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Preserving the evolutionary potential of floras in biodiversity hotspots

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One of the biggest challenges for conservation biology is to provide conservation planners with ways to prioritize effort. Much attention has been focused on biodiversity hotspots¹. However, the conservation of evolutionary process is now also acknowledged as a priority in the face of global change². Phylogenetic diversity (PD) is a biodiversity index that measures the length of evolutionary pathways that connect a given set of taxa^{3,4}. PD therefore identifies sets of taxa that maximize the accumulation of 'feature diversity'. Recent studies, however, concluded that taxon richness is a good surrogate for PD^{5–9}. Here we show taxon richness to be decoupled from PD, using a biome-wide phylogenetic analysis of the flora of an undisputed biodiversity hotspot—the Cape of South Africa. We demonstrate that this decoupling has real-world importance for conservation planning. Finally, using a database of medicinal and economic plant use¹⁰, we demonstrate that PD protection is the best strategy for preserving feature diversity in the Cape. We should be able to use PD to identify those key regions that maximize future options, both for the continuing evolution of life on Earth and for the benefit of society.

The Cape of South Africa is an area of less than 90,000 km². Botanically, it is one of the most species-rich areas of the world. There are more than 9,000 plant species, of which about 70% are endemic¹¹. For decades it has been noted that a longitudinal gradient in species richness exists across the Cape¹². The western part, with a predominantly winter rainfall regime, has about twice the density of plant species of the eastern region, which receives rainfall year-round¹³. Higher species richness in the western part has been attributed to variation in speciation and extinction rates as a consequence of differences in historical ecological conditions¹⁴. In the west, species richness also varies with topography, with the more uniform lowlands having fewer species than the rugged mountain landscapes¹³. Similarly, there are higher numbers of endemic genera in the western part of the Cape¹⁵.

We collected and compiled distribution data for the entire Cape and created an inventory of species and genera per quarter-degree square (QDS; the finest scale available). After extensive fieldwork (2003–2005), we reconstructed the phylogeny of the Cape flora, on the basis of plastid ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcL*). We used an exemplar from 735 genera, each indigenous to the Cape. Because of computing limitations imposed by the size of the data matrix, phylogenetic relationships were

reconstructed using the parsimony ratchet¹⁶. Molecular branch lengths were optimized using maximum likelihood. Using non-parametric rate smoothing¹⁷, the branch lengths were then transformed to units of absolute time for PD calculation. This is the largest phylogenetic tree yet built for an entire flora.

We compared per-QDS species and genus richness with per-QDS PD (calculated as the length of the subtree that joins the genera in each QDS to the root of the tree³). As expected^{5–9}, we found these diversity indices to be distributed in a similar manner (Fig. 1b, c; linear regressions: PD versus species richness $R^2 = 0.77$, PD versus genus richness $R^2 = 0.96$). These results initially indicated a limited role for PD in conservation planning in this region^{6,8,18}. However, this similarity in overall distribution hides key differences in the distribution of these metrics. We found PD to scale with taxon richness, but the scaling to be complex: some regions have more or less PD than would be expected from their taxon richness. Using two tests (a loess regression of per-QDS PD on genus richness, Fig. 1d; and comparing the observed PD in each QDS against an empirical randomization of PD, Fig. 1e) we found a distinctive east–west division in the distribution of PD that broadly corresponds to the climatic zones defined previously¹³, with PD for a given number of taxa being higher in the eastern region than in the western.

These results demonstrate that the flora (within QDS) of the western part of the Cape is phylogenetically clustered: it is made up of relatively closely related genera, resulting from multiple radiations over at least the last 25 million years^{19–21}. This results in a higher proportion of both shared and short branches, relative to the east, and therefore a lower PD score for a given number of lineages. In contrast, the flora (within QDS) of the eastern region is phylogenetically 'over-dispersed' relative to the western region: it contains genera that are, on average, less closely related to one another. These patterns result from fundamental evolutionary and palaeoclimatic processes in the west^{22–24}. Relative over-dispersion in the east is likewise explicable: the eastern flora abuts another biodiversity hotspot (Maputaland–Pondoland–Albany), is highly ecotonal, and contains occasional exemplar genera from unusual ecotypes¹¹.

