Contributed Paper

Incorporating Geographical and Evolutionary Rarity into Conservation Prioritization

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Abstract: *Key goals of conservation are to protect both species and the functional and genetic diversity they represent. A strictly species-based approach may underrepresent rare, threatened, or genetically distinct species and overrepresent widespread species. Although reserves are created for a number of reasons, including economic, cultural, and ecological reasons, their efficacy has been measured primarily in terms of how well species richness is protected, and it is useful to compare how well they protect other measures of diversity. We used Proteaceae species-occurrence data in the Cape Floristic Region of South Africa to illustrate differences in the spatial distribution of species and evolutionary diversity estimated from a new maximum-likelihood molecular phylogeny. We calculated species richness, phylogenetic diversity (i.e., summed phylogenetic branch lengths in a site), and a site-aggregated measure of biogeographically weighted evolutionary distinctiveness (i.e., an abundance weighted measure that captures the unique proportion of the phylogenetic tree a species represents) for sites throughout the Cape Floristic Region. Species richness and phylogenetic diversity values were highly correlated for sites in the region, but species richness was concentrated at a few sites that underrepresented the much more spatially extensive distribution of phylogenetic diversity. Biogeographically weighted evolutionary diversity produced a scheme of prioritization distinct from the other 2 metrics and highlighted southern sites as conservation priorities. In these sites, the high values of biogeographically weighted evolutionary distinctiveness were the result of a nonrandom relation between evolutionary distinctiveness and geographical rarity, where rare species also tended to have high levels of evolutionary distinctiveness. Such distinct and rare species are of particular concern, but are not captured by conservation schemes that focus on species richness or phylogenetic diversity alone.*

Keywords: Cape Floristic Region, conservation biogeography, evolutionary distinctiveness, phylogenetics, species prioritization

Incorporación de la Rareza Geográfica y Evolutiva en la Priorización de la Conservación

Resumen: *Las metas clave de la conservación son proteger tanto a especies como a la diversidad funcional y genética que representan. Un enfoque basado estrictamente en especies puede dejar de representar a especies raras, amenazadas o distintas genéticamente y sobrerepresentar especies de distribución amplia. Aunque las reservas son creadas por diversas razones, incluyendo económicas, culturales y ecológicas, su eficacia ha sido medida principalmente en términos de qué tan bien se protege la riqueza de especies. Utilizamos datos de la ocurrencia de especies de Proteaceae en la Región Florística del Cabo en Sudáfrica para ilustrar diferencias en la distribución espacial de especies y diversidad evolutiva estimadas a partir de una filogenia molecular nueva. Calculamos la riqueza de especies, la diversidad filogenética (i.e., suma de longitudes de ramas filogenéticas en un sitio) y una medida agregada de la unicidad evolutiva ponderada biogeográficamente (i.e., una medida ponderada de abundancia que captura la proporción única del árbol filogenético que representa una especie) para diferentes sitios en la Región Florística del Cabo. La riqueza de especies y*

los valores de diversidad filogenética estuvieron altamente correlacionados en sitios de la región, pero la riqueza de especies se concentró en unos cuantos sitios que no representaron la distribución más extensa espacialmente de la diversidad filogenética. La diversidad evolutiva ponderada biogeográficamente produjo un esquema de priorización distinto de las otras 2 medidas y resaltó a los sitios sureños como prioridades de conservación. Los altos valores de diversidad evolutiva ponderada biogeográficamente en estos sitios fueron el resultado de una relación no aleatoria entre la unicidad evolutiva y la rareza geográfica, donde las especies raras también tendieron a presentar altos niveles de unicidad evolutiva. Tales especies únicas y raras son de particular preocupación, pero no son capturadas por los esquemas de conservación que solo enfocan la riqueza de especies o la diversidad filogenética.

Palabras Clave: biogeografía de la conservación, filogenia, priorización de especies, Región Florística del Cabo, unicidad evolutiva

Introduction

Thirty-four regions with high species diversity, levels of endemism, and probability of habitat loss are currently defined as "biodiversity hotspots" (Mittermeier & Cemex 2004). These criteria implicitly assume species (with a focus on endemic species) are the focus of conservation efforts. Similarly, evaluation of the effectiveness of existing conserved areas often focuses on taxonomic diversity (Fleishman et al. 2006). Conservation efforts seek to protect not only species, but also the underlying functional and genetic diversity they represent. A strictly species-based approach may underrepresent rare, threatened, or genetically distinct species and overrepresent widespread species (Faith 1992; Moritz 2002). The evolutionary relations of species capture the genetic and likely the phenotypic and ecological similarities among species (Erwin 1991; Harvey & Pagel 1991). Phylogenetic information therefore provides a convenient way to capture the multidimensional differences and similarities among species (Faith 1994, 2002). Phylogenetic diversity (PD) is commonly measured with (Faith's 1992) method, which is the sum of branch lengths in the tree connecting all resident species of interest in a site. It may also be useful to account for evolutionary distinctiveness among species, which can be applied to the conservation of multiple, often unmeasured, and hard to measure ecological traits (Crozier 1997).

