

A taxonomic comparison of local habitat niches of tropical trees

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Abstract The integration of ecology and evolutionary biology requires an understanding of the evolutionary lability in species' ecological niches. For tropical trees, specialization for particular soil resource and topographic conditions is an important part of the habitat niche, influencing the distributions of individual species and overall tree community structure at the local scale. However, little is known about how these habitat niches are related to the evolutionary history of species. We assessed the relationship between taxonomic rank and tree species' soil resource and topographic niches in eight large (24–50 ha) tropical

forest dynamics plots. Niche overlap values, indicating the similarity of two species' distributions along soil or topographic axes, were calculated for all pairwise combinations of co-occurring tree species at each study site. Congeneric species pairs often showed greater niche overlap (i.e., more similar niches) than non-congeneric pairs along both soil and topographic axes, though significant effects were found for only five sites based on Mantel tests. No evidence for taxonomic effects was found at the family level. Our results indicate that local habitat niches of trees exhibit varying degrees of phylogenetic signal at different sites, which may have important ramifications for the phylogenetic structure of these communities.

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Introduction

An understanding of the rate at which species' ecological niches evolve—and consequently the degree to which closely related species occupy similar niches—is a topic that is relevant to many aspects of ecological and evolutionary biology (Wiens and Graham 2005; Wiens et al. 2010). The tendency for closely related taxa to share similar traits and occupy similar niches is often termed 'phylogenetic signal' sensu Losos (2008). This idea is also the basis for Darwin's hypothesis that competition is greater among close relatives (Darwin 1859), which has become known as phylogenetic limiting similarity. Many empirical studies have documented similarity of observed ecological niches among closely related species for a variety of taxa and ecological traits (e.g., Peterson et al. 1999; Prinzing 2001; Chazdon et al. 2003; Burns and Strauss 2011; Violle et al. 2011). Phylogenetic signal is widely accepted in the biological community, and sometimes takes on the role of an untested assumption. This assumption often underlies the interpretation of community assembly processes in phylogenetic community ecology (Webb 2000; Webb et al. 2002), and is often implicit in species distribution modeling and historical biogeography (Wiens and Donoghue 2004).

However, in a review of studies examining phylogenetic signal of ecological traits, Losos (2008) called attention to several instances where no relationship between evolutionary relatedness and ecological similarity was found, or where the relationship was negative (indicating rapid niche evolution). For example, Silvertown et al. (2006b) found no phylogenetic signal in the hydrological niches of co-occurring meadow plants, Cavender-Bares et al. (2004) found phylogenetic signal in some traits but not others in Floridian oak communities, and Losos et al. (2003) found no phylogenetic signal in the habitat and feeding niches of *Anolis* lizards in Cuba. Additionally, Blomberg et al. (2003) tested for phylogenetic signal in a variety of continuous traits and phylogenies taken from the literature, and found that most traits exhibited less phylogenetic signal than expected based on Brownian motion evolution. The results of these studies and others reviewed by Losos (2008) caution against the use of a priori assumptions of phylogenetic signal for all ecological systems and traits.

Adaptation to specific soil and topographic conditions is known to be an important part of the niche of tropical tree species. Small-scale variation in soil type, soil resource availability, and topography influences tropical tree species distributions at the local scale (<1 km) (Harms et al. 2001; Davies et al. 2005; Gunatilleke et al. 2006; John et al. 2007; Chuyong et al. 2011). Furthermore, species responses to both soil and topographic gradients have been shown to influence tropical forest community structure within many tropical forest dynamics plots (Valencia et al. 2004; Legendre et al. 2009; Baldeck et al. 2013). However, despite the importance of species' habitat niches in structuring tropical forest communities, it is unknown whether tree species sort independently along environmental gradients or whether evolutionary history influences the sorting of species along these gradients.

The question of how species' habitat niches are influenced by their evolutionary history is particularly relevant to the field of phylogenetic community ecology. The analysis of phylogenetic community structure attempts to reveal the relative importance of community assembly processes, with a primary focus on competitive exclusion and habitat filtering (Webb 2000; Webb et al. 2002; reviewed in Cavender-Bares et al. 2009; Vamosi et al. 2009). In the most common framework, the phylogenetic relationships among species occurring in a sample are analyzed and the sample may be described as phylogenetically even (species in the sample tend to be more distantly related than expected by chance, also called overdispersion), clustered (species in the sample tend to be more closely related than expected by chance), or neither (Webb 2000). It is usually assumed at the outset that the phylogenetic relatedness between two species is an indicator of their ecological similarity—that closely related species generally share more similar habitat

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requirements but also compete more strongly with one another. The presence of phylogenetic clustering then indicates the predominance of habitat filtering in structuring the community, while the presence of phylogenetic evenness indicates the predominance of competitive exclusion. However, tests of the assumption of phylogenetic signal in the ecological niches of the organisms under investigation are rare (e.g., Swenson et al. 2007).

