



Rarest of the rare: advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales

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ABSTRACT

Aim In an era of global habitat loss and species extinction, conservation biology is increasingly becoming a science of triage. A key approach has been the designation of global biodiversity hotspots – areas of high species richness and endemism – prioritizing regions that are disproportionately valuable. However, traditional hotspot approaches leave absent information on species evolutionary histories. We argue that prioritizing the preservation of evolutionary diversity is one way to maximize genotypic and functional diversity, providing ecosystems with the greatest number of options for dealing with an uncertain future.

Location Global.

Methods We review methods for encapsulating phylogenetic diversity and distinctiveness and provide an illustration of how phylogenetic metrics can be extended to include data on geographical rarity and inform conservation prioritization at biogeographic scales.

Results Abundance-weighted metrics of evolutionary diversity can be used to simultaneously prioritize populations, species, habitats and biogeographical regions.

Main conclusion Policy makers need to know where scarce conservation funds should be focused to maximize gains and minimize the loss of biological diversity. By incorporating these evolutionary diversity metrics into prioritization schemes, managers can better quantify the valuation of different regions based on evolutionary information.

Keywords

Biodiversity, conservation biogeography, evolutionary distinctiveness, phylogenetics, phylogeography, species prioritization.

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INTRODUCTION

We live in an era of unprecedented global change. The unfortunate casualty of this is the Earth's biological diversity – from individual genes to entire ecosystems – we are losing aspects of diversity at an increasing rate. Scientists from a multitude of disciplines are now called upon both to offer solutions to reduce diversity loss and to inform policy makers about where to place limited resources to minimize the consequences of diversity loss. The science of conservation biology emerged in the early 1980s but was largely species specific, focussed at local scales and management orientated (Soulé, 1985, 1986). However, by the late 1980s, conservation

biologists were increasingly recognizing the global extent of the current diversity crisis and the need for global solutions (Myers, 1989). A scientific call-to-arms was put out to develop strategies to reduce the magnitude and impact of global diversity loss (Myers, 1989). A new discipline of conservation biogeography was soon to emerge, growing rapidly and in 2005 provided with a dedicated platform in the newly titled journal of *Diversity and Distributions: A Journal of Conservation Biogeography* (Whittaker *et al.*, 2005). The purview for conservation biologists had suddenly increased vastly in scale, and as a consequence, solutions were required for a new paradigm and to bridge the large gap between the urgency and scale of the problem and the resources available to mitigate it.

Conservation biogeography needed to become a science of triage – to focus scarce conservation resources to maximize conservation returns (Pressey *et al.*, 1993; Pressey, 1994; see also a more recent review by Marris, 2007). The critical challenge therefore was how to objectively prioritize among taxa and regions – the ‘agony of choice’ (Vane-Wright *et al.*, 1991).

In 1988, Norman Myers (Myers, 1988) published the first of a series of high-impact articles on global biodiversity hotspots (Myers, 1990, 2003; Myers *et al.*, 2000; Mittermeier *et al.*, 2004; Brooks *et al.*, 2006), identifying regions of high endemism and habitat loss as global conservation priorities. Currently, 34 global *hotspots* are recognized by Mittermeier *et al.* (2004), covering 2.3% of terrestrial habitats on Earth; this would, they argued, be the most effective approach to minimize species extinctions. Designating and protecting global hotspots represents the single largest conservation effort to date, with over \$750 million dollars invested (Brooks *et al.*, 2006). A common feature of these efforts was a species-based focus and, along with it, the implicit assumption that all species are of equal value. In a seminal article, Vane-Wright *et al.* (1991) argued that species are not all equal, and there should be added value to those that are more evolutionarily distinct – that is those that lack close relatives. By prioritizing evolutionary distinct species, conservation schemes may maximize the preservation of the evolutionary diversity of a clade. There are two major arguments for protecting evolutionary diversity, one pragmatic and one ethical. The pragmatic rationale is that by maximizing the conservation of evolutionary diversity, we maximize genotypic, phenotypic and functional diversity, thus providing biological systems with the most options to respond to a changing world (Vane-Wright *et al.*, 1991; Faith, 1992; Yachi & Loreau, 1999). The ethical rationale argues that, like the impulse to value and preserve buildings or landscapes with perceived cultural and historical value, maximizing the conservation of evolutionary diversity best preserves the immense history of the Earth, of which we are a small part. Weighting species differentially might alter our order of conservation prioritization – the price of misaligning conservation effort is high both for biodiversity and scarce conservation dollars.

