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Perspective

Difficult decisions: Strategies for conservation prioritization when taxonomic, phylogenetic and functional diversity are not spatially congruent

Marc W. Cadotte^{a,b,*}, Caroline M. Tucker^{c,d}

^a Department of Biological Sciences, University of Toronto-Scarborough, 1265 Military Trail, Toronto, ON M1C 1A4, Canada

^b Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks St., Toronto, ON M5S 3B2, Canada

^c Department of Biology, University of North Carolina at Chapel Hill, Coker Hall, CB #3280 120 South Road, Chapel Hill, NC 27599-3280, United States of America

^d Centre d'Ecologie Fonctionnelle et Evolutive, CNRS, 1919 Route de Mende, 34293 Montpellier Cedex 5, France

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ABSTRACT

Preventing further loss of biodiversity is the most important challenge for conservation biology. The loss of species and the functions and services they provide has negative implications for human well-being. However, conservation efforts focussed on sites with high numbers of species may inadvertently under-represent other facets of biodiversity such as phylogenetic and functional diversity. Further, because these different biodiversity facets vary in their degree of spatial congruence, methods of site selection that maximize phylogenetic, functional, and species diversity are necessary to represent biodiversity in a holistic fashion. In this paper we discuss approaches to such multi-faceted site-level prioritization. Specifically, we examine complementarity algorithms and provide strategies to weight species selection by their trait or phylogenetic distinctiveness. Further, we explore approaches that integrate diversity facets into a single measure of prioritization and incorporate complementarity such that the goal is not just optimizing the protection of biodiversity, but to prioritize the addition of sites representing unprotected biodiversity across different facets. We highlight the strengths and limitations of such an approach. These types of holistic approaches to reserve design should provide flexibility in the face of changing knowledge and priorities.

1. Introduction

Estimates of human impacts on biodiversity vary with spatial scale (Vellend et al., 2017), ecosystem type, and the approach to measuring biodiversity (Gruner et al., 2017), but it is clear that human activities have greatly altered species diversity from regional to global scales (Pimm et al., 2014). Conservation efforts attempt to avoid or mitigate some of the negative impacts by protecting either species at risk (e.g. those species experiencing low population sizes, habitat loss, habitat fragmentation) or with a particular value (e.g. for human activities or ecosystem services), or else by identifying intact or otherwise valuable places for protection. The influential ‘global hotspots’ approach falls between these, prioritizing sites that harbour high diversity and disproportionate numbers of endemic species and face high rates of habitat loss (Myers, 2003; Myers et al., 2000). Such multi-pronged approaches are becoming more common, and reflect the fact that conservation policy and management have multiple priorities and costs that need to be incorporated (Groves et al., 2002). Thus, approaches that implicitly capture a more holistic set of costs and benefits of prioritizing sites may be most appropriate (Karp et al., 2015).

It is increasingly recognized that biodiversity has multiple components, including diversity in form and function (often measured from traits), diversity in the number of species and their abundances, and diversity in species genetic composition and evolutionary histories, with each offering potentially different information and value (McNeely et al., 1990; Purvis and Hector, 2000). Reserves should represent the full biodiversity of life, a goal that requires alternatives to species-centred approaches be applied. There have been numerous calls for conservation prioritization to consider phylogenetic and trait (often referred to as ‘functional’) information in order to identify ecologically, genetically, or phenotypically unique species and the sites harbouring such species (Brum et al., 2017; Cadotte and Davies, 2010; Carvalho et al., 2017; de Bello et al., 2010; Faith, 1992; Isaac et al., 2007; Pollock et al., 2017; Rolland et al., 2012; Thuiller et al., 2015; Van Meerbeek et al., 2014; Veron et al., 2017). Particular biodiversity facets may be differentially associated with particular utilities, such as option value, resilience or maximizing ecosystem function; further, spatial incongruencies in the distributions of different facets are common (e.g. Devictor et al., 2010; Pollock et al., 2017). The challenge in protecting multiple facets of biodiversity is that trade-offs are inevitable (Wilson

* Corresponding author at: Department of Biological Sciences, University of Toronto-Scarborough, 1265 Military Trail, Toronto, ON M1C 1A4, Canada.
E-mail address: mcadotte@utsc.utoronto.ca (M.W. Cadotte).

and Law, 2016), and yet policy-makers and managers require optimal solutions that can address the reality of competing priorities (Bennett et al., 2014; Faith and Walker, 2002).

