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Balancing phylogenetic diversity and species numbers in conservation prioritization, using a case study of threatened species in New Zealand

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ABSTRACT

Funding for managing threatened species is currently insufficient to assist recovery of all species, so management projects must be prioritized. In attempts to maximize phylogenetic diversity conserved, prioritization protocols for threatened species are increasingly weighting species using metrics that incorporate their evolutionary distinctiveness. In a case study using 700 of the most threatened species in New Zealand, we examined trade-offs between emphasis on species' evolutionary distinctiveness weights, and the numbers of species prioritized, as well as costs and probabilities of success for recovery projects. Increasing emphasis on species' evolutionary distinctiveness weights in the prioritization protocol led to greater per-species costs and higher risk of project failure. In a realistic, limited-budget scenario, this resulted in fewer species prioritized, which imposed limits on the total phylogenetic diversity that could be conserved. However, by systematically varying the emphasis on evolutionary distinctiveness weight in the prioritization protocol we were able to minimize trade-offs, and obtain species groups that were near-optimal for both species numbers and phylogenetic diversity conserved. Phylogenetic diversity may not equate perfectly with functional diversity or evolutionary potential, and conservation agencies may be reluctant to sacrifice species numbers. Thus, we recommend prioritizing species groups that achieve an effective balance between maximizing phylogenetic diversity and number of species conserved.

1. Introduction

Global biodiversity loss is accelerating (Butchart et al., 2010), and current funding levels are inadequate to reverse this trend (McCarthy et al., 2012). Funding tends to be allocated unevenly, with taxonomic biases towards charismatic vertebrate species (Martín-López et al., 2009; Laycock et al., 2011). Both scientists and conservation agencies increasingly recognize that systematic prioritization schemes must be developed to efficiently allocate funding to minimize biodiversity loss (e.g. Bottrill et al., 2008; Wilson et al., 2011; IUCN, 2013). A number of frameworks exist for prioritizing threatened species management based on criteria such as threat level (Master, 1991; Carter et al., 2000), socio-political significance (Rodríguez et al., 2004), ecological importance, and potential for recovery (Marsh et al., 2007).

Phylogenetic diversity is considered a key component of biodiversity, reflecting life's evolutionary heritage, its functional diversity and potentially its ability to adapt to future conditions (Vane-Wright et al., 1991; Cadotte and Davies, 2010). Thus, the evolutionary distinctiveness of species has repeatedly been proposed as a key consideration in conservation prioritization, under the assumption that distinct species with few extant relatives are more important to maintaining phylogenetic diversity than species from diverse lineages, which are assumed to have greater genetic redundancy (e.g. May, 1990; Vane-Wright et al., 1991; Crozier, 1997).

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In attempts to shift the emphasis of conservation programmes from maximizing the total number of species conserved to maximizing conserved phylogenetic diversity, a variety of prioritization schemes have been proposed that weight species according to metrics incorporating their evolutionary distinctiveness. Redding and Mooers (2006) proposed a scheme that weights species according to the 'equal splits' distinctiveness metric, which divides evolutionary time of a branch equally among daughter branches, as well as probability of extinction. Isaac et al. (2007) designed a similar scheme, which weights species according to a slightly different measure of evolutionary distinctiveness (see *Methods* below) and International Union for Conservation of Nature (IUCN) threat status. Other methods (e.g. Vane-Wright et al., 1991; Faith, 1992, 2008) consider phylogenetic complementarity of the prioritized suite of taxa, with the goal of choosing a species group that protects as much total phylogenetic diversity as possible. Rosauer et al. (2009) and Cadotte and Davies (2010) proposed methods that explicitly consider both evolutionary distinctiveness and species ranges when prioritizing areas to maximize retained phylogenetic diversity. Cofré and Marquet (1999) designed a conservation priority index that includes an ordinal metric of taxonomic singularity, which assigns higher values to taxa with fewer closely-related species. Their metric also considers endemism and additional aspects such as threat status and geographic distribution. Joseph et al. (2009) devised a method that integrates prioritization of species based on distinctiveness as well as cost, probability of project success and expected change to probability of species' survival.

Given limited budgets, a shift in emphasis towards conserving phylogenetic diversity of a planning area by prioritizing evolutionarily distinct species may result in trade-offs leading to fewer individual species being conserved. If conserving maximum phylogenetic diversity in a planning area is the primary goal, this trade-off may be unimportant. However, the evolutionary distinctiveness of species may not be a perfect reflection of their long-term ecological importance. In particular, phylogenetic clustering of extinction risk in some older lineages (Gaston and Blackburn, 1997; Vamosi and Wilson, 2008) raises the possibility that such lineages may be maladapted to current conditions, and that prioritizing according to evolutionary distinctiveness could sacrifice the rapid evolutionary potential contained in some diverse, recently-radiated clades. Although conserving phylogenetic diversity may be an important consideration in setting conservation priorities, the trade-offs with other factors such as cost and probability of management success must also be explored.

