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Evaluating Trade-Offs between Target Persistence Levels and Numbers of Species Conserved

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Abstract

A focus of conservation planning is to maximize the probability of species persistence, but this may reduce the number of species that can be secured with a limited budget. Using a data set of 700 New Zealand species, we examine the trade-off between providing a high level of persistence for some species and a lower level of persistence for more species. We find that the target persistence level that delivers the highest conservation outcome is a function of the annual budget, such that lower budgets have lower optimal targets. However, it is never optimal to manage species below a 75% probability of persistence. We introduce a prioritization approach that maximizes biodiversity gains based on a flexible persistence target, and demonstrate how strategies with fixed high-persistence targets can be inefficient. We also illustrate the risks in spreading conservation resources too thinly by undertaking low levels of management on more species.

Introduction

Target-setting is crucial for translating the complexities of conserving natural resources into clear "rules of thumb" for conservation practitioners and forms the basis against which management actions are prescribed and assessed (reviewed in Tear *et al.* 2005; Carwardine, Wilson *et al.* 2008b). Examples of common management targets include species' "minimum viable population" size (Traill *et al.* 2007), and the optimum percentage (and location) of land that should be protected (i.e., Aichi target 11; Soulé & Sanjayan 1998; Convention on Biological Diversity 2011; Venter *et al.* 2014). Despite the prevalence of papers debating the efficacy of "one-size-fits-all" targets (e.g., Flather *et al.* 2011; Santini *et al.* 2014), only one study, to our knowledge, has explored whether lowering the threshold of species security allows more species to be saved (Chadés *et al.* 2015). No studies have explicitly investigated the optimal persistence target for maximizing conservation outcomes given a set budget, nor have they explored the trade-offs faced by managers when deliberately lowering target persistence levels in order to spread conservation effort across more species in situations where funding is limited.

Species persistence targets are central to multispecies conservation plans, through which, due to a lack of sufficient funding, certain species are prioritized for management over others based on a variety of formal frameworks. These range from ranking species according to only one criterion, such as level of endangerment (Master 1991) or evolutionary distinctiveness (Faith 1992; Weitzman 1992), to frameworks which explicitly trade-off species' costs, benefits, taxonomic uniqueness, and likelihood of success of particular management actions to achieve a balanced, cost-efficient allocation of resources (Joseph *et al.* 2009). A key assumption in conservation planning is that management is carried out to guarantee the highest probability of species' persistence (e.g., Williams & Araújo 2000; Nicholson & Possingham 2006), where persistence is mainly portrayed in a "binary" manner (see Table S1). However, high targets may result in a greater management cost per species, therefore reducing the number of species that can be secured under limited budgets and potentially decreasing the resilience of conservation investments to environmental stochasticity (e.g., Ando & Mallory 2012).

The New Zealand (NZ) Department of Conservation (DOC) applied a "Project Prioritization Protocol" (PPP) framework (Joseph *et al.* 2009) to optimize resource allocation across high-ranking threatened species projects in 2011 (detailed in Department of Conservation 2013) that could be adapted to evaluate the effect of lowering persistence targets on multispecies conservation planning outcomes. In this study, we use a data set of 700 threatened species projects gathered during DOC's use of the PPP framework to test how changes in targets levels ranging from 95% down to 5% probability of persistence affect the overall expected number of species persisting after 50 years, including all managed and unmanaged species within the system. We perform this analysis under a series of budget constraints, and using two functional relationships relating the number of sites managed to a species' probability of persistence.

Materials and Methods

Data set filtering

Our data set is based on a collection of 700 species "projects," designed to ensure long-term persistence of "Threatened" and "At Risk" NZ species listed by Hitchmough *et al.* (2005). Each species "project" is a set of actions across a number of different sites, delivering 95% probability of persistence over 50 years for each species as determined through expert elicitation. We filtered this data set by excluding all monitoring actions as these actions do not contribute directly to species persistence, and removed 18 species' projects with an expected probability of persistence following management (b_1) of less than 95%. The final data set of 682 species spanned 13 orders (including birds, mammals, fish, amphibians, reptiles, freshwater and terrestrial vertebrates, and vascular and nonvascular plants), with 6198 management actions at 1388 sites, over a period of 50 years. Management actions included weed control, animal pest control, species and habitat management, biosecurity management, fire and water management, managing human-wildlife interactions, and conservation advocacy activities. All data manipulation and analyses were carried out in R v.3.0.1 (R Development Core Team 2013).