Classically, conservation actions focussed on species, whether the goal was to protect particular species with high conservation value (e.g., *Roberge and Angelstam, 2004*) or to protect places with large numbers of species (*Myers, 1988*). Despite some difficulties in estimating species abundances or richness from imperfect data (e.g., *Chao and Jost, 2012; Chen et al., 2009; Kellner and Swihart, 2014; MacKenzie et al., 2009; Royle et al., 2005*), taxonomic-based metrics are far easier to estimate than functional or phylogenetic ones. However, species per se should have the weakest relationship with utility values like ecosystem function, since the species concept contains no particular information about form or function (*Cadotte et al., 2011; Cadotte and Davies, 2016; Diaz et al., 2013*). Protecting increasing numbers of species may increase, for example, the protection of ecosystem functions (see examples in *Cardinale et al., 2012*), simply by increasingly sampling the complete range of ecological diversity in a group of taxa (*Hooper et al., 2005; Loreau and Hector, 2001; Loreau et al., 2001*). However, this can be an inefficient approach, especially if resources or available areas are extremely limited, and in many cases policymakers and managers will be ‘choosy’ about what to protect. For that reason, approaches that focus directly on the range of traits (i.e., functional diversity) could increase efficiency. Functional diversity may be correlated in turn with increased ecosystem function and service delivery (*Cadotte et al., 2011; Diaz and Cabido, 2001*). Phylogenetic diversity may be a useful proxy for trait diversity (including unmeasured or difficult-to-measure traits) (*Cadotte et al., 2017; Kraft et al., 2007*), and may capture the sites likely to have higher ecosystem functioning (e.g. *Cadotte, 2013*). Protecting phylogenetic diversity or functional diversity could also provide the raw material (directly or via unmeasured traits) for ongoing biodiversity production through evolution or greater stability in the face of uncertain futures (*Faith, 1992*). Note that although phylogenetic diversity, functional diversity, and species richness can be tied to specific indices, we only use them to refer to the facets conceptually and do not imply any particular metric or approach to their measurement.

Different biodiversity facets may align with conservation priorities in different ways. For instance, prioritizing functional diversity logically aligns with the goal of ensuring future diversity of ecological traits. Trait-based conservation requires that we have the a priori knowledge of which traits should be measured for a given taxon, or that we have measured a sufficient number of traits to adequately estimate species differences (e.g. *Chan et al., 2006*). It also requires that current methodologies meaningfully describe trait-ecosystem relationships and that we have adequately identified traits that will be crucial in future scenarios. Trait-based conservation is further complicated by the fact that within-species trait variation can be substantial (*Albert et al., 2012*) and this variability should potentially be incorporated. As a result, an approach prioritizing phylogenetic diversity might be preferable, since modern phylogenies rely on molecular data and so their quality is independent of the availability and quality of trait data. Phylogenetic relationships only assume that species evolve differences and that closely related species on average tend to be more similar than distantly related ones. However, the value of phylogenetic distance as a proxy for species dissimilarity depends on the underlying rate of trait evolution and specific models of evolution (*Cadotte et al., 2017*). Further, phylogenetic relationships might be preferable to traits since they can capture meaningful differences between species even when different combinations of traits are important for estimating dissimilarity for different pairs of species. Yet, phylogenies do not provide direct evidence of proximate mechanisms. For many practitioners, given these important qualifications about the robustness of trait and phylogenetic approaches, taxonomic counts remain a valid way to maximize diversity without need to collect time consuming and expensive genetic and trait data. Alternatively, in the face of uncertainty about all

biodiversity facets, it might preferable to develop methods maximizing diversity across all facets (*Bennett et al., 2014*).

