

## FORUM

# Climate change, connectivity and conservation decision making: back to basics

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## Summary

1. The challenge of climate change forces us to re-examine the assumptions underlying conservation planning.
2. Increasing ‘connectivity’ has emerged as the most favoured option for conservation in the face of climate change.
3. We argue that the importance of connectivity is being overemphasized: quantifying the benefits of connectivity *per se* is plagued with uncertainty, and connectivity can be co-incidentally improved by targeting more concrete metrics: habitat area and habitat quality.
4. *Synthesis and applications.* Before investing in connectivity projects, conservation practitioners should analyse the benefits expected to arise from increasing connectivity and compare them with alternative investments, to ensure as much biodiversity conservation and resilience to climate change as possible within their budget. Strategies that we expect to remain robust in the face of climate change include maintaining and increasing the area of high quality habitats, prioritizing areas that have high environmental heterogeneity and controlling other anthropogenic threatening processes.

**Key-words:** adaptation, biodiversity, conservation prioritization, habitat quality, landscape planning, spatial ecology, species–area relationship, uncertainty

## Introduction

How should we adapt our conservation strategies in the face of climate change? Of the multitude of suggested answers, the single most repeated suggestion is to increase ‘connectivity’ (Heller & Zavaleta 2009). ‘Connectivity conservation’ (Crooks & Sanjayan 2006) is gathering pace and political support (e.g. Australian Government 2004; IUCN WCPA 2006; Kettunen *et al.* 2007). The idea is to maintain and build connected environments that will enable species to move with the climate. Whilst laudable, our concern is that this strategy could cause more harm than good if it inadvertently redirects resources and attention away from more certain and effective conservation actions.

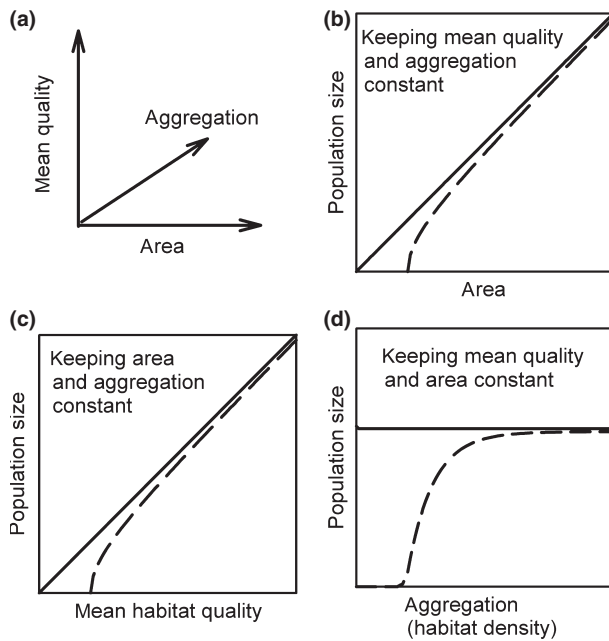
In this study, we revisit the principles of spatial ecology and conservation planning. We summarize how connectivity emerges as a complicated function of habitat area, habitat quality, the spatial arrangement of habitat and species-spe-

cific dispersal. We argue that uncertainty associated with connectivity is generally higher than uncertainty about habitat area and quality, and threatening processes such as habitat destruction. We aim for a more balanced approach to developing climate change conservation strategies where connectivity is treated as a potentially useful tool, but not as an end in itself.

## Spatial conservation planning: the basics

We start from a consideration of individual species; the population theory we discuss applies to any species, but we apply this primarily to spatial planning for terrestrial landscapes. The regional carrying capacity, and hence the population size of a species depends principally on the area of suitable habitat, the quality of that habitat and on the spatial arrangement of suitable habitat (Fig. 1; Andrewartha & Birch 1954; MacArthur & Wilson 1967). Habitat arrangement has multiple dimensions, but we consider the main one to be ‘aggregation’ (Fig. 1); how habitat is concentrated in space. We consider habitat ‘quality’ to be a measure of potential population

