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Ecological–economic optimization of biodiversity conservation under climate change

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Substantial investment in climate change research has led to dire predictions of the impacts and risks to biodiversity. The Intergovernmental Panel on Climate Change fourth assessment report[1] cites 28,586 studies demonstrating significant biological changes in terrestrial systems[2]. Already high extinction rates, driven primarily by habitat loss, are predicted to increase under climate change[3–6]. Yet there is little specific advice or precedent in the literature to guide climate adaptation investment for conserving biodiversity within realistic economic constraints[7]. Here we present a systematic ecological and economic analysis of a climate adaptation problem in one of the world's most species-rich and threatened ecosystems: the South African fynbos. We discover a counterintuitive optimal investment strategy that switches twice between options as the available adaptation budget increases. We demonstrate that optimal investment is nonlinearly dependent on available resources, making the choice of how much to invest as important as determining where to invest and what actions to take. Our study emphasizes the importance of a sound analytical framework for prioritizing adaptation investments[4]. Integrating ecological predictions in an economic decision framework will help support complex choices between adaptation options under severe uncertainty. Our prioritization method can be applied at any scale to minimize species loss and to evaluate the robustness of decisions to uncertainty about key assumptions.

A high proportion of the world's biodiversity is threatened with extinction due to direct and synergistic influences of climate change[3–6]. The problem of shifting or disappearing niches compounds existing threats, including habitat loss and fragmentation, interactions with invasive species, increased spread of infectious diseases and altered disturbance regimes. Climate adaptation investment decisions range in scale from allocation of funding between global biodiversity hotspots, to determining optimal investment in continental habitat connectivity, to catchment-level initiatives for conserving local populations of threatened species. At each of these scales, the question is how best to invest limited conservation and climate adaptation resources to minimize the risk of extinction. Climate adaptation investment decisions for biodiversity conservation will centre on choices between multiple management options within high-priority conservation areas. Recent reviews highlight the fact that these choices are made with imperfect information about conservation values, existing and future threats, and costs and efficacy of the management options at hand, making the demand for a sound analytical framework acute[4,8].

Decision science provides the tools necessary for rational decision-making under uncertainty and complexity[8,9]. Decision science has been discussed in the Intergovernmental Panel on Climate Change assessment reports as conceptually and practically relevant to mitigation and adaptation choices[1]. Like all decision theory problems, climate adaptation will include a problem formulation phase in which broad goals and a set of specific, measurable objectives are defined (Fig. 1). This is followed by the identification of a set of candidate management actions, the construction of a system model that characterizes system dynamics and predicts expected benefits of investment options, and the implementation of a decision model that identifies the best portfolio of actions in light of the information at hand (Fig. 1). For sequential investment decision problems, an evaluation phase is used to reflect on the performance of actions and to incorporate learning in future decisions. Here we explicate this framework with an analysis of climate adaptation investment options aimed at minimizing species extinctions in the mega-diverse and highly threatened fynbos biome of South Africa.

The fynbos is a centre of endemism, containing over 6,200 endemic plant species that are highly dependent on local fire regimes[10]. Climate change is likely to increase fire risk in Mediterranean ecosystems, posing a significant threat to shrubland species worldwide[11]. A large portion of fynbos shrub flora are known as 'obligate seeders' because standing plants are killed by fire and they can regenerate only from seed. Increasing fire frequency (decreasing fire return interval (FRI)) may lead to the destruction of adult plants before they reach sexual maturity, and hence local extinction. Exacerbating these impacts is the rapid loss