2. Different facets need not agree

If different biodiversity facets are highly congruent in space, then concerns about trade-offs are less relevant and a scheme focussing on a single facet (e.g., species richness) can be the optimal strategy to prioritize all facets (*Rodrigues et al., 2005, 2011*). Indeed, at the whole-assemblage scale, species richness, phylogenetic diversity, and functional diversity are not independent, since the functional diversity and phylogenetic diversity metrics necessarily sum across the species present (*Pavoine and Bonsall, 2011; Tucker et al., 2017*). However, in practice these biodiversity measures can still vary in their relationship or be only weakly correlated for many reasons (*Rodrigues et al., 2005; Tucker and Cadotte, 2013*). The relationship between phylogenetic diversity and species richness is dependent on the shape of the phylogenetic tree representing taxa, which is influenced by historical biogeographical processes that influence speciation and extinction. Very imbalanced trees (e.g., with a combination of highly distinct species and clades with many closely related species) and trees with few species will tend to produce weaker correlations with richness than more balanced trees (*Tucker and Cadotte, 2013*), for example. Empirically, many studies find that strong spatial congruence of multiple diversity facets is the exception, not the rule (*Albouy et al., 2017; Brum et al., 2017; Dehling et al., 2014; Devictor et al., 2010; Pollock et al., 2017; Safi et al., 2011; Tucker et al., 2012*).

This spatial incongruence may result from a number of mechanisms (see *Fig. 1* as an example). The relationship between functional diversity and phylogenetic diversity depends on the tempo and trajectory of evolution (often estimated with evolutionary models), and the shape of the phylogenetic tree, all of which can produce weaker or stronger relationships between phylogenies and traits (*Cadotte et al., 2017; Mazel et al., 2017*). This necessary linkage between evolution and traits also translates into uncertainty about the relationship between richness and functional diversity. Further, biases may produce imperfect data that alter diversity estimates in non-random ways (*Diniz-Filho et al., 2013; Stephens et al., 2015*). Specifically, species' detection probabilities might be functionally and phylogenetically non-random (*Jarzyna and Jetz, 2016; Si et al., 2018*) with some traits resulting in lower detection probabilities (e.g., brightly coloured birds vs. those with brown and mottled plumage). This could result in phylogenetic diversity and functional diversity being over- or underestimated relative to species richness estimates depending on the nature of detection biases (e.g., distinct species vs. those in dense clades) (*Jarzyna and Jetz, 2016*). Finally, when biodiversity facets are measured at the local site scale, ecological assembly processes create species compositions non-randomly from regional species pools, and incongruence among biodiversity facets can arise as a result of these processes (*Gerhold et al., 2015; Mayfield and Levine, 2010; Ricklefs, 1987*). The choice of spatial scale can thus greatly alter the degree of congruence between facets by altering the relative importance of different evolutionary and ecological processes and making it an important consideration.

3. Prioritization of sites using different facets of diversity

Too often the tendency has been to search for best-case scenarios in conservation prioritization, e.g. scenarios in which spatial congruence of multiple diversity facets allows efficient protection of multiple conservation priorities (*Pollock et al., 2017; Wilson and Law, 2016*). Given that trade-offs do occur (*Devictor et al., 2010; Forest et al., 2007; Laity et al., 2015; Tucker et al., 2012; Zupan et al., 2014*), it is surprising that the question of how to optimize the protection of multiple facets of diversity for spatial reserve design has not received more attention (but see: *Bennett et al., 2014; Pollock et al., 2017*). Take as an example *Fig. 1*: in this hypothetical landscape richness, traits, and phylogeny all

