

Estimating the benefit of well-managed protected areas for threatened species conservation

STEPHEN G. KEARNEY, VANESSA M. ADAMS, RICHARD A. FULLER
HUGH P. POSSINGHAM and JAMES E. M. WATSON

Abstract Protected areas are central to global efforts to prevent species extinctions, with many countries investing heavily in their establishment. Yet the designation of protected areas alone can only abate certain threats to biodiversity. Targeted management within protected areas is often required to achieve fully effective conservation within their boundaries. It remains unclear what combination of protected area designation and management is needed to remove the suite of processes that imperil species. Here, using Australia as a case study, we use a dataset on the pressures facing threatened species to determine the role of protected areas and management in conserving imperilled species. We found that protected areas that are not resourced for threat management could remove one or more threats to 1,185 (76%) species and all threats to very few ($n = 51$, 3%) species. In contrast, a protected area network that is adequately resourced to manage threatening processes within their boundary could remove one or more threats to almost all species ($n = 1,551$; $c. 100\%$) and all threats to almost half ($n = 740$, 48%). However, 815 (52%) species face one or more threats that require coordinated conservation actions that protected areas alone could not remove. This research shows that investing in the continued expansion of Australia's protected area network without providing adequate funding for threat management within and beyond the existing protected area network will benefit few threatened species. These findings highlight that as the international community expands the global protected area network in accordance with the 2020 Strategic Plan for Biodiversity, a greater emphasis on the effectiveness of threat management is needed.

Keywords Aichi targets, Australia, Environment Protection and Biodiversity Conservation Act, EPBC Act, protected area effectiveness, protected area management, threats, threat management

The supplementary material for this article is available at <https://doi.org/10.1017/S0030605317001739>

Introduction

Nationally designated protected area networks are now central to biodiversity conservation strategies globally (Coetsee et al., 2014; Watson et al., 2016) as they are considered the most effective way to overcome the threats that are causing the current biodiversity crisis (Rands et al., 2010). Although recent research has found that protected areas generally support greater species richness and abundance than comparable areas that are not protected (Barnes et al., 2016; Gray et al., 2016), and they are mostly effective at mitigating vegetation clearing by human activity (Naughton-Treves et al., 2005; Joppa et al., 2008), there is also evidence that under current levels of funding many protected areas are unable to abate the many other processes that cause species declines (Craigie et al., 2010; Joppa & Pfaff, 2011). Despite pronounced protected area expansion over recent decades and ambitious global targets for future growth under the 2020 Strategic Plan for Biodiversity (CBD, 2011; UNEP-WCMC & IUCN, 2016), little is known about the extent to which they can abate the full range of threatening processes that imperil species (Watson et al., 2014).

Given the central, and sometimes sole, focus on the establishment of protected areas to fulfil international conservation targets (Joppa & Pfaff, 2011; Lopoukhine & de Souza Dias, 2012; Dudley et al., 2014), it is important to understand the extent to which protected areas can mitigate threatening processes. For example, Australia's National Reserve System is the country's most important investment in biodiversity conservation (Commonwealth of Australia, 2013b) and in 2014 the Environment Minister announced to the World Parks Congress that Australia had achieved its international commitments because it reached the areal component of the goal of 17% of land within protected areas as outlined in Aichi Target 11 of the Strategic Plan for Biodiversity (Secretariat of the CBD, 2010; Hunt, 2014). Many other nations are making progress towards their own protected area coverage targets. For example, both South Africa and Canada are planning a significant increase to their protected area networks to make their contribution to the global 17% target by 2020 (Government of South Africa, 2010; Government of Canada, 2016).

STEPHEN G. KEARNEY (Corresponding author) and JAMES E. M. WATSON* School of Earth and Environmental Sciences, University of Queensland, Steele Building, Brisbane, Queensland 4072, Australia. E-mail stephen.kearney@uq.edu.au

VANESSA M. ADAMS, RICHARD A. FULLER and HUGH P. POSSINGHAM School of Biological Sciences, University of Queensland, Queensland, Australia

*Also at: Global Conservation Program, Wildlife Conservation Society, Bronx, New York, USA

Received 18 July 2017. Revision requested 21 September 2017.

Accepted 13 November 2017. First published online 31 May 2018.