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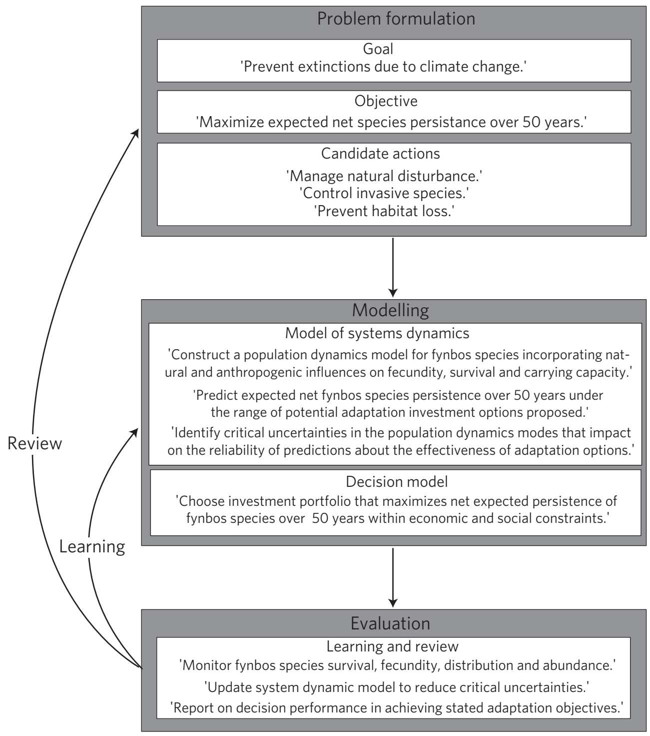

Figure 1 | A framework for climate adaptation investment decision-making. The six headings in the white boxes define the steps of a general framework for prioritizing climate adaptation investment options. By way of example, activities relevant to the fynbos case study are included in inverted commas. These are an emblematic subset of the range of activities likely to be considered in a complex decision problem. Our relatively simple objective may be augmented with a range of competing social, economic, and ecological objectives that may need to be traded-off. Where more complex objectives are proposed, a richer system model is required to make predictions about how multiple criteria perform under the actions being considered. Decision optimization may be adapted to reflect different attitudes to risk and uncertainty.

and fragmentation of the fynbos under urban and agricultural development[12], and invasion by exotic plant species[13]. Given an objective to maximize net species' persistence in the fynbos over the next 50 years, how should a limited adaptation investment budget be most efficiently invested?

Climate adaptation options for conserving biodiversity are well documented[7]. Numerous adaptation actions aim to increase the resilience of species to climate change by reducing new or existing threats. These include managing disturbance and invasive species, reducing rates of habitat loss and fragmentation, reducing rates of exploitation, restoring habitat area and connectivity, and reorienting protected area networks. Alternative actions, such as managed relocations and captive breeding, aim to secure particular species deemed most likely to be impacted by climate change, although they tend to be used as last resort actions because of cost and other risks[14]. In the fynbos, two competing actions for maximizing species persistence are proposed: (1) fire management to avoid excessive reduction below current return intervals of around 15 years[15], and (2) habitat protection, including invasive species management. Ignition reduction and fire suppression are plausible strategies for protecting fynbos ecosystems from a decreasing FRI, whereas fuel reduction burning is relatively inefficient and potentially damaging[15]. Based on predictions about the number of extreme fire weather days in Mediterranean climate ecosystems under current emissions scenarios[16], we estimated the costs of maintaining FRI between 6 and 18 years (Fig. 2 and Methods). Wilson *et al.*[12] identified avoiding loss of fynbos vegetation to urban and agricultural development as a key conservation priority. They estimated the cost of purchase and management of fynbos at US\$45,000 km^{-2}, which is commensurate with more recent estimates[17]. They identified approximately 15,000 km^2 of fynbos under threat of loss. We annualized purchase costs over 50 years and built in annual costs of management (not including fire) and invasive species control, giving an estimated cost of protection of US\$3,920 $km^{-2}\ yr^{-1}$.