We found that these conflicting patterns of taxon diversity and PD invalidate the sole use of taxon richness for conservation actions. Conservation planning is not just about total numbers, but also about marginal gains. To mimic the critical decisions that conservation planners face in the Cape, we set up a series of conservation

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scenarios based upon complementarity. In each scenario, an additional locality that maximizes gain in a biodiversity index is to be included in an existing partial set of conservation areas. We initially chose additions to partial sets based upon taxon richness, and examined the marginal gain in PD experienced. We then contrasted these gains by choosing additions to partial sets based directly on PD. The results show that gains in taxon richness and gains in PD are decoupled (Fig. 2 and Supplementary Information). Typically, selection for conventional taxon complementarity misses localities that would provide large gains in PD.

Why does it matter that PD is not well captured by conventional taxon-based policies? We argue that maximizing PD is the best bet-hedging strategy. By maximizing feature diversity we maximize

option value: the possibility of having the right feature at hand in an uncertain future. We use a practical example to illustrate this point. We identified all genera in the Cape with species of medicinal or economic importance¹⁰. We divided these genera into three types of use (food, medicine and other). Using a randomization test, we found that each type of use is phylogenetically clumped (all $P < 0.01$) and that different categories of use are clustered in different parts of the phylogeny (Supplementary Information). So how should we have designed a conservation strategy to preserve useful plants if this distribution were not known? Simply choosing samples of the largest possible number of genera permits the selection of a set of genera that are themselves phylogenetically clumped: such a set might include many genera of one type of use but this must come at a cost to the

