

Contributed Paper

Effects of threat management interactions on conservation priorities

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Abstract: *Decisions need to be made about which biodiversity management actions are undertaken to mitigate threats and about where these actions are implemented. However, management actions can interact; that is, the cost, benefit, and feasibility of one action can change when another action is undertaken. There is little guidance on how to explicitly and efficiently prioritize management for multiple threats, including deciding where to act. Integrated management could focus on one management action to abate a dominant threat or on a strategy comprising multiple actions to abate multiple threats. Furthermore management could be undertaken at sites that are in close proximity to reduce costs. We used cost-effectiveness analysis to prioritize investments in fire management, controlling invasive predators, and reducing grazing pressure in a bio-diverse region of southeastern Queensland, Australia. We compared outcomes of 5 management approaches based on different assumptions about interactions and quantified how investment needed, benefits expected, and the locations prioritized for implementation differed when interactions were taken into account. Managing for interactions altered decisions about where to invest and in which actions to invest and had the potential to deliver increased investment efficiency. Differences in high priority locations and actions were greatest between the approaches when we made different assumptions about how management actions deliver benefits through threat abatement: either all threats must be managed to conserve species or only one management action may be required. Threatened species management that does not consider interactions between actions may result in misplaced investments or misguided expectations of the effort required to mitigate threats to species.*

Keywords: action prioritization, Australia, cost-effectiveness analysis, management action, return on investment, threats, threatened species

Efectos de las Interacciones del Manejo de Amenazas sobre las Prioridades de Conservación

Resumen: *Se necesita tomar decisiones sobre acciones de manejo de biodiversidad a emprender para mitigar las amenazas y sobre dónde implementar estas acciones. Sin embargo, las acciones de manejo pueden interactuar; es decir, el costo, el beneficio y la viabilidad de una acción pueden cambiar cuando se emprende otra acción. Existe poca orientación sobre cómo priorizar explícita y eficientemente el manejo para amenazas múltiples, incluido el decidir en dónde actuar. El manejo integrado podría enfocarse en una acción de manejo para abatir una amenaza dominante o en una estrategia que comprende acciones múltiples para abatir amenazas múltiples. Más allá, el manejo podría emprenderse en sitios que se encuentran en proximidad para así reducir los costos. Usamos un análisis de rentabilidad para priorizar las inversiones en el manejo de incendios, el control de depredadores invasores y en la reducción de la presión de pastoreo en una región*

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biodiversa del sureste de Queensland, Australia. Comparamos los resultados de cinco estrategias de manejo basadas en suposiciones diferentes sobre las interacciones y cuantificamos cómo la inversión necesaria, los beneficios esperados y las localidades priorizadas para la implementación difirieron cuando se tomaron en cuenta las interacciones. Manejar por interacciones alteró las decisiones sobre dónde invertir y en cuáles acciones invertir y tuvo el potencial de entregar una incrementada eficiencia de inversión. Las diferencias en las localidades y acciones de alta prioridad fueron mayores entre las estrategias cuando hicimos suposiciones diferentes sobre cómo entregan beneficios las acciones de manejo por medio del abatimiento de amenazas: ya sea que todas las amenazas deben ser manejadas para conservar a las especies o que sólo sepueda requerir una acción de manejo. El manejo de especies amenazadas que no considera las interacciones entre las acciones puede resultar en inversiones mal asignadas o en expectativas mal guiadas del esfuerzo requerido para mitigar las amenazas para las especies.

Palabras Clave: acción de manejo, amenazas, análisis de rentabilidad, Australia, especies amenazadas, priorización de acción, retorno de la inversión

Introduction

Understanding how and where to reduce known threats to biodiversity, and thereby enhance the persistence of species, is a major focus of conservation science (Salafsky et al. 2002). Typically species are threatened by numerous processes (Darling & Côté 2008), and characterizing these threats can be a first step toward clarifying management priorities (Burgman et al. 2007). Managers are then faced with complex practical decisions about which actions to implement and where they should be implemented. Furthermore, there can be non-additive interactions between management actions such that the whole (an integrated strategy for abating multiple threats) is not the same as the sum of the parts (acting to abate each threat independently; Didham et al. 2007). These interactions introduce management complexity because it may not be clear whether a strategy of taking one action in isolation will sufficiently improve the persistence of a species or whether an integrated strategy of managing every threat is required.

