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BIODIVERSITY RESEARCH

Spatial incongruence among hotspots and complementary areas of tree diversity in southern Africa

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ABSTRACT

Aim Biodiversity hotspots have important roles in conservation prioritisation, but efficient methods for selecting among them remain debated.

Location Southern Africa.

Methods In this study, we used data on the dated phylogeny and geographical distribution of 1400 tree species in southern Africa to map regional hotspots of species richness (SR), phylogenetic diversity (PD), phylogenetic endemism (PE), species endemism (CWE), and evolutionary distinctiveness and global endangerment (EDGE). In addition, we evaluated the efficiency of hotspots in capturing complementary areas of species richness and phylogenetic diversity. We examined the spatial overlap among hotspots for each metric, and review how well one metric may serve as a surrogate for others. We then evaluated the effectiveness of current conservation areas in capturing these different facets of diversity and complementary areas. Lastly, we explored the environmental factors influencing the distribution of these diversity metrics in southern Africa.

Results We reveal large spatial incongruence between biodiversity indices, resulting in unequal representation of PD, SR, PE, CWE and EDGE in hotspots and currently protected areas. Notably, no hotspot area is shared among all five measures, and 69% of hotspot areas were unique to a single diversity metric. Areas selected using complementarity are even more dispersed, but capture rare diversity that is overlooked by the hotspot approach.

Main conclusions An integrative approach that considers multiple facets of biodiversity is needed if we are to maximise the conservation of tree diversity in southern Africa.

Keywords
Complementarity, EDGE, hotspots, phylogenetic endemism, protected areas, trees of southern Africa.

INTRODUCTION

To protect biodiversity within the constraints of limited conservation funding, it is essential that we prioritise conservation efforts. A fundamental challenge in the selection of priority areas for conservation is therefore deciding on which elements of biodiversity to protect. In the past, conservation areas have often been chosen based on concentrations of species richness, endemism, rarity, degree of threat (Dinerstein *et al.*, 1995, 2000; Williams *et al.*, 1996; Myers *et al.*, 2000; Ceballos & Ehrlich, 2006). Typically, geographic regions harbouring high concentrations of one or more of these diversity components are given high priority (Prendergast *et al.*, 1993; Myers *et al.*, 2000; Ceballos & Ehrlich, 2006). A high congruence among these diversity measures would allow one metric to serve as a surrogate for the others and thus might provide a silver bullet for conservation strategy. However, even among traditional diversity metrics (e.g. richness, endemism, rarity), spatial mismatches are frequently reported (Orme *et al.*, 2005; Ceballos & Ehrlich, 2006). If incongruence among metrics is a general feature of the spatial distribution of biodiversity then an integrative strategy that considers multiple facets of diversity should be considered. Such a strategy might better represent the essential elements

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of biodiversity important for maintaining ecosystem functioning in a world faced with increasing threats due to human pressure, competing land uses, climate change and invasive species (Devictor *et al.*, 2010).

Recent work has suggested that a more integrative approach for selecting among conservation areas is provided by metrics that consider evolutionary components, for example, phylogenetic diversity (Faith, 1992), evolutionary distinctiveness (Isaac *et al.*, 2007), phylogenetic endemism (Rosauer *et al.*, 2009), or a combination of evolutionary distinctiveness and species vulnerabilities (e.g. the EDGE metric of Isaac *et al.*, 2007). Phylogenetic diversity (PD) represents the summed length of phylogenetic branches linking a group of species (Faith, 1992). This metric is often characterised in units of time and incorporates one aspect of species complementarity as it accounts for the shared branch lengths among species such that the contribution of a given taxon depends on its relatedness to other taxa in a set (Faith, 1992). PD has been used for identifying priority areas for conserving plants (Forest *et al.*, 2007) and animals (Davies *et al.*, 2008). Evolutionary distinctiveness (ED) partitions branch lengths by the total number of species subtending them, and then, weights species based on the amount of 'unique' evolutionary history they represent (see Isaac *et al.*, 2007; Cadotte & Davies, 2010). Although PD is a property of an area and ED is a property of species, the spatial distribution of ED might be equivalent to PD under some models of speciation. For example, at the extreme, when radiations are geographically restricted, the sum of the ED of species in a region will equal PD. Differences in the spatial distribution of PD and PE might therefore provide additional information useful for conservation planning, although we do not consider this explicitly here.

Phylogenetic endemism (PE; Rosauer *et al.*, 2009) provides an alternative evolutionary metric for prioritising species and areas. PE integrates phylogenetic diversity and geographical distribution of species allowing identification of geographic regions harbouring high degree of restricted evolutionary history (Mooers & Redding, 2009; Rosauer *et al.*, 2009). Similarly, evolutionary distinctiveness and threat have been combined in the EDGE (evolutionary distinctiveness and global endangerment) metric of Isaac *et al.* (2007). This metric identifies species that have few extant relatives and face high risk of extinction.

Whilst hotspots approaches have attracted much attention, it is nonetheless well recognised that conservation prioritisation based on selecting the most diverse set of regions does not necessarily maximise the overall representation of biological diversity, particularly when the number of species is very large (Williams *et al.*, 1996). For example, two highly diverse regions might capture similar elements of diversity, and therefore, including both areas in a conservation network would result in high redundancy. Whilst we might value redundancy as an insurance mechanism, we frequently wish to first ensure that each element of biodiversity is represented at least once. Complementarity approaches attempt to find the set of areas that maximises the number of target species or clades conserved within a minimum set (Vane-Wright *et al.*, 1991). The PD complementarity of a species is measured by the additional branch length it represents that is not spanned by a reference set of species (Faith, 1992). Because EDGE is a property of species, not areas, it is not naturally fitted to complementarity approaches. However, a recent reformulation (HEDGE) by Steel *et al.* (2007) considers the extinction risk of all species subtending from a particular branch, such that a highly threatened species is downweighted if it has close relatives that are less threatened. A similar approach could be applied in space, such that complementary grid cells could be selected to increase the total protected EDGE score. In part, this might be considered equivalent to combining EDGE with PE approaches and could be a useful avenue to explore in the future.

There is growing interest in the application of integrative approaches in identifying biodiversity hotspots (Devictor *et al.*, 2010; Davies & Cadotte, 2011; Gonza´lez-Orozco *et al.*, 2012; Tucker *et al.*, 2012; Mazel *et al.*, 2014). However, to date, empirical studies have been relatively narrow in their taxonomic or geographic focus (e.g. Rosauer *et al.*, 2009; Ribeiro *et al.*, 2012; Gudde *et al.*, 2013). In this study, we integrate data on phylogeny and geographical distribution of tree species of southern Africa (an area that includes Botswana, Mozambique, Zimbabwe, Namibia, South Africa, Swaziland and Lesotho) and explore congruence among different facets of tree diversity in the region: species richness (SR), phylogenetic diversity (PD), phylogenetic endemism (PE), species endemism (CWE), and evolutionary distinctiveness and global endangerment (EDGE). We also contrast hotspot approaches to methods based on complementarity for PD and SR. We then assess the representation of the selected hotspots within the current network of protected areas. Last, we explore the correlations between various environmental variables, including human population density, and the different diversity metrics to gain insights into the processes structuring these different facets of tree diversity within southern Africa.