The potential for such trade-offs when conserving phylogenetic diversity versus species richness was noted by Davies and Buckley (2011), who found a disconnect between patterns of species richness and phylogenetic diversity in Neotropical mammals. In addition, Joseph et al. (2009) found in limited tests that a prioritization strategy that weighted species based exclusively on their evolutionary distinctiveness could lead to fewer species being prioritized for management versus other strategies. Such trade-offs have not previously been demonstrated in realistic prioritization scenarios involving an entire suite of threatened species being considered for prioritization.

Here, we use systematic prioritization scenarios from a dataset of 700 of the most threatened species in New Zealand to examine trade-offs when there is increasing emphasis on species' evolutionary distinctiveness. We examine the relationships between emphasis on individual species' evolutionary distinctiveness, and number of species prioritized, cost and probability of project success. We also examine the relationships between the total evolutionary distinctiveness weights of prioritized species (a measure of the phylogenetic diversity conserved) and the number of species conserved, cost and probability of project success. We examine these patterns using three alternative evolutionary distinctiveness weights: an iteratively-updated method that accounts for endemism, an additional iteratively-updated method that incorporates probability of extinction, and a static method that accounts for threat level. Our aim is to derive efficient prioritization solutions that minimize the potential loss of both phylogenetic and species diversity, recognizing the potential importance of conserving both aspects of biodiversity.

2. Methods

2.1. Dataset

We designed prioritization scenarios using potential recovery projects for 700 of the most threatened species in New Zealand, encompassing all species in New Zealand's 'Threatened' and 'At Risk' categories that have declining populations (Hitchmough et al., 2005). Each species had an associated 'project', which included the specific actions that, based on expert opinion, would be necessary to ensure reasonable probability (~95%) of the species' persistence over 50 years, as well the costs, assumed benefits and probability of project success. The New Zealand government has used this dataset to help prioritize budget allocations (NZ Department of Conservation, 2011), using a protocol developed by Joseph et al. (2009). New Zealand represents an excellent test case for prioritization, as it is undergoing an extinction crisis that may forecast future global patterns (Jenkins, 2003), and for which there is currently insufficient funding to protect all threatened species.

2.2. Prioritization protocol

We used the project prioritization protocol (PPP) framework of Joseph et al. (2009), which ranks the efficiencies of threatened species projects based on species' evolutionary distinctiveness weight, project benefits to species, probabilities of project success, and cost:

$$E_i = \frac{W_i \times B_i \times S_i}{C_i}, \tag{1}$$

where E_i is the project efficiency for species i; W_i is the species' evolutionary distinctiveness weight; B_i is the project benefit to the species, defined as the difference between the estimated probabilities that a species will be secure in 50 years with and without the project; S_i is the estimated probability of project success; and C_i is the cost of all actions associated with the species project. Costs of actions that benefit multiple species are shared among the beneficiaries. Values were assigned to B_i, S_i and C_i through consultation with >100 threatened species experts. Further details regarding estimation of these parameters are found in Joseph et al. (2009).

The prioritization process begins with all species being funded, then sequentially removes species with the lowest project efficiencies until pre-determined targets for budget or number of species prioritised are reached. At each stage, cost and phylogenetic weight parameters for remaining species are updated, both of which may increase as species are excluded.

2.3. Evolutionary distinctiveness weights (W_i)

While a variety of methods exist for assigning species weights that incorporate evolutionary distinctiveness (e.g. May, 1990; Vane-Wright et al., 1991; Redding and Mooers, 2006; Isaac et al., 2007), a major distinction among them is whether they consider complementarity of the species group, updating weights according to changes in the prioritized species list, or whether they statically assign distinctiveness weights to species based on original conditions (Faith, 2008). We assessed the effects of systematically increasing evolutionary distinctiveness weights on prioritization outcomes using both types of weights and the following specific methods: (1) a measure developed for prioritization in New Zealand, the 'phylogeny, threat and endemism' (PTE) method, which updates based on threat status changes as species are removed from prioritization and emphasizes threatened endemics; (2) an additional method, expected phylogenetic diversity (expected PD; Faith, 2008) that updates as species are removed from prioritization and incorporates probabilities of extinction; and (3) the 'evolutionary distinct and globally endangered' (EDGE) static method of Isaac et al. (2007). We chose the PTE method because it is currently used in prioritization of species recovery programs in New Zealand and it updates weights according to changes in the prioritized species list, and we chose the expected PD measure because it demonstrates an alternative approach that incorporates estimates of extinction probabilities, and also updates weights as species are removed from prioritization. For the sake of brevity, we present detailed methods and results for expected PD in the Appendix. We chose EDGE because it is a static measure that has been used extensively to demonstrate prioritization for large suites of species (e.g. Collen et al., 2011; Isaac et al., 2012). In addition, these measures do not explicitly consider species ranges, which was a necessary criterion since species ranges have not been fully characterized for many threatened New Zealand species, particularly marine species that are difficult to survey. For all three measures, the lack of a detailed phylogenetic tree across our diverse group of threatened species necessitated the use of species' taxonomic relationships as a surrogate for evolutionary distinctiveness. Although this approach is less precise than methods using phylogenetic branch lengths and thus may suffer from errors where taxonomy inaccurately or imprecisely reflects phylogenetic relatedness (Cadotte and Davies, 2010), it has been shown to be a reasonably robust measure of distinctiveness for conservation prioritization (Crozier et al., 2005; Rodrigues et al., 2011).

