

Optimal timing for managed relocation of species faced with climate change

Eve McDonald-Madden^{1,2,3*}, Michael C. Runge^{4,5,6}, Hugh P. Possingham^{2,3} and Tara G. Martin^{1,3}

Managed relocation is a controversial climate-adaptation strategy to combat negative climate change impacts on biodiversity. While the scientific community debates the merits of managed relocation^{1–12}, species are already being moved to new areas predicted to be more suitable under climate change^{13,14}. To inform these moves, we construct a quantitative decision framework to evaluate the timing of relocation in the face of climate change. We find that the optimal timing depends on many factors, including the size of the population, the demographic costs of translocation and the expected carrying capacities over time in the source and destination habitats. In some settings, such as when a small population would benefit from time to grow before risking translocation losses, haste is ill advised. We also find that active adaptive management^{15,16} is valuable when the effect of climate change on source habitat is uncertain, and leads to delayed movement.

Rapid climate change is leading to shifts in the distribution of many species^{17–22} and will have economic and social consequences for human societies^{23,24}. Predicting the impact of different climate-change scenarios on biodiversity has been the overwhelming focus of research effort so far^{21,25}; far less attention has been devoted to developing and choosing between adaptation actions for biodiversity management.

Managed relocation (also known as assisted colonization) is a controversial adaptation action for combating the impacts of climate change on biodiversity^{1–12} and has recently been identified as a key priority for conservation research²⁶. Managed relocation involves physically moving species from habitat predicted to become unsuitable under climate change to locations where the habitat is predicted to become suitable, but where they have never occurred before. At present, debate is focused on whether to undertake managed relocation, in light of its potential risks and benefits^{2,5,9,11}. While this debate continues, species are being moved in anticipation of the risks of climate change^{13,14}. There is now an urgent need for a framework to underpin decisions about when to implement managed relocation, a framework that recognizes the potential for learning to reduce uncertainty and improve future decisions.

A decision framework for managed relocation

We propose a decision framework for managed relocation that includes learning. We focus on a situation where the risk of species extinction as a result of not undertaking managed relocation is considered greater than the risks to the recipient ecological community of undertaking managed relocation⁹. In this case, the

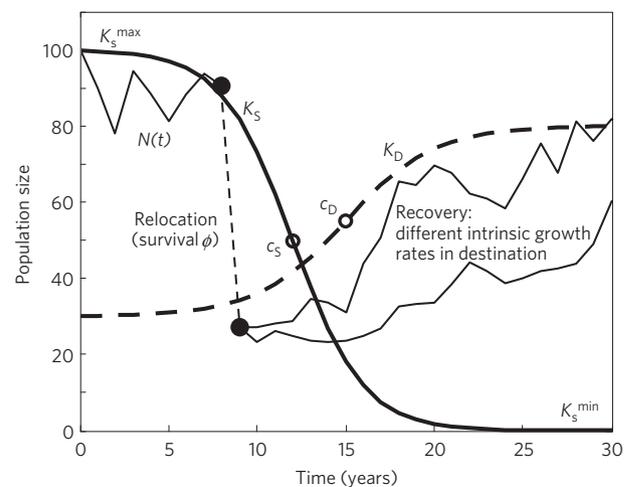


Figure 1 | System model for managed relocation. Carrying capacities in the source (K_S) and destination (K_D) are shown with thick solid and dashed lines respectively; the population size, N , is shown with a thin solid line. The population size represents the state of the system by which decisions are specified. Note, N can decline with K_S or increase towards K_S , depending on the starting population size. The premise of managed relocation is that the suitability of the source habitat will decline with climate change and a destination habitat will become suitable. c_S and c_D represent the times at which half the suitable habitat in the source and destination populations are expected to be lost. The demographic cost of moving a population is expressed as the relocation survival rate, ϕ . The thin dashed line represents population change after relocation based on ϕ .

manager is left with the decision about when, if ever, to implement managed relocation. We articulate several key elements of this decision framework: the objectives, the alternative actions, the assumptions about the system dynamics, the key uncertainties and the role of monitoring.