It may be possible, for example, to reduce the effects of one threat by undertaking an action that aims to mitigate another threat. For instance, lack of a suitable refuge increases the vulnerability of small mammals to predation by invasive predators. Restoring degraded areas could potentially provide additional habitat and thereby enhance the persistence of species without requiring the additional action of invasive predator control (Stokes et al. 2004; Robley et al. 2013). In other situations, such as with pest control, an integrated strategy for managing multiple threats may be necessary. Control of one pest species alone may be counter-productive because other pest species may be released from competition or predation. For example, when invasive fox and rabbit pests are both present in an Australian landscape, control of rabbits alone may lead to intensified predation by foxes on native prey, whereas control of foxes alone may result in increased rabbit populations and competition with native herbivores (Glen & Dickman 2005).

The costs and benefits of actions can be affected by the actions that occur nearby. Budget constraints dictate that

management actions cannot be implemented everywhere at once. However, by choosing to spend resources on threat mitigation in a specific location, the cost of managing nearby locations is likely to decrease. Coordination and management of adjacent sites could result in reduced labor and transportation costs due to local economies of scale (Armsworth et al. 2011), although spatial interactions between management costs are typically not taken into consideration in systematic conservation planning (e.g., Carwardine et al. 2008). Managing locations in close proximity can result in both cost savings and increased management effectiveness. For example, clustering artificial tunnels for threatened burrow-nesting birds facilitates nest maintenance and results in better nesting success (Gummer et al. 2015). Another example is invasive species control that is more successful when neighboring land owners cooperate as a group in preventing weed spread or invasive predator dispersal into adjacent properties, resulting in more effective management across a landscape (Epanchin-Niell et al. 2009; McLeod et al. 2010). Clarifying how cost savings may be found by managing sites in close proximity could also result in a better return on investment in threat management.

A major focus of systematic conservation planning is on efficiently protecting species (Hughey et al. 2003; Murdoch et al. 2007; Moran et al. 2010). Therefore, a growing body of research explores ways to prioritize threat management and protect species through cost-effectiveness analysis (e.g., Joseph et al. 2009; Carwardine et al. 2012; Auerbach et al. 2014). Cost-effectiveness is calculated as the ratio of the expected benefit of an action (expressed in non-monetary terms) and the cost of that action (Weitzman 1998). Prioritizing locations for threat-specific management can help direct where actions are likely to achieve the greatest benefits to species when funding is limited (e.g., Wilson et al. 2007). Progress has been made in considering interactions for more cost-effective conservation, but most of the research that considers interactions only addresses the issue of complementarity, which avoids redundancy in species protection (e.g., Underwood et al. 2008; Withey et al. 2012) or conservation actions

(Chadès et al. 2015). There are few examples of where interactions between threat management actions have been explicitly addressed in the prioritization process.

Threats and consequently the effects of actions to mitigate them are usually assumed to be independent and additive, or the focus of management is on abating a dominant threat (e.g., Didham et al. 2007; Halpern & Fujita 2013; Ng et al. 2014). As such, the biological and economic complexity of many conservation problems has been neglected (Polasky et al. 2001; Brook et al. 2008). From a practical perspective, managers may not be aware of such interactions (Sala et al. 2000) or may be limited in the extent to which they can undertake multiple actions due to economic constraints (Bottrill et al. 2008) or socio-political pressures (Miller & Hobbs 2002). However, integrated management that explicitly accounts for interactions can increase efficiency (Wu & Boggess 1999; Duke et al. 2013). It has been demonstrated that when management is integrated, limited resources are allocated across space more efficiently and cost-effectively at a continental scale than when actions are enacted independently (Evans et al. 2011). However, it has not been shown that management actions could be better targeted for many species at a fine scale when interactions are taken into account. A clearer understanding of the size of the efficiencies that could be gained by accounting for interactions could potentially guide better returns on investment in threat mitigation at the fine scale, where regional management takes place.

