

## Modeling dynamics of native and invasive species to guide prioritization of management actions

CHERYL A. LOHR,<sup>1,†</sup> JIM HONE,<sup>2</sup> MICHAEL BODE,<sup>3</sup> CHRISTOPHER R. DICKMAN,<sup>4</sup>  
AMELIA WENGER,<sup>3</sup> AND ROBERT L. PRESSEY<sup>3</sup>

<sup>1</sup>Department of Parks and Wildlife, Science and Conservation Division, 37 Wildlife Pl, Woodvale, Western Australia 6026 Australia

<sup>2</sup>Institute for Applied Ecology, University of Canberra, Canberra, Australian Capital Territory 2601 Australia

<sup>3</sup>Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4811 Australia

<sup>4</sup>School of Life and Environmental Sciences, University of Sydney, Sydney, New South Wales 2006 Australia

**Citation:** Lohr, C. A., J. Hone, M. Bode, C. R. Dickman, A. Wenger, and R. L. Pressey. 2017. Modeling dynamics of native and invasive species to guide prioritization of management actions. *Ecosphere* 8(5):e01822. 10.1002/ecs2.1822

**Abstract.** Action to achieve biodiversity conservation is usually expensive, and resources are limited relative to conservation goals. Prioritizing management investment therefore is essential if important goals are to be achieved. New software, the “Islands DSS,” has been developed to prioritize the mix of management actions that will optimally mitigate biodiversity loss. Here, we present novel temporally dynamic models of species population growth, interaction, and management efficacy that have been incorporated into the software. We have analyzed the sensitivity of these models to uncertainty in four parameters: maximum rate of population growth ( $r_{\max}$ ), coefficient of species interaction ( $\alpha_{ij}$ ), quantity of food resources required to maintain species equilibrium ( $J_i$ ), and the coefficient of management efficacy ( $\theta_i$ ). We focused on the projected abundance of species by simulating interactions among one to four species, both invasive and native, on a hypothetical arid-tropical island that is 1000 ha in size and consists of five evenly distributed habitat types. Sensitivity analysis revealed significant variation in species abundance due to uncertainty in  $r_{\max}$  (coefficient = 51.34;  $P < 0.001$ ) and  $\alpha_{ij}$  ( $N_i = -16.48$ ;  $P = 0.43$ ;  $N_j = -2.33^2$ ;  $P = 2.00^{-16}$ ), a significant but potentially stabilizing effect of modeling multiple species simultaneously (coefficient =  $-65.80$ ;  $P = 2.00^{-16}$ ), and mirroring by species response trajectories of threat mitigation trajectories. There are several benefits of using temporally dynamic models of species responses to threat mitigation in systematic conservation planning including increased accuracy in estimates of the cost of management; locally relevant understanding of lag-times between threat establishment and unacceptable impacts on valued species; understanding of threat abundance and required intensity of control for biodiversity features to persist; site- and species-specific understanding of time to eradication and threat recovery when management is interrupted; and an improved understanding of the opportunity cost, in terms of threat levels and responses of native species, for islands not selected for management. Our models and associated software are based on decades of ecological research, potentially useful in a wide range of situations, including islands, the mainland, and marine regions, and we suggest that they provide managers with novel and powerful tools to efficiently prioritize conservation actions via the new systematic conservation planning software, “Islands DSS.”

**Key words:** conservation planning; invasive species; sensitivity analysis; species response trajectory; threat mitigation.

**Received** 8 December 2016; revised 30 March 2017; accepted 3 April 2017. Corresponding Editor: Lucas N. Joppa.

**Copyright:** © 2017 Lohr et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** cheryl.lohr@dpaw.wa.gov.au

## INTRODUCTION

Invasive species are one of the primary threats to the persistence and conservation of native species (Butchart et al. 2010, Ehrenfeld 2010, Duncan et al. 2013). These species can be controlled or eradicated (Veitch and Clout 2002), but effective control is usually costly and resource intensive and may compete with other threats such as persecution by people or loss of habitat as priorities for mitigation. Prioritization of threat management is therefore essential because human and material resources are limited relative to the cost of achieving many conservation goals.

While conservation goals are best pursued using a range of management actions, most prioritization research has focused on the design of networks of conservation reserves rather than considering the mix of management actions that will optimally mitigate biodiversity loss (Pressey et al. 2004, Wilson et al. 2007, Spring et al. 2010, Visconti et al. 2010). Previous prioritization exercises that have considered a range of possible actions (Bottrill et al. 2008, Joseph et al. 2008) have either modeled the effect of management on a threat and the responses of protected species to threat mitigation separately, or assumed that threats are static and eliminated instantaneously (or uniformly over time) when conservation actions are applied (Watts et al. 2009, Klein et al. 2010, Wilson et al. 2010, Januchowski-Hartley et al. 2011).

New systematic conservation planning software, the “Islands DSS,” has been developed to prioritize the mix of management actions that will optimally mitigate biodiversity loss. The optimization algorithm within the software is designed to use continuous ecosystem or community models with temporally variable trajectories of species abundance, henceforth referred to as “species response trajectories” (Brotankova et al. 2015, Urli et al. 2016). The shape of a species response trajectory may be influenced by the presence of other interacting species or threat mitigation activities. Incorporating continuous species response trajectories into systematic conservation planning models can improve the accuracy of estimates of the cost of management by up to 20% (Cattarino et al. 2016). Ultimately, the software uses a constraint programming model built upon robust optimization principles and a large neighborhood search scheme to

select a suite of management actions that will maximize the total conservation benefit achieved given a limited budget (Urli et al. 2016). It can also help to identify the most cost-effective management actions to implement (Margules and Pressey 2000). Here, we present the novel temporally dynamic and spatially implicit ecological community models with dynamics that are directly and indirectly influenced by management actions that have been embedded in the new software.

Modeling the effects of invasive species on protected native species can be complex and, to be effective, needs to be underpinned by sound ecological understanding. This is because, when invasive species become established in ecological communities, they often become involved in webs of direct and indirect interactions with other species that can generate surprising relationships (Dickman 2007). For example, on Boullanger Island, Western Australia, the removal of invasive mice (*Mus musculus*) led to a short-term depression in numbers of a threatened native marsupial (the dibbler, *Parantechinus apicalis*) and concomitant increases in litter-dwelling skinks (*Ctenotus fallens* and *Morethia lineocellata*) (Dickman 2007). Unexpected interactions may also occur due to hyperpredation or mesopredator release, exemplified by rabbits killing birds (Courchamp et al. 2000) and coyotes protecting birds by reducing other predators (Crooks and Soule 1999), or to synergistic interactions between invasive species and other threats (Doherty et al. 2015).

At a community level, invasive species may facilitate native species (Rodriguez 2006) and increase species diversity, which can in turn increase the stability of an ecosystem in the face of perturbations (Ives and Carpenter 2007). Invasive species alternatively may have no effects in their host community, or may drive declines in species diversity (Hejda et al. 2009) and possibly even ecosystem collapse (MacDougall et al. 2013). Hence, modeling community dynamics and the effects of invasive species and their control should investigate the effects of the invader on community dynamics and stability. Despite their potential advantages in such explorations, continuous models of threat mitigation and species response have not been incorporated into systematic conservation planning until recently because they are computationally challenging (Cattarino et al. 2016).

Users of the “Islands DSS” software need a sound understanding of the ecological community model and associated assumptions embedded within the code to assess the quality of the recommendations generated by the optimization algorithm. Therefore, we present the components of the ecological community model and discuss the data input requirements. We also present the results of sensitivity analysis of uncertainty in four model components: maximum intrinsic rate of population growth ( $r_{\max}$ ), coefficient of species interaction ( $\alpha_{ij}$ ), quantity of food resources required to maintain species equilibrium ( $J_i$ ), and the coefficient of management effectiveness ( $\theta_i$ ), by simulating interactions among one to four species on a hypothetical 1000-ha island.

Inputs for the sensitivity analysis are based on species found on the Pilbara Islands, Western Australia, a hotspot for endemic species that has recently been the focus of intense conservation research. The software and our sensitivity analysis use islands as a case study because the numbers of species present on islands are limited, thus reducing computational demands, and because islands often contain endemic species as well as invasive species that threaten native species via competition or predation (e.g., Dickman 1992). The modeling approach could, however,

be used for mainland and marine applications. The ecological community models and the associated software synthesize decades of ecological research to provide conservation practitioners with estimates of site- and species-specific community dynamics.

## METHODS

### *Modeling population dynamics for conservation planning software*

Broadly, the ecological community models are built upon theories of bioenergetics (Ney 1993) and resource availability (McLeod 1997). Many species are limited primarily by food availability and secondarily by density-dependent factors that intensify as carrying capacity is approached. To reduce the data input requirements for the software, we assumed that populations within the community are closed, existing on islands with limited external resources. We use finite difference equations to describe temporal changes in abundance of species  $i$ , using a one-year time step. For all species, in the absence of competitors, consumers, and management, a population of species  $i$  will show logistic growth. Concurrently, we assume management inputs ( $A_a$ ) have diminishing returns (Hone et al. 2015). Model parameters are defined in Table 1.

Table 1. Description of parameters within the two models (Eqs. 1 and 2) of population dynamics for island species.

