BIODIVERSITY RESEARCH

Unifying measures of biodiversity: understanding when richness and phylogenetic diversity should be congruent

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ABSTRACT

Aim Biogeographical theory and conservation valuation schemes necessarily involve assessing how biodiversity is distributed through space and 'biodiversity' encapsulates many different aspects of biological organization and information. While biogeography may try to explain biodiversity patterns, successful conservation strategies should attempt to maximize different aspects of diversity. Ultimately, diversity patterns are the product of evolutionary history, and research and conservation efforts seek to understand the unequal distribution of evolutionary history. For conservation efforts, results have been inconsistent as to whether species richness (SR) provides sufficient surrogacy for evolutionary history. Here, we provide a conceptual framework allowing for the direct comparison of taxonomic richness and phylogenetic diversity (PD), both in terms of their mechanistic relationship and the relationship between their spatial distributions.

Location Global.

Methods We present a framework that relates regional SR, PD, biogeographically weighted evolutionary distinctiveness and biogeographically weighted SR. Further, we use simulations to illustrate how the size of the species pool, topological patterns within the phylogeny and autocorrelation in spatial distributions affect the correlation among metrics.

Results In regions that include both recently diversified groups and ancient species poor lineages, large species pools and low spatial autocorrelation, the correlation between biodiversity measures is lower than regions with low richness, balanced phylogenetic trees and high spatial autocorrelation.

Main conclusions We can now understand and predict when regional richness and PD should be strongly correlated. This congruency is the product of evolutionary and ecological processes that determine species pool membership and community assembly. Further, in regions where SR is not expected to be congruent with phylogenetic distinctiveness, re-examining how existing reserve networks protect the multiple aspects of biodiversity is critically important.

Keywords

Biogeography, conservation prioritization, evolutionary history, habitat protection, phylogenetic diversity, spatial distributions.

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INTRODUCTION

Global patterns of biological diversity reveal stark contrasts. Some regions contain thousands of species in relatively small areas, while elsewhere there may only be a few species over extremely large areas. Understanding this inequality in the distribution of species has been the focus of the creative energy of numerous scientists (e.g. MacArthur & Wilson, 1967; Gaston & Blackburn, 2000) and has served as the basis of global conservation prioritization (Myers *et al.*, 2000;

Fleishman *et al.*, 2006). The recognition that the term diversity is not synonymous with species richness (SR), but instead encompasses organismal variety at all levels, from genetic variation to the differences in the richness of higher taxa, and includes the diversity in ecosystem structure and function (Wilson & Peter, 1988), has led researchers to measure the spatial distribution of different aspects of diversity (Faith, 1992; Forest *et al.*, 2007; Devictor *et al.*, 2010; Huang *et al.*, 2011; Tucker *et al.*, 2012). Such comparisons aim to understand the biogeographical relationship between different facets of diversity. This type of research has been motivated, in part, by the fact that historically reserves have not focused on aspects of diversity beyond richness and endemism. Therefore, it is reasonable to examine the efficacy of existing reserves in protecting other facets of biodiversity (Devictor *et al.*, 2010; Huang *et al.*, 2011; Tucker *et al.*, 2012). In addition, comparing different biogeographical distributions of diversity allows researchers to potentially infer different mechanisms generating and maintaining different aspects of diversity. For example, studies examining latitudinal gradients of SR often infer the influence of climate on speciation rates (Weir & Schluter, 2007), whereas biogeographical studies that focus on genetic diversity often find that vicariance or natural barriers are critically important (Kuo & Avise, 2005).

There is a long history of measuring and mapping patterns of SR across biogeographical regions throughout the world (Wallace, 1876; Whittaker, 1954, 1960; Preston, 1960; Stevens, 1989). As the importance of alternative forms of diversity is increasingly recognized (Faith, 1992, 1994; Diaz & Cabido, 2001; Cadotte *et al.*, 2011), documenting patterns of other measures of diversity such as phylogenetic and functional diversity become an important exercise. For diversity and conservation research, having a precise estimate of ecological or functional diversity is beneficial. However, ecologically meaningful functional diversity is often difficult to quantify due to a lack of comprehensive trait information for species in a region, or an incomplete understanding of how traits correspond to ecological differences.

