-CENTRE OF BIODIVERSITY AND SUSTAINABLE LAND USE-
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Interactive effects of elevation and forest-use intensity on tropical tree diversity in Veracruz, Mexico.

Dissertation

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“What beautiful mountains in Mexico!” those cones of perpetual snow are the most beautiful thing in the world; those majestic heads that rise among the shimmering vegetation of the tropics”

Alexander von Humboldt (1769-1859)

“¡Que hermosas montañas las de México! aquellos conos de nieve perpetua es lo más hermoso del mundo; esas cabezas de nieve majestuosa que se elevan en medio de la brillante vegetación de los trópicos”

Alexander von Humboldt (1769-1859)

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Thesis abstract

Land-use change and intensification have a substantial impact on tropical mountain ecosystems worldwide. However, our understanding of how anthropogenic changes affect different facets of tree diversity and community composition as well as ecosystem functioning along elevational gradients remains limited. Therefore, the main objective of my doctoral dissertation was to examine how interactive effects of elevation and forest-use intensity impact tree species diversity, community composition, functional diversity, functional redundancy and forest structure patterns along an elevational gradient. To do that, I used a sampling design in which elevation was crossed with three different levels of forest-use intensity: old-growth, degraded and secondary forest. I developed my research in an elevational gradient located within a global biodiversity hotspot in central Veracruz, Mexico, covering from sea level to tree line.

In chapter 1, I assessed how the interactive effect of elevation and forest-use intensity affects tree diversity patterns and community composition. In general, my results showed that interactive effects of elevation and forest-use intensity strongly alter tree diversity patterns and community structure along the elevational gradient. My findings revealed that degraded forests were similar to old-growth forests, in terms of species diversity and composition, suggesting that degraded forest represent important reservoirs of species and may act as a safeguard of tree diversity in human-dominated tropical landscapes.

In chapter 2, I investigated how the interactive effects of land-use intensity and elevation impact functional diversity and redundancy of tropical forests, and their implications in term of forest biomass and structure. To the best of my knowledge, the response of functional redundancy along a tropical elevational gradient has not been investigated before. Overall, my results revealed that functional diversity and functional redundancy varied greatly with elevation, but within elevations these two different facets of biodiversity were largely similar across levels of forest-use intensity. Lowland and pre-montane forests had highly redundant and functionally diverse tree communities, suggesting that these forest ecosystems are likely to be resilient to future disturbances. Montane forests,

however, were functionally less redundant, suggesting that they could be highly affected by land-use and climate change.

In chapter 3, I compiled a novel tree database named BIOVERA-Tree: tree diversity, community composition, forest structure and functional traits along gradients of forest-use intensity and elevation in Veracruz, México. BIOVERA-Tree contains information of 215 tree species distributed in 80 families and 154 genera, BIOVERA-Tree includes on tree diversity abundance, community composition, forest structure, and functional eight traits. My database is a fundamental resource providing detailed ecological information on tropical mountain forest ecosystems.

In conclusion, the findings of my doctoral dissertation represent a paramount contribution providing new insights into how the interactive effects between elevation and forest-use intensity affect different facets of tree diversity, tree community composition and forest structure in tropical mountains. Understanding these interactive effects have implications in term of ecosystem resilience of tree communities as well as conservation strategies of tropical mountain forests.

Author contributions

Chapter 1

Response of tree diversity and community composition to forest-use intensity along a tropical elevational gradient

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MLM-G, HK and TK conceived the study, MLM-G, AH-S and GC-C collected data; MLM-G,D.C and NG-R analysed the data; MLM-G wrote the paper with contributions from HK,DC, NG-R, VG-J and TK; all the authors discussed the results and commented on the manuscript.

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Chapter 2

Interactive effects of land-use intensity and elevation reduce functional redundancy of tropical tree communities

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M.L.M-G, H.K., and T.K. conceived the study; M.L.M-G collected data; M.L.M-G, D.C., and N.G-R. analyzed the data; M.L.M-G wrote the paper with contributions from all authors.

Manuscript under review at *Journal of Applied Ecology*.

Chapter 3

BIOVERA-Tree: tree diversity, community composition, forest structure and functional traits along gradients of forest-use intensity and elevation in Veracruz, Mexico.

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M.L.M-G, H.K., and T.K conceived the study; M.L.M-G collected data; P.W., D.C and N.G-R. contributed to data management and designed the database, M.L.M-G wrote the paper with contributions from H.K., P.W., N.G-R., G.C-C. and D.C. All the authors commented on the manuscript.

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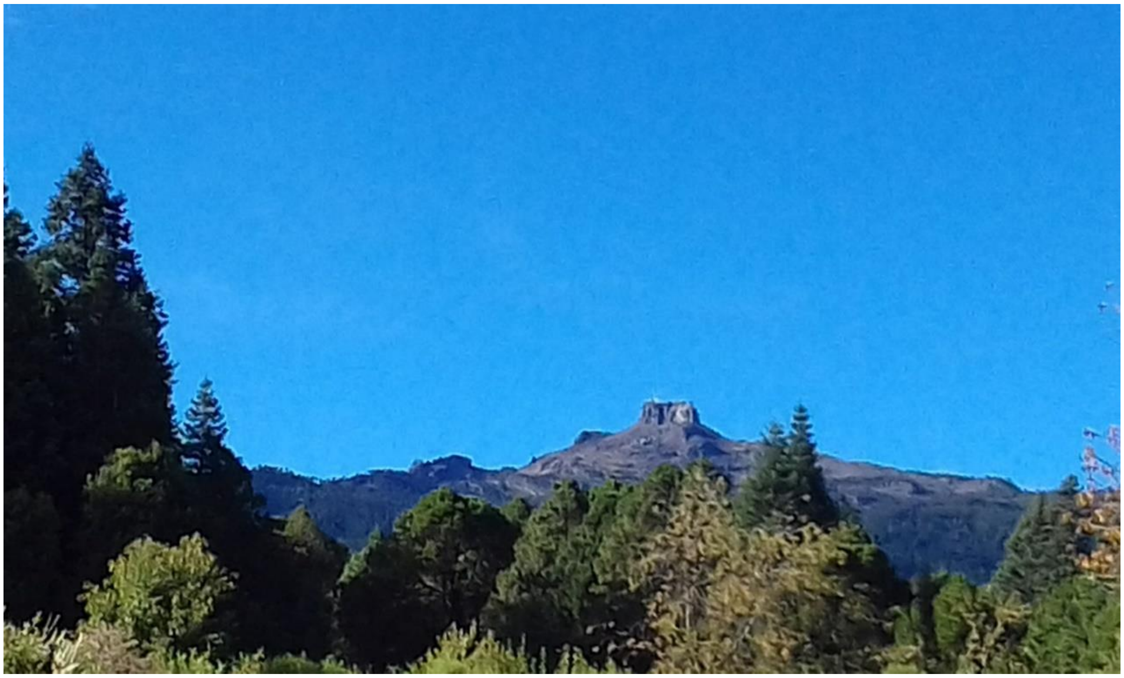

Cofre de Perote mountain, Central Veracruz (Mexico).

General introduction

Tropical mountains as important ecosystems

Tropical mountains are fascinating ecosystems as they are considered natural laboratories for evolutionary and ecological research as they encompass a variety of different climatic conditions, geology, and topography histories over short distances (Körner 2004; Malhi et al. 2010; Rahbek, Borregaard, Colwell, et al. 2019). Unsurprisingly, mountains have captivated scientists since Alexander von Humboldt's (1806) seminal research in the Neotropics, and they still contribute to our understanding of how environmental conditions affect plant diversity patterns, or how diversity may be impacted by land-use change (Körner 2004; Malhi et al. 2010; McCain & Grytnes 2010; Morueta-Holme et al. 2016; Perrigo et al. 2020).

High biodiversity in tropical mountains regions is associated with environmental heterogeneity, orography and elevational gradients that heavily influence climatic conditions (Currie 1991; Kerr & Packer 1997; Fjeldså et al. 2012). These climatic gradients, characterized by a decrease in temperature and air pressure with increasing elevation, are especially strong in the tropics (McCain & Grytnes 2010). Mountains also obstruct atmospheric circulation patterns; prevailing winds cause increased air and precipitation on the slopes on the windward side of a mountain followed by a rain shadow on the lee side. This change affects the taxonomic composition and vegetation types along slopes (Antonelli et al. 2018). These processes have resulted in tropical mountain regions that are cradles for species origination and diversification, but that are also museums maintaining remnant populations and graves with high rates of extinction (Myers et al. 2000; Rahbek, Borregaard, Antonelli, et al. 2019).

Mountains cover 24% of the earth's surface and account for 32% of the world's protected areas, with 10% of the world's population living in tropical mountains (Körner 2004; Kohler et al. 2010). These areas provide vital ecosystem services from biodiversity over water regulation to carbon sequestration, benefitting the human population. Appropriate management and conservation of tropical mountain ecosystems are hence crucial for humankind (Malhi et al. 2010; Kohler et al. 2010; Kidane et al. 2012). However, tropical mountains are the most threatened ecosystems by climate change as well as land-use change and intensification (Payne et al. 2017). In this context, ecological mountain research elucidates how environmental and biophysical factors influence the diversity and distribution of species as well as their community structure, in areas that are important for conservation.

Tree diversity patterns along tropical elevational gradients

Species richness distribution patterns along elevational gradients exhibit different curves (Fig. 1.0). Each pattern can be described as follows; A) monotonic pattern show that species richness decreases with increasing elevation, B) low-plateau pattern has the highest species richness at the lower portion of the mountain and afterwards decreasing species richness monotonically, and C) hump-shape pattern shows a peak in richness at intermediate elevations and declines towards both ends of the elevational gradient (McCain & Grytnes 2010)

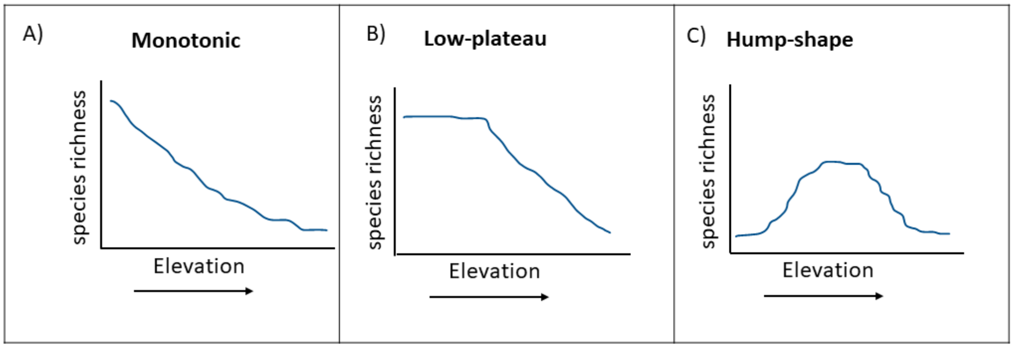

Figure 1.0. Schematic diagram illustrating species richness patterns along elevational gradients. A) monotonic, B) low-plateau, and C) hump-shape.

For tropical tree communities, previous studies showed a monotonically decreasing with increasing elevation (Slik et al. 2009; Homeier et al. 2010; Toledo-Garibaldi & Williams-Linera 2014). The potential drivers that explain this pattern are related to climate, the mosaic of edaphically different habitats, less area with increasing elevation, hostile soils in highlands, and physical and chemical soil properties e.g. C: N ratio, pH, moisture storage capacity and top soil base saturation (Slik et al. 2009; Homeier et al. 2010; Toledo-Garibaldi & Williams-Linera 2014). Other studies report a hump-shaped pattern with a peak at mid-elevations (Zhang et al. 2013; Rutten et al. 2015). The shape of this pattern is driven by environmental factors, for example litter thickness, slope, climate, and land-use change (Zhang et al. 2013; Rutten et al. 2015).

Interactive effects of land-use intensity and elevation on functional diversity, functional redundancy, and forest structure of tropical tree communities

Land-use change and intensification alter forest structure and plant community composition, thereby impacting tropical mountain ecosystem functions (Peters et al. 2019; Monge-González et al. 2020). The impact of land-use type and increasing forest-use intensity on functional diversity and redundancy may change along elevational gradients in relation to climate, which varies with elevation (Laliberté et al. 2010; Peters et al. 2019). Functional diversity is defined as the value and range of functional traits of an organism in an assemblage (Díaz & Cabido 2001). A high functional diversity is essential to ensure a high level of ecosystem functioning in plant communities. Functional redundancy is defined as a group of species that perform similar functions (Naeem 1998; Ricotta et al. 2016). Redundancy is an important property of community ecosystem functioning, as a high redundancy maintains ecosystem processes and stability. For example in case of disturbances, redundant species provide ecological resilience (Yachi & Loreau 1999).

Tree functional diversity along tropical elevational gradients often peaks at mid-elevations (Zhang et al. 2014), or decreases monotonically with increasing elevation (Wieczynski et al. 2019; Thakur & Chawla 2019). Tree functional diversity and redundancy patterns along elevational gradients are thought to be driven by environmental filtering and climate. The environmental filtering hypothesis predicts that the abiotic environment selects species that can tolerate specified conditions, thereby favoring species with similar functional traits (Keddy 1992; Bagousse-Pinguet et al. 2017).

Aboveground tree biomass and basal area patterns also vary along elevational gradients. Homeier et al. (2010) found a monotonically decreasing basal area pattern in Ecuador, the principal drivers that explains low basal area of tree communities at higher elevations were low temperatures, and hostile soil properties. In contrast, Toledo-Garibaldi & Williams-Linera (2014) found that basal area increased monotonically in Mexico. This pattern is thought to be driven by the high levels of humidity and precipitation at high elevations. Ensslin et al. (2015), reported a mid-elevational peak pattern for tree above ground biomass in Tanzania, which was strongly correlated with a peak in precipitation at mid-elevation.

Human activities also shape tree biomass and basal area gradients on tropical mountains: agriculture, timber extraction or cattle grazing strongly impact forest structure, biomass, and ecosystem functioning (Chapin et al. 2000; Payne et al. 2017). Previous studies revealed that intermediate land-use intensity increases forest biomass (Marín-Spiotta et al. 2007) whereas high land-use intensity reduces tree biomass and stem density (Ensslin et al. 2015). However, our understanding of the interactive effect of elevation and forest-use intensity on forest structure is very limited.

Importance of diversity data compilation and data sharing in tropical mountain ecosystems

Data sharing makes data accessible to other researchers and allows investigators to re-use data from previous studies to answer new research questions and fill gaps in science (Michener 2015). Data contribute to ecological research and may also be beneficial for decision making in the context of natural resource management and conservation in tropical mountain ecosystems (Slik et al. 2009; Michener 2015). Here, alarming deforestation rates and ubiquitous land-use change, have already altered tree diversity and community composition along tropical elevational gradients. To document these changes, the compilation, integration, and use of diversity data collected in the field (e.g. tree diversity inventories) provide key ecological information on the current state of tropical forests. Ecological data in the form of tree diversity databases that describe the distribution and abundance of species along with functional traits along elevational and land-use intensity gradients can hence provide an important baseline for generations to come.

Study outline

In this thesis, I examined how the interaction effect of elevation and forest-use intensity affects different facets of tree diversity, community composition, and forest structure along an elevational gradient from sea level to tree line within a global biodiversity hotspot in central Veracruz, Mexico. This thesis is divided into three chapters. The first chapter focuses on species diversity, community composition. The second chapter focuses on functional diversity and redundancy, forest structure. The third chapter describes a database containing the data used in chapters one and two.

In chapter 1, I assessed the response of tree diversity and community composition to forest-use intensity along an elevational gradient. Tree diversity showed a low-plateau pattern for old-growth and a bimodal pattern for degraded and secondary forests. My results revealed that the interaction between elevation and forest-use intensity affected tree diversity as well as community composition. The effects of forest-use intensity on tree diversity were not consistent along the elevational gradient, with tree diversity decreasing significantly in secondary compared to old-growth forests at only three elevations (0, 500, and 1500 m). Degraded forests were very similar to old-growth forests in terms of diversity and species composition, suggesting that degraded forests represent important reservoirs of species and may act as a safeguard for tree diversity. In conclusion, the interactive effects between land-use and how forest-use intensity alter diversity patterns of tree communities.

In chapter 2, I examined how functional diversity, functional redundancy, and forest biomass and structure change along an elevational gradient from the tropical lowlands to near the tree line. My findings revealed that interactive effects between elevation and forest-use intensity significantly affected functional diversity and redundancy. Overall, one main finding in this thesis was high functional diversity and redundancy from lowland to pre-montane tree communities, suggesting that tree communities from sea level to 2000 m are more resilient against future human disturbances than tree communities at higher elevations. Specifically, functional diversity and redundancy to exhibit a low-plateau pattern in old-growth forests and a bimodal pattern in degraded forests, whereas secondary forests showed a hump-shaped pattern for functional diversity and a bimodal pattern for functional redundancy. One finding in this study was positive relationships between biomass and stem density, with functional diversity and redundancy. Yet, these relationships were not consistent along the elevational gradient, suggesting that multiple approaches are needed for conserving both biodiversity and ecosystem functioning in tropical mountain ecosystems.

In chapter 3, I assembled the BIOVERA-Tree database. I compiled a database that provides detailed information on tree diversity, community composition, forest structure, and functional traits of tropical tree communities along crossed elevation and forest-use intensity gradients. BIOVERA-Tree includes information for 4548 tree individuals with a diameter at breast height ≥ 5 cm belonging to 215 species, 154 genera, and 80 families and measurements of eight functional traits, namely wood density (n = 159 species), maximum height (n = 216 species), specific leaf area, leaf dry matter content, Leaf thickness, lamina density, chlorophyll content, and leaf area (n = 156 species). BIOVERA-Tree is a new database that contributes to the understanding of how interactive effects of forest-use intensity and elevation affect tree diversity, community composition and functional traits in tropical forests. By releasing BIOVERA-Tree to the public, I make the data available to researchers today and in the future.

Chapter 1:

Response of tree diversity and community composition to forest-use intensity along a tropical elevational gradient

Pine forest at 3000 m elevation, Cofre de Perote mountain, Central Veracruz (Mexico).

1 Response of tree diversity and community composition to forest-use intensity along a tropical elevational gradient

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1.1 Abstract

Question:

Land-use change and intensification are currently the most pervasive threats to tropical biodiversity. Yet, their effects on biodiversity change with elevation is unknown. Here we examine how tree diversity and community composition vary with elevation and how the effects of forest-use intensity on tree diversity and community composition change within elevations.

Location: Eastern slopes of the Cofre de Perote mountain, state of Veracruz, Mexico.

Methods:

We assessed tree diversity and composition using a sampling design in which elevation was crossed with three levels of forest-use intensity: old-growth, degraded, and secondary forests. We established 120 20 x 20 m forest plots, located at eight sites between 0 and 3545 m. At each site, five replicate plots were inventoried for each level of forest-use intensity.

Results:

Our analyses revealed an interactive effect between elevation and forest-use intensity affecting tree diversity and community composition along the elevational gradient. Contrasting effects of forest-use intensity within elevation resulted in tree diversity following a low-plateau pattern for old-growth and a bimodal pattern for degraded and secondary forests. Along the entire elevational gradient, 217 tree species distributed within 154 genera and 80 families. Species accumulation curves revealed that forests at 0 and 1500 m elevation showed differences in species richness among forest-use intensities. In contrast, species richness did not differ between old-growth forest and the other forest-use intensities in five of the eight studied elevations. In terms of community composition, secondary forests differed from old-growth and degraded forests.

