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Priority threat management of invasive animals to protect biodiversity under climate change

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Abstract

Climate change is a major threat to global biodiversity, and its impacts can act synergistically to heighten the severity of other threats. Most research on projecting species range shifts under climate change has not been translated to informing priority management strategies on the ground. We develop a prioritization framework to assess strategies for managing threats to biodiversity under climate change and apply it to the management of invasive animal species across one-sixth of the Australian continent, the Lake Eyre Basin. We collected information from key stakeholders and experts on the impacts of invasive animals on 148 of the region's most threatened species and 11 potential strategies. Assisted by models of current distributions of threatened species and their projected distributions, experts estimated the cost, feasibility, and potential benefits of each strategy for improving the persistence of threatened species with and without climate change. We discover that the relative cost-effectiveness of invasive animal control strategies is robust to climate change, with the management of feral pigs being the highest priority for conserving threatened species overall. Complementary sets of strategies to protect as many threatened species as possible under limited budgets change when climate change is considered, with additional strategies required to avoid impending extinctions from the region. Overall, we find that the ranking of strategies by cost-effectiveness was relatively unaffected by including climate change into decision-making, even though the benefits of the strategies were lower. Future climate conditions and impacts on range shifts become most important to consider when designing comprehensive management plans for the control of invasive animals under limited budgets to maximize the number of threatened species that can be protected.

Keywords: adaptive management, climate adaptation, climate variability, complementarity, decision theory, ecological cost-benefit analyses, EPBC Act 1999, IPCC RCP6 scenario, IUCN Red list, Maxent, multi-objective optimization, synergistic threats to biodiversity

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Introduction

Preventing the catastrophic loss of the world's native species and ecosystems under anthropogenic climate change is one of the most significant challenges of the coming 50–100 years (Franklin, 1999; Woinarski et al., 2001; Monastersky, 2014). Climate change impacts are threatening native biodiversity by altering resource availability and biotic interactions within ecosystems (Thomas et al., 2004). A changing climate exacerbates pre-existing threats to biodiversity, such as the spread and impact of invasive species (Hellmann et al., 2008).

To date, climate change research efforts have focused on understanding the potential shifts in the geographic

distribution of native species of concern in response to projected climate models (Thomas et al., 2004). However, species responses to climate change alone are not sufficient to inform decision-makers about the most cost-effective adaptation strategies for managing threats to biodiversity under climate change (Dawson et al., 2011). Managers cannot undertake all possible strategies to manage biodiversity threats in all places and at all times and must decide where, when, and how much to invest in various management strategies (Wilson et al., 2009; Martin et al., 2014). To make informed decisions in a changing climate, we need approaches for assessing different adaptation strategies and their likely cost-effectiveness under future climate change conditions (Shoo et al., 2013; Pacifici et al., 2015).

Research efforts on conservation decision-making are increasingly reliant on effective methods for combining

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expert opinion and scientific data, allowing for more rapid and adaptable decision-making in the face of looming biodiversity losses (Burgman et al., 2011; Martin et al., 2012). To date, expert information has been used to evaluate the cost-effectiveness of strategies in a range of settings to assist decision-making for saving threatened species, wildlife, and other ecological assets (Possingham et al., 2002; Joseph et al., 2009; Carwardine et al., 2012; Pannell et al., 2012; Chades et al., 2014). The cost-effectiveness of a strategy is measured by the expected benefits it provides divided by the expected costs (Cullen et al., 2005). The potential benefits of strategies are measured as the improvement in species habitat protected (Carwardine et al., 2008), improvement in species persistence (Joseph et al., 2009; Carwardine et al., 2012), or a reduction in the habitat occupied by an invasive species (Firn et al., 2015). Conservation costs can include financial management costs and/or opportunity costs (Naidoo et al., 2006).

To date, however, none of these approaches have been used to determine whether climate change considerations are likely to affect which conservation strategies we should choose. Research on conservation decisions such as protected area expansion (Hannah et al., 2007; Alagador et al., 2014; Bush et al., 2014) and threatened species translocation under climate change (McDonald-Madden et al., 2011) finds significant efficiency gains are possible by considering future climate scenarios. Hence, it is likely that priority threat management approaches that ignore climate change may miss cost-effective opportunities for managing threats to native species as future climate shifts are realized (Pacifi et al., 2015).

In this study, we develop a prioritization approach for assessing the cost-effectiveness of threat management strategies to conserve biodiversity under climate change. Specifically, we identify how the relative cost-effectiveness of strategies to improve the persistence of native species will change under a future climate scenario, while considering threats that interact with climate change. We demonstrate our approach by prioritizing strategies to abate the interacting threats of invasive animals and climate change on native species persistence over a vast area of Australia, the Lake Eyre Basin (LEB), for the next 50 years.

Invasive animals are a leading cause of the decline of native species in Australia (Evans et al., 2011) and globally (Butchart et al., 2010). Invasive animals predate upon native species, compete for resources, and contribute to further habitat alterations (Gurevitch & Padilla, 2004; Woinarski et al., 2015). A shared characteristic of invasive animals is their ability to reproduce and spread quickly, as they are highly adaptable to changing weather and biotic conditions (Hellmann

et al., 2008). Invasive animal populations are subject to both pressures and opportunities provided by climate change. The combined pressure from climate change and invasive animals is likely to have a profound impact on threatened native species already disadvantaged by habitat and environmental conditions that will be indirectly impacted by anthropogenic climate change (Isaac & Cowlshaw, 2004; Brooks, 2008). Invasive animals also impact on other sectors – for example, the costs of management, administration, and research to address the impacts of invasive animals to Australia's agricultural and horticultural sectors are estimated at \$700 million annually (Gong et al., 2009).

The approach we develop here could be applied to other regions facing combined impacts from multiple threats including climate change. Our findings influence how conservation policy and financial investments to manage threats to native biodiversity should be planned today for longer term climate change impacts.

Materials and methods

Case-study region

The LEB covers approximately 120 million ha of arid and semiarid central Australia. This is a large area, one-sixth of the Australian continent and equivalent to the combined area of Germany, France, and Italy (Habeck-Fardy & Nanson, 2014). The LEB spans multiple states, including Queensland, South Australia, New South Wales (smallest land area), and the Northern Territory. This makes trans-boundary cooperation pivotal to the success of natural resource management efforts across the region. In recognition of this need for coordination of management efforts, the LEB Intergovernmental Agreement was established in 2001. The purpose of this Agreement 'is to provide for the development or adoption, and implementation of Policies and Strategies concerning water and related natural resources in the LEB Agreement Area to avoid or eliminate so far as reasonably practicable adverse cross-border impacts' (Anon, 2000).

Lake Eyre or Kati Thanda is the fourth largest terminal lake in the world. It lies in the most arid part of Australia, with an average annual rainfall of less than 125 mm and an evaporation rate of 2.5 m (Anon, 2000). Only a small fraction of the rain that falls in the Basin flows to Lake Eyre. On the rare occasions when large volumes of water do flow, exceptionally large flocks of water birds gather in the Basin to breed, attracted by masses of fishes and aquatic invertebrates in the flooded waterways (Kingsford, 1995).