As national and global protected area networks are dramatically expanded to halt biodiversity decline (Venter et al., 2014; Watson et al., 2014; Barr et al., 2016), it is vital to understand their effectiveness at conserving biodiversity. Given Australia is one of the first nations to have claimed to have met the 17% terrestrial area target, it is a useful case study in which to assess the extent that protected areas can abate those processes that threaten species. Despite having a large protected area network, the country has a history of recent extinctions (Woinarski et al., 2017) and with > 1,700 species currently listed as threatened with extinction nationally (Commonwealth of Australia, 2015), further extinctions are likely (Woinarski et al., 2015). Furthermore, most Australian species face multiple threats (Evans et al., 2011) that require a variety of actions to mitigate. These range from protected area designation and targeted threat management across protected and non-protected areas, to stronger legislation and better land-management practices (Lindenmayer, 2015; Woinarski et al., 2015, 2017).

Quantifying the variety of actions needed to mitigate the impacts of threats on imperilled species is vital for understanding the response required to conserve threatened species. Where legal support for protected areas is strong, their designation alone will be effective at mitigating a number of threats, particularly those that cause habitat loss (e.g. agriculture, urbanization). Nevertheless, many threats operate irrespective of land tenure and, as such, management is required to mitigate their impacts. Where threats can be dealt with at a local or point-basis, targeted management within a protected area will effectively mitigate these (e.g. invasive species, fire), but some threats are pervasive across the landscape and therefore require a systematic management approach both inside and outside protected areas (e.g. invasive diseases and pathogens). In Australia, for example, threats such as inappropriate fire regimes and invasive species are contributing to the severe decline of numerous mammal species in one of Australia's premiere protected areas (and a UNESCO Natural World Heritage site), Kakadu National Park (Woinarski et al., 2011). To adequately conserve these threatened species, protected area managers must be resourced to undertake intensive management of these threats. In evaluating the role of protected areas in threatened species conservation it is vital to recognize that in many circumstances protected area designation must be complemented with management to conserve species effectively.

Here we provide the first holistic assessment of the extent to which a continental protected area network mitigates the range of threats to species at risk of extinction. In doing this we aim to understand how effective protected areas are at removing the processes that threaten species with extinction. Using a recently compiled national database on the threats to Australian species, we summarize the range of management actions required to mitigate these threats.

Using this summary we quantify the role that protected areas play in separating threatened species from the processes that threaten their persistence.

Methods

Australian threatened species data

Species that have been classified as threatened by the Australian Department of the Environment and Energy's Threatened Species Scientific Committee and Minister are listed under the Environment Protection and Biodiversity Conservation Act 1999 (Commonwealth of Australia, 2017b). We undertook this study in early 2017, at which time there were 1,749 Australian species listed as threatened under the Act. We followed previous studies (Carwardine et al., 2008; Evans et al., 2011) and included all terrestrial and freshwater vertebrate, invertebrate and plant species, as well as marine species that rely on land or freshwater for a part of their life-cycle. We only considered threats to marine species that originate and require management on land. Excluded from the analysis were extinct species, species that face uncertain threats and exclusively marine species. In total, 1,555 Australian threatened species were considered in this analysis.

Data on threatening processes

Information on Australian threatened species and the threats reported as impacting them are available through the Species Profiles and Threats database (Commonwealth of Australia, 2015). This database provides threat data on species protected under the Environment Protection and Biodiversity Conservation Act and has been used in a number of studies that assess threatening processes on Australian species (Evans et al., 2011; Walsh et al., 2013). For this study we used information from the database that was current as of late 2015.

The information on threats is compiled using a range of sources including listing advice, recovery and action plans, published literature and expert knowledge (Commonwealth of Australia, 2015). It is likely that this information is not exhaustive and the listed threats are likely to be those that are obvious and tangible to managers of threatened species, meaning subtle threats may be overlooked and not reported. The Species Profiles and Threats database follows the standardized Threats Classification Scheme outlined by Salafsky et al. (2008). These threat classifications are the same as those used by IUCN for the Red List process and allow comparison across regions and taxonomic groups (IUCN, 2016). This threat classification scheme contains 11 direct threat types and one type for new and emerging threats ('Other options'; Salafsky et al., 2008). The classification scheme is

based on a three-level hierarchy, with each level increasing in detail and specificity. The first level (major threat) being the broadest, the second level (sub-threat) being more defined and the third level (specific threat) being at a finer scale. Each major threat has between three and six sub-threat classifications. [Table 1](#) provides a full description and specific details for each major threat classification.

