

EFFECTS OF SOIL NUTRIENT AVAILABILITY ON THE DEVELOPMENT OF TROPICAL  
MONODOMINANCE AND SUBORDINATE SPECIES COMPOSITION IN MONTANE  
FORESTS

BY

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THESIS

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## ABSTRACT

Although tropical forests are well known for harbouring some of the highest levels of plant diversity in the world, natural areas occur where a single tree species dominates the forest stand. The presence of these monodominant forests therefore represents an unusual and intriguing phenomenon. Several studies over the past 30 years have attempted to explain how monodominance arises and how monodominant species persist in otherwise highly diverse tropical forests. Proposed mechanisms can be grouped into the “exceptional trait” and “ecosystem modification” hypotheses. Using the framework of these hypotheses, this study aimed to understand how an ectomycorrhizal tree species, *Oreomunnea mexicana*, achieves high abundance. The study assessed soil properties along with species composition using a paired plot design consisting of mixed forest and nearby *Oreomunnea*-dominated forest sampled at four sites in montane forest in western Panama. We found support for the “ecosystem modification” hypothesis as *Oreomunnea*-dominated stands mostly differed in soil properties from mixed forest stands that shared the same soil parent material. Alterations to soil conditions via a positive plant-soil feedback were also associated with differences in the composition of the subordinate tree species community. Species diversity not affected by the presence of *Oreomunnea*, and compositional beta-diversity was lower across *Oreomunnea*-dominated forests, suggesting that the plant-soil feedback imposed additional environmental filtering on the tree community. However, the capacity to generate plant soil feedback is itself a consequence of an “exceptional trait”, the presence of ectomycorrhizal fungi associations in *Oreomunnea*-dominated forests, in a community otherwise consisting of trees that form arbuscular mycorrhizal associations.

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# CHAPTER 1: EFFECTS OF SOIL NUTRIENT AVAILABILITY ON THE DEVELOPMENT OF TROPICAL MONODOMINANCE AND SUBORDINATE SPECIES COMPOSITION IN MONTANE FORESTS

## INTRODUCTION

Tropical forests are among the most biodiverse ecosystems in the world, where hundreds of plant species can exist in a single hectare of forest. The presence of forest patches dominated by a single tree species therefore represents an unusual and intriguing phenomenon. A forest is considered as monodominant when a single tree species accounts for more than 60% of basal area, or of the number of individuals >10 cm of diameter at breast height (DBH), in a forest stand (Hall et al., 2020; Hart et al., 1989). These monodominant forests, while rare, have been reported in all biogeographic regions within the wet tropical forest biome. Examples of monodominant tree species include *Dicymbe corymbosa* Spruce ex Benth. in Guyana (Henkel, 2003), *Gilbertiodendron dewevrei* (De Wild.) J. Léonard in Congo (Tovar, Harris, Breman, Brncic, & Willis, 2019), *Brosimum rubescens* Taub. in Southern Amazonia (Marimon-Junior et al., 2020), *Dipterocarpus tuberculatus* Roxb. in Vietnam (Nguyen & Baker, 2016), and *Oreomunnea mexicana* (Standl.) J.-F. Leroy in Panama (Corrales et al., 2016). Various drivers of tropical monodominance acting differently across tropical monodominant forests may be the reason of that no single hypothesis has been successful in explaining the presence of these unusual and fascinating ecosystems.

One barrier to our understanding of how tropical monodominance arises may stem from the fact that previous studies have focused on the traits of the monodominant species itself, rather than the forest community as a whole. Indeed, little attention has been given to how the presence of the monodominant species shapes the composition and diversity of the subordinate species. Investigating the subordinate community composition could provide information about how the monodominant species affects ecosystem functioning and plant-plant interactions. The study of community composition and diversity is especially important since patterns in plant diversity can only be explained by integrating species traits in relation to environmental conditions and habitat heterogeneity (Kneitel & Chase, 2004). Therefore, the analysis of the effects of monodominance on subordinate species could provide additional insight into how monodominance is maintained.

A recent resurgence of interest in the study of tropical monodominance reflects the insights that these forests might provide in understanding how high levels of biodiversity are maintained in tropical forests. This is because current ecological theory has supported the idea that conspecific negative density-dependence (CNDD), where the negative effect of biotic enemies scales with population density (Laliberté et al., 2015), is an important driver of high plant species diversity in tropical forests (Chen et al., 2019; Mangan et al., 2010; Song et al., 2020). In this context, tropical monodominant forests represent a clear anomaly. High local population densities, the hallmark of monodominance, represent the potential escape from negative density dependent population regulation. Thus, understanding how monodominance is achieved can provide insights in the broader question of how diversity is maintained.

Peh et al. (2011) proposed multiple mechanisms to explain the occurrence of monodominance in tropical forests. However, despite numerous studies which have attempted to better understand the formation and maintenance of tropical monodominant forests, no single hypothesis has emerged. Existing hypotheses to explain tropical monodominance can generally be sorted into two classes: “ecosystem modification” hypotheses and “exceptional trait” hypotheses. While evidence to support these groups of hypotheses has been found in various tropical monodominant forest systems, the question of how and why tropical monodominant forests form is still unanswered.

The “ecosystem modification” hypotheses posit that the presence of the monodominant species changes the ecosystem to favour conspecific individuals. Suggested ways in which the ecosystem is modified include low rates of leaf litter decomposition which decrease rates of nutrient cycling (Hart et al., 1989; Torti et al., 2001), the production of deep layers of leaf litter (Torti et al., 2001), as well as the production of defensive chemicals that inhibit the germination of competitor species (Gris et al., 2019). One final process through which the monodominant species may modify the ecosystem is a process known as plant-soil feedback (Bennett & Klironomos, 2019). Plant soil feedback occurs when a plant species is able to alter the biotic and abiotic conditions of the soil in which they grow. Low C:N and C:P ratios (Guillot, 1981; Hall et al., 2020) and low extractable nitrogen (Brookshire & Thomas, 2013; Corrales et al., 2016; Torti et al., 2001) may be the result of this process, and have previously been reported in monodominant soils. This is particularly important because nitrogen is a key limiting nutrient for plants in tropical montane forests (Corrales et al. 2016; Hall et al. 2020). In addition, plant soil feedback has been

suggested to influence species coexistence, making it a potentially important mechanism in the formation and maintenance of monodominant forest in the tropics (Corrales et al., 2016).

Contrary to the “ecosystem modification” hypotheses, the “exceptional trait” hypotheses propose that monodominant species possess characteristics that confer a fitness advantage relative to competitors. Proposed traits include species adaptations that allow them to persist over time after a low level of disturbance (Connell & Lowman, 1989), higher seedling survival rates in the understory in disadvantageous environments (Hart, 1995) and nutritional benefits arising from ectomycorrhizal fungal associations (Corrales et al., 2016). Limited seed dispersal (Hart et al., 1989), large seed size (Torti et al., 2001), low levels of leaf herbivory (Gross et al., 2000; Hart, 1995), mast fruiting events (Hart, 1995), high plasticity in different light environments (Hall et al., 2020), high resprouting capacity (Ter Steege et al., 2019), and more efficient water transport (Kearsley et al., 2017) may also be traits that promote the formation and maintenance of tropical monodominant forest. If the monodominant species were to possess these competitively advantageous traits, then this may explain why different plant species from phylogenetically diverse plant families have been able to form tropical monodominant forest across biogeographic regions.

The monodominant forest in our study system is formed by *Oreomunnea mexicana*, a canopy tree from the walnut family. *Oreomunnea* has been reported to establish monodominant stands throughout Mesoamerica (Corrales et al., 2016; Veintimilla et al., 2019; Williams-Linera et al., 2013), and can establish high densities of conspecific individuals under a variety of soil fertility levels (Corrales et al., 2015). The formation of *Oreomunnea*-dominated stands has been suggested to be influenced by processes which bridge the “exceptional trait” hypotheses and the “ecosystem modification” hypotheses. Individuals of *Oreomunnea* possess several notable traits. Mast seeding has been reported in *Oreomunnea*, which could promote high reproductive success and therefore a continued pattern of high local population density (Pacheco-Cruz et al., 2019). *Oreomunnea* also associates with ectomycorrhizal (EM) fungi, which is uncommon in the tropical forests in which it occurs (Corrales et al., 2016). Notably, this same mycorrhizal relationship has been observed in several other monodominant species, where co-occurring competing species lack this association (Connell & Lowman, 1989; Corrales & Ovrebo, 2021; Hall et al., 2020; Torti & Coley, 1999). The presence of these mycorrhiza may additionally act as a driver of ecosystem modification, since they both supply nitrogen to the monodominant host and reduce the availability of inorganic

nitrogen in the ecosystem (Frey, 2019; Lindahl & Tunlid, 2015; Phillips et al., 2013). In addition, in temperate ecosystems ectomycorrhizal fungi reduce the rate of nutrient cycling since decomposition rates are lower in stands dominated by these fungi (Phillips et al., 2013). Thus, the multiple potential causes of *Oreomunnea*-dominated stands remain unresolved as is the case for other monodominant taxa.

Here, we used paired adjacent plots with and without *Oreomunnea* to examine how this dominant species affects soil conditions and the subordinate tree community in montane forests in Panama. This design allowed us to evaluate three different hypotheses. Our first hypothesis states that monodominance is contingent on the existence of particular edaphic conditions (Hall et al., 2020; Ter Steege et al., 2019), while plant-soil feedback plays only a minor role in determining community composition. Under this scenario, subordinate species are adapted to the same soil conditions as *Oreomunnea*, and therefore tree community composition is similar in the presence or absence of *Oreomunnea* (Figure 1a). Our second hypothesis is that monodominance arises from plant traits that are independent of soil fertility and represent highly localized plant-soil feedback effects on soil microbial communities and nutrient supply, with limited impact on neighbouring individuals of subordinate species. This hypothesis is consistent with observations of lower nitrate and ammonium concentrations beneath *Oreomunnea* tree crowns than neighbouring subordinate species in a nitrogen addition experiment (Dalling and Turner, unpublished data), and soil microbial data that shows distinct microbial communities beneath monodominant species and subordinate species in the same plots (Edwards and Yang, unpublished data). In this scenario, although *Oreomunnea* modifies the ecosystem, effects are so localized that the composition and diversity of the subordinate community is unaffected. Thus, we would predict that the diversity and composition of the subordinate species community would vary across soil types but would be unchanged (after accounting for stem number) in plots on the same soil type with and without the monodominant species (Figure 1b).