Measures of evolutionary distinctiveness partition branches on the basis of the number of species descending from them, and the measure gives priority to species with less redundant genetic information (Isaac 2007; Redding et al. 2008). Biogeographically weighted evolutionary distinctiveness (BED) values scale evolutionary distinctiveness values by species' range sizes. When BED is summed for all species in a site, this represents the site or total biogeographically weighted evolutionary distinctiveness (BED$_T$), and BEDT allows BED to be compared with other site-level variables such as species richness or PD. A focus on evolutionary distinctiveness suggests that species lacking close relatives, and thereby representing a greater proportion of the unshared evolutionary diversity of a clade, should be prioritized (Vane-Wright et al. 1991).

Just as it is common to consider the geographical distribution of species diversity, it is becoming common to examine the geographical distribution of PD throughout biogeographical regions (e.g., Sechrest et al. 2002; Forest et al. 2007). However, it is unclear whether PD provides additional information about the distribution of diversity beyond simple maps of species richness (Moritz 2002; Rodrigues & Gaston 2002; Forest et al. 2007). Using simulations, Rodrigues et al. (2002) showed that in the majority of cases, species richness is a good surrogate for PD. They concluded that only where species with high evolutionary distinctiveness have narrow geographic distributions does PD provide additional information. Therefore, in most theoretical scenarios, species richness is an acceptable proxy for PD.

Contrary to theoretical expectations, several researchers have found that PD may diverge significantly from taxonomic richness (Moritz 2002; Forest et al. 2007). For example, in the Cape of South Africa, there is a strong biogeographical gradient in the relation between taxonomic richness and PD, whereby the relative level of PD, adjusted for species richness, increases from west to east, though this was observed for a phylogenetic tree resolved to the level of genus (rather than species) (Forest et al. 2007). Rodrigues et al. (2005) suggest species richness and PD are uncorrelated when phylogenetic trees are very asymmetrical; thus, there are both species with long- and short-terminal branches, and ancient species tend to have limited ranges. One method for capturing this variation is to use metrics that incorporate both PD and range size.

Methods for integrating evolutionary history and geographical rarity have been developed (Rosauer et al. 2009; Cadotte & Davies 2010). BED$_T$ (Cadotte & Davies 2010) weights diversity as a function of range size and evolutionary distinctiveness (sensu Isaac 2007) such that phylogenetic branch lengths are inversely weighted in proportion to the descendant species' number of populations or range sizes. Thus, species with high evolutionary distinctiveness and greater rarity receive more weight (Rosauer et al. 2009; Cadotte & Davies 2010). Higher weights are assigned to more geographically restricted species because species with small ranges, on average, have a higher probability of extinction than their more

widely distributed congeners (Gaston 2003; Jones et al. 2003). Such range-weighted metrics are also beginning to be used for assessments of biological diversity. For example, Huang et al. (2011) used these metrics to assess the distribution of diversity (species richness and BED_T) in China.

The positioning of reserves is often motivated by economics or politics rather than (or in addition to) ecological principles. However, assessing the effectiveness of existing reserve networks is critical if one is to maximize conservation returns by making efficient choices about the use of future resources. In addition, as the importance of alternative conservation measures is increasingly recognized, contrasting alternative diversity metrics may help highlight gaps in current reserve networks and focus discussion on identifying conservation priorities. Here we used 4 alternative metrics of diversity–species richness, PD, BED_T, and biogeographically weighted species richness (BSR)—to examine the distribution of biological diversity of Proteaceae in the Cape Floristic Region of South Africa.