The LEB supports a diverse array of ecosystems. Given the arid climate, the most extraordinary are those associated with the ephemeral wetlands and large permanent waterholes. Examples include the internationally recognized Coongie Lakes (Ramsar listed), Astrebla Downs National Park, and Munga-Thirri National Park. Mound springs, which occur at points of natural water seepage from the LEB Great Artesian Basin (GAB), are listed as endangered under the Australian

Commonwealth Environmental Protection and Biodiversity Conservation Act 1999. Mound springs support many rare species including at least 13 endemic plant species and 65 endemic fauna species (Fensham et al., 2007).

Data collection

We used a structured expert elicitation approach to identify control strategies for managing the impacts of invasive animals on threatened species in the LEB. This approach also provided estimates of the actions, costs, feasibility, and benefits of each strategy. We conducted elicitations during two workshops. The first was a 3-day workshop (April 2013; 22 participants) to structure the problem and gather expert predictions under current conditions. The second was a 2-day workshop (April 2014; 24 participants), which gathered expert predictions under expected climate change. Nine participants attended both workshops. Overall, 37 participants attended the workshops, which included representatives from federal, state and local governments, indigenous landholders, pastoralists, and nongovernment organizations, and nine members from the LEB advisory committees (Scientific and Community).

Participants who were experts in the biodiversity of the LEB (14 participants) agreed on 148 threatened native flora (74 spp.) and fauna (74 spp.) to be included in the study. See Table S1 in the supplementary material for a complete list. These included 80 species listed by the Australian federal government Environmental Protection and Biodiversity Conservation (EPBC) Act, 34 listed by both the EPBC and the IUCN Red list, 27 listed only on the IUCN Red list, and 7 additional floral species also considered threatened and important in the region by the experts. Participants grouped these threatened species into 31 species groups; 18 for fauna spp., and 13 for floral spp. Species groups included critical weight range ground-dwelling mammals (defined as mammals with an intermediate body mass between 35 g and 5500 g), rock wallabies, bats, granivorous birds, ground-dwelling birds, parrots, individual rare species (*Erythrorhynchus radiatus*, *Manorina melanotis*, and *Falco hypoleucos*), water birds (*Rostratula australis* and *Botaurus poiciloptilus*), amphibians, snakes, lizards and geckos, GAB mound spring fish, other fish, butterfly (i.e., *Croizetana aestiva*), yabbie (*Cherax destructor*), GAB mound spring invertebrates, endangered forbs, other forbs, endangered graminoids, other graminoids, endangered shrubs, other shrubs, endangered trees, other trees, endangered vines, other vines, endangered other plants, other listed 'others', and GAB mound spring plant species. None of the participants were able to estimate benefits for the following floral species groups: endangered graminoids, other vines, endangered other or other 'listed' other such as epiphytes.

We collated information on the occurrence of 37 invasive animals recorded in the LEB from the scientific literature and the Atlas of Living Australia (Atlas of Living Australia website), accessed on March 15, 2014. Participants agreed on a total of 11 strategies for invasive species management: 9 control strategies targeting different invasive animals either individually or in groups: *Sus scrofa* (hereafter pigs), *Equus ferus caballus*

(hereafter horses) and *Equus asinus* (hereafter donkeys), *Capra hircus* (hereafter goats), *Camelus dromedaries* (hereafter camels), *Oryctolagus cuniculus* (hereafter rabbits), *Bufo marinus* (hereafter cane toads), predators (*Felis catus* (hereafter cats), *Canis familiaris* (hereafter dogs), and *Vulpes vulpes* (hereafter foxes), *Gambusia holbrooki* (hereafter gambusia), and other aquatic invaders; an overarching strategy to set up an Institution for natural resource management; and a total combined strategy of all of the above strategies (Table 1). Each strategy was made up of a number of actions required to successfully implement the strategy.

Threatened species distribution models. We modeled the current distribution and made projections about the future distribution of the threatened species of the LEB to aid experts to estimate the benefits to biodiversity of implementing different strategies under climate change. The focal threatened species are known to occur in very few localities; therefore, guidance on their current and projected future distributions under climate change was key data needed to support estimates by the experts. The potential distributions of the threatened species in the LEB under current and future climate conditions were modeled according to the method described in Maggini et al. (2013) and explained below.

Spatial data on the occurrence of threatened native fauna and flora in the LEB were extracted from the Australian Natural Heritage Assessment Tool database. This toolbase includes species location records from Australian museums, Australian herbaria, Birdlife Australia, CSIRO, and state and territory governments. The precise distribution of threatened/rare species is sensitive information; therefore, data were supplied in a denaturated form of occurrences within a 0.01° (~1 km) grid cell. Modeling was undertaken for species with a minimum of 20 occupied grid cells at a resolution of one decimal degree across Australia (total 100 species, consisting of 3 amphibians, 12 reptiles, 15 birds, 28 mammals, and 42 plants) (Table S2 in the supplementary materials). This threshold was set to ensure a robust modeling outcome (Maggini et al., 2013). We were not able to model fishes and crustaceans as the method used is only suitable for terrestrial species.

The current and future distributions of the species were modeled at the continental scale using the same bioclimatic and substrate predictors that proved to be effective for the modeling of threatened species in Australia by Maggini et al. (2013). The bioclimatic predictors were related to temperature (annual mean temperature, temperature seasonality) and precipitation (precipitation seasonality, precipitation of the wettest and driest quarters). Substrate predictors were the solum average clay content, hydrological scoring of pedality, solum average of median horizon saturated hydraulic conductivity, and mean geological age (Williams et al., 2010, 2012). Species distributions were modeled using the software Maxent (Philips et al., 2006). Presence records were compared against a background sample (10 000 grid cells), which was defined separately for each species and chosen randomly from within the IBRA regions (Interim Biogeographic Regionalisation of Australia, v.7 <http://www.environment.gov.au/land/nrs/science/ibra>) currently occupied by the species. IBRA classifies landscapes

Table 1 Management strategies and description of actions with and without consideration of climate change. More detailed descriptions of suggested actions are provided in Table S11 in the supplementary material

Management strategies	Brief description of actions
1. Institution for facilitating natural resource management (overarching strategy)	A general contingency fund that could be used to respond to unanticipated threats such as new pests or unexpected outbreaks
2. Predator control (cat, fox, and dog control)	Cat and fox trapping and baiting at key assets Fox aerial baiting Monitoring Early response 'control' team in each state Training of guardian dogs community program PhD research projects to improve control efforts Additional actions with climate change Additional eight research projects on the impacts of climate change on cat populations and mesopredator release effects
3. Pig control	Aerial baiting and/or shooting around water Monitoring program every 10 years Special asset management PhD research projects to improve control efforts
4. Cane toad control	Asset protection PhD research projects on control efforts Monitoring and trapping: localized eradication Surveillance and biosecurity hotspots Education
5. Gambusia	Chemical control (e.g., rotenone) of gambusia Surveillance and biosecurity Research program on chemical controls Education and public awareness campaigns Identification of key threats and triage ranking Modeling to predict the impact of changes to natural flows because of planned irrigation projects in the Queensland section of the LEB

