THE EFFECTS OF LOCAL-SCALE RESOURCE HETEROGENEITY ON
TROPICAL TREE COMMUNITIES

BY

CLAIRE A. BALDECK

DISSERTATION

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Doctoral Committee:

      Associate Professor James W. Dalling, Chair, Director of Research
      Professor Carol K. Augspurger
      Assistant Professor Michael C. Dietze
      Associate Professor Michelle M. Wander

ABSTRACT

The role of niche assembly processes in shaping ecological communities is a subject of great interest to ecologists, especially in species rich communities such as tropical forests, as niche processes may play an important part in biodiversity maintenance. An important part of the environmental niche for tropical tree species is their specialization for particular soil resource conditions. My dissertation research examines the soil resource and topographic niches of tropical forest tree species and how they affect local (< 1 km) tree community structure. This research draws upon data from eight large (24-50 ha) tropical forest plots located around the globe, for which all trees > 1 cm in diameter have been mapped. Additionally, topographic variation has been mapped within these plots and I use data from a recent, extensive soil sampling effort that mapped the small-scale heterogeneity in many soil variables (including P, Ca, Mg, K, Mn, Al, and pH) within these plots. Previous research using these data has demonstrated that many tree species are non-randomly distributed with respect to soil resource and topographic variation, indicating that local-scale soil resource specialization is common and widespread for tropical trees.

I use a variety of multivariate techniques to investigate whether the soil resource and topographic niches of individual tree species have important emergent effects at the community level. I demonstrate that environmental variation is often a strong driver of variation in community composition within these forest plots. I also relate the soil resource and topographic niches of species to their evolutionary relationships and show that closely related species often have more similar habitat niches than distant relatives. The combined effects of habitat heterogeneity on community structure and phylogenetic signal in habitat niches create communities where soil resource and topographic variation affects the overall phylogenetic

structure of the community. Furthermore, I examine a possible mechanism for the controls of soil resources on spatial variation in leaf chemistry, an important component of ecosystem biogeochemical cycling. I find that leaf nutrient profiles are highly conserved within a species and thus I predict that soil resources are likely to influence community-level variation in leaf chemistry through their effects on species composition, rather than by intraspecific responses to soil nutrients. Overall, my dissertation has helped to reveal and explain local-scale environmental controls on community structure and to clarify likely controls of soil resources on spatial variation in ecosystem biogeochemistry.

To Morrill,

You are as lovely on the inside as you are ugly on the outside

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CHAPTER 1: INTRODUCTION

A major unresolved question in ecology is how ecological niches influence community structure. An understanding of ecological niches is needed, especially in highly species diverse communities such as tropical forests, because species' ecological niches lie at the heart of many putative explanations for species coexistence and biodiversity maintenance. These theories revolve around the idea that niche partitioning may facilitate species coexistence by reducing interspecific competition (Hutchinson 1959, Tilman 1982, Chesson 2000). For plants, soil resources are likely to be an important part of the ecological niche. Previous work has shown that soil nutrient availability influences the local-scale distributions of c. 30-40% of tropical tree species in three neotropical forest plots (John et al. 2007). This indicates that tropical tree species have specific soil resource niches and that niche partitioning along soil resource axes may play an important role in shaping tropical forest community structure at the local scale.

In contrast to theories of coexistence that are based upon species niche differentiation, neutral theory (Hubbell 2001) proposes that species are ecologically equivalent. Ecological equivalency means that species in the same trophic level are demographically identical; that is, they have similar birth, death, and speciation rates, and similar dispersal capabilities. It is a well known fact that species differences exist, but neutral theory asks whether this simplified model is sufficient to explain patterns of community assembly in nature. In the neutral model, communities are assembled via stochastic dispersal events and community species richness is a product of random local extinction and migration from the outside regional species pool. To refute neutral theory, it is not enough to show that species are ecologically non-equivalent, or that they exhibit differences in their environmental niches (e.g. Harms et al. 2001, John et al. 2007). One must show that species' environmental niches are important for community

assembly. This may be tested by examining how environmental heterogeneity influences overall community structure within these tropical forest communities. Beyond neutral theory, it is crucial to understand how tree species' soil resource niches impact tree community structure in order to better understand the factors that shape community assembly and local-scale patterns of biodiversity.

The main focus of my dissertation is on the influence of local-scale environmental heterogeneity on overall community structure. The analyses for my dissertation draw upon data from eight long-term tropical forest plots located around the world from the Center for Tropical Forest Science (CTFS) network. At each of these sites essential plant nutrients (including N, P, Ca, Mg, K) and topography have been intensively mapped and individual trees have been mapped and identified to species. The CTFS data sets, containing information on over 1.5 million individual trees, offer an extraordinary opportunity to explore local-scale soil resource niches and how soil resource variation affects the structure of these tropical forest communities.

In the second chapter I explore how the effects of soil resources and topography on the distributions of individual species scale up to the community level. I examine whether soil resources and topography influence overall community structure by examining how variation in these environmental factors influences beta diversity, or how community composition changes across space. Using variation partitioning with canonical redundancy analysis, I partitioned total community compositional variation (a form of beta diversity; Legendre et al. 2005) into fractions explained by spatial, soil, and topographic variables. I found that soil resources and topography both exhibited strong and roughly equal influences on the overall tree community structure. At the same time, there is a large portion of variation that is spatially structured yet unexplained by environmental factors, which indicates an important role for limited dispersal and unmeasured environmental variables in shaping community structure. Furthermore, I mapped overall

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community structure within these forests by displaying the multivariate dispersion of the tree community as an RGB image. The results of this analysis demonstrate that local-scale variation in community composition is strongly driven by variation in soil resources and topography within many tropical forest communities.

The third chapter asks whether tree species that are evolutionarily more closely related have more similar habitat niches. I calculated the niche overlap (a value that indicates the similarity of two species' environmental niches) for all pairwise combinations of co-occurring tree species along soil resource and topographic axes. These niche overlap values were compared with the taxonomic relatedness among species. I found that species belonging to the same genus had significantly higher niche overlap than more distantly related species pairs along at least one axis in five study sites. However, a similar effect was not found at the family level, indicating that similarities in habitat niches may be restricted to the level of congeners. The results indicate that tree species' local habitat niches exhibit phylogenetic signal (i.e., close relatives are more ecologically similar) and they have implications for the overall structure of tropical tree communities in terms of how closely related species are distributed in space with respect to one another, a subject that is addressed in the fourth chapter.

The fourth chapter explores how the phylogenetic structure of these tropical forest communities is affected by the interaction of soil resource niches and phylogenetic signal in soil resource niches of trees. Because soil resource niches are known to affect the compositional structure of these forests, and these soil resource niches may exhibit phylogenetic signal, it is reasonable to expect that soil resource variation may affect the phylogenetic structure of these communities. Using composite phylogenetic trees that approximate the evolutionary relatedness of the species in the forest plots, I examined how variation in soil resources and topography affect phylogenetic community structure. I examined phylogenetic community structure using a

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newly derived metric called phylogenetic beta diversity (Graham & Fine 2008), which measures how the evolutionary relatedness of the tree community changes across space. I found that soil resource variation explained a significant portion of the phylogenetic structure of a community. Furthermore, I found that these effects were generally independent of geographic distance. This means that areas that share a more similar soil nutrient composition tend to contain more phylogenetically similar tree communities.

The fifth chapter examines how leaf nutrient concentrations, indicating the nutrient composition of the plant, are related to available soil nutrients within a species. Previous biogeochemical work in the tropics has indicated a connection between soil nutrient availability and leaf chemistry at the ecosystem scale (e.g. McGroddy et al. 2004, Townsend et al. 2007, Asner et al. 2010); however, variation in leaf chemistry may be caused by turnover in species composition along soil nutrient gradients, or by intraspecific responses to soil nutrient availability. I conducted extensive within-species sampling of 15 tree species along gradients of key soil nutrients in the 50-ha plot of Barro Colorado Island, Panama. I found species' leaf nutrient profiles are highly constrained, and that leaf chemistry was generally not correlated with soil nutrient availability within a species. My results indicate that ecosystem-level variation in leaf nutrients along soil nutrient gradients is likely to be more strongly driven by species composition than by intraspecific responses to soil nutrient gradients.

Understanding the role of ecological niches in shaping emergent community properties such as community structure, phylogenetic structure, and variation in ecosystem biogeochemical processes is central to the study of ecology. This information is crucial to our understanding of how communities are assembled, how biodiversity is structured across space, and for making predictions of how communities may respond to changing environmental conditions. Previous work in tropical forests has focused primarily on tree species' light and water requirements,

while soil resource niches have received far less attention. The previous work that has been done on the effects of soil resources in tropical forests has mainly focused on large-scale, landscape and regional patterns. The work of John et al. (2007) was among the first to indicate that soil resource heterogeneity influences species distributions at the local-scale. My work is the first to take these observations from the species- to the community-level, and to place these observations in an evolutionary context. Furthermore, using eight replicate study sites I examine these issues on an unprecedented scale, allowing me to make pantropical generalizations. Further, I examine a possible mechanism which may control ecosystem-level variation in leaf chemistry, which may have important implications for understanding how spatial variation in biogeochemical processes is driven by soil resource variation.

CHAPTER 2: SOIL RESOURCES AND TOPOGRAPHY SHAPE LOCAL TREE
COMMUNITY STRUCTURE OF TROPICAL FORESTS

ABSTRACT

Both habitat partitioning and dispersal limitation influence the compositional structure of

forest communities, but little is known about the relative contributions of these two processes, or

the roles of different types of environmental variation. I used variation partitioning based on

canonical redundancy analysis to decompose community compositional variation within eight

large (24-50 ha) tropical forest plots into fractions explained by spatial, soil resource, and

topographic variables. All environmental variables together explained 13-39% of compositional

variation within a plot, with both soil resources and topography accounting for significant and

approximately equal variation (9-34% and 5-29%, respectively). Additionally, a large fraction of

variation (19-37%) was spatially structured yet unexplained by the environment, suggesting an

important role for dispersal processes. My results, illustrated using a new graphical depiction of

community structure within these plots, demonstrate the importance of small-scale

environmental variation in shaping local community structure in diverse tropical forests around

the globe.

INTRODUCTION

A major challenge for community ecology is to understand the importance of niche-

assembly processes in shaping community structure. This is of particular interest in species rich

communities such as tropical forests, because niche partitioning is thought to facilitate species

coexistence and may therefore play an important role in biodiversity maintenance (Chesson

2000, Chave et al. 2002). Evidence for the role of habitat partitioning among tropical forest tree

species has been found from local to landscape scales, and comes from observed non-random

associations between species distributions and environmental variables and observations of species turnover along environmental gradients (Clark et al. 1998, Harms et al. 2001, Potts et al. 2002, Phillips et al. 2003, Valencia et al. 2004, Fine et al. 2005, Paoli et al. 2006, John et al. 2007). However, at local scales (<1 km^2), limited dispersal also plays an important role in determining species distributions, resulting in aggregated seedling and adult populations (Condit et al. 2000, Plotkin et al. 2000, Dalling et al. 2002). Disentangling the relative importance of niche and dispersal mechanisms to local community structure is problematic because both contribute to spatial autocorrelation in species composition at this scale. Dispersal processes lead to spatially aggregated species distributions and, therefore, spatially structured communities. Additionally, habitat partitioning leads to spatial community structure due to the high spatial autocorrelation of environmental variables.

Despite substantial evidence for the importance of niche partitioning in structuring communities, surprisingly little is known about the relative influence of different environmental factors. At local scales, evidence for niche partitioning has been based mostly on topographic variation (Harms et al. 2001, Potts et al. 2002, Valencia et al. 2004, Gunatilleke et al. 2006, Legendre et al. 2009, Chuyong et al. 2011), as topography is relatively easily measured and acts as a useful proxy for habitat heterogeneity because it influences both water availability and soil biogeochemical processes. However, recently created fine-scale soil resource maps for several tropical forest dynamics plots greatly enhance the ability to directly examine the effects of resource variation on tropical forest community structure. In a previous analysis using these soil maps at three neotropical forest plots, John et al. (2007) found that *c*. 30-40% of tree species were non-randomly distributed with respect to soil nutrient variation. While these results indicate that soil resource variation influences many individual species, the community-level effects of soil resource variation have not yet been examined extensively, nor has any study combined soil

resource and topographic data to examine their relative contributions to local community structure.

Variation partitioning (Borcard et al. 1992, Borcard & Legendre 1994) via canonical redundancy analysis (RDA; Rao 1964) provides one way to assess the relative importance of habitat niche and dispersal-assembly processes, or of different sets of environmental variables on community structure. With variation partitioning, the total variation in community composition within a study area (an expression of the beta diversity of the area (Legendre et al. 2005, Anderson et al. 2011) may be decomposed into fractions explained by different sets of variables (see Fig. 1 in 20). To address the relative contribution of habitat niche and dispersal processes, the geographic coordinates of the sampling sites may be used to derive a set of spatial variables (Borcard & Legendre 2002), and when paired with environmental variables, compositional variation can be partitioned into fractions explained by pure spatial variation, pure environmental variation, spatially structured environmental variation, and the unexplained remainder (Legendre et al. 2005). The component of compositional variation that is explained by environmental variables (the pure environmental plus the spatially structured environmental component) is generally interpreted as resulting from species responses to measured environmental variation, whereas the component explained by pure spatial variation is thought to result from the influence of dispersal processes and species responses to unmeasured environmental variation (Legendre et al. 2005, Legendre et al. 2009, Anderson et al. 2011).

My analysis combines detailed data on both topographic and soil resource variation for eight tropical forest plots that range from 24-50 ha in size (Table 2.1), span a number of biogeographic regions, and vary in soil fertility and precipitation regime (from continuously wet to seasonally dry). Here I assess the relative influence of small-scale environmental variation and dispersal processes on tree community structure using the variation partitioning approach. I

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further decompose the influence of environmental variation into the contributions of soil resource and topographic variation. These analyses are accompanied by among-plot comparisons that examine the role of topographic heterogeneity on the importance of topography, and the relationship between the inferred importance of niche and dispersal processes and plot diversity.

Based on previous analyses (Harms et al. 2001, Potts et al. 2002, Valencia et al. 2004, Gunatilleke et al. 2006, Legendre et al. 2009, Chuyong et al. 2011), I predicted that topographic variables would have an important effect on community composition, although the magnitude was expected to be positively related to the amount of topographic heterogeneity present. I expected soil resource variables to exert an even greater influence on community structure because they provide a more direct measure of factors that influence plant growth and survival. To visualize compositional variation within a study site I adapted a technique from landscape and regional mapping where an ordination of community composition is converted into an RGB image (Thessler et al. 2005). I use these "beta diversity" maps to inform my interpretation of the variation partitioning results and illustrate that local habitat heterogeneity may be more important to tropical forest community structure than commonly assumed.

METHODS

Study sites and environmental data

The data come from eight long-term tropical forest dynamics plots of the Center for Tropical Forest Science (CTFS) network: Barro Colorado Island (BCI), Panama; Huai Kha Khaeng and Khao Chong, Thailand; Korup, Cameroon; La Planada, Colombia; Pasoh, Peninsular Malaysia; Sinharaja, Sri Lanka; and Yasuni, Ecuador. Within each plot, all free-standing trees larger than 1 cm dbh have been mapped, identified to species, and measured for

dbh according to a standard protocol (Condit 1998). Information on plot size as well as vegetation and soil characteristics of the plots is presented in Table 2.1.

Topographic variables consisted of elevation, slope, convexity (the relative elevation of a quadrat with respect to its immediate neighbors), and aspect. 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. Finally, aspect was the direction of the steepest slope of a quadrat, calculated in ArcMap 9.3 (www.esri.com).

Soil samples were collected throughout each plot, analyzed, and the variables were kriged using comparable methods (John et al. 2007). In each study site soil samples were taken at the intersections of a 40 or 50 m grid across the study area, with additional samples taken near alternate grid points to estimate fine scale variation in soil variables. The first 10 cm of topsoil was sampled, excluding the top organic horizon. Non-nitrogen elements were extracted with Mehlich-III solution and analyzed on an atomic emission-inductively coupled plasma (AE-ICP, Perkin Elmer Inc., Massachusetts, USA), with the exception of phosphorus at the Yasuni study site, which was extracted with Bray extract solution and analyzed by automated colorimetry on a Quickchem 8500 Flow Injection Analyzer (Hach Ltd., Colorado, USA). For the three neotropical study sites (BCI, La Planada, and Yasuni) an estimate of the *in situ* N-mineralization rate was taken at each sample location by measuring nitrogen before and after a 28 day incubation period. Nitrogen was extracted as NH_4^+ and NO_3^- with 2M KCl and analyzed with an auto analyzer (OI FS 3000, OI Analytical, Texas, USA). Sample values were kriged to obtain estimated

concentrations of soil nutrients at the 20×20 m quadrat scale. The set of soil variables for each study site contained 6–12 variables, generally including Al, Ca, K, Mg, Mn, P, and pH, but where available also included the N-mineralization rate, B, Cu, Fe, and Zn (Table 2.1).