Qualitative generalizations about the most appropriate strategies for saving species under climate change are of limited value because ecological, social, and economic complexities demand that each investment option be judged on its case-specific merits. Instead, we need robust predictive models that can be applied rapidly to a range of taxa to determine the expected benefits of competing investment options. Models should quantify the expected outcomes of management using measures that directly reflect stated objective(s). Measures of persistence such as net expected minimum abundance (EMA; ref. 18) are most appropriate when the objective is to maximize net species persistence. Models of population viability are a well-documented means of predicting persistence[19].

Keith *et al.*[11] used population demographic models to quantify the risks posed by climate change to fynbos species. They found that the viability of fynbos species over a period of 50 years was driven by complex interactions between environmental and demographic processes, although the influence of fire frequency on persistence was paramount. They did not include loss of habitat to development or weed invasion in their analyses. Building on their modelling, we parameterized population models for fynbos species to evaluate the impacts of changes to FRI, habitat loss and weed invasion and to test the conservation management actions described above (Methods). Impacts were modelled in a spatially explicit way, allowing for synergies between multiple threats and management actions to occur.

The complexity of adaptation decisions increases with increasing numbers of options, with uncertainty about expected benefits and with the number of decision criteria. Dealing with complexity and uncertainty is the domain of decision theory, and tools exist to help, ranging from simple cost-effectiveness analyses[20], to sophisticated optimization and uncertainty analysis techniques[9,21]. Cost-effectiveness analysis has been used to allocate health funding and pharmaceutical subsidies to maximize 'quality of life years'[22], to guide energy policy[23], to support military spending decisions[24] and to underpin systematic conservation planning and resource allocation[25]. Maximizing the cost-effectiveness of investments is a sensible and transparent way to expend limited conservation resources that can be adapted to deal with particular social preference, such as iconic or economically valuable species[20].

We use a relatively simple cost-effectiveness analysis to identify optimal allocations to fire management and habitat protection and then apply a more sophisticated uncertainty analysis to measure the robustness of optimal (and nominally sub-optimal) allocations to uncertainty about the effectiveness of management actions. The optimal mix of fire and habitat protection was determined for annual budgets ranging from US\$0–120 M yr^{-1}, based on the efficiency with which they reduced medium-term (50 yr) threats to species' persistence (Methods). Our analysis indicates that if climate change drives FRI to low levels (<8 years), there is a high probability of extinction for the species modelled in this system (Fig. 2). Under relatively conservative climate change scenarios, and in the absence of investment in fire protection, this is a real possibility. Consequently, it was most efficient to invest almost solely in fire management, especially when available budgets are small (Fig. 2). When the available budget exceeds US\$43 M, marginal returns from