Threat management

We used government threat abatement plans and peer-reviewed literature to identify potential management actions to mitigate each threat. Although there are potentially a number of ways to remove each threat and local context influences what is the most appropriate action, we identify what would generally be the conservation action or combination of actions used to mitigate each threat. For clarity we followed the standardized lexicon provided by Salafsky et al. (2008) for conservation actions. [Table 1](#) contains a summary of the threats and conservation actions required and Supplementary Table 1 contains the reasoning for the choice of each action.

Assessing the effectiveness of the protected area network to manage threats

There is no dataset available that provides information on how each individual protected area mitigates the threats occurring within it. We therefore classified each threat relative to how effective the protected area network could be in overcoming it. We followed the standardized conservation actions as defined by Salafsky et al. (2008). Conservation actions are interventions that need to be undertaken to reduce the extinction risk of a species (Salafsky et al., 2008). Using these conservation actions, we defined three distinct threat management scenarios for protected areas.

The first, which we label ‘unmanaged’, considers protected areas as a legally designated land use, which can overcome threats causing vegetation clearance and habitat loss but where threat management such as invasive species control and fire management does not occur ([Table 1](#)). This scenario captures a situation in which protected area managers are inadequately resourced to undertake threat management, as is likely to be the case in some protected areas across Australia (Taylor et al., 2011a; Craigie et al., 2015). In some countries, protected areas are ineffective at achieving their primary goal because of poor legislative support (Watson et al., 2014). Protected areas designated but never implemented (commonly referred to as paper parks) are unlikely to be able to abate the threats we discuss here.

The second scenario, which we label ‘well-managed’, considers a protected area as not only a legally designated land use, and hence able to halt habitat loss, but one

where there is adequate funding and resources provided to undertake effective management of threats within its boundary. Here, management is a broad term that refers to activities that mitigate the processes that threaten species within the protected area boundary. Management actions range from invasive species control and fire management, to enforcement and habitat restoration ([Table 1](#) provides full details).

Additionally, a number of threats to Australian species are unable to be adequately mitigated by protected areas, no matter how well resourced and managed (Gaston et al., 2008). These threats require a coordinated response across protected and non-protected areas, which we label ‘landscape management’ ([Table 1](#)). An example of threats that require a landscape management approach are the invasive diseases and pathogens listed as key threatening processes under the Environment Protection and Biodiversity Conservation Act (Commonwealth of Australia, 2017a). These diseases impact 161 Australian threatened species and are thought to have caused or contributed to at least four extinctions of Australian species (Commonwealth of Australia, 2005, 2006, 2014). The threat abatement plans for these diseases emphasize a number of management actions to be coordinated nationally. These are minimizing the spread of the disease by controlling dispersal through quarantine actions and controlling the movement of infected species, mitigating the impact on species at infected sites through identified means, and the establishment of a captive breeding programme for species at high risk of extinction (Commonwealth of Australia, 2005, 2006, 2014). Although effectively managed protected areas play a vital role in mitigating the impact of threats such as this, a coordinated threat management approach across the broader landscape is needed to ensure effective conservation.

There are local factors that require interpretation to determine the most appropriate management action. These factors influence both the impact of threats and the effectiveness of the management action required to deal with it. For example, the impact of salinity can vary widely in its scale and severity. Where its impact is localized, a protected area with restoration efforts can effectively mitigate this. Whereas when salinity impacts an entire landscape, as is occurring in Australia’s Murray-Darling Basin, a landscape management approach is required (Murray-Darling Basin Authority, 2015). Similarly, to mitigate adequately the impact of a number of invasive species, multiple levels of management may be required. For example, to abate the immediate impact of an invasive plant species, control (e.g. spraying, physical removal) is first needed (IPAC, 2016) but then should be complemented with local (and potentially national) policies aimed at minimizing its spread and establishment in new areas (IPAC, 2016). Additionally, the size of a protected area has a significant impact on its effectiveness at mitigating threats. For example, the conservation

TABLE 1 A description of the threat classifications, the typical conservation actions taken to mitigate these and our assessment of the corresponding protected area management scenario. Threat classification, description and conservation actions taken from Salafsky et al. (2008).