The PTE method of evolutionary distinctiveness weighting was designed to fulfil the following criteria: (1) to account for threatened species within the same lineages, since risk to sister species increases risk to phylogenetic lineages (Faith, 2008), and species with lineages containing many threatened species should be weighted higher to help conserve a representative group of species; (2) to update values as species are managed and threats change, rather than statically partition distinctiveness weight (e.g. Isaac et al., 2007); and (3) to include endemism as an important consideration for threatened taxonomic groups, to reflect the fact that a planning area (in our case, New Zealand) bears the responsibility for conserving the evolutionary history of its endemic lineages.

The PTE method uses the following formula:

$$W_i = R_i \times M_i, \tag{2}$$

where W_i is the evolutionary distinctiveness weight of species i. R_i (representativeness of species i) is calculated as follows:

$$R_i = 1 + \sum_{z=s,g,f} T_{i_z} \frac{A_{i_z}}{B_{i_z}}, \tag{3}$$

where s, g and f are species, genus and family taxonomic levels; $T_{iz} = 1$ for each level if all taxa at this level are threatened in the planning area and $T_{iz} = 0$ otherwise; A_{iz} is the number of threatened taxa at this level, within the next-highest taxonomic level (for $z = s$, number of threatened species in the genus; for $z = g$, number of threatened genera in the family; for $z = f$, number of threatened families in the order); and B_{iz} is the total number of taxa at this level, within the next-highest taxonomic level (for $z = s$, the total number of species in the genus, etc.). The addition of 1 to the summed proportion of threatened taxa scales ensures $W_i \geqslant 1$ in Eq. (1), allowing tests on evolutionary distinctiveness weight outlined below. Thus, a species from a genus containing three species, two of which are threatened, would have $R_i = 1 + 2/3 + 0 + 0 = 1.66$, while the sole species from a genus in a family containing another genus that is secure would have $R_i = 1 + 1/1 + 1/2 + 0 = 2.5$. This formula gives greater weight to threatened species from lineages containing a greater proportion of threatened taxa, in recognition of the risk to the evolutionary distinctiveness of these lineages. Species from more diverse lineages receive relatively low weight, unless their lineages contain a high proportion of threatened taxa.

M_i is a multiplier for endemism of threatened taxa, which was added to recognize species that are endemic to New Zealand, and thus wholly dependent on the planning area for survival:

$$M_i = 1 + \sum_{z=s,g,f} U_{i_z}, \tag{4}$$

where $U_{iz} = 1$ if all threatened taxa at a given level are endemic to the planning area. Thus, an endemic species whose entire genus is threatened and endemic, but whose family is not endemic, would have $M_i = 1 + 1 + 1 + 0 = 3$, while a threatened non-endemic species would have $M_i = 1 + 0 + 0 + 0 = 1$. When calculating the initial W_i for a given species, closely-related species that are retained in the prioritized list are considered to be managed and therefore secure. However, species' W_i are re-calculated with each iteration of the prioritization algorithm. As species are dropped from the prioritized list, they are considered threatened and W_i for remaining species are updated accordingly.

EDGE weighting was designed to prioritize species by both evolutionary distinctiveness and threat level (Isaac et al., 2007). We calculated EDGE weights using the following formula:

$$W_i = 1 + \mathrm{EDGE}_i, \tag{5}$$

where W_i is the EDGE measure of evolutionary distinctiveness weight of species i, with a value of 1 added to scale the minimum W_i to 1. EDGE assigns static, one-time species weights based on the following formula:

$$\mathrm{EDGE}_i = \ln(1 + \mathrm{ED}_i) + \mathrm{GE}_i \times \ln(2), \tag{6}$$

where ED_i is the evolutionary distinctiveness of species i, calculated as the sum of all branch lengths divided for each branch by the number of subtended species (Isaac et al., 2007), and GE_i is the threat status of the species, assigned a number of one to four. We used New Zealand threat categories (Hitchmough et al., 2005; Hitchmough, 2012; see Appendix Table A1 for details) instead of the IUCN Red List Categories used by Isaac et al. (2007) because some New Zealand species have not yet been ranked by the IUCN. Since we were using taxonomic relationships as a surrogate for phylogenetic relationships, branch lengths were assumed to be one. As opposed to the original EDGE approach that uses EDGE as the sole criterion in developing proposed species priority lists, we incorporated EDGE-based W_i into the Joseph et al. (2009) prioritization framework in Eq. (1) above.