Conclusion:

Our results suggest that the interactive effects of elevation and forest-use intensity change tree diversity patterns and community composition along a tropical elevational gradient. Degraded forests were similar to old-growth forests in terms of species diversity and composition, suggesting that they may act as a safeguard of tree diversity in human-dominated tropical landscapes.

Keywords: Degraded forest, Elevational gradient, Land-use, Mexico, Old-growth forest, Secondary forest, Tropical montane forest.

1.2 Introduction

Tropical mountains are characterized by steep gradients in climate and other environmental conditions that lead to rapid changes in diversity and species composition with elevation. Globally, tropical mountains are centers of plant diversity and endemism (Barthlott et al. 2005; Kier et al. 2009) resulting from the high environmental heterogeneity that affects both ecological and evolutionary processes (Stein et al. 2014; Antonelli et al. 2018). Tropical elevational gradients are considered as natural laboratories where drivers of diversity patterns and ecosystem functions can be studied over short geographical distances (Sanders & Rahbek 2012; Körner et al. 2017). However, tropical mountain ecosystems are also highly vulnerable to land use (Malhi et al. 2010; Kidane et al. 2012) and climate change (Cuesta et al. 2017), yet our understanding of how anthropogenic change may affect plant diversity and community composition along elevational gradients remains limited (Peters et al. 2019).

In tropical mountain ecosystems, tree diversity often peaks at mid-elevations (Huerta Martínez et al. 2014; Toledo-Garibaldi & Williams-Linera 2014; Clark et al. 2015; Rutten et al. 2015) or decreases monotonically from the lowlands with increasing elevation (Aiba & Kitayama 1999; Slik et al. 2009; Homeier et al. 2010). Explanations of elevational gradients in tree diversity have focused principally on temperature and precipitation, soil nutrient concentrations, mixing of biotas, spatial constraints associated with area and mid-domain effects, and – to a lesser extent - anthropogenic disturbances (Slik et al. 2009; Homeier et al. 2010; Zhang et al. 2013; Toledo-Garibaldi & Williams-Linera 2014; Rana et al. 2019; Peters et al. 2019). The effect of land-use type and intensity on species richness and composition might change along elevational gradients (McCain & Grytnes 2010), as it might be amplified or weakened by climate that changes with elevation (Peters et al. 2019). For example, if the impact of land-use on diversity is higher at lower elevations than at higher elevations, species richness patterns could shift from monotonic to hump-shaped. Conversely, if the impact of land-use on diversity is stronger at mid-elevations than at lower ones, species richness patterns could change from hump-shaped to monotonic.

Forest-use intensity, hereon defined as the conversion of (near-) natural, complex structured forest ecosystems to simplified, managed ecosystems with more frequent resource use or extraction (Nepstad et al. 1996; Vitousek et al. 1997; Tscharntke et al. 2005), may also influence the composition of forest communities by altering environmental conditions. In tropical forest ecosystems, highly intensive forest uses, such as cattle grazing and agroforestry, increase light availability and air temperature, reduce air humidity, soil moisture and have negative effects on propagule dispersion (Holl 1999; Lebrija-Trejos et al. 2011). High forest-use intensity may shift tree species composition to forests dominated by species better adapted to tolerate such conditions, e.g. fast-growing and light-demanding pioneer species, whereas more shade-tolerant late successional species are often unable to persist (Lohbeck et al. 2013; Craven et al. 2015). As a result of high-intensity forest use, light conditions increase and favor the establishment of early successional tree species. Therefore, floristic composition - and to a lesser extent species richness - of young secondary and degraded forests usually differs markedly from that of old-growth tropical forests (Gossner et al. 2013; Rozendaal et al. 2019). Yet, how such changes in species compositions are mediated by climatic changes along elevational gradients is largely unknown (but see Peters et al. 2019).

Human impacts on tropical mountain forests, such as logging and deforestation for agriculture, have transformed large parts of these ecosystems into human-dominated forested landscapes (Laurance et al. 2014). Globally, the direction and magnitude of changes in species richness depend strongly on the kind, intensity, severity, incidence, and timing of disturbances (Foley et al. 2005; Gibson et al. 2011; Newbold et al. 2015; Barlow et al. 2018). Yet, we know little about the impacts of forest-use intensity on tree diversity and composition along environmental gradients, particularly elevational gradients in tropical forests. While it is likely that these impacts will shift because tree communities differ in their resilience to similar forest uses (Crouzeilles et al. 2016), there is no *a priori* expectation whether the impacts will be stronger, weaker, or similar with changes in elevation.

Here, we examined how the interaction of elevation and forest-use intensity affects tree diversity and community composition along an elevation gradient from sea level to treeline within a global biodiversity hotspot in central Veracruz, Mexico. Specifically, we asked: i) How do tree diversity and community composition vary with elevation? and ii) How do the effects of forest-use intensity on tree diversity and community composition change within elevational sites? We hypothesized that tree diversity monotonically decreases with increasing elevation (Aiba & Kitayama 1999; Slik et al. 2009; Homeier et al. 2010; Toledo-Garibaldi & Williams-Linera 2014) , that high forest-use intensity at lower elevations may shift species richness from monotonic to hump-shaped pattern (McCain & Grytnes 2010) and expected a consistently negative effect of forest-use intensity on tree diversity and associated shifts in tree species composition (Gibson et al. 2011; Newbold et al. 2015).

1.3 Methods

1.3.1 Study area

Our study was conducted along an elevational gradient, from sea level close to the Gulf of Mexico (19.5894 N, -96.375167 W) to close to the treeline at 3545 m elevation (19.5182 N, -97.154525 W) along the eastern slopes of Cofre de Perote, an extinct volcano of 4282 m in Veracruz, Mexico (Carvajal-Hernández & Krömer 2015; Gómez-Díaz et al. 2017) (Fig. 1.1). Climatic conditions along the elevational gradient vary from tropical-dry at lower elevations, to temperate-humid at mid-elevations and cold-dry at high elevations (Soto-Esparza & Giddings-Berger 2011; Gómez-Díaz et al. 2017) . Temperature decreases with elevation, with mean annual temperature ranging from 26 °C near sea level to 9 °C at the highest site. Mean annual precipitation varies from 1222 mm at low elevations, 2952 mm at mid-elevations and 708 mm at high elevations (Table 1.1).

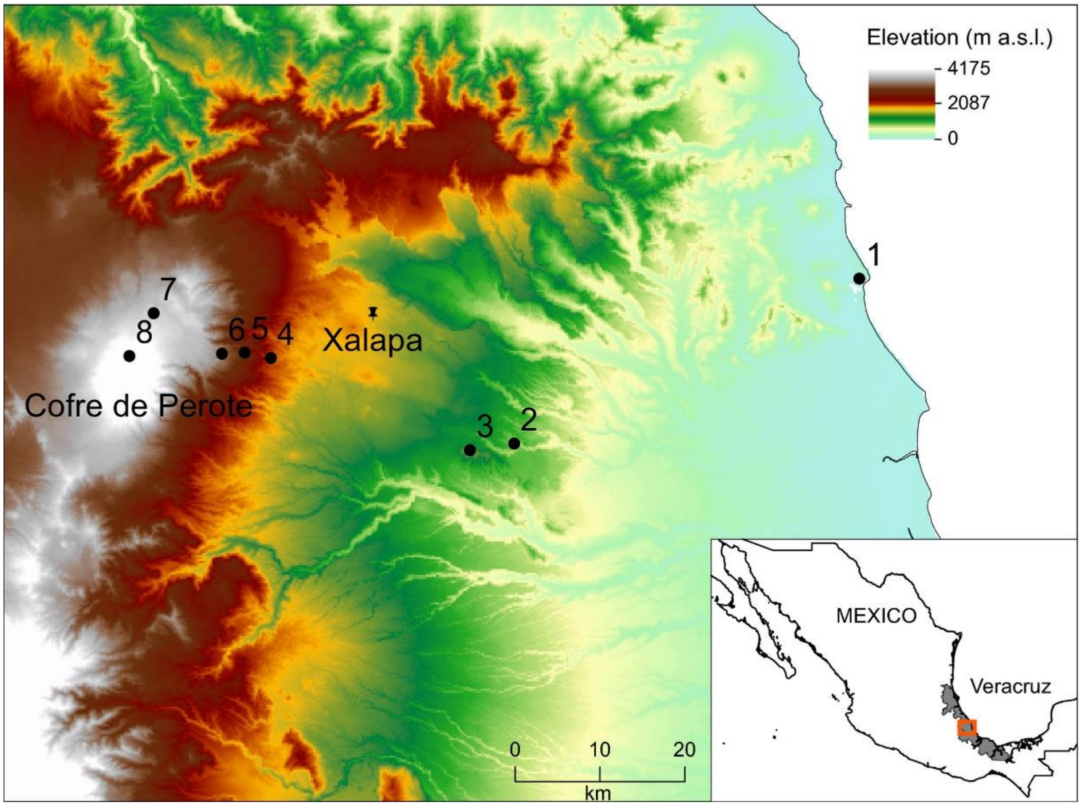

Figure 1.1. Location of the eight study sites along the elevational gradient at the eastern slopes of Cofre de Perote in Veracruz, Mexico. Black dots show the location of sites along the elevational gradient 1. 0 m; 2. 500 m; 3. 1000 m; 4. 1500 m; 5. 2000 m; 6. 2500 m; 7. 3000 m; 8. 3500 m.

The study area is located in the transition zone between two biogeographic regions, the Neotropical and Nearctic, in the Mesoamerica biodiversity hotspot (Myers et al. 2000; Morrone 2006). Biogeographically, the upper part of the elevational gradient falls into the convergence zone between the Trans-Mexican Volcanic Belt and the Sierra Madre Oriental (Rodríguez et al. 2010). Along the elevation gradient, there are six main vegetation types including tropical semi-humid deciduous, tropical oak, humid montane, pine-oak, pine, and fir forests (Table 1.1; Leopold 1950).

Table 1.1. Location and climatic conditions of the eight study sites in central Veracruz, Mexico. Vegetation types according to Leopold (1950), mean annual temperature (MAT; °C), mean annual precipitation (MAP; mm/a). Climate data were obtained from National Meteorological Service of México (SMN 2019) for 1951-2010.

Site	Elevation (m)	N Latitude	W Longitude	MAT (°C)	MAP (mm/a)	Vegetation type
1	0-60	19.58	-96.37	26	1222	Tropical semi-humid deciduous forest
2	569-695	19.54	-96.89	23	946	Tropical oak forest
3	913-1023	19.42	-96.79	21	1331	Tropical oak forest
4	1501-1650	19.52	-96.98	19	1436	Humid montane forest
5	2008-2240	19.51	-97.03	14	2952	Humid montane forest
6	2487-2575	19.52	-97.05	12	1104	Pine-oak forest
7	3014-3139	19.56	-97.13	9	708	Pine forest
8	3305-3545	19.51	-97.15	9	708	Fir forest

1.3.2 Study design and data collection

The study was conducted at eight sites along the elevational gradient, separated by about 500 m in elevation (Fig. 1.1). Hereafter, we refer to every elevation as 0, 500, 1000, 1500, 2000, 2500, 3000, and 3500 m. At each site, we established 15 plots of 20 x 20 m, including five plots each in old-growth, degraded, and secondary forests. In total, 120 non-permanent forest plots (4.8 ha) were inventoried. Forest-use intensity was defined following Leuschner et al. (2006), Carvajal-Hernández & Krömer (2015) and Gómez-Díaz et al. (2017): i) old-growth forest (OF): a mature forest with tall, large diameter trees and without any visible signs of recent human disturbance, classified as low forest-use intensity; ii) degraded forest (DF): a forest subjected to selective logging and / or cattle grazing, classified as intermediate forest-use intensity; iii) secondary forest (SF): a young forest (15 – 20 years since abandonment) recovering after clearcutting, sometimes with cattle grazing, with small diameter trees, classified as high forest-use intensity. In each plot, we measured and identified all trees with a diameter at breast height (DHB) $\geq$ 5 cm (Homeier et al. 2010;

Toledo-Garibaldi & Williams-Linera 2014). In total, 64.5 % of the individuals could be identified to species, 19.3% were identified to genus level, 8.2% to family level and 7.8% were unidentified species see Table A1 tree species list; species names follow The Plant List version 1.1 (2013). Tree species were identified by specialists (Dr. Francisco Lorea Hernández, M. Sc. Claudia Gallardo Hernández and Biol. Carlos M. Durán Espinosa, Instituto de Ecología, A. C.). Vouchers of specimens were deposited at the herbarium XAL of Instituto de Ecología, A.C. at Xalapa, Mexico. The sampling was conducted from November 2015 to August 2016.

1.3.3 Data analysis

Tree diversity

We estimated species diversity as species richness (Hill number, q = 0), Shannon diversity (q = 1), and Simpson diversity (q = 2) in terms of effective species numbers (Jost 2006). These diversity indices give increasing weight to species abundances; while species richness gives equal weight to common and rare species, Shannon and Simpson diversities emphasize the contributions of common and abundant species, respectively. For each diversity index, we estimated species accumulation curves using sample-based rarefaction and extrapolation (Chao et al. 2014), pooling data by forest-use intensity for each elevation. We used rarefaction and extrapolation because the number of individuals may vary systematically with forest-use intensity, which may bias estimates of species diversity in plots with more individuals. As we observed similar patterns for Shannon and Simpson diversities, we only present and discuss results for species richness. At the plot level, we estimated species diversity using a fixed sample coverage of 95% with the 'iNeXT' package (Hsieh et al. 2016) to permit unbiased comparisons of species diversity across forest-use intensities and elevations. To meet model assumptions of normality, we natural-log transformed all diversity indices.

At the plot level, we examined the effect of forest-use intensity at each elevation on species richness and Shannon and Simpson diversities using a nested analysis of variance (ANOVA) using the R function *aov*, where forest-use intensity and elevation were treated as categorical variables. We performed post-hoc comparisons using a Tukey's Honest Significant Differences test with the packages 'car' (Fox & Weisberg 2011) and 'multcomp' (Hothorn et al. 2008).

We examined changes in tree community composition among elevational sites and levels of forest-use intensity using non-metric multidimensional scaling (NMDS) with both incidence-based Jaccard dissimilarity and abundance-based Bray-Curtis dissimilarity (adjustment noshare=0.1; 999 permutations) using the packages *ecodist* (Goslee & Urban

2007) and *vegan* (Oksanen et al. 2019). We then tested for differences in tree community composition across elevations and levels of forest-use intensity using a nested permutational multivariate analysis of variance (PERMANOVA, 999 permutations) using the *adonis* function in vegan package (Oksanen et al. 2019), followed by pairwise comparisons using the *pairwise.adonis* function in the *pairwiseAdonis* package. The *p*- values for the pairwise comparisons were Bonferroni corrected to tested differences in species composition among levels of forest-use intensity within elevation. For data manipulation and visualization, we used the R packages '*dplyr'* (Wickham et al. 2019) and '*ggplot2'* (Wickham 2009), respectively. We performed all analyses in R version 3.5.1 (R Core Team 2018).

1.4 Results

1.4.1 Changes in tree diversity along the elevation gradient

We recorded a total of 4555 individual trees belonging to 217 species distributed among 80 families and 154 genera (Table A1). The most diverse families were Fagaceae (15 species), Leguminosae (13), Moraceae (10), and Pinaceae (8). At lower elevations (below 1000 m), tropical genera such as *Ficus*, *Acacia,* and *Bursera* were the most abundant, while at mid-elevations *Quercus*, *Carpinus,* and *Liquidambar* and at 2500 m (transitional pine-oak forest) *Pinus*, *Quercus,* and *Juniperus* were the most common. At higher elevations (3000-3500 m), the most abundant genera were *Abies*, *Pinus,* and *Alnus*. Across all elevations, 18 % of all species exclusively occurred in old-growth forest followed by 16 % in secondary forest, and 9 % in degraded forest.

At most elevations (500, 1000, 2000, 3000 and 3500 m) species accumulation curves overlapped across forest-use intensities, revealing that species pools in degraded and secondary forests were of similar size (indicated by overlapping 95% confidence intervals) as those of with old-growth forests (Fig. 1.2). In contrast, at 0 and 1500 m species accumulation curves showed significant differences in species richness between forest-use intensities (95 % confidence intervals did not overlap). Species accumulation curves at 2500 m showed that tree species richness in degraded forests was higher than species richness of old-growth forests (Fig. 1.2). For most levels of forest-use intensity, species accumulation curves did not reach an asymptote at elevations between 0 to 2500 m (except for secondary forests at 0 m). At 3000 and 3500 m, species accumulation curves for all levels of forest-use intensity reached an asymptote, indicating that these forests have been fully sampled (Fig. 1.2).

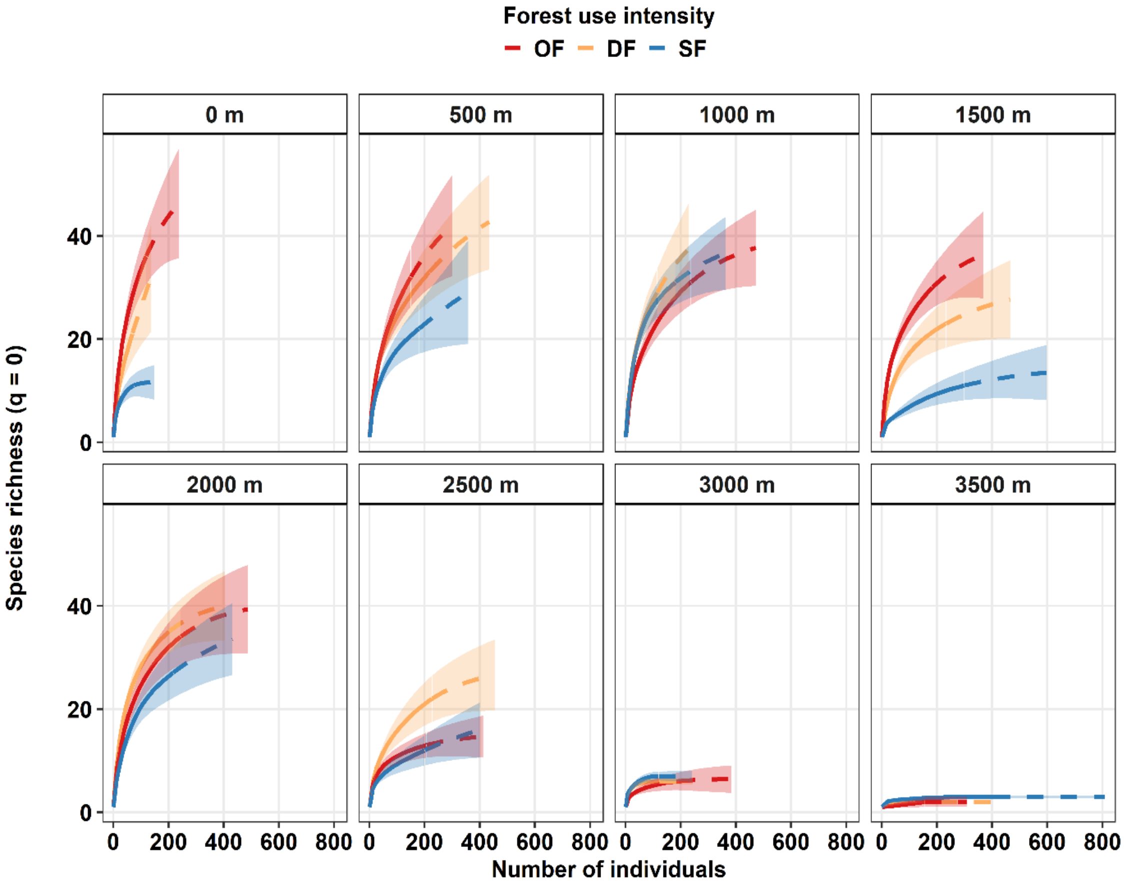

Figure 1.2. Rarefaction (solid lines) and extrapolated (dashed lines) curves for species richness (Hill number = 0, pooling data by forest-use intensity within each elevation). The 95 % confidence intervals (shaded areas). Forest-use intensity levels are: old-growth forest (OF, red), degraded forest (DF, yellow) and secondary forest (SF, blue).