Table 1 (continued)

Management strategies	Brief description of actions
6. Other aquatic spp. control	Research program on eDNA Education campaign and signage Surveillance and biosecurity Increased investment into LEBRA Quarantine of pristine GAB mound springs Translocation projects Protection of natural flows
7. Horse and donkey control	Education including regular training workshops Aerial culling with helicopters Monitoring program Public engagement program Industry partners for meat production market depending on local regulations
8. Camel control	Education including regular training workshops Monitoring program of control efforts Public engagement program Commercial muster for sale Aerial culling with helicopters Fencing with steel spider structures for key waterhole/cultural protection
9. Goat control	Education including regular training workshops Aerial culling with helicopters Monitoring program of control efforts Public engagement program Industry partners for meat production market depending on local regulations Incentive/assistance program to encourage mustering of goats Fencing with steel spider structures to protect biodiversity assets
10. Rabbit control	Monitoring program Biological control Habitat modification (warren destruction) Fumigation Baiting with 1080 Education and regular training workshops Engagement staff and programs
11. Total combined strategies	All strategies 1 to 10 combined

into large geographically distinct bioregions based on common climate, geology, landform, native vegetation, and species presence. Modeling was performed using R scripts on the high-performance computing facilities at The University of Queensland.

Species' distributions were projected (from 1990) into the future under three climate change scenarios and for three time horizons, namely 2015, 2035, and 2055. The climate change scenario used for the projections was three of the new Representative Concentration Pathways (RCPs) adopted by the IPCC's fifth assessment report: a high-emission business as usual scenario RCP 8.5, a moderate mitigation scenario RCP 6 requiring a climate-policy intervention, and a stronger mitigation scenario RCP 4.5 assuming the imposition of a series of emission mitigation policies (Masui et al., 2011; Riahi et al., 2011; Thomson et al., 2011). To simplify the task of the experts, workshop participants were only presented results in relation to the intermediate scenario, namely RCP 6 (scenario without overshoot pathway leading to 850 ppm CO₂ eq), and time horizon 2055.

Species' distributions were projected for 18 different Global Circulation Models (GCMs; see Table 3 in Maggini et al., 2013) to avoid the bias related to the choice of a particular GCM. Projections were summarized using the median of the predicted probabilities of occurrence across the 18 GCMs within each grid cell. Finally, the realized distribution of a species was obtained by removing from the potential distribution all areas that were not within a currently occupied or neighboring IBRA region. Given that IBRA regions are vast areas of similar biogeographic characteristics, species are unlikely to expand their range beyond neighboring IBRA regions within the modeled time frame.

The probabilistic map of each species was transformed into a presence/absence map according to a threshold that equated the entropy of the distributions before and after applying the threshold (Philips et al., 2006). The presence/absence maps for all species within each group were stacked into one data layer and used to calculate the species richness within each grid cell to produce maps of the current and future distributions of species groups (example presented in Fig. 1). The species richness per grid cell in the maps can vary from zero to a maximum corresponding to the number of species in the group (n) specified next to the group name in the title of the figure. Some groups are composed of a single species while others contain up to 19 species (Fig. 1, see Annex S1 in the supplementary material to view all species group maps provided to workshop participants).

Estimating benefits, costs, and feasibility of strategies. Workshop participants estimated the benefits of each strategy, the costs and feasibilities of each of the individual actions required to implement the strategy, using existing information where available and the species group distribution maps described above.

To estimate the benefits of each strategy, biodiversity experts estimated the probability of functional persistence of each species group under a 'baseline scenario' where none of the management strategies would be implemented. They then estimated the probabilities of species group persistence if each

strategy was implemented independently. The probability of functional persistence was given by the likelihood that a species would persist at levels high enough to achieve their 'ecological function' (Carwardine et al., 2011). Participants estimated benefits individually following a modified Delphi approach (Speirs-Bridge et al., 2010), where following the workshop summarized estimates were anonymized and provided to participants with the opportunity to revise their estimates (McBride et al., 2012).

Two elements of feasibility were collected for each action detailed with the strategies: the probability of uptake (the likelihood that the strategy would be implemented, taking into account economic, social, and political factors) and the probability of success of the action (the likelihood that the action would achieve its desired impact). Feasibility for each action was calculated as the product of the probabilities of uptake and success. The feasibility of each strategy was calculated by averaging the estimated values across all actions in each strategy.

Fixed and variable cost estimates over 50 years for each action were estimated in small groups. Costs were converted to present-day values using a discount rate of 7%, the recommended rate for public investments in Australia (Council of Australian Governments, 2007). We also conducted sensitivity analyses to assess how a 3% or a 10% discount rate may change the priority rankings of strategies.

Experts had the opportunity to estimate benefits, feasibility, and direct costs of each management strategy under current climatic conditions and under the climate change scenario at horizon 2055 (see following section). Experts decided that strategies and costs would not change under the climate scenario considered apart from the strategy on predator control (which would become more expensive due to the addition of research projects), but did suggest changes to benefit and feasibility estimates. The difference in estimated benefits and feasibility was used to compute the expected changes in persistence of species and the cost-effectiveness of strategies under climate change.

Cost-effectiveness ranking approach. We estimated the cost-effectiveness of a strategy *i* (CE_{*i*}) by the total expected benefit of the strategy divided by the expected cost (C_{*i*}). The expected benefit for each strategy was estimated by multiplying the potential benefit (B_{*i*}) by the feasibility (F_{*i*}), providing an indication of the likely improvement in persistence across the threatened species in LEB if that strategy was implemented:

$$CE_i = \frac{B_i F_i}{C_i} \tag{1}$$

The potential benefit B_{*i*} of implementing strategy *i* across the LEB was defined by the cumulative difference in persistence probability of threatened species groups in the region with and without implementation of that strategy, averaged over the experts who made predictions for the species group:

$$B_i = \frac{1}{k} \sum_{j=1}^k \frac{P_{ij}}{M_j} \tag{2}$$

where P_{*ijk*} is the probability of persistence of threatened species groups *j* if strategy *i* is implemented, estimated by expert