As the NZ data set only reports the actions required to maintain a 95% probability of persistence, we processed it to target levels from 95% down to 5% probability of persistence in decrements of 5%. In order to determine how many fewer actions might be required under each lower target persistence, we fit linear and asymptotic functions (which we term "site-persistence relationships") between each species' likelihood of persistence without any management (b_0) and the number of sites reported as required for 95% probability of persistence (n_{95}; equations detailed in Supporting Information; Table S1). We selected these functional forms out of four proposed representations (Carwardine, Klein *et al.* 2008; van Teefelen & Moilanen 2008; Wilson *et al.* 2009). An alternative logistic/s-shaped relationship (where the first several sites contribute little to persistence, up to a threshold point past which persistence rapidly asymptotes; e.g., Carwardine, Wilson *et al.* 2008b) was also modelled, but these results have not been presented on account of the lack of precise data supporting this functional relationship.

Due to a lack of information on the relative importance of particular sites and management actions for species' persistence, we assumed all sites and actions contributed equally to species' persistence. We then selected which actions to remove from the data set using the following steps for each species under each functional relationship and target persistence level (summarized in Figure 1b). We first increased all probabilities of management success (defined as the joint probability of "implementation success" and "technical success") of 95% (the maximum value used by experts to represent "successful" actions) to 100% to avoid penalizing sites with many highly successful actions. To validate the effect of this treatment of probability of success on our results, we re-ran the analyses in two additional manners: (1) leaving actions with management success of 95% at 95% and (2) increasing the probability of success of all actions by 5%. We then ranked sites in descending order of their cost-effectiveness, which we defined by dividing the product of the success of all actions at a particular site by their total cost (Equation S2 in Supporting Information). In cases where sites had the same score, we randomly allocated them different ranks. Finally, we removed all actions that were applied across those sites ranked higher (i.e., with lower cost-effectiveness) than the number of sites predicted as necessary under a given target persistence level based on the selected site-persistence function.

Resource allocation algorithm

We prioritized species for conservation using a PPP approach (Joseph *et al.* 2009; Figure 1a). We used annual budgets of 0.5, 1, 5, and 10 million NZD, and at all intervals of 1 million between 30 and 40 million NZD. We