Partitioning beta diversity

Spatial patterns in community compositional variation were modeled with principal components of neighbor matrices (PCNM) according to the methods described in Borcard & Legendre (2002). PCNM is a powerful technique that is able to model spatial structure in a data set at any spatial scale that can be resolved by the sampling design (here, the 20×20 m spatial resolution) (Borcard & Legendre 2002, Borcard et al. 2004, Dray et al. 2006). To calculate PCNM eigenfunctions, a truncated geographic distance matrix was produced for all 20×20 m quadrats in a study site. In this matrix, neighboring quadrats were determined using the queen criterion of contiguity (i.e., each quadrat has up to eight neighbors). The geographic distance between neighbors was retained, but the distances between all non-neighbor quadrats was replaced with a value of four times the distance between diagonally contiguous quadrats. A principal coordinates analysis was then performed on this truncated geographic distance matrix, and all eigenfunctions with positive eigenvalues were retained. These PCNM eigenfunctions made up the set of spatial variables used to model spatial structure in the community data.

I used canonical redundancy analysis (RDA; Rao 1964) to partition the total compositional variation in a community into portions explained by spatial and environmental variables at the 20×20 m scale. Before performing the RDA, I expanded the set of environmental variables according to the method of Legendre et al. (2009) to increase model flexibility and to facilitate comparison among studies. I added to the set of environmental variables the squared and cubed values of each variable, with the exception of aspect. I included

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the sine and cosine of aspect as the only aspect variables. This created a set of 11 topographic variables and 18-36 soil variables for each study site.

First, I partitioned the variation in community composition within each plot into fractions explained by environmental and spatial variables, then the proportion of variation explained by environmental variation was partitioned between topographic and soil variables. This decomposition was performed in two steps to simplify interpretation. The sets of soil and topographic variables were then separately subjected to forward selection; note that the use of forward selection obviates the statistical significance of both the soil and topographic variable sets in explaining compositional variation at each study site. Variation partitioning with RDA and forward selection were performed using the 'vegan' and 'packfor' packages in R, respectively.

To check the robustness of my variation partitioning results to the type of canonical analysis used, I repeated the variation partitioning analysis with a distance-based RDA (Legendre & Anderson 1999), based on square-root transformed Bray-Curtis distances among quadrats. Fractions of explained variation from the ordinary RDA were compared to those from the distance-based RDA. I also checked my results for robustness to plot size. Larger plots may be expected to have a higher beta diversity due to the species-area relationship, and they may encompass greater environmental variation. For the five 50-ha plots, I compared the variation partitioning results with those obtained from their two 25-ha plot halves. Methodological details, results, and discussion of these analyses are presented in Appendix A. The relative sizes of the variation fractions were found to be robust to the type of canonical analysis used and to differences in plot size; therefore, only the results of the ordinary RDA for original plot sizes are discussed here.

Topographic heterogeneity

I tested whether the effect of topography was related to the topographic heterogeneity of a site by correlating the elevational range of a plot (calculated as the highest elevation minus the lowest within the plot; Table 2.1) with the proportion of variation explained by topographic variables. The results for the Gutianshan CTFS plot from Legendre et al. (2009) were added to this analysis, for a total sample size of nine plots. A similar investigation of the effects of soil resource heterogeneity is not attempted here, given differences in the soil resource variables included for each site and the interacting effects of soil resource abundance, heterogeneity, and ratios.

Plot diversity

To test whether the importance of niche or dispersal processes explain among-plot diversity patterns, I tested for correlations between the sizes of four of the variation fractions and plot species richness and overall beta diversity (Table 2.1). The variation fractions used were the total explained, representing niche plus dispersal processes; environmental, representing habitat niche partitioning; topographic, representing habitat niche partitioning with uniform data across study sites; and pure spatial, representing dispersal. The overall beta diversity of a plot was calculated as the multiplicative partition of gamma diversity by alpha diversity ($\beta = 1 - \bar{\alpha} / \gamma$; Whittaker 1960, Tuomisto 2010). Here, $\bar{\alpha}$ is the mean 20×20 m quadrat species richness and γ is the plot species richness.

Beta diversity maps

To produce a map of community structure within a study site I first calculated the Bray-Curtis distances among all 20×20 m quadrats within a study site, then this distance matrix was

subjected to non-metric multidimensional scaling on three ordination axes. Each quadrat's position in three dimensional ordination space was then translated into an RGB color by assigning quadrat positions on ordination axes 1, 2 and 3 to intensities of red, green, and blue, respectively (Thessler et al. 2005). I applied the same translation from axis position to color intensity to all axes simultaneously so that the variation shown by each of the colors is proportional to the variation explained by its respective axis. The red, green, and blue components of each quadrat were combined to create RGB colors that were then mapped. This method of mapping community structure displays a greater portion of community variation than possible by displaying one species or ordination axis at a time.

RESULTS

Niche and dispersal assembly

The ability to explain local tree community structure varied markedly among sites. Total explained variation, from environmental and spatial variables together, ranged from 32% at La Planada to 74% at Korup and Sinharaja (table 2.2). Across study sites, nearly all of the total explained variation was accounted for by the spatial variables, resulting in a lack of pure environmental variation. The proportion of variation explained by environmental variables also varied widely from site to site, from as little as 13% at La Planada to as much as 39% at Khao Chong (table 2.2). The proportion of variation explained by spatial variables alone (after controlling for the effect of environmental variation) ranged from 19-37%, similar in magnitude to the variation explained by environmental variables.

Soil resource and topographic effects

The sets of soil and topographic variables each explained a statistically significant proportion of compositional variation at every study site. Soil variables explained more variation than topographic variables in seven of the eight study sites (table 2.3). However, there were generally 2-3 times as many soil variables included in the analysis as topographic variables. I therefore compared the variation explained among soil and topographic variables, controlling for the number of variables included from a forward selection of variables (table 2.3). Viewing the contributions of soil and topographic variables in this way, I found that three study sites (Huai Kha Khaeng, Korup, and Sinharaja) had a greater proportion of variation explained by topographic variables than soil variables. Additionally, the variation explained by the first (explaining the greatest amount of variation) soil and first topographic variables were similar, indicating that the primary topographic variable is as important as the primary soil variable in explaining community structure across study sites (figure A.1).

Among-plot comparisons

When the elevational range of a plot was used as a proxy for topographic heterogeneity I found a weak positive relationship with the amount of variation explained by topography (figure 2.1). However, this relationship was not statistically significant at the traditional 0.05 α level (Pearson's r = 0.64, P = 0.065), an unsurprising result given the small sample size.

None of the fractions of explained variation tested, including total explained, environmental, topographic, and pure spatial, were related to the species richness of the plot or to the overall beta diversity of a plot.

Beta Diversity Maps

Maps of plot beta diversity are presented alongside site elevation maps in figure 2.2. In the beta diversity maps, quadrats of similar color contain similar tree communities (lower Bray-Curtis dissimilarity), providing a visual interpretation of both the turnover between any two quadrats within a study site and the total variation in community composition. The maps for Korup and Sinharaja (figure 2.2A, 2.2F), where 74% of the variation in community composition is explained by environmental and spatial variables, clearly show far more spatial structure than the La Planada map (figure 2.2E), where only 32% of variation is explained. These maps also reveal community responses to certain environmental features, such as the stream bed running east to west across the Pasoh study site (figure 2.2C) and the swamp located near the center of the Barro Colorado Island study site (figure 2A; cf. figure 1 in Harms et al. 2001).

DISCUSSION

My analysis illustrates the importance of previously unmeasured environmental variation in contributing to compositional variation in tropical forests. The inclusion of soil resource data for these plots elevates the inferred importance of habitat niche partitioning and decreases the inferred importance of dispersal processes compared to an analysis using only topographic data (as seen by variation explained by soil resources after topography has been taken into account; table 2.3). It is almost certain that there is still important unmeasured environmental variation (i.e., light, soil moisture and drainage) that contributes to the community structure of these forests. However, the data for any one study site are among the most complete environmental datasets for any tropical forest community.

The considerable explanatory power of both pure spatial and environmental variation suggests an important role for dispersal assembly alongside habitat niche processes in shaping

community structure in these forests. However, interpretation of the relative roles of niche and dispersal processes is complicated by the fact that the purely spatial fraction of compositional variation is attributed to the effects of dispersal assembly and species responses to unmeasured environmental variation. Additionally, some important unmeasured environmental variables may exhibit spatial structure that is not captured by the 20×20 m resolution of my study design, such as light availability which may vary more dramatically over smaller spatial and temporal scales than topography and soil resource availability. Species responses to such environmental variables are likely to contribute to the unexplained portion of compositional variation. Moreover, some of the variation explained by the environment may be confounded with species spatial aggregation due to dispersal processes (Anderson et al. 2011).

The spatial resolution of my analysis is also expected to affect the balance between the proportion of variation explained by environmental and pure spatial variation (Legendre et al. 2009), and thus the inferred relative importance of habitat niche and dispersal assembly processes. As the spatial resolution of the analysis decreases (or quadrat size becomes larger), smaller-scale dispersal effects and environmental heterogeneity are smoothed over, causing the explanatory power of the environment to increase (Legendre et al. 2009). For this analysis, I chose the 20×20 m resolution because this quadrat size best represents soil resource variation as measured by the sampling scheme, and it is the scale at which elevation was measured. Therefore, the size of the fractions of compositional variation that are explained by environmental and pure spatial variation are specific to the 20×20 m resolution of this analysis.

This study is the first to combine and examine the relative contributions of soil resource variation and topography to community structure within any of these study sites. Although soil resources explained more variation in community composition than topography, I found rather similar contributions of soil resource and topographic factors when variable number was taken

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into account. Furthermore, the primary topographic and primary soil resource variables explained very similar amounts of variation. The greater amount of variation explained by soil resources is therefore likely caused by the higher dimensionality of soil chemical variation. Neither effect was entirely nested within the other, indicating that both soil resources and topography independently influence community structure in a wide variety of tropical forest communities.

The beta diversity maps I generated help inform the interpretation of my variation partitioning results. From these maps one can see that the topographic signature on community structure is strong at many of the sites even though the set of topographic variables always accounts for less than 30% of compositional variation (figure 2.2). The variable selection procedure identified slope as the most important topographic variable at the BCI study site, explaining 3.4% of compositional variation, yet this small effect can be discerned from the RGB map (figure. 2.2A; cf. figure 1 in Harms et al. 2001). The four most important topographic variables from the variable selection procedure (elevation, convexity, slope and cosine of aspect) explain a combined 9.6% of the community variation at the Yasuni study site, and there is a strong similarity between the beta diversity and topographic maps for this site. The strongest effect of any single environmental variable on community structure in my study is elevation at Sinharaja, explaining 14.7%, which coincides with sharply defined features of the community (figure 2.2F). Therefore, in the context of my analysis, a variable that explains 3% of variation in community composition has a discernable but subtle effect on community structure, whereas a variable that explains 15% has a very strong effect.

My results demonstrate remarkable variability among study sites in the importance of niche and dispersal processes in shaping local community structure. One putative explanation for among-plot variability in the importance of environmental control is that the degree of habitat

heterogeneity affects the strength of habitat-based niche partitioning – strong community responses to topography are not expected in plots that are relatively flat. Although I found weak support for this relationship, a few problems arise from such a comparison. First, my study sites differ in climatic conditions and forest type. The study site for which topography explains the smallest proportion of beta diversity is La Planada. La Planada is the only montane forest represented, with a continuously wet climate. If topography primarily reflects heterogeneity in soil moisture conditions (e.g. Comita & Engelbrecht 2009), then there may be little topographic influence in continuously wet soils. Second, elevational range may inadequately represent topographic heterogeneity at Khao Chong compared to other sites, as the topography of this plot can mainly be characterized by a single slope (figure A.2).

Both habitat partitioning and dispersal limitation are mechanisms that are expected to promote species coexistence (Chesson 2000, Chave et al. 2002). I therefore hypothesized that the importance of these processes, as measured by the fractions of explained variation, would be positively related to plot diversity, measured as either beta diversity or plot species richness. However, I did not find any evidence for such relationships among study sites. The absence of a relationship between the strength of limited dispersal or the influence of the environment and plot beta diversity or species richness should not imply that they do not contribute to the maintenance of biodiversity within a plot. The fact that compositional variation arises as a result of the environmental variation indicates that environmental variation allows a greater number of species to exist within a plot than would exist in a homogenous environment.

My findings suggest that the influence of environmental variation on local community structure may be underappreciated; maps of beta diversity plotted as an RGB image indicate that environmental factors that account for <5% of compositional variation may nonetheless produce an important signal in compositional structure. My results also highlight the large differences

among sites in the inferred importance of niche and dispersal processes. I offer some evidence that topographic heterogeneity is correlated with the explanatory power of topographic variables, a reasonable expectation when comparison is restricted to similar forest types. Further investigation into the factors shaping differences among study sites in the role of habitat niche and dispersal processes offers a promising track for future research.

TABLES AND FIGURES

Table 2.1. Study site characteristics.

Study site	Size (ha)	Forest type	No. species	β*	Elev. range (m)	Soil order	Soil variables used
BCI	50	semidecid. lowland moist	298	0.84	38	Oxisol	Al,B,Ca,Cu,Fe,K,Mg,Mn,Nmin,P,Zn,pH
Huai Kha Khaeng	50	seasonal dry evergreen	233	0.90	85	Ultisol	Al,B,Ca,Cu,Fe,K,Mg,Mn,P,Zn,pH
Khao Chong	24	mixed evergreen	571	0.88	239	Ultisol	Al,Ca,Fe,K,Mg,Mn,P,Zn,pH
Korup	50	lowland evergreen	452	0.85	95	Ox./Ult.	Al,Ca,Fe,K,Mg,Mn,P,Zn
La Planada	25	pluvial premontane	192	0.75	67	Andisol	Al,Ca,Cu,Fe,K,Mg,Mn,Nmin,P,pH
Pasoh	50	lowland mixed dipterocarp	790	0.86	24	Ult./Ent.	Al,Ca,Cu,Fe,K,Mg,Mn,P
Sinharaja	25	mixed dipterocarp	199	0.76	145	Ultisol	Al,Ca,Fe,K,P,pH
Yasuni	50	evergreen lowland wet	1088	0.88	32	Ultisol	Al,Ca,Cu,Fe,K,Mg,Mn,Nmin,P,Zn,pH

[*]The overall beta diversity of a plot, calculated as $\beta = 1 - \bar{\alpha} / \gamma$, where $\bar{\alpha}$ is the average species richness of a 20×20 m quadrat and γ is the species richness of the entire plot.

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Table 2.2. Variation partitioning results for spatial variables and the total set of environmental variables. Total = the proportion of variation explained by both spatial and environmental variables combined, Space = the proportion explained by spatial variables, Env. = the proportion explained by environmental variables, Space|Env. = the pure spatial component, Overlap = the spatially structured environmental component, and Env.|Space = the pure environmental component.

	Total	Space	Env.	Space|Env.	Overlap	Env.|Space
BCI	0.54	0.54	0.25	0.29	0.25	0.00
Huai Kha Khaeng	0.47	0.45	0.14	0.33	0.11	0.02
Khao Chong	0.61	0.57	0.39	0.22	0.35	0.03
Korup	0.74	0.74	0.38	0.36	0.38	0.00
La Planada	0.32	0.29	0.13	0.19	0.10	0.03
Pasoh	0.47	0.47	0.20	0.28	0.19	0.01
Sinharaja	0.74	0.73	0.37	0.37	0.36	0.01
Yasuni	0.50	0.49	0.22	0.28	0.21	0.01

Table 2.3. Variation partitioning results for soil and topographic variables. Total Env. = the proportion of variation explained by both soil and topographic variables combined, Soil = the proportion explained by soil variables, Topo. = the proportion explained by topographic variables, Soil|Topo. = the pure soil component, Overlap = the topographically structured soil component, and Topo.|Soil = the pure topographic component. Soil FS is the proportion of variation explained by soil variables from the forward selection procedure, holding the number of soil variables chosen equal to the number of topographic variables chosen by forward selection; the number of variables used is given in parentheses. The proportion of variation explained by the topographic variables from the forward selection results is equal to the amount given by regular variation partitioning (Topo.).