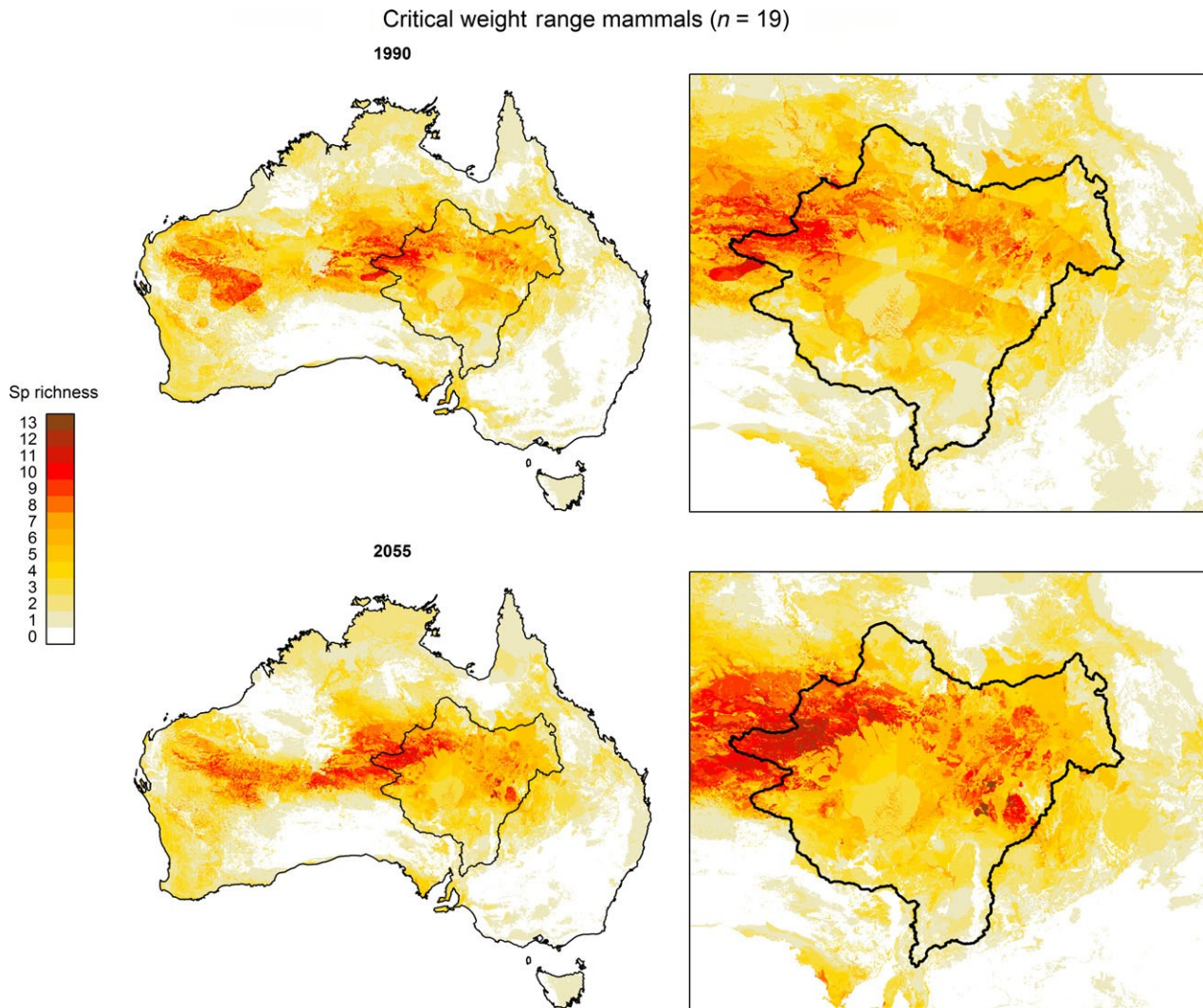


Fig. 1 Richness (sum of single species' modeled presence) of threatened species belonging to the group of critical weight range mammals ($n = 19$) at current time (1990) and in 2055 under the climate change scenario RCP6, across Australia and within the Lake Eyre Basin (zoom on the right panel).

k . P_{0jk} is the probability of persistence of functional groups j if no strategy is implemented (baseline scenario), estimated by the same expert k . N is the number of functional groups, and M_j is the number of workshop participants who made predictions for the functional group j .

Complementary sets of strategies at various budgets

Because the cost-effectiveness approach evaluates strategies individually, there is a possibility that multiple strategies that are highly cost-effective would benefit the same species. If funding was available to implement several strategies at once, strategies selected from the top of a ranked list based on their individual cost-effectiveness may not be the most complementary set. In other words, some species receive more protection than necessary, while other species receive no protection at all. In contrast, using complementarity approaches, strategies

are evaluated jointly so that strategies selected benefit as many different species as possible (Chades et al., 2014). In our case, we sought to identify optimal sets of strategies that could maximize the number of species saved for any given budget. This is useful when decision-makers have the dual objectives of maximizing the number of species secured at a minimum cost. We investigated three thresholds of species group persistence (i.e., probability of functional persistence): $>85\%$, $>70\%$, and $>50\%$, over 50 years with and without climate change. We assumed that when multiple strategies were implemented, the persistence of an individual species was equal to the persistence provided by the most beneficial strategy. While it is likely in many cases that implementing multiple strategies would increase persistence beyond that of individual strategies, we were unable to collect information on positive or negative interactions between strategies and as such took a conservative approach. However, the combined strategy 11

provided an indication of the persistence of species when all strategies are implemented.

Finding the optimal sets of strategies that secure as many species groups as possible above any one of these thresholds for any given budget requires solving a multi-objective optimization problem:

$$\max \sum_{j \in N} p_{ij} x_i \text{ and } \min \sum_i C_i x_i \quad \delta 3b$$

where x_i is a binary decision variable that denotes whether ($x_i = 1$) or not ($x_i = 0$) a strategy is included in the optimal set of strategies. A vector $x \in \{0, 1\}^S$ represents a combination of selected strategies. The S represents the set of strategies listed in Table 1; p_{ij} identifies whether species j is expected to reach a given persistence threshold if strategy i is implemented; $p_{ij} = 1$ if the expected benefit of applying strategy i for species j is above the persistence threshold (i.e., $B_{ij} + B_{0j} > s$ with $B_{ij} = \frac{1}{4} \frac{M_j \delta}{M_j + o_{jk}}$; $p = 0$ if this threshold is not exceeded. The persistence p_{ijk} of each strategy was elicited independently, that is, assuming no other strategy was implemented.

Because multi-objective problems rarely have a unique solution that maximizes all objectives simultaneously, Pareto-optimal solutions are sought. Pareto-optimal solutions are solutions that cannot be improved in one objective without degrading at least one other objective (Nemhauser & Ullmann, 1969; Ruzika & Wiecek, 2005). Formally, a decision x^0 is dominated by a decision x if it secures fewer species per unit cost of implementation. We found the Pareto-optimal solutions by formulating our problem as an integer linear programming problem.

Results

Habitat distribution models for species groups

The distribution models for the 100 species were all considered valid as evaluated with the area under the curve (AUC) of a receiver-operating characteristic plot (Training.AUC) and a ten-fold cross-validation (average Test.AUC; provided in Table S2 of the supplementary materials). The median value for the training AUC across all species was 0.938 and 0.906 for the cross-validated AUC, which corresponds to ‘very good’ discrimination ability (Swets, 1988).

