TREE COMMUNITY ASSEMBLY AND BIOGEOCHEMICAL PROCESSES ALONG AN ELEVATIONAL GRADIENT IN WESTERN PANAMA

BY

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DISSERTATION

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ABSTRACT

Tropical montane forests (TMF) are unique ecosystems with remarkable contributions to global diversity and C cycle regulation. Understanding factors responsible of TMF dynamics are critical to predicting their plant community response to global change. Elevational and environmental gradients are key elements in our understanding of the effect of climate, edaphic and biotic interactions in plant community assembly and biogeochemical processes. Changes in environmental and biotic conditions are expected to influence tree diversity, floristic composition, nutrient and C cycling. My dissertation evaluates how edaphic factors, climate, and mycorrhizal associations drive tree community assembly, C storage, and biogeochemical processes along environmental gradients. Using a set of twelve plots in a premontane forest established along a natural fertility gradient, I was able to determine that soil fertility, geology, and annual rainfall account for tree species compositional variation in these forests. In a set of nine plots along an elevational gradient, within which forest patches are dominated by either ectomycorrhizal (EM) or arbuscular mycorrhiza (AM) trees, I show that variation in tree species composition is in part explained by the tree species' mycorrhizal associations, even when controlling for elevation. I further evaluate how climate, edaphic factors and mycorrhizal associations influence biomass and soil C stocks. I report an exceptionally high C stock attributed to the presence of *Quercus* species at upper elevations and to recent geological history. Finally, I found *Quercus*-dominated forests are depleted in available N compared to mixed forests, resulting in low N foliar concentrations and low seedling growth rates. This dissertation highlights the importance of incorporating both abiotic and biotic interactions in our understanding of the effects of climate change on forest dynamics. Specifically, I emphasize the role of oak forests on species composition, C stocks and nutrient availability.

INDEX WORDS: biogeochemical processes, elevational gradient, mycorrhizal associations, nutrient limitation, tropical montane forests, Volcan Baru National Park

Dedico mi trabajo de tesis de grado a
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CHAPTER 1: INTRODUCTION

BACKGROUND

Tropical regions enclose the most biodiverse biomes in the world and are a major component of global terrestrial carbon cycle (Willig & Presley, 2017). While lowland tropical forests in Amazonia are renowned as being the most biodiverse ecosystems on the planet (Ter Steege et al., 2013), richness in tropical montane forests (TMF) is higher than the Amazon (Rahbek et al., 2019) when taking their area into account. Moreover, TMF are increasingly recognized for their importance as stores of terrestrial carbon (C) (Duque et al., 2021; Spracklen & Righelato, 2014). Despite the remarkable value of TMF forests in global ecological and biogeochemical processes, the mechanisms and factors controlling these processes are still not well understood. Furthermore, studies the factors influencing TMF responses to global change are critical to predicting future community dynamics, ecosystem function, and atmospheric CO_2 levels.

Elevational gradients in the tropics provide a powerful tool to examine plant community responses to climate factors that change with altitude. Studies in these gradients have shown how changes in temperature affect tree community composition (Fadrique et al., 2018; Jones et al., 2011), carbon storage (Girardin et al., 2014; Nottingham et al., 2015) or nutrient availability (nitrogen (N) mineralization rates: Kitayama et al., 1998; Marrs et al., 1988). However, there are environmental variables that are not directly tied to elevation (e.g., precipitation, phosphorus (P) availability), but that nonetheless have been shown to be very important in explaining ecological patterns. Precipitation regimes, in combination with temperature, influence forest productivity (Hofhansl et al., 2015). At the same time changes in nutrient availability can emerge from geological processes (i.e., parent materials) influencing tree species turnover (Prada et al., 2017, Dalling et al., 2021). A less studied aspect in TMF is the role of mycorrhizal associations in regulating biogeochemical processes (Cheeke et al., 2017; McGuire et al., 2010; Phillips et al., 2013; Tedersoo et al., 2020).

While patterns of tree community assembly have been widely explored in lowland forest, these factors have received much less attention in TMF. Studies in TMF have focused, however, on evaluating the effect of climate and edaphic factors on biogeochemical process. The role of biotic interactions such as mycorrhizal associations on nutrient availability and C storage are rare in montane forests (Corrales et al., 2016), and their effect on forest composition is even more rare. This dissertation integrates climate, edaphic and biotic interactions to evaluate the effect of the factors on tree species composition, distribution, and biogeochemical processes in TMF.

STUDY SITES

Panama's unique geographic position with exceptionally diverse geological history and climate variability, results in high biodiversity (Condit et al., 2020, D'Arcy,1987). In montane areas of Panama, species that migrated from temperate forests and from neotropical South America have converged, resulting in the biodiversity hotspot it is today. Through the activities of the Smithsonian Tropical Research Institute (STRI), Panama has become a hub for studies on tropical ecosystems recognized by countries and institutions all over the world. Work at STRI however, has mostly focused on lowland forests, especially Barro Colorado Island (BCI) and the canal area, with less attention given to montane forests. Montane forests in Panama are located along the Central Cordillera, with the highest points situated on the western side of the country (Cavelier et al., 2009; Monro et al., 2017). This project was performed in two locations: The premontane forests of Fortuna Forest Reserve (FFR) and at the northeastern side of the Volcan Baru National Park (VBNP).

Fortuna Forests Reserve: premontane and lower montane forests

The Fortuna Forest Reserve (19,500 ha) is located in the north of the province of Chiriqui (8º 42' N, 82º12' W) adjacent the Palo Seco Reserve. Fortuna supports per-humid to super-humid premontane forest (700-1000 m asl) and lower montane forest (1000-2000 m), as well as small areas of per-humid montane forest (> 2000 m) (Holdridge, 1947). Fortuna is characterized by locally variable climate regimes with high rainfall and cloud cover; mean annual rainfall ranging from 2812 to 7728 mm yr $^{-1}$ and mean annual temperatures vary between 17.1 to 19.9 ºC (Dalling et al., 2021). Variation in parent material reflects the complexity of the topography and geology of the region resulting in remarkable differences in soil fertility (Turner & Dalling, 2021).

Twelve permanent 1-ha plots were established in Fortuna from 2003-2013 (800-1000 m asl) in which all trees > 5 cm diameter at breast height (DBH) are mapped, measured, and identified to species. These plots have been the foundation of extensive studies including flora inventories of trees, epiphytes, understory palm and fern communities (Prada et al., 2017); Gómez et al., 2021; Viana et al., 2021; Andersen et al., 2021). The outcomes of this inventories suggest the complex geology in Fortuna translates into remarkable plant diversity associated with the soil fertility.

Volcan Baru National Park: lower montane and upper montane forests

The Volcan Baru National Park (14,000 ha) is located in the west of the province of Chiriqui (8º 48.5' N, 82º 32.5' W) and about 30 km west of Fortuna. Volcan Baru National Park supports six life zones (ANAM, 2004) with humid premontane forests (1400- 1700 m asl), super-humid montane forests (1800-3000 m asl) and subalpine paramo at the summit (3.475 m asl; Holdridge, 1947). In VBNP mean annual temperatures vary from 12.5 to 20ºC and mean annual rainfall from 2138 to 3710 mm yr $^{-1}$ (ANAM, 2004). At least four eruptions of Volcan Baru have occurred in the last 1600 years. The last episode, 500 years ago, may have included widespread tephra fallout, pyroclastic flows, and lahars across the area (Sherrod et al., 2008).

Since the foundation of the park in 1974 flora inventories have been developed across the region (Monro et al., 2017; ANAM, 2004). However, to our knowledge there have been no long-term studies using permanent plots. In 2015 we established nine plots — four 1-ha (100 × 100 m) and five 0.2-ha (50 × 40 m) —along an elevational gradient from 1600 to 3400 m a.s.l., where all trees > 5 cm DBH have been mapped, measured, and identified to species. Seven of these plots were established within Finca El Velo, a private in-holding in Volcan Baru National Park, one was located at La Esperanza, a private farm in a valley 5 km east of El Velo, and one plot was located just below the tree line near the summit of Volcan Baru.

OVERVIEW

In Chapter 2, I evaluate how environmental filtering structures tree communities in terms of floristic composition in a premontane forest at FFR. I compared alpha and beta diversity among thirteen 1-ha plots established along a soil fertility gradient at elevations between 800 and 1100 m asl. I found alpha diversity varied from 68 to 180 species and that species turnover was very high over short distances. Additionally, ecological dominance of plant functional groups differed among palm, N-fixer and mycorrhizal association type. With this study I was able to show that tree species composition in this forest is largely determined by parent material and annual rainfall. This paper was coauthored by James W. Dalling, Arturo Morris, Kelly M.

Andersen, Benjamin L. Turner and Pedro Caballero. The resulting manuscript was published in the *Journal of Vegetation Science*.

In chapter 3, I evaluate how environmental filtering and mycorrhizal association's structure tree communities in montane and cloud montane forests at VBNP. I established nine plots distributed along an elevational gradient ranging from 1600 to 3200 m a.s.l. where across the gradient forest patches are dominated by either EM or arbuscular mycorrhiza (AM) trees. I found that the diversity of EM-dominated forests was lower than that of AM-dominated forests. Compositional similarity declined with elevation and distance, while at intermediate elevations variation was largely due differences in forest type (EM versus AM-dominated forests). I found both climate and biotic factors strongly influence the structure of tree community composition in montane forest. These results highlight the role of biotic interactions in forest composition in TMF. This chapter was coauthored by James W. Dalling and Maria Juliana Pardo and will be submitted to *Biotropica*.

In chapter 4, I evaluated how edaphic conditions, climate, and the type of mycorrhizal association influence carbon storage in forests in FFR and VBNP. I estimated aboveground biomass (AGB), coarse wood debris (CWD), and soil C among ten 1-ha plots. I found remarkably high C stocks in these forests in AGB and soil C compared to other TMF in the Andes and Central America. I found high AGB was attributable to the presence of EM associated *Quercus* in the highest elevations. However, EM association had no effect on total soil C; exceptionally high values of soil C at the highest elevations maybe a consequence of volcanic eruptions that buried C rich surface soils in the past. In this chapter I demonstrate that *Quercus* species are strong determinants of ecosystem C cycling. This chapter was coauthored by James

W. Dalling, Katie Heineman, Maria Juliana Pardo, Camille Piponiot and Benjamin L. Turner, and will be submitted to *Biogeosciences*.

In chapter 5, I devised an experiment to evaluate how patches of oak (EM-dominated) forest, and mixed (AM-dominated) forest influence the growth of EM and AM-seedlings. I found EM-dominated stands were characterized by significantly lower N availability and accumulation of organic matter. AM seedlings, transplanted into EM-dominated stands had lower foliar N than those transplanted to nearby mixed forest, however reduced N availability did not translate to a large reduction in seedling growth. The results of this experiment point to limited effects of alterations in soil nitrogen availability on seedling growth in a montane forest. This paper was coauthored by James W. Dalling and Benjamin L. Turner and is in revision for publication in *Functional Ecology*.

In chapter 6, I summarize the results of my research, and explore directions for future research in tropical montane forests, especially in oak forests.

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CHAPTER 2: SOILS AND RAINFALL DRIVE LANDSCAPE-SCALE CHANGES IN THE DIVERSITY AND FUNCTIONAL COMPOSITION OF TREE COMMUNITIES IN PREMONTANE TROPICAL FOREST[1]

ABSTRACT

Premontane tropical forests harbour exceptionally high plant species diversity; understanding which factors influence their species composition is critical to conserving them, and to predicting how global environmental change will affect them. We asked: (1) how does alpha and beta diversity vary at the landscape scale? (2) how important is environmental filtering in structuring these communities? (3) which soil and climate variables account for the most compositional variation? Location: Old-growth premontane forest, Fortuna Forest Reserve, western Panama. All trees ≥ 5 cm DBH were censused in twelve 1 ha plots up to 13 km apart. For each plot, we measured soil properties (0-10 cm depth) at thirteen locations, and estimated or measured monthly rainfall. To evaluate how the environmental and spatial variables are associated with community composition, we used ordination and Mantel tests. Diversity varied nearly three-fold among plots (68 – 184 species ha^{-1}). Beta diversity was also high, with only one of 364 species present in all plots. Turnover reflected distinct forest community types that have developed on different parent materials: forests on rhyolite had an abundance of either ectomycorrhizal-associated trees or canopy palms, while forests on the other rock types (andesite, dacite and basalt) were dominated by trees that form arbuscular mycorrhizal associations. While NMDS ordination showed that seasonality of rainfall

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[1] Prada et al., 2017. Soils and rainfall drive landscape-scale changes in the diversity and functional composition of tree communities in premontane tropical forest. Journal of Vegetation Science, 28(4)

was significantly correlated with species turnover, turnover also covaried with geographic distance. Nonetheless, large compositional differences were apparent among sites <2 km apart with similar rainfall but differing soils. Partial Mantel tests controlling for geographic distance highlighted the relationship between total phosphorus and species composition. Soil nutrient availability and rainfall seasonality in premontane forests at Fortuna is associated with striking variation in the taxonomic and functional composition of nearby tree communities, and with plot differences in species richness comparable in magnitude to those reported over >1000 m of elevation in previous studies. Accounting for how local edaphic conditions structure premontane and montane tropical forests will be critical to predicting how tree communities will respond to climate change.

INTRODUCTION

Montane forests are among the world's most diverse habitats (Kappelle & Brown, 2001). Despite their limited area and geographic extent, some support plant species diversity comparable to lowland tropical forests (Henderson *et al.*, 1991), harbour unique assemblages of epiphytic and hemi-epiphytic plants, and contain many locally and regionally endemic species (D’Arcy, 1977; Gentry, 1992). Despite this diversity we understand far less about the ecology and biogeography of montane forests than lowland forests. In particular, montane and premontane forests have few permanent forest plots with data on species richness and composition (Scatena *et al.*, 2010).

Without adequate base-line data on species distribution patterns and on factors determining these patterns, such as soils and climate, we cannot predict how environmental change will affect montane forests. Montane forest communities may be especially at risk from regional changes in precipitation regime when lowland forests are replaced by fields, or when global climate change affects both temperature and rainfall (Ray *et al.*, 2006; Barradas *et al*., 2010). While lowland and montane taxa are predicted to move to higher elevations, numerous biotic and abiotic barriers to plant migration cause uncertainty about future forest communities (Feeley & Silman, 2010; Feeley *et al*., 2013).

Plant communities in montane forest often have narrow environmental ranges constrained by steep gradients of rainfall and mist interception (Young, 1994; Vazquez, 1995; Jump *et al*., 2009). Precipitation regime can vary dramatically over short distances particularly at the lower elevational limits of cloud formation, and when passing from windward to leeward mountain slopes (Shreve, 1914; Haber, 2000). Aspect may also influence disturbance regime through exposure to prevailing winds or hurricanes (Bellingham, 1991). Moreover, in common with lowland forests, soils of montane forests can vary greatly in fertility, reflecting heterogeneity in age, parent material, and topography, in interaction with climate and forest composition (Silver *et al*., 1994; Benner *et al*., 2010).

To date most studies have emphasized the importance of elevation as a correlate of species diversity and structural variation in montane forests (Lieberman *et al*., 1996; Vazquez & Givnish, 1998; Asner *et al*., 2014; Girardin *et al*., 2014). However, these transect-based studies may under-sample much of the compositional variability within elevational zones or ecotones that is attributable to topography, soils and microclimate (Aiba & Kitayama, 1999; Homeier *et al*., 2010). In particular, premontane forests mark an elevational transition between lowland forests, where productivity and species composition is often considered to be determined by phosphorus (P) availability

(Vitousek, 1984; Condit *et al.,* 2013), and montane forests, where nitrogen (N) availability is considered most limiting (Vitousek, 1984; Tanner *et al*., 1998). Forests growing at this elevational transition may therefore be subject to N and P co-limitation, or may shift between N and P limitation over short spatial scales depending on parent material, disturbance history and plant-soil feedbacks, leading to high compositional turnover across the landscape.

Here we explored the alpha (α) and beta (β) diversity of forests in 12 1-ha forest plots distributed across 13 km within a relatively narrow elevational band between lowland and montane forest (850-1330 m a.s.l) in western Panama. Our previous work, at a sub-set of seven of these plots, has shown that the Fortuna forests occupy a geologically complex terrain that includes rhyolitic tuff, andesite, dacite and basalt (Andersen *et al*., 2010). These different parent materials are associated with contrasting soil physical and chemical properties, and form a mosaic in soil nutrient availability influencing understory palm community composition (Andersen *et al*., 2010), functional trait composition (Andersen *et al*., 2012) and seedling growth performance (Andersen *et al*., 2014). Here we explore broader compositional patterns within the tree community over a more intensively sampled rainfall and soil fertility gradient at Fortuna. If understorey palm and the overstorey tree community composition are controlled by similar processes, then we predict high compositional dissimilarity across the plot network, and that climate and soil variables, particularly soil N and cation availability, will be important correlates of species distributions (Andersen *et al*., 2010). However, inclusion of additional sites, and a focus on the tree community, may also reveal an important role for P availability, a major driver of beta diversity in tree communities in lowland forest in Panama (Condit *et al*., 2013). In Central America and S.E. Asia, premontane forests often define the lower elevational limits of forests that are dominated by temperate plant lineages, primarily Fagales, that form associations with ectomycorrhizal fungi (Whitmore & Burnham, 1975; Kappelle, 2006). The occurrence of plant lineages associated with N limited temperate forest ecosystems may therefore indicate sites with a predominance of N limitation. We therefore also describe how the broader functional group composition of tree communities (palms vs. dicots; angiosperms vs. gymnosperms; arbuscular vs. ectomycorrhizal trees; N-fixing legumes vs. non-legumes) are distributed along the same environmental gradients.

MATERIALS AND METHODS

Study site

The study was carried out in the Fortuna Forest Reserve (19,500 ha), and the southern edge of the adjacent Palo Seco Forest Reserve (125,000 ha), in western Panama (8°45'N, 82°13'W; Figure 2.1). The study area supports super-humid premontane forests (Holdridge, 1947) between 700 and 1500 m above sea level. Mean annual rainfall ranges between 4600 and 6300 mm (Table A.1). Although there is seasonality in rainfall across all but the most northerly sites along the Caribbean slope of the continental divide, mean rainfall in the drier months (January–April) is rarely <100 mm mo^{-1} except at the most southerly (leeward) side of Fortuna (Figure A.3).

Within the study region we established 12 permanent 1 ha (100 × 100 m) forest inventory plots (Figure 2.1; Figure A.1,2). Plots were located on relatively gentle slopes, avoiding exposed ridge tops. Plot area was corrected for slope inclination. Six plots were established in 2003, with an additional six plots added in 2008. Data from the 2013 recensus are reported, which included all trees ≥5 cm diameter at breast height (d.b.h.). Analyses of α-diversity includes all confirmed tree species identifications (333 species), and an additional 106 morphospecies for which species epithets are provisional. Vouchers of fertile specimens have been deposited at the University of Panama (PMA) herbarium. Analyses of β-diversity are restricted to the 364 species or morphospecies for which we have high confidence identifications are consistent across plots. Species were classified as ectomycorrhizal (EM) if they occurred in families known to contain EM taxa (Smith & Read, 2008), and if subsequent examination of fine roots revealed the presence of a hyphal mantle (15 species; A. Corrales, unpublished data). Remaining tree taxa are assumed to be arbuscular mycorrhizal with the exception of non-mycorrhizal Proteaceae (two species at the study site). A list of 44 potentially nitrogen-fixing taxa (including 26 species of *Inga*) consisted of all species in the legume sub-families Mimosoideae and Papilionoidae.

Rainfall and soils data

Rainfall data were collected every two weeks from 2007-2009 and 2011-2014 in a rain gauge 2-5 m above the ground in the center of a large gap close to a sub-set of sites spanning the study area (Table A1, Figure A.3). For the sites of Pinola and Alto Frio, rainfall data were only available for 2013 and 2014. However, annual rainfall averaged across sites measured over the five years from 2007-2012 (5772 ±1039 mm; mean ± 1 SD) was similar to that in 2013-14 (5506 ± 809 mm). For four sites (Bonita, Chorro B, Verrugosa A and B) that lacked rainfall gauges, data were used from the closest sites (<3 km away) that had similar slope position (Table A.1).

Soil variation reflects the complex geology at Fortuna, with two distinct mountain ranges -- the Cordillera Central (parent material: rhyolitic tuff, basalt, and andesite) and Cerro Hornito (dacite outcrops) separated by a few kilometers. The twelve plot sites sample these contrasting parent materials. Soil from each 1-ha plot was analyzed for pH, bulk density, total C, N and P, extractable inorganic nitrogen (NH_4 and NO_3), resin extractable P, extractable cations (Al, Ca, Fe, K, Mg, Zn), effective cation exchange capacity (ECEC), and total exchangeable bases (TEB). All samples were collected in the mid-wet season (July 2010). Soil samples were collected after removing undecomposed litter from the surface 0-10 cm of soil, where most fine roots are located (Cavalier, 1992), at 13 locations per plot, and from a subset of five locations per plot at 20-50 cm depth. Inorganic N extractions were completed within 6 h of sample collection, and other extractions within 24 h.

Bulk density (BD) was determined by drying a known volume of soil at 105°C. Soil pH was measured in water with a glass electrode in a 1:2 dry soil:water solution ratio. Nitrogen fractions (ammonium, nitrate) were determined by extraction in 0.5 M K_2SO_4 for 1 h with detection by automated colorimetry on a Lachat Quikchem 8500 (Hach Ltd.). Readily exchangeable phosphate (resin phosphorus) was determined by extraction with anion-exchange membranes. Exchangeable cations were determined by extraction in 0.1M $BaCl_2$ (2 h, 1:30 soil to solution ratio), with detection by inductively-coupled plasma spectrometry on an Optima 7300 DV (Perkin-Elmer Ltd, Shelton, CT, USA) (Hendershot *et al.*, 2008). Total exchangeable bases (TEB) was calculated as the sum of Ca, K, Mg, and Na; ECEC was calculated as the sum of Al, Ca, Fe, K, Mg, Mn, and Na; base saturation was calculated as (TEB ÷ ECEC) × 100. Total P was determined by ignition (550°C for 1 h) and acid extraction (1 M H_2SO_4 for 16 h), with phosphate detected by molybdate colorimetry (Walker & Adams, 1958). Total C and N was determined by elemental analysis (Thermo Flash 1112 analyzer, Bremen, Germany).

Data analysis

Analyses of tree communities and environmental variables were implemented using the statistical software package “vegan” (version 2.0-10, http://CRAN.R-project.org/package=vegan) in R (Foundation for Statistical Computing, Vienna, AT)

Alpha diversity and compositional variation

Species accumulation curves were compared among plots using 95% confidence intervals of species richness after rarefaction of 1000 stems per plot. Fisher's alpha was used to compare species diversity among plots. Variation in species composition was assessed using a Steinhaus dissimilarity matrix, calculated using the Bray–Curtis method, double-standardized by species maxima and plot totals of square root-transformed species abundance data for each plot. Non-metric multidimensional scaling (NMDS), an unconstrained ordination technique, was used to visualize compositional variation among sites. Analysis of similarity (ADONIS; http://CRAN.R-project.org/package=vegan) was then used to examine plot differences and parent material effects (andesite, rhyolite, dacite and basalt) on species composition. To describe geographic distance-decay in similarity, a matrix of three-dimensional Euclidean geographic distances among plots was calculated from GPS coordinates for the SW corner of each plot; elevation was measured using a digital altimeter (Suunto USA, Ogden, UT, USA).

Relationship between compositional variation, geographic distance and environmental variables

To explore how environmental variables varied among plots, the 21 soil variables and two rainfall variables (Table A.1) were jointly subject to principal components analyses (PCA). To assess the strength of correlation between tree community composition, environment variables and geographic distance we used Mantel tests. The environmental matrix was constructed based on Euclidean distance using the first three axes of the PCA of soil and rainfall data combined. Mantel tests were used to correlate environmental matrices with geographic distance, and partial Mantel tests to correlate the tree community with environmental variables while controlling for geographic distance (a test of 'pure environmental' effects) and between the tree community and geographic distance controlling for environmental variables ('pure spatial'). Standardized Mantel statistics are based on Pearson's correlation coefficients, and significance was assessed using randomization tests with 1000 permutations (Legendre & Legendre, 2012). We assessed the strength of association of individual environmental variables with the Steinhaus dissimilarity matrix of tree community composition by fitting environmental variables *a posteriori* to the NMDS, maximizing their correlation to the ordination configuration. Finally, we also used detrended correspondence analysis (DCA) to explore species responses to environmental gradients.

RESULTS

Functional and compositional variation among plots

Plots varied considerably in stem number (range 1112-2435 stems $\geq$5 cm d.b.h.) and basal area (range 30.3-50.3 m^2 ha^{-1}) (Table 2.1). However, only basal area varied significantly with parent material (F=5.16; d.f.=2.9; P=0.032), with lower values on andesite-derived soils (mean 34.2 m^2 ha^{-1}) than dacite derived soils (mean 46.35 m^2 ha^{-1}; Tukey HSD, $P<0.05$).

There were also striking differences in the ecological dominance of different plant functional groups (Table 2.1). Most notable were differences between adjacent pairs of plots at Chorro and Honda (all on rhyolite geology, but with different soil orders), and between Honda and the nearby plots with similarly aseasonal rainfall patterns: Pinola (on basalt), Bonita (on andesite), and Samudio (rhyolite-andesite transition). The two Chorro plots were dominated by three species of palm (*Colpothrinax aphenopetala*, *Wettinia quinaria* and *Euterpe precatoria*) that accounted for 25-41% of basal area. In contrast, palms accounted for <1% of basal area in the two Honda plots, which were instead dominated by the ectomycorrhizal (EM) tree *Oreomunnea mexicana* (Juglandaceae; 25-46% of basal area). *Oreomunnea* rarely occurred in other plots. A single species of conifer, *Podocarpus oleifolius* (Podocarpaceae, exclusively AM), also occurred on the two Chorro plots (6-8% of basal area); otherwise it only occurred at Honda B. Finally, plots showed substantial variation in the abundance of potentially nitrogen fixing taxa (primarily *Inga* spp), with low representation in the Hornito and Chorro plots.

Alpha and beta diversity

In total 18,856 trees ≥ 5 cm d.b.h. were censused in the 12 1-ha plots, representing 439 species and 73 families. Species richness per plot ranged between 68 and 184 species per hectare, and between 59 and 170 species per 1000 stems (Table 2.1, Figure A.1). The three lowest diversity sites (Alto Frio, Chorro A, Chorro B), each with <90 species per hectare, also had the highest stem density per hectare. Similar diversity patterns were observed for canopy trees (>30 cm d.b.h.; Table A.2).

Compositional similarity declined linearly with the logarithm of distance over the 13 km spanning the sites (r^2=0.26, P<0.001; Figure 2.2). Similarity values dropped to

<0.2 for plots 10 km apart, however, similarity at the intermediate spatial scale (2-4 km) varied greatly, reflecting in part the effect of parent material on compositional similarity (ADONIS: *F*=2.09, *P*=0.003). Only one tree species, *Tapirira guianensis* (Anacardiaceae), was present in all plots, and 27.4% of species were only recorded in a single plot (Figure 2.3).

Rainfall and soil variation among plots

Rainfall varied considerably across the 13 km separating plot locations (Table A.1). However, only the two dacite plots, Hornito and Alto Frio, at the southern side of the Fortuna reserve, experienced dry season moisture deficits. Over a seven year period, Hornito had eight different months with <100 mm of rainfall (Figure A.3). In contrast, plots further North, and East of Pinola received >5 m of rain annually and had <1 month with <100 mm of rainfall over the same seven years.

Soil nutrient concentrations also varied greatly among plots, with pH ranging from 3.6-5.6, 20-fold variation in resin extractable P, 8-fold variation in NH_4, 13-fold variation in NO_3, and 6-fold variation in cation exchange capacity (Table A.1). Extractable nutrients are expressed on a per volume basis because soil bulk density also varied 5-fold across the plots, primarily reflecting differences in soil total carbon (Table A.1).

The first two axes of the PCA of the rainfall and soil environmental variables measured at 0-10 cm depth (Figure 2.4) explained 68.8% of the variance in the dataset, and indicated that, with some exceptions, plots grouped according to parent material. The two dacite derived plots grouped with Pinola, a basalt plot, and were characterized by relatively high plant available P, Ca, and extractable ammonium. The low pH andesite plots clustered in a group along PC1 characterized by high rainfall and low total exchangeable bases. The rhyolite plots of Chorro and Honda were characterized by low bulk density, pH, inorganic N and resin P. Much of the overall variation in soil nutrient availability (captured in the first PC axis) was encompassed by five plots (Pinola, Chorro A and B, Honda A and B) distributed over only 3 km. A similar PCA generated for less intensively sampled sub-surface mineral soils 20-50 cm depth (Figure A.4) explained a similar proportion of variance in the dataset (69.6%), and for the most part revealed similar grouping of plots and correlations with environmental variables.

Compositional variation in relation to rainfall and soil nutrients

The NMDS ordination of plant communities revealed that plots grouped according to underlying geology and geographic location (Figure 2.5). The andesite plots on the Caribbean slope (Palo Seco, Verrugosa A and B) formed a cluster distinct from the andesite plots closer to the reservoir (Samudio and Bonita). The two rhyolite plots at Honda also grouped with the nearby rhyolite-andesite transition plot of Samudio, despite the abundance of the EM tree *Oreomunnea* at Honda. The two rhyolite sites at Chorro were also distinct (high values on MDS axis 1, Figure A.4b), while Alto Frio was distinct in having by far the lowest value on the same axis. The basalt site, Pinola, geographically close to Samudio and Honda, was also distinct in the vegetation ordination.

Environmental vectors fitted to the ordination showed that dry season rainfall, annual rainfall, elevation, ECEC, pH, and total P were all significantly correlated with compositional variation ($P<0.05$). The two sites on the southern side of Fortuna, Hornito and Alto Frio, were characterized by high ECEC, and drier and more seasonal rainfall, while the rhyolite sites and basalt site (Pinola) were distributed across the gradient of P availability. The Caribbean slope sites (Verrugosa A and B, Palo Seco) were not strongly associated with any of the significant environmental vectors except elevation (Figure 2.5). Analysis of the sub-surface mineral soils resulted in correlations with environmental variables that were largely congruent with those of surface soils (Figure A.4b), as was a detrended correspondence analysis (DCA) of the same data (Figure A.5).

Mantel test results did not differ for species abundance or presence/absence (Table 2.2). Floristic dissimilarity was significantly correlated with geographic distance, the PCA environmental matrix, dry rainfall season, pH, bulk density, total P, calcium, ECEC and TEB. After controlling for spatial variation, the 'pure environmental' partial Mantel test showed that only the PCA environmental matrix, bulk density and total P were correlated with floristic dissimilarity.

DISCUSSION

We found striking variation in α and β-diversity, and in the functional group composition of tree communities in forest plots <13 km apart in premontane forest in western Panama. In part, compositional variation reflects dispersal limitation as floristic similarity between plots declined with distance, a result we found previously for understory palm communities at Fortuna (Andersen *et al.*, 2010). Differences in diversity and composition, however, are also attributable to a combination of soil fertility effects, the amount of rainfall and its seasonality. In common with lowland forests, differences in fertility reflect co-variation in pH, P variables, inorganic N and ECEC in soils that developed on diverse parent materials (Turner & Engelbrecht 2011), and to a lesser extent may reflect differential rates of leaching under different rainfall regimes.

Diversity of premontane forest tree communities

To date, the most extensive analysis of the composition of premontane and montane forest tree communities is based on 0.1 ha transect samples arrayed across Andean and Central American sites (Gentry, 1995; Clinebell *et al*., 1995). These studies found remarkable consistency in patterns of species and familial diversity in both Andean and Central American montane forests. For Andean forests, elevation explained 71% of variation in species richness, with twice as many species on average in premontane forest at 1200 m a.s.l. than in montane forest at 2500 m a.s.l. (Figure 2.2 in Gentry, 1995). Similar patterns have been reported for 1 ha plots arrayed along elevational transects in Central America and Peru (Lieberman *et al*., 1996; Fierer *et al*., 2011; Girardin *et al*., 2014).

While these broad-scale studies highlight the importance of elevation in structuring communities, they have overlooked the variation in composition and richness that occurs within narrow elevational limits. For example, Clinebell *et al.* (1995) concluded in their study that "tropical forest species richness is surprisingly independent of soil quality". Here we found that forests distributed across a few kilometres, with similar elevation, and often with very similar climate, can vary threefold in species richness - equivalent to the mean richness differences that occur over >1000 m elevation (Gentry, 1995). This variation appears to be attributable to differences in parent material, and therefore, soil nutrient availability.

Tree diversity is expected to peak at the lower elevational limits of montane forest. This could arise if less seasonal premontane forests support the inclusion of species otherwise excluded from lowland forests by dry season water deficits (Wright, 1992). A mid-elevational peak in diversity has been reported for elevational transects in Peru and Bolivia (Girardin *et al*., 2014), and Costa Rica (Lieberman *et al*., 1996) and almost certainly exists in Panama. At Fortuna, the highest species richness was recorded at Palo Seco (145 species ≥10 cm d.b.h.), and is only exceeded by two lower elevation and relatively wet sites, both in central Panama: Santa Rita (400 m a.s.l.; 152 species; Pyke *et al*., 2001) and Nusagandi (350 m a.s.l.; 191 species; Paredes unpublished data, cited in Leigh, 1999).

Structural and compositional variation at Fortuna

Differences in species richness at Fortuna are also accompanied by large variation in stem density and basal area, and in the representation of different functional and taxonomic groups (Table 2.1). Whereas tree communities on andesite, dacite and basalt are almost exclusively composed of species that form arbuscular mycorrhizal (AM) associations, forests on relatively infertile rhyolite-derived soils in the Honda watershed, and to a lesser extent at Chorro, have a substantial representation of ectomycorrhizal (EM) taxa from the predominantly temperate order of Fagales.

At the Honda B plot, EM taxa account for nearly half of basal area, an effect that is largely attributable to a single EM tree species, *Oreomunnea mexicana* (Juglandaceae; Corrales *et al*., 2016a). EM associations may be particularly beneficial in high elevation forests because the ability of EM to acquire nitrogen from a variety of organic sources (Read & Perez-Moreno, 2003; Treseder *et al*., 2008) may compensate for a decline in nitrogen mineralization with decreasing temperature and increasing soil moisture content (Marrs, 1988; Raich *et al*., 1997). Rhyolite plots, however, did not appear to be especially N-limited relative to other plots (Table A.1). Furthermore, the EM tree *Oreomunnea* *mexicana* also grows in soil relatively rich in mineral N close to the Alto Frio plot (Corrales *et al*., 2016a). Instead, EM associated tree species may induce feedback effects on soil N availability. In the Honda watershed resin-extractable nitrate and ammonium are lower beneath *Oreomunnea* trees than neighbouring AM tree species, an effect attributed to direct uptake of organic N by EM fungi and a suppression of microbial mineralization of organic matter by free-living saprobes (Corrales *et al*., 2016b).

Although *Oreomunnea* is locally dominant at Honda, it is absent from the two most infertile plots in the adjacent Chorro watershed <1 km away. Chorro is dominated by three species of canopy palms that collectively account for 29-37% of stems. The slow leaf production rate and tall stature (>25 m) achieved by these palms, particularly *Colpothrinax aphanopetalum* (Heineman *et al*., 2015), suggests that they may be particularly strong competitors under extremely infertile conditions, where long-lived leaves with low nutrient concentrations, as well as reduced investment in wood, results in higher nutrient use efficiency and potentially allows greater allocation to reproductive biomass than dicot trees (Heineman *et al*., 2015). Chorro also supports a population of the only conifer at Fortuna, *Podocarpus oleifolius*, a pattern consistent with the affinity for low fertility soils shown by other tropical and temperate Podocarpaceae (Coomes & Bellingham, 2011; Punyasena *et al.*, 2011). In contrast, nitrogen-fixing taxa, primarily *Inga* (Fabaceae), the largest genus in neotropical lower montane forests (Gentry, 1995), were far rarer at Chorro than all other sites except Hornito (Table 2.1). The rarity of N fixers at Chorro may reflect critical limitation of P or molybdenum (Vitousek & Field, 1999; Wurzburger *et al*., 2012).

More generally, species turnover was high across sites, with low floristic similarity even for plots <1 km apart. Although there is a significant effect of geographic distance on compositional similarity when controlling for environmental variables, consistent with dispersal limitation, compositional similarity also reflects variation both in soil properties and in rainfall regime. While annual rainfall exceeds 4 m at all plots, occasional dry season moisture deficit may still act as an ecological filter for tree species occurring on the Pacific side of the reserve. A study at the Monteverde Reserve in Costa Rica also found low community similarity between nearby Pacific and Atlantic slope plots at similar elevation along a 2.5 km transect (Häger, 2010). As seasonally drier sites also tend to be more fertile, with higher pH, cation exchange capacity, inorganic nitrogen and extractable phosphorus (Figure 2.4), the effects of climate and soils cannot be completely distinguished. Overall, sites generally clustered in the NMDS ordination of forest composition data based on underlying soil properties and rainfall (Figure 2.5). However, the composition of plots located at sites near the center of the reserve (Pinola, Samudio, Honda and Chorro), with similar total dry season rainfall, differed markedly, reflecting a clear effect of soil properties.

Given the high degree of covariation in soil variables across the Fortuna sites (Figure 2.4) it remains unclear whether compositional variation reflects differential sensitivity among taxa to the same soil nutrient or a combination of soil nutrients. Our earlier analysis of understory palms at Fortuna highlighted base cations and inorganic nitrogen as the soil variables most strongly correlated with compositional similarity (Andersen *et al*., 2010). In addition, N limitation to productivity appears to be important for the overstorey tree community in the rhyolite derived soils at Honda, where N fertilization increases litterfall and stem growth (Adamek *et al*., 2009; Heineman *et al*., 2015). The absence of N as a significant correlate of compositional variation in the tree community ordination in this study however may also indicate that neither total N nor inorganic N effectively characterize plant available N pools when plants use both organic and inorganic sources of N (Lipson & Nasholm 2001, Andersen & Turner 2013).