Our final hypothesis is that monodominant species can occur on a range of soil types and achieve high local abundance through positive plant-soil feedback, which generates more expansive changes to soil conditions that favour the monodominant species. This is consistent with the observation that stand-level soil inorganic N and resin P is negatively correlated with the basal area of *Oreomunnea* in 20 x 20 m plots in the Honda watershed of the Fortuna Forest Reserve (Corrales et al., 2016). In this scenario, the presence of *Oreomunnea* conditions the soil, selecting



for subordinate species that tolerate the soil conditions *Oreomunnea* generates. Consequently, *Oreomunnea*-associated subordinate species may be rare or absent from neighbouring plots that share the same soil type or parent material, but where *Oreomunnea* is absent (Fig. 1c). This hypothesis also yields the prediction that species diversity in *Oreomunnea*-dominated plots will be lower than in the corresponding mixed forest paired plot, reflecting an additional layer of environmental filtering imposed by plant-soil feedback.

## METHODOLOGY

### *Study site and experimental design*

The study was performed in western Panama in the Fortuna Forest Reserve (8°45 N, 82°15 W) and at Finca La Esperanza, in Boquete (8°48 N, 82°25 W), Chiriqui. These sites are classified as per-humid premontane and lower montane forests in the Holdridge life zone system. The Fortuna Forest Reserve has a mean annual rainfall range between 4600 and 6300 mm (Prada et al., 2017), and an annual mean temperature range of 17°C to 20°C (Dalling et al., 2021). Meanwhile, the study site at Finca La Esperanza has a mean annual rainfall range between 2600 and 2800 mm, and an annual mean temperature range of 16°C to 17°C. A paired plots study design was used to survey three sites: Honda, Zorro, and Hornito within the Fortuna Forest Reserve and one site: Hope at Finca La Esperanza. At each site, one plot in each pair contained the monodominant species *Oreomunnea mexicana* (Standl.) J.-F. Leroy (Juglandaceae), while an adjacent plot contained mixed forest. Plots were either 1 ha (100 × 100 m; established in 2003), or 0.2 ha (40 × 50 m; established in 2018). Within each plot, all trees ≥5 cm DBH were identified. Pairs of plots were located within the same watersheds in the Fortuna Forest Reserve, at Finca La Esperanza which is located at the base of the Baru volcano. Paired plots within each site were 100 m to 500 m apart (Table 1).

### *Study site species composition*

All plots support species-rich primary forest. Across the permanent plots established in Fortuna Forest Reserve, half of the species richness is composed of species within the families Euphorbiaceae, Fabaceae, Lauraceae, Melastomataceae, Meliaceae, Primulaceae, Rubiaceae, and Sapotaceae (Dalling et al., 2021). Species composition data were taken from census data of the permanent plots in Fortuna Forests Reserve and Boquete. Species were identified in the field and

herbarium samples were taken. All free-standing woody species  $\geq 5$  cm DBH were identified to species or morphospecies.

*Oreomunnea* is a canopy tree which grows up to 40 m tall and is distributed from southern Mexico to Panama at elevations between 600-1900 m (D E Stone, 2011). Where found, *Oreomunnea* consistently forms monodominant forest (Veintimilla et al., 2019). *Oreomunnea* possesses certain functional characteristics which may potentially be important to its success. Unlike most Juglandaceae, it has small wind dispersed seeds (Stone, 1972) which can disperse up to 35 meters away from the parent tree (Pacheco-Cruz et al., 2019). In our study sites, *Oreomunnea* is able to establish extensive areas of monodominant forest (Corrales et al., 2015). Contrary to the vast majority of plant species in lower montane forests in Panama, which form arbuscular mycorrhizal associations, *Oreomunnea* is associated with a high diversity of ectomycorrhizal fungi. This ectomycorrhizal community is highly variable at local and regional scales (Corrales et al., 2021, 2015). Previous work in our study site found that the most abundant genera of ectomycorrhizal fungi in forests dominated by *Oreomunnea* are *Russula*, *Cortinarius*, *Tomentella* and *Laccaria*. These functional characteristics associated with dispersal and nutrient relations may account for the ability of *Oreomunnea* to generate high seedling densities, often  $>50$  seedlings/m<sup>2</sup> in the understory (Z. Mijango, personal observation).

#### *Soil and climate data*

Broadly, the soils at Fortuna are finely textured and range from acidic to strongly acidic (Turner & Dalling, 2021). Soil fertility varies in relation to parent material at the local scale (Prada et al., 2017). The plots in this study were distributed across four soil parent material types: rhyolite (Honda), tephra-granodiorite (Hope), dacite (Hornito) and granodiorite (Zorro). Soils on rhyolite parent material are classified as having low nutrient availability and an organic surface horizon (Andersen et al., 2012). Soils on tephra-granodiorite are characterized as having high fertility and carbon-rich minerals which originate from volcanic ash (Minasny et al., 2021). Soils on dacite and granodiorite are classified as having high nutrient availability and an organic surface horizon (Turner & Dalling, 2021)(Table 2).

In this study, soil samples in each plot at Hornito and Honda were collected in July 2008 and 2010 during the mid-wet season. In two of the plots, Zorro and Hope, soil samples were collected in December 2018 at end of the wet season. In all plots, we collected soil samples

systematically across the plot, sampling 13 out of 25 of the 20 × 20 m subplots within each of the 1 ha plots and 10 out of 20 of the 10 × 10 m subplots of the 0.2 ha plots. At each sampling location we removed fresh litter and collected soil from the surface 0-10 cm of mineral soil. In addition, we collected soil from a subset of five locations per plot at 10-50 cm depth.

We analyzed a suite of soil environmental variables, soil extractable N (NH<sub>4</sub>, NO<sub>3</sub>) and P (resin extractable phosphorus), total N and P, exchangeable bases (Ca, Mg, K, Na), and pH. Extractable N was determined by extraction in 0.5 M K<sub>2</sub>SO<sub>4</sub> for one hour, with detection by a colorimetric analyzer (Lachat QuickChem 8500). Extractable P was measured by extraction with anion-exchange membranes (resin P). Total N and P were quantified using an elemental analyzer (Thermo Flash 1112) and acid extraction (1 M H<sub>2</sub>SO<sub>4</sub> for 16 h) using molybdate to detect P. Exchangeable bases were determined by extraction in 0.1 M BaCl<sub>2</sub> (at 2 h, 1:30 soil to solution ratio), with detection using inductively coupled plasma spectrometry on an Optima 7300 DV. Finally, soil pH was measured in water with a glass electrode in a 1:2 dry soil:water solution ratio.

Mean annual temperature and precipitation, mean of wettest and driest month, mean diurnal range, isothermality, temperature seasonality, max and min temperature, and mean temperature range were obtained for each plot from the Climatologist at High Resolution for the Earth's Land Surface Areas (CHELSA) (Karger et al., 2017) using maps with 0.5 arc sec grid resolution layers.

### *Statistical analysis*

A plant species matrix in subplots of 20 × 20 m, along with the soil and climate environmental variables, was constructed to examine how the presence of *Oreomunnea* is related to the composition of subordinate species relative to that of adjacent mixed forest. An ordination analysis was used to test the effect of soil environmental variables (extractable N and P, total N and P, Ca, Mg, K, Na, and pH; Table 2) and CHELSA derived climate variables (Table 3). Species compositional changes between forest types were measured using Bray-Curtis dissimilarity with square root transformation with the function *vegdist* and visualized with a nonmetric multidimensional scaling (NMDS) plot using the function *metaMDS*. We used the same NMDS output to display the correlations of soil and climate variables with species compositional data using the function *envfit*. Additionally, we performed a permutational multivariate analysis of variance (Anderson, 2014), PERMANOVA, using the function *adonis*, to test the effect of parent

material, the presence of *Oreomunnea*, and their interaction on the species community composition. All these analyses were implemented with the software R (R Core Team, 2020) using the package “vegan” (Oksanen et al. 2019)

Rarefaction and extrapolation analyses was used to determine whether the presence of *Oreomunnea* affects subordinate species richness and diversity. Since plot size, and therefore sample size, varies between paired plots, we estimated and compared species diversity using the Hill numbers of order  $q=0$  (species richness) and  $q=1$  (Shannon diversity; for calculations refer to (Chao et al., 2014)), and used rarefaction and extrapolation curves to display our results (Colwell et al., 2012). Species richness and Shannon diversity were compared between paired plots. These comparisons were done with both the inclusion and exclusion of *Oreomunnea* stems in the monodominant plots using the “iNEXT” package in R (Hsieh et al., 2016).

Analysis of beta-diversity was implemented to compare species composition between mixed and *Oreomunnea*-dominated forests. For this comparison, a Bray-Curtis matrix dissimilarity using subplots of  $20 \times 20$  m was calculated grouping the four mixed and the four *Oreomunnea*-dominated forests. Then, to calculate multivariate dispersion among the groups (mixed and *Oreomunnea*-dominated forests), the function *betadisper* from the “vegan” package was used, and then utilized one-way Anova to examine the differences in dispersion between groups. Comparisons within both, mixed and *Oreomunnea*-dominated forests, for each of the four sites were conducted by calculating Jaccard dissimilarity values for each plot based on their corresponding  $20 \times 20$  m<sup>2</sup> subplots. Then, a t-test analysis was done for each set of paired plots to compare the similarity values. Both matrixes of dissimilarity were calculated using the function *vegdist*.

An indicator species analysis was performed to determine whether subordinate species were indicators of the presence of *Oreomunnea*. Using the species abundance from each pair of plots, we calculated the indicator species index (IndVal) which is the product of the specificity or uniqueness of a species to a specific habitat (component A) and the fidelity or the frequency of occurrence of a species in a habitat (component B), multiplied by 100. We used the function *multipatt* from the R package “indicpecies” (Cáceres & Legendre, 2009).

## RESULTS

### *Species community composition*

The NMDS ordination (stress=0.2) showed that plots grouped by sites for plant communities in both monodominant and mixed forest plots (Figure 2). Distinct clusters of mixed and monodominant forests were most apparent for the Honda sites and to a lesser extent the Hornito and Zorro sites (Figure 3). Plot pair centroids were most distant for the Hope site. Spe

### *The effect of *Oreomunnea* on beta-diversity*

Overall, compositional beta-diversity was significantly higher in mixed forest plots compared to the *Oreomunnea*-dominated forest plots (Table 4; Figure 4a). Beta-diversity in Honda and Hornito was higher in mixed forests compared to the *Oreomunnea*-dominated forest, but this was only significant for the paired plots at Honda (Table 4; Figure 4b, 4d). For the paired plots located at Hope beta-diversity was not significantly different (Table 4; Figure 4c). Unexpectedly, significantly higher beta-diversity was found in the *Oreomunnea*-dominated forest compared to the mixed forest in the site located at Zorro (Table 4; Figure 4e).