The habitat distribution models predicted that in the next 50 years, the species groups will generally shift in a southeast direction within the LEB under the climate change scenario considered with a stronger emphasis on the southern, respectively, eastern component depending on the group (Fig. 1 and see Annex S1 in supplementary material for all maps generated). This southeastward shift is consistent with other large-scale climate projections of Australian biodiversity for the continent (Dunlop et al., 2012). For the species’ groups with a distribution centered on the central arid zones of

Australia, such as the critical weight range mammals, parrots, and skinks, distributions are expected to move out of the center generally toward the southeast but in different directions depending on the species group. As a consequence, in the LEB, species are mainly expected to move from the west and the north and to leave the basin from the south and the east.

Cost-effectiveness appraisal with and without climate change

The cost-effectiveness ranks of strategies were robust to the consideration of the climate change scenario. The pig control strategy was the most cost-effective, followed by horses and donkeys, and goats control the least cost-effective (Table 2). The combined strategy that included the implementation of all strategies

remained the 7th (of nine) most cost-effective with and without consideration of climate change impacts on the distribution of the threatened species.

The total cost (net present value, NPV) of implementing all of the proposed strategies for the control of invasive animals across the LEB over the next 50 years was \$439 million, equivalent to an average annualized cost of \$32 million. These costs increased slightly with consideration of the climate change scenario to a total cost of \$442 million and an average annualized cost of \$33 million (Table 2). Eight of the strategies focused on the control of invasive animals with substantial existing populations, while one strategy, cane toad control, focused on preventing a future risk to threatened species in the LEB. The only strategy with a different cost under climate change was the predator control strategy, because of the addition of eight research projects (including PhD scholarships) aimed at investigating cat populations and mesopredator release effects. Workshop participants decided that the ‘Institution for facilitating natural resource management strategy’ would be overarching. Benefits were not estimated separately for this strategy, but participants were asked to consider the benefits of this strategy when making estimates for the other strategies.

Feasibility estimates increased when the climate change scenario was considered for most strategies, except for gambusia and other aquatic invasive strategies where participants predicted a decrease in feasibility (Table 2). Benefits of implementing the strategies for the persistence of threatened species were estimated as lower under the climate change scenario for gambusia, cane toads, other aquatic invaders, and goats (Table 2). For the remaining five strategies, benefits were estimated as higher under the climate change scenario.

Priority rankings of cost-effective strategies differed for particular categories of animals and plants such as

Table 2 Appraisal of key conservation strategies across the Lake Eyre Basin, estimated: uptake (%), success (%), average expected benefits, average net present value, annual equivalent value, and cost-effectiveness. Appraisal values estimated without consideration of the climate change scenario are shown in brackets for comparison

Strategy	CE rank	Cost-effectiveness score	Uptake (proportion 0–1)	Success (proportion 0–1)	Expected benefit (50 years)	Rank expected benefit	Expected NPV (50 years)	Average annualized cost
Pigs	1 (1)	1.93 (1.79)	0.93 (0.925)	0.76 (0.75)	543 (504)	3 (3)	\$28 M (\$28 M)	\$2 M (\$2 M)
Horses and donkeys	2 (2)	1.38 (1.43)	0.80 (0.80)	0.90 (0.80)	581 (562)	2 (2)	\$41 M (\$41 M)	\$3 M (\$3 M)
Cane toads	3 (3)	1.12 (1.22)	0.88 (0.88)	0.80 (0.77)	438 (476)	5 (4)	\$39 M (\$39 M)	\$3 M (\$3 M)
Camels	4 (4)	1.04 (1.00)	0.90 (0.95)	0.80 (0.70)	425 (410)	6 (5)	\$41 M (\$41 M)	\$3 M (\$3 M)
Rabbits	5 (5)	0.73 (0.57)	1 (1)	0.50 (0.50)	471 (363)	4 (6)	\$64 M (\$64 M)	\$5 M (\$5 M)
Gambusia	6 (6)	0.42 (0.55)	0.67 (0.67)	0.56 (0.63)	83 (109)	8 (9)	\$20 M (\$20 M)	\$2 M (\$2 M)
All strategies	7 (7)	0.38 (0.38)	0.9 (0.9)	0.80 (0.80)	1698 (1652)	1 (1)	\$442 M (\$439 M)	\$33 M (\$32 M)
Predators	8 (8)	0.31 (0.29)	0.72 (0.62)	0.84 (0.87)	374 (353)	7 (7)	\$123 M (\$120 M)	\$9 M (\$9 M)
Other aquatic	9 (9)	0.19 (0.28)	0.89 (0.89)	0.64 (0.69)	81 (119)	9 (8)	\$43 M (\$43 M)	\$3 M (\$3 M)
Goats	10 (10)	0.15 (0.19)	0.5 (0.50)	0.25 (0.20)	63 (80)	10 (10)	\$44 M (\$44 M)	\$3 M (\$3 M)
Institution for NRM	na	na	0.60 (0.60)	0.60 (0.60)	na	na	\$2 M (\$2 M)	\$141 T

NPV, net present values; NRM, natural resource management; M, millions; T, thousands.

mammals, birds, and fauna or flora group together (Table 3). Pig control was the most cost-effective strategy when considering persistence benefits for all species groups. It remained the most cost-effective with climate change for the following animal types: fauna, birds, amphibians, reptiles, and aquatic species (Table 3). The most cost-effective strategy for threatened mammals was the predator control strategy both with and without climate change (Table 3). For increasing the persistence of threatened plant species, the most cost-effective strategy was horse and donkey control with and without climate change. Cane toad control was the most cost-effective strategy for increasing the probability of persistence for GAB mound spring species and also for aquatic species but without consideration for climate impacts. The gambusia control strategy was co-ranked as the most cost-effective for threatened amphibians along with pig control (Table 3).

The cost-effectiveness of strategies increased with the climate change scenario for the control of camels, horses and donkeys, pigs, predators, and rabbits (Fig. 2a). Cost-effectiveness of strategies decreased for strategies that targeted aquatic invaders such as gambusia, cane toads, and other aquatic invaders such as red claw, tilapia, and sleepy cod (Fig. 2a). The cost-effectiveness of controlling goats was also estimated to decrease with climate change (Fig. 2a).

For threatened fauna, cost-effectiveness of strategies decreased under climate change for the control of horses and donkeys, gambusia, other aquatic invaders, goats, and all strategies combined. Cost-effectiveness estimates increased in the cases of predator, camel, and rabbit control (Fig. 2b). For threatened flora, cost-effectiveness of all strategies was estimated to increase with climate change, except for the control of camels and goats (Fig. 2c). Under the climate change scenario, the cost-effectiveness of strategies increased or remained similar for threatened GAB mound spring species, mammals, and reptiles (Fig. 2g, h, and i), but not for aquatic species where strategies were estimated to decrease in cost-effectiveness except with camel control (Fig. 2e). Cost-effectiveness estimates varied little under climate change for the two threatened amphibian species (Fig. 2d).