A related measure that is used as a surrogate for functional diversity is phylogenetic or evolutionary diversity, which quantifies the amount, distribution or evenness of evolutionary information contained within species assemblages. There are a number of ways to measure phylogenetic diversity (PD) in communities (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009; Cadotte *et al.*, 2010b), but methods that quantify either the amount of evolutionary history or the evolutionary distinctiveness of a set of species are most appropriate to examine spatial patterns of diversity (Faith, 1992; Isaac, 2007; Cadotte & Davies, 2010; Davies & Cadotte, 2011). The most often used measure is Faith's (1992) PD, which is the sum of all phylogenetic branch lengths connecting species together. Evolutionary distances are often correlated with potential multidimensional phenotypic differences among species (Vane-Wright *et al.*, 1991; Faith, 1992). There are many subtleties associated with this assumption, including the degree of phylogenetic conservatism among traits and the degree that trait divergence follows Brownian motion evolution. Specific traits and lineages often fail to meet these assumptions, and some researchers have found functional diversity and PD vary independently (Safi *et al.*, 2011). Regardless, researchers often use phylogenetic information to represent unknown aspects of species ecologies or simply as a representation of similarities in the information contained within their genomes. To this end, a number of studies have examined the spatial distribution of PD and delineate sites with disproportionately high PD (Moritz, 2002; Rodrigues & Gaston, 2002; Forest *et al.*, 2007; Devictor *et al.*, 2010; Tucker *et al.*, 2012).

On its own, SR is not ecologically meaningful, and considering other forms of diversity that capture species differences becomes important. With a particular focus on conservation, a number of studies have questioned the efficacy of richness as a surrogate for other types of diversity and have called for more multifaceted approaches to conservation (Crozier, 1997; Bonn & Gaston, 2005; Fleishman *et al.*, 2006; Devictor *et al.*, 2010; Davies & Cadotte, 2011). Studies that examine the congruence between species (or generic) and PD have been inconsistent. For example, Devictor *et al.* (2010) found a large spatial mismatch between the species, functional and PD of birds across France; these measures were congruent in some areas and incongruent in others, possibly depending on the history of the regional species pool in each area. They found that phylogenetic and functional diversity was underrepresented in the current reserve network, relative to SR. Two papers that compared the spatial distribution of generic or species diversity in the Cape Floristic Region of South Africa (Forest *et al.*, 2007; Tucker *et al.*, 2012) similarly found evidence of spatial incongruence between SR and PD. Conversely, several studies found that PD and taxonomic diversity to have similar spatial distributions: for example, Rodrigues & Gaston (2002) found that phylogenetic and generic richness of birds in north-west South Africa showed high spatial congruence, and reserve site selection was complementary. Perez-Losada *et al.* (2002) found little difference in conservation priorities for Chilean freshwater crabs, regardless of whether SR or PD was considered (although Faith & Baker, 2006 raise doubts about these results). Similar conclusions were made regarding Ozark crayfishes (Crandall, 1998). This marked variation in the observed relationship between SR and PD appears to makes it difficult to draw conclusions regarding the relationship between these measures.

The relationship between PD and species diversity depends on the phylogenetic topology and the geographical distribution of species (Rodrigues *et al.*, 2005). For example, in regions with large, diverse species pools, particularly in the case of randomly accumulating species, PD increases at a similar rate as SR, and thus, PD is likely to be highly correlated with SR (Fjeldsa, 1994; Mace *et al.*, 2003). This suggests that a framework predicting the degree of correlation expected between different measures of diversity could make

an important contribution to our understanding of the biogeographical distribution of diversity.

While there has been substantial effort to measure alternative aspects of diversity, there is a surprising dearth of studies that explicitly incorporate abundances into phylogenetic metrics of any kind (but see: Cadotte *et al.*, 2010b; Scheiner, 2012). Given the importance of species range sizes and abundances for understanding basic biogeographical processes as well as their role in extinction risk, this is an area that deserves further study. One method of weighting richness by abundances, here referred to as 'biogeographically weighted species richness' (BSR)[1]. BSR sums the inverse of the range sizes or number of sites or populations of all species at a site or in a region: $\text{BSR} = \sum_{i=1}^{s} \frac{1}{n_i}$, where S is the number of species at a specific site and n_i is the number of sites (or populations or range size) that species i occurs at over the larger region (Crisp *et al.*, 2001; Rosauer *et al.*, 2009). Thus, BSR is small if a site contains species with large ranges and is large if the site has many range-restricted species. A measure-like BSR may show quite different patterns than non-range size-related measures of diversity, especially if rich sites disproportionately contain large-ranged or abundant species (Rosauer *et al.*, 2009; Tucker *et al.*, 2012).