Parameters	Description
$V_i$	Present abundance of ( $V_i$ ), the space-limited species to be modeled, or ( $V_j$ ) a competing space-limited species: whole numbers for fauna and hectares for flora
$N_i$	Present abundance of ( $N_i$ ), the consumer species to be modeled, or ( $N_j$ ) a consumer that is preying upon the modeled species: whole numbers
$r_{mi}$	Maximum biologically achievable population growth rate of species $i$
$\alpha_{ij}$	Coefficient of the effect of species $i$ on species $j$
$H_i$	Total area of habitat, including optimal and sub-optimal habitat, available for a space-limited species $i$ : hectares
$M_i$	Area of sub-optimal habitat available for a space-limited species $i$ : hectares
$J_i$	Quantity of food resources required to maintain species equilibrium: hectares of forage per herbivore per year or number of prey species per consumer per year
$F_i$	Present abundance of consumable species (i.e., food) for $N_i$ , which may be space-limited species ( $V_i$ ) or other consumers ( $N_i$ )
$K_i$	Carrying capacity or maximum abundance obtainable by a species: proportion covered per hectare for space-limited species or individuals per hectare
$\theta_{ai}$	Coefficient of the effectiveness ( $\theta$ ) of management action ( $a$ ) applied to species $i$ $\theta_{ai} = (X_i/A_{ai}) + X_i A_{ai}$
$A_a$	Amount ( $A$ ) of action ( $a$ ) applied: \$/ha
$X$	Efficacy of management action on species $i$ per hectare
$t$	Time

The ecological community models consist of two equations. The first describes the dynamics of space-limited species under competition from other space-limited species (Eq. 1), which are defined as either primary producers or species that consume resources from outside a given island's environment (e.g., marine turtles, seabirds). The abundance of these latter species is limited by the area of suitable habitat for non-consumptive purposes (e.g., nest sites). Access to this habitat and reproductive success may be suppressed by competition with other species.

Two space-limited species ( $V_i$  and  $V_j$ ) with competition (competitive coexistence or competitive exclusion) is shown in below

$$V_i(t+1) = V_{i,t} + r_{mi}V_{i,t} \left( 1 - \frac{V_{i,t} + \sum_{j \in B_i} \alpha_{ij}V_{j,t}}{K_iH_i - K_iM_i \frac{\sum_{j \in C_i} \alpha_{ij}V_{j,t}}{1 + \sum_{j \in C_i} \alpha_{ij}V_{j,t}}} \right) - \sum_{j \in D_i} \alpha_{ij}V_{i,t}N_{j,t} - \sum_a V_{i,t} \left( \frac{\theta_{ai}A_a(t)}{1 + \theta_{ai}A_a(t)} \right) \quad (1)$$

Two outcomes of interspecific competition are included within Eq. 1: competitive coexistence and exclusion. The form of competition (resource or interference) is not defined to accommodate a wide variety of potential species interactions, but we assume linear effects of competition (Table 3) to reduce data input requirements. If two species can coexist despite interspecific competition (Bengtsson et al. 1994), they may occupy the same habitat type simultaneously but the carrying capacity for each species is suppressed by the coefficient of the species interaction (Table 1:  $\alpha_{ij}$ ). The identity of a species that competes with (but does not exclude) species  $i$  is contained in set  $B_i$  (Eq. 1:  $j \in B_i$ ). Under competitive exclusion, by contrast, two competing species may not coexist within a given habitat type and instead will retreat from any sub-optimal habitat types to their respective optimal habitat types where they retain competitive dominance. The identity of species that exclude species  $i$  is contained in set  $C_i$  (Eq. 1:  $j \in C_i$ ).

The second equation describes the dynamics of consumers whose resources are contained within the boundary of a given island (Eq. 2). The

abundance of a consumer is limited primarily by the amount of energy it requires to reproduce ( $J_i$ ) and the abundance of its food resources ( $N_i/\Sigma F_i$ ) (Table 1), and secondarily by other density-dependent factors ( $K_i$ ), such as space. It is assumed in Eq. 1 that consumers have a linear (type 1) functional response (Holling 1965). The numerical response of consumers to their food includes a ratio term. Empirical evidence for such a ratio response has been reported for wolves (*Canis lupus*) eating moose (*Alces alces*) in North America (Eberhardt and Petersen 1999), ferrets (*Mustela furo*) eating rabbits (*Oryctolagus cuniculus*) in New Zealand (Barlow and Norbury 2001), least weasels (*Mustela nivalis*) eating voles (*Microtus agrestis*) in Scandinavia (Hanski et al. 2001), and lynx (*Lepus canadensis*) eating snowshoe hare (*Lepus americanus*) in Canada (Hone et al. 2007).

Consumers ( $N_i$ ) that consume food ( $F_i$ ) and may in turn be consumed ( $N_j$ ) is shown in below

$$N_i(t+1) = N_{i,t} + r_{mi}N_{i,t} \left( 1 - J_i \left( \frac{N_{i,t}}{\Sigma F_i} \right) \right) \left( 1 - \frac{N_{i,t}}{K_i} \right) - \sum_{j \in D_i} \alpha_{ij}N_{i,t}N_{j,t} - \sum_a N_{i,t} \left( \frac{\theta_{ai}A_a(t)}{1 + \theta_{ai}A_a(t)} \right) \quad (2)$$

### Parameterizing the models

A limitation of some models is that their input requirements can appear to be complex or daunting. Here, we describe the ideal sources of data that should be used in our models, and also indicate alternative data sources that are more likely to be available in real-world situations (Table 2) such as those available for islands in the Pilbara.

### Present abundance of a species ( $N_i$ or $V_i$ )

The present abundance of a species provides a starting point for modeling population growth or decline and is measured in individuals for animals, or area of land (hectares) covered for plant species (Table 1). Ideally, when using the software, the present abundance of a species would be provided by a comprehensive census on each island over multiple years to account for fluctuations in population size. When such ideal data are not available, values may be extrapolated from

Table 2. Ideal and actual sources of data on population parameters for island species.

Parameter type	Ideal data source	Actual data source
Species abundance ( $V_i$ or $N_i$ )	Comprehensive recent census of each species on each island, quantifying the fluctuations in populations over time	<ul style="list-style-type: none"> <li>• Extrapolation from geographically limited surveys and species attributes</li> <li>• Estimates of abundance from experts for all species on each island</li> <li>• Sporadic or old measures of abundance</li> <li>• Presence-only data and: <ul style="list-style-type: none"> <li>◦ assuming long-term resident species present at carrying capacity</li> <li>◦ assuming newly arrived species are at minimum propagule size</li> </ul> </li> </ul>
Maximum population growth rate ( $r_{mi}$ )	Empirically measure on each island using a small and growing population of each species	<ul style="list-style-type: none"> <li>• Use field-based estimates from other environments</li> <li>• Estimate from complete set of demographic variables (e.g., Leslie matrix or Lotka-Euler equation)</li> <li>• Estimate using minimal set of demographic variables</li> </ul>
Carrying capacity ( $K_i$ )	Empirically measure the maximum density obtained by a species in each habitat type	<ul style="list-style-type: none"> <li>• Use estimates of maximum density obtained by a species in other, preferably similar environments</li> </ul>
Optimal/sub-optimal habitat classification ( $H_i$ or $M_i$ )	Empirically measure the density obtained by a species in each habitat type	<ul style="list-style-type: none"> <li>• Use descriptions of habitat use from other environments</li> </ul>
Food requirement ( $J_i$ and $\bar{F}_i$ )	Empirically measure in the field the quantity of food consumed by individuals when the species exists in equilibrium	<ul style="list-style-type: none"> <li>• Calculate the megajoules of energy required or provided by individuals given the average mass of the species</li> </ul>
Species interaction coefficient ( $\alpha_{ij}$ )	Empirically measure in multiple field sites to derive species-specific damage–density curves for each pair of species, in the presence of different combinations of other species	<p>For space-limited species:</p> <ul style="list-style-type: none"> <li>• Estimate pairwise coefficients using the identification of optimal and sub-optimal habitat types to calculate the proportion of total habitat availability that must be shared by two species</li> </ul> <p>For consumers:</p> <ul style="list-style-type: none"> <li>• Assume an existing damage–density curve is applicable to multiple species</li> <li>• Use field-based estimates from other environments and assume that the quantity of damage is not density dependent</li> </ul>
Efficacy of management action ( $\theta_i$ )	Empirically measure in the field the efficacy of each management technique on each threat	<ul style="list-style-type: none"> <li>• Use field-based estimates of the efficacy of management from other environments</li> <li>• Use expert knowledge to define efficacy</li> <li>• Assume that efficacy is consistent across related or similar species</li> </ul>
Cost of management ( $A_a$ )	Use the cost of implementing actions from similar environments for each species	<ul style="list-style-type: none"> <li>• Assume that the cost of implementing actions is related to quantified island or species attributes (e.g., island size, distance from mainland, transportation costs, rate of application per individual)</li> </ul>

Notes: Actual data sources are listed in order of higher (top) to lower (bottom) data quality. See discussion of each parameter for details on derivation of actual data.

temporally or geographically limited survey data and species attributes (Potts and Elith 2006), elicited from experts (Anadon et al. 2009, Martin et al. 2012), or replaced with presence-only data (Table 2). The use of presence-only data requires some assumptions: (1) For pest species that have

been present for a long time or for native unthreatened species, we assume species abundance is at carrying capacity ( $K_i$ ); (2) for newly arrived pest species, we assume that current abundance is at or just above the minimum propagule size for population establishment



(Forsyth and Duncan 2001); and (3) for native species that have been in the presence of a threat for a moderate to long period of time, we assume that their abundance has been suppressed to half of carrying capacity ( $K_i/2$ ).

#### *Intrinsic rate of population growth ( $r_{mi}$ )*

The instantaneous rate of population growth ( $r_{mi}$ ) is a critical parameter for modeling changes in abundance in species over time. Actual rate of population growth may vary greatly across the landscape, with optimal habitats allowing populations to grow more rapidly than sub-optimal habitats (Pulliam and Danielson 1991). Species in equilibrium should have a realized growth rate of approximately zero as the population fluctuates around carrying capacity. The maximum annual population growth rate,  $r_{max}$ , is the increase in numbers that occurs when resources are not limiting and there are no predators, parasites, or competitors (Sibly and Hone 2002). Our models calculate the realized growth rate by combining  $r_{max}$  with data on the number of predators, competitors, or resources available on a given island at a given time.