	Total Env.	Soil	Soil FS	Topo.	Soil|Topo.	Overlap	Topo.|Soil
BCI	0.25	0.20	0.16 (10)	0.13	0.12	0.08	0.04
Huai Kha Khaeng	0.14	0.09	0.06 (8)	0.08	0.06	0.03	0.04
Khao Chong	0.39	0.34	0.30 (10)	0.17	0.22	0.12	0.05
Korup	0.38	0.30	0.26 (11)	0.28	0.10	0.19	0.09
La Planada	0.13	0.11	0.09 (10)	0.05	0.08	0.03	0.02
Pasoh	0.20	0.17	0.14 (11)	0.10	0.10	0.07	0.03
Sinharaja	0.37	0.20	0.18 (10)	0.29	0.08	0.12	0.17
Yasuni	0.22	0.17	0.13 (11)	0.11	0.11	0.06	0.05
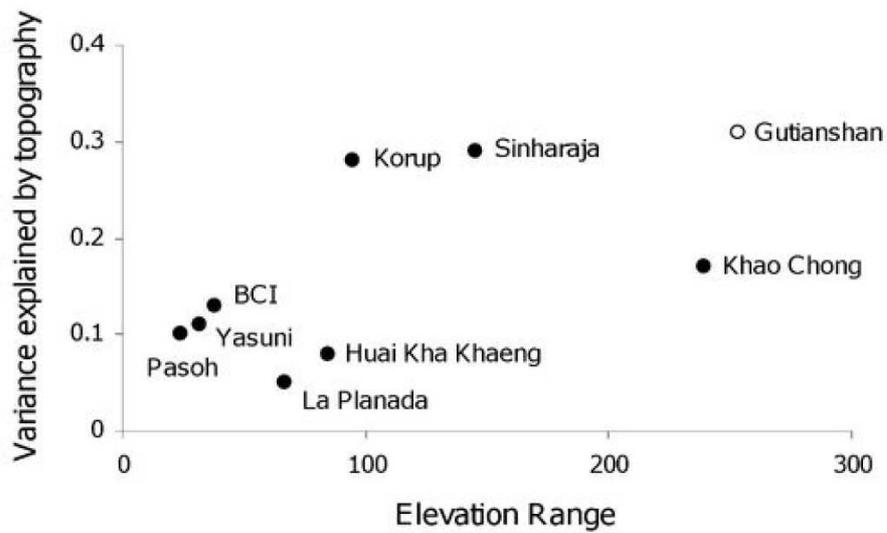
Figure 2.1. The elevational range of a study site (table 2.1) versus the proportion of variation in community composition explained by the set of topographic variables (table 2.3). The open circle represents the results of the same variation partitioning method for the Gutianshan CTFS plot in China (Legendre et al. 2009).
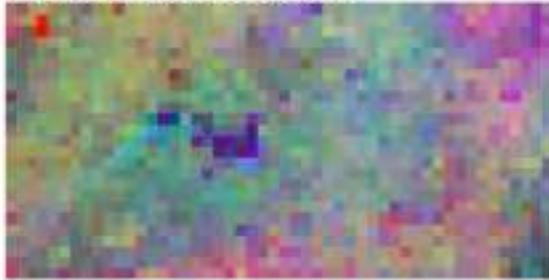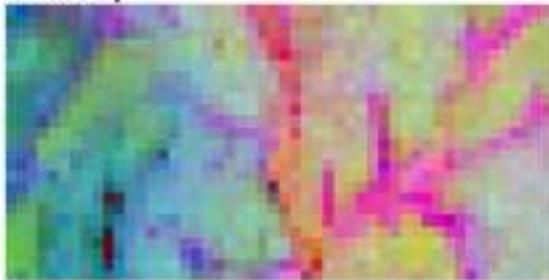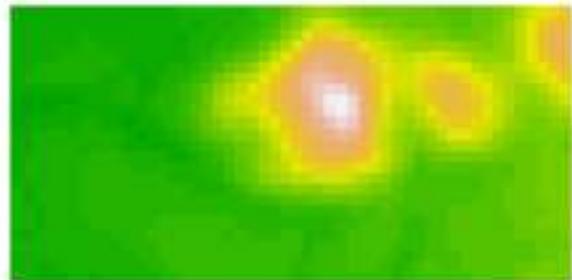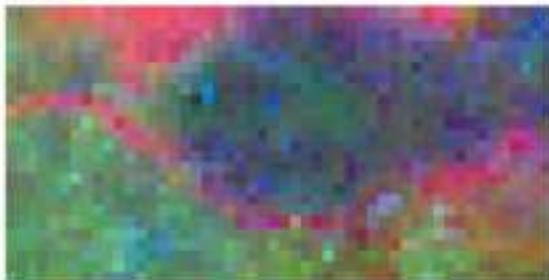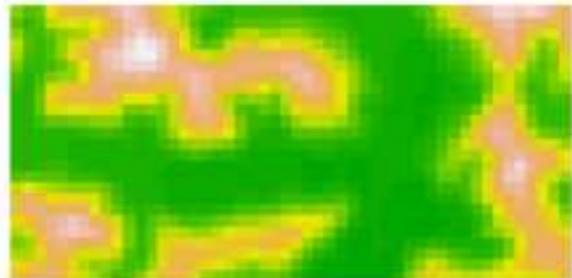
Figure. 2.2. Beta diversity maps along with elevation maps for six of the eight study sites: A) Barro Colorado Island, Panama; B) Korup, Cameroon; C) Pasoh, Penninsular Malaysia; D) Yasuni, Ecuador; E) La Planada, Colombia; and F) Sinharaja, Sri Lanka. Beta diversity and elevation maps for Huai Kha Kheng and Khao Chong, Thailand are in figure A.2. In elevation maps, the color scheme moves from dark green (low elevation) to white (high elevation).

E. La Planada
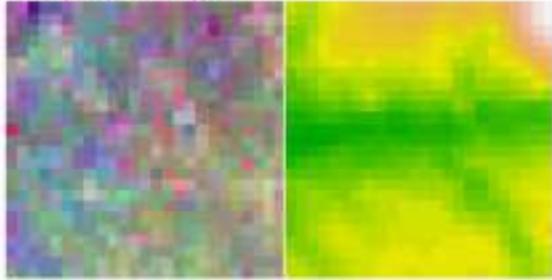
F. Sinharaja
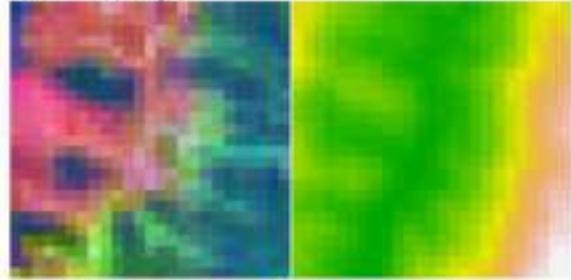
Figure 2.2. (Continued)

CHAPTER 3: A TAXONOMIC COMPARISON OF LOCAL HABITAT NICHES OF
TROPICAL TREES

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. I 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 generally showed greater niche overlap (i.e., more similar niches) than
non-congeneric pairs along both soil and topographic axes, though effects were significant for
only five sites based on Mantel tests. This analysis was unable to uncover evidence for similar
effects at the family level. The results suggest that local habitat niches of trees exhibit
phylogenetic signal, which may have important ramifications for the phylogenetic structure of
these communities.

INTRODUCTION

The assumption that closely related species tend to be ecologically similar 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 in historical
biogeography (Wiens & Donoghue 2004). The tendency for evolutionarily related taxa to share

similar traits is often termed 'phylogenetic signal' *sensu* Losos (2008). The presence of

phylogenetic signal in ecological traits has been supported by the congruency of morphological

phylogenies with those constructed from molecular data (Vamosi et al. 2009). More directly,

several studies have documented similarity of observed ecological niches among closely related

species, including the climatic niches of sister taxa in birds, mammals, and butterflies in Mexico

(Peterson et al. 1999), the hydrological, soil, and light niches of plants in central Europe

(Prinzing 2001), and reproductive traits and growth-forms of trees in Costa Rican forests

(Chazdon et al. 2003).

However, in an informal review of studies examining phylogenetic signal of ecological

traits, Losos (2008) cited several instances where no relationship between evolutionary

relatedness and ecological similarity was found, or where the relationship was negative. 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 the Floridian oak community, 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 contrasting results of these studies and others reviewed by

Losos (2008) caution against making *a priori* assumptions of phylogenetic signal.

Adaptation to specific soil and topographic conditions is known to be an important part of

the ecological niche of tropical tree species. Small-scale variation in soil type, soil resource

availability, and topography has been shown to influence tropical tree species distributions at the

local scale (< 1 km) (Chuyong et al. 2011, Davies et al. 2005, Gunatilleke et al. 2006, Harms et

al. 2001, John et al. 2007). For example, John et al. (2007) found that 30-40% of tree species are

non-randomly distributed with respect to soil resource gradients in three neotropical forest dynamics plots. Furthermore, species responses to both soil and topographic gradients have been shown to influence tropical forest community structure within these and several other plots (Legendre et al. 2009, Valencia et al. 2004, Baldeck et al. in review). However, it is unclear whether tree species are sorting independently along environmental gradients or whether evolutionary history influences the sorting of species along these gradients. If tree species' niches are found to be more similar or dissimilar among close relatives, this would have important consequences for the phylogenetic structure of these communities.

In this study, I examine the relationship between taxonomic rank and similarity in soil resource and topographic niches of co-occurring tropical tree species. My taxonomic approach 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, for which high-resolution phylogenies are not currently available. I compare soil and topographic niche similarity of species pairs belonging to the same genus or family to that of more distantly related species pairs.

I 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 are shown to have more similar habitat niches than more distant relatives, this would be indicative of phylogenetic signal in local habitat niches. The presence of phylogenetic signal in habitat niches indicates that adaptation to new environmental conditions occurs slowly over evolutionary timescales (Losos 2008). It would also suggest that habitat filtering via soil and topographic variation could contribute to phylogenetic clustering within tropical tree communities (Webb 2000). Alternatively, local habitat niches may be highly

evolutionarily labile, or may be convergent, which may contribute to the coexistence of closely related species within the same habitat (Silvertown et al. 2006a) and may cause phylogenetic evenness of tropical forest communities.

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; Huai Kha Khaeng and Khao Chong Thailand; Korup, Cameroon; La Planada, Colombia; Pasoh, Peninsular Malaysia; Sinharaja, Sri Lanka; and Yasuni, Ecuador (see table 3.1 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. Detailed descriptions of the study areas and forest dynamics plots are provided by Losos & 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 Inc., Massachusetts, 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 Ltd., Colorado, 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 NH4+ and NO3- extracted with 2M KCl and analyzed with an auto analyzer (OI FS 3000, OI Analytical, Texas, 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 as not all variables generated useable soil maps at all sites. At least five soil variables were included in the analysis for each of the study sites (table B.1).

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 analysis was performed to extract the main axes of soil nutrient variation for each site. The first two principal component (PC) axes were used in the subsequent analysis. Among the eight study sites, the first two principal components combined represented between 60-87% of the total variation present in the raw soil data (summary information on PC axes is provided in table B.1). Topographic variables were not

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converted to principal components, 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. The 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 principal component 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, I used 1-D as my 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 3.1). 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. Statistical significance was assessed by a two-tailed test ($\alpha = 0.025$ for each tail).

The use of two PC axes to represent soil resource variation and my taxonomic approach focusing on genus and family comparisons helped to reduce the total number of tests performed.

While the soil resource PC axes may be considered orthogonal (and the resulting Mantel tests independent), the topographic variables are highly related to one another, as well as to the soil resource PC axes. This resulted in several non-independent Mantel tests for each study site, with no clearly appropriate α level adjustment. Additionally, although Mantel tests have received some criticism for having low power (Harmon & Glor 2010), Mantel tests are useful and appropriate for these data, which occur naturally as distances among species both in the niche overlap and in genus and family co-membership.

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. Kembel & Hubbell 2006, Swenson et al. 2007, Webb 2000). 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. I 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. 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.

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 (figure 3.1A, table B.2A). Additionally, congneric species pairs showed significantly higher niche overlap than expected for at least one topographic variable at four study sites (figure 3.1B, table B.2B). 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 B.1). 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 B.3A). 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 B.3B). However, when topographic maps were swapped among sites, significantly higher niche overlap was found for Khao Chong (elevation and convexity; data not shown).

DISCUSSION

The presence of significantly higher habitat niche overlap among congeneric pairs of species in five of the eight study sites indicates that closely related tropical tree species often exhibit similar habitat preferences. 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.

In contrast to the results at the genus level, evidence for similar habitat niches at the family level is relatively weak. 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 indicate that the spatial structure of the environmental variables and the tree community may underlie observed niche overlap patterns at the family level. Additionally, a taxonomic 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, meaning that confamilial species pairs will vary more in their evolutionary divergence times than congeneric species pairs.

I 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. I found that congeneric species pairs had significantly higher niche overlap than expected for one soil PC axis at BCI. In a previous study, using a barcode phylogeny for the tree community on BCI from Kress et al. (2009), Schreeg et al. (2010), found no phylogeny-wide signal in mean soil values and ranges using an analysis of traits approach. I believe this discrepancy occurred because my analysis incorporates more information on species

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distributions across gradients and focuses on close relatives, where effects are most likely to be found. Thus, although taxonomic comparisons may break down at higher taxonomic ranks, I would argue that they 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 (i.e., Kress et al. 2009), it may soon be possible to obtain better estimates of the temporal extent of phylogenetic signal in species' ecological niches.

At the genus level, even though significance was only achieved in five of the sites, and only one or two environmental gradients per site, the majority of the effect sizes were positive, indicating an overall 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. Failure to detect significant effects at some sites may reflect limited power of the Mantel test. For example, the effect sizes for gradients at Huai Kha Kheng is similar in magnitude to significant effects at other sites; however, there were only 10 congeneric species pairs included in the analysis of Huai Kha Kheng, an order of magnitude fewer than for most other sites (table 3.1).

Understanding the degree to which ecological similarity is correlated with evolutionary relatedness is especially pertinent to the field of phylogenetic community ecology. 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). Phylogenetic signal links the evolutionary relatedness of species to their phenotypes, and through their phenotypes to the assembly processes that determine their distributions. 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. For

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example, Cavender-Bares et al. (2004) and Ackerly et al. (2006) both showed that differences in the phylogenetic signal and the adaptive significance of traits explained observed phylogenetic community structure patterns in their respective study systems. Using simulated communities with known assembly processes, Kraft et al. (2007) and Kembel (2009) showed that differences in phylogenetic signal of traits strongly affect the outcome of phylogenetic community structure tests.

Considering the results from all study sites taken together, the results suggest that very close relatives (i.e., congeners) tend to have more similar local habitat niches, though these similarities may be lost or undetectable at the family level. These results are indicative of phylogenetic signal in the habitat niches of tropical trees. 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. Kraft & Ackerly 2010, Swenson et al. 2007, Webb 2000). Of the study sites included in this analysis, phylogenetic community structure has only been thoroughly examined at BCI (Kembel & Hubbell 2006, Swenson et al. 2007, but see Kress et al. 2009) and Yasuni (Kraft & 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.

TABLES AND FIGURES

Table 3.1. Environmental and vegetation characteristics of the study sites.

Study site	Size (ha)	Forest type	Elev. (m)	Soil order	Species	Congen.	Confam.
BCI	50	Semidecid. lowland moist	120	Oxisol	143	70	409
Huai Kha Khaeng	50	Seasonal dry evergreen	549	Ultisol	74	10	137
Khao Chong	24	Mixed evergreen	120	Ultisol	202	185	857
Korup	50	Lowland evergreen	150	Oxisol/Ultisol	209	239	933
La Planada	25	Pluvial premontane	1796	Andisol	106	75	279
Pasoh	50	Lowland mixed dipterocarp	80	Ultisol/Entisol	417	1017	3725
Sinharaja	25	Mixed dipterocarp	424	Ultisol	126	126	365
Yasuni	50	Evergreen lowland wet	230	Ultisol	313	532	2012

Footnotes: Forest type taken from Losos & 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.
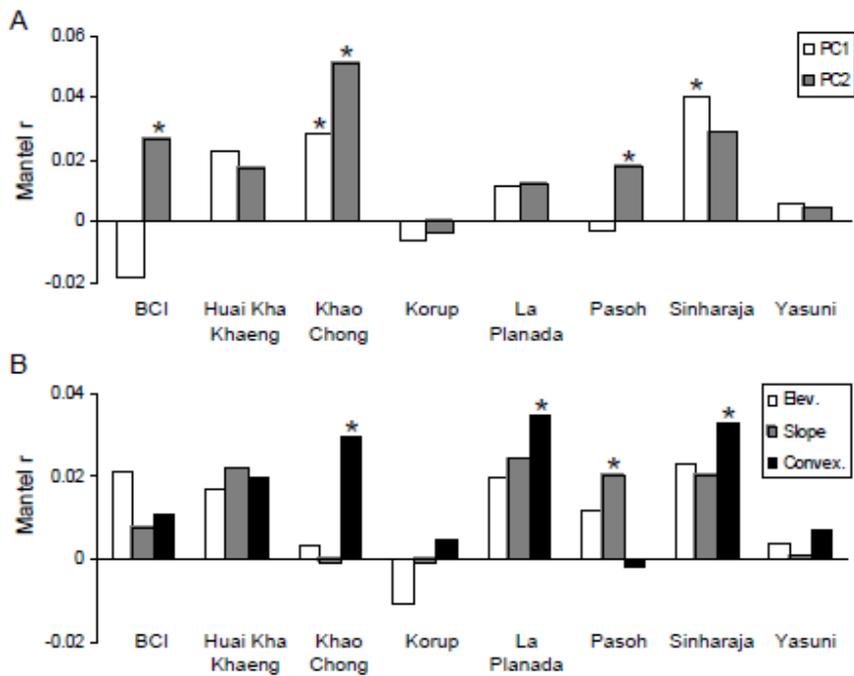
Figure 3.1. The Mantel r values for the genus level Mantel test test of (A) soil PC axes and (B) topographic variables. Positive values indicate that members of the same genus have higher niche overlap than members of different genera. Stars indicate significance ($\alpha = 0.025$ for each tail of a two-sided test).