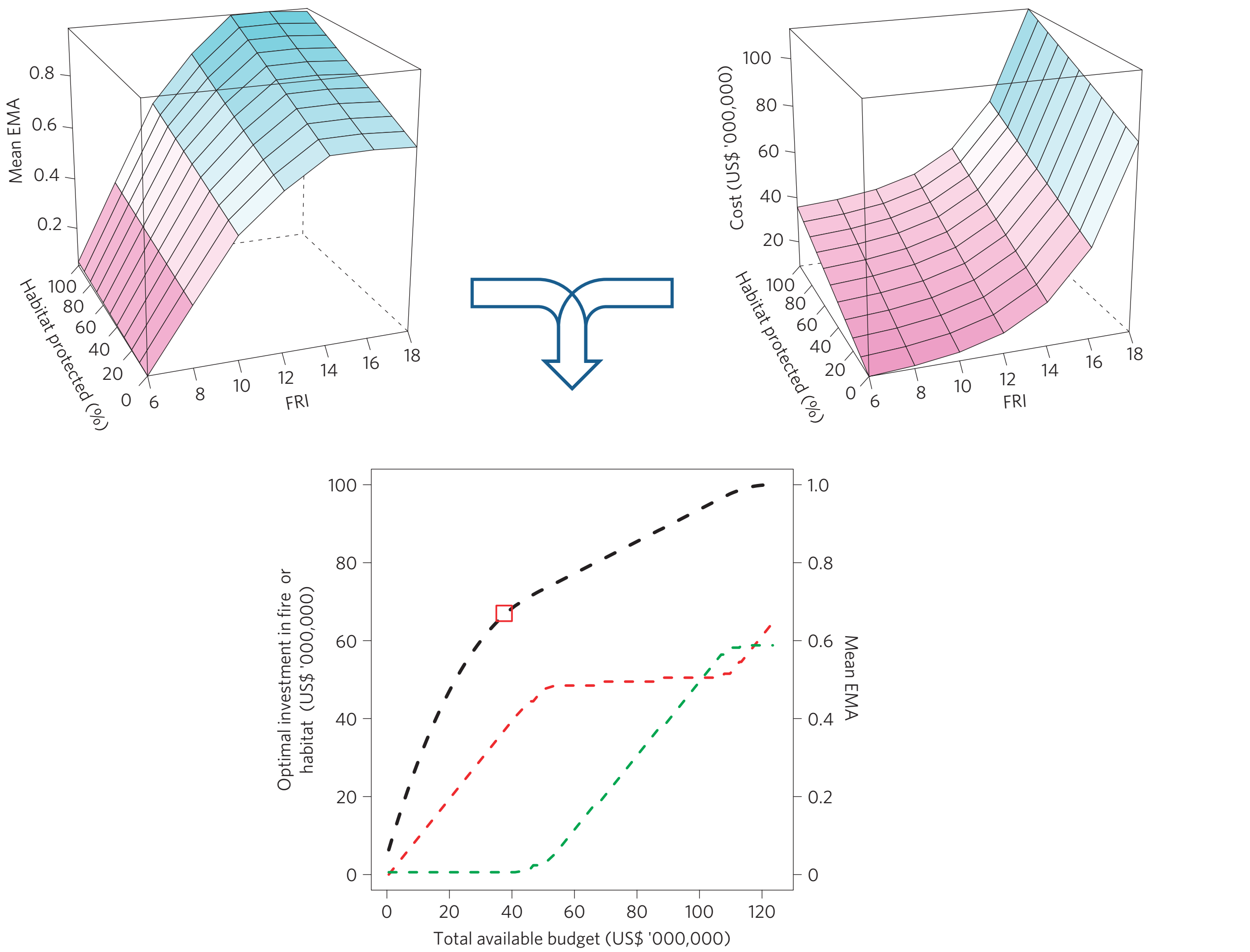

Figure 2 | Optimal allocation of management effort under varying budget constraints. The top left plot shows how the species' EMA varies with the proportion of habitat protected and FRI. The top right plot shows how overall conservation cost varies with habitat protected and FRI. The central plot shows the optimal investment allocation between fire management (red line) and habitat protection (green line) as a function of available budget (axis on the left). The black line on the central plot shows how species' mean EMA (axis on the right) increases as the budget increases. The red box indicates the level of investment that provides the greatest return per dollar.

fire management decrease relative to habitat protection, leading to a mixed investment strategy (Fig. 2). At around US$105 M no further gains in EMA can be made with further investment in habitat protection, after which the remaining budget goes into fire management. This illustrates a key result; that the optimal investment strategy depends on the available budget, in this case in a highly nonlinear fashion. The preference for fire management at low budgets arises because every dollar invested in fire management delivers a relatively large increase in FRI and therefore population persistence, and if FRIs are too low to maintain species, habitat protection is irrelevant. At higher budgets, the switch to habitat management and then back to fire management simply reflects diminishing returns from each activity as the total available budget increases. These results have important implications for climate adaptation investors. First, investing in just one type of adaptation action (for example increasing habitat connectivity) irrespective of available resources is unlikely to be an optimal strategy; a careful evaluation of the optimal strategy, given the resources available, is necessary. Second, analytical methods such as those used here can be used to quantify how much extra conservation benefit can be obtained for a given increase in budget, providing a powerful tool for guiding policy.