In an ideal situation, values of  $r_{max}$  would be estimated empirically for each species of interest on each island (Table 2). Unsurprisingly,  $r_{max}$  has not been estimated in the field for the vast majority of species (Duncan et al. 2007), typically because long-term field studies are logistically and financially difficult. However,  $r_{max}$  may be estimated from minimal demographic data, namely age at first reproduction, given demographic data on related species (Hone et al. 2010). While there is considerable uncertainty around predicted values of  $r_{max}$ , they confer the advantage of consistent assumptions and level of uncertainty across species and islands when used in conservation planning software.

Estimating  $r_{max}$  for plants is less reliable. Plants have a wider variety of reproductive strategies and may produce hundreds or thousands of diaspores per parent per year. However, many of these will never contribute to the next generation. Where possible, estimates of  $r_{max}$  should be derived from field studies of small but rapidly growing plant populations (Gimeno and Vila 2002). Alternatively, knowledge of a plant's reproductive strategy and a patch expansion rate (Dixon et al. 2002), or relative growth rate

(Traveset et al. 2008), could be used to calculate a rate of population growth.

#### *Carrying capacity ( $K_i$ )*

Carrying capacity generally refers to the maximum sustainable number of individuals that can be achieved in a given habitat (McLeod 1997). Quantifying carrying capacity is necessary for defining the upper bounds on species abundance and subsequently for modeling increases and decreases in interacting species. It is a particularly pertinent variable for species that are naturally rare vs. those that are rare due to threatening processes (Partel et al. 2005) because conservation actions are unlikely to generate the desired outcome if a species is subject to natural causes of rarity.

Where ideal data are not available (Table 2), carrying capacity for space-limited species may be based on the maximum density a species has achieved in similar environments multiplied by the amount of suitable habitat present. In the equations above, the increase in consumers (Eq. 2) is limited by two carrying capacity terms. First, carrying capacity is defined by food availability (see *Food required ( $J_i$  and  $F_i$ )*) as the point at which resource consumption by a species is equal to population growth rates of its prey (McLeod 1997). Second, in the event that food resources are exceedingly abundant, consumer population growth may be limited by other density-dependent factors ( $K_i$ ; e.g., shelter, space, water).

Separating food from other density-dependent factors is particularly relevant in tropical arid environments where food resources may be sporadically abundant and interspersed with harsh, dry periods. For example, the carrying capacity for black rats (*Rattus rattus*) in dry forests and grassland is approximately 30 rats/ha, whereas the maximum observed on wet tropical islands is 119 rats/ha (Harper and Bunbury 2015). Two terms for carrying capacity are useful when prioritizing conservation actions because it allows the effective carrying capacity (food requirement) to differ among islands despite a consistent coefficient of carrying capacity for each species.

#### *Optimal and sub-optimal habitat ( $H_i$ and $M_i$ )*

Optimal foraging theory was developed in 1966 and has since spawned myriad models that address optimal habitat selection (Emlen 1966, MacArthur and Pianka 1966). At the core of the

theory is the idea that organisms will enlarge an activity as long as the resulting gain in time spent per unit food exceeds the loss (MacArthur and Pianka 1966). The most productive habitat types will be optimal until density-dependent factors reduce the amount of resources available per individual within patches of that habitat, at which point individuals will disperse into other, less optimal habitat patches. Current application of this theory is frequently seen in habitat suitability models where regressions link species occupancy data with landscape-scale habitat maps and identify sub-optimal and optimal habitat types (e.g., Carvalho and Gomes 2003) or patches of high species density (Guthlin et al. 2014).

The continuum of variable habitats across a landscape will usually have to be grouped into a limited number of classes (Table 2). Depending on the available literature, allocation of optimal or sub-optimal habitat types to each species should then be biased toward sub-optimal habitats to limit the invasive potential of generalist species within the models (e.g., Appendix S1: Table S1).

#### Food required ( $J_i$ and $F_i$ )

The primary limit to population growth is built on bioenergetics theory (Ney 1993) and relies on  $J_i$ , the estimated amount of food per head of species  $i$  required to maintain a population at equilibrium. Unfortunately, many bioenergetics models require large quantities of species-specific data to calculate multiple parameters, and hence have potential for inaccuracy (Ney 1993). Encouraging land managers to use a systematic conservation planning tool requires that we minimize data requirements. We used estimates of species basal metabolic rate (BMR) to derive the amount of food required by each species. Despite debate regarding modeling techniques and variation among species (see Roberts et al. 2010, Seymour and White 2011), current models for BMR in animals weighing less than 2.5 kg do not deviate dramatically from Brody's equation (Eq. 3), in which daily BMR is measured in megajoules MJ and  $W$  is weight in kilograms (Brody 1945). Given advances in island conservation and eradication, it is now rare that managers would be required to prioritize the management of invasive species that are considerably larger than 2.5 kg (Clout and Veitch 2002).

$$\text{BMR (MJ)} = 0.27W^{0.75} \quad (3)$$

Basal metabolic rate alone will underestimate the energy requirements of wild animals, because foraging, movement, and reproduction consume energy. Efficiency of digestion and metabolism varies, with efficiencies of 70–80% being typical (Case 1973, McDonald et al. 2002). To account for the energy requirements of foraging and reproduction in the wild, we multiplied BMR by 150%. Similarly, to account for metabolic efficiency, we divided BMR by 75% for carnivores and omnivores and by 50% for herbivores to estimate the total amount of energy an animal needs to survive (Eq. 4).

$$\begin{aligned} \text{Annual consumption (MJ)} \\ = 365 \left( \frac{1.5 \times 0.27W^{0.75}}{0.75} \right) \text{ or} \\ 365 \left( \frac{1.5 \times 0.27W^{0.75}}{0.50} \right) \end{aligned} \quad (4)$$

The gross energy (GE) content of prey items depends on the proportions of carbohydrates, fats, and proteins within the food (McDonald et al. 2002). In lieu of measuring the chemical energy present in all prey items within an ecosystem (Table 2), we used average GE content per weight ( $W_i$ ) of animal prey and vegetation class. Since vegetation abundance is measured in hectares, the GE content of vegetation must be multiplied by biomass of each plant species as if it achieved complete coverage of a hectare. If relevant biomass functions are unavailable, biomass functions for similar species may be used. For example, in lieu of biomass functions for tropical arid zone plants on the Pilbara Islands (Table 4), we used a foliage biomass function for sagebrush (*Artemesia tridentata*; Gholz et al. 1979), which grows in arid and semi-arid conditions of northwest America. The total number of prey items or hectares of vegetation required by a predator is a function of prey size or vegetation biomass and energy requirements of the consumer (Eq. 5).

$$\begin{aligned} J_i \text{ (Number of prey required annually)} \\ = \frac{365 \left( \frac{1.5 \times 0.27W_i^{0.75}}{0.75} \right)}{\text{GE} \times W_i} \end{aligned} \quad (5)$$

Table 3. Actual methods of calculating species interaction coefficients.

Influence of species $i$ on species $j$	Type of interaction	Calculation method
No interaction	No interaction	$\alpha_{ij} = 0$
Negative	Competition	$\alpha_{ij} = \text{Area shared habitat (ha)}/\text{Area total habitat (ha)}$
	Herbivory/predation	Published damage–density curve if available. If published damage–density curve is not available, and if abundance of threat species and affected native species is available, assume linear relationship as per: $\alpha_{ij} = \text{proportion } j \text{ damaged}/N_i$ If published damage–density curve is not available, and if only the proportion of $j$ damaged is available, assume a linear relationship as per: $\alpha_{ij} = \text{Max proportion } j \text{ damaged}/K_i$

### Species interactions ( $\alpha_{ij}$ )

The coefficient of species interaction is based upon the concept of a damage–density curve, which is a linear or curved relationship between the amount of damage done by a pest and the abundance of the pest (Hone 2007). Within the systematic conservation planning software, a coefficient must be defined for every pair of interacting organisms. For space-limited species, the coefficient is calculated as the proportion of habitat that two species share (Eq. 1; Table 3). For consumers, the coefficient is derived from the proportion of a population of a prey species taken by each individual predator per annum (Table 3).

Due to the number and complexity of species interactions that may occur in a community (Polis and Strong 1996), estimates of species interaction coefficients are made pairwise. They hence assume a linear functional response (Holling 1965) and that interaction coefficients may be conveyed among similar species (Table 3; Appendix S1: Table S2). We assumed that all relationships have an intercept of zero and that there is no variation in predator search effort or capture success across similar prey items. For example, given similarities in size, habitat use, and reproductive strategy, the herbivorous marsupial *Lagorchestes conspicillatus* would be similarly susceptible to predation by feral cats (*Felis catus*) as *Bettongia penicillata* (Dickman 1996). Similarly, we assume that rooting of soil by pigs (Hone 2007) will have an equivalent negative influence on all plant species that are not disturbance specialists.

### Efficacy of management actions ( $\theta_{ai}$ and $A_a$ )

The purpose of these equations is to create a temporally dynamic model of island species

abundance that may be modified directly or indirectly by management actions. The term for management efficacy describes the portion of a threat population that is removed by a given management action. The estimated efficacy of an action may vary depending on the measurement technique, management site, time of year, and the extent and magnitude of application (Table 1), but may be derived from the literature (e.g., Williams and Moore 1995, Johnston et al. 2010, VanderWerf et al. 2011, Coddou et al. 2014) or from expert knowledge of how the techniques have worked in different environments (Table 2).