Methods

Study Area

The Cape Floristic Region is known for its floristic diversity and high degree of endemism: 70% of the 9000 plant species found there are endemic to the region (Goldblatt & Manning 2002; Myers et al. 2000). It is located on the southwestern tip of South Africa and had an original extent of <80,000 km^2. One-third of the region's flora are classified as of conservation concern on the International Union for Conservation of Nature Red List and a high proportion of those are threatened or near-threatened (Raimondo et al. 2009). The region is characterized by cool, wet winters and hot, drought-prone summers. It includes regions of Mediterranean-type climate in the southwest. Rain falls in the summer in the east and in winter in the west (Schultze 1997). A longitudinal gradient of taxonomic richness exists; the western Cape has the highest species richness (Forest et al. 2007). The Fynbos biome is 1 of the 2 biomes in the Cape Floristic Region. It consists of Mediterranean shrublands. Proteaceae species are a major component of the Fynbos biome; there are over 330 taxa in the region and all are endemic or nearly endemic (>80% of range within the Cape Floristic Region).

Data Sources

The Protea Atlas Project provides estimates of Proteaceae species presence and abundance in the Fynbos biome. It has over 250,000 species records that were collected from 1991 to 2001 (Protea Atlas Project 2006) (Rebelo 2002). Species records were treated as point values and placed within 1'×1' grid cells (~1.55 × 1.85 km rectangles). The resulting area for which records were available covered ~36,000 grid cells. Range size was defined as the number of cells in which a species was recorded as present.

Phylogeny

We constructed a molecular phylogeny containing all Proteaceae species found in the Cape Floristic Region. To reduce the effects of biased taxon sampling in the region of interest on tree construction, we included all global Proteaceae genera that had sequences available GenBank and then pruned the tree to include only those taxa in the data set. We used the PhyLoTA browser to identify 30 informative sequence clusters available in GenBank (Bilofsky & Burks 1988; Sanderson et al. 2008) (Supporting Information). When there were multiple sequences for a species, we chose the sequence with the fewest missing base pairs. We then aligned and combined these sequences into a supermatrix with ClustalX (version 2.0) (Larkin et al. 2007). This supermatrix included over 25,000 characters across the 30 gene sequences and 466 Proteaceae species. We used PhyML to estimate phylogenies of the supermatrix with maximum likelihood. This is a "fast algorithm" that accurately estimates the tree topology, branch lengths, and parameters of the Markov model of substitution (Guindon & Gascuel 2003). We used the general time reversible (GTR) model of nucleotide substitution (Lanave et al. 1984), with the rate of substitution within each group initially set to 1.0, rates of nucleotide substitution were then optimized based on our data. We then optimized tree topology to maximize the likelihood; branch support is indicated with bootstrap values. This phylogenetic tree is included in the Supporting Information; most nodes were highly supported (e.g., values >0.75). On the basis of the Proteaceae phylogeny published in Sauquet et al. (2009), we treated *Bellendena montana* as the outgroup when we rooted the tree. We generated a chronogram by converting this phylogeny—pruned to contain only the Cape Floristic Proteaceae—to an ultrametric tree.

For 311 Proteaceae species, we had >1 observation, and we used this subset of observations for further analyses. Of the 311 retained species, 154 had sequence data available and could be included in the supermatrix. Sequences were available for at least 1 species in all 13 Cape Floristic Proteaceae genera (*Aulax, Diastella, Faurea, Leucadendron, Leucospermum, Mimetes, Orothamnus, Paranomus, Protea, Serruria, Sorocephalus, Spatalla, Vexatorella*). However, we subsequently pruned the tree to represent only species with >1 observation and thus included only 11 genera in our analyses. To account for the effect of missing species for which sequence data were not available, we explored 3 alternate tree

topologies: a tree consisting of only species for which sequences were available (none); a tree in which missing species were added as polytomies at the node where their congener had the highest evolutionary distinctiveness (high); and a tree in which the missing species were added as polytomies at the node where their congener had the lowest evolutionary distinctiveness (low) (Supporting Information).

To examine potential discrepancy between PD measured with trees resolved to species versus genera, we also pruned the phylogenetic tree to the genus level (e.g., Forest et al. 2007). This tree included 11 genera of Proteaceae. In our genus-level analyses, we used this tree and community data aggregated to the level of genus.

Diversity

We calculated measures of taxonomic richness, PD, BSR, and BED_T for each grid cell in the region containing >2 species, which is the minimum number of species necessary for determining the PD within a cell without specifying the length of the root branch (see below). Our analyses included 4935 cells when the missing species were included and 4029 cells when they were not. We repeated these calculations at the genus level (i.e., we included only those cells that contained >2 genera [4492 cells]). We used the R package ecoPD to calculate all metrics (R Development Core Team 2009; Regetz et al. 2009). We treated all Proteaceae subspecies as separate taxa and included them in the phylogeny as polytomies with uninformative branch lengths (i.e., branch lengths set to zero). We based our quantification of taxonomic diversity on Proteaceae species richness (number of species per cell) or on genera-level richness, as applicable.