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**Fig. 1.** Fundamental variables of spatial population biology. (a) Habitat area, habitat quality and habitat aggregation (see text for definitions) are independent axes that all affect regional population size (they also affect functional connectivity, see Fig. 2). (b–d) For each factor, there is a threshold below which the regional population is unable to persist. Solid lines indicate potential carrying capacity, whilst dashed lines denote the long-term expected population size.

growth and/or density, and area to be the total area with a positive quality. Importantly, each of these three quantities has a threshold below which the regional population of the species will not persist (Fig. 1) – too little habitat area, too low habitat quality or excessive dispersion of habitat will all lead to regional extinction of the focal species (Fig. 1; With & King 1999; Hanski & Ovaskainen 2000). Even though area, habitat quality and aggregation are abstractions and their exact definitions might be debated, there is very good evidence for their effects on single species (e.g. Thomas, Thomas & Warren 1992), and they are used as the basis of much conservation planning (Margules & Pressey 2000; Moilanen & Wintle 2006).

Defining area, quality and aggregation for multiple species simultaneously is not straightforward because the requirements of species vary. The relationship between species and area is most strongly established (MacArthur & Wilson 1967; Simberloff 1976a,b). More area generally means more individuals, more resources and more environmental variation, giving opportunities for niche specialization. Quality is a difficult notion when considering multiple species, but for practical purposes can be described in terms of freedom from anthropogenic degradation, disturbance, pollution, etc. Influences of habitat aggregation and isolation on diversity are seen for many communities (e.g. MacArthur & Wilson 1967; Simberloff 1976b; Hanski 1998), but differences among species in their habitat requirements and dispersal characteristics mean that there is no universal relationship.

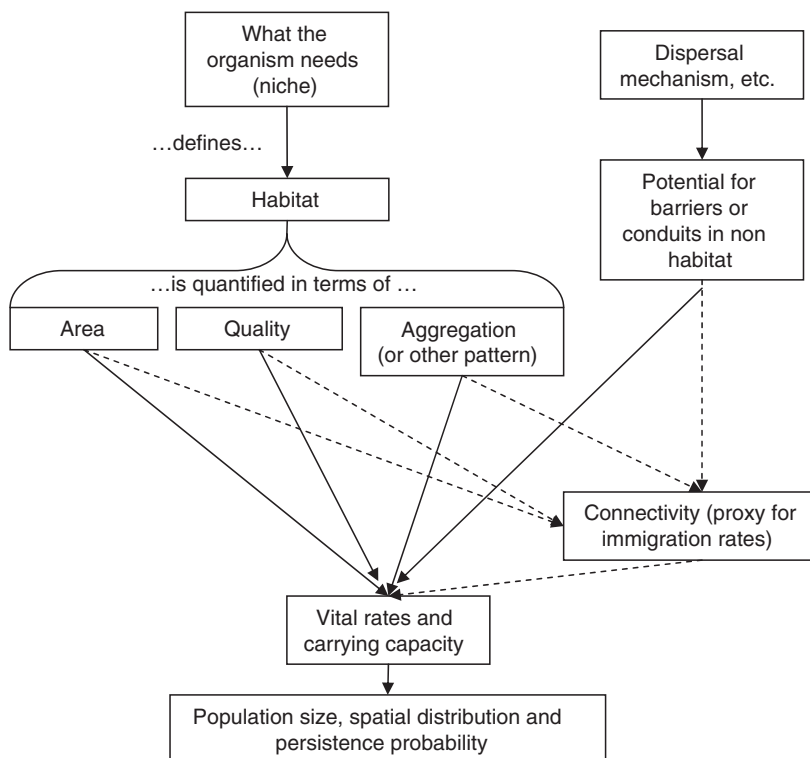
## Connectivity and uncertainty

Connectivity is seen as something that should be accounted for in conservation planning (Margules & Pressey 2000; McCarthy, Thompson & Possingham 2005; Moilanen *et al.* 2005), but there are numerous overlapping definitions (Tischendorf & Fahrig 2000; Moilanen & Hanski 2001; Goodwin 2003; Fagan & Calabrese 2006). Broadly, 'functional connectivity' estimates the actual or potential rate of immigration into a point, cell, or patch on the landscape (Hanski 1998; Tischendorf & Fahrig 2000), and thus depends on several attributes of the species, as well as the interaction between the species and the landscape (Fig. 2). As a result, most connectivity measures subsume influences of habitat area, quality and spatial aggregation, and some also include information about heterogeneities in the non-habitat (Fig. 2).

