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Dispersal, isolation and diversification with continued gene flow in an Andean tropical dry forest

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The Andes are the world's longest mountain chain, and the tropical Andes are the world's richest biodiversity hot spot. The origin of the tropical Andean cordillera is relatively recent because the elevation of the mountains was relatively low (400–2500 m palaeoelevations) only 10 MYA with final uplift being rapid. These final phases of the Andean orogeny are thought to have had a fundamental role in shaping processes of biotic diversification and biogeography, with these effects reaching far from the mountains themselves by changing the course of rivers and deposition of mineral-rich Andean sediments across the massive Amazon basin. In a recent issue of Molecular Ecology, Oswald, Overcast, Mauck, Andersen, and Smith (2017) investigate the biogeography and diversification of bird species in the Andes of Peru and Ecuador. Their study is novel in its focus on tropical dry forests (Figure 1) rather than more mesic biomes such as rain forests, cloud forests and paramos, which tend to be the focus of science and conservation in the Andean hot spot. It is also able to draw powerful conclusions via the first deployment of genomic approaches to a biogeographic question in the threatened dry forests of the New World.

KEYWORDS
conservation, dispersal, dry forest, speciation, vicariance

The field of Biogeography has been influenced over two centuries by an often heated debate between those believing in the power of dispersal to shape distributions and those who have a view that geological events in earth history are the key factor. For example, Darwin was a dispersalist who carried out various eccentric experiments to validate his view of the power of dispersibility, including forcing seeds into dead fish, feeding the fish to storks and pelicans and then demonstrating that the seeds taken from their excrement could germinate. Darwin's friend and contemporary, the botanist Joseph Hooker, though a great supporter of evolutionary theory, considered long-distance dispersal events to be so improbable that he was amongst an "extensionist" group that hypothesized historical land connections amongst continents more than a century before the acceptance of plate tectonics, which led to a more general acceptance of explanations of geographic distributions that emphasized earth history. Such "vicariance" explanations include the rifting of continents or building of mountain chains that might split distributions and lead to diversification. The vicariance–dispersal debate has continued, with some emphasising a fundamental importance of earth history (e.g., Parenti & Ebach, 2013), whilst recent empirical studies, many based upon phylogenetic trees calibrated with a dimension of time, give results consistent with distributions, even those across major oceans or with high levels of intracontinental geographic structure, being the result of dispersal (e.g., Lavin et al., 2004; Pennington, Daza, Reynel, & Lavin, 2011; de Queiroz, 2014).

The study system used by Oswald et al. (2017) is a prime candidate for a vicariance explanation—six pairs of bird taxa with each pair separated by the Andean cordillera. The study taxa are known to be most closely related to each other (i.e., sister taxa), with five of the taxon pairs recognized as subspecies, and the final one a pair of

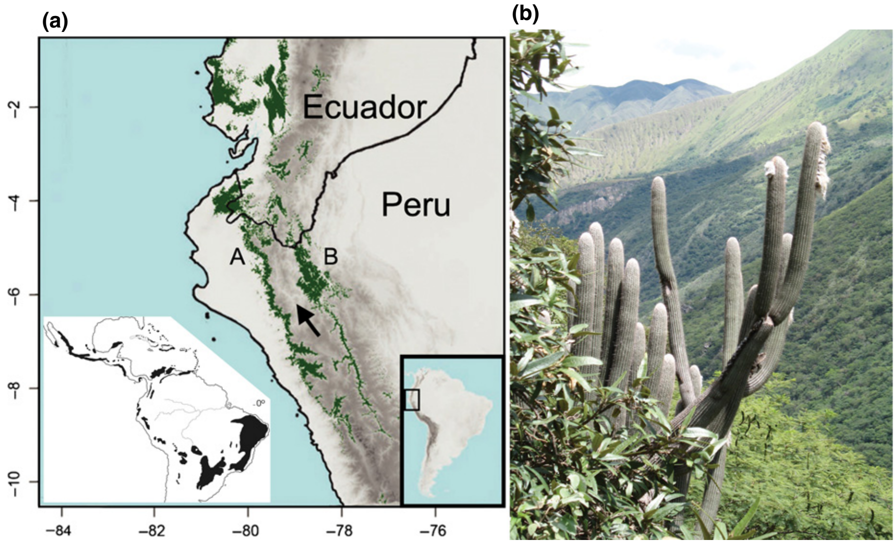

FIGURE 1 (a) The dry forests of northern Peru and southern Ecuador are divided by the Andean mountains into the Tumbes dry forests (A) and the Marañón dry forests (B). In this area, known as the Huancabamba depression, the cordillera has its lowest point, (arrow) reaching only 2145 m (map kindly provided by Jessica Oswald). Inset: schematic distribution of tropical dry forests in the Neotropics. (b) Dry forest in the Marañón valley, Peru, in the wet season. Neotropical dry forests are often characterized by abundant succulent Cactaceae (photograph: RT Pennington). Neotropical dry forests have high species endemism but are underprotected, despite their widespread destruction (DRYFLOR, 2016)

