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Spatial Predictions of Phylogenetic Diversity in Conservation Decision Making

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Abstract: *Considering genetic relatedness among species has long been argued as an important step toward measuring biological diversity more accurately, rather than relying solely on species richness. Some researchers have correlated measures of phylogenetic diversity and species richness across a series of sites and suggest that values of phylogenetic diversity do not differ enough from those of species richness to justify their inclusion in conservation planning. We compared predictions of species richness and 10 measures of phylogenetic diversity by creating distribution models for 168 individual species of a species-rich plant family, the Cape Proteaceae. When we used average amounts of land set aside for conservation to compare areas selected on the basis of species richness with areas selected on the basis of phylogenetic diversity, correlations between species richness and different measures of phylogenetic diversity varied considerably. Correlations between species richness and measures that were based on the length of phylogenetic tree branches and tree shape were weaker than those that were based on tree shape alone. Elevation explained up to 31% of the segregation of species rich versus phylogenetically rich areas. Given these results, the increased availability of molecular data, and the known ecological effect of phylogenetically rich communities, consideration of phylogenetic diversity in conservation decision making may be feasible and informative.*

Keywords: angiosperms, conservation planning, predictive modeling, proteaceae, South Africa, spatial overlap, species richness

Predicciones Espaciales de la Diversidad Filogenética en la Toma de Decisiones de Conservación

Resumen: *Durante mucho tiempo se ha argumentado que la consideración de las relaciones genéticas entre especies es un paso importante hacia la medición más precisa de la diversidad biológica, en lugar de solo basarse en la riqueza de especies. Algunos investigadores han correlacionado medidas de la diversidad filogenética y de la riqueza de especies en una serie de sitios y sugieren que los valores de la diversidad filogenética no difieren suficientemente de los valores de riqueza de especies para justificar su inclusión en la planificación de la conservación. Comparamos las predicciones de riqueza de especies y 10 medidas de diversidad filogenética mediante la creación de modelos de distribución de 168 especies de una familia de plantas muy rica en especies, Proteaceae. Cuando utilizamos cantidades promedio de terrenos protegidos para comparar áreas seleccionadas con base en la riqueza de especies con áreas seleccionadas con base en*

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la diversidad filogenética, las correlaciones entre riqueza de especies y las diferentes medidas de diversidad filogenética variaron considerablemente. Las correlaciones entre riqueza de especies y medidas que se basaron en la longitud de las ramas de los árboles filogenéticos y la forma del árbol fueron más débiles que las que se basaron solamente en la forma del árbol. La elevación explicó hasta 31% de la segregación de áreas ricas en especies versus las áreas filogenéticamente ricas. Dados estos resultados, la mayor disponibilidad de datos moleculares, y el efecto ecológico conocido de las comunidades filogenéticamente ricas, la consideración de la diversidad filogenética en la toma de decisiones de conservación puede ser factible e informativa.

Palabras Clave: angiospermas, modelado predictivo, Proteaceae, riqueza de especies, Sudáfrica, traslape espacial

Introduction

Although ecosystem services, potential conflicts between people and nature, and other social and economic factors have been used to set theoretical conservation priorities (Moore et al. 2004; Eigenbrod et al. 2009), assessments of biological diversity are still the primary basis on which locations are prioritized for conservation. Complementing traditional data (e.g., species richness) with information on evolutionary history has long been argued as a more meaningful way to measure biological diversity (Faith 1992).

Phylogenetic diversity represents the accumulation of evolutionary adaptations in a group of species and may be related to the evolutionary potential of those species (Forest et al. 2007), but it is also positively correlated with ecosystem functions, such as primary productivity (Cadotte et al. 2009). Because species share evolutionary history with related species (which can be numerous or few, distant, or close) by definition, communities that are species rich may not have equally high levels of phylogenetic diversity (Devictor et al. 2010). If phylogenetic diversity patterns were similar to those of species richness patterns, there would be no reason to consider phylogenetic diversity because species richness is easier, cheaper, and quicker to measure. In some cases, patterns of species richness and phylogenetic diversity are closely related (Rodrigues & Gaston 2002; Schipper et al. 2008), whereas in others they differ greatly (Rissler et al. 2006; Forest et al. 2007; Devictor et al. 2010). As a general rule, however, species richness is thought to be an inaccurate surrogate of phylogenetic diversity only when species restricted to species-poor areas correspond to the ancient branches of an unbalanced phylogenetic tree (i.e., a tree containing long branches that accounts for a disproportionate amount of phylogenetic diversity [Rodrigues & Gaston 2002]).

Information on phylogenetic diversity has been measured in a limited number of taxonomic groups and spatial extents at either the genus (Rodrigues & Gaston 2002; Forest et al. 2007; Proches et al. 2009) or species level (e.g., Winter et al. 2009; Redding et al. 2010; Vamosi & Queenborough 2010). Many researchers conducting studies at a global extent have used distribution data that have a coarse resolution to identify potential areas for conservation. If one is to incorporate information on phylogenetic diversity in conservation prioritization efforts, one must determine whether phylogenetic diversity measures are congruent with species richness at finer extents (Devictor et al. 2010).