We argue that uncertainties in the estimation and effects of connectivity make it potentially inefficient as a primary conservation metric. Conservation planning is plagued with uncertainties (Regan, Colyvan & Burgman 2001). Uncertainty about area and quality derive from uncertainty about which environmental and biotic factors explain the local carrying capacity for a given species (Elith, Burgman & Regan 2002). Uncertainty about the functional connectivity of the species automatically includes uncertainties relating to area, quality and habitat pattern because functional connectivity depends partly on the distribution and quality of habitats in the landscape (Fig. 2). Additional uncertainties about the measurement of connectivity include: species-specific influences of distance on dispersal; tails of dispersal distributions, which are notoriously difficult to estimate; effects of source and target habitat quality on emigration and immigration; how dispersing individuals search for habitat; how movement behaviour is affected by the spatial structure of non-habitat, and the influence of spatially correlated environmental stochasticity on population-dynamical processes (Moilanen & Nieminen 2002). By combining all of these, uncertainty about measuring and predicting connectivity is always higher than uncertainty about the constituent factors that contribute to connectivity.

Not only is the measurement of connectivity uncertain, but so are its effects on long-term expected population size. *Total* carrying capacity always steadily increases with increasing habitat area and quality, but does not do so with increasing habitat aggregation (Fig. 1b–d) or increasing dispersal, the other components of connectivity. There is only a relatively narrow window at intermediate levels of habitat aggregation where increased aggregation makes a major difference to expected population size (because once habitats are close enough to be colonized, further benefits of aggregating habitat or increasing dispersal are diminished). Thus, increasing area and quality are more certain to increase population size than are increases in aggregation and dispersal, unless isolation is already known to be the main constraint for a particular species and landscape.

As uncertainties about connectivity tend to be high, and increases in habitat quantity and quality coincidentally improve connectivity, we conclude one should generally



**Fig. 2.** A schematic of the place of (functional) connectivity in spatial ecology and conservation. Functional connectivity is a quantity that always incorporates some aspect of spatial pattern, but it usually also includes information about the amount and quality of habitats and factors influencing dispersal behaviour and success.

provide higher weight in decision-making to actions that increase area and quality. Theoretically, we know that populations will sometimes benefit more from a small, well-connected piece of habitat than a larger, more isolated one, but the relative uncertainties and the probability of worse-than-expected outcomes should also affect our decision making. From a decision theoretic perspective, when faced with two options that convey similar expected (mean) returns, one should choose the option with the lowest variance of expected outcome to maximize the probability of achieving one's conservation goal (e.g. Ben-Haim 2001).

We are particularly concerned that in a planning process, people who want to release areas from conservation, e.g. for development, could actually exploit the profusion of connectivity measures (Kindlmann & Burel 2008) to choose one that 'works' for them (Walker *et al.* 2009). For example, restored corridors, stepping stones or 'softening' of the anthropogenic matrix will cause increases in some connectivity measures. Depending on the connectivity metric used, a large percentage increase in 'connectivity' could be used to argue that a large percentage decrease in habitat area is acceptable – allowing a development to proceed. Loss of habitat implies certain and immediate decreases in population sizes, whereas compensating long-term benefits of additional connectivity might be largely unknown and possibly small (Falcu & Estades 2007).

Notwithstanding these misgivings, the functional connectivity of landscapes applied to single species is a very useful concept in appropriate circumstances, when the constraints on a particular species are known. But, ultimately, conservation is a multi-species enterprise. In this context, various measures of 'structural connectivity' have been proposed, that generalize

the connectivity of vegetation types without reference to particular species. Combining species' responses in this way magnifies uncertainty because multi-species responses are not a simple function of each individual species' response. There is an attractive simplicity to increasing structural connectivity for multi-species conservation, but the scientific basis for such a strategy is largely absent and the applicability of this concept under climate change is also highly uncertain. The trade-off between increased structural connectivity *per se* and increased protection for existing natural or semi-natural habitats are always very difficult to calculate. However, maintaining and increasing the area of natural or semi-natural habitats will add useful habitat area for many species and, as described above, will usually coincidentally increase connectivity.