While the theoretical justification for including information on species evolutionary histories in conservation has been made strongly (Vane-Wright *et al.*, 1991; Faith, 1992; Crozier, 1997; Mace *et al.*, 2003; Purvis *et al.*, 2005), data on evolutionary relationships have frequently been lacking. However, with the advent of rapid molecular DNA-sequencing technologies, following the development of PCR in the 1980s, there has been a phylogenetic revolution, with large advances in both the amount and quality of information on species phylogenies, depicting their evolutionary relationships (Savolainen & Chase, 2003), and phylogenetic methods (Gascuel, 2005). For the first time, it is now possible to quantify evolutionary value of species or habitats for large clades [e.g. mammals (Sechrest *et al.*, 2002; Davies *et al.*, 2008), birds (Mooers & Atkins, 2003) and flowering plants (Forest *et al.*, 2007)]. At the same time,

how we quantify evolutionary diversity has progressed, with a sophisticated set of metrics emerging. We briefly review existing approaches and draw attention to one current limitation – the lack of integration between phylogenetic diversity (PD) metrics and measures of biogeographic distribution and abundance. We provide an illustration of how information on both species evolutionary diversity and geographic range characteristics (e.g. the population density, range size or number of sites occupied by a species) can be combined to fill this gap.

CONSERVING BIODIVERSITY – WHAT DO WE MEAN BY ‘BIODIVERSITY’

The term biological diversity or ‘biodiversity’ became mainstream following the 1992 United Nations Earth Summit in Rio de Janeiro and was defined as ‘the variability among living organisms from all sources, including, “inter alia”, terrestrial, marine and other aquatic ecosystems, and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems’. The broad remit of conservation biologists has been to maximize the preservation of biodiversity or minimize its rate of loss – the stated goal of the Convention on Biological Diversity 2010 Biodiversity Target (Secretariat of the Convention on Biological Diversity 2003). Despite the inclusive definition of biodiversity, practical conservation efforts have remained focused on species (but see, Rissler *et al.*, 2006). One practical reason for this focus is that species richness is relatively easy to quantify and provides an intuitive metric that allows simple rankings (Gaston, 1996). In contrast, it can be very difficult to measure feature diversity directly or even determine which features we should be measuring (Roy & Foote, 1997; Purvis & Hector, 2000). One approach is to focus efforts on habitats rather than species, maintaining a diversity of habitats will likely ensure that a diversity of taxa are represented (Margules & Usher, 1981). Nonetheless, habitat-based approaches are likely to be insufficient on their own. Habitats differ widely in the taxonomic diversity they represent and the ecosystem services they provide, hence, as is the case for species, all habitats are not equal – there is still then the requirement to prioritize among them. Information on the shared and non-shared evolutionary diversity of species provides a common currency to compare both the conservation worth of habitats and individual species.

Phylogenetic trees – branching diagrams depicting the evolutionary relationships of species – allow us to quantify the evolutionary information represented within groups of taxa (see succeeding section for formal derivations). The central tenet underlying phylogenetic approaches is the assumption that closely related taxa will tend to be more similar in their physiologies and ecologies than more distantly related taxa (Harvey & Pagel, 1991; Harvey, 1996), a concept that can be traced back to Darwin’s observation that ‘*species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure*’. Phylogenetic metrics therefore provide a more

encompassing measure than ones based upon a single or a few select traits (Faith, 1994, 2002; Crozier, 1997). As a consequence, maximizing the preservation of PD will also tend to maximize the preservation of feature diversity, including unmeasured, but ecologically important traits.