A thorough study of the relation between species richness and phylogenetic diversity showed a decoupling of the number of plant genera and their phylogenetic diversity in the Cape Floristic Region (South Africa) (Forest et al. 2007), which is likely due to different processes of species diversification in the western and eastern part of the region. Richness of genera was high throughout the Cape, but multiple recent radiations led to phylogenetically clustered diversity in the Western Cape. Diversity in the eastern Cape reflects a set of genera with unusual ecotypes (Forest et al. 2007).

We used a complementarity algorithm (defined by Margules and Pressey [2000] as a measure of the extent to which an area, or set of areas, contributes unrepresented biological features to an existing area or set of areas) to examine whether increases in phylogenetic diversity are associated with increases in taxon richness (Forest et al. 2007; Devictor et al. 2010). Moreover, we assessed the correlation between spatially explicit predictions of species richness and predictions of several measures of phylogenetic diversity in the Cape Floristic Region. We used 10 phylogenetic diversity measures (Schweiger et al. 2008) that are calculated in very different ways.

Branch length on a phylogenetic tree is the preferred measure of phylogenetic diversity (Crozier 1997) because, assuming it is estimated correctly, branch length accurately reflects the evolutionary distances between species. Data on branch lengths are not always available, in which case measures that consider only the number of nodes separating species along a phylogenetic tree (i.e., topology-based measures) are an alternative (Schweiger et al. 2008). In studies that do not explicitly consider evolution, pairwise distances between species are sometimes used as measures of biological diversity (e.g., Warwick & Clarke 1998; Izsak & Papp 2000). Recently researchers have used information on species' relatedness to address questions in community ecology and conservation prioritization and have based their conclusions on Faith's (1992) measure of phylogenetic diversity (e.g., Sechrest et al. 2002; Forest et al. 2007; Redding et al.

2010). Therefore, little is known about the properties of other distance- and topology-based measures of phylogenetic diversity. Regardless of the motivation for using phylogenetic diversities, comparing these measures provides a comprehensive assessment of the spatial relation between measures of phylogenetic diversity and species richness.

In addition, we conducted an analysis of the plant family Proteaceae, which occurs in the Cape Floristic Region, to relate potential discrepancies between species richness and phylogenetic diversity patterns with environmental gradients.

The Cape Floristic Region contains one of the highest levels of species richness and endemism of plants in the world (Myers et al. 2000; Linder 2003). The Proteaceae include over 300 low-growing shrubs and trees with a wide variety of pollination and fire-survival strategies (Rebelo 2001). Of the 13 genera that occur in mainland Africa, 10 are endemic to the fynbos vegetation of the Western Cape (Barker 2002). The Cape Floristic Region differs from other high-diversity areas, such as tropical forests, in that it is made up of dissimilar local communities, in which most species are relatively abundant and few are rare (Latimer et al. 2005). This pattern is explained by migration rates in the fynbos, which are two orders of magnitude lower than in tropical forests, and by speciation rates of plants associated with this vegetation type, which are higher than in any previously studied plant system (Latimer et al. 2005).

Methods

Species Distribution Predictions

The quality of the occurrence data for species of plants in the Cape Floristic Region is high, but data are not available for all subregions. Thus, we used species-distribution modeling to provide a probability distribution of the occurrence of each Proteaceae species in the entire Cape Floristic Region. We built models at a resolution of $1' \times 1'$ (approximately 1.6×1.6 km at 33° latitude) for 168 endemic Proteaceae species for which both occurrence and nuclear genetic data were available and that had been recorded in a minimum of 20 locations. We took distributional data from the *Protea* Atlas Project (Rebelo 2001). For each species, presences and pseudoabsences consisted, respectively, of $1' \times 1'$ cells occupied and unoccupied by the species. By using a resolution of >150 m, we assumed no spatial autocorrelation (Fischer 1990) and used all occupied cells to fit the models as in Thuiller et al. (2005).

We calibrated generalized additive models (Hastie & Tibshirani 1990) in BIOMOD (Thuiller 2003). We included seven bioclimatic variables in the models (mean annual evapotranspiration, evapotranspiration of the wettest quarter, sum of annual precipitation, precipitation of the wettest quarter, precipitation of the driest quarter, mean annual temperature, and temperature of the coldest quarter), which were derived from WorldClim (Hijmans et al. 2005). These climatic variables summarize the main temperature and precipitation gradients in the study area (including seasonal variations) and are considered critical to plant physiology (Woodward 1987). We used a random sample of the initial data (70%) and stepwise selection. We used Akaike's information criterion (AIC) (Burnham & Anderson 2002) to identify the best model, which we defined as the one with the lowest AIC (delta AIC < 4.0).

We multiplied the probabilities of occurrence resulting from the models by 1 – human-footprint index (Sanderson et al. 2002). This measure is a consistent way to represent intensity of human activity worldwide. We rescaled the values of the index to represent a range between zero and one (i.e., completely transformed by human use). Given the vulnerability of the fynbos vegetation, including Proteaceae, to changes in land use (Rouget et al. 2003), our weighting procedure ensured that our use of climatically suitable grid cells with intensive human use would not lead to an overestimate of the overall habitat quality for a species.

We transformed the weighted predictions to binary predictions with a probability threshold at which sensitivity (i.e., the rate of correctly predicted presences) equaled specificity (i.e., the rate of correctly predicted absences) (Liu et al. 2005). To evaluate the predictive power of each model on the remaining 30% of the initial data set, we used the values obtained from the area under the curve in a plot of the receiver operating characteristic (Fielding & Bell 1997).