CHAPTER 4: THE EFFECTS OF SOIL RESOURCES AND TOPOGRAPHY ON TROPICAL
FOREST PHYLOGENETIC COMMUNITY STRUCTURE

ABSTRACT

Previous research in tropical forests has demonstrated that local-scale heterogeneity in soil

resources and topography influences the distributions of many tree species, and that species' habitat

niches have important impacts on emergent community structure. Additionally, there is evidence that

the soil resource and topographic niches of tropical tree species often exhibit phylogenetic signal

(i.e., closely related species often have more similar niches). It may therefore be expected that the

phylogenetic structure of forest communities is shaped by habitat heterogeneity. Here I examine how

phylogenetic beta diversity (indicating the degree of phylogenetic similarity of two communities) is

related to soil resource and topographic variation within eight 24-50 ha tropical forest plots. Using

distance-based redundancy analysis, I found that phylogenetic beta diversity, expressed as either

nearest neighbor distance or mean pairwise distance, was significantly influenced by both soil and

topographic variation. Furthermore, patterns of nearest neighbor phylogenetic beta diversity are

consistent with previously observed patterns of niche similarity among congeneric species pairs:

sites where congeneric species have more similar habitat niches show a positive relationship

between habitat similarity and phylogenetic similarity of the tree community. These results

demonstrate that patterns of evolutionary lability in species' habitat niches determine the relationship

between habitat heterogeneity and the phylogenetic structure of these communities.

INTRODUCTION

Both ecological and evolutionary processes interact to determine the distribution and

abundance of species within a community. Species' ecological niches are play a central role in

determining community assembly, and these niches in turn are influenced by the evolution of

ecological traits that respond to environmental gradients. The evolutionary lability of such traits determines the phylogenetic signal in ecological niches, or the degree to which closely related species are more ecologically similar (Losos 2008). Phylogenetic community structure, or the pattern of relatedness among community members across space, has been shown to be directly related to the direction and degree of phylogenetic signal in species' ecological niches (Cavender-Bares et al. 2004, Ackerly 2006, Kraft et al. 2007, Kembel 2009). Therefore, it is expected that the strength of niche partitioning and the strength and direction of phylogenetic signal in species' ecological niches interact to determine the relationship between environmental variation and phylogenetic community structure. If niche partitioning along environmental gradients is absent, or if phylogenetic signal in species' habitat niches is absent, phylogenetic community structure should be unrelated to environmental variation.

Niche partitioning along environmental gradients has been shown to have important consequences for community structure at the local scale (<1 km). Topographic variation has been shown to influence the distributions of individual tree species and the overall structure of many tropical forest communities (Harms et al. 2001, Valencia et al. 2004, Gunatilleke et al. 2006, Legendre et al. 2009, Chuyong et al. 2011, chapter two). The role of soil resources in influencing species distributions (Davies et al. 2005, John et al. 2007) and community structure (chapter two) at the local-scale has come to light more recently as a result of fine-scale mapping of soil variables in eight large forest dynamics plots. A recent study that incorporated information on both soil resource and topographic variation within these plots (chapter two) demonstrated that niche partitioning along soil and topographic gradients has important emergent effects on tropical forest community structure.

Given the demonstrated importance of environmental niches within these forests, the evolutionary lability of traits that confer environmental niches may be expected to play a role in

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shaping the phylogenetic structure of these communities. Chapter three compared the taxonomic rank of species to their soil resource and topographic niches in the same set of eight forest plots. It was found that congeneric species pairs had more similar niches than more distantly related species along at least one environmental (soil resource or topographic) gradient in five of the study sites, which suggests the presence of phylogenetic signal in the local habitat niches of tropical trees. However, when examining pairs of species belonging to the same family, the results were relatively weak and prone to type I error, suggesting that phylogenetic signal in tree species' habitat niches may be restricted primarily to close relatives. Because habitat niches have been shown to be important in shaping these communities (chapter two), and evidence of phylogenetic signal in habitat niches is often present (chapter three), I expect the phylogenetic structure of these communities to be linked to environmental variation.

A phylogenetic approach to the analysis of community variation along environmental gradients can compliment analyses of compositional variation. Examining variation in community composition along environmental gradients can help resolve the community imprint resulting from habitat-based niche partitioning (Legendre 2009, chapter two). When the importance of niche partitioning has been assessed, a phylogenetic approach allows an assessment of the importance of phylogenetic signal in habitat niches in shaping phylogenetic community structure (Cavender-Bares et al. 2004, Cavender-Bares et al. 2009, Fine & Kembel 2010).

Phylogenetic beta diversity is a useful tool for examining phylogenetic community structure that compares the phylogenetic relatedness of two sample communities (Webb et al. 2008). In microbial ecology, phylogenetic beta diversity has proven useful for identifying important environmental gradients among microbial communities (reviewed in Faith et al. 2009). More recently, phylogenetic beta diversity has attracted attention of non-microbial ecologists

(Graham & Fine 2008) and has yielded useful insights into the evolutionary processes that contribute to animal and plant community structure. For example, Graham et al. (2009) examined patterns of phylogenetic beta diversity among hummingbird communities in the Ecuadorian Andes, highlighting the role of the Andes as a biogeographic barrier and as a strong environmental driver of phylogenetic community patterns in hummingbirds. Additionally, Fine & Kembel (2010) used phylogenetic beta diversity to elucidate the roles of habitat specialization, historical biogeographic and evolutionary processes in shaping regional phylogenetic patterns among trees in an Amazonian forest.

Here I examine the effect of phylogenetic signal in habitat niches on phylogenetic community structure by examining patterns of phylogenetic beta diversity along soil resource and topographic gradients within eight tropical forest plots. Because closely related species were generally found to have more similar habitat niches, I predict that areas with similar habitats will have more closely related tree communities. I examine phylogenetic beta diversity in two ways: as the mean nearest neighbor (phylogenetic) distance and mean pairwise (phylogenetic) distance among quadrats. These two measures of phylogenetic beta diversity may detect effects occurring at different depths in the phylogenetic tree – mean nearest neighbor distance detects relationships among close phylogenetic relatives while mean pairwise distances detects deep phylogenetic patterns. As evidence was found for phylogenetic signal of soil resource niches at the genus level, but not beyond, I expected that mean nearest neighbor distance to be more strongly related to environmental variation than mean pairwise distance. Furthermore, I expected the relationship between soil resource variation and phylogenetic beta diversity among study sites to reflect patterns of phylogenetic signal in soil resource niches observed in chapter three.

METHODS

Study sites

The tree data come from eight Center for Tropical Forest Science (CTFS) forest dynamics plots: Barro Colorado Island (BCI), Panama; Huai Kha Khaeng and Khao Chong Thailand; Korup, Cameroon; La Planada, Colombia; Pasoh, Peninsular Malaysia; Sinharaja, Sri Lanka; and Yasuni, Ecuador (Losos & Leigh 2004). All of the plots are either 24-25 or 50 ha in size. At each study site, all trees >1cm dbh have been mapped, measured, and identified to species.

Soil resource and topographic data

To create maps of soil resource concentrations, soil samples were taken every 40 or 50 m throughout each plot, and continuous maps of the soil variables were kriged to create estimates at the 20×20 m quadrat scale following the methods of John et al. (2007). The variables used vary by study site, but where available included the nitrogen mineralization rate, phosphorus, base cations (calcium, potassium and magnesium), boron, copper, iron, manganese, zinc, aluminum and pH. For a complete list of the variables included for each study site, see table 2.1.

Topographic variables were derived from elevation measurements made at each intersection of a 20×20 m grid throughout a plot. Mean elevation, slope, convexity, and aspect were each calculated for 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 of the corners of a quadrat at a time. Convexity was the elevation of a quadrat minus the average elevation of all immediate neighbor quadrats. Lastly, aspect was the direction of the steepest slope of a quadrat, and was calculated in ArcMap 9.3 (www.esri.com).

Phylogenetic beta diversity

A master phylogenetic tree was created by pooling species from all eight study sites and submitting this species list to the online tool Phylomatic (Webb & Donoghue 2005). Tree ferns, and the few species that were not identified to genus were left out of the species pool. This created a phylogenetic tree containing all species in all plots, the backbone of which was taken from the most recent Angiosperm Phylogeny Group classification (APGIII; www.mobot.org, accessed May 2011). This tree was assigned branch lengths according to the bladj algorithm of the community phylogenetic software Phylocom (Webb et al. 2008), which anchors certain nodes at fossil and molecular dates estimated by Wilkstrom et al. (2001) and evenly spaces intervening nodes. Phylogenies were created for each study site by pruning the dated master tree to contain only species from that study site, and the analysis for each study site was performed using its respective pruned tree.

Each study site was divided into 20×20 m quadrats and pairwise phylogenetic beta diversity indices were calculated for all quadrat pairs within a study site. Here, I use the two types of phylogenetic beta diversity established by Webb et al. (2008). The first, mean pairwise distance (betaMPD), expresses the mean pairwise phylogenetic distance between pairs of taxa between two samples. The second, mean nearest taxon distance (betaMNTD), expresses the mean phylogenetic distance between each taxon in the first sample and its nearest phylogenetic neighbor in the second sample and vice versa. Mean nearest taxon distance expresses the phylogenetic similarity between samples at the tips of the phylogenetic tree and may be interpreted as scaling with the frequency of finding close phylogenetic relatives between samples.

Because compositional beta diversity affects the values of betaMPD and betaMNTD among quadrats, observed values of betaMPD and betaMNTD were standardized with respect to

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expected values calculated under a null model. The null model randomizes the positions of species on the phylogeny, preserving the compositional beta diversity and species richness of the samples. The standardized versions of betaMPD and betaMNTD are termed betaNRI (net relatedness index) and betaNTI (nearest taxon index), respectively, and are the beta diversity analogs to the NRI and NTI metrics that are used for examining the phylogenetic structure of a single sample (Webb 2000). Randomizations were repeated 99 times and the following standardizations were performed:

$$betaNRI = -1 \times (Mean(betaMPD_{Random}) - betaMPD_{Observed}) / SD(betaMPD_{Random})$$
$$betaNTI = -1 \times (Mean(betaMNTD_{Random}) - betaMNTD_{Observed}) / SD(betaMNTD_{Random})$$

BetaNRI and betaNTI values were multiplied by -1, as shown above, to convert them to a dissimilarity measurement. Thus, positive values of betaNRI and betaNTI indicate that taxa are less closely related between quadrats and negative values indicate that taxa are more closely related. Note that this is the opposite of some previous uses of betaNRI and betaNTI (e.g. Fine & Kembel 2010).

Analysis

I first tested for the ability of the entire set of environmental variables (soil plus topographic variables) to explain phylogenetic community structure and subsequently tested soil and topographic variables separately. I tested whether the set of explanatory variables accounted for a significant amount of variation in the multivariate dispersion among quadrats given as phylogenetic beta diversity using distance-based canonical redundancy analysis (dbRDA; Legendre & Anderson 1999). Distance-based RDA works similarly to RDA; however, whereas an RDA of a community matrix preserves the Euclidian distances among samples, dbRDA allows the use of any distance measurement. In this analysis, the phylogenetic beta diversity

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indices were used as the distance measure among samples. In dbRDA, a principal coordinates

analysis is performed on the matrix of phylogenetic beta diversity among quadrats, and all

eigenfunctions with positive eigenvalues are retained as the quadrat coordinates. These

coordinates are then used as the response matrix in RDA. The significance of a set of

explanatory variables was tested using permutation of the phylogenetic beta diversity matrix 999

times, and was carried out in the program DISTLM (McArdle & Anderson 2001).

The use of the null model in the calculation of phylogenetic beta diversity among

quadrats controls for the effects of shared species among quadrats and, therefore, the effects of

species aggregation patterns caused by dispersal. However, it is possible that spatial

autocorrelation in the phylogenetic clustering or evenness of the community may cause

phylogenetic beta diversity to be influenced by geographic distance among quadrats. I therefore

tested for the effects of environmental differences on phylogenetic beta diversity, while

controlling for the effect of geographic distance using partial Mantel analysis. The distance

among quadrats along the first canonical axis from the dbRDA was used as the measure of

environmental dissimilarity in the partial Mantel analysis. The first canonical axes from the

dbRDA combines and weighs the environmental variables so as to explain the greatest amount of

multivariate dispersion among quadrats, and preliminary analysis showed that the distance along

the first canonical axis (as a measure of environmental distance) explained much more variation

in phylogenetic beta diversity than various combinations of all environmental variables weighted

equally. However, the goal was to test whether this environmental dissimilarity could still

explain phylogenetic beta diversity after the effect of the geographic distance among quadrats

was removed.

The phylogenetic structure of each study site was mapped according to each phylogenetic

beta diversity index following an adaptation of the methods of Thessler et al. (2005). Briefly, the

pairwise phylogenetic beta diversity matrices were subjected to nonmetric multidimensional scaling in three dimensional space. Then, the position of each quadrat on the three ordination axes was translated to color intensity of red, green, and blue. The color assigned to each quadrat represents its position in ordination space based on the phylogenetic relationships among quadrats, and quadrats of similar color are interpreted as containing more closely related species than quadrats of dissimilar colors. The quadrats were then mapped with their corresponding colors, and the entire map gives a summary of plot phylogenetic structure.

RESULTS

Maps of phylogenetic structure reveal broad spatial patterns in phylogenetic community structure within many of the study sites (Fig 4.1). All three variable sets – environmental, soil, and topographic – explained a significant amount of phylogenetic beta diversity at every site as tested by the dbRDA (table 4.1). The entire set of environmental variables explained 3.9-12% of variation when phylogenetic beta diversity was expressed as nearest neighbor distance, betaNTI, and 6-19% of variation when expressed as mean pairwise distance, betaNRI. Across study sites and different sets of explanatory variables, more variation was explained when phylogenetic beta diversity was expressed as mean pairwise distances than when expressed as nearest neighbor distances. In general, a greater proportion of variation was explained by soil resource variables than was explained by topographic variables.

Neither phylogenetic beta diversity index was consistently related to geographic distance across study sites (table 4.2), which is unsurprising given that the null model approach to calculating the indices of phylogenetic beta diversity control for the effects of aggregated species distributions. When the effects of environmental, soil, or topographic variables on phylogenetic beta diversity were tested using a distance matrix approach, the results were usually significant,

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but not always. Some loss of significance was expected given the lower power of Mantel tests as compared to the raw data approach (such as dbRDA) to detect an effect (Legendre & Legendre 1998, Harmon & Glor 2010). Importantly, the distance matrix approach revealed that in a few instances (Korup for betaNTI and Huai Kha Khaeng for betaNRI), the relationship between environmental dissimilarity and phylogenetic beta diversity is negative. This relationship was not revealed by the dbRDA as response matrices expressed as either similarities or dissimilarities produce the same result.

The majority of significant effects retained their significance after the effect of geographic distance was removed in the partial Mantel analysis. This indicates that, in the majority of cases, the effects of these environmental variables on the phylogenetic structure of the community operate independently of spatial autocorrelation that may be caused by aggregated species distributions or spatial autocorrelation in the phylogenetic clustering or evenness of the tree community.

DISCUSSION

Soil resource and topographic variation have previously been shown to influence the distributions of individual species as well as shape tree community compositional variation at local scales (e.g., Davies et al. 2005,Valencia et al. 2004, Gunatilleke et al. 2006, John et al. 2007, Chuyong et al. 2010, chapter two). Furthermore, evidence of phylogenetic signal in soil resource and topographic niches has been found in many of the tropical forest communities examined in this study (chapter three). It was therefore expected that environmental variation would also affect the phylogenetic community structure of these forests, at least at the sites where phylogenetic signal in soil resource niches is observed. Because phylogenetic signal in chapter two was interpreted as being restricted to the level of very close phylogenetic relatives,

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(i.e. congeners), I expected phylogenetic beta diversity expressed as nearest neighbor distance to be most influenced by soil resource variation. High correspondence between these two measurements was expected because a member of the same genus is the nearest possible phylogenetic neighbor given the resolution of phylogenies created using Phylomatic.

In fact, both soil resource and topographic variation were found to significantly influence both types of phylogenetic beta diversity of all communities studied. The high significance of all environmental data sets in explaining phylogenetic beta diversity was surely influenced by the increased power of raw-data approaches (e.g. dbRDA) as compared to distance matrix approaches (the Mantel approach of chapter three) and the ability of the approach to use all available community data rather than a subset of the species occurring within a site. It was a bit surprising that phylogenetic beta diversity was generally more strongly related to environmental variation when expressed as mean pairwise distance than when expressed as nearest neighbor distance, the opposite of my expectation. However, the prediction that nearest neighbor distance would be more strongly related to environmental gradients was made in the absence of any evidence for phylogenetic signal at levels of relatedness greater than congeneric pairs. Additionally, previous examination of phylogenetic signal in habitat niches of trees did not lead to a strong prediction of how mean pairwise phylogenetic beta diversity would be related to the environment, as family level phylogenetic signal does not correspond to mean pairwise distances within these phylogenies.