We measured PD for all Proteaceae species using the PD metric, which calculates the sum of the branch lengths for a restricted tree that included only the taxa present in the cell, irrespective of the total regional species pool:

$$PD = \sum_{i=1}^{S} \sum_{e \in s(T,i,r)} \left(\lambda_e \cdot \frac{1}{S_e} \right), \qquad (1)$$

where e is the edge of length λ in the set $s(T,r,i)$ connecting species i to the root r of tree T, and S_e is the number of species (or genera for the genus-level tree) that descend from edge e.

Biogeographically Weighted Evolutionary Distinctiveness

To calculate BED_T of a species, one can partition phylogenetic branch lengths by descendant species' abundances or by the number of populations or in our case, the number of occupied grid cells. We calculated BED as

$$BED(T,i) = \sum_{e \in q(T,i,r)} \frac{\lambda_e}{n_e}, \qquad (2)$$

where n_e is the number of grid cells in which a species is present, below branch e, in the set $q(T,i,r)$, which includes the branches connecting species i to the root r of tree T. (Cadotte and Davies [2010] provide a detailed description and graphical representation of how this metric partitions internal branches.) The metric BED_T is then the summation of the BED values of all species in a site; thus, sites with species that are narrowly distributed will have higher BED_T than sites with widely distributed species.

BED shares with an alternative measure, phylogenetic endemism (Rosauer et al. 2009), the partitioning of internal branches by range size. However, phylogenetic endemism weights internal branch lengths by the union of subtending ranges and splits evolutionary distinctiveness among populations of different species if their ranges overlap. As a consequence, the phylogenetic endemism metric does not sum to PD as BED does (e.g., via BED_T), which makes it difficult to compare phylogenetic endemism and PD. We also calculated species richness weighted by range size with the BSR metric, which is equivalent to weighted endemism (Williams et al. 1994; Linder 1998; Rosauer et al. 2009)

$$BSR = \sum_s \sum_i \frac{1}{n_i}, \qquad (3)$$

where i is the species, s is the number of species in the cell, and n is range size (in our case, the number of occupied cells).

Metrics with Genera-Level Trees

For all metrics (species richness, PD, BED_T, and BSR), we repeated the calculations at the level of genus rather than species with the genera-level tree and site data aggregated across species at each site. We examined the concordance among species richness, PD, BSR, and BED_T with Pearson correlation coefficients. We did not correct for spatial autocorrelation directly because autocorrelation tends to strengthen the perceived relation between spatially structured variables, whereas we were interested in departures between the various metrics; hence, our comparisons are conservative.

Maps representing the distribution of species richness, PD, and BED_T values (all standardized at mean[SD] = 0 [1]) across the Cape Floristic Region were constructed in arcEditor (ESRI, Redlands, California) with 8 quantile intervals from blue to red. The mapped values were derived from the most conservative tree (low), where species lacking sequence data were included at low evolutionary diversity positions.

Reserve Representation Indices

We used a weighted index to compare how the prioritization of areas outside the current reserve system differed when applying phylogenetic and species-diversity metrics. We weighted species as an inverse function of the

number of times sites in which they were present were contained in reserves. For species richness, this calculation was similar to BSR, except that the number of sites in reserves was used instead of range size. We used a modification of the BED_T metric to calculate the representation of phylogenetic richness in reserves. In this case, however, we partitioned phylogenetic branch lengths by the number of sites a species occupied in the reserve system, rather than by range size. We used 8 quantile intervals from blue to red to map the results for the Cape Floristic Region. The mapped values illustrated standardized (mean 0, SD 1) values derived from the most conservative (low) tree, in which species lacking sequence data were included at low evolutionary diversity positions. To explore further the relation between evolutionary distinctiveness and range size, we plotted one against the other (including only species for which sequence data were available).

Results

The cells analyzed in the Cape Floristic Region contained between 2 and 26 Proteaceae species (mean [SD] = 5.28 species [3.83]). Pearson's correlation coefficients among the 3 metrics were calculated separately for metrics from the no added species, lowest and highest evolutionary distinctiveness and genus-level trees (Fig. 1). For the 4 trees, PD was strongly correlated with species richness ($r = 0.68$–0.85), whereas the correlation between BED_T and species richness was much weaker ($r = 0.18$–0.56). The PD measure was similarly correlated with BED_T ($r = 0.26$–0.53). All correlations were positive, but BED_T was distinct from the other metrics (Fig. 1).