We summed predicted probabilities of occurrence of individual species for each site to obtain species-richness predictions, which we then used in combination with the phylogenetic tree to calculate corresponding measures of phylogenetic diversity. Modeled distributions were therefore the basis for both species richness and phylogenetic diversity predictions.

Measures of Phylogenetic Diversity

On the basis of 23 genes, we assembled a calibrated phylogenetic tree for the Proteaceae from existing data for the South African and for some Australian Proteaceae in GenBank.

We followed the clustering method described by McMahon and Sanderson (2006). The tree had 284 species and was built with MrBayes software (version 3.1.2; Huelsenbeck et al. 2001). We performed two runs of four Markov chain Monte Carlo chains for 10 millions generations with the GTR+Gamma (Tavaré 1986; Yang 1993) model of DNA evolution (as determined by likelihood ratio tests) and default priors. We assessed the

convergence of the two runs with Tracer (Drummond & Rambaut 2007). We used previously described fossils (Sauquet et al. 2009) and penalized likelihood (Sanderson 2002) as implemented in the R package ape (Paradis et al. 2004) to date the phylogenetic trees (Supporting Information). We assessed the consistency of the date estimates by performing penalized likelihood on 100 randomly sampled trees from the posterior distribution generated in MrBayes. We pruned the tree to remove species for which distribution data were not available.

For each grid cell in the study area, we calculated in R each of the measures of phylogenetic diversity listed in Schweiger et al. (2008). Two measures are based on topology (node information only) (W, standardized taxic weights, and Q, basic taxic weights), five are based on pairwise distances (J, intensive quadratic entropy; F, extensive quadratic entropy; AvTD, average taxonomic distinctness; TTD, total taxonomic distinctness; Dd, pure diversity), and three so-called minimum-spanning measures (PDroot, phylogenetic diversity with basal branches; PDnode, phylogenetic diversity; AvPD, average phylogenetic diversity) are based on both branch length and node information. These measures can be classified on the basis of whether they sum (Q, W, PDnode, PDroot, F, TTD, Dd) or average (AvTD, J, AvPD) the evolutionary history of all species present in an area. Details on the mathematical properties of each of these measures are in Table 1 of Schweiger et al. (2008). We followed the naming convention used in Schweiger et al. (2008) for all phylogenetic measures. Several of the metrics we used, in particular the averaged indices, are not specifically developed for conservation prioritization. Although we think the term *phylogenetic diversity* should be less inclusive and relate more specifically to topology, for completeness we include all measures that may be considered in conservation prioritization.

Discrepancy Values

We normalized species richness and phylogenetic diversity at each grid cell by subtracting the mean and dividing by the standard deviation over the whole region. We then subtracted species richness from phylogenetic diversity to obtain discrepancy values (positive when phylogenetic diversity was greater than species richness and negative otherwise).

Species Richness versus Phylogenetic Diversity

We used Spearman correlations to describe the relation between species richness and phylogenetic diversity. We ran a complementarity algorithm (from Forest et al. [2007]; see Margules and Pressey [2000] for complete explanation of the complementarity concept) to investigate how increases in phylogenetic diversity and species richness may change as a function of which measure is maximized and whether sites selected by maximizing phylogenetic diversity or species richness overlap spatially. To do this, the grid cell with the highest species richness was selected first and then grid cells were added in descending order of complementary diversity until all species in the phylogenetic tree were represented.

Finally, we quantified the spatial overlap between species richness and each of the measures for different hypothetical percentages (1% to 100%) of protected land. We compared the highest ranking grid cells measured with species richness and each of the phylogenetic diversity measures when conserving different percentages of the landscape. We calculated the spatial overlap as the percentage of grid cells identified by both measures.

Environmental Variables and Quadratic Regression

We carried out a principal component analysis (PCA) of the environmental variables used to predict individual species distributions in the R package ade4 (Franquet et al. 1995). The scores corresponding to relatively high normalized phylogenetic diversity or species richness were used to examine possible spatial and climatic segregation between the two groups of scores. We conducted a polynomial quadratic regression to describe the relation between elevation and discrepancy values.

Results

Correlations, Complementarity, and Discrepancy

The accuracy of the species-distribution models was consistently high. Average area under the curve was 0.98 over all species (range 0.88–0.99).

The correlation of phylogenetic diversity with species richness varied greatly among measures. Topology measures were highly correlated with species richness (Spearman rho 0.98 for W and 0.99 for Q). Use of both node and branch-length information resulted in considerably different correlations with species richness: from −0.75 to 0.94 with minimum-spanning measures (0.92, 0.94, and −0.75 for PDnode, PDroot, and AvPD, respectively) and from −0.06 to 0.99 for pairwise-distance measures (−0.06, −0.03, 0.99, 0.98, and 0.7 for AvTD, J, F, TTD, and Dd, respectively). The measures W and TTD were linearly related to species richness and PDnode, PDroot, Dd, Q, and F were positively correlated with species richness with a nonlinear upward slope (Supporting Information).