We considered the fine-scale management of 3 dominant threats that affect native species in Australia (Burgman et al. 2007; Woinarski et al. 2015). We developed and applied approaches for accounting for interactions in a typical spatial conservation prioritization problem to increase understanding of how management recommendations differ when interactions between management actions are taken into consideration. Specifically, we investigated how interactions affect the relative level of required investment in different actions and where these actions should be implemented.

Methods

Case study

The case study applied to a natural resource management region in southeastern Queensland, Australia, in which a conservation practitioner must make decisions about managing threats to species across a landscape. We divided the region (approximately 55,000 km²) into a grid of 25-ha management sites for a fine-scale analysis. We analyzed only those sites ($n = 129894$) with remaining or regrown native vegetation. Seventy-two species prioritized for regional and state government management (DERM 2010; Supporting Information) are listed under state (Nature Conservation Act 1992) or Commonwealth

(Environment Protection and Biodiversity Conservation Act 1999) legislation or are species of regional concern. We derived potential habitat maps of priority species from species distribution models (Auerbach et al. 2014), range maps, or point locations (data sets referenced in Supporting Information). We addressed the management of three threats (IUCN 2014) that have been identified by experts as affecting the priority species (DERM 2010): too frequent and intense fire, an invasive predator (red fox [*Vulpes vulpes*]), and habitat degradation caused by domestic stock (threats to individual species listed in Supporting Information). Species are affected by different combinations of the three threats. Targeted actions in our case study were proactive fire management for biodiversity according to vegetation type, predator control by lethal baiting, and grazing reduction or removal through a stewardship agreement.

Approaches to threat management

We took the view of a typical land manager acting under budget constraints. We considered 5 approaches to managing threats that were based on different assumptions about the interactions between the threat management actions.

In the first approach, there were no interactions between management actions and management actions were additively and proportionally beneficial in conserving each priority species (action proportional approach). In the second approach, there were interactions between management actions, such that one management action in a specific location conserved each priority species (any one action approach). In the third approach, there were interactions between management actions, such that addressing all threats to each priority species in a specific location was necessary to conserve them (only all actions approach). We used outcomes from the first approach (with no interactions) as a baseline against which to compare outcomes from the second 2 approaches (with interactions). In the fourth approach, there was no spatial dependence (there were no interactions) in the cost of implementing management actions (no spatial dependence approach). In the final approach, there was spatial dependence in the costs of implementing management actions (there were interactions), and when one location was selected for management, the cost of taking action in nearby locations was lower relative to a location farther away (spatial dependence approach). We used outcomes from the fourth approach (with no interactions) as a baseline against which to compare outcomes from the final approach (with interactions).

Solving the problem

We evaluated how interactions affected investments in threat management within a decision-theoretic

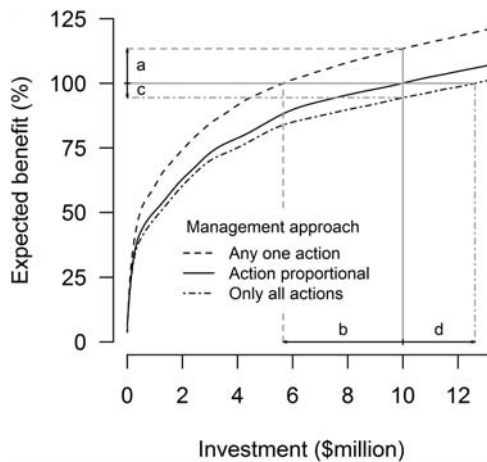


Figure 1. Return-on-investment (benefits) for approaches to management of threats to priority species: baseline approach (management actions are not interactive and effects of actions are proportional and additive) versus approaches that account for interactions among management actions under the assumption either that threats will be mitigated by any one action or only by all actions. Returns are normalized to those expected from a \$10 million investment in the baseline (no interactions) approach (differences in expected benefit and required investment: a, 13%; b, −\$4.3 million; c, −5.6%; d, \$2.6 million).

framework (Possingham et al. 2001). Our objective was to maximize benefits for a set of species within a budget constraint and given options about which threat-mitigating actions could be carried out at a particular site.