In contrast to the weak influence of N, there was a strong effect of P availability on compositional variation across the landscape. This effect is consistent with observed patterns of species turnover across similar gradients of P availability at larger spatial scales in lowland forest in central Panama (Condit *et al*., 2013) and with structural and compositional change across the Amazon basin (ter Steege *et al*., 2006; Quesada *et al*., 2009). Productivity responses to N fertilization at Fortuna further suggests the potential for N co-limitation among species adapted to the prevailing conditions of P availability, consistent with evidence for co-limitation by N and P observed in other montane forests (Tanner *et al*., 1992; Homeier *et al.*, 2012).

Implications of variation in species composition for understanding responses to climate change

Tropical montane forests are vulnerable to climate change because their biota is adapted to continually moist conditions involving high rainfall and frequent cloud immersion (Pounds *et al*., 1999). Rising temperatures could dramatically shift moisture regimes, particularly at transitional sites in premontane forests by increasing the basal altitude at which cloud cover forms (Foster, 2001; Nair *et al*., 2010; but see van der Molen *et al.*, 2010). Decreases in the frequency of cloud cover, as has been observed in lower montane forests in Costa Rica and Mexico (Pounds *et al*., 1999; Barradas *et al*., 2010), could therefore result in upward migration of species from the lowlands, or horizontal migration of species adapted to similar temperature regimes, from leeward mountainsides.

Variation in soil properties on mountains adds another dimension to potential global change effects. At Fortuna, where differences in soil and parent material play an important role in shaping forest composition, migrations must contend with both a reduction in habitat area as migration pushes species off the top of mountains, and with the potential of encountering unfavourable edaphic conditions.

CONCLUSIONS

The premontane forest tree communities at Fortuna differ markedly in diversity and species composition, with almost complete species turnover across just 13 km. As noted in previous studies, compositional variation potentially reflects climate and dispersal limitation, but here we show that soil properties also matter. These effects are unlikely to be unique to Fortuna; mountain uplift often results in landscapes composed on heterogeneous parent material and substrate age (e.g., Aiba & Kitayama 1999). A recent compilation of forest diversity and structure data from elevational transects from Peru, Ecuador and Bolivia shows regional variation in richness at 1000 m elevation (Figure 2.5 in Girardin *et al.*, 2014) that is similar to the local variation observed at Fortuna. Furthermore, and in accordance with plot networks in lowland tropical forests, soil P as well as rainfall patterns appear to drive variation in α and β-diversity in this mid-elevation forest. Nonetheless, the importance of edaphic specialization, and the relative importance of N, P and base cation limitation has received little consideration when interpreting plant responses to environmental change along elevational transects. Additional exploration of ecosystem properties and plant response to fertility gradients may provide new insights into the biogeographic patterns of montane taxa and their future response to global change.

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TABLES

Table 2.1. Number of stems, species number (including morphospecies), rarifed species number per 1000 stems and Fisher's alpha for individuals ≥5 cm and ≥10 cm d.b.h. Percentage of stems ≥5 cm d.b.h. that are of species forming ectomycorrhizal associations (EM), palms, conifers, potential nitrogen fixing taxa (all mimosid and papilionid legumes). Total basal area per plot (m^2 ha^{-1}), and percentage of basal area in each group.

		Rhyolite				Rhy/And transition	Andecite				Basalt	Dacite	
		ChorroA	ChorroB	HondaA	Honda B	Samudio	Bonita	P. Seco	Verrug.A	Verrug.B	Pinola	Hornito	A. Frio
≥10cm d.b.h	Stems	1015	1143	787	935	754	649	617	562	696	784	647	964
	No. Spp.	59	53	120	102	103	77	145	114	126	80	89	75
	Fisher α	13.65	11.49	39.44	29.15	32.25	22.74	59.73	43.17	44.96	22.29	27.95	19.00
≥5cm d.b.h	Stems	1866	2435	1597	1578	1781	1314	1246	1233	1425	1424	1112	1845
	No. Spp	80	68	149	128	141	98	184	151	163	98	108	90
	Spp/1000	67	59	132	113	126	93	170	143	148	91	106	84
	Fisher α	16.9	12.9	40.2	32.9	35.9	24.5	59.6	45.2	47.5	23.9	29.5	19.8
	B. Area	35.1	40.4	46.3	47.4	35.6	32.6	32.5	30.3	30.3	43.6	50.3	42.4
	% for B. Area												
	% EM	8.7	21.8	24.9	46.1	1.8	-	3.9	2.4	1.8	0.02	3.8	7.4
	% Palm	41.9	25.7	0.7	0.3	1.6	0.2	4.5	3.5	4.3	0.2	0.05	0.04
	% Conifer	8.2	6.5	-	0.4	-	-	-	-	-	-	-	-
	% N fixer	0.4	0.1	4.4	4.2	10.8	10.1	16.0	6.9	5.9	11.5	0.3	13.7
	No. Stems												
	Palm	686	697	48	15	86	25	196	190	81	25	9	7
	Conifer	7	5	-	1	-	-	-	-	-	-	-	-

Table 2.2. Mantel and Partial Mantel tests results showing correlation between floristic composition, environmental and geographic distance matrices among twelve lower montane forest plots in Panama. The Env PCA matrix encompasses the first three axes of the principal component analysis (PCA) of all environmental variables. To assess the correlation of individual environmental variables we only included those that were significant ($p<0.05$) in the multidimensional scaling analysis (MDS). Mantel tests were performed between compositional dissimilarity matrices based on Steinhaus index (for abundance and presence/absence) and each environmental matrix. Additionally, each environmental variable matrix was correlated to the geographic distance matrix (Geo. distance) to evaluate if environmental variables are correlated with the spatial component. The floristic composition matrix was also correlated with geographic distance. Partial Mantel tests were performed to evaluate the correlation of floristic dissimilarity with (1) 'Pure environmental' variables, after partialling out the influence of the geographical distance and (2) 'Pure spatial' variables, after partialling out the influence of environmental variables. Values in the table represent the Pearson correlation coefficient (r) and significance was based on 999 permutations (***$p < 0.001$, **$p< 0.01$, *$p< 0.05$).

				Partial Mantel Test			
	Mantel Test			Pure environmental		Pure spatial	
Environmental Variable	Abundance	Pre/Abs	Geo. distance	Abundance	Pre/Abs	Abundance	Pre/Abs
Env PCA	0.54^{***}	0.48^{**}	0.31	0.47^{**}	0.38^{*}	0.42^{**}	0.51^{**}
Rainfall	0.19	0.23	0.13	0.15	0.19	0.49^{**}	0.57^{**}
Dry rain	0.40^{**}	0.50^{**}	0.64^{***}	0.11	0.20	0.35^{*}	0.39^{*}
pH	0.25^{*}	0.29^{*}	0.26	0.14	0.17	0.46^{**}	0.54^{**}
Bulk Density	0.42^{**}	0.53^{**}	0.28	0.33^{*}	0.47^{**}	0.44^{**}	0.52^{***}
Total P	0.45^{**}	0.37^{*}	-0.08	0.57^{***}	0.51^{**}	0.61^{***}	0.66^{***}
Ca	0.46^{**}	0.50^{**}	0.54^{*}	0.26	0.27	0.34^{*}	0.42^{**}
Fe	0.18	0.15	0.11	0.14	0.10	0.49^{**}	0.57^{**}
ECEC	0.45^{**}	0.50^{*}	0.56^{**}	0.24	0.26	0.33^{*}	0.41^{**}
Total Exchangeable Bases	0.47^{**}	0.51^{**}	0.56^{*}	0.26	0.28	0.33^{*}	0.41^{**}
Geographic distance	0.50^{**}	0.58^{**}					

`

FIGURES

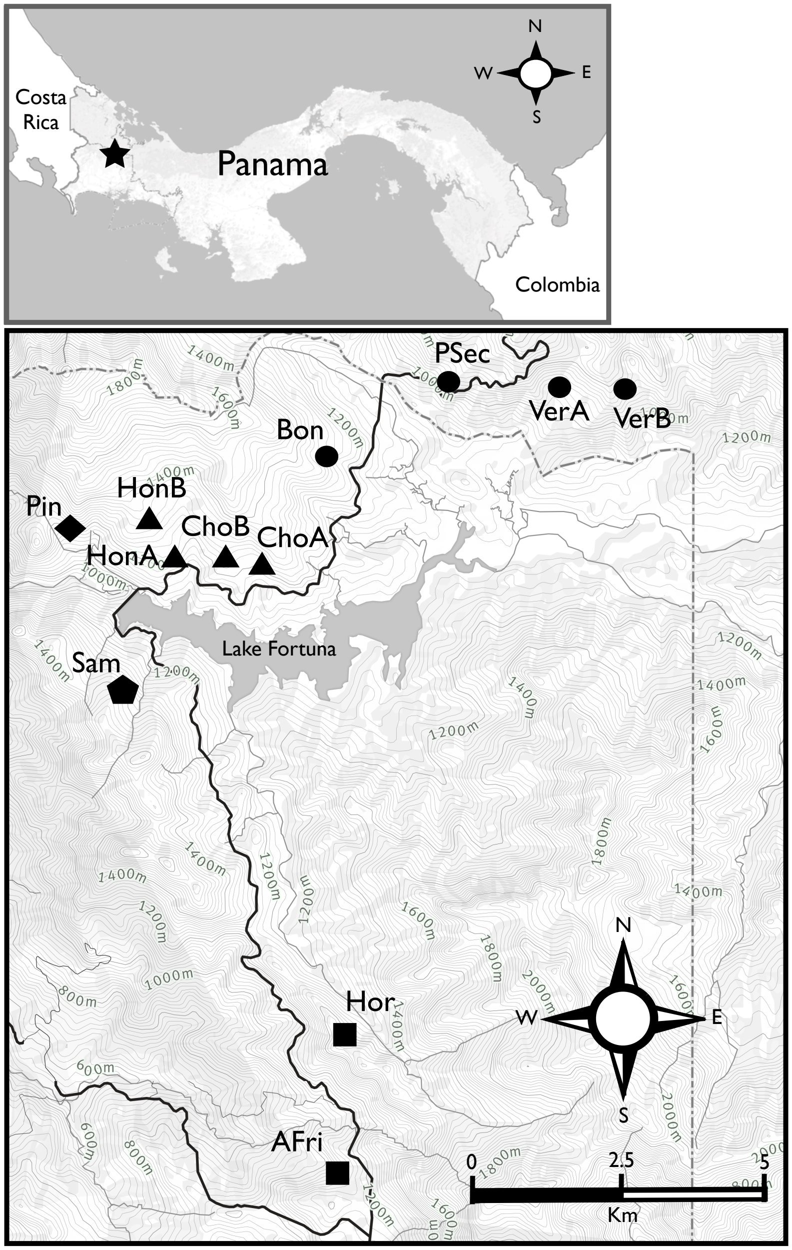

Figure 2.1. Location of the twelve one-hectare forest plots in the Fortuna and Palo Seco forest reserves. High fertility sites derived from porphrytic dacite are shown by square symbols, intermediate fertility andesite (circles) and basalt (diamond), low fertility rhyolite (triangles) and transition between andesite and rhyolite (pentagon)

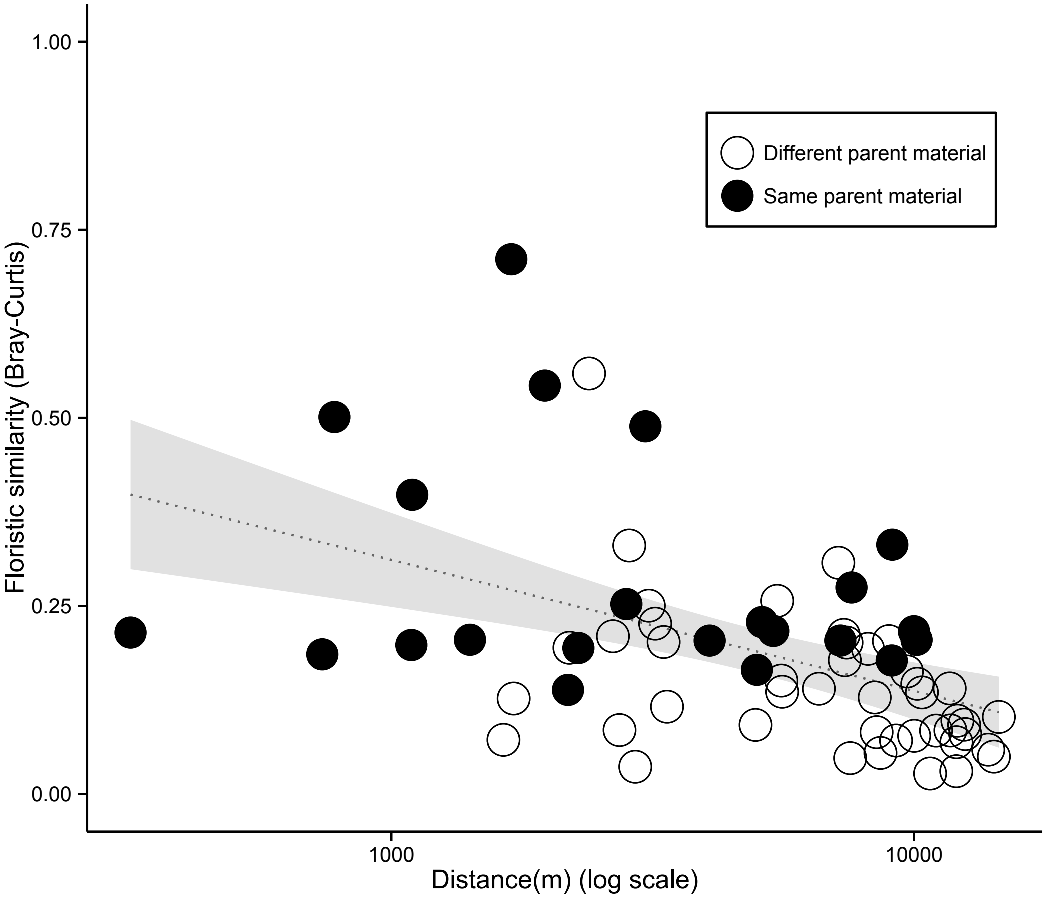

Figure 2.2. Decay in Bray-Curtis floristic similarity based on species abundance between all pairs of one-hectare plots with geographic distance across the Fortuna and Palo Seco forest reserves. Linear regression fit and 95% confidence intervals are shown. Pairs of plots on different parent materials are shown by open circles and pairs on the same parent material by filled circles.

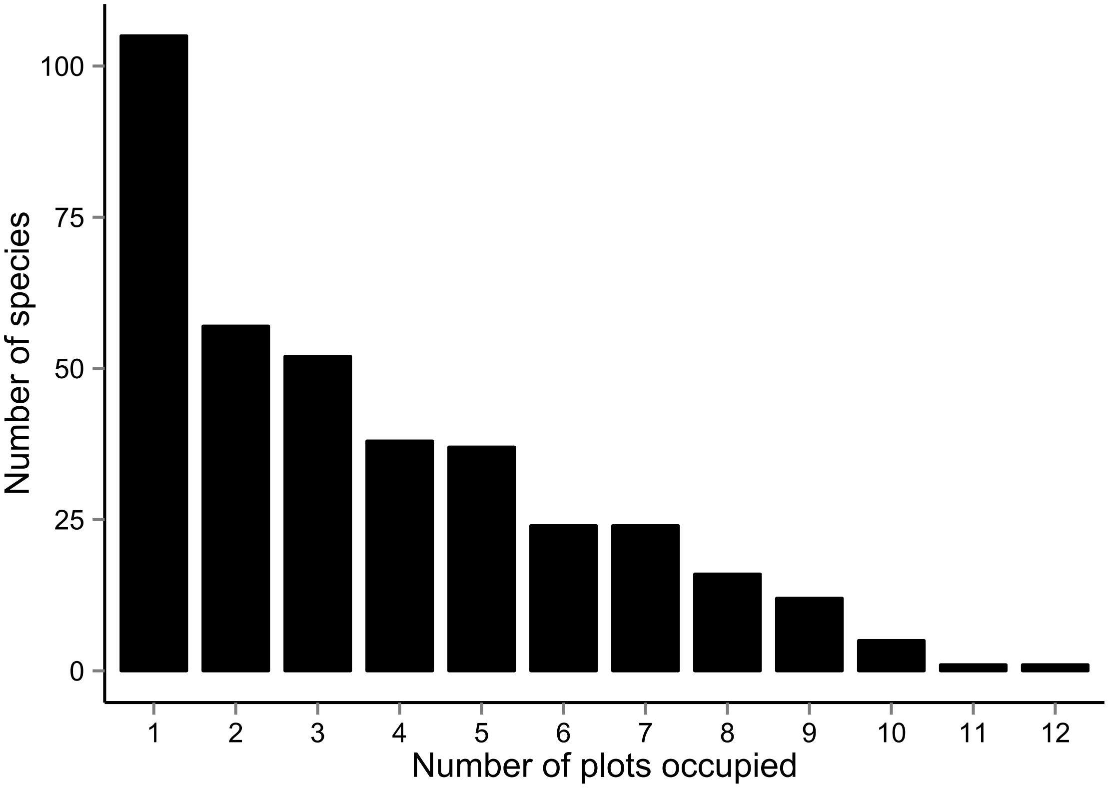

Figure 2.3. The number of plots occupied by each tree species with individuals >5cm DBH.

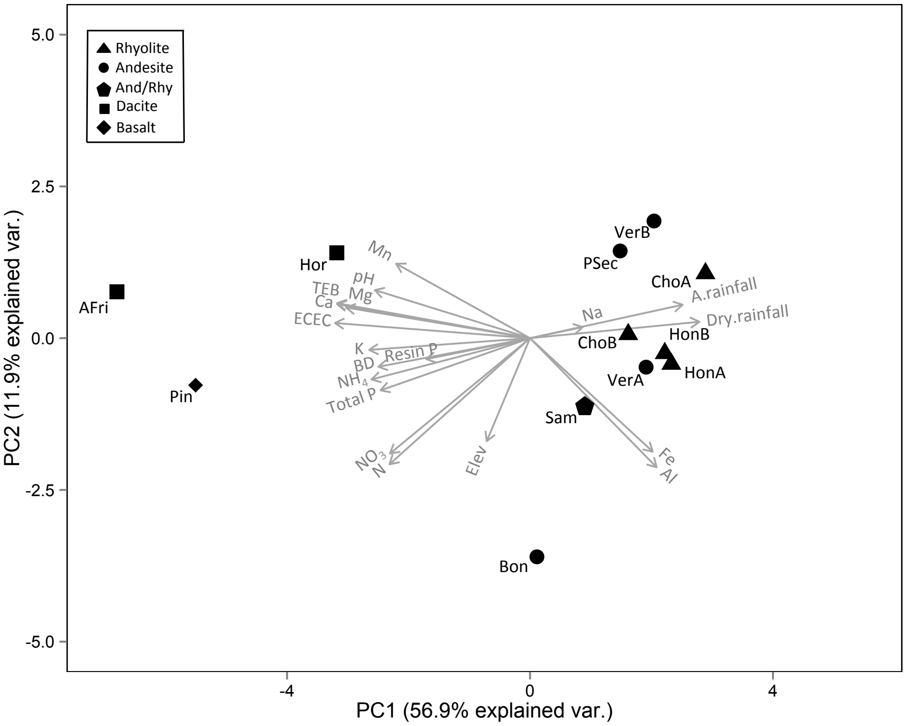

Figure 2.4. Principal components analysis of variation in elevation, rainfall and soils variables for 12 one-hectare plots.

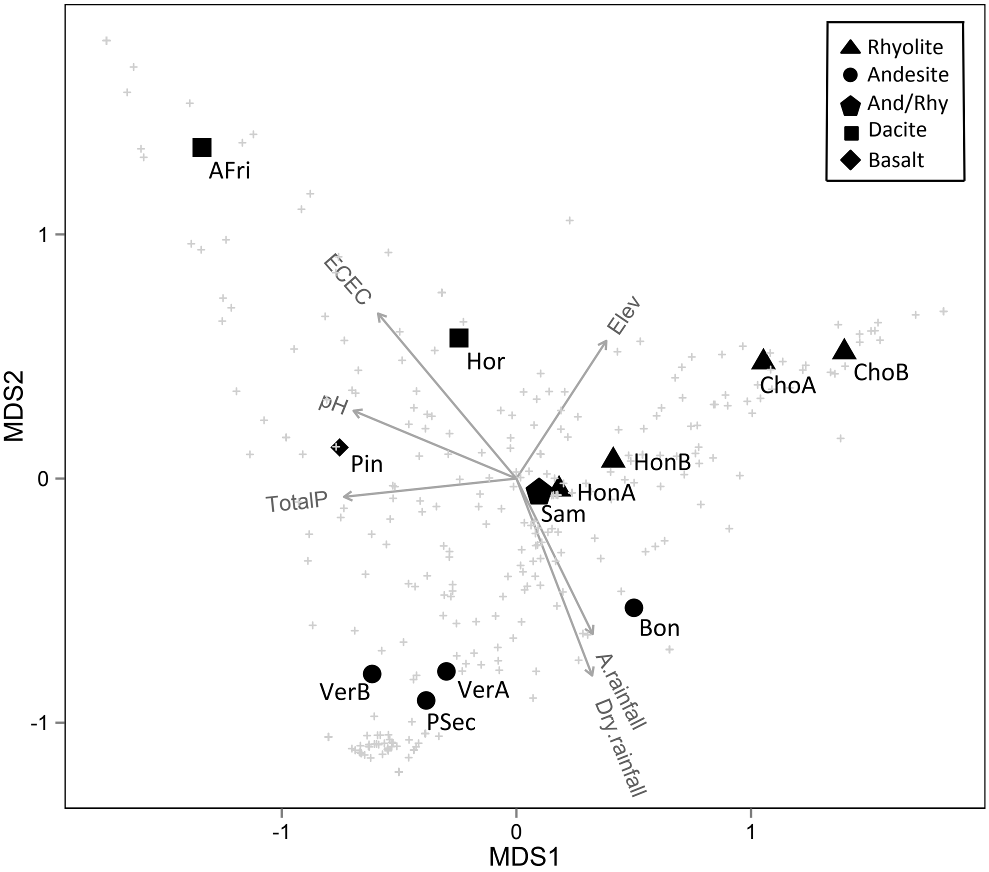

Figure 2.5. Non-metric multi-dimensional scaling (NMDS) ordination for 12 one-hectare plots based on species abundance data. Environmental variables with $P \geq 0.05$ were fitted in the NMDS represented by arrows. Parent material are symbolized by the geometric figures and species are in grey.

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CHAPTER 3: TREE SPECIES COMPOSITION IS ASSOCIATED WITH ENVIRONMENTAL AND BIOTIC INTERACTIONS ALONG AN ELEVATIONAL GRADIENT IN WESTERN PANAMA

ABSTRACT

Tropical montane forests (TMF) have fascinated ecologists for centuries, nevertheless, factors explaining their community assembly are not yet fully resolved. While climate is a major contributor to ecological processes in these forests, recent studies have also highlighted the role of biotic interactions with mycorrhizal fungi in determining biogeochemical processes. Here we take the next step to evaluate the impact of these interactions on tree community assembly. We established nine plots distributed along an elevational gradient ranging from 1600 to 3200 m a.s.l., and where patches are dominated by either EM (oak) or AM (mixed) forest. All trees ≥ 5 cm DBH were censused. We evaluated the effect of elevation on diversity and floristic similarity and the role of EM and AM domination on these patterns. Specifically, we asked: Do potential EM-soil feedbacks impact the beta diversity of montane forests? We found tree species richness declined markedly with elevation, ranging from 7–31 species per 0.1-ha. Furthermore, Fisher's alpha, was significantly lower in EM-oak forests than in AM-forests, averaging 7.7 and 11.1, respectively. We also found that species composition differed between AM and EM dominated forests, with 32% of tree species restricted to EM forest. While floristic similarity decreased with elevation and distance, at intermediate elevation, forests that shared the same mycorrhizal type were more similar in species composition. Finally, after controlling by geographic distance, Partial Mantel analysis showed annual precipitation was also associated with species composition. Our study highlights the importance of key taxa (EM associated oaks) in addition

to climate parameters in shaping the species composition of TMF. Additional studies are needed to fully reveal the mechanisms that generate oak dominance and therefore determine community assembly.

INTRODUCTION

Tree species diversity and composition along elevational gradients in tropical forests has been a focus of attention for scientists since Alexander von Humboldt's expeditions over 200 years ago (Von Humboldt & Bonpland, 1808). Scientists' fascination with tropical montane forests (TMF) reflects the unique hydrological and ecological conditions of these ecosystems, such as high fog water inputs, continually cool temperatures, and topographic and edaphic heterogeneity (Shreve, 1914). Collectively, these contribute to the unique physiognomy of montane forests. Global change predictions suggest tropical forests are responding to changes in temperature, precipitation, and nutrient deposition (Lewis et al., 2004) and that TMF communities are more likely than other tropical forest ecosystems to be severely impacted by these changes in the future (Fadrique et al., 2018; Feeley et al., 2013). Understanding the current determinants of species diversity and composition in TMF is therefore essential to predicting the effects of environmental change on TMF communities and their ecosystem function.

Climate is a major controller of ecological processes in montane forests, as it plays an important role in shaping temperature, precipitation, and can influence soil properties via weathering and leaching. Temperature regimes are tightly coupled to elevation (Muller-landau et al., 2020), which is therefore often used as a proxy for climate. Changes in temperature also affect precipitation regimes, altering fog water input and rainfall patterns by impacting saturation vapor, relative humidity and dew point (Scholl et al., 2011). In montane forests, soil nutrient pools and fluxes also change with elevation, an increase in elevation is generally associated with decrease in N availability and net nitrogen mineralization (Kanehiro Kitayama & Aiba, 2002; Marrs et al., 1988).

Elevational gradients have been used extensively to evaluate changes in species diversity and composition (Clark & Clark, 2000; Culmsee et al., 2010; Gentry, 1995; Gentry, 1988; Lieberman et al., 1996) in tropical montane forests (Aiba et al., 2005; Gentry, 1988; Homeier et al., 2010; Kitayama, 1992). Changes in species diversity with elevation has been attributed to environmental factors such as temperature and precipitation (Gentry, 1995; Vázquez & Givnish, 1998). As has been shown in latitudinal gradients, warmer temperatures are associated with higher diversity (Willig & Presley, 2017).

Shifts in climate and in soil biogeochemistry along elevational gradients can result in narrow elevational and environmental distributions of species. These narrow distributions are expected to be accompanied by shifts in floristic composition. Species in montane forests, especially those at the highest elevations, have low thermal tolerances (Feeley et al., 2020), a condition that limits species distributions across temperature gradients. Species therefore are restricted to particular temperature and precipitation regimes that result in life-zone patterns that were initially described in a general way in Costa Rica by Holdridge et al. (1971), and later extended to several other montane forests (Aiba & Kitayama, 2010; Hemp, 2011; Maarten et al., 1995). Despite clear changes in communities due to temperature and precipitation, plant communities also shift with changes in soil fertility (Condit et al., 2013; Prada et al., 2017).

A less studied aspect of tropical montane forests is the role that biotic interactions such as mycorrhizas and N-fixers have in driving forest diversity and composition. In neotropical lowland forest, the vast majority of trees associate with arbuscular mycorrhizal fungi (AM), that are thought to provide advantages for phosphorus (P) acquisition in P-limited soils (Smith et al., 2003, but see Liu et al., 2018). In Central America, as elevation increases, ectomycorrhizal (EM) associations become more common, providing a competitive advantage in N-limited environments (Read & Perez-Moreno, 2003; Treseder, 2016). In Central America, *Quercus* is one of the most diverse genera of EM hosts (García-Guzmán et al., 2017), providing important ecosystem services (Kappelle & van Uffelen, 2006; Nixon, 2006; Narango et al. 2020). In Panama, the large individual size and basal area of *Quercus* in upper montane forests results in large impacts on key biogeochemical processes of C and nitrogen cycling (Prada et al., chapter 4; Prada et al., chapter 5). While some species of *Quercus* occur in mixed forests, at least two species, *Q. salicifolia* and *Q. costaricensis* in Panama, form monotypic stands (Kappelle et al., 1995; Nixon, 2006). Stand dominance by *Quercus* may be facilitated by their EM association, where mycorrhizal uptake of N from organic matter reduces inorganic N availability to competing AM associated tree species, altering forest composition (Corrales, et al., 2016).

Diversity and composition in montane forests is generally studied in an elevational context where climate is the major driver of community assembly. In this study we include climate, edaphic and mycorrhizal associations to explore the combined effect on these factors on tree communities. To address this aim we established four 1-ha and five 0.2-ha plots distributed across an elevational gradient from 1600 to 3300 m a.s.l in Volcan Baru National Park in western Panama. Across the gradient forest patches are dominated by either EM-associated or AM-associated trees, while nitrogen-fixing trees are rare or absent. We investigated tree species richness and species composition across the elevation gradient and surveyed patches of EM (oak) and AM (mixed) forest to explore how mycorrhizal type covaries with soil characteristics and forest composition. In addition to characterizing alpha and beta diversity patterns we asked whether the presence of EM-associated oak trees reduces the richness of less abundant (subordinate) species. Positive plant-soil feedbacks generated by EM species provide a mechanism that favors conspecific recruitment and that alters nutrient availability (Corrales et al., 2016; Hall et al., 2020; Prada, chapter 5), potentially excluding species adapted to higher nutrient levels. We therefore predict that EM-forests will have lower diversity than mixed AM-forests at similar elevation, and that beta diversity among EM-dominated forests will be lower than that of AM-dominated forests.

MATERIALS AND METHODS

Study Site

This study was conducted on the northeastern slope of the Volcan Baru National Park (VBNP, 8˚49"11'N, 82˚28"58'W) in western Panama. Volcan Baru National Park extends from lower montane forests (1800- 2000 m asl), through cloud forests (>2000 m), to subalpine paramo at the summit (3374 m) (Holdridge 1971). At 2300 m asl, mean annual temperature is 14 ˚C and annual rainfall during 2019 was 2003 mm (C.M. Prada unpublished). The parent material of VBNP is Holocene lahar flow deposits with periodic tephra inputs and the soils can be classified as basaltic, or andesite (Sherrod et al., 2008).

In 2015, nine plots — four 1-ha (100 × 100 m) and five 0.2-ha (50 × 40 m) — were established along an elevational gradient from 1600 to 3300 m asl (Figure 3.1). Seven plots were established within Finca El Velo, a private in-holding in Volcan Baru National Park, along the eastern slope of the volcano. Of the remaining plots, Hope A was located at La Esperanza, a private farm valley 5 km east of the lowest elevation El Velo plot, while the Volcan plot was located just below the tree line 2 km west of the highest elevation El Velo plot along the road to the summit of Volcan Baru (Figure 3.1). All trees with ≥ 5 cm diameter at breast height (DBH) were measured, tagged, mapped, and identified to the lowest taxonomic level possible. When a species identification was not determined a morphospecies was designated. Species were designated to ecological groups based on literature (AM and EM associated species: Averill et al., 2019; Corrales et al., 2018; Soudzilovskaia et al., 2020) and N-fixers (Huss-Daniel, 1997; Sprent, 2009). Species from the genus *Quercus* (Fagaceae) and *Oreomunnea mexicana* (Juglandaceae) were the EM-associated trees on this gradient.

Environment and climate across the elevation

Soil data for the 1-ha plots were collected in May 2016, and in December 2018 for the 0.2-ha plots. Soil samples were taken from the surface 0–10 cm of soil after removing the litter layer. For the larger plots, thirteen locations were sampled per plot, and ten locations per plot for the smaller plots. Bulk density (BD), pH, extractable inorganic N (NH_4 and NO_3), total N, P, and C were quantified. Inorganic N concentrations (ammonium, nitrate) were determined by extraction in 0.5 M K_2SO_4 for 1 h, with detection by automated colorimetry on a Lachat Quikchem 8500 (Hach, Manchester, UK) following the same protocols in Prada et al. (2017). One soil sample was collected in every other 20 × 20 m subplot within the 1-ha plot and every other 10 × 10 m in the 0.2-ha plot for a total of thirteen and ten locations, respectively. For the small plots BD, total C, N, and P were not available from plot sampling locations; data from the surface 0–10 cm of a profile pit 1.5 m from the edge of the plot was used instead.

Climate data across the gradient were obtained from the CHELSA database (http://chelsa-climate.org) at 30 arc-sec spatial resolution (Karger et al., 2017; Karger et al., 2018) for each plot. We extracted three variables that have that have been shown to be important in structuring forest composition: MAT (mean annual temperature), MAP (mean annual precipitation) and ISO (isothermality). Isothermality represents the ratio of diurnal to annual temperature variation. Additionally, to account for the topography in the plots we extracted the slope from the 30 m digital elevation model (DEM) (https://stridata-si.opendata.arcgis.com/datasets/panama-30m-dem).

A principal components analysis (PCA) was used to examine differences in environmental variables among plots. The eleven soil and climate variables were standardized with zero mean and standard deviation of 1 before the analysis. Interactions between soil variables (BD, pH, extractable inorganic N (NH_4-N and NO_3-N), total N, P, and C) and forest type (AM vs EM) were analyzed using a MANCOVA with elevation included as a covariate. The analysis was performed using the *jmv* R package (Ravi et al., 2020)

Species richness and composition

Variation in species richness among plots was compared using accumulation curves, with 95% CI of species richness after rarefaction of 100 stems per plot. Fisher's alpha was used to compare species diversity among plots. However, due to differences in sizes, 1-ha plots were divided into twenty 50 × 10 m subplots and 0.2-ha plots into four 50 × 10 m subplots, and mean values of Fisher's alpha for subplots used to compare plots. To evaluate species turnover across the sites a Steinhaus dissimilarity matrix was calculated using the Bray–Curtis method based on species abundance. This matrix was converted to a similarity matrix to examine the decay of floristic similarity with elevation and geographic distance. The plots' coordinates were recorded using a Garmin GPSMAP 60CSx GPS to establish elevation and geographic location. Using GPS location, geographic distances between plots were calculated the *raster* R package (Robert et al., 2020). Elevation and geographic distances were converted to two matrices using a Euclidean index. Analysis of similarity (ADONIS) was used to examine differences in plots and forest types (EM- vs AM-dominated) on species composition.

Environmental variables and species composition

To visualize compositional variation among sites we performed a NMDS ordination using species abundances. Edaphic, climate and slope variables were fitted to the NMDS to evaluate how environmental variables are associated with floristic composition. Additionally, mantel tests were performed to examine correlations between floristic composition based on abundances, environmental, and geographic distance matrices. Partial mantel tests were used to correlate floristic composition with environmental and biotic factors while controlling for geographic distance ("pure environmental/biotic") and between tree community and geographic distance controlling for environmental variables ("pure spatial"). In addition, we generated a biotic matrix to examine the contribution of ecological groups (EM, N-fixers) calculated as the percentage of the total basal area of the plot on species composition. Pearson correlation coefficients were generated for pairs of matrices using randomization tests with 999 permutations in the *vegan* R package (Jari et al., 2019). All statistical analyses were conducted in R version 3.6.3 (R Development Core Team, 2020).

RESULTS

Collectively, for the nine plots established along the elevation gradient there were 5861 trees ≥ 5 cm DBH, 94 species and 117 morphospecies —74 identified at least to genus level, 26 to family, and 17 unidentified, distributed in 63 families (Table B.1). Three forest types were distinguished across the elevation gradient: two types of EM-dominated forests — oak-dominated and *Oreomunnea mexicana* (Juglandaceae)-dominated, and mixed (AM-dominated) forests (Table 3.1). The oak-dominated forests were located at the high elevations, starting at 2100 and continuing to approximately 3000 m asl, however, some small patches of this forest type were observed at lower elevations, extending down to 1900 m asl. Oak forests were dominated by either *Quercus salicifolia* (AUL and CASA), *Q. costaricensis* (QUE and COP) or a mix of the two species (CASB) representing 46.6 to 63.8% of the total basal area of the plot. An *Oreomunnea mexicana*-dominated forest (HOPA) was located at 1679 m asl, with this species contributing 48.2% of the total basal area. Mixed forests (that lack a dominant species) occurred at 1762, 1987, and 3253 m asl (Table 3.1). The dominant taxa in the lower elevation plots were *Ulmus mexicana*, *Ocotea laetevirens*, *Cornus discifloral* and *Magnolia sororum* and in the high elevation plot (VOL) *Oreopanax striatus*, and an unidentified *Miconia* sp and some individuals of *Vaccinium consanguineum.* At the lower elevation mixed forest plots a third oak species, *Q. insignis*, was present in low densities. Relative abundances of trees associated with EM, as well as N-fixers, varied across plots (Table 3.1).

Alpha and beta diversity

Using 50 × 10 m subplots we found number of species ranged between 7 ± 0.4 and 31 ± 0.7, while between 9 to 34 species were found when 100 stems per plot are sampled (Table 3.1, Figure B.1). The richness by subplots and richness per 100 stems significantly decreased with increasing elevation (both $r^2 = 0.7$, $p < 0.001$, Figure 3.2a,b). Richness was highest at the lowest elevation plot (HOPA) and lowest at the highest elevation plot (VOL). Richness in oak-dominated forest show a range of 11-21 tree species. After controlling for elevation, Fisher's alpha determined for 50 × 10 m was significantly different between oak and mixed forests ($F_{(1,93)} = 69.6$, $p < 0.001$). Fisher's alpha was low in the oak forest compared to mixed forest stands (7.7 ± 0.7 and 11.1 ± 3.6, respectively). Fisher's alpha determined for 50 × 10 m subplots showed a near-identical pattern to richness (Table 3.1). Compositional similarity was conducted by plot and not by 50 × 10 m subplots to avoid pseudo-replication. Compositional similarity declined across 1574 m of elevation and 12 km of geographic distance ($r^2 = 0.31$, $p < 0.0001$ and $r^2 = 0.24$,

$p < 0.001$; Figure 3.2 c,d), with an almost complete turnover of species across the entire gradient (floristic similarity <0.1). At middle elevations among plot variation in compositional similarity was partly due to differences in forest type, with greater similarity among plots that shared the same mycorrhizal dominance class (EM vs AM forests) (ADONIS: F = 1.4, $p < 0.05$), even when controlled by elevation (ADONIS: F = 1.5, $p < 0.05$). Out of a total of 211 taxa, 75 were only found in the EM forests and 50 were only found in AM forests. Comparing MIR-mixed forests and CASA-oak forest that are 1284 m apart, have the same size (1-ha) and similar elevation (1987 and 2248, respectively), we found in total 89 species, of which 29 were only present in the oak forest (32%), 43 were only present in the mixed forest (48%), and only 17 were in common. The most important species associated with oak forests based on stem number include *Rogiera amoena, Ardisia subsessilifolia, Vaccinium consanguineum and Weinmannia pinnata*. No species were found in all EM forest plots. However, *W. pinnata*, *Turpinia occidentalis* and *Dendropanax sp1* were present in five out of six plots.

