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INSIGHTS

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Neither species geographic range size, climatic envelope nor intraspecific leaf trait variability capture habitat specialization in a hyperdiverse Amazonian forest

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Abstract

Many plant species exhibit strong association with topographic habitats at local scales. However, the historical biogeographic and physiological drivers of habitat specialization are still poorly understood, and there is a need for relatively easy-to-measure predictors of species habitat niche breadth. Here we explore whether species geographic range, climatic envelope or intraspecific variability in leaf traits is related to the degree of habitat specialization in a hyperdiverse tropical tree community in Amazonian Ecuador. Contrary to our expectations, we find no effect of the size of species geographic ranges, the diversity of climate a species experiences across its range or intraspecific variability in leaf traits in predicting topographic habitat association in the ~300 most common tropical tree species in a 25-ha tropical forest plot. In addition, there was no phylogenetic signal to habitat specialization. We conclude that species geographic range size, climatic niche breadth and intraspecific variability in leaf traits fail to capture the habitat specialization patterns observed in this highly diverse tropical forest.

RESUMEN

Muchas especies de plantas muestran una fuerte asociación con los hábitats topográficos a escalas locales. Sin embargo, las causas biogeográficas históricas y fisiológicas de la especialización de hábitat continúan siendo poco entendidas. Por esto es necesario encontrar predictores de fácil medición de la amplitud del nicho de las especies. Aquí se explora si el rango geográfico de las especies, su amplitud climática o la variación intraespecífica de las características de las hojas están relacionadas con el grado de especialización de hábitat en un bosque megadiverso de la Amazonía ecuatoriana. Contrario a lo esperado, no se encontró un efecto del tamaño de los rangos geográficos de las especies, ni de la diversidad climática que la especie experimenta a lo largo de su rango geográfico o de la variabilidad intraespecífica en las características funcionales de las hojas que permita predecir la asociación al hábitat topográfico en las ~300 especies más comunes de árboles estudiadas en una parcela de 25 hectáreas. Adicionalmente, tampoco se encontró una señal filogenética de especialización de hábitat. Se concluye que el rango geográfico de las especies, la amplitud climática del nicho y la variabilidad intraespecífica de las características funcionales de las hojas no capturaron los patrones de especialización de hábitat en este bosque tropical altamente diverso.

Keywords

Functional traits, geographic range, climatic envelope, habitat association, intraspecific trait variability, topographic gradient, tropical trees

Introduction

Multiple mechanisms act simultaneously across spatio-temporal scales to generate plant species distributions (HilleRisLambers *et al.* 2012). Global-scale climate patterns define contrasting plant biomes (Holdridge 1967, Whittaker 1975). Regional-scale soil and climate variation further contributes to shape plant species distributions within biomes (Moncrieff *et al.* 2015). Local-scale topographic variation (<1km²) influences soil nutrients and water availability, generating strong species association with high or low elevation habitats (Harms *et al.* 2001, Brown *et al.* 2013). Physiological tolerance to environmental factors are thus expected to be major drivers of plant species distributions (Prentice *et al.* 1992) and be reflected in species geographic range size, climatic envelope and functional strategies (Guisan & Thuiller 2005, McGill *et al.* 2006). However, it remains unclear to what extent large- or small-scale species niche differences contribute to local habitat specialization.

Tropical forests span broad climatic and soil gradients (Quesada *et al.* 2010, Alden *et al.* 2016) and exhibit high species turnover across regional (Condit *et al.* 2002, ter Steege *et al.* 2006) and local (Condit *et al.* 2000, Valencia *et al.* 2004) scales. In particular, the Amazon basin ranges from aseasonal to seasonal climates from west to east (Davidson *et al.* 2012). Some Neotropical tree species cover broad geographic ranges, while others appear more restricted (ter Steege *et al.* 2013), suggesting that broadly-distributed species may have larger climatic envelopes than spatially-restricted species (Brown 1984). Because local topographic habitats can strongly differ in microclimate and soil water availability (Chen *et al.* 1999, Suggitt *et al.* 2011), species climatic envelope may contribute to topographic habitat specialization (Sedio *et al.* 2013). If these niche differences are conserved through species evolutionary history (Losos 2008, Sexton *et al.* 2017), closely-related species may also be more similar in habitat association.