The positioning of species missing phylogenetic information in the trees had little effect on the relation between metrics, regardless of whether these species were added in positions of low or high evolutionary distinctiveness (Fig. 1). However, metrics calculated with a tree resolved to the level of genus resulted in different patterns of correlation than the equivalent values calculated from the species-level tree. There was a stronger correlation between BED_T and PD ($r = 0.45$) and BED_T and species richness ($r = 0.37$) and a weaker correlation between species richness and PD ($r = 0.67$) for genus-level than for species-level trees.

To determine whether the distribution of BED_T values resulted only from the inclusion of information on range size, independent of phylogeny, we compared BED_T with our metric BSR, which incorporates both species richness and range size, but not phylogenetic branch lengths. The correlation between the BSR and BED_T metrics was weak ($r = 0.21$–0.22) (Fig. 1), which indicated BED_T's differential performance was the result of a nonrandom distribution of range size in relative to evolutionary history. In addition, BSR was not correlated with species richness ($r = -0.21$).

Species richness and PD had similar spatial distributions (Fig. 2). However, PD was less concentrated than species richness such that many regions had moderate levels of PD, whereas species richness tended to have high values in relatively fewer locations. The map of BED_T showed far fewer areas of high diversity than the maps of either species richness or PD and highlighted sites in the south and southwest as having higher diversity and thus higher priority for conservation.

Species with high evolutionary distinctiveness tended to have smaller ranges, whereas a subset of species with low evolutionary distinctiveness had very large ranges (Fig. 3). However, species' range sizes were not correlated with relatedness (Blomberg's $K = 0.18$, $p > 0.05$), which indicated close relatives did not tend to have similar range sizes.

The representation of species and PD in the current reserve system differed greatly (Appendix S2). The correlation between the species and phylogenetic representation indices was not significant ($r = 0.17$, $p = 0.86$). Furthermore, the spatial distributions of these representation indices across the region were strikingly different (Supporting Information). Few areas had a high concentration of underrepresented species, and those that did were primarily near the southern border of the region. There were numerous areas with high levels of underrepresented phylogenetic richness near both the south and northeastern edges of the region.

Discussion

It is necessary to determine whether and when phylogenetic and species diversity represent complementary or comparable information. We found that different metrics of diversity identified different areas in the Cape Floristic Region as having high levels of diversity. These differences may provide additional information for conservation planning, such as in the selection of areas for augmenting an existing reserve network. For example, the spatial distribution of our multivariate metric, BED_T, which incorporated both evolutionary distinctiveness and regional species rarity, departed from the distribution of more traditional diversity metrics and highlighted additional areas (e.g., areas in the southern edge of the region) that might be considered for protection by identifying areas with species that were both relatively distinct and rare compared with the regional species pool.

Metrics accounting for evolutionary history may help identify sites overlooked by diversity metrics that focus on species richness (Polasky et al. 2001; Forest et al. 2007). Divergence between phylogenetic diversity (measured with PD) and species richness may be sizeable in only particular cases, for example, when evolutionarily distinct species have narrow geographic distributions and occur in species-poor sites (Rodrigues et al. 2005). Here,
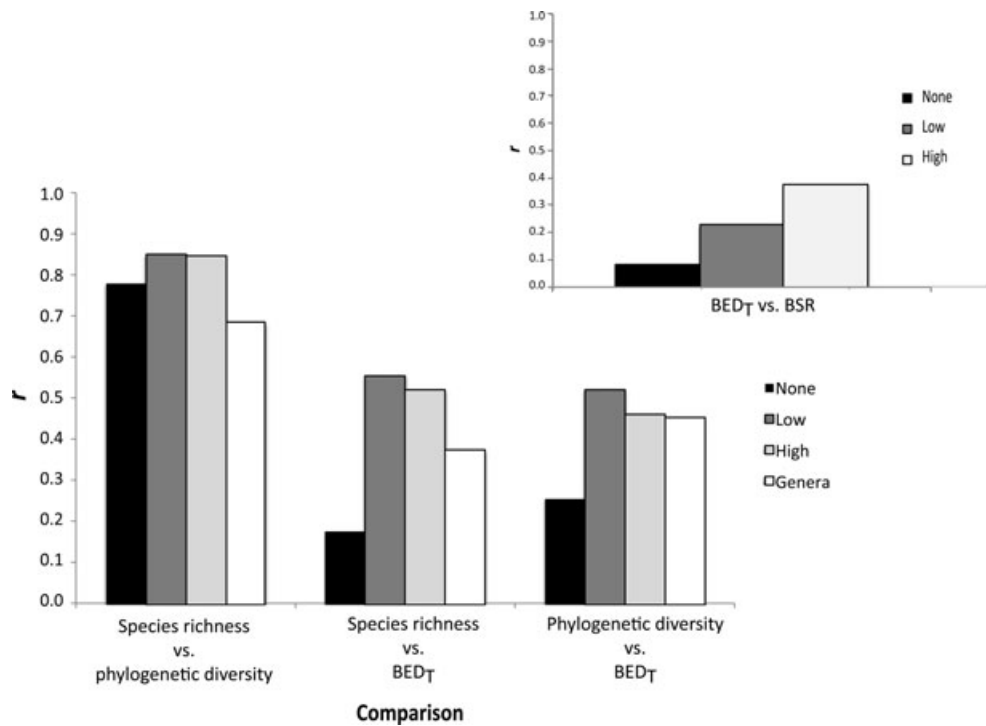
Figure 1. *Pearson correlation coefficients showing the strength of the relations among species richness, phylogenetic diversity (PD), and biogeographically weighted evolutionary distinctiveness (BED_T, summation of the biogeographically weighted evolutionary distinctiveness values of all species in a site) metrics for Proteaceae in the Cape Floristic Region, South Africa (none, species lacking sequence data not included; low, species lacking sequence data included at low evolutionary diversity position; high, species lacking sequence data included at high evolutionary diversity position; genera, resolved only to the level of genus). The inset shows the Pearson correlation coefficients between the 2 range-weighted metrics, BED_T, and biogeographically weighted species richness (BSR) for the none, low, and high trees.*