### Sensitivity analysis of model components

The above equations were recreated in RStudio (2015) using R version 3.2.5 for a hypothetical island of 1000 ha that contains five evenly distributed habitat types and a community of one to four interacting species, both native and invasive (Table 4; Appendix S1: Tables S1, S2). Both the habitat types and species were chosen to represent those that occur in the Pilbara case study region, with the native and invasive species among those that are most commonly targeted by managers for conservation and control, respectively. The modeling time frame was limited to 20 yr; few management agencies are likely to forecast species declines or recoveries more than 20 yr in advance.

The sensitivity of model results to variation in four key components ( $r_{\max}$ ,  $\alpha_{ij}$ ,  $J_i$ , and  $\theta_{ai}$ ) was assessed by independently randomizing the input value of each component over 100 simulations. We varied the values for  $r_{\max}$ ,  $\alpha_{ij}$ , and  $J_i$  using a normal distribution (mean, Table 4). We used a uniform distribution between 0 and 1 to



Table 4. Input values for simulations of species trajectories on an island that is 1000 ha in size and has five habitat types (Appendix S1: Table S1).

Species	Trophic level	Residence	$r_{\max}$	$K_i$	$J_{\text{provided}}$ MJ	$J_{\text{required}}$ MJ
Wirewood ( <i>Acacia coriacea</i> )	SL-Eq1	Native	0.02	0.8	11,624	0
Kapok bush ( <i>Aerva javanica</i> )	SL-Eq1	Invasive	1.50	1	17,551	0
Buffel grass ( <i>Cenchrus ciliaris</i> )	SL-Eq1	Invasive	1.50	1	25,284	0
Spinifex ( <i>Triodia wiseana</i> )	SL-Eq1	Native	0.22	1	5644	0
Wedge-tailed shearwater ( <i>Ardenna pacifica</i> )	SL-Eq1	Native	0.33	7400	8.23	0
Spectacled hare-wallaby ( <i>Lagorchestes conspicillatus</i> )	C-Eq2	Native	0.73	0.68	62.77	428.92
Cat ( <i>Felis catus</i> )	C-Eq2	Invasive	0.99	0.79	101.73	616.06
Black rat ( <i>Rattus rattus</i> )	C-Eq2	Invasive	3.59	30	3.92	53.60

†  $J_{\text{required}} = 0$  for space-limited species (SL-Eq1) as they consume resources external to the island ecosystem; consumers (C-Eq2);  $K_i$  for plants is proportion of hectare;  $K_i$  for animals is number of individuals per hectare.

vary the values for  $\theta_{ii}$ . We then analyzed the variation in species abundance in year 20 in relation to variation in the model component using linear regression models with fixed and random effects (Pinheiro et al. 2017). Data were not transformed prior to analysis. With combinations of one to four species, two models for competition, and 100 simulations, up to 16,000 results for year-20 abundance were analyzed. The input values in Table 4 and Appendix S1: Tables S1, S2 were derived from an extensive literature review (C. Lohr, unpublished data).

## RESULTS

### Sensitivity analysis of species population growth rate $r_{\max}$

As would be expected, variation in the input value of  $r_{\max}$  significantly affects the 20-yr abundance of species (coefficient = 51.34;  $P < 0.001$ ; Appendix S1: Table S3). Increasing the number of species included in the modeled ecosystem significantly reduces the median and variation in 20-yr abundance of the modeled species due to competition for resources ( $P < 1.00^{-5}$ ; Fig. 1; Appendix S1: Table S3). Similarly, within a given number of species, the choice between defining a competitive exclusion relationship or a competitive coexistence relationship between two space-limited species makes a difference in the average abundance of species  $i$  in year 20 ( $P < 1.00^{-5}$ , Fig. 1; Appendix S1: Table S3). The influence of the variation in  $r_{\max}$  is more constrained in species interactions that involve competitive exclusion because species are pushed out of sub-optimal habitats and effectively confined to optimal habitat

types, or parts thereof, whereas competitive coexistence allows two or more species to occupy the same habitat type. With fewer habitats to effectively occupy under competitive exclusion, there is less room for variation in species abundance. A mixed-effects model with  $r_{\max}$ , competition type, and number of species included as variables explains 79% of the variation in the data (Appendix S1: Table S3).

### Sensitivity analysis of species interaction coefficients $\alpha_{ij}$

Variation in the species interaction coefficient does not have a significant influence on the variation in the year-20 abundance for modeled species  $i$  when it is involved in a competitive relationship ( $p_{\alpha_{ij}} = 0.43$ ; competitive coexistence linear regression for species  $i$ ;  $F_{12, 7764} = 1807$ ,  $P < 2.00^{-16}$ ,  $r^2 = 0.73$ ). The total number of species included in the ecosystem, however, does have a significant indirect effect on the year-20 abundance for modeled species  $i$  ( $P = 2.00^{-16}$ , Fig. 2; Appendix S1: Table S4). In contrast, variation in both the species interaction coefficient and the number of species included in the ecosystem has a significant indirect effect on the year-20 abundance of competing species  $j$  ( $p_{\alpha_{ij}} = 2.00^{-16}$ ;  $p_{\text{no. of species}} = 2.00^{-16}$ ;  $F_{12, 15627} = 414.3$ ,  $P < 2.20^{-16}$ ,  $r^2 = 0.24$ , Fig. 3; Appendix S1: Table S5). It is also evident in Fig. 3 that the identity of the species involved in interactions also significantly influences the year-20 abundance of species (Appendix S1: Tables S4, S5).

### Sensitivity analysis of prey consumed $J_i$

$J_i$  is a component of the food resource-based carrying capacity term in Eq. 2. Increasing  $J_i$

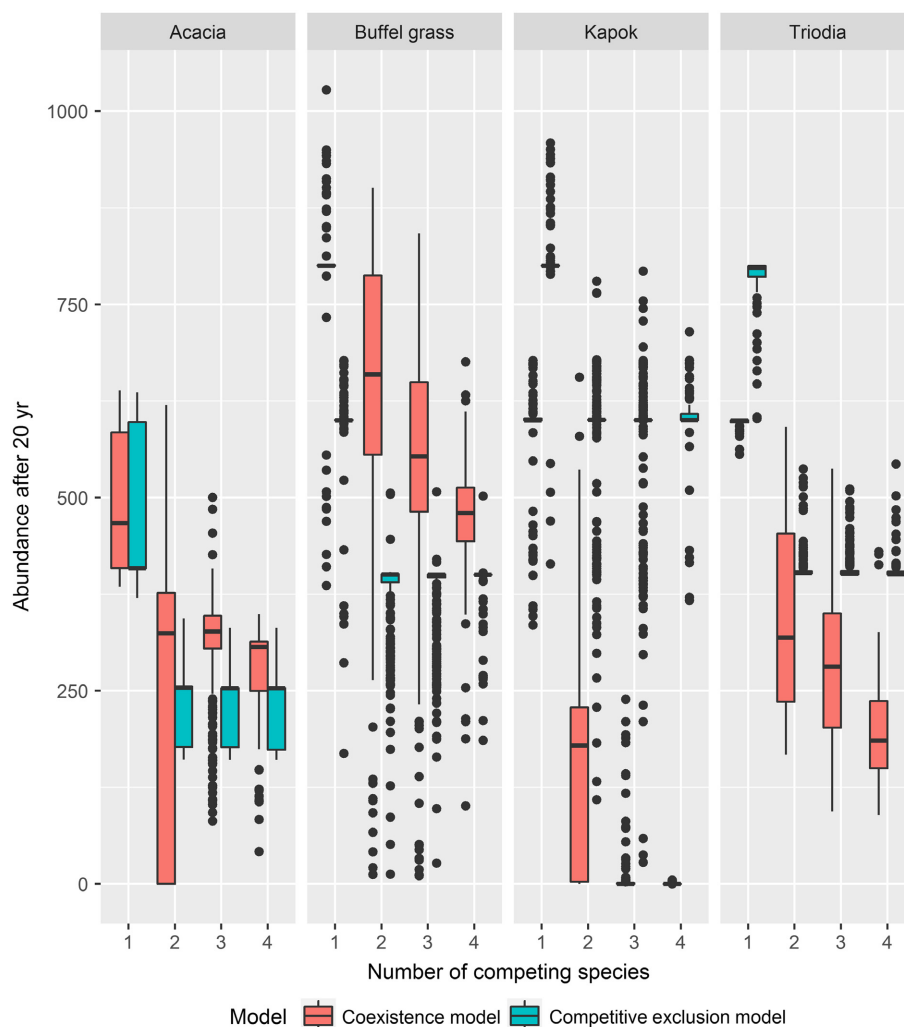


Fig. 1. Influence of variation in growth rate ( $r_{\max}$ ) on the abundance of the labeled species in year 20 given simultaneous competition (competitive coexistence or competitive exclusion models) with one to three other space-limited species. Variation seen in scenarios with zero competitors is due solely to variation in  $r_{\max}$  of the labeled species and model selection. Boxplots with median (horizontal bar), quartiles 1 (lower whisker), 2 (lower box edge), 3 (upper box edge), 4 (upper whisker), and outliers (points).

reduces the margin between current species abundance and the food-based carrying capacity of the ecosystem, alters the magnitude of fluctuations around the food-based carrying capacity, and acts as a linear brake on the growth of the modeled species ( $i$ ) population. Depending on the food resources available on an island,  $J_i$  and the corresponding  $F_i$  (food resources available) can prevent population growth before species  $i$  reaches its ultimate carrying capacity ( $K_i$ ).  $J_i$  had an insignificant effect on the abundance of

species  $i$  ( $P = 1.00$ ) when compared to the significant influence of the number of species ( $P = 8.00 \times 10^{-4}$ ) included in the modeled ecosystem and the trophic level of species  $i$  (linear mixed-effects model  $r^2 = 0.73$ ; Appendix S1: Table S6). The abundance of food items (e.g., plants) is indirectly related to the  $J_i$  of herbivores (e.g., rats or wallabies). The abundance of consumers is indirectly related to their assigned values of  $J_i$ . The interaction between  $J_i$  and the plant or predator trophic level was not significant due to their very