1.4.2 Effects of forest-use intensity on local tree species diversity along the elevation gradient

Elevation significantly affected plot-level tree species richness (Hill number = 0; $F_{7,96} = 57.02$, *p*-value <0.001), Shannon diversity (Hill number = 1; $F_{7,96} = 49.44$, *p*-value <0.001) and Simpson diversity (Hill number =2; $F_{7,96} = 37.74$, p-value <0.001, Appendix A 2: Table A2). Within elevations, tree diversity varied significantly among forest-use intensity levels ($F_{16,96}$ = 4.38 for species richness, $F_{16,97} = 5.47$ for Shannon diversity and, $F_{16,96} = 4.91$ for Simpson diversity, *p*-value <0.001; Appendix A 2: Table A2). Pairwise comparisons among forest-use intensity levels within elevation showed significant differences in tree species richness between old-growth and secondary forests at 0, 500, 1500 and 3500 m (*p*-value <0.05;

Appendix A 2: Table A2, Fig. 1.3). While these differences were associated with higher species richness in old-growth forests than in secondary forests at 0, 500 and 1500 m, the inverse pattern was observed at 3500 m, i.e., higher species richness in secondary forests than in old-growth forests. Similarly, we found significant differences in tree species richness between degraded and secondary forests at 1500, 2500 and 3500 m (p-value < 0.05; Appendix A 2: Table A2), with higher tree species richness in degraded than in secondary forests at 1500 and 2500 m but the inverse trend at 3500 m.

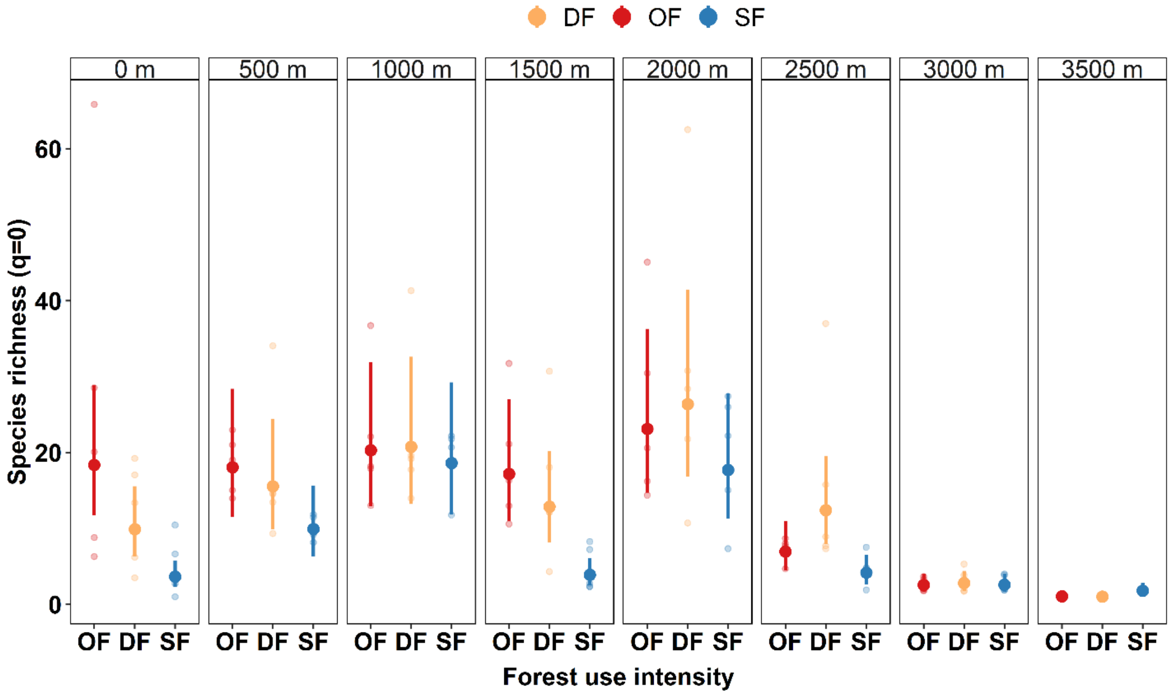

Figure 1.3. Tree species richness (Hill number = 0) along the elevation gradient and different levels of forest use intensity (n = 120 plots). Tree species richness was significantly affected by elevation ($F_{7,96}$ = 57.02, p-value < 0.001) and forest-use intensity within elevation ($F_{16, 96}$ = 4.38, p-value <0.001; Supplementary Table A 2). Bold points are predicted means from the nested ANOVA (lines are 95 % confidence intervals). Light points are plot-level values. Forest-use intensity levels are old-growth forest (OF), degraded forest (DF) and secondary forest (SF).

In old-growth forests, tree species richness along the elevational gradient was best described as a low-plateau pattern, where species richness was highest from 0 m to 2000 m after which it decreased monotonically (Fig. 1.3). Tree species richness in degraded and secondary forests showed a bimodal pattern with peaks at 1000 m and 2000 m and declines towards both ends of the elevational gradient (Fig. 1.3). Similar patterns were observed for Shannon and Simpson diversities (Appendix A: Figs. A1 and A2).

1.4.3 Tree community composition among gradients of forest-use intensity and elevation

We found that tree community composition varied significantly along the elevational gradient (PERMANOVA $F_{7,96} = 8.69$, $R^2 = 0.30$, p-value <0.001 and $F_{7,96} = 14.94$, $R^2 = 0.40$, p-value <0.001 based on Jaccard and Bray-Curtis dissimilarity, respectively; Appendix A 2: Tables A4 and A5) and among forest-use intensity levels within elevation (PERMANOVA $F_{16,96} = 2.88$, $R^2 = 0.23$, p-value <0.001 and $F_{16,96} = 3.82$, $R^2 = 0.23$, p-value <0.001 based on Jaccard and Bray-Curtis dissimilarity, respectively; Appendix A 2: Tables A6 and A7). Within elevations, floristic composition differed significantly between old-growth forest and secondary forest (p-value adjusted <0.05), except at 2500 m (Appendix A 2: Tables A6 and A7, Figs. 1.4 and A3). In contrast, within elevations, floristic composition only varied significantly between old-growth and degraded forests at 500, 1000 and 1500 m based on Jaccard dissimilarity and at 1000 and 1500 m based on Bray-Curtis dissimilarity (p-value adjusted <0.05; Appendix A 2: Tables A6 and A7). At these elevations, floristic composition differed significantly among old-growth, degraded and secondary forests (pairwise comparisons within elevation, p-value adjusted <0.05; Appendix A2: Tables A6 and A7, Figs. 1.4 and A 3). Tree community composition varied between degraded and secondary forests in most elevations except at 2000 and 3000 m based on Jaccard dissimilarity and at 500, 2000, and 3000 m based on Bray-Curtis dissimilarity (Appendix A 2: Tables A6 and A7).

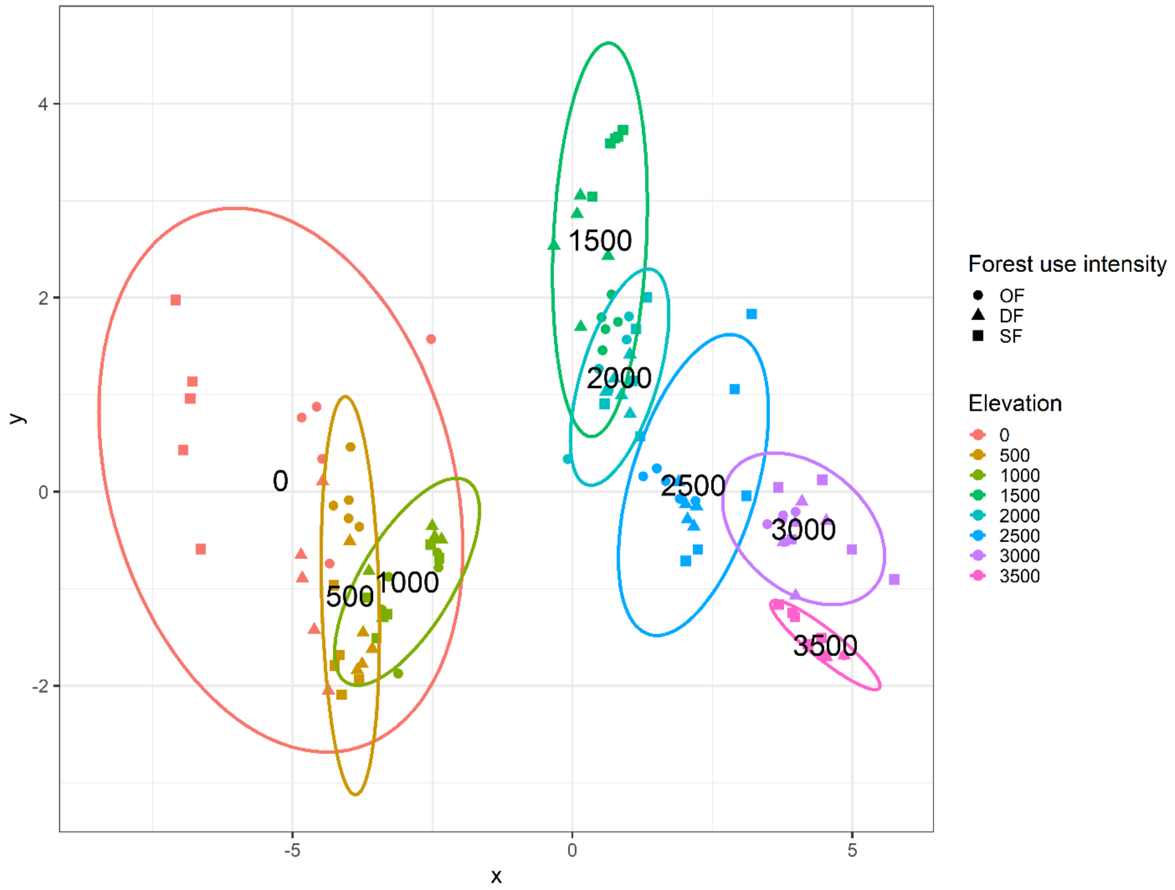

Figure 1.4. Tree community composition along eight elevational sites and three different forest-use intensity levels. Non-metric multidimensional scaling (NMDS) based on Jaccard dissimilarity (n = 5 plots per forest-use intensity within elevation), ellipses show the range of each elevation site. Forest-use intensity levels are old-growth forest (OF, circles), degraded forest (DF, triangles) and secondary forest (SF, squares).

1.5 Discussion

Our results revealed that the interaction between elevation and forest-use intensity affected tree diversity, i.e. species richness, Shannon and Simpson diversity as well as community composition. Importantly, we found that the effects of forest-use intensity on tree diversity were not consistent along the elevational gradient, with tree diversity decreasing significantly in secondary compared with old-growth forests at only three elevations (0, 500 and 1500 m). Together, our results suggest that the direction and magnitude of the effects of anthropogenic forest disturbance on tree diversity in tropical forests are context dependent and will be difficult to generalize more broadly.

1.5.1 Forest-use intensity affects tree diversity along the elevational gradient

Forest-use intensity affected tree diversity, and we found significant interactive effects of forest-use intensity and elevation on diversity and species composition. While our analyses revealed that an increase in forest-use intensity may result in a decrease of tree diversity, this pattern was not consistent along the elevational gradient. Anthropogenic forest use is generally thought to reduce species richness in tropical forest landscapes (Ramírez-Marcial et al. 2001; Kessler et al. 2009; Williams-Linera & Lorea 2009; Gibson et al. 2011). Yet the effects of land-use change are context dependent and depend on the timing, frequency, type and intensity of disturbances (Ramírez-Marcial et al. 2001; Carreño-Rocabado et al. 2012; Newbold et al. 2015), factors which likely varied along the elevational gradient in this study.

Old-growth and degraded forests exhibited similar plot-level species diversity at all elevations, a pattern that is consistent with previous studies (Zhang et al. 2013; Rutten et al. 2015) and that suggests that high local-scale diversity can be maintained under moderate levels of disturbance. Furthermore, these results suggest that degraded forests may act as reservoirs of native tree diversity and, thus, play an important role in the conservation of diverse tropical forests (Chazdon et al. 2009; Rozendaal et al. 2019). A potential explanation of the observed pattern is that low or medium forest-use intensities or the creation of gaps in the forest canopy may create new habitats that favor the establishment of fast-growing and light-demanding tree species (Ramírez-Marcial et al. 2001; Zhang et al. 2013) or may facilitate the growth of advanced regeneration of shade tolerant species into larger size classes (Brokaw 1985; Denslow 1987). However, forests subjected to frequent disturbances may be vulnerable to biological invasions in the future (Alpert et al. 2000), although we did not detect the presence of any non-native woody species in our inventory. On the other hand, we found that secondary forests had lower tree diversity compared to old-growth forests at half of the elevational sites. This suggests that high forest-use intensity reduces diversity and that tree communities, particularly old-growth forests, need more time to recover in species composition (Crouzeilles et al. 2016; Gossner et al. 2016; Rozendaal et al. 2019; Peters et al. 2019). Yet the effects of both low and high forest-use intensity, and the subsequently trajectory of recovery, may depend on intrinsic biotic and abiotic conditions within each elevation, e.g. differences in dispersal limitations, distance from adjacent forest, and propagule sources (Holl 1999; Martínez-Garza & González-Montagut 1999; Breugel et al. 2013).

The interactive effects of elevation and forest-use intensity resulted in contrasting tree diversity patterns along the elevational gradient. The low-plateau elevational gradient for tree diversity in old-growth forests gradually changed into a bimodal pattern for degraded and especially secondary forests. These results are broadly in line with a recent multi-taxon study from Mount Kilimanjaro in Tanzania that showed interactive effects of climate and land-use change on diversity trends (Peters et al. 2019). Specifically, in our study, the low plateau pattern in old-growth forest was driven by similar values in species richness between sea-level and 2000 m, above which it decreased strongly towards the treeline. Such an elevational pattern in tree diversity has been described before, although it appears to be uncommon (Jankowski et al. 2013; Rana et al. 2019). The high species diversity between sea-level and 2000 m may be linked to climatic conditions. For instance, tree diversity usually increases with temperature and precipitation (Homeier et al. 2010; Toledo-Garibaldi & Williams-Linera 2014). In this regard, it is interesting that the highest species richness observed in our study occurred in the warm but comparatively dry lowlands (Portillo-Quintero & Sánchez-Azofeifa 2010). However, this observation is in line with previous studies concerning trees along elevational gradients showing that temperature is the primary climatic predictor of tree diversity and stronger than precipitation (Toledo-Garibaldi & Williams-Linera 2014; Sharma et al. 2019). We attribute the sharp decrease in tree diversity above 2000 m mainly to low minimum temperatures and the frequent occurrence of frost (–3° C absolute minimum temperature in winter; C.I. Carvajal-Hernández, unpubl. data; Pereyra et al. 1992; Toledo-Garibaldi & Williams-Linera 2014). These thermal conditions represent strong biophysical constraints that likely limit the occurrence of tropical tree species (Zanne et al. 2014; Veintimilla et al. 2019), which is consistent with patterns reported from the Himalayas by Bhattarai and Vetaas (2006) and Rana et al. (2019). Interestingly, this decrease in tree diversity above 2000 m was also observed for degraded and secondary forests, suggesting a strong role of ecological factors associated with elevation.

1.5.2 Floristic composition along the elevational gradient and forest-use intensity

We found marked differences in tree composition related to forest-use intensity at most elevations, especially between old-growth and secondary forests. This suggests that, at most elevations, high intensity forest-use strongly affected community composition, which supports results from previous studies in Neotropical forests (Norden et al. 2009; Dent et al. 2013). This observed shift in forest composition may be explained by the fact that the time needed to recover species composition may be longer than for species richness (Rozendaal et al. 2019), as strong environmental filtering in tropical secondary forests limits the diversity of adaptive trait combinations (Lebrija-Trejos et al. 2011). For instance, the abiotic conditions in secondary forests typically favor light-demanding, fast-growing species over shade-tolerant, slow-growing species, which are better adapted to abiotic conditions found in old-growth forests (Gómez-Pompa & Vásquez-Yanes 1974; Bazzaz & Pickett 1980; Ewel 1980; Finegan 1984; Swaine & Whitmore 1988; Guariguata & Ostertag 2001; Crouzeilles et al. 2016). Other factors may similarly contribute to the differentiation in species composition of old-growth and secondary forests, such as previous forest-use type and proximity of seed sources (Guariguata & Ostertag 2001; Muñiz-Castro et al. 2006; Zhang et al. 2013; Rozendaal et al. 2019). In contrast, the composition of tree communities did not vary significantly between old-growth and degraded forests within five or six of the eight studied elevations (based on incidence or abundance-based dissimilarities, respectively). This suggests that moderate forest-use intensity in most degraded tropical forests did not appreciably alter abiotic conditions, as many common species (probably shade-tolerant, slow-growing ones) that also occurred in old-growth forests were able to persist in degraded ones. Our finding is in line with that of a previous study on herbaceous species along the same elevational gradient, which also reported similar floristic composition of old-growth and degraded forests (Gómez-Díaz et al. 2017). It is important to note that our study did not consider the possible impacts of forest-use intensity on the tree seedling community, which may capture the impacts of disturbances more readily than the mature tree community (Ramírez-Marcial 2003; Alvarez-Aquino et al. 2004). While forest disturbances of even moderate intensity may result in extinction debts in the long term (Moreno-Mateos et al. 2017), the similar floristic composition of old-growth and degraded forests in most elevations supports the idea that degraded forests may act as important reservoirs of biodiversity in human-modified tropical landscapes.

1.6 Conclusions

We found that forest-use intensity significantly altered tree species diversity and composition, and that this effect was modified by elevation. Our results provide evidence that, even in human-dominated tropical landscapes, degraded and secondary forests may safeguard considerable levels of tree diversity. Due to their greater similarity to old-growth forests, degraded forests may act as reservoirs for biodiversity conservation and restoration. In conclusion, the interactive effects between land-use and elevation render predictions across elevations difficult and highlight the value of examining how forest-use intensity may alter diversity patterns along elevational gradients in tropical forests.

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Chapter 2:

Interactive effects of land-use intensity and elevation reduce functional redundancy of tropical tree communities

“El Zapotal” humid montane forest at 2000 m elevation

2 Interactive effects of land-use intensity and elevation reduce functional redundancy of tropical tree communities

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2.1 Abstract

1. Land-use change and intensification alter tropical mountain ecosystems, influencing diversity and ecosystem functioning. Tree communities with high functional redundancy, i.e. communities in which species are functionally similar, may be more resilient to human disturbances. However, interactive effects of forest-use intensity on functional diversity and redundancy along tropical elevation gradients remain poorly understood.
2. Here, we examined the interactive effects of forest-use intensity and elevation on tree functional diversity and redundancy, and their relationships with forest biomass and structure, along an elevational gradient from the tropical lowlands to near tree line in Mexico. In our sampling design, elevation was crossed with three levels of forest-use intensity: old-growth, degraded, and secondary forests. At eight elevational sites, five replicate plots were inventoried for each level of forest-use intensity (total n = 120 plots). In addition, leaf and wood traits of 144 tree species were measured.
3. Interactive effects between elevation and forest-use intensity significantly affected functional diversity and redundancy. We found high functional diversity from sea level to 2000 m, which declined thereafter for all three forest-use intensities. Across

forest-use intensities, functional redundancy exhibited either a hump-shaped or a bimodal pattern and was lowest at the two highest elevations.