For each of our 5 management approaches, we prioritized suites of actions at a site (strategies) with a greedy heuristic algorithm in which we ranked priorities by iteratively selecting the most cost-effective site-by-action strategy combination relative to the other site-by-action strategy combinations previously selected. Rankings of highest to lowest priority were site-by-action strategy combinations with highest to lowest cost-effectiveness values. We calculated cost-effectiveness as being the ratio between the expected benefits and costs of threat management. We determined expected benefit for each species at each site on the basis of stated assumptions, as well as on whether a species was predicted to have habitats at the site and known to be affected by a specific threat or set of threats. We then summed expected benefits for all species at a site.

We modeled management costs for taking one action against each threat at each site and summed the costs for different potential strategies (e.g., fire plus grazing). Detailed methods for estimating benefits and costs of threat management with our 5 management approaches,

and for prioritizing sites and action strategies, are in Supporting Information.

We plotted return-on-investment curves for all 5 management approaches as investment (cumulative summed cost) against expected benefit fitted with a cubic smoothing spline in R. Normalized units were used to represent the percentage of total benefit expected when managing under the assumption of no interactions (\$10 million budget) or spatial dependence (\$5 million budget). We compared differences in return on investment in terms of expected benefits for an equivalent investment and differences in investment for an equivalent expected benefit. We then mapped priority sites and actions and determined the area selected for each management action strategy.

We evaluated the similarity between the spatial locations prioritized for management. Differences between plans from different approaches were quantified using Cohen's kappa ($\kappa = 1$, perfect agreement; $\kappa = 0$, agreement no better than expected by chance) (Cohen 1960). We used the same methods to contrast the original analysis (above) with a sensitivity analysis in which we adjusted (increased) known threats to species to compare how managing for more threats would change conservation priorities. In the sensitivity analysis, we tested for outcomes if all plants in the region were threatened by both fire and grazing and assessed differences as above (Supporting Information). For the spatial dependence approach comparison, we tested whether prioritized sites were grouped closely together with a measure of their compactness (Possingham et al. 2000): the ratio of boundary length to area of sites selected for management under a \$10 million budget. We measured nearest-neighbor distances between the center points of management sites with the Geospatial Modeling Environment (<http://www.spatial ecology.com>) point distances function.

Results

Effects of different assumptions of management interactions on priorities

The expected benefit to species from a \$10 million investment in managing threats with any one action by explicitly accounting for the possibility for interactions between actions (any one action approach) was 13% greater than the species benefit using the baseline assumption (no interactions; action proportional approach) (Fig. 1a; gap between any one action versus action proportional curves). Alternatively expressed, for the same level of expected benefit to species, managing threats with any one action by accounting for interactions was \$4.3 million less expensive than the cost of the benefit to species using the baseline assumption