Measures of PD may also provide additional information when they incorporate range size. When Isambert *et al.* (2011) examined PD patterns in Malagasy national parks, they found that PD was negatively correlated with numbers of endemic species, as these endemics are the product of recent species radiations in Madagascar. Abundance information is straightforward to incorporate into phylogenies, because stopping a phylogenetic tree at the species level is arbitrary, and a tree can be resolved to the individual or population level by extending the tree via adding further tips (Cadotte *et al.*, 2010b). (In cases where additional genetic information is not available for individuals or populations, intraspecific tips can still be added as uninformative polytomies). As a result, the evolutionary distinctiveness of a species would explicitly account for the numbers of individuals or populations and therefore a measure of extinction risk. Several weighted PD metrics have been proposed that explicitly incorporate species abundances or range sizes into prioritization schemes (Rosauer *et al.*, 2009; Cadotte & Davies, 2010). There are other useful measures that use extinction risk (Redding & Mooers, 2006; Faith, 2008) or IUCN species ranks (Isaac, 2007) to weight phylogenetically based prioritization. IUCN ranks and extinction risk are used because of the availability and accessibility of this data and the fact that such conservation ranks are based on abundance and range size.

An example of a metric that combines evolutionary distinctiveness with abundances is the biogeographically

weighted evolutionary distinctivness (BED) metric (Cadotte & Davies, 2010), which partitions internal branches in a phylogenetic tree by the range or population size of the subtending taxa: $\text{BED}(T, i) = \sum_{e \in q(T,i,r)} \frac{\lambda_e}{n_e}$, where n_e is the number of grid cells in which a species is present, below branch e, of length λ, in the set $q(T, i, r)$, which includes the branches connecting species i to the root r of tree T. (Cadotte & Davies (2010) provide a detailed description and graphical representation of how this metric partitions internal branches – see also Fig. 1d). It should be noted that how abundances are calculated (e.g. number of sites occupied vs. geographical extent vs. total number of individuals) can affect BED values and their interpretation, and researchers should be cognizant of the potential implications of their measure of rarity (Rabinowitz, 1981). Species with long branches and low abundances or ranges are weighted highly (i.e. distinct and rare), while species that share the majority of their genetic heritages with many other species and have high abundances receive less weight. As a result, in a biogeographical setting, BED highlights sites containing species that have greater extinction risk and also have few close relatives.

UNIFYING BIODIVERSITY MEASURES

Given seemingly contradictory results from empirical studies (Rodrigues & Gaston, 2002; Forest *et al.*, 2007; Devictor *et al.*, 2010; Tucker *et al.*, 2012), reconciling results from different biodiversity metrics, and further, predicting how these differing metrics will relate is clearly necessary. There have only been a few studies published that investigate the effect of phylogenetic topology and abundance distributions on the relationship between phylogenetic- and species-based metrics of diversity (Rodrigues *et al.*, 2005; Schweiger *et al.*, 2008) and there remains a need for frameworks relating PD with SR (whether they are weighted by abundance or not). Comparing the spatial distributions of biodiversity measures informs conservation decision-making because incongruence between measures highlights how different aspects of diversity (SR, evolutionary history, geographical rarity) are differentially distributed through space. It also provides an opportunity to understand why patterns of diversity vary among biogeographical regions. In the following, we present a conceptual unification of these measures and then explore the effects of (1) tree structure, (2) spatial structure, (3) species pool size on the relationship between diversity metrics.

Conceptual underpinning of biodiversity measures

It is relatively straightforward to compare counts of the number of species with Faith's PD. Metrics based on SR implicitly assume that species are all equally weighted (weight of 1). This is synonymous to a phylogenetic tree where the phylogenetic relationships are removed and the tip-to-root distance is equal to 1 for an ultrametric tree (Fig. 1a) – that is, a star phylogeny where all terminal branches originate from a single polytomy (Helmus *et al.*,

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[1]Crisp and colleagues referred to this metric as 'weighted endemism' and we refer to it as BSR to make the terminology comparable to the other measures in this paper and because endemism is a scale dependent measure with specific connotations.

2007). If an informative ultrametric phylogeny is also scaled with a tip-to-root length of 1 (Fig. 1b), then the more distantly related the individual species, the closer the value of PD is to SR. The alternative scaling method would be to multiply SR by the real tip-to-root distance from the phylogeny. Regardless of the scaling method, PD will diverge from SR as the tree becomes increasingly imbalanced and as the mean nearest neighbour distance decreases. Thus, in regions with incongruent site rankings between PD and SR, we should expect less balanced evolutionary relationships among species.

When we weight the branches by species abundances or range sizes for BSR or BED (Fig. 1c,d), then there is a second axis to compare. BED can deviate from SR due to topology, abundance or their combined effect. Thus, BED must be compared with both PD and BSR to draw conclusions about the mechanisms that affect diversity distributions. Like the relationship between SR and PD, when the phylogeny is relatively balanced and has long terminal branches, the expectation is that BSR and BED give similar values. Both BSR and BED sum to their unweighted counterparts when each species value is multiplied by its abundance, for example:

$$\text{PD} = \sum_{i=1}^{s} n_i \cdot \text{BED}_i$$

or PD is approximated by:

$$\bar{n} \cdot \sum_{i=1}^{s} \text{BED}_i$$

where S is the number of species or terminal tips in the phylogeny and n is a measure of abundance. Thus, if abundance lacks variation (i.e. all species have roughly equivalent abundances), then PD and site-summed BED values are highly correlated.