### The new world order

So far, our discussion has been most relevant to situations where the regional distributions of species can be assumed to be relatively stationary. Given climate change and the lagged responses of species (Menéndez *et al.* 2006), dynamic change will be the norm for the foreseeable future. At large scales there are shifts to higher latitudes and elevations (Hickling *et al.* 2006; Parmesan 2006; IPCC 2007) and movements along moisture gradients, and at smaller scales there are shifts in preferred microclimates and changes to the nature of the vegetation that constitutes 'habitat' (Thomas *et al.* 2001; Davies *et al.* 2006).

These changes undermine three common presumptions in conservation planning. First, we often presume that vegetation type can be used as a reasonable proxy for habitat availability for one or many species. Quaternary evidence shows that

species exhibit individualistic responses to climate change, and vegetation types change with the climate (Williams, Shuman & Webb 2001), so that the community classification schemes we now use to describe vegetation types will become redundant in the long term. Secondly, we assume that structural connectivity, measured on the basis of land cover types, is a reasonable proxy for functional connectivity of multiple species. As with the first assumption, this will become less reasonable the more climate change advances and changes communities.

Thirdly, we commonly assume that protecting locations with the most populations of a species will maximize the chances of persistence in both the short- and long-term survival. Under climate change, prioritizing only existing core populations carries the danger of promoting short-term persistence in current strongholds at the expense of long-term survival; but prioritizing only marginal populations that are predicted to expand is risky because of massive uncertainties about the true consequences of climate change. In essence we are required to deal with trade-offs through time, as well as continuing to pay attention to trade-offs in space and trade-offs between species. We have to address the additional question 'How much short-term conservation success should we forgo in order to increase the long-term probability of achieving our targets?' Perhaps not much, as benefits that are to materialize a long time in the future may have a tendency of disappearing on the way (Walker *et al.* 2009). Such considerations need to be incorporated within population viability analyses and decision frameworks, which can no longer assume long-term stasis in environmental conditions.

### Reasons to be cheerful

It is easy to be overwhelmed by the complexity and uncertainty involved in conservation planning for a world with climate change. There is a huge desire to 'do something' but what exactly is it that we should do? A vast number of suggestions have been made, and there is limited direct evidence to assess which of these is likely to be most effective (Heller & Zavaleta 2009). So, can we step back and ask if any principles hold true with or without climate change, and thereby which conservation strategies are most likely to be robust?

One such principle is that increasing numbers of species are associated with increasing area (Connor & McCoy 1979; Guilhaumon *et al.* 2008). But how much area is enough? Effective conservation requires sufficient habitat where a species currently occurs and additional locations that will support populations whilst the distribution is changing, until it reaches a new equilibrium (assuming the climate does; Araújo *et al.* 2004). Any previously used target [e.g. the 10% terrestrial protected area target (IUCN 2004)] will deliver lower conservation outcomes under climate change than originally hoped. Therefore, renewed effort and additional funding to conserve extra land is warranted. Locations that have low human impacts should remain good for many species, even if the identities of those species change. Maintaining sites of high value to biodiversity should be feasible, but management that attempts to

retain a particular community composition may be expensive and ultimately doomed to failure.

A second generalization is that environmental heterogeneity provides opportunities for populations to survive different extremes by shifting between different types of vegetation, soils, aspects or elevations (Thomas *et al.* 2001; Davies *et al.* 2006). Species diversity and endemism are also increased in regions with high topographic and habitat diversity (e.g. Simberloff 1976a), especially where there are steep elevation and climatic gradients (Ohlemüller *et al.* 2008). Our second message is that focussing efforts on regions with high existing environmental heterogeneity is likely to be a robust strategy. In a sense, we are identifying the importance of a different kind of connectivity – that between cooler and warmer (and drier and moister), habitats rather than between currently similar habitats. Further research is needed to quantify the benefit of habitat diversity, especially when there might be a trade-off between this and the aggregation of existing habitat for many species.