As we touched upon in the preceding section, there are two broad arguments for maximizing evolutionary (or feature) diversity, one pragmatic, the other ethical. For purposes here, we focus on the former. First, theory and experimental data suggest ecosystem services increase with the number of species because of greater dispersion over niche space (Naeem *et al.*, 1994; Tilman *et al.*, 1997; Cardinale *et al.*, 2006). If closely related species share similar ecologies, we would predict them to fall into similar functional groups, and the distribution of trophic interactions will reflect phylogeny (Cattin *et al.*, 2004; Ives & Godfray, 2006). Evolutionary diversity might then be important for maintaining ecosystem services, perhaps more so than species richness (e.g. Cadotte *et al.*, 2008). Second, the phylogenetic structure of ecological communities might also influence community susceptibility to invasion, for example, if invasive species require empty niches to invade, phylogenetically depauperate communities may be more vulnerable – Darwin's naturalization hypothesis – although evidence is conflicting (Duncan & Williams, 2002; Strauss *et al.*, 2006; Procheş *et al.*, 2008). Third, evolutionary diversity might be key to maximizing options in an uncertain future (Vazquez & Gittleman, 1998; Avise, 2005).

In the absence of detailed phylogenetic trees, one approach is to use taxonomy as a surrogate for phylogeny. Higher taxonomic levels, for example genera or families, might equate to clades deeper in the phylogenetic tree, so maximizing the representation of families or genera rather than species would perform better at capturing evolutionary diversity (Rodrigues & Gaston, 2002); or taxonomic hierarchies can be surrogate phylogenies (Crozier *et al.*, 2005). However, taxonomies can at best only approximate evolutionary relationships and frequently rely upon untested assumptions of monophyly. In addition, taxonomy-based approaches cannot capture the variation in age and diversity of higher taxa (Crozier *et al.*, 2005). Nonetheless, taxonomies may still provide a useful approximation, especially if they are phylogenetically informed. One relevant example is provided by the Angiosperm Phylogeny Group (APG, APGII APGIII), which has provided a reclassification of flowering plant families based upon reciprocal monophyly (Chase *et al.*, 2000). Of course, it is important to note that detailed phylogenetic information is required to construct such 'phylo-taxonomies', and the APG group represents the combined output of a multi-institute consortium over many years.

HISTORY OF CONSERVATION PHYLOGENETICS

Modern conservation phylogenetics can be traced back to two key articles published by Vane-Wright *et al.* (1991) and Faith (1992). These authors developed two general metrics for encapsulating phylogenetic information that differed in

approach; the first, taxonomic distinctness (TD) (Vane-Wright *et al.*, 1991; see Box 1), measures a species distinctiveness relative to other species, as the number of evolutionary divergences preceding the species in question within the clade of interest. The second, Faith's (1992) PD sums the branch lengths of the phylogenetic tree representing the extant species in a region. As practical conservation tends to focus on areas rather than species and because TD cannot be simply summed across species to provide an aggregate index evolutionary distinctiveness (Rodrigues *et al.*, 2005), PD has been the more commonly adopted metric in the conservation phylogenetic literature. We follow this lead, but end by reviewing recent developments that have seen a resurgence of interest in TD-type approaches.

Phylogenetic diversity

If branch lengths between nodes are scaled in units of time (e.g. millions of years), PD can be represented in millions of years of evolutionary history (e.g. Purvis *et al.*, 2000a; Sechrest *et al.*, 2002; Mooers & Atkins, 2003; Mooers *et al.*, 2003). Alternatively, branch lengths might also be scaled to represent number of substitution events or character state changes (e.g. Crozier, 1992; Diniz-Filho, 2004), which might be of interest given *a priori* information on the importance of particular traits or genes. For simplicity, we here assume branch lengths are calibrated in units of time, and variance in feature diversity increases in proportion to the phylogenetic distance separating taxa, for example, as might be characterized by a model of Brownian evolution (Felsenstein, 1985), although this assumption can be modified (Diniz-Filho, 2004). Mooers *et al.* (2005) argue that time is the best metric for deriving PD, because (1) it might best capture information content as measured on other scales if the probability of character state change is correlated with time (cf. Brownian); (2) it provides a metric comparable across taxa and (3) it is a readily comprehensible metric for policy making and public understanding.

