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A genomic perspective on Amazon tree diversity

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If the traveler notices a particular species and wishes to find more like it, he may often turn his eyes in vain in every direction. Trees of varied forms, dimensions, and colours are around him, but he rarely sees any one of them repeated. Time after time he goes towards a tree which looks like the one he seeks, but a closer examination proves it to be distinct. A. R. Wallace, 1878

In our current moment of rampant deforestation and climate change, research on the adaptive potential of tropical trees takes on new urgency. In a From the Cover article in this issue of *Molecular Ecology*, Brousseau et al (2021) map out a genomic approach to studying local to regional-scale adaption in tropical trees.

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Tropical tree diversity is a perennial source of fascination for ecologists and evolutionary biologists. Consider that a single hectare of Amazon rain forest harbors more tree species (N=644) than all the temperate forests of Europe and North America combined (Fine & Ree, 2006; Valencia et al., 2004). The broader Amazon basin contains an estimated 16,000 tree species (ter Steege et al., 2016). The question that intrigues evolutionary biologists – how did this diversity arise? – complements the ecological question of how so many species can coexist.

Evolutionary studies of Amazon tree diversity trace back to the 18th century. Alfred Russel Wallace (1878) famously described the varied forms of Amazon tree species. In his view, tropical tree diversity was best understood in a historical context. Unlike the recently glaciated landscapes of Europe and North America, the lowland tropics have been environmentally stable through deep geological time. Tropical forests are akin to museums, in a sense, and accumulate more species than they lose through extinction (Stebbins, 1974).

The geneticist Theodosius Dobzhansky (1950) highlighted the role that biotic diversity itself must play in generating diversity. Tropical trees are embedded in a network of symbiotic relationships on which they depend for nutrients and reproduction, and they directly compete with hundreds of other plant species. And pest pressures (pathogens, herbivores, seed predators) are intense in tropical moist forests. Hence there are many possibly axes of biotic niche differentiation.

The Janzen-Connell hypothesis – also called the enemies hypothesis – posits a central role of pests in regulating the population densities of tropical trees (Connell, 1971; Janzen, 1970). Pests can keep any single species from becoming dominant if they act in a density dependent fashion, and divergence in plant defenses can promote coexistence insofar as related species do not attract the same enemies. In the species-rich Neotropical tree genus *Inga* the evolution of defense traits far outpaces neutral genetic divergence and was inferred to promote coexistence (Kursar et al., 2009).

Like all Amazon trees, the focal species of the featured study, *Eperua falcata* (Fabaceae), exists within a nexus of biotic and abiotic interactions. It depends on bats for pollination and – somewhat unusually for rain forest trees – on the explosive dehiscence of its fruit pods for seed dispersal (see figure 1). *Eperua falcata* ranks 13th in overall Amazon tree species abundance and forms near monocultures in the Guiana shield. Forget (1989) reported high densities of *E. falcata* seedlings in defiance of Janzen-Connell expectations. It is a hyperdominant tree species, which means that it is one of 227 tree species that comprise half of Amazon forest biomass and stem numbers, and thus contributes inordinately to ecosystem processes (ter Steege et al., 2013). Like some other hyperdominant species, *E. falcata* thrives in both floodplain and *terra firme* (unflooded) forest.

Brousseau and colleagues designed a brilliantly symmetrical experiment in which to study adaptive genomic differentiation of *E. falcata* in French Guiana. The authors paired populations in microgeographic floodplain and *terra firme* habitats separated by 30 meters. These habitat pairs were then replicated in a different site 300 km away. The authors pooled DNA from each of the four subpopulations and analyzed SNPs obtained from genome wide shotgun sequencing. To detect selection, they developed a hierarchical Bayesian analyses that distinguishes F_{ST} outlier loci from background levels of divergence. To complement the genomic analyses, the authors performed a reciprocal transplant experiment across microhabitats and between regions.

The authors found SNPs under selection between regions and between habitat types. Remarkably, similar trends of genetic turnover between *terra firme* and floodplain habitats were detected in the two study sites for many SNPs, suggesting parallel selection over microgeographic scales. The outlier SNPs were neighbors to 106 genes, including ones involved in pathogen defense and physiological response to flooding and soil hypoxia.

The reciprocal transplant studies showed some measure of heritable variation between regions and microhabitats, although significance tended to fade over longer monitoring periods. There were significant maternal effects associated with all measured traits, which in turn varied across sites and microhabitats, suggesting that foresters might consider sourcing seeds on the basis of matched maternal habitat.

The Amazon has been broadly characterized by flooded forest and *terra firme* and periodic barriers to gene flow. It is not hard to envision evolution along biotic and abiotic axes leading to speciation. In support of this view, several phylogenetic studies have documented sister species divergence in clades of trees across soil and habitat types in the Amazon basin (Dick & Pennington, 2019).

The study signals an exciting direction in molecular ecology and especially in its application to the origins and maintenance of tropical tree diversity. It will be interesting to see these methods replicated in other species and habitats, such as the fingers of dry forest and islands of white sand soils in the Amazon basin. Such methods are sorely needed to understand the mechanisms driving diversification in rapidly evolving clades such as *Inga* (Bermingham, 2001). Genomic approaches such as these will undoubtedly lead to a deeper understanding of the varied forms of tropical trees.

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