Thirdly, the majority of small-range terrestrial species are clustered into a small percentage of the land surface (centres of endemism/areas of high irreplaceability, cf. Wilson, Carwardine & Possingham 2009), many of which are mountain ranges. A high percentage of the species threatened with extinction from climate change are found in such locations: they are expected to show range retractions within the regions where they currently occur, and are unlikely to achieve long distance colonization of other parts of the world (Midgley *et al.* 2002; Williams, Bolitho, & Fox 2003; Thomas *et al.* 2004; Malcolm *et al.* 2006; Ohlemüller *et al.* 2008). So, our third message is that concentration of conservation effort in centres of endemism remains a valid strategy.

Fourthly, almost all threatened species are negatively impacted by multiple factors. In some instances, mitigating known threats other than climate change may be sufficient to permit a population to persist, even if the local climate has deteriorated. When this strategy cannot ensure persistence in its own right, mitigating known threats should be regarded as an essential first step in making populations robust to climate change. We recommend dealing with known (stoppable) threats for which there are known solutions before addressing uncertain and/or unstoppable threats with less certain or less feasible solutions (Pressey *et al.* 2007; Wilson *et al.* 2007).

These four principles, increasing protected area, maintaining and in some cases increasing environmental heterogeneity, concentrating efforts in centres of endemism, and reducing other pressures are likely to be beneficial and robust, with or without climate change. However, these are rules of thumb, and there is great potential for improved planning at regional scales with improved adaptive decision-making methods. Importantly, decision-making tools need to weight strategies according to their relative costs, expected benefits and the uncertainty in achieving that benefit (Burgman, Lindenmayer & Elith 2005; McDonald-Madden, Baxter & Possingham 2008). Ecological research needs to contribute by quantifying benefits (including the benefits of connectivity and the benefits of habitat heterogeneity) in terms of a common currency, e.g. long-term species persistence, and by quantifying

**Table 1.** Suggested re-assessment of basic ideas in conservation planning, assuming climate change

Ideas to keep	Ideas to modify and develop	Ideas that hold us back
More total area is beneficial; including expanding present conservation areas	The time frame for conservation planning (the trade-off between current and future benefit; and incorporation of environmental change in population viability assessment)	Attempting to maintain existing or past community composition
Biodiversity hotspots/centres of endemism should be prioritized	The role of connectivity, including trade-offs between connecting landscapes and other conservation actions	Using permanently fixed conservation targets (e.g. 10% terrestrial area target)
Environmental/habitat heterogeneity facilitates diversity and persistence		
Human activities that diminish diversity should be minimized or reversed		

uncertainty. Research is required in the development of decision frameworks (Hoegh-Guldberg *et al.* 2008) to integrate and visualize the costs and benefits, and to ensure that methods are easy to adapt and update as new information becomes available.

## Conclusion

In summary, we think that the political and ecological reality of climate change should prompt us to reassess which ideas to keep, which to modify and which to abandon (Table 1). Connectivity usefully reminds people that excessive isolation is a threat to populations, but, as increased attention is paid to the spatial arrangement of habitats and dispersal, more fundamental issues may be overlooked (Fig. 1; Table 1). Whilst climate change adds extra challenges, potential damage can still be alleviated by removing other sources of threat. Land conversion and land-use change leading to habitat loss is still the most cited threat to currently endangered species, and the most straightforward way to tackle this is to maintain and restore larger areas of natural habitat. Species will not be able to survive where they are or shift their distributions to new climatically suitable areas unless there are sufficient habitats for them, and it should be remembered that increasing habitat area is an effective way of increasing 'connectivity'. Furthermore, conserving habitats will be beneficial even if the particular species found in an area are gradually replaced by others as the climate changes. The conservation of high quality existing habitats should therefore remain the primary focus of conservation efforts to maintain biodiversity.