Managed relocation will be invoked as an adaptation strategy to conserve species threatened by climatic changes, so a likely objective for managed relocation is to maximize the persistence of the species. We assume that probability of persistence is a monotonically increasing function of population size, so our explicit objective is to maximize population size at some point in the future, T . Other objectives, such as maximizing growth rate, are of course possible. (For a discussion of the effect of risk tolerance, see Supplementary text and Supplementary Figs S1 and S2.)

¹Climate Adaptation Flagship, CSIRO Ecosystem Sciences, Ecosciences Precinct 41 Boggo Rd, Dutton Park 4102, Australia, ²Centre for Applied Environmental Decision Analysis, The University of Queensland, School of Biological Sciences, St Lucia, Queensland 4072, Australia, ³ARC Centre for Excellence in Environmental Decisions, University of Queensland, St Lucia, Queensland 4072, Australia, ⁴United States Geological Survey, Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, Maryland 20708, USA, ⁵Australian Centre of Excellence for Risk Analysis, The University of Melbourne, Parkville, Victoria 3010, Australia, ⁶Centre for Applied Environmental Decision Analysis, The University of Melbourne, School of Botany, Parkville, Victoria 3010, Australia. *e-mail: eve.mcdonald-madden@csiro.au.

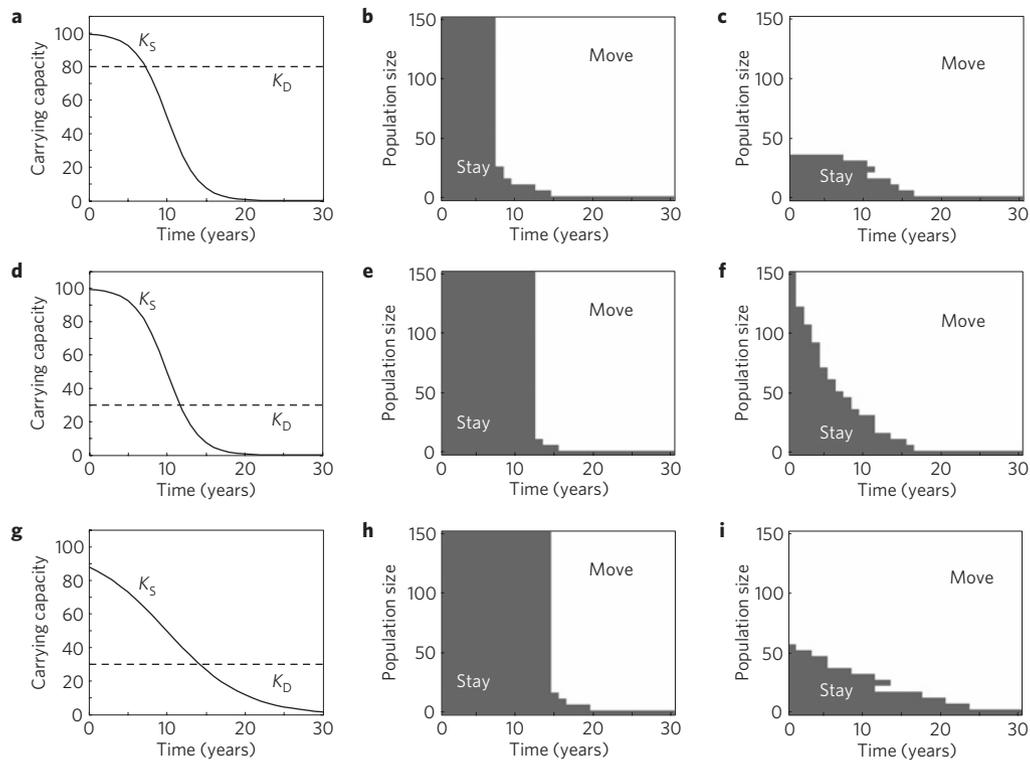


Figure 2 | Optimal timing of managed relocation, as a function of population size in the source, when the change in the carrying capacity under climate change is known. a,d,g. Known habitat carrying capacity over time in the source (K_S , solid line) and destination (K_D , dashed line), for three scenarios. **b,c,e,f,h,i.** Optimal state- and time-dependent decision strategy for the corresponding habitat scenario when the relocation survival rate is high ($\phi = 0.95$; **b,e,h**), and when the relocation survival rate is low ($\phi = 0.3$; **c,f,i**).