Here, we examine the relationship between the evolutionary relatedness of co-occurring tropical tree species and the similarity in their local-scale habitat niches. We use the taxonomic rank of the species to approximate their evolutionary relationships, which allows us to use data from eight long-term tropical forest dynamics plots from the Center for Tropical Forest Science (CTFS) network, including approximately 1.4 million individuals of 1,513 species. We thus compare soil and topographic niche similarity of species pairs belonging to the same genus or family to that of more distantly related species pairs.

We expected that any effects of evolutionary relatedness on local habitat niches would be stronger at the genus level than at the family level, simply because congeneric species pairs will have diverged more recently, on average, than confamilial species pairs. If congeneric or confamilial species pairs have more similar habitat niches than more distant relatives, this would indicate phylogenetic signal in local habitat niches. It would also suggest that habitat filtering via soil and topographic variation could contribute to phylogenetic clustering within tropical tree communities. Alternatively, if congeneric or confamilial species pairs have more dissimilar habitat niches than more distant relatives, this would indicate that local habitat niches are highly evolutionarily labile, or convergent. This outcome could contribute to the coexistence of closely related species within the same habitat (Silvertown et al. 2006a) and could result in phylogenetic evenness of tropical forest communities.

Materials and methods

Study sites

This study uses vegetation and soil data from eight long-term tropical forest plots from the CTFS network: Barro Colorado Island (BCI), Panama (Hubbell et al. 1999, 2005); Huai Kha Khaeng and Khao Chong Thailand; Korup, Cameroon; La Planada, Colombia; Pasoh, Peninsular Malaysia; Sinharaja, Sri Lanka; and Yasuni, Ecuador (see Table 1 for environmental and vegetation characteristics of each study site). The plots range from 24 to 50 ha in size. Within each plot, all trees >1 cm diameter at breast height were measured, mapped, and identified to species (protocol described

in Condit 1998). Detailed descriptions of the study areas and forest dynamics plots are provided by Losos and Leigh (2004).

Soil and topographic data

Soil sampling and kriging methods followed those described in John et al. (2007). Briefly, soil samples were taken in a 40 or 50 m grid across the 24–50 ha study area, with additional samples taken near alternate grid points to estimate fine scale variation in soil variables. Soil nutrient extractions were conducted at each site using a standardized protocol. Non-nitrogen elements were extracted with Mehlich-III solution and analyzed on an atomic emission-inductively coupled plasma (AE-ICP; Perkin Elmer, MA, USA), with the exception of phosphorus at the Yasuni study site, which was extracted with Bray extract solution and analyzed calorimetrically on a Quickchem 8500 Flow Injection Analyzer (Hach, CO, USA). For the three neotropical study sites (BCI, La Planada, and Yasuni), an estimate of the in situ nitrogen mineralization rate was taken at each sample location by measuring nitrogen before and after a 28-day incubation period (see John et al. 2007 for a more detailed description). Nitrogen was measured as NH_4^+ and NO_3^- extracted with 2 M KCl and analyzed with an auto-analyzer (OI FS 3000; OI Analytical, TX, USA). Sample values were kriged to obtain estimated concentrations of soil nutrients at the 20×20 m quadrat scale. The non-nitrogen soil variables included in this study were phosphorus, calcium, potassium, magnesium, manganese, aluminum, and pH, but the number of variables included in the analysis varied from site to site. At least five soil variables were included in the analysis for each of the study sites (Table S1).

Topographic variables consisted of elevation, slope, and convexity (the relative elevation of a quadrat with respect to its immediate neighbors). Throughout each plot, elevation was recorded at the intersections of a 20×20 m grid and used to calculate topographic variables at the 20×20 m quadrat scale. Mean elevation was calculated as the mean of the elevation measurements at the four corners of a quadrat. Slope was calculated as the average slope of the four planes formed by connecting three corners of a quadrat at a time. Convexity was the elevation of a quadrat minus the average elevation of all immediate neighbor quadrats.

Niche overlap test

To reduce the complexity of the soil resource data, which included up to eight highly intercorrelated variables, a principal components (PC) analysis was performed to extract the main axes of soil nutrient variation for each site. The first two PC axes were used in the subsequent analysis.