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## References

- Andrewartha, H.G. & Birch, L.C. (1954) *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago, IL.
- Araújo, M.B., Cabeza, M., Thuiller, W., Hannah, L. & Williams, P.H. (2004) Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology*, **10**, 1618–1626.

- Australian Government (2004) *The National Biodiversity and Climate Change Action Plan 2004–2007*. Australian Government, Department of the Environment and Heritage, Canberra, ACT.
- Ben-Haim, Y. (2001) *Information-Gap Decision Theory: Decisions Under Severe Uncertainty*, 1st edn. Academic Press, San Diego.
- Burgman, M.A., Lindenmayer, D.B. & Elith, J. (2005) Managing landscapes for conservation under uncertainty. *Ecology*, **86**, 2007–2017.
- Connor, E.F. & McCoy, E.D. (1979) Statistics and biology of the species–area relationship. *American Naturalist*, **113**, 791–833.
- Crooks, K.R. & Sanjayan, M. (2006) *Connectivity Conservation*. Cambridge University Press, Cambridge.
- Davies, Z.G., Wilson, R.J., Coles, S. & Thomas, C.D. (2006) Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology*, **75**, 247–256.
- Elith, J., Burgman, M.A. & Regan, H.M. (2002) Mapping epistemic uncertainties and vague concepts in predictions of species distribution. *Ecological Modelling*, **157**, 313–329.
- Fagan, W.F. & Calabrese, J.M. (2006) Quantifying connectivity: balancing metric performance with data requirements. *Connectivity Conservation* (eds K.R. Crooks & M. Sanjayan), pp. 297–317. Cambridge University Press, Cambridge.
- Falcy, M.R. & Estades, C.F. (2007) Effectiveness of corridors relative to enlargement of habitat patches. *Conservation Biology*, **21**, 1341–1346.
- Goodwin, B.J. (2003) Is landscape connectivity a dependent or independent variable? *Landscape Ecology*, **18**, 687–699.
- Guilhaumon, F., Gimenez, O., Gaston, K.J. & Mouillot, D. (2008) Taxonomic and regional uncertainty in species–area relationships and the identification of richness hotspots. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 15458–15463.
- Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41–49.
- Hanski, I. & Ovaskainen, O. (2000) The metapopulation capacity of a fragmented landscape. *Nature*, **404**, 755–758.
- Heller, N.E. & Zavaleta, E.S. (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation*, **142**, 14.
- Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.
- Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D.B., Parmesan, C., Possingham, H.P. & Thomas, C.D. (2008) Assisted colonization and rapid climate change. *Science*, **321**, 345–346.
- IPCC (2007) *Climate Change 2007 – Impacts, Adaptation and Vulnerability: Contribution of Working Group II to the Fourth Assessment Report of the IPCC*. Cambridge University Press, Cambridge.
- IUCN (2004) *The Durban Accord – Vth IUCN World Parks Congress*. IUCN, Gland.
- IUCN WCPA (2006) *The Papallacta Declaration, a declaration Relating to Connectivity Conservation Developed at the IUCN WCPA (Mountains Biome)*, Workshop at Papallacta, November 14–17 2006. IUCN WCPA, Papallacta. <http://protectmountains.com/connectivityconservation/>.
- Kettunen, M., Terry, A., Tucker, G. & Jones, A. (2007) *Guidance on the Maintenance of Landscape Features of Major Importance for Wild Flora and Fauna – Guidance on the Implementation of Article 3 of the Birds Directive (79/409/EEC) and Article 10 of the Habitats Directive (92/43/EEC)*. Institute for European Environmental Policy (IEEP), Brussels.
- Kindlmann, P. & Burel, F. (2008) Connectivity measures: a review. *Landscape Ecology*, **23**, 879–890.

- MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- Malcolm, J.R., Liu, C.R., Neilson, R.P., Hansen, L. & Hannah, L. (2006) Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology*, **20**, 538–548.
- Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature*, **405**, 243–253.
- McCarthy, M.A., Thompson, C.J. & Possingham, H.P. (2005) Theory for designing nature reserves for single species. *American Naturalist*, **165**, 250–257.
- McDonald-Madden, E., Baxter, P.W.J. & Possingham, H. (2008) Making robust decisions for conservation with restricted money and knowledge. *Journal of Applied Ecology*, **45**, 1630–1638.
- Menéndez, R., Megias, A.G., Hill, J.K., Braschler, B., Willis, S.G., Collingham, Y., Fox, R., Roy, D.B. & Thomas, C.D. (2006) Species richness changes lag behind climate change. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 1465–1470.
- Midgley, G.F., Hannah, L., Millar, D., Rutherford, M.C. & Powrie, L.W. (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biogeography*, **11**, 445–451.
- Moilanen, A. & Hanski, I. (2001) On the use of connectivity measures in spatial ecology. *Oikos*, **95**, 147–151.
- Moilanen, A. & Nieminen, M. (2002) Simple connectivity measures in spatial ecology. *Ecology*, **83**, 1131–1145.
- Moilanen, A. & Wintle, B.A. (2006) Uncertainty analysis favours selection of spatially aggregated reserve structures. *Biological Conservation*, **129**, 427–434.
- Moilanen, A., Franco, A.M.A., Early, R.I., Fox, R., Wintle, B. & Thomas, C.D. (2005) Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. *Proceedings of the Royal Society B-Biological Sciences*, **272**, 1885–1891.
- Ohlemüller, R., Anderson, B.J., Araújo, M.B., Butchart, S.H.M., Kudrna, O., Ridgely, R.S. & Thomas, C.D. (2008) The coincidence of climatic and species rarity: high risk to small-range species from climate change. *Biology Letters*, **4**, 568–572.
- Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, **37**, 637–669.
- Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M. & Wilson, K.A. (2007) Conservation planning in a changing world. *Trends in Ecology & Evolution*, **22**, 583–592.
- Regan, H.M., Colyvan, M. & Burgman, M.A. (2001) A taxonomy and treatment of uncertainty for ecology and conservation biology. *Ecological Applications*, **12**, 618–628.
- Simberloff, D. (1976a) Experimental zoogeography of islands – effects of island size. *Ecology*, **57**, 629–648.
- Simberloff, D. (1976b) Species turnover and equilibrium island biogeography. *Science*, **194**, 572–578.
- Thomas, C.D., Thomas, J.A. & Warren, M.S. (1992) Distributions of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia*, **92**, 563–567.
- Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M. & Conrad, L. (2001) Ecological and evolutionary processes at expanding range margins. *Nature*, **411**, 577–581.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Tischendorf, L. & Fahrig, L. (2000) On the usage and measurement of landscape connectivity. *Oikos*, **90**, 7–19.
- Walker, S., Brower, A.L., Stephens, R.T.T. & Lee, W.G. (2009) Why bartering biodiversity fails. *Conservation Letters*. Preprint doi:10.1111/j.1755-263X.2009.00061.x.
- Williams, J.W., Shuman, B.N. & Webb, T. (2001) Dissimilarity analyses of late-Quaternary vegetation and climate in eastern North America. *Ecology*, **82**, 3346–3362.
- Williams, S.E., Bolitho, E.E. & Fox, S. (2003) Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 1887–1892.
- Wilson, K.A., Underwood, E.C., Morrison, S.A., Klausmeyer, K.R., Murdoch, W.W., Reyers, B., Wardell-Johnson, G., Marquet, P.A., Rundel, P.W., McBride, M.F., Pressey, R.L., Bode, M., Hoekstra, J.M., Andelman, S., Looker, M., Rondinini, C., Kareiva, P., Shaw, M.R. & Possingham, H.P. (2007) Conserving biodiversity efficiently: What to do, where, and when. *PLoS Biology*, **5**, 1850–1861.
- Wilson, K.A., Carwardine, J. & Possingham, H.P. (2009) Setting conservation priorities. *Annals of the New York Academy of Sciences*, **1162**, 237–264.
- With, K.A. & King, A.W. (1999) Extinction thresholds for species in fractal landscapes. *Conservation Biology*, **13**, 314–326.

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