sister species. In each case, one taxon of each pair is found in tropical dry forests on just one side of the Andes mountains in northern Peru and southern Ecuador in the Tumbes region (the Pacific coastal plain west of the Andes) and in the valley of the Marañón River to the east of the cordillera (Figure 1). They collected data from thousands of loci from individuals of both sides of the mountains using double-digest restriction site-associated DNA (ddRAD) sequencing. Using coalescent-based approaches, they assessed the timing of divergence across the Andean cordillera, how ancestral effective population sizes have varied, and which demographic models best-fitted the divergence of the taxon pairs.

The divergence times discovered by Oswald et al. (2017) demonstrate that the polarized vicariance–dispersal debate is not needed given their evidence that barriers, though important, are dynamic and do not necessarily limit dispersal. They show that the cross-Andes disjunctions in their study system occurred at different times from 0.1 to 2.9 Ma, long after the onset of the final Andean uplift and hence cannot be due to the simultaneous disruption of distributions that were continuous before the Andean orogeny. The nonsimultaneous isolation might be due to the effects of climatic cycles on distributions through the Pleistocene or to chance long-distance dispersal events. What is clear is that whatever the underlying reason for dispersal, the mountain barrier is fundamental in restricting it—if dispersal was unfettered, resulting gene flow would prevent divergence, which is clearly not the case given both morphological evidence (i.e., recognisable taxonomic entities) and the genetic data (clear divergence either side of the mountains). However, demographic models suggest that divergence has occurred in the face of continuing gene flow in every case, adding to the examples supporting this mode of speciation (Pinho & Hey, 2010). Dispersal may have been facilitated by the low elevation of the Andean mountains in the Huancabamba depression region of southern Ecuador and northern Peru, but in every case, this gene flow has also been from the Pacific coastal plain into the Marañón valley. The authors suggest that this unusual unidirectionality of dispersal might reflect the larger size of the population in the Pacific region coupled with the effects of extreme El Niño climatic events there.

This article corroborates for birds a biogeographic model suggested for Neotropical dry forests, including the Andean ones studied by Oswald et al. (2017), based on data sets for plants. Geologically old divergences amongst woody plant clades found in disjunct dry forest areas reflect processes of stochastic dispersal, successful establishment and subsequent isolation amongst geographically separate dry forest patches (Pennington et al., 2011; Särkinen, Pennington, Lavin, Simon, & Hughes, 2012). These studies are based upon dated phylogenies and show that geographical disjunctions amongst neotropical dry forest nuclei, including Andean ones, occurred at different times (Särkinen et al., 2012) exactly as Oswald et al. (2017) demonstrate. However, the Oswald et al. (2017) study has the added power and sophistication of genomic data, which, for example, allows the estimation of ancestral effective population sizes. Their analyses show that ancestral bird populations in these dry forest areas were larger than at present, providing some support for ideas that dry forests may have been more extensive in historically drier periods (Prado & Gibbs, 1993). The evidence shown by Oswald et al. (2017) for changes in bird species population sizes in these dry forest areas may provide the explanation for the distinctive phylogenetic signatures seen in dry forest plants, where long stems and short crowns may indicate prior population bottlenecks or any process limiting effective population size (Fig. 4 in Pennington & Lavin, 2016).

Seasonally dry tropical forests are the most threatened of the major lowland biomes in tropical America, with less than 10% of their original extent remaining in many countries (DRYFLOR, 2016). The dry forests of the Marañón valley in Peru, which are one of the foci of this article, are no exception, being highly degraded. This is the first article to deploy genomic data to understand the evolution of an organismal group in the Marañón drainage and adds to a growing body of work that shows the dry forests there to have a highly distinct and ancient island-like biota that has evolved largely in isolation from the dry forests of the Pacific coast of the South American continent (Särkinen et al., 2012). The evidence for the genetic distinctiveness of birds in the Marañón dry forests shown by Oswald et al. (2017) adds compelling weight to arguments that the unique forests there, which are not covered by any national protected area, require better protection.

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