METHODS

Description of data

The sampling in this study covers over 1400 woody plant species of southern Africa (Maurin *et al.*, 2014). We defined trees according to O'Brien (1993) as woody species with stems or pseudostems > 0.5 m in height. The woody plants of southern Africa include monocots, gymnosperms, and angiosperms and comprise approximately 115 families, 541 genera and ~2200 species. The data were obtained by first, compiling a checklist of the region's woody species from literature (Coates Palgrave, 2002; Schmidt *et al.*, 2007; Boon, 2010; Van Wyk *et al.*, 2011; Germishuizen & Meyer, 2013) and cross-checking the names for synonyms and family names using The Plant List (www.plantlist.org) and the

Angiosperm Phylogeny Group (APG III, 2009), respectively. Second, over a 6-year period, leaf samples were collected from across southern Africa, from which the two plant DNA barcoding regions (*matK* and *rbcLa*) were sequenced and used to reconstruct a phylogenetic tree of the region's flora.

Species distribution data

We used range maps representing the maximum geographic area encompassing the known extent of each species distribution for the over 1400 species. These maps were sourced from Coates Palgrave (2002) and Van Wyk *et al.* (2011). All maps were scanned at 300 dpi and processed in ArcMap v.10.0 (Esri, CA, USA). Each species' range map was projected into a Behrmann equal area cylindrical projection and overlaid onto a 50 × 50 km grid to generate a species richness map (Fig. 1a) and a matrix of species presence/absences for the 1563 grid cells. Coastal grid cells with < 50% land area were excluded to minimise the influence of unequal sampling area.

Species phylogeny

A matching, dated molecular phylogeny was obtained from (Maurin *et al.*, 2014). This tree was reconstructed using Bayesian inference and 28 independent fossil calibrations from plant DNA barcodes, *matK* and *rbcLa* (see Maurin *et al.*, 2014, for full description of tree reconstruction).

Measures of diversity hotspots

We computed five common diversity indices from the biodiversity literature (Myers *et al.*, 2000; Orme *et al.*, 2005; Isaac *et al.*, 2007; Gonza´lez-Orozco *et al.*, 2012): SR, PD, PE, CWE and EDGE. SR, PD, PE and CWE were calculated using Biodiverse v.0.18 (Laffan *et al.*, 2010), and EDGE was computed in R (R Core Team, 2013).

SR is simply the total number of species within each grid cell. PD is defined as the sum of branch lengths connecting a set of taxa on a rooted phylogenetic tree (Faith, 1992) and was estimated on the presence/absence matrix in the software Biodiverse v.0.18 (Laffan *et al.*, 2010).

CWE measures the distribution of narrow-ranged or endemic species (Crisp *et al.*, 2001). This metric is obtained by dividing weighted endemism (WE), the number of species within a grid weighted by the inverse of their range sizes, by species richness (Crisp *et al.*, 2001). CWE thus represents the mean endemism of the species in each grid cell and was calculated in Biodiverse v.0.18 (Laffan *et al.*, 2010).

PE is similar to WE except that it is calculated based on shared branches of a phylogenetic tree (Rosauer *et al.*, 2009), whereas WE is only weighted based on shared grid cells in

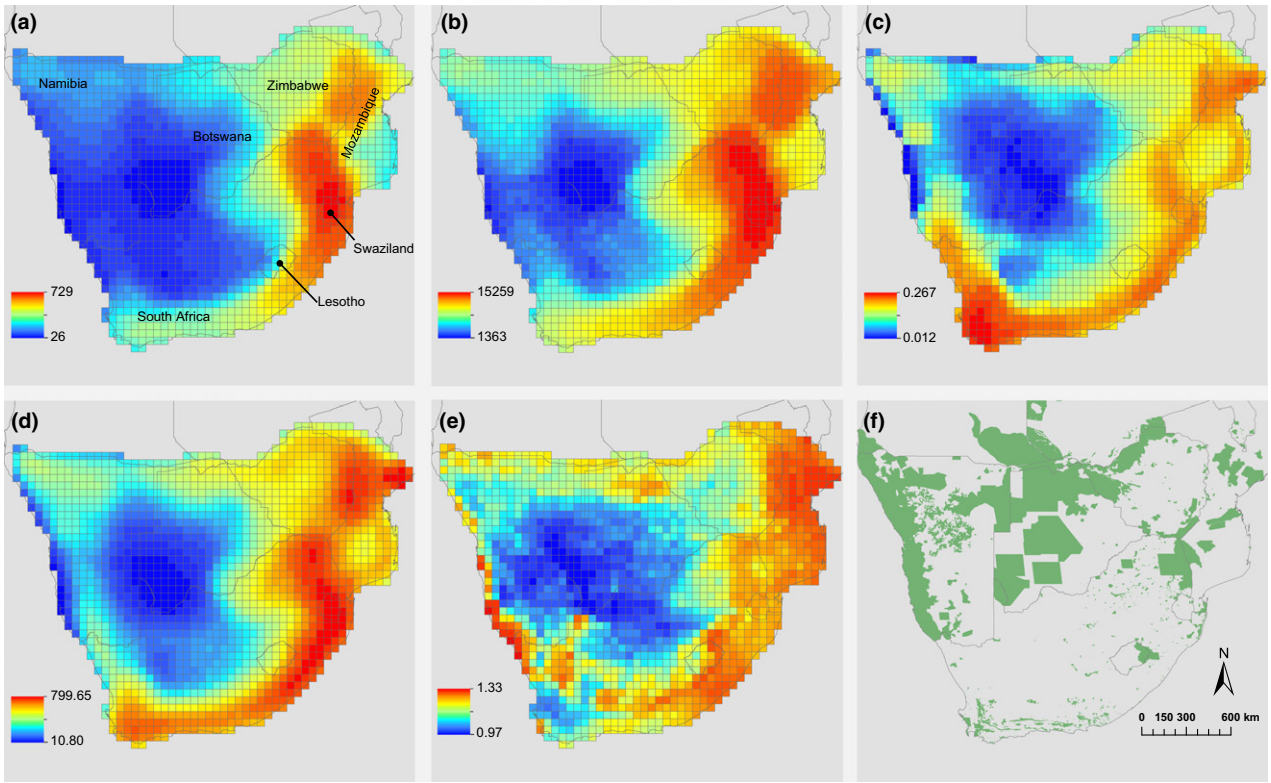

Figure 1 Spatial distribution of tree biodiversity components across 50 × 50 km equal area grids (Behrmann projection); (a) species richness, (b) phylogenetic diversity, (c) mean species endemism, (d) phylogenetic endemism, (e) mean EDGE and (f) currently protected area network obtained from UNEP-WCMC (2012). Data for *a–e* are depicted divided into 30 classes using natural breaks.

geographic space. Following Rosauer *et al.* (2009), PE is expressed as:

$$\mathrm{PE} = \sum_{\{a \in A\}} \frac{L_a}{R_a}$$

where $\{A\}$ encapsulates the set of branches connecting species to the root of a phylogenetic tree, L_a is the length of branch a, expressed as proportion of the total length of the tree and R_a is the range size of the clade. Thus, the proportion of branch lengths allocated to a grid cell represents the PE in that cell (Mooers & Redding, 2009; Rosauer *et al.*, 2009).