Overall, nonaveraged measures were positively correlated with species richness, whereas, as expected, some averaged measures (AvTD and J) showed no correlation with species richness. Another averaged measure (AvPD) was negatively correlated with species richness. The complementarity algorithm identified the minimum set of sites representing 100% of Proteaceae species across the Cape Floristic Region (12 noncontiguous

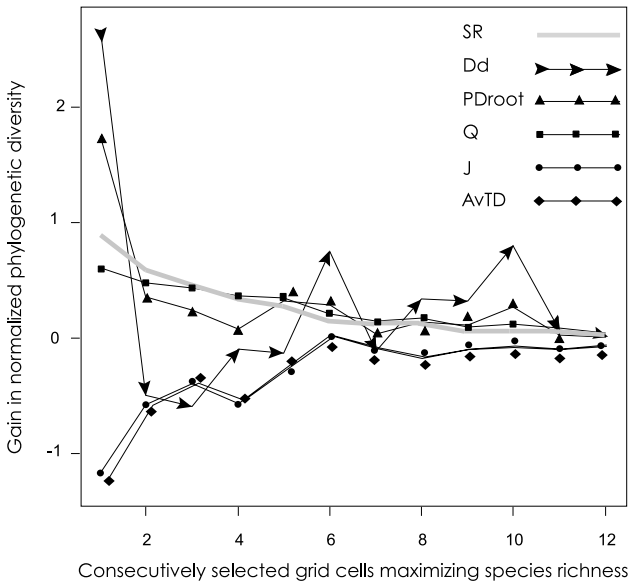

Figure 1. Increases in species richness (SR) and phylogenetic diversity as measured by Dd (pure diversity); PDroot (phylogenetic diversity including basal branches); Q (basic taxic weights); J (intensive quadratic entropy); and AvTD (average taxonomic distinctness) when a complementarity algorithm is used to maximize species richness. This algorithm identifies the minimum set of sites representing 100% of Proteaceae species across the Cape Floristic Region, which in this case is 12 noncontiguous grid cells.

grid cells) and showed that corresponding increases in different phylogenetic diversity measures were not highly correlated (Fig. 1). Moreover, when we maximized increases in species richness for each measure separately, only increases in Q matched increases in species richness (data not shown). Phylogenetic diversity as measured by PDroot was not highly correlated with species richness. Phylogenetic diversity as measured by Dd decreased when the second and third cells were added. Phylogenetic diversity as measured by AvTD and J decreased as the number of cells increased and was not correlated with species richness (Fig. 1).

The spatial patterns of discrepancy between species richness and phylogenetic diversity varied considerably depending on the measure of phylogenetic diversity (Fig. 2). High phylogenetic diversity as measured by W, Q, and F occurred in locations with high species richness (Fig. 3c). Areas with higher than expected phylogenetic diversity as measured by PDroot, AvPD, J, AvTD, and Dd were different from locations with high species richness. These areas included the Koebeeberge Mountains in the northern portion of the Cederberg range (Fig. 3a), lower-elevation areas between Knysna and Port Elizabeth (Fig. 3d), and parts of the Cederberg, KoueBokkeveld, and Groot Winterhoek mountains (Fig. 3b).

Spatial Overlap of Areas with High Diversity

The overlap between species richness and various measures of phylogenetic diversity varied as an increasing, nonlinear function of the amount of area considered (Fig. 4). The highest overlaps were between species richness and two topology-based measures of phylogenetic diversity, Q and W (93% and 89% of the cells with the highest phylogenetic diversity measured by Q and W, respectively, also had the highest species richness), and two of the pairwise-distance measures, F and TTD (95% and 93%, respectively). Correlations between species richness and one of the pairwise-distance measures of phylogenetic diversity, Dd, and two of the minimum-spanning distance measures, PDroot and PDnode, were 53%, 79%, and 78%, respectively. Species richness was not correlated with phylogenetic diversity as measured by J, AvTD, and AvPD.

PCA of Environmental Variables and Quadratic Regression

The PCA scores for three measures of phylogenetic diversity (AvTD, TTD, and PDroot) that were representative of the level of correlation between species richness and phylogenetic diversity were separated along the climatically driven principal component axes (Figs. 5a, 5b, & 5c). Segregation between these points was more evident in measures of phylogenetic diversity that had low correlation with species richness (e.g., AvTD, AvPD, and J) (Fig. 5c) and less evident in measures that correlated highly with species richness (e.g., TTD, F, W, and Q) (Fig. 5a). In general, scores corresponding to grid cells with higher than expected phylogenetic diversity were associated with higher temperatures and evapotranspiration and less precipitation (Fig 5). Elevation explained 31%, 11%, and 9% of the variation in the discrepancies among TTD ($t[27,243] = -76.82$, $p < 0.001$) (Fig. 6a), PDroot ($t[27,243] = -40.32$, $p < 0.001$) (Fig. 6b), and AvTD ($t[27,243] = -28.12$, $p < 0.001$) (Fig. 6c), respectively.

Discussion

Only topology-based measures of phylogenetic diversity of the Cape Proteaceae were highly correlated with species richness. Moreover, regions with high species richness and phylogenetic diversity were, to some extent, segregated climatically and spatially.

Highly significant correlations between species richness and phylogenetic diversity were often matched by an equally significant level of overlap in spatial patterns. We expect phylogenetic diversity measures that are not averaged to show a positive relation with species richness, but the functional form of this relation is likely to vary among different classes of such measures.

