

**ON THE NATURE OF THINGS: ESSAYS** *New Ideas and Directions in Botany* 

## Flora of the hot deserts: emerging patterns from phylogenybased diversity studies

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Manuscript received 29 May 2020; revision accepted 20 July 2020.

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Citation: Scherson, R. A., F. Luebert, P. Pliscoff, and T. Fuentes-Castilllo. 2020. Flora of the hot deserts: emerging patterns from phylogeny-based diversity studies. American Journal of Botany. 107(11): 1467–1469.

doi:10.1002/ajb2.1555

**KEY WORDS** arid environments; Australia; California; Chile; complementarity; conservation priorities; neoendemism; option value; phylogenetic diversity; phylogenetic endemism.

Relatively recent increases in molecular and geographic data for many taxa in different areas of the world have provided scientists with tools to evaluate biodiversity using evolutionary or phylogeny-based indices (reviewed by Laffan, 2018). These measures provide quantitative estimates of the portion of the tree of life contained in a taxon or community, aiming to answer the question of what percentage of the phylogeny would be lost if that taxon or community is not conserved (Faith, 1992; Purvis et al., 2000). One of the most widely used phylogenetic indices is phylogenetic diversity (PD), which measures the evolutionary history captured by a set of species (or any biodiversity unit) on the tree of life (Faith, 1992). A higher PD value can represent either a set of taxa that represent longer branches than expected and/or are overdispersed in the phylogeny (Fig. 1A, B). Use of PD was proposed more than two decades ago (Faith, 1992) as a method for finding sets of taxa that could be highlighted as priorities for conservation and has recently been proposed as a biodiversity metric by several international conservation organizations (see IPBES, 2019). For example, the International Union for the Conservation of Nature (IUCN) has recently established a Phylogenetic Diversity Task Force (https://www.iucn.org/commissions/ssc-groups/disciplina ry-groups/phylogenetic-diversity-task-force), a global expert

group, aimed at incorporating PD into practical conservation strategies.

Several studies of geographic patterns of PD have been conducted for the floras of different ecoregions (for a review, see Scherson et al., 2018), generally showing that relatively more humid regions (temperate and tropical) tend to concentrate more PD than arid zones. Coincident with the concentration of PD, plant diversity in hot deserts is lower than the diversity in more humid regions when measured in terms of species richness (Barthlott et al., 2005), and humid regions tend to have lower extinction rates leading to higher species accumulation over time. Greater resource availability contributes to the increased species richness in humid compared to arid zones (Worm and Tittensor, 2018).

Tropical regions in the world constitute most of the biodiversity hotspots (Myers et al., 2000), and only 1.82% of hotspots correspond to arid zones (Olson et al., 2001), leaving deserts underprioritized in national and international biodiversity conservation strategies. However, hot deserts are areas of high endemism (meaning that their taxa are unique and geographically restricted) and vulnerability. In addition, plant species in these areas are adapted to dry conditions, a relevant attribute when considering their evolutionary, ecological, and economic potential in the face of global change (Ward, 2016).



Phylogenetic diversity

FIGURE 1. Upper panel (A, B): Theoretical example to illustrate the calculation of PD. The phylogenetic tree represents the hypothetical relationship among species A-G. Branch lengths indicate amount of evolution (e.g., molecular divergence) of each taxon (numbers above branches). The two panels represent taxa present in two areas (orange branches), and each area has three species. The area in panel A contains species A, C, and D, while the area in panel B contains species B, F, and G. Phylogenetic diversity (PD) is calculated by summing the branch lengths of the taxa present in each area. An area with more taxa in short branches and/or clustered in the tree of life (A) will have lower PD than areas in which taxa are in long branches and/or spread in the tree of life (B). Lower panel (C-E): Phylogenetic diversity and location of hot deserts in Chile (modified with permission from Scherson et al. [2017], copyright license from Elsevier via Copyright Clearance Center's RightsLink\*), Australia (modified with permission from Thornhill et al. [2016], copyright license from Wiley via Copyright Clearance Center's RightsLink\*) and California (modified with permission from Thornhill et al. [2017], available under Creative Commons license http://creativecommons.org/licenses/by/4.0/). The PD is indicated with a color code: the darker the grid cell, the higher the PD for that area. Desert areas are depicted as black polygons. The percentage of phylogenetic neoendemisms within each desert with respect to the total is indicated for each map.