The actions that the decision-maker needs to evaluate regarding managed relocation include whether and where to move individuals, which kinds of individual to move, how many to move, whether to move all at once or in staggered cohorts, what methods to use for release and whether a period of temporary captivity is required. We examine what we believe to be the primary consideration with respect to our uncertainty about the impacts of climatic shifts: at what time to move. To illustrate our framework, we assume that the relocation involves moving every individual all at once. This strategy is applicable in situations where wild populations are perilously small (for example, California condor, *Gymnogyps californianus*, and orange-bellied parrot, *Neophema chrysogaster*²⁷). Our framework, however, could easily be extended to consider more complex methods of implementation such as staggered movement.

Predicting the consequences of alternative management strategies in terms of their ability to achieve objectives requires making explicit assumptions about the system dynamics. There are a number of assumptions that have been implicit in past discussions of managed relocation. First, the motivation for managed relocation is that the suitability of the current (source) habitat, for example, population growth rate or carrying capacity, will decline over time owing to climate change ($K_S(t)$, Fig. 1). Second, the notion of managed relocation assumes that there is somewhere else that will be better for the species at some point in the future ($K_D(t)$, Fig. 1). Third, for managed relocation to be effective, at least one of the source and destination sites must be suitable at any one time (unless temporary captivity is being considered). Fourth, there is a demographic cost to moving individuals and only a fraction, ϕ , will survive and become established at the destination (Fig. 1). Fifth, the quality of the habitat in the destination needs to be sufficiently high that recovery of the population is feasible within the desired time period, T ; this habitat quality could be expressed as the expected intrinsic growth rate in the destination.

The success of a managed relocation programme hinges on these assumptions; the difficulty is that there is likely to be considerable uncertainty about many of these. How much and how quickly will the source habitat decline? How much and how quickly will the destination habitat improve? What fraction of the population might die during relocation? What will be the intrinsic growth rate of the species in the destination? Three tools are valuable in the face of this uncertainty: predictive habitat modelling with explicit articulation of uncertainty, for example, by coupling general circulation models with species-specific habitat suitability models²⁸, monitoring of key response variables and Bayesian updating of the predictions in light of emerging monitoring data. In the face of uncertainty, a full-fledged decision framework should include explicit articulation of critical uncertainties and an ongoing monitoring programme designed to resolve that uncertainty, both key components of adaptive management^{15,16,29}.

Decision-making without uncertainty

We discovered that, when we are certain about how the system will change in the future, the optimal timing of relocation is strongly affected by the suitability of the destination site, K_D , relative to the source site, K_S , the relocation survival rate, ϕ (Fig. 2), and the intrinsic growth rate of the population in both the destination and source sites. If the relocation survival rate is high ($\phi = 0.95$), then regardless of the number of individuals in the population, N , we should not move our threatened species until the carrying capacity in the source population, K_S , is less than that in the destination, K_D (Fig. 2b,e,h). A small difference in the maximum carrying capacities leads to an early crossing point of the two habitat models (Fig. 2a, $t = 7.2$ yr) and a correspondingly early optimal relocation time (Fig. 2b). An increase in this difference (Fig. 2d) increases the time at which the source carrying capacity falls below that of the destination ($t = 11.7$ yr),

Table 1 | Trade-off table for a decision to move a population when belief about the impact of climate change is static.

Model	Truth		Expected value
	No impact (K_S model 1)	Impact (K_S model 2)	
Belief	w	$1-w$	
Stay	K_S^{\max}	K_S^{\min}	$wK_S^{\max} + (1-w)K_S^{\min}$
Move	K_D^{\max}	K_D^{\max}	K_D^{\max}

The uncertainty concerns whether the source carrying capacity will, in fact, decrease (impact) or not (no impact). The consequences of taking a particular action, as a function of the true system dynamics, are expressed as the expected long-term population size. The expected value of each action is the belief-weighted average across the two system models—there is impact and there is no impact of a changing climate. Here K_S is the carrying capacity in the source area, K_S^{\max} is the maximum carrying capacity in the source area, K_D^{\max} is the maximum carrying capacity in the destination area and w is our belief that there is no impact of climate change on the carrying capacity of the source population.

and therefore also increases the optimal time of relocation (Fig. 2e; also compare Fig. 2g,h).