The EDGE metric identifies species that have few or no extant relatives and which are threatened with extinction. It is expressed as:

$$\mathrm{EDGE} = \ln(1 + \mathrm{ED}) + \mathrm{GE} \times \ln(2)$$

where GE is global endangerment and corresponds to the IUCN conservation status of each species (LC, NT, VU, EN, CR) see Isaac *et al.* (2007); ED is the amount of unique evolutionary history represented by a species. First, values of ED and GE were calculated separately for each species. Second, we calculated EDGE scores per species using the equation expressed above. Third, we generated per-cell scores by taking the mean species values.

It is important to note that SR, PD and PE represent summations and are a property of an area, whereas CWE and our per-cell EDGE measure represent average species values; thus, these two sets of metrics capture intrinsically different dimensions of diversity. We use CWE rather than WE to reflect usage in the conservation literature (e.g. Crisp *et al.*, 2001; Laffan & Crisp, 2003), and we therefore use mean EDGE for comparison (see Safi *et al.*, 2013 for a different approach); however, we additionally include maps of WE and summed EDGE in the supplementary material (Figure S1).

Analyses

Following common practice, we defined hotspots as the top 2.5% of the grid cells in each category. This threshold has been shown to perform well in representing a significant proportion of terrestrial biodiversity in several taxonomic groups (Myers *et al.*, 2000; Orme *et al.*, 2005; Ceballos & Ehrlich, 2006). The sensitivity of our hotspot criteria was evaluated by steadily increasing the hotspot threshold percentage.

We evaluated congruence among the different hotspots by calculating the degree of spatial overlap between hotspots and the correlations between them using simultaneous autoregressive (SAR) models with Moran's I correction for spatial autocorrelation implemented in SAM v.4.0 (Rangel *et al.*, 2010).

Complementary areas were identified for both SR and PD to identify the minimum number of cells to maximise coverage of both metrics in turn. The species complementarity algorithm was calculated in R (R Core Team, 2013) by first selecting the grid cell of highest species richness. Subsequent cells are added to the first cell based on species richness of the unrepresented species. The algorithm then selects the cell with the highest richness of the remaining unrepresented species. The process is iterated until all species are represented at least once in the minimum set of sites (Vane-Wright *et al.*, 1991). PD complementarity was quantified using an equivalent metric but maximising unique phylogenetic branch lengths rather than species, where each cell was assigned the phylogenetic branches linking the species within the cell to the root of the phylogeny (Faith *et al.*, 2004), and cells were selected to maximise the addition of unrepresented branches. We set the SR- and PD-complementarity algorithm to represent the same species richness of trees as captured in the 2.5% SR and PD hotspots.

We then assessed the representation of hotspots and complementary areas within polygons of currently protected areas. We overlaid our diversity hotspots and complementary areas on a GIS layer of legally protected areas from the UNEP World Conservation Monitoring Centre (UNEP-WCMC, 2012) and calculated the proportion of each hotspot area found within protected areas.

Finally, we evaluated the correlations between the diversity metrics and various environmental factors and human population density (HPD) known to correspond with regional-scale diversity gradients and ecosystem processes. We explored mean altitude, mean annual precipitation (MAP), mean annual temperature (MAT) and net primary productivity (NPP). Altitude, MAP and NPP were obtained from the worldclim database (Hijmans *et al.*, 2005), NPP from Kucharik *et al.* (2000). HPD was obtained from the AfriPop project (Linard *et al.*, 2012). Each environmental variable was extracted by overlaying the 50 × 50 km grid cells and calculating the mean value per cell in the R package RASTER (Hijmans, 2013). Correlation strengths were estimated using spatial autoregressive models correcting for spatial non-independence among grid cells using Moran's I as implemented in SAM v.4.0 (Rangel *et al.*, 2010).

RESULTS

The distribution of overall tree SR, PD, CWE, PE and EDGE are summarised in Fig. 1. We reveal areas of high tree SR in the east, running from Mthatha district in the Eastern Cape to KwaZulu-Natal, Swaziland, Mpumalanga, Limpopo, southern Zimbabwe and parts of Mozambique (Fig. 1a). The distribution of PD (Fig. 1b) is similar to SR but more evenly dispersed. Areas with high mean endemism (CWE) are more centred in Western Cape and some parts of the Northern Cape within the Cape floristic region (CFR) of South Africa, and to a lesser extent in the Eastern Cape and Mozambique (Fig. 1c). In contrast, PE is higher in the east, with centres of high diversity in the CFR, stretching from Port Elizabeth in Eastern Cape to Limpopo provinces of South Africa, and Mozambique (Fig. 1d). The EDGE metric is more unevenly

dispersed, with higher values in south-western Namibia, Northern Cape, Eastern Cape and Mozambique (Fig. 1e).

Our hotspot analysis based on the top 2.5% grid cells (Fig. 2) reveals the low overlap among the various diversity metrics, with the exception of SR and PD (Fig. 2a,b). Cumulatively, hotspots for the five metrics occupied a total of 345,000 km^2 (representing 8.8% of the total grid cells; Fig. 2f), of which no cell was shared among all five measures (Fig. 3). Further, 69% (95 of 138) of hotspot cells were unique to one of the five diversity measures (Fig. 3). The remaining 31% (43 of 138) hotspot cells were shared between pairs of hotspots types. The total number of species captured by the 2.5% hotspot criterion varied with diversity metric (Table 1), notably PE captured a greater proportion of tree species (76.7% representing 1074 species), followed by PD (62%) and SR (61.2%), and CWE captured the fewest species (22.6%).

A lack of congruence among diversity hotspots could reflect the small size of hotspot areas. We predicted greater congruence with increasing hotspots size (i.e. increasing the percentage of cells considered as hotspots). However, using small increments in the percentage of cells considered as hotspots, we found no obvious increase in congruence (Fig. 4) until the percentage of hotspot cells was increased to > 7.5%. Further, increments from 15% to 50% of cells result in large overlap among biodiversity components (Fig. 4). The cumulative 5% hotspot threshold (i.e. union of the 5% hotspots for all diversity measures combined) encompassed 101 more cells than in the 2.5% criterion (Fig. 2), representing 15% of the total number of cells. At this threshold, the

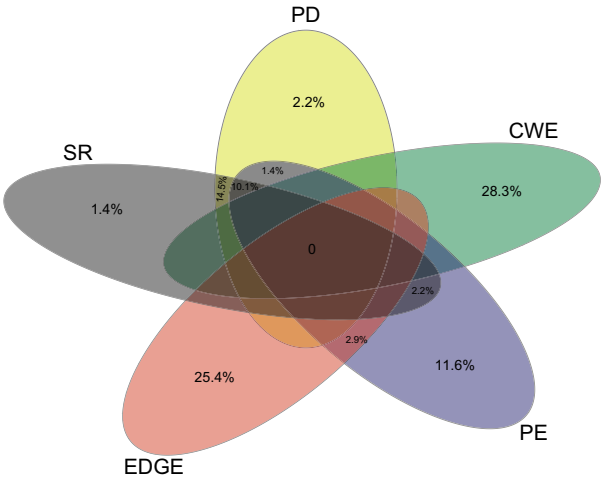

Figure 3 Venn diagram of spatial overlap and mismatch for the hotspot components; SR species richness, PD phylogenetic diversity, CWE corrected weighted endemism, PE phylogenetic endemism, and EDGE evolutionary distinctiveness and global endangerment.