### *The effect of *Oreomunnea* on subordinate species richness and diversity*

Of a total of 467 tree species recorded in the eight plots, 173 were only found in *Oreomunnea*-dominated forests, 159 in mixed forests and 135 were shared between these two forest types. Species richness was significantly higher in mixed than *Oreomunnea*-dominated forests for two of four sites, both when including *Oreomunnea* stems and when excluding *Oreomunnea* (Table 5; Figure 5). The exceptions were Honda and Zorro. Honda had overlapping species accumulation curves with and without *Oreomunnea* stems (Figure 5a, 5e); Zorro had significantly higher species richness in the *Oreomunnea*-dominated forest when including and excluding *Oreomunnea* stems (Figure 5d, 5h).

Shannon diversity was significantly higher in mixed than monodominant forests in all our sites when *Oreomunnea* stems were included. However, when *Oreomunnea* stems were excluded, the diversity difference was no longer significant for Honda, Hornito and Hope (Table 5; Figure 6). Contrary to expectation, in Zorro Shannon diversity was significantly higher in monodominant than mixed forest even when *Oreomunnea* stems were excluded (Figure 6h).

### *Soil and climate variables in mixed and Oreomunnea-dominated forests*

Soil environmental vectors fitted to the ordination showed that  $\text{NH}_4$ ,  $\text{NO}_3$ , total N and P, Resin P and exchangeable bases were all significantly correlated with species compositional variation (Table 6). The lack of a complete soil data set, however, limited the interpretation of our ordination analysis. Thus, only complete data from variables of Table 2 were used to support and interpret the results of soil ordination analysis in this section. In the Hornito and Zorro sites, the *Oreomunnea*-dominated stands were characterized by soils with relatively high extractable nitrogen in the form of  $\text{NH}_4$  and high total N. In contrast, the mixed forests in Hope and Zorro were distinguished by soils with high extractable nitrogen in the form of  $\text{NO}_3$ . The *Oreomunnea*-dominated stand in Honda was differentiated by soils with low exchangeable nitrogen in the form of  $\text{NO}_3$ .

With regards to the bioclimatic variables fitted in the ordination, mean annual temperature and precipitation, mean of the wettest month, mean of the driest month, mean diurnal temperature range, relative temperature oscillation day to night throughout an annual season (isothermality) and temperature seasonality were all found to be significantly correlated with species compositional variation in the sites considered in this study (Table 6). The Honda site was characterized by high mean diurnal temperature range and isothermality, but low temperature seasonality. The site located at Hope was distinguished by low mean annual precipitation and low mean precipitation of the wettest month, but high temperature seasonality. The Hornito site had high mean annual temperature, high mean annual precipitation and mean annual precipitation of wettest month, but low precipitation in the driest month. Lastly, the site at Zorro was characterized by a high mean annual temperature.

Permanova analysis showed a significant effect of soil parent material ( $df= 3$ ,  $F= 22.54$ ,  $p= 0.001$ ), the presence/absence of *Oreomunnea* ( $df= 1$ ,  $F=21.35$ ,  $p= 0.001$ ) and their interaction ( $df= 3$ ,  $F=8.76$ ,  $p=0.001$ ) on species composition. Notably, 32% of the variation of the species composition within the 8 plots was explained by soil parent material, 10% by the presence/absence of *Oreomunnea* independent of parent material, and 12% by the interaction of parent material and *Oreomunnea*.

### *Indicator species of Oreomunnea forests*

No single species had a significantly positive association with the presence of *Oreomunnea* across the four *Oreomunnea* dominated forest plots (Table 7). However, the presence of *Inga exalata*, *Inga acuminata*, *Inga punctata* from the Fabaceae family, and *Posoqueria latifolia*, *Rondeletia buddleioides* and *Arachnothryx bertieroides* from the Rubiaceae family were positively associated with *Oreomunnea*-dominated forests in three out of the four sites (Table 7).

## **DISCUSSION**

In this study, three hypotheses were explored to explain the occurrence of tropical monodominant forests. Of these three hypotheses, support was mostly found for the third hypothesis, in which the presence of the monodominant species conditions soil properties to favour high conspecific local abundance and in the process, selects for subordinate species which can tolerate these new conditions.

The finding that *Oreomunnea*-dominated plots had lower availability of nitrate (NO<sub>3</sub>) and an overall more restricted species compositional beta-diversity than mixed forest plots provides support for the hypothesis that *Oreomunnea* modifies local soil conditions and therefore alters the subordinate tree species community. However, the diversity of subordinate species did not differ significantly between *Oreomunnea*-dominated and mixed forests in most sites studied. Furthermore, at one site (Zorro), subordinate species diversity was higher in the *Oreomunnea* dominated plot than in the adjacent mixed forest plot. These results suggest that *Oreomunnea* may be able to achieve high local abundance by changing soil properties that favour its own recruitment, but that this capacity may be dependent on environmental factors. Where the presence of *Oreomunnea* does lead to local plant-soil feedback, monodominance may be maintained along with the selection of subordinate species that tolerate these new properties. Our results therefore somewhat support the “ecosystem modification” hypothesis, indicating that tropical monodominance could be driven by the dominant species altering local ecosystem conditions.

### *Soil and climate variables in monodominant forests*

Previous studies have suggested that the formation of monodominant forests is dependent on the existence of specific soil conditions which confer an advantage to the monodominant species (Hall et al., 2020; Ter Steege et al., 2019). Based on these studies, we hypothesised that

we would see that plant communities with and without *Oreomunnea* would be adapted to the same initial low-fertility soil conditions and, apart from *Oreomunnea*, would have similar community composition. My design, using multiple plots on different soil parent materials, allowed me to evaluate this hypothesis.

I found that *Oreomunnea* achieves high abundance independent of pre-existing soil conditions because it is capable of forming monodominant stands on a variety of soil parent materials and soil fertility levels. Monodominance by *Oreomunnea* was found under rhyolite, tephra-over granodiorite, dacite and granodiorite soil parent material; however, *Oreomunnea* has not been registered to establish monodominance on andesite-derived soils, the most common parent material at Fortuna. Furthermore, there is no evidence that *Oreomunnea* is an early-successional tree species dependent on disturbance. *Oreomunnea* populations consist of mixed size classes and co-occur with large individuals of shade-tolerant tree species (e.g. *Micropholis melinoniana*, *Eschweilera panamensis*). I also found that soil parent material was a primary determinant of plant species composition across our study site. Soil parent material type can strongly influence mineralogy and soil texture in tropical ecosystems (Araujo et al., 2017), as well as the microbial community composition within these soils (Stone et al., 2015; Wagai et al., 2011). Notably, it has been shown that at the Fortuna Forest Reserve, variation in species composition at the local scale is driven by differences in soil nutrient availability associated with the composition soil parent material (Prada et al., 2017). However, while differences in soil chemistry can explain a large fraction of the variation in overall plant community composition, parent material cannot entirely explain the local dominance of *Oreomunnea*.

In this study, I had an incomplete soil dataset; however, despite this issue, my data reveal some potentially interesting patterns. I expected to find soils with low extractable nitrogen in *Oreomunnea*-dominated stands compared to the adjacent mixed forests as the result of ecosystem modification. I found that *Oreomunnea*-dominated forests varied in  $\text{NH}_4$  availability relative to adjacent mixed forest but were more generally characterized by low extractable  $\text{NO}_3$ . This result in part supports a general finding where soils under monodominant species are depleted in  $\text{NH}_4$  and nitrate due to resource competition between ectomycorrhizal fungi and saprophytes, which slows down decomposition rates in the soil (Brookshire & Thomas, 2013; Corrales et al., 2016; Hall et al., 2020; Torti et al., 2001). Low extractable nitrogen and phosphorus have previously been reported in *Oreomunnea*-dominated stands compared to the mixed forest in Honda (Corrales



et al. 2016), however I did not find a similar pattern for the rest of the sites considered in this study. In fact, mean  $\text{NH}_4$  values in two of the four monodominant forests (Hornito B and Zorro A; Table 2) were almost two times higher  $\text{NH}_4$  than the adjacent mixed forests. I attribute this difference to temporal fluctuations in nitrogen availability that may mask differences in time-averaged values between plots. Inorganic nitrogen availability can be difficult to measure under field conditions (Powlson, 1993), because  $\text{NH}_4$  and  $\text{NO}_3$  can be mobilized up or down in the soil profile over very short time periods due to changes in climate variables and the presence of microbes (Dahnke & Johnson, 1990). This might explain the differences in inorganic nitrogen in the paired plots at Hornito, because soil samples were taken at different times. Variation in nitrogen availability has also been shown to be influenced by soil horizon, such that the depth at which soil samples are taken and the presence of a surface organic layer are important (Torti et al., 2001).

Alternatively, the high variability of the ectomycorrhizal community associated with different *Oreomunnea*-dominated stands under different soil fertility gradients may affect the reduction in nitrogen availability, such that nitrogen availability is not reduced as much where the nitrogen availability is high (Corrales et al., 2021, 2015). Variation in the strength of this feedback is most likely related to differences among ectomycorrhizal taxa in their hyphal exploration types (Agerer, 2001) and enzymatic capacities (Buée et al., 2007; Pritsch & Garbaye, 2011), such that they differ in the degree and spatial extent to which they immobilize nitrogen in the soil. Further work with a complete soil data set is needed to determine if this pattern is present in *Oreomunnea*-dominated plots throughout the study site. In addition, I found varying climatic conditions across the four sites. Honda was characterized by high monthly temperature fluctuations, whilst Hope had annual low rates of rainfall with high temperature variability over the year. Hornito had annual high temperature and precipitation, whereas Zorro was depicted by high annual temperature levels. These results suggest that *Oreomunnea*-dominated stands are not constrained to a narrow range of climatic niche space.

In summary, I found variability in both the climatic and soil conditions across the four sites in this study. This result suggests that *Oreomunnea*-dominated stands are not constrained to a narrow range of climatic or edaphic niche space. This leads me to reject the first hypothesis in which monodominance is dependent on the existence of particular edaphic conditions. The evaluation of the remaining two hypotheses cannot be explained by only looking at soil properties.

Therefore, in this study I also assessed the diversity and composition of subordinate species associated with *Oreomunnea*-dominated stands.

### *Species diversity in monodominant forests*

While in this study I found evidence that some soil conditions differ between *Oreomunnea*-dominated and mixed forests, potentially as a result of dominance by *Oreomunnea* (Table 2), additional data can be informative in determining whether *Oreomunnea* dominance arises from plant-soil feedback. Under the ecosystem modification hypothesis, I predicted that the presence of *Oreomunnea* would affect both the composition and diversity of the tree community through environmental filtering, indirectly imposed by alterations to soil nutrient availability.

In the present study, the diversity of subordinate species was analysed both including and excluding *Oreomunnea* stems. Here, I focus on the results observed when stems of *Oreomunnea* in *Oreomunnea*-dominated plots and an equivalent number of random stems from mixed forest plots were omitted. This analysis allows the comparison of similar stem densities between plots and the calculation of diversity indices excluding the influence of *Oreomunnea*.