Many tropical tree species specialize to ridge or valley habitats, or alternatively range across the topographic gradient (Clark *et al.* 1998, Lasky *et al.* 2013). Trait differences can reflect species topographic associations: ridge-associated species have lower specific leaf area (SLA), greater maximum size, denser wood and heavier seeds than valley-associated species (Kraft *et al.* 2008, Allié *et al.* 2015). Key leaf traits such SLA and leaf area (LA) notably vary along water gradients (Reich *et al.* 1997) and relate to species sensitivity to soil water availability (Mitchell *et al.* 2008). Most trait-based studies examined the role of species mean trait values, but intraspecific trait variability (ITV) may also influence species response to topography (Violle

et al. 2012). First principles suggest that generalists should display a greater degree of intraspecific variability in traits related to habitat use than specialists because they experience a wider range of environmental conditions and/or have inherently higher levels of phenotypic plasticity (Albert *et al.* 2011).

We examined geographic range, climatic envelope and ITV in the Yasuní forest dynamics plot in Ecuadorian Amazon, one of the most diverse tree communities on the planet. The plot encompasses distinct topographic habitats formed by a ridge and valley system, with a number of species identified as ridge or valley specialists, or generalists (Valencia *et al.* 2004), that differ in their mean trait values (Kraft *et al.* 2008). Previous work at Yasuní shows how environmental filtering, species interactions and dispersal limitation contribute to habitat specialization (Kraft *et al.* 2008, Fortunel *et al.* 2018, McFadden *et al.* 2019). Here, we specifically ask:

(i) Do habitat generalists span greater climatic niche breadth across their geographic ranges than specialists? We expect ridge-associated species to have geographical ranges falling within drier climates than valley-associated species. We also expect closely-related species to show similar habitat associations.

(ii) Does species niche breadth correlate with intraspecific variability in leaf traits related to habitat use? We expect generalists to display a larger degree of ITV in LA and SLA than ridge and valley specialists.

Methods

The Yasuní forest dynamics plot is a 25-ha plot in lowland, old-growth rainforest in Yasuní National Park and Biosphere Reserve in Eastern Ecuador. The climate is aseasonal, with a mean annual rainfall of 2826mm and mean monthly temperatures range between 22 and 34°C. Soils are clay-rich, acidic and relatively nutrient poor (Baldeck *et al.* 2013). From elevation data recorded on a 10x10m grid, the plot ranges from 216 to 248m a.s.l and contains distinct topographic habitats: two ridges rise 25-40m above a main intervening valley, plus a smaller valley in the northeastern corner (Valencia *et al.* 2004). Relative to ridges, valleys have greater soil moisture, but 20% lower stem density and 30% lower biomass, leading to greater light availability (Valencia *et al.* 2009).

All stems ≥ 1 cm DBH are identified to species, tagged and mapped, with a total of over 150,000 mapped trees from $\sim 1,100$ species, liana excluded (Valencia *et al.* 2004). The forest was censused in 1997, 2004 and 2008. We evaluated species-level associations with plot elevation for 467 species with over 70 individuals across censuses (Wiegand *et al.* 2007). To control for bias due to spatial autocorrelation in plot elevation (Allié *et al.* 2015), we used a Monte Carlo test of pairwise association. We calculated the Pearson correlation coefficient ($r_{Pearson}$) between species abundance maps and the original plot elevation map (Canty & Nielsen 2008). To evaluate significance, we used a two-tailed test with 999 $r_{Pearson}$ values obtained between species abundance maps and 999 randomized plot elevation maps preserving the autocorrelation of the original plot elevation map (Deblauwe *et al.* 2012). We ran species-level association test at each census and averaged standard effect size (SES) values to categorize species as generalists ($-1.96 \leq SES \leq 1.96$), ridge ($SES > 1.96$) or valley ($SES < -1.96$) specialists. We found 151 ridge-associated species and 94 valley-associated species, while the remaining 222 species were generalists with respect to elevation (Fig. 1).