EXPLORING THE CORRELATION BETWEEN METRICS

The four biogeographical measures of diversity considered here (Fig. 1) can vary from one another depending on the topology of the phylogeny and the geographical range sizes or abundances of species. We now ask how variation in these aspects can affect the strength of the correlation between metrics. To do this, we simulated thousands of trees and abundance distributions (see Appendix S1 for full methodology) and compared the four diversity metrics. Specifically, we assess whether variation in topology, the strength of the spatial autocorrelation in species occupancy patterns and species pool size have consequences for the strength of the relationship between richness and phylogenetic measures of diversity.
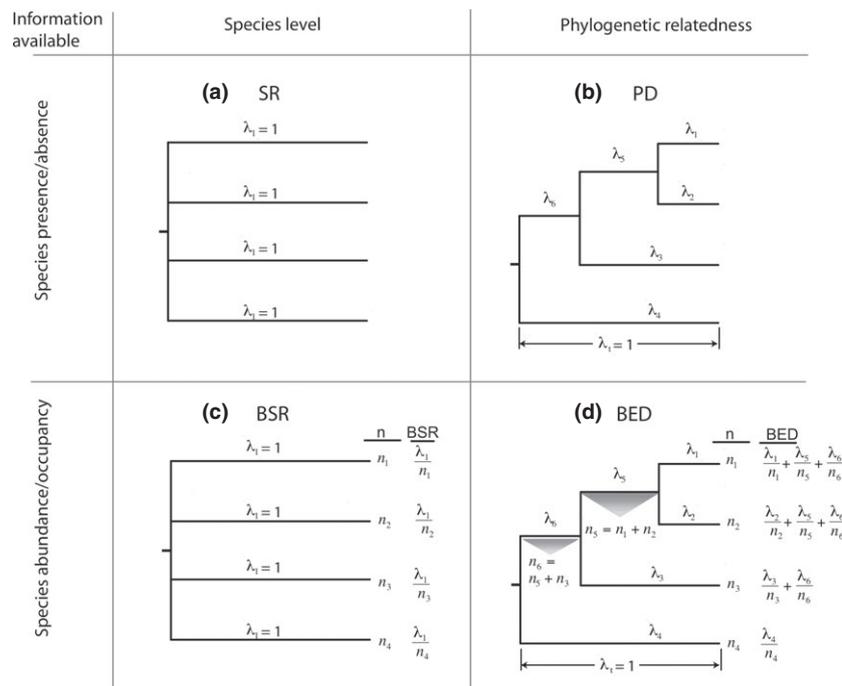
Figure 1 Comparison of the four types of biogeographical diversity metrics that use different types of information. When only species presence/absence information is available, the similarity of (a) species richness and (b) phylogenetic diversity (PD) depends on the deviation of the phylogeny from equal relatedness. Adding abundance or occupancy information to either richness as (c) biogeographically weighted species richness or PD as (d) biogeographically weighted evolutionary distinctiveness, weights individual tips by t relative abundances. In this schematic, the tip-to-root distance (λ) is set to 1, but this value can be the actual distance from the phylogeny, in which case, corrected richness is SR $\times$ λ_t. Lambdas with numeric subscripts are branch lengths and n is the abundance or range size of species.

Tree structure

If all species are equally related to a polytomy or star phylogeny (i.e. all species have identical amounts of unshared evolutionary information), with tip-to-root branch lengths equal to 1, then SR and PD are equivalent (e.g., Fig. 1). When a tree's topology diverges from that of a star phylogeny (as is common) so that information is no longer symmetrically distributed through clades and/or through time (see Fig. 2), we can expect systematic changes in the relationship between SR and PD.

