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Commentary

Rapid plant diversification in the Andes does not require flowers

Across their many heterogeneous habitats, the tropical Andes are incredibly species-rich. Their biodiversity and the geographical distribution have fascinated natural historians and biologists stretching back generations (von Humboldt & Bonpland, 1807), and continue to be a major theme in the study of plant evolution today. As a result of methodological advances, the last decade has seen an increase in our understanding of the evolutionary processes that have generated this incredible species richness. We are now able to infer the rates of diversification in relation to mountain uplift (Lagomarsino *et al.*, 2016), understand the prevalence of hybridization and introgression among recently diverged relatives (Vargas *et al.*, 2017), and identify the genomic basis of adaptive evolution in morphologically diverse lineages (Pease *et al.*, 2016). This increased statistical rigor has resulted in a nuanced understanding of plant diversification patterns within and between the different habitat types that constitute the tropical Andes (Pennington *et al.*, 2010; Hughes, 2016). In this issue of *New Phytologist*, Testo *et al.* (pp. 604–613) contribute to this rich body of literature via an in-depth examination of diversification patterns in a clubmoss genus.

‘Phlegmariurus displays the same macroevolutionary hallmarks of Andean diversification as myriad angiosperms clades – including recent, rapid diversification.’

Most of our knowledge of plant evolution in the tropical Andes comes from the study of flowering plants. However, other major clades, including lycophytes and ferns, have similarly high levels of diversity in this region (Ulloa Ulloa *et al.*, 2017). To date, few macroevolutionary studies have incorporated molecular phylogenetic data with statistical models of diversification to explain species richness patterns in Andean-centered pteridophyte groups. This bias precludes a full understanding of evolutionary dynamics in the world’s most species-rich biodiversity hotspot – which, in turn, contributes to a common misconception about fern and lycophytes: that they are evolutionary relicts, ancient groups that thrived long ago and now persist in the face of strong extinction pressure. However, while pteridophytes may be older than either

gymnosperms or angiosperms, most extant lineages evolved long after the initial origin of their containing clades (e.g. Schuettpelz & Pryer, 2009). Importantly, ferns and lycophytes continue to evolve into the present, responding to the adaptive regimes in which they may find themselves.

Unlike their seed-producing relatives, the life history of lycophytes and ferns is marked by the production of haploid spores that give rise to free-living gametophytes. These spores, generally 30–70 µm in diameter, are dust-like and act as the dispersal unit for these plants. This small size confers incredible dispersal potential, and fern and lycophyte spores often travel over 3000 km (Tryon, 1972). Spores, and the occasional spore-producing structure (or sporangium), can even be found in the jet stream (Moran, 2008)! Consistent with the importance of long-distance dispersal in the biogeography of pteridophytes, there are hundreds of widespread fern species whose ranges span multiple disjunct regions, even within tropical America (Tryon, 1972). While there is great variation in the life history of ferns and lycophytes, the production of bisexual, self-compatible gametophytes that are independent from the sporophytes in many species enhances the potential for establishment after long-distance dispersal events (Barrington, 1993). These properties lead to fundamental differences in dispersal biology as compared to seed-producing lineages, which have relatively heavy seeds and, in angiosperms, fruits that often rely on animals for dispersal. Pteridophytes, then, may be able to cross environmental barriers in a heterogeneous landscape, such as the tropical Andes, much more readily than seed plants.

A new study by Testo *et al.* is among the first to explicitly examine the role of Andean uplift on diversification in a free-sporing vascular plant lineage, the primarily Neotropical clubmoss genus *Phlegmariurus* (Lycopodiaceae; Fig. 1). Applying a model recently published in *New Phytologist* that correlates diversification rates to past elevation using data derived directly from the geological literature (Lagomarsino *et al.*, 2016), they find that Andean uplift is associated with increased speciation rates across the 150 species of *Phlegmariurus*. While the genus originated during the Eocene *c.* 45.8 million years ago, most of the well-supported species groups of *Phlegmariurus* began accumulating species in the mid-Miocene *c.* 10–15 million years ago. The genus experienced subsequent increases in diversification rate in the late Miocene, *c.* 10 million years ago, during a period marked by intense mountain building (Garzzone *et al.*, 2008). These rates remained elevated as high elevation grasslands originated and spread, facilitating the radiation of large species groups. Together, these results add to a growing consensus about evolutionary patterns in the Andes, with diversification beginning in the last 15 million years as the cloud forests emerged, and accelerating as islands of páramo vegetation developed (Hughes, 2016).