We compiled geographic range size and climate variables for 311 species from the Botanical Information and Ecology Network database (Morueta-Holme *et al.* 2013, Enquist *et al.* 2016) that extracted climatic variables from Worldclim (worldclim.org). To reduce dimensionality between climate variables (Appendix S1), we used a Principal Component Analysis (PCA): the first four PCA axes together explained 80.9% of the variance, the first PCA axis explaining 45.5%. To test whether species climatic niche breadth translates into topographic specialization, we kept the single climate variables best describing each of the first four PCA axes (Appendix S2), species coordinates on the first PCA axis, and mean annual precipitation (as a proxy for species position on a dry-to-wet climatic zone). Variables were log-transformed prior to analysis. Because geographical range size was correlated with these climate factors (Appendix S2), we ran separate ANOVAs with Bonferroni-corrected P-values to evaluate their variation between generalists, ridge specialists and valley specialists.

We recovered a phylogenetic tree for 309 species from Kraft and Ackerly (2010). To evaluate if niche breadth is evolutionarily conserved, we determined the observed phylogenetic signal in species habitat association using Blomberg's K on mean SES values. Blomberg's K values vary between zero and >1 , values close to zero indicate no phylogenetic signal while values close to 1 indicate trait evolution according to Brownian motion (i.e. random walk

divergence in species trait similarity). To evaluate significance, we used a rank-based P-value with Blomberg's K for 999 randomizations of phylogeny tips.

We estimated ITV for 43 locally-abundant species at Yasuní, including 12 ridge specialists, 12 valley specialists and 19 generalists. We measured LA and SLA on randomly selected, censused individuals. For ridge and valley specialists, we sampled 10-12 individuals in their preferred habitat. For generalists, we sampled 4-10 individuals in the valley habitat and 5-10 individuals in the ridge habitat. Traits were log-transformed prior to analysis. For each species, we evaluated ITV as the variance in leaf traits. To explore differences in ITV in LA and SLA between habitat generalists, ridge specialists and valley specialists, we ran separate ANOVAs for each trait.

All analyses were conducted in the R 3.4.3 statistical platform (R Development Core Team 2018) using packages *ape* (Paradis *et al.* 2004) and *picante* (Kembel *et al.* 2010).

Results

We found no differences in geographic range size and climatic envelope between habitat generalists, ridge and valley specialists (Fig. 2a-g). In particular, ridge specialists did not fall within drier climates than valley specialists (Fig. 2g). Yet, ridge species tend to exhibit higher maximum temperature of the warmest month on average than valley species, with generalists exhibiting intermediate values (Fig. 2d). In addition, we found no strong phylogenetic conservatism in habitat specialization, and the observed phylogenetic signal in topographic association among the studied species did not differ from the null expectation ($K_{\text{Blomberg}}=0.198$, $P=0.822$). Finally, we found no evidence that generalists were more variable in LA and SLA than ridge and valley specialists (Fig. 2h,i).

Discussion

Improving predictions of species responses to global change requires a better understanding of the drivers of habitat specialization. Despite evidence for the role of species mean trait differences in habitat specialization (Cavender-Bares *et al.* 2004, Fine *et al.* 2006), the role of regional-scale and within-species niche differences remains poorly understood. As a first step, we examined whether geographic range, climatic envelope or ITV can capture differences

in topographic association in the most common tree species in a 25-ha forest plot in Amazonian Ecuador.

Species niche breadth is linked to geographical range size and position (i.e. resource availability within a species niche) in many organisms (Slatyer *et al.* 2013). In Panama, species drought resistance drives regional distribution along a rainfall gradient (Engelbrecht *et al.* 2007) and local-scale topographic habitat association (Comita & Engelbrecht 2009). At Yasuní, we conversely found no evidence that generalists cover broader geographical areas than ridge or valley specialists, or that ridge-associated species have geographical ranges linked to drier climates than valley-associated species. Niche breadth effects on habitat specialization may be largely idiosyncratic at Yasuní, which may stem from the diversity of mechanisms contributing to species geographic ranges (Gaston 1996, McGill *et al.* 2007).

Evolutionary relationships have the potential to inform species niche differences (Webb *et al.* 2002). For example, in Panama, pioneer tropical tree species were associated with over-dispersed clades for phosphorus acquisition (Zalamea *et al.* 2016). However, habitat specialization at Yasuní showed no phylogenetic signal. Neotropical clades can include many habitat-specialist species found only in restricted parts of soil gradients (Bardon *et al.* 2012, Fine *et al.* 2014), suggesting that species evolutionary relationships may be a poor predictor of similarity in habitat preference. Moreover, assuming that topographic differences in soil water availability drive habitat specialization, detecting phylogenetic patterns in habitat specialization may be difficult because species can be drought resistant in many different ways (Delzon 2015) and drought resistance likely evolved multiple, independent times in different clades (Larter *et al.* 2017).