2.4. Tests on evolutionary distinctiveness weight

We examined the trade-offs incurred when the emphasis on evolutionary distinctiveness weight of individual species is systematically increased vis-à-vis other parameters, and when the total distinctiveness weight conserved by the prioritized species (a measure of the phylogenetic diversity conserved) increases. To do so, we ran sets of prioritization protocols that progressively increased the emphasis on species' W_i in Eq. (1) using an exponent:

$$E_i = \frac{W_i^x \times B_i \times S_i}{C_i}, \tag{7}$$

where x is the exponent used to emphasize evolutionary distinctiveness weight in prioritization iterations. Increasing x increased the emphasis on evolutionary distinctiveness weight in the prioritization protocol, allowing us to efficiently test scenarios ranging from no consideration of distinctiveness to strong emphasis on distinctiveness weights. The exponent was incrementally increased from zero to five, in increments of 0.125 from zero to one, and 0.25 from one to five, and the prioritization protocol was run at each increment. An exponent of zero represents no consideration of evolutionary distinctiveness weight ($x = 0$ so $W_i^x = 1$ for all species i); an exponent of one represents emphasis on distinctiveness weight as calculated in Eq. (1); an exponent of five strongly favors species with larger distinctiveness weights. Increasing x also increased the total evolutionary distinctiveness weight conserved by the prioritized species group (calculated as the sum of W_i for all prioritized species), allowing us to explore potential trade-offs in phylogenetic diversity conserved versus number of species prioritized and mean probability of project success.

We ran this analysis for W_i based on PTE, EDGE, and expected PD, using two budget scenarios: (1) a fixed maximum annual budget of \$30M NZD, which reflects recent budgets allocated by the New Zealand government for conserving threatened species (NZ DOC, 2013); and (2) a flexible budget to ensure a prioritization target of 300 species, which is the number of species currently prioritized for management by the New Zealand Department of Conservation (NZ DOC, 2012). Analyses were conducted using R v. 2.15.2 (R Development Core Team, 2012); data and code are available on request from the corresponding author. For the \$30M scenarios we plotted the exponent on W_i and total distinctiveness weight (summed W_i of prioritized species) versus number of species prioritized and mean probability of project success. For the 300 species scenarios, we plotted the exponent on W_i and total distinctiveness weight versus total annual budget and mean probability of project success. To compare these results with those obtained considering only evolutionary distinctiveness weight, we also ran the prioritization protocol for \$30M and 300 species constraints using only W_i to rank species ignoring cost and feasibility. In addition, to determine whether results might be influenced by dependencies among input variables, we examined relationships among input variables using linear models.

3. Results

3.1. \$30M budget scenario

As we increased the emphasis on individual species' distinctiveness weights (i.e., increased x in Eq. (7)), the number of species prioritized for a \$30M budget progressively decreased for PTE, EDGE and expected PD methods, while the total distinctiveness weight conserved initially increased (Fig. 1; Appendix, Fig. A1). However, for the PTE method total distinctiveness weight conserved reached an asymptote, after which relatively constant total distinctiveness weight was conserved in progressively fewer species (Fig. 1c). For EDGE and expected PD, gains in total distinctiveness weight were reversed when the emphasis on evolutionary distinctiveness of species rose to a certain level ($x = 3.75$ for EDGE), as increases due to more distinct species being prioritized could not compensate for losses due to fewer species being prioritized (Fig. 1d; Appendix, Fig. A1 and Table A2). This difference between the methods occurred because dropped species in the PTE method are assumed to not contribute to future phylogenetic diversity, and thus weights increase more than for EDGE (which is static), or expected PD (for which the additional weight in retained species is multiplied by the extinction probabilities of all related dropped species). Retention of species with greater complementarity in PTE thus helped to compensate for loss of total PTE distinctiveness weight as species were dropped. At each successive increase (via exponent x) on species' W_i, newly-retained species at this level contributed a mean of 13.0 (±1.4 SE) to the total PTE weight. Mean PTE weight of these species prior to updating when others were removed was 3.4 (±0.3 SE).