Table 1 Environmental and vegetation characteristics of the study sites

Study site	Country	Size (ha)	Forest type	Elev. (m)	Soil order	Species	Congen.	Confam.
BCI	Panama	50	Semideciduous lowland moist	120	Oxisol	143	70	409
Huai Kha Khaeng	Thailand	50	Seasonal dry evergreen	549	Ultisol	74	10	137
Khao Chong	Thailand	24	Mixed evergreen	120	Ultisol	202	185	857
Korup	Cameroon	50	Lowland evergreen	150	Oxisol/Ultisol	209	239	933
La Planada	Colombia	25	Pluvial premontane	1,796	Andisol	106	75	279
Pasoh	Malaysia	50	Lowland mixed dipterocarp	80	Ultisol/Entisol	417	1,017	3,725
Sinharaja	Sri Lanka	25	Mixed dipterocarp	424	Ultisol	126	126	365
Yasuni	Ecuador	50	Evergreen lowland wet	230	Ultisol	313	532	2,012

Forest type taken from Losos and Leigh (2004)

Elev. is the lowermost elevation in the forest dynamics plot. *Species* indicates the number of species included in the study from each site, using only species with at least 100 individuals, *Congen.* and *Confam.* are the number of congeneric and confamilial species pairs from each study site, respectively

Among the eight study sites, the first two PCs combined represented between 60 and 87 % of the total variation present in the raw soil data (summary information on PC axes is provided in Table S1). Topographic variables were not converted to PCs, as elevation, slope, and convexity were generally non-linearly related to one another.

To measure the degree of similarity between two species' niches along an environmental gradient, a measure of niche overlap was calculated. Our niche overlap metric is adopted from Potts et al. (2004) and is derived from a Kolmogorov–Smirnov (K–S) test. A K–S test was calculated between two species' distributions along a PC axis or topographic variable, yielding a D statistic. The D statistic is a value between 0 and 1 that describes the degree of dissimilarity between the two distributions, and accounts for differences in central tendency, spread, and skewness. The test is non-parametric and therefore no assumption of normality regarding the distributions of species along soil gradients was needed. To express similarity between two distributions, we used 1–D as our measure of niche overlap.

All species with at least 100 individuals present at a study site and that were identified to genus were included in the analysis. A minimum sample size of 100 individuals was set to reduce spurious results due to low sample sizes, though results were found to be robust to smaller minimum sample sizes. Study sites varied considerably in the number of species included in the study, ranging from 74 species at Huai Kha Khaeng to 417 species at Pasoh (Table 1). Information on the families and genera represented in each study site is presented in Table S2. For each study site, the niche overlap metric was calculated for all pairwise combinations of species, for the two soil PC axes and the three topographic variables. Mantel tests were used to test whether species pairs belonging to the same genus or the same family have higher or lower niche overlap than expected based on a randomization of the data. Tests at the two taxonomic levels were performed for each environmental gradient,

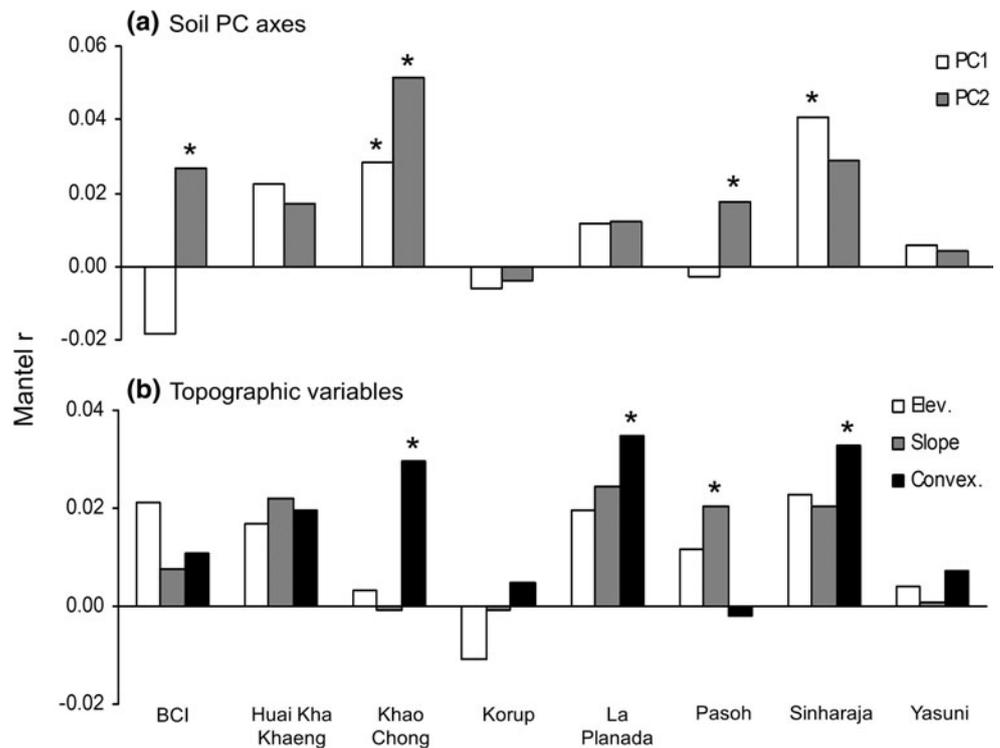
resulting in ten non-independent Mantel tests for each study site. Statistical significance was assessed by a two-tailed test ($\alpha = 0.025$ for each tail). Our analysis makes the assumption that congeneric species pairs are more closely related on average than confamilial species pairs, which are more closely related on average than non-confamilial species pairs.