## PHYLOGENY-BASED MEASURES OF DIVERSITY IN HOT DESERTS

This essay reflects upon spatial patterns of phylogeny-based measures of diversity for three desert areas in the world and is meant to provide material for discussion of how to interpret these spatial patterns. Three recent studies using comparable methods calculated spatial patterns of PD in three large areas: California (Thornhill et al., 2017), Chile (Scherson et al., 2017) and Australia (Thornhill et al., 2016). Along with hot desert vegetation, these three areas also encompass humid (i.e., temperate or tropical) and Mediterranean areas. In all three, the observed patterns of phylogeny-based measures are similar in that hot deserts have lower PD, meaning that they concentrate a significantly higher proportion of taxa in short branches and/ or have more clustered branches on the tree of life, than the other vegetation types (Fig. 1C-E). If PD by itself was to be considered in the future as an indicator for conservation by any local or global organization, then the deserts present in the three studies could appear as areas of low conservation priority compared to neighboring regions. Geologically, hot deserts are relatively recent with origins ranging from Oligocene to Miocene times (35 to 5 million years ago [Ma]; Fujioka et al., 2009; Graham, 2011; Ritter et al., 2018). By contrast, other major formations such as tropical rainforests originated around 100 Ma (Couvreur and Baker, 2013). An exception might be the Namib Desert, which has been proposed to be as old as 65 Ma (Ward and Corbett, 1990). This comparatively greater age may explain why the Namib desert is the only hot desert that is highly diverse (Barthlott et al., 2005). Because of their recent origin, many desert plant species are in "younger" branches of the tree of life, resulting in lower phylogenetic diversity when compared to relatively more humid environments. Thus, if we consider the relative contribution of desert taxa to PD compared to other vegetation types (tropical, temperate, and/or Mediterranean), hot deserts are likely to appear as regions of low PD.

Another similarity among the spatial patterns shown by these studies is that the highest level of phylogenetic neoendemism is found in the three hot deserts (Fig. 1C–E), a measure that has not been yet considered as a criterion for setting conservation priorities. Phylogenetic endemism indicates areas with a high proportion of geographically restricted portions of the tree of life (Rosauer et al., 2009), and phylogenetic neoendemism means areas with geographically restricted short branches (Mishler et al.,

2014). In fact, these three deserts concentrate more than half of the centers of phylogenetic neoendemism found in California, Australia and Chile (56, 60.5, and 62%, respectively; Fig. 1C–E). In contrast, species in longer branches of the green plant phylogeny that are more characteristic of humid areas, for example, magnoliids, are largely absent from drier environments.

As a consequence of high levels of phylogenetic neoendemism, deserts tend to contribute unique lineages (endemic to the deserts), which means hot deserts may be areas of high complementarity, i.e., the marginal gain in overall biodiversity that the area offers (Véron et al., 2018). Even though these taxa tend to represent short branches, because of their uniqueness, they may complement the total diversity (PD or any other measure). Deserts may provide a diversity that is not been accounted for in other areas, given that many lineages present in deserts are not present elsewhere.

However, most studies of phylogeny-based diversity measures have not focused on complementarity, perhaps because the importance of this approach has been highlighted in only few, recent studies. For example, Veron et al. (2018) measured total PD of the Mediterranean Basin for three groups of vertebrates and contrasted the spatial distribution of PD with the network of protected areas, which are areas designated by states to protect biodiversity, identifying phylogenetic lineages that are not protected. To add protection to these lineages, they proposed a new network of protected areas that could maximize the gain in PD by sequentially adding areas to the current network.

PD complementarity contributed by hot desert taxa is directly linked to the concept of "option value" (the unexpected future benefits of biodiversity for human societies, such as medicinal plants or any other goods that humans can obtain from nature), meaning that by complementing existing PD in a protected area network, the storehouse of potential benefits of biodiversity can be enhanced (IPBES, 2019). These potential future benefits are especially relevant today when our society is facing global changes with unpredictable consequences. In fact, most of the climate-change scenarios predict an increase in aridity due to an imminent rise in global temperature, highlighting the importance of conserving arid-adapted taxa (IPCC, 2018).

We end this discussion by arguing that there are special areas in the world with sets of taxa that are unique, vulnerable and important for current and especially future climatic conditions. For these areas, PD measures could be effectively complemented with other strategies that may help establish conservation priorities. We propose that conservation evaluations for hot deserts include PD and additionally consider: (1) high priority for endemic (mostly neoendemic) lineages, (2) complementarity of areas and taxa, and (3) priority for arid-adapted species in the face of global change.

## ACKNOWLEDGEMENTS

We thank ANID-Chile for grants Fondecyt 1171586 and CONICYT PII20150091. We also thank Pamela K. Diggle, Nisha Owen, and an anonymous reviewer for constructive suggestions to the manuscript.

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