I found that species diversity did not differ significantly between *Oreomunnea*-dominated forests and the adjacent mixed forests in three out of four sites. This indicates that the diversity of the subordinate community in these plots may be relatively unaffected by *Oreomunnea* – other than the effect of reducing stem density. The exception was the paired plots in Zorro, where the species diversity was significantly higher in *Oreomunnea*-dominated forests compared to the mixed forest. Low species diversity in the mixed forest plot at Zorro may be attributed to the steep slopes (Homeier et al., 2010; Zhang et al., 2016) on which this plot is situated compared to the adjacent *Oreomunnea*-dominated plot which is less steep. Finally, the soil in the *Oreomunnea*-dominated forest plot in Zorro had much higher concentrations of ammonium than soils at other sites (with the exception of Hornito), implying that the effect of *Oreomunnea* on these soils, and therefore on the subordinate species, may be weaker.

Overall, this result indicates that the presence of *Oreomunnea* does not strongly affect tree diversity. Another possibility, however, is that *Oreomunnea* may impact community composition, but that species unable to coexist with *Oreomunnea* are replaced by an equally diverse group of taxa adapted to grow where *Oreomunnea* has changed the soil properties. If this

is the case, I would expect a significant effect of *Oreomunnea* on the compositional beta-diversity of tree community but not on species diversity.

#### *Lower beta-diversity among Oreomunnea-dominated forests than mixed forests*

I found that compositional beta-diversity was significantly lower in *Oreomunnea*-dominated forests than mixed forests. Differences in beta-diversity in tropical forests can be driven by a host of variables including rainfall, geology, soil gradients and dispersal limitation (Condit et al., 2002; González & Duque, 2010; Prada et al., 2017). However, our paired plot study design allowed us to reduce the influence of these factors. Therefore, the differences in beta-diversity found here appear to be consistent with the prediction that community composition is in part determined by species which can tolerate the presence of *Oreomunnea*.

In addition to significant differences in beta-diversity between *Oreomunnea*-dominated and mixed forests, I examined beta-diversity in each of the paired plots at our four study sites. I found that species compositional beta-diversity was lower in the *Oreomunnea*-dominated forest compared to the adjacent mixed forest in Honda and Hornito, but this result was only significant for Honda. This result suggests *Oreomunnea* has a weaker impact on community composition at Hornito. Species compositional beta-diversity was not significantly different in Hope. Consistent with the pattern for alpha diversity, significantly higher beta-diversity was found in the *Oreomunnea*-dominated forest compared to the mixed forest in the site located at Zorro. I attribute this result to the same causes that potentially affect species diversity in these paired of plots. In particular, the high ammonium to low nitrate that was found in this plot may be affecting species composition (Liu et al., 2017). Overall, I found more evidence which supports the third hypothesis, wherein the presence of *Oreomunnea* alters soil conditions, independent of soil parent material, implying the presence of plant-soil feedback.

Given the high beta diversity in this forest, the indicator species analysis found no single species associated with the presence of *Oreomunnea*. However, species of the genus *Inga*, and some species of the plant family Rubiaceae were associated as indicator species with *Oreomunnea*-dominated forests. This study, however, was restricted to taxa  $\geq 5$ cm DBH, the size class cut off for the permanent plots. Herbaceous plants and shrubs may be more strongly associated with the presence of *Oreomunnea*. For example, *Psychotria elata*, a shrub species from the coffee plant

family, was consistently observed in the understory in three out of four *Oreomunnea*-dominated forest plots (Z. Mijango personal observation).

#### *Mechanisms associated with Oreomunnea monodominance*

My study provides evidence that *Oreomunnea mexicana* can influence tree community composition and soil chemistry. These results are consistent with positive plant-soil feedback, where the monodominant tree species and the symbiotic ectomycorrhizal fungi alter soil conditions to benefit conspecifics. Positive ectomycorrhizal-mediated feedback was previously posited to promote monodominance in tropical forests (McGuire, 2014). This research suggested that the presence of ectomycorrhizal fungi confers a growth and survival advantage to seedlings of the monodominant species under conspecific trees through positive ectomycorrhizal-mediated feedback. While ectomycorrhizal associations may be important in some cases, different classes of ectomycorrhiza behave differently according to the soil in which they are present. In my study system, the ectomycorrhizal fungi community is highly variable (Corrales et al., 2021), where different ectomycorrhizal taxa have different enzymatic mechanisms to cope with a gradient of soil fertility. Additionally, in this study, evidence of positive plant-soil feedback is found, in which both the dominant species, *Oreomunnea*, and the associated ectomycorrhizal fungi mediate changes in the ecosystem in favour of the monodominant species. Therefore, instead of the mere presence of ectomycorrhizal fungi giving rise to monodominance in tropical forests, I have shown that ectomycorrhizal fungi may form one part of a larger process of ecosystem modification, which may drive monodominance in my study system.

One previous study in Bornean rainforest has shown positive plant-soil feedback affecting the growth of seedlings of ectomycorrhizal plant species in the Dipterocarpaceae, a family which is also able to establish monodominant stands (Segnitz et al., 2020). The positive plant-soil feedback in seedlings under conspecific individuals was attributed to conditioning of the soil microbial community by conspecific individuals. The positive plant-soil feedback generated in the Bornean forest and the positive plant-soil feedback found in *Oreomunnea*-dominated forest both fit the ecosystem modification hypothesis, although the positive plant-soil feedback in *Oreomunnea*-dominated forests may be driven by changes in the soil chemistry. This result suggests that ecosystem modification can take several forms in monodominant forests. Ectomycorrhizal fungal networks acting through hyphal interactions between conspecific trees

have also been shown to affect conspecific seedlings, increasing their survival and growth, and serving as antagonists to pathogens, resulting in positive plant-soil feedback (Liang et al., 2020). However, earlier research by Corrales et al. (2016) found no evidence that soil microbial feedback affects *Oreomunnea* seedling growth nor that seedlings benefitted from a common mycorrhizal network linking conspecific trees.

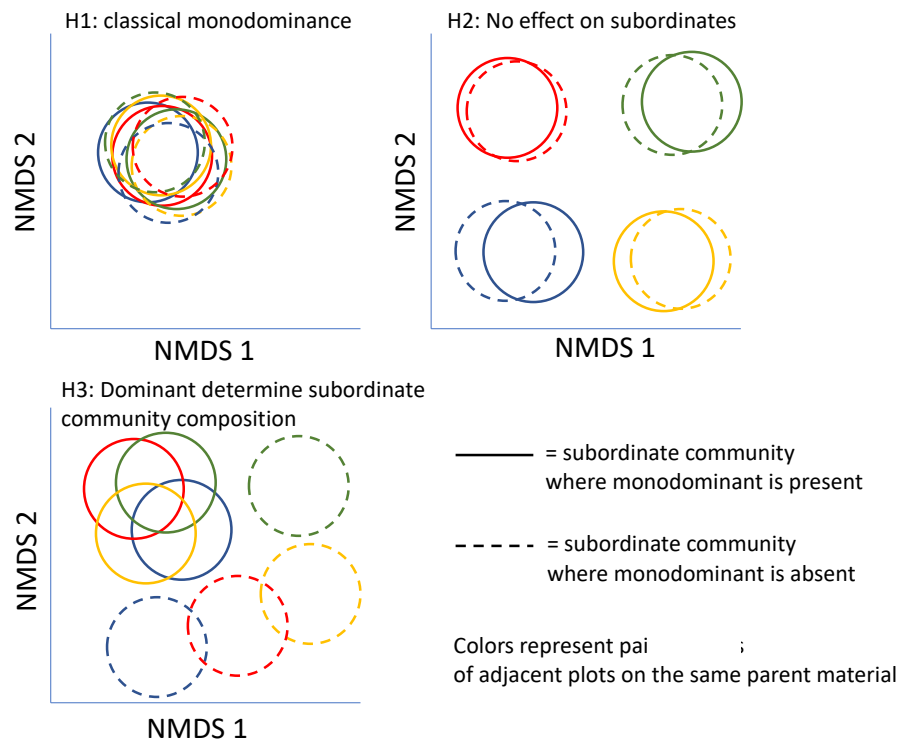
Even though in this study I could not find support for changes in extractable phosphorus in *Oreomunnea*-dominated forest soils, organic phosphorus could also play a fundamental role in the modification of soil properties by monodominant species. For instance, lower resin P in *Oreomunnea*-dominated forests compared to the adjacent mixed forests has been reported in our study system (Corrales et al., 2016). Low phosphorus availability in monodominant forests could be the result of the capacity of *Oreomunnea* and its associated ectomycorrhizal fungal to acquire P in different forms compared to the adjacent arbuscular mycorrhizal tree species (Liu et al., 2018). Thus, low organic phosphorus in *Oreomunnea*-dominated forests may also further support the hypothesis of soil chemistry modification.

Overall, this study highlights the potential for multiple mechanisms that could lead to monodominance across species and regions. Therefore, in order to expand this work to other tropical monodominant systems, more studies looking at species diversity and composition within tropical monodominant forests need to be done. Similarly, special attention must be paid to the type of study design and sampling scale utilized, whilst investigating monodominant forests.