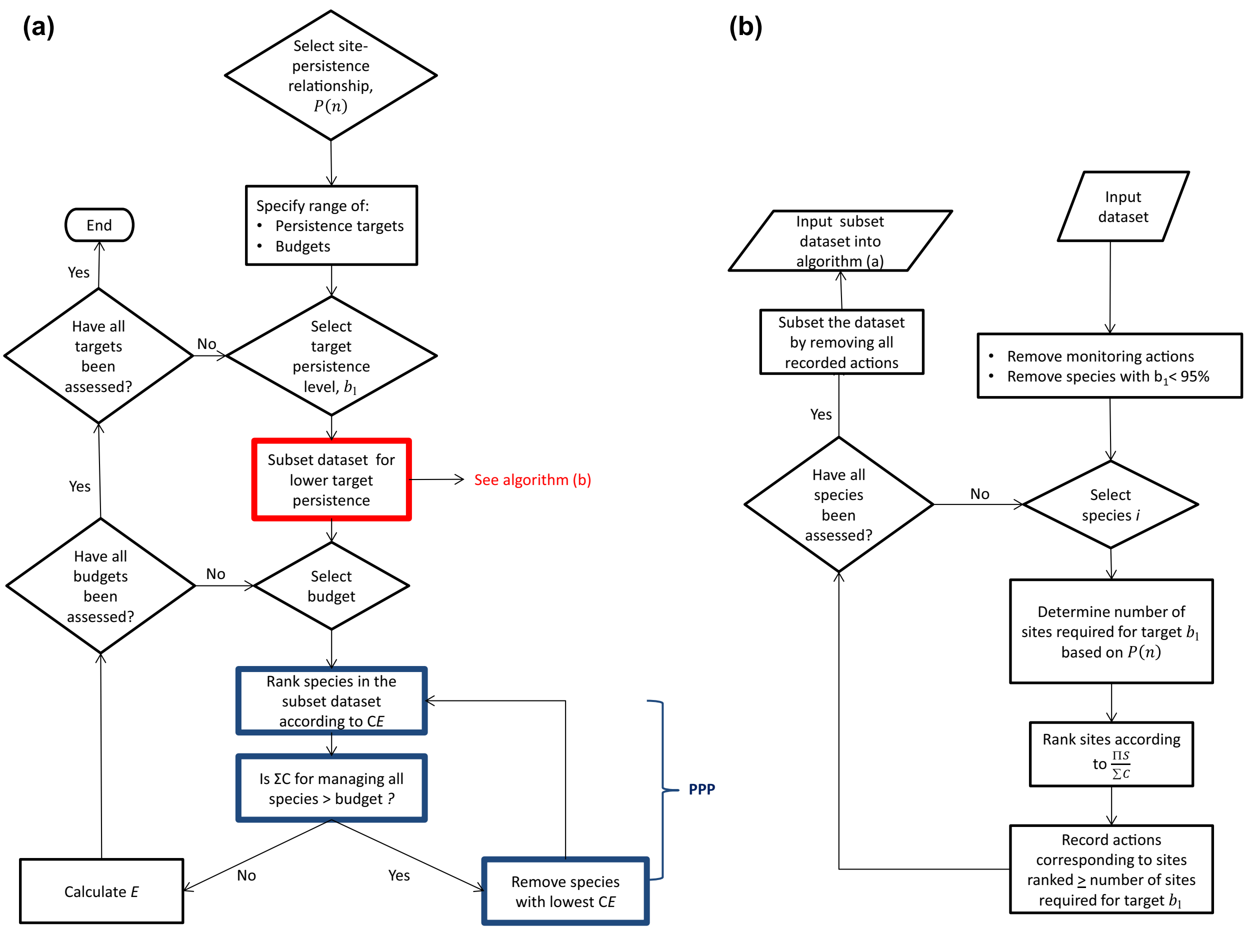

Figure 1 (a) Resource allocation algorithm used to calculate conservation outcomes under a range of target persistence levels and budgets and (b) steps used to subset data set according to a lower persistence target. The blue sections correspond to Joseph *et al.*'s (2009) PPP framework. *P*(*n*) refers to the asymptotic or linear site-persistence relationship (described in the main text), b_1 refers to the probability of persistence following management action, *CE* refers to cost-efficiency, calculated using Equation (1), *S* is the probability of success of actions required at a particular site, and *C* is the cost of all required actions at a particular site. *E* refers to the overall expected number of species persisting after 50 years, detailed in Equation (2).

selected this range to take into account annual NZ DOC threatened species budgets, which are estimated between 17-32 million NZD. PPP ranks species according to their cost-effectiveness (CE_i) using the following equation:

$$CE_i = \frac{W_i \times B_i \times S_i}{C_i}. \qquad (1)$$

where W_i is a weighting of phylogenetic distinctiveness of species i, B_i indicates the benefit of management to species i; S_i is the probability of project implementation and technical success; and C_i is the cost of all required actions. The process of prioritization starts by funding all species projects, then iteratively excludes projects with the lowest cost-effectiveness until the target budget is met. Further details regarding B_i, S_i, W_i, and C_i are described in Joseph *et al.* (2009), Bennett *et al.* (2014), Tulloch *et al.* (2015), and in this manuscript's Supporting Information. The resource allocation algorithm is freely available from M.M.I.D.F.

Calculating resource allocation outcomes

Because most species have some probability of persistence without any management, we used the overall expected number of species persisting after 50 years including all managed and unmanaged species (E) to describe the output of the resource allocation. We calculated E in the following way:

$$E = \sum_{i \in T} b_{1,i} + \sum_{i \in T'} b_{0,i}. \qquad (2)$$

where T is the set of managed species, $b_{1,i}$ is the probability of persistence following management of species i