Previous work from some CTFS plots and other forests around the world has demonstrated that forest communities may be phylogenetically clustered at distances of up to 100 m and that community phylogenetic structure is spatially autocorrelated (e.g., Webb 2000; Kembel and Hubbell 2006; Swenson et al. 2007). It was therefore necessary to check whether the results of this study were the result of coincident spatial structure of soil resources and the phylogenetic structure of the tree community. We checked for spurious results by repeating the Mantel tests for each site after swapping its soil PC or topographic maps with maps from another study site of the same or larger size (in the method of John et al. 2007). This created a null model that preserved both the spatial structure of the environmental gradients and the phylogenetic structure and spatial aggregation patterns of the tree communities. Statistically significant results for the swapped soil PC or topographic maps at either the genus or family level would indicate that the results of the tests at that taxonomic level may arise only due to the spatial structure of the community and the environmental variables.

Results

Congeneric species pairs showed significantly higher niche overlap than expected for at least one soil resource PC axis in four out of the eight study sites (Fig. 1a; Table S3a). Additionally, congeneric species pairs showed significantly higher niche overlap than expected for at least one

Fig. 1 Summary of Mantel tests comparing niche overlap among species from the same or different genera based on **a** soil PC axes and **b** topographic variables from eight sites. Positive values indicate that members of the same genus have higher niche overlap than members of different genera. *Asterisks* indicate significance ($\alpha = 0.025$ for each tail of a two-sided test)



topographic variable at four study sites (Fig. 1b; Table S3b). Of the topographic variables, convexity was the significant variable at three sites while slope was the significant variable at one site. Overall, congeneric species pairs generally had higher niche overlap than non-congeneric pairs (positive values of Mantel r), though a significant effect was only found for five sites total. When soil PC and topographic maps were swapped among sites, no spurious significant results were found at the genus level (data not shown).

In the genus-level Mantel tests, the PC axes for which congeneric species pairs showed significantly greater niche overlap than non-congeneric pairs tended to be highly correlated with aluminum (BCI PC2, Khao Chong PC2, Pasoh PC2, and Sinharaja PC1), with phosphorus (BCI PC2, Khao Chong PC2, and Pasoh PC2), base cations (Khao Chong PC1, Sinharaja PC1, and Yasuni PC2 as potassium), and manganese (Pasoh PC2, Yasuni PC2, Khao Chong PC1) having nearly equal overall importance to these axes (Table S1). Nitrogen mineralization rate was not found to be a large contributor to these axes, though it was only included for three sites.

The family level test results were more ambiguous. Significantly higher niche overlap along at least one soil PC axis was found for confamilial pairs at Khao Chong and Sinharaja, but the opposite result, significantly lower niche overlap, was found for La Planada (Table S4a). When soil PC maps were swapped among sites, a significantly higher niche overlap between members of the same family was

found for Sinharaja (PC2), and significantly lower niche overlap was found for Yasuni (PC1; data not shown). Significantly higher niche overlap along at least one topographic axis was found for confamilial pairs at Khao Chong and Yasuni, and significantly lower overlap was found for La Planada (Table S4b). However, when topographic maps were swapped among sites, significantly higher niche overlap was found for Khao Chong (elevation and convexity; data not shown).

Discussion

Over all eight study sites, we found that very close relatives (i.e., congeners) often have more similar local habitat niches, indicating phylogenetic signal in the habitat niches of tropical trees. The genus-level results do not appear to be the consequence of coincident spatial structure of environmental variation and phylogenetic community structure, as no significant correlations were observed when habitat maps were swapped among sites. Although results were significant for five of the sites, and for only one or two environmental gradients per site, the majority of the effect sizes were positive, indicating a weak trend for congeneric species pairs to have higher niche overlaps than non-congeneric species pairs. However, there was considerable variability in the results from site to site, thus it may not be appropriate to assume phylogenetic signal in habitat niches

of species across all sites. Additionally, the effects (Mantel r values) were small and it is unclear whether they are ecologically meaningful.