For PTE, an exponent on W_i of 1.25 offered the best compromise between maximum species retained and maximum total distinctiveness weight conserved, with 296 species retained (versus a maximum across all iterations of 301 species), and total PTE weight of 581 (versus a maximum of 603; Fig. 1e). For EDGE, an exponent on W_i of 1.5 offered the best compromise, with 305 species retained (versus a maximum across all iterations of 306 species), and total EDGE weight of 722 (versus a maximum of 724; Fig. 1f). For all methods, mean probability of project success for prioritized species was lowest at the highest degree of emphasis on

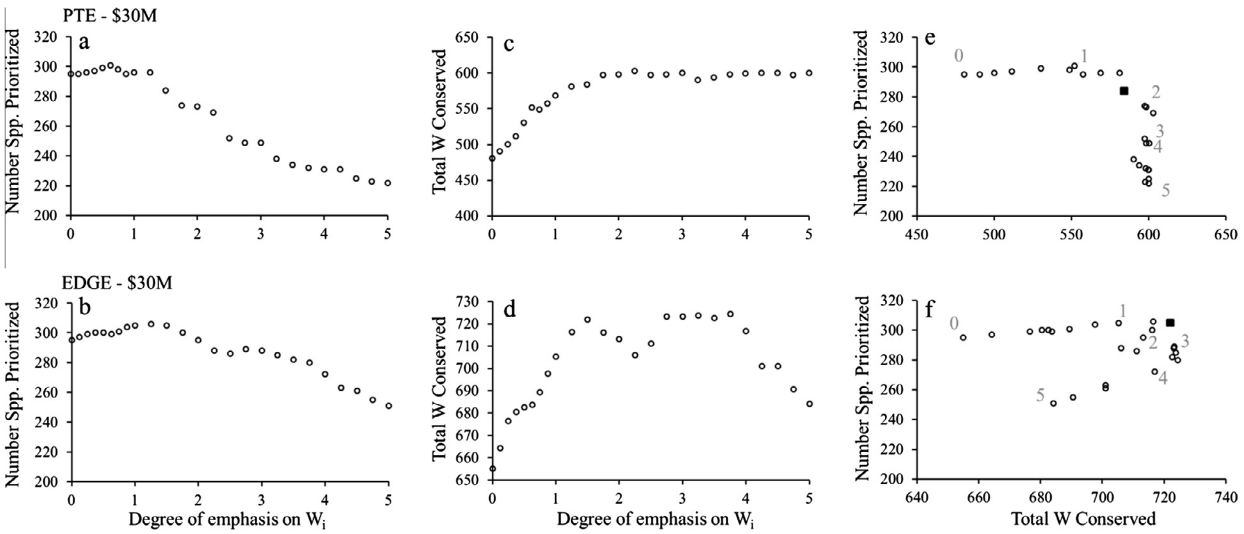

Fig. 1. Effect of increasing emphasis on evolutionary distinctiveness weight (W_i) with a \$30M NZD budget: degree of emphasis on species' distinctiveness weight (exponent x on W_i) versus number of species prioritized for PTE (a) and EDGE (b); degree of emphasis on W_i versus total distinctiveness weight (W) conserved for PTE (c) and EDGE (d); and total distinctiveness weight conserved versus number of species prioritized for PTE (e) and EDGE (f). Grey numbers represent the degree of emphasis on W_i for selected points. Filled squares in (e) and (f) represent iterations with the best compromise between total distinctiveness weight conserved and number of species prioritized. Note that distinctiveness weight is measured differently for PTE and EDGE, and is not directly comparable between these measures.

W_i (Appendix, Fig. A2). The iterations offering the largest combined proportion of maximum species retained and total distinctiveness weight conserved also offered an optimal or near-optimal compromise with mean probability of project success (Appendix, Table A2).

For PTE and EDGE methods, correlations among input variables were non-significant or trivial (Appendix, Table A3), and thus results for both the $30M and 300 species scenario were not dependent on relationships among input variables. However, expected PD was highly correlated with the benefit parameter B (the difference between estimated probabilities that species will be secure with and without their projects), because its formula incorporated B_i from Eq. (1) as an estimate of extinction probability (Appendix, Table A3).

3.2. 300 Species scenario

With a fixed target of 300 species prioritized, increased emphasis on individual species' evolutionary distinctiveness weight and increased total distinctiveness weight conserved were both accompanied by increased annual budget and decreased mean probability of success (Fig. 2, Appendix, Figs. A3 and A4). For the EDGE method, a 21% increase in estimated annual cost from $36.9 million to $44.8 million (for a 1.3% increase in total distinctiveness weight) occurred when the exponent on W_i increased from 3.5 to 3.75. This cost increase was driven largely by the addition of the critically-endangered shrub *Carmichaelia carmichaeliae*, which contributed ~50% of the added cost and ~20% of the total evolutionary distinctiveness weight of the five species added at this level.