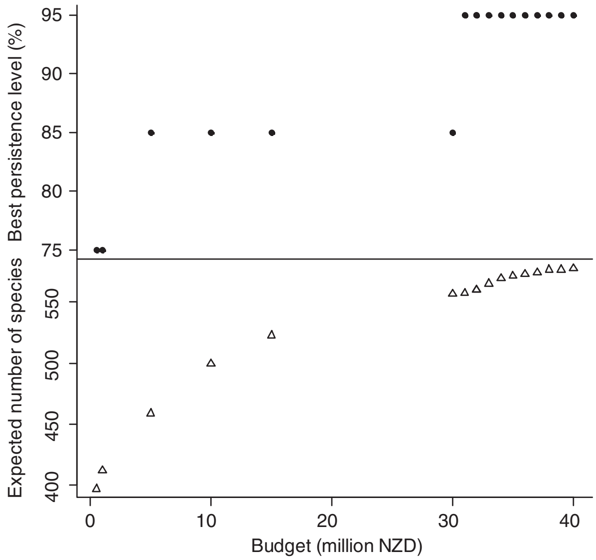

Figure 2 The upper points indicate the target persistence level (in terms of % probability of persistence) which results in the highest overall expected number of species persisting (*E*) under a range of budgets. The lower triangles display the highest *E* under each budget (and corresponding best persistence target).

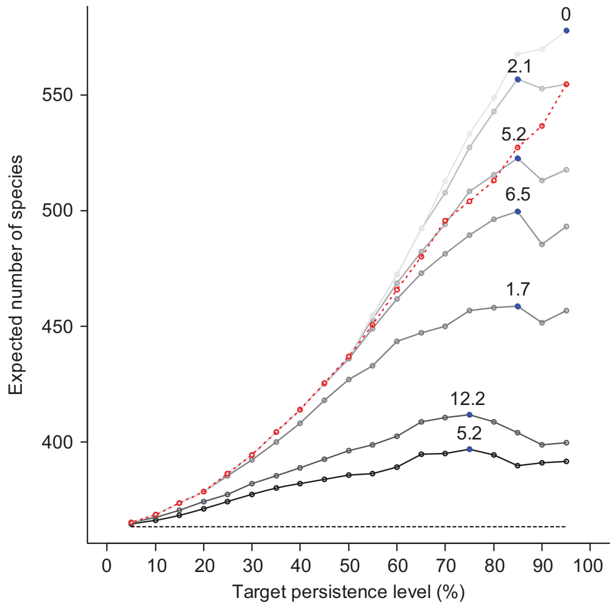

Figure 3 Expected number of NZ species (*E*) given different target persistence levels, under 0.5, 1, 5, 10, 15, 30, and 40 million NZD per year (from darkest to lightest line). The blue points indicate the level of persistence which results in the highest *E*; the numbers above the blue points indicate how many expected species higher this outcome is than if the prioritization were carried out with a target of 95% persistence. The lower dotted line represents *E* without any management. The red dashed line represents changes in *E* at 30 million NZD, based on a linear site-persistence relationship.

(based on the target persistence level), T' is the set of unmanaged species, and $b_{0,i}$ is the probability of persistence of unmanaged species *i*. It is important to note that the algorithm will only rank species for management if their b_0 is lower than the target persistence level. This will result in an initial increase in conservation outcomes with increasing target persistence levels as more species qualify for cost-effectiveness ranking (detailed in Figure S1). For each scenario, we recorded the target level which resulted in highest *E*, and in cases where two persistence targets resulted in the same near-optimal *E*, we selected the higher target.

Results

When we assumed an asymptotic site-persistence relationship, we identified a positive relationship between best persistence level and available budget (Figure 2). We found that it is only near optimal to manage NZ species at 95% probability of persistence when the annual budget is greater than 30 million NZD. We define our results as near optimal as we analyzed persistence levels at intervals of 5%, resulting in approximate optimal persistence values. When the budget is lowered, we identify consecutively lower target persistence levels as delivering a greater overall expected number of species persisting (*E*), down to a target of 75% probability of persistence. It is never optimal to manage NZ species below a 75% probability of persistence under the wide range of budgets analyzed. When we analyzed changes in *E* under increasing target persistence levels across different budgets, we identified a left-skewed relationship that is most visible under the lower budget scenarios (Figure 3). As the budget is increased, the skewed relationship weakens as more funding is available to work on a greater number of species at higher persistence levels. Under a linear persistence relationship (red dashed lined in Figure 3), *E* increases monotonically as the target persistence level is increased. We found that it would always be optimal to manage for a target of 95% probability of persistence under any budget when using this persistence relationship (results not presented).