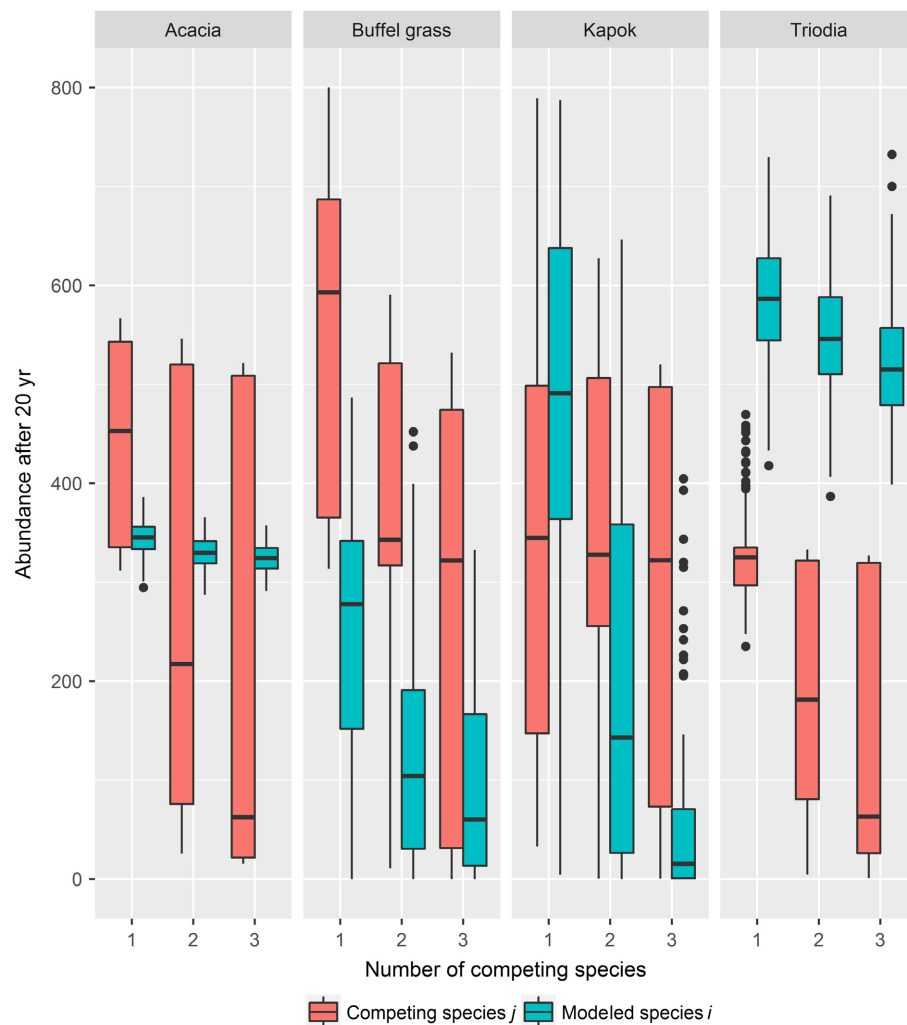


Fig. 2. Influence of variation in species interaction coefficients ( $\alpha_{ij}$ ) on the abundance of the labeled species in year 20 given one to three competing space-limited species (competitive coexistence model). The labeled species was positioned as either the modeled species  $i$  or the competing species  $j$ . Boxplots with median (horizontal bar), quartiles 1 (lower whisker), 2 (lower box edge), 3 (upper box edge), 4 (upper whisker), and outliers (points).

different roles in the ecosystem. Plants were pushed to a minimal abundance that maintained the rat population at equilibrium, whereas cats were not food limited and were maintained at maximum density ( $K_{\text{cat}}$ ) regardless of  $J_i$  (Appendix S1: Table S6). When all four species were included in the ecosystem, wallabies became extinct within 7 yr due to hyperpredation by cats, whereas rats became food limited (20-yr abundance  $\sim 0.5 \times K_{\text{rat}}$ ), following a reduction in plant resources when two herbivores were present (Fig. 4).

#### *Sensitivity analysis of the effectiveness of management ( $\theta_i$ )*

As expected, the coefficient of management efficacy had a negative effect on the abundance of the threat being controlled and a positive effect on the abundance of the native species being protected (Appendix S1: Table S7). We analyzed variation in the year-20 abundance of cats (predators) and wallabies (native prey), when the effectiveness of annual cat control ( $\theta_{\text{cat}}$ ) varied (Fig. 5). As  $\theta_{\text{cat}}$  increased, the year-20 abundance of cats decreased (coefficient =  $-26.90$ ;  $P < 2.00 \times 10^{-16}$ ; Model

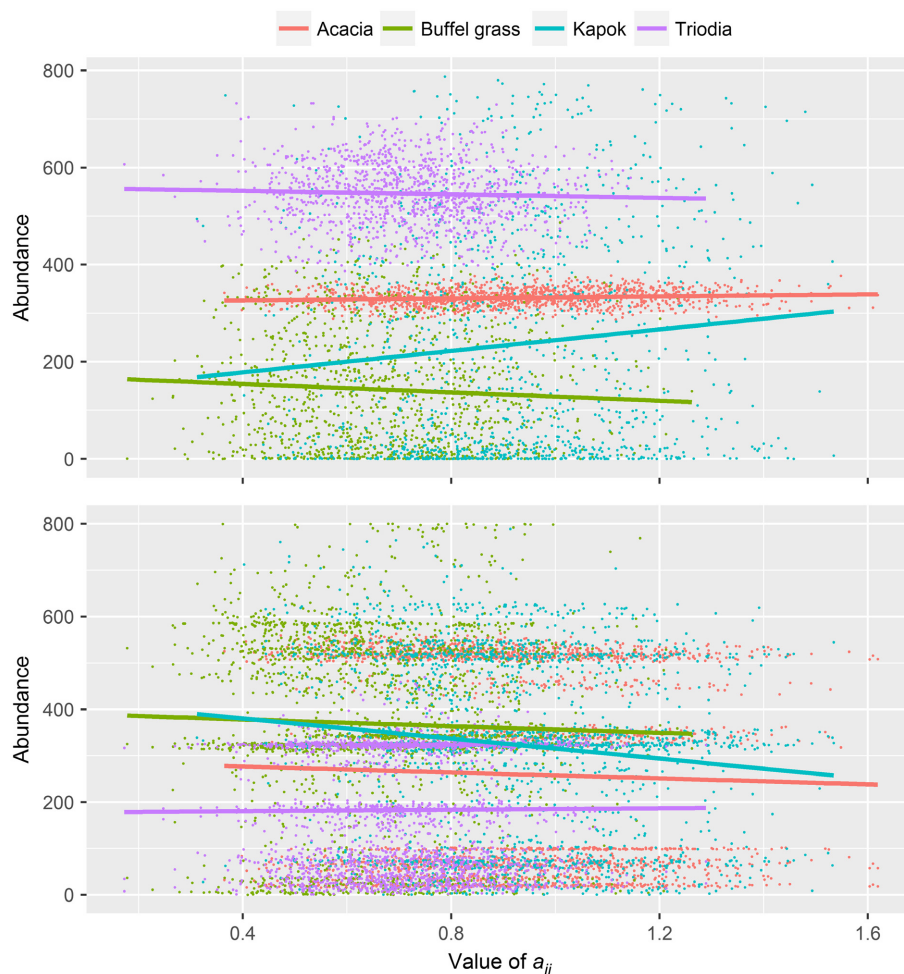


Fig. 3. Influence of variation in the species interaction coefficient ( $\alpha_{ij}$ ) on the year-20 abundance of a labeled species when it is modeled as species  $i$  (a) in the presence of one competitor, or as the competing species  $j$  (b). Points and lines indicate the scatter of data associated with each species, and the linear relationship derived from the data.

$F_{1, 298} = 2.34$ ; adj  $r^2 = 0.87$ ) and the year-20 abundance of wallabies increased (coefficient = 1164.36;  $P < 2.00 \times 10^{-16}$ ; Model  $F_{1, 298} = 69.96$ ; adj  $r^2 = 0.86$ ; Appendix S1: Table S7). The proportion of cats removed per year explained approximately 87% of the variation in the year-20 abundance of cats and wallabies. Fitting a three-parameter logistic equation to the efficacy of management against the proportional reduction in year-20 cat abundance ( $r^2 = 0.99$ ), we calculated an inflection point of 0.40 (95% CI 0.36–0.50), which coincided with the difference between cat populations that stabilized within 20 yr vs. populations that were continuing to decline after 20 yr (Fig. 5). Cat

extinction occurred within 20 yr if  $\theta_{\text{cat}}$  was more than 0.54.