When there is a large demographic cost to the relocation (that is, a low relocation survival rate, $\phi = 0.3$), the optimal timing of relocation is driven not only by habitat dynamics but also by the number of individuals in the source population (Fig. 2c,f,i). When the carrying capacity in the destination, K_D^{\max} , is high (Fig. 2a), the timing depends largely on the population size in the source: if the population is large, the optimal strategy calls for immediate relocation, which allows recovery from the move to start sooner; if the population size is small, there is an advantage in leaving the population in the source to allow some recovery towards the carrying capacity before incurring the relocation cost (Fig. 2c). When the carrying capacity in the destination is much lower than the source (Fig. 2d), there is no point introducing more individuals than the destination can hold (Fig. 2f). Still, relative to the case when the relocation survival rate is high (Fig. 2e), the timing of relocation is earlier, to allow more time to recover from the demographic costs of relocation. Under all habitat suitability scenarios, below a certain population size we should never implement managed relocation as a result of the relatively high demographic costs of relocation.

Decision-making with uncertainty

Decision-makers are invariably uncertain about the response of species to climate change. Incorporating uncertainty about how the system will respond to changes in climate alters both what drives our actions and when we should act. We capture this uncertainty with a belief state, w . In our illustration w describes our belief that there will be no impact of climate change on the carrying capacity of the source population. We consider two cases: a static case, in which the belief state is fixed and does not change over time; and an active adaptive case, in which the belief state is dynamic and updated with ongoing monitoring data. The static case represents a likely scenario where insufficient resources are in hand to proceed with active adaptive management^{15,16,29} and instead the best available knowledge regarding the impact of climate change is used to inform managed relocation.

In the static case, we assume that the future population size is determined by the long-term carrying capacity in the final location of the population, which is a function of both the decision (‘stay’ or ‘move’) and the reality about the effects of climate change (Table 1). We find that the expected long-term value of keeping the population in the source (‘staying’) is greater than the expected long-term value of moving when our belief in the no-impact model is above a critical threshold: $w > w_c$, where $w_c = (K_D^{\max} - K_S^{\min}) / (K_S^{\max} - K_S^{\min})$. In other words, if our initial

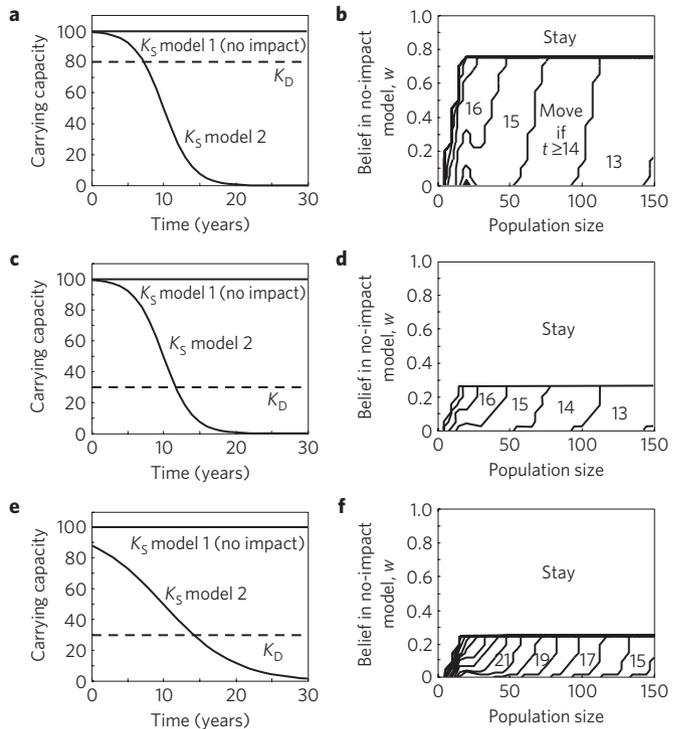


Figure 3 | Optimal timing of managed relocation in the face of uncertainty about the impact of climate change. a,c,e, For each scenario, there are two potential models for the carrying capacity in the source, one in which there is no impact of climate change (K_S model 1), and one in which carrying capacity declines with time (K_S model 2). The three scenarios of decline correspond to the scenarios in Fig. 2. b,d,f, Optimal state-, time-, and belief-dependent decision strategy for the corresponding habitat scenario, when the relocation success rate is low ($\phi = 0.3$).

belief in the no-impact model is greater than w_c then we do not move the species and no further decision is made. Conversely, if our initial belief in the no-impact model is less than w_c , we move the species.