When the relationships between environmental, soil, or topographic dissimilarity and indices of phylogenetic beta diversity were examined, the orientations of these relationships were revealed. In general, phylogenetic beta diversity was positively related to environmental, soil resource, or topographic dissimilarity. This pattern indicates that areas with more similar environments are likely to contain more closely related tree communities – the expected result

when species exhibit phylogenetic signal in their environmental niches. However, neutral or negative relationships were found at a few study sites. A neutral or negative relationship could arise from one or both of two things: environmental niches may not be important at that study site or environmental niches may not exhibit phylogenetic signal. A negative relationship between environmental dissimilarity and phylogenetic beta diversity could arise as a result of convergent evolution in species' environmental niches. The results of chapter two demonstrated that environmental niches are important for shaping community structure at these sites; therefore, the explanation is likely to lie in the pattern of phylogenetic signal in species' environmental niches.

The across-site pattern in the effects of soil resource dissimilarity on betaNTI was consistent with the observed phylogenetic signal in habitat niches from chapter three. In chapter three, congeneric species were generally found to have more similar soil resource and topographic niches, with the main exception of the Korup study site, though statistically significant results were only found for five study sites. The results of the congeneric test of phylogenetic signal in soil resource niches are shown alongside the results of the partial Mantel test for the effect of soil resource dissimilarity on betaNTI in figure 4.2. The congruence of the results of the two tests supports the hypothesis that phylogenetic beta diversity, expressed as nearest neighbor distance, is influenced by habitat, with the effect contingent on the presence of phylogenetic signal in habitat niches.

For example, Korup exhibited a negative relationship between soil dissimilarity and betaNTI, suggesting convergent evolution for soil resource niches at Korup. It has been previously demonstrated that soil resource variation strongly influences compositional community structure at Korup, and thus soil resource niches are important for structuring this community (chapter two). In fact, there is some support for convergent evolution of soil resource

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niches, or at least the lack of phylogenetic signal in soil resource niches, from the test of soil

resource niche overlap among congeners in chapter three (figure 4.2). Additionally, a negative

relationship was found between topographic dissimilarity and betaNRI at Huai Kha Khaeng

(likely causing the negative relationship between environmental dissimilarity and betaNRI at this

site) and Korup. These relationships also suggest convergent evolution of topographic niches, but

at a much deeper level of the phylogeny.

By examining patterns of phylogenetic beta diversity in relation to soil resource variation,

I was able to uncover the role of soil resources and topography in shaping phylogenetic

community structure. The examination of phylogenetic community structure through the analysis

of patterns of phylogenetic beta diversity differs significantly from localized methods that

examine the relative relatedness of species occurring in the same quadrat. My examination of

phylogenetic beta diversity highlights patterns of relatedness that are present at the across-plot

scale (< 1 km), while localized measures of phylogenetic clustering and evenness such as NRI

and NTI (Webb et al. 2002) generally examine patterns within much smaller areas (generally 25

m^2-1 ha quadrats) with emphasis on determining the relative importance of habitat filtering and

competitive effects at these scales (e.g. Webb et al. 2000, Cavender-Bares et al. 2006, Kembel &

Hubbell 2006). These results do not indicate whether phylogenetic clustering or evenness is

present at within localized areas, or give any indication as to the importance of interspecific

competition. However, in sites where betaNTI is positively related to soil dissimilarity, this

suggests a combination of habitat filtering and phylogenetic signal in environmental niches that

may be expressed as phylogenetic clustering of close relatives at smaller scales.

The strong influence of soil resources and topography on tree community compositional

structure at spatial scales < 1 km reveals the importance of small-scale environmental variation

and species' local habitat niches as drivers of local community structure. The present study puts

these observations into an evolutionary context, tying the phylogenetic signal observed in habitat niches of trees (chapter three) to outcomes of phylogenetic community structure. The relationships between soil dissimilarity and phylogenetic beta diversity were consistent with the patterns of phylogenetic signal present among congeners observed in chapter three. While habitat niches are found to be highly important in nearly all forest communities, patterns of phylogenetic signal may vary among communities. Overall, soil resource and topographic variation play an important role in shaping phylogenetic community structure, and the nature of this role can be better understood by first understanding differences in the importance of niche partitioning and the nature of phylogenetic signal among communities.

TABLES AND FIGURES

Table 4.1. The proportion of variation explained (R^2) by each of the three sets of variables. All effects tested as highly significant (P = 0.001) based on random permutation of the data.

	betaNTI			betaNRI		
	Env.	Soil	Topo.	Env.	Soil	Topo.
BCI	0.056	0.044	0.018	0.094	0.077	0.037
Huai Kha Khaeng	0.052	0.037	0.019	0.079	0.059	0.034
Khao Chong	0.116	0.088	0.042	0.143	0.105	0.073
Korup	0.048	0.035	0.023	0.119	0.094	0.077
La Planada	0.074	0.055	0.021	0.110	0.084	0.036
Pasoh	0.039	0.028	0.014	0.063	0.049	0.026
Sinharaja	0.088	0.051	0.052	0.190	0.111	0.139
Yasuni	0.047	0.034	0.016	0.090	0.066	0.041

Table 4.2. Mantel tests for the effects (Mantel r values) of environmental dissimilarity on betaNTI (A) and betaNRI (B). Mantel r values shown in bold have P<0.025. The first four columns show the results of ordinary two-way Mantel tests of the correlation between each explanatory matrix (calculated as the pairwise difference along the first canonical axis (CA1) of the dbRDA) and phylogenetic beta diversity. The last three columns show the partial Mantel correlation between environmental dissimilarity and phylogenetic beta diversity after controlling for the effect of geographic distance among quadrats.

A) BetaNTI

		Two-way Mantel				Partial Mantel		
Study site	Geog.	Env. CA1	Soil CA1	Topo. CA1		Env. CA1	Soil CA1	Topo. CA1
BCI	0.00	**0.13**	**0.12**	**0.04**		**0.13**	**0.12**	**0.04**
Huai Kha Khaeng	0.01	**0.13**	**0.06**	**0.13**		**0.13**	**0.06**	**0.12**
Khao Chong	**0.11**	0.38	0.34	0.13		0.37	0.33	0.11
Korup	-0.02	-0.01	**-0.03**	-0.01		0.00	**-0.03**	0.00
La Planada	**-0.06**	0.07	0.05	-0.03		**0.08**	0.06	-0.02
Pasoh	**0.05**	0.14	0.11	0.12		0.13	0.10	0.11
Sinharaja	**0.07**	0.27	0.15	0.20		0.26	0.14	0.18
Yasuni	**-0.04**	0.09	0.09	0.05		0.09	0.09	0.06

B) BetaNRI

		Two-way Mantel				Partial Mantel		
Study site	Geog.	Env. CA1	Soil CA1	Topo. CA1		Env. CA1	Soil CA1	Topo. CA1
BCI	**0.08**	**0.18**	**0.15**	**0.15**		**0.18**	**0.15**	**0.14**
Huai Kha Khaeng	**-0.07**	**-0.09**	**-0.05**	**-0.14**		**-0.06**	-0.01	**-0.13**
Khao Chong	0.01	0.04	**0.06**	-0.01		0.04	**0.05**	-0.01
Korup	**0.10**	**0.08**	**0.07**	**0.05**		0.01	0.00	**-0.03**
La Planada	**0.05**	**0.12**	**0.10**	0.05		**0.11**	**0.09**	0.05
Pasoh	**0.05**	**0.08**	**0.09**	**0.04**		**0.08**	**0.09**	0.03
Sinharaja	0.03	**0.26**	**0.11**	**0.20**		**0.27**	**0.11**	**0.21**
Yasuni	**0.04**	**0.23**	**0.21**	**0.09**		**0.23**	**0.21**	**0.09**
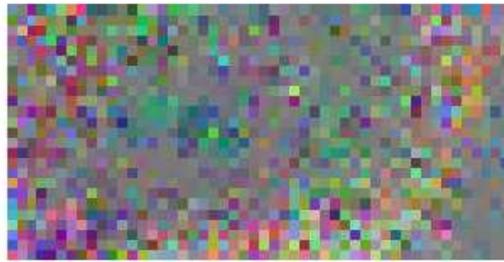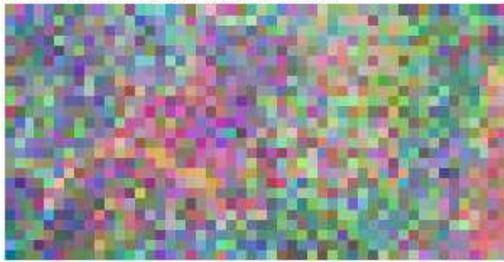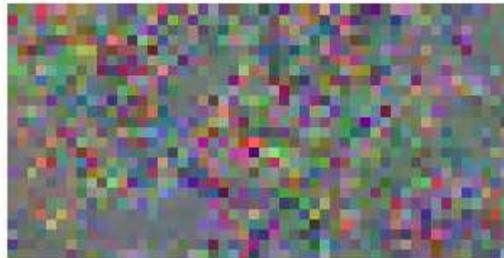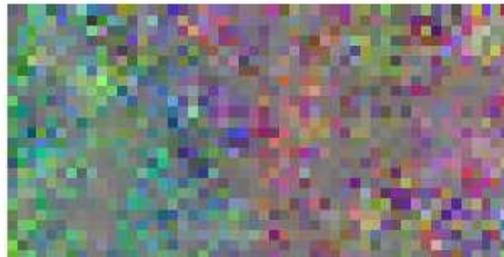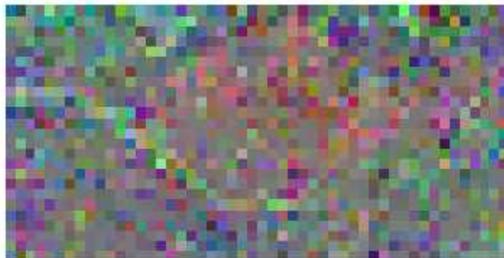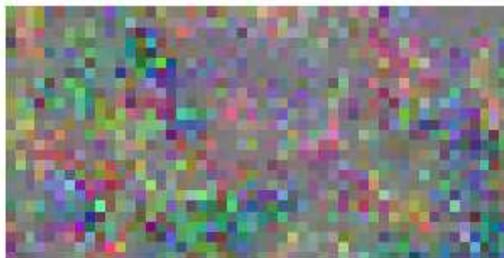
Figure 4.1. Maps of phylogenetic community structure for each of the eight plots, created from phylogenetic beta diversity matrices in the method of Thessler et al. (2005). Maps shown on the left side are based on betaNTI and maps on the right side are based on betaNRI.

F. Khao Chong
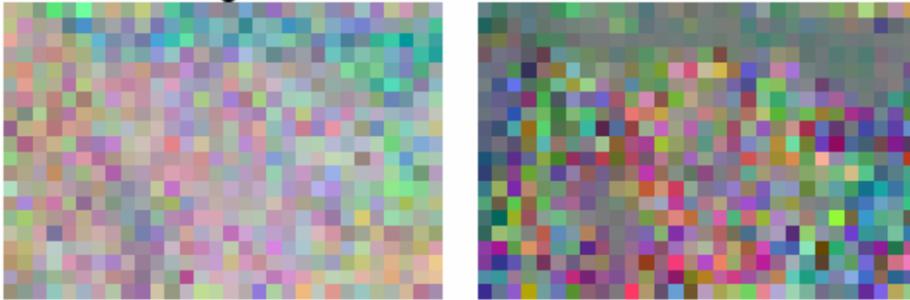
G. La Planada
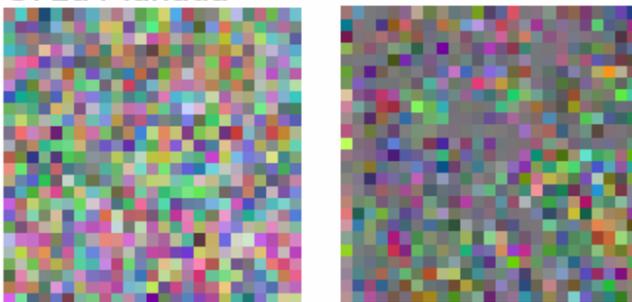
H. Sinharaja
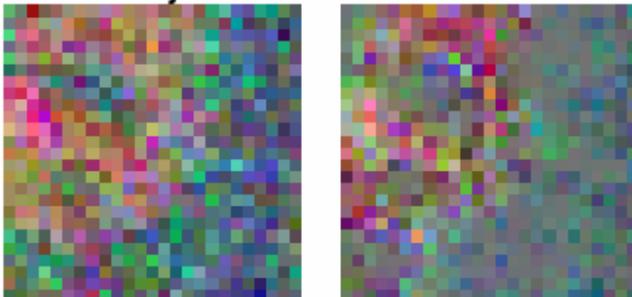
Figure 4.1. (Continued)
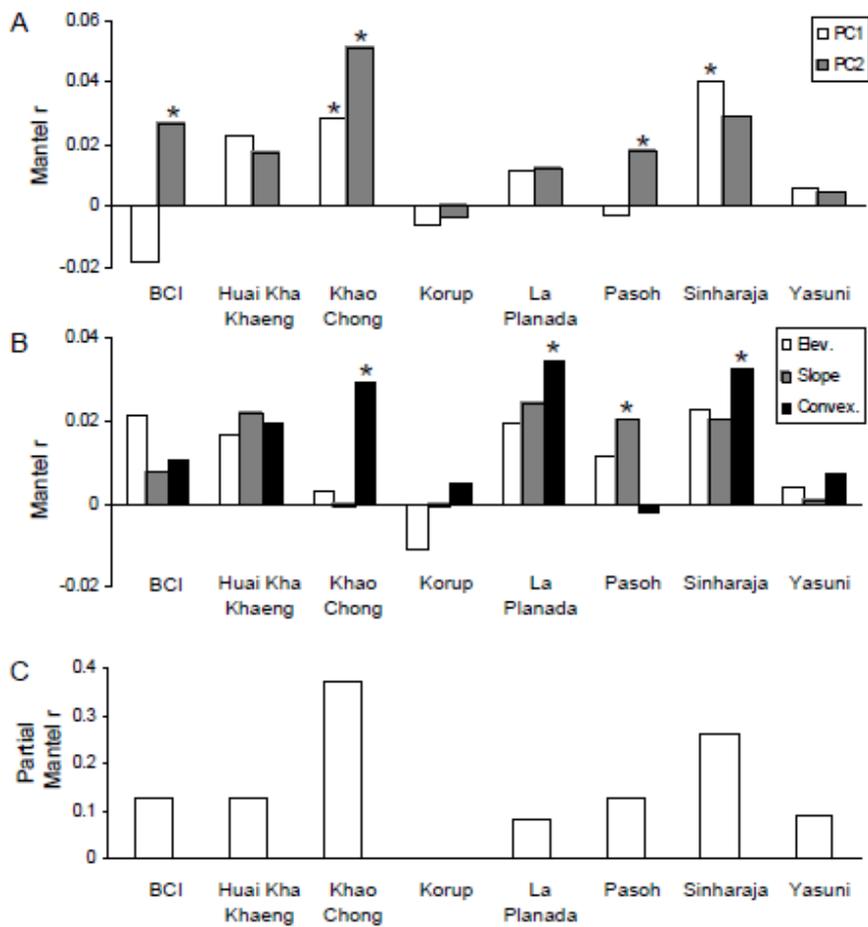
Figure 4.2. Comparison of Mantel results between the test for greater soil resource (A) and topography (B) niche overlap among congeneric species of chapter three and (C) the partial Mantel correlation between environmental (soil plus topography) dissimilarity on betaNTI (table 4.2A).

CHAPTER 5: INTRASPECIFIC VARIATION IN FOLIAR NUTRIENTS ALONG SOIL RESOURCE GRADIENTS

ABSTRACT

Leaf chemistry is an important determinant of ecosystem processes, and has been shown to vary within forests along soil nutrient gradients. However, previous investigations of variation in leaf chemistry have not performed enough within-species sampling to determine whether variation in leaf chemistry is driven by species turnover or intraspecific responses to soil resource gradients. This study investigates the stoichiometric responses of tree species to six key soil resource gradients (N, P, Ca, K, Mg, and Mn) that vary from six to over 50 fold for phosphorus and cations. I examined the within-species relationship between foliar and soil nutrients for 15 species growing in a tropical forest in Panama. Evidence for relationships between foliar and soil nutrients within a species was weak: with one exception, there were no significant relationships between soil nutrient concentration and foliar nutrients for any given species $\times$ nutrient combination. However, overall results suggest that weak intraspecific relationships may exist for P and K. Differences within species, even growing in very different soil resource conditions, were very small compared with differences among species: intraspecific variation made up less than 3.5% of total sample variation in any given nutrient, and a linear discriminant analysis based on only seven foliar nutrients was able to successfully classify 80% of leaf samples to species. These results indicate that species' internal stoichiometry is highly conserved, suggesting that spatial variation in leaf chemistry is more driven by species compositional turnover than by intraspecific differences in foliar nutrients.