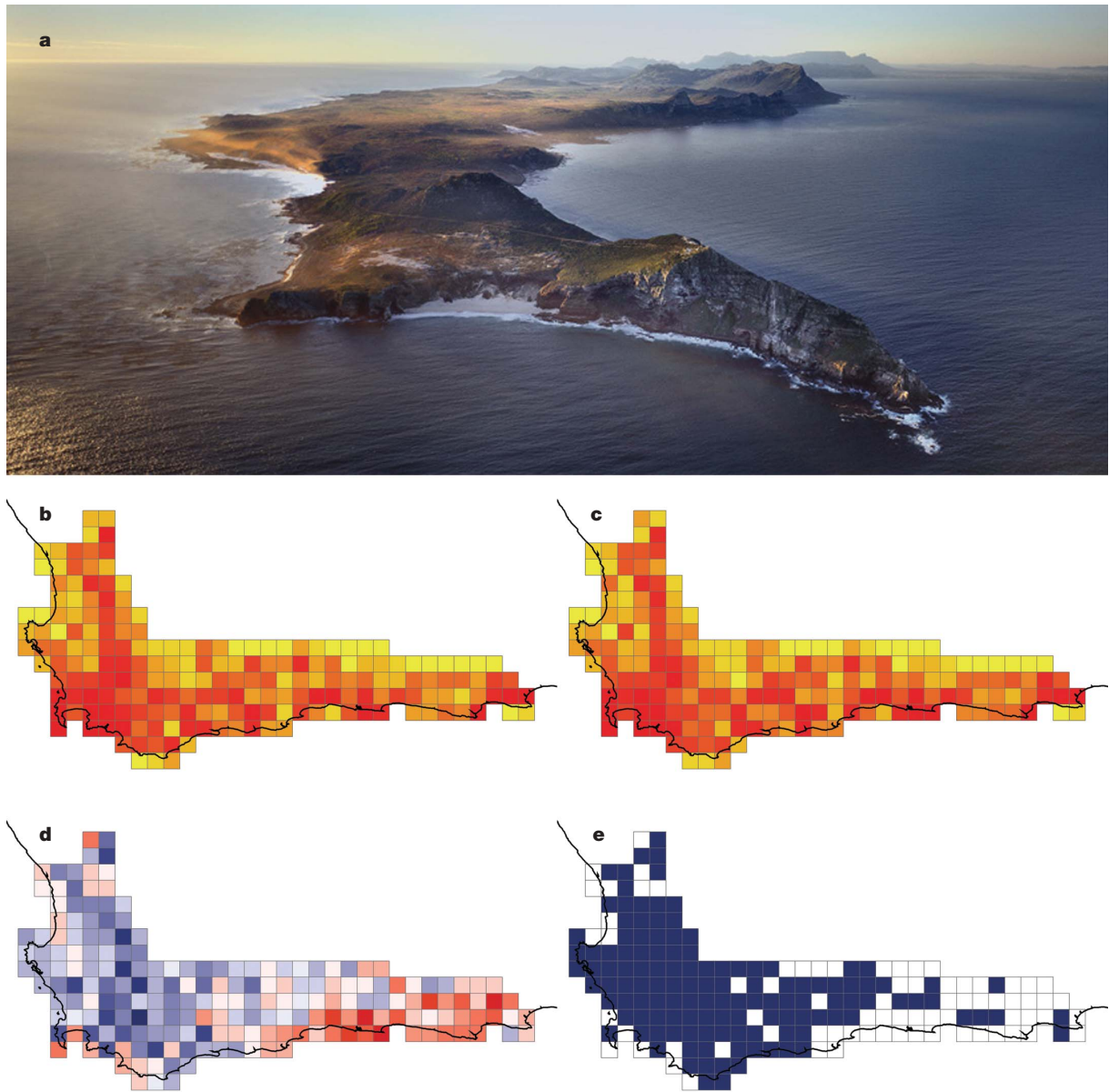


Figure 1 | Taxon richness and phylogenetic diversity in the Cape. **a**, This biodiversity hotspot, which includes the renowned Cape Peninsula, Cape of Good Hope and Table Mountain (in the distance), dominated by fynbos vegetation, is situated at the southern tip of Africa. Picture credit: A. Proust/iAfrika. **b–e**, Maps of 201 QDS covering the entire Cape region. **b**, Genus richness (ten quantile intervals from yellow to deep red). **c**, PD calculated using NPRS absolute age estimates in million years (colour code as for **b**). **d**, Residuals from a loess regression of PD (calculated using NPRS absolute age estimates) on genus richness. QDS with negative residuals are

indicated in blue, and those with positive residuals are shown in red (shading increments of half a standard deviation). **e**, The spatial distribution of unusual PD values, as assessed by comparing the observed PD in each QDS with 10,000 PD values calculated by random selection of the same number of genera from the Cape flora. Cells with significantly lower PD ($P < 0.05$, two-tailed) than expected are shaded in blue. A similar pattern was found when the tree was simplified to reflect the phylogeny-based taxonomy of the Angiosperm Phylogeny Group³⁰ (Supplementary Information).

other two types, because they are found in different parts of the phylogeny. Choosing a selection of over-dispersed taxa based on PD would have maximized the probability of having representatives of each of the three classes of use. In fact, we found that a set of cells chosen to maximize PD complementarity (blue line, Fig. 2) samples all useful genera in 13 QDS, while a set chosen to maximize taxon complementarity (black line, Fig. 2) requires 15 QDS to do so, although the majority of useful genera in both cases are sampled in the first few QDS. In an uncertain future, where we are not yet sure of the sort of plant features we will need, we argue that incorporating gains in PD into conservation planning is the best strategy.

It is not just our own options, though, that we need to keep open. We do not know the characteristics that species in the Cape will need to adapt and diversify in a future of climatic change. We therefore argue that maximizing PD will in turn maximize the options for future diversification. The many radiations in the western part of the Cape may well be a reason²⁵ to see the region as one of high evolutionary potential. However, although it is possible, we see no reason why future speciation regimes must be the same as those that gave rise to the historical diversification in the western part of the Cape. Throughout the history of angiosperms, diversification has been a complex process in which the propensity to diversify was highly labile and dependent upon many different traits at different times²⁶. Our recommendation would not be to reject recently diversifying sites in the west as conservation targets, but to ensure that PD is maximized by inclusion of suitable areas in the east into existing conservation schemes. Balancing these two diversity indices is now at least an algorithmic problem for which we have suitable tools²⁷. We also note that scale is important. For example, our phylogenetic tree does not include lineages that are not found in the Cape, but we have chosen the most biologically sound limits: a phylogeographic delimitation²⁸ that falls within a single country and can therefore be managed under a single coordinated conservation response²⁹. Any conservation plan that operates at less than a global scale will always be at risk of finding solutions that are optimal only within the region being considered.