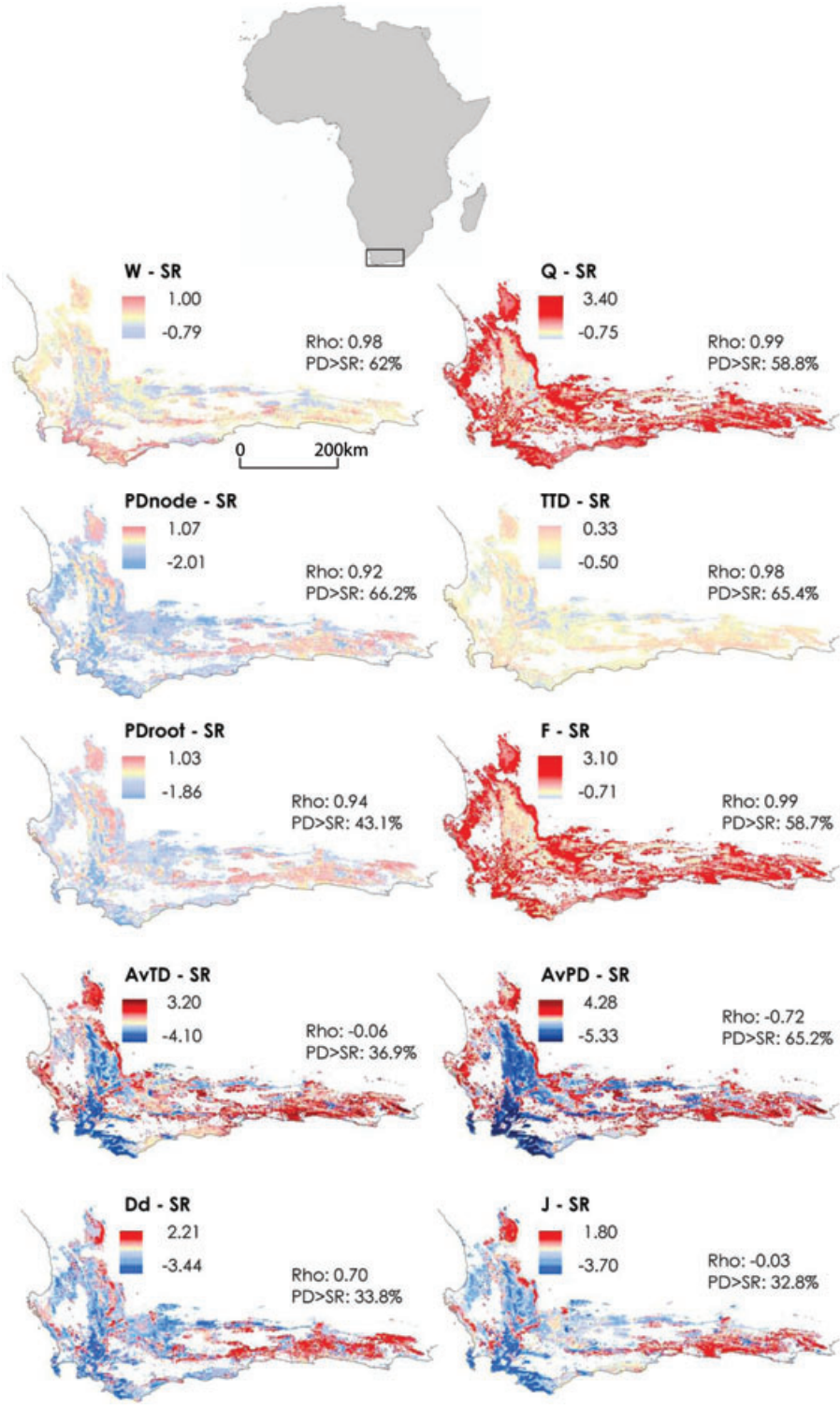

Figure 2. Discrepancy maps resulting from the subtraction of species richness (SR) from 10 measures of phylogenetic diversity (F, extensive quadratic entropy; TTD, total taxonomic distinctness; W, standardized taxic weights; PDnode, phylogenetic diversity; AvPD, average phylogenetic diversity; Dd, PDroot, Q, J, and AvTD defined in Fig. 1) for Proteaceae in the Cape Floristic Region. Red indicates areas where phylogenetic diversity is greater than species richness, and blue indicates areas where species richness is higher than phylogenetic diversity. Values are normalized so that a difference of zero (light yellow) means species richness and phylogenetic diversity are identical. The Spearman rank correlation (rho) between species richness and phylogenetic diversity and the percentage of grid cells where phylogenetic diversity is higher than species richness are indicated.

Although Rodrigues and Gaston (2002) found a linear relation between genera richness and phylogenetic diversity (for PDroot), we found that was not the case for all phylogenetic diversity measures. Besides the effects of tree imbalance (Rodrigues & Gaston 2002), it is likely that diversification rates among lineages will have a large influence on the correlation of phylogenetic diversity with species richness. For example, we expect areas with clades that originated from recent periods of diversification (characterized by many closely related taxa with shorter branches) to have lower phylogenetic diversity than areas inhabited by a relatively high proportion of older monotypic clades.