INTRODUCTION

Leaf chemical properties are important determinants and indicators of plant physiology and biogeochemical processes in terrestrial ecosystems (Vitousek 1982, Aerts & Chapin 2000, Hedin 2004). However, little is known about the spatial variation of leaf chemistry in tropical forests. The little information that exists comes from sparse field-based data sets focused on just a few elements, usually nitrogen (N) and phosphorus (P), and from just a handful of tropical forests sites globally (Townsend et al. 2007). This research also generally focuses on broad sampling of foliar nutrients at ecosystem levels across different tropical forests (e.g. Vitousek 2004, Townsend et al. 2007, Asner & Martin 2011).

A major insight arising from these studies is that ecosystem-level leaf chemistry varies along soil resource gradients in tropical forests. For example, Townsend et al. (2007) found differences in foliar nutrient concentrations in tropical forests on different soil types, with higher foliar N:P ratios among trees growing on P-impoverished Ultisols and Oxisols compared to more fertile soils. These differences in N:P ratios were the result of lower foliar P concentrations in trees growing in the P-poor Ultisols and Oxisols, whereas foliar N was relatively constant among study sites. Additionally, Asner & Martin (2011) found that species from higher fertility Inceptosols sites had higher P and base cation concentrations than species from low fertility Ultisols in the Amazon. However, neither study sampled widely within any one species, and the sampling designs were not able to tease apart whether differences in leaf chemistry between soil types was a result of species turnover or intraspecific responses to soil resources. Therefore, the relative contribution of intra- and inter-specific variation in leaf chemical properties, as well as how these sources of variation are affected by soil fertility, are poorly understood.

Previous work by John et al. (2007) has shown that *c*. 30-40% of tropical tree species are nonrandomly distributed with respect to soil nutrient concentrations at the local scale (< 1 km) in

three neotropical forest dynamics plots (25-50 ha), while subsequent research has shown this to be true in several other paleotropical forest plots (Baldeck, unpublished data). Furthermore, these species-soil associations have emergent effects at the community level: chapter two showed that soil resource variation affects whole tree community structure within these same plots. Soil resources are known to also affect tree species distributions and species turnover at meso-, landscape, and regional scales (Swaine 1996, Clark et al. 1998, Potts et al. 2002, Phillips et al. 2003, Fine et al. 2005, Paoli et al. 2006). Soil resources clearly play a critical role in shaping the distributions of individual species and the overall community structure of tropical forests.

Because there is high species turnover along soil gradients in tropical forests, the species that are sampled are usually different for the different soil types. Extensive sampling of leaf nutrients within a single species along soil resource gradients has not been conducted, so the intraspecific responses of foliar nutrients to soil resource gradients is not known. If species are found to be have highly conserved leaf nutrient profiles along soil fertility gradients, this would indicate that spatial variation in leaf nutrients is driven by species turnover rather than by plastic responses to soil resources within a species. If however, species are found to have highly plastic leaf nutrient profiles, this would indicate that spatial variation in leaf nutrients is also driven by intraspecific responses to soil resource gradients.

In this study I investigate the within-species relationship between soil nutrient abundance and foliar nutrients. I conducted extensive within-species leaf sampling along six important soil nutrient gradients for 15 common species on Barro Colorado Island (BCI), Panama. Leaf samples were taken along soil nutrient concentration gradients that varied up to 20 fold for phosphorus, and up to 14 fold for major base cations. John et al. (2007) demonstrated that tree species distributions are affected by soil resource availability at the spatial scales and levels of

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soil resource abundance and heterogeneity found within the BCI 50-ha plot. Therefore, the soil

nutrient gradients covered in this study are ecologically relevant. Here I ask whether foliar

nutrients are influenced by soil nutrients within a species. I expected that intraspecific foliar P is

related to soil P concentration, as tropical forests are generally considered to be P-limited

(Vitousek 2004, McGroddy et al. 2004), BCI is located on P-poor Oxisols, and ecosystem-level

foliar P has been shown to be responsive to soil P availability (Townsend et al. 2007).

METHODS

Study Site and soil nutrient maps

Leaves were collected from within the 50-ha forest dynamics plot of Barro Colorado

Island (BCI), Panama. BCI is a semideciduous moist forest that receives 2,600 mm of rain

annually (Losos & Leigh 2004). The 50-ha plot contains approximately 300 tree species. The

soils at BCI are mostly well weathered Oxisols that are relatively high in cations and poor in

phosphorus compared to other tropical plots from the Center for Tropical Forest Science network

(Dalling, unpublished data).

Soil samples of the top 10 cm of mineral soil were taken and measured for their

concentrations of P, Ca, K, Mg, Mn, and N mineralization. Samples were taken at the

intersections of a 50 m grid with additional samples taken near alternate grid points to estimate

fine scale variation in soil variables. Non-nitrogen elements were extracted with Mehlich-III

solution and analyzed on an atomic emission-inductively coupled plasma (AE-ICP, Perkin Elmer

Inc., Massachusetts, USA). Nitrogen was extracted as NH_4^+ and NO_3^- with 2M KCl and analyzed

with an auto-analyzer (OI FS 3000, OI Analytical, Texas, USA). 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. Complete soil maps for each nutrient were created for the entire

plot by kriging. The kriged values for each 20x20 quadrat within the 50-ha plot are used in this study. A more detailed description of the soil sampling methods and kriging can be found in John et al. (2007).

Leaf Chemistry

Leaf samples were collected from 15 common species in the 50-ha plot: *Alseis blackiana, Chrysophyllum argenteum, Chrysophyllum cainito, Garcinia intermedia, Guarea sp., Guarea guidonia, Hirtella triandra, Protium panamense, Protium tenuifolium, Quararibea asterolepis, Swartzia simplex var. grandiflora, Swartzia simplex var. ochnacea, Tetragastris panamensis, Trichilia pallida,* and *Trichilia tuberculata*. These species were chosen because they are among the most common species of the BCI 50-ha plot, they represent a variety of different families, and contain five congeneric species pairs which show contrasting soil associations (table 5.1). Twenty-seven individuals of each species were sampled for analysis of intraspecific variation in foliar chemistry.

For each species, sampled individuals were selected to maximize variation along soil nutrient gradients. Exact ranges of soil nutrient abundances vary by species, but on average ranged from 344 – 4603 ppm dry weight for Ca, 60 – 396 ppm for K, 58 – 826 ppm for Mg, 13 – 719 ppm for Mn, 0.37 – 7.9 ppm for P, and -6.3 – 46 ppm for N mineralization rate. These nutrient ranges capture most of the range of soil nutrient concentrations for the 50-plot. Leaf samples were collected from June to August, 2006. Leaves were collected with a pruning pole, with a maximum height of 10m. Due to the height constraints imposed by the pruning pole, only juvenile trees (~3-8 cm dbh in 2005 census) were sampled and only shade leaves were collected. Each individual was sampled by making three or more subsamples at different locations, and selecting an equal amount of leaf material from each subsample. All leaf material collected from

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an individual tree was combined to make a composite sample. Only mature leaves with little or no visible damage were included in the sample.

Foliar material was oven dried for a minimum of 48 hours at 60°C, pulverized in a Kleco ball mill, then digested in concentrated HNO_3 acid at 100^oC for 22 minutes in a MARS microwave digester (CEM Co.). The concentrations of P, Ca, K, Mg, and Mn were measured with an inductively coupled plasma optical emission spectrometer (ICP-OES, Perkin Elmer Optima 2000). Total foliar nitrogen and carbon were analyzed on a CHN analyzer.

I tested for the correlation between soil nutrients and foliar nutrients within each species for the six nutrient gradients. The proportion of total sample variation that was attributed to intraspecific variation was quantified as the mean squared error among samples of the same species divided by the total mean squared error. To test for the ability of foliar chemical profiles to differentiate among species, a linear discriminant analysis was performed on leaf N, C, P, Ca, K, Mg, and Mn. Linear discriminant analysis was performed using the 'MASS' package of the R programming language.

RESULTS

Leaf nutrients and N:P ratios varied strongly among species (table 5.2). With only a few exceptions, leaf nutrients were not significantly related to soil nutrients for the nutrient gradients tested (table 5.3). There were four instances where the correlation between soil resource abundance and leaf nutrient concentration was significant at an alpha level of 0.01 (shown in bold in table 5.3). However, if a Bonferroni correction is applied to the total of 90 correlation tests performed, the alpha level decreases to 0.0005. Using this alpha, only the correlation between soil and leaf phosphorus for *Hirtella triandra* remains significant (P<0.0004). On

average, correlations between soil and foliar nutrients were greatest for K (average r value ~0.2) and P (average r value ~0.16).

Intraspecific variation in foliar nutrients was small compared to interspecific variation: within-species variation made up 0.05 – 3.1% of the total variation among samples for all seven measured leaf nutrients. Linear discriminant analysis was able to correctly classify 80% of leaf samples based only on N, C, P, Ca, K, Mg, and Mn. Clear separation of several species can be observed based on a plot of leaf samples against the first two discriminant axes, especially *Garcinia intermedia*, *Hirtella triandra*, *Alseis blackiana*, and *Tetragastris panamensis* (figure 5.1). Forty-three percent of misclassification errors were between members of the same genus, and many of these errors were between the two varieties of Swartzia. Excluding the two Swartzia varieties, the rate of correct classification by linear discriminant analysis increases to 83%. Species-specific N:P ratios ranged from a low of 15.5 to a high of 35.5. Species' average N:P ratios were consistently greater than 16, which is indicative that P is more limiting that N on Barro Colorado Island.

DISCUSSION

Low intraspecific variation in foliar nutrients as compared to the total variation (< 3%), and the ability of the linear discriminant analysis to correctly classify leaves to species in 80% of cases based on leaf nutrient data, both support the conclusion that species' foliar nutrient profiles are highly conserved. Although sampling was constricted to the soil nutrient gradients found within the BCI 50-ha plot, it has previously been shown that these soil resource gradients influence individual species distributions and play an important role in shaping overall community structure. As these soil resource gradients are responsible for species turnover within the 50-ha plot, they were expected to be long enough to potentiate intraspecific responses in

foliar nutrients. Intraspecific foliar sampling must inevitably cover shorter soil nutrient gradients than interspecific or ecosystem level foliar sampling, because the presence of community turnover precludes intraspecific sampling over long gradients for most species.

Evidence for intraspecific relationships between soil and foliar nutrients is weak, at least at the sampling intensity used in this study. Power analyses based on the results of this study indicate that the power of a correlation test for any given species × nutrient combination is quite low. For example, if the true population r value is taken as the mean r value between soil and foliar K for all species (~0.2), a correlation test of only 27 individuals along a soil gradient has a power of ~0.17 (at $\alpha = 0.05$). Conversely, if we were to design a sampling scheme for a test with a power of 0.8 given the same population r value, we would need to sample ~200 individuals. This suggests a far greater sampling intensity than is practical for most species in order to detect an effect that is likely to be small (r ~0.2 on average for K and ~0.16 on average for P).

Although evidence for an intraspecific correlation between soil and foliar nutrients for any given species × nutrient combination is weak, examining the results across all nutrients and species together gives the impression that there may be important differences among nutrients in the potential to find such relationships. The average r value for K is ~0.2 and that of P is ~0.16, which contrasts to the average r values of N, Ca, Mg, and Mg, which are all very close to zero or negative (Table 5.3). This suggests that if intraspecific foliar values are related to soil nutrient availability, this relationship is likely to be restricted to a few important elements at a given site.

Although intraspecific relationships between soil and foliar P have not been explored previously, Townsend et al. (2007) found differences in foliar P related to seasonal changes in soil P availability within individual trees in Costa Rica. The responses of individual tree foliar P to seasonal changes in soil P availability, in addition to ecosystem-level correlations between foliar and soil P, suggest that conspecific individuals growing along a P gradient should show

correlated foliar P. Though foliar and soil P were not significantly correlated in this study, with one exception, the majority of these correlations are positive (table 5.3). This suggests that a weak relationship between soil P and intraspecific foliar P may exist. However, much more intensive sampling within a species along soil P gradients would be needed to detect such a relationship.

Foliar N:P ratios are regarded as an index of plant nutrient status that provides insight into soil nutrient limitation and ecosystem biogeochemical cycling (Aerts & Chapin 2000). Specifically, foliar N:P ratios less than 14 are considered to reflect N limitation and ratios greater than 16 are considered to reflect P limitation (values 14-16 reflect N and P co-limitation) (Koerselmann & Mueleman 1996, Aerts & Chapin 2000, Reich & Oleksyn 2004). The species-specific foliar N:P ratios found in this study varied widely among species. All species-specific N:P ratios were greater than 16 with the exception of one species, *Quararibea asterolepis*. In general, foliar N:P values indicate P limitation over N limitation for BCI. However, the considerable variability in N:P ratios among species highlights the possibility that different species may be differentially limited within the same ecosystem (Townsend et al. 2008).

My results suggest that variation in leaf chemistry across space may be more influenced by interspecific differences in leaf chemical profiles than by intraspecific variation. Previous studies of variation in leaf traits or of variation in leaf traits in relation to soil properties has focused on broad sampling of many species, with few replicates within a species (e.g. Townsend et al. 2007, Asner & Martin 2011). The results presented here generally support the robustness of this sampling strategy as variation within a species was found to be much smaller than variation among species, even when individuals within a species were sampled across heterogeneous soil resource environments.

The lack of strong evidence for intraspecific changes in foliar nutrients along soil nutrient gradients also suggests that interspecific differences in foliar chemistry drives ecosystem-level relationships between soil nutrients and foliar nutrients. However, if this is true then species-specific foliar nutrient profiles must be correlated with their soil resource associations. Broad sampling of foliar chemistry across many species, as well as linking these foliar chemical data species' distributions with respect to soil resources is needed to explore the relative roles of intra- and interspecific variation in foliar nutrients. Across-species sampling within the Center for Tropical Forest Science (CTFS) plots, where the soil resource associations of most species has already been quantified (John et al. 2007, Baldeck, unpublished data) would be one good way to test this idea. Linking species-specific foliar chemistry to species' soil resource associations would go a long way to establishing a mechanistic understanding of observed species-soil associations in the tropics. Furthermore, species-specific foliar chemical profiles could be tested for the presence of phylogenetic signal, which may contribute to a mechanistic understanding of phylogenetic signal in species' soil resource niches (chapter three) and the influence of soil resources on phylogenetic community structure (chapter four).

TABLES AND FIGURES

Table 5.1. Species included in study, their family, and associations with soil nutrients as determined by John et al. (2007). Plus signs indicate that a species has been found to have a positive association with concentrations of that nutrient in the soil, and minus signs indicate negative associations.

Species	Family	Nmin	P	Ca	K	Mg	Mn
Alseis blackiana	Rubiaceae	-			-		
Chrysophyllum argenteum	Sapotaceae		-				+
Chrysophyllum cainito	Sapotaceae		+				
Garcinia intermedia	Clusiaceae	+					
Guarea sp.	Meliaceae						
Guarea guidonia	Meliaceae	+		+	+		
Hirtella triandra	Chrysobalanaceae	+	-	+	+	+	
Protium panamense	Burseraceae	-	-				
Protium tenuifolium	Burseraceae	+	-	+	+	+	
Quararibea asterolepis	Bombacaceae						
Swartzia sim. grandiflora	Fabaceae						
Swartzia sim. ochnacea	Fabaceae		-	+		+	
Tetragastris panamensis	Burseraceae	-					
Trichilia pallida	Meliaceae			-	-	-	-
Trichilia tuberculata	Meliaceae						

Table 5.2. The mean foliar nutrient concentrations and N:P ratio by species, the within-species coefficient of variation is given in parentheses. The values for C and N reported as percent, for other elements reported in ppm.

Species	C (%)	N (%)	P (ppm)	Ca (ppm)	K (ppm)	Mg (ppm)	N:P
Alseis blackiana	45.8(0.02)	4.68(0.10)	1787(0.22)	11460(0.34)	20465(0.25)	4171(0.29)	32.9(1.16)
Chrysophyllum argenteum	45.1(0.04)	2.10(0.10)	874(0.13)	19170(0.25)	10386(0.26)	3372(0.37)	24.3(0.14)
Chrysophyllum cainito	46.1(0.02)	2.19(0.07)	965(0.11)	17170(0.21)	9959(0.26)	2745(0.23)	22.9(0.10)
Garcinia intermedia	50.3(0.02)	1.54(0.07)	886(0.12)	8014(0.21)	10577(0.16)	1573(0.19)	17.7(0.16)
Guarea guidonia	46.9(0.02)	3.06(0.07)	1651(0.13)	13059(0.36)	15208(0.25)	4199(0.22)	18.7(0.11)
Guarea sp.	47.8(0.02)	2.91(0.08)	1412(0.10)	14933(0.24)	16890(0.17)	3106(0.22)	20.8(0.11)
Hirtella triandra	41.9(0.04)	1.93(0.07)	849(0.13)	9427(0.19)	9158(0.27)	3658(0.14)	23.1(0.12)
Protium panamense	46.1(0.02)	2.16(0.08)	1086(0.22)	5352(0.45)	9053(0.40)	1973(0.17)	20.5(0.16)
Protium tenuifolium	43.2(0.02)	2.01(0.09)	1012(0.15)	17339(0.23)	11311(0.28)	2434(0.13)	20.2(0.13)
Quararibea asterolepis	42.8(0.02)	2.54(0.08)	1684(0.16)	12790(0.31)	22490(0.22)	3699(0.24)	15.5(0.19)
Swartzia sim. grandiflora	48.1(0.02)	3.77(0.09)	1095(0.13)	13497(0.29)	9229(0.30)	2726(0.15)	34.8(0.12)
Swartzia sim. ochnacea	47.7(0.04)	3.41(0.13)	980(0.15)	15371(0.35)	8177(0.35)	2736(0.19)	35.1(0.11)
Tetragastris panamensis	44.9(0.06)	1.96(0.31)	787(0.15)	4980(0.19)	7343(0.27)	2223(0.22)	25.3(0.34)
Trichilia pallida	47.1(0.03)	3.26(0.10)	1826(0.18)	15549(0.31)	20913(0.18)	2781(0.15)	18.4(0.19)
Trichilia tuberculata	47.7(0.02)	2.77(0.08)	1410(0.17)	14051(0.39)	19055(0.20)	2887(0.25)	20.2(0.17)

Table 5.3. Correlation coefficients for the correlation between soil nutrient abundance and leaf nutrient concentration for 15 species along six soil nutrient gradients. Bold correlation coefficients are significant at P < 0.01.