4. We found significant but inconsistent bi-variate relationships of functional diversity and redundancy with tree biomass along the elevational gradient. Further, our results suggest that the ability of high-elevation tropical tree communities to provide vital ecosystem functions may be particularly susceptible to climate change and increasing forest-use intensity.
5. Synthesis and applications. We found high functional diversity and functional redundancy from lowland to premontane tree communities, suggesting that these forest ecosystems can be resilient against future disturbances. Context-dependent bi-variate relationships of functional diversity and redundancy with tree biomass suggest that multiple criteria are needed for conserving forests both biodiversity and ecosystem functioning in tropical mountain ecosystems. Finally, our study shows that macroecological constraints are important to understand the influence of land-use changes on biodiversity and ecosystem functioning relationships.

Keywords: Degraded forest, Ecosystem functioning, Functional traits, Land-use, Mexico, Old-growth forest, Secondary forest, Tropical montane forest

2.2 Introduction

Human activities lead to an alarming loss of biodiversity and alter ecosystem functioning worldwide (Chapin et al. 2000). The implications of biodiversity loss go beyond decreases in species diversity and also include the variation, range, or dispersion of traits, i.e. functional diversity (Díaz & Cabido 2001; Maire et al. 2015). Species with unique traits and functions contribute to functional diversity in an ecosystem and guarantee the integrity of its functioning (Díaz & Cabido 2001). Species that perform similar ecological functions, i.e. functionally redundancy, helps to maintain ecosystem functioning and improve the resilience of ecological communities to global change drivers (Pillar et al. 2013).

Land-use change and increasing forest-use intensity are affecting tropical montane forests around the world by habitat loss, fragmentation (Payne et al. 2017) and by negatively impacting species and functional diversity (Laliberté et al. 2010; Peters et al. 2019). However, land-use intensity may have both positive and negative effects on functional redundancy in tropical forests (Laliberté et al. 2010). Therefore, the response of functional redundancy to forest-use intensity along environmental gradients remains uncertain.

Land-use intensity in the form of timber extraction or cattle grazing is one of the main drivers that modifies forest structure. For instance, high land-use intensity in forests may reduce tree biomass and stem density (Whitfeld et al. 2014; Ensslin et al. 2015), while intermediate land-use intensity may increase biomass (e.g. Marín-Spiotta et al. 2007). Forest structure varies strongly along elevational gradients, and opposing elevational trends in biomass and stem density have been reported ranging from monotonous increases with increasing elevation (e.g. Clark et al. 2015), monotonous decreases with elevation (e.g. Homeier et al. 2010) to unimodal mid-elevation peaks (e.g. Ensslin et al. 2015). A key factor driving changes in forest structure along elevational gradients is climate. Yet, how such changes in forest structure are interactively affect by elevation and land-use intensity is largely unknown.

Tropical mountains encompass, over short distances, diverse climatic, geological, and topographical conditions. Consequently, tropical mountains are natural laboratories to study responses of plant diversity, community composition, and ecosystem functioning in relation to elevation (Körner et al. 2017). One of the principal drivers that explains plant species diversity is the availability of ambient energy and water, which is thought to control the number of individuals (more individuals hypothesis; MIH) thereby influencing species abundances and diversity (Wright 1983; Storch et al. 2018). Consequently, higher elevations with lower energy availability are expected to have smaller tree populations and thus lower diversity than lower, warmer elevations (e.g. Givnish 1999). Together, these (and other) drivers usually generate monotonously decreasing, low-plateau or hump-shaped patterns of tree species diversity along tropical elevation gradients (Rana et al. 2019; Monge-González et al. 2020).

Environmental filtering is an alternative mechanism that structures diversity along elevational gradients by limiting the number of viable trait combinations and, therefore affecting species and functional diversity (Bello et al. 2013; Dainese et al. 2015; Wieczynski et al. 2019). At low elevations, where environmental conditions are usually not limiting species with contrasting ecological strategies may co-exist, resulting in greater taxonomic and functional diversity. In contrast, under more severe environmental limitations frequently found at higher elevations, the number of viable ecological strategies is limited, thus constraining species and functional diversity.

Similar to species diversity, elevational patterns of functional diversity can also be highly variable, and reports range from hump-shaped (Luo et al. 2019), linearly increasing (Thakur & Chawla 2019) to no relationship (Durán et al. 2019) with elevation. The inconsistent relationship of functional diversity with elevation could be due to idiosyncratic variation in water and soil nutrient availability along some elevational gradients (Luo et al. 2019; Durán et al. 2019). Furthermore, functional diversity is multi-faceted, and the variety of indices and traits used to estimate it may contribute to the heterogeneity of observed patterns. To the best of our knowledge, the response of functional redundancy along a tropical elevational gradient has still to be examined.

Functional diversity and functional redundancy are important facets of biodiversity linked to ecosystem functioning (Paquette & Messier 2011; Jucker et al. 2014), with the relationships between different biodiversity facets and ecosystem functioning being altered by land-use intensity (Cardinale & Palmer 2002). and mediated by environmental conditions and affected by current and future climate change (Peters et al. 2019). Functional diversity also captures the effect of disturbances on ecosystem functioning (Naeem 1998; Flynn et al. 2009). Functional redundancy is associated with the resilience of ecosystem functioning, i.e. the capacity to recover ecosystem functioning after disturbance (Mori et al. 2013). One key ecosystem function is aboveground biomass, particularly in tropical forests, which account for an estimated 58% of the stored carbon globally (Meister et al. 2012). Patterns of tree biomass along elevational gradients could be associated with multiple facets of biodiversity (Paquette & Messier, 2011), particularly in intact old-growth forests (Ensslin et al. 2015; Poorter et al. 2016).

This study aimed at examining i) how do forest-use intensity and elevation interact as drivers of functional diversity and redundancy and forest biomass and structure? and ii) how do bi-variate relationships between functional diversity and functional redundancy and forest biomass and structure differ with elevation? We expected that the interaction between forest-use intensity and elevation will reduce functional diversity and functional redundancy. Further, we expect positive association between these facets of biodiversity and forest biomass (tree biomass) and structure (stem density).

2.3 Materials and methods

2.3.1 Study region

The study was conducted along an elevational gradient ranging from sea level close to the Gulf of Mexico (19.5894° N, 96.375167° W) to near tree line at 3545 m elevation (19.5182° N, 97.154525° W) on the eastern slopes of Cofre de Perote, an extinct stratovolcano of 4282 m, in the state of Veracruz, Mexico. The flora in the study region combines elements of Nearctic and Neotropical origin, with an elevational sequence of tropical semi-humid deciduous, tropical oak, humid montane, pine-oak, pine, and fir forests (Leopold 1950). Forests in the study region are affected by deforestation, extraction of timber, agriculture, conversion into pastures and cattle grazing, resulting in high levels of forest cover loss, fragmentation, and forest degradation (Gómez-Díaz et al. 2018) with associated changes in tree species diversity and community composition (Monge-González et al. 2020).

2.3.2 Study design and data collection

We selected eight sites at approximately 500 m intervals along the elevational gradient between 30 and 3545 m; to simplify, we refer here to each site as 0, 500, 1000, 1500, 2000, 2500, 3000, and 3500 m. At each site, we established 15 plots of 20 m x 20 m each, with five plots each in old-growth forest (a mature forest with low forest-use intensity), degraded forest (classified as intermediate forest-use intensity), and secondary forest (high forest-use intensity). In total, we sampled 120 plots covering an area of 48,000 m^2. In each plot, all trees with a diameter at breast height (DBH; 1.3 m) > 5 cm were measured and identified to the lowest possible taxonomic resolution, vouchers of specimens were deposited at the herbarium XAL of Instituto de Ecología, A.C. at Xalapa, Mexico. We also counted the number of stems, and measured DBH (cm) and tree height (m) following the protocol of Homeier et al. (2010).

Functional traits sampling

We selected seven plant functional traits: maximum tree height (m), wood density (g cm^{-3}), specific leaf area (m^2 kg^{-1}), leaf dry matter content (g g^{-1}), lamina density (g cm^{-3}), chlorophyll content (µg cm^{-2}), and leaf area (cm^2). We chose these traits because they capture variation in plant growth and function and are likely to respond to changes in land-use intensity and climate. Traits were measured following standardized measurement protocols (Chave 2005; King, Davies, et al. 2006; Pérez-Harguindeguy et al. 2016). Because we were not able to collect traits for all species in our plots, we obtained wood density values for 44 species from the Botanical Information and Ecology Network (BIEN) database (Enquist et al. 2016). We also performed phylogenetic trait imputation for species with missing leaf traits following Penone et al.(2014), for details see Supplementary Methods. We restricted our analysis to the 111 plots for which we had trait data for at least 90% of all individuals (Pakeman & Quested 2007).

2.3.3 Data analysis

Species and functional diversity

We used new approach by Chao et al. (2019) to calculate functional diversity, because traditional functional diversity indices (Laliberté et al. 2010) often give similar values to communities with different levels of functional diversity. To overcome these issues, the new approach uses a threshold of functional distinctiveness ("τ") between any two species, which quantifies effective numbers of functionally distinct species (Chao et al. 2019). In addition, for any value of τ, functional diversity can be estimated for any Hill number (Jost 2006).

As the framework of Chao et al. (Chao et al. 2019) is consistent with Hill numbers, functional diversity can be expressed in similar units, i.e. effective number of functionally distinct species. Species diversity assumes that each species is maximally distinct from other species, while functional diversity quantifies the extent to which each species is distinct (Chao et al. 2019). Therefore, we estimated species and functional diversity using different distinctiveness thresholds: d_{min} and d_{mean}, respectively. For both species and functional diversity, we calculated richness (Hill number q = 0), which counts species irrespective of their abundance, and diversity, which weighs species' abundance to different extents (Hill numbers q = 1 and 2), and we expressed both measures in terms of effective numbers of species (or functional groups) following Jost (2006). Prior to calculating functional diversity, we estimated the number of functional dimensions that maximized the quality of functional spaces (Maire et al. 2015); with five dimensions for our study (Fig. B1, Table B1).

Functional redundancy

Following Ricotta et al. (2016), we estimated functional redundancy for each Hill number as the difference between species and functional diversity. Functional redundancy is based on functional similarity among species, i.e. species with similar functional trait values are assumed to fulfill similar ecological functions (Ricotta et al. 2016) and thus quantifies the capacity of a community to maintain ecosystem processes under biodiversity change. For example, communities with high functional redundancy are comprised of species with similar trait values, meaning that if one species is lost, another will provide similar ecological functions. In contrast, communities with low functional redundancy are comprised of functionally dissimilar species that provide ecological functions that cannot be replaced by another species in the community.

Tree biomass

From our plot data, we estimated tree above-ground biomass (AGB) following Chave et al. (2014) with tree diameter *D* (cm), tree height *H* (m) per plot, and wood density *WD* (g cm^{-3}). We used the allometric equation for tropical forests as: $AGB = 0.0673(WD * H * D^2)^{0.967}$, with the '*BIOMASS*' package (Réjou-Méchain et al. 2017).

Statistical analysis

We examined the effect of forest-use intensity at each elevation on functional diversity and redundancy and tree biomass separately using a nested analysis of variance (ANOVA) Type III using the "*car*" package (Fox & Sanford 2019). We used natural logarithmic transformation for functional diversity and biomass to meet assumptions of normality. In the case of stem density, where our data were counts, we used a generalized linear model with a Poisson distribution as implemented in the R function '*glm'.* In this model, we treated forest-use intensity and elevation as factors.

We performed a Standardized Major Axis (SMA) regression analysis to quantify the relationships between functional diversity and redundancy with tree biomass and stem density along elevations. SMA regression analysis was performed using the R package '*smatr*' (Warton et al. 2012). For data manipulation and visualization, we used the R packages '*dplyr'* (Wickham et al. 2019) and '*ggplot2'* (Wickham 2009), respectively. We performed all analyses in R version 3.6.3 R Core Team (2020).

2.4

2.5 Results

2.5.1 Effects of elevation and forest-use intensity within elevation on functional diversity and redundancy

Functional diversity varied significantly with elevation (Hill number q = 0; $F_{7,87} = 25.76$, *p*-value < 0.0001) and forest-use intensity within elevation (Hill number q = 0; $F_{16,87} = 1.68$, *p*-value < 0.0001; Table B2). In old-growth forests, functional diversity showed a low-plateau pattern, with higher functional diversity between 0 to 2000 m followed by a monotonic decrease thereafter. In contrast, we observed a bimodal pattern for degraded forests, which peaked at 1000 m and 2000 m. In secondary forests, functional diversity peaked at 1000 m and then declined monotonically (Fig. 2.1). We observed similar patterns for functional diversity when weighted by species abundances (q = 1 and q = 2; Table B2, Figs B2 and B3). Within elevations, functional diversity did not vary significantly between forest-use intensities, except for 1000 m, where we detected significant differences between old-growth and secondary forest.

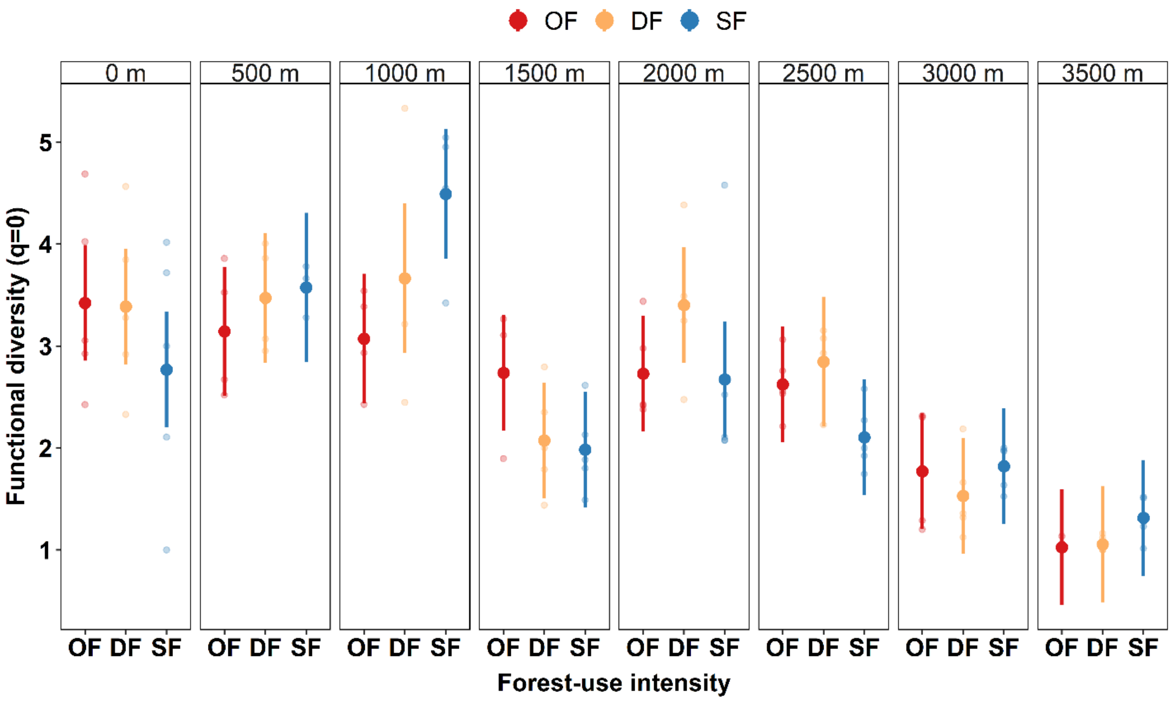

Figure 2.1. Functional diversity (Hill number q = 0) along the elevation gradient and different levels of forest-use intensity (n = 111 plots). Functional diversity was significantly affected by elevation ($F_{7,87}$ = 25.76, *p*-value = 9.81^{e-19}) and forest-use intensity within elevation ($F_{16,87}$ = 1.68, *p*-value = 6.55^{e-02}). Bold points are predicted means from the nested ANOVA (lines are 95 % confidence intervals). Light points are plot-level values. Forest-use intensity levels are old-growth forest (OF), degraded forest (DF), and secondary forest (SF).

We found significant differences for functional redundancy across elevations (Hill number q = 0; $F_{7,87}$ = 43.36, *p*-value < 0.0001) and forest-use intensity within elevation (Hill number q = 0; $F_{16,87}$ = 5.88 *p*-value < 0.0001; Table B2). Functional redundancy for old-growth forests followed a low-plateau elevational pattern and bimodal pattern for degraded forests, reaching its highest values between 0 and 2000 m, and then decreasing monotonically. In contrast, secondary forests showed a bimodal pattern, with functional redundancy peaking at 1000 and 2000 m (Fig. 2.2). Functional redundancy with Hill numbers q = 1 and q = 2 yielded similar results (Table B2, Figs B4 and B5). Within elevations, we only observed significant differences in functional redundancy among forest-use intensities between old-growth and secondary forests at 0 m and 1500 m.

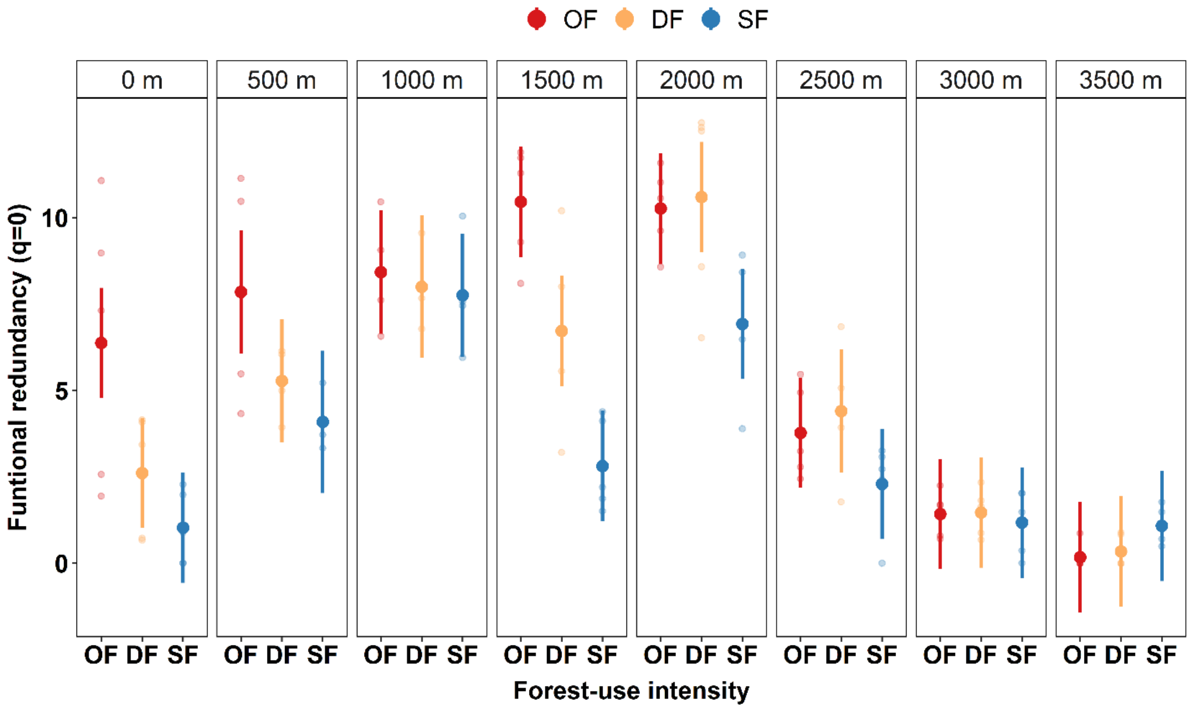

Figure 2.2. Functional redundancy (Hill number q = 0) along the elevation gradient and different levels of forest-use intensity (n = 111 plots). Functional redundancy was significantly affected by elevation ($F_{7,87}$ = 43.36, *p*-value = 9.59^{e-26}) and forest-use intensity within elevation ($F_{16,87}$ = 5.88, *p*-value = 1.81^{e-08}). Bold points are predicted means from the nested ANOVA (lines are 95 % confidence intervals). Light points are plot-level values. Forest-use intensity levels are old-growth forest (OF), degraded forest (DF), and secondary forest (SF).