Surprisingly, phylogenies can be relatively robust to even catastrophic extinction scenarios. Using simulations, Nee & May (1997) demonstrated that over 80% of PD may be preserved even when 95% of species are lost. However, their model assumed that extinction strikes taxa at random – coined the '*field of bullets*' (Raup *et al.*, 1973), in which survival is not contingent upon inherent species attributes, but simply down to chance – that is, the bullets are not targeted. Empirical data suggest phylogenetic non-randomness in extinction risk is a common feature in many taxa, including mammals (Purvis *et al.*, 2000a); flowering plants (Vamosi & Wilson, 2008), birds (Russell *et al.*, 1998; Von Euler, 2001) and amphibians (Cooper *et al.*, 2008). In addition, Nee and May evaluated the expected loss (EL) of PD from coalescent trees, which tend to be more topologically balanced than observed phylogenetic topologies (Heard, 1992). The loss of PD under phylogenetically non-random extinction is much greater because we lose not only the unique evolutionary branches from which extinct species descend, but also the network of branches that form

Box 1: Measures of evolutionary distinctiveness (ED)

The original concept to evaluate the conservation value of a species according to its taxonomic distinctiveness was introduced by Vane-Wright *et al.* (1991) and can be represented by the equation (following Redding *et al.*, 2008):

$$TD(T, i) = \frac{1}{\sum_{v \in q(T, i, r)} \text{deg}_{\text{out}}(v)}$$

where, for a tree, T , the set $q(T, i$ and $r)$ includes the node splits between species i and the root of the tree, r . The value of $\text{deg}_{\text{out}}(v)$ for any node is 2 in a perfectly resolved bifurcating tree and > 2 for a node containing a polytomy. Branch lengths are not included in this formulation, and it is sensitive to the resolution of the phylogeny.

Two approaches for adding branch information to metrics of taxonomic distinctiveness have recently been proposed. The first, equal splits (ES; Redding & Mooers, 2006; Redding *et al.*, 2008), distributes phylogenetic diversity (PD) among species as:

$$ES(T, i) = \sum_{e \in q(T, i, r)} \left(\lambda_e \prod_{v \in a(T, i, e)} \frac{1}{\text{deg}_{\text{out}}(v)} \right)$$

where the length of each branch, λ_e , is partitioned by the number of branches directly subtending the node, v , down to the tip, species i (see Fig. 1a for an illustration). A conceptually similar measure, fair proportion or ED (Isaac *et al.*, 2007), instead partitions branches by the total number of species subtending it, not just the branches directly below it (see Fig. 1b). It is calculated as:

$$ED(T, i) = \sum_{e \in q(T, i, r)} \left(\lambda_e \cdot \frac{1}{S_e} \right)$$

where e is an branch of length λ in the set $s(T, i, r)$ connecting species i to the root, r , and S_e is the number of species that descend from edge e . A nice feature of both ES and ED is that they both sum to PD. In this article, we use the latter, ED, metric to derive a biogeographically weighted evolutionary distinctiveness measure to help inform conservation prioritization.

connections amongst them (Purvis *et al.*, 2000a). Furthermore, greater topological imbalance also elevates PD loss, even under random extinction, because of greater frequency of species-poor clades with long, distinct evolutionary histories (Heard & Mooers, 2002). The actual loss of evolutionary history under projected extinction scenarios is therefore likely to be much greater than suggested from Nee and May's simulations.