Species	N	P	Ca	K	Mg	Mn
Alseis blackiana	0.22	0.07	-0.35	0.31	-0.30	-0.10
Chrysophyllum argenteum	0.10	0.36	0.21	0.27	-0.02	0.01
Chrysophyllum cainito	0.17	0.09	0.32	0.27	-0.34	0.25
Garcinia intermedia	0.40	-0.09	-0.26	0.12	0.38	-0.32
Guarea guidonia	-0.14	0.14	0.09	0.17	-0.08	-0.19
Guarea sp.	-0.44	0.16	-0.10	0.23	-0.08	-0.37
Hirtella triandra	-0.20	**0.63**	-0.24	0.14	-0.21	-0.01
Protium panamense	-0.15	0.01	0.20	-0.03	0.24	-0.03
Protium tenuifolium	0.15	0.41	-0.35	0.31	0.28	**-0.52**
Quararibea asterolepis	-0.35	0.19	-0.23	**0.53**	-0.08	-0.09
Swartzia sim. grandiflora	-0.13	0.31	0.13	-0.12	0.13	-0.14
Swartzia sim. ochnacea	-0.32	0.18	0.23	0.23	**0.49**	-0.06
Tetragastris panamensis	0.24	-0.28	0.01	0.36	0.05	-0.06
Trichilia pallida	-0.08	0.09	0.32	-0.11	0.25	-0.07
Trichilia tuberculata	-0.31	0.18	-0.15	0.26	-0.16	-0.55
Average	-0.06	0.16	-0.01	0.20	0.04	-0.15
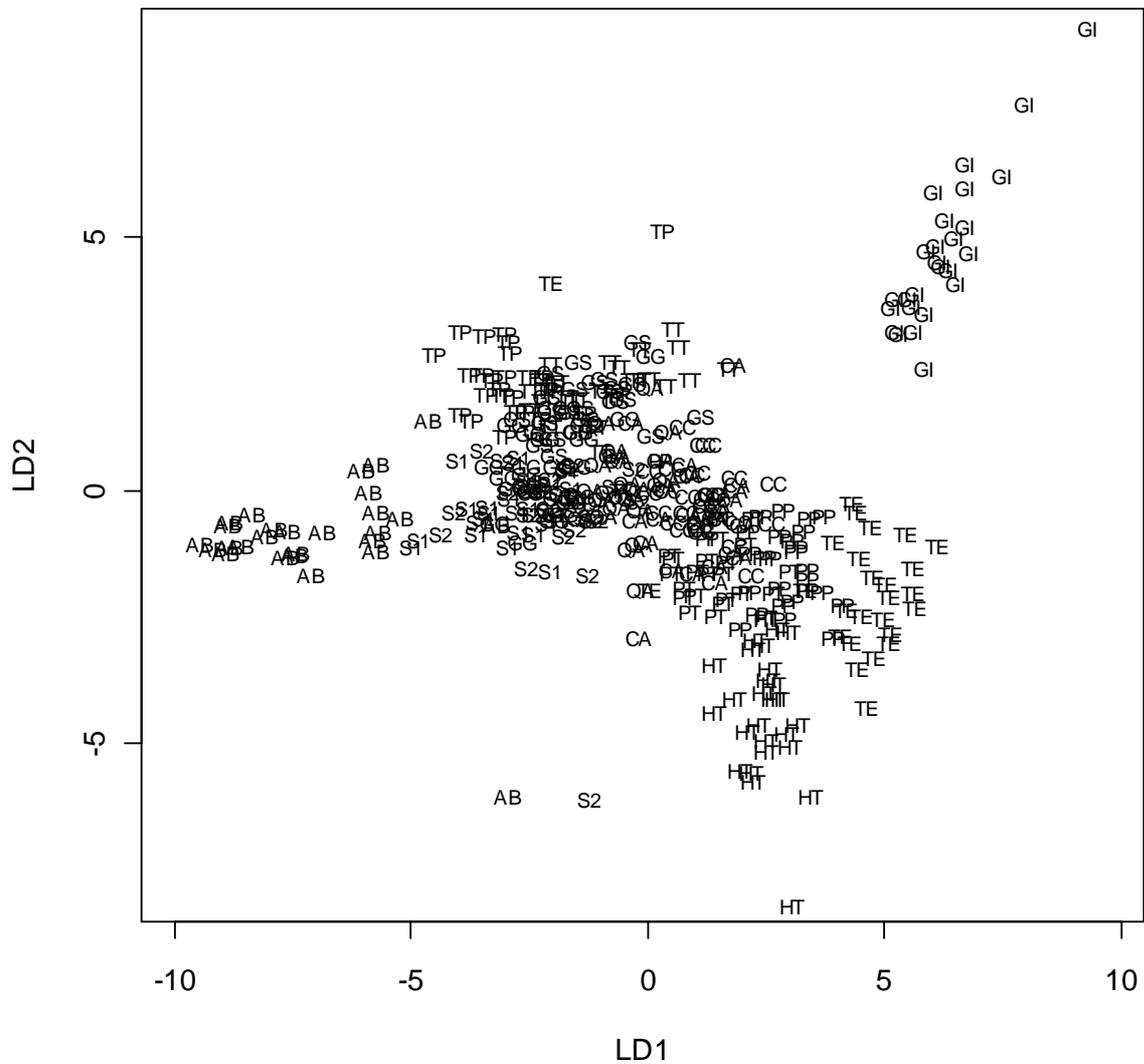
Figure 5.1. Plot of leaf samples against the first two linear discriminant axes. Two character codes represent the species: AB = *Alseis blackiana*, CA = *Chrysophyllum argenteum*, CC = *Chrysophyllum cainito*, GI = *Garcinia intermedia*, GG = *Guarea guidonia*, GS = *Guarea sp.*, HT = *Hirtella triandra*, PP = *Protium panamense*, PT = *Protium tenuifolium*, QA = *Quararibea asterolepis*, S1 = *Swartzia sim. grandiflora*, S2 = *Swartzia sim. ochnacea*, TE = *Tetragastris panamensis*, TP = *Trichilia pallida*, TT = *Trichilia tuberculata*.

CHAPTER 6: CONCLUSIONS

SUMMARY

My dissertation examined how local-scale habitat heterogeneity affects emergent properties of tropical tree communities. Previous research has shown that local-scale variation in soil resources and topography affect the distributions of individual tree species (e.g. Harms et al. 2001, John et al. 2007). My research is the first to show the effects of soil resource variation on local-scale forest compositional and phylogenetic community structure. I found that local-scale soil resource and topographic variation strongly influences compositional community structure. I also tested whether tree species that are close relatives have more similar soil resource and topographic niches, and found that this is the case for many study sites. I further showed that soil resource and topographic variation significantly influence the phylogenetic structure of these communities. I linked phylogenetic signal in soil resource niches to the phylogenetic structure of these communities and showed that patterns of phylogenetic signal are tied to the relationship between environmental variation and phylogenetic community structure. Finally, I examined intraspecific variation in foliar chemistry along soil resource gradients, which helped to clarify how ecosystem-level variation in leaf chemistry is likely to be driven more by species turnover than by intraspecific responses to soil resource gradients.

These analyses provide insight into environmental controls on tropical tree community structure at a smaller spatial scale than is usually investigated. I showed that local-scale environmental variation strongly drives compositional variation in these communities, providing a strong refutation of the idea that community assembly is primarily determined by stochastic processes (Hubbell 2001). I went beyond showing the importance of environmental variation to community structure by further exploring how this influences phylogenetic community structure

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and how it is likely to influence spatial variation in biogeochemical processes. My dissertation sheds light on the various community-level influences of local-scale environmental heterogeneity, and offers insight on promising tracks for future research.

CHAPTER SUMMARIES

In chapter two I showed that individual species' soil resource and topographic niches have important community-level effects. I used a multivariate statistical method called canonical redundancy analysis to partition total community compositional variation (a form of beta diversity) in to fractions explained by spatial, soil, and topographic variables. I found that both soil resource and topographic variation significantly influence tree community structure in these communities. However, there was a large amount of community compositional variation that was spatially structured yet unexplained by environmental variables. This indicates that other spatially structured community assembly processes, such as limited dispersal and species responses to unmeasured environmental variation, are also important determinants of community structure. To demonstrate the ecological importance of environmental variation in shaping these communities, I used a visualization technique from regional mapping to depict community compositional variation in these communities for the first time. These maps provide striking visual support of the argument that community organization is driven by species' responses to environmental gradients.

The evolutionary lability of species ecological traits, such as their soil resource niches, may also affect local tree community structure. In chapter three I tested for the presence of phylogenetic signal (the tendency for close relatives to be more similar) in the local soil resource and topographic niches of tropical trees by comparing the soil and topographic niche overlaps of trees in the same community to their taxonomic relatedness. Species belonging to the same genus

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showed significantly higher niche overlap than expected along at least one environmental axis in five of the study sites; however, I was not able to detect evidence for phylogenetic signal at the family level. These results indicate that phylogenetic signal differs from site to site, and that phylogenetic signal in local-scale soil resource niches may be restricted to close relatives.

Soil resource niches and phylogenetic signal in soil resource niches may then be expected to influence the phylogenetic structure of these communities. In chapter four I examined the effect of soil resource and topographic variation on phylogenetic community structure using phylogenetic beta diversity, which measures the overall phylogenetic relatedness of two community samples. I used distance-based redundancy analysis to test for effects of soil resource and topographic variation on phylogenetic beta diversity, and found that both significantly affected phylogenetic community structure. Furthermore, relationships between soil and phylogenetic beta diversity reflected patterns of phylogenetic signal in soil resource niches found in chapter three: sites that showed evidence for phylogenetic signal in soil resource niches also show a relationship between soil and phylogenetic beta diversity.

Finally, in chapter five I investigated possible mechanisms by which soil resources may shape ecosystem-level variation in foliar nutrients. Previous biogeochemical research in tropical forests has found ecosystem differences in foliar nutrients related to soil type and soil nutrient concentrations. However, because intensive sampling within any one species had not been done, intraspecific variation in foliar nutrients along soil resource gradients was entirely unknown. Therefore it was not known whether ecosystem-level variation in foliar nutrients along soil gradients is caused by species turnover along soil gradients or intraspecific changes in foliar chemistry, or both. I investigated intraspecific variation in foliar nutrients for multiple species along six key soil resource gradients within the Barro Colorado Island 50-ha plot. I found that foliar nutrients were generally not related to soil nutrient concentrations within a species,

although the power to detect modest correlations was low. Because species-specific foliar nutrient profiles were found to be highly conserved along soil nutrient gradients, this suggests that observed ecosystem-level variation in foliar nutrients along soil resource gradients is driven by species compositional turnover, rather than intraspecific variation in foliar nutrients. Furthermore, this analysis provided insight into the stoichiometry of tropical trees, suggesting that they generally have rigid nutrient requirements that are relatively invariant within a species. This study recommends future research focusing on relating species-specific foliar chemistry to species' soil resource associations.

FUTURE DIRECTIONS

There is a great deal of work that remains to be done in order to better understand soil resource niches, how they arise, how they are related to species stoichiometry, and how they influence spatial patterns of biodiversity and biogeochemical processes. My dissertation work has highlighted the importance of small-scale soil resource and topographic heterogeneity in shaping community compositional and phylogenetic structure, and provided insight into one aspect of spatial variation in leaf chemistry along soil resource gradients. However, a large amount of work lies ahead to test resource theories of coexistence that link environmental niche partitioning to species coexistence and biodiversity. Further, we are lacking a mechanistic understanding of how soil resource niches arise at multiple levels, from individual tree growth and mortality responses along soil resource gradients, to species' stoichiometric requirements, to site biogeochemistry and how this determines nutrient limitation and thus soil resource niche axes. Successful research along this path has the potential to connect ecosystem biogeochemistry to species' niches and to species coexistence and biodiversity.

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APPENDIX A: SUPPLEMENTARY MATERIAL FOR CHAPTER 2

Distance-based RDA

For the distance-based RDA (Legendre & Anderson 1999), principal coordinate analysis was performed on the square-root transformed Bray-Curtis distance matrix to create a Euclidian representation of quadrat relationships. Bray-Curtis distances were square-root transformed to allow distance relationships to be fully represented in Euclidian space (i.e., eliminate negative eigenvalues; Legendre & Legendre 1998). The principal coordinates were then submitted to variation partitioning with RDA. The Euclidian distances among quadrats preserved by the RDA are thus equal to the square-root of the Bray-Curtis distance.

The variation partitioning results for the distance-based RDA using square-root transformed Bray-Curtis distances are presented in tables A.1 and A.2. For comparison, the variation explained by each of the two variation partitioning methods (distance-based RDA and plain RDA) are plotted in figure A.3. In general, the magnitude of the explained variation fraction was larger when based on the plain RDA than when based on the distance-based RDA. However, the results were highly correlated between the two methods (figure A.3). Based on these results, I concluded that the relative sizes of the explained variation fractions were robust to the method used to calculate them. My results also highlight the fact that the proportion of variation found to be explained by a set of explanatory variables depends heavily on the method of canonical analysis chosen.

Plot size

To test for the robustness of my results to plot size, I split each of the five 50-ha plots in half and recalculated the variation partitioning results for each of the 25-ha halves. The variation

partitioning results for both halves of the 50-ha plots are presented in tables A.3 and A.4. In general, the proportion of variation explained by the environment was slightly greater, and the proportion of variation explained by spatial variables was slightly smaller, for the 25-ha subsections than for the entire 50-ha plots. However, these differences were very small (1-3 percent of the total variation, comparing the average value for the two 25-ha subplots to the value from the 50-ha plot). This difference is usually less than the differences among variation fractions within the same plot, or among the same variation fraction at different plots. These effects do not change the overall interpretation of the results, in terms of the relative importance of different sets of variables. However, it is worth noting that in my analysis, I found a slight tendency toward greater spatial variation and less environmental variation with larger plot size within the same plot. More extreme differences in plot size may result in larger biases that need to be factored into variation partitioning analyses.

Table A.1. Variation partitioning results for spatial variables and the total set of environmental variables from a distance-based RDA using square-root transformed Bray-Curtis distances among subplots. Total = the proportion of variation explained by both spatial and environmental variables combined, Space = the proportion explained by spatial variables, Env. = the proportion explained by environmental variables, Space|Env. = the pure spatial component, Overlap = the spatially structured environmental component, and Env.|Space = the pure environmental component.

	Total	Space	Env.	Space|Env.	Overlap	Env.|Space
BCI	0.26	0.26	0.13	0.13	0.13	0.00
Huai Kha Khaeng	0.23	0.22	0.09	0.13	0.09	0.00
Khao Chong	0.31	0.30	0.18	0.13	0.18	0.00
Korup	0.41	0.41	0.22	0.20	0.21	0.01
La Planada	0.17	0.16	0.08	0.09	0.07	0.01
Pasoh	0.22	0.21	0.10	0.12	0.10	0.00
Sinharaja	0.47	0.46	0.26	0.21	0.25	0.01
Yasuni	0.20	0.20	0.10	0.10	0.10	0.00

Table A.2. Variation partitioning results for spatial for soil and topographic variables from a distance-based RDA using square-root transformed Bray-Curtis distances among subplots. Total Env. = the proportion of variation explained by both soil and topographic variables combined, Soil = the proportion explained by soil variables, Topo. = the proportion explained by topographic variables, Soil|Topo. = the pure soil component, Overlap = the topographically structured soil component, and Topo.|Soil = the pure topographic component.