When we re-ran our prioritizations by: (1) leaving actions with management success of 95% at 95% and (2) increasing the probability of success of all actions by 5%, we identified a similar positive relationship between best persistence levels and the available budget, except under a budget of 5 million NZD, where the best persistence level was 95% (10% higher than under a budget of 10 million NZD). Results for option 1 are presented in Figures S2 and S3. Closer analysis showed that *E* was only 2.6 species greater under a target of 95% probability of persistence compared to the second best target of 80%, suggesting that this was due to a minor change in the species being prioritized following modifications of their overall probability of success.

Discussion

Our findings suggest that the overall expected number of species persisting (E) is not always maximized under a management objective that focuses on a very high (i.e., 95%) probability of persistence (Figure 2). Rather, the target persistence level that delivers the highest E is dependent on the relative budget available for conservation. This pattern arises when improvement in species' persistence is represented by a conservative asymptotic functional form, where the first few sites contribute the most to species' persistence, after which each successive site has a diminishing return on investment. Our analyses of NZ threatened species show that it is only optimal to manage those final sites that result in 95% probability of persistence when the budget is over 30 million NZD. For budgets of 30 million NZD or less, we identify a trade-off between the numbers of species that can be managed and the maintenance of high-persistence targets. Our study thus confirms NZ's management objective of maximizing the number of unique species with 95% probability of persistence is the best choice of target persistence level for budgets greater than 30 million NZD, and provides clear guidelines concerning which target persistence to apply if the annual budget were to be reduced. We also show that it would never be optimal to manage projects to levels of less than 75% probability of persistence.

A closer analysis of the change in E with increasing persistence targets identified a left-skewed relationship that is most visible under the lower budget scenarios (Figure 3). This relationship occurs partly because at very low target persistence levels, few species will have a probability of persistence without management that is low enough to qualify for ranking (see exact numbers in Figure S1), and partly because the numbers of species that can be managed at high persistence levels are constrained by the budget. As the budget increases, the left-skewed relationship becomes less prominent as greater numbers of species can be managed at higher persistence levels.

Here, we provide the first evidence of how the optimal conservation target for a given system may depend on the available budget. Our results have broad reaching implications for global conservation interventions, most notably in tropical, developing countries with high concentrations of threatened species and limited financial resources. Our analyses of a comprehensive NZ data set suggest that managers should be very wary of undertaking small numbers of actions across a higher number of sites in order to maximize the number of species being managed. Unless the target probability of persistence from these actions is high (i.e., greater than 75%, in our example), managers risk wasting resources through spreading their conservation efforts too thinly, causing unnecessarily high probabilities of species extinction as a result. To extend this framework to other jurisdictions, we recommend managers and analysts develop standard conservation plans (e.g., based on expert-elicited data) containing explicit costed actions to conserve species.

The manner in which species' probability of persistence was represented in this study will have an impact on how near-optimal persistence targets are defined. First, for lack of more precise information, we assumed that there was no ecological interactions between species (such as competition, symbiosis, and predation; e.g., Berg *et al.* 2012), and we did not account for the effect of nontargeted management actions on species' persistence (e.g., Chauvenet *et al.* 2012). Estimating interactions and codependencies for all 700 NZ threatened species would have been challenging, and we acknowledge that the data set is likely to represent an oversimplification of the system. The PPP algorithm does allow for sharing of common costs where sites and actions between species overlap, however, we did not apply this option due to uncertainty regarding how the removal of actions in low *CE* ranking sites for one species might affect the persistence of overlapping species with different site rankings.

Second, we carried out most analyses using an asymptotic relationship, also used in Tear *et al.* (2005) and McCarthy *et al.* (2005). We acknowledge that this is a simplification of metapopulation theory, which assumes that a threshold number of geographically distinct local populations are required for the rate of local colonization to exceed the rate of extinction (Levins 1969; Lande 1987; Ovaskainen & Hanski 2003). Based on this hypothesis, persistence should be represented as increasing in a sigmoidal manner with the number of managed sites, rising exponentially to a threshold habitat area (Hanski 1999). Third, we applied the same functional persistence form across all species, which we altered solely according to the number of sites required to reach 95% probability of persistence. Based on allometric scaling relationships, it could be expected that larger, longer-lived species require more sites for long-term persistence, whereas smaller, shorter-lived species reach high probabilities of persistence after fewer sites (Peters 1983; Hendricks 2007). Species that live under more variable habitat conditions (e.g., extreme weather or high threat) should also be expected to require more sites to buffer against stochastic events. Differences in site connectivity and species' dispersal abilities may also influence how a species' probability of persistence rises with increasing sites managed, though these conditions were not relevant within the NZ system as each site was managed as an independent population. In order to refine our understanding of individual species' site-persistence relationships, we recommend carrying out additional expert elicitation surveys with a focus on describing changes in species persistence in the presence of interacting species, in response to potential nontarget actions, and under increasing levels of management intensity.