Edaphic and climate variation among plots

Soil characteristics varied markedly across plots (Table B.2). Bulk density varied seven-fold, and pH ranged from 3.94 to 5.98. Variation in nitrogen availability across plots was also high; there was 20-fold variation in NH_4-N and nearly 200-fold variation in NO_3-N. Plot differences in total nutrient pools were smaller, and mostly reflected differences in organic matter content. Total N was highly correlated with total C ($r^2 = 0.90$, $p < 0.001$). Total N varied three-fold and total P six-fold across plots. Edaphic variables measured in this study did not correlate with elevation (Table B.3). However, MAT was negatively correlated, and MAP and ISO positively correlated with elevation (Table B.3). The first two axes of the PCA of soil and climate data explained 68.9% of the variation across plots. Plots did not group together according to forest type (Figure 3.3a). Climate variables loaded most strongly on PC1 and soils on PC2 (Figure B.2). When elevation was included as a covariate the edaphic variables did not differ between forest types (AM vs EM) (Wilk's $\lambda = 0.28$, $F_{(6,1)} = 0.526$, $p = 0.78$).

Environmental effects on compositional variation

Elevation, and the three climate variables MAT, MAP, and ISO, were significantly correlated with tree species composition, with vectors broadly aligned with NMDS axis 1 (Figure 3.3b). The second axis of the NMDS largely separated the three mixed forest plots from EM-dominated forests. In the EM-oak dominated forests three plots, CASB, CASA and QUE, which are dominated by *Q. salicifolia* were grouped together. Species composition in these plots was associated with high values of NH_4 and BD, however, edaphic factors were not significantly correlated with compositional variation. Species composition, determined for 50 × 10 m subplots, showed AM-mixed forests grouped together by plots and that there was a separation from EM-forest. EM-oak forests subplots clustered together by plot, however, overall the oak forest plots grouped together (Figure 3.4).

Simple mantel tests showed that environmental variables (env PCA), climate factors including MAP and ISO, biotic factors (% EM and % N-fixers), elevation, and geographic distance all showed significant correlations with floristic dissimilarity among plots (Table 3.2). Partial mantel tests showed floristic dissimilarity was significantly correlated with MAP and biotic factors after controlling for spatial variation (geographic distance).

DISCUSSION

We examined α- and β diversity of tree communities and its relationship to environmental variation along an elevational gradient in western Panama. While alpha diversity decreased markedly with elevation as expected, beta diversity also revealed large compositional shifts in tree species often over very short spatial scales. Soil conditions were highly variable among the plots, particularly for macronutrients (N and P) that potentially limit plant growth. Overall, tree community composition and diversity were correlated with climate and soil variables, and with the presence of key functional groups quantified as the percent of EM associated.

Plant diversity in montane forests

We found tree species diversity decreased with elevation, a trend that has been well-documented for several tropical montane forests (Aiba et al., 2010; Homeier et al., 2010; Kappelle et al., 1995; Lieberman et al., 1996). We recorded a total of 221 taxa in this study, at sites ranging from 1600 to 3200 m asl. This is a relatively small species pool compared to Andean forest (125 species at 1800 and 2100 m, compared to 73 species in this study; Webster & Rhode, 2007; Homeier et al., 2010). Lower species richness is consistent with smaller regional species pools in Central American montane forests, but may also reflect the predominance of oak-dominated forest at our sites. In our study, at 50 × 10 m diversity was low in oak forest compare to mixed forest with species richness ranging between 11 (44 stems) and 21(76 stems). Richness in oak forest in Colombia in two 0.1-ha plots was lower (39 – 42 in 357 and 453 stems respectively), compare to mixed forests (55- 81 in 297 and 361 stems respectively) (Prada & Stevenson, 2016). At the EM forest site of HOPA (1679 m) dominated by *Oreomunnea*, species richness per 100 stems was similar to EM forest dominated by *Oreomunnea* at 1100–1200 m asl, in the Fortuna Forest Reserve (Prada, unpublished data) (34 and 42, respectively).

Changes in edaphic and climate factors related to floristic composition

In montane forests environmental variables such as temperature, precipitation or nutrient availability vary significantly across sites. In general in the tropics variation in temperature is explained by changes in elevation (Muller-Landau et al., 2020). In our study, precipitation was also highly correlated with elevation – a pattern that has been found in mountains in Bolivia (Schawe et al., 2011). However, this pattern may also reflect interpolation algorithms used to generate precipitation estimates in CHELSA. More generally, rainfall patterns in montane forests tend to be complex, reflecting the movement of air masses along windward slopes (Kappelle & van Uffelen, 2006) or microhabitats created by local topography (Moser et al., 2008, Dalling et al. 2021). At the same time, climate regimes and elevation in montane forests contribute to edaphic heterogeneity. High precipitation and low temperatures are known to decrease nutrient availability due to leaching (Homeier et al., 2010; Schawe et al., 2007) and low N mineralization rates caused by low decomposition rates at high elevations (Marrs et al., 1988; Tanner et al., 1998). Under these conditions it is common to find species with higher nutrient use efficiency (Asner & Martin, 2016; Dalling et al., 2016). In our system we found large variation in inorganic N which is attributable to elevation and mycorrhizal effects (Prada et al., chapter 5) and also in total P among plots, which may be explained by the geological history of the site. The last eruptive episode, on Volcan Baru, 500 years ago, likely included widespread tephra fallout, pyroclastic flows, and lahars (Sherrod et al., 2008); recent volcanic ash inputs may therefore have increased phosphorus availability.

In tropical montane forests, rapid tree species turnover can reflect aspect and even quite small elevational changes (Shreve 1914; Gentry, 1988; Gentry, 1995; Clark & Clark, 2000; Culmsee et al., 2010). Supporting these well-known patterns, we found in our system species similarity decreased with elevation and geographic distance. Likewise, changes in soil properties have a significant effect on floristic distribution and composition (Condit et al., 2013; John et al., 2007; Prada et al., 2017; Umaña et al., 2021). For example, in lowland forest in central Panama compositional turnover in the Panama Canal watershed is strongly associated with soil P availability (Condit et al., 2013).

In a premontane forest at Fortuna, Panama, high species turnover reflects differences in parent material and is associated with soil fertility (Prada et al., 2017). At Fortuna, EM trees—represented mainly by *Oreomunnea* are most abundant on infertile rhyolite-derived soils resulting in large changes in soil N associated with EM composition. EM trees are capable of driving declines in N availability, generating feedbacks that favor conspecific recruitment (Corrales et al., 2016; Hall et al., 2020). Furthermore, low nitrogen availability associated with EM trees is expected to alter forest structure and composition by conditioning the forest to species that tolerate the new soil conditions.

Species composition in EM and AM forests

Studies have shown forest dominated by EM trees have low N mineralization rates and are depleted in N availability in temperate forests (Lin et al., 2017; Phillips et al., 2013) and in the tropics (Corrales et al., 2016; Dalling et al., 2021; Prada et al., chapter 5). Non-EM species may need particular functional traits for N uptake or use efficiency to maintain populations in EM-dominated forest . We found floristic composition in EM and AM-dominated forests were significatively different even when controlling for elevation. Ectomycorrhizal forests occurred all across the elevational gradient, except at the highest plot (VOL: 3235 m a.s.l), and EM dominated forest plots were censused close to AM dominated forests. For example, two EM forest stands (AUL: 0.2-ha and CASA: 1-ha) were close in distance (<150 and < 1500 m, respectively) to MIR, a mixed forest. When sites of similar size and elevation were compared we found 32% of tree species were restricted to EM forest plots. Furthermore, we found that the most abundant AM tree species that occurred in EM forests tended to be sub-canopy species (e.g., *Rogiera amoena* and *Ardisia subsessilifolia*).

In Central America and the Colombian Andes, oak forests are majors components of ecosystems in which they occur (Kappele & van Uffelen, 2006; Nixon, 2006; Narango et al. 2020). Their contribution to biogeochemical processes such as C and N cycling is remarkable (Prada et al., chapter 4; Prada et al., chapter 5). Additionally, oak forests harbor unique tree communities and contribute to the landscape beta diversity of montane forests. Understanding factors influencing biogeochemical processes in these forests will e indispensable to predicting their responses to climate which could thus inform conservation efforts.

TABLES

Table 3.1. Summary statistics for trees ≤ 5 cm DBH found in nine plots along an elevational gradient in western Panama. Number of stems per plot, species per plot and per 50 × 10 m subplot, species per 100 individuals, Fisher alpha by plot and for 50 × 10 m subplots, basal area per ha, and percentage of stems represented by species forming EM associations and N-fixers.

Plot name	**Plot code**	**Elevation (m a.s.l)**	**Size (ha)**	**Type of forest**	**No. Stems**	**No. Spp**	**No. Spp (50 × 10 m)**	**No. sp/ 100**	**Fisher α plot**	**Fisher α subplots**	**Basal area (m^2ha^{-1})**	**% EM**	**% N-fixers**
HopeA	HOPA	1679	0.2	EM-*O. mexicana*	377	55	31±0.7	34	17.0	16.2 ±0.4	71.8	52.1	0.8
Bodega	BOD	1762	0.2	AM-mixed	156	31	16.5±2	26	11.6	10.9±1.1	72.4	0.4	0.0
Mirador	MIR	1987	1	AM-mixed	998	60	21.1±0.7	32	14.82	14.9±1.02	47.9	1.16	4.9
Aulladores	AUL	2014	0.2	EM-oak	304	37	21.0±0.7	25	11.04	9.89±1.02	63.2	61.5	5.2
CasitaA	CASA	2248	1	EM-oak	1519	46	17.8±0.5	21	8.9	7.54±0.2	51.7	68.9	0.4
CasitaB	CASB	2380	0.2	EM-oak	329	30	19±0.9	19	8.0	8.22±1.3	62.9	63.4	0.0
Quetzal	QUE	2599	1	EM-oak	1152	54	16.5±0.5	23	11.11	8.08±0.3	59.2	46.69	1.9
Copete	COP	2923	1	EM-oak	879	34	10.8±0.4	17	7.0	4.99±0.3	59.2	63.8	6.7
Volcan	VOL	3235	0.2	AM-mixed	147	10	7±0.4	9	2.42	2.61±0.03	64.4	0.0	0.0

Table 3.2. Mantel and partial Mantel test results showing correlations between floristic distance, environmental, biotic and geographic distance matrices among nine plots in an elevational gradient in western Panama. Env PCA encompasses the first three axes of the PCA of all environmental variables. Only variables that were significant ($p < 0.05$) in the MDS were used for individual correlations. Values represent the Pearson correlation coefficient (r) and significance was based on 999 permutations.

	Mantel		Partial Mantel	
Variable	Abundance	Geo. Distance	Pure environmental/biotic	Pure Geographic
Env PCA	0.54***	0.31	0.42*	0.43
MAT	0.60***	0.66**	0.40*	0.19
MAP	0.74***	0.61*	0.62**	0.10
ISO	0.54**	0.29	0.48*	0.44
Biotic	0.35*	-0.09	0.47*	0.59*
Geographic	0.51*			

***$p < 0.001$, **$p < 0.01$, *$p < 0.05$

FIGURES

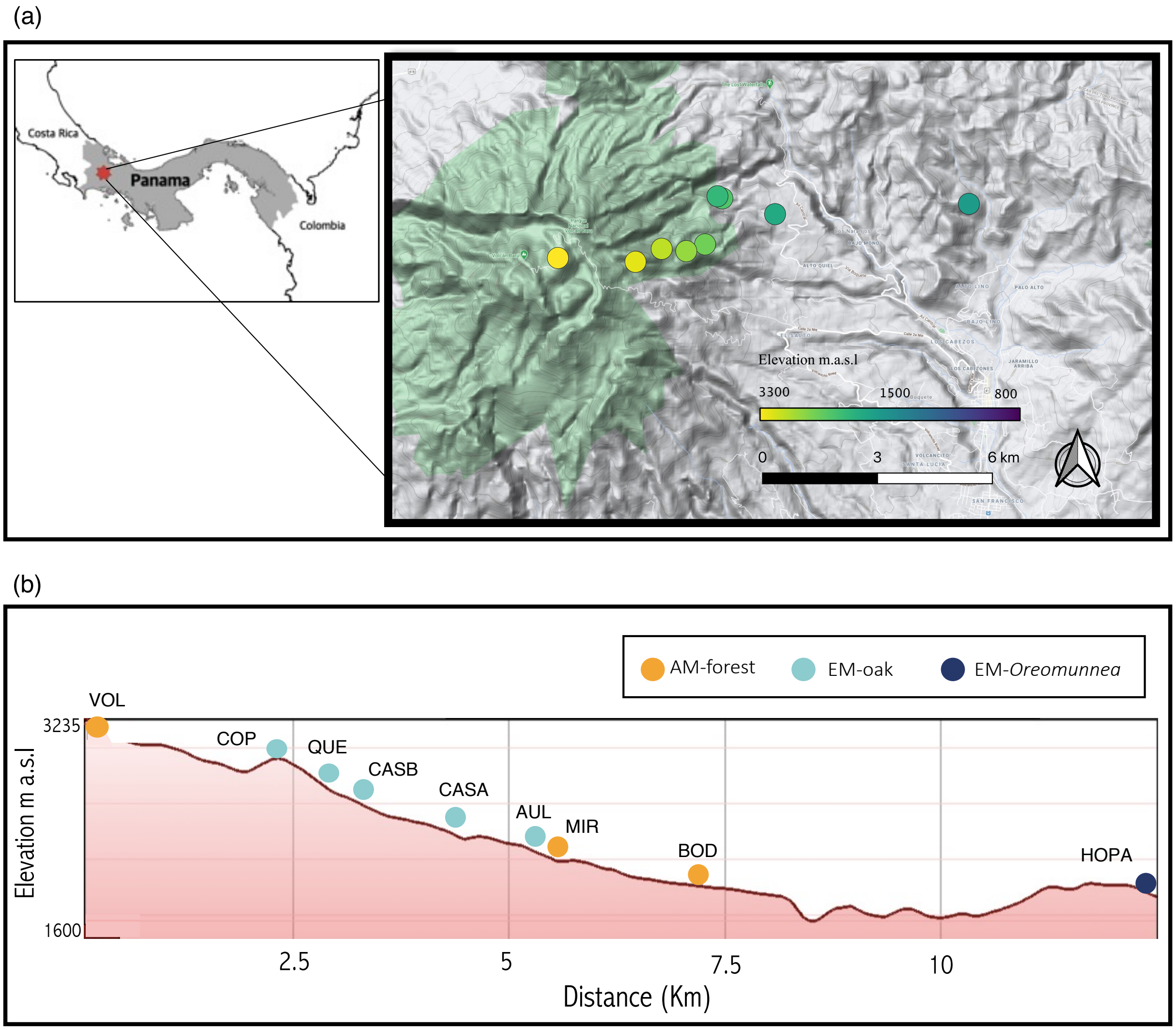

Figure 3.1. Map of Volcan Baru National Park (VBNP) showing the location of nine plots across an elevational gradient in western Panama. Each circle represents a plot, colors represent (a) elevation and (b) forest type (plots are designated as EM-oak or EM-Oreomunnea if EM taxa accounted for > 50 % of plot basal area).

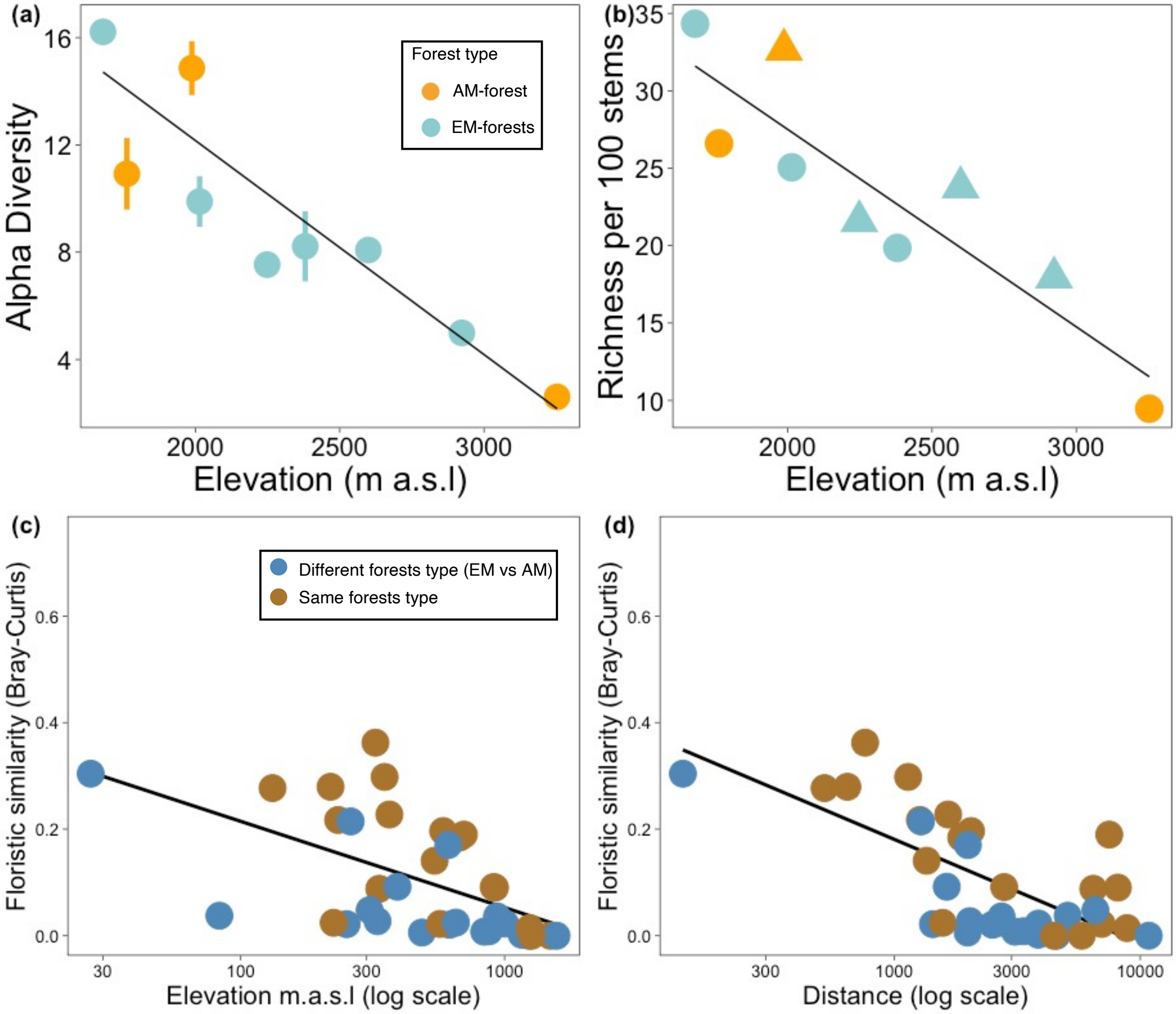

Figure 3.2. Alpha diversity (a, b) and β-diversity (c, d) of nine plots along an elevational gradient in western Panama. (a) Mean species richness by 50 × 10 m subplots data ± SE (missing bars are too small to appear in the figure); (b) Richness per 100 stems, circles represent 0.2-ha and triangles represent 1-ha plots. Relationship between β-diversity and (c) interplot elevational difference, and (d) geographic distance. Each point represents one pair of plots.

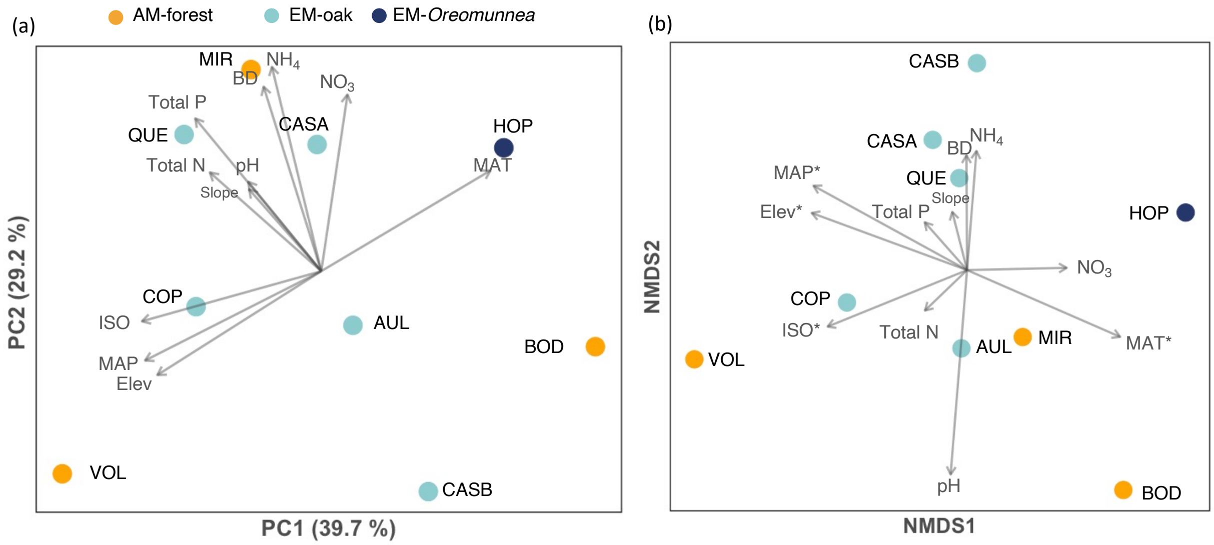

Figure 3.3. (a) PCA of edaphic and climate variables associated with nine sites; (b) NMDS ordination based on species abundance. Environmental variables fitted to the NMDS are represented by arrows. * represents variables where $p < 0.05$. BD = Bulk density; MAT = mean annual temperature; MAP = mean annual precipitation; ISO (isothermality).

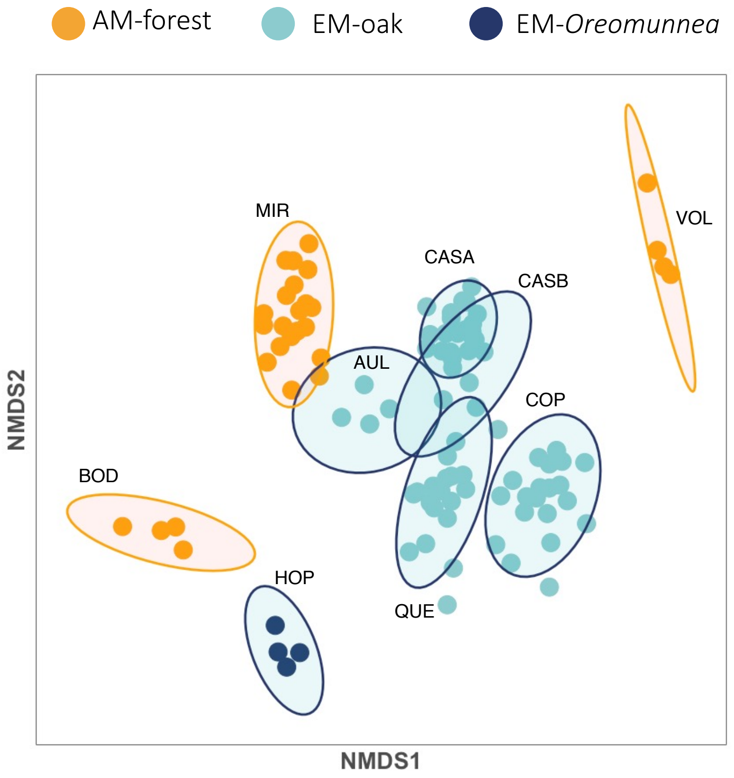

Figure 3.4. NMDS ordination based on species abundance in 50 × 10 m subplots. Ellipses represent 95% confidence intervals for plot.

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CHAPTER 4: DRIVERS OF EXCEPTIONALLY HIGH SOIL AND BIOMASS CARBON STORAGE IN CENTRAL AMERICAN MONTANE FORESTS

ABSTRACT

Tropical montane forests (TMF) play a key role in the global carbon cycle and in climate regulation by sequestering large amounts of above and belowground carbon. Elevation gradients in TMF have helped reveal the influence of environmental factors, and more recently, mycorrhizal associations on carbon stocks. However, the influence of elevation and soil nutrient availability on C stocks have not been evaluated for ectomycorrhizal (EM) associated forests in the Neotropics. We estimated aboveground biomass (AGB), coarse wood debris (CWD), and soil C based on field inventories in ten 1 ha plots along an elevational gradient from 880 to 2920 m a.s.l varying in relative abundance of EM-trees in western Panama. Trees ≥ 10 cm diameter at breast height (DBH) and CWD ≥ 10 cm diameter were measured to calculate biomass and necromass. Soil C to 1 m depth was estimated. Furthermore, climate and edaphic characteristics were described for each plot to evaluate the influence on these variables on each C pool. AGB, downed CWD and soil C were strongly positively correlated with elevation. We found exceptionally high AGB, up to 574.3 Mg ha^{-1}, and soil C, up to 577.9 Mg ha^{-1} at higher elevations. Variation in total CWD within and among plots was high ranging from 14.75 to 326.5 Mg ha^{-1}. After controlling for elevation, neither nutrient availability nor EM-dominance had an effect on AGB or soil C. High AGB at high elevations was attributed to the presence of *Quercus* species. Remarkably high soil C at high elevations might be a consequence of low temperatures decreasing decomposition rates that accumulate soil C, or geological history, where volcanic eruptions buried surface soil organic layers. Our results highlight the uncertainty in C pool

estimates in tropical montane forests, where further research is needed to correctly estimate and evaluate C stocks.

INTRODUCTION

Tropical forests store ~40-50% of the total C in terrestrial ecosystems (Meister et al., 2012; Pan et al., 2011, 2013), and therefore play a key role in the global carbon cycle and climate regulation (Keenan & Williams, 2018; Malhi & Grace, 2000; Mitchard, 2018). This carbon is sequestered in several pools, consisting of live biomass, necromass (i.e. coarse woody debris), and soil. Estimating of the size of each pool is critical to evaluating uncertainty in future global C budget predictions. While it is well known that climate and edaphic processes influence carbon stocks (Clark et al., 2002; Girardin et al., 2010; Gerald Moser et al., 2011), mycorrhizal interactions have also been shown to have a significant impact on C cycling at the global scale (Averill et al., 2014; R. P. Phillips et al., 2013; Steidinger et al., 2019). Evaluating the effects of these factors on tropical forest C stocks is an important step in predicting future atmospheric CO_2 levels (Keenan & Williams, 2018).

Studies along elevational gradients in the tropics, especially in the Andes, have been shown to be powerful natural experiments to understand how the environment directly and indirectly influences processes related to carbon cycling (Malhi *et al.* 2010, 2017, Girardin *et al.* 2014, Nottingham, *et al.* 2015, Duque *et al.* 2021). Factors such as temperature, cloud cover, precipitation, nutrient availability, and species turnover change as elevation increases, affecting aboveground biomass, woody debris and the soil C stock. High temperatures in the lowlands are typically associated with fast plant growth rates; in the Amazon, studies have shown faster growth rate is associated with lower mean wood density (Baker et al., 2004; Malhi et al., 2004), which may suggest low aboveground biomass at low elevations. On the other hand, in upper montane forests, low temperatures can have an effect on soil carbon accumulation (Nottingham, et al., 2015).

While elevational gradients can help us to understand how temperature influences ecosystem carbon stocks, additional confounding factors may vary with elevation. In montane forests soil nutrient availability can vary over short geographic scales, associated with variation in parent material and substrate age (Prada et al., 2017). It is clear that soil nutrient availability impacts forest productivity and therefore carbon sequestration (Muller-Landau et al., 2020). However, effects of soil properties on AGB in the tropics are often contradictory, showing positive, negative, and no relationship (Muller-Landau et al., 2020). Furthermore, soil nutrient availability influences tree tissue nutrient content and therefore litter quality and decomposition rate (Aerts & Chapin, 2000). Recalcitrant tissues with low nutrient concentrations decompose slowly and increase soil carbon sequestration due to their long residence time in soil (De Deyn et al., 2008). However, it has also been suggested that fast-decomposing labile tissues can remain in the soil as mineral-stabilized soil organic matter protected in the soil, and thus increase soil C (Cotrufo et al., 2013).

While environmental factors play a critical role in forest structure and function, plant mutualisms with microbes also strongly impact soil C storage. Ectomycorrhizas (EM) and arbuscular mycorrhizas (AM) are thought to influence C stocks via effects in decomposition rates (Averill et al., 2014; De Deyn et al., 2008; R. P. Phillips et al., 2013). Studies have found forest trees associated with EM fungi promote slow C cycling compared to tress associated with AM fungi (R. P. Phillips et al., 2013; Soudzilovskaia et al., 2019). In temperate forests this may in part result from lower quality litter in EM than AM-trees, resulting in slower decomposition (Craig et al., 2018; Keller & Phillips, 2019). Additionally, soil C storage through the soil profile also appears to depend on mycorrhizal type; soil beneath EM trees stores more C in the surface layers while a greater proportion of soil C can be stored in deeper soil layers beneath AM-trees (Craig et al., 2018).

In this study we estimated the size of three C pools: aboveground biomass (AGB), coarse wood debris (CWD), and soil C in ten 1 ha plots along an elevational gradient in western Panama to further evaluate the influence of climate, edaphic and biotic factors on each pool.
This is the first study in EM-associated forests that integrates both the effect of soil nutrient availability and elevation on C stocks in the Neotropics. Studies in western Panama provide new insights into the drivers of carbon storage because the dominant ecological group shifts with elevation, from AM dominated forests at low elevations to EM dominated forests at high elevation. We hypothesized that i) a reduction in temperature with increasing elevation results in reduced growth rates, increased wood density and therefore increased AGB, CWD, and soil C storage; ii) decreasing nutrient availability favors trees with conservative nutrient cycling strategies (Soong et al., 2020) (i.e., high wood density, low nutrient concentration), resulting in higher AGB accumulation in low soil nutrient availability sites. Furthermore, wood from low soil nutrient availability sites has lower nutrient concentrations (Heineman et al., 2016), resulting in slower decomposition and the accumulation of CWD and soil C. iii) Forests associated with EM tree species have high overall C storage, EM taxa that form monodominant stands in tropical forests have previously been associated with low nutrient soils (Hall et al., 2020), tend to have conservative nutrient cycling strategies (Phillips et al., 2013) and have been associated with soils with higher C:N (Averill et al., 2014; Lin et al., 2017). Therefore, following our previous hypothesis, we expect the presence of EM trees to increase AGB. Additionally, if mycorrhizal type alters decomposition rates due to differences in litter quality or nutrient immobilization

(McGuire et al., 2010; Read & Perez-Moreno, 2003), we expect accumulation of CWD and soil C associated with EM-trees.

MATERIALS AND METHODS

Study Site

The study was conducted at ten sites in western Panama along an elevational gradient ranging from 880 to 2920 m a.s.l within the Fortuna Forest Reserve (FFR), the southern edge of the adjacent Palo Seco Forest Reserve (8˚45'N, 82˚13'W) and at Finca El Velo (8˚49"11'N, 82˚28"58'W), on the northeastern slope of Volcan Baru National Park (VBNP). The elevational gradient extends from super-humid premontane forests (700-1000 m asl) and lower montane forest (1000-2000 m asl) (Holdridge 1947) in the FFR, and lower montane forests (1700-2000 m asl) to upper montane cloud forests (>2000) at VBNP. At the FFR, mean annual rainfall ranges between 4600 and 6300 mm (Prada et al 2017; Dalling et al 2021), while at 2300 m asl at VBNP, mean annual temperature is 14 ˚C and annual rainfall during 2019 and 2020 was 2003 and 2464 mm, respectively. For this study, ten permanent 1-ha plots were established: six plots at FFR in 2003 and four at VBNP in 2015, where all trees with ≥ 5 cm diameter at breast height (DBH) were measured. In this study to facilitate comparisons with other published datasets only trees ≥ 10 cm DBH were included in the analyses.

Across the elevational gradient, plots differ in relative abundances of different ecological groups that are known to have important ecological role in tropical forests, including trees associated with ectomycorrhizal fungi (EM) and arbuscular mycorrhiza (AM), N-fixers, and palms (Table 4.1). Based on literature, trees were classified depending on mycorrhizal type (Averill et al., 2019; Corrales et al., 2018; Soudzilovskaia et al., 2020) and N-fixing ability

(Huss-Daniel, 1997; Sprent, 2009). The representation of ecological groups (EM, N-fixers and palms) was calculated as the percentage of the total basal area of the plot.

Soil sampling variables

Soil data are described in detail for the plot network in the FFR (Dalling et al., 2021; Turner & Dalling, 2021). For this study, soil data were used for six plots from the FFR plots network collected in July 2008 or July 2010 (Prada et al., 2017) and from four VBNP plots, collected in May 2016. Soil from each 1-ha plot was analyzed for bulk density (BD), pH, resin extractable P (ResinP), extractable inorganic N (NH_4 and NO_3), extractable cations (Al, Ca, Fe, K, Mg, Zn), effective cation exchange capacity (ECEC), total exchangeable bases (TEB), and total N and P. Following the protocols described in Prada et al. (2017), soil samples were collected from the surface 0–10 cm of soil after removing the litter layer. Soil samples were collected in a regular grid (every other 20 × 20 m subplot) within each 1-ha plot for a total of thirteen sampling locations.

Climate variables

To evaluate the climate regime across the elevational gradient we obtained data from the CHELSA database (http://chelsa-climate.org) at 30 arc-sec spatial resolution (Karger et al., 2017, 2018) for each plot. We obtained ten variables that have been shown to be important in determining forest structure: MAT (mean annual temperature), MATvar (mean temperature range), MTmax (max temperature), MTmin (min temperature), TS (temperature seasonality), MAP (mean annual precipitation), MPdry (mean of driest month), MPwet (mean of wettest month), ISO (isothermality) and MDR (mean diurnal range). Additionally, we extracted the average climatic water deficit (WD) data from a global climate layer for the long-term at 2.5 arc-minute resolutions (http://chave.ups-tlse.fr/pantropical_allometry.htm). Climatic WD describes seasonal moisture limitation, with very negative WD values being strongly seasonally water-stressed.

Carbon stock calculations

Aboveground biomass

We used the BIOMASS R package to estimate AGB (Réjou-Méchain et al., 2017); functions in this section are all part of this package. For each plot, tree DBH was measured, including multiple stems, if ≥ 10 cm DBH. The DBH used for the analyses was the value from the last re-census measured from FFR and VBNP (2018 and 2015 respectively). We estimated the height of a subsample of 78 ± 11 trees from each plot using a triangulation approach, measuring the angle to the tree base, the angle to treetop and the distance to the tree. The angles were measured using a manual clinometer (PM5/360PC, Suunto, Finland). To estimate the height of each tree in each plot, we created a plot height-diameter model using the *log 1* equation in the function *modelHD()*. *Log 1* was the best model for seven of the plots based on the AIC index compared to the other models proposed in Réjou-Méchain et al (2017). To estimate the wood density of each tree we calculated the density of 117 species across all plots, with an average of eight individuals measured for each species. Wood density in the field was calculated using the water displacement method (Jerome Chave, 2006). This dataset was incorporated into the function *getWoodDensity*(), assigning a density to each tree based on our field wood density, then the nearest species, genus or family measurement if the field data were missing . Trees without any identification (23% of the total trees) were assigned the average plot level measurement. Finally, to estimate the AGB we used the Chave *et al*. (2014) allometric equation:

$$\mathrm{AGB} = 0.0673 * (\rho * \mathrm{H} * \mathrm{D}^2)^{0.976} \tag{1}$$

Where ρ is the wood density, H is the height, and D is the DBH of each tree. We used the function *AGBmonteCarlo*() to estimate 95 % confidence intervals at a plot level.

To evaluate differences in the variation in AGB between lowland and montane forests we used 212 plots from twelve studies in the Neotropics, including 10 plots from this study (Table C.4). Distribution between forests was assessed by bootstrapping the AGB with 1000 resamples.

Downed coarse wood debris

To estimate the downed CWD (DCWD) we used a line-intersect sample method following (Gora et al., 2019; Larjavaara & Muller-Landau, 2011). Downed CWD was defined as wood debris fallen to ground level that was ≥ 10 cm diameter and crossed the transect. For each plot, we measured DCWD along twenty-two transects of 0.1 km. For the PS plot we only conducted 10 transects given the difficulty of traversing this plot. Transects were oriented south to north and east to west every 10 m within and including the edge of the plot. For each piece of DCWD we used a large caliper to measure the diameter at the point the transect crossed the sample. Using a qualitative classification method, each sample was classified into three decomposition categories 1) 'Hard', if the sample was hard to the touch, 2) 'Medium', if the sample was still somewhat solid but soft to the touch, 3) 'Soft', if the sample was visually rotten and collapsed easily. For each decomposition category and for each plot we took destructive samples consisting of a cross-section that was weighed, measured, and dried to estimate the necromass (Gora et al., 2019). With the destructive samples we used linear regressions to estimate the necromass of the samples, where the necromass was a function of diameter, decomposition category, and plot. All cross-section masses were corrected by the random angle correction factor ($\pi/2$), summed and divided by the transect length. For the final estimates of the

DCWD we calculated the 95% confidence intervals by bootstrapping over unit samples (10 m) (Gora et al., 2019).