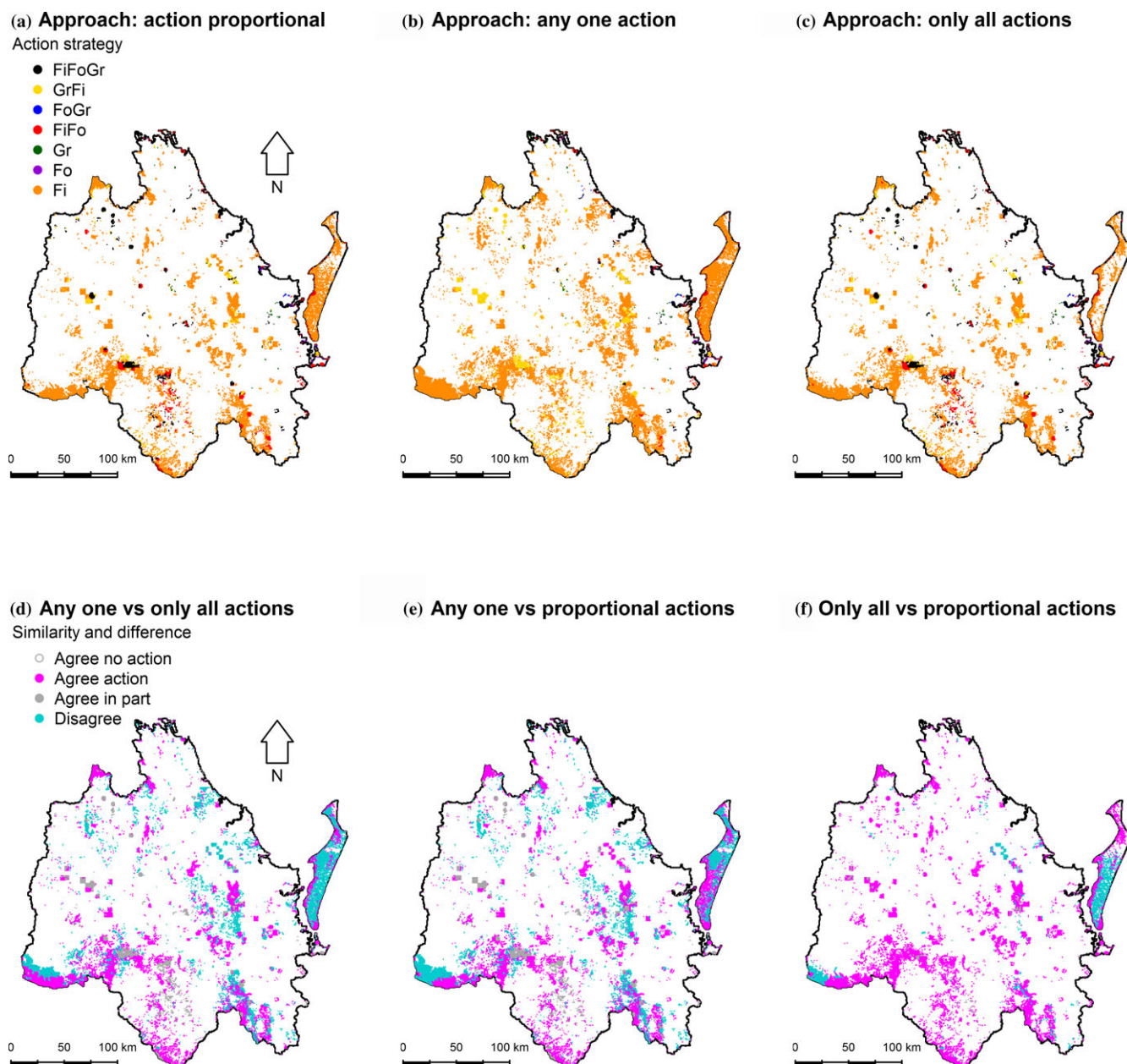


Figure 2. Conservation management priorities for a \$10 million investment in different approaches to management of threats to priority species. (In [a], baseline approach, management actions are not interactive and effects of actions are proportional and additive; in [b], approach explicitly accounts for interactions between management actions because it is assumed threats will be mitigated by any one action; and in [c], approach explicitly accounts for interactions between management actions because it is assumed threats will be mitigated only by all actions) (action strategy fi, proactive fire management for biodiversity; fo, invasive predator [fox] control by lethal baiting; gr, grazing reduction or removal of domestic stock through a stewardship agreement). In (d-f) Similarities and differences in locations of priority action strategies between approaches (similar if both approaches are in agreement with action strategy prioritized in a location; different if in disagreement; partially similar if one action in a 2-action strategy is in agreement or 2 actions are agreement in a 3-action strategy).

(Fig. 1b). In contrast, for a \$10 million investment, the expected benefit to species was nearly 5.6% lower than the benefit to species using the baseline assumption when the assumption was that all actions must be undertaken

to manage threats by explicitly accounting for interactions (only all actions approach) (Fig. 1c; gap between only all actions and action proportional curves). In other words, for the same level of expected benefit to species,