Finally, we evaluated trade-offs between target persistence levels and numbers of species conserved using an index-based cost-effectiveness ranking approach; however, it is important to acknowledge that other conservation decision-making processes are available, such as spatially explicit prioritization algorithms (i.e., Marxan and Zonation; Moilanen 2007; Ball *et al.* 2009). We focused on this approach as it is the first conservation decision-making process to generate data at a national scale in NZ and at the state level in Australia (New South Wales Government 2013), which makes our target-setting study especially policy-relevant.

Our analyses of NZ species persistence plans under lowered target persistence levels and differing budgets introduces several new concepts to the field of multispecies conservation planning. We demonstrate the importance of careful target-setting of species' persistence for delivering the greatest conservation gains and advise conservation planners to ascertain whether setting an overprecautionary goal of ensuring 95% probability of persistence is optimal given their budget. The idea that lower management targets may result in greater gains, but too great a reduction would be suboptimal, is worthy of further testing in other management environments. Although managers may be interested in diversifying investments to better insure their assets against environmental stochasticity (e.g., Ando & Mallory 2012; Hoekstra 2012), and there may be pressure to work on many species at low levels so that many more species can be "counted" as managed, we show that this practice could lead to perverse outcomes, with fewer species saved overall. Our study demonstrates the existence of a potential threshold for target persistence levels, below which the practice of undertaking low levels of management on more species at more sites becomes very inefficient. We encourage further exploration of the advantages of setting lower thresholds in multispecies conservation planning through quantification of the trade-off between long-term target persistence levels and conservation outcomes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Table S1. Equations used to represent the relationship between species' probability of persistence (P) with respect to the number of sites that are currently managed.

Figure S1. Cumulative number of species which qualify for efficiency ranking by the PPP as the target persistence level is increased.

Figure S2. The upper dots indicate the target persistence level (in terms of % probability of persistence) which results in the highest expected number of species persisting (E) under a range of budgets, based on a PPP where actions with 95% probability of success are not increased to 100% success.

Figure S3. Expected number of NZ species (E) given different target persistence levels based on a PPP where actions with 95% probability of success are not increased to 100% success, under 0.5, 1, 5, 10, 15, 30, and 40 NZD million per year (from darkest to lightest line; all runs were carried out using an asymptotic site-persistence relationship).

References

Ando, A.W. & Mallory, M.L. (2012) Optimal portfolio design to reduce climate-related conservation uncertainty in the Prairie Pothole Region. *P. Natl. Acad. Sci. USA*, **109**, 6484-6489.

Ball, I.R., Possingham, H.P. & Watts, M. (2009) Marxan and relatives: software for spatial conservation prioritisation. Pages 185-195 in A. Moilanen, K.A. Wilson, H.P. Possingham, editors. *Spatial conservation prioritisation: quantitative methods and computational tools*. Oxford University Press, Oxford, UK.

Bennett, J.R., Elliott, G., Mellish, B. *et al*. (2014) Balancing phylogenetic diversity and species numbers in conservation prioritization. *Biol. Conserv*., **174**, 47-54.

Berg, M.P., Kiers, E.T., Driessen, G. *et al*. (2012) Adapt or disperse: understanding species persistence in a changing world. *Glob. Change Biol*., **16**, 587-598.

Carwardine, J., Klein, C.F., Wilson, K.A., Pressey, R.L. & Possingham, H.P. (2008a) Hitting the target and missing the point: target-based conservation planning in context. *Conserv. Lett*., **2**, 3-10.

Carwardine, J., Wilson, K.A., Ceballos, G. *et al*. (2008b) Cost-effective priorities for global mammal conservation. *P. Roy. Soc. Lond. B*., **105**, 11446-11450.

Chadés, I., Nicol, S., vanLeeuwen, S. *et al*. (2015) Benefits of integrating complementarity into priority threat management. *Conserv. Biol*. **29**, 525-536.

Chauvenet, A.L., Durant, S.M., Hilborn, R. & Pettorelli, N. (2012) Unintended consequences of conservation actions: managing disease in complex ecosystems. *PLoS One* **6**, e28671.