## FIGURES AND TABLES

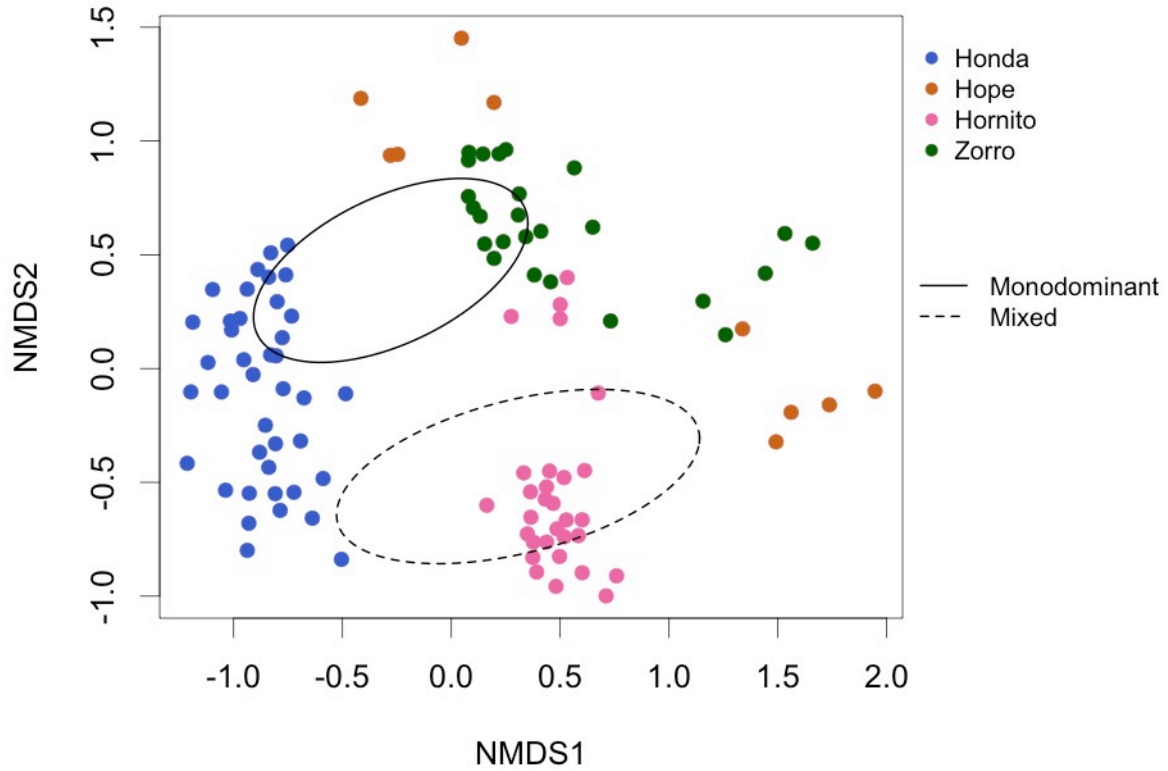
**Figure 1**

Hypothetical ordination of tree community composition given the hypotheses proposed for this study. Lines represent hypothetical ellipses delimiting compositional variation across a given plot. Solid lines are for communities where the monodominant species (*Oreomunnea*) is present and dashed lines were absent. Colors represent pairs of adjacent plots that occur on the same parent material. (a) Classical monodominance hypothesis: communities with and without *Oreomunnea* are adapted to the same initial low-fertility soil conditions and have similar community composition. Monodominance is consistent with the ‘exceptional traits’ hypothesis; (b) Exceptional traits or localized feedback effects do not impact subordinate species: subordinate species vary across soil types while the presence/absence of *Oreomunnea* does not impact species composition. (c) Feedback effects determine subordinate community composition; monodominant species selects for subordinate species able to tolerate the same soil conditions. Community composition is more divergent across plots in the absence of *Oreomunnea*.



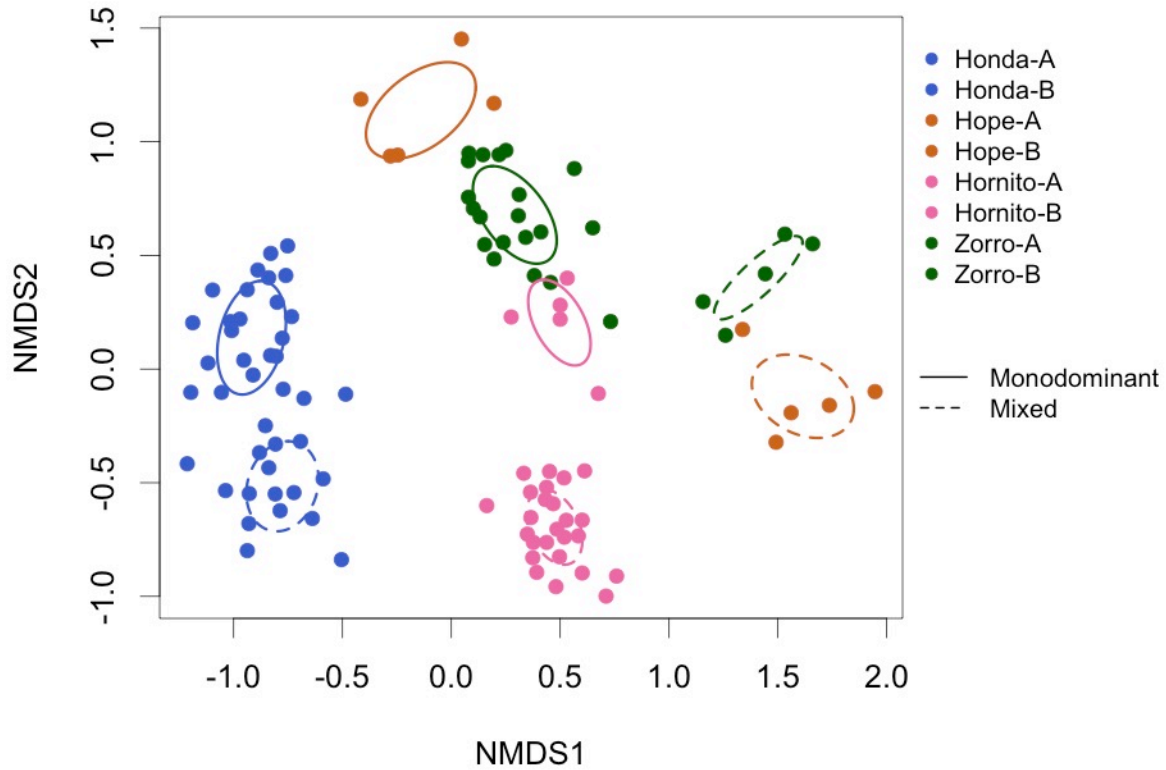
**Figure 2**

Nonmetric multidimensional analysis (NMDS) plot using Bray-Curtis dissimilarity distance (stress=0.2). Community species composition of four sites in The Fortuna Forest Reserve and Finca La Esperanza. Colors represent sites, solid line represent the mean community species composition of the *Oreomunnea*-dominated forests and the mixed forests.



**Figure 3**

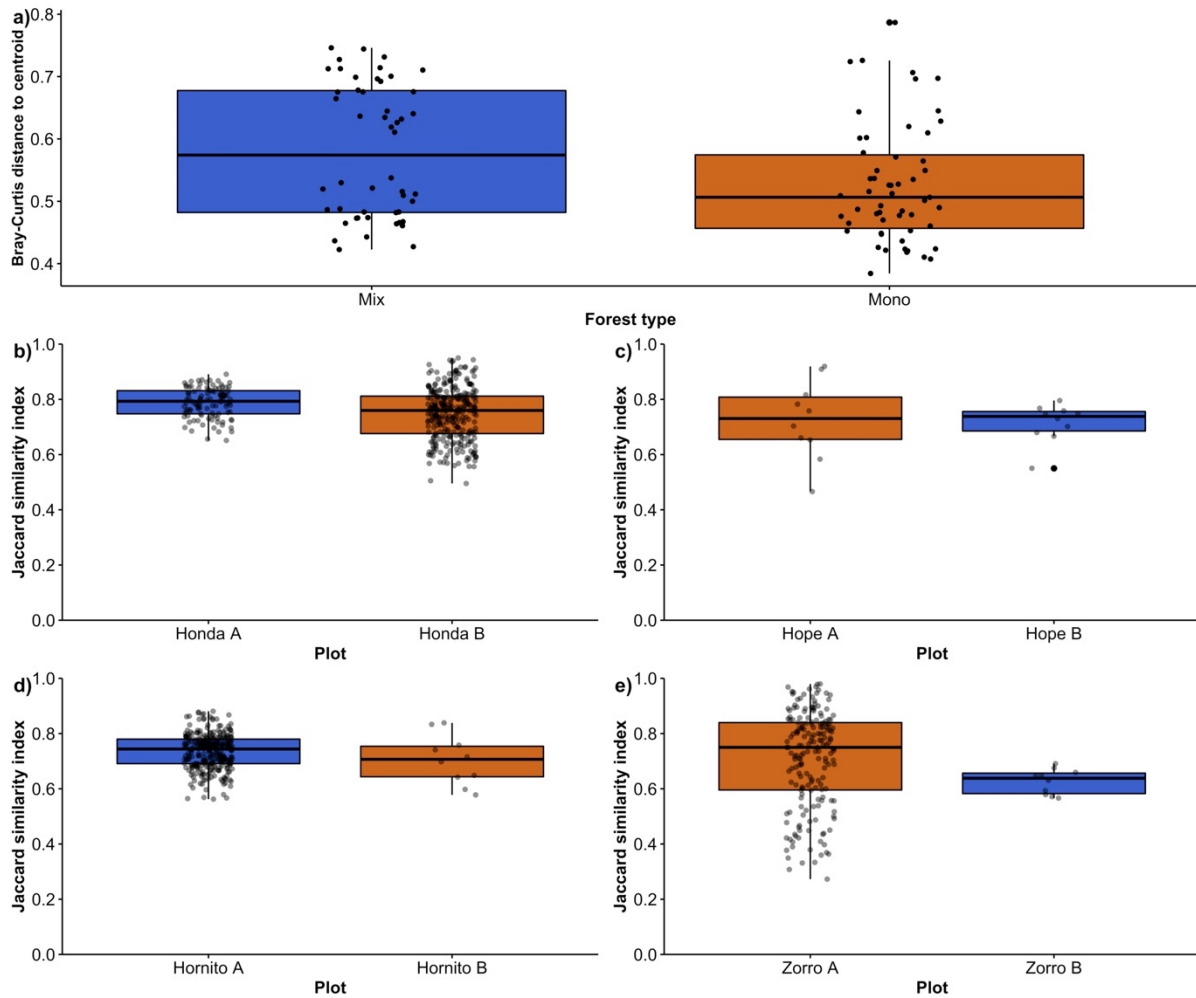
Nonmetric multidimensional analysis (NMDS) plot using Bray-Curtis dissimilarity distance (stress=0.2). Species community composition where colors represent paired plots of four sites considered in this study in the Fortuna Forests Reserve and Finca La Esperanza, solid lines represent the mean distribution of species composition of a given site with *Oreomunnea*-dominated forest and dashed lines represent the mean distribution of species composition of a given site with mixed forest.