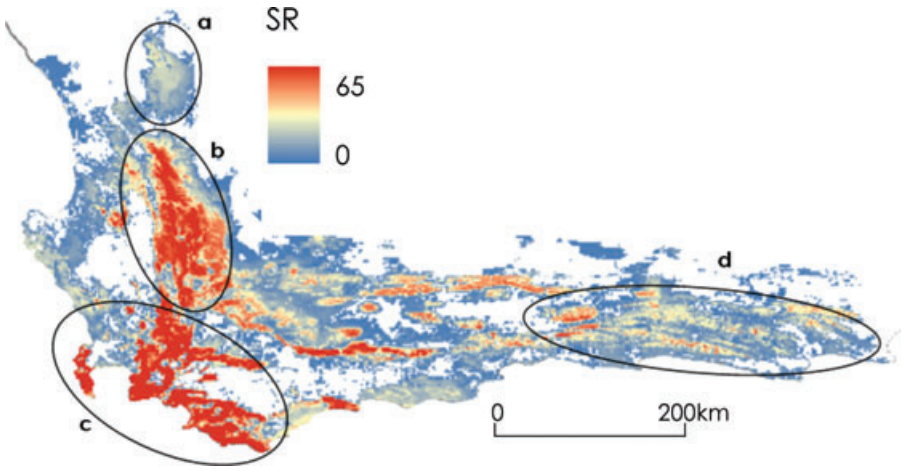

Figure 3. Predicted species richness (SR) for the Proteaceae of the Cape Floristic Region in South Africa per 1′ × 1′ cell (range: 1 species [blue] to 65 species [red]). Particularly diverse areas are demarcated: (a) Koebeeberge Mountains in the northern portion of the Cederberg range, (b) parts of the Cederberg, KoueBokkeveld, and GrootWinterhoek mountains, (c) Hawekwas, Hottentots Holland, and Kogelberg mountains, Cape Peninsula, and the Agulhas plain, and (d) areas between Knysna and Port Elizabeth.

Spatial and Climatic Discrepancies

Soil characteristics, colonization history, pollinator specificity, occurrence of seasonal fire, and climate regimes are thought to explain the unusual species richness of plants in the Cape Floristic Region (Goldblatt & Manning 2002; Linder 2003; Bergh & Linder 2009).We found that areas with relatively high species richness had more precipitation and less evapotranspiration than areas with relatively low species richness (Fig. 5). Moreover, higher elevations (normally associated with high levels of precipitation and low rates of evapotranspiration) had higher relative species richness than phylogenetic diversity (Fig. 6).

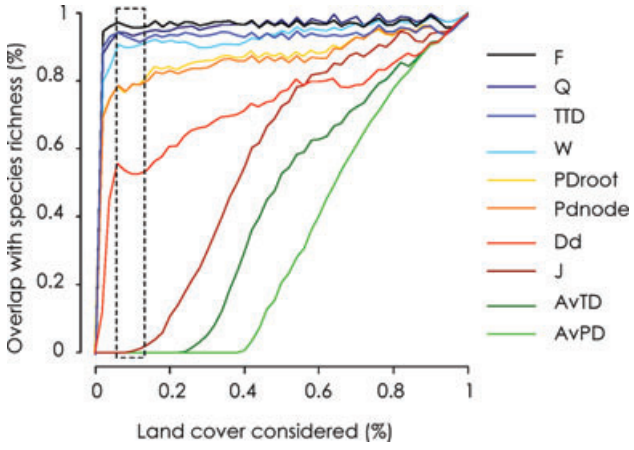

Figure 4. Changes in the overlap between predicted species richness and 10 measures of phylogenetic diversity (F, Q, TTD, W, PDroot, PDnode, Dd, J, AvTD, AvPD; defined in legends of Figs. 1 & 2) as the amount of land set aside for conservation changes (dashed-line rectangle, average values for the percentage of land area set aside for conservation [UNEP-WCMC 2008]).

High species richness in the mountains in the Cape region is thought to reflect allopatric speciation processes with very low extinction rates, which may have resulted from particularly stable climates (Dynesius & Jansson 2000; Lawes et al. 2000). Moreover, mountains have steep environmental gradients along which species can move and survive climatic fluctuations (Loarie et al. 2009). Therefore, relatively stable mountain climates may have allowed original species in each clade to persist and evolve over time. Extinction rates at lower elevations may have been much higher. Today these areas may contain only the surviving members of historically more diverse clades, which represent higher levels of phylogenetic diversity resulting from more distant evolutionary relations among species.

Weighting predictions of species richness on the basis of human footprint instead of considering potential species richness (i.e., no weighting) may change the relation between species and phylogenetic diversity at lower elevations because lower elevations are more likely to be affected by human activity (mostly intensive agriculture). But there are relatively few such areas in the study region and use of the human footprint to weight species' probabilities of occurrence does not change our general conclusions.