2.5.2 Effects of elevation and forest-use intensity within elevation on tree biomass and stem density

Tree biomass and stem density were also significantly affected by elevation (tree biomass: $F_{7,87}$ = 5.65, *p*-value < 0.0001; stem density: $F_{7,96}$ = 5.70, *p*-value= < 0.0001) and forest-use intensity within elevation (tree biomass: $F_{16,96}$ = 3.37, *p*-value = < 0.0001; stem density: $F_{16,96}$ = 2.98, *p*-value < 0.0001). Tree biomass varied non-linearly with elevation for all forest-use intensities; the highest tree biomass in old-growth and degraded forests occurred at 3500 m. In secondary forests, the highest tree biomass was observed at 1500 m and the lowest tree biomass occurred at 0 m (Fig. 2.3). Values of stem density did not differ strongly along the elevational gradient for old-growth forests. In degraded and secondary forests, we found the lowest stem densities at 0 m, with stem density increasing up to 1500 m. In secondary forests, stem density peaked at 3500 m (Fig. 2.4).

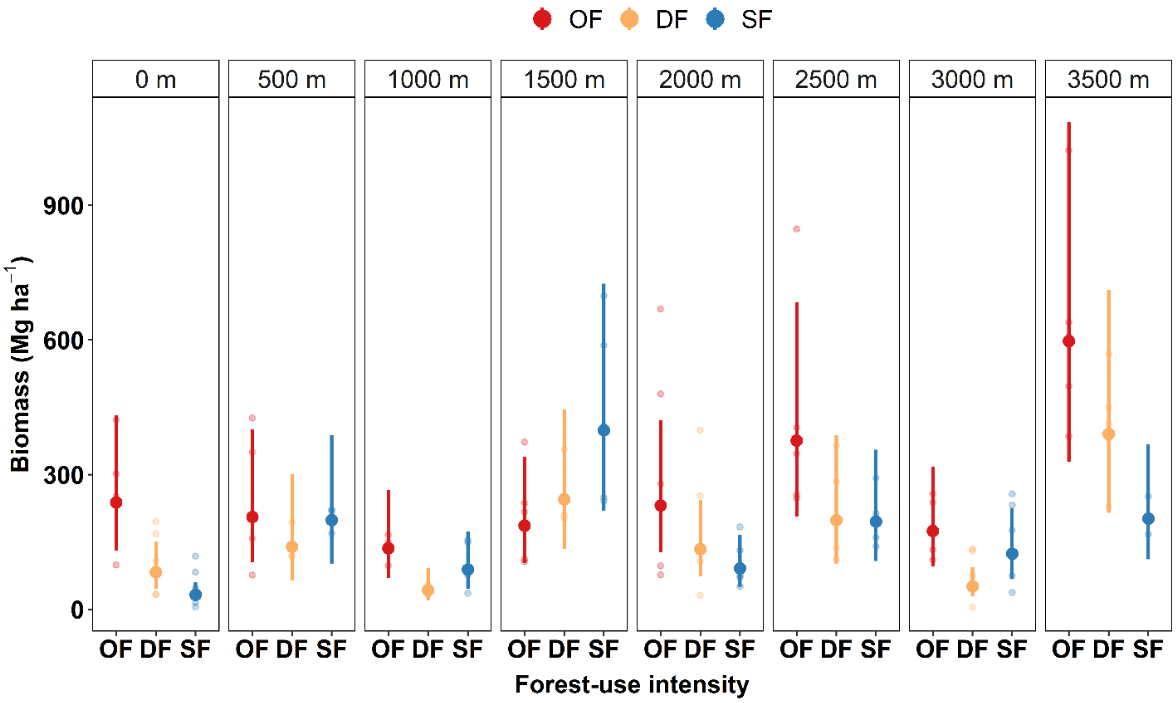

Figure 2.3. Biomass along the elevation gradient and different levels of forest-use intensity (n = 111 plots). Biomass varied significantly along elevation ($F_{7,87}$ = 5.65, *p*-value = 2.09^{e-05}) and forest-use intensity within elevation ($F_{7,87}$ = 3.37, *p*-value = 0.0001). Bold points are predicted means from the nested ANOVA (lines are 95 % confidence intervals). Light points are plot-level values. Forest-use intensity levels are old-growth forest (OF), degraded forest (DF), and secondary forest (SF).

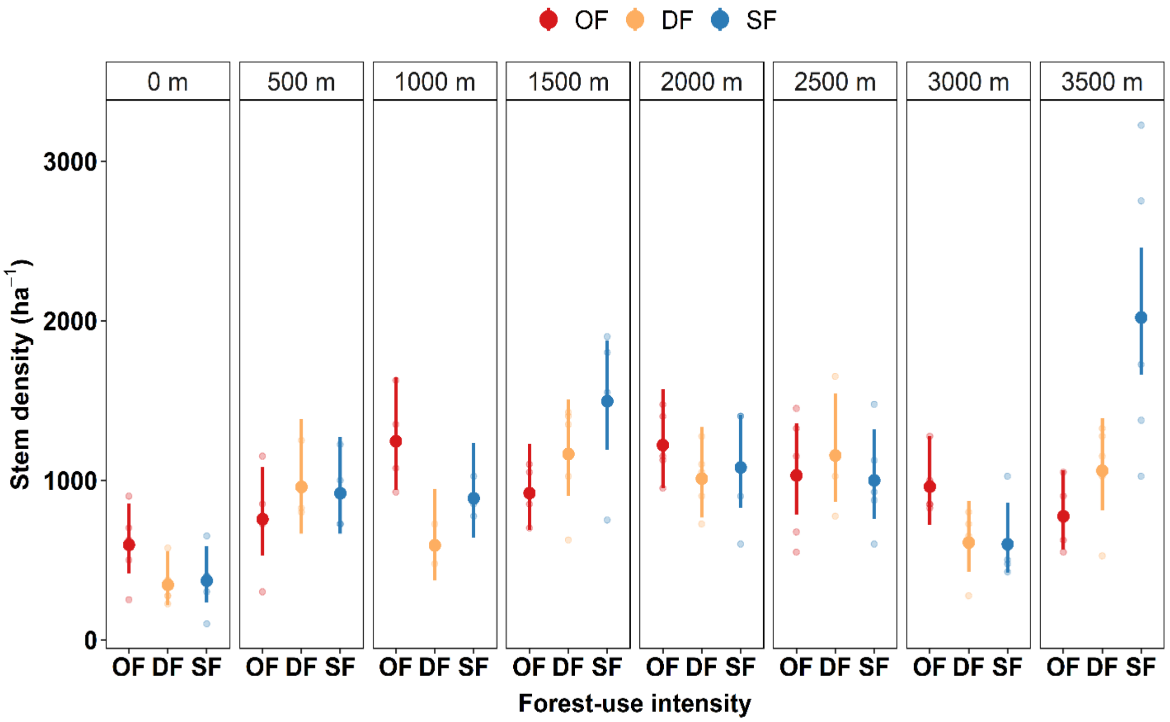

Figure 2.4. Stem density along the elevation gradient and different levels of forest-use intensity (n = 111 plots). Stems density was significantly affected by elevation ($F_{7,87}$ = 5.70, *p*-value = 1.90^{e-05}) and forest-use intensity within elevation ($F_{7,87}$ = 3.77, *p*-value = 2.9^{e-05}). Bold points are predicted means from the nested ANOVA (lines are 95 % confidence intervals). Light points are plot-level values. Forest-use intensity levels are old-growth forest (OF), degraded forest (DF), and secondary forest (SF).

2.5.3 Bi-variate relationships between functional diversity and redundancy and biomass and stem density

Functional diversity and redundancy were significantly associated with tree biomass and stem density, respectively (Fig. 2.5; Tables B3 - B6). Yet, these relationships were not consistent across elevations. For the relationship between functional diversity and tree biomass, we found significantly positive relationships at 0 m (R^2 = 0.37, slope = 0.32, *p*-value = 0.01), at 2000 m (R^2 = 0.32, slope = 0.29, *p*-value = 0.02), and 3500 m (R^2 = 0.42, slope = -0.27, *p*-value = 0.008; Fig. 2.5, Table B3). Further, we found a significant, positive relationship between functional redundancy and biomass at 0 m (R^2 = 0.43, slope = 6.36, *p*-value = 0.007) and 1500 m (R^2 = 0.26, slope = -16.45, *p*-value =0.048), and a negative relationship at 3500 m (R^2 = 0.55, slope = -2.55, *p*-value = 0.001; Fig. 2.5; Table B4). Finally, the relationships between functional diversity and redundancy and stem density were significantly positive at 0 m (functional diversity: $R^2 = 0.44$, slope = 0.69, *p*-value = 0.006, redundancy: $R^2 = 0.43$, slope = 13.72, *p*-value = 0.007), at 2500 m (functional diversity: $R^2 = 0.32$, slope = 0.54, *p*-value = 0.03) and 3500 m (functional diversity: $R^2 = 0.44$, slope = 0.28, *p*-value = 0.006, redundancy: $R^2 = 0.33$, slope = 2.61, *p*-value = 0.02; Fig. 2.5; Tables B5 and B6).

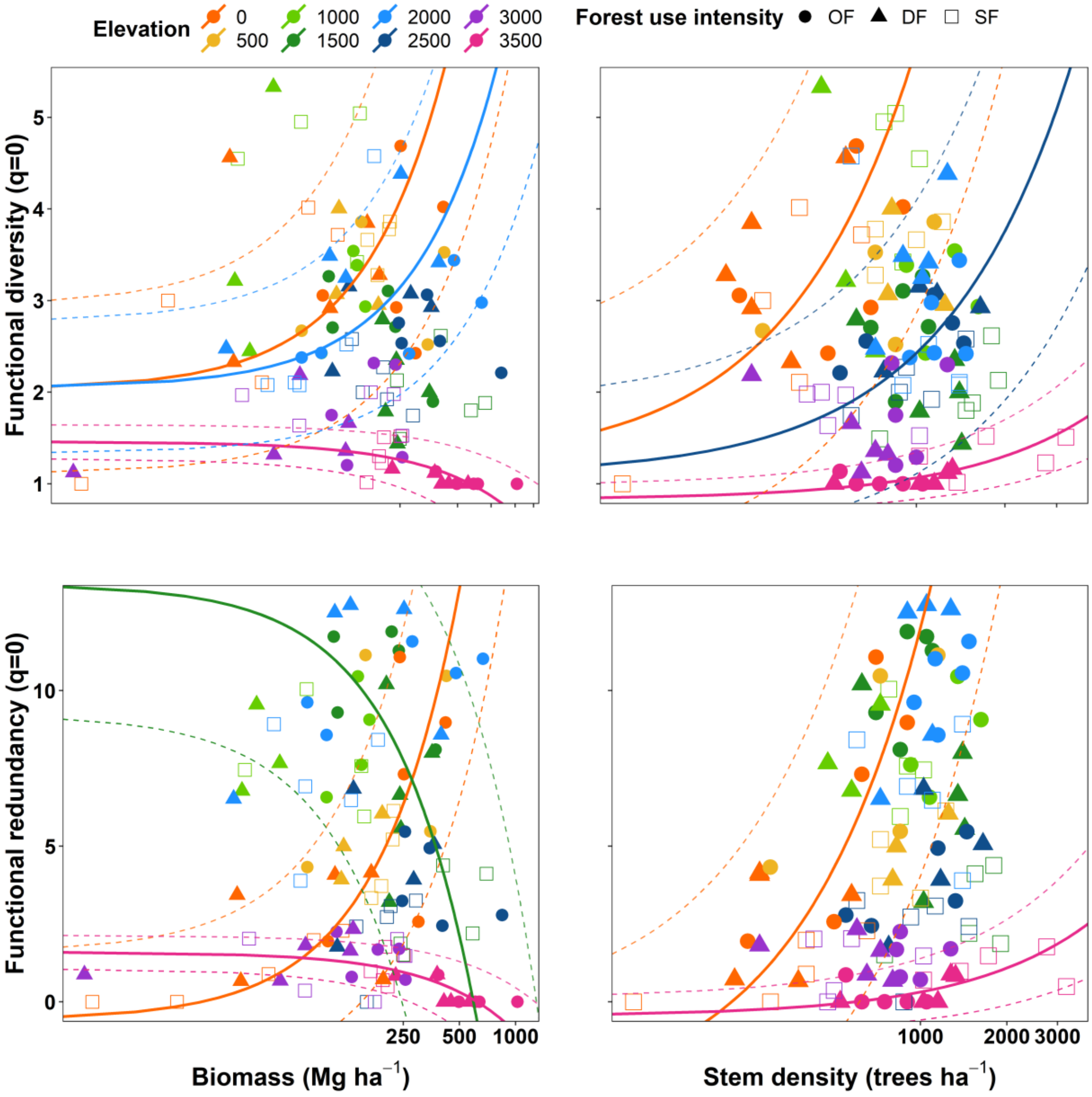

Figure 2.5. Relationships between functional diversity and redundancy (Hill number q = 0) with biomass and stem density on logarithmic scale, fitted with standardized major axis (SMA) regression. Solid lines represent the regression model and show significant relationships (p-value < 0.05) and dashed lines indicate confidence intervals 95%. Forest-

use intensity levels are old-growth forest (OF, circles), degraded forest (DF, triangles), and secondary forest (SF, squares).

2.6 Discussion

Previous research provides strong evidence for elevation and forest-use intensity affecting species diversity and, to a lesser extent, for the influence of their interactive effects on species diversity (Peters et al. 2019; Monge-González et al. 2020). Our study is one of the first that assessed the interactive effects of elevation and forest-use intensity on other facets of biodiversity, as well as their repercussions on forest structure and ecosystem functioning. Our results revealed that functional diversity and redundancy are affected by the interaction between elevation and forest-use intensity, resulting in a low-plateau pattern in old-growth forests and a bimodal pattern in degraded forests, whereas secondary forests showed a hump-shaped and bimodal pattern for functional diversity and redundancy, respectively. At most elevations, forest-use intensity did not affect functional diversity. This means that from sea level to 2000 m tree communities had a high functional diversity and redundancy, making them more resilient to disturbances than tree communities at higher elevations. Further, the relationships between functional diversity and redundancy with tree biomass and stem density varied with elevation, shifting in both direction and magnitude, suggesting that species conservation alone may not suffice to maintain key ecosystem processes in tropical mountain ecosystems.

2.6.1 Interaction effect of elevation and forest-use intensity affects tree functional diversity and redundancy

We found a low-plateau elevational pattern for functional diversity and redundancy in old-growth forests, with functional diversity and redundancy decreasing above 2000 m. This mirrors similar patterns for tree species diversity reported in a related study by Monge-González et al. (2020), suggesting that more diverse tree communities at lower elevations may be more resilient than species-poor tree communities at higher elevations. At higher elevations (particularly 3000-3500 m), lower functional diversity and redundancy may reflect strong environmental filtering (Spasojevic & Suding 2012). Decreases in temperature with increasing elevation are known to affect changes in plant functional traits and to cause functional convergence at high, cold elevations by constraining trait variation (Bagousse-Pinguet et al. 2017; Durán et al. 2019). However, the low-plateau elevational pattern for functional diversity and redundancy observed in our study indicates that elevational shifts in the strength of environmental filtering are non-linear. This suggests that other environmental factors also influence functional diversity and redundancy but may not change linearly with elevation (e.g. precipitation; McCain & Grytnes,2010), and/or that the increase in the strength of environmental filtering corresponds to where freezing temperatures occur along the elevational gradient. Indeed, our results are consistent with those of macroecological studies (Qian et al. 2017), which report greater phylogenetic relatedness of trees (i.e. low phylogenetic diversity) in colder and drier biomes, a pattern driven by the evolution of traits to tolerate freezing temperatures and prolonged periods of drought. Low functional redundancy at higher elevations of 3000-3500 m suggests that these tree communities are functionally similar because they are dominated by a few species of conifers adapted to harsh environmental conditions and may be less resilient to species loss or future climate change (Fadrique et al. 2018).

Our results reveal that the impacts of forest-use intensity on functional diversity and redundancy in degraded and secondary forests were not consistent across elevations. Specifically, at certain elevations, forest-use intensity affected functional diversity and functional redundancy, while for functional diversity at 1000 m, we detected significant differences between old-growth and secondary forests, with the highest functional diversity in secondary forest. While unexpected, this result coincides with those of previous studies that have shown variable responses of functional diversity to land-use intensity (e.g. Flynn et al. 2009). For functional redundancy, we found significant differences between old-growth, degraded, and secondary forests at 0 m, and between degraded and secondary forests at 1500 m, which is consistent with previous studies in tropical and subtropical forests (Laliberté et al. 2010) and suggests that an increase in forest-use intensity may result in a decrease of functional redundancy. However, in other cases, land-use intensity increased functional redundancy in two tropical forests (Laliberté et al. 2010). In our study, forest-use intensity did not significantly affect functional redundancy within five elevations, suggesting that ecosystem processes of tropical mountain forests can be resilient to forest uses of varying intensities (Norden et al. 2009; Poorter et al. 2016).

2.6.2 Relationships between biomass, stem density and functional diversity and redundancy

We found highly variable relationships between biomass, functional diversity, and functional redundancy across the elevational gradient. Usually, when statistically significant, there was a positive relationship between biomass and functional diversity at elevations (0, and 2000 m), while we found significant, positive relationship between functional redundancy and biomass at 0 m, respectively. A positive relationship is expected because evidence suggests that functionally diverse forests provide higher levels of ecosystem functioning and are likely to be more resilient to global change (Paquette & Messier 2011; Craven et al. 2016). For instance, previous studies have shown a positive relationship between species diversity or functional diversity with productivity in grasslands (Cardinale et al. 2011) and forests (Liang et al. 2016). However, functional diversity and biomass were not significantly correlated at five elevations (500, 1000, 1500, 2500 m and 3000 m) and were even negatively correlated at 3500 m; for functional redundancy and biomass we found a positive correlation at 0 m and negative correlations at 1500 and 3500 m, but these were not significantly correlated at 500, 1000, 2000, 2500, and 3000 m. Together, these results provide further evidence that relationships between multiple facets of biodiversity and ecosystem functioning in natural forest ecosystems are complex and highly context-dependent (Ratcliffe et al. 2017) (Tables B7 - B8 Fig. B6). The positive relationships between functional redundancy and biomass indicate that forests with high functional diversity and redundancy enhance ecosystem functioning (Díaz & Cabido 2001), while negative relationships between functional redundancy and biomass indicate that ecosystem functioning is dependent on a small number of functionally similar species

(Petchey et al. 2007) and that losing these species would have large impacts on ecosystem functioning (Díaz & Cabido 2001).