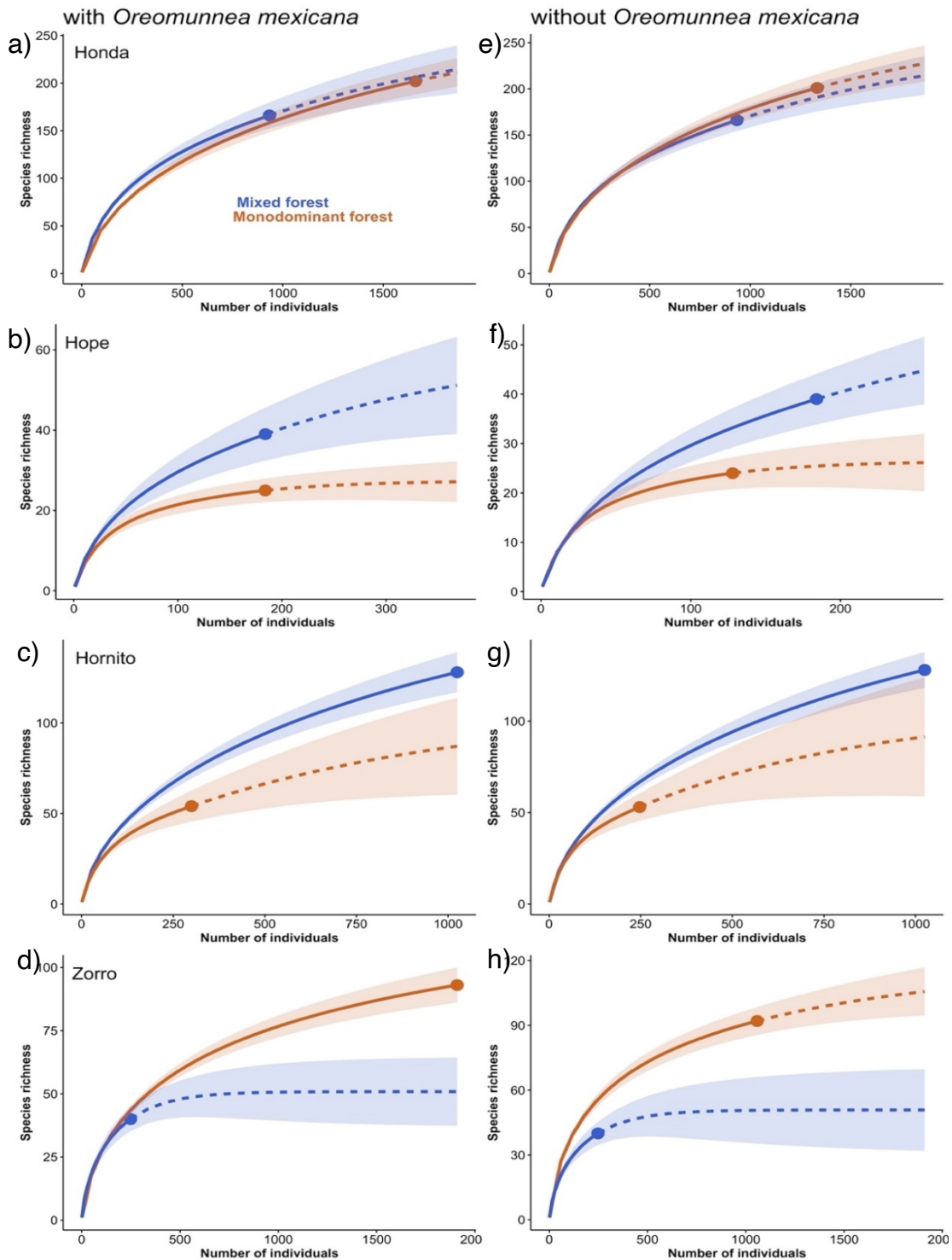
**Figure 4**

Box plots comparison of Bray-Curtis distance between groups as a measured of beta-diversity in eight plots located in Fortuna Forest Reserve and Finca La Esperanza in Boquete, and Jaccard similarity index as a measure of beta-diversity between paired plots. Beta-diversity comparison between 4 mixed and 4 monodominant forests plots (a), and paired plots in Honda (b), Hope (c), Hornito (d), and Zorro (e).



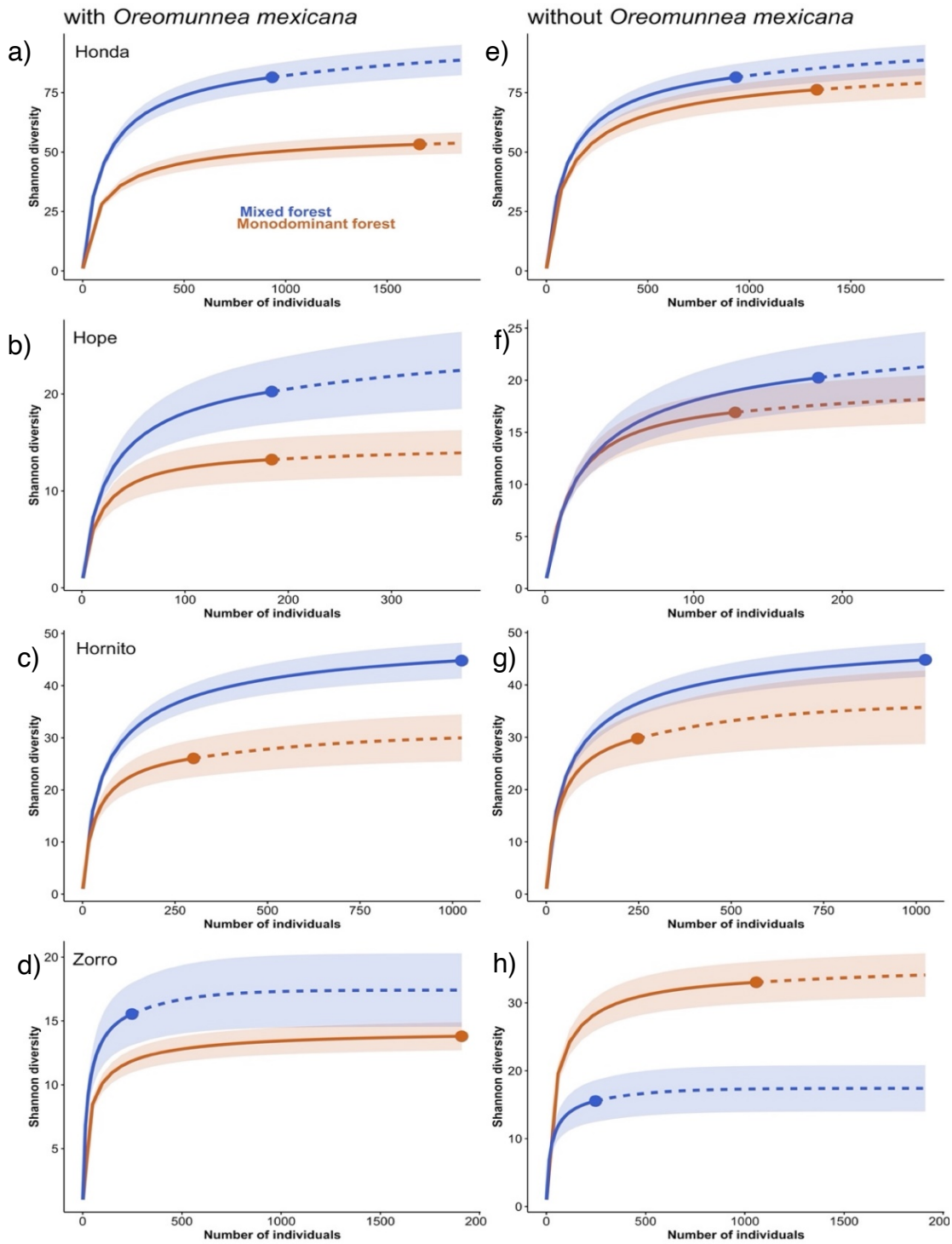
**Figure 5**

Rarefaction (solid line) and extrapolation (dashed line) curves between the 4 paired plots in the study, 3 in Fortuna Forest Reserve and 1 in Finca La Esperanza, Boquete. Species richness comparison between mixed and monodominant forest, including (a-d) and excluding individuals of *Oreomunnea mexicana* (e-h). Shaded areas represent the 95% CI of each curve.



**Figure 6**

Rarefaction (solid line) and extrapolation (dashed line) curves between the 4 paired plots in the study, 3 in Fortuna Forest Reserve and 1 in Finca La Esperanza, Boquete. Shannon diversity comparison between mixed and monodominant forest, including (a-d) and excluding individuals of *Oreomunnea mexicana* (e-h). Shaded areas represent the 95% CI of each curve.



**Table 1**

Site characteristics of eight plots at The Fortuna Forest Reserve and Finca La Esperanza in western Panama. Paired plots are segregated by forest type.

	<i>Oreomunnea</i> -dominated forests				Mixed forests			
	Honda B	Hope A	Hornito B	Zorro A	Honda A	Hope B	Hornito A	Zorro B
Coordinates	8.76 N, 82.24 W	8.82 N, 82.44 W	8.68 N, 82.21 W	8.76 N, 82.26 W	8.75 N, 82.24 W	8.82 N, 82.43 W	8.68 N, 82.21 W	8.76 N, 82.26 W
Major location	Fortuna	Baru	Fortuna	Fortuna	Fortuna	Baru	Fortuna	Fortuna
Plot size (subplots)	1 ha (25)	0.2 ha (5)	0.2 ha (5)	0.8 ha (20)	0.6 ha (15)	0.2 ha (5)	1 ha (25)	0.2 ha (5)
Vegetation								
Species richness	202	25	54	93	166	39	128	40

**Table 2**

Soil properties with the means and standard deviation values of eight plots at The Fortuna Forest Reserve and Finca La Esperanza in western Panama.

Forest type Parent material	Honda-A		Honda-B		Hope-B		Hope-A	
	Mix		Mono		Mix		Mono	
	Rhyolite		Rhyolite		Tephra over granodiorite		Tephra over granodiorite	
	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd
Total N ( $\mu\text{g cm}^{-3}$ )	2.92	0.71	2.39	0.71	2.28		2.4	
Total P ( $\mu\text{g cm}^{-3}$ )	180.64	41.06	127.7	63.69	384.8		231.9	
NH4 ( $\mu\text{g cm}^{-3}$ )	2.25	1.68	1.78	1.48	1.94		1.64	
NO3 ( $\mu\text{g cm}^{-3}$ )	1.2	1.07	0.43	0.64	5.84		1.97	
Resin P ( $\mu\text{g cm}^{-3}$ )	0.23	0.19	1.93	1.36				
Ca ( $\text{cmol L}^{-1}$ )	0.05	0.01	0.11	0.14				
Mg ( $\text{cmol L}^{-1}$ )	0.04	0.01	0.06	0.05				
K ( $\text{cmol L}^{-1}$ )	0.02	0.004	0.03	0.01				
Na ( $\text{cmol L}^{-1}$ )	0.02	0.01	0.02	0.01				
pH	3.59	0.18	3.84	0.63	5.1		4.71	
Forest type Parent material	Hornito-A		Hornito-B		Zorro-B		Zorro-A	
	Mix		Mono		Mix		Mono	
	Dacite		Dacite		Granodiorite		Granodiorite	
	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd
Total N ( $\mu\text{g cm}^{-3}$ )	2.87	0.49	1.62		3.4		4.47	1.44
Total P ( $\mu\text{g cm}^{-3}$ )	280.16	72.55						
NH4 ( $\mu\text{g cm}^{-3}$ )	1.82	0.91	3.54		2.9		5.16	2.53
NO3 ( $\mu\text{g cm}^{-3}$ )	1.19	0.64	0.47		3.9		1.34	2.3
Resin P ( $\mu\text{g cm}^{-3}$ )	2.23	0.57					1.42	1.61
Ca ( $\text{cmol L}^{-1}$ )	4.94	2.69					0.63	0.84
Mg ( $\text{cmol L}^{-1}$ )	1.02	0.53					0.17	0.2
K ( $\text{cmol L}^{-1}$ )	0.18	0.06					0.12	0.04
Na ( $\text{cmol L}^{-1}$ )	0.04	0.01					0.03	0.02
pH	5.03	0.66	4.3				4.41	0.32

**Table 3**

Climate variables obtained using CHELSA at 0.5 resolution capacity in eight plots at The Fortuna Forest Reserve and Finca La Esperanza in western Panama.