Two carrying capacity terms ( $K$  and prey availability) induced compensatory population growth of cats in response to the removal of cats from the population. When these two terms were included as factors in the analysis of the variation in the year-20 abundance of cats, the model adjusted  $r^2$  value increased to 0.99 (Appendix S1: Table S8). In these modeling scenarios,  $K$  was the more stringent limiting factor, and hence, prey availability was not a significant explanatory variable for cat abundance (coefficient =  $-0.02$ ;  $P = 0.86$ ; Appendix S1: Table S8). The magnitude



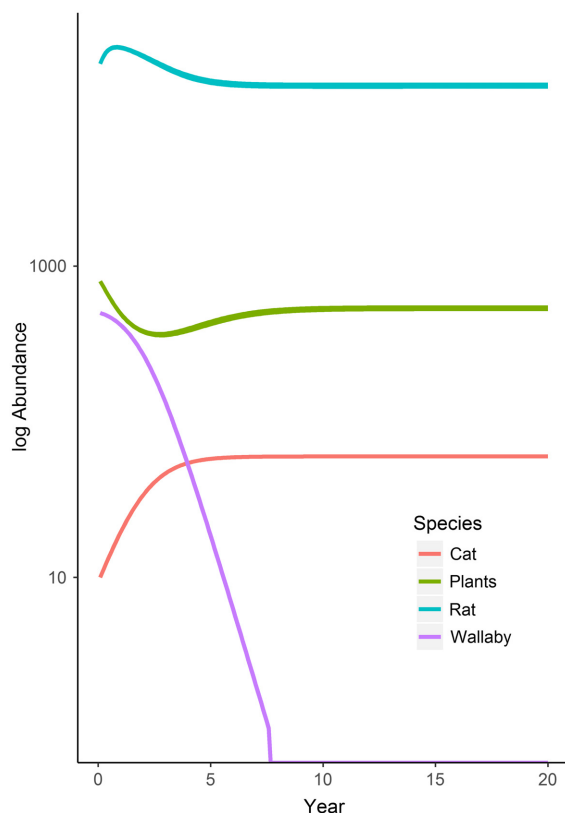


Fig. 4. An example of hyperpredation with insignificant variation (each line depicts the results of 100 model simulations) in species abundance due to variation in  $J_i$ , the quantity of food required to maintain species equilibrium. Note that the  $y$ -axis is on a logarithmic scale.

of the effect of the coefficient of management efficacy on the abundance of the protected feature was indirectly determined by the coefficient of species interaction ( $\alpha_{ij}$ ). The year-20 abundance for species  $j$  (i.e., the feature) significantly decreased as  $\alpha_{ij}$  increased, meaning when  $a_{ij}$  is high an individual predator has greater impact on a population of a feature than when  $a_{ij}$  is low. Therefore, threat mitigation activities will yield greater returns when  $a_{ij}$  is high than when  $a_{ij}$  is low.

## DISCUSSION

Conservation goals can be achieved using a variety of management actions, with optimal actions being identified and prioritized most often

for single species (Wilson et al. 2007, Bottrill et al. 2008, Joseph et al. 2008, Januchowski-Hartley et al. 2011). Our equations of community dynamics and management extend these approaches using spatially and temporally dynamic threat mitigation and species response trajectories that we incorporate into new systematic conservation planning software. While the use of dynamic species response trajectories can reduce total budget costs by up to 20% compared with traditional static methods (Cattarino et al. 2016) and hence significantly alter recommended management actions, a prioritization algorithm that could incorporate dynamic species models is a recent development (Brotankova et al. 2015, Urli et al. 2016).

Unfortunately, most ecosystems include some poorly studied species that are a priority for management agencies. The input values for these species will necessarily involve uncertainty that may not be reduced in the near future. The novel purpose of our sensitivity analysis was to reveal, in the context of uncertain population parameters, the behavior of the threat mitigation and species response trajectories and facilitate understanding of model components for users of the conservation planning software. Other research has demonstrated that halving the variance on parameters with the largest correlation coefficients produces the greatest refinement to model predictions (Gardner et al. 1981). For many species, those parameters are going to be the initial species abundance and environmental carrying capacity (Appendix S1: Table S8), given that the influence of all other parameters is constrained by this ceiling.

The three key model behaviors revealed by our sensitivity analysis are significant variation in 20-yr species abundance due to parameter uncertainty, a significant and potentially stabilizing effect of modeling multiple species simultaneously (Fig. 1), and response curves of native species mirroring threat mitigation trajectories, albeit with species-specific lag-times (Fig. 5).

Increasing the number of species included in the ecosystem model reduced the influence of uncertainty in the species growth rate (Fig. 2). The number of species included in the ecosystem was also a significant covariate when there was uncertainty in the coefficient of species interaction ( $\alpha_{ij}$ ) or food required to maintain species equilibrium ( $J_i$ ), but it influenced the value of species

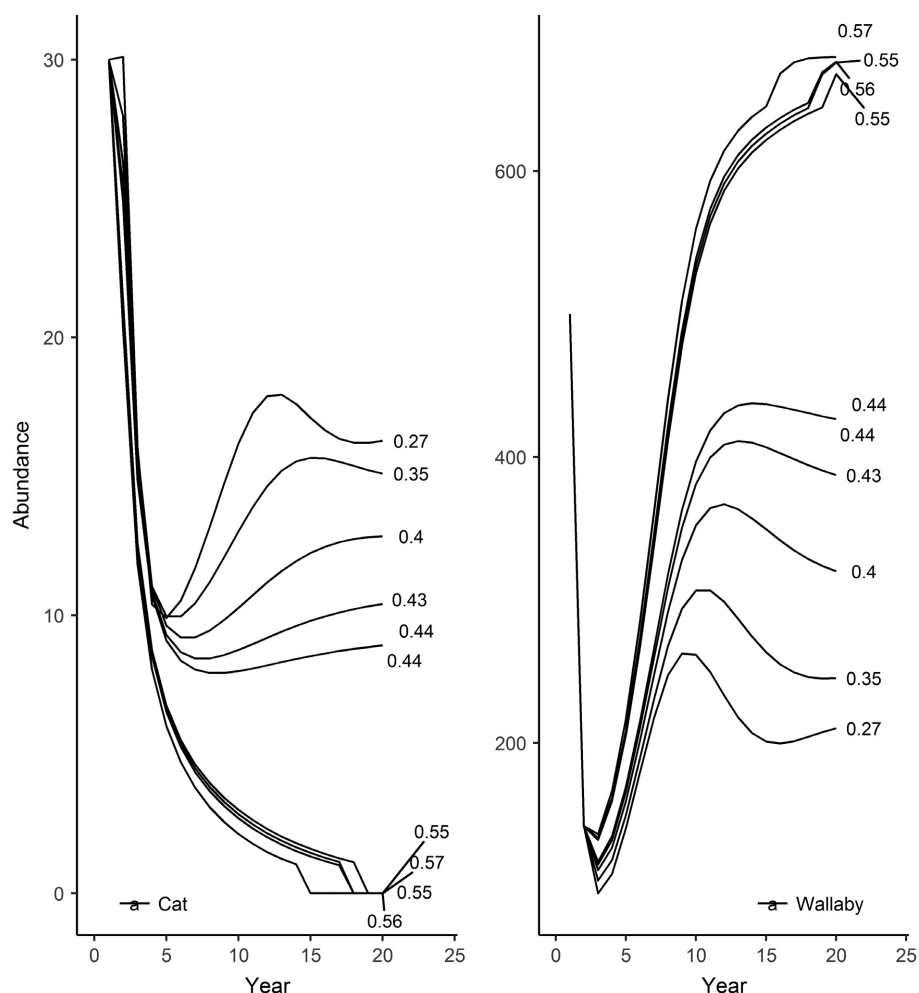


Fig. 5. Variation in abundance of an introduced predator (cat) and native prey (wallaby) in response to variation in the coefficient of effectiveness of a management action ( $\theta_{cat}$ , rounded 2 decimal places): (a) variation in abundance of predator with management action applied annually and (b) variation in abundance of native prey in response to that of the predator.

year-20 abundance rather than variation in abundance by altering the amount of resources (i.e., habitat or food) available. While ecosystem stability can be measured by many metrics, our results are consistent with the consensus view that greater species diversity within an ecosystem increases ecosystem stability in the face of perturbations (Ives and Carpenter 2007). Similarly, the construction of food webs with plausible interaction strengths (species interaction matrix;  $\alpha_{ij}$ ; Appendix S1: Table S2) also improves stability of the modeled ecosystem (McCann 2000). More importantly, it suggests that the results of the

prioritization process will be less subject to uncertainty if multiple species are included.

Multi-annual cycles of population density may occur because of combinations of nonlinear responses to density or because of time-lags in response to environmental change (Batzli 1992). We have embedded the former into our equations through the use of logistic growth curves. The volatility of these cycles is influenced directly by the rate of population growth and indirectly by the ratio of a population with carrying capacity. We created the latter via a linear functional response that describes the interactions between

two species ( $\alpha_{ij}$ ) and generates dampening oscillations around equilibrium levels of predator and prey abundance. Increasing the value of  $\alpha_{ij}$  increases the magnitude of the oscillations. Lag-times generated by the latter case provide crucial information for managers to visualize, because the return (i.e., increase in species targeted for conservation) on management investment may take years or decades (e.g., protecting marine turtle nests when turtles take 30–50 yr to reach reproductive maturity).

The linear (type I) functional response between predators and prey (Holling 1965) is responsible for the species response trajectories mirroring threat mitigation. As mentioned, the decision-support software that will use these equations may be applied to poorly studied areas with many understudied species. A linear functional response provides the simplest relationship between predators and prey and hence reduces the effort to define input values. However, when compared with type II or III functional response curves, which are both asymptotic, a linear functional response will overestimate the effects of an invasive species when prey is at high densities, and potentially underestimate the number of prey taken when predators are at low density but engage in targeted or surplus killing (Zimmerman et al. 2015). Surplus killing has been linked to low prey densities and sporadic food supply (e.g., breeding seabird populations; Oksanen et al. 1985, Major and Jones 2005), both of which are common occurrences on islands. In a biosecurity context, surplus killing has also been linked to the reinvasion/invasion of an ecosystem by an invasive species that is not currently established (Short et al. 2002). A type III sigmoidal functional response is the more appropriate curve for describing the impact of predators that engage in prey switching or surplus killing, but would be more complicated to define for lesser-studied species.