In trees with proportionally more information in the terminal branches – that is, when there are few recent radiations (Fig. 2) – SR and PD should be highly correlated. A star phylogeny is the extreme of this situation, in which internal branches are minimized so the ratio between branch number and species number approaches one, at which point SR and PD are equivalent (Fig. 3). This suggests that in communities with species from anciently diverged lineages (Hawkins *et al.*, 2006; Lopez-Fernandez & Albert, 2011) or where community assembly selects distantly related species (Webb, 2000; Webb *et al.*, 2002), we would expect stronger correlations between SR and PD. Conversely, when trees have long internal branches and many short terminal branches representing recent speciation events (e.g. the Cape Flora, Linder, 2005; cichlids, Seehausen, 2006) or assembly processes that select for clades of closely related species (Cadotte *et al.*, 2010a; Helmus *et al.*, 2010), the correlation between SR and PD should be weaker. When the evolutionary information in the tree is biased towards particular clades – that is, some clades contain more evolutionary diversity than others – the correlation between SR and PD is also weakened (Fig. 3). Asymmetrical trees are likely more common in some regions with a long history of climatic or geological instability, as diversity in these regions is largely defined by unequal or temporally contingent speciation and extinction rates (Stebbins, 1974; Weir & Schluter, 2007). Symmetrical trees may be more likely in regions in which rates of extinction and speciation are relatively similar or more stable, such as in the tropics (Hawkins *et al.*, 2006; Weir & Schluter, 2007).

The relationship between the two abundance-weighted metrics (BSR and BED) is also dependent on the shape of the phylogenetic tree. A symmetrical tree with long internal branches yields a stronger correlation between BSR and BED (Fig. 4 a-i, iii). This is because short terminal branches (recent radiations) minimizes the variation in evolutionary diversity, so that BSR and BED are more similar. In addition, the strength of the correlation between range size and evolutionary distinctiveness alters the correlation between BSR and BED (Fig. 4a-ii). When range size and evolutionary distinctiveness are negatively correlated, that is rare species do not tend to be distinct and *vice versa*, the correlation between BSR and BED is stronger. This is because the relationship between BSR and BED is weakened when rare species also tend to be distinct and so receive high BED values, causing BED values to diverge from the abundance-weighted – but not phylogenetically informed – BSR metric.

Balance of information across clades
Symmetrical<-------->Asymmetrical

Balance of information across time
Terminal branches<------>Internal branches
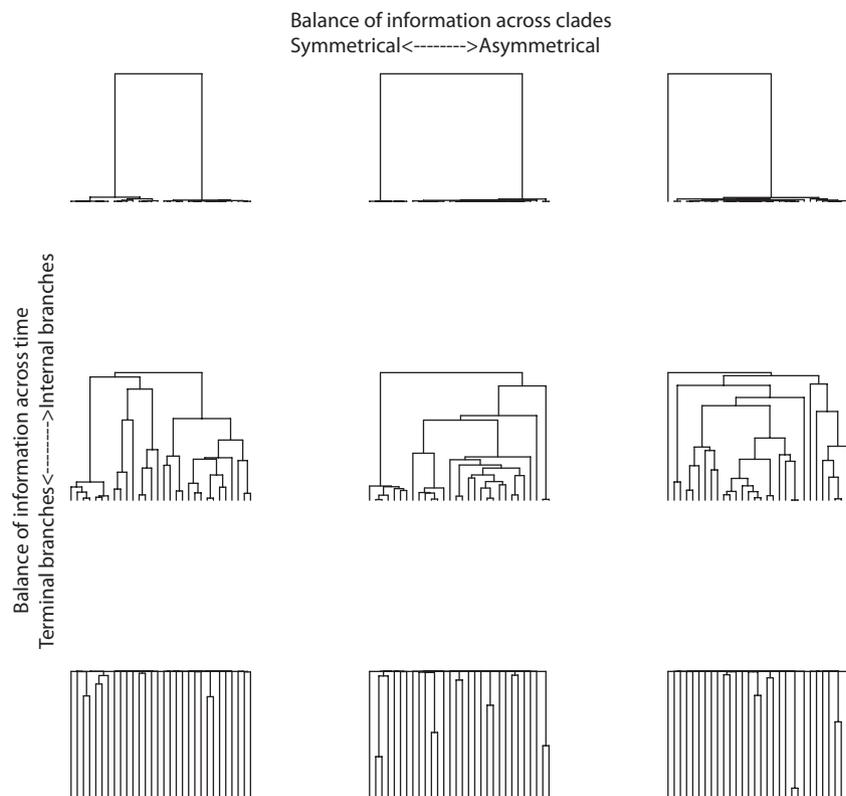
Figure 2 Examples of the range of tree topology are simulated. Trees vary in the distribution of information among species (*x*-axis), which is manifested as the degree of symmetry in dichotomous branching, and the distribution of information over time (*y*-axis), which is seen in the proportion of total branch length accounted for by internal vs. terminal branches.
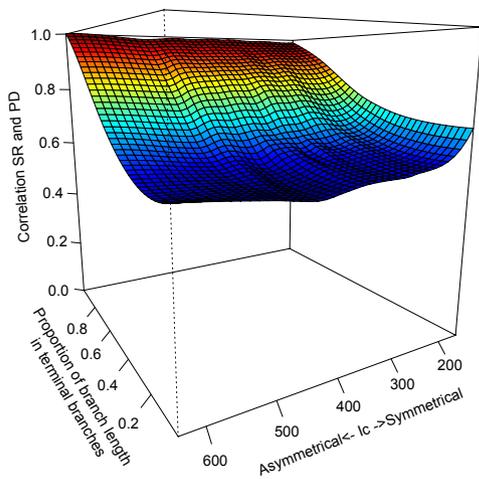
Figure 3 Spearman's correlation (*r*) between species richness and phylogenetic diversity as a function of tree topology.