Despite evidently strong theoretical grounds for incorporating PD into conservation prioritization schemes, PD and species richness frequently covary closely (e.g. Sechrest *et al.*, 2002; Davies *et al.*, 2008). Significant divergence in gross spatial patterns is only predicted under a rather narrow set of circumstances: the phylogeny should be imbalanced to allow differential contribution of PD between assemblages, there should be a phylogenetic component to the spatial distribution of species, and older species should inhabit smaller ranges and species-poor areas (Rodrigues *et al.*, 2005). However, because conservation tends to work at the margins, even small gains can impact prioritization schemes (Faith, 1992; Faith & Baker, 2006). Furthermore, when the factors shaping regional diversity patterns encompass evolutionary processes, including speciation and extinction, different areas might sample from different species pools with different underlying phylogenies, causing divergence in the distribution of taxonomic richness and PD (e.g. Forest *et al.*, 2007).

Even when we do not predict large differences in taxonomic versus PD patterns, PD might still be a powerful conservation metric because (1) time-based evolutionary heritage provides a powerful metaphor and can easily be equated to cultural heritage (Mooers *et al.*, 2005); (2) PD is less sensitive to the changing whims of taxonomists (Isaac *et al.*, 2004) – but may be more sensitive to incomplete taxonomic sampling; (3) advances in molecular techniques allow rapid biodiversity assessment where taxonomy is poorly understood, or species identification is problematic (Pons *et al.*, 2006).

Taxonomic distinctiveness

Vane-Wright's TD measure enumerates the number of splits in a species ancestral lineage (Box 1), and thus a species with few preceding splits is more taxonomically distinct than one nested within a larger radiation. We consider two recent derivations that incorporate branch lengths into calculations of distinctiveness. The first, equal splits (ES – Redding & Mooers, 2006; Redding *et al.*, 2008; see Box 1) divides an edge by the number of subtending branches directly below it (Box 1, Fig. 1a). In the second metric, called ED or fair proportion (Isaac *et al.*, 2007; see Box 1), internal branches are equally divided by all species below it, regardless of nested tree structure (Box 1, Fig. 1b). Cadotte *et al.* (2010) incorporated abundance information into the latter, ED, measure to generate a metric of

abundance-weighted evolutionary distinctiveness (AED). Here, we extend upon this approach to evaluate distinctiveness at biogeographical scales, which encapsulates the conservation worth of both species and regions.

PHYLOGENETIC LINKS TO BIOGEOGRAPHICAL RARITY

While evolutionary diversity can encapsulate variation among many traits, it only represents a single axis of conservation importance. Other important, although not necessarily independent, axes include abundance rarity, geographical rarity, utilitarian services, ecological function and charisma (Avisé, 2005). Of greatest concern for conservationists are species of low abundance and restricted range, with range size frequently the single most important predictor of extinction risk (Purvis *et al.*, 2000b,c; Cardillo *et al.*, 2005). Species with small ranges are vulnerable, because a single localized threat can impact their entire distribution, whereas species with low abundances are increasingly susceptible to demographic stochasticity. In addition, low abundance is frequently associated with species traits linked to high risk, for example, large body size and low fecundity (Cardillo *et al.*, 2005). Species with both small ranges and low abundance therefore suffer double jeopardy, from extrinsic threats and intrinsic vulnerability (Rabinowitz, 1981).

Both the ES and ED measures of distinctiveness (Box 1) have been extended to incorporate extinction risk for assessing conservation worth. Redding & Mooers (2006) quantify the loss of evolutionary history, EL, as:

$$EL_i = ES_i \cdot Pe_i \tag{1}$$

where the ES of species *i* is multiplied by its probability of extinction, *Pe*. Similarly, Isaac *et al.* (2007) extended their ED measure to include global endangerment (GE). Their metric, EDGE (evolutionarily distinct and globally endangered), is calculated as:

$$EDGE_i = \ln(1 + ED_i) + GE_i \cdot \ln(2) \tag{2}$$

In their formulation, GE values are taken from the International Union for Conservation of Nature (IUCN) Red

List categories (<http://www.iucnredlist.org>). EDGE values are interpreted as the log-transformed, species-specific EL of evolutionary diversity, where each increment in Red List ranking represents a doubling of extinction risk (Isaac *et al.*, 2007). Equations 1 and 2 are formulated identically, save a log-transformation and what differs is how they measure ED and estimate extinction risk.