Major threat classification	Description	Sub-threats	Key conservation actions	Threat management scenario
Residential & commercial development	Threats from human settlements or other non-agricultural land uses with a substantial footprint	Commercial & industrial areas, housing & urban areas, residential & commercial development, tourism & recreation areas	Site/area protection	Unmanaged
Agriculture & aquaculture	Threats from farming & ranching as a result of agricultural expansion & intensification, including silviculture, mariculture & aquaculture (includes the impacts of any fencing around farmed areas)	Agriculture, aquaculture, livestock farming/grazing, timber plantations	Site/area protection	Unmanaged
Energy production & mining	Threats from production of non-biological resources	Oil & gas drilling, mining, quarrying & renewable energy	Site/area protection	Unmanaged
Transportation & service corridors	Threats from long, narrow transport corridors & the vehicles that use them including associated wildlife mortality	Roads & railroads, shipping lanes, transportation & service corridors, utility & service lines	Site/area protection	Unmanaged
Biological resource use	Threats from consumptive use of wild biological resources including both deliberate & unintentional harvesting effects; also persecution or control of specific species	Fishing/harvesting/collecting/gathering terrestrial, marine & aquatic species	Site/area protection & management, compliance & enforcement	Well-managed
Human intrusion & disturbance	Threats from human activities that alter, destroy & disturb habitats & species associated with non-consumptive uses of biological resources	Commercial logging Human intrusion & disturbance, recreational activities, work & other activities, military exercises	Site/area protection Site/area protection & management	Unmanaged Well-managed
Natural system modifications	Threats from actions that convert or degrade habitat in service of managing natural or semi-natural systems, often to improve human welfare	Dams & water management Fire & fire suppression, other ecosystem modification	Policies & regulations Site/area protection & management	Landscape management Well-managed
Invasive & other problematic species, genes & diseases	Threats from non-native & native plants, animals, pathogens/microbes, or genetic materials that have or are predicted to have harmful effects on biodiversity following their introduction, spread &/or increase in abundance	Invasive non-native species, problematic native species Invasive diseases, pathogens & parasites	Site/area protection & invasive/problematic species control Invasive/problematic species control	Well-managed Landscape management
Pollution	Threats from introduction of exotic &/or excess materials or energy from point & non-point sources	Garbage & solid waste Agricultural & forestry pollutants, excess energy, urban sewage & waste water; industry/military pollution	Site/area management, compliance & enforcement Legislation & policies & regulations	Well-managed Landscape management
Geological events	Threats from catastrophic geological events	Landslides	Habitat & natural process restoration	Well-managed
Climate change & severe weather	Threats from long-term climatic changes that may be linked to global warming & other severe climatic/weather events that are outside of the natural range of variation, or potentially can wipe out a vulnerable species or habitat	Climate change, severe weather, droughts, storms & flooding, temperature extremes, habitat shifting/alteration	Habitat & natural process restoration & species re-introduction	Well-managed

of large, intact landscapes is the best response to the impacts of climate change (Watson et al., 2009; Gross et al., 2015). As such, small protected areas that comprise a high proportion of Australia's protected area network (Commonwealth of Australia, 2013a) are unlikely to be able to mitigate the impacts of such threats. Here, we determined the typical actions used to mitigate each threat. Supplementary Table 1 provides a full reasoning for the choice of the conservation action required to mitigate each threat to Australian species.

Level of threat abatement

To estimate the role of protected areas in threatened species conservation in Australia, we quantify the level of threat abatement provided by each management scenario. We do this by calculating the proportion of threats removed by each scenario to Australian threatened species, and the number of species that have one or more and all threats abated by each management scenario. Although these calculations are theoretical, by comparing the effectiveness of the two protected area management scenarios we approximate the role that well-managed and unmanaged protected areas play in threatened species conservation in Australia.

Results

The threats impacting Australian species

Australian threatened species face 11 major threat classes, with invasive and other problematic species impacting the greatest proportion of species ($n = 1,274$, 82%; Fig. 1). Two other major threats, natural system modifications and agriculture, impact over half of Australia's threatened species ($n = 1,136$, 73% and $n = 874$, 56%, respectively; Fig. 1). The sub-threats of invasive non-native species (within the major threat class 'invasive and other problematic species'; 80%) and fire and fire suppression (within the major threat class 'natural system modifications'; 65%) threaten the greatest number of Australian threatened species.

The number of threats reported as impacting Australian species

Each Australian threatened species is impacted by 1–10 major threats (Fig. 2a) and 1–54 specific threats (Fig. 2b). On average, each species faces $7.6 \pm \text{SD } 5.8$ specific threats. Only 95 species (6%) face a single specific threat and 1,025 species (66%) face five or more specific threats (Fig. 2b).