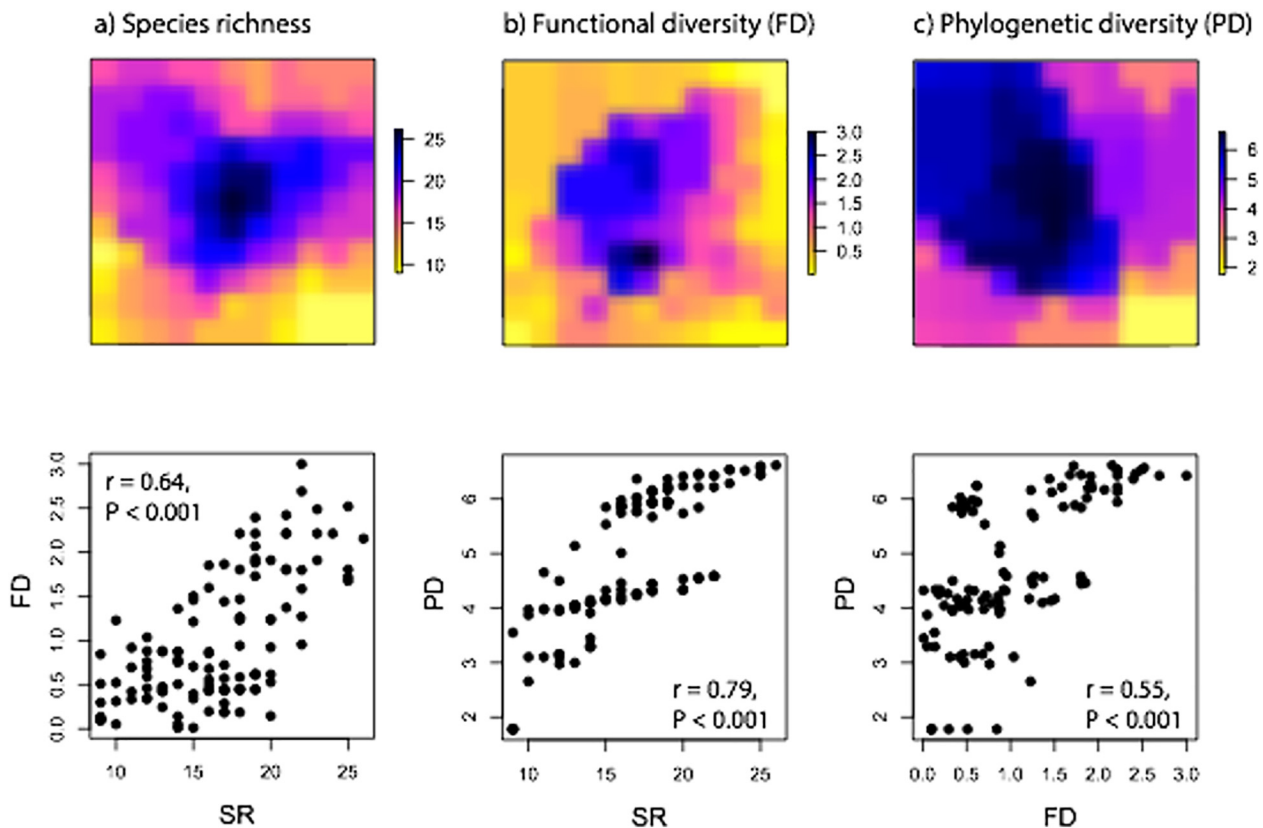


Fig. 1. The spatial distribution of the three biodiversity facets in hypothetical 11×11 grid cell landscapes. The top three panels show species richness (a), functional diversity (b), and phylogenetic diversity (c), respectively. The three facets, though correlated (bottom three panels), appear to highlight different grid cells as being the most diverse, as highlighted by cell colours (see legend to right of landscapes). The landscapes in the top row were created using the *scape* function in the *pez* R package. This function creates phylogenetically non-random spatial distributions. Traits were then evolved using *fastBM* in the *phytools* package. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

highlight different sites with high diversity. Moving from simply reporting incongruent patterns towards making conservation management recommendations is not straightforward. One approach would be to a priori identify the single facet believed to be of greatest importance (e.g., Vane-Wright et al., 1991), but mechanistic uncertainties, incomplete information, and poorly understood ecological ramifications make this a risky choice. Alternatively, it is possible to incorporate all diversity facets of interest into the prioritization scheme.