As the degree of emphasis on W_i increased, total distinctiveness weight conserved by the 300 retained species reached an asymptote for the PTE method, but continued to increase for EDGE (Fig. 2). This was due to two differences in how the distinctiveness weights are calculated. In the PTE method, updating of distinctiveness weight for retained species meant that species added as emphasis on W_i increased contributed diminishing additional distinctiveness weight to the complementary core group of species (Appendix, Fig. A5). However, the static partitioning of distinctiveness weight in EDGE meant that complementarity of species groups was not considered. In addition, the influence of threat level in EDGE calculation resulted in greater numbers of critically endangered species being prioritized as the degree of emphasis on W_i increased (Appendix, Fig. A4), with total EDGE distinctiveness weight increasing accordingly. Results for the expected PD method were intermediate between the PTE and EDGE methods (Appendix, Fig. A3 and A5 and A5).

For the 300 species scenario, total distinctiveness weight conserved per dollar spent was optimal at intermediate levels of total distinctiveness weight. The optimum value for PTE, the was 19.7 PTE units per million NZD at an exponent on W_i of 1.3, while for EDGE it was 24.5 EDGE units per million NZD at an exponent of 1.5 (Appendix, Table A4).

3.3. W_i-only rankings

For PTE, EDGE and expected PD $30M scenarios, species rankings using only W_i resulted in considerably lower total evolutionary distinctiveness weight conserved, numbers of species conserved and mean probabilities of success than any of the runs considering other factors (Appendix, Table A5). Scenarios for 300 species using only W_i resulted in the maximum total weight that could be conserved in 300 ranked species (Appendix, Table A5). However, mean probabilities of success were low, and annual budgets were nearly four times recent annual budgets for conserving threatened species in the planning area (NZ DOC, 2013).

4. Discussion

Given limited funding, there is potential tension between conservation objectives emphasizing either the number of species secured or phylogenetic diversity conserved. Within the objective of maximizing phylogenetic diversity conserved, there is also potential tension between prioritizing species according to their evolutionary distinctiveness weights, and maximizing the total distinctiveness (i.e., phylogenetic diversity) among all prioritized species (Faith, 2008). We examined trade-offs among these objectives using a dataset of 700 of New Zealand's most threatened species that has been used to prioritize funding for conservation projects. Our tests used three types of evolutionary distinctiveness weights, and included the additional realistic constraints of project costs, benefits and probabilities of success.

Our tests showed that increasing the emphasis on the distinctiveness weight of individual species in prioritization leads to

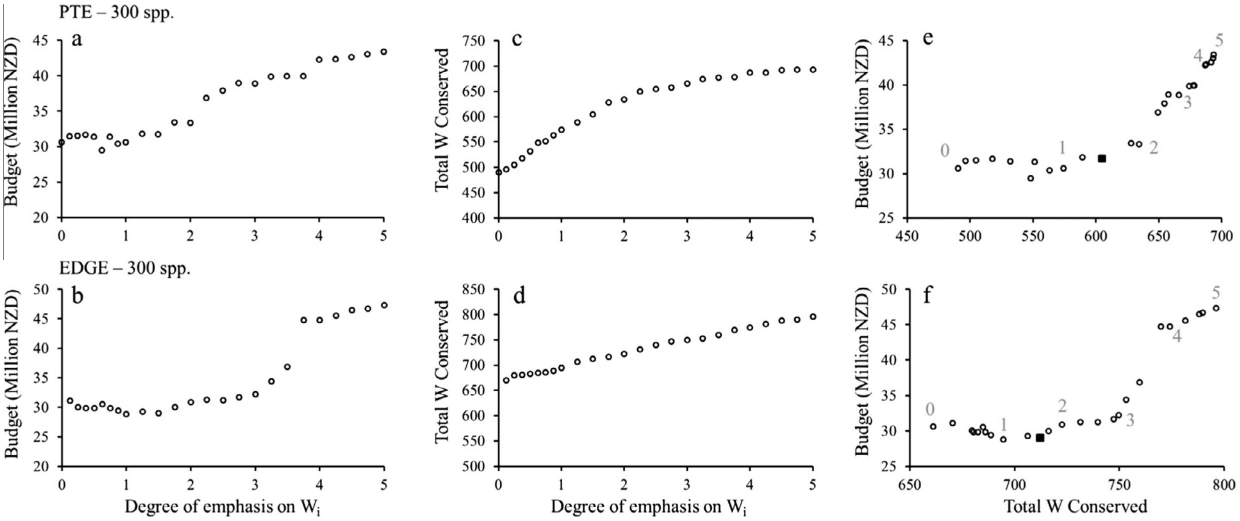

Fig. 2. Effect of increasing emphasis on evolutionary distinctiveness weight (W_i) with a fixed target of 300 species: degree of emphasis on species' distinctiveness weight (exponent x on W_i) versus annual budget for PTE (a) and EDGE (b); degree of emphasis on W_i versus total distinctiveness weight (W) conserved for PTE (c) and EDGE (d); and total distinctiveness weight conserved versus annual budget for PTE (e) and EDGE (f). Grey numbers represent the degree of emphasis on W_i for selected points. Filled squares in (e) and (f) represent iterations with the highest total distinctiveness weight per dollar spent.