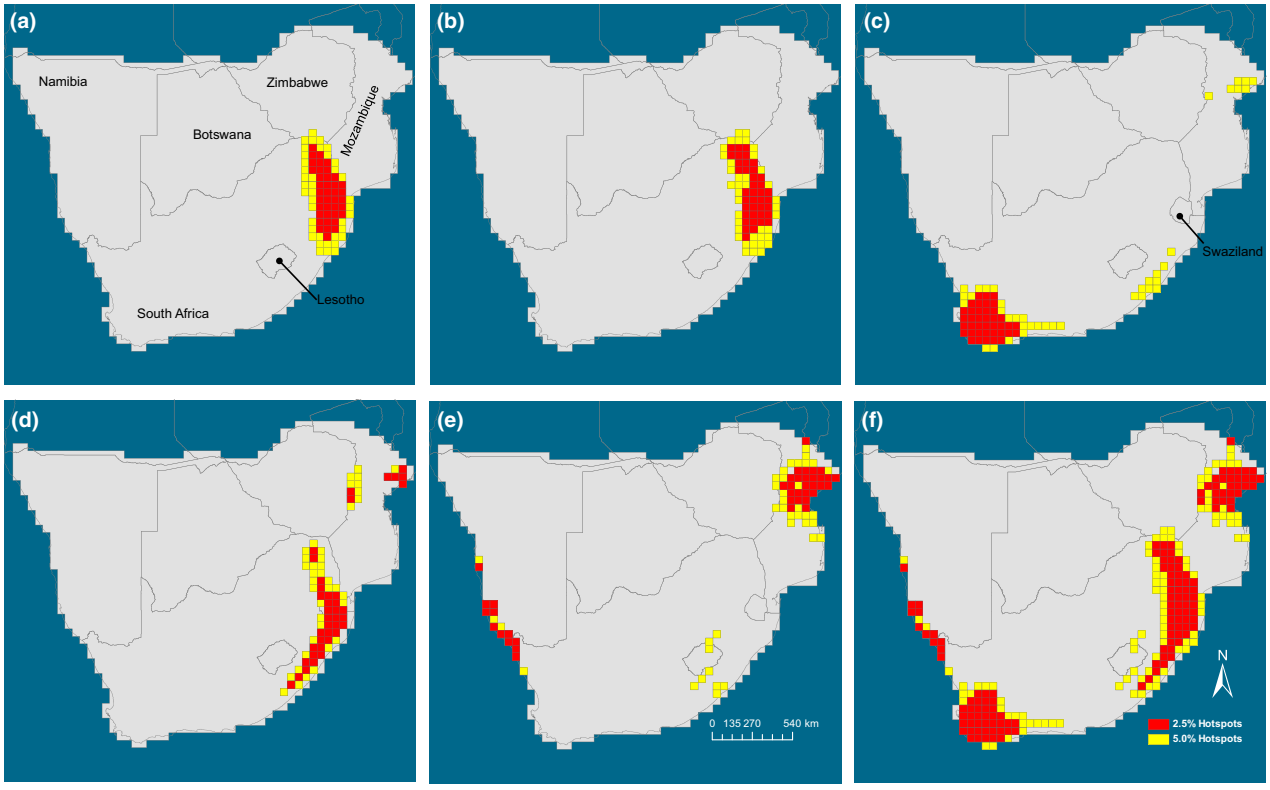

Figure 2 Diversity hotspots of (a) species richness, (b) phylogenetic diversity, (c) mean species endemism, (d) phylogenetic endemism, (e) mean EDGE and (f) cumulative map of all five hotspots combined together. The hotspots are grid cells with the highest 2.5% of the diversity scores (shown in red), and the 5.0% hotspots are shown in yellow.

Table 1 Representation of tree richness and evolutionary distinctiveness in the five hotspot diversity indices based on the 2.5% and 5% hotspot criteria. Regional total (total richness = all species included in analysis, 1400)

Hotspots	Richness (2.5% criterion)	Richness (5.0% criterion)	Largest contributing reserves
SR	857 (61.2)	904 (64.6)	Kruger to Canyons UNESCO-MAB Biosphere Reserve; Kruger National Park; Selati Game Reserve; Greater St Lucia Wetland Nature Reserve; Zona de Vigilancia da REM; Sabi Sand Provincial Nature Reserve; Klaserie Private Nature Reserve; Motlatse Canyon Nature Reserve; Timbavati Game Reserve; Songimvelo Provincial Nature Reserve
PD	867 (62)	908 (65)	Kruger to Canyons UNESCO-MAB Biosphere Reserve; Kruger National Park; Selati Game Reserve; Sabie Sand Provincial Natural Reserve; Klaserie Private Nature Reserve; Motlatse Canyon Nature Reserve; Timbavati Game Reserve; Songimvelo Provincial Nature Reserve; UNESCO-MAB Biosphere Reserve; Ithala Provincial Nature Reserve
CWE	316 (22.6)	1122 (80)	Cape Floristic Region; Cape West Coast UNESCO-MAB Biosphere Reserve; Cape Winelands UNESCO-MAB Biosphere Reserve; Groot Swartberg Provincial Nature Reserve; Koue Bokkeveld Mountain Catchment Area; Riviersonderend Mountain Catchment Area; Matroosberg Mountain Catchment Area; Tankwa-Karoo National Park; Cederberg Provincial Nature Reserve; Langeberg-wes Mountain Catchment Area
PE	1074 (76.7)	1109 (79)	Kruger to Canyons UNESCO-MAB Biosphere Reserve; Taveuni Reserved Forest; Marromeu Complex Ramsar Wetland; Gorongosa National Park; Coutada N. 12 Hunting Reserve; Natal Drakensberg Park; Coutada Oficial No. 10 Hunting Reserve; Selati Game Reserve; Greater St Lucia Wetland Nature Reserve; Coutada Oficial No. 11 Hunting Reserve
EDGE	580 (41.4)	961 (68.6)	Namib-Naukluft National Park; Sperrgebiet National Park; Skeleton Coast Park National Park; Taveuni Reserved Forest; Lesotho National Park; Coutada Oficial 5 Hunting Reserve; Coutada Oficial No. 13 Hunting Reserve; Ai-Ais Hot Springs National Park; Marromeu Complex Ramsar Site; Gorongosa National Park
Total in all hotspots	1312 (93.7)	1348 (96.3)	

Numbers in parenthesis are percentages. Data for contributing reserves obtained from UNEP-WCMC (2012).

number of species represented for all hotspots combined increased from 93.7% (1312 of 1400 species) to 96.3%. Thus, an almost doubling in the size of the combined hotspot area captures only an additional 2.6% of species.

The patterns of congruence and incongruence are also reflected in the correlations among diversity metrics. Correlation strengths ranged from 8% for EDGE against CWE, to 98% for PD against SR (Table 2).

We found that large-ranged species tend to be well represented within hotspots, complementary and protected areas (Figure S2). The species which were best represented by all the criteria were thus the most widely distributed, such as *Boscia albitrunca* (Capparaceae) (1086 grid cells; 2,715,000 km^2) or *Terminalia sericeae* (Combretaceae) (982 grid cells; 2,455,000 km^2). Conversely, the most poorly represented species were all narrow ranged, such as *Brachystegia stipulata* (Fabaceae; two grid cells; 5000 km^2) and *Drypetes mossambicensis* (Putranjivaceae) (three grid cells, 7500 km^2).