Standing coarse wood debris

To estimate the standing CWD (SCWD) we used a plot approach following Gora et al. (2019) and Larjavaara & Muller-Landau (2011). Standing CWD was defined as dead trunks with a DBH ≥ 10 cm. We measured SCWD in five 20×20 m subplots, for a total of 0.2 ha area sampled in each plot. For each SCWD sample we measured the DBH, classified it in the same decomposition categories as the DCWD, and additionally classified it in two qualitative branch categories: 1) With branches, if the sample retained between 20-100% of branches, and 2) without branches, if the sample retained < 20% of branches.

We estimated the necromass of the standing dead wood using two steps. For standing dead wood with branches we used the BIOMASS package (Réjou-Méchain *et al*., 2017) using *equation 1* in this study. In this case ρ was calculated using the DCWD destructive samples. Since the wood densities differed between DCWD decomposition categories ($F_{(2,326)} = 87.35$, $P = <0.001$), wood density was calculated as the average of each decomposition category by plot. Height (H) was the total height of the sample measured in the field. Necromass was calculated as 87.5% of the total original AGB estimated using *equation 1* (Gora et al. 2019).

For standing dead wood without branches we calculated the volume and density of each sample. We used a taper function to estimate the diameter at the top using the Kozak *et al*. (1969) equation in Cushman et al. (2014) and the volume was calculated as a truncated cone for samples ≥ 3 m high. For samples < 3 m high we calculated the volume as a cylinder. Densities were calculated in the same way as branched SCWD. We summed the necromass of all of the samples in all categories and we divided by the total area to finally estimate the SCWD by plot.

We calculated the 95% confidence intervals by bootstrapping over unit samples (20×20 m subplots) (Gora et al., 2019).

Soil Carbon

To estimate the soil C stocks in each plot we collected soil in depth increments from 0 to 100 cm at a subset of five of the thirteen locations sampled for soil nutrients. For the FFR network plots the 50-100 cm depth soil C value was based on a single estimate from profile pits excavated to 1.5–2.0 m (Turner & Dalling, 2021). The 0-10 cm and 10–20 cm depth samples were taken with a 5 cm diameter core, and for 50–100 cm depth samples we used a 6.25 cm diameter core. Total C stock was calculated as the product of the total C%, BD and the increment of each depth. Total C was determined by elemental analysis (Thermo Flash 1112 analyser, Bremen, DE). The 95% confidence interval of the total C stock was calculated by bootstrapping over locations for each plot.

Data analysis

All variables including environmental variables, and C pools were standardized to mean of zero and standard deviation of one to perform the analyses. One-way ANOVA was used to evaluate differences among plots. To explore and visualize the variation of environmental variables among plots, soil and climate variables were analyzed separately by principal component analysis (PCA). To compare EM and AM wood density a linear mixed-effects model was used, implemented in the package lme4 (Bates et al., 2015). We included mycorrhizal type as a fixed effect and species as random effect. *P*-values of the main effects were estimated using model simplification (Crawley, 2013).

To examine the relationship between environmental variables and elevation across the different carbon pools we used simple linear regression. Due to correlation among the different variables, we used path analysis to partition the variance of responses. Path analysis evaluates the effect of each variable – environmental, edaphic, and EM% – on each carbon pool, using the *piecewiseSEM* R package (Lefcheck, 2016). An *a priori* model (Figure C.1) was hypothesized based on our predictions and simple linear regressions between the parameters. To discriminate between models, we followed the approach of Glassmire et al., (2020) for adding and dropping variables. Akaike's information criterion (AIC) was used to compare the alternative models. The best model was the most parsimonious; the fit of the best model was evaluated using Fisher's C statistic (Lefcheck, 2016). A low Fisher's C value represents a small difference between the model and the data. For the path analysis, soil and climate parameters were included as the first and second axes of the PCA scores for each plot (respectively). For the path analysis, a second PCA was performed where scores of resin-extractable P and NH_4 were not included since we were interested in the direct effect of these variables (Figure C.2). To correct collinearity the model included the correlation between variables that are highly correlated ($r > 0.5$). Representation of EM trees was incorporated in the model as the percent of trees based on basal area (Table 4.1).

RESULTS

Edaphic and climate variation

Edaphic characteristics were highly heterogenous across plots – inorganic N varied 6-fold in NH_4 and 12-fold in NO_3, and resin-extractable P varied 87-fold (Table C.1). The first two axes of the soil PCA of environmental variables (Figure 4.1a) explained 68.6% of the variance in the edaphic variables among plots. In the first axis (PC1), two plots, MIR and AF were grouped together by variables associated with high fertility (i.e., ECEC). The FFR plots CA, HA, PS and SAM grouped together and were associated low pH and high Fe in the soil. The second axis

(PC2) described soil variation with elevation (Figure 4.1a). The plots at the highest elevation are at the bottom of the figure and are associated with high values of resin P.

The first two axes of the climate PCA variables (Figure 4.1b) explained 87.9% of the variance in the climate variables among plots. The first axis (PC1) grouped plots by the sites FFR and VBNP and shows the association between climate variation and elevation (Figure 4.1b). The plots at the highest elevations are at the right of the figure and are associated with low MAT values and high mean precipitation during the driest month (MPdry). The second axis (PC2) groups together three plots, CA, HA, and PS, which are associated with high values of mean diurnal range (MDR). The plots HOR and AF group together related to high mean precipitation during the wettest month (MPwet). Although there is high variation in the water-stressed seasonally (WD) (Table C.1), its contribution to the climate variation was low (Figure 4.1b).

Total carbon stock estimates

Total carbon stocks for the ten plots ranged from 371.8 to 1156.4 Mg ha^{-1} (Table 4.2, Figure 4.2a). Aboveground biomass and soil C were the most important carbon pools, contributing 38–68% and 25.7–55.2%, respectively, of the total carbon budget of the forest (Figure 4.2b). The contribution of CWD to the total carbon budget was highly variable, ranging from 5.1–34.8% between plots. For example, for QUE and HOR the plot total CWD was nearly 10 times smaller than AGB, while for HA the total CWD contribution was similar to AGB (Figure 4.2.b).

Aboveground Biomass

To estimate the AGB, 7434 trees (from 91 plant families) and 780 tree heights were measured across all of the ten plots. Aboveground biomass varied three-fold among plots, ranging from 186.2 to 574.3 Mg ha^{-1} (Table 4.2). Different taxa contributed to AGB in different plots (Table S5), with important contributors including Fagaceae (57.0-83.8%), Sapotaceae (22.1-38.8%) and Arecaceae (37.2%). In addition to taxon differences, contributions of ecological groups to AGB also differed across plots. EM trees ranged from 0.98-83.8% of AGB across plots. EM trees in the genus *Quercus* were the most important contributors to AGB at the highest elevation plots, and at the HA plot, where EM trees accounted for 24% of basal area and 35% of the AGB. N-fixing trees accounted for 0.33-19.2% of the total AGB of the plots. Palms were the most important ecological group in the CA plot, accounting for 37.3% of AGB, whereas palms contributed < 1% of total AGB in the remaining plots. EM trees had higher wood density compared to AM trees ($\chi^2 = 18.5$, d.f. = 1, $p < 0.001$). Mean wood density (g cm^3) for EM trees was 0.71 ± 0.02 and for AM trees 0.54 ± 1 (SE).

Combining data from this study and eleven published studies in neotropical forests (Table C.4) we found that variance in AGB for montane forests (1037-3537 m asl) was exceptionally high, compared to lowland forests (41-1000 m asl) (Figure C.3a,b).

Coarse wood debris

In total, 2037 samples of DCWD were found in 20.8 km of transect, and 232 samples of SCWD were measured in 0.2 ha per plot. Total CWD varied across plots, ranging from 14.75 to 326.51 Mg ha^{-1} (Table 4.2) and accounted for 3.2% - 34.8% of the total C budget. Across plots there was no clear pattern in the contribution of DCWD and SCWD to the total CWD. For PS, HOR, MIR, QUE and COP dead wood was mainly stored in the form of DCWD, contributing 4.1-7.3% to the total carbon of the plot, while for AF, CA, SAM, CASA and HA, SCWD was the main CWD pool, contributing 6.7 to 30%.

Soil carbon

Total soil C calculated from 0-100 cm depth differed among plots, and was similar in magnitude and variance to AGB, ranging from 119.0 to 577.9 Mg ha^{-1} (Table 4.2). There were differences among plots ($F_{(9,181)} = 10.9$, $p = < 0.001$) and depth categories ($F_{(3,181)} = 31.5$, $p = <0.001$). Plots at the highest elevation (1900 – 2923 m asl) accumulated notably large amounts of carbon in the deeper soil layers (50-100 cm), ranging from 92.8 to 246.3 Mg ha^{-1} (Figure C.4). The proportion of C not associated with % EM at any depth (Figure C.5). However, at 10-20 cm depth was positively correlated with the percent of basal area contributed by EM trees (% EM; $r^2 = 0.36$, $p < 0.05$,), however this effect was not significant after controlling for elevation.

Effect of elevation on abiotic and biotic factors, and carbon pools

Most climate variables were strongly correlated with elevation (Table C.2); variables related to temperature (MAT, MTmax, MTmin and MATvar), water deficit and mean diurnal range were negatively correlated with elevation. Precipitation during the driest month was positively correlated with elevation. Among edaphic variables only resin P was correlated with elevation, increasing with elevation ($r = 0.88$, $p < 0.001$, Table C.2). Additionally, % EM was also highly positively correlated with elevation ($r = 0.80$, $p < 0.001$, Table C.2). Resin P and % EM were therefore also highly correlated with temperature ($r = -0.89$, $p < 0.001$ and $r = -0.76$, $p < 0.05$, respectively).

Aboveground biomass and soil C showed a significant positive relationship with elevation ($r^2 = 0.73$ $p < 0.001$; $r^2 = 0.76$, $p < 0.001$, respectively, Figure 4.3a,b). Total CWD was not correlated with elevation ($r^2 = -0.06$, $p =$ NS), even after removing plot HA, an outlier, ($r^2 = 0.001$, $p =$ NS). However, DCWD was positively correlated with elevation ($r^2 = 0.76$, $p < 0.001$, Figure 4.3c). Low values of AGB, DCWD and soil C are significantly correlated with high values of variables related with temperature (Table C.3), and soil C decreased with increasing wood density ($r^2 = 0.76$, $p < 0.001$), however, this effect was not significant after controlling for elevation.

Among the AGB components, elevation was correlated with basal area but not with wood density or canopy height (Figure 4.3d-f). Basal area was positively correlated with elevation, more than doubling over the elevation range of the study ($r^2 = 0.65$, $p < 0.001$). The number of stems per plot tended to decrease with elevation, but was not significant ($r^2 = 0.18$, p = NS).

We used predicted relationships among environmental variables to develop a structural equation model (SEM) including soil, climate variables, AGB, DCWD, and soil C (Figure C.1). Temperature was the variable that best predicted AGB and soil C, after controlling for soil and other climate parameters (Figure 4.4). Temperature was significantly negatively associated with AGB and soil C. In the model resin P was negatively correlated with temperature (r = -0.47) but not significant. Resin P, NH_4 and other soil parameters (represented in the first PCA axis, Figure C.2), and % EM showed a significant association with DCWD. Downed CWD decreased significantly with high values of resin P, NH_4 and soil parameters and increased with high values of % EM. Additionally, % EM was significantly related with resin P; high values of % EM were associated with high values of resin P. The effect of climate parameters other than temperature, represented in the second PCA axis, did not have a significant effect on C pools. Standing CWD was not included in the SEM analysis since it was not correlated with any of the abiotic or biotic factors.

DISCUSSION

Exceptionally high carbon storage was observed along this elevational gradient in Panama. In contrast to most published data from elevational gradients in TMFs, we found total carbon stocks were strongly *positively* correlated with elevation a pattern attributable to the presence of EM associated *Quercus* species at the highest elevations. Temperature was a strong predictor of AGB and soil C. In contrast, we found resin P and % EM explained more variation in DCWD stocks than temperature; DCWD accumulation was associated with increasing % EM and decreasing resin P and NH_4. Estimates of SCWD were poorly constrained in this study, with exceptionally high values restricted one site. We found high soil C was also associated with high elevation sites. We predicted soil C storage would be associated with EM-trees, however we found no effect of % EM on total soil C. The plot with patches dominated by *O. mexicana* had intermediate values of soil C while plots at the VBNP site showed the highest values of soil C, possibly reflecting volcanic activity that buried C rich surface soils in the past.

Carbon stocks in comparison with other studies

Comparing the results reported in this study with other Neotropical forests at similar elevations revealed remarkably high AGB at FFR and VBNP. In lowland forest in the Amazon high AGB is associated with low productivity and low tree turnover rate (Quesada et al. 2009). In lowland forests using plot inventories, AGB in Mg ha^{-1} using trees $\geq$ 10 cm DBH has been estimated as 262 in BCI, Panama (Chave et al., 2003), 160.5 in La Selva, and ranged from 114 to 172 in the Área de Conservación Osa (ACOSA), Costa Rica (Clark & Clark, 2000; Hofhansl et al., 2020) and 397 ± 30 in Brazil (Nascimento & Laurance, 2002). Studies along elevational gradients have shown there is an irregular pattern between elevation and AGB, increasing the uncertainty of estimates of this C pool (Muller-landau et al., 2020; Sierra et al., 2007). Variation in AGB arises from variation in tree height and wood density, which differs across sites due to changes in environmental factors (Chave et al., 2014; Malhi et al., 2004). Comparing this study with four studies conducted on Neotropical elevational gradients indicates AGB in

Colombia (González-Caro et al., 2020) and Panama (this study) had higher AGB compared to Peru (Malhi et al., 2017), Ecuador (Moser et al., 2008) and Venezuela (Delaney et al., 1997; Vilanova et al., 2018) (Figure 4.5a). At high elevations AGB in our study was between three and seven times higher than AGB reported from other comparable elevational gradients.

Our results showed a significant increase of AGB with increasing elevation. This positive relationship between AGB and elevation has also been found in Brazilian Atlantic forest at much lower elevations (0-1200 m; Alves et al., 2010). The opposite pattern has generally been found in elevational gradients in Neotropical forests in Peru (120-3537, Malhi et al. 2017), Ecuador (1050-3050, Moser et al., 2008) and Puerto Rico (725-1000, Weaver et al., 1990), and a hump-shaped relationship between AGB and elevation was found in Colombia (41-2928, González-Caro et al., 2020)

In common with previous studies, soil C stocks in western Panama were highly variable, and in general increased with elevation. In striking contrast with other neotropical studies (Figure 4.5b) we found the highest soil C stocks in the highest elevation plots, supporting our initial hypothesis of increases in soil C with increasing elevation. At our highest elevation site, COP, soil C to 1 m depth (578 Mg ha^{-1}) was more than four times higher than comparable measurements in lowland forests in Panama (133 Mg ha^{-1}, Cusack et al., 2018). Similarly, in our study, the soil C stock was five times higher in lower montane forest (1500-2000) and two times higher in upper forest (2000-3600), compared to studies in Colombia (Phillips et al., 2019), Ecuador (Schrumpf et al., 2001) and Venezuela (Delaney et al., 1997).

Differences in methodologies and sample sizes across studies make comparisons of CWD difficult. Furthermore, variation in total CWD within and among plots in this study was exceptionally high. One plot, HA had exceptionally high SCWD (313 Mg ha^{-1}) with correspondingly large confidence intervals. The presence of a few large standing dead trees can greatly skew estimates of SCWD (Gora et al. 2019) necessitating large sample sizes to capture the true mean pool size. Nonetheless, our study highlights the potential importance of this pool to the ecosystem C budget, and adequately constraining SCWD measurements to detect climate change effects via elevated tree mortality rates.

Responses of carbon pools to environmental and biotic factors

Aboveground biomass

After controlling for elevation we found no effect of fertility (measured as NH_4-N and resin P) nor % EM on AGB, leaving temperature as the main determinant of AGB in this system. We hypothesized decreasing temperatures will result in greater AGB because of the relationship between reduced growth rates at higher elevation and increased wood density. Species that have slow growing are associated with denser wood following the wood economic spectrum (Chave et al., 2009). More generally, species with long life spans are associated with high wood density as a result of slow height and diameter growth rates (Muller-Landau, 2004). Species at high elevations that are exposed to harsher conditions (e.g., higher windspeeds), may face selection for greater resource investment in building stronger trunks with high wood density. Lower growth rates also mean that trees need to build stronger, longer-lasting trunks to live long enough to achieve reproductive size (Poorter et al., 2005). Low wood density does not always imply vulnerability; lower wood density may lead to higher maintenance costs but lower construction cost for the same strength as a high cost, high wood density trunk (Larjavaara & Muller-Landau, 2010). Although AGB was associated with elevation, we were not able to confirm that wood density was correlated with elevation. Nonetheless, EM tree species showed higher wood densities compared to AM trees, and EM species such as *Quercus costaricensis* and *Q. salicifolia* had a large contribution to AGB.

In tropical forests in Colombia and Indonesia, AGB increases due to the significant contribution of temperate-affiliated families such as Fagaceae and conifers such as *Podocarpus* in highland forests (Culmsee et al., 2010; González-Caro et al., 2020; Peña et al., 2018). Recent studies have shown that the evolutionary history of tree communities can explain forest structure in tropical forests, where a phylogenetic signal was detected for AGB (de Aguiar-Campos et al., 2021; González-Caro et al., 2020). In an elevation gradient in Colombia, González-Caro et al. (2020) found high AGB in intermediate elevation (1800-2200) was associated with a high proportion of temperate-affiliated species. One of the most important temperate-affiliated genera is *Quercus*, which contributes to high AGB in upper montane forests in Colombia (González-Caro et al., 2020; Peña et al., 2018). This aligns with our results, where except for one of the four plots in the highest elevations, *Quercus* was the largest contributor to AGB. The EM genus *Quercus* appears to be well adapted to the cold conditions of tropical high elevation forests, where it reaches large sizes and high wood densities (Cavender-Bares, 2019).

Ectomycorrhizal tree taxa in the Neotropics are mainly distributed in montane forests in northern South America and Central America (Corrales et al., 2018) compared to Southeast Asian forests, where the most important EM family (Dipterocarpaceae) is distributed in lowland forests (Brearley et al., 2016; Corrales et al., 2018). Our results fit the broader Neotropical distribution, as we found % EM was highly correlated with elevation. However, there was no significant effect of % EM on AGB in this system after accounting for elevation. For example, at the VBNP plots, the MIR plot had high AGB despite very low % EM basal area. Therefore, non-EM trees may need to have similar values for canopy height and wood density in order to be able to co-occur in oak forests. These results contrast with AGB patterns at a smaller spatial scale in a 50 ha plot in a temperate forest in China, where AGB was positively associated with the proportion of EM basal area in the stand (Mao et al., 2019).

In the China 50 ha plot, differences in AGB associated with EM trees appeared to be mediated by soil fertility. However, more generally, responses of AGB to soil nutrient availability are highly inconsistent among studies (Muller-Landau et al., 2020). For example, in lowland tropical forests in the Guiana Shield (Soong et al., 2020) AGB did not respond to soil P, whereas more broadly across the Amazon basin low AGB was found to be associated with high soil P (Quesada et al., 2012). In contrast to our hypothesis, here we found that AGB was not correlated with nutrient availability after accounting for the effect of elevation. Evaluating the effects of nutrient availability on AGB along elevational gradients is challenging as direct fertility effects may be masked by the strong correlations between elevation and soil N and P.

Coarse woody debris

Coarse woody debris in tropical forests is a critical component of the C cycle, with highly variable distributions in space and time, rendering it hard to study (Gora et al., 2019; Iwashita et al., 2013). The amount of CWD in the forest can depend on wood quality, climatic conditions including temperature and stand turnover rates (Chambers et al., 2000, 2001). Here we found that the responses of CWD to environmental and biotic factors depended on the different CWD pools — downed (DCWD) and standing (SCWD). Total CWD and SCWD were not correlated with elevation. After controlling for elevation we found resin P, NH_4 and % EM was correlated with DCWD. Similarly, a study in tropical montane forests in Hawaii found DCWD did not change with temperature (Iwashita et al., 2013).

We found that the accumulation of DCWD was associated with low fertility (low resin P and NH_4) and with increases in % EM. Previous studies in the Fortuna site have shown that wood from trees associated with low nutrient soils had higher wood density and lower wood nutrient concentrations than those of higher nutrient soils (Heineman et al., 2016). Although climate can be the best predictor of decomposition in Neotropical forests (Cusack et al., 2009), litter quality is also important (Zhang et al., 2008). Low litter N and P concentration is associated with slow decomposition (Zhang et al., 2008), which may account for the high accumulation of DCWD on the forest floor on this study. Additionally, in the Amazon, high wood density is associated with lower decomposition rates (Chambers et al., 2000). In this study, DCWD accumulation with increasing % EM may be explained by higher values of wood density in EM trees compared to AM trees, and potentially also lower soil nitrogen availability in EM stands (Lin et al., 2017; Phillips et al., 2013; Prada, chapter 5).

Soil Carbon

We found that temperature was the most important factor influencing soil C stocks. Soil C accumulated with increases in elevation, a pattern that has been reported previously for tropical montane forests (de la Cruz-Amo et al., 2020; Girardin et al., 2010; Kitayama & Aiba, 2002; Gerald Moser et al., 2011; Schrumpf et al., 2011). Continually cool temperatures at high elevation decrease microbial activity, which results in a decrease in decomposition rates and mineralization of soil organic matter (Davidson & Janssens, 2006; Nottingham, Whitaker, et al., 2015; Zimmermann et al., 2009). Following Microbial Efficiency-Matrix Stabilization (MEMS) framework (Cotrufo et al., 2013), slow decomposition rates at high elevations suggest C in the soil would be present as particulate soil organic matter (POM). Additionally, in montane forests POM would be expected to increase in EM forests (Craig et al, 2018). In this study, we cannot separate the effect of elevation and mycorrhizal association on POM accumulation. Additionally, on elevational gradients, general patterns can be confounded by other interactions, such as soil nutrient availability. For example, in TMF, an increase in elevation is usually associated with a decline in N and an increase in P availability (Dalling et al., 2016; Nottingham, et al., 2015). In this study we found elevation was not correlated with inorganic N (neither NH_4-N nor NO_3-N), but was highly positively correlated with resin P. This strong correlation makes it hard to unravel the true effect of both temperature and P on soil C stock.

Increasing evidence show significantly higher soil C stock in topsoil beneath EM trees in both temperate and tropical forests (Averill et al., 2014; Craig et al., 2018; Lin et al., 2017, Steidinger et al., 2019). However, greater soil C stock has also been observed at greater soil depths in AM forest (Craig et al., 2018). Mechanisms explaining differences in soil C stock have been attributed to differences in the enzymatic capacity of AM and EM species to mineralize OM, or differences in decomposition rates (McGuire et al., 2010; Read & Perez-Moreno, 2003). In this study we found the effect of % EM on soil C may have been confounded by the correlation between % EM and elevation. However, a clear example of how high soil C stocks are not necessarily dependent on the presence of EM taxa is provided by the MIR plot— a mixed forest in which EM taxa accounted for only 1.1% of basal area and yet had one of the highest soil C stocks. An additional complication at this site is that soil C accumulation on the slope of Volcan Baru may also have been affected by the volcano's recent eruptive history as some of the deeper soil C stores show evidence of burial by volcanic ash (C. Prada, personal observation). At least four eruptions of Volcan Baru have occurred in the last 1600 years (Sherrod et al., 2008). The last episode, 500 years ago, may have included widespread tephra fallout, pyroclastic flows, and lahars across the area occupied by our plots (Sherrod et al., 2008). Volcanic eruptions result in the burial of the existing organic layer at the time of the event, and can result in the long-term persistence of significant quantities of soil organic carbon (Chaopricha & Marín-Spiotta, 2014). For example on Mt. Kilimanjaro, Tanzania, soil organic carbon below 1 m depth ranged from 117 to 627 Mg ha^{-1} in elevations from 2100 to 2800 m asl (Zech, 2006). Particulate soil organic matter is expected to be more vulnerable to disturbance than C that is as mineral-associated organic matter MAOM (Poeplau et al, 2018) in low land forests. Volcanic eruptions may protect POM, increasing soil C accumulation in these montane forests.

Role of tropical elevational gradients in global C stocks

Our results from the FFR-VBNP gradient highlight the significance of these forests in the global C cycle, as they sequester large amounts of C in tree biomass and in the soil. While tropical forests represent a large proportion of the terrestrial carbon sink (Spracklen & Righelato, 2014; Duque et al., 2021), the contribution of montane forests and of the temperate family Fagaceae has only been recognized more recently (Culmsee et al., 2010; González-Caro et al., 2020; Peña et al., 2018). Nonetheless, factors explaining the dynamics and accumulation of C in the soil are still ambiguous. Large uncertainty in C pool estimates suggests that further research is needed to correctly estimate and evaluate C stocks in tropical montane forests.

TABLES

Table 4.1. Summary of characteristics of ten 1-ha plots along an elevational gradient in western Panama including trees >10 cm DBH. Percent of basal area of species that form ectomycorrhizal associations (EM), N-fixing, and palm taxa. FFR= Fortuna Forest Reserve, VBNP = Volcan Baru National Park.

Plot	Plot code	Site	Type of forest	Elevation (m a.sl)	No. trees	No. stems*	Basal area (m^2ha^{-1})	% EM	% N-fix	% Palms
PaloSeco[‡]	PS	FFR	Mixed	880	630	646	31.2	2.4	17.4	2.3
AltoFrio[§]	AF	FFR	Mixed	1100	1019	1042	44.6	7.1	8.5	0.0
ChorroA[†]	CA	FFR	Palm-dominated[b]	1100	979	1002	32.6	9.2	0.4	41.7
HondaA[†]	HA	FFR	Mixed/ EM-dominated[c]	1155	800	804	41.6	24.0	4.4	0.4
Samudio[*]	SAM	FFR	Mixed	1215	1049	1071	33.7	0.78	10.4	0.8
Hornito[¤]	HOR	FFR	Mixed	1330	681	694	55.2	2.2	2.2	0.0
Mirador[þ]	MIR	VBNP	Mixed	1987	457	477	46.7	1.1	4.9	0.0
CasitaA[þ]	CASA	VBNP	EM-dominated[a]	2248	646	686	50.5	74.1	0.4	0.0
Quetzal[þ]	QUE	VBNP	EM-dominated[a]	2599	543	564	59.0	48.1	3.2	0.04
Copete[þ]	COP	VBNP	EM-dominated[a]	2923	630	728	63.0	63.3	7.3	0.0

Geology: [‡] mafic volcanic; [§] undifferentiated volcanics; [†]rhyolite; [*] mafic/rhyolite; [¤] dacite; [þ] Holocene lahar flow. Forest type: [a] *Quercus*-dominated; [b] *Colpothrinax aphanopetala*-dominated; [c] *Oreomunnea mexicana*-dominated *No. of stems used for the analyses includes multiple stems of individual trees

Table 4.2. Total estimated carbon pools in Mg ha^{-1} with 95% confidence intervals for ten 1ha plots in an elevational gradient for trees and CWD samples with diameter ≥10 cm. AGB = Aboveground biomass; CWD = Coarse wood debris.

Plot	Plot code	Elevation	AGB	CWD			Soil C	Total Carbon
				Downed	Standing	Total CWD		
PaloSeco	PS	880	231.7 (211.6, 255.7)	12.14 (8.72,15.59)	9.03 (1.68,19.09)	21.17	119.0 (76.2, 170.8)	371.8
AltoFrio	AF	1100	311.2 (292.4, 336.4)	10.35 (7.14,14.1)	86.06 (17.56,178.98)	96.41	260.5 (215.5, 307.2)	668.2
ChorroA	CA	1100	186.2 (174.6, 200.5)	7.35 (5.79,9.1)	52.72 (15.28,119.86)	60.07	233.4 (143.6, 296.7)	479.4
HondaA	HA	1155	370 (334.1, 420)	13.49 (10.48,17.08)	313.02 (20.69,757.09)	326.51	241.3 (138.7, 318.5)	937.1
Samudio	SAM	1215	264.8 (249.6, 281.3)	16.1 (13.39,18.98)	39.64 (2.27,103.53)	55.74	193.3 (115.3, 274.9)	513.5
Hornito	HOR	1330	408.3 (375.3, 445.6)	11.38 (7.77,15.37)	3.37 (0.92,5.83)	14.75	174.3 (133.6, 213.8)	597.3
Mirador	MIR	1987	381.6 (346.9, 425.2)	20.37 (15.7,25.94)	13.83 (0.66,31.13)	34.2	524.7 (428.7, 640.6)	940.5
CasitaA	CASA	2248	468.3 (432.4, 512.8)	21.32 (16.94,26.23)	50.4 (3.78,108.02)	71.72	317.3 (273.4, 361.2)	856.4
Quetzal	QUE	2599	574.3 (524.8, 628.6)	26.97 (21.06,33.87)	7.9 (2.97,14.49)	34.87	473.1 (400.2, 544)	1082.2
Copete	COP	2923	518.3 (482.8, 559.1)	48.9 (35.81,63.01)	11.08 (1.83,26.02)	59.98	577.9 (474.2, 642.9)	1156.4

FIGURES

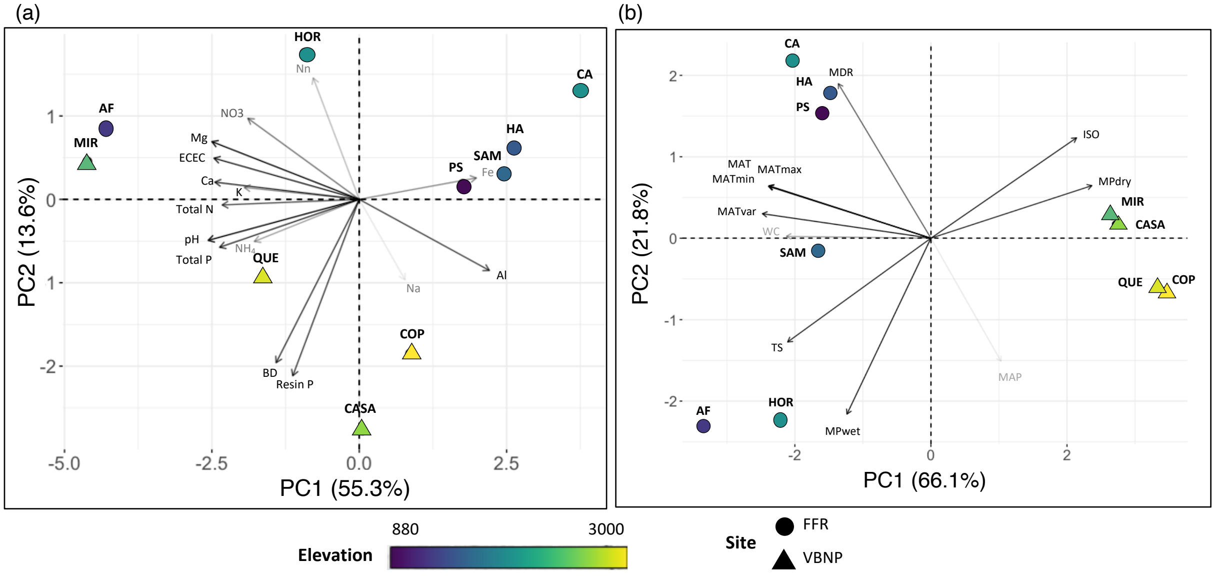


Figure 4.1. Principal component analysis (PCA) for (a). soil variables 0-10 cm depth, and (b). climate variables of ten 1ha plots in an elevational gradient in Panama. Direction and length of vectors indicates the effect of the variable. Color represents the elevation of the plot and the symbols represent the site. FFR= Fortuna Forest Reserve, VBNP=Volcan Baru National Park.

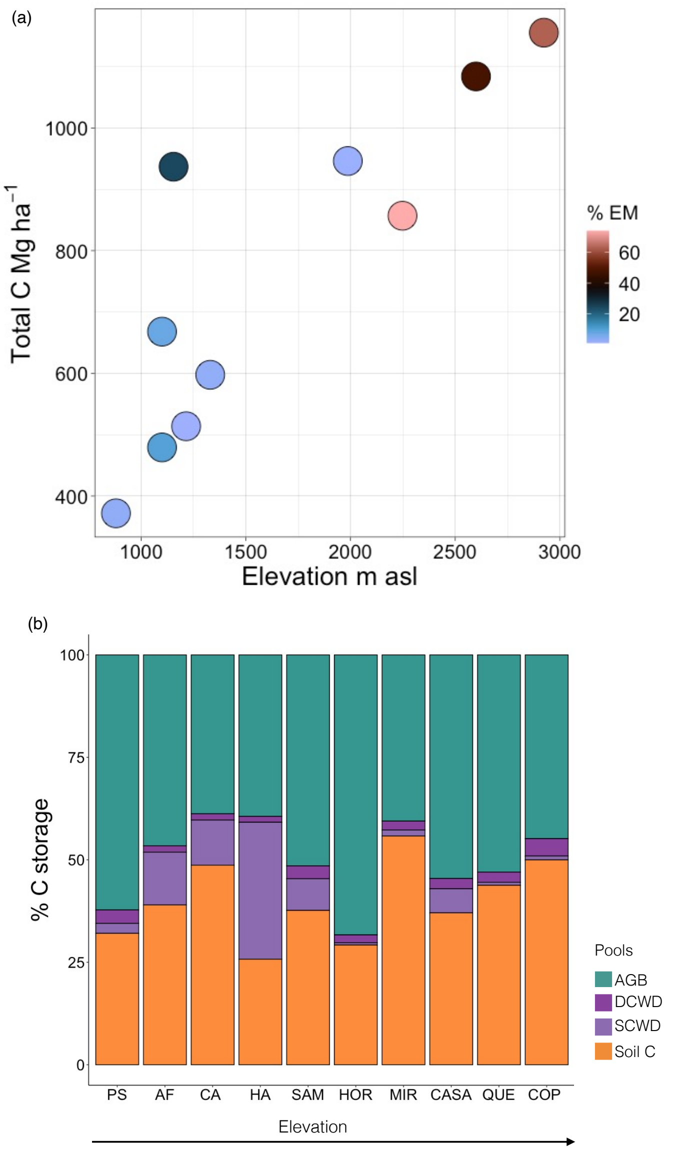


Figure 4.2. Total C stocks (a) and contribution (b) of the different pools to the total carbon stocks for ten 1ha plots in an elevational gradient in western Panama. AGB = Aboveground biomass; DCWD= Downed coarse wood debris; SCWD = Standing coarse wood debris; % EM= percent of plot basal area occupied by EM trees.

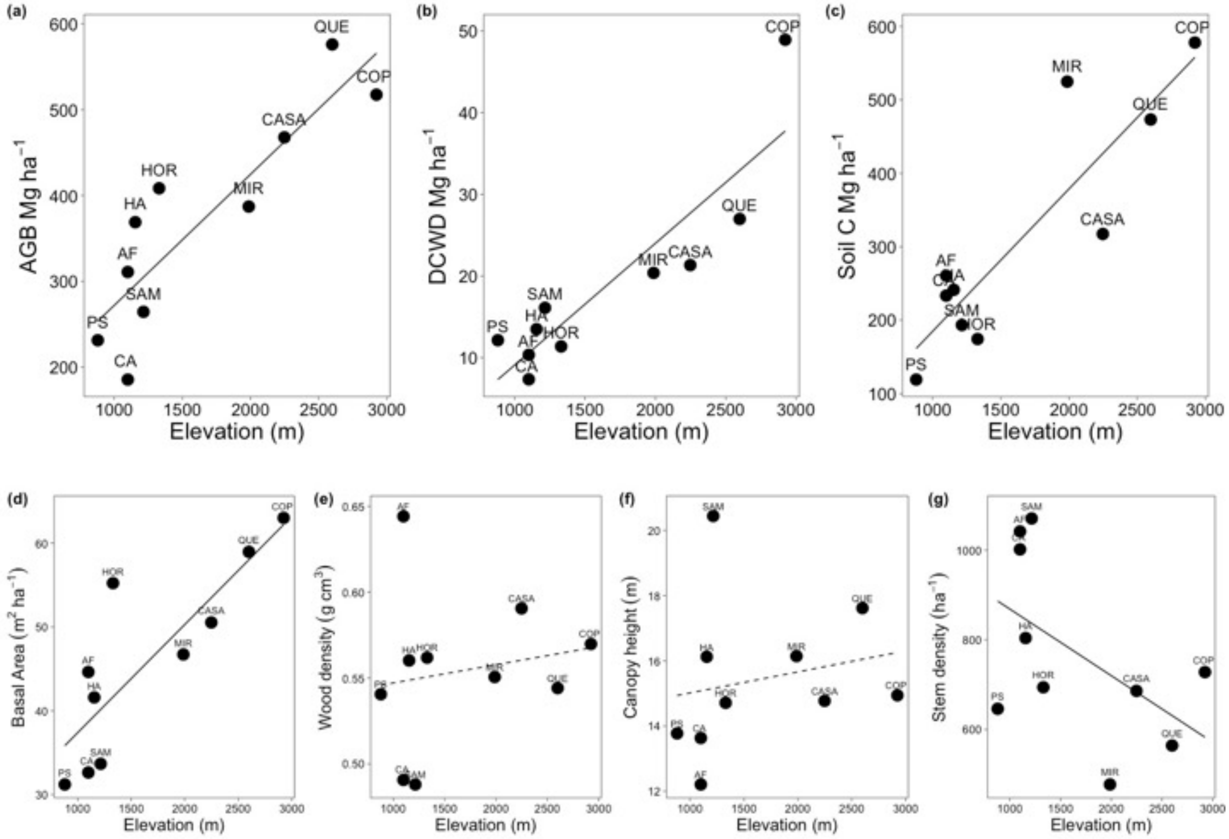
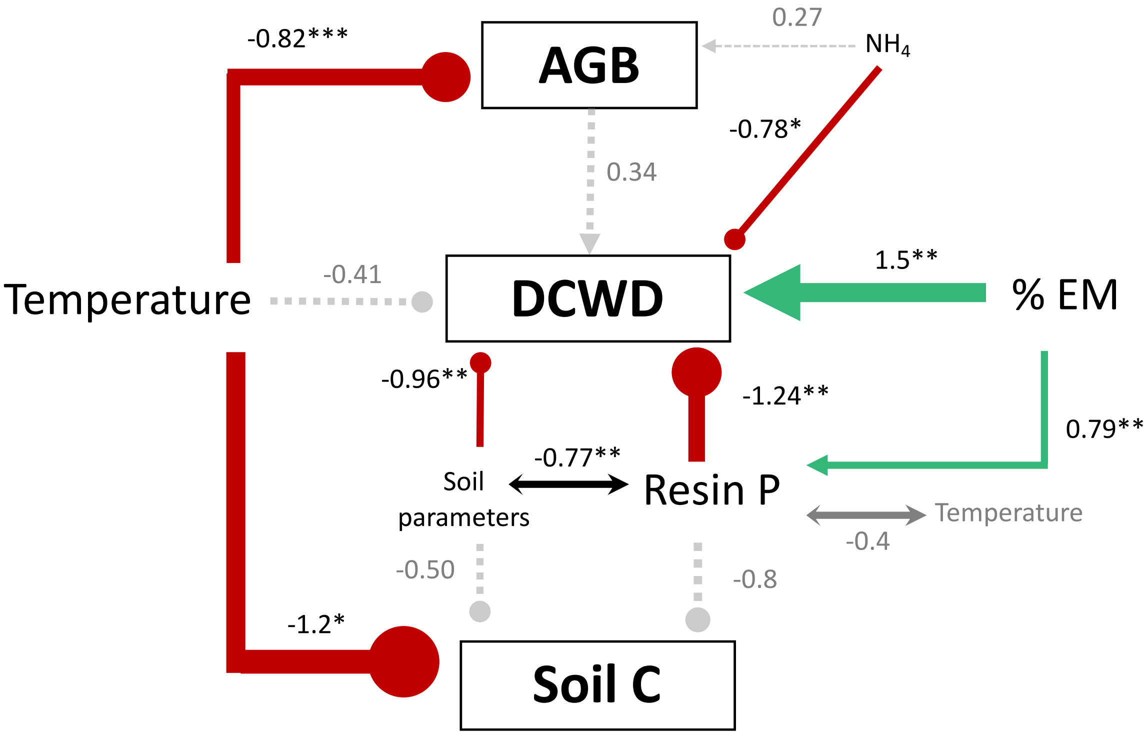


Figure 4.3. Effect of elevation on a) above ground biomass, b) downed coarse wood debris, c) total soil C, (d) basal area, (e) wood density, (f) canopy height and (g) stem density for ten 1ha plots. Lines are linear regressions between the response variables and elevation. Solid lines indicate significance while dashed lines not significance. Each point is the mean value for each plot except for (d) that is the total basal area of the plot. AGB = Aboveground biomass; ; DCWD= Downed coarse wood debris.