Cost-effectiveness analyses were robust to possible inaccuracies of $\pm 30\%$ made by participants when estimating benefits and costs. We found no change in the priority ranking of the top ten strategies both with and without climate change when biodiversity benefit estimates were varied from 70% to 130% of the original values (Table S3 in supplementary material). We found cost-effectiveness rankings were also generally robust to changes in discount rates. The only difference in rankings occurred at the discount rate of 10%, where

Table 3 Appraisal of key invasive animal control strategies across the Lake Eyre Basin by species group – estimated cost-effectiveness (CE) overall (all threatened flora and fauna), fauna only, flora only, birds, mammals, amphibians, aquatic fish and invertebrates, reptiles, and all species recorded as threatened in the GAB mound springs. CE values are shown with and without considering climate change scenarios (denoted by WOC). The highest ranking strategy is shaded in blue, and the second and third ranking strategy shaded in gray

Strategy	Overall	WOC_			WOC_			WOC_			WOC_			WOC_			WOC_GAB		
		Birds	Mammals	Amphibians	Mammals	Amphibians	Amphibians	Aquatic	Aquatic	Reptiles	Reptiles	Reptiles	GAB Springs	GAB Springs	GAB Springs	Reptiles	Reptiles	Reptiles	springs
Pigs	1.93	1.79	1.44	1.55	0.48	0.11	0.26	0.28	0.12	0.01	0.03	0.74	0.96	0.22	0.13	0.68	0.46		
Horses and donkeys	1.43	1.38	0.75	0.83	0.68	0.10	0.05	0.12	0.08	0	0.003	0.35	0.58	0.16	0.12	0.62	0.30		
Cane loads	1.12	1.22	1.00	1.22	0.12	0.01	0.01	0.06	0.06	0.006	0.006	0.73	1.06	0.20	0.10	0.70	0.48		
Camels	1.04	1	0.71	0.56	0.33	0.08	0.04	0.13	0.09	0.006	0.006	0.34	0.32	0.15	0.10	0.35	0.29		
Rabbits	0.73	0.57	0.30	0.23	0.44	0.06	0.05	0.14	0.12	0	0.003	0	0.01	0.08	0.06	0	0		
Gambusia	0.42	0.55	0.42	0.55	0	0	0	0	0	0	0.03	0.41	0.52	0	0	0.41	0.42		
All	0.38	0.38	0.23	0.24	0.15	0.04	0.04	0.10	0.10	0.003	0.004	0.05	0.06	0.02	0.02	0.04	0.05		
Predators	0.31	0.29	0.31	0.29	0	0.03	0.07	0.22	0.19	0	0.002	0	0	0.03	0.03	0	0		
Aquatics	0.19	0.28	0.19	0.28	0	0	0	0	0	0.004	0.003	0.18	0.27	0	0	0.12	0.09		
Goats	0.14	0.19	0.07	0.09	0.07	0.01	0.01	0.03	0.03	0	0	0	0.04	0.03	0.02	0.05	0		

WOC_ Mammals Birds

the gambusia control strategy moved from the sixth ranked to seventh ranked strategy swapping with all strategies combined (Table S4 in supplementary material). This occurred because the gambusia control strategy includes a number of costs early on during the 50-year period.

Species persistence under limited budgets

The optimal combination of strategies depends on the budget available to implement strategies, on the species group persistence threshold selected and whether climate change is considered (Fig. 3). Overall, it is predicted to be more difficult and costly to secure species under the predicted future climate scenario. Without a budget for effective invasive animal control strategies, some 29 species (analyses were run at the species group level; here we sum the number of species within each of the groups) are likely to be lost from the LEB over the next 50 years under climate change, having a persistence estimate of less than 50%. If targeting a minimum species group persistence level (i.e., ≥50% likelihood of persistence), all groups are estimated to reach this threshold by implementing two management strategies: predator control and pig control at an annual estimated cost of \$10.8 million over 50 years (Fig. 3, Table S5). Under the climate change scenario, two species (*Cherax destructor* (common yabbie) (42%) and *Manorina melanotis* (black-eared miner) (44%)) would not reach the 50% persistence threshold even if all strategies were implemented (\$31.8 million yr⁻¹, Table S6).

If targeting a higher persistence threshold of 70%, 115 species are predicted to reach this threshold by combining the strategies of pig control, predator control, and cane toad control (\$15.4 million yr⁻¹, Fig. 3). Implementing all strategies would secure three additional species groups (rock wallabies, spring fish, and granivorous birds) and additionally increase the probability of persistence for four species: black-eared miner (64.5%), yabbie (52.9%), *Scaturiginichthys vermeilipinnis* (red-finned blue eye) (64.1%), and the butterfly (60%, Table S7). When climate change impacts are considered, two species groups would not be secured even if all strategies were implemented (i.e., granivorous birds and CWR mammals, Table S8).

If targeting an 85% persistence threshold, the majority of floral species groups are predicted to reach this threshold with the implementation of the rabbit and camel strategies, whereas none of the faunal species groups will reach this threshold even if all control strategies were implemented. The flora species groups, ‘endangered trees’ (83.6%) and ‘endangered shrubs’ (84.4%), were close to reaching the 85% threshold (Table S9). Under the climate change scenario, the only