Advances in our knowledge of species distributions and threats have allowed biologists to make detailed recommendations about areas with rare and threatened species (Cowling *et al.*, 2003; Rouget *et al.*, 2003). For the most part spatial mapping has not considered phylogenetic metrics, which could help refine habitat prioritization. Although some recent work has also begun to look at spatial hotspots of PD (Sechrest *et al.*, 2002; Forest *et al.*, 2007), information on species vulnerabilities has not been considered. For reasons outlined previously, lineages that are both evolutionary distinct and geographically restricted may be of greatest conservation concern and should therefore be weighted accordingly. Recently Rosauer *et al.* (2009) introduced a new metric, phylogenetic endemism (PE), to weight the CV of a region by both the phylogeny and range size of constituent species, as:

$$PE = \sum_{e \in p(T,c,r)} \frac{\lambda_e}{R_e} \tag{3}$$

where, for each branch length, λ_e , in the set of branches for tree *T*, connecting the set *c* species within a cell (or spatial unit/sites) to the root, *r*, is divided by the range size, *R_e*, for that edge. Thus, high PE regions are those where species capture a large fraction of a clade’s evolutionary diversity and tend to have small ranges. PE provides a relative measure for comparing multiple regions. Later, we outline an alternative approach that allows us to quantify the amount of ED at either a single site or across larger regional scales. Our approach simultaneously measures the conservation worth of individual species, multispecies sites and multisite regions. We reformulate the AED from Cadotte *et al.* (2010), which partitions phylogenetic information among individuals, derived from the Isaac *et al.* ED metric (see Box 1):

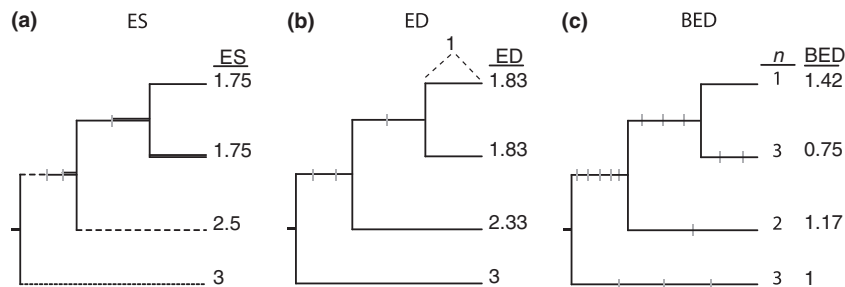


Figure 1 Three methods of partitioning phylogenetic diversity (PD). (a) Equal splits (Redding *et al.*, 2008), ES, hierarchically partitions branch lengths by the number of descendent edges. (b) Evolutionary distinctiveness (Isaac *et al.*, 2007), ED, partitions branches by the total number of species descending from them. (c) Biogeographically weighted evolutionary distinctiveness, BED, extends ED by partitioning PD by the numbers of populations or sites (*n*) descending from a branch.