Numerous ecological and economic assumptions underpin the analysis presented here, so how confident can we be about the answers? For example, we assume a linear relationship between net cost and area of habitat protected. Similarly, we assume a particular relationship between target FRI and cost, based on the best available expert information, which is highly uncertain in a changing climate. Concern about the robustness of intricate analyses leads naturally to uncertainty analysis. Techniques for dealing with uncertainties about project costs, benefits, and implementation success can be drawn from examples in spatial conservation planning and conservation investment[26]. We conducted an uncertainty analysis using 'info-gap' decision theory[21] that derives from Wald's maximin, which ranks options based on their worst-case outcome[9]. A maximin-optimal investment option is the option under which the worst possible outcome is at least as good as the worst outcome of any other option. In the fynbos analysis, the worst-case outcome for a given investment in fire and habitat management was defined as the lowest net EMA predicted to result from that investment, given uncertainty about the effectiveness of management actions. Info-gap generalizes the maximin strategy by identifying worst-case outcomes at increasing levels (horizons) of uncertainty. This permits the construction of 'robustness curves' that describe the decay in guaranteed minimum performance (or worst-case outcome) as uncertainty increases. Robustness curves are useful in decision-making because they allow the analyst to identify the decision option that is most robust to a range of plausible levels of uncertainty, and the minimum level of performance that can be expected for a given level of uncertainty

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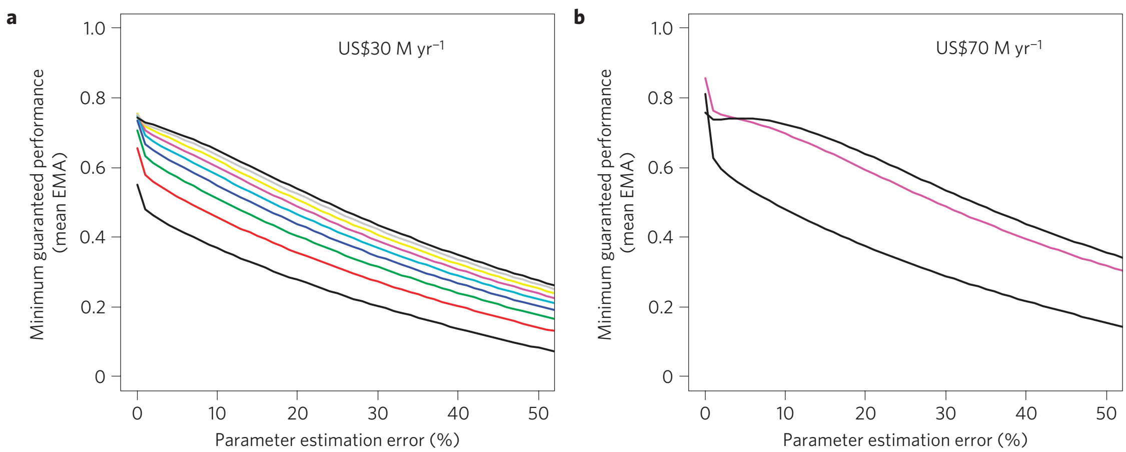

Figure 3 | The robustness of fynbos climate adaptation investment options to uncertainty about fire management and habitat protection effectiveness. **a**, Minimum guaranteed performance in terms of EMA diminishes as uncertainty about fire and habitat management effectiveness increases for a total budget of US\$30 M yr^{-1}. Individual curves represent the proportion of the total budget allocated to fire management, ranging from 10% (bottom black curve) to 90% (top black curve). **b**, Robustness curves at total budget of US\$70 M yr^{-1} for the nominal optimal investment (pink line: 60% investment in fire management), a 10% investment in fire management (lower black line), and a 90% investment in fire management (upper black line).