Broader niche breadth is expected to relate to greater variability in key traits related to habitat use (Albert *et al.* 2011). However, we found no evidence for greater intraspecific variability in leaf traits in habitat generalists at Yasuní, in line with findings in temperate grasslands (Boulangeat *et al.* 2011, Mitchell *et al.* 2017). Selecting only species present across the elevation gradient at Yasuní omitted species tolerant of local abiotic conditions but excluded by biotic interactions, which may have limited our ability to evaluate ITV accurately. Moreover, LA and SLA are traits integrative of several functions and, while mean values capture species responses to topography (Kraft *et al.* 2008, Allié *et al.* 2015), trait variability may be driven by other factors such as light availability or attacks by natural enemies (Russo & Kitajima 2016).

Variation in traits related to physiological response to water and soil gradients (e.g. Bartlett *et al.* 2014) may be more tightly linked to habitat specialization. Future studies would need to use reciprocal transplant experiment to evaluate species phenotypic plasticity (Merilä & Hendry 2014) and expand measurements on traits more closely-linked to species physiological responses to abiotic gradients (Craine *et al.* 2012).

To summarize, examining geographic range, climatic niche breadth and intraspecific variability in leaf traits in tropical tree species in a hyperdiverse tropical forest, we found that none capture local topographic association, suggesting that habitat specialization at Yasuni may be mainly driven by other processes such as environmental filtering, species interactions and dispersal limitation (Kraft *et al.* 2008, Fortunel *et al.* 2018, McFadden *et al.* 2019).

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CF, IM and NJBK designed the study, formatted data, performed the analyses and analyzed output data. RV collected demographic data; NJBK and IM collected trait data. CF wrote the first draft of the manuscript. All authors contributed to revisions and gave final approval for publication.

Data Availability: Species range and climate data are from version 2 of the BIEN database (<http://bien.nceas.ucsb.edu/bien/biendata/bien-2>) and can be accessed using the BIEN R package (<https://cran.r-project.org/web/packages/BIEN/index.html>) or the BIEN data portal

(<http://biendata.org>). Species leaf trait data are deposited in the TRY Plant Trait Database [DOI]. Plot data is available upon request to Renato Valencia (LRVALENCIA@puce.edu.ec).