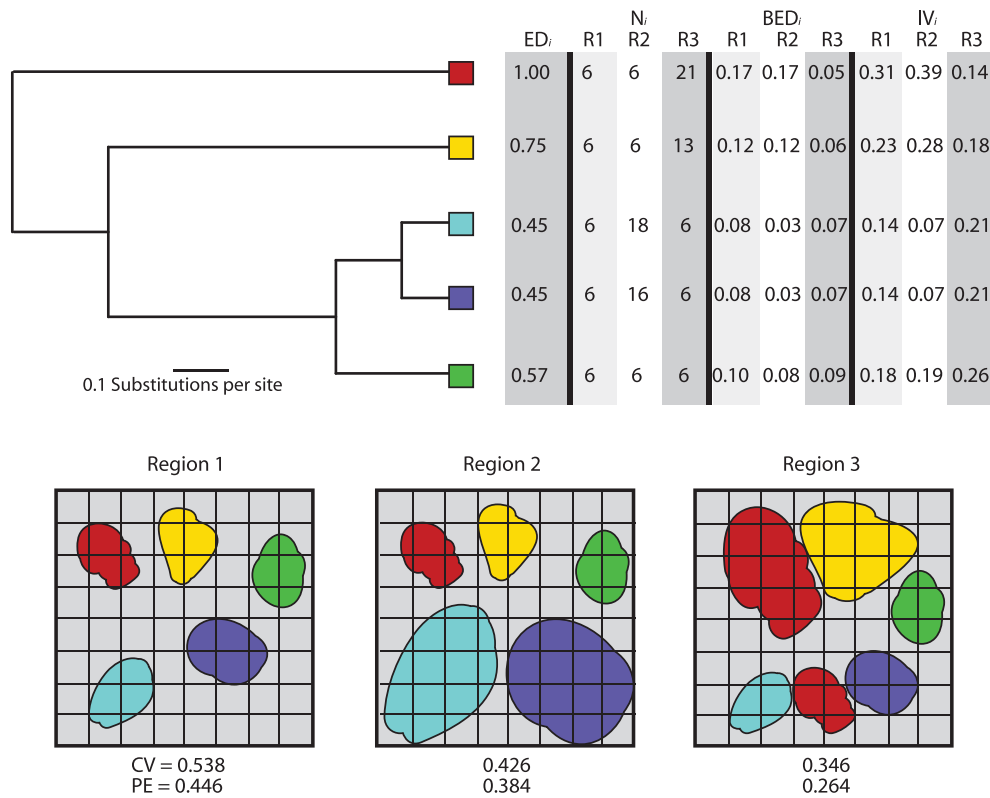


Figure 2 An example using a phylogeny and three hypothetical regions to illustrate the metrics proposed here. Each species (represented by different colours) occupies some number of sites (grid cells) in three regions, R1, R2 and R3. Biogeographically weighted evolutionary distinctiveness and the species-specific importance value (IV) are shown for each species. For regions R1 and R2, the red and yellow species are the most distinct and have the highest IV values. However, in R3, the less distinct species (cyan, purple and green) have higher IV values because of their rarity. Region R1 has the highest conservation value, because all species are rare, while region R3 has the lowest value because the most evolutionary distinct species are common.

$$AED(T, i) = \sum_{e \in q(T, i, r)} \frac{\lambda_e}{n_e} \quad (4)$$

where n_e is the total abundance of species that descend from branch e , in the set $q(T, i, r)$ which includes the branches connecting species i to the root, r , of tree T [see ‘biogeographically weighted evolutionary distinctiveness (BED)’ Fig. 1c]. We note the obvious similarity between PE and AED, both independently developed. We use the different notations here to highlight the simple difference that PE, as formulated, is evaluated across all species within a clade, whereas AED can be estimated at the species, population or individual level.

A WAY FORWARD: MEASURING SITE CONTRIBUTION TO EVOLUTIONARY DIVERSITY

By reformatting Equation (4), we calculate a BED measure for each site or population of species i , BED_i with n_e representing the number of sites or populations (Fig. 1c), but unlike PE, calculated to the individual species or population level, which may themselves be the target of conservation action.