$C_{(12)}$= 11.41; p=0.494; AIC= 55.4

Figure 4.4. Structural equation model to evaluate the effect of environmental and edaphic variables on the different carbon pools in a montane forest. Soil and edaphic parameters are represented by the first and second axes of a PCA for each group of variables where resin P and NH_4 where not included. The best model was selected based on Akaike's information criterion (AIC) comparing alternative models. Positive effects are in green and represented by arrows and negative effects in red with blunt-ended lines; arrow width represents the relative importance of each factor. Gray dashed arrows represent nonsignificant relationships. Lines with doble arrows represent correlations between variables. Numbers are the standardized path coefficients. AGB = Aboveground biomass; DCWD= Downed coarse wood debris; % EM= percent of plot basal area occupied by EM trees.

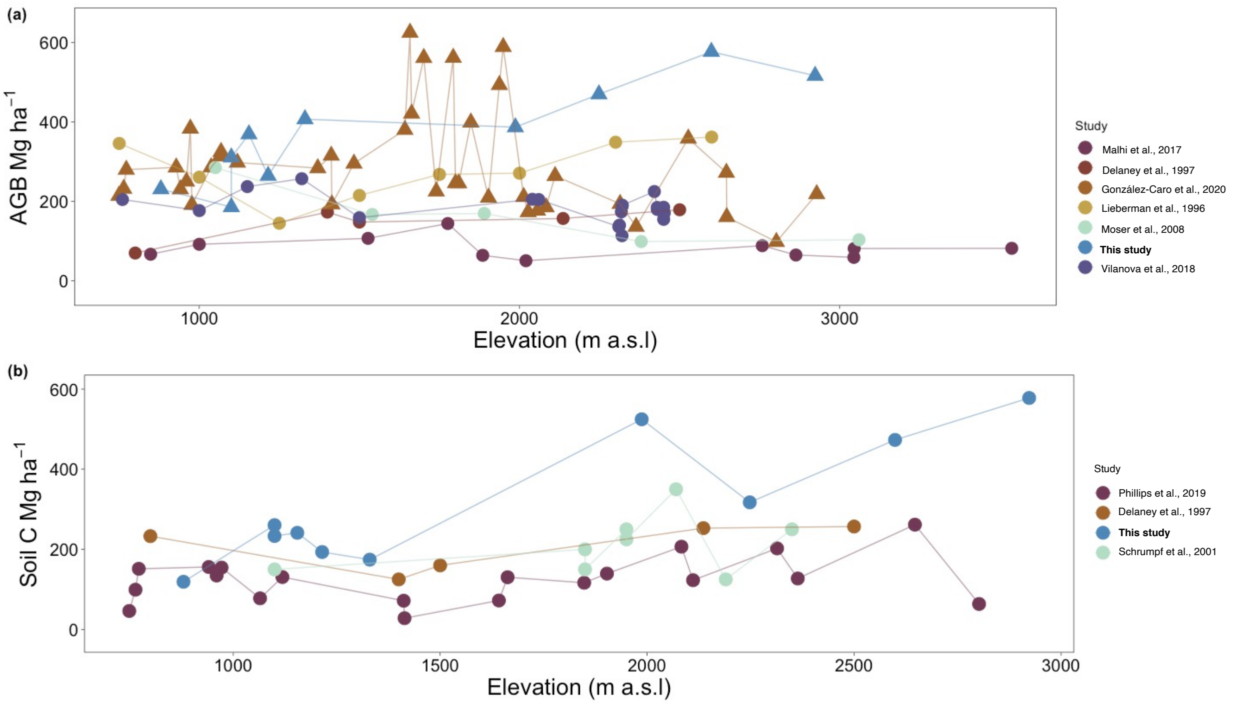


Figure 4.5. Comparison of above-ground biomass (a) and soil C (b) stocks among studies in the Neotropics. (a) Points represent AGB Mg ha^{-1} in one plot for five studies; symbols indicate sites with presence of EM dominated forests (triangle) or absence (circles). (b) Points represent Soil C Mg ha^{-1} at 1 m depth for four studies. Studies were performed in Peru (Malhi et al., 2017), Ecuador (Moser et al., 2008; Schrumpf et al., 2001), Venezuela (Delaney et al., 1997; Vilanova et al, 2018), Costa Rica (Lieberman et al., 1996) and Colombia (González-Caro et al., 2020; Phillips et al., 2019)

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CHAPTER 5: GROWTH RESPONSES OF ECTOMYCORRHIZAL AND ARBUSCULAR MYCORRHIZAL SEEDLINGS TO LOW SOIL NITROGEN AVAILABILITY IN OAK FOREST STANDS IN TROPICAL MONTANE FOREST

ABSTRACT

Differences in nutrient acquisition pathways between arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi are associated with greater soil organic matter (SOM) accumulation and reduced inorganic nitrogen (N) availability in EM-dominated forests. These plant–soil feedbacks (PSFs) are expected to influence seedling recruitment and the maintenance of diversity. Montane forests of Central America are characterized by a mosaic of AM and EM dominance. We used a seedling transplant and soil manipulation experiment on Volcan Baru, Panama, to evaluate whether patches of oak (EM-dominated) forest, and mixed (AM-dominated) forest affect seedling growth. We predicted that (1) PSF would result in lower soil inorganic N availability in oak than in mixed forests; (2) consequently AM seedlings would grow more slowly and have lower foliar N concentrations in oak forest; and (3) dependence of EM seedlings on organic N uptake via mycorrhiza would mean that inorganic N addition would increase seedling performance for AM but not EM (i.e., oak) seedlings. As SOM accumulation may affect seedling performance beyond altering nutrient supply, we also tested whether SOM removal differentially affected AM and EM seedlings. Nitrogen availability was six times lower and the soil organic layer three times deeper in oak-dominated stands compared to mixed stands. Foliar N was lower for AM seedlings growing in oak than in mixed forest, but did not differ for oak seedlings and was increased only marginally by N addition for both AM and EM seedlings growing in both AM and EM forests. Seedling growth did not respond to N addition or OM

removal. However, AM seedlings generally grew slower in oak forest compared with AM forest, consistent with lower foliar N concentration and low light availability. These results suggest that changes in soil nitrogen availability have a limited effect on seedling growth. In the neotropics, EM tree communities occur at high elevation. Future upslope migration of trees may result in AM-dominated tree communities encountering unfavorable soil conditions generated by EM-dominated canopies. While longer-term experiments are needed, our results suggest that AM seedlings may not be able to tolerate low N conditions associated with EM forest.

INTRODUCTION

Recent studies have highlighted the key role that mycorrhizal associations play in regulating biogeochemical processes in temperate and tropical forests (Cheeke et al., 2017; McGuire et al., 2010; Phillips et al., 2013; Tedersoo et al., 2020). The two principal groups of mycorrhizas, arbuscular mycorrhizas (AM) and ectomycorrhizas (EM), have different nutrient acquisition strategies that influence soil carbon (C) storage and nitrogen (N) availability (Phillips et al., 2013). At the global scale, forests dominated by trees that form EM associations store high soil C when compared to forests dominated by AM species (Averill et al., 2014; Steidinger et al., 2019). These differences have been attributed to differences in the enzymatic capacity of AM and EM species to mineralize OM, or to differences in the rates fungal-mediated decomposition of AM and EM tree litter (Fernandez & Kennedy, 2016; Hobbie & Högberg, 2012; Jacobs et al., 2018; McGuire et al., 2010; Read & Perez-Moreno, 2003).

These proposed differences in nutrient cycling have been summarized by Phillips et al. (2013) in the mycorrhizal-associated nutrient economy (MANE) framework. In temperate forests of North America, MANE predicts that forest dominated by AM has relatively small stocks of soil organic matter (SOM) as a consequence of high litter quality allowing fast decomposition rates and therefore rapid mineralization of N and C. In contrast, trees that associate with EM fungi accumulate SOM and the soil beneath them has relatively small fluxes of inorganic N. In turn, the accumulation or loss of SOM influences soil physical properties including bulk density and water-holding capacity (Schmidt et al., 2011).

Ectomycorrhizal trees can dominate in both lowland and montane tropical forests (Corrales et al., 2018). In the neotropics, EM forests are typically dominated by a single tree species, which has led to the suggestion that alterations to N cycling associated with EM trees can generate positive feedbacks favoring conspecific recruitment (Corrales et al., 2016; Hall et al., 2020). For example, in a premontane forest in Panama, Corrales et al. (2016) concluded that EM fungi promote monodominance by reducing N availability, driven by the depletion of N from OM by EM fungi. Several subsequent studies have also shown that positive feedbacks favor the recruitment and growth of EM seedlings (Bennett et al., 2017; Teste et al., 2017) although these may be unrelated to N availability.

Positive feedback generated by changes in soil nutrient availability might be counterbalanced by negative feedback, whereby increasing local abundance leads to greater herbivory rates or transmission of host-specific pathogens. The direction and strength of the feedback may also depend on mycorrhizal type (Bennett & Klironomos, 2019; Mao et al., 2019). Soil conditioning experiments using AM species have shown that seedlings perform poorly when grown with conspecific versus heterospecific soil biota, creating conditions for heterospecific recruitment and therefore the maintenance of species coexistence in AM dominated tropical forests, temperate grasslands, and Mediterranean shrublands (Klironomos, 2002; Mangan et al., 2010; Teste et al., 2017). It has been suggested that the EM hyphal sheath can serve as a barrier to pathogen entry and, therefore, that EM tree species are less susceptible to pathogen induced negative plant–soil feedback (PSF) (Bennett et al., 2017). Guild assignment of fungal sequences obtained from roots provides some support for this hypothesis, because EM seedlings harbor fewer sequence reads of putative pathogens than AM species (Chen et al., 2019; Liang et al., 2020). In contrast, in a monodominant EM species, *Oreomunnea mexicana* (Juglandaceae), in lower montane forest in Panama suffered stronger negative PSF than a range of co-occurring AM species (Corrales et al., 2016).

Oaks (*Quercus*) are common EM trees in tropical montane forests (TMFs) in Central America, the Colombian Andes, and Southeast Asia (Kappelle 2006). Although some oak species occur in mixed forest, others such as *Q. salicifolia* in Panama, form monotypic stands (Kappelle et al., 1995; Nixon, 2006). Such conditions should promote strong negative feedback, based on accumulation of natural enemies, thus favoring heterospecifics. However, oak stands are also associated with a deep organic horizon at the soil surface and low inorganic N availability. These conditions potentially inhibit the recruitment of heterospecific seedlings and contribute to oak dominance. Here we used a seedling transplant experiment to explore how soil conditions created by *Q. salicifolia* stands affect seedling recruitment. We predicted (1) that the oak-dominated forest in the study site would be depleted in inorganic N relative to the mixed forest. Further, we hypothesized that (2) EM associations allow oaks to maintain N supply and outperform AM species that are strongly N limited in oak forest. (3) Increasing soil inorganic N to replace N depleted from SOM by EM would improve the performance of AM-associated species, but not of oaks. (4) OM that accumulates in oak forest differentially impacts AM and EM species; removal of the organic layer to create conditions similar to those below AM stands would benefit AM species.

MATERIALS AND METHODS

Study Site

We established a field experiment at El Velo (8˚49"11'N, 82˚28"58'W), on the northeastern slope of Volcan Baru National Park in western Panama. At 2300 m elevation, mean annual temperature is 14 ºC (max 22 ºC; min 9 ºC), and annual rainfall during 2019 was 2003 mm, with an average monthly rainfall of 42 mm in the dry months (November to April) and 291 mm in the wet months (May to October). The parent material of the area is Holocene lahar flow deposits with periodic tephra inputs (Sherrod et al., 2008). Soil at the experimental site is a well-drained Andisol (Soil Survey Staff, 1999), with a shallow organic horizon over a deep black A horizon (> 60 cm) with a sandy loam texture, common pumice gravel, and andic properties. The field experiment was established at 1900 m a.s.l, where the forest is a mosaic of mixed forests, dominated by trees in the Lauraceae, Myrtaceae, and Magnoliaceae families, and oak forest dominated by *Quercus salicifolia*. We established three 2.7 × 7.4 m plots at similar elevation in each forest type (Figure 5.1a). Mixed forest plots had no oak trees within 50 m; inter-plot distance ranged from 390 to 580 m. Some logging occurred in the vicinity of the study plots in the 1930s (Price Peterson, personal communication); human disturbance since then has been minimal. For oak forest plots, trees ≥10 cm diameter at breast height (DBH) within 15 m of the plots were measured. Oak trees (*Quercus salicifolia*) accounted for 94–96% of the total basal area.

Mineral soil characteristics of mixed and oak dominated forest, based on 1 ha plots at similar elevation < 2 km from the experiment sites, differed in pH, bulk density (BD), and the concentrations of total C, total N, resin P and effective cation exchange capacity (ECEC) (Table D.1). Specifically, pH, BD, resin P and total C:N ratio were significantly higher in the oak dominated forest, while total C, total N, total P and ECEC concentrations were significantly higher in the mixed forest.

Environmental conditions

We collected soil samples at three locations in each plot in December 2018. Separate samples were taken from the surface organic horizon, excluding recognizable leaf litter, and from the upper 10 cm of mineral soil. At each location we measured the depth of the OM layer, based on the abrupt change in texture and color at the transition to mineral soil. Inorganic N concentrations (ammonium, nitrate) were determined by extraction in 0.5 M K_2SO_4 for 1 h, with detection of ammonium and nitrate (NH_4-N and NO_3-N) by automated colorimetry on a Lachat Quikchem 8500 (Hach, Manchester, UK). In addition, to estimate the availability of NH_4-N and NO_3-N over time, we buried resin bags containing 5 g of mixed-bed anion and cation exchange resins (Dowex Marathon Mr-3 Supelco, Bellefonte, PA, USA) sealed inside 220 μm polyester mesh. Separate bags were placed in the organic horizon and 10 cm deep in the mineral soil. In July 2019, 60 bags were buried in each plot, with one resin bag buried in each treatment (described in the next section). After 36 days in the field, resin bags were collected, rinsed with deionized water to remove adhering soil, extracted with 75 mL of 0.5 M HCl, and then nitrate + nitrite (resin-NO_3-N) and ammonium (resin-NH_4-N) were determined by automated colorimetry on a Lachat QuikChem 8500 (Hach Ltd., Loveland, CO, USA). The effect of N addition on resin-N was calculated for each plot as the N addition treatment divided by the N control treatment value and then ln-transformed.

Photosynthetically active radiation (PAR) was measured in each plot with a Li-COR LI-2500 quantum sensor (Li-COR, Lincoln, NE). We recorded PAR measurements on a cloudy day (September 2018) between 1:30 to 3:00 pm, for three minutes per reading. In addition, we quantified percent canopy openness from hemispherical photographs taken using a Nikon D7500 and an AF-S fisheye NIKKOR 8-15mm f/3.5-4.5E ED and analyzed them using GLA version 2.0 software (Frazer et al., 1999).

Experimental design and treatments

In September 2018 we transplanted 441 seedlings of three AM and one EM tree species in a combination of three treatments based on a split-split plot design. We selected seedlings of *Q. salicifolia* Née (Fagaceae) to represent EM associated species and *Ocotea cernua* (Nees) Mez, *Nectandra salicina* C.K. Allen, and *Ocotea laetevirens* Standl. & Steyerm (all Lauraceae), to represent AM associated species. AM species were selected to match *Q. salicifolia* ecology and seed size; all species had an average seed size of 1.5 to 2 cm. We did not evaluate the root mycorrhizal colonization of our study species, but the genera *Nectandra* and *Ocotea* are known to form AM associations, while *Quercus* associates with EM (Averill et al., 2019; Soudzilovskaia et al., 2020). *Quercus salicifolia* is the only EM taxon that occurs at the study site; seedlings of *Q. costaricensis* and *Q. insignis*, that occur at lower and higher elevations respectively, were collected to include in the experiment but did not survive transplantation. Seedlings were collected from forests surrounding the plots, planted in soil collected from three sources along a roadside close to both the oak and mixed forest patches, and grown in a greenhouse for one month until transplanting.

Experimental plots were divided into two treatments: N addition and OM manipulation subplots (Figure 5.1b). In the first split, half of each plot received 4.16 g m^{-2} of slow-release N fertilizer in the form of urea comprised of 44% nitrogen (ESN, Nutrien, Saskatoon, Canada) every three months (+N), with the other (slightly upslope) half of the plot designated as the control-N. This N application equates to 69.33 kg N ha^{-1} yr^{-1}. The N treatment and control subplots were further split into sub-subplots by the OM treatment, which consisted of three levels: (i) an OM removal (O_{rem}) plot; (ii) removal and replacement of the OM from the same plot and forest type, and (iii) reciprocal replacement of the OM from the other forest type within the same block (O_{mix} or O_{oak}; Figure 5.1b). Existing seedlings and herbaceous vegetation were removed at the beginning of the experiment. In each plot, three seedlings of each of the AM species and an average of five seedlings for *Q. salicifolia* were transplanted into each treatment combination. To evaluate the effect of mycorrhizal type on seedling performance, we planted AM associated species and EM associated species into separate 90 × 90 cm quadrats within each subplot. Within each sub-subplot, seedlings were planted 30 cm apart. In each treatment a total of nine AM seedlings and an average of five EM seedlings were transplanted.

Seedling measurements

Approximately every three months over 13 months we censused seedling stem height, root collar diameter, number of leaves, leaf length and leaf width. In October 2019 all seedlings were harvested and separated into leaf, stem, and root components. Each component was dried at 60°C for 48 h and weighed to calculate total plant biomass. Due to uncertainty in allometric models to estimate the initial biomass for each plant we used the relative growth rates of the leaf area and stem. Relative growth rate of the leaf area (RGR_L, $mm^2\ cm^{-2}\ d^{-1}$) was calculated as the natural log of final leaf area minus the natural log of initial leaf area divided by the number of days in the experiment. Relative growth rate of the stem height (RGR_S, $cm\ mm^{-1}\ d^{-1}$) was calculated in the same way. We determined RGR_L and RGR_S at the initial and final measurements and at 3 month intervals. Average seedling size at the time of transplant varied by species (Figure D.1, D.2)

We calculated leaf mass fraction (LMF g g^{-1}), stem mass fraction (SMF g g^{-1}), and root mass fraction (RMF g g^{-1}) as the proportion of each component of the total plant dry mass. Leaves were digitally scanned to calculate final areas and leaf damage, and total root length was calculated using ImageJ2 software (Rueden et al., 2017) and Smartroot (Lobet et al., 2011). Percent leaf damage was calculated as the difference between observed leaf area and the estimated total area for each leaf. We also calculated leaf area per unit leaf mass (specific leaf area, SLA cm^2 g^{-1}) and root length per unit root mass (SRL cm g^{-1}). We calculated leaf area ratio (LAR cm^2 g^{-1}) as the total leaf area per unit plant biomass. We quantified foliar C and N concentrations for each seedling by dry combustion using an elemental analyzer (Vario Micro Cube, Elementar, Hanau, Germany).

Statistical analyses

Edaphic and light variables were compared between oak-dominated and mixed forests using one-way ANOVA with log or square root transformation. NH_4-N and NO_3-N, which were not normally distributed after transformation, were compared using a Wilcoxon rank sum test. To estimate treatment effects on RGR_L, RGR_S, biomass allocation, functional traits, and foliar nutrient content, linear mixed-effects models were used, implemented in the package *lme4* (Bates et al., 2015). We created a model for each species, including forest type, N treatment, and OM treatment as fixed effects and plots as nested random effects. Canopy openness was used as a covariate in the model for RGR_L and for RGR_S; PAR, and canopy openness were covariates for LAR, biomass allocation, and SLA. To meet distributional assumptions, OM depth was log transformed, PAR, SLA and SRL were square root transformed, and LMF, SMF and RMF were logit transformed. *P*-values of the main effects and interactions were estimated using model simplification (Crawley, 2013). Models were compared using a likelihood-ratio test in the package *lmerTest* (Kuznetsova et al., 2017). For post-hoc tests among treatment levels, we used the package *emmeans* (Lenth, 2020) applying Tukey correction for significance. For the final analyses we used the 315 seedlings that survived until the end of the experiment. Statistical analyses were conducted in R version 3.6.3 (R Core Team, 2020).

RESULTS

Soil conditions and light environments

Mixed and oak-dominated forest differed markedly in the depth of the organic horizon and in N availability. The organic layer in the oak-dominated forest was on average three times as thick as that of the mixed forest (Table 5.1). In this layer, extractable NH_4-N and NO_3-N were significantly higher in the mixed forest compared to the oak-dominated forest (Table 5.1). In the mineral soil there was significantly higher NO_3-N in the mixed forest compared to the oak-dominated forest, but NH_4-N did not differ between forests (Table 5.1). Photosynthetically active radiation did not differ between forest types, while canopy openness was significantly greater in the mixed forest (Table 5.1). There was a significant positive correlation between PAR and canopy openness ($r = 0.46$, $p = 0.05$).

Nitrogen addition markedly increased inorganic N availability measured in both organic and mineral soil using resin bags 36 days after N application (Table D.2). In the organic horizon, resin-extractable NH_4-N and NO_3-N were 37 and 9 times higher in the +N compared to control-N treatment respectively in the mixed forest, and 75 and 16 times higher in oak forest. Similar patterns were observed in the mineral soil layer (Table D.2, Figure D.3).

Plant growth responses

Seedlings mean leaf area growth (RGR_L) ranged 0.03 to 0.08 $mm^2\ cm^{-2}\ d^{-1}$ across species. In general, AM species produced more leaf area in mixed forest than in oak forest

(Figure 5.2). This relationship was significant for *N. salicina* over the full length of the experiment ($\chi^2 = 3.5$, d.f. = 1, $p = 0.05$) and for the last census ($t = 2.5$, $p < 0.05$, Figure 5.2c), but not for the other species. The EM species, *Q. salicifolia*, produced more leaf area in the mixed forest, but only in the last census ($t = 2.8$, $p < 0.01$, Figure 5.2e). Leaf production did not respond significantly to N or OM treatments. For stem height growth (RGR_S) there was no significant effect of forest type for AM species over the whole experiment (Figure 5.3a), while *O. cernua* seedlings grew taller in mixed forest in the last census ($t = 2.4$, $p < 0.05$, Figure 5.3b). In *Q. salicifolia,* RGR_S was faster in mixed forest ($\chi^2 = 4.3$, d.f. = 1, $p < 0.05$). Mortality rates were similar for AM seedlings growing in mixed and oak-dominated forest (29% and 37%, respectively). Likewise, mortality of *Q. salicifolia* was nearly identical in mixed and oak dominated forest (26% and 27%, respectively).

Seedlings of the AM-associated species also had significantly lower LAR in the oak than in the mixed forest (Figure 5.4; *O. cernua*: $\chi^2 = 5.9$, d.f. = 1, $p < 0.05$, *N. salicina*: $\chi^2 = 8.4$, d.f. = 1, $p < 0.01$ and *O. laetevirens*: $\chi^2 = 4.6$, d.f. = 1, $p < 0.05$). In addition, *N. salicina* showed a significant interaction between N and OM treatments ($\chi^2 = 7.5$, d.f. = 2, $p < 0.05$), whereby N addition in the O_{mix} treatment was associated with lower LAR ($t = 2.8$, $p < 0.01$). There were no significant differences in LAR for EM *Q. salicifolia* between forests ($\chi^2 = 0.09$, d.f. = 1, p = n.s).

Seedling SLA, SRL, foliar N and herbivory damage

Seedlings of the AM-associated species had significantly denser leaves (lower SLA) in the oak forest than in the mixed forest (Figure 5.5a; *O. cernua*: $\chi^2 = 4.6$, d.f. = 1, $p < 0.05$; *N. salicina*: $\chi^2 = 7.7$, d.f. = 1, $p < 0.01$; *O. laetevirens*: $\chi^2 = 6.1$, d.f. = 1, $p < 0.05$). In addition, *O. cernua* showed a two-way interaction between forest type and OM treatment ($\chi^2 = 7.3$, d.f. = 2, $p < 0.01$), with seedlings in the O_{mix} and O_{oak} treatments having higher SLA in the mixed forest than oak forest ($t = 2.8$, $p < 0.01$ and $t = 3.1$, $p < 0.01$, respectively), with no differences in the O_{rem} treatment. In contrast, there were no significant differences in SLA for the EM species *Q. salicifolia* between forest types. There were no significant differences in SRL for the AM species nor *Q. salicifolia* (Figure 5.5b)

Seedlings of the AM associated species had significantly higher foliar N concentration (Fig 5c) in mixed than oak forest (*O. cernua*: $\chi^2 = 5.5$, d.f. = 1, $p < 0.5$; *N. salicina*: $\chi^2 = 7.2$, d.f. = 1, $p < 0.01$; *O. laetevirens*: $\chi^2 = 5.2$, d.f. = 1, $p < 0.05$). Foliar N concentration was also higher in the N addition treatment for two species: *O. cernua* and *O. laetevirens* ($\chi^2 = 3.8$, d.f. = 1, $p = 0.05$ and $\chi^2 = 5.9$, d.f. = 1, $p < 0.05$). There were no significant interactions between N treatments and forest type for any species (Figure 5.6). Foliar damage tended to be greater in the mixed forest where foliar N was higher, although differences were only statistically significant for *N. salicina*: $\chi^2 = 8.1$, d.f. = 1, $p < 0.01$ (Figure 5.5c, d). For *Q. salicifolia,* foliar N did not vary between forests (Figure 5.5c, Figure 5.6d), but differed among OM treatments ($\chi^2 = 7.6$, d.f. = 2, $p < 0.05$), with lower values in the OM_{rem} compared to the OM_{oak} treatment ($t = -2.5$ $p < 0.05$).

Biomass allocation to shoot and root tissues differed among treatments and species (Figure 5.7). There was a significant effect of forest type on the shoot:root mass relationship for all AM species (*O. cernua*: $F_{1,72.6} = 6.44$, $p < 0.05$; *N. salicina*: $F_{1,71} = 5.01$, $p < 0.05$; *O. laetevirens*: $F_{1,80.9} = 5.62$, $p < 0.05$). Larger seedlings of the AM species allocated more resources to shoot mass in the mixed forest than in the oak forest. For *Q. salicifolia* the shoot:root biomass relationship was unaffected by forest type. In the mixed forest, LMF was significantly higher compared to the oak forest for *O. cernua* ($\chi^2 = 4.1$, d.f. = 1, $p < 0.05$) and *N. salicina* ($\chi^2 = 4.9$, d.f. = 1, $p < 0.05$), but not for *O. laetevirens* or *Q. salicifolia* (Figure D.4a). Species' SMF responded differently low to the treatments, with no main effects of forest (Figure D.4b) or N addition except for *O. cernua*, which responded to the main effect of OM treatment. For AM species, RMF tended to be higher in the oak forest compared to the mixed forest (Figure D.4c) but was significant only for *N. salicina* ($\chi^2 = 5.0$, d.f. = 1, $p < 0.05$). *Quercus salicifolia* SMF and RMF did not respond to the treatments.

DISCUSSION

We found a large reduction in inorganic N availability beneath oak forest stands consistent with the mycorrhizal associated nutrient economy (MANE) framework (Phillips et al., 2013). We further found that low N availability in oak stands translated to low foliar N concentration for AM seedlings but not for oak seedlings. Reduced N availability had a small effect on seedling leaf or stem growth rates, although both oak and AM seedlings grew slower in oak forest. . Likewise, manipulations of the SOM layer did not influence seedling growth. These results point to limited effects of alterations in soil N availability on seedling growth.

Differences in soil chemistry and physical properties between adjacent oak and mixed forest stands

Nitrogen availability was six times lower, and the OM layer three times thicker, in oak-dominated forest compared to adjacent mixed forest. These results are consistent with (i) the nutrient economy framework for EM forests (Phillips et al., 2013), and (ii) observations of generally low N mineralization rates in Central American montane forests (Marrs et al., 1988). In EM-dominated sites, OM accumulates in the soil due to a low decomposition rate, while mycorrhizal uptake of N directly from organic matter reduces inorganic N availability (Lin et al., 2017; Phillips et al., 2013). However, differences in OM accumulation and N availability can appear even when decomposition rates are similar for litter produced by AM and EM trees (Kyaschenko et al., 2017; Seyfried et al., *in review*). Reductions in N availability and increases in

OM have also been observed at 1000 m a.s.l., associated with the EM tree *Oreomunnea mexicana* when compared to nearby mixed forest (Corrales et al., 2016; Dalling et al., 2021). Oak forests in Costa Rica at 2900 m a.s.l. have similar values for OM thickness compared to EM-dominated forests in this study (Hertel et al., 2003). A reduced N availability and greater accumulation of organic matter at the soil surface is therefore a widespread feature of tropical montane EM forests, and follow global patterns of greater soil C:N in EM-dominated vegetation (Averill et al., 2014, but see Ushio et al., 2017).

Seedling growth performance in mixed and oak forest

We predicted that AM-associated seedlings would have significantly lower growth rates in oak forest due to greater N limitation. This prediction is consistent with observations of reduced growth rates of non-mycorrhizal *Roupala montana* (Proteaceae) seedlings inside versus outside *Oreomunnea*-dominated forest patches (Corrales et al., 2016). We found that greatly reduced N availability coupled with OM accumulation in oak forest had only a small effect of leaf or stem growth rate of transplanted seedlings, although AM seedlings generally grew faster in mixed forest, consistent with higher foliar N concentration and higher light availability.

We expected AM seedling performance to respond positively to N addition, especially in oak forest, due to the low soil N. Nitrogen addition experiments in lowland and premontane tropical forests have shown increases in tissue N concentration in seedlings (Andersen et al., 2010; Santiago et al., 2012) and increases in adult AM tree growth rate (Tanner et al., 1990, J. Dalling, unpublished). However, numerous experiments in lowland and montane forests have also failed to find growth responses to N addition (Wright et al., 2018). Consistent with our results, N fertilization in a wet forest in Ecuador at 1000 m showed limited responses of seedling foliar N and biomass allocation to N addition (Cárate-Tandalla et al., 2018). Lack of a N treatment response given the strong effect on soil N availability is surprising, and may reflect multiple nutrient limitation (Santiago et al. 2012), or potentially a decline in soil pH associated with urea addition (Yavitt et al., 2011).

The AM-associated seedling response potentially reflects low nutrient availability. Seedlings of the AM species showed lower SLA and foliar N concentrations in oak stands, although the effect on leaf growth rate was weak. In lower montane forest in western Panama, Andersen et al. (2010) found that N addition to understory palm species (that form AM associations) significantly increased both foliar N concentrations and photosynthetic rates, but did not increase relative growth rates because increased foliar N was associated with increased levels of herbivory. In this study, the contribution of herbivory in RGR_L was minor, as foliar damage tended to be higher in the mixed forest for all AM species, but was only significant for *N. salicina*.

For EM trees, substantial evidence supports positive PSF on the growth or survival of seedlings in EM-dominated forest stands in temperate (Bennett et al., 2017; Teste et al., 2017) and subtropical forests (Liang et al., 2020). Mechanisms potentially facilitating the success of EM seedlings where conspecifics are present include protection from pathogens (Bennett et al., 2017) and resource transfer via EM fungal networks (Liang et al., 2020; McGuire, 2007). However, here we found that stem growth of *Q. salicifolia* was slower in the oak-dominated than the mixed forest stands, either reflecting lower light availability or a possible negative PSF. These findings are consistent with a pot experiment in nearby lower montane forest, where two EM species (*Oreomunnea mexicana* and *Quercus insignis*) showed negative PSF effects on seedling growth rate when planted in soil collected from beneath conspecific trees (Corrales et al., 2016).

We also found that larger seedlings of AM species in oak forests allocated less biomass to shoots relative to roots than in mixed forests, and that LAR was lower in oak forest as a consequence of reduced SLA and LMF. Allocation and leaf traits reflect the relative importance of above-ground (light) and below-ground resources (moisture and nutrients) (Ericsson, 1995; Kitajima, 1994; Poorter, 1989; Wright et al., 2010). Here, leaf trait results were consistent with seedlings responding to nutrient availability rather than differences in light availability. Plants in part compensate for lower light availability by making leaves with higher SLA and allocating more resources above-ground (Kitajima, 1994; Poorter, 1989). While we found that canopy openness was significantly higher in the mixed compared to oak forests, so too were SLA and LAR. Meta-analyses and a global experimental test have shown that at sites with low N availability species have low SLA (Hodgson et al., 2011; Ordoñez et al., 2009), so from the perspective of resource economy, low SLA should be expected in resource-poor environments (Weemstra et al., 2020). Intraspecific variation in SLA shows a similar response to variation in nitrogen availability in subtropical forest (He et al., 2018). Thus, while some differences in forest structure arise comparing mixed and oak forests, compositional effects on soil nutrient cycling likely outweigh effects on light availability for recruiting seedlings.

In addition to effects on soil fertility, accumulation of SOM can reduce moisture availability (Werner & Homeier, 2015), creating conditions that reduce seedling survival. We predicted that removal of the thick OM layer associated with oak forest would benefit AM species by increasing bulk density and moisture availability. Contrary to expectation, we found SOM treatments had little effect on AM and EM seedling growth, and therefore the deep organic layer was not a significant barrier to seedling performance in this experiment.

Responses of *Q. salicifolia* to N addition

Differences in biogeochemical cycling beneath EM and AM associated forest stands have been related to differences in nutrient acquisition strategies between mycorrhizal groups (Phillips et al., 2013). Extracellular enzymes produced by EM fungi enable them to access organic sources of nutrients inaccessible to AM fungi (Kohler et al., 2015; Lindahl & Tunlid, 2015; Martin et al., 2016). Consistent with the use of organic sources of N, *Q. salicifolia* did not respond to the N addition treatment. Similarly, in a pot experiment using *Q. costaricensis*, which occurs in higher elevation forest adjacent to *Q. salicifolia* in Panama, N addition did not influence tissue nutrient content or seedling biomass (Holste et al., 2017). Differences in N nutrition between AM and EM seedlings are also unlikely to reflect seed reserves. In this study AM and EM seedlings were of similar size, AM seedlings were grown for one month before transplanting and at that point none of them had the seed attached. Seedlings of *Q. salicifolia* had seeds attached at the time of transplant, but by harvest only three of 61 seedlings had a seed remnant attached.

Implications for global change

Compelling evidence indicates that tropical tree distributions are moving upslope on mountains in response to warming (Fadrique et al., 2018; Feeley et al., 2013; Tito et al., 2020; Wright et al., 2009). However, projections for future species distributions focus on the climatic niche, with little consideration of edaphic effects. In Central America and the northern Andes, where lowland forests are dominated by AM taxa, and montane forests by EM taxa, upslope migration suggests that AM associated species will encounter a compositional legacy — soils generated beneath an EM canopy. In our study, AM seedlings transplanted beneath oak (EM) canopies tended to grow more slowly than on their home soil type, and after a year had much reduced foliar N concentrations, suggesting their fitness may decline with time. Seedlings of AM species in this study were also first collected in the field, planted in soil combined from oak and mixed forest patches, and then transplanted in the treatments. This approach may have bypassed a series of important biotic filters that constrain initial seedling establishment. Conservation assessments for tropical montane forests, and future studies of species migration potential need to evaluate the distribution and dominance of EM taxa, and the impact of EM derived soils on all life stages of AM trees.

TABLE

Table 5.1. Initial conditions of the soil and environmental characteristics before the experiment by forest type. Data are means (± SE) of nine samples for each forest.