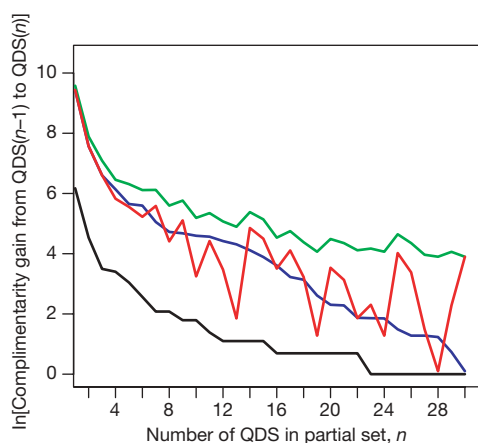


Figure 2 | Complementarity analysis of PD and genus richness. A series of conservation scenarios based on complementarity were set up with a simple greedy algorithm: for each partial set defined along the x axis, we identified the additional QDS that provided the highest possible genus-based complementarity (black). We then calculated the PD complementarity that would be provided by this same QDS (red), as well as the alternative additional QDS that would provide the highest possible PD complementarity (green). Whereas comparisons of diversity measures have usually focused on richness, it is now apparent that decision-making depends on marginal gains (complementarity values) and these must be the basis for comparisons. Here we show that gains in genus richness are poor predictors of gains in PD (contrast red and green lines). We also show the independent series of QDS that provide the highest PD-based complementarity (blue).

We have shown that a simple correspondence between taxon richness and PD can hide a fundamental decoupling of biodiversity indices, with drastically different conservation outcomes if only one of the indices is used. The Cape is one of the most well-studied hotspots, so our findings clearly raise the possibility that similar decoupling may be found in others. Further, we know from simulations⁷ that a decoupling of PD and taxon richness is most likely when the underlying phylogeny is unbalanced and there is strong phylogeographic structure; both these are epiphenomena of endemic radiations. We conclude by suggesting that because biodiversity hotspots are defined in part by their richness in endemics¹, they are precisely the areas in which a decoupling of PD and taxon richness is most likely—as is observed here.

METHODS

DNA sequencing and phylogeny reconstruction. We sampled one exemplar species for 735 of the 943 genera of angiosperms currently recognized in the Cape (~78%) and obtained sequence data for the plastid *rbcl* exon (ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit). Phylogenetic relationships were reconstructed using the parsimony ratchet¹⁶ method with 15% of the characters perturbed and 200 iterations; ten independent parsimony ratchet searches were performed and the shortest trees resulting from these independent searches were used to create a consensus tree. Clade support was assessed with 500 bootstrap replicates. One of the most parsimonious trees from the parsimony ratchet analysis was chosen as a best hypothesis of relationships for the Cape plant genera. PD calculations were performed using branch lengths (maximum parsimony and maximum likelihood) and age estimates (non-parametric rate smoothing¹⁷; relative time divergences were transformed into absolute ages using twelve well-characterized fossils; see Supplementary Information).

Distribution of phylogenetic diversity. The distribution of genera within the Cape was compiled as a binary matrix of absence/presence per quarter degree square (QDS; approximately 25 km × 27 km) using data from the Pretoria National Herbarium database (PRECIS). The spatial pattern of the relationship between PD and taxon richness was revealed by plotting the residuals for a loess regression of per-QDS PD on taxon richness. To locate QDS with significantly higher or lower PD than expected from their taxon richness, the PD in each QDS was compared with 10,000 PD values for sets of genera of the same size, sampled without replacement (Supplementary Information).

Medicinal and economic species. A randomization procedure was used to assess whether the distribution of medicinal and economic species is constrained by the phylogeny or randomly distributed across lineages. To be considered of medicinal and/or economic use, a given genus must have at least one species found in the Cape that is recorded in the database of the Survey of Economic Plants for Arid and Semi-Arid Lands (SEPASAL¹⁰; Supplementary Information).

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Information DNA sequences have been deposited at GenBank/EMBL under accession numbers AM234779–AM235167 (see also Supplementary Information). Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Correspondence and requests for materials should be addressed to F.F. (f.forest@kew.org) and V.S. (v.savolainen@kew.org).