Relationships between stem density, functional diversity, and functional redundancy were generally weak across the elevational gradient, only exhibiting positive, significant correlations at two elevations. These results suggest that the more-individuals hypothesis of species diversity may not hold for other facets of biodiversity, such as functional diversity and redundancy, possibly due to natural population variability, as short-term sampling may mask the true effects of stem density (Vagle & McCain 2020). Moreover, the lack of a consistent relationship between stem density and functional diversity and redundancy reflects the non-linear changes in forest structure along the elevational gradient. Indeed, other measures of forest structure that capture stand structural complexity (Ali et al. 2019), which may vary more predictably with elevation, may mediate the relationship between functional diversity and redundancy and stem density. In more practical terms, our results suggest that changes in forest structure due to forest-use intensity may not have consistent impacts on forest diversity and redundancy.

2.7 Conclusions and application

We found that functional diversity and functional redundancy of tropical tree communities greatly varied with elevation, yet within elevations these two different facets of biodiversity were largely similar across levels of forest-use intensity. Lowland and premontane communities (with few exceptions) had highly redundant and functionally diverse tree communities, suggesting that these forest ecosystems are likely to be resilient to future disturbances. Context-dependent relationships of biomass with functional diversity and redundancy suggest that multiple criteria should be used for conserving tree diversity and ecosystem functioning in tropical mountain ecosystems. Specifically, our study shows that macroecological constraints, e.g. changes in energy and water availability and the strength of environmental filtering along elevational gradients, need to be considered to better understand the influence of land-use changes on biodiversity and ecosystem functioning relationships.

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Chapter 3:

BIOVERA-Tree: tree diversity, community composition, forest structure and functional traits along gradients of forest-use intensity and elevation in Veracruz, Mexico

“Poza Azul” tropical oak forest at 500 m elevation

3 BIOVERA-Tree: tree diversity, community composition, forest structure and functional traits along gradients of forest-use intensity and elevation in Veracruz, Mexico

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Unpublished manuscript

3.1 Abstract

Here, we describe BIOVERA-Tree, a database on tree diversity, community composition, forest structure, and functional traits collected in 120 forest plots distributed along an extensive elevational gradient in Veracruz State, Mexico. BIOVERA-Tree includes information on forest structure from three levels of forest-use intensity, namely old-growth, degraded, and secondary forest, replicated across eight elevations from sea-level to near the tree line at 3500 m and on size and location of 4548 tree individuals with a diameter at breast height ≥ 5 cm belonging to 216 species, 154 genera, and 80 families. We also report measurements of seven functional traits, namely wood density for 159 species, maximum height for 216 species and leaf traits including: specific leaf area, lamina density, chlorophyll content, and leaf area for 156 species and leaf dry matter content for 152 species.

New information

BIOVERA-Tree is a new database comprising data collected in a rigorous sampling design along forest-use intensity and elevational gradients, contributing to our understanding of how interactive effects of forest-use intensity and elevation affect tree diversity, community composition, and functional traits in tropical forests.

Keywords: Degraded forest, Elevational gradient, Forest plots, Functional traits, Land-use, Mexico, Old-growth forest, Secondary forest, Tree communities, Tropical montane forest.

3.2 Introduction

Mountains are fascinating ecosystems and natural laboratories for evolutionary and ecological research as they encompass a wide variety of different climatic conditions over short distances (Körner 2004; Malhi et al. 2010). Mountains have captivated and inspired scientists since the seminal research by Alexander von Humboldt (von Humboldt 1806), and mountain research still contributes to our understanding of how environmental conditions affect plant distributions and how diversity may be impacted by global change (Körner 2004; Malhi et al. 2010; McCain & Grytnes 2010; Morueta-Holme et al. 2016; Perrigo et al. 2020). Mountains cover 25% of the Earth's land surface and support an estimated one third of all terrestrial species (Körner 2004). Tropical mountains account for 10% of the terrestrial land area, and are reservoirs of species diversity and hotspots of endemism with the potential to provide safe havens for species under current and predicted future anthropogenic global warming (Körner 2004; Sundqvist et al. 2013; Perrigo et al. 2020). Finally, tropical mountain forests provide a plethora of important ecosystem functions, e.g. water storage and yield, carbon storage, and pollination, that underpin ecosystem services and are a basis for human well-being (Díaz et al. 2018). Yet increasing human population and land-use intensification are altering forest structure, tree species diversity, and functional diversity of tropical mountain forests around the world.

Land-use change and intensification are occurring at rapid rates and are strongly impacting mountain ecosystems (Payne et al. 2017). For instance, during a period of high deforestation in Mexico between 1980-2010, the state of Veracruz experienced the second highest rate of deforestation among all states, with 75% of its area being deforested (Ellis et al. 2011; SEMARNAT 2016). Specifically between 1990-2000, Veracruz lost approximately 4.8% of its natural and secondary vegetation during this period, while only 8.6% of its vegetation remains conserved (Ellis et al. 2011). Afterwards, however, the region experienced a mild recovery in forest cover between 2000-2014 (Gómez-Díaz et al. 2018).

Land-use change and intensification for timber extraction, agriculture, and cattle pastures alter tree species diversity and community composition in this region (Monge-González et al. 2020). Further, land-use change is not only a major threat to species diversity, but also has consequences for ecosystem functioning (Chapin et al. 2000; Newbold et al. 2015; Hooper et al. 2016). Therefore, high-quality databases of tree diversity and ecosystem functions are essential to understand the impacts of land-use change and elevation on tropical forests. Here, our objective is to contribute to the knowledge on how elevation and forest-use intensity interactively affect tropical tree diversity, community composition, functional traits, and forest structure.

General description:

BIOVERA-Tree originated from the interdisciplinary research project BIOVERA, which aims at documenting and understanding biodiversity patterns along gradients of altitude, climate, soil, and disturbance along an elevational transect at the Cofre de Perote in central Veracruz, Mexico (Carvajal-Hernández et al. 2017; Gómez-Díaz et al. 2017; Bautista-Bello et al. 2019; Guzmán-Jacob et al. 2020; Monge-González et al. 2020). BIOVERA-Tree comprises forest plot data from eight elevational sites and three levels of forest-use intensity, namely old-growth, degraded, and secondary forests. It contains descriptions of 120 non-permanent forest plots of 20 x 20 m and a community matrix including abundances for 217 species. Further, it contains measurements for 216 species including diameter at breast height (DBH) and tree height of 4548 and 4549 individuals, respectively. BIOVERA-Tree also includes functional traits, with data for wood density of 159 species calculated based on 525 individuals, maximum height for 216 species calculated based on 4549 individuals, and leaf traits for 156 species, specific leaf area (n = 3262 leaves), leaf thickness (n=156), lamina density (n = 3310 leaves), chlorophyll content (n = 3393 leaves), and leaf area (n = 3320 leaves) and leaf dry matter content for 152 species (n = 3179 leaves).

3.3 Study area

The study area is located along an elevational gradient from sea level close to the Gulf of Mexico to near the tree line at 3545 m on the eastern slopes of the Cofre de Perote volcano, in the central part of the state of Veracruz, Mexico (Figure 3.1). This region is located at the intersection of the Trans-Mexican volcanic belt and the Sierra Madre Oriental, resulting in complex geological conditions, and is a transition zone where floristic elements from the Neotropics and Nearctic mix. Veracruz (including the study area) is part of the Mesoamerican biodiversity hotspot (Myers et al. 2000). The state harbors a diverse vascular flora of approximately 8500 species, which represents about 36% of the Mexican flora (Villaseñor 2016). The elevational gradient is characterized by a wide range of different environmental conditions. For instance, climate varies between tropical-dry at lower elevations, to temperate-humid at mid-elevations and cold-dry at high elevations (Soto-Esparza & Giddings-Berger 2011). The mean annual temperature ranges from 26 °C near sea level to 9 °C at the highest site. Mean annual precipitation varies between 1222 mm at low elevations, 2952 mm at mid-elevations, and 708 mm at high elevations (Servicio Meteorológico Nacional 2019). Six main vegetation types along this elevation gradient are typically recognized, including tropical semi-humid deciduous, tropical oak, humid montane, pine-oak, pine, and fir forests (Leopold 1950; Carvajal-Hernández et al. 2020). However, land-use change has altered these ecosystems into mostly degraded and secondary forests. The forests in the lowlands (0, 500, and 1000 m) have been largely replaced by agricultural systems, e.g. sugar cane, corn, mango, and lemon plantations, and grasslands for cattle (Travieso-Bello et al. 2006; Thiébaut et al. 2017), while the forests at mid-elevations (1500, 2000, and 2500 m) have been transformed by illegal logging for charcoal production and firewood and converted into cattle pastures, coffee plantations, and agricultural fields (Cruz-Angón et al. 2010), and the forests in the highlands (3000 and 3500 m) have been altered by timber extraction, agricultural fields for potatoes and broad beans, as well as pastures for goats and sheep (Pineda-López et al. 2013). Land-use modifications at every elevational site change with the primary economic activities.

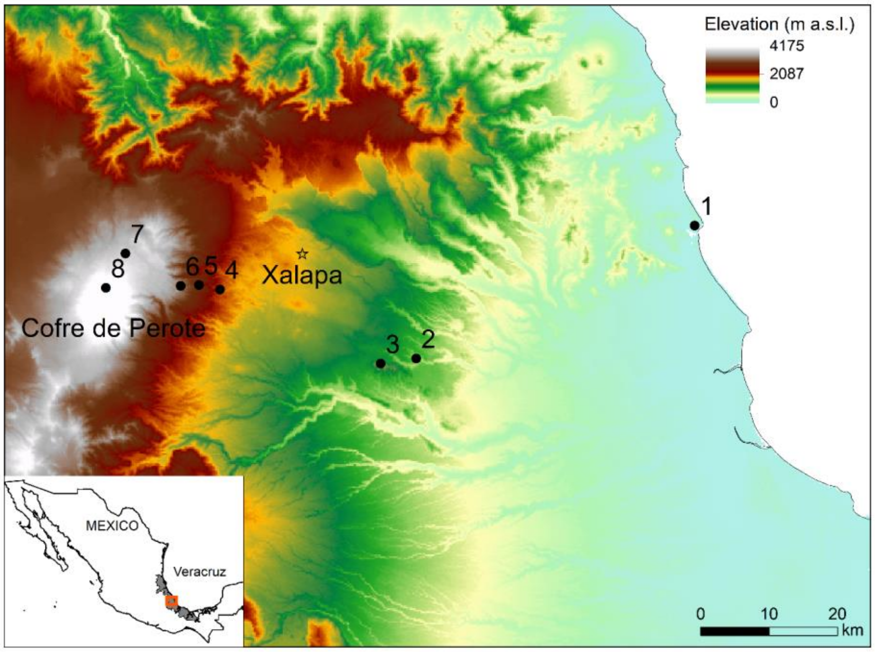

Figure 3.1. Location of the eight study sites along the elevational gradient at the eastern slopes of Cofre de Perote in Veracruz, Mexico.Black dots show the location of sites along the elevational gradient 1) 0 m; 2) 500 m; 3) 1000 m; 4) 1500 m; 5) 2000 m; 6) 2500 m; 7) 3000 m; 8) 3500 m.

3.4 Sampling methods

We selected eight sites along the elevational gradient, separated by about 500 m in elevation (Fig. 3.1). At each site, we established 15 plots of 20 x 20 m, with five plots located in old-growth, degraded, and secondary forests, respectively, (for plot descriptions see Data set 1). This study design led to a total of 120 non-permanent forest plots (120 x 0.04 ha = 4.8 ha) inventoried along the elevation gradient.

Old-growth forests were defined as mature forests with low forest-use intensity and showed no signs of recent human use. Degraded forests were classified as intermediate forest-use intensity which had been subjected to selective logging, and grazing by cattle or goats at high elevations. Finally, secondary forests were defined as high forest-use intensity, having regenerated following clearcutting 15-20 years prior or with cattle grazing (Gómez-Díaz et al. 2017). In each plot, we inventoried all trees with a DBH $\geq$ 5 cm and identified individual trees to the highest taxonomic resolution possible. For each individual we measured its DBH (in cm) and tree height (in m), which was measured with a Leica laser (Homeier et al. 2010; Monge-González et al. 2020). We calculated maximum tree height for each species following King et al. (2006) and classified the trees into three groups: 1) species with more than 20 individuals, 2) species with between 5-19 individuals, and 3) species with less than five individuals. For the first group, we calculated maximum tree height as the mean of the tallest three individuals. For the second group, we estimated maximum tree height as the mean of the tallest two individuals; and for the third group, we used the height of the tallest individual (King et al. 2006).

In addition, we measured the following functional traits: maximum height, wood density, specific leaf area, leaf dry matter content, leaf thickness, lamina density, chlorophyll content, and leaf area (Table 3.1). We selected these traits because they are expected to respond to both elevation and forest-use intensity (Díaz et al. 2016). For instance, the abundance of species with slow growth and conservative resource acquisition is expected to decrease, while that of species with fast growth and acquisition rates should increase with forest-use intensity (Table 3.1) (Lavorel & Garnier 2002; Díaz et al. 2016). For trait measurements, we selected one to three tree individuals per species and collected at least five to ten leaves per individual, and one to three wood cores per species along the gradients of elevation and forest-use intensity.

Table 3.1. Number of individuals and species with measurements of eight functional traits.

Ecological relevance	Functional Trait	Unit	Measured individuals	Number of species
Seed dispersion, competitive ability	Maximum height	m	4549†	216
Structure and mechanical support	Wood density	g cm-^{3}	525	159
Leaf energy and water balance, physical strength	Specific leaf area	m^2 kg^{-1}	3262	156
	Leaf dry matter content	g g^{-1}	3179	152
	Leaf thickness	mm	3406	156
	Lamina density	g cm^{-3}	3310	156
Photosynthesis	Leaf area	cm^2	3320	156
	Chlorophyll content	µg cm^{-2}	3393	156

†Individual used to calculate mean species values reported as maximum height.

For wood density, we collected wood samples using an increment borer. We used the water-displacement method for measuring wood sample volume and oven-dried samples at 70 °C for 48 to 72 hours until they reached a constant dry weight (Chave 2005). We determined maximum height for each species following King et al. (2006). For leaf traits, we followed standardized trait measurement protocols (Pérez-Harguindeguy et al. 2016). We weighed the fresh leaves and then oven dried them at 60 °C for 48 hours, or until they had reached a constant dry weight. We measured leaf thickness with a digital caliper. For chlorophyll concentration, we used a SPAD-502 chlorophyll meter (Spectrum Technologies, Plainfield, IL, USA) and converted measurements to chlorophyll concentration following Coste et al. (2010). We calculated leaf area using WinFOLIA (Version 2016b Pro, Regent Instruments Canada, 2016). In total, we collected wood samples for 159 species and leaf samples for 156 species, except leaf dry matter content for which we have samples for 152 species.

Geographic coverage

The BIOVERA elevational gradient is located close to the Gulf of Mexico and spans from close to sea level (19.5894 N, -96.375167 W) to close to the treeline at 3545 m elevation (19.5182 N, -97.154525 W) along the eastern slopes of Cofre de Perote volcano (4282 m) in Veracruz State, Mexico (Fig. 3. 1).

Taxonomic coverage

Taxonomic information on valid species, genus, and family names was obtained from The Plant List version 1.1 (2013). Individuals were identified to the species level by specialists (Dr. Francisco Lorea-Hernández, M.Sc. Claudia Gallardo-Hernández, and Biol. Carlos M. Durán-Espinosa, Instituto de Ecología, A. C.), while some individuals could only be identified to the family or genus level, or could not be identified. Vouchers of specimens were deposited at the herbarium XAL of Instituto de Ecología, A.C. at Xalapa, Mexico.

Tree diversity and community composition

The database contains information of 216 tree species distributed among 80 families and 154 genera and tree abundances across plots along the forest-use intensity and elevation gradients (Dataset 2). The number of species per plot ranged from 1 to 18, with a mean 8.1 species (Table 3.2).

Table 3.2. Mean tree species and individual numbers per plot.

Elevation (m)	**Species (mean ± SD)**	**Individuals (mean ± SD)**
0	6.8 ± 4.16	17.46 ± 8.68
500	11.06 ± 3.63	36.4 ± 11.91
1000	13.33 ± 2.22	35.4 ± 12.7
1500	9.6 ± 4.56	44.73 ± 15.9
2000	13.13 ± 2.94	44.13 ± 10.4
2500	6.8 ± 2.99	42.20 ± 13.2
3000	3.06 ± 0.96	28.93 ± 10.5
3500	1.66 ± 0.72	51.4 ± 30.81

The number of individuals per plot ranged from 4 to 120 with a mean of 8.19 individuals (Table 3.2). Species-abundance distributions across levels of forest-use intensity indicated a higher proportion of rare species in old-growth and degraded forests than in secondary forests (Fig. 3.2 A). Species-abundance distributions across elevations revealed that forests at high elevations (3000-3500 m) are dominated by a small number of species, while forests at low elevations (0-1000 m) and mid-elevations (1500-2000 m) exhibited higher evenness (Fig. 3.2).

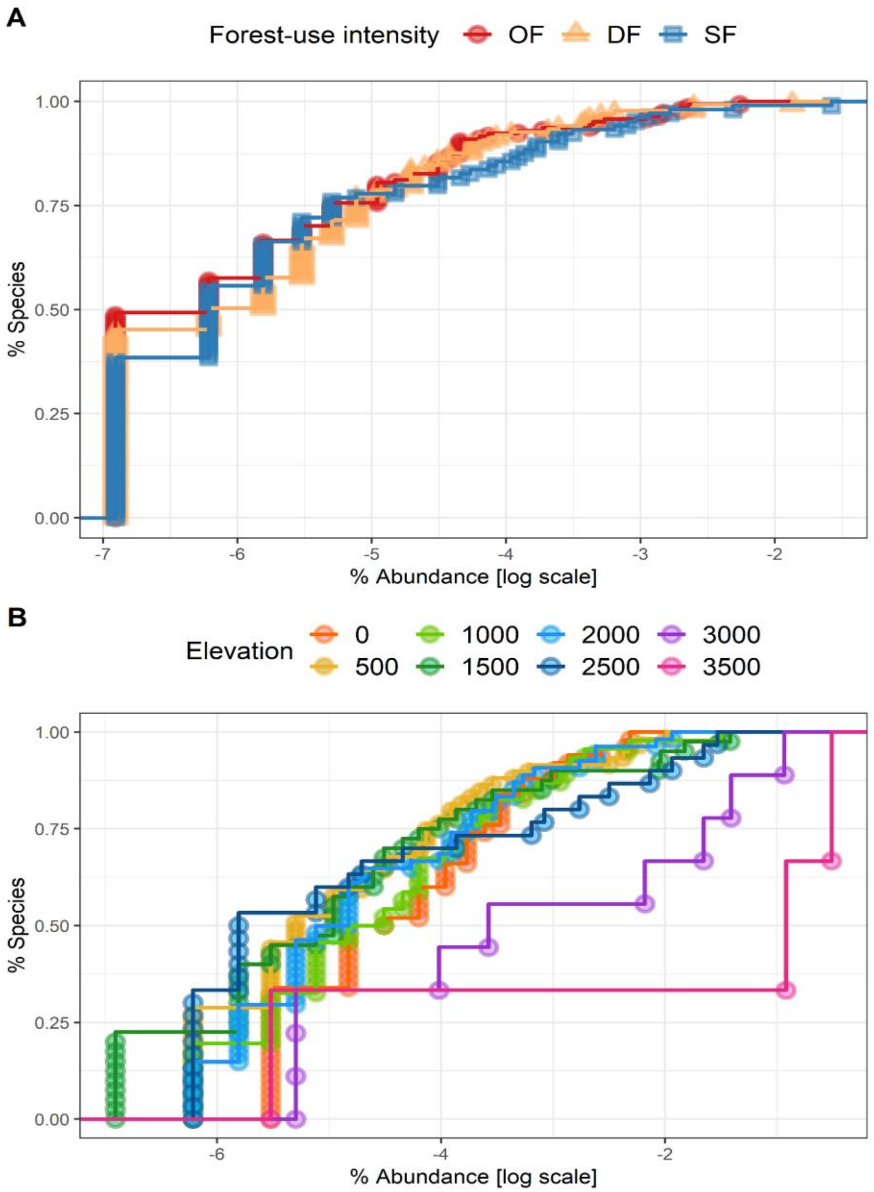

Figure 3.2. Species-abundance distributions (n = 120 plots) using an empirical cumulative distribution function A for different levels of forest-use intensity and B for eight sites along the elevation gradient. Vertical axis shows each species from most to least abundant. Horizontal axis shows the relative abundance of the species on a logarithm scale. Forest-use intensity levels are old-growth forest (OF), degraded forest (DF), and secondary forest (SF).