we found that PD and species richness are, unsurprisingly, strongly correlated in the Cape Floristic Region. Nonetheless, their mapped values indicated species richness was concentrated in fewer sites, which underrepresented the more spatially extensive distribution of PD, particularly in the eastern Cape Floristic Region. Significant differences among the metrics were evident in the Cape Floristic Region even in the absence of a highly unbalanced phylogeny or structured species distribution. Relatively few Proteaceae in the region have very large or very small range sizes, and the phylogenetic tree we used was not greatly unbalanced ($I_c = 0.067$, which is not significantly different than an equal-rates Markov null model [$I_c = 0$]). We therefore suggest that even modest departures in tree shape or structuring of the distribution of species ranges may therefore result in realized differences among metrics. In particular, phylogenetic metrics and species richness can be decoupled when the focus is on sites within an extensive region because sites may contain very different subsets of the species pool, which would alter the shape of the tree (Cadotte & Davies 2010).

Forest et al. (2007) examined PD for the entire Cape Floristic flora at a coarser spatial grain than we applied in

our analyses. Our results for patterns of divergence between species richness and evolutionary diversity were similar to theirs. However, because Forest et al. examined genus-level rather than species-level richness, it is possible their estimates of PD are biased downward because branching relations among species within genera were not included. When we compared the relation between PD and species richness at the genus level, we observed an approximately 10% drop in correlation strength compared with the species-level analyses, which may suggest the coarser taxonomic resolution overestimated the mismatch between PD and species richness. Despite this difference in spatial and taxonomic resolutions between studies, our results were generally congruent: PD and species richness covaried closely when considered in the absence of spatial context, but departed significantly in their spatial distribution.