If we adopt an active adaptive management approach¹⁵, for each year the population remains in the source habitat, our belief about the impact of climate change will change in response to monitoring data, specifically, to observed changes in the population size, N . Now, because we are implementing active adaptive management, our decisions are guided by the number of individuals in the population, as well as our belief, w , in whether climate change is having an impact on the carrying capacity of the source population (Fig. 3). When the belief in the no-impact model is above the critical threshold, w_c , the optimal decision is to keep the population in the source, no matter what the population size. When managed relocation is warranted, the optimal timing of movement is driven by our expectations about how the system will change and how rapidly the alternative models of system change can be distinguished from each other via learning (Fig. 3). When the rate of decline in the source habitat impact model (K_S model 2) is high (Fig. 3a,c), the optimal timing of relocation is between 13 and 18 years, depending on population size (Fig. 3b,d). This is later than in the corresponding case of known dynamics (Fig. 2c,f) for two reasons: first, as a bet-hedging strategy, we leave the population in the source longer, in case the source is not being affected by climate change; and second, we can only distinguish the alternative models if individuals remain in the source; leaving animals in the source population is the only way to monitor and learn in this population. Intriguingly, the value of learning does not last forever; if 16 or 17 years have gone by, and there is not enough evidence for the

Table 2 | Performance of three managed relocation approaches under climate change.

Prob. model 1	Performance metrics	Initial belief in model 1			Initial belief in model 1		Initial belief in model 1	
		Case 1	Case 2	Case 3	Case 2	Case 3	Case 2	Case 3
0.8	<i>P</i> (extinction)	0.00	0.22	0.00	0.22	0.00	0.00	0.00
	Terminal <i>N</i>	29.7	99.1	80.5	99.1	80.5	29.7	80.4
	Freq. relocation	1.000	0.000	0.266	0.000	0.266	1.000	0.268
0.4	<i>P</i> (extinction)	0.00	0.63	0.00	0.63	0.00	0.00	0.00
	Terminal <i>N</i>	29.7	99.2	53.1	99.2	53.1	29.7	53.0
	Freq. relocation	1.000	0.000	0.662	0.000	0.662	1.000	0.664
0.2	<i>P</i> (extinction)	0.00	0.81	0.00	0.81	0.00	0.00	0.00
	Terminal <i>N</i>	29.7	100.3	42.2	100.3	42.2	29.7	42.1
	Freq. relocation	1.000	0.000	0.822	0.000	0.822	1.000	0.824

Case 1 is the time- and state-dependent strategy of Fig. 2f; case 2 is the belief-dependent strategy of Table 1; case 3 is the active adaptive strategy of Fig. 3d. Three performance metrics are shown, the probability of extinction after 100 years, *P* (extinction); the mean population size at 100 years for populations that did not become extinct; terminal *N* and the frequency with which managed relocation occurred, Freq. relocation. Parallel simulations were run for scenarios in which the underlying probability of the model with no impact of climate change (Prob. model 1) was 0.8, 0.4 and 0.2, and in which the initial belief in this probability was 0.8, 0.4 and 0.2.

climate having no impact, it is best to move the population and avoid the risk of population collapse. When the rate of decline in the impact model (K_S model 2) is slower (Fig. 3e), the optimal timing of managed relocation is later, between 15 and 28 years (Fig. 3f). As a result of the slower loss of habitat in the impact model, more time is required to distinguish between the no-impact (K_S model 1) and impact (K_S model 2) models through monitoring.

Using simulation, we compare the performance of our managed relocation strategies (Table 2). Allowing for learning through our active adaptive strategy (time–state–belief-dependent strategy) outperforms our strategy where the belief is fixed (belief-dependent strategy) and our strategy where we assume the dynamics about climate change impacts are known (time–state-dependent strategy). See Supplementary Information for more detail on the simulation results.