Similarly, the abundance-weighted BED metric should have predictable relationships with PD and SR depending on the topology of the phylogenetic tree. In addition to the shape of the tree, the distribution of the abundance information in relation to the phylogenetic branch lengths changes the relationship between BED and PD. The correlation

between BED and PD should be strongest under those conditions that minimize the importance of the abundance weighting (as previously, when there is a negative correlation between range size and evolutionary distinctiveness) (Fig. 4b-ii) and when the phylogenetic tree has long terminal branches and high symmetry (Fig. 4b-i,iii).

Spatial structure and abundance distribution

The spatial structure of species ranges in a region can alter the expected relationship between the different types of diversity. We examined the role of spatial structure in species' ranges, in particular the likelihood that conspecifics be present in neighbouring sites. High autocorrelation in species presences' tends to result in small, compact ranges, while low autocorrelation results in patchy, but larger ranges. This spatial structure can create variation in the spatial distribution overall of SR. High autocorrelation could be reflected in the clumped distribution of tropical tree species, for example, while in other forests species might be highly dispersed, representing a system with low autocorrelation in species presences (Condit *et al.*, 2000). The correlation between metrics tends to be lowest when there is low spatial autocorrelation in species presences (Supplementary Fig. S1A). When spatial
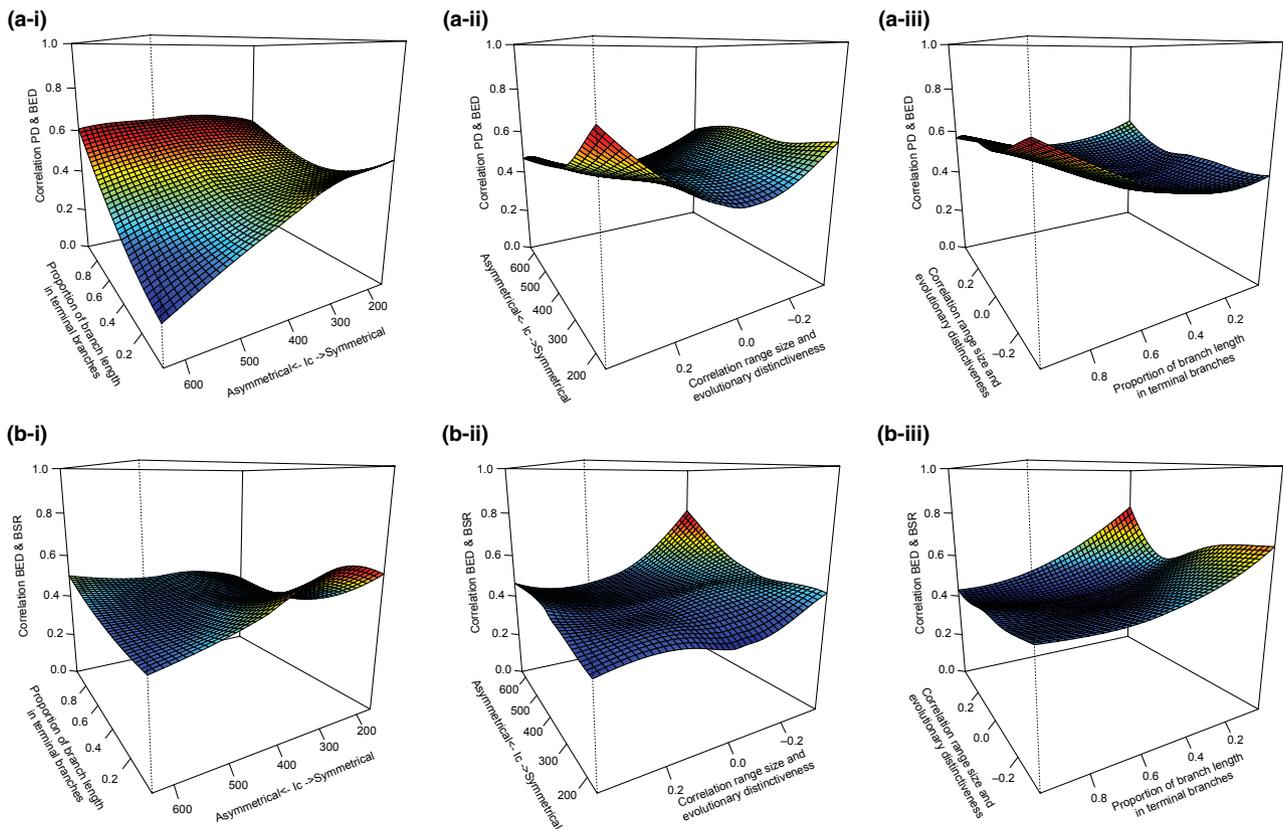
Figure 4 (a) Spearman's correlation (*r*) between biogeographically weighted species richness (BSR) and biogeographically weighted evolutionary distinctivness (BED), as a function of tree topology and species range sizes. (b) Spearman's correlation (*r*) between phylogenetic diversity and BED as a function of tree topology and species range sizes.