		Forest				
	Variable	**Mixed**	**Oak**	**F $_{(1,16)}$**	**W[*]**	**P**
Organic layer	NH_4-N[‡]	40.8±14.1	9.1±1.3	-	78	<0.001
	NO_3-N[‡]	19.6±8.3	0.003±0.003	-	81	<0.001
	depth (cm)	3.8±0.5	9.4±0.3	68.7	-	<0.001
Mineral layer	NH_4-N[‡]	1.7±0.3	1.3±0.2	-	48	n.s
	NO_3-N[‡]	6.15±1.3	0.07±0.03	-	81	<0.001
	PAR[§]	11.73±1.6	9.9±1.2	0.76	-	n.s
	Canopy openness[†]	15.3±0.6	12.9±0.5	8.13	-	<0.05

[‡]mg kg^{-1}; [§]µmol m^{-2} s^{-1}, [†]Percent (%); *n=18

FIGURES

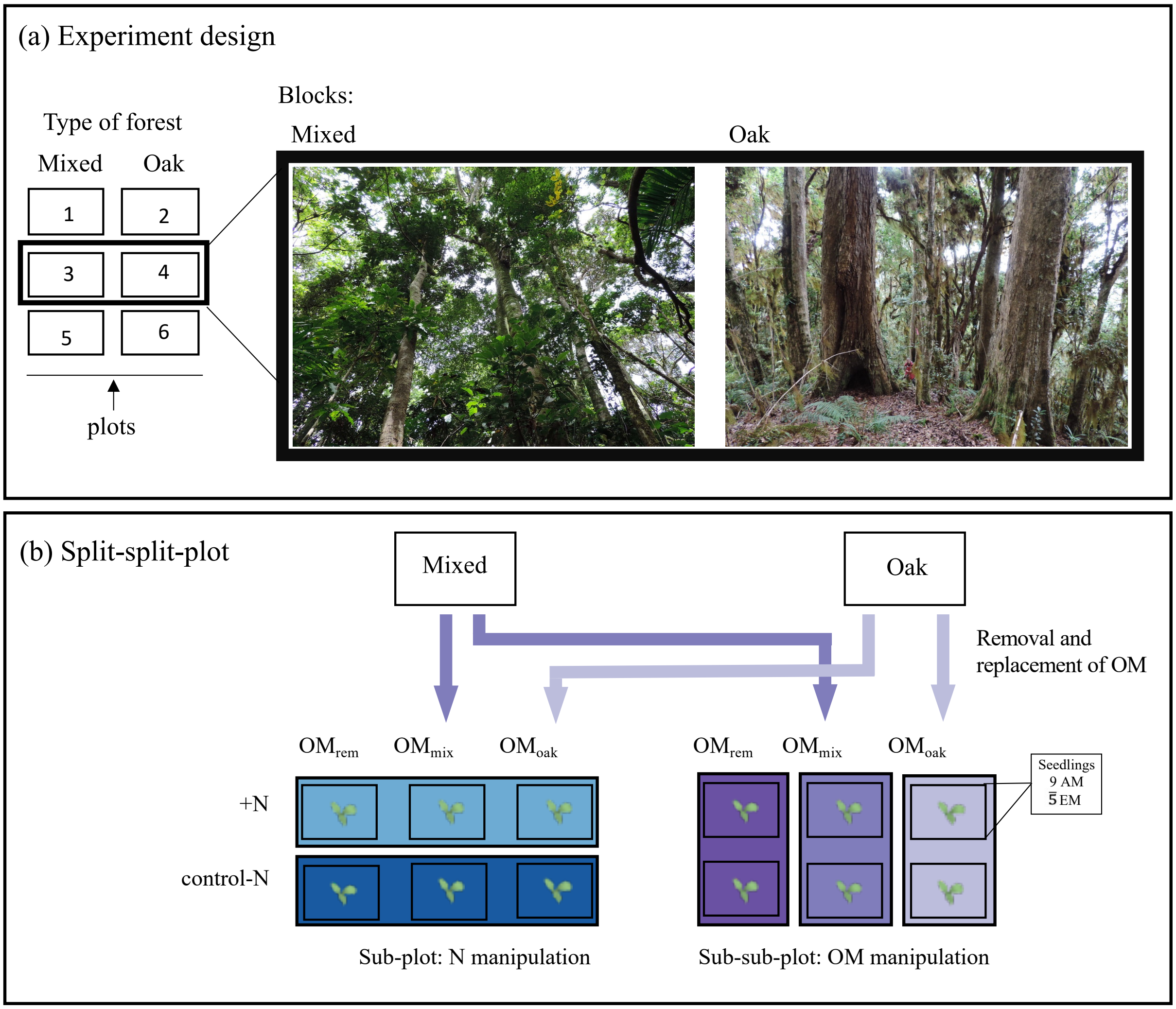

Figure 5.1. Split-split-plot experiment design in Volcan Baru National Park. (a) General experiment design. Block includes the pair of plots for which the OM was exchanged. (b) Split-split-plot description. Blue color represents the first split, by nitrogen treatment. Purple color represents the second sub split, by organic matter (OM) treatment.

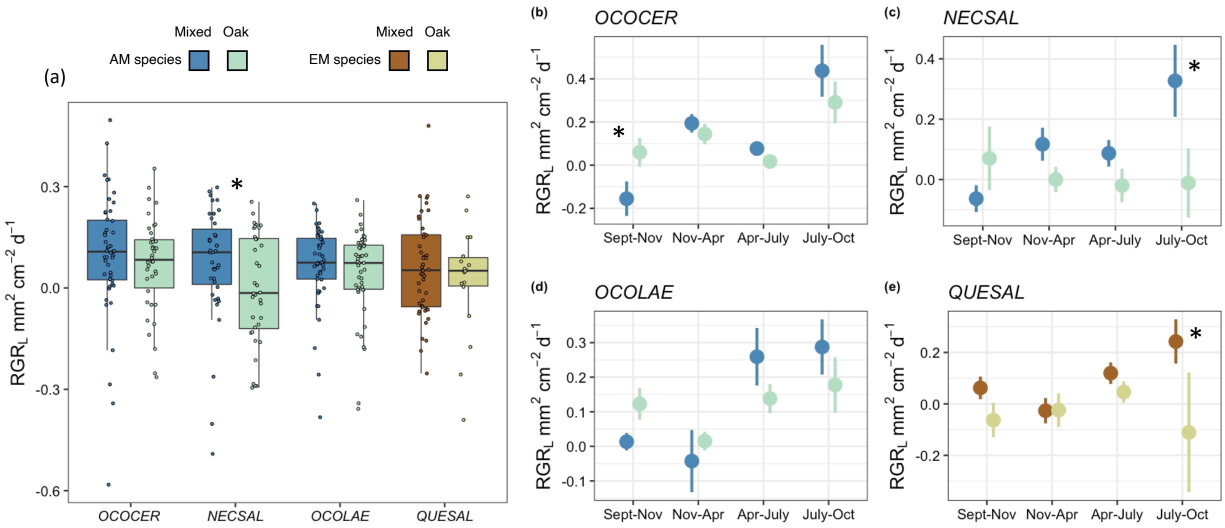

Figure 5.2. (a) Variation in leaf growth rate (RGR$_L$) over the entire period; (b-e) by census, data are the mean ± 1SE. * significant difference between forest types ($p < 0.05$). OCOCER= *O. cernua*, NECSEL= *N. salicina*, OCOLAE= *O. laetevirens*, and QUESAL= *Q. salicifolia*.

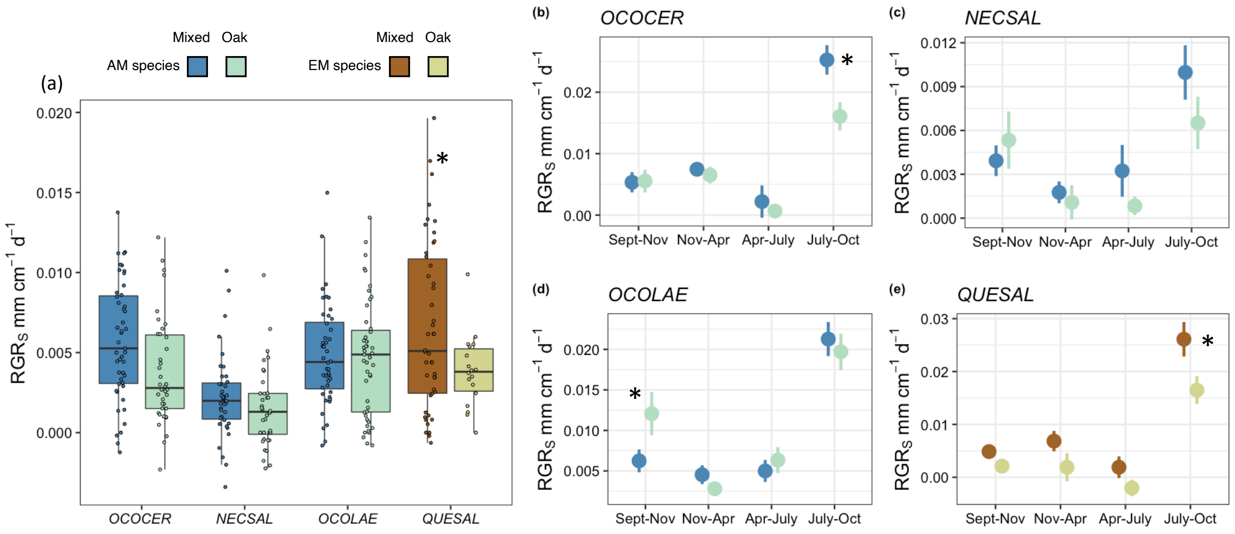

Figure 5.3. (a) Variation in stem growth rate (RGR$_S$) over the entire period; (b-e) by census, data are the mean ± 1SE. * significant difference between forest types ($p < 0.05$). OCOCER= *O. cernua*, NECSEL= *N. salicina*, OCOLAE= *O. laetevirens*, and QUESAL= *Q. salicifolia*.

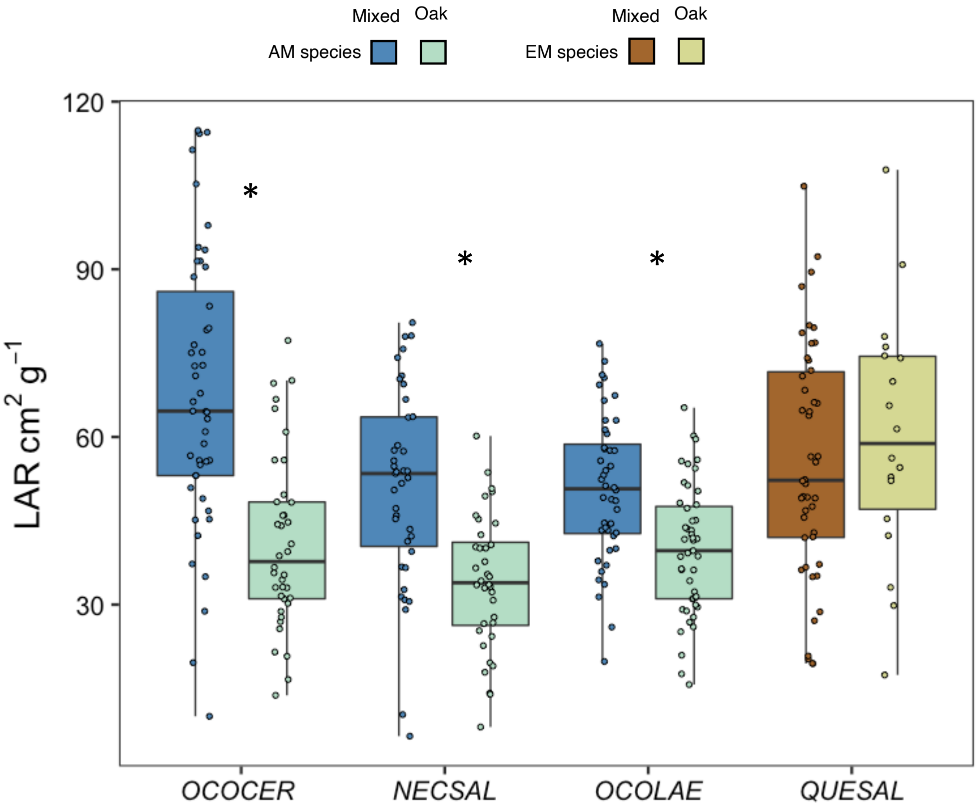

Figure 5.4. Variation in leaf area ratio (LAR) for seedlings associated with arbuscular mycorrhiza (AM) and ectomycorrhiza (EM) in mixed and oak forest. * significant difference between forest types ($p < 0.05$). OCOCER= *O. cernua*, NECSEL= *N. salicina*, OCOLAE= *O. laetevirens*, and QUESAL= *Q. salicifolia*.

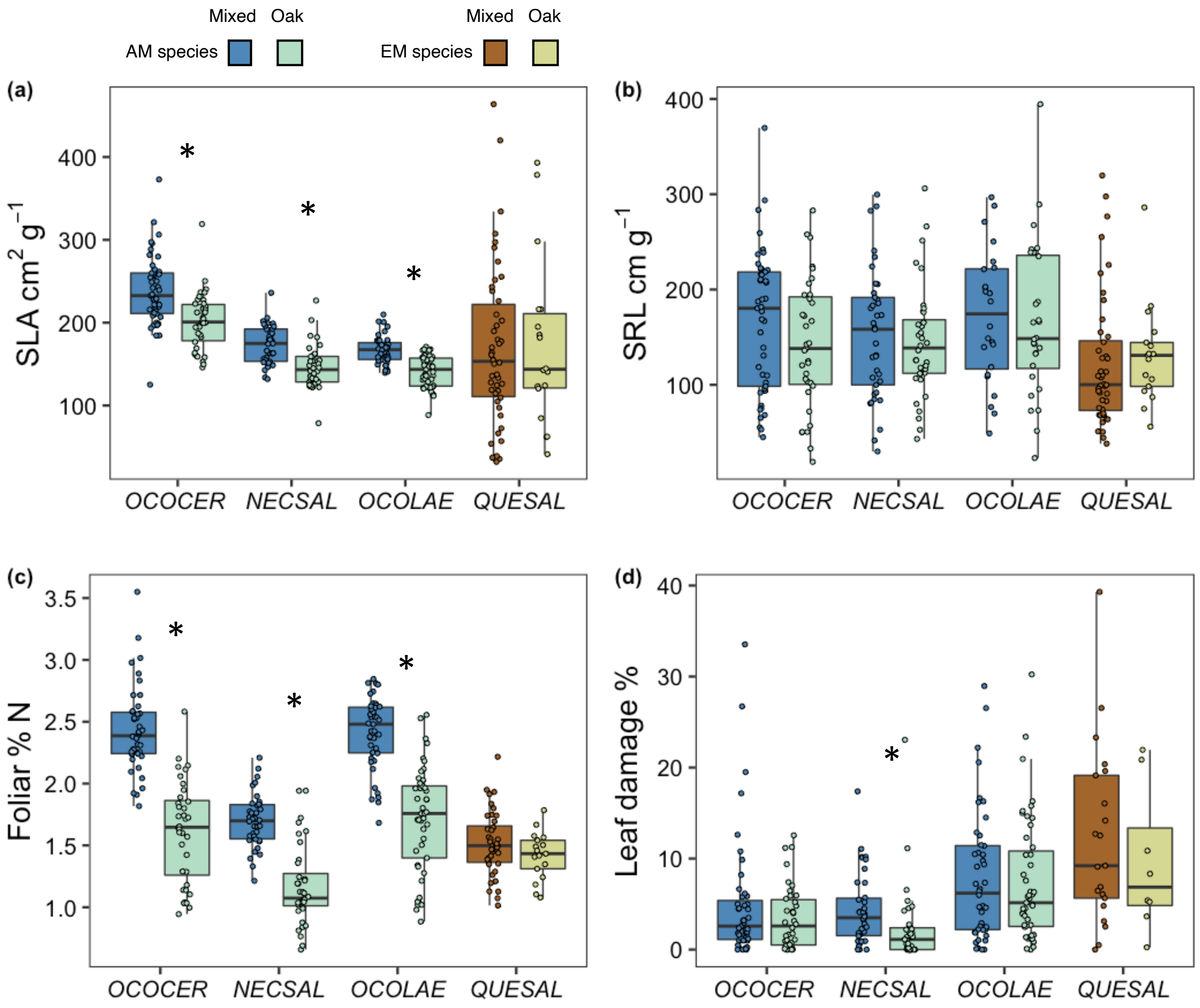

Figure 5.5. Specific leaf area (a), specific root length (b), foliar N (c) including all N treatments, and foliar damage variation (d) between forest types for seedlings associated with arbuscular mycorrhiza (AM) and ectomycorrhiza (EM). * significant difference between forest types. OCOCER= *O. cernua*, NECSEL= *N. salicina*, OCOLAE= *O. laetevirens*, and QUESAL= *Q. salicifolia*.

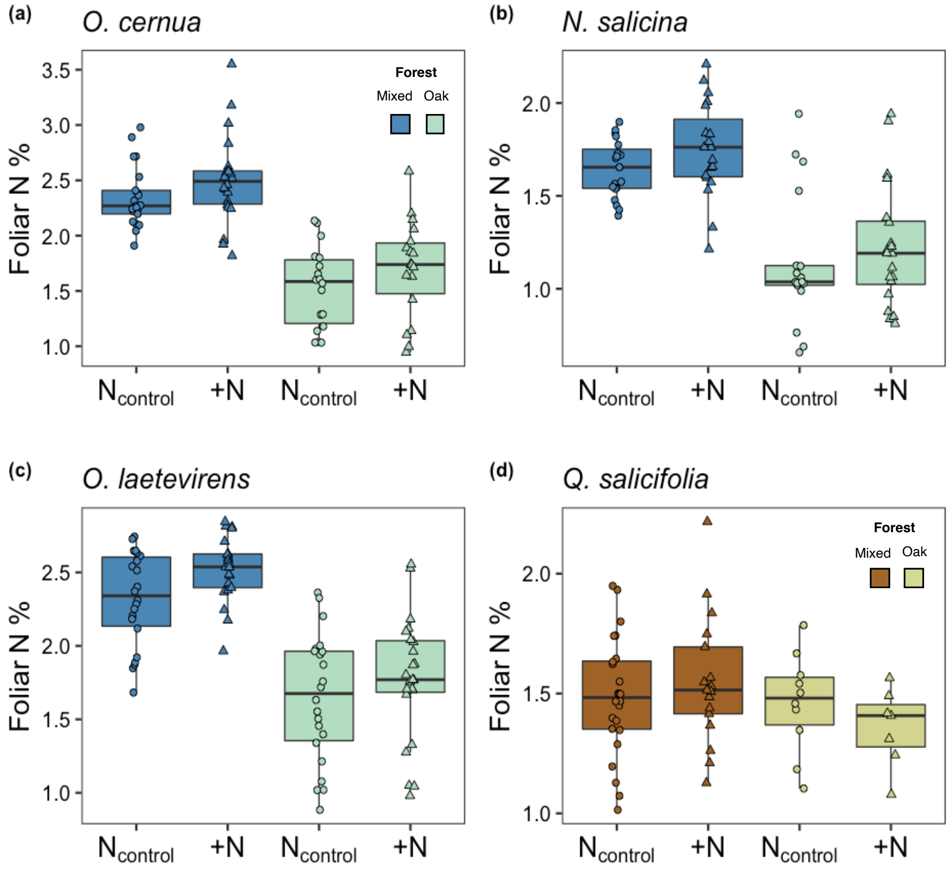

Figure 5.6. Interaction between forest type and nitrogen treatment for seedlings associated with arbuscular mycorrhiza (AM) and ectomycorrhiza (EM).

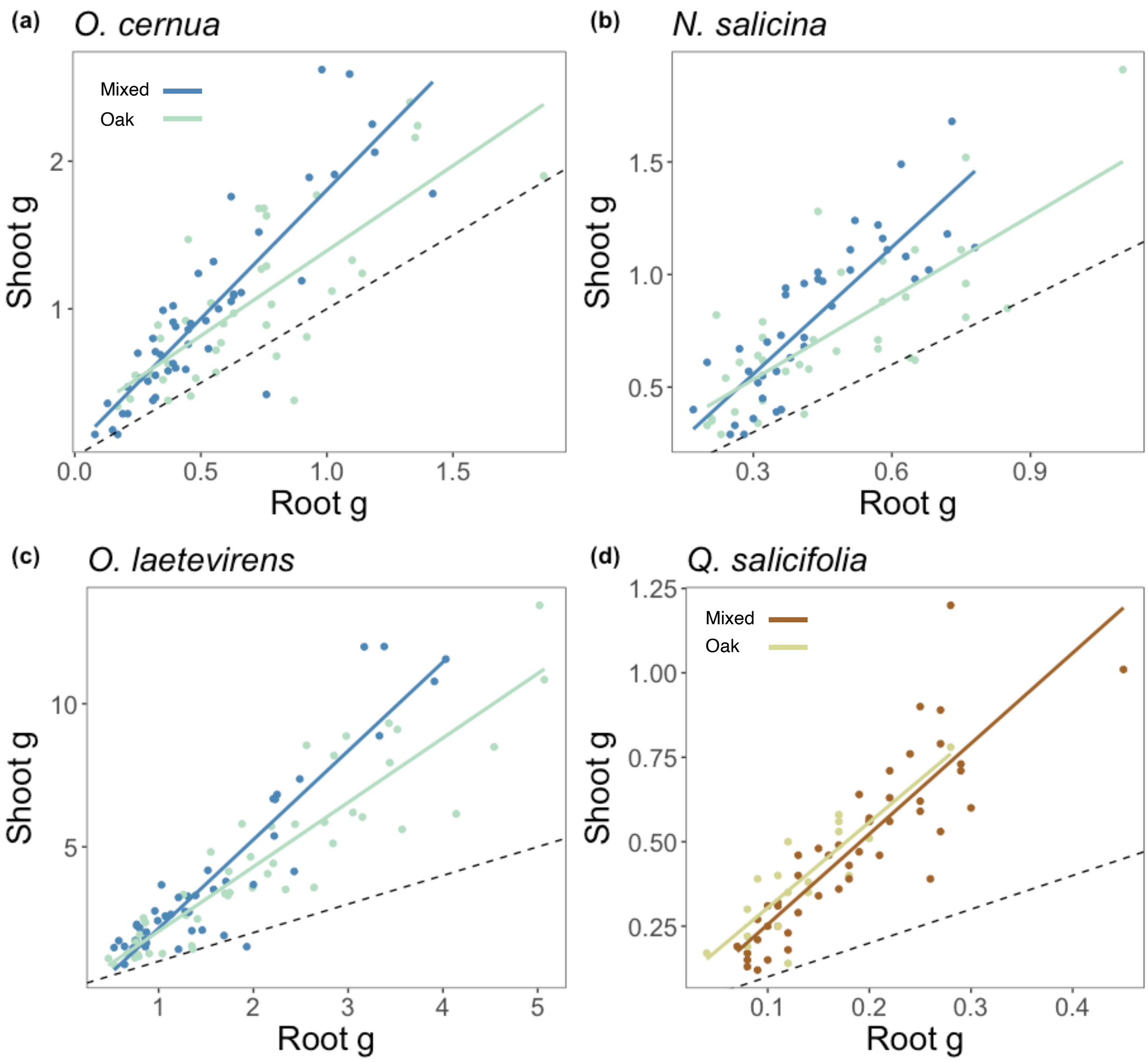

Figure 5.7. Shoot (leaf + stem) to root biomass relationships for AM seedlings (a-c) and EM seedlings (d). Points are individual seedlings. Solid lines represent the linear relationship between shoot and root biomass. Dashed line represents the 1:1 ratio. Dark color = mixed forests, light color = oak forests.

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CHAPTER 6: CONCLUSION

SUMMARY AND SYNTHESIS

This dissertation research highlights the importance of tropical montane forests in biogeochemical processes, especially C cycling, and emphasizes the role of EM-associated trees, specifically the genus *Quercus*, as a critical contributor to C storage and soil nutrient cycling. Changes in tree community composition along environmental gradients can reflect species adaptations to particular habitats, and therefore changes in resource acquisition strategies. In chapters 2 and 3 I demonstrated high species turnover in response to variation in soil and climate variability at a relatively local scale. In chapter 2, the high diversity in premontane forests reflects the influence of both lowland and highland species on this pattern. Additionally, tree communities change nearly completely as a consequence of geological patterns that influence soil parent materials across just 13 km. Consistent with other studies in lowland forests, fertility gradients, especially variation in soil P, as well as rainfall, appear to drive species composition in premontane forests.

In chapter 3, diversity in upper montane forests decreased with elevation and was similar to other comparable forests (Aiba et al., 2010; Homeier et al., 2010; Kappelle et al., 1995; Lieberman et al., 1996). However, we found large compositional shifts in tree species along the elevational gradient in response to environmental and biotic factors. We found that climate variables varied with elevation as expected, and that soils exhibited high variation in edaphic variables, especially in inorganic N and total P. Patterns in soil variables may reflect Volcan Baru's geological history, as eruptive episodes may have influenced nutrient pools, as well as biotic interactions. Tree composition was significantly different in arbuscular mycorrhizal (AM)-

mixed forests and ectomycorrhizal (EM)-tree forests; in chapter 4 we were able to determine that EM-oak forests are associated with low N availability.

Factors influencing C stock include abiotic variables (Clark et al., 2002; Girardin et al., 2010; Gerald Moser et al., 2011) as well as biotic interactions (Averill et al., 2014; Phillips et al., 2013; Steidinger et al., 2019). In chapters 2 and 3 we were able to show high variation in these factors in our system, and in chapter 4 we evaluated the effect of these factors on the forests' C stocks. We found large amounts of aboveground biomass and soil C in this system compared to others in the Neotropics. In contrast to expectation, soil C stocks were not correlated with the percent of EM. Instead, we suggest that the highest values of soil C reflect volcanic activity that buried C-rich surface soils in the past. Large aboveground biomass in cool environments was attributed to the presence of EM-associated *Quercus* species. Given the large contribution of some *Quercus* species to the C stock in montane forest in Panama, in chapter 5 we explored how the presence of *Q. salicifolia* influences soil properties and affects seedling performance.

We found a large accumulation of organic matter, and a reduction in inorganic N availability beneath oak forest stands, consistent with the mycorrhizal associated nutrient economy (MANE) framework (Phillips et al., 2013). We found foliar N was lower for AM seedlings growing in oak than in mixed forest. Reduced N availability had a small effect on seedling leaf or stem growth rates, although both oak and AM seedlings grew slower in oak forest. These results suggest that changes in soil nitrogen availability may have a limited effect on seedling growth, at least over the relative.

SIGNIFICANCE

This work strongly reinforces the remarkable importance of montane forests in their global contributions to C cycling and biogeochemical processes (Duque et al., 2021; Spracklen

& Righelato, 2014). Numerous studies have been conducted in lowland forests to evaluate factors influencing C stocks (Chave et al., 2003; Clark & Clark, 2000; Hofhansl et al., 2020; Nascimento & Laurance, 2002; Quesada et al., 2012). Less work has been done in montane forests, and most studies are limited to the Andes in Peru, Ecuador, and Colombia (Girardin et al., 2010; González-Caro et al., 2020; Malhi et al., 2017; G. Moser et al., 2008). We were able to highlight the value of premontane and montane forests on processes related to C cycling as a respond to temperature a geology history. Evaluating the effects of these factors on tropical forest C stocks is key in predicting future atmospheric CO2 levels in a changing world.

Furthermore, we were able to provide important insights into the effects of alterations in soil nutrient availability on seedling growth in EM-dominated stands in tropical montane forest. Compelling evidence indicates that tropical tree distributions are moving upslope on mountains in response to warming (Fadrique et al., 2018; Feeley et al., 2013; Wright et al., 2009). In Central America and the northern Andes, upslope migration suggests that AM associated species will encounter a compositional legacy — soils generated beneath an EM canopy. Our study provide an insight of how species may respond to this new conditions, although longer-term experiments are needed to fully understand.

FUTURE RESEARCH

In this study I was able to highlight the exceptionally high C storage in the AGB and soil C at the VBNP site, however, factors explaining this pattern are still not clear. I suggest that the exceptionally high soil C at the VBNP site may be a consequence of volcanic activity. Still, more studies are needed to determine if this pattern is due to volcanic activity or is a general phenomenon associated with TMF. If the latter case is true, regional and global mapping of soil and AGB needs to be updated (Asner et al., 2013). Additionally, this study found oak forests are astonishing ecosystems with important contributions to C and nutrient cycles. With current projections of global change, a key question that needs to be answered is how resilient will oak forests be to climate change and upward species migrations?

Work on my thesis has inspired me to conduct future research on the question of what maintains *Quercus* dominance in montane forests. Understanding how tropical forests support and maintain diversity is a key question that remains unanswered. Recent studies have demonstrated that below ground traits (root and biotic associations) hold the key to understanding species distribution and diversity. Yet, there are few studies addressing these topics in TMF, and they have focused on just one species. *Quercus* species in the TMF often cluster together, creating monodominant stands. However, some *Quercus* species are rarer in the forest, where a single tree is isolated from conspecifics or more highly dispersed in mixed forests. *Quercus* therefore is the perfect focal genus to answer my general question of how monodominance sometimes occurs at local scales, yet TMF maintain high diversity overall in the forest. Are there differences in *Quercus* species' root traits, including ectomycorrhizal colonization and diversity, that provide a competitive advantage over heterospecific trees?

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APPENDIX A: SUPPLEMENTARY MATERIAL FOR CHAPTER 2

Table A.1. Environmental characteristics of 12 one-hectare plots located in a premontane forest in western Panama. Plots are grouped by parent material (rhyolitic tuff, andesite, basalt, and dacite). Plot names are given along with their abbreviations used in figures. Rainfall is the annual mean (mm ± 1SE) from 2007-9 and 2011-14. Dry rainfall data are the monthly means (± 1SE) for the dry season (1 January - 30 April). Soils data are means (± 1SE) of 13 samples of 0-10 cm depth per plot. Superscripts report significant differences among sites, based on one-way ANOVA and Kruskal-Wallis analysis for parametric and non-parametric variables respectively. pH was measured in water. BD: Bulk density units are g cm^{-3}; all other soil variables are expressed on a volume basis. ECEC: Effective cation exchange capacity; TEB: Total exchangeable bases (see text for details).

	Rhyolite				Rhy/And transition	Andesite				Basalt	Dacite	
	Chorro A 'ChoA'	Chorro B 'ChoB'	Honda A 'HonA'	Honda B 'HonB'	Samudio 'Sam'	Bonita 'Bon'	P. Seco 'PSec'	Verrug. A 'VerA'	Verrug. B 'VerB'	Pinola 'Pin'	Hornito 'Hor'	Alto Frio 'AFri'
Location												
Lat	8.749	8.749	8.751	8.756	8.731	8.767	8.778	8.778	8.777	8.754	8.674	8.654
Lon	-82.229	-82.232	-82.239	-82.243	-82.248	-82.215	-82.198	-82.180	-82.170	-82.259	-82.214	-82.215
Elev (m)	1100	1240	1155	1240	1215	1300	880	970	850	1135	1330	1100
Temp (C)	20.5	19.7	20.2	19.7	19.7	19.4	21.8	21.4	22.0	20.1	19.2	20.5
Rainfall	5507 ± 247^{a}	6159 ± 617^{a}	6255 ± 962^{a}	6159 ± 617^{a}	4833 ± 219^{a}	5507 ± 247^{a}	6257 ± 310^{a}	6257 ± 310^{a}	6257 ± 310^{a}	$4964{*}\pm863^{a}$	5164 ± 232^{a}	$4641{*}\pm623^{a}$
Dry rainfall	351 ± 53^{ab}	332 ± 51^{abc}	381 ± 51^{abc}	332 ± 34^{abcd}	215 ± 30^{bcd}	351 ± 53^{ab}	445 ± 33^{a}	445 ± 33^{a}	445 ± 33^{a}	$159{*}\pm27^{d}$	203 ± 28^{cd}	$94{*}\pm27^{d}$
pH	3.7 ± 0.1^{e}	4.7 ± 0.1^{bcd}	3.6 ± 0.05^{e}	3.8 ± 0.2^{de}	4.2 ± 0.2^{de}	4.5 ± 0.06	4.4 ± 0.1^{cde}	4.6 ± 0.1^{bcd}	5.1 ± 0.04^{abc}	5.4 ± 0.1^{ab}	5.0 ± 0.2^{abc}	5.6 ± 0.1^{a}
BD	0.13 ± 0.01^{e}	0.31 ± 0.04^{cde}	0.29 ± 0.02^{cde}	0.17 ± 0.02^{de}	0.40 ± 0.01^{bcd}	0.34 ± 0.04^{bc}	0.41 ± 0.04^{bcde}	0.42 ± 0.01^{bc}	0.40 ± 0.03^{bcd}	0.50 ± 0.02^{ab}	0.26 ± 0.03^{cde}	0.66 ± 0.02^{a}
NH_4-N‡	0.8 ± 0.06^{ab}	2.4 ± 0.3^{ab}	2.25 ± 0.4^{ab}	1.78 ± 0.4^{abc}	0.6 ± 0.1^{b}	1.9 ± 0.3^{ab}	0.8 ± 0.07^{ab}	1.6 ± 0.3^{ab}	0.85 ± 0.1^{ab}	6.98 ± 0.89^{ab}	1.8 ± 0.25^{ab}	3.76 ± 0.6^{a}
NO_3-N‡	0.2 ± 0.1^{b}	1.17 ± 0.16^{ab}	1.2 ± 0.3^{ab}	0.43 ± 0.2^{ab}	1.17 ± 0.1^{ab}	1.77 ± 0.3^{a}	0.8 ± 0.12^{ab}	0.98 ± 0.1^{ab}	0.67 ± 0.08^{ab}	2.3 ± 0.3^{a}	1.2 ± 0.18^{ab}	2.5 ± 0.2^{a}
Total N†	1.8 ± 0.1^{c}	2.7 ± 0.3^{bc}	2.9 ± 0.2^{abc}	2.3 ± 0.2^{abc}	3.6 ± 0.2^{abc}	3.8 ± 0.6^{b}	2.2 ± 0.2^{abc}	2.7 ± 0.2^{abc}	2.2 ± 0.1^{c}	4.5 ± 0.1^{a}	2.8 ± 0.1^{abc}	4.7 ± 0.2^{ab}
Resin P‡	0.1 ± 0.03^{a}	0.01 ± 0.01^{a}	0.2 ± 0.01^{ab}	1.9 ± 0.38^{bc}	0.4 ± 0.08^{abc}	1.1 ± 0.2^{abc}	0.4 ± 0.1^{abc}	0.5 ± 0.1^{abc}	0.3 ± 0.03^{abc}	1.8 ± 0.1^{bc}	2.2 ± 0.2^{c}	1.4 ± 0.1^{abc}
Total P‡	57.2 ± 8.6^{c}	86.3 ± 10^{cd}	$180.6\pm11.4.5^{acd}$	127.7 ± 18^{acd}	270 ± 10^{abcd}	351 ± 57^{abcd}	369.2 ± 23^{abd}	241 ± 23^{abdc}	317 ± 35^{abcd}	617.5 ± 20^{b}	280 ± 20^{abcd}	503 ± 27^{ab}
Total	26.95 ± 3.0^{d}	31.53 ± 2.3^{d}	17.46 ± 0.9^{acd}	16.10 ± 1.9^{cd}	13.76 ± 0.5^{acd}	10.75 ± 0.6^{abc}	7.67 ± 0.6^{b}	11.16 ± 0.6^{abc}	8.00 ± 2.6^{b}	7.52 ± 0.3^{b}	10.38 ± 0.6^{abc}	9.60 ± 0.4^{ab}

Table A.1. (cont.)