In contrast to the results at the genus level, there was no evidence for similar habitat niches at the family level. Although four sites showed significantly higher or lower niche overlap among members of the same family for at least one environmental gradient, three sites showed significant results at the family level when maps were swapped. The presence of spurious significant results at the family level indicates that the spatial structure of the environmental variables and the tree community may underlie observed niche overlap patterns at the family level. Additionally, our approach may be less able to detect patterns at the family level than at the genus level because of poorer representation of evolutionary divergence times at higher taxonomic ranks (i.e., confamilial species pairs will vary more in their evolutionary divergence times than congeneric species pairs).

We would expect that the use of taxonomic ranks would yield less power to detect evidence of phylogenetic signal than a well-resolved molecular phylogeny for the tree species in a community. However, this may not be the case when focusing on relationships among close relatives. For example, we found that congeneric species pairs had significantly higher niche overlap than expected for one soil PC axis at BCI. A previous study by Schreeg et al. (2010), using a barcode phylogeny for the tree community on BCI from Kress et al. (2009), found no phylogeny-wide signal in mean soil values and ranges using an analysis of traits approach. This discrepancy may have occurred because our analysis incorporates more information on species distributions across gradients and focuses on close relatives, where effects are most likely to be found. Thus, although taxonomic comparisons may be less effective at higher taxonomic ranks, they may yield decent power to detect effects at the genus level. As molecular phylogenies are increasingly available for many more tropical tree species, and are being created for some tropical forest communities (e.g., Kress et al. 2009), it may soon be possible to obtain estimates of the temporal extent of phylogenetic signal in species' ecological niches.

The variability in the genus level results do not display any global pattern that we can discern. The three sites that did not show any evidence for phylogenetic signal at the genus level were Huai Kha Kheng (Thailand), Korup (Cameroon), and Yasuni (Ecuador). These sites are located on three different continents, vary widely in their biogeographic history, climate, disturbance regimes, forest type, and species richness (Losos and Leigh 2004). There is no apparent commonality among these sites that differentiates them from the other sites, and thus we cannot infer any broad biogeographic trends in evolutionary lability of species' local habitat niches from this study.

However, our results may have important implications for the phylogenetic structure of these forest communities. It has been shown that, when patterns of phylogenetic signal in traits are incorporated into studies of phylogenetic ecology, they are tightly linked to observed patterns of phylogenetic community structure. Cavender-Bares et al. (2004) and Ackerly et al. (2006) showed that differences in the phylogenetic signal and the adaptive significance of traits explained observed phylogenetic community structure patterns in their study systems. For example, the convergent evolution of species' functional traits associated with habitat use in Floridian oaks explained the phylogenetic evenness of Floridian oak communities (Cavender-Bares et al. 2004). Additionally, Kraft et al. (2007) and Kembel (2009) used simulated communities with known assembly processes to show that differences in phylogenetic signal of traits strongly affect the outcome of phylogenetic community structure tests.

Further study is needed to understand how the patterns observed in the habitat niches of congeners is related to the phylogenetic structure of these communities. Phylogenetic signal in habitat-use niches may underlie some of the observed phylogenetic clustering of tree species at large scales in some CTFS and other tropical forest plots (e.g., Webb 2000; Swenson et al. 2007; Kraft and Ackerly 2010). However, if closely related species have more similar habitat niches at the plot scale, it does not necessarily follow that they will tend to be found within the same small-scale locations (i.e., a 5×5 or 10×10 m quadrat). Of the study sites included in this analysis, phylogenetic community structure has only been thoroughly examined at BCI (Kembel and Hubbell 2006; Swenson et al. 2007; but see Kress et al. 2009) and Yasuni (Kraft and Ackerly 2010). Future analyses connecting habitat variability with phylogenetic community structure could reveal the importance of phylogenetic signal in local-scale habitat niches in shaping phylogenetic structure in tropical forest communities.

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Author contributions GBC, DK, DWT, SM, NG, SG, SB, SK, AY, MNNS, RV, HN, SJD, and SPH coordinated collection of tree census and topographic data, JWD, KEH, JBY, and RJ designed the soil sampling protocol, BLT, HN, GBC, SM, SB, SK and AY collected soil data, RJ kriged the soil data, CAB designed and carried out the statistical analysis with JWD as advisor, CAB wrote the manuscript, and JWD and SWK contributed substantially to revisions.

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