Moving the debate from whether to when

The decision to move a species to a new area given the impact of climatic change is far from simple. Indeed, predictions and uncertainty about the effect of climate change on the source and the destination populations, the demographic cost of relocation and the growth rates of the population in both areas all influence the optimal timing of managed relocation. Alternative programme objectives (for example, maximize growth rate) and the consideration of a different suite of actions (for example allowing staggered movement) also may alter the optimal timing of relocation. The counterintuitive nature of some results and the sensitivity of the decision to these different factors highlight the need for an explicit structure that considers the anticipated system dynamics, uncertainty about these dynamics, and the benefits of active learning. The framework we present provides the scaffolding for careful analysis of managed relocation decisions.

There are additional factors that managers may want to consider. For example, first, the destination habitat is also likely to be changing with time; in fact, the suitability of this habitat may improve with time, affecting the best time to move a species (see, for example, Fig. 1). In an extreme case, where the destination habitat may not become viable until after the source population is lost, the establishment of an insurance captive population may need to be considered as an interim strategy. Second, how the destination habitat is changing with time may be uncertain, requiring learning about the destination before making a decision to move the species. Third, environmental stochasticity may be an important dynamic to include in the population model, particularly for highly threatened species at low numbers. The framework we have provided could

be expanded to incorporate all these intricacies and others, and we would expect this expansion to give rise to further novel patterns in the optimal strategies.

Our decision science framework provides a platform to increase our understanding of decision making in the face of climate change. There are two key components of climate change that are particularly challenging: management in the face of system changes; and management in the face of uncertainty surrounding these changes. Regarding the first challenge, we have shown that by using time-dependent dynamic optimization methods we can make informed decisions in the face of system change. The second challenge has paralyzed the ability of agencies to make decisions in a changing world, and caused some to advocate broad-based monitoring to reduce uncertainty without any link to what should actually be done if the systems are found to be in decline. Instead, we have shown here that by explicitly articulating uncertainty in the form of alternative models of system change, and evaluating the evidence for these different models with information gained about the system, we can make informed decisions regarding adaptation in the face of uncertain climate change.

Methods

Once the broader risks and benefits of implementing managed relocation have been considered, the question becomes one of optimal timing. We frame this problem as a time-dependent Markov decision process³⁰, and use stochastic dynamic programming to find the optimal time to implement managed relocation, conditional on full knowledge about the system dynamics, which in this case is the impact of climate change on the carrying capacity of the species. We also consider the case when we are uncertain about the system dynamics. Here, a tension may arise between actions that are optimal given uncertainty and actions that are most informative about uncertainty^{15,16}; are the short-term costs of learning offset by their long-term benefits?

To illustrate the complexity of the decision on when to relocate a species and thus the value of a framework to aid this decision, we present the optimal timing of relocation given that our objective is to maximize population size, the action is to move all at once and the impact of climate change is modelled as carrying capacity changing through time. Further, we present the changes in this optimal strategy that occur when we vary the specified parameters within the framework (for example, the parameters within the models of carrying capacity and demographic cost of relocation). A detailed description of the methods can be found in Supplementary Information.

Received 17 May 2011; accepted 24 June 2011; published online 24 July 2011

References

1. McLachlan, J. S., Hellmann, J. J. & Schwartz, M. W. A framework for debate of assisted migration in an era of climate change. *Conserv. Biol.* **21**, 297–302 (2007).