Prioritization of multiple diversity facets has some similarities to—and can be informed by—multi-taxon approaches, which incorporate different targets iteratively or use integrative measures to value sites (e.g. Kremen et al., 2008). Site prioritization schemes have a long history in conservation (Kirkpatrick, 1983; Margules and Pressey, 2000; Pressey et al., 1993) and modern prioritization schemes rely on the principle that optimal selection requires knowledge about multiple sites and priorities (Ball et al., 2009; Carvalho et al., 2017; Moilanen et al., 2005). Generally, these approaches attempt to minimize the cost of sites and isolation from other sites while trying to maximize the representation of certain conservation targets or features.

Here we outline two approaches that build on existing spatial prioritization methods but allow biodiversity facets to be considered through the addition of functional and phylogenetic information. Spatial prioritization algorithms, such as Zonation (Moilanen et al., 2005), attempt to minimize the loss of value from removing a site from a regional set of sites by maximizing the inclusion of sites (δ_k) by:

$$\delta_k = \max_i \frac{q_{ki} \cdot w_i}{Q_i(S) \cdot c_k} \quad (1)$$

where q_{ki} is the proportion of species i 's regional distribution captured by site k . This can be based on the proportion of a species' range (e.g.,

km^2) or some other abundance measure (from: Moilanen et al., 2005). w_i is the weight of species i , c_k is the cost of including site k , and $Q_i(S)$ is the proportion of the original distribution of species i found in the set of remaining sites. This equation prioritizes rare and restricted species, those given high weights, and those that occur in low cost sites.

For our purposes, w_i is the variable of interest. We can weigh the priority of a species according to any value, such as increasing the weight of a charismatic species or down weighting an undesirable species (e.g., an invasive species) to zero. A taxonomic approach would be reflected by setting $w_i = 1$ for taxa to be included, and so only range size and rarity would affect site selection. Functional or phylogenetic information could also be incorporated using w_i , as we explore below.

1) Weighting species based on either phylogenetic or functional information

To calculate functional and phylogenetic weights, we use a measure of species distinctiveness (D_i) calculated from a pairwise distance matrix (following: Violle et al., 2017):

$$D_i = \frac{\sum_{j=1, i \neq j}^N d_{ij}}{N-1} \quad (2)$$

where d_{ij} is the functional or phylogenetic distance (from a pairwise distance matrix—see: Cadotte and Davies, 2016; Swenson, 2014) between species i and species j , and N is the total number of species. The R package *funrar* calculates this (Grenié et al., 2017). D_i could be any value since d_{ij} can be estimated from data measured in millions of years, rate of nucleotide substitution, or dimensionless values from a principal component analysis measuring trait variation. For comparison across multiple datasets, w_i should be

standardized:

$$w_i = \frac{D_i}{D_{\max}} \quad (3)$$

2) Weighting species by combined phylogenetic and functional information

The previous scheme treats functional and phylogenetic information as independent sources of weighting information; potentially the user could compare the resulting site prioritization resulting from each, but this ignores the fact that the functional and phylogenetic distances could variously be redundant, complementary, or unrelated. An alternative approach is to use a composite measure of distance that combines both functional and phylogenetic distance measures and so does not make assumptions about the relationship or relative value of the two measures (Cadotte et al., 2013).

For this composite distance, functional and phylogenetic pairwise distances (d_{ij}) can be combined as orthogonal vectors to create a hybrid distance measure (Cadotte et al., 2013), referred to as functional-phylogenetic distance (FPd_{ij}). The functional and phylogenetic vectors can be differentially weighted, allowing the assessment of different weightings of the two distances, from pure functional to pure phylogenetic distance:

$$FPd_{ij} = (aPd_{ij}^p + (1 - a)Fd_{ij}^p)^{1/p} \quad (4)$$

where Pd_{ij} and Fd_{ij} are the phylogenetic and functional distances, respectively, a is the weighting parameter, which ranges from pure functional ($a = 0$) to pure phylogenetic ($a = 1$), and p is a non-linear term, and a value of 2 returns a Euclidean distance. Pd_{ij} and Fd_{ij} are normalized so they have similar relative magnitudes. The value $a = 0.5$ would return a distance matrix that equally combines functional and phylogenetic distances. Calculation of this measure is available in the R package *pez* (Pearse et al., 2015).