Climate variables	Honda		Hope		Hornito		Zorro	
	Honda A	Honda B	Hope A	Hope B	Hornito A	Hornito B	Zorro A	Zorro B
Mean annual temperature (°C)	18.9	18.8	16.8	16.7	18.1	26	18.5	25.4
Mean annual precipitation (mm)	2708	2639	2620	2830	3024	2084	2726	2164
Mean of wettest month (mm)	343	335	308	334	439	346	344	353
Mean of driest month (mm)	54	51	73	82	38	13	55	15
Mean diurnal range (°C)	43	43	42	42	42	41	43	41
Isothermality (°C)	6.03	6.03	6.06	6.07	5.95	5.63	6.03	5.68
Temperature seasonality (°C)	49.3	49.2	47.8	47.3	52.1	66.5	49	64.2
Max temperature (°C)	23.1	23	20.9	20.7	22.3	30.5	22.6	29.8
Min temperature (°C)	16	15.9	13.9	13.7	15.1	23.3	15.5	22.6
Mean temperature range (°C)	7.1	7.1	7.0	7.0	7.1	7.2	7.1	7.2

**Table 4**

Group dispersion Anova-one way test results as a measured of beta-diversity using eight plots and t-test result of pairwise comparison in four sites considered in this study. Plots were in Fortuna Forest Reserve and Finca La Esperanza in Boquete. Beta-diversity comparison between 4 mixed and 4 monodominant forests plots (a), pairwise comparison using Jaccard similarity index between mixed and monodominant forests in the four sites considered in this study (b)

<b>a: Multivariate dispersion test between mixed and monodominant forests using Bray-Curtis distance</b>					
Anova	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Groups	1	0.078	0.078	7.70	0.0066
Residuals	103	1.04	0.010		

<b>b: Pairwise comparison between mixed and monodominant forests in each site using Jaccard similarity index</b>			
t-test	Df	t value	P-value
Honda	318.83	5.15	< 0.001
Hope	18	0.21	0.8334
Hornito	308	1.43	0.1549
Zorro	4.39	27.56	< 0.001

**Table 5**

Comparison of species richness (Ri) and Shannon diversity (D) in four mixed forest plots and the adjacent monodominant forest based on rarefaction and extrapolation analysis. Values shown for the analysis done both, with the inclusion and the exclusion of stems of the monodominant tree species *Oreomunnea Mexicana*. Standard errors and 95% confidence intervals were obtained by bootstrap.

		Species richness				
<b>With <i>Oreomunnea</i></b>	n	Ri	Ri <sub>es</sub> <sup>1</sup>	Ri se <sup>2</sup>	Ri LCI <sup>3</sup>	Ri UCI <sup>4</sup>
Honda						
Mixed	934	166	264	32.83	217.28	351.33
Monodominant	1661	202	286	25.22	249.48	351.63
Hope						
Mixed	184	39	63	15.96	46.3	117.22
Monodominant	184	25	28	2.94	25.4	40.58
Hornito						
Mixed	1025	128	182	20.45	154.59	238.87
Monodominant	300	54	109	37.21	70.48	237.19
Zorro						
Mixed	248	40	51	7.58	43.15	77.35
Monodominant	1910	93	117	12.68	102.09	156.48
<b>Without <i>Oreomunnea</i></b>						
Honda						
Mixed	934	166	264	32.83	217.28	351.33
Monodominant	1333	201	285	25.22	248.47	350.6
Hope						
Mixed	184	39	63	15.96	46.3	117.55
Monodominant	128	24	26	2.94	24.4	39.54
Hornito						
Mixed	1025	128	182	20.45	154.59	238.87
Monodominant	247	53	107.9	37.18	69.46	236.06
Zorro						
Mixed	248	40	51	7.58	43.15	77.35
Monodominant	1058	92	116	12.68	101.09	155.45
		Species diversity				
<b>With <i>Oreomunnea</i></b>	n	D	D <sub>es</sub> <sup>5</sup>	D se <sup>6</sup>	D LCI <sup>7</sup>	D UCI <sup>8</sup>
Honda						
Mixed	934	81.44	94.68	4.19	86.47	102.88
Monodominant	1661	53.24	58.57	2.74	53.24	63.93



**Table 5 cont.**

Hope						
Mixed	184	20.25	24.29	2.31	20.25	28.81
Monodominant	184	13.23	14.32	1.19	13.23	16.64
Hornito						
Mixed	1025	44.81	49.42	2.26	44.99	53.85
Monodominant	300	26.04	30.90	2.71	26.04	36.21
Zorro						
Mixed	248	15.54	17.41	1.45	15.54	20.25
Monodominant	1910	13.80	14.27	0.62	13.80	15.49
<b>Without <i>Oreomunnea</i></b>						
Honda						
Mixed	934	81.44	94.68	4.12	86.61	102.74
Monodominant	1333	76.23	85.82	3.28	79.40	92.25
Hope						
Mixed	184	20.25	24.29	2.50	20.25	29.19
Monodominant	128	16.92	18.89	1.41	16.92	21.65
Hornito						
Mixed	1025	44.81	49.42	2.27	44.98	53.86
Monodominant	247	29.75	36.54	3.52	29.75	43.45
Zorro						
Mixed	248	15.54	17.41	1.55	15.54	20.45
Monodominant	1058	33.02	35.05	1.52	33.02	38.04

<sup>1</sup>Richness estimate based on extrapolation, <sup>2</sup>richness standard error, <sup>3</sup>lower 95% confidence interval of richness estimate, <sup>4</sup>upper 95% confidence interval of richness estimate; <sup>5</sup>Shannon diversity estimate based on extrapolation, <sup>6</sup>Shannon diversity standard error, <sup>3</sup>lower 95% confidence interval of Shannon diversity estimate, <sup>4</sup>upper 95% confidence interval of Shannon diversity estimate.

**Table 6**

Nonmetric multidimensional analysis (NMDS) result of soil and climate variables fitted in the ordination of species abundance in eight plots located in Fortuna Forest Reserve and Finca La Esperanza in Boquete. Factors are represented by location between pair plots.

	NMDS1	NMDS2	r <sup>2</sup>	Pr (>r)
<b>Vectors</b>				
pH	0.15992	-0.98713	0.0461	0.09
Total N	0.47753	0.87861	0.1758	0.001
Total P	0.1468	-0.98917	0.4351	0.001
NH <sub>4</sub>	0.34866	0.93725	0.3766	0.001
NO <sub>3</sub>	0.99071	0.13597	0.5108	0.001
Resin P	-0.43132	-0.9022	0.0952	0.011
Ca	0.40744	-0.91323	0.4939	0.001
Mg	0.38652	-0.92228	0.4796	0.001
K	0.56407	-0.82573	0.2591	0.001
Na	0.10402	-0.99457	0.0885	0.009
Temp	0.7749	0.63208	0.0587	0.049
Preci	0.08224	-0.99661	0.2665	0.001
Iso	-0.98525	0.17112	0.2041	0.001
Diurnal range	-0.96343	0.26795	0.5114	0.001
Wettest month	0.39334	-0.91939	0.6055	0.001
Driest month	-0.54562	0.83803	0.1179	0.005
Temp season	0.99179	-0.12785	0.1796	0.001
Max temp	0.79409	0.6078	0.0524	0.066
Min temp	0.74834	0.66332	0.0541	0.061
Temp range	0.548	-0.83648	0.0095	0.617
<b>Centroids</b>				
Hornito	0.4815	-0.5492	0.6903	0.001
Zorro	0.5219	0.6299		
Honda	-0.87	-0.1099		
Hope	0.7304	0.5125		

<sup>1</sup>Annual mean temperature, <sup>2</sup>annual mean precipitation, <sup>3</sup>isothermality, <sup>4</sup>mean diurnal temperature range, <sup>5</sup>mean of wettest month, <sup>6</sup>mean of driest month, <sup>7</sup>temperature seasonality, <sup>8</sup>max temperature, <sup>9</sup>min temperature, <sup>10</sup>mean temperature range.

**Table 7**

List of indicator species in eight plots at the Fortuna Forest Reserve and Finca La Esperanza in western Panama. Component A represents the uniqueness of a species and component B represents the frequency of occurrence of a species within a habitat. The IndVal index represents the goodness of a given species as an indicator species for a particular habitat. The IndVal index is represented by a value between 0 and 100 where 100 is the best indicator of indicator species. P-value was obtained by permutational analysis.

Family	Species	A	B	Indval	Stat	p-value
<b>Honda A (mix)</b>						
Euphorbiaceae	<i>Croton schiedeanus</i>	1.00	0.87	86.67	0.93	0.0001
Chloranthaceae	<i>Hedyosmum bonplandianum</i>	0.97	0.87	84.42	0.92	0.0001
Arecaceae	<i>Wettinia quinaria</i>	0.93	0.87	81.02	0.90	0.0001
Actinidaceae	<i>Saurauia sp.</i>	1.00	0.73	73.33	0.86	0.0001
Rubiaceae	<i>Elaeagia auriculata</i>	0.81	0.87	70.13	0.84	0.0002
Vochysiaceae	<i>Vochysia gatemalensis</i>	1.00	0.67	66.67	0.82	0.0001
Icacinaceae	<i>Calatola costaricensis</i>	0.94	0.67	62.71	0.79	0.0002
Monimiaceae	<i>Mollinedia sp.</i>	1.00	0.53	53.33	0.73	0.0003
Myrsinaceae	<i>Ardisia spl</i>	1.00	0.47	46.67	0.68	0.0002
Euphorbiaceae	<i>Alchornea glandulosa</i>	0.85	0.53	45.20	0.67	0.0044
Euphorbiaceae	<i>Richeria obovata</i>	0.74	0.60	44.12	0.66	0.0140
Rubiaceae	<i>Psychotria inelata</i>	0.94	0.47	44.03	0.66	0.0012
Celastraceae	<i>Quetzalia occidentalis</i>	0.68	0.60	40.54	0.64	0.0362
Asteraceae	<i>Koanophyllum hylonomum</i>	1.00	0.40	40.00	0.63	0.0014
Myrtaceae	<i>Plinia sp.</i>	1.00	0.40	40.00	0.63	0.0015
Rubiaceae	<i>Psychotria panamensis</i>	1.00	0.40	40.00	0.63	0.0014
Elaeocarpaceae	<i>Sloanea cf. brenesii</i>	1.00	0.40	40.00	0.63	0.0017
Apocynaceae	<i>Tabernaemontana sp.</i>	1.00	0.40	40.00	0.63	0.0015
Salicaceae	<i>Casearia arborea</i>	0.87	0.40	34.78	0.59	0.0124
Erythroxylaceae	<i>Erythroxylum macrophyllum</i>	0.85	0.40	33.90	0.58	0.0140
Fabaceae	<i>Inga leonis</i>	1.00	0.33	33.33	0.58	0.0042
Moraceae	<i>Pseudolmedia spuria</i>	1.00	0.33	33.33	0.58	0.0051
Myristicaceae	<i>Virola surinamensis</i>	0.83	0.40	33.33	0.58	0.0192
Myrtaceae	<i>Myrtaceae spl</i>	0.92	0.33	30.70	0.55	0.0148
Malvaceae	<i>Pachira aquatica</i>	1.00	0.27	26.67	0.52	0.0132
Rubiaceae	<i>Pentagonia nuciformis</i>	1.00	0.27	26.67	0.52	0.0135
Sapotaceae	<i>Pouteria glomerata</i>	1.00	0.27	26.67	0.52	0.0160
Rubiaceae	<i>Chomelia sp.</i>	1.00	0.20	20.00	0.45	0.0438
Lauraceae	<i>Endilcheria browniana</i>	1.00	0.20	20.00	0.45	0.0430
Annonaceae	<i>Guatteria dolichopoda</i>	1.00	0.20	20.00	0.45	0.0490