autocorrelation is low, the distribution of evolutionarily distinct species is more uneven through space, meaning that some sites may contain more phylogenetic information despite containing fewer species, and this weakens the relationship between the different metrics.

The distribution of species abundances should also affect the relationship between the SR, PD and the abundance-weighted BED and BSR metrics. When the relative abundance distribution is uniform (e.g. each abundance is equally likely to be observed), the correlation between abundance-weighted BED and BSR with SR and PD metrics should be highest. As the abundance distribution reflects the more realistic scenario in which most species have low abundances, and increasingly few species have high abundances (often represented with a log-normal distribution), abundance-weighted and non-abundance-weighted metrics will diverge.

Species pool size

The number of species in the regional species pool impacts the strength of the correlations between metrics. When species pools are small, the correlation between PD and SR is stronger, as communities contain relatively few species and proportionally more of the species pool; this means that the subtree for that community is relatively depauperate and the importance of tree shape is minimized (Supplementary Fig. S1B). Only for relatively large regional pools, above about 80 species, do sites with very low SR-PD correlations regularly appear. PD will always be highly correlated with SR for regional pools with relatively few species.

While species pool size has important consequences for PD-SR correlations, it is much less consequential for metrics that incorporate species range sizes or abundances. The effect of the abundance distribution or the degree of autocorrela-tion in species occupancy patterns is critically important for the abundance-weighted metrics and appears to mask any effect of the pool size.

CONCLUSIONS: SECURING THE PLACE FOR EVOLUTION AND RARITY IN CONSERVING BIODIVERSITY

If we are to conserve the diversity of life on Earth, then biodiversity conservation is an invaluable endeavour. It necessarily involves emphasizing or accommodating multiple priorities including social and economic valuations (Meffe & Viederman, 1995), the functioning of ecosystems and accounting for the services they provide (Chan et al., 2006) and the preservation of the diversity of life. Conservation efforts have focused on numerous aspects of diversity and have produced conflicting priorities (Fleishman et al., 2006). Species diversity, composition, rarity and evolutionary distinctiveness are three important aspects of diversity that are often considered, and conceptual approach that provides a meaningful way to compare differing aspects of diversity is of value. While incongruities in biodiversity metrics can highlight additional sites to protect in a conservation network (Forest et al., 2007; Devictor et al., 2010; Tucker et al., 2012), understanding how and why metrics diverge is important for larger scale conservation schemes, as well as informing our basic understanding of the evolutionary and ecological processes generating patterns of biodiversity. With a priori knowledge about several aspects of diversity, such as basic information about the evolutionary topology, species pool size or how species are distributed through space, one can predict whether different metrics should be weakly or strongly correlated (Fig. 5). This in turn would inform the types of diversity that should be prioritized in conservation
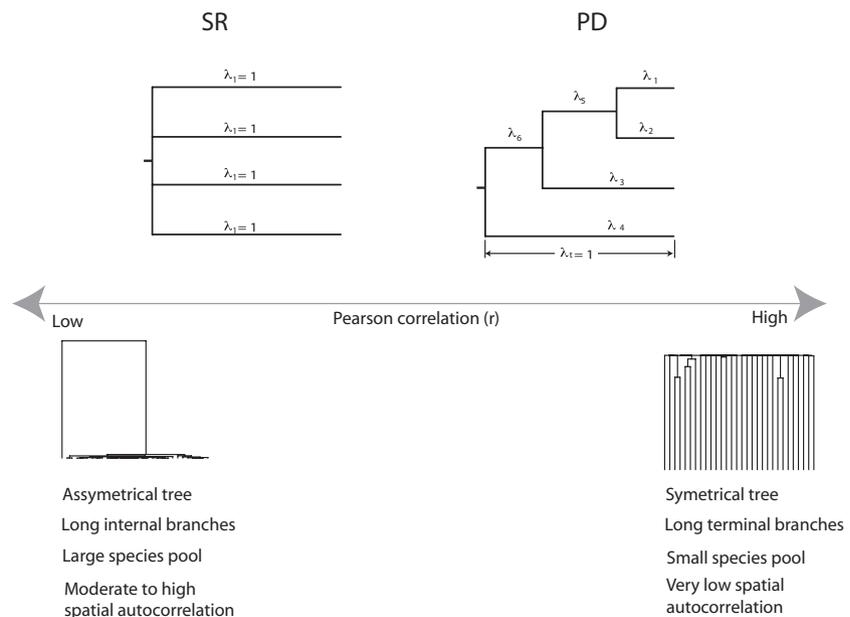
Figure 5 The expected correlation between species richness and phylogenetic diversity as a function of tree topology, species pool size and spatial autocorrelation.