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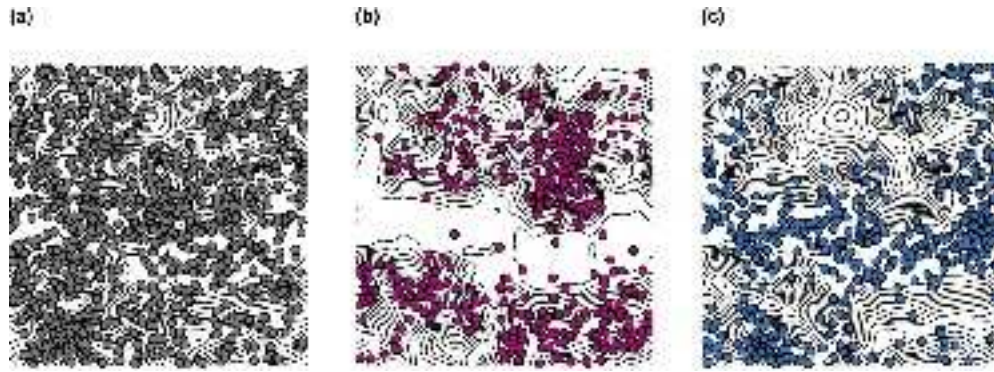
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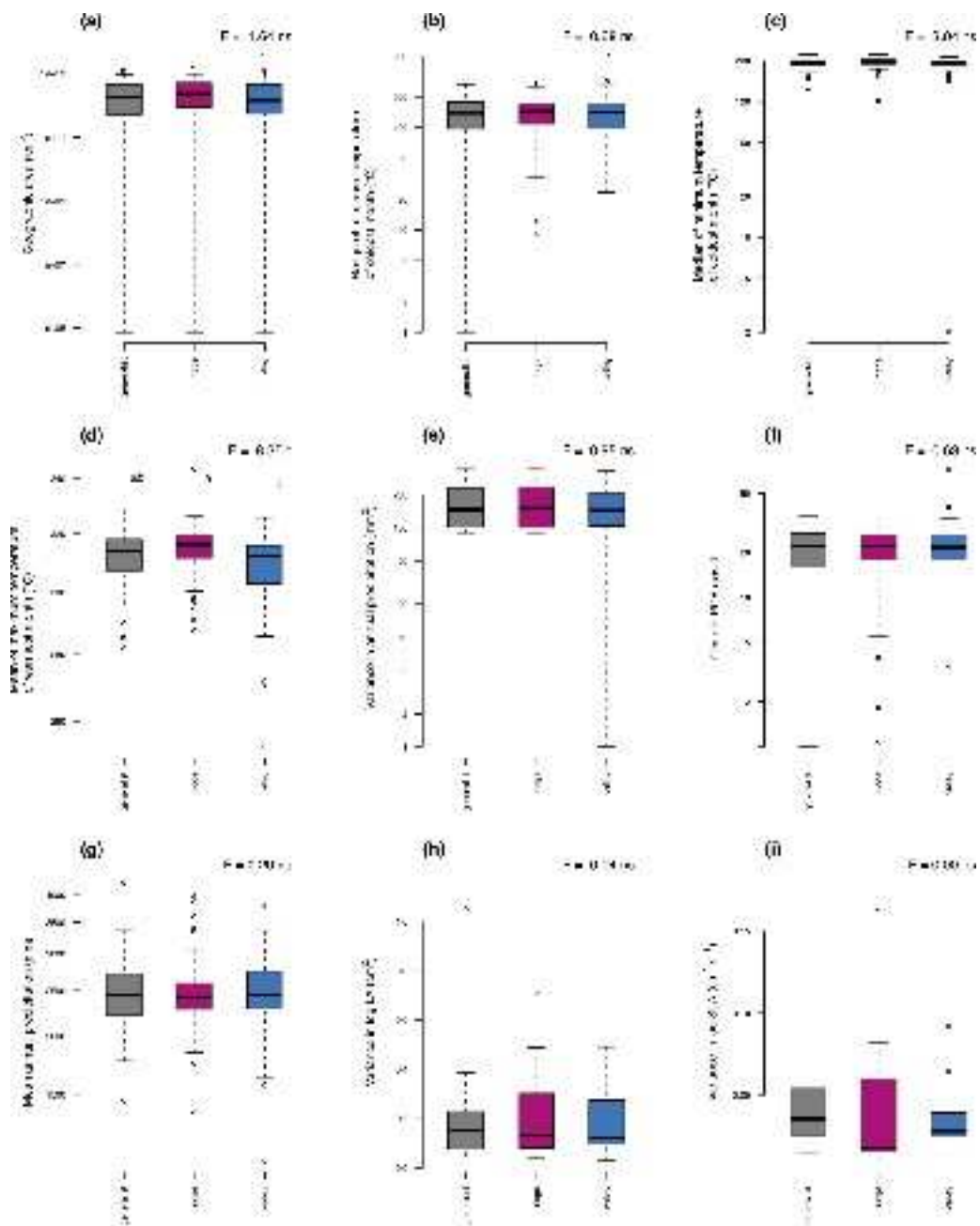
Figure legend

Figure 1: Stem distributions on the 25-ha Forest Dynamics Plot of Yasuní, Ecuador, for: (a) *Inga capitata* (Fabaceae), a habitat generalist, (b) *Pouteria vernicosa* (Sapotaceae), a ridge specialist and (c) *Eschweilera 'giga'* (Lecythidaceae), a valley specialist. Individual stems are shown as dots and contours represent topography within the plot.

Figure 2: Differences between habitat generalist, ridge and valley specialists in (a-g) geographic area and climatic variables, plotted on a log scale (467 species total), and (h,i) intraspecific variability in leaf traits (43 species total). F values and significance are indicated (*: Bonferroni-corrected $P < 0.007$ in panels (a-g), $P < 0.05$ in panels (h,i); ns: non-significant). With three habitat categories, the degree of freedom equals 2 for all tests. When significant, Tukey's 'Honest Significant Difference' (HSD) *post hoc* tests are shown.



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