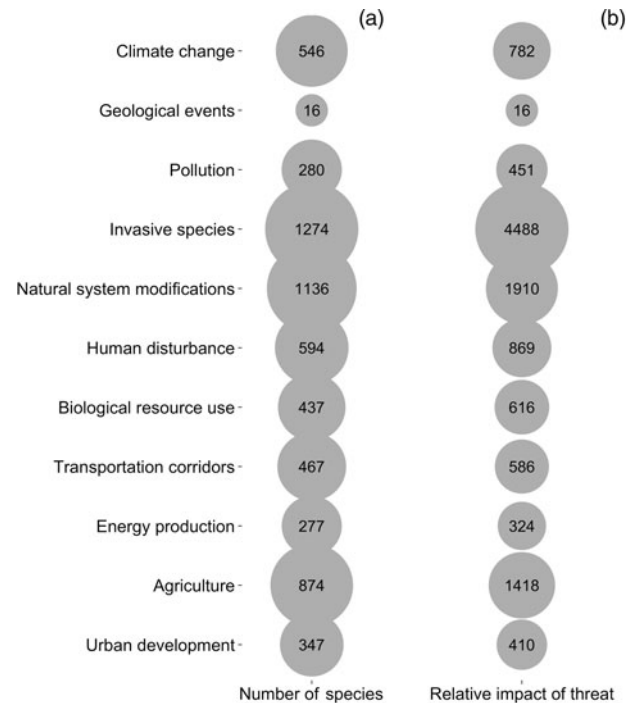


FIG. 1 The number of Australian threatened species facing each of Salafsky et al.'s (2008) major threat classifications (a) and the relative impact of each major threat classification on Australian threatened species (b). The relative impact is defined as the cumulative number of specific threats within a major threat that impacts a species. It takes into account that species may face more than one specific threat under each major threat. For example, a species may be threatened by an invasive plant species and an invasive animal species and as such is impacted twice by the major threat classification 'invasive and problematic species'. Threat information is compiled using a range of sources including listing advice, recovery and action plans, published literature and expert knowledge (Commonwealth of Australia, 2015). It is likely that this information is not exhaustive and the listed threats are likely to be those that are obvious and tangible to species' managers, meaning subtle threats may be overlooked and not reported.

The number of threats mitigated by each management scenario

Under our unmanaged protected area management scenario, in which protected areas are not resourced for threat management, the Australian protected area network can remove 26% of all threats to Australian threatened species (Table 2). We found that although the protected area network could mitigate one or more threats to 1,185 (76%) species, it could only remove all threats to 51 (3%) species (Table 2). In contrast, under the well-managed scenario, in which protected areas are adequately resourced for threat management, Australia's protected area network can remove 86% of threats to all threatened species. Similar to the unmanaged scenario, we found that although the well-managed scenario can remove one or more threats to almost

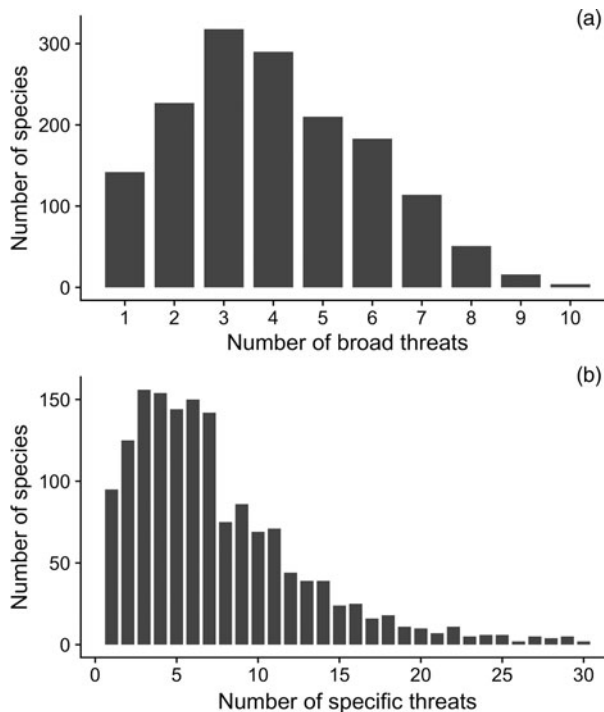


FIG. 2 The number of Australian threatened species that face one or more major threat classifications (a) and the number of threatened species facing one or more specific threats (b). Species facing more than 30 specific threats ($n = 9$, 0.006%) were excluded from (b) to facilitate presentation. Threat information is compiled using a range of sources including listing advice, recovery and action plans, published literature and expert knowledge (Commonwealth of Australia, 2015). It is likely that this information is not exhaustive and the listed threats are likely to be those that are obvious and tangible to species' managers, meaning subtle threats may be overlooked and not reported.