The sum of the individual BED values equals total PD, meaning that we can assess the proportion of the total PD

contained by single populations or sites. Furthermore, we can use the BED_i values to evaluate species importance values, IV_i , within and across sites, relative to other species.

$$IV_i = BED_i / \sum_{i=1}^S BED_i \quad (5)$$

Thus, high IV species have populations with high ED relative to those for populations of other species. This formulation assumes that the branches connecting individual populations together, within a species, have a length of zero. This equation can easily be extended to account for intraspecific differences (see Appendix 2 in Cadotte *et al.*, 2010) – for example, the set used to calculate BED could be to the population, where populations have differing branch lengths, or to the species, where it is the mean of population metrics. The total ED encapsulated within site t with overlapping species is then:

$$ED_t = \sum_{i=1}^S BED_i \quad (6)$$

Thus, to calculate the conservation value (CV) of region L , we can sum the ED_t values standardized by the total number of sites sampled, N :

$$CV_L = \frac{\sum_{t=1}^N \sum_{i=1}^S \left(\sum_{e \in q(T,i,r)} \frac{\lambda_e}{n_e} \right)}{N} \text{ or } CV_L = \frac{\left(\sum_{t=1}^N ED_t \right)}{N} \quad (7)$$

This set of metrics allows us to consider the conservation worth of species (IV), sites with multiple species (ED_t), and regions encompassing multiple sites (CV_L). These metrics will be available in the forthcoming R package: *ecoPD* (Regetz, Cadotte and Davies). We use an example phylogeny and three regions to illustrate how to interpret these metrics (Fig. 2). The red species is the most evolutionarily distinct ($ED = 1$), the blue and purple are the least evolutionary distinct species (both $ED = 0.45$). The species occupy between 6 and 21 sites (a site is a grid square in Fig. 2), and BED_i values represent the fraction of total PD (3.225) represented by an individual site of species i (i.e. $PD = \sum_i^S BED_i \cdot n_i$). In region 1 (R1), a loss of a red site (site containing a red species) would be of more than twice as much concern than the loss of a purple site (site containing a purple species: $BED_{lost} = 0.17$ vs. 0.08, respectively). These values show the relative uniqueness of each individual site, and thus their relative conservation worth within the region. In region 2, the relative value of red sites is further emphasized as the number of purple and blue sites increases. Using these BED_i values, we calculate the regional conservation worth, standardized by the number of sites in the region (CV_L ; Equation 7). In this example, region 1 has the highest value, since all species are rare, and region 2 is the next most valuable, since the most evolutionarily distinct species are relatively rarer. Region 3 is given the lowest ranking, because evolutionary distinct species are the most common. Rosauer's PE (Rosauer *et al.*, 2009) also ranks the regions in the same order as our metric (Fig. 2). The key feature of our metrics is the ability to partition evolutionary information across different scales. At the regional scale, CV is a product of individual BED values, which in turn reflect the amount of PD contained within single populations or sites and can thus be linked to individual species values. For simplicity, this example does not contain overlapping ranges, but these metrics work with more complicated distributional data – allowing conservation valuation of diverse regions.

CONCLUSION

The global biodiversity crisis requires global solutions. However, because conservation resources are limited, it is essential that we develop robust methods for prioritizing conservation efforts. Increasing availability of detailed phylogenetic and distribution data now allows conservation biologists to use the evolutionary diversity of species to inform conservation priorities. Evolutionary diversity might be important in representing feature diversity, and thus future options in an era of global change. We have presented a new metric that provides the potential to simultaneously quantify the evolutionary distinctiveness of populations or sites, and the conservation worth of individual species or

entire regions. These new tools provide additional information with which to guide conservation decision-making. However, the value of these metrics relies on the quality of the underlying phylogenetic and distributional data. While taxonomy-based hierarchies or broad distributional categories provide some basis for informing decision-making, at more local scales, at which conservation acts, the availability of detailed and high-quality data will be critical.

ACKNOWLEDGEMENTS

The authors thank Dave Richardson for the invitation to write this article and to Jim Regetz for help with creating the R code for some of these metrics. For T.J.D., part of this work was conducted as a Postdoctoral Associate at the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant #DEB-0553768), the University of California, Santa Barbara and the State of California.

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BIOSKETCHES

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Author contributions: Both authors conceived, carried out the analysis and wrote the article.

Editor: David Richardson