2. Hoegh-Guldberg, O. *et al.* Assisted colonization and rapid climate change. *Science* **321**, 345–346 (2008).
3. Fazey, I. & Fischer, J. Assisted colonization is a techno-fix. *Trends Ecol. Evol.* **24**, 475–475 (2009).
4. Hunter, M. L. Climate change and moving species: Furthering the debate on assisted colonization. *Conserv. Biol.* **21**, 1356–1358 (2007).
5. Ricciardi, A. & Simberloff, D. Assisted colonization is not a viable conservation strategy. *Trends Ecol. Evol.* **24**, 248–253 (2009).
6. Sandler, R. The value of species and the ethical foundations of assisted colonization. *Conserv. Biol.* **24**, 424–431 (2010).
7. Schlaepfer, M. A., Helenbrook, W. D., Searing, K. B. & Shoemaker, K. T. Assisted colonization: Evaluating contrasting management actions (and values) in the face of uncertainty. *Trends Ecol. Evol.* **24**, 471–472 (2009).
8. Seddon, P. J. *et al.* The risks of assisted colonization. *Conserv. Biol.* **23**, 788–789 (2009).
9. Richardson, D. M. *et al.* Multidimensional evaluation of managed relocation. *Proc. Natl Acad. Sci. USA* **106**, 9721–9724 (2009).
10. Sax, D. F., Smith, K. F. & Thompson, A. R. Managed relocation: A nuanced evaluation is needed. *Trends Ecol. Evol.* **24**, 472–473 (2009).
11. Schwartz, M. W., Hellmann, J. J. & McLachlan, J. S. The precautionary principle in managed relocation is misguided advice. *Trends Ecol. Evol.* **24**, 474–474 (2009).
12. Mueller, J. M. & Hellmann, J. J. An assessment of invasion risk from assisted migration. *Conserv. Biol.* **22**, 562–567 (2008).
13. Willis, S. G. *et al.* Assisted colonization in a changing climate: A test-study using two U.K. butterflies. *Conserv. Lett.* **2**, 46–52 (2009).
14. Fox, D. *Conservation Vol. 8* (Society for Conservation Biology, 2007).
15. Walters, C. J. & Hilborn, R. Ecological optimization and adaptive management. *Annu. Rev. Ecol. Syst.* **9**, 157–188 (1978).
16. Holling, C. S. *Adaptive Environmental Assessment and Management* (Blackburn Press, 1978).
17. Hughes, L. Biological consequences of global warming: Is the signal already apparent? *Trends Ecol. Evol.* **15**, 56–61 (2000).
18. Pounds, J. A., Fogden, M. P. L. & Campbell, J. H. Biological response to climate change on a tropical mountain. *Nature* **398**, 611–615 (1999).
19. Root, T. L. *et al.* Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60 (2003).
20. Parmesan, C. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Syst.* **37**, 637–669 (2006).
21. Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42 (2003).
22. Walther, G. R. *et al.* Ecological responses to recent climate change. *Nature* **416**, 389–395 (2002).
23. Levy, M. *et al.* *Millennium Ecosystem Assessment, 2005* (Island Press, 2005).
24. Hooper, D. U. *et al.* Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol. Monogr.* **75**, 3–35 (2005).
25. Thomas, C. D. *et al.* Extinction risk from climate change. *Nature* **427**, 145–148 (2004).
26. Sutherland, W. J. *et al.* A horizon scan of global conservation issues for 2010. *Trends Ecol. Evol.* **25**, 1–7 (2010).
27. Butchart, S. H. M., Stattersfield, A. J. & Collar, N. J. How many bird extinctions have we prevented? *Oryx* **40**, 266–278 (2006).
28. Durner, G. M. *et al.* Predicting 21st century polar bear habitat distribution from global climate models. *Ecol. Monogr.* **79**, 25–58 (2009).
29. Peterson, G. *et al.* Uncertainty, climate change, and adaptive management. *Ecol. Soc.* **1**, 1–7 (1997).
30. Puterman, M. L. *Markov Decision Processes: Discrete Stochastic Dynamic Programming* (Wiley, 1994).

Acknowledgements

This work was supported by a CSIRO Julius Career Award to T.G.M.; E.M-M. was supported by an OCE Fellowship from CSIRO, Queensland International Fellowship and an ARC APD Fellowship. H.P.P. was supported by an ARC Federation Fellowship. This work was further supported by the ARC Centre for Excellence in Environmental Decisions. We thank S. Ferrier, S. McIntyre, I. Chades and J. Nichols for comments on this manuscript and the late S. Schneider for his insights on this work.

Author contributions

E.M-M., T.G.M., M.C.R. and H.P.P. designed the research. M.C.R. and E.M-M. carried out the analysis. E.M-M., T.G.M. and M.C.R. 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 E.M-M.