all threatened species ($n = 1,551$; c. 100%), it can only remove all threats to 740 (48%) threatened species (Table 2). Of great concern is that 815 species face threats that require co-ordinated landscape-scale management for adequate mitigation (Table 2). Protected areas alone, no matter how well-managed, cannot remove all threats to these species.

The disparity between scenarios can be explained by the variety of threats to Australian species and the number of threats each species faces. Unmanaged protected areas can only effectively mitigate threats causing habitat loss, particularly agriculture, urbanization and transport corridors (Table 1). As the majority of Australian species face multiple threats, of which many require management to abate, unmanaged protected areas cannot remove the majority of threats to Australian species. In contrast, well-managed protected areas can abate the two greatest threats to Australian species: invasive and other problematic species, and natural system modifications as well as threats causing habitat loss (Table 1). Hence, well-resourced protected areas can remove all threats to many more species than unmanaged protected areas. Although this accounts for the conservation of c. 50%

of Australia's threatened species, the other 50% require well-managed protected areas complemented with threat management in non-protected lands. Threats from invasive diseases and pathogens, air and waterborne agricultural pollutants, and altered flow regimes from dams require combined management across the entire landscape. As such, for all threats to be removed to all species and ensure the effective conservation of species in Australia, well-resourced protected areas must be complemented with effective landscape-scale threat management.

Discussion

Using the actions required to mitigate threats to species, we evaluated the potential effectiveness of protected areas, the predominant action taken to protect biodiversity globally, at conserving threatened species. Using Australia as a case study, we found that even in the best-case scenario where protected areas are well-resourced and effectively managed, only 48% of threatened species will have all threats removed by the nation's protected area network. These results are likely to be an overestimate of the effectiveness of the current protected area network, as the few studies that have discussed the adequacy of funding for management of protected areas in Australia have shown that there are significant shortfalls across much of continent (Taylor et al., 2011a; Craigie et al., 2015). Taylor et al. (2011a), for example made the case for an estimated seven-fold increase in investment needed to fill the current management and protection gap in Australia's protected area network. Where protected areas are inadequately funded to undertake threat management, few species ($n = 51$, 3%) will have all threats removed.

Similarly, this analysis overestimates the benefit to threatened species conservation provided by Australia's current protected area network. With the majority of Australian threatened species inadequately represented in protected areas and 10% of species having no coverage (Watson et al., 2011), protected areas provide little to no benefit to these species. This highlights the importance of a landscape scale approach to threat management as many threatened species occur outside protected areas, and half ($n = 815$, 52%) of Australia's threatened species face threats requiring concerted efforts across protected and non-protected areas. This emphasizes the need to fund not only establishment of new protected areas but also to adequately fund management within and outside the current protected area network.

These findings have significant implications for biodiversity conservation globally. As the international community undertakes concerted efforts to halt biodiversity decline (Juffe-Bignoli et al., 2014), too narrow of a focus on protected area network expansion will probably lead to an insufficient response. The threat of invasive species, pollution and fire impact thousands of species globally (Rodrigues

TABLE 2 The total number (and percentage of total) of threats to all Australian species, the number of species with one or more threats, and all threats removed by the two protected area management scenarios. The unmanaged scenario represents a network of protected areas that receives no funding for threat management, whereas the well-managed scenario represents a protected area network that is well-funded and all necessary threat management occurs. Landscape-scale management is required to mitigate threats that either originate outside protected areas or require coordinated management across all land-tenures.