	Rhyolite				Rhy/And transition	Andesite				Basalt	Dacite	
	Chorro A 'ChoA'	Chorro B 'ChoB'	Honda A 'HonA'	Honda B 'HonB'	Samudio 'Sam'	Bonita 'Bon'	P. Seco 'PSec'	Verrug. A 'VerA'	Verrug. B 'VerB'	Pinola 'Pin'	Hornito 'Hor'	Alto Frio 'AFri'
Total N:P	26.95±3.0^{d}	31.53±2.3^{d}	17.46±0.9^{acd}	16.10±1.9^{cd}	13.76±0.5^{acd}	10.75±0.6^{abc}	7.67±0.6^{b}	11.16±0.6^{abc}	8.00±2.6^{b}	7.52±0.3^{b}	10.38±0.6^{abc}	9.60±0.4^{ab}
Total C	29.6±2.2^{d}	50.6±6.1^{ab}	43.9.0±2.0^{abc}	40.9±4.0^{abcd}	51.3±2.5.6^{ab}	47.6±7.2^{abcd}	32.5±4.3^{cd}	37.9±3.1^{abcd}	28.7±1.7^{d}	54.2±1.6^{a}	35.0±1.6^{bcd}	51.1±2.3^{ab}
Al†	0.8±0.2^{ab}	1.3±0.2^{ab}	1.1±0.2^{ab}	1.2±0.3^{ab}	1.5±0.4^{ab}	2.5±0.5^{b}	1.1±0.2^{ab}	1.7±0.1^{b}	1.17±0.1^{ab}	0.3±0.1^{ab}	0.48±0.3^{ab}	0.03±0.02^{a}
Ca§	0.5±0.2^{ab}	1.2±0.4^{ab}	0.04±0.01^{b}	0.1±0.04^{b}	1.1±0.2^{ab}	0.3±0.05^{ab}	1.0±0.2^{ab}	0.4±0.05^{ab}	0.31±0.05^{ab}	6.6±0.3^{a}	4.9±0.75^{a}	8.47±0.3^{a}
Fe§	0.1±0.01^{b}	0.04±0.02^{b}	0.02±0.0^{ab}	0.03±0.1^{ab}	0.06±0.03^{ab}	0.05±0.02^{ab}	0.01±0.06^{ab}	0.05±0.01^{b}	<0.01^{ab}	<0.01^{ab}	<0.01^{ab}	<0.01^{a}
K§	0.1±0.01^{bcd}	0.07±0.02^{cd}	0.02±0.0^{e}	0.02±0.0^{e}	0.07±0.01^{bcd}	0.11±0.03^{abcd}	0.06±0.0^{cd}	0.06±0.0^{cd}	0.04±0.01^{de}	0.1±0.0^{ab}	0.18±0.02^{a}	0.12±0.01^{abc}
Mg§	0.28±0.03^{c}	0.07±0.1^{c}	0.04±0.0^{e}	0.06±0.02^{de}	0.32±0.05^{bc}	0.35±0.1^{bc}	0.33±0.06^{bc}	0.17±0.0^{c}	0.15±0.02^{cd}	1.09±0.06^{a}	1.01±0.2^{ab}	2.29±0.2^{a}
Mn§	0.01±0.01^{ef}	0.04±0.04^{def}	<0.01 ^{f}	<0.01 ^{f}	0.14±0.06^{bcd}	0.03±0.02^{cdef}	0.19±0.09^{abcd}	0.04±0.01^{cd}	0.07±0.01^{bcd}	0.15±0.01^{abc}	0.71±0.1^{a}	0.42±0.09^{ab}
Na§	0.01±0.01^{abc}	0.03±0.02^{abc}	0.01±0.0^{bc}	0.01±0.0^{c}	0.05±0.0^{a}	0.03±0.02^{ab}	0.04±0.0^{a}	0.03±0.0^{abc}	0.04±0.01^{a}	0.02±0.0^{abc}	0.03±0.0^{abc}	0.02±0.0^{abc}
ECEC§	1.8±0.1^{bc}	3.1±1.1^{abc}	1.3±0.2^{b}	1.5±0.3^{b}	3.4±0.2^{abc}	3.4±0.7^{abc}	2.8±0.2^{abc}	2.5±0.1^{abc}	1.8±0.1^{bc}	8.5±0.04^{ac}	7.4±1.1^{ac}	11.4±0.5^{a}
TEB§	0.9±0.2^{ab}	1.7±0.8^{ab}	0.1±0.01^{b}	0.2±0.08^{b}	1.6±0.2^{ab}	0.8±0.2^{ab}	1.5±0.3^{ab}	0.6±0.08^{ab}	0.6±0.1^{ab}	8.0±0.5^{a}	6.2±1.4^{a}	10.9±0.5^{a}

*Data available only for 2013-2014; ‡units μg cm^{-3}; †units mg cm^{-3}; §units C$_{M}$ L^{-1}

Table A.2. Stem number, species number and Fisher's alpha for trees ≥ 30 cm d.b.h

	Rhyolite				Rhyo/Ande transition	Andecite				Basalt	Dacite	
	ChorroA	ChorroB	HondaA	Honda B	Samudio	Bonita	P. Seco	Verrug.A	Verrug.B	Pinola	Hornito	A. Frio
Stems	75	88	153	187	119	117	117	93	87	167	178	115
No. Spp.	14	14	36	43	37	33	54	41	37	43	44	29
Fisher α	5.07	4.69	14.84	11.62	18.40	15.29	38.89	28.02	24.32	18.75	18.69	12.47

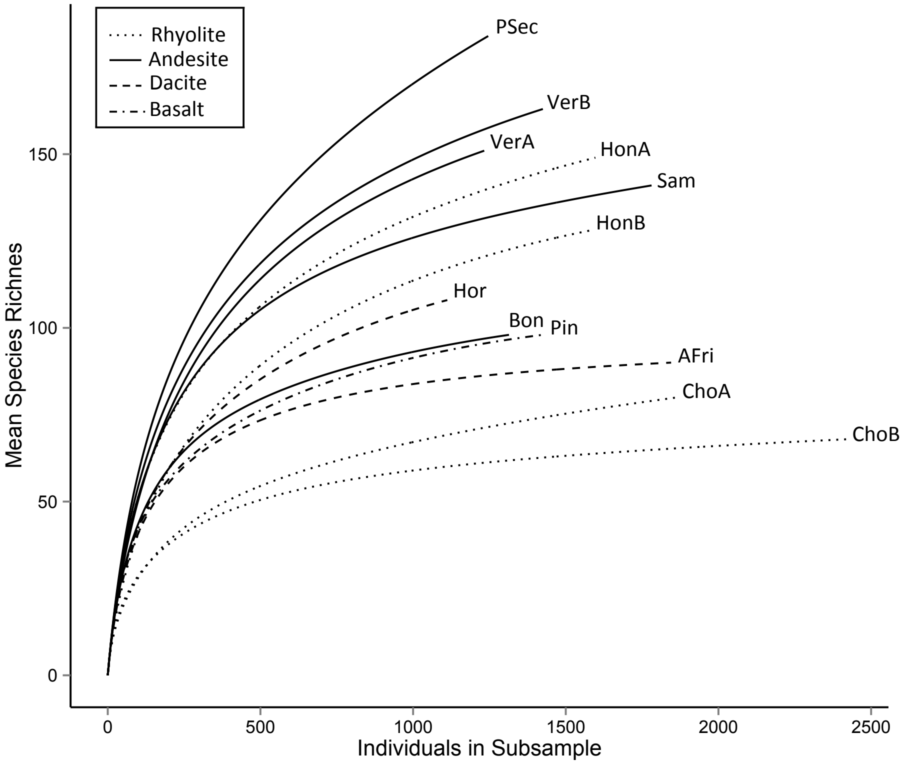

Figure A.1. Species accumulation curves for twelve one-hectare plots in the Fortuna and Palo Seco forest reserves. Line types indicate underlying geology (see Figure 1).

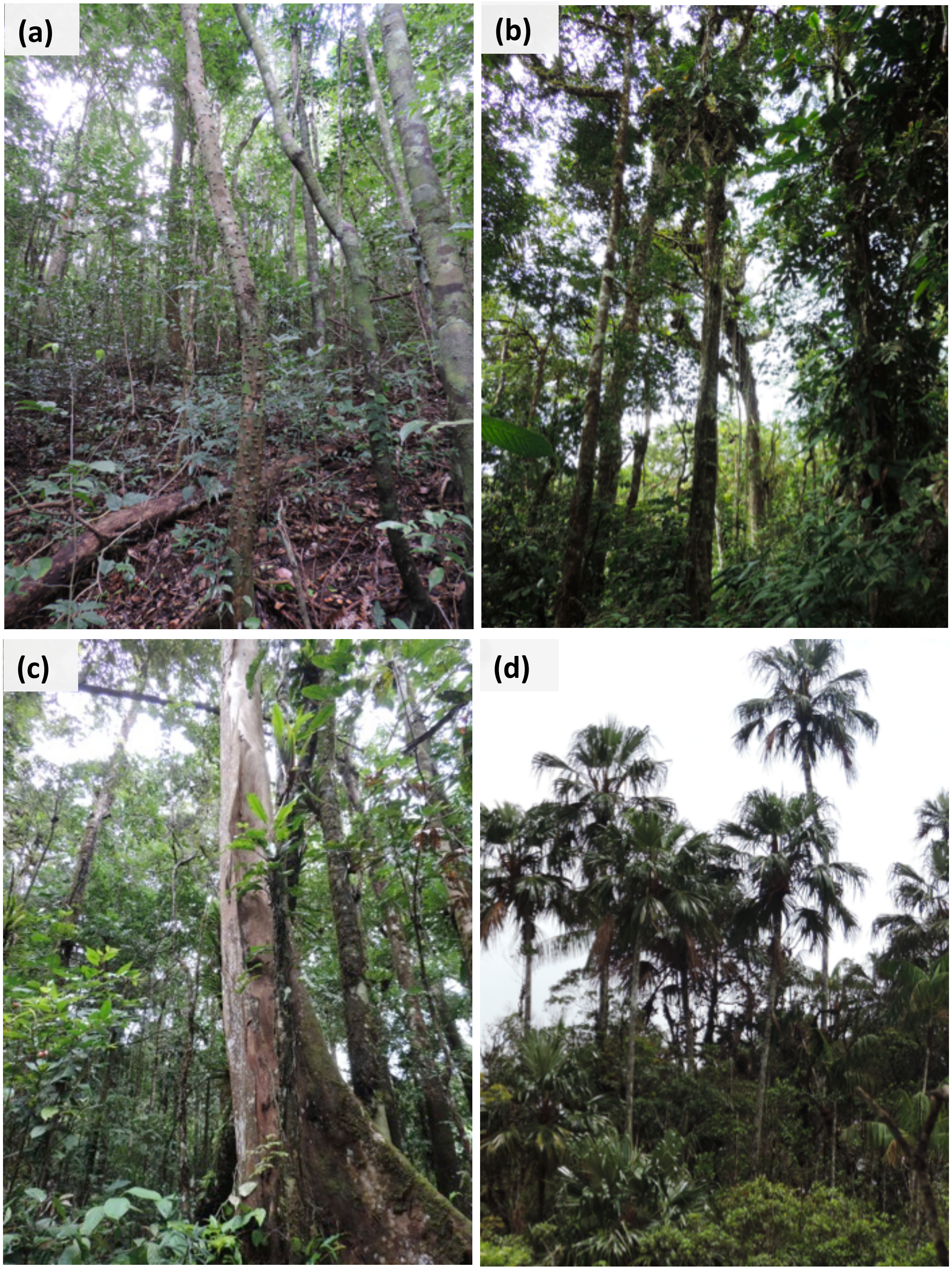

Figure A.2. Views of the different forest types found at Fortuna (a) Hornito: Tall mixed forest on dacite dominated by Lauraceae, (b) Samudio: mixed forest on andesite with a dense understorey layer, (c) Honda: forest on the periphery of rhyolite deposit dominated by *Oreomunnea mexicana* (Juglandaceae), (d) Chorro: forest on deep rhyolite deposit dominated by the palm *Colpothrinax aphenopetala*.

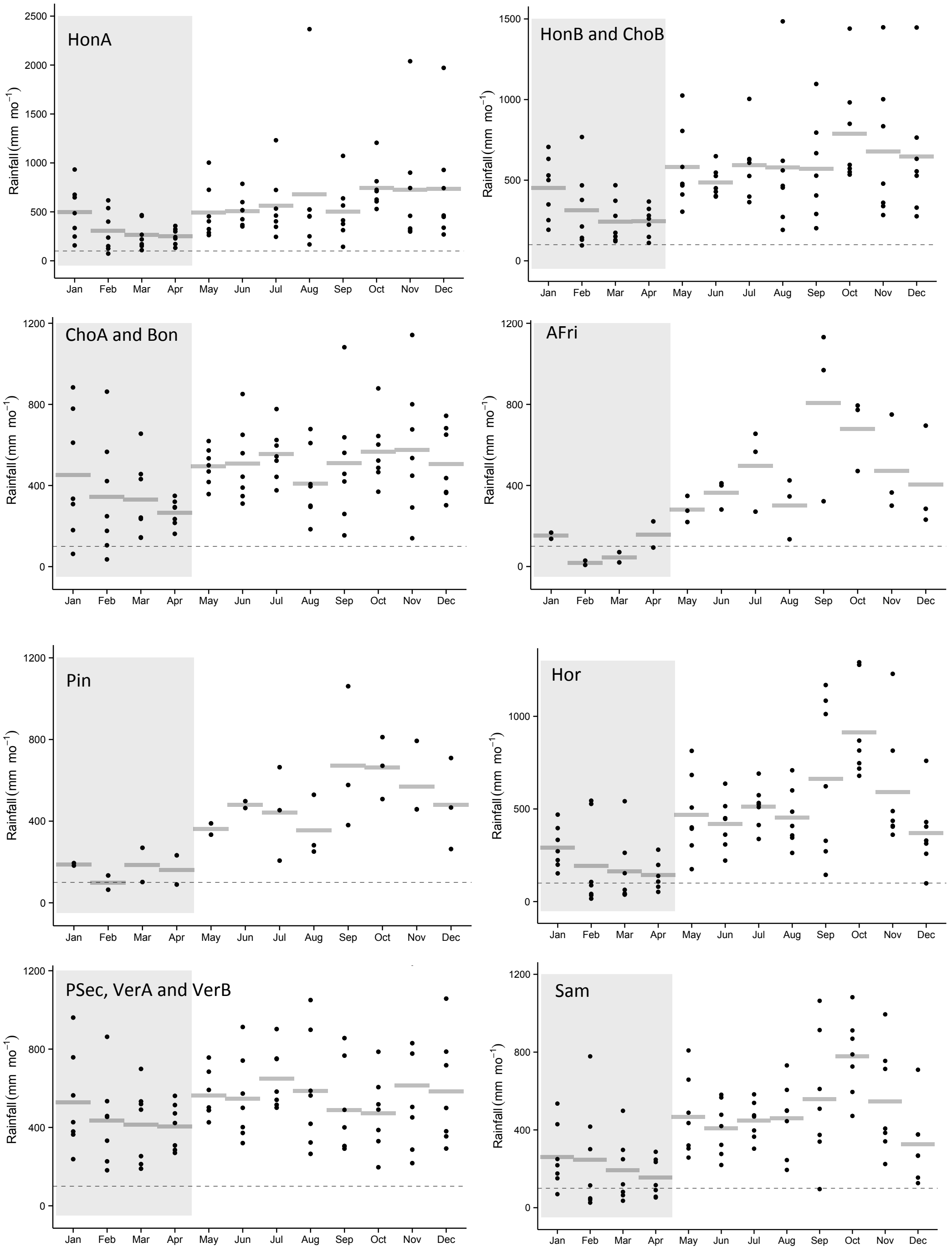

Figure A.3. Monthly rainfall (mm) from 2007-2009 and 2011-2014 for raingauges at permanent plot sites. Shade part of the figure represents the dry season, horizontal dashed line represents 100 mm/mo^{-1} and grey horizontal bars represent the mean of the seven years. Points represent individual year data. HonA = Honda A, HonB = Honda B, ChoB = Chorro B, ChoA = Chorro A, Bon = Bonita, AFri = Alto Frio, Pin = Pinola, Hor = Hornito, PSec = Palo Seco, VerA = Verrugosa A, VerB = Verruogosa B, Sam = Samudio.

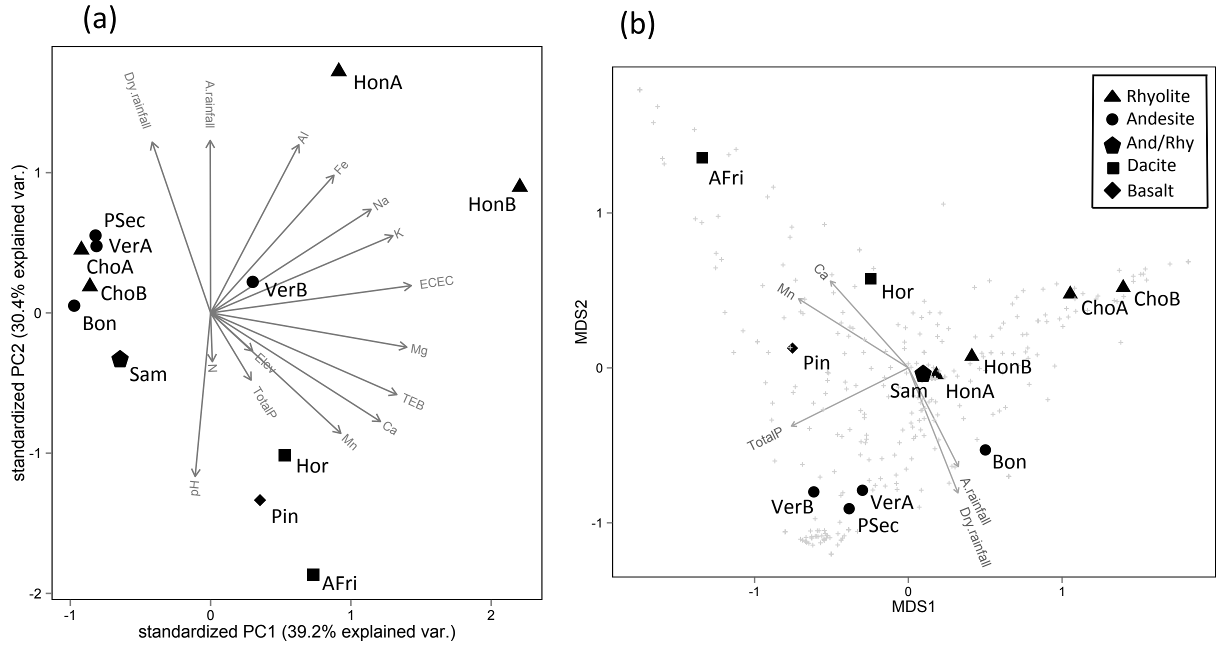

Figure A.4. Beta diversity analysis for 12 one-hectare plots in the Fortuna and Palo Seco forest reserves. Environmental variables are a mean of 5 samples of 20-50 cm depth per plot. A. Representation of the environmental variation by a principal component analyses (PCA). B. Non-metric multi-dimensional scaling (NMDS) ordination. Species abundances were used to compute the analyses. In the figure only significant variables (*P*<0.05) are shown.

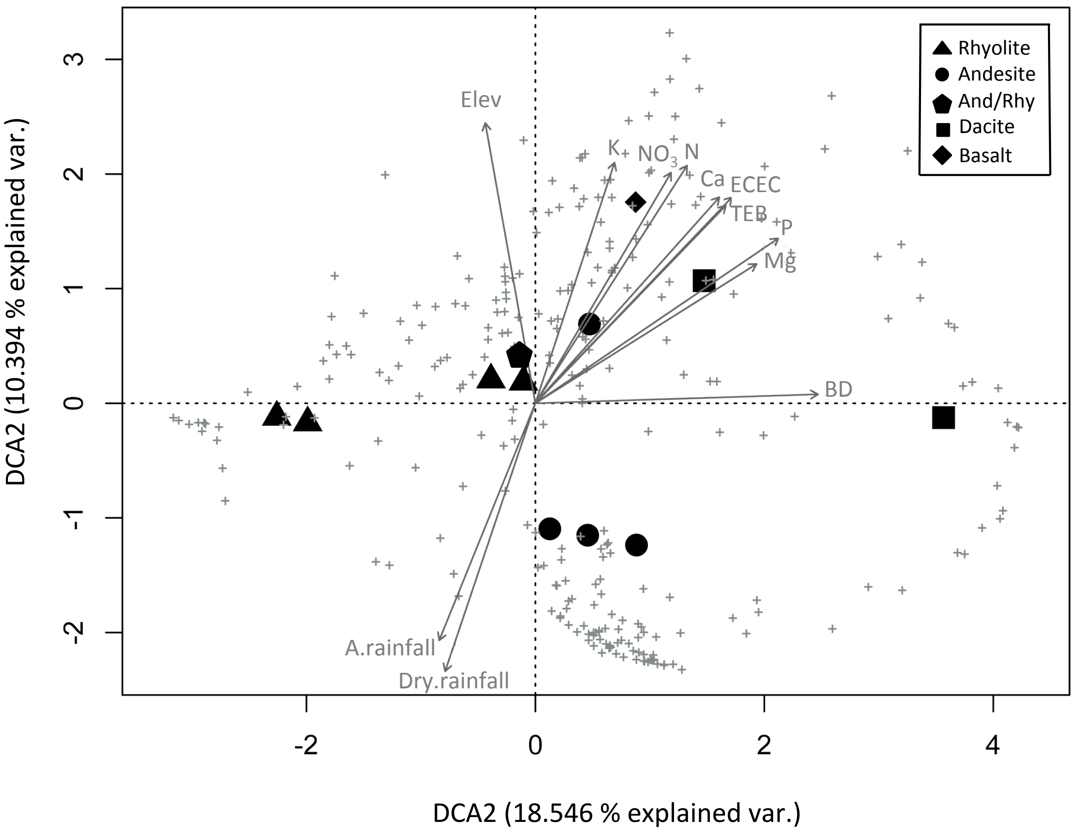

Figure A.5. Detrended correspondence analysis (DCA) for 12 one-hectare plots in the Fortuna and Palo Seco forest reserves, respond to environmental and soil (0-10 cm depth) variables. Species abundances were used to compute the analyses. In the figure only significant variables (P<0.05) are shown.

APPENDIX B: SUPPLEMENTARY MATERIAL FOR CHAPTER 3

Table B.1. Tree species ≥ 5 cm DBH in 9 permanent pots in an elevational gradient in Panama, including the number of individuals. Status indicate if the sample is a morphospecies (y) or a species (n).

Family	Genus	Species	Status	No. ind
Actinidaceae	*Saurauia*	*montana*	n	31
		sp2	y	2
Adoxaceae	*Viburnum*	*costaricanum*	n	336
Anacardiaceae	*Mauria*	*heterophylla*	n	5
Annonaceae	*Guatteria*	*acrantha*	n	4
Apiaceae	*Myrrhidendron*	*donnellsmithii*	n	1
Apocynaceae	*Rauvolfia*	*aphlebia*	n	6
Aquifoliaceae	*Ilex*	*pallida*	n	76
		sp3	y	5
		sp5	y	1
		sp6	y	5
		vol3	y	4
Araliaceae	*Dendropanax*	sp1	y	63
		sp3	y	26
		sp5	y	3
		sp6	y	12
		sp7	y	4
	Oreopanax	*oerstedianus*	n	1
		striatus	n	11
		xalapensis	n	128
	Schefflera	CASB3	y	1
		sp2	y	37
Arecaceae	*Prestoea*	*acuminata*	n	2
Asteraceae	*Jessea*	*multivenia*	n	4
	Koanophyllon	*hylonomum*	n	2
	Neomirandea	sp	y	1
Betulaceae	*Alnus*	*acuminata*	n	14
Boraginaceae	*Tournefortia*	*glabra*	n	5
Buddlejaceae	*Buddleja*	*nitida*	n	39
Burseraceae	*Protium*	*sp*	y	2
Caricaceae	*Carica*	*sp*	y	9
	Vasconcellea	*pubescens*	n	1

Table B.1. (cont.)

Family	Genus	Species	Status	No. ind
Celastraceae	*Crossopetalum*	*panamense*	n	4
	Maytenus	*woodsonii*	n	3
	Perrottetia	*multiflora*	n	1
	Salacia	*cordata* sub *patenensis*	n	15
Chloranthaceae	*Hedyosmum*	*mexicanum*	n	21
Clusiaceae	*Clusia*	sp	y	19
	Tovomita	sp	y	1
Cornaceae	*Cornus*	*disciflora*	n	148
Cunoniaceae	*Weinmannia*	*pinnata*	n	109
Cyatheaceae	*Alsophila*	*erinacea*	n	6
		sp2	y	1
	Cyathea	*caracasana*	n	1
		divergens	n	1
		sp2	y	2
		sp4	y	7
Dryopteridaceae	*Megalastrum*	*sp*	y	4
Elaeocarpaceae	*Sloanea*	*sp*	y	9
Ericaceae	*Comarostaphylis*	*arbutoides*	n	28
	Vaccinium	*consanguineum*	n	94
		vol4	y	2
Euphorbiaceae	*Acalypha*	*sp*	y	2
	Alchornea	*latifolia*	n	2
	Croton	*sp1*	y	1
	Sapium	*glandulosum*	n	8
		sp2	y	5
Fabaceae	*Erythrina*	*fusca*	n	7
	Inga	*oerstediana*	n	23
		sp2	y	1
Fagaceae	*Quercus*	*costaricensis*	n	511
		insignis	n	16
		salicifolia	n	186
Hypericaceae	*Vismia*	*sp*	y	1
Juglandaceae	*Oreomunnea*	*mexicana*	n	56
Lauraceae	*Aiouea*	*costaricensis*	n	2
	Beilschmiedia	*ovalis*	n	78
	Cinnamomum	*paratriplinerve*	n	9

Table B.1. (cont.)

Family	Genus	Species	Status	No. ind
	Indet	*AULsp10*	y	3
		BODsp12	y	5
		COPsp1	y	5
		COPsp2	y	2
		COPsp3	y	1
		COPsp9	y	1
		HOPAsp13	y	2
		lau_sp5	y	42
		lau_sp7	y	3
		QUEsp11	y	1
		QUEsp6	y	6
		QUEsp8	y	1
	Nectandra	*sp1*	y	10
		sp2	y	6
		sp3	y	1
		sp4	y	34
		sp5	y	6
	Ocotea	*cernua*	n	36
		laetevirens	n	31
		sp4	y	18
		sp5	y	9
		sp6	y	1
	Persea	*sp2*	y	28
Loranthaceae	*Gaiadendron*	*punctatum*	n	49
Magnoliaceae	*Magnolia*	*panamensis*	n	1
		sororum	n	35
		sp2	y	10
Malphiciaceae	*Bunchosia*	*macrophylla*	n	24
Malvaceae	*Heliocarpus*	*americanus*	n	2
	Malvaviscus	*arboreus*	n	102
Melastomataceae	*Conostegia*	*cinnamomea*	n	50
	Indet	*Hop_mel_sp6*	y	1
		MIR_mela_sp2	y	11
	Maconia	*sp1*	y	12
	Meriania	*macrophylla*	n	4
		panamensis	n	3

Table B.1. (cont.)

Family	Genus	Species	Status	No. ind
		sp1	y	3
		sp4	y	1
		sp5	y	1
	Miconia	*0*	y	4
		sp.volcan	y	48
		sp2	y	27
		sp3	y	2
		sp5	y	7
Meliaceae	*Cedrela*	*tonduzii*	n	3
	Guarea	*adenophylla*	n	16
		glabra	n	11
		sp1	y	7
	Trichilia	*havanensis*	n	44
Monimiaceae	*Mollinedia*	*sp1*	y	13
Moraceae	*Sorocea*	*sp*	y	11
Myrtaceae	*Eugenia*	*gomezii*	n	35
		sp_broc	y	13
		sp2	y	5
	Indet	*Myta_1*	y	2
		Myta_sp1	y	1
		Myta_sp10	y	9
		Myta_sp3	y	1
		Myta_sp5	y	1
		Myta_sp6	y	1
		Myta_sp7	y	9
		Myta_sp8	y	1
Oleaceae	*Forestiera*	*cartaginensis*	n	10
Onagraceae	*Fuchsia*	*paniculata*	n	2
Pentaphylacaceae	*Cleyera*	*theaeoides*	n	226
Phyllanthaceae	*Hieronyma*	*oblonga*	n	6
	Margaritaria	*0*	y	2
Piperaceae	*Piper*	*obliquum*	n	28
		zhorquinense	n	4
Primulaceae	*Ardisia*	*furfuracea.sub.furfuracea*	n	32
		glandulosomarginata	n	278
		subsessilifolia	n	236

Table B.1. (cont.)

Family	Genus	Species	Status	No. ind
		pellucidopunctata	n	35
	Parathesis	*glabra*	n	43
Rhamnaceae	*Frangula*	*oreodendron*	n	7
	Rhamnus	*sp1*	y	8
Rhizophoraceae	*Cassipurea*	*0*	y	4
Rosaceae	*Prunus*	*0*	y	1
		brachybotrya	n	5
		rhamnoides	n	6
		sp2	y	3
		sp3	y	4
		sp4	y	4
Rubiaceae	*Amaioua*	*sp*	y	8
	Arachnothryx	*buddleioides*	n	58
	Chiococca	*pachyphylla*	n	29
	Faramea	*multiflora*	n	2
		vol2	y	33
	Guettarda	*crispiflora*	n	2
	Indet	*Rub_sp4*	y	1
		Rub_sp5	y	1
	Palicourea	*angustifolia*	n	7
		discolor	n	89
	Posoqueria	*sp1*	y	1
	Psychotria	*chiriquensis*	n	236
		padifolia	n	84
	Rogiera	*amoena*	n	186
Rutaceae	*Zanthoxylum*	*melanostictum*	n	135
	Zanthoxyllum	*sp2*	y	3
Sabiaceae	*Meliosma*	*0*	y	132
Salicaceae	*Casearia*	*sp*	y	20
		tacanensis	n	3
	Hasseltia	*guatemalensis*	n	1
		sp1	y	2
		sp2	y	1
	Xylosma	*sp2*	y	9
Sapindaceae	*Billia*	*rosea*	n	15
Sapotaceae	*Pouteria*	*4*	y	12

Table B.1. (cont.)

Family	Genus	Species	Status	No. ind
Solanaceae	*Indet*	*Sola_sp1*	y	4
	Solanum	*sp1*	y	2
		sp2	y	4
		sp3	y	1
Staphyleaceae	*Turpinia*	*occidentalis*	n	12
Styracaceae	*Styrax*	*argenteus*	n	574
Symplocaceae	*Symplocos*	*chiriquensis*	n	18
		serrulata	n	79
		sp2	y	3
Ulmaceae	*Ulmus*	*mexicana*	n	3
Urticaceae	*Cecropia*	*angustifolia*	n	2
	Coussapoa	*0*	y	1
	Phenax	*mexicanus*	n	2
Verbenaceae	*Citharexylum*	*donnell-smithii*	n	21
	Lippia	*torresii*	n	5
Winteraceae	*Drymis*	*granadensis*	n	4
Indet	*Indet*	*CASA1*	y	1
		CASA3	y	1
		CASA4	y	29
		CASA5	y	1
		CASA6	y	1
		CASB1	y	1
		CASB2	y	1
		Cop5	y	1
		HOPA1	y	1
		HOPA2	y	1
		HOPA3	y	1
		HOPA4	y	2
		MIR2	y	1
		QUE6	y	1
		QUE7	y	1
		QUE8	y	1
		QUE9	y	1

Table B.2. Environmental and topographic characteristics for nine plots along an elevational gradient in Panama. Soil data are means (±1 SE) of 13 samples (1 ha plots) or a single pit location (0.2 ha plots). Samples are 0-10 cm depth per plot. Climate data are from the CHELSA database.

Plot name	HopeA*	Bodega*	Mirador	Aulladores*	CasitaA	CasitaB*	Quetzal	Copete	Volcan*
Plot code	HOPA	BOD	MIR	AUL	CASA	CASB	QUE	COP	VOL
Elevation (m a.s.l)	1679	1762	1987	2014	2248	2380	2599	2923	3253
BD	0.46	0.11	0.43±0.03	0.17	0.74±0.04	0.1	0.54±0.05	0.51±0.05	0.19
pH	4.71±0.22	5.23±0.9	5.98±0.11	5.4±0.19	5.04±0.15	3.94±0.1	5.08±0.19	4.81±0.14	5.57±0.06
$\mathrm{NH_4}$‡	1.64±0.3	0.33±0.07	1.8±0.2	0.26±0.05	2.81±1.0	0.12±0.02	2.58±0.2	1.29±0.2	0.43±0.05
$\mathrm{NO_3}$‡	1.97±0.4	0.84±0.01	1.55±0.13	0.18±0.1	0.23±0.01	0.01±0.001	1.96±0.4	0.28±0.1	0.13±0.03
Total C†	32.56	27.17	63.12±2.7	45.61	48.36±3.1	42.16	47.45±2.5	39.19±3.5	54.01
Total N†	2.41	1.91	5.51±0.2	4.11	3.2±0.2	2.63	3.66±0.2	2.98±0.2	3.57
Total P§	231.97	80.96	512.34±42	330.08	371.82±44.7	150.64	376.73±54	276.13±60.5	309.9
MAT	16.8	16.3	14.4	14.4	13.9	12.5	10.9	10.9	7.9
MAP	2620	2515	2948	2948	2937	3040	3102	3102	3554
ISO	606	605	607	607	606	606	608	608	610
Slope	27.36	13.99	18.33	14.33	20.38	13.54	37.13	46.44	16.65

*Data for 0.2 ha plots are from the soil pits; ‡units µg cm^{-3}; †units mg cm^{-3}; §units µg cm^{-3}

Table B.3. Correlation between variables and elevation

Variable	r	P	Variable	r	P
BD	0.15	0.73	MAT	-0.98	<0.001
pH	-0.13	0.75	MAP	0.92	<0.001
NH_4	0.03	0.94	ISO	0.86	<0.001
NO_3	-0.23	0.577			
Total N †	-0.04	0.91			
Total P †	0.09	0.82			

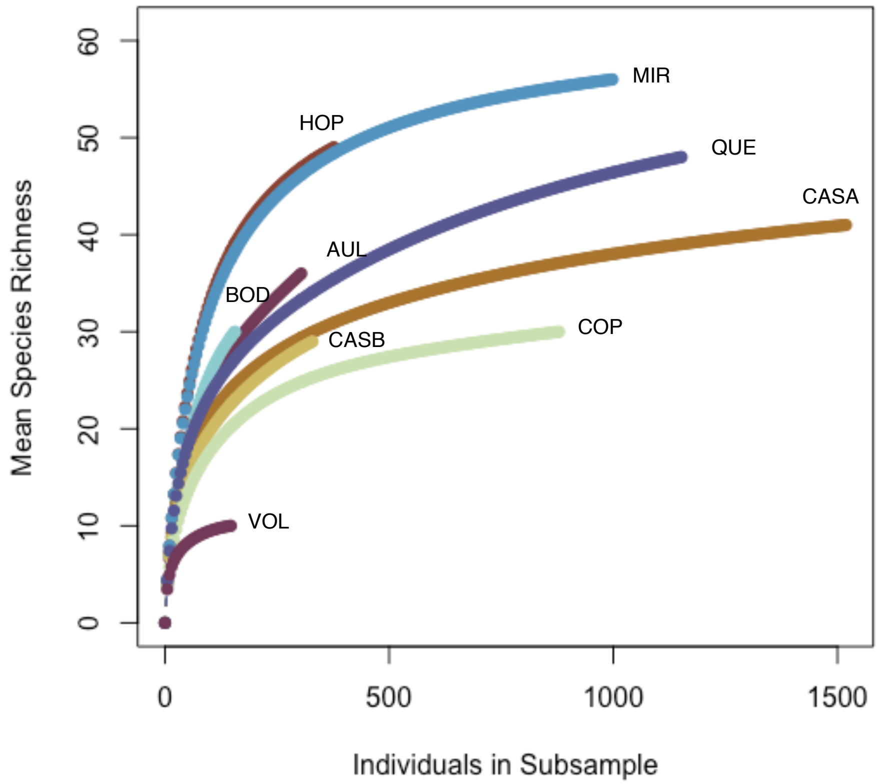

Figure B.1. Species accumulation curves for nine plots along an elevational gradient in western Panama.

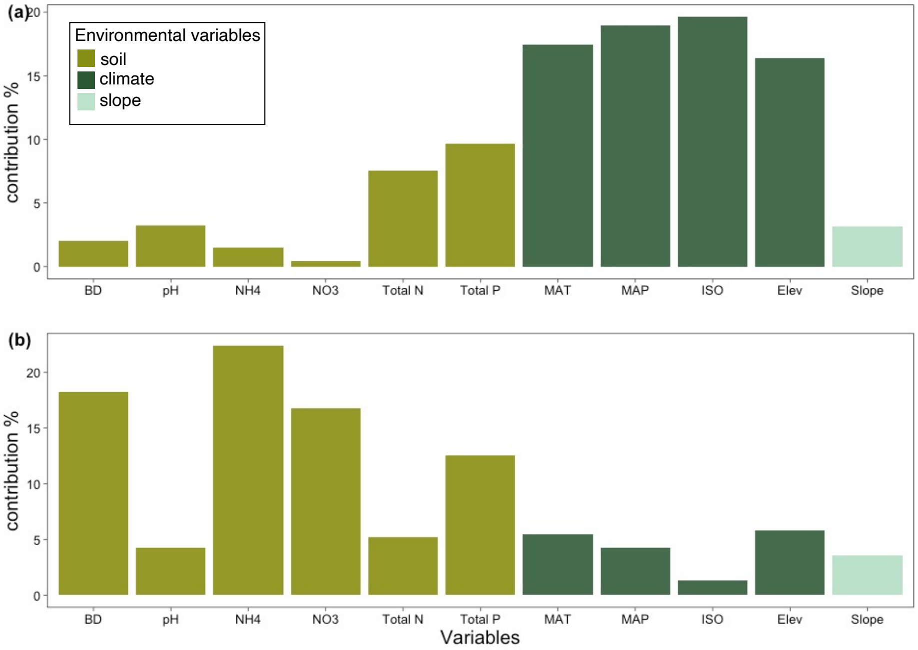

Figure B.2. Contribution of environmental and topographic variable to the variation across plots. (a) First axis, PC1 and (b) Second axis, PC2.

APPENDIX C: SUPPLEMENTARY MATERIAL FOR CHAPTER 4

Table C.1. Environmental characteristics of ten 1ha plots along an elevational gradient in Panama. Soil data are means (±1 SE) of 13 samples of 0-10 cm depth per plot. Superscripts report significant differences among sites, based on one-way ANOVA. Climate data from the CHELSA database.