about key assumptions. We constructed robustness curves for every combination of investment allocation ranging from 100% investment in fire management to 100% investment in habitat protection and weed management (Methods). The analysis reveals that the 'optimal' allocation between management options (the one that maximizes net EMA without considering any uncertainty about key assumptions) is the most robust allocation to uncertainty about management effectiveness at low budgets (for example, US\$30 M); remaining dominant over other solutions up to high levels of uncertainty (Fig. 3). At high budgets (for example US\$60 M), the 'optimal' allocation is not the most robust decision when taking into account plausible levels of uncertainty, but it is only marginally less robust in that the minimum level of guaranteed performance is very close to that of the most robust allocation (Fig. 3). In general, high allocations to fire management tended to be more robust than high allocations to habitat protection.

The robustness analysis provides some confidence in the optimal allocations identified by the cost-effectiveness analysis. However, the uncertainty analysis focussed only on assumptions about the cost-effectiveness of the two management actions. These two parameters are good targets for uncertainty analysis because they subsume much of the important uncertainty about how climate changes will influence fire regimes, the rate of weed invasion, the availability of habitat to protect and cost of habitat protection. Other assumptions not incorporated in this uncertainty analysis include the rate of climate change and its influence on survival, fecundity and carrying capacity of fynbos species. Therefore, estimates of worst-case outcomes should be interpreted with caution.

Demonstrating the performance of conservation investment is critical for both the ongoing credibility of conservation investments[27] and the process of learning about the value of investments and reducing decision uncertainty[28]. Because climate adaptation strategies will be developed under severe uncertainty, it is critical to incorporate uncertainty in decisions using a method such as info-gap, and plan for reducing uncertainty by learning about management effectiveness and other key parameters[29]. In the case of fynbos climate adaptation, monitoring the outcomes of investment will aid learning about the relative cost-effectiveness of competing investment options. This is only valuable if there is a willingness to adapt decisions as new information comes to hand[30]. Because the impacts of stressors and the benefits of conservation actions evolve slowly and data will be noisy, categorical corroboration of investment choices will not be possible within the time horizons usually required by auditors of public spending. Therefore, investments must be seen as long-term experiments that will be improved over time[29].

Structured approaches to decision-making, including cost-effectiveness uncertainty analysis, are politically challenging because they demand recognition of uncertainty and acknowledgement of the trade-offs between competing social, economic and environmental objectives. Decision analytic methods have been successfully applied in sectors where complex socio-environmental decisions are made. Unfortunately, they are rarely applied in biodiversity conservation. This may be because we are frightened of setting explicit objectives and performance measures which can erode political control over decisions. Because threats to biodiversity are large and time is of the essence, the costs of delay, pork-barrelling and political game-playing will be very high. Although ecological-economic analyses such as the one conducted here provide just one of many inputs to real-world decision-making, more widespread application of these approaches to evaluating adaptation options will help reduce the politicization of decisions, thereby enhancing the credibility of those who make them.

Methods

Population dynamics models. We adapted stochastic population models for serotinous obligate seeding shrub species of the Cape Proteaceae originally built by Keith and colleagues[11]. Spatially explicit age/stage-based matrix models were run in RAMAS GIS (ref. 31). The models included distance-declining seed dispersal, environmental and demographic stochasticity, and stochastic fire. Density dependence was implemented using a ceiling model to reduce survival and growth in particular life stages whenever a population exceeds the carrying capacity (K) of its habitat patch[11]. Climate change alters K, as determined by the time series of habitat suitability maps for each species. Habitat loss is implemented as population deletion. The influences of fire management and habitat protection were propagated through the population models. The EMA of each species over the 50-year period (2001–2050) was calculated under a suite of fire and habitat management investment scenarios, based on 1,000 replicate simulations. Each species' EMA for each investment scenario was standardized against a no-climate change and no-habitat-loss EMA to enable comparison of EMA across species for the purposes of evaluating management performance across species.