Our complementarity analysis revealed that all tree species could be represented at least once within just 48 grid cells (195,000 km^2) (Fig. 5a), much fewer than expected under a null model of selecting cells randomly (Figure S3). The areas selected based on the species complementarity are widely dispersed, incorporating distinct habitat types in northern Namibia and Botswana that were not captured by the hotspots analysis. We contrasted the total number of species

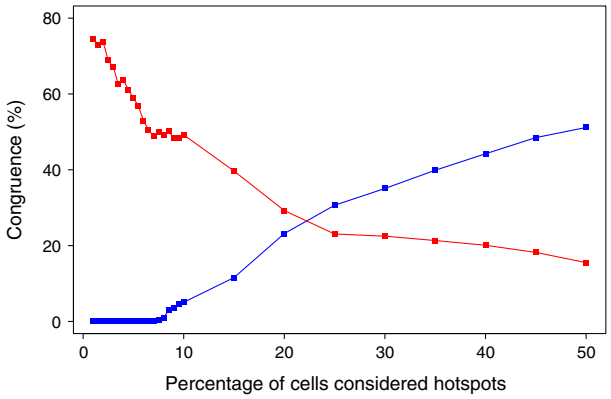

Figure 4 Relationship between the threshold per cent of cells considered hotspots and congruence among the five hotspot indices (species richness, phylogenetic diversity, mean species endemism, phylogenetic endemism and mean EDGE). Congruence corresponds to the percentage of cells that are shared by all five types of hotspots (blue line); the red line indicates the percentage of hotspot grid cells that are unique to individual metrics.

captured by the 2.5% SR hotspots with the species complementarity approach by constraining the complementarity algorithm to capture 60% of species diversity. Surprisingly, using this threshold, equivalent tree species diversity (including

Table 2 Pairwise correlation of diversity metrics using spatial autoregression

	PD	CWE	PE	EDGE
SR	**0.98**	0.22	**0.83**	0.31
PD		0.22	**0.80**	0.37
CWE			0.43	0.08
PE				0.31

The explained variances (r^2) above 50% are indicated in bold. In all cases, $P < 0.001$.

narrowly distributed species such as *Diospyros verrucosa* and *D. mossambicensis*) can be represented in just three grid cells (Fig. 5a). As we increased the number of cells represented, the algorithm rapidly yields an asymptote such that further increments in the number of cells did not result in increase in species diversity (Figure S4). We also evaluated phylogenetic diversity within the minimal number of grid cells – PD complementarity. We found that 49 cells are selected to capture total phylogenetic diversity, one more cell than to capture species richness, indicating slight differences in efficiency in the respective optimisation algorithms. When we constrained the PD-complementarity analysis to select 60% of phylogenetic diversity, we identify an optimal set of two grid cells (Fig. 5b).

In all cases, more than 50% of our hotspots and complementary areas fell outside currently protected areas (Fig. 6; Table 1). The best-protected hotspot is EDGE with 40.60% of its area within currently protected areas. Hotspots of PD and SR have 32.7% and 34.7% of their area within protected area, respectively. Although we did not find a significant correlation between species richness and geographic area across protected areas ($r = -0.031$, $P = 0.23$), the Kruger National Park, is the largest park and also captures the most PD and SR. Hotspots of PE and CWE are the least protected, with only 15.8% and 18.5%, respectively of their area within currently protected areas. The coverage of complementary areas by the currently protected areas is also poor, 26.1% for SR complementarity and 23.9% for PD complementarity (Fig. 6).

NPP followed by MAP was the best predictors of all diversity metrics, with NPP explaining > 50% of the variation in PD, SR and PE (Table S1). However, EDGE and CWE were less well predicted by the environmental variables (correlation with NPP = 0.26 and 0.15, respectively). We found moderate correlation strengths with altitude, whereas MAT and HPD explained little or no variation in tree diversity irrespective of metric (Table S1).

DISCUSSION

We show lack of overlap and unequal coverage among hotspots of tree SR, PD, CWE, PE and EDGE within southern Africa. Nonetheless, we identify several high diversity areas that correspond to regions which have been identified as conservation hotspots in southern Africa (Van Wyk & Smith, 2001; Conservation International, 2005). We note that complementarity methods are much more efficient in selecting minimal areas for conservation, protecting maximum species/branch lengths in a small geographic area and high priority complementary areas are more widely dispersed across the study area than those based on the hotspot approach. Our results suggest that currently protected areas are insufficient for protecting tree diversity in southern Africa irrespective of the biodiversity metric evaluated.

SR and PD covary closely but overlap little with hotspots of EDGE or PE, and the different facets of tree diversity correlate differently with different environmental factors. Concentrations of high PD, PE and SR in the east correspond to regions of high NPP and MAP. Climate and environmental heterogeneity play important roles in determining the geographic distribution of species richness and community assembly at various spatial scales (Hawkins *et al.*, 2003; Field *et al.*, 2008). In southern Africa, water, energy and primary productivity have been shown to strongly influence the distribution of plant species richness along a longitudinal gradient, from west to east (O'Brien, 1993). The strong association found for NPP and MAP with PD, PE and SR may be consistent with habitat filtering due to energy-moisture-productivity dynamics supporting both greater biomass and species diversity. Endemic radiations might also shape patterns of richness and endemism regionally, although evolutionary rates might be driven more by temperature and environmental heterogeneity rather than productivity (Davies *et al.*, 2005).

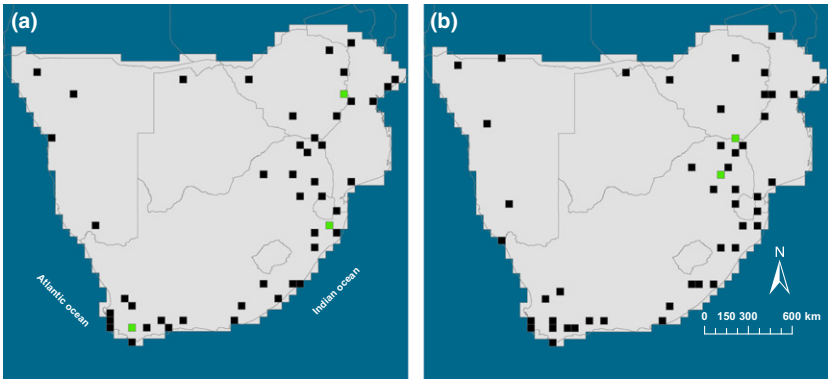

Figure 5 Distribution of grid cells chosen by the complementarity algorithm to represent tree diversity based on (a) species richness and (b) phylogenetic diversity. Grid cells in green are the top grid cells required to capture 60% of total tree species richness. Compare with Figure S3a,b to evaluate equivalent accumulation curves selecting cells at random.

