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Asymmetrical niche determinism across geological units shapes phylogenetic tree communities in the Colombian Amazonia

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ABSTRACT

We evaluate the role of differences in substrate age and environmental conditions, as represented by different geological units, in determining the phylogenetic structure and distribution of tree communities in the northwest Amazon. We used 412 0.1-ha plots distributed across the three main geological units (craton, tertiary and alluvial) in the Colombian Amazon, to answer the following research questions: i) To what extent do environmental filtering and dispersal limitation determine the phylogenetic composition of tree communities across geological units in the Colombian Amazon? and ii) Are there differences between geological units in the extent to which niche conservatism shapes the phylogenetic structure of indicator species (i.e., strong habitat-specialists) in tree communities? The results of our study give support for both environmental filtering and dispersal being important drivers of the phylogenetic structure and turnover of tree communities. Nonetheless, the extent to which geology explained the phylogenetic turnover of tree communities was surpassed by the geographic distance between plots, which was used to account for effects of dispersal limitation. This finding suggests that most of the lineages have had sufficient time to migrate and establish into adjacent geological units, contradicting claims that geological conditions are the dominant factors determining the distribution of tree communities across northwestern Amazonia. However, in the craton unit, indicator species were more closely related than expected by chance, while in the alluvial and tertiary units, observed relationships were not statistically different from null expectations. These results indicate that environmental filtering is asymmetrical among geological units, with the craton environment being the most restrictive. In contrast, the alluvial unit may be relatively easy to colonize and hence ecological strategies may be more labile through evolutionary history.

1. Introduction

The Amazon basin harbors one of the most diverse tree communities on Earth (Slik et al., 2015; Duque et al., 2017). Such a high diversity has been attributed to a complex geological history resulting from the Andean uplift and involving different tectonic movements, changes in the direction of rivers, and processes of sedimentation (Hoorn et al., 2010). Therefore, Amazon forests have evolved on highly variable geological conditions that change in terms of age (2.5–65 my), soil fertility, and patterns of drainage from the eastern white-sand Guiana shield dominated systems (hereafter craton unit) to the western Andean foothills (ter Steege et al., 2006). The extent to which these geological differentiations can be translated into evolutionary processes that determine the floristic differences in the Amazon forests has been intensively debated (Fine and Kembel., 2011; Dexter et al., 2012, 2017; Guevara et al., 2016). Although different mechanisms, such as environmental filtering or dispersal ability, have been suggested as being important historical drivers of the current biota in Amazon forests, the relative importance that each plays in structuring the phylogenetic structure of tree communities remains controversial (Fine and Kembel, 2011; Fortunel et al., 2016; Dexter et al., 2017).

Under the environmental filtering view of Amazonian diversity, we expect abrupt changes in tree community composition across different geological units (Higgins et al., 2011; ter Steege et al., 2006). A comparison of functional traits between contrasting geological units, such as the white-sands in French Guiana and the tertiary terra firme forests in Peru, indicates strong habitat filtering as the main driver of the tree community composition in these areas (Fortunel et al., 2014). These

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findings suggest that dispersal plays a weak role in shaping the species composition of tree communities across geological units, and that environmental conditions primarily determine the capability of tree species to establish and reproduce in specific environments (Fortunel et al., 2016). In cases such as this, we can expect a high phylogenetic turnover between geological units controlled by plant-habitat specialization due to a constrained evolution of the species' niches through time (niche conservatism *sensu* Wiens and Graham, 2005). High niche conservatism between geographically separate geological units may influence allopatric speciation (Wiens and Harrison, 2004; Guevara et al., 2016), which will produce a pattern of geographically structured phylogenies with a high abundance of closely related species associated with each environmental unit.

In contrast, under a dispersal-mediated view of Amazonian diversity, we assume that species movement has been a primary determinant of floristic composition and diversity independent of the geological features. In other words, according to this viewpoint, species distributions in the Amazon basin have historically been determined by the species' differential dispersal abilities and with only a relatively weak influence of geographical barriers (Dexter et al., 2012, 2017; Smith et al., 2014). If there is effective establishment of propagules of clades with origins in different geological units through time, the ecological traits associated to each geological unit (*sensu* Fortunel et al., 2014) should be labile through evolutionary history. If this is true, ecological speciation may have been an important driver of Amazon diversification (Misiewicz and Fine, 2014). Based on this scenario of evolutionary convergence, we will expect that the local coexistence of tree species will be geographically structured by distantly related species (Dexter et al., 2017), which may also be widespread across geological units (Pitman et al., 1999). We also expect larger (Wang et al., 2013), older geological units to support more diverse communities due to greater likelihood and time to accumulate species (Fine and Ree, 2006). This idea of Amazon forests structured by geological units floristically differentiated just by the capability of species to migrate and colonize new areas in geographical space (Hubbell, 2001) has received recent support at evolutionary timescales as well (Dexter et al., 2017).