With regard to threat mitigation, one of the most important outputs for managers to be able to access is the extinction threshold, which is also known as the sustainable harvest threshold (Slade et al. 1998, Hone et al. 2010), and the associated time to extinction. Removing the threshold amount of a population annually will stop population growth and stabilize species abundance, whereas removing more of a population than is defined by the threshold will eventually drive it

to extinction. The extinction threshold is directly related to a species' maximum annual rate of population growth ( $r_{\max}$ ). For cats, with  $r_{\max}$  of 0.99 (Table 4), Hone et al. (2010) predicted that the extinction threshold will be 0.57. In our simulations, which started with 20 cats, at least one cat was still present after 20 yr if the proportion of cats removed annually was less than or equal to 0.54. If 57% of the population was removed annually, cats were extinct within 15 yr.

Other software has been designed to calculate species interactions for the purposes of managing an environment, including Ecosim/Ecopath (Christensen and Walters 2004). Ecosim/Ecopath uses a similar bioenergetics framework to model species interactions. However, Ecosim/Ecopath, which is designed for use in managed fisheries, requires many variables, including biomass accumulation rate, diet composition, and migration rate, that could not be defined for poorly studied terrestrial ecosystems or species. Our equations have a reduced data requirement through the use of several assumptions: (1) Islands are closed ecosystems with no net migration; (2) species abundance is limited by the amount of habitat and food available; (3) the quantity of habitat shared by two species is a suitable proxy for competition, which may occur via many different interactions; and (4) species interact with their habitat, other species, and management, which occurs in a consistent manner across the landscape.

The limitations associated with our assumptions are (1) difficulties in defining the carrying capacity or management targets (Didier et al. 2009) for migratory species (e.g., shorebirds) or species with low site fidelity (e.g., fairy tern, *Sterna nereis*); (2) difficulties including information regarding dietary preferences and prey switching; and (3) due to the bioenergetics framework, ensuring that enough primary producers are included in the modeled ecosystem to feed consumers, and prevent the extirpation of threats without management. Modeled consumers (Eq. 2), like real consumers, cannot survive on barren islands. Careful parameterization of primary producers and species interactions may allow predictions of ecosystem collapse due to invasional meltdown (O'Dowd et al. 2003) or alternatively facilitate hypothesis development regarding why cosmopolitan species have failed to invade some island ecosystems (e.g., *Rattus*

*rattus* in the Kimberley Island group; Conservation Commission of Western Australia 2010). Another advantage of the bioenergetics framework is that it allows for some aspects of the hyperpredation process (Courchamp et al. 2000), in that a population of a consumer can increase in abundance despite declining abundance of their primary prey species because the model uses a web of species interactions.

The advantages of temporally dynamic threat mitigation and species response trajectories, especially when they are embedded as visual graphics in decision-support software, include giving managers access to (1) locally relevant lag-times between the establishment of a threat and unacceptable adverse impacts on valued features (native species, habitats, or processes); (2) visual estimates of levels of control that suppress threats sufficiently to allow conservation targets to persist; (3) an estimate of the time required to eradicate threats when the efficacy of control is less than 100%; (4) an understanding of how quickly a threat may rebound when management actions are interrupted or terminated; and (5) an understanding of what threats and conservation targets will do on islands not selected for management actions (the missed opportunity cost of actions taking place only on selected islands). This latter advantage is highly relevant to common situations in which conservation budgets are insufficient to deal with all invasive species on all sites of concern.

While many of these concepts have been discussed in detail in the ecological literature and are understood by managers, they are difficult to quantify and use in decision-making because it is rare for an agency to have access to high-resolution, locally relevant studies that cover their suite of threats and conservation targets. Our software and associated models pull decades of ecological and threat mitigation research together and make it accessible to those who implement conservation. Regardless of (reasonable) parameter uncertainty, the use of temporally dynamic threat mitigation and species response trajectories in systematic conservation planning software will increase the decision-making power of island managers by giving them access to site- and species-specific models of the ecological community.

## ACKNOWLEDGMENTS

This project was funded by the Gorgon Barrow Island Net Conservation Benefits Fund. RLP and CRD acknowledge the support of the Australian Research Council. Appendix S1 contains detailed statistical results associated with our sensitivity analysis.

## LITERATURE CITED

- Anadon, J., A. Gimenes, R. Ballestar, and I. Perez. 2009. Evaluation of local ecological knowledge as a method for collecting extensive data on animal abundance. *Conservation Biology* 23:617–625.
- Barlow, N., and G. Norbury. 2001. A simple model for ferret population dynamics and control in semi-arid New Zealand habitats. *Wildlife Research* 28:87–94.
- Batzli, G. 1992. Dynamics of small mammal populations: a review. Pages 831–850 in D. R. McCullough and R. H. Barrett, editors. *Wildlife 2001: populations*. Elsevier Science Publishers LTD, Essex, England.
- Bengtsson, J., T. Fagerstrom, and H. Rydin. 1994. Competition and coexistence in plant communities. *TREE* 9:246–250.
- Bottrill, M. C., et al. 2008. Is conservation triage just smart decision making? *Trends in Ecology and Evolution* 23:649–654.
- Brody, S. 1945. *Bioenergetics and growth*. Reinhold, New York, New York, USA.
- Brotankova, J., M. Randall, A. Lewis, R. L. Pressey, and A. Wenger. 2015. A genetic algorithm solver for pest management control in island systems. Pages 273–285 in S. Chalup, A. Blair, and M. Randall, editors. *Proceedings of the First Australasian Artificial Life and Computational Intelligence Conference (8955)*. ACALCI 2015. Newcastle, New South Wales, Australia, 5–7 February 2015. Springer International Publishing, Cham, Switzerland.
- Butchart, S. H., M. Walpole, B. Collen, A. Van Strien, J. P. Scharlemann, R. E. Almond, J. E. Baillie, B. Bomhard, C. Brown, and J. Bruno. 2010. Global biodiversity: indicators of recent declines. *Science* 328:1164–1168.
- Carvalho, J., and P. Gomes. 2003. Habitat suitability model for European wild rabbit (*Oryctolagus cuniculus*) with implication for restocking. *Game and Wildlife Science* 20:287–301.
- Case, R. 1973. Energetic requirements for egg-laying bobwhites. Pages 205–212 in J. A. Morrison and J. C. Lewis, editors. *Proceedings of the 1st National Bobwhite Quail Symposium*. Oklahoma State University, Stillwater, Oklahoma, USA.
- Cattarino, L., V. Hermoso, L. W. Bradford, J. Carwardine, K. A. Wilson, M. J. Kennard, and S. Linke.



2016. Accounting for continuous species' response to management effort enhances cost-effectiveness of conservation decisions. *Biological Conservation* 197:116–123.
- Christensen, V., and C. Walters. 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* 172:109–139.
- Clout, M. and C. Veitch. 2002. Turning the tide of biological invasion: the potential for eradicating invasive species. Pages 1–3 in C. R. Veitch and M. N. Clout, editors. *Turning the tide: the eradication of invasive species*. Occasional Paper of the IUCN Species Survival Commission No. 27. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.
- Coddou, A., H. Mills, N. Hamilton, and D. Algar. 2014. Baiting effectiveness for introduced rats (*Rattus* sp.) on Christmas Island. *Raffles Bulletin of Zoology Supplement* 30:54–59.
- Conservation Commission of Western Australia. 2010. Status Performance Assessment: Biodiversity Conservation on Western Australian Islands, Phase 2 - Kimberley Islands, Final Report. The Government of Western Australia, Perth, Western Australia, Australia.
- Courchamp, F., M. Langlais, and G. Sugihara. 2000. Rabbits killing birds: modelling the hyperpredation process. *Journal of Animal Ecology* 69:154–164.
- Crooks, K., and M. Soule. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400:563–566.
- Dickman, C. 1992. Conservation of mammals in the Australasian region: the importance of islands. Pages 175–214 in J. Coles and J. Drew, editors. *Australia and the global environmental crisis*. Academy Press, Canberra, Australian Capital Territory, Australia.
- Dickman, C. R. 1996. Overview of the impacts of feral cats on Australian native fauna. Australian Nature Conservation Agency, Canberra, Australian Capital Territory, Australia.
- Dickman, C. 2007. The complex pest: interaction webs between pests and native species. Pages 208–215 in D. Lunney, P. Eby, P. Hutchings, and S. Burgin, editors. *Pest or guest: the zoology of overabundance*. Royal Zoological Society of New South Wales, Mosman, New South Wales, Australia.
- Didier, K. A., M. J. Glennon, A. Novaro, E. W. Sander-son, S. Strindberg, S. Walker, and S. DiMartino. 2009. The landscape species approach: spatially-explicit conservation planning applied in the Adirondacks, USA, and San Guillermo-Laguna Brava, Argentina, landscapes. *Oryx* 43:476–487.
- Dixon, I., K. Dixon, and M. Barrett. 2002. Eradication of buffel grass (*Cenchrus ciliaris*) on Airlie Island, Pilbara coast, Western Australia. Pages 92–101 in M. Clout and C. Veitch, editors. *Turning the tide: the eradication of invasive species*. IUCN SSC Invasive Species Specialist Group, Gland, Switzerland and Cambridge, UK.
- Doherty, T., C. Dickman, D. Nimmo, and E. Ritchie. 2015. Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. *Biological Conservation* 190:60–68.
- Duncan, R., A. Boyer, and T. Blackburn. 2013. Magnitude and variation of prehistoric bird extinctions in the Pacific. *Proceedings of the National Academy of Science USA* 110:6436–6441.
- Duncan, R., D. Forsyth, and J. Hone. 2007. Testing the metabolic theory of ecology: allometric scaling exponents in mammals. *Ecology* 88:324–333.
- Eberhardt, L., and R. Petersen. 1999. Predicting the wolf-prey equilibrium point. *Canadian Journal of Zoology* 77:494–498.
- Ehrenfeld, J. 2010. Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution and Systematics* 41:59–80.
- Emlen, J. 1966. The role of time and energy in food preference. *American Naturalist* 100:611–617.
- Forsyth, D., and R. Duncan. 2001. Propagule size and the relative success of exotic ungulate and bird introductions to New Zealand. *American Naturalist* 157:583–595.
- Gardner, R., R. O'Neill, J. Mankin, and J. Carney. 1981. A comparison of sensitivity analysis and error analysis based on a stream ecosystem model. *Ecological Modelling* 12:173–190.
- Gholz, H., C. Grier, A. Campbell, and A. Brown. 1979. Equations for estimating biomass and leaf area of plants in the Pacific northwest. Research Paper 41, Oregon State University, Corvallis, Oregon, USA.
- Gimeno, I., and M. Vila. 2002. Recruitment of two *Opuntia* species invading abandoned olive groves. *Acta Oecologica* 23:239–246.
- Guthlin, D., I. Storch, and H. Kuchenhoff. 2014. Toward reliable estimates of abundance: comparing index methods to assess the abundance of a mammalian predator. *PLoS ONE* 9:e94537.
- Hanski, I., H. Henttonen, E. Korpimäki, L. Oksanen, and P. Turchin. 2001. Small-rodent dynamics and predation. *Ecology* 82:1505–1520.
- Harper, G., and N. Bunbury. 2015. Invasive rats on tropical islands: their population biology and impacts on native species. *Global Ecology and Conservation* 3:607–627.
- Hejda, M., P. Pyšek, and V. Jarosik. 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology* 97:393–403.