Forest structure

Across all plots, DBH ranged from 5 to 148 cm, with a mean of 14 ± 15.5 SD (Fig. 3.3). DBH mean per forest-use intensity varied from 20.84 ± 17.6 SD in old-growth forests, 19.3 ± 15.2 SD in degraded forests, and 17.4 ± 13.3 SD in secondary forests. The five species with the highest mean DBH were *Pseudobombax ellipticum*, *Salix humboldtiana*, *Diphysa robinioides*, and *Pachira aquatica*.

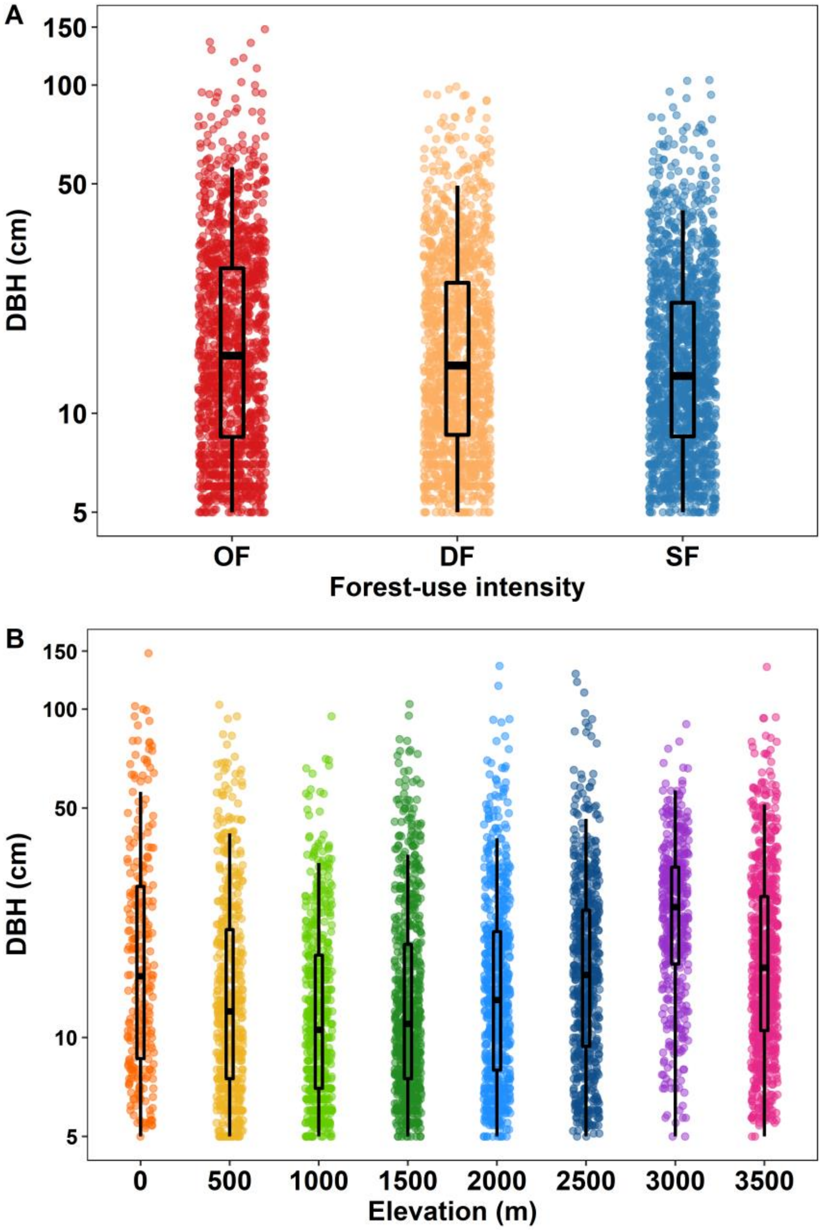

Figure 3.3. Diameter at breast height (DBH; n = 4127 individuals) for A different levels of forest-use intensity and for B eight sites along the elevation gradient. Vertical axis shows tree diameter at breast height (DBH) on a logarithm scale. Forest-use intensity levels are old-growth forest (OF), degraded forest (DF), and secondary forest (SF). Boxes are second and third quartile, whiskers upper and lower quartile and horizontal lines indicate mean values.

Tree functional traits

This dataset contains seven functional traits (Table 3.1; Fig. 3. 4). The number of species per functional trait varies, from 216 species for maximum height, to 159 for wood density, and 152- 156 species for leaf traits.

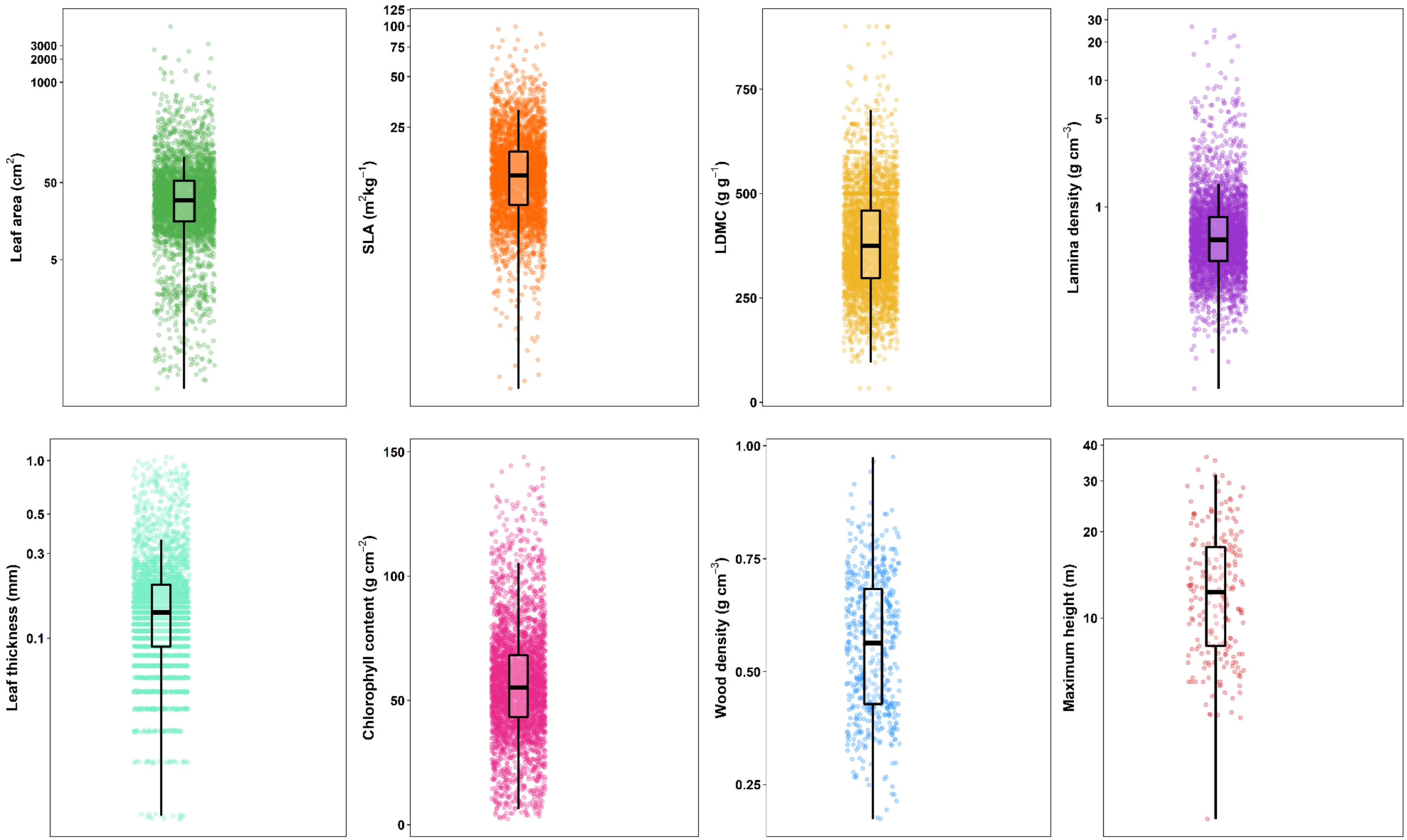

Figure 3.4. Distribution of seven functional traits along elevation and forest-use intensity gradients in the BIOVERA-Tree. Points represent leaf-level data for specific leaf area (n = 3262), leaf dry matter content (n = 3179), lamina density (n= 3310), leaf area (n = 3320), leaf thickness (n = 3406), and chlorophyll content (n = 3393); individual-level data for wood density (n = 525); and species-level data for maximum height (n = 216). Boxes are second and third quartile, whiskers upper and lower quartile and horizontal lines indicate mean values.

Data resources

Data package title BIOVERA-Tree: community, functional traits, and forest structure along forest-use intensity and elevational gradients in Veracruz, Mexico.

Number of data sets: 6

Data set 1: BIOVERA-Tree forest plots description

Description: Location of the 120 plots along the elevational gradient at the eastern slopes of Cofre de Perote in Veracruz, Mexico.

Data set 2: BIOVERA-Tree scientific name

Description: List of tree species along the elevational gradient and different levels of forest-use intensity.

Data set 3: BIOVERA-Tree community matrix

Description: Tree community matrix composition along eight elevational sites and three different forest-use intensity levels of 217 tree species (n = 5 plots per forest-use intensity within elevation).

Data set 4: BIOVERA-Tree forest structure

Description: Diameter at breast height (DBH) and tree height for 217 species along the elevational gradient, and different levels of forest-use intensity. Forest-use intensity levels are old-growth forest (OF), degraded forest (DF), and secondary forest (SF).

Data set 5: BIOVERA-Tree functional traits

Description: Plant functional traits measured along the elevational gradient and different levels of forest-use intensity; including leaf traits, wood density, and maximum height.

Data set 6: BIOVERA-Tree metadata, with definition and categories according with Darwin Core, Functional Diversity thesaurus and this research.

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General discussion

“La Mancha” at 0 m elevation

4 General discussion

My thesis contributes to the field of ecology of tropical mountains, providing new and relevant insights into tree biodiversity patterns and ecosystem functioning. In my thesis, I assessed the response of different facets of tree diversity and forest structure to forest-use intensity along an elevational gradient in Veracruz, México. My results revealed that the interactive effects of elevation and forest-use intensity change tree diversity patterns and community composition. Firstly, I showed that degraded forests were similar to old-growth forests in terms of species diversity and composition. This result is relevant for conservation and restoration because it shows that degraded forests have the capacity to protect similar species as those that occur in old-growth forests. I also found high functional diversity and functional redundancy in lowland and premontane tree communities, indicating that these tree communities are expected to be resilient to potential anthropogenic disturbances. In contrast, forests at high elevations of 3000-3500 m may be vulnerable to climate change and species loss, because they had low functional diversity and redundancy. My thesis also increases our knowledge about the response of tropical tree biodiversity to land-use change and elevation by making the underlying data on tree diversity, functional traits, and forest structure easily accessible to the scientific community. Sharing ecological data allows other researchers to ask new research questions, and, possibly, to synthesize how land-use intensity affects different aspects of biodiversity along elevational gradients across multiple sites in tropical regions.

4.1 The interactive effects of elevation and forest-use intensity on tree diversity

I found that the interactive effects of elevation and forest-use intensity changed tree species diversity patterns along the elevational gradient. This result is consistent with a previous multi-taxon study that demonstrated the effects of climate and land-use change on diversity patterns in Tanzania (Peters et al. 2019). In my study, tree diversity in old-growth forests exhibited a low-plateau pattern along the elevational gradient and changed into a bimodal pattern for degraded forests. The highest tree species diversity values in old-growth forests were observed between 0 and 2000 m, decreasing strongly towards the treeline. This pattern is unusual, yet has been described before(Reich et al. 2010; Toledo-Garibaldi & Williams-Linera 2014). The high species diversity between sea-level and 2000 m could be related to climatic conditions. Previous studies showed that precipitation and temperature increase tree diversity (Rana et al. 2019). However, previous studies of trees along elevational gradients showing that temperature is the primary climatic predictor of tree diversity (Sharma et al. 2019). A potential explanation for this pattern is the low minimum temperatures at this elevation, which represents a strong biophysical restriction that limits the occurrence of tropical tree species (Zanne et al. 2014; Veintimilla et al. 2019). Qian et al. (2020) assessed the relations between the phylogenetic structure of angiosperm trees in North America, and found that winter cold temperatures had a stronger effect on community composition than temperature seasonality. Another study showed that some tree angiosperm lineages exhibit functional traits that help them to avoid freezing induced embolism, enabling them to grow at high latitudes (Zanne et al. 2014; Segovia et al. 2020). To identify the ecological mechanisms that underpin the observed elevational patterns of diversity, I would propose examining trait-environment relationships using leaf and wood traits associated with drought tolerance, for example photosynthetic capacity, leaf water potential, and water use efficiency.

4.2 Floristic composition along the elevational gradient and forest-use intensity

My results showed that tree community composition varied along the elevational gradient and between forest-use intensity levels within elevation. In a new study, Feeley et al. (2020) demonstrated that the floristic composition and distribution of plant communities are changing owing to climate change. Specifically, they show that plant species that tolerate heat are increasing in abundance as temperatures increase. This phenomenon is termed thermophilization and primarily affects regions with intermediate temperatures, like temperate broadleaf and mixed forests moreover as temperate grasslands, savannas, and shrublands (Feeley et al. 2020). Along the elevational gradient of Cofre de Perote, where I conducted my studies, pinus and fir forests at high elevations, and other species with Nearctic affinities, could even be particularly prone to global climate change. Species from lowlands or with Neotropical affinities, on the other hand, may be more resilient to a warming climate. In other parts of the Neotropics, tropical and subtropical tree communities are observed to undergo changes in floristic composition, and are shifting towards communities being dominated by species from warm lowlands (Fadrique et al. 2018). Another global driver that´s is currently altering the floristic composition of tree communities is land-use change and a rise in land-use intensity, as also demonstrated in my thesis. Studying the tree seedling community, rather than the mature tree community, may capture the consequences of disturbances, e.g. wood extraction, cattle grazing, and fire, more quickly. In tropical forests of Mexico, Ramírez-Marcial (2003) found that the density of seedlings decreased with increasing land-use intensity or disturbance, because of changes in radiation and air temperatures to raised. To better understand the joint impacts of land-use intensity and global climate change on temporal changes in composition of forests along the elevational gradient at Cofre de Perote, I propose establishing a network of permanent plots in which repeated measurements of the tree and seedling communities are taken. This data would allow to evaluate the abundance of seedling species and their survival, facilitating conclusion on the impact of climate change on this potentially vulnerable mountain ecosystem.

4.3 Interactive effects of elevation and forest-use intensity on tree functional diversity and redundancy

I found that the interactive effect of elevation and forest-use intensity alters tree functional diversity and redundancy patterns. For functional diversity and redundancy, old-growth forests showed a low-plateau pattern and a bi-modal pattern for degraded forests, while secondary forests showed a hump-shaped pattern for functional diversity and a bi-modal pattern for functional redundancy. Previous studies of functional redundancy were focused on grasslands (Joner et al. 2011; Pillar et al. 2013) and forests (Laliberté et al. 2010). However, none evaluated the interactive effects of elevation and forest-use intensity on facets of biodiversity, or their potential impacts on ecosystem functioning and forest structure. At most elevations, I found that forest-use intensity did not affect functional diversity. This suggests that from sea level to 2000 m, tree communities had a high functional diversity and redundancy, making them more resilient to disturbances than tree communities at higher elevations. Tree communities at 3000-3500 m elevation have low functional redundancy, suggesting that these forests are less resilient and may be vulnerable to climate change, which supports the idea that environmental filtering is stronger in harsher environmental contexts (Spasojevic & Suding 2012).

4.4 Relationships between biomass and stem density with functional diversity and redundancy

Functionally diverse forests provide higher levels of ecosystem functioning and are likely to be more resilient to global change (Craven et al. 2016). I found positive relationships between functional redundancy and biomass at 0 m, indicating that forests with high functional diversity and redundancy increase ecosystem functioning (Díaz & Cabido 2001). I also found negative relationships between functional redundancy and biomass at 1500 and 3500 m, indicating that ecosystem functioning is dependent on a small number of functionally similar species (Petchey et al. 2007). The inconsistent relationships between stem density and functional diversity as well as functional redundancy suggest that changes in forest structure due to forest-use intensity may not have constant impacts on forest diversity and redundancy. Context-dependent bi-variate relationships of functional diversity and redundancy with tree biomass and stem density reveal that numerous criteria are necessary for safeguarding both biodiversity and ecosystem functioning in tropical mountain ecosystems. A possible explanation for the inconsistent relationships may be spatial grain at which these relationships were tested, although previous studies have found a tendency for these relationships to be stronger, not weaker, at smaller spatial grains (Chisholm et al. 2013). Similarly, our measurement of stem density may reflect demographic stochasticity that may obscure relationships between stem density and biodiversity facets (Vagle & McCain 2020). To test the robustness of my results to spatial grain, I propose establishing a network of permanent, nested plots with multiple sizes (e.g. 200 m^2, 400 m^2, and 800 m^2) to test for scale-dependent changes in biodiversity-ecosystem functioning relationships (Gonzalez et al. 2020) along the elevational gradient in Cofre de Perote. Repeated measurements of these plots would help to improve the probability of detecting the more-individuals hypothesis.

4.5 Future perspectives

Studies on elevational gradients in Mexico

Mexico is a megadiverse country that has a high plant and animal diversity and a variety of ecosystems and vegetation types spanning from deserts over grasslands to tropical and temperate forests (Mittermeier 1988). The northern part of Mexico belongs to the Nearctic region while the southern part of the country belongs to the Neotropical region. Where the Sierra Madre and the Trans-Mexican Volcanic Belt cross is known as the Mexican transition zone (Morrone 2006; Halffter et al. 2008; Morrone 2019). The complex orography and the Mexican transition zone contributes to Mexico's high diversity of natural communities, soils, and climates. For the reasons mentioned before, and given the limitations of my thesis, future studies along elevational and forest-use intensity gradients in this biodiverse zone should include permanent, nested plots to facilitate the monitoring of different facets of diversity and ecosystem functions over time and space (Anderson-Teixeira et al. 2015). For example, long-term studies may capture temporal changes in forest structure, as well as changes in land use and land-use intensity (Becker et al. 2007). Long-term studies along elevation and forest-use intensity gradients are ideal to understand and to make predictions about changes in the diversity and composition of tropical tree communities and ecosystem responses to climate change. To enable broader generalization of the results from the Cofre de Perote study system, I would establish similar studies along other elevational gradients in México, taking advantage of its unique biogeography and large diversity of environmental contexts.