To use this composite distance for site prioritization, we can revisit Eq. (2) and find the maximal distinctiveness across all possible a values, from 0 to 1:

$$D_i = \max_a \left(\frac{\sum_{j=1, i \neq j}^N FPd_{ij, a}}{N - 1} \right) \quad (5)$$

The distinctiveness (D_i) value should be standardized as in Eq. (3) to facilitate comparison of different sites. It is important to note that the maximal value of a can be different for different species. It represents the value that maximizes the distinctiveness (D_i) value for a given species in comparison to the other species in the set. One species may be closely related to the other species in a set but have large trait differences arising from strong divergent evolution and so for this species D_i will be maximized as $a \rightarrow 0$. Another species might be distantly related but due to convergent evolution, have similar traits to other species in the set, and for this species D_i will be maximized as $a \rightarrow 1$. Finally, a species may be distinct as a result of both their trait values and phylogenetic relationships, so that $0 < a < 1$.

3) Comparing different prioritizations

Using the above two modifications for weighting sites, we here highlight several alternative spatial prioritization scenarios incorporating taxonomic, functional and phylogenetic information. These provide modifications to selection algorithms like Zonation but incorporate weights for species contributions to different diversity facets. Note this approach increases the range of potential prioritization outputs: the first approach allows users to create three separate spatial prioritization schemes maximizing each of

taxonomic, functional or phylogenetic diversity, while the second allows users to compare two different schemes, one maximizing taxonomic diversity and one the combined functional-phylogenetic diversity index. Having produced multiple prioritization schemes, planners and managers still need to evaluate whether they are spatially congruent, and to assess which sites to select given their own priorities. They could choose a single scheme to follow; they could select sites according to one weighting scheme (e.g., taxonomic or functional-phylogenetic weighting) but then augment this selection with sites with high value according to another weighting approach. Or they could simply select some number of top sites indicated for each scheme, or alternate between the different facets (e.g., first ranked site for taxonomic diversity, then first ranked for functional-phylogenetic, and so on) until conservation resources are exhausted. One could employ more sophisticated algorithms that estimate conditional benefits of adding sites, for example adding a site not because it is the highest ranked for one facet but gives maximal return on more than one facet. For example, there might not be a single site that maximizes all three facets, but there could be sites that achieve, for example, a minimum of 85% of the maximum values for each facet. These could be prioritized over sites that maximize a single facet as a bet-hedging strategy.

We also recognize that it's not likely that a conservation planning process would be tasked with designing a set of reserves de novo, but rather augmenting or complementing existing reserves. In this case, the approach outlined here could be used to assess how well existing reserves protect biodiversity facets, and to identify if certain facets are underrepresented. New conservation sites can be added to the reserve network according to how well they provide distinctive additions of taxonomic or functional and phylogenetic diversity.

4. Conclusions and future directions

Identifying sites for conservation must take into account numerous potentially competing priorities ranging from sociological, to economic, to biological (Bennett et al., 2014; Faith and Walker, 2002). Given such priorities, methods that integrate across multiple sources of information are particularly valuable, especially if they identify high-priority sites that were undervalued when using species-centric approaches. It may be that there are no optimal solutions that would result in adequate protection of all forms of diversity, but at least by accounting for multiple biodiversity facets researchers can provide best-case scenarios for managers and policy-makers. Given that many conservation reserves already exist, and these rarely have explicitly incorporated the protection of phylogenetic or functional diversity, one advantage of these algorithms is that they can be used to add new sites meant to supplement the phylogenetic and functional diversity in the existing system. Historically reserves were not selected to protect multiple forms of diversity, but new additions can redress this shortfall (Pollock et al., 2017). At a minimum, the conservation efficacy of existing reserve networks should be assessed relative to broader regional diversity patterns to identify gaps and shortcomings that would indicate which facets to prioritize for additional conservation investment.

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