Metrics such as BED_T, which combines evolutionary diversity and rarity into a single measure of diversity, may allow a more holistic approach to conservation prioritization. Nonrandom relations between evolutionary distinctiveness and range size can produce rankings different from those of any single input variable. Comparing
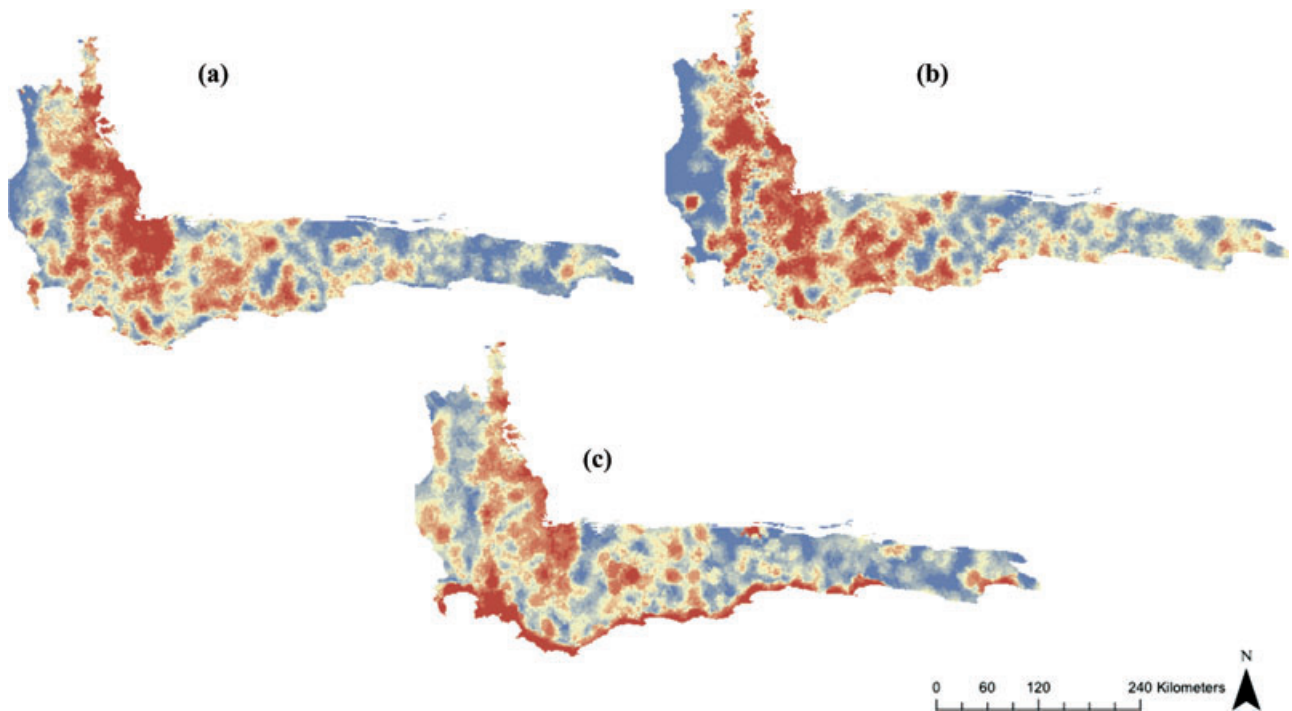
Figure 2. *Proteaceae diversity of 311 species in the Cape Floristic Region on the southern tip of Africa measured on the basis of (a) species richness, (b) phylogenetic diversity, and (c) biogeographically weighted ecological distinctiveness ([b] and [c] were calculated with the low tree, where species lacking sequence data were included at low evolutionary diversity positions). All diversity measures are scaled with mean 0 and SD 1. Colors are scaled over 8 quantile intervals from blue (low diversity) to red (high diversity).*
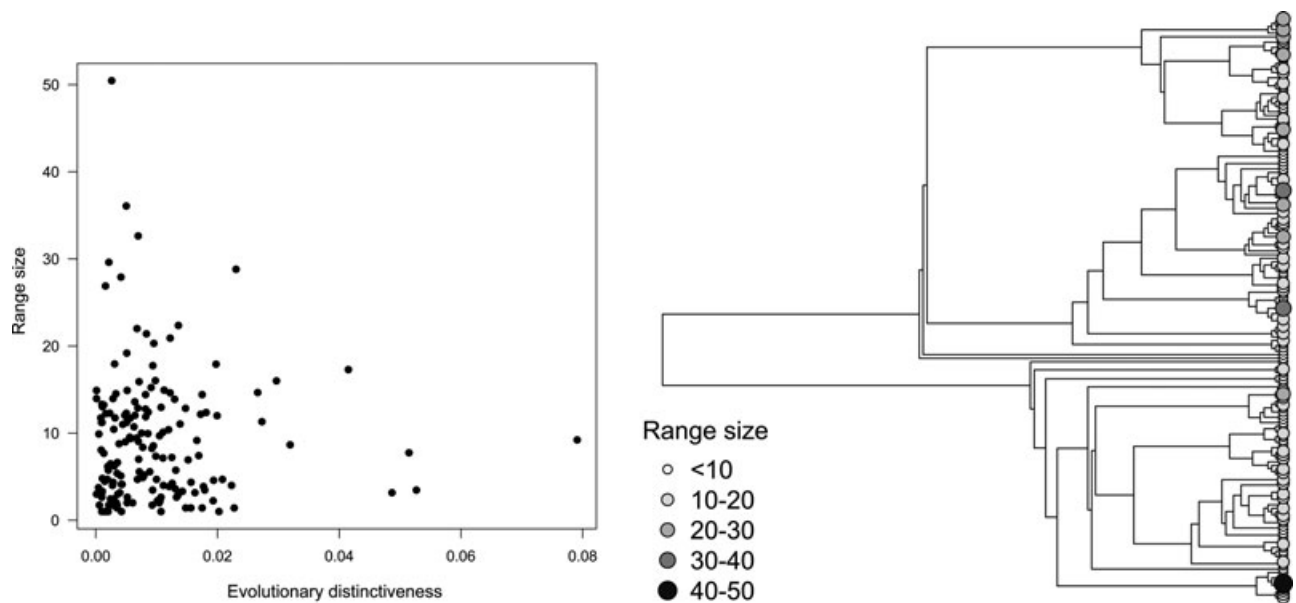