	'Unmanaged' protected area scenario	'Well-managed' protected area scenario	Landscape management	All management types combined
Total number of threats removed to all threatened species	3,056 (26%)	10,220 (86%)	1,651 (14%)	11,871 (100%)
Number of threatened species with one or more threats removed	1,185 (76%)	1,551 (~100%)	815 (52%)	1,555 (100%)
Number of threatened species with all threats removed	51 (3%)	740 (48%)	4 (<1%)	1,555 (100%)

et al., 2014; Maxwell et al., 2016) and in many countries, invasive species impact a significant proportion of native species (e.g. the USA; Wilcove et al., 1998). Therefore, we expect our findings to be similar in many other nations. Although protected areas play a crucial role in solving the biodiversity crisis, we have shown here that this investment will only be of value if complemented by effective threatened species management.

The protected area management scenarios defined in this analysis are the two extremes of a spectrum. In Australia, few protected areas are probably receiving no threat management actions within their boundary, just as few are likely to be adequately and effectively managed for all threats within their boundaries. Where Australia's current protected area network is on this management spectrum is difficult to determine; however, based on reported funding for protected area management, it is likely to be highly variable (Taylor et al., 2011a). Taylor et al. (2011a) report that in 2008–2009, the average funding for protected area management across Australia was AUD 9.56/ha. Although New South Wales has reported that impacts to threatened species in protected areas are stable or improving for the majority, in 6.6% of protected areas, impacts are increasing (N.S.W. Government, 2007). Considering the national average for protected area management funding is less than one third of New South Wales (Taylor et al., 2011a), it is likely that many of Australia's protected areas are inadequately resourced for effectively managing all threats within their boundaries.

Our analysis emphasises the importance of all threats being removed from threatened species. Although it is unlikely that every threat must be removed to prevent species' extinction, recent Australian extinctions suggest that a more holistic approach to threat management is needed. Insufficient management of just a few threats resulted in these preventable extinctions (Woinarski et al., 2017). Well-funded, strategically planned and coordinated threat management across protected and non-protected areas in Australia is needed to conserve its unique biodiversity. Currently, available funding for

threatened species protection and recovery in Australia is inadequate (Taylor et al., 2011a; Waldron et al., 2013). Additionally, the allocation of the limited available resources is currently biased (Walsh et al., 2013) and often ineffectively spent (Bottrill et al., 2011; Taylor et al., 2011b). Although it is unlikely the suggested seven-fold increase in funding (Taylor et al., 2011a) for Australia's protected area network will occur soon, efficiency can be addressed with a strategic planning process for threatened species management (Watson et al., 2010). Systematic and strategic investment of available funding through management action-specific planning protocols has proven effective and efficient (Bottrill et al., 2008; Joseph et al., 2009). These protocols incorporate cost, benefit and likelihood of success to ensure effective and efficient outcomes for threatened species. Such protocols have been used in some states across Australia (Tasmanian Government, 2010; N.S.W. Government, 2013) but a national approach is required given that threatened species and the threats they face are unaffected by state borders.

As the global protected area network continues to expand in an attempt to halt biodiversity decline, it is vital to understand its effectiveness in achieving this goal. We have provided the first continental evaluation of how effective a network of protected areas is at removing the suite of threats that imperil species. We discovered that a protected area network well-resourced for threat management within its boundaries could abate all known threats to half of Australia's threatened species. Although protected areas will play a role in reducing threats to the other half of Australia's threatened species, they are unable to mitigate all of the processes that impact these species. A coordinated approach across protected and non-protected areas is therefore required to conserve these species adequately.

Acknowledgements

We are grateful to the Commonwealth Department of the Environment and Energy for access to the Species Profile and Threats Database, and to J. Woinarski and two anonymous reviewers for helpful comments on the text. This research received support from

the Australian Government's National Environmental Science Program through the Threatened Species Recovery Hub.

Author contributions

Conception and design of study: SK, VA, RF, HP, JW; analysis and interpretation of data: SK, JW; drafting the text: SK, JW; revising the text: SK, VA, RF, HP, JW.

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Biographical sketches

STEPHEN KEARNEY is interested in understanding the pressures on threatened species and how to mitigate these efficiently. VANESSA ADAMS focuses on the human dimensions of conservation and systematic environmental decision-making. RICHARD FULLER is interested in understanding how people have affected the natural world around them, and how some of their destructive effects can best be reversed. HUGH POSSINGHAM is interested in decision-making for conservation, including spatial planning, optimal monitoring, value of information, population management, prioritization of conservation actions, structured decision-making, bird ecology and dynamic systems control. JAMES WATSON is a conservation biogeographer interested in identifying conservation solutions in a time of rapid anthropogenic change.