	Total Env.	Soil	Topo.	Soil|Topo.	Overalap	Topo.|Soil
BCI	0.13	0.11	0.07	0.06	0.05	0.02
Huai Kha Khaeng	0.09	0.07	0.06	0.03	0.04	0.02
Khao Chong	0.18	0.15	0.10	0.08	0.06	0.04
Korup	0.22	0.17	0.17	0.05	0.12	0.05
La Planada	0.08	0.06	0.04	0.04	0.02	0.02
Pasoh	0.10	0.08	0.05	0.04	0.04	0.02
Sinharaja	0.26	0.15	0.21	0.05	0.10	0.11
Yasuni	0.10	0.07	0.06	0.04	0.03	0.03

Table A.3. Variation partitioning results for spatial variables and the total set of environmental variables from the two 25-ha subplots created by halving each of the five 50-ha plots. Total = the proportion of variation explained by both spatial and environmental variables combined, Space = the proportion explained by spatial variables, Env. = the proportion explained by environmental variables, Space|Env. = the pure spatial component, Overlap = the spatially structured environmental component, and Env.|Space = the pure environmental component.

	Total	Space	Env.	Space|Env.	Overlap	Env.|Space
BCI	0.54 / 0.49	0.55 / 0.49	0.27 / 0.28	0.27 / 0.21	0.28 / 0.28	0.00 / 0.00
Huai Kha Khaeng	0.44 / 0.50	0.37 / 0.48	0.18 / 0.16	0.25 / 0.34	0.12 / 0.14	0.06 / 0.02
Korup	0.73 / 0.70	0.72 / 0.68	0.42 / 0.37	0.31 / 0.33	0.41 / 0.35	0.01 / 0.01
Pasoh	0.47 / 0.45	0.46 / 0.44	0.24 / 0.21	0.23 / 0.24	0.23 / 0.20	0.01 / 0.01
Yasuni	0.47 / 0.49	0.46 / 0.48	0.26 / 0.27	0.21 / 0.22	0.25 / 0.26	0.01 / 0.01

Table A.4. Variation partitioning results for soil and topographic variables from the two 25-ha subplots created by halving each of the five 50-ha plots. Total Env. = the proportion of variation explained by both soil and topographic variables combined, Soil = the proportion explained by soil variables, Topo. = the proportion explained by topographic variables, Soil|Topo. = the pure soil component, Overlap = the topographically structured soil component, and Topo.|Soil = the pure topographic component.

	Total Env.	Soil	Topo.	Soil|Topo.	Overalap	Topo.|Soil
BCI	0.27 / 0.28	0.22 / 0.24	0.16 / 0.16	0.11 / 0.12	0.11 / 0.13	0.05 / 0.04
Huai Kha Khaeng	0.18 / 0.16	0.15 / 0.11	0.09 / 0.11	0.10 / 0.06	0.05 / 0.05	0.03 / 0.05
Korup	0.42 / 0.37	0.26 / 0.27	0.31 / 0.25	0.11 / 0.12	0.15 / 0.15	0.16 / 0.10
Pasoh	0.24 / 0.21	0.21 / 0.18	0.11 / 0.11	0.13 / 0.10	0.08 / 0.07	0.03 / 0.04
Yasuni	0.26 / 0.27	0.21 / 0.22	0.13 / 0.15	0.14 / 0.13	0.08 / 0.10	0.05 / 0.05
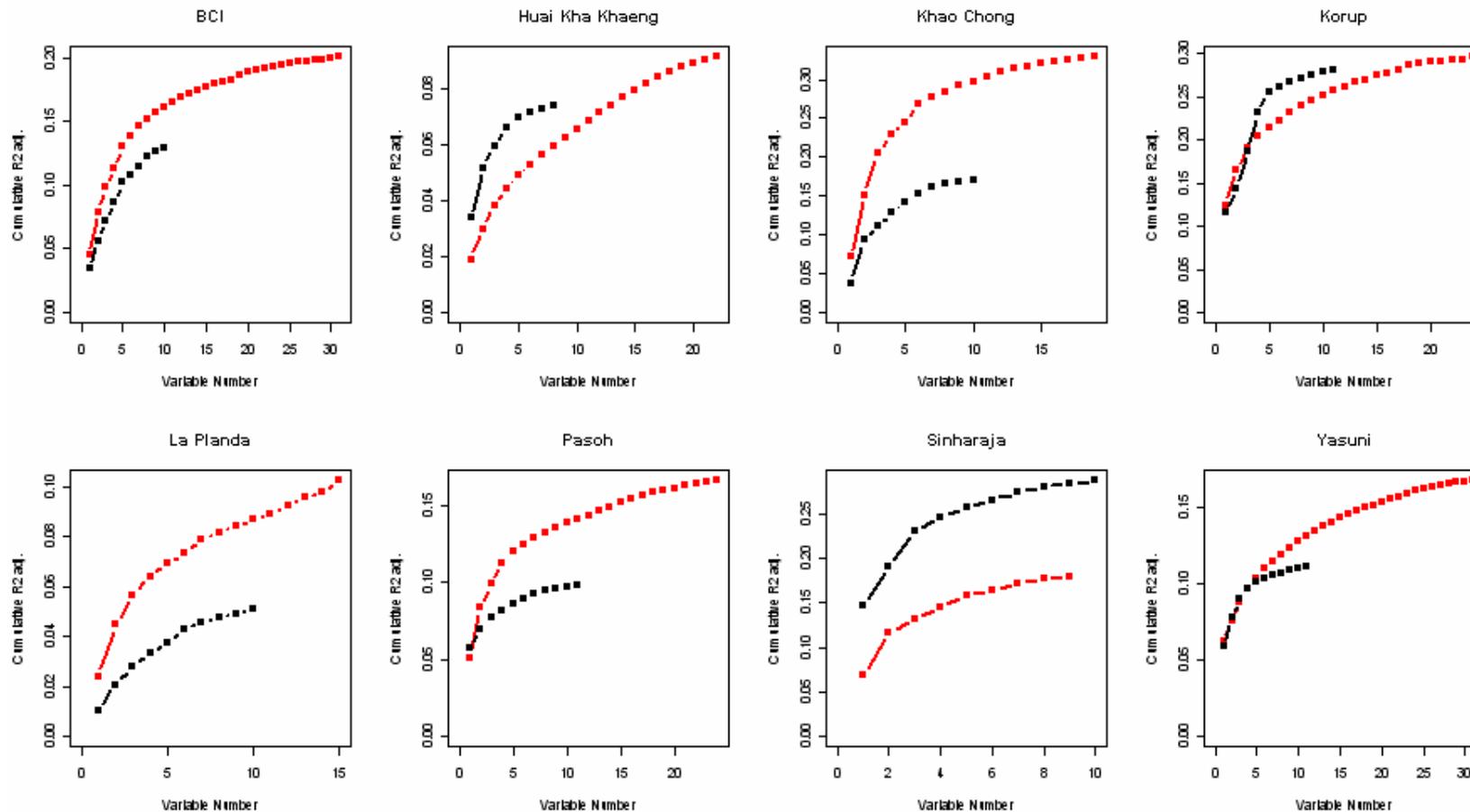
Figure A.1. The cumulative proportion of variance explained (cumulative adjusted R^2) with increasing number of variables included in RDA model from the forward selection of variables performed separately for the sets of soil and topographic variables. Variables accumulate in the order of decreasing importance, or variance explained. Red represents soil variables and black represents topographic variables.
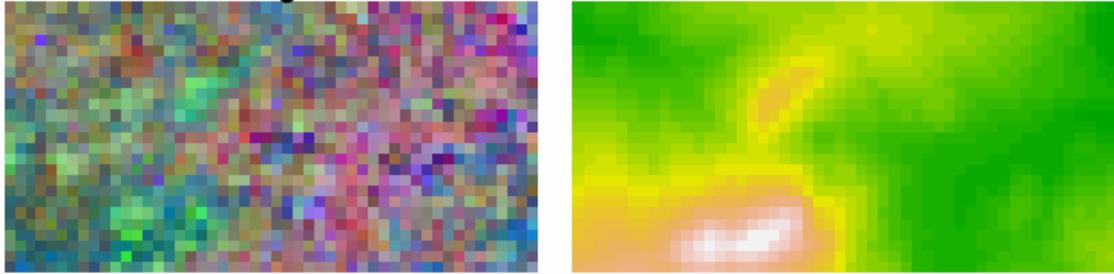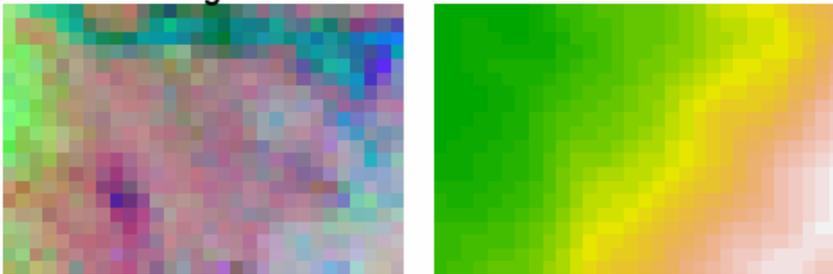
Figure A.2. Beta diversity maps along with elevation maps for the two Thai study sites: A) Huai Kha Khaeng, and B) Khao Chong.
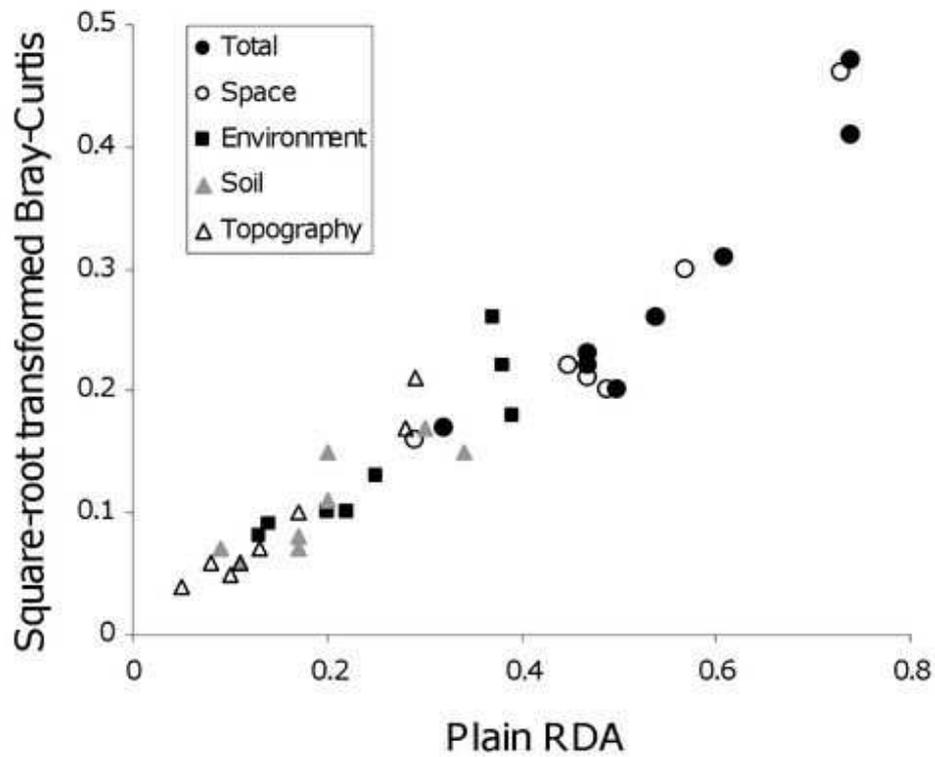
Figure A.3. The proportion of variation explained calculated using plain RDA and using distance-based RDA based on square-root transformed Bray-Curtis distances among quadrats. The results are given for five explained variation fractions: total variation explained and the variation explained by spatial, environmental, soil, and topographic variables.

APPENDIX B: SUPPLEMENTARY MATERIAL FOR CHAPTER 3

Table B.1. The loadings of each soil variable with each of the first two PC axes and the total variance explained by the two PC axes combined.

BCI	PC1	PC2
Al	0.26	-0.64
Ca	-0.46	-0.11
K	-0.45	-0.11
Mg	-0.43	-0.11
Mn	-0.31	-0.28
Nmin	-0.35	0.00
P	0.08	-0.69
pH	-0.32	0.05
Variance explained: 69%		

| La Planada	PC1	PC2
Al	0.10	-0.66
Ca	0.44	0.14
K	0.47	0.00
Mg	0.47	0.08
Mn	-0.09	0.61
Nmin	0.11	0.27
P	0.43	0.20
pH	-0.39	0.25
Variance explained: 68%		

Huai Kha Khaeng	PC1	PC2
Al	-0.33	0.60
Ca	-0.47	0.15
K	-0.50	-0.12
Mg	-0.39	-0.18
Mn	-0.23	-0.43
P	-0.29	0.43
pH	-0.36	-0.45
Variance explained: 67%		

Pasoh	PC1	PC2
Al	0.31	0.51
Ca	0.50	-0.15
K	0.45	0.22
Mg	0.53	-0.25
Mn	0.27	-0.66
P	0.30	0.41
Variance explained: 69%		

Khao Chong	PC1	PC2
Al	-0.09	0.77
Ca	-0.43	-0.08
K	-0.43	0.25
Mg	-0.41	0.28
Mn	-0.43	-0.11
P	-0.29	-0.46
pH	-0.43	-0.20
Variance explained: 81%		

Sinharaja	PC1	PC2
Al	-0.51	0.22
Ca	-0.49	-0.49
K	-0.55	-0.32
P	-0.36	0.29
pH	0.27	-0.72
Variance explained: 67%		

Yasuni	PC1	PC2
Al	-0.39	0.04
Ca	0.51	0.23
K	0.26	-0.45
Mg	0.44	0.30
Mn	0.14	-0.59
Nmin	-0.22	0.50
P	0.05	0.21
pH	0.51	0.13
Variance explained: 58%		

Korup	PC1	PC2
Al	0.21	0.93
Ca	-0.46	0.00
K	-0.43	0.10
Mg	-0.46	0.08
Mn	-0.45	-0.04
P	-0.39	0.34
Variance explained: 87%		

Table B.2. Exact Mantel r values and significance for the genus level Mantel tests for (A) soil PC axes and (B) topographic variables. Positive values indicate that members of the same genus have higher niche overlap than members of different genera. Bold font indicates significance (α = 0.025 for each tail of a two-sided test).

(A)

Study site	PC1 Mantel r	PC1 P value	PC2 Mantel r	PC2 P value
BCI	-0.0184	0.879	**0.0268**	**0.019**
Huai Kha Khaeng	0.0224	0.122	0.017	0.202
Khao Chong	**0.0283**	**0.013**	**0.0517**	**<0.001**
Kroup	-0.0057	0.684	-0.0038	0.623
La Planada	0.0119	0.291	0.0121	0.314
Pasoh	-0.0028	0.63	**0.0178**	**0.013**
Sinharaja	**0.0409**	**0.007**	0.0287	0.031
Yasuni	0.0059	0.174	0.0040	0.303

(B)

Study site	Elevation Mantel r	Elevation P value	Slope Mantel r	Slope P value	Convexity Mantel r	Convexity P value
BCI	0.0211	0.077	0.0077	0.338	0.0109	0.236
Huai Kha Khaeng	0.0167	0.202	0.0218	0.124	0.0198	0.154
Khao Chong	0.0033	0.404	-0.0008	0.541	**0.0296**	**0.008**
Korup	-0.0107	0.803	-0.0007	0.527	0.0048	0.366
La Planada	0.0194	0.172	0.0246	0.105	**0.0347**	**0.024**
Pasoh	0.0117	0.075	**0.0203**	**0.003**	-0.0021	0.607
Sinharaja	0.0228	0.084	0.0206	0.110	**0.0329**	**0.021**
Yasuni	0.0041	0.259	0.0009	0.450	0.0070	0.126

Table B.3. Exact Mantel r values and significance for family level Mantel tests for (a) soil PC axes and (b) topographic variables. Positive values indicate that members of the same family have higher niche overlap than members of different families. Bold font indicates significance ($\alpha = 0.025$ for each tail of a two-sided test).

(A)

Study site	PC1		PC2	
	Mantel r	P value	Mantel r	P value
BCI	-0.0178	0.792	0.037	0.033
Huai Kha Khaeng	-0.0102	0.648	-0.0417	0.937
Khao Chong	**0.0399**	**0.003**	**0.0537**	**<0.001**
Kroup	0.0129	0.163	-0.0051	0.63
La Planada	**-0.055**	**0.979**	-0.0517	0.957
Pasoh	-0.0098	0.868	0.0021	0.398
Sinharaja	0.0257	0.055	**0.03**	**0.022**
Yasuni	0.0128	0.032	0.0029	0.366

(B)

Study site	Elevation		Slope		Convexity	
	Mantel r	P value	Mantel r	P value	Mantel r	P value
BCI	0.0268	0.104	0.0205	0.173	0.0188	0.184
Huai Kha Khaeng	-0.0250	0.815	0.0081	0.385	-0.0422	0.935
Khao Chong	**0.0384**	**0.006**	**0.0311**	**0.022**	**0.0491**	**<0.001**
Korup	0.0135	0.158	0.0187	0.090	0.0207	0.082
La Planada	-0.0336	0.879	-0.0081	0.628	-0.0397	0.903
Pasoh	-0.0014	0.563	0.0055	0.253	**-0.0202**	**0.989**
Sinharaja	0.0253	0.054	0.0114	0.238	0.0166	0.136
Yasuni	0.0126	0.029	**0.0146**	**0.020**	**0.0131**	**0.022**