**Table 7 cont.**

Family	Species	A	B	Indval	Stat	p-value
Proteaceae	<i>Panopsis suaveolens</i>	1.00	0.20	20.00	0.45	0.0483
Picramniaceae	<i>Picramnia teapensis</i>	1.00	0.20	20.00	0.45	0.0454
<b>Honda B (mono)</b>						
Rubiaceae	<i>Posoqueria latifolia</i>	0.89	0.92	81.95	0.91	0.0001
Annonaceae	<i>Guatteria acrantha</i>	1.00	0.76	76.00	0.87	0.0001
Unknown	Morfo1	0.84	0.84	70.23	0.84	0.0004
Lecythidaceae	<i>Eschweilera panamensis</i>	0.83	0.76	63.16	0.80	0.0017
Fabaceae	<i>Inga exalata</i>	1.00	0.48	48.00	0.69	0.0018
Unknown	Morfo 52056	1.00	0.44	44.00	0.66	0.0058
Adoxaceae	<i>Viburnum costaricanum</i>	1.00	0.44	44.00	0.66	0.0065
Unknown	Morfo2	1.00	0.40	40.00	0.63	0.0085
Melastomataceae	<i>Graffenrieda bella</i>	0.91	0.36	32.79	0.57	0.0480
Arecaceae	<i>Euterpe precatória</i>	1.00	0.32	32.00	0.57	0.0299
Theaceae	Theaceae1	1.00	0.28	28.00	0.53	0.0314
<b>Hope A (mono)</b>						
Apocynaceae	<i>Rauvolfia aphlebia</i>	1.00	1.00	100.00	1.00	0.0075
Elaeocarpaceae	<i>Sloanea sp.</i>	1.00	1.00	100.00	1.00	0.0075
Myrtaceae	<i>Eugenia sp1</i>	1.00	0.80	80.00	0.89	0.0456
Fagaceae	<i>Quercus insignis</i>	1.00	0.80	80.00	0.89	0.0473
Rubiaceae	<i>Rondeletia buddleiodes</i>	1.00	0.80	80.00	0.89	0.0473
Celastraceae	<i>Salacia cordata</i> subsp. <i>patenensis</i>	1.00	0.80	80.00	0.89	0.0456
Salicaceae	<i>Xylosma sp2</i>	1.00	0.80	80.00	0.89	0.0473
<b>Hope B (mix)</b>						
Rubiaceae	<i>Coffea arabica</i>	1.00	1.00	100.00	1.00	0.0075
Lauraceae	<i>Ocotea cernua</i>	1.00	1.00	100.00	1.00	0.0075
Rubiaceae	<i>Psychotria panamensis</i>	1.00	1.00	100.00	1.00	0.0075
Salicaceae	<i>Casearia arborea</i>	1.00	0.80	80.00	0.89	0.0469
Araliaceae	<i>Dendropanax sp5</i>	1.00	0.80	80.00	0.89	0.0445
Lauraceae	Lauraceae sp12	1.00	0.80	80.00	0.89	0.0466
Melastomataceae	<i>Miconia variabilis</i>	1.00	0.80	80.00	0.89	0.0469
<b>Hornito A (mix)</b>						
Sapotaceae	<i>Pouteria juruana</i>	0.95	1.00	95.05	0.98	0.0001
Moraceae	<i>Brosimum guianense</i>	1.00	0.88	88.00	0.94	0.0004
Araliaceae	<i>Dendropanax arboreus</i>	1.00	0.84	84.00	0.92	0.0011
Myrtaceae	Myrtaceae sp6	1.00	0.84	84.00	0.92	0.0007
Apocynaceae	<i>Rauvolfia aphlebia</i>	0.92	0.88	80.67	0.90	0.0018
Myrtaceae	<i>Eugenia sp1</i>	1.00	0.72	72.00	0.85	0.0158

**Table 7 cont.**

Family	Species	A	B	Indval	Stat	p-value
Picramniaceae	<i>Picramnia teapensis</i>	0.88	0.76	66.73	0.82	0.0419
Salicaceae	<i>Hasseltia floribunda</i>	1.00	0.60	60.00	0.78	0.0495
<b>Hornito B (mono)</b>						
Araliaceae	<i>Dendropanax sp2</i>	1.00	1.00	100.00	1.00	0.0001
Rhizophoraceae	<i>Cassipourea elliptica</i>	0.88	1.00	87.84	0.94	0.0004
Araliaceae	<i>Dendropanax sp1</i>	1.00	0.80	80.00	0.89	0.0003
Fabaceae	<i>Inga sierra</i>	1.00	0.80	80.00	0.89	0.0002
Melastomataceae	<i>Miconia lonchophylla</i>	1.00	0.80	80.00	0.89	0.0001
Sapotaceae	<i>Pouteria aff. reticulata</i>	1.00	0.80	80.00	0.89	0.0001
Sapotaceae	<i>Pouteria reticulata</i>	1.00	0.80	80.00	0.89	0.0003
Rubiaceae	<i>Arachnothryx bertieroides</i>	0.93	0.80	74.58	0.86	0.0010
Monnimiaceae	<i>Mollinedia viridiflora</i>	0.88	0.80	70.59	0.84	0.0024
Annonaceae	<i>Guattera costaricensis</i>	1.00	0.60	60.00	0.78	0.0009
Fagaceae	<i>Quercus gulielmi-treleasei</i>	1.00	0.60	60.00	0.78	0.0027
Fagaceae	<i>Quercus insignis</i>	1.00	0.60	60.00	0.78	0.0025
Burseraceae	<i>Protium panamensis</i>	0.96	0.60	57.69	0.76	0.0073
Lauraceae	<i>Aiouea sp.</i>	1.00	0.40	40.00	0.63	0.0195
Myrsinaceae	<i>Ardisia cf. crassipedicellata</i>	1.00	0.40	40.00	0.63	0.0251
Myrsinaceae	<i>Ardisia rigidifolia</i>	1.00	0.40	40.00	0.63	0.0195
Salicaceae	<i>Casearia arborea</i>	1.00	0.40	40.00	0.63	0.0220
Melastomataceae	<i>Graffenrieda bella</i>	1.00	0.40	40.00	0.63	0.0239
Meliaceae	<i>Guarea sp4</i>	1.00	0.40	40.00	0.63	0.0235
Salicaceae	<i>Hasseltia sp1</i>	1.00	0.40	40.00	0.63	0.0235
Myrtaceae	Myrtaceae sp8	1.00	0.40	40.00	0.63	0.0219
Fabaceae	<i>Inga punctata</i>	0.95	0.40	38.10	0.62	0.0235
<b>Zorro A (mono)</b>						
Lauraceae	<i>Aiouea sp.</i>	1.00	0.95	95.00	0.98	0.0002
Araliaceae	<i>Dendropanax arboreus</i>	1.00	0.95	95.00	0.98	0.0001
Annonaceae	<i>Guattera costaricensis</i>	1.00	0.90	90.00	0.95	0.0005
Sapindaceae	<i>Billia rosea</i>	1.00	0.80	80.00	0.89	0.0016
Adoxaceae	<i>Viburnum costaricanum</i>	0.89	0.85	75.90	0.87	0.0120
Sapotaceae	<i>Pouteria aff. reticulata</i>	1.00	0.75	75.00	0.87	0.0076
Burseraceae	<i>Protium panamensis</i>	1.00	0.75	75.00	0.87	0.0107
Magnoliaceae	<i>Talauma sp.</i>	1.00	0.75	75.00	0.87	0.0151
Fabaceae	<i>Inga acuminata</i>	1.00	0.70	70.00	0.84	0.0279
Fabaceae	<i>Inga exalata</i>	1.00	0.65	65.00	0.81	0.0365

**Table 7 cont.**

Family	Species	A	B	Indval	Stat	p-value
<b>Zorro B (mix)</b>						
Lauraceae	Lauraceae sp4	1.00	1.00	100.00	1.00	0.0001
Asteraceae	<i>Koanophyllom hylonomum</i>	0.98	1.00	98.49	0.99	0.0001
Lauraceae	<i>Ocotea cernua</i>	0.89	1.00	88.73	0.94	0.0001
Lauraceae	<i>Ocotea insignis</i>	0.86	1.00	86.27	0.93	0.0009
Myrtaceae	Myrtaceae sp1	0.85	1.00	84.62	0.92	0.0025
Fabaceae	<i>Inga oerstediana</i>	0.77	1.00	76.60	0.88	0.0060
Melastomataceae	Melastomataceae sp2	1.00	0.60	60.00	0.78	0.0036
Actinidaceae	<i>Saurauia pittieri</i>	0.90	0.60	54.19	0.74	0.0209
Clusiaceae	<i>Chrysochlamys psychotriifolia</i>	1.00	0.40	40.00	0.63	0.0358
Fabaceae	<i>Erythrina sp1</i>	1.00	0.40	40.00	0.63	0.0354
Malvaceae	<i>Hampea appendiculata</i>	1.00	0.40	40.00	0.63	0.0338
Actinidaceae	<i>Saurauia montana</i>	1.00	0.40	40.00	0.63	0.0311
Actinidaceae	<i>Saurauia seibertii</i>	1.00	0.40	40.00	0.63	0.0358
Arecaceae	<i>Chamaedorea woodsoniana</i>	0.63	0.60	37.90	0.62	0.0403

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