A model of fire regimes and suppression costs under climate change. The number of extreme fire days in Mediterranean ecosystems is predicted to increase by up to 40% in 2020 and 200% in 2050 under the A1FI Intergovernmental Panel on Climate Change emissions scenario[32]. This indicates a reduction of current FRI to between 6 and 8 years by the mid-point of our simulations (2025) based on current fire suppression investment. We developed a model to predict FRI in the fynbos under fire suppression investments ranging from current levels up to US$120 M yr^{-1}. We represented the relationship between fire suppression investment (c_f) and FRI using a right-shifted power function (Fig. 2, top right plot):

$$c_f = -0.0909 + 6.5 \times 10^{-5} \times (\text{FRI} - 1.74)^{5.11} \quad (1)$$

We assumed that suppression costs would increase gradually with an increase in aspired FRI until around 16 years, after which costs would rapidly increase owing to the necessarily high surveillance and early-strike capacity.

Modelling habitat protection and management costs. If habitat loss continues unabated in high-threat areas, approximately 25% of available habitat will be lost[12,15]. If these threats are managed everywhere they exist, we assume that the available habitat is determined by fire, climate change and the environmental variables described by Keith and colleagues[11]. We aggregate the cost of avoiding clearing (including a purchase cost annualized over 50 years, plus maintenance and administration = US$1,920 $\text{km}^{-2}\,\text{yr}^{-1}$; refs 12,17) and the cost of protection from weed invasion (surveillance and weed eradication programs = US$2,000 $\text{km}^{-2}\,\text{yr}^{-1}$; ref. 12), resulting in a net expected cost of US$3,920 $\text{km}^{-2}\,\text{yr}^{-1}$. The actual cost of any given protection scenario scales linearly with the total area protected, such that the expected cost is:

$$c_h = 0.58 \times P \quad (2)$$

where P is the percentage of the total area of currently threatened habitat that is protected.

Optimization and uncertainty analysis. We searched across the range of possible investments in fire and habitat protection to identify the allocation predicted to yield the highest net EMA across all species. This process was repeated over a range of possible budgets to: (1) identify the budget that achieved the maximum marginal return on investment, and (2) to explore how the optimal mix of investments varied with the total size of the budget. We evaluated the robustness of the optimized investment strategy to uncertainty about the cost effectiveness of fire management and habitat protection. We generalized the two cost functions that define the marginal benefits of increasing investment in fire and habitat management (equations (1) and (2)) to generate a family of cost functions that represent a plausible range of relationships between the cost and effectiveness of management options (Supplementary Fig. S1). The upper bound (worst case) of habitat protection costs was obtained from Osano *et al.*[17], who studied real-estate prices in areas of high conservation significance in South Africa. They found that purchase prices varied by four orders of magnitude, from around US$15 ha^{-1} to US$172,000 ha^{-1}, with 90% of purchase prices falling below US$15,000 ha^{-1}. The worst-case fire management cost-effectiveness occurred when the maximum available allocation to fire (US$100 M) achieves the worst-case FRI modelled in the population models (six years). The worst-case management performance (EMA) was determined for each level of uncertainty about cost-effectiveness, ranging from 0% to 100%. Worst-case management performance was then plotted against estimation error to generate robustness curves (*sensu* Wald, Ben Haim[9,21]) that indicate the lowest level of EMA that can be guaranteed at a given level of estimation error (Fig. 3). We constructed robustness curves for every combination of investment allocation, ranging from 100% investment in fire to 100% investment in habitat protection.

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Author contributions

B.A.W., S.A.B., D.A.K., and H.P.P. designed the research. B.A.W., D.A.K., and B.W.v.W. performed the analysis. B.A.W., S.A.B, M.C., B.S., S.B.C., L.B., A.F., L.M., C.R., T.J.R., and H.P.P. wrote the paper. All authors discussed the results and edited the manuscript.

Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/natureclimatechange. Reprints and permissions information is available online at http://www.nature.com/reprints. Correspondence and requests for materials should be addressed to B.A.W.