In the Amazon, the oldest geological craton units with precambric origin are derived from the Guiana shield; however, we know that there are fewer species, genera, and families in these units than in the younger tertiary sedimentary terra firme and the quaternary floodplains (Duivenvoorden, 1995; Duque et al., 2002), contradicting the expectation of the time-integrated species-area effect (Fine and Ree, 2006). This phenomenon, named by Hoorn et al. (2010) as the craton paradox, is by itself a strong argument supporting niche conservatism and environmental filtering as important mechanisms that shape the phylogenetic structure of tree communities in the Amazon basin (Fine and Kembel, 2011; Guevara et al., 2016; but see Dexter et al., 2017). The low-nutrient content, seasonal anoxia, and bad drainage of soils in white-sand systems (Lips and Duivenvoorden, 1996) may increase the level of environmental stress, and thus promote the development of convergent adaptive strategies. Likewise, in Amazon floodplains, the reported dominant pattern of phylogenetic clustering for tree communities (Aldana et al., 2016; Umaña et al., 2012), gives additional support to the assumption of environmental filtering as one of the most important mechanisms determining the phylogenetic structure of tree communities across geologic units in the Amazon basin (Fine et al., 2005; Fortunel et al., 2016). Therefore, comparative regional assessments of the phylogenetic structure and turnover of tree communities that include the most contrasting geological units, such as craton, tertiary sedimentary plains, and quaternary floodplains, are needed to help unravel the role played by asymmetric environmental filtering across geologic units in determining the distribution of tree communities in the Amazon. This prediction implies that the degree of niche conservatism will change between different evolutionary and ecological scales, and as so, between geological units.

Here, we aim to evaluate the role of differences in substrate age and environmental conditions, as represented by the main geological units, in determining the phylogenetic structure and distribution of tree communities in the Colombian Amazon. The Colombian Amazon has a strong longitudinal gradient of geological formations and substrates, which varies from the western Andean mountains to the eastern craton dominated formations, crossing through tertiary sedimentary plains and floodplains. The overall geological variation in the Colombian Amazon reflects the variation found throughout the Amazon basin, allowing us to use it as a benchmark to assess the extent to which environmental filtering determines the evolution and distribution of Amazon tree communities more generally. It is important to note that the use of phylogenetic indices to infer the main structuring mechanisms of plant communities has previously been criticized (Cavender-Bares et al., 2009). In particular, it has been argued that using assemblages of either distantly or closely related species to disentangle the roles played by competition vs. habitat filtering is "out of date" in modern species coexistence theory (Mayfield and Levine, 2010). According to this argument, more fundamental problems can arise when we assume that increasing phylogenetic differences favor species coexistence. To bypass some of these concerns, we employ phylogenetic turnover and structure, focusing on the main theoretical frame introduced above, to assess the extent to which dispersal (represented by geographical distances) and environmental filtering (represented by geological units) determine tree community composition in the Colombian Amazon, but avoiding any reference to competition. In other words, we assume that environmental filtering is due to a combination of both species' strict abiotic habitat requirements and competitive exclusion based on species' differential competitive abilities in different settings (Mayfield and Levine, 2010).

The main research questions and associated hypotheses addressed in this study are:

i) To what extent do environmental filtering and dispersal limitation determine the phylogenetic composition of tree communities across geological units in the Colombian Amazon? We expect a high correlation of phylogenetic turnover with geology as well as a high phylogenetic clustering of indicator species in each geological unit, which would support environmental filtering as the main factor shaping the evolution of tree communities in the Amazon forests.
ii) Are there differences between geological units in the extent to which niche conservatism shapes the phylogenetic structure of indicator species (i.e., strong habitat specialists) in tree communities? We hypothesize that niche conservatism increases with the age of the geological unit. In geological units with greater environmental stress, such as craton and floodplains, we expect the associated species to have evolved similar ecological traits that allow them to be abundant and widely distributed within each geological unit. In other words, the indicator species associated to each geological unit will be phylogenetically clustered if ecological advantages (traits) evolved in a conserved fashion.

2. Methods

2.1. Study region

The Colombian Amazon covers an area of roughly 483,119 km^2, which represents 41% of the countrýs continental territory, and 8.7% of the Amazon basin (Fig. 1). Although the Colombian Amazon includes the largest deforestation hotspot in the country, the natural forests are still well preserved in more than 70% of the region. The Colombian Amazon has the lowest population density (1.5 people km^{-2}), and harbors the highest portion of indigenous communities of the whole country. To date, 84% of the regiońs territory is consolidated into protected areas including Indigenous Reserves and National Parks.

The Colombian Amazonia can be divided into three main geological