Plot	PaloSeco	Alto Frio	ChorroA	HondaA	Samudio	Hornito	Mirador	CasaA	Quetzal	Copete
Plot code	PS	AF	CA	HA	SAM	HOR	MIR	CASA	QUE	COP
Edaphic										
BD	0.41 ± 0.03^{cde}	0.65 ± 0.02^{ab}	0.12 ± 0.01^{f}	0.29 ± 0.02^{def}	0.39 ± 0.0^{cde}	0.25 ± 0.02^{ef}	0.43 ± 0.03^{cb}	0.74 ± 0.04^{a}	0.54 ± 0.05^{bc}	0.51 ± 0.05^{bc}
pH	4.37 ± 0.09^{cde}	5.6±0.06ab	3.67 ± 0.08^{e}	3.58 ± 0.05^{3}	4.18 ± 0.13^{de}	5.03 ± 0.18^{bcd}	5.98 ± 0.11^{a}	5.0 ± 0.15^{bc}	5.08 ± 0.19^{bc}	4.81 ± 0.14^{cd}
ResinP‡	0.43 ± 0.06^{d}	1.39 ± 0.13^{cd}	0.08 ± 0.02^{d}	0.22 ± 0.05^{d}	0.41 ± 0.08^{d}	2.22 ± 0.15^{bcd}	3.67 ± 0.33^{bc}	7.01 ± 1.08^{a}	6.51 ± 0.93^{a}	4.57 ± 0.67^{ab}
$NH_4^{\ddagger}$	0.78 ± 0.06^{b}	3.75 ± 0.66^{a}	0.81 ± 0.06^{b}	2.24 ± 0.46^{ab}	0.63 ± 0.1^{b}	1.81 ± 0.25^{ab}	1.8 ± 0.2^{ab}	2.81 ± 1.09^{ab}	2.58 ± 0.26^{ab}	1.29 ± 0.25^{b}
$NO_3^{\ddagger}$	0.81 ± 0.12^{cd}	2.56 ± 0.23^{a}	0.2 ± 0.06^{d}	1.19 ± 0.29^{bcd}	1.17 ± 0.14^{bcd}	1.18 ± 0.17^{bcd}	1.55 ± 0.13^{bc}	0.23 ± 0.15^{d}	1.96 ± 0.4^{ab}	0.28 ± 0.13^{d}
Al§	1.1 ± 0.15^{ab}	0.03 ± 0.0^{c}	0.82 ± 0.13^{abc}	1.13 ± 0.13^{ab}	1.59 ± 0.3^{a}	0.48 ± 0.22^{abc}	0.06 ± 0.01^{c}	1.31 ± 0.19^{a}	0.44 ± 0.15^{bc}	0.8 ± 0.18^{abc}
Ca§	1.08 ± 0.2^{c}	8.47 ± 0.28^{b}	0.54 ± 0.13^{c}	0.04 ± 0.0^{c}	1.12 ± 0.15^{c}	4.93 ± 0.74^{bc}	16.33 ± 0.96^{a}	2.44 ± 0.42^{c}	7.02 ± 1.24^{b}	3.55 ± 1.11^{bc}
Fe§	0.01 ± 0.0^{bc}	$<0.01^{c}$	0.05 ± 0.0^{ab}	0.02 ± 0.0^{abc}	0.06 ± 0.02^{a}	$<0.01^{c}$	$<0.01^{c}$	0.02 ± 0.0^{bc}	0.01 ± 0.0^{bc}	0.01 ± 0.0^{c}
K§	0.06 ± 0.0^{ab}	0.12 ± 0.0^{ab}	0.07 ± 0.0^{ab}	0.02 ± 0.0^{b}	0.07 ± 0.0^{ab}	0.18 ± 0.01^{a}	0.16 ± 0.02^{a}	$0.11\ 0\pm0.02^{ab}$	0.1 ± 0.01^{ab}	0.11 ± 0.01^{ab}
Mg§	0.33 ± 0.03^{bc}	2.29 ± 0.14^{a}	0.28 ± 0.03^{bc}	0.04 ± 0.0^{c}	0.32 ± 0.03^{bc}	1.01 ± 0.14^{b}	1.96 ± 0.25^{a}	0.44 ± 0.04^{bc}	0.77 ± 0.1^{bc}	0.41 ± 0.1^{bc}
Mn§	0.19 ± 0.05^{bc}	0.42 ± 0.06^{b}	0.01 ± 0.0^{c}	$<0.01^{c}$	0.14 ± 0.04^{c}	0.71 ± 0.1^{a}	$<0.01^{c}$	$<0.0^{c}$	0.02 ± 0.0^{c}	0.01 ± 0.0^{c}
Na§	0.04 ± 0.0^{b}	0.02 ± 0.0^{b}	0.03 ± 0.0^{b}	0.01 ± 0.0^{b}	0.05 ± 0.0^{b}	0.03 ± 0.0^{b}	0.01 ± 0.0^{b}	0.02 ± 0^{b}	0.02 ± 0.0^{b}	0.11 ± 0.01^{a}
ECEC§	2.83 ± 0.17^{d}	11.37 ± 0.36^{b}	1.82 ± 0.07^{d}	1.29 ± 0.14^{d}	3.37 ± 0.13^{cd}	7.39 ± 0.69^{bcd}	18.47 ± 1.16^{a}	3.03 ± 0.45^{b}	7.93 ± 1.34^{bc}	4.2 ± 1.19^{cd}
TEB§	1.52 ± 0.23^{d}	10.91 ± 0.33^{b}	0.93 ± 0.16^{d}	0.13 ± 0.0^{d}	1.57 ± 0.18^{d}	6.17 ± 0.87^{bcd}	18.55 ± 1.15^{a}	4.37 ± 0.33^{cd}	8.41 ± 1.23^{bc}	5.03 ± 1.13^{cd}
Total N†	2.28 ± 0.23^{cd}	4.71 ± 0.22^{a}	1.76 ± 0.15^{d}	2.91 ± 0.19^{bc}	3.6 ± 0.17^{b}	2.86 ± 0.13^{bc}	5.51 ± 0.25^{bc}	3.2 ± 0.2^{bc}	3.66 ± 0.25^{b}	2.98 ± 0.29^{bc}
Total P*	369.21 ± 23.2^{ab}	503.02 ± 27.02^{a}	57.16 ± 8.64^{d}	180.6 ± 11.3^{cd}	269.11 ± 9.8^{bc}	280.1 ± 20.1^{bc}	512.34 ± 42.01^{a}	371.82 ± 44.7^{ab}	376.73 ± 54.6^{ab}	276.1 ± 60.5^{bc}

Table C.1. (cont.)

Plot	PaloSeco	Alto Frio	ChorroA	HondaA	Samudio	Hornito	Mirador	CasaA	Quetzal	Copete
Plot code	PS	AF	CA	HA	SAM	HOR	MIR	CASA	QUE	COP
Climate										
MAT	20.8	19.4	19.4	18.9	18.5	18.1	14.4	13.9	10.9	10.9
MAP	2972	2901	2573	2708	3142	3024	2948	2937	3102	3102
MPwe	367	447	326	343	393	439	345	343	365	365
MPdry	71	31	51	54	58	38	90	89	88	88
MDR	43	42	43	43	43	42	42	42	42	42
ISO	605	592	601	603	600	595	607	606	608	608
TS	48.2	53.3	49.6	49.3	50.1	52.1	47.8	47.9	47.2	47.2
MTmax	25	23.6	23.6	23.1	22.7	22.3	18.4	17.9	14.9	14.9
MTmin	17.8	16.5	16.4	16	15.6	15.1	11.5	11	8	8
MATvar	7.1	7.1	7.1	7.1	7.1	7.1	6.9	6.9	6.9	6.9
WC	0	-0.62	-1.66	-75.16	-1.66	-42.16	-225.08	-225.08	-117.83	-117.8

[‡]units µg cm^{-3}; [§]units C$_M$ L^{-1}; [†]units mg cm^{-3}; [*]units µg cm^{-3}

Table C.2. Correlations of soil and climate variables with elevation.

Variable	r	P	Variable	r	P
BD	0.49	0.1492	MAT	-0.99	<0.001***
pH	0.41	0.2339	MAP	0.48	0.1636
ResinP[‡]	0.88	0.0008***	MPwe	-0.26	0.4635
NH4[‡]	0.19	0.6061	MPdry	0.77	0.0092**
NO3[‡]	-0.16	0.6685	MDR	-0.67	0.0331*
Al[§]	-0.14	0.6904	ISO	0.66	0.0381*
Ca[§]	0.31	0.3847	TS	-0.65	0.0429*
Fe[§]	-0.3	0.408	MTmax	-0.99	<0.001***
K[§]	0.34	0.3372	MTmin	-0.99	<0.001***
Mg[§]	0	0.9948	MATvar	-0.93	<0.001***
Mn[§]	-0.41	0.2369	WC	-0.72	0.0196*
Na[§]	0.43	0.2113	A. Cloud	-0.51	0.133
ECEC[§]	0.19	0.5913			
Total.N[†]	0.23	0.518	EM %	0.80	0.005**
Total.P[†]	0.22	0.532			

Table C.3. Linear regressions for carbon pools with environmental factors.

	AGB		D_CWD		S_CWD		Soil C	
Variable	r	P	r	P	r	P	r	P
BD	0.16	0.13	0.05	0.253	-0.08	0.614	0.02	0.305
pH	0.09	0.204	-0.06	0.508	0.15	0.141	0.15	0.143
ResinP[‡]	0.71	0.001*	0.3	0.055 *	0.03	0.287	0.39	0.03*
NH4[‡]	0.1	0.194	-0.12	0.918	-0.04	0.47	-0.08	0.598
NO3[‡]	-0.11	0.779	-0.05	0.498	-0.11	0.801	-0.12	0.928
Al[§]	-0.07	0.554	-0.12	0.989	-0.07	0.54	0.06	0.243
Ca[§]	-0.02	0.413	-0.1	0.725	0	0.352	0.24	0.084
Fe[§]	0.14	0.149	-0.05	0.498	-0.11	0.779	0.02	0.308
K[§]	0.02	0.292	-0.09	0.67	0.31	0.054	0	0.33
Mg[§]	-0.12	0.873	-0.1	0.725	-0.05	0.488	-0.05	0.479
Mn[§]	-0.1	0.716	0.04	0.263	-0.07	0.569	0.14	0.15
Na[§]	-0.07	0.566	0.5	0.012*	0	0.334	0	0.342
ECEC[§]	-0.08	0.582	-0.12	0.928	0	0.366	0.12	0.171
Total.N[†]	-0.04	0.452	-0.11	0.757	-0.11	0.805	0.12	0.17
Total.P[†]	-0.02	0.4	-0.1	0.731	0	0.357	-0.01	0.38
MAT	0.76	0*	0.68	0.001*	0	0.361	0.77	0*
MAP	0.16	0.13	0.2	0.107	0.22	0.093	-0.02	0.403
MPwe	-0.12	0.976	-0.08	0.595	-0.08	0.586	-0.02	0.392
MPdry	0.22	0.093	0.39	0.03*	-0.01	0.378	0.41	0.025*
MDR	0.49	0.013*	0.12	0.173	0.06	0.233	0.31	0.054
ISO	0.1	0.184	0.31	0.053	-0.1	0.728	0.29	0.061
TS	0.08	0.216	0.3	0.058	-0.09	0.66	0.25	0.078
MTmax	0.76	0*	0.68	0.001*	0	0.359	0.77	0*
MTmin	0.76	0*	0.68	0.001*	0	0.351	0.77	0*
MATvar	0.56	0.007*	0.5	0.012*	0.01	0.321	0.74	0*
WC	0.36	0.039*	0.13	0.16	-0.11	0.802	0.41	0.025*

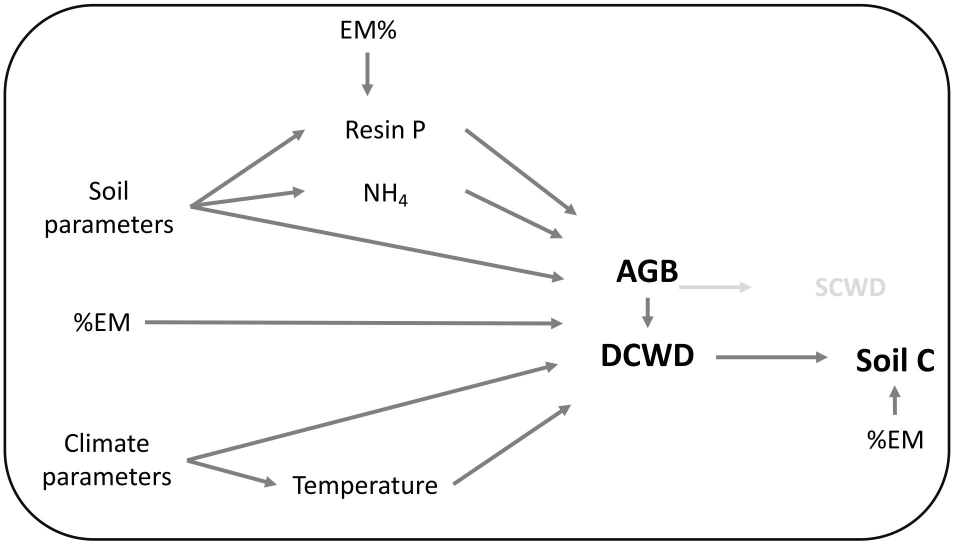

Figure C.1. *A priori* structural equation model based on predicted relationships among environmental variables to evaluate the effect of environmental and edaphic variables on the different carbon pools in a montane forest.

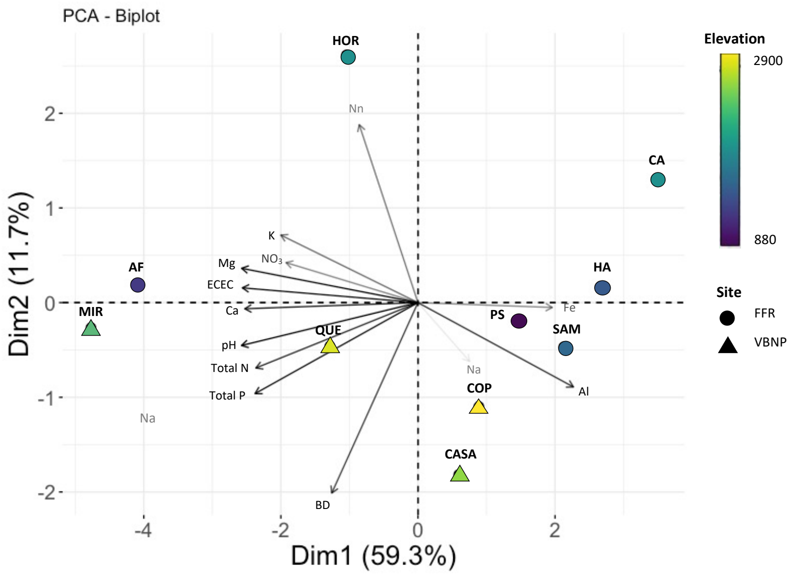

Figure C.2. Principal component analysis (PCA) soil variables 0-10 cm depth for path analysis excluding resin P and NH_4 of ten 1ha plots in an elevational gradient in Panama. Direction and length of vectors indicates the effect of the variable. Color represents the elevation of the plot and the symbols represent the site. FFR= Fortuna Forest Reserve, VBNP=Volcan Baru National Park.

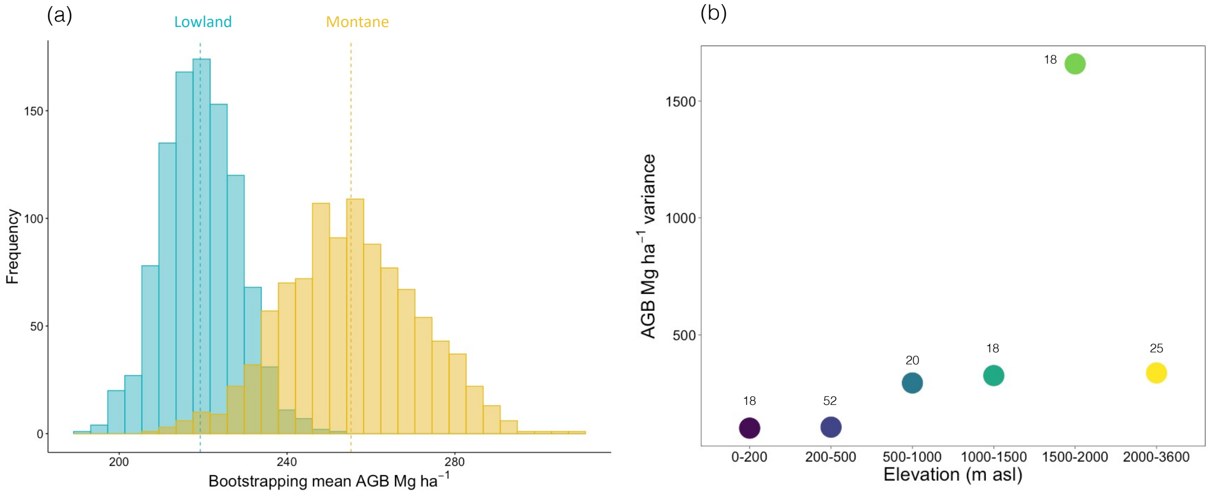

Figure C.3. Variation in AGB by bootstrapping the mean AGB of 212 plots across twelve studies in Neotropical forests. Variation in AGB (a) between lowland forests and Montane forests and (b) across elevation categories. Numbers above data points represent the number of plots in each elevation category. Distributions were assessed by bootstrapping of 1000 resamples.

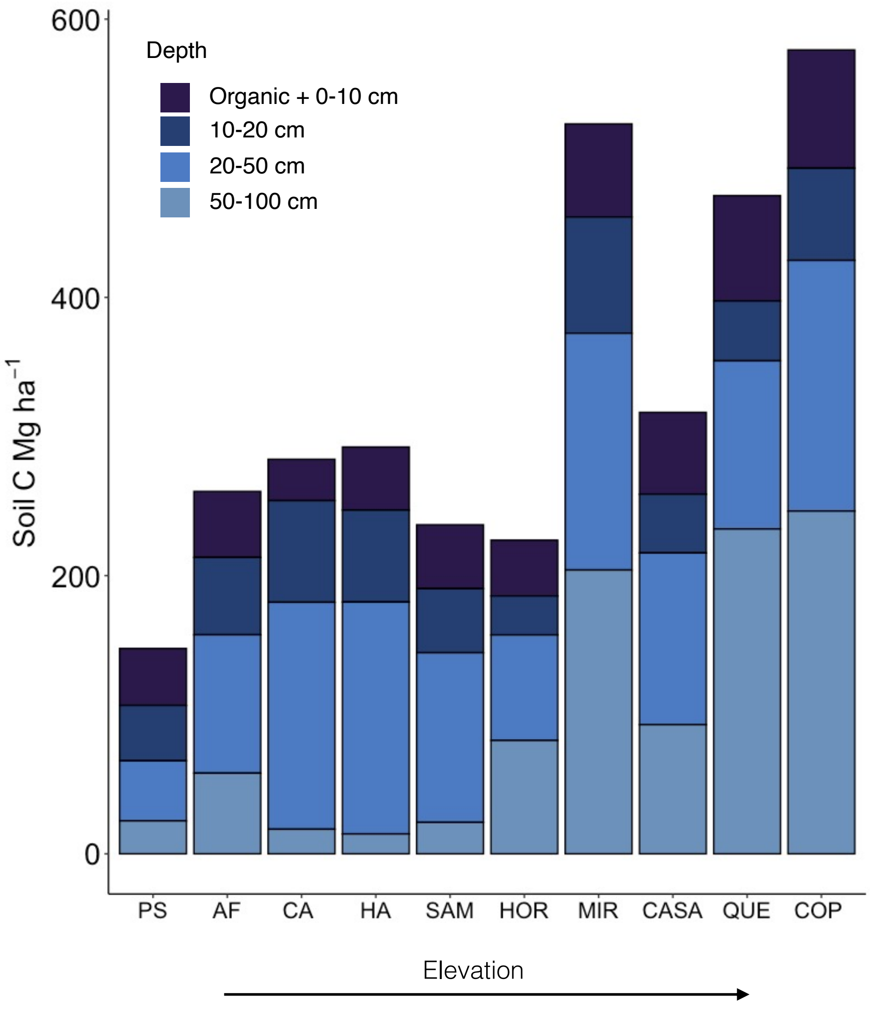

Figure C.4. Variation in soil C at different depths among ten 1-ha plots in western Panama.

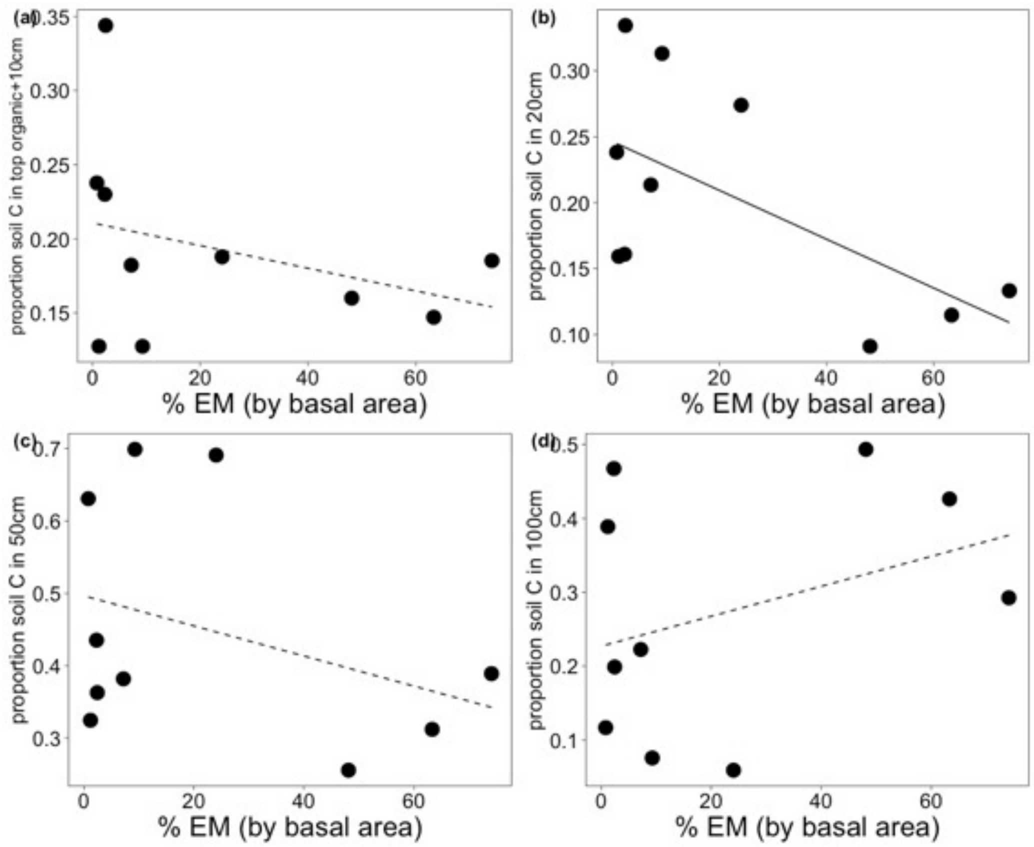

Figure C.5. Relationship between percent of basal area contributed by EM associated tree species and soil C accumulation for ten 1-ha plots. Each point represents plot soil C at each depth. Solid line represents a significant basal area effect.

APPENDIX D: SUPPLEMENTARY MATERIAL FOR CHAPTER 5

Table D.1. Soil characteristics of one-hectare mixed forest and oak forest plots located near to the experiment. Data are means (± SE) of thirteen samples for each plot. pH was measured in water. BD: Bulk density; ECEC: Effective cation exchange capacity.

	Variable	**Mixed**	**Oak**	**F**	***p***
Mineral layer					
	pH	5.04±0.15	5.90±0.11	25.2	<0.001
	BD*	0.43±0.03	0.74±0.04	25.3	<0.001
	Total C†	63.1±2.7	48.3±3.1	12.27	<0.01
	Total N†	5.51±0.25	3.20±0.20	49.74	<0.001
	Total C:N	11.49±0.52	15.26±0.22	44.06	<0.001
	Resin P‡	3.67±0.33	7.01±1.08	8.7	<0.01
	ECEC§	18.47±1.16	3.03±0.45	152.4	<0.001

*g cm^{-3}; †mg cm^{-3}; ‡units µg cm^{-3}; §units CM L^{-1}

Table D.2. Effects of N (urea) addition on resin extractable nitrate and ammonium in the organic and mineral soil layers of mixed and oak forests. Data are means (± 1SE).

	Forest	**Mixed**					**Oak**			
	N treatment	**control**	**addition**				**control**	**addition**		
	Variable			**n**	***F***	***p***			**F**	***p***
Organic layer	Resin NH_4-N[‡]	1.5±0.4	56.5±20.7	12	56.9	<0.001	1.16±0.2	87.15±36.6	23.4	<0.001
	Resin NO_3-N[‡]	8.9±2.3	84.4±28.04	12	13.9	<0.01	5.21±2.5	42.01±23.6	6.1	<0.05
Mineral layer	Resin NH_4-N[‡]	1.8±0.74	59.2±21.3	18	15.15	<0.01	1.0±0.2	103.9±40.3	37.4	<0.001
	Resin NO_3-N[‡]	19.6±3.2	125.7±18.69	18	44.7	<0.001	2.7±1.2	126.0±55.0	17.5	<0.001

[‡] mg kg^{-1}day^{-1}

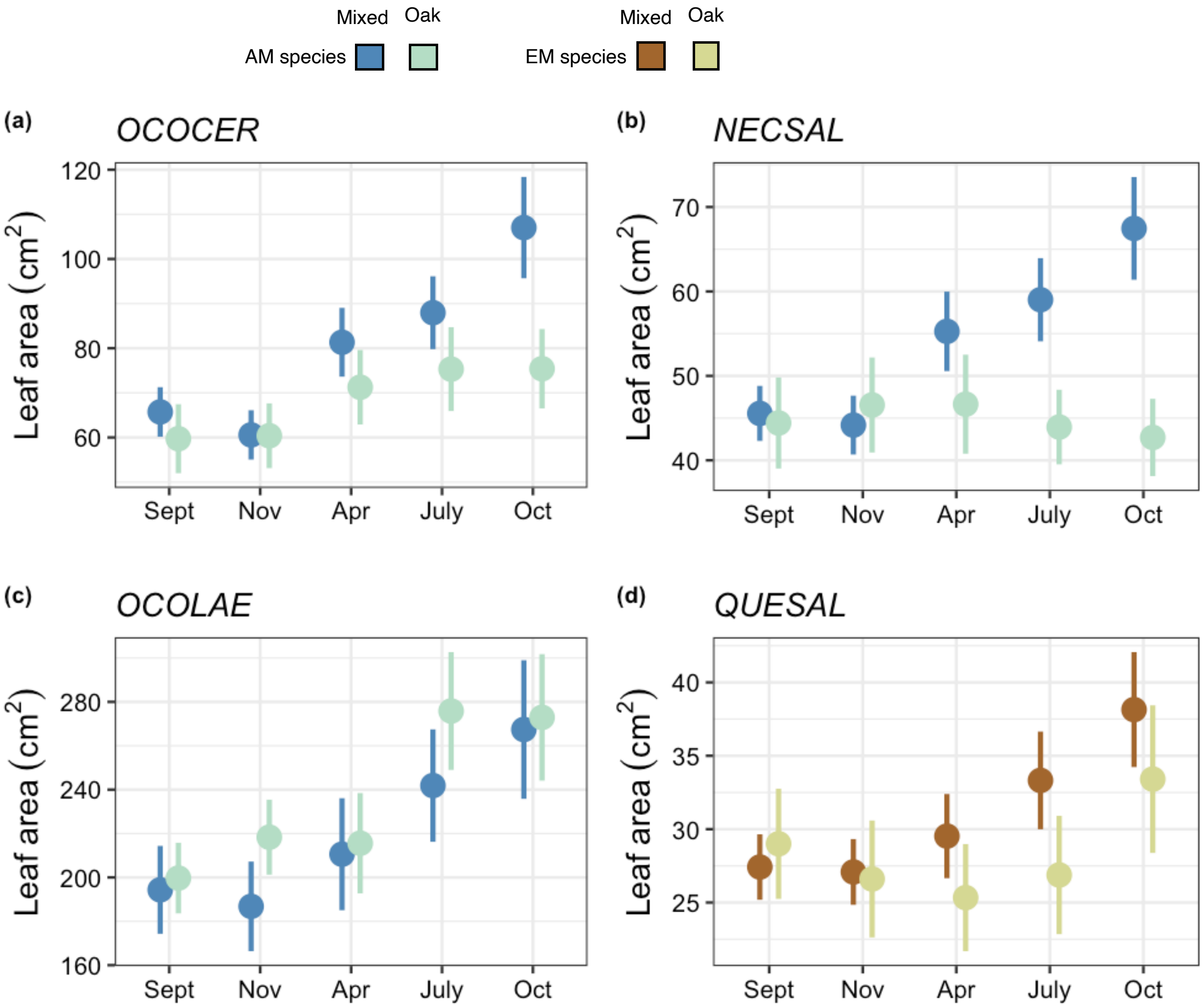

Figure D.1. Variation in total leaf area through time. Data are means ± 1SE for seedlings associated with arbuscular mycorrhiza (AM) and ectomycorrhiza (EM) in mixed and oak forest. OCOCER= *O. cernua*, NECSEL= *N.salicina*, OCOLAE= *O. laetevirens*, and QUESAL= *Q. salicifolia*.

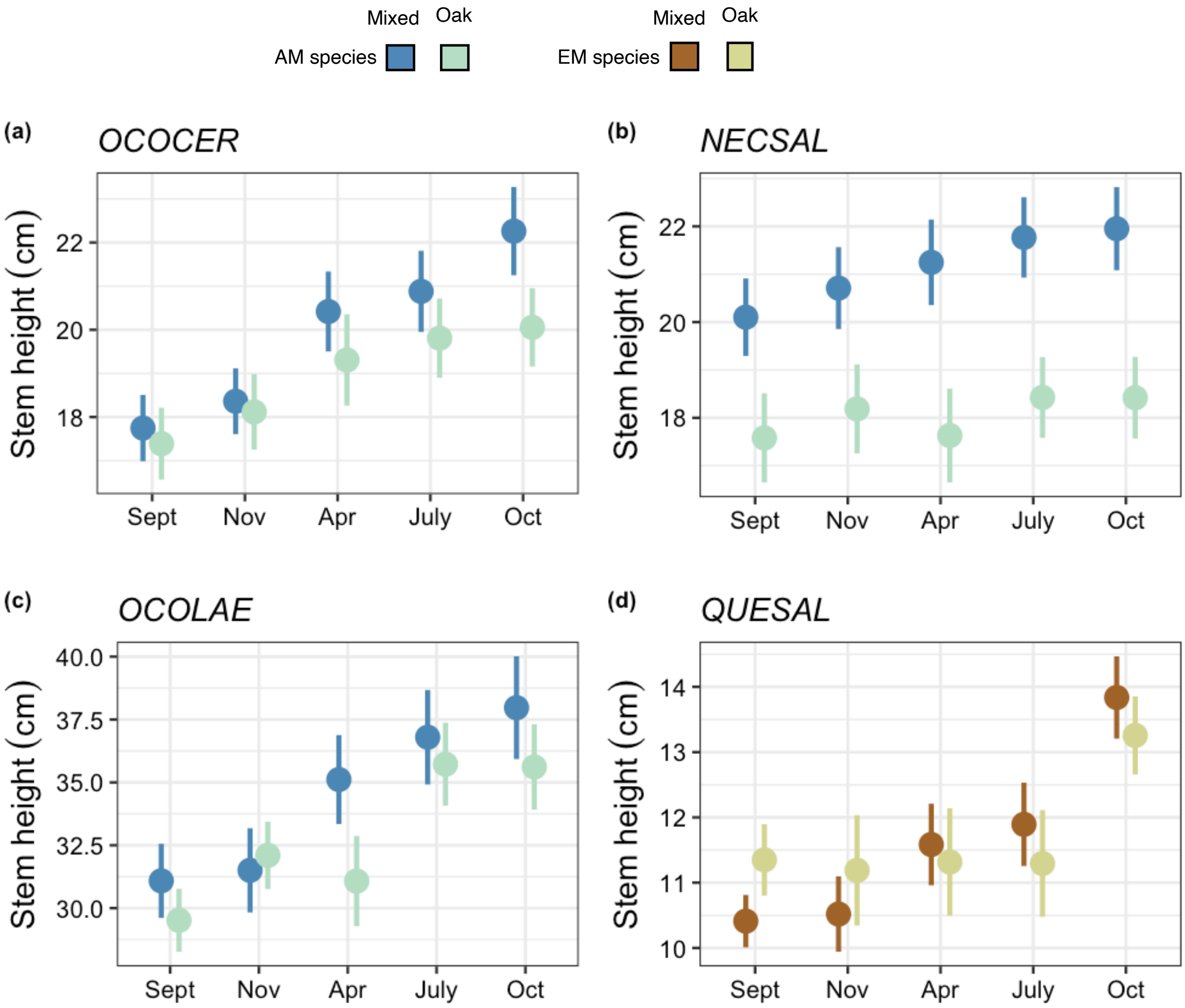

Figure D.2. Variation in total stem height through time. Data are means ± 1SE for seedlings associated with arbuscular mycorrhiza (AM) and ectomycorrhiza (EM) in mixed and oak forest. OCOCER= *O. cernua*, NECSEL= *N.salicina*, OCOLAE= *O. laetevirens*, and QUESAL= *Q. salicifolia*.

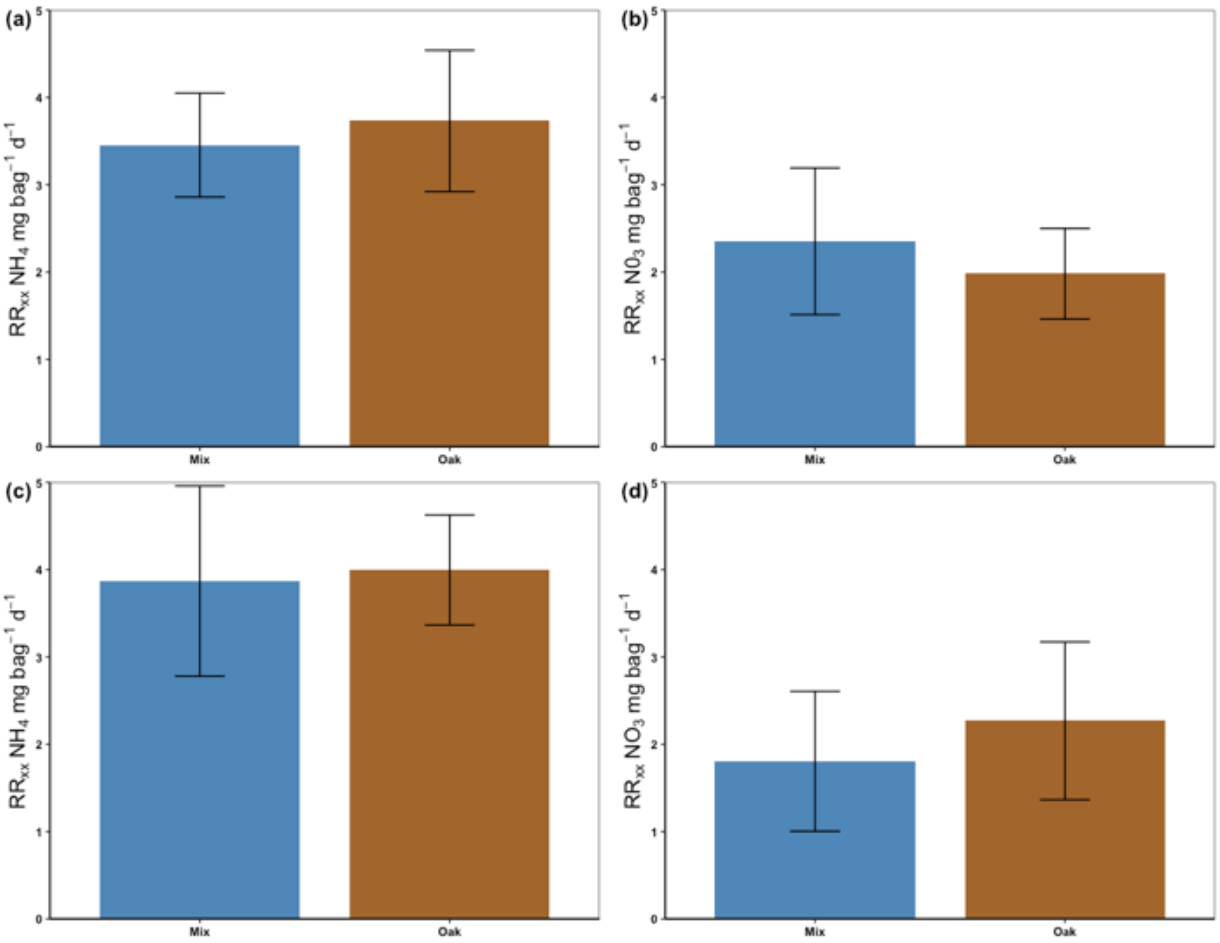

Figure D.3. Effect of nitrogen addition treatment on inorganic N availability using resin bags in the organic matter layer (a, b), and mineral soil (c, d). The effect (response ratio; RRxx) is the N+ treatment divided by the control treatment and then ln transformed. Mean ± SE of resin-NH_4-N and resin-NO_3-N.

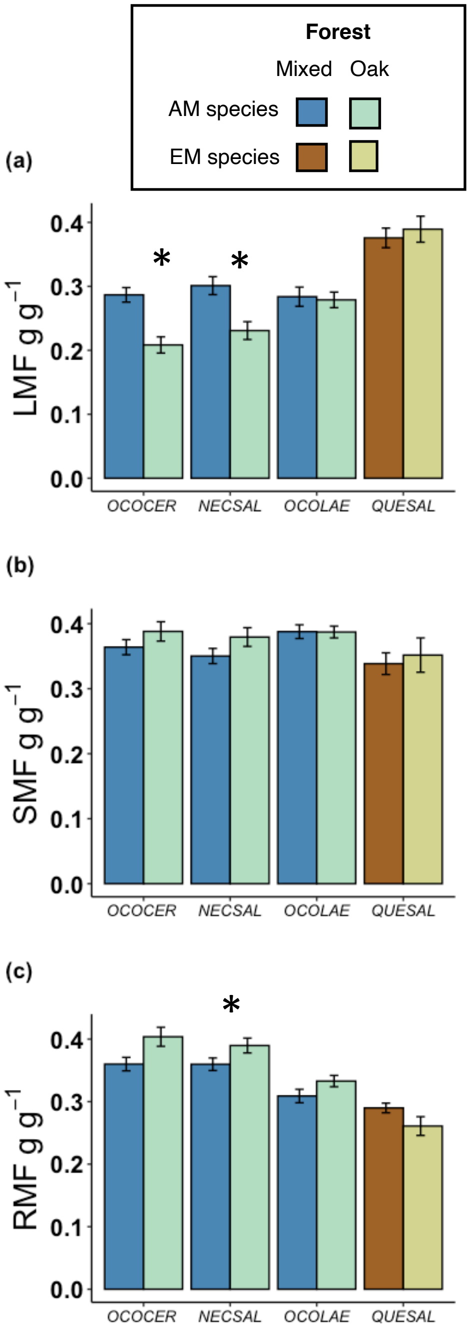

Figure D.4. Leaf (LMF), stem (SMF), and root (RMF) mass fraction means (± 1SE) for four species measured for the experiment. OCOCER= *Ocotea cernua*, NECSEL= *Nectandra salicina*, OCOLAE= *Ocotea laetevirens*, and QUESAL= *Quercus salicifolia*.