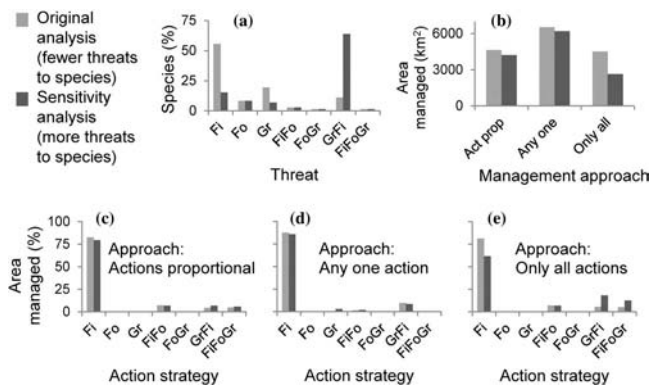


Figure 3. Differences in (a) percentage of priority species affected by each threat or combination of threats in the original analysis relative to the sensitivity analysis (with more threats to species); differences in (b) total area prioritized for management under different management approaches; and (c-e) percentage of total area prioritized for different action strategies with \$10 million investments in different management approaches ([a]: fi, too frequent and intense fire; fo, an invasive predator [fox]; gr, habitat degradation caused by domestic stock grazing; [b]: act prop, approach in which management actions are not interactive and effects of actions are proportional and additive; any one, approach that explicitly accounts for interactions between management actions because it is assumed threats to priority species will be mitigated by any one action; only all, approach that explicitly accounts for interactions between management actions because it is assumed threats to priority species will be mitigated only by all actions; [c-e]: fi, proactive fire management for biodiversity; fo, invasive predator (fox) control by lethal baiting; gr, grazing reduction or removal of domestic stock through a stewardship agreement).

it was \$2.6 million more expensive to manage all threats to species by explicitly accounting for the interactions between management actions (Fig. 1d). The differences in return on investment between the same approaches were greater when species were affected by more threats (Supporting Information).

Priority locations and action strategies for cost-effective threat mitigation differed among management approaches (Fig. 2a-c). Differences in priority management maps were greatest between the two approaches that explicitly accounted for the possibility of interactions (Fig. 2d; $\kappa = 0.72$). Sites and action strategies prioritized when accounting for interactions by managing for any one threat were more dissimilar to the baseline assumption (Fig. 2e; $\kappa = 0.73$) than when accounting for interactions by managing for all threats (Fig. 2f; $\kappa = 0.91$) (see Supporting Information). Those strategies that

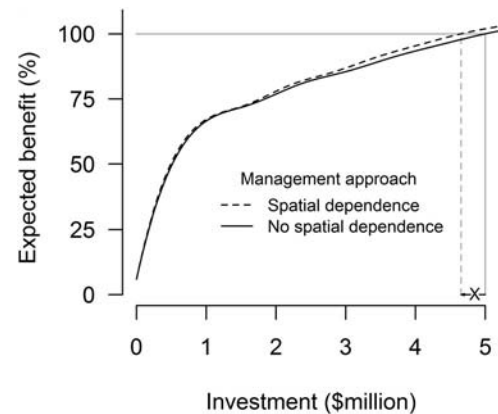


Figure 4. Return-on-investment (benefits) for different approaches to management of threats to priority species (no spatial dependence approach, management actions across space are not interactive and costs of actions are additive; spatial dependence approach, accounts for interactions between management actions, management costs are assumed to be lower in sites nearer to each other; x is difference in investment and equals \$350,000). Returns are normalized to those expected from a \$5 million investment in the baseline (no spatial dependence) approach.

included fire management were prioritized as being the most cost-effective for the greatest percentage of area chosen for action in all approaches (Figs. 2a-c).

More species were vulnerable to more threats in the sensitivity analysis than in the original analysis (Fig. 3a). When prioritizing management for more threats to species, the total area selected for the same budget (\$10 million) was smaller in all approaches relative to managing for fewer threats (Fig. 3b). With more threats to be managed, a greater percentage of the total area was selected for multiple-action strategies that included fire and grazing management (Figs. 3c and 3e; strategies GrFi and FiFoGr), except when accounting for interactions by managing for only one threat (Fig. 3d). Differences in priority locations and action strategies were greater when managing more threats (sensitivity analysis) than when managing fewer threats (original analysis), especially between the approach with the baseline assumption of no interactions and the approach that accounted for interactions by managing for all threats ($\kappa = 0.51$ and 0.91 , respectively). See Supporting Information for more detailed results of the sensitivity analysis.