Spatial Patterns of Species Richness and Phylogenetic Diversity

There was considerable difference in the spatial correlation between species richness and different measures of phylogenetic diversity. Measures that were based on topology were always highly spatially correlated with

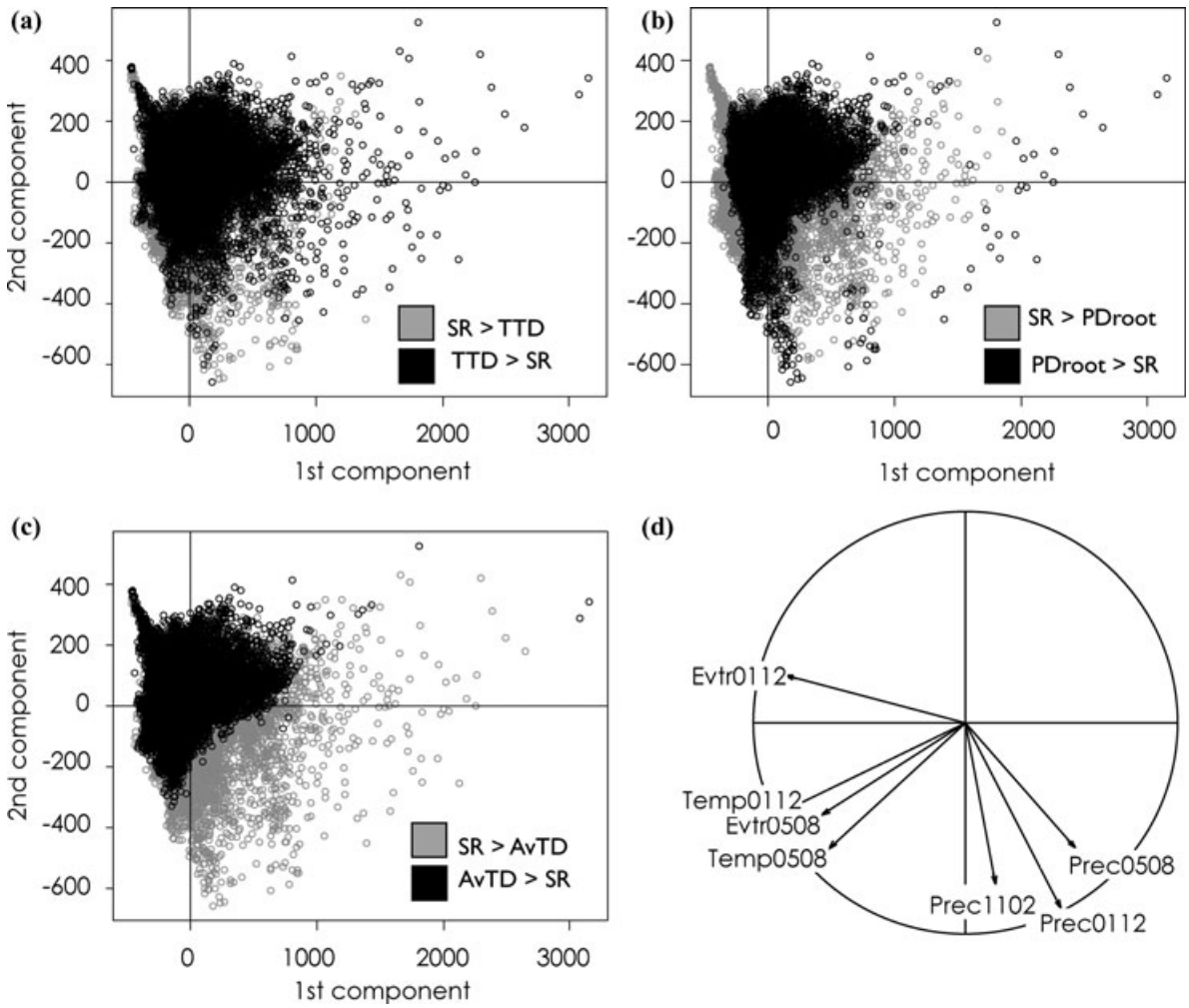

Figure 5. Results of principal component analysis (PCA) of locations with relatively high species richness (SR) versus phylogenetic diversity distributed in a multidimensional climatic space. Scores corresponding to grid cells where values for measures of phylogenetic diversity (TTD, PDroot, AvTD; defined in legends of Figs. 1 & 2) are higher than species richness (SR) (TTD > SR in [a], PDroot >SR in [b], and AvTD > SR in [c]) are highlighted in black, whereas those where species richness is higher than phylogenetic diversity (SR > TTD in [a], SR > PDroot in [b], and SR > AvTD in [c]) are in gray. (d) Correlation circle illustrating the projection of the seven climatic variables used in the analysis (mean annual evapotranspiration [Evtr0112], evapotranspiration of the wettest quarter [Evtr0508], mean annual temperature [Temp0112], temperature of the coldest quarter [Temp0508], sum of annual precipitation [Prec0112], precipitation of the wettest quarter (Prec0508), and precipitation of the driest quarter [Prec1102] [5d]) on the first two axes of the PCA.

species richness, whereas averaged measures were not. The fact that topology-based measures were most closely associated with species richness in the Cape Proteaceae likely reflects some of the characteristics of the diversification process in this region, a process that leads to similar speciation rates in the different lineages.

It has been shown that the correlation between species richness and phylogenetic diversity (measured as PDroot; Rodrigues et al. 2005) is highest with balanced topologies, which is the case for the Proteaceae tree here (Colless index for the tree was 0.863). The *Protea* diversity in the Cape Floristic Region could be the result of microevolutionary processes repeated across many clades and over millions of years (Prunier & Holsinger 2010). Strong geographical isolation is also associated with diversification of the *Protea* in this region, as is prolonged accumulation of species at a moderate rate, rather than by recent, rapid radiation (Valente et al. 2010).