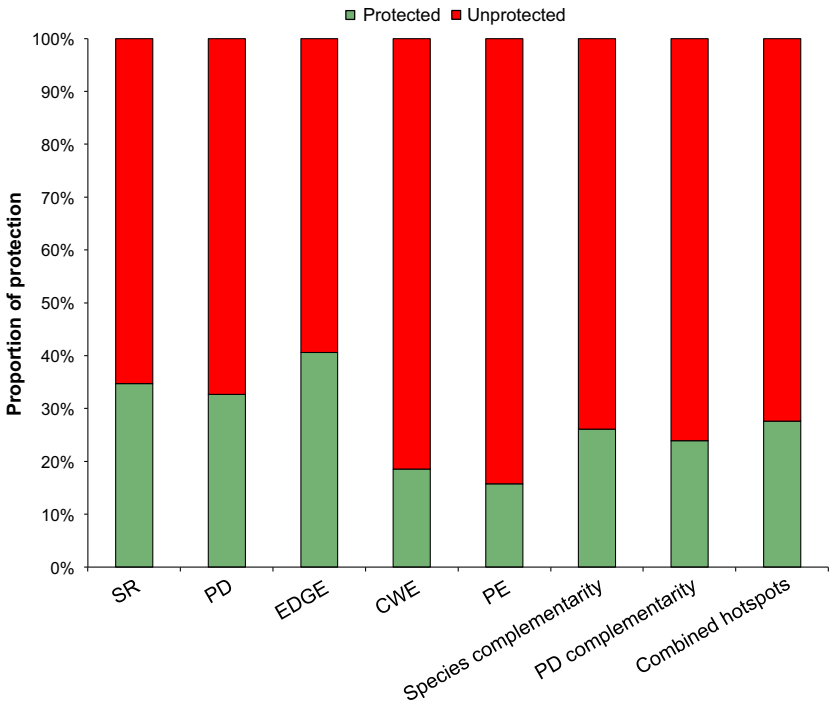

Figure 6 Barplot showing the degree of protection of hotspots and complementary areas within currently protected areas in southern Africa.

The EDGE hotspots are mainly distributed along the west coast in southern Namibia, and the largest is in the north-east covering parts of Chimoio, Gorongosa National Park, Chinizuia forest and Marromeu National Reserve in Mozambique (Fig. 1e). These hotspots are represented by species that have few close relatives on the tree of life for southern African woody flora and are highly threatened with extinction such as *Brackenridgea zanguebarica* (Ochnaceae), *Khaya anthotheca* (Meliaceae) in the north-east and *Aloe pillansii* (Asphodelaceae) in southern Namibia. It is possible that these high EDGE regions, that fall outside areas of high species richness, host lineages from once more diverse clades. However, because our measure of ED only considers the relationships among the tree flora of southern Africa, it is also possible that these regions capture species within clades that are better represented in other biomes.

Previous work has suggested that hotspots of richness, threat and endemism might demonstrate different spatial distributions (e.g. Orme *et al.*, 2005) and differ between taxonomic groups (Grenyer *et al.*, 2006), making it difficult to select among areas for conservation prioritisation. Phylogenetic approaches may provide a more integrative metric, capturing multiple facets of biodiversity (Faith, 1992; Forest *et al.*, 2007; Davies & Cadotte, 2011). However, our study reveals that hotspots defined using different metrics of phylogenetic diversity, including those weighted by endemism (PE) and threat (EDGE) also demonstrate large incongruence. Such spatial mismatch could imply differences in the biogeographical and evolutionary histories underlying the distribution of species or more fundamental differences in the drivers of different facets of biodiversity (Prinzing *et al.*, 2008; Cumming & Child, 2009) and the intrinsic properties of the metrics themselves (Pavoine & Bonsall, 2011). For example, although EDGE, PE and PD all incorporate information on the evolutionary history of species, in our usage here PE and PD represent summations, whereas EDGE represents a mean species value. It would be possible to explore how much variation is due to differences in the distribution of ED versus GE, for example, by comparing the explanatory power of the correlation or relationship between ED vs. EDGE, ED vs. PD and ED vs. PE, as described in Safi *et al.* (2013). Such comparisons could be useful in weighting conservation decisions when faced with multiple metrics, each with a different spatial distribution.

Our study emphasises how different diversity metrics can present very different conservation scenarios. For example, if the goal is to maximise the protection of species endemism, a metric that focuses solely at the species level, then we should prioritise the CFR. The high endemism of the CFR is well recognised (Goldblatt, 1978; Cowling & Hilton-Taylor, 1994) and distinguish it as one of the six floral hotspots of the world (Goldblatt & Manning, 2002; Linder, 2003), emphasising its importance as a global conservation priority. However, this area contains a high representation of short phylogenetic branches with lineages of recent divergence and locally restricted to the landscape of the area (Forest *et al.*, 2007). Thus, a narrow focus on species endemism might be suboptimal for capturing phylogenetic diversity, phylogenetic endemism or EDGE, that may be higher in other parts of southern Africa. A focus on phylogenetic diversity would, for example, centre conservation efforts to the east around Swaziland, Mpumalanga, Limpopo, southern Zimbabwe and parts of Mozambique. This region captures both high PD and PE and might therefore retain relict clades with

present-day distributions reflecting the history of past climatic changes and range contraction (see Mishler *et al.*, 2014). Our results therefore not only high-light hotspots of present-day diversity, but also provide insights into the biogeographical and evolutionary history of the southern African flora. This information might additionally be incorporated into conservation decision-making if we wish to protect centres of evolutionary radiations or past refugia.

We show that different metrics vary greatly in their ability to act as surrogates for other metrics. For example, for hotspots of CWE, EDGE and PE, 28.3%, 25.4% and 11.6% of cells, respectively, were unique to that metric. However, PD is perhaps the best overall surrogate measure, sharing 27% and 11.6% of cells, respectively, with SR and PE. The strong positive correlation between species richness and phylogenetic diversity has been reported previously (Rodrigues & Gaston, 2002; Morlon *et al.*, 2011), and therefore, this result is not unexpected. Congruence between PD and EDGE or CWE is in general much lower, reflecting the important distinction between metrics that represent summations (PD, SR and PD) versus those that represent mean values (CWE and EDGE). Nonetheless, there is some overlap between PE and EDGE in Sofala, Mozambique, with 3% of cells shared. Perhaps most surprisingly, we found that our PE hotspots captured a higher proportion of species richness (76.7%, 1074 species) than the SR hotspots. A similar pattern has been previously shown for birds (Orme *et al.*, 2005) and likely reflects the wider geographic dispersal of endemism hotspots (see also Rosauer *et al.*, 2009).

Our classification of 'hotspots' follows convention, but the 2.5% threshold is arbitrary. It is possible that congruence among hotspots is scale dependent, such that increments in the percentage of hotspots cells increase spatial overlap between metrics. However, we found that a significant increase in spatial overlap among metrics was only observed when the threshold for delineating hotspots was increased above 7.5% of cells, representing an unrealistically large geographic area under the constraints of limited conservation funds and competing land uses (Meffe & Carrol, 1994). Area selection based on complementarity provides an efficient solution for maximising diversity under a minimal cost scenario (Vane-Wright *et al.*, 1991). Here, we show that total species and phylogenetic diversity can be represented within a surprisingly small cell set (see also Williams *et al.*, 1996; Howard *et al.*, 1998; Kati *et al.*, 2004). The minimal set includes areas harbouring species that were missed by the hotspots identification, such as those in northern Botswana, which correspond to the Zambezian Domain of White (1983). However, complementarity approaches also have drawbacks. First, hotspots selected based on complementarity are not spatially clustered, potentially leading to problems associated with isolation and habitat fragmentation. Second, complementary approaches which select minimum cell sets may leave little buffer for future biodiversity loss, such that losses due to stochastic events can be intensified. In addition, complementary approaches, when focused on one or a few biodiversity metrics fail to account for other criteria important in planning a protected area network, such as socioeconomic factors.