Effects of different assumptions of spatial dependence on priorities

For equivalent management effects (benefit to species), prioritizing predator control investment in adjacent

sites, which accounted for the possibility that there was spatial dependence between sites, was marginally more efficient than the baseline approach (assuming no interactions; \$0.35 million less expensive) (Fig. 4). In the spatial dependence approach, the management area was also more compact and the boundary length-to-area ratio smaller than in the baseline (no spatial dependence) approach (see Supporting Information). Furthermore, for \$10 million, more area was prioritized for management with the spatial dependence approach than with the baseline approach (1994.25 km² and 1806.00 km², respectively). The average distance to the nearest neighboring management site was smaller for the spatial dependence approach than for the baseline approach (mean of 582.52 m [SE 3.97] and mean of 590.92 m [SE 4.58], respectively), although the average distances were not statistically different (2-group *t* test, *p* = 0.1659; descriptive statistics in Supporting Information).

Discussion

Interactions are rarely addressed when spatially prioritizing investment in threat management. Maximizing return on investment while accounting for interactions and spatial dependence in costs can complicate an analysis and interpretation of results, and data on them are often lacking. Therefore, these aspects are often ignored.

A common management approach considers effects of actions to be cumulative (Didham et al. 2007; Halpern & Fujita 2013). Our results indicate that investment priorities are different when management interactions are explicitly considered. Investment costs are lower if one expects management interactions to protect a species by abating any one of their threats (Fig. 1). Our results indicate this might be a risky approach if in fact interactions are such that a species can only be conserved by managing all threats: the benefits expected from managing one threat could be negligible. Thus, our results concur with previous findings that expected benefits may be overestimated when investing in abating only one threat to species if interactions exist (Evans et al. 2011). However, our results showed that this is also true at the fine scale, where threats are managed on the basis of the specific habitat needs of multiple species. In contrast, if one assumes that abating all threats is necessary to conserve species, the required investment will be greater (Fig. 1). Spending an entire budget on managing multiple threats, when managing any one threat would be sufficient, runs the risk of managing some sites too intensively and not leaving enough money for managing threats in other sites (Figs. 1, 2, and 3). Importantly, considering interactions affects expected return on investment in threat management (Fig. 1) and alters decisions about where to manage with which actions (Fig. 2).

In a landscape in which 83% of the species are known to be affected by at least a single threat (that might be different between species [Fig. 3a]), we found that collectively managing for any one threat to each species changed the sites to be managed (Fig. 2e) more than collectively managing all threats to conserve species (Fig. 2f). In managing any one of all the threats that might impact a species, the least expensive sites and actions were prioritized (Fig. 3b); these were primarily sites for fire management. In comparison, managing more threats to each species was more restrictive. When more threats must be managed to conserve species, management priorities were multiple-action strategies that required higher investment and that occurred in limited locations in the landscape (Figs. 3a and 3c and sensitivity analysis in Supporting Information).

Investment decisions also differed when spatial interactions are incorporated. We demonstrated a way to account for the spatial dependence of management costs when allocating funding across a landscape. However, we found that prioritizing management in nearby sites was only marginally more cost-effective than not considering the spatial dependence of management costs (Fig. 4). The modest difference may be partly attributed to the degree of habitat fragmentation in our case study region. We found that in highly fragmented landscapes almost the same outcomes may be achieved by ignoring spatial interactions as by including them, especially when budgets were low (e.g., \$2.5 million, Fig. 4). Beneficial effects of invasive predator control from neighboring parcels may be limited if distances between management sites are >5 km (McLeod et al. 2010). Spatial interactions are likely to be more important in landscapes that are more connected. Managers looking for savings in highly fragmented landscapes may consider that alternative actions not addressed in this study, such as habitat restoration to restore connectivity, may be required in combination with predator control (Zavaleta et al. 2001).