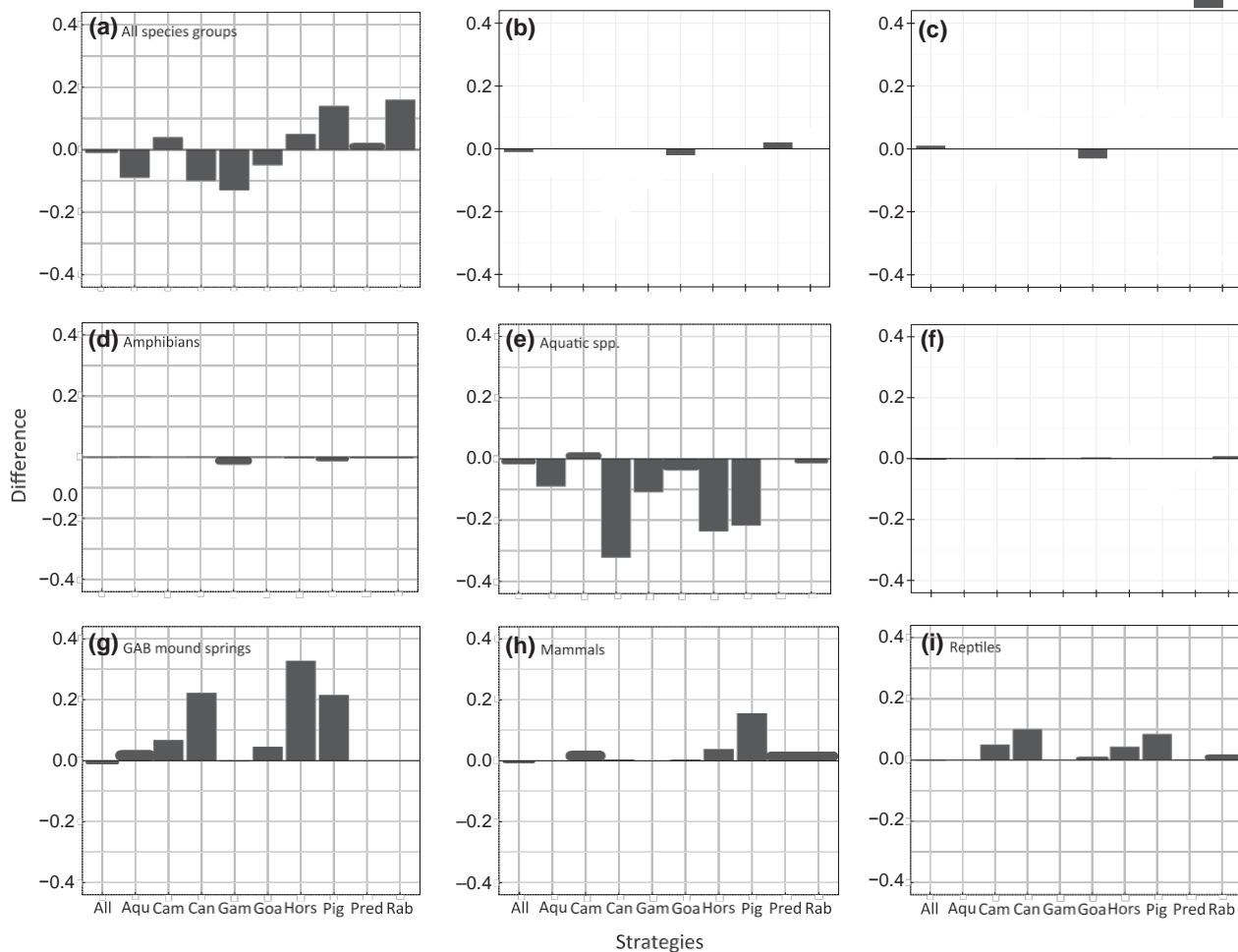


Fig. 2 Differences between the cost-effectiveness estimates with and without considering a climate scenario for all species groups and different categories. Negative values indicate experts estimated a reduction in the cost-effectiveness of invasive animal control strategies for increasing the persistence of threatened species with climate change.

species groups reaching the threshold were ‘Other shrubs’ and ‘Other trees’ (40 species), which equates to 23 species less than when the climate scenario was not considered. The species group ‘reptiles’ (83.7%) was close to the threshold in consideration of climate change (Table S10).

Discussion

Habitats worldwide are experiencing what is described as the Earth’s sixth mass extinction, which is already being exacerbated by climate change (Settele et al., 2014). Here we develop a framework for prioritizing threat management strategies considering climate change. Our application to the management of invasive animals in the LEB indicates that the priority ranking of strategies is robust to climate change predictions. However, we discover that the ecological cost-effectiveness for protecting threatened species generally decreases

under the most likely climate scenario and it will cost more money and effort spent on specific sets of strategies to ensure species persistence above target levels under climate change. Priority strategies differed for specific threatened species groups, indicating the importance of targeting actions toward species of concern. Our approach and findings are potentially applicable to other regions globally, especially those facing multiple threats including the complex synergies with climate change.

The most cost-effective strategy for improving the overall persistence of native threatened species was the management of feral pigs, at approximately \$2 million yr⁻¹ in specific locations throughout the region. We found that invasive predator control is one of the top priority strategies for the protection of threatened mammals with and without considering climate change impacts, which supports the current focus on predator control strategies for protecting biodiversity in Australia

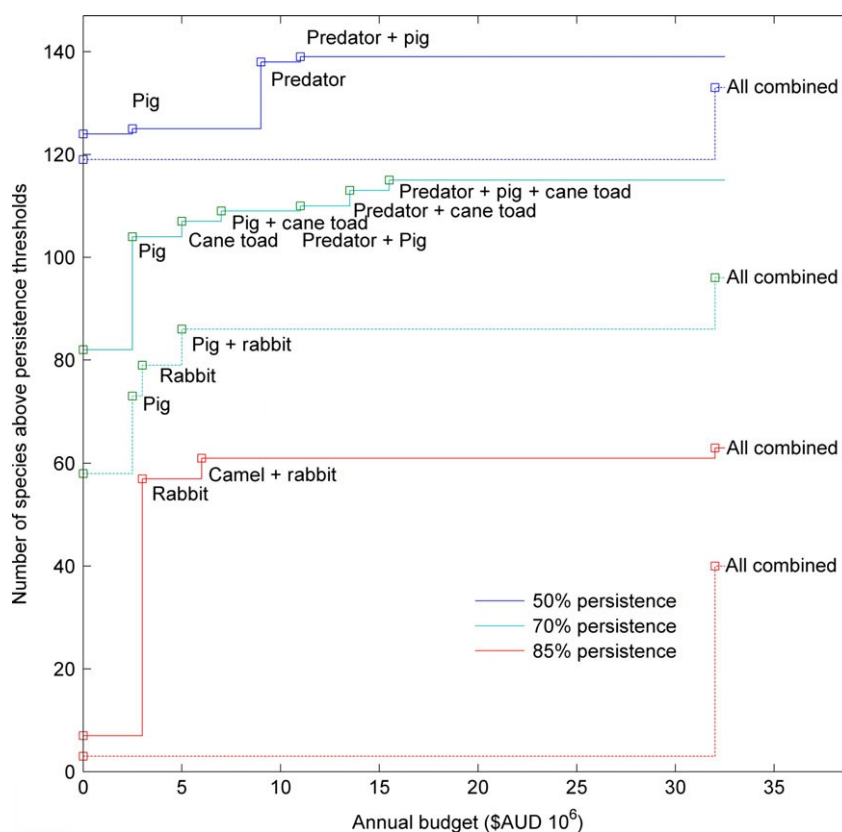


Fig. 3 The optimal strategies selected at a range of budget increments from \$0 to 32 million yr⁻¹ for improving the persistence of species above three thresholds (50%, 70%, and 85% chance of persistence), both with (solid line) and without (dashed line) considering the climate change scenario. This complementarity analysis accounts only for the benefits of strategies that improve the persistence of species to exceed each threshold. As shown by the cost-effectiveness ranking approach, there are benefits to undertaking all strategies, but not always sufficient benefits to improve species persistence above one of these thresholds.

(Woinarski et al., 2015). Pig control was a top priority for the majority of species groups and becomes a higher priority under climate change for birds, reptiles, amphibians, and aquatic species. *Gambusia* control was the most cost-effective strategy for threatened aquatic species without consideration of climate change, while pig control was expected to be more cost-effective under climate change. This shift from *Gambusia* to pig control when considering climate change impacts is supported by the IPCC predictions of reduced river flows within Australia and reduced water availability is likely to hinder the negative impacts of *Gambusia* but inhibiting its spread (Reisinger et al., 2014).