- Holling, C. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada* 97:5–60.
- Hone, J. 2007. *Wildlife damage control*. CSIRO Publishing, Collingwood, Victoria, Australia.
- Hone, J., V. Drake, and C. Krebs. 2015. Prescriptive and empirical principles of applied ecology. *Environmental Reviews* 23:170–176.
- Hone, J., R. Duncan, and D. Forsyth. 2010. Estimates of maximum annual population growth rates ( $rm$ ) of mammals and their application in wildlife management. *Journal of Applied Ecology* 47:507–514.
- Hone, J., C. Krebs, M. O'Donoghue, and S. Boutin. 2007. Evaluation of predator numerical responses. *Wildlife Research* 34:335–341.
- Ives, A., and S. Carpenter. 2007. Stability and diversity of ecosystems. *Science* 317. <https://doi.org/10.1126/science.1133258>
- Januchowski-Hartley, S. R., P. Visconti, and R. L. Pressey. 2011. A systematic approach for prioritizing multiple management actions for invasive species. *Biological Invasions* 13:1241–1253.
- Johnston, M., D. Algar, N. Hamilton and M. Lindeman. 2010. A Bait Efficacy Trial for the Management of Feral Cats on Christmas Island. Technical Report Series No. 200. Arthur Rylah Institute for Environmental Research, Department of Sustainability and Environment, Government of Australia, Heidelberg, Victoria, Australia.
- Joseph, L. N., R. F. Maloney, and H. P. Possingham. 2008. Optimal allocation of resources among threatened species: a project prioritization protocol. *Conservation Biology* 23:328–338.
- Klein, C. J., J. C. Steinbeck, M. Watts, A. J. Scholz, and H. P. Possingham. 2010. Spatial marine zoning for fisheries and conservation. *Frontiers in Ecology and Environment* 8:349–353.
- MacArthur, R., and E. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* 100: 603–609.
- MacDougall, A., K. McCann, G. Gellner, and R. Turkington. 2013. Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature* 494:86–89.
- Major, H., and I. Jones. 2005. Distribution, biology and prey selection of the introduced Norway rat *Rattus norvegicus* at Kiska Island, Aleutian Islands, Alaska. *Pacific Conservation Biology* 11:105–113.
- Margules, C., and R. Pressey. 2000. Systematic conservation planning. *Nature* 405:243–253.
- Martin, T. G., M. A. Burgman, F. Fidler, P. M. Kuhnert, S. Low-Choy, M. McBride, and K. Mengersen. 2012. Eliciting expert knowledge in conservation science. *Conservation Biology* 26:29–38.
- McCann, K. 2000. The diversity-stability debate. *Nature* 405:228–233.
- McDonald, P., R. Edwards, J. Greenhalgh, and C. Morgan. 2002. *Animal nutrition*. Sixth edition. Pearson Education Limited, Essex, UK.
- McLeod, S. 1997. Is the concept of carrying capacity useful in variable environments? *Oikos* 79:529–542.
- Ney, J. 1993. Bioenergetics modeling today: growing pains on the cutting edge. *Transactions of the American Fisheries Society* 122:736–748.
- O'Dowd, D., P. Green, and P. Lake. 2003. Invasional 'meltdown' on an oceanic island. *Ecology Letters* 6:812–817.
- Oksanen, T., L. Oksanen, and S. D. Fretwell. 1985. Surplus killing in the hunting strategy of small predators. *American Naturalist* 126:328–346.
- Partel, M., R. Kalamees, U. Reier, E. L. Tuvi, E. Roosaluste, A. Vellak, and M. Zobel. 2005. Grouping and prioritization of vascular plant species for conservation: combining natural rarity and management need. *Biological Conservation* 123:271–278.
- Pinheiro, J., D. Bates, S. DebRoy, S. Sarkar, EISPACK authors, S. Heisterkamp, B. Van Willigen, and R-core. 2017. Linear and nonlinear mixed effects models: package 'nlme'. The R Foundation for Statistical Computing, Vienna, Austria.
- Polis, G., and D. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* 147:813–846.
- Potts, J., and J. Elith. 2006. Comparing species abundance models. *Ecological Modelling* 199:153–163.
- Pressey, R. L., M. E. Watts, and T. W. Barrett. 2004. Is maximising protection the same as minimizing loss? Efficiency and retention as alternative measures of the effectiveness of proposed reserves. *Ecology Letters* 7:1035–1046.
- Pulliam, H., and B. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* 137 (Supplement):S50–S66.
- Roberts, M., E. Lightfoot, and W. Porter. 2010. A new model for the body-size-metabolism relationship. *Physiological and Biochemical Zoology* 83:395–405.
- Rodriguez, L. 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biological Invasions* 8:927–939.
- RStudio Team. 2015. RStudio: integrated development for R. RStudio Inc, Boston, Massachusetts, USA.
- Seymour, R., and C. White. 2011. Can the basal metabolic rate of endotherms be explained by biophysical modeling? Response to "A new model for the body size-metabolism relationship". *Physiological and Biochemical Zoology* 84:107–110.
- Short, J., J. Kinnear, and A. Robley. 2002. Surplus killing by introduced predators in Australia - evidence

- for ineffective anti-predator adaptations in native prey species? *Biological Conservation* 103:283–301.
- Sibly, R., and J. Hone. 2002. Population growth rate and its determinants: an overview. *Philosophical Transactions of the Royal Society, London B* 357: 1153–1170.
- Slade, N., R. Gomulkiewicz, and H. Alexander. 1998. Alternatives to Robinsons and Redford's method of assessing overharvest from incomplete demographic data. *Conservation Biology* 12:148–155.
- Spring, D., J. Baum, R. MacNally, M. MacKenzie, A. Sanchez-Azofeifa, and J. R. Thomson. 2010. Building a regionally connected reserve network in a changing and uncertain world. *Conservation Biology* 24:691–700.
- Traveset, A., E. Moragues, and F. Valladares. 2008. Spreading of the invasive *Carpobrotus aff. acinaciformis* in Mediterranean ecosystems: the advantage of performing in different light environments. *Applied Vegetation Science* 11:45–54.
- Urli, T., J. Brotankova, P. Kilby, and P. Van Hentenryck. 2016. Intelligent habitat restoration under uncertainty. *Proceedings of the Thirtieth AAAI Conference on Artificial Intelligence* 3908–3914.
- VanderWerf, E. A., S. M. Mosher, M. D. Burt, P. E. Taylor, and D. Sailer. 2011. Variable efficacy of rat control in conserving Oahu elepaio populations. Pages 124–130 in C. Veitch, M. Clout and D. Towns, editors. *Island invasives: eradication and management*. IUCN, Gland, Switzerland.
- Veitch, C. and M. Clout. 2002. Turning the tide: the eradication of invasive species. Occasional Paper of the IUCN Species Survival Commission No. 27. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.
- Visconti, P., R. L. Pressey, D. B. Segan, and B. A. Wintle. 2010. Conservation planning with dynamic threats: the role of spatial design and priority setting for species' persistence. *Biological Conservation* 143:756–767.
- Watts, M. E., I. R. Ball, R. S. Stewart, C. J. Klein, K. Wilson, C. Steinbeck, R. Lourival, L. Kircher, and H. P. Possingham. 2009. Marxan with zones: software for optimal conservation based land- and sea-use zoning. *Environmental Modelling and Software* 24:1513–1521.
- Williams, C., and R. Moore. 1995. Effectiveness and cost-efficiency of control of the wild rabbit, *Oryctolagus cuniculus* (L.), by combinations of poisoning, ripping, fumigation and maintenance fumigation. *Wildlife Research* 22:253–269.
- Wilson, K. A., et al. 2007. Conserving biodiversity efficiently: what to do, where, and when. *PLoS Biology* 5:e223.
- Wilson, K. A., et al. 2010. Conserving biodiversity in production landscapes. *Ecological Applications* 20:1721–1732.
- Zimmerman, B., H. Sand, P. Wabakken, O. Liberg, and H. P. Andreassen. 2015. Predator-dependent functional response in wolves: from food limitation to surplus killing. *Journal of Animal Ecology* 84:102–112.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1822/full>