Convention on Biological Diversity. (2011) Conference of the parties decision X/2: strategic plan for biodiversity 2011-2020. Nagoya, Japan.

Department of Conservation. (2013) *Annual report for the year ended 30 June 2012. New Zealand Government*, Wellington, New Zealand.

Faith, D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biol. Conserv*., **61**, 1-10.

Flather, C.H., Hayward, G.D., Beissinger, S.R. & Stephens, P.A. (2011) Minimum viable populations: is there a 'magic number' for conservation practitioners?. *Trends Ecol. Evol*. **26**, 307-316.

Hanski, I. (1999) *Metapopulation ecology*. Oxford University Press, Oxford.

Hendricks, A.J. (2007) The power of size: a meta-analysis reveals consistency of allometric regressions. *Ecol. Model*. **205**, 196-208.

Hoekstra, J.M. (2012) Improving biodiversity conservation through modern portfolio theory. *P. Natl. Acad. Sci. USA*,**109**, 6360-6361.

Joseph, L.N., Maloney, R.F. & Possingham, H.P. (2009) Optimal allocation of resources among threatened species: a project prioritization protocol. *Conserv. Biol*., **23**, 328-338.

Lande, R. (1987) Extinction thresholds in demographic models of territorial populations. *Am. Nat*., **130**, 624-635.

Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am*., **15**, 237-240.

Master, L.L. (1991) Assessing threats and setting priorities for conservation. *Conserv. Biol*., **5**, 559-563.

McCarthy, M.A., Thompson, C.G. & Possingham, H.P. (2005) Theory for desigining nature reserves for single species. *Am. Nat*., **165**, 250-257.

Moilanen, A. (2007) Landscape zonation, benefit functions and target-based planning. Unifying reserve selection strategies. *Biol. Conserv*., **134**, 571-579.

New South Wales Government. (2013) *Saving our species*. Office of Environment and Heritage, Sydney, New South Wales.

Nicholson, E. & Possingham, H.P. (2006) Objectives for multiple-species conservation planning. *Conserv. Biol*., **20**, 871-881.

Ovaskainen, O. & Hanski, I. (2003) Extinction threshold in metapopulation models. *Annales Zoologici Fennici* **40**, 81-97.

Peters, R.H. (1983) *The ecological implications of body size*. Cambridge University Press, Cambridge.

R Development Core Team (2013) *R: a language and environment for statistical computing. R Foundation for Statistical Computing*, Vienna, Austria.

Santini, L., Di Marco, M., Boitani, L., Maiorano, L. & Rondinini, C. (2014) Incorporating spatial population structure in gap analysis reveals inequitable assessments of species protection. *Diversity Distrib*., **20**, 698-707.

Soulé, M.E. & Sanjayan, M.A. (1998) Conservation targets: do they help? *Science*, **279**, 2060-2061.

Tear, T.H., Kareiva, P., Angermeier, P.L. *et al*. (2005) How much is enough? The recurrent problem of setting measurable objectives in conservation. *BioScience*, **55**, 835-849.

Traill, L.W., Bradshaw, C.J.A. & Brook, B.W. (2007) Minimum viable population size: a meta-analysis of 30 years of published estimates. *Biol. Conserv*., **139**, 159-166.

Tulloch, A.I.T., Maloney, R.F., Joseph, L.N. *et al*. (2015) Effect of risk aversion on prioritizing conservation projects. *Conserv. Biol*., **29**, 513-524.

van Teefelen, A.J.A. & Moilanen, A. (2008) Where and how to manage: optimal selection of conservation actions for multiple species. *Biodiversity Informatics* **5**, 1-13.

Venter, M., Fuller, R.A., Segan, D.B. *et al*. (2014) Targeting global protected area expansion for imperiled biodiversity. *PloS Biology* **12**, e1001891.

Weitzman, M. (1992) On diversity. *Q. J. Econ*., **107**, 363-405.

Williams, P.H. & Araújo, M.B. (2000) Using probability of persistence to identify important areas for biodiversity conservation. *P.Roy.Soc.Lond.B*., **267**, 1959-1966.

Wilson, K.A., Carwardine, J. & Possingham, H.P. (2009) Setting conservation priorities. *Ann. NY Acad. Sci*. **1162**, 237-264.