Finally, we show that the performance of the current network of protected areas in southern Africa varies depending on the diversity metric considered. EDGE, SR and PD are relatively well represented in National Parks, but hotspots of PE and CWE are predominantly distributed outside of protected areas. Notably, our results highlight the need to increase protected areas within the CFR. Cumulatively, 72% of hotspot areas were not protected. The reserve networks also performed relatively poorly in protecting complementary areas (< 50% of cells fall within protected areas). We suggest protecting the remaining complementary areas should be considered a priority for future conservation action within southern Africa.

In conclusion, to effectively maximise the protection of biodiversity under the unprecedented pressures imposed by anthropogenic habitat modification and climate change, it is essential that we focus conservation strategies on priority taxa and areas. Many conservation frameworks identify the same or similar areas as conservation priorities globally (Brooks *et al.*, 2006) and focus on areas of overlap. However, we show that at much finer scales, the different indices of tree diversity in southern Africa are distributed unequally. Our results therefore emphasise the general lack of congruence among different biodiversity metrics, posing a challenge for conservation biologists, and highlight the need to adopt a more integrative approach in identifying areas of high conservation priority. Nonetheless, we suggest incongruence between metrics might, however, provide insights into the different processes structuring diversity and thus help in our understanding of the origin of biodiversity gradients.

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REFERENCES

Angiosperm Phylogeny Group (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society*, **161**, 105–121.

Boon, D. (2010) *Pooley's trees of eastern South Africa – a complete guide*. Flora and Fauna Publication Trust, Durban, South Africa.

Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D. & Rodrigues, A.S.L. (2006) Global biodiversity conservation priorities. *Nature*, **313**, 58–61.

Cadotte, M.W. & Davies, T.J. (2010) Rarest of the rare: advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales. *Diversity and Distributions*, **16**, 376–385.

Ceballos, G. & Ehrlich, P.R. (2006) Global mammal distributions, biodiversity hotspots, and conservation. *Proceedings of the National Academy of Sciences USA*, **103**, 19374–19379.

Coates Palgrave, M. (2002) *Keith Coates Palgrave trees of southern Africa*, 3rd edn. Struik, Cape Town, South Africa.

Conservation International (2005) *Biodiversity hotspots*. CI Facts (www.conservation.org).

Cowling, R.M. & Hilton-Taylor, C. (1994) Patterns of plant diversity and endemism in southern Africa: an overview. *Botanical diversity in southern Africa* (ed. by B.J. Huntley), pp. 31–52. National Botanical Institute, Pretoria.

Crisp, M.D., Laffan, S., Linder, H.P. & Monro, A. (2001) Endemism in the Australian flora. *Journal of Biogeography*, **28**, 183–198.

Cumming, G.S. & Child, M.F. (2009) Contrasting spatial patterns of taxonomic and functional richness offer insights into potential loss of ecosystem services. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **364**, 1683–1692.

Davies, T.J. & Cadotte, M.W. (2011) Quantifying biodiversity – does it matter what we measure? *Biodiversity hotspots* (ed. by F.E. Zachos and J.C. Habel), pp. 43–60. Springer-Verlag, Berlin, Heidelberg.

Davies, T.J., Savolainen, V., Chase, M.W., Goldblatt, P. & Barraclough, T.G. (2005) Environment, area and diversification in the species-rich flowering plant family Iridaceae. *The American Naturalist*, **166**, 418–425.

Davies, T.J., Fritz, S.A., Grenyer, R., Orme, C.D.L., Bielby, J., Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., Gittleman, J.L., Mace, G.M. & Purvis, A. (2008) Phylogenetic trees and the future of mammalian biodiversity. *Proceedings of the National Academy of Sciences USA*, **105**, 11556–11563.

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W. & Mouquet, N. (2010) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecology Letters*, **13**, 1030–1040.

Dinerstein, E., Olson, D.M., Graham, D.J., Webster, A.L., Primm, S.A., Bookbinder, M.P. & Ledec, G. (1995) *A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean*. The World Bank, Washington, DC.

Dinerstein, E., Powell, G., Olson, D., Wikramanayake, E., Abell, R., Loucks, C., Underwood, E., Allnutt, T., Wettengel, W., Ricketts, T., Strand, H., O'connor, S. & Burgess, N. (2000) *A workbook for conducting biological assessments and developing biodiversity visions for ecoregion-based conservation. Part 1: terrestrial ecoregions*. Conservation Science Program, World Wildlife Fund, Washington, DC.

Faith, D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation*, **61**, 1–10.

Faith, D.P., Reid, C.A.M. & Hunter, J. (2004) Integrating phylogenetic diversity, complementarity, and endemism for conservation assessment. *Conservation Biology*, **18**, 255–261.

Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G. (2008) Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, **36**, 132–147.

Forest, F., Grenyer, R., Rouget, M., Davies, T.J., Cowling, R.M., Faith, D.P., Balmford, A., Manning, J.C., Proches, S., van der Bank, M., Reeves, G., Hedderson, T.A.J. & Savolainen, V. (2007) Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature*, **445**, 757–760.

Germishuizen, G. & Meyer, N.L. (2013) *Plants of southern Africa: an annotated checklist*. Strelitzia 14. 1231 pp. National Botanical Institute, Pretoria, South Africa.

Goldblatt, P. (1978) An analysis of the flora of southern Africa: its characteristics, relationships, and origins. *Annals of the Missouri Botanical Garden*, **65**, 369–436.

Goldblatt, P. & Manning, J.C. (2002) Plant diversity of the Cape region of southern Africa. *Annals of the Missouri Botanical Garden*, **89**, 281–302.

Gonza´lez-Orozco, C.E., Brown, A.H.D., Knerr, N., Miller, J.T. & Doyle, J.J. (2012) Hotspots of diversity of wild Australian soybean relatives and their conservation in situ. *Conservation Genetics*, **13**, 1269–1281.

Grenyer, R., Orme, C.D.L., Jackson, S.F., Thomas, G.H., Davies, R.G., Davies, T.J., Jones, K.E., Olson, V.A., Ridgely, R., Rasmussen, P., Ding, T.-S., Bennett, P.M., Blackburn, T.M., Gaston, K.J., Gittleman, J.L. & Owens, I.P.F. (2006) The global distribution and conservation of rare and threatened vertebrates. *Nature*, **444**, 93–96.

Gudde, R.M., Joy, J.B. & Mooers, A.O. (2013) Imperilled phylogenetic endemism of Malagasy lemuriformes. *Diversity and Distributions*, **19**, 664–675.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.

Hijmans, R.J. (2013) *raster: Geographic data analysis and modeling*. R package version 2.1-49. Available at: http://CRAN.R-project.org/package=raster (accessed 22 December 2013).

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Howard, P.C., Viskanic, P., Davenport, T.R.B., Kigenyi, F.W., Baltzer, M., Dickinson, C.J., Lwanga, J.S., Matthews,

R.A. & Balmford, A. (1998) Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature*, **394**, 472–475.

Isaac, N.J., Turvey, S.T., Collen, B., Waterman, C. & Baillie, J.E. (2007) Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS One*, **2**, e296.