Selection of Phylogenetic Measures

We agree with Schweiger et al. (2008) that there is no overall best measure of phylogenetic diversity and that in different situations certain measures may be better than

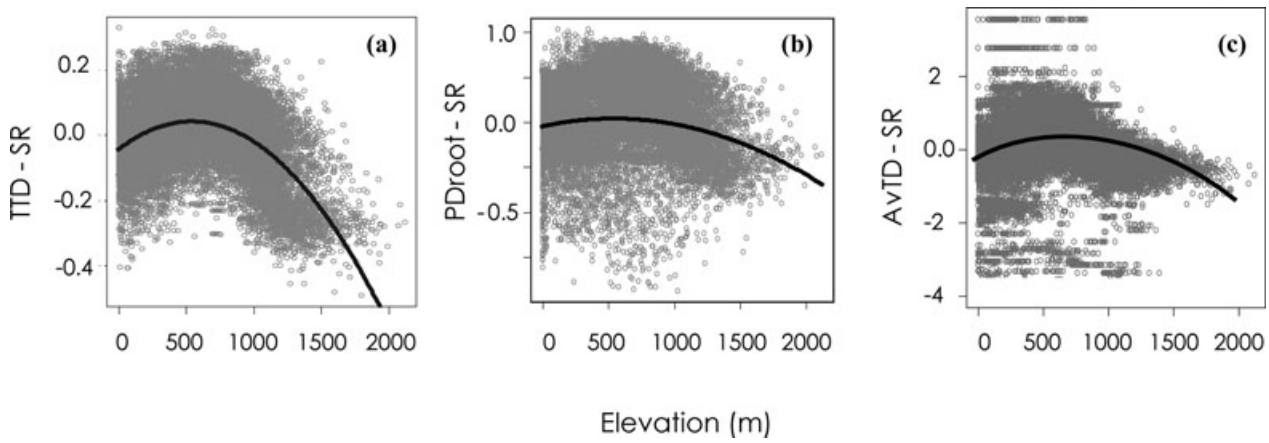

Figure 6. Results of a quadratic regression with elevation as the explanatory variable and the discrepancy between species richness and the following three phylogenetic diversity indices as response variables: (a) total taxonomic distinctness (TTD), (b) phylogenetic diversity including basal branches (PDroot), and (c) average taxonomic distinctness [AvTD].

others. It has been argued that a low correlation with species richness, such as that exhibited with averaged measures of phylogenetic diversity, is a desirable property for a measure of phylogenetic diversity (Schweiger et al. 2008) because it increases the effect of phylogeny in such measures. However, if information on phylogenetic diversity is included in a complementarity algorithm, we discourage the use of averaged measures. Our results showed (Fig. 1) that the increase in phylogenetic diversity from adding a new site may be offset by the number of new species that would be added ultimately, which would cause a reduction in averaged estimates of phylogenetic diversity. This seems counterintuitive, but it is due to the scaling of the branches in the Proteaceae phylogeny expressed in millions of years. Most branch lengths were <1 (mean [SD] $= 0.031$ [0.103]). Adding a new species will of course increase total phylogenetic diversity, but we found that the division by the number of species to obtain average measures increased faster than the numerator, which resulted in an unexpected decrease of phylogenetic diversity.

We therefore conclude that nonaveraged measures of phylogenetic diversity that include both topology and branch-length information, such as PDroot, PDnode, and Dd, provide stronger inference for conservation prioritization. Recently, PDroot and PDnode have been used extensively because they are intuitive measures of phylogenetic diversity; the only difference between these measures is the inclusion of basal branches in PDroot and not in PDnode (with minimal differences in the patterns of these two measures). A measure that focuses on the pairwise distance between a species and its nearest neighbor, Dd, has a lower spatial overlap with species richness compared with PDnode, PDroot, TTD, and F.

An alternative, perhaps more informative, null model with which to compare the different measures would be to resample the entire species pool with the same number of species several times and compare this to observed measurements. This would allow one to assess whether observed patterns are different from those obtained from random assemblages.

The choice of whether to include phylogenetic diversity as a criterion for conservation-area selection (and if so which metric to use) also depends on what society hopes to protect. Presently preserving a large complement of interspecific genetic diversity is considered by conservation professionals beneficial to conservation (Mooers et al. 2005; Forest et al. 2007; Cadotte et al. 2009). The phenotypic diversity that is added by conserving very old monotypic lineages is likely to be greater than phenotypic diversity of closely related species. However, these older monotypic lineages are also more susceptible to extinction (Purvis et al. 2000). Nevertheless, there is evidence that phylogenetically diverse communities have higher biomass than less diverse communities (Cadotte et al. 2009). If the discrepancies between species richness and phylogenetic diversity we found are similar in other groups of organisms (as they are in birds [Devictor et al. 2010]) and the evidence for the link between phylogenetic relations and ecosystem productivity or function is strengthened (Cadotte et al. 2009), we believe there is value in using measures of phylogenetic diversity in conservation planning.

Supporting Information

Supporting information is available online. The authors are 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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