Few research analyses account for interactions in the context of investing in managing many species and threats and the benefits and costs of management actions to abate those threats across a landscape at a fine scale. Spatially, threats often are assessed independently and added together to evaluate cumulative effects (e.g., Halpern et al. 2008; Allan et al. 2013). Threats are synergistic when their combined effect is greater than would be expected from their additive effects and antagonistic when it is less. The possibility of either synergistic or antagonistic interactions between multiple threats further complicates the process of prioritization (Sala et al. 2000). However, assuming there are no interactions could lead to an incorrect identification of sites requiring management (Brown et al. 2013). The consequences of ignoring synergisms, such as between climate change and habitat loss (Mantyka-Pringle et al. 2012) or between fire

and disease (Regan et al. 2011), could lead to missed opportunities in areas where action could abate not only one threat but also its interaction with another threat. The consequences of ignoring antagonisms could have negative outcomes if reducing one threat worsens another threat (Didham et al. 2007; Evans et al. 2011; Brown et al. 2013). With synergistic threats, one management action may be enough to conserve species, whereas with antagonistic threats, a set of management actions may be required. Our results demonstrate differences in investment required, expected benefit, and locations for management under different assumptions that take management interactions into account. The approaches we tested could inform investment in management of synergistic and antagonistic threats such as these.

We did not consider all aspects of management interactions. Analyses of problems with smaller decision spaces than those we explored here show that species can be protected more efficiently when an estimate of the likelihood of management success and feasibility is included (Joseph et al. 2009; Carwardine et al. 2012; Chadès et al. 2015). Potentially, multiple actions may be appropriate for abating a given threat (Carwardine et al. 2012). Our approach can be translated to multiple actions for addressing each threat by weighting additional strategies by their likelihood of delivering the desired outcome (Joseph et al. 2009) (i.e., species security from threat). However, accounting for more actions requires additional prior information on the likelihood of each action benefiting each species, either from experts or empirical data (Carwardine et al. 2012; Martin et al. 2012; Chadès et al. 2015). We assumed binary outcomes (the species will persist or not), but probabilities occur on a continuum. Associating upper and lower uncertainty boundaries would lead to more confidence in assessing risks of management actions (Tulloch et al. 2015).

We did not account for species complementarity (Kirkpatrick 1983) because our focus was on less-studied interactions among actions. Other research that has been conducted in a decision space with smaller dimensionality than the problem outlined here shows that addressing species complementarity increases management efficiency (Underwood et al. 2008; Withey et al. 2012; Chadès et al. 2015). Linear programming could be used to integrate species complementarity into our approach and could involve setting management area targets for each species and then tracking and summing the area managed for each species during the iterative ranking of site-by-action combinations (e.g., Withey et al. 2012). Once a species' target is met, there would be no more value in adding more management area for that species. Systematic conservation planning software (e.g., Moilanen et al. 2009; Watts et al. 2009) may also be used to account for complementarity; each zone would be a management strategy of combined or single actions (Auerbach 2015). Decision makers can assess whether it is worth collecting

more information on different potential actions to address each threat or on the level of interactions between the threats through value-of-information analysis (e.g., Polasky & Solow 2001). We recommend these approaches as avenues of future research.

We assessed how considering interactions changes investment strategies for managing multiple threats at a fine scale. The traditional assumption is that benefits of managing threats are additive (Didham et al. 2007). However, particularly when it is known that two or more threats affect a system, it is likely they interact in some way, and should be managed accordingly (Sala et al. 2000; Didham et al. 2007; Darling & Côté 2008). When acting under the constraint of a limited budget, considering threat management interactions can make a substantial difference to investment decisions, the magnitude of which partially depends on the number of interacting threats per species. We recommend that considering interactions will maximize return on investment in threat management and lead to the needs of threatened species being more efficiently and effectively addressed.

Acknowledgments

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Supporting Information

Priority species and their threats (Appendix S1), detailed methods (Appendix S2), the fire management cost model (Appendix S3), results of the sensitivity analysis with more threats (Appendix S4), results of similarity analyses (Appendix S5), results of spatial dependence analyses (Appendix S6), area prioritized (Appendix S7), descriptive statistics for outcome layers (Appendix S8), descriptive statistics for cost layers (Appendix S9), and variations in expected benefits and costs of different threat mitigation budgets (Appendix S10) are available online. The authors are solely responsible for the content and

functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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