sacrifices the number of species that can be managed with a fixed budget. These sacrifices limited the total distinctiveness weight that could be conserved in a chosen suite of species, as the addition of more distinct (and more expensive) species was offset by the removal of greater numbers of less distinct species. Fortunately, the trade-off between total distinctiveness weight conserved and number of species that could be managed for a set budget was convex for all methods of measuring distinctiveness weight, and near-optimal total distinctiveness weight could be retained while retaining a near-optimal total number of species. In scenarios where a fixed number of species was chosen regardless of budget, costs increased as individual species' weight was given greater priority, especially at the highest level of emphasis, for which relatively small increases in total distinctiveness weight conserved were often accompanied by large budget increases.

There are strong arguments for considering the importance of evolutionary history in prioritizing the conservation of species (Cadotte and Davies, 2010; Collen et al., 2011). Prioritizing species according to weights based on evolutionary distinctiveness may help to conserve the functional diversity of life, including its resilience to environmental change, and its genetic capacity to evolve as new conditions arise (Vane-Wright et al., 1991; Cadotte and Davies, 2010). Indeed, where resources are limited and conserving phylogenetic diversity is the primary consideration, a potentially attractive approach could be prioritizing the minimum number of species necessary to achieve near-maximum attainable total distinctiveness weight, thereby allowing more focussed, efficient conservation efforts.

However, such an approach has three potential flaws. First, it relies on an accurate quantification of phylogeny and distinctiveness. In our case, realistic prioritization across a full suite of threatened species necessitated the use of taxonomic relationships as a proxy for phylogenetic relationships. While this technique may be useful for conservation prioritization (Crozier et al., 2005; Rodrigues et al., 2011), it is also accompanied by considerable uncertainty. Even meticulously constructed phylogenies are subject to debate and revision (e.g. Wiens et al., 2010; Pagel, 2012). Second, the link between functional and phylogenetic diversity is strong in some cases (e.g. Cadotte et al., 2008), but not in others (e.g. Kluge and Kessler, 2011), potentially weakening the argument for conserving phylogenetic diversity as a proxy for functional diversity (Winter et al., 2012). Third, positive relationships between evolutionary distinctiveness and extinction probability for some groups (Redding and Mooers, 2006; Vamosi and Wilson, 2008) but not others (Verde Arregoitia et al., 2013), indicate that the link between phylogenetic distinctiveness and ability to adapt to emerging conditions is unclear. In addition, highly-radiated lineages sometimes show remarkable adaptability to change (Schluter, 2001; Seehausen, 2004).

Including evolutionary distinctiveness weight in prioritization schemes also introduces an additional parameter that must be traded off with other important considerations. In our prioritization scenarios, increasing emphasis on distinctiveness weight was generally accompanied by increases in cost and decreases in mean probability of project success across species. Lower probabilities of project success indicate greater risk that some species, and their associated evolutionary distinctiveness, may be lost despite being prioritized for management intervention.

Exploring a range of emphasis on distinctiveness weight allowed us to find species combinations that were a useful compromise between species-based and phylogenetic approaches. For the PTE method with a $30M budget, the prioritized suite of species that offered the best compromise between the number of species prioritized and total distinctiveness weight conserved represented 98% of the maximum species number and 96% of the maximum total distinctiveness weight attained across all iterations. For EDGE and expected PD, the compromise group represented ~99% of the maximum number of species and maximum total distinctiveness weight of all iterations. Where our goal was to conserve 300 species, exploring the range of emphases on distinctiveness weights revealed a useful compromise between total distinctiveness weight conserved and money spent. Given the potential benefits and uncertainties in either a phylogenetic or species-based approach, we suggest that exploring a range of possible compromises is preferable to using either approach in isolation. While extreme approaches strongly emphasizing species numbers sacrificed conserved distinctiveness weight, and extreme approaches emphasizing distinctiveness weight sacrificed species numbers, the optimal combinations of both approaches were near-optimal for both distinctiveness weight and number of species prioritized.