Figure 3. *The relation between evolutionary distinctiveness and range size (calculated as the square-root transformed number of cells occupied by the species) (left) and distribution of range size for the none phylogenetic tree (i.e., Proteaceae species lacking sequence data not included) (right) for the 154 species in the Cape Floristic Region, South Africa with sequence data.*

BED_T and BSR allowed us to determine whether differences between BED_T and PD resulted simply from the incorporation of range-size information (in which case BED_T and BSR should have a similar relation to the relation between species richness and PD) or from more complex relations between range size and evolutionary distinctiveness.

We found that BED_T differed from the similarly range-size weighted BSR, which suggests evolutionarily distinct species tended to have more restricted geographical distributions. The relation between evolutionary distinctiveness and range size could be of interest for species conservation. Species that are evolutionarily distinct are of high conservation value (Crozier 1997), and species with small ranges have greater risk of extinction (Purvis et al. 2000*a*; Purvis et al. 2000*b*; Cardillo et al. 2005). Although species-based prioritization schemes that incorporate range size more likely emphasize these species, such schemes cannot differentiate between species with small ranges that are not evolutionarily distinct and species that have small ranges and are more evolutionary distinct (Davies et al. 2011).

Other metrics of PD also incorporate measures of extinction risk (Redding & Mooers 2006; Isaac 2007; Faith 2008), but they rely on inferred estimates of extinction risk that require detailed species data such as probability of extinction. In contrast, BED_T requires information only on range size (or abundance or population numbers), which is perhaps the most widely available type of species data. We suggest BED_T might therefore have much greater practicality, especially for less well-described clades. Species prioritization rankings are often developed at global or national scales, which means sites may be assigned a high priority that may not contain the rarest species at the scale of interest.

A common criticism of alternative diversity metrics is that they are sensitive to the calculations and the weighting scheme used to construct them. Although this criticism is valid, weighting schemes are implicit in all reserve-selection approaches (e.g., measures of species richness assume all species have equal weights). Alternative weighting schemes allow one to make explicit those aspects of biological diversity that are valued and encourages debate over what aspects of biological diversity should be valued. In addition, all metrics depend on the calculations used to construct them. Comparing alternative metrics and performing sensitivity analyses (here, differing phylogenetic construction methods) makes it clear that there are differences in the distribution of biological diversity that are worth considering and that are due to more than choice of metric construction alone.

The Protea Atlas Project (Rebelo 2001) produced one of the most detailed surveys of species occurrence in the world (presence or absence of approximately 330 species over 36,000 sites). These data are being used to guide reserve selection and predict how range sizes, locations,

and extinction risks will change as temperatures increase (Lombard et al. 2003; Midgley et al. 2003; Bomhard et al. 2005). Proteaceae species in the Cape Floristic Region currently receive considerable protection; the majority of species occur in at least one reserve. Our analyses are primarily an illustration of how the distribution of evolutionary history can differ from the distribution of species richness. Our results suggest that sites near the southern edge of the region contain species that have high levels of evolutionary distinctiveness and limited ranges, but are not assigned high conservation-priority rankings on the basis of species richness or PD. That these areas in the south and southwest contain sites with many rare and evolutionary distinct species may relate to the presence of lowland fynbos, which is restricted to areas between the coast and interior mountains and contains different vegetation than other fynbos types. Many species in this region have small ranges, and mountains and coastal areas may form barriers to dispersal. The resulting negative relation between evolutionary distinctiveness and range size that resulted in this area is important to consider because it means that in some cases the species that capture the greatest evolutionary diversity will also be the species most vulnerable to extinction. Further, modest differences in the distribution of phylogenetic and species richness in the region may suggest different conservation scenarios for protecting phylogenetic versus species richness and may lead to different conclusions regarding the future positioning of protected areas.

Acknowledgments

Supporting Information

The Cape Floristic Region protea phylogeny (Appendix S1) and the maps showing the distribution of the reserve representation index (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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