Kati, V., Devillers, P., Dufrêne, M., Legakis, A., Vokou, D. & Lebrun, P. (2004) Hotspots, complementarity or representativeness? Designing optimal small-scale reserves for biodiversity conservation. *Biological Conservation*, **120**, 471–480.

Kucharik, C.J., Foley, J.A., Delire, C., Fisher, V.A., Coe, M.T., Lenters, J.D., Young-Molling, C., Ramankutty, N., Norman, J.M. & Gower, S.T. (2000) Testing the performance of a dynamic global ecosystem model: water balance, carbon balance, and vegetation structure. *Global Biogeochemical Cycles*, **14**, 795–825.

Laffan, S.W. & Crisp, M.D. (2003) Assessing endemism at multiple spatial scales, with an example from the Australian vascular flora. *Journal of Biogeography*, **30**, 511–520.

Laffan, S.W., Lubarsky, E. & Rosauer, D.F. (2010) Biodiverse, a tool for the spatial analysis of biological and related diversity. *Ecography*, **33**, 643–647.

Linard, C., Gilbert, M., Snow, R.W., Noor, A.M. & Tatem, A.J. (2012) Population distribution, settlement patterns and accessibility across Africa in 2010. *PLoS One*, **7**, e31743.

Linder, H.P. (2003) The radiation of the Cape flora, southern Africa. *Biological Reviews*, **78**, 597–638.

Maurin, O., Davies, T.J., Burrows, J.E., Daru, B.H., Yessoufou, K., Muasya, A.M., van der Bank, M. & Bond, W.J. (2014) Savanna fire and the origins of the 'underground forests' of Africa. *New Phytologist*, **204**, 201–214.

Mazel, F., Guilhaumon, F., Mouquet, N., Devictor, V., Gravel, D., Renaud, J., Cianciaruso, M.V., Loyola, R., Diniz-Filho, J.A.F., Mouillot, D. & Thuiller, W. (2014) Multifaceted diversity–area relationships reveal global hotspots of mammalian species, trait and lineage diversity. *Global Ecology and Biogeography*, **23**, 836–847.

Meffe, G. & Carrol, R. (1994) What is conservation biology? *Principles of conservation biology* (ed. by G. Meffe and R. Carrol), pp. 3–23. Sinauer Associates, Inc., Massachusetts, USA.

Mishler, B.D., Knerr, N., González-Orozco, C.E., Thornhill, A.H., Laffan, S.W. & Miller, J.T. (2014) Phylogenetic measures of biodiversity and neo- and paleo-endemism in Australian *Acacia*. *Nature Communications*, **5**, 4473.

Mooers, A.O. & Redding, D.W. (2009) Where the rare species are. *Molecular Ecology*, **18**, 3955–3957.

Morlon, H., Schwilk, D.W., Bryant, J.A., Marquet, P.A., Rebelo, A.G., Tauss, C., Bohannan, B.J.M. & Green, J.L. (2011) Spatial patterns of phylogenetic diversity. *Ecology Letters*, **14**, 141–149.

Myers, M., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

O'Brien, E.M. (1993) Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. *Journal of Biogeography*, **20**, 181–198.

Orme, C.D., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T.S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston, K.J. & Owens, I.P. (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature*, **436**, 1016–1019.

Pavoine, S. & Bonsall, M. (2011) Measuring biodiversity to explain community assembly: a unified approach. *Biological Reviews*, **86**, 792–812.

Prendergast, J., Quinn, R.M., Lawton, J.H., Eversham, B.C. & Gibbons, D.W. (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature*, **365**, 335–337.

Prinzing, A., Reiffers, R., Braakhekke, W.G., Hennekens, S.M., Tackenberg, O., Ozinga, W.A., Schaminée, J.H.J. & Van Groenendael, J.M. (2008) Less lineages – more trait variation: phylogenetically clustered plant communities are functionally more diverse. *Ecology Letters*, **11**, 809–819.

R Core Team (2013) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rangel, T.F., Diniz-Filho, J.A.F. & Bini, L.M. (2010) SAM: a comprehensive application for Spatial Analysis in Macroecology. *Ecography*, **33**, 46–50.

Ribeiro, P.L., Rapini, A., Silva, U.C.S., Konno, T.U.P., Damascena, L.S. & van den Berg, C. (2012) Spatial analyses of the phylogenetic diversity of *Minaria* (Apocynaceae): assessing priority areas for conservation in the Espinhaço Range, Brazil. *Systematics and Biodiversity*, **10**, 317–331.

Rodrigues, A.S.L. & Gaston, K.J. (2002) Maximising phylogenetic diversity in the selection of networks of conservation areas. *Biological Conservation*, **105**, 103–111.

Rosauer, D., Laffan, S.W., Crisp, M.D., Donnellan, C. & Cook, L.G. (2009) Phylogenetic endemism: a new approach for identifying geographical concentrations of evolutionary history. *Molecular Ecology*, **18**, 4061–4072.

Safi, K., Armour-Marshall, K., Baillie, J.E.M. & Isaac, N.J.B. (2013) Global patterns of evolutionary distinct and globally endangered amphibians and mammals. *PLoS One*, **8**, e63582.

Schmidt, E., Lotter, M. & McCleland, W. (2007) *Trees and shrubs of Mpumalanga and Kruger national park*. Jacana Education, Johannesburg, South Africa.

Steel, M., Mimoto, A. & Mooers, A.Ø. (2007) Hedging our bets: the expected contribution of species to future phylogenetic diversity. *Evolutionary Bioinformatics*, **3**, 237–244.

Tucker, C.M., Cadotte, M.W., Davies, T.J. & Rebelo, T.G. (2012) Incorporating geographical and evolutionary rarity into conservation prioritization. *Conservation Biology*, **26**, 593–601.

UNEP-WCMC (2012) *Data standards for the world database on protected areas*. UNEP-WCMC, Cambridge, UK.

Van Wyk, A.E. & Smith, G.F. (2001) *Regions of floristic endemism in southern Africa. A review with emphasis on succulents*. Umdaus Press, Hatfield, South Africa.

Van Wyk, B., van der Berg, E., Coates Palgrave, M. & Jordaan, M. (2011) *Dictionary of names for southern African trees*, 1st edn. Briza, Pretoria, South Africa.

Vane-Wright, R.I., Humphries, C.J. & Williams, P.H. (1991) What to protect – systematics and the agony of choice. *Biological Conservation*, **55**, 235–254.

White, F. (1983) *The vegetation of Africa. A descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa*. UNESCO, Paris.

Williams, P., Gibbons, D., Margules, C., Rebelo, A., Humphries, C. & Pressey, R. (1996) A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. *Conservation Biology*, **10**, 155–174.

SUPPORTING INFORMATION

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

Table S1 Spatial autoregressive models of the distribution of tree diversity metrics in southern Africa against human population density and environmental variables that are known to influence floristic diversity at regional scales.

Figure S1 Spatial distribution of tree diversity as (a) summed endemism, and (b) summed EDGE, across 50 × 50 km equal area grids (Berhmann projection).

Figure S2 Relationship between species representation against range size for the diversity metrics.

Figure S3 Gains in species richness and PD complementarity in comparison to a null model selecting cells at random.

Figure S4 Relationship between percentages of species captured versus number of complementary cells.

BIOSKETCHES

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