We discovered that improving the persistence of native threatened species would become more challenging under the climate change scenario in LEB with biodiversity experts predicting lower probabilities of threatened species persistence (Letnic & Dickman, 2010). The cost-effectiveness of strategies was overall lower with climate change, predominantly because the potential biodiversity benefits would decrease for all

but two strategies (i.e., pig and rabbit control strategies). The costs of implementation increased under climate change with one strategy, predator control. Participants estimated that feasibility of most of the strategies would increase with climate change as invasive animal populations were expected to decline in density and range due to lower rainfall and unpredictable climatic events, making them easier to locate and control (Spencer et al., 2012). Feasibility decreased for strategies focused on the aquatic invasive animals, due to the difficulty of finding populations with less water flowing through the LEB and potentially more sporadic and even less predictable flooding events (Roshier et al., 2001).

Our complementarity analysis indicates that more strategies are needed to improve the persistence of species above higher critical thresholds under climate change. When we considered persistence thresholds of 50% and 70%, we found that pig control and predator control (with the additional of cane toad control at 70%) were consistently the optimal strategies to secure the

maximum number of species. If climate change is considered and the threshold target is 70% or more, all strategies should be implemented but even then fewer species groups will be secured and no faunal species groups will reach a persistence threshold of 85%. These results reflect empirical studies that have found remote areas and relatively intact habitats of Australia to be experiencing high rates of extinctions particularly in comparison with other continents such as North America (Woinarski et al., 2015).

Cost-effectiveness rankings and complementarity sets provided us with different recommendations on the optimal strategies to implement; the most relevant recommendations depend upon the conservation objective and available budget (Chades et al., 2014). If funds are available for one or two strategies only, managers may choose the highest ranked strategy in terms of cost-effectiveness as this maximizes the overall benefit, but does not ensure that this benefit is spread evenly among species of concern. Risk-averse managers may wish to focus on the complementary set of strategies that is predicted to provide a minimum persistence threshold for as many species as possible given the resources available. Managers focused on specific groups of species may implement the strategies that benefit those species. Further, managers may wish to consider broader objectives, values, and preferences than those considered in our study, such as the cultural values of invasive animals and the management priorities to reduce the impacts of invasive animals to agriculture.

The naturally variable climate of the LEB and the response of exotic and native species to variable climates suggest that establishing an 'Institution for facilitating natural resource management' is a key strategy. The LEB is already characterized by a highly variable climate, and climate change impacts are predicted to increase this variability (Williams, 2002; Reisinger et al., 2014). This poses a significant challenge as public funding for natural resource management is typically earmarked for an activity in a given financial year. At the start of a financial year, it may not be possible to anticipate favorable invasive animal control climatic conditions, so allocating resources in advance to mitigate threats like invasive animal control can be inefficient (Spencer et al., 2012). This strategy would allow managers to find the funds needed to respond early to rising issues and would allow funding to be carried over into future years if it is likely to be better spent later, when conditions are more conducive for high invasive animal populations. Without such an institution, it is unlikely that annual funding could be used cost-effectively. The concept of a responsive institution could act as a key model for managing pests under climate change globally.

Our findings are applicable to other parts of the globe that are characterized by climates similar to the LEB (Brooks, 2008; Mainka & Howard, 2010). The LEB has a climate that is naturally difficult to predict and often extreme, usually in a state of flood or drought (Habeck-Fardy & Nanson, 2014). Many workshop participants were natural resource managers who have been making decisions on how to adapt actions to climate variability for decades. To develop climate change adaptation strategies for biodiversity conservation, we must capitalize on this expertise to develop recommendations for cost-effective strategies in regions not already accustomed to managing under these conditions.

Our approach presents some assumptions and limitations. Participants gave estimates for the persistence of species groups for which they were confident in having the knowledge to do so; therefore, we have variable numbers of estimates for each species group. We were unable to create species distribution models for all threatened species considered in this study because presence data were not available or insufficient for some species, and the technique is only robust for terrestrial species. Due to data paucity, the expert predictions used in these analyses may not always be formed on the basis of published, peer-reviewed scientific research or on the real costs of management strategies. We assumed that strategies could be fully funded or not funded, but in reality actions could be partially funded. Our approach also does not consider interactions between invasive animal threats, nor additional threats to native species that operate across the basin, such as habitat clearing, fire, cattle grazing, or invasive plants. We show that managing for invasive animals under climate change is insufficient to secure the persistence of all native species considered in this study (i.e., common yabby and black-eared miner). We assumed that any combination of strategies delivered the maximum benefit of the independent strategies being combined, where in reality a combined strategy could deliver a higher benefit than the maximum of individual strategies.

Climate change and invasive animals are considered two of the leading causes of biodiversity loss globally (Millennium Ecosystem Assessment, 2005; Monasterky, 2014). Synergies between these global threats necessitate a re-think of how we manage invasive animals for the protection of native biodiversity, as adapting to climate change is a multifaceted problem (Brooks, 2008; Dawson et al., 2011). Effectively responding to the threat of invasive animals under climate change, within financial and logistic constraints will be key to successfully meeting the challenge of protecting native species.

The approach we present here can be adapted and applied to any region of the world and for other threats, because it is flexible, transparent, systematic, and knowledge based. Analyses can be updated as improved information on the costs and benefits of invasive animal control becomes available. This is likely to be vital for effectively conserving biodiversity as climate conditions become increasingly unpredictable. Taking into consideration, future climate conditions when planning for biodiversity conservation will assist to ensure limited resources are used most efficiently. Further, our analysis indicates that ignoring climate change may result in optimistic estimates of species persistence, leaving us with insufficient resources to adequately manage native biodiversity to avoid further species losses.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Focal list of threatened fauna and flora considered in this study and how the species were organised into ‘species groups’ for the purposes of the estimates and analyses. The Environmental Protection and Biodiversity Conservation Act (the EPBC Act 1999) refers to the Australian federal government key legislation to protect and manage nationally and internationally important flora, fauna, ecological communities and heritage places.

Table S2. Species where there was sufficient data to conduct species distribution models of current (1990) and based on future predictions. Validity of the distribution models were evaluated using Training. AUC and Average Test.AUC. These tests validated the models generated and our shown here.

Table S3: Sensitivity of the CE rankings for each of the strategies in the LEB. We conducted these analyses to test the effectiveness of the CE rankings to inaccuracies in estimates of species benefits, costs or feasibility. Ranks in brackets are for climate change scenarios.

Table S4. Sensitivity analysis of cost effectiveness values and appraisal of key conservation strategies, depending on discount rates of 3%, 7% and 10%. Appraisal values estimated without consideration of the climate change scenario are shown in brackets for comparison.

Table S5. Details of Pareto results for persistence threshold of 50% without CC.

Table S6. Details of Pareto results for persistence threshold of 50% with CC.

Table S7. Details of Pareto results for persistence threshold of 70% without CC.

Table S8. Details of Pareto results for persistence threshold of 70% with CC.

Table S9. Details of Pareto results for persistence threshold of 85% without CC.

Table S10. Details of Pareto results for persistence threshold of 85% with CC.

Table S11. Management strategies and description of actions with and without consideration of climate change.

Annex S1. Copies of species richness maps provided to workshop participants.