Despite broad agreement among tests using PTE, EDGE and expected PD on compromises between species numbers and evolutionary distinctiveness weight, there were differences in results among the methods that were indicative of the contrasting ways in which each method calculates distinctiveness weight. The PTE method explicitly includes complementarity based on threats to related species and updates this measure as species are dropped from prioritization, while EDGE statically partitions distinctiveness weight. Expected PD is intermediate between PTE and EDGE. It updates weights as species are dropped; however, it multiplies the contributions of dropped species to retained species' updated weights by the dropped species' probabilities of extinction. For the $30 M scenario and the PTE method, species losses at higher emphases on distinctiveness weight were compensated by increased weight assigned to retained species. This did not occur for EDGE or expected PD.

As noted by Faith (2008), static partitioning without considering complementarity may lead to inefficient prioritization. Permanent assignment of low priority to species from a diverse lineage may mean that no species from such a lineage is prioritized, putting the entire lineage at risk. Likewise, permanent assignment of high priority to all species from a highly-distinct lineage would not reflect the total phylogenetic diversity at risk once one or more species in the lineage are made secure. For example, Isaac et al. (2012) derived a global EDGE-based prioritization list for threatened amphibians, of which the top five species were in the genus *Epicrionops*. If one or more of these species were protected to the point where the highly-distinct *Epicrionops* genus itself was safe, the other *Epicrionops* species could move down the list of priorities if threats to other lineages posed greater threat to global phylogenetic diversity.

In addition, if non-prioritized threatened species are likely to go extinct, the importance of secure species to the survival of lineages may be misconstrued if evolutionary distinctiveness weights are not updated to reflect the insecurity of the non-prioritized species. Updating based on complementarity and threat in the PTE method is therefore prudent in that it assumes non-prioritized threatened species may not contribute to future diversity, and responsibility for persistence of phylogenetic diversity rests with prioritized or non-threatened relatives. Although non-prioritized species may still persist without management, their continued survival and the persistence of their associated evolutionary distinctiveness cannot be assumed. The expected PD method offers a less conservative approach, by considering extinction probabilities for dropped species. Depending on the timescale of planning and the perception of accuracy in extinction probability estimates, either technique may be appropriate.

Another key difference among the PTE, EDGE and expected PD methods is that PTE calculations consider endemism of threatened taxa. Again, this is a cautious, prudent approach, especially in the New Zealand context. Though ideally conservation efforts should be prioritized globally (Wilson et al., 2006; Brooks et al., 2006), individual planning areas routinely bear the burden of conserving their threatened species, and therefore the responsibility for survival of their endemics. As a center of endemism (Mittermeier et al., 1998; Wallis and Trewick, 2009), New Zealand bears a disproportionate responsibility for conserving threatened endemics. By weighting prioritization towards threatened endemic taxa, the PTE method helps to prioritize the only chance of survival for these lineages.

In other planning areas, where threatened species ranges cross political boundaries, the strategy for considering endemism may need to be more nuanced. For example, Cofré and Marquet (1999) included an ordinal measure of endemism in a ranking system for species conservation, with species found in fewer countries receiving a higher endemism score. In some cases, species may not be endemic to a planning area, but may be shared with areas lacking environmental protection, where their survival cannot be assumed (e.g. Abbitt et al., 2000). In such cases, managers may still wish to weight such species as if they were endemic in prioritization protocols. Finally, there may be ecological, social or political considerations that can influence weighting of species in either quantitative or informal prioritization processes. For example, there may be strong impetus for preserving keystone species (Soulé et al., 2005), iconic species (Schwartz, 2008), or those that are economically important or part of cultural traditions (Rodríguez et al., 2004).

5. Conclusion

The earth is experiencing a biodiversity crisis for which current funding and political will is sufficient to do little more than attenuate (Butchart et al., 2010; McCarthy et al., 2012). Thus, scarce resources must be prioritized to focus on projects that minimize biodiversity loss within current constraints (Bottrill et al., 2008). Since the unique genetic information contained in threatened species is valuable from both practical and philosophical standpoints (Cadotte and Davies, 2010), it is important to include evolutionary distinctiveness weights in prioritizing threatened species for conservation. Indeed, as detailed understanding of phylogenetic relationships among species improves, there may be increasing incentive at global and local levels to explicitly rank species according to their evolutionary distinctiveness.

However, species' evolutionary distinctiveness is not the only consideration: other aspects such as cost and probability of project success must be taken into account. Given that there are still many uncertainties in phylogenetic trees as well as links between evolutionary distinctiveness and potential adaptive ability, it is also prudent to seek a balance between a phylogenetic and species-based approach. For better or worse, 'species' is also the currency with which governments and conservation agencies often measure conservation progress. Conservation planners have been slow to incorporate evolutionary distinctiveness into prioritization schemes (Collen et al., 2011; Isaac et al., 2007, 2012), perhaps due to a perceived lack of compelling justification for phylogenetic approaches (Winter et al., 2012), or continued allegiance to traditional methods. As we have shown, a combined approach that minimizes loss in both species and phylogenetic diversity is possible.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.03.013.

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