assessments, as well as inform hypotheses about the processes behind the origin and maintenance of diversity in a region.

Two studies that conclude that SR and PD are highly correlated and thus recommend using SR as a surrogate for PD (Rodrigues *et al.*, 2005, 2011), can be contextualized given our understanding of how topology and species distributions affect SR-PD correlations. In one of these studies, which examines the surrogate value of SR for PD using an artificially simulated set of species and phylogenetic data (Rodrigues *et al.*, 2005), the species pool chosen was quite small – about 16 species. Given the influence of pool size on the strength of the correlations (Supplementary Fig. S1), we would expect that there would be a high correlation. This highlights an important message that when the number of species being evaluated for conservation is relatively small number, and especially if they are all members of a single clade (e.g., bumblebees, seahorses, etc.), then finding sites that maximize richness is sufficient to meet multiple conservation priorities.

In the second study that examines how well sites selected for SR also protect global mammal PD (Rodrigues *et al.*, 2011) also finds high surrogate value in SR. As Rodrigues and colleagues examined an extremely large species pool of 5258 mammal species globally, the expectation should be for a low correlation between SR and PD, although results become more variable as species pool size increases (Supplementary Fig. S1). It could be that for mammals, SR is an efficacious surrogate for PD. Alternately, other aspects of the Rodrigues study may lead to a higher correlation. Their phylogeny relied on a backbone supertree, and many species were added as polytomies, and polytomies necessarily increase the SR-PD correlation. Further, the spatial information that they were able to obtain was at a very coarse resolution with cells corresponding to approximately 23,000 km^2. This scale likely contains many species and phylogenetic branches, but would also undoubtedly mask subtle spatial patterns of species occupancy, autocorrelation and rarity. We have shown that spatial patterns of occupancy are quite important, and we have not assessed the consequences of aggregating spatial patterns into larger scales, but lumping together would increase the SR-PD correlation. While the study by Rodrigues *et al.* (2011) has important value for global conservation, the scale of this study may be mismatched to the finer scales that many managers focus on.

Widening the focus of conservation programs to account for multiple aspects of biodiversity is a worthy goal, but given the limited resources available for conservation and the lack of consensus about multiple forms of diversity, different measures of diversity have not often been used in biodiversity assessments. One approach to rectifying this is to develop a clearer understanding of how different measures of biodiversity relate to each other in a region. Here, we have attempted to reconcile inconstant findings on congruencies among different diversity. In regions where SR is not expected to be congruent with phylogenetic distinctiveness, re-examining how existing reserve networks protect the multiple aspects of biodiversity is critically important.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Simulation methods.

Figure S1 a) Effect of spatial autocorrelation in species occupancy on the correlation between the four biodiversity metrics; b) Effect of regional species pool size on the strength of the correlation between the four biodiversity metrics.

BIOSKETCH

Marc Cadotte is an Assistant Professor in the Department of Biological Sciences at the University of Toronto Scarborough and in Ecology and Evolutionary Biology at the University of Toronto. His research interests focus on the mechanisms generating patterns of diversity, from communities to biogeographical regions, and the consequences of changes in diversity. This work employs tools and hypotheses from models of species coexistence to patterns of evolutionary history, and applies to understanding the threats facing biodiversity.

Caroline Tucker is a doctoral student in the Department of Ecology and Evolutionary Biology at the University of Toronto. Her research interests include the mechanisms that maintain diversity in communities, particularly the role for environmental variability in species coexistence, and how these contribute to understanding and managing threats to biodiversity. She is also interested in developing multifaceted approaches to conservation prioritization to facilitate more complete protection of biodiversity and its associated functions.

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