Testo *et al.* also demonstrate the importance of geographic isolation in structuring the diversification history of *Phlegmariurus*.

This article is a Commentary on Testo *et al.*, 222: 604–613.



Fig. 1 Phenotypic diversity of *Phlegmariurus* found in Colombia, showing variation in growth form, leaf shape, and plant color: (a) *P. brevifolius*; (b) *P. amentaceus*; (c) an undescribed species. Photographs provided courtesy of W. L. Testo.

By exploring correlations between diversification rates and various parameters related to species ecology and distribution, they show that diversification rates are highest for species with small range sizes, as well as for those at high elevation. These results are consistent with a predominant pattern of allopatric speciation in geographically isolated mountaintops. Given the extraordinary dispersal potential of spores, these results are counterintuitive. Despite occurring in relatively close geographic proximity, gene flow between populations of *Phlegmariurus* species on different mountain slopes seems to have been infrequent enough that speciation in allopatry was able to proceed at a rapid rate. The Andes – one of the world's tallest mountain chains – are an imposing barrier to dispersal, even to plants with dust-like spores (Moran, 2008).

Besides mountain uplift, biotic interactions are often invoked as drivers of diversification in Andean-centered angiosperm lineages. Pollinators and seed dispersers are particularly important, and many Andean angiosperm lineages are considered morphologically diverse in the traits that facilitate mutualisms with the animals that play these roles (Lagomarsino *et al.*, 2017). No such mutualisms occur in *Phlegmariurus*. Despite this, the genus displays variation in many traits, including growth form, leaf shape, presence or absence of leaf dimorphy, and stem color (Fig. 1). It is likely that the


opening of new ecological niches drove the evolution of some of these traits. For example, Testo *et al.* describe a transition from an epiphytic (e.g. Fig. 1b) to a terrestrial growth form (e.g. Fig. 1a,c) in two subclades of *Phlegmariurus* that are endemic to páramos, grasslands above the treeline where there are few appropriate substrates for epiphytes. That biotic interactions are not necessary to drive shifts in morphology that allow free-sporing plants to exploit divergent niches is corroborated by convergent evolution in the páramo habitat in other groups (Sánchez-Baracaldo & Thomas, 2014). However, the lack of substantial ecological differentiation within a habitat and a propensity to hybridize across relatively large distances may stymie morphological evolution in ferns and lycophytes (Barrington, 1993). Further, there are relatively few mechanisms by which pteridophytes can form barriers to gene flow, including via divergence in allopatry and polyploidization. By contrast, the reproductive biology of angiosperms provides many additional avenues through which speciation can proceed, including shifts in specialized pollination systems, the origin of self-incompatibility mediated by the stigmatic surface, and shifts in flowering time. This allows flowering plant radiations to support more species diversity than even the largest fern and lycophyte radiations, and may explain why divergences in ecological niche, as opposed to morphological innovation, predominate in species-rich tropical pteridophyte groups (Barrington, 1993; Hauffler *et al.*, 2000; Sundue *et al.*, 2015).

The most important lasting contribution of Testo *et al.* will not lie in any single result: we have long understood that mountain uplift, geographic isolation, and the opening of new ecological niches promote rapid evolutionary diversification. Instead, this study will be remembered for its rigorous statistical methodology to document these forces in an understudied branch of the Tree of Life – importantly, one that is often misconceived to be an ancient lineage currently in evolutionary decline. Given this common misconception, it may be surprising to some to learn that *Phlegmariurus* displays the same macroevolutionary hallmarks of Andean diversification as myriad angiosperm clades – including recent, rapid diversification. By no definition is *Phlegmariurus* a relict. Furthermore, it seems that flowers and fruits, and the rich biotic interactions they engender, are not essential in the arena of rapid montane diversification. Instead, the tropical Andean mountains are so dissected and include such steep environmental gradients that geographic isolation can quickly lead to allopatric speciation no matter the dispersal potential of the propagules involved. I argue, as Testo *et al.* do, that this region's exceptional species richness is largely a product of its fragmented landscape, and not solely the species properties of its biota. With or without flowers, tropical Andean plant lineages have all been along for the geological ride, responding to shared evolutionary pressures and competing to establish and radiate in new environments.

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