4.6 Conclusion

The key results of my thesis have multiple implications for forest management and the conservation of tropical mountain forests. Conservation strategies usually focus on a single facet of diversity, particularly species diversity. However, other facets of diversity are crucial for the maintenance and stability of ecosystem functions (Cadotte et al. 2011; Naeem et al. 2016; Craven et al. 2018), indicating the need to integrate other facets of biodiversity into conservation policy (Pollock et al. 2017). However, it may be difficult for stakeholders and decision makers to integrate ecological concepts, such as functional diversity and redundancy, into forest management and conservation. One way of bridging this gap would be to develop spatial products that map functional diversity and redundancy over time. Such a product could be used to inform decision making in biodiversity hotspots, such as Veracruz, to identify areas that are important for enhancing ecological resilience. In addition to providing policy-relevant science, future studies along elevational gradients should also aim to explain the relevance of research findings to people who live in mountains and receive ecosystem services from mountain ecosystems. Doing so will raise awareness of how their well-being depends on functional ecosystems and may strengthen their support for biodiversity conservation.

In conclusion, my results show that interactive effects of land-use intensity and elevation determine species diversity, functional diversity and redundancy patterns and alter tree community composition. This demonstrates that Integrating various facets of biodiversity beyond species richness is paramount for tropical forest conservation and management strategies.

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6 Appendix

6.1 Appendix A-supporting information to chapter 1

Monge-González, M.L. et al. Response for tree diversity and community composition to forest-use intensity along a tropical elevational gradient. *Applied Vegetation Science*.

Table A1. List of tree species recorded at different levels of forest-use intensity along an elevational gradient in central Veracruz, Mexico. Total number of individuals recorded on 120 plots distributed along the elevational gradient (Ind.). The elevation and forest-use intensity (present = 1 or absent = 0) in which the species was observed is provided. Forest-use intensity levels are old-growth forest (OF), degraded forest (DF) and secondary forest (SF). Species nomenclature follows The Plant List < http://www.theplantlist.org/> (accessed on May 2019).

Family	**Species**	**Ind.**	**Elevation (m)**	**Forest-use intensity**		
				OF	**DF**	**SF**
Achatocarpaceae	*Achatocarpus nigricans* Triana	1	0	1	0	0
Actinidiaceae	Saurauia leucocarpa Schltdl.	18	1500, 2000	1	1	1
	Saurauia sp.	2	2500	0	1	0
Adoxaceae	*Sambucus canadensis* L.	1	2500	0	0	1
	Viburnum sp.	3	2000	1	0	0
Altingiaceae	*Liquidambar styraciflua* L.	93	1500	1	1	1
Anacardiaceae	*Comocladia macrophylla* (Hook. & Arn.) L.Riley	12	500	1	1	0
	Mangifera indica L.	25	0, 500, 1000	1	0	1
Annonaceae	*Annona cherimola* Mill.	1	1500	0	0	1
	Annona glabra L.	1	0	0	1	0
	Anonaceae sp. 2	2	500	1	1	0
	Guatteria sp.	1	500	1	0	0
	Mosannona depressa (Baill.) Chatrou	3	500, 1000	1	1	0
Apocynaceae	*Stemmadenia* sp.	21	0, 500, 1000	1	1	1
	Thevetia sp.	3	500	0	0	1
	Tonduzia longifolia (A.DC.) Markgr.	14	1000	0	1	1
Aquifoliaceae	*Ilex* sp.	4	500, 1000	1	1	0
Araliaceae	*Dendropanax arboreus* (L.) Decne. & Planch.	13	1000, 2000	1	1	1
	Dendropanax sp.	2	0	1	0	0
	Oreopanax echinops (Schltdl. & Cham.) Decne. & Planch.	1	2000	1	0	0
	Oreopanax flaccidus Marchal	1	2500	0	1	0
	Oreopanax xalapensis (Kunth) Decne. & Planch.	17	1500, 2000, 2500	1	1	0
Asteraceae	Asteraceae sp. 1	2	1500	1	0	0
	Asteraceae sp. 2	9	2000	0	1	1

	Asteraceae sp. 3	2	2500	0	1	0

Family	Species	Ind.	Elevation (m)	Forest-use intensity		
				OF	DF	SF
	Eupatorium sp.	92	1500	0	1	1
	Senecio sp.	3	2000	1	1	0
Betulaceae	*Alnus acuminata* Kunth	42	2000	1	1	1
	Alnus jorullensis Kunth	106	3000	1	1	1
	Carpinus caroliniana Walter	140	1500, 2000	1	1	1
Bignoniaceae	*Handroanthus chrysanthus* (Jacq.) S.O.Grose	2	0	0	0	1
Boraginaceae	Ehretia tinifolia L.	1	0	1	0	0
Burseraceae	*Bursera simaruba* (L.) Sarg.	153	0, 500, 1000	1	1	1
	Protium copal (Schltdl. & Cham.) Engl.	12	500, 1000	1	1	0
Cannabaceae	*Celtis caudata* Planch.	4	0	0	1	1
	Celtis iguanaea (Jacq.) Sarg.	2	0	1	0	0
	Celtis monoica Hemsl.	37	500, 1000	1	1	1
	Trema micrantha (L.) Blume	9	1500, 2000	1	1	1
Capparaceae	*Crateva tapia* L.	6	0	1	0	0
Celastraceae	Celastraceae sp. 1	9	500	0	1	0
	Celastraceae sp. 2	1	1000	1	0	0
	Celastraceae sp. 3	1	2500	0	1	0
	Gyminda tonduzii Loes.	44	500, 1000	1	1	1
	Schaefferia frutescens Jacq.	2	500	1	1	0
	Schaefferia sp.	6	0	1	1	0
	Wimmeria concolor Cham. & Schltdl.	1	1000	1	0	0
	Zinowiewia sp.	2	1000	0	0	1
Chloranthaceae	*Hedyosmum mexicanum* C.Cordem.	221	1500, 2000	1	1	1
Clethraceae	*Clethra alcoceri* Greenm.	4	2000	1	0	0
	Clethra mexicana DC.	57	1500, 2000	1	1	1
	Clethra occidentalis (L.) Kuntze	26	2500	1	1	0
Clusiaceae	*Clusia* sp.	3	500	0	0	1
Cochlospermaceae	*Cochlospermum vitifolium* (Willd.) Spreng.	5	0	0	0	1
Combretaceae	*Terminalia amazonia* (J.F.Gmel.) Exell	4	0	1	0	0
Compositae	*Roldana schaffneri* (Sch.Bip. ex Klatt) H.Rob. & Brettell	1	1500	0	0	1
Cunoniaceae	*Weinmannia pinnata* L.	19	2000, 2500	1	1	1
Cupressaceae	*Cupressus lusitanica* var. benthamii (Endl.) Carrière	52	2500	1	0	1
Dipentodontaceae	*Perrottetia longistylis* Rose	1	2000	0	1	0

Family	**Species**	**Ind.**	**Elevation (m)**	**Forest-use intensity**		
				OF	**DF**	**SF**
Ebenaceae	*Diospyros digyna* Jacq.	5	0	1	1	0
	Diospyros oaxacana Standl.	11	1000	1	0	1
Ericaceae	*Arbutus xalapensis* Kunth	8	3000	1	0	1
	Vaccinium leucanthum Schltdl.	21	1500, 2000	1	1	1
Euphorbiaceae	*Acalypha* sp.	3	2000	0	1	1
	Adelia barbinervis Cham. & Schltdl.	4	1000	0	0	1
	Alchornea latifolia Sw.	97	1500, 2000	1	1	1
	Croton glabellus L.	11	500	1	1	0
	Euphorbiaceae sp. 1	4	500	0	0	1
	Jatropha sp.	2	1000	0	1	1
	Sapium nitidum (Monach.) Lundell	1	0	0	0	1
	Sapium sp.	1	2000	1	0	0
Fagaceae	*Quercus affinis* Scheidw.	29	2500	1	1	1
	Quercus corrugata Hook.	144	2000, 2500	1	1	1
	Quercus cortesii Liebm.	21	1500	1	1	1
	Quercus delgadoana S. Valencia, Nixon & L.M. Kelly	20	1500, 2000	1	1	0
	Quercus germana Schltdl. & Cham.	47	500, 1000	1	1	1
	Quercus lancifolia Schltdl. & Cham.	100	1500, 2000, 2500	1	1	1
	Quercus leiophylla A.DC.	4	2500	0	1	0
	Quercus ocoteifolia Liebm.	27	1500, 2000	1	1	0
	Quercus oleoides Schltdl. & Cham.	9	500	0	1	1
	Quercus peduncularis Née	54	500,1000	1	1	1
	Quercus sapotifolia Liebm.	45	500	0	0	1
	Quercus sartorii Liebm.	35	1500	1	1	0
	Quercus sp. 1	4	500	0	1	0
	Quercus sp. 2	3	1500	0	1	0
	Quercus xalapensis Bonpl.	1	2000	1	0	0
Icacinaceae	*Oecopetalum mexicanum* Greenm. & C.H. Thomps.	2	500	1	0	0
Lauraceae	*Cinnamomum effusum* (Meisn.) Kosterm.	9	1500, 2500	1	1	0
	Cinnamomum pachypodum (Nees) Kosterm.	3	2000	0	1	0
	Cinnamomum psychotrioides (Kunth) Kosterm.	6	1500, 2000	1	1	1
	Lauraceae	1	500	0	1	0
	Nectandra salicifolia (Kunth) Nees	24	500, 1000	1	1	1
	Nectandra sp. 1	5	0	1	0	0

Family	**Species**	**Ind.**	**Elevation (m)**	**Forest-use intensity**		
				OF	**DF**	**SF**
	Nectandra sp. 2	1	1000	0	0	1
	Ocotea disjuncta Lorea-Hern.	4	2000	1	0	0
	Ocotea effusa (Meisn.) Hemsl.	5	2000	1	1	0
	Persea chamissonis Mez	5	2000	0	0	1
Leguminosae	*Acacia cornigera* (L.) Willd.	2	0	1	1	0
	Acacia pennatula (Schltdl. & Cham.) Benth.	12	1000	1	1	1
	Acacia sp. 1	6	0	1	1	1
	Acacia sp. 2	22	500,1000	1	1	1
	Caesalpinia sp.	6	0	1	1	0
	Diphysa americana (Mill.) M.Sousa	8	0	1	1	0
	Gliricidia sepium (Jacq.) Walp.	25	0	1	0	1
	Inga sp. 1	1	0	0	1	0
	Inga sp. 2	1	1500	1	0	0
	Leucaena sp.	2	0	1	0	0
	Lonchocarpus orizabensis Lundell	1	1500	1	0	0
	Lonchocarpus sp 1.	1	1000	0	1	0
	Lysiloma divaricatum (Jacq.) J.F.Macbr.	4	0	0	1	1
Malpighiaceae	*Byrsonima crassifolia* (L.) Kunth	4	500	1	0	1
Malvaceae	*Ceiba pentandra* (L.) Gaertn.	9	500, 1000	1	0	1
	Guazuma ulmifolia Lam.	20	0	1	0	1
	Heliocarpus americanus L.	10	0	1	0	1
	Luehea candida (Moc. & Sessé ex DC.) Mart.	1	0	0	1	0
	Malvaceae	2	500	1	0	0
	Pachira aquatica Aubl.	8	0	1	0	0
	Pseudobombax ellipticum (Kunth) Dugand	2	0,500	1	0	0
	Timiliaceae	1	1000	0	1	0
Melastomataceae	*Conostegia arborea* Steud.	1	1500	0	1	0
	Miconia glaberrima (Schltdl.) Naudin	90	1500, 2000	1	1	1
Meliaceae	*Cedrela odorata* L.	8	0	1	1	0
	Trichilia havanensis Jacq.	17	0, 500, 1000	1	1	0
Moraceae	*Brosimum alicastrum* Sw.	64	0, 500, 1000	1	1	1
	Castilla sp.	1	500	0	1	0
	Ficus cotinifolia Kunth	1	0	0	0	1
	Ficus insipida Willd.	2	0	1	1	0
	Ficus obtusifolia Kunth	9	500, 1000	1	1	1
	Ficus sp. 1	7	0	1	1	0

Family	Species	Ind.	Elevation (m)	Forest-use intensity		
				OF	DF	SF
	Ficus sp. 2	3	0	1	0	0
	Ficus sp. 3	6	500	1	0	1
	Maclura tinctoria (L.) D. Don ex Steud	18	500, 1000	1	1	0
	Trophis racemosa (L.) Urb.	1	500	0	0	1
Myrtaceae	*Calyptranthes* sp.	1	1000	1	0	0
	Eugenia capuli (Schltdl. & Cham.) Hook. & Arn.	4	0	1	0	0
	Eugenia naraveana Cházaro & Franc.-Gut.	1	2000	0	0	1
	Eugenia sp. 2	23	500, 1000	1	1	0
	Pimenta dioica (L.) Merr.	1	2000	0	0	1
Oleaceae	*Fraxinus dubia* (Willd. ex Schult. & Schult.f.) P.S.Green & M.Nee	13	500	0	1	1
	Fraxinus schiedeana Cham. & Schltdl.	8	1000	0	1	1
	Osmanthus sp.	2	2000	0	1	1
Pentaphylacaceae	*Cleyera theoides* (Sw.) Choisy	1	1500	1	0	0
	Ternstroemia sylvatica Schltdl. & Cham.	14	2000, 2500	0	1	1
Phyllonomaceae	*Phyllonoma laticuspis* (Turcz.) Engl.	3	2000	0	1	1
Pinaceae	*Abies hickelii* Flous & Gaussen	2	3000	0	1	0
	Abies religiosa (Kunth) Schltdl. & Cham.	473	3000, 3500	1	1	1
	Pinus ayacahuite Ehrenb. ex Schltdl.	93	2500, 3000	1	1	1
	Pinus hartwegii Lindl.	356	3000, 3500	1	1	1
	Pinus montezumae Lamb.	175	2500, 3000	1	1	1
	Pinus patula Schiede ex Schltdl. & Cham.	11	2000, 2500, 3000	0	1	1
	Pinus pseudostrobus Lindl.	77	2000, 2500	1	1	1
	Pinus teocote Schied. ex Schltdl. & Cham.	223	2500, 3000, 3500	1	1	1
Piperaceae	*Piper nudum* C. DC	5	500	1	0	0
	Piper sp.	1	1500	0	0	1
Polygonaceae	*Coccoloba humboldtii* Meisn.	1	0	0	1	0
Primulaceae	*Myrsine coriacea* (Sw.) R. Br. ex Roem. & Schult.	21	1500, 2000	1	1	1
Proteaceae	*Macadamia integrifolia* Maiden & Betche	5	1500	0	1	0
Rhamnaceae	*Rhamnus humboldtiana* Willd. ex Schult.	15	0	0	1	1
	Rhamnus sp.	14	2000, 2500	1	1	1

Family	Species	Ind.	Elevation (m)	Forest-use intensity		
				OF	DF	SF
	Sageretia sp.	1	0	0	1	0
Rosaceae	*Prunus brachybotrya* Zucc.	2	2500	0	1	0
	Prunus serotina Ehrh.	29	1500, 2000, 2500	1	1	1
	Rosaceae sp. 1	3	1000	1	1	1
	Rosaceae sp. 2	1	2500	1	0	0
Rubiaceae	*Chiococca alba* (L.) Hitchc.	119	1000	1	1	1
	Exostema mexicanum A.Gray	1	500	0	1	0
	Palicourea sp.	2	2000	1	0	0
	Psychotria galeottiana (M.Martens) C.M.Taylor & Lorence	2	1500	1	0	0
	Psychotria perotensis Cast.-Campos	5	2000	0	1	0
	Psychotria sp.	7	500, 1000	1	0	1
	Rubiaceae sp. 1	2	0	1	0	0
	Rubiaceae sp. 2	5	500	1	1	0
	Rubiaceae sp. 3	8	1000	1	1	1
	Rubiaceae sp. 4	1	2000	0	0	1
	Rubiaceae sp. 5	1	1500	0	1	0
	Stenostomum aromaticum (Cast.-Campos & Lorence) Borhidi	9	500	1	1	0
Rutaceae	*Citrus reticulata* Blanco	8	1000	0	1	0
	Zanthoxylum melanostictum Schltdl. & Cham.	29	1500, 2000	1	1	1
	Zanthoxylum sp.	32	500, 1000	1	1	1
Salicaceae	*Casearia corymbosa* Kunth	3	0, 500	1	0	1
	Salix humboldtiana Willd.	1	0	1	0	0
Sapindaceae	*Cupania dentata* Moc. & Sessé ex DC.	4	0, 1000	1	0	1
	Exothea copalillo (Schltdl.) Radlk.	94	500, 1000	1	1	1
Sapotaceae	*Manilkara zapota* (L.) P.Royen	1	0	1	0	0
	Pouteria sp.	3	500	1	0	0
	Sideroxylon contrerasii (Lundell) T.D.Penn.	5	2000	0	1	0
	Sideroxylon salicifolium (L.) Lam.	6	1000	1	0	1
Scrophulariaceae	Buddlejaceae sp.	2	2000	0	0	1
Solanaceae	*Solanum* sp. 1	2	1000	0	0	1
	Solanum sp. 2	4	1500, 2000	1	1	0
Staphyleaceae	*Turpinia insignis* (Kunth) Tul.	10	1500, 2000	1	1	0
	Turpinia occidentalis (Sw.) G.Don	5	2000, 2500	1	1	0
Styracaceae	*Styrax glabrescens* Benth.	20	1500, 2000	1	1	0

Family	Species	Ind.	Elevation (m)	Forest-use intensity		
				OF	DF	SF
Symplocaceae	*Symplocos limoncillo* Humb. & Bonpl.	10	1500, 2500	1	1	1
	Symplocos longipes Lundell	15	2000	1	1	1
Symplocaceae	*Symplocos speciosa* Hemsl.	7	1500	0	1	0
Unidentified	Unidentified species 1	1	0	1	0	0
	Unidentified species 2	1	0	0	1	0
	Unidentified species 3	1	0	1	0	0
	Unidentified species 4	2	500	0	1	0
	Unidentified species 5	1	500	0	1	0
	Unidentified species 6	10	500, 1000	1	1	1
	Unidentified species 7	5	500, 1000	1	1	1
	Unidentified species 8	4	500, 1000	1	1	0
	Unidentified species 9	1	500	0	1	0
	Unidentified species 10	1	500	0	0	1
	Unidentified species 11	1	500	1	0	0
	Unidentified species 13	3	2000	1	1	0
	Unidentified species 14	1	2500	0	1	0
	Unidentified species 15	2	2500	0	1	0
	Unidentified species 20	8	1500	1	1	1
	Unidentified species 221	1	2000	1	0	0
	Unidentified species 232	6	2500	0	1	0
Urticaceae	*Cecropia peltata* L.	2	500	1	0	0
	Urera sp.	1	500	1	0	0
Verbenaceae	*Citharexylum hidalgense* Moldenke	3	1500, 2500	1	1	0
	Citharexylum mocinoi D.Don	23	0, 500, 1000	1	1	1
Winteraceae	*Drymis* sp.	3	2000	1	0	1

Supporting information to the paper

Table A2. Results of the analysis of variance (ANOVA) for the models evaluating the effects of elevation and forest-use intensity nested in elevation on tree species richness. Shannon and Simpson diversity using effective number of species, i.e., Hill numbers q = 0, q = 1, and q = 2, respectively. Species richness and all diversity indices were natural-log transformed. Bold values are statistically significant at <0.05.

	Species richness (q = 0)		**Shannon (q = 1)**		**Simpson (q = 2)**	
	F-value	*p*-value	F-value	*p*-value	F-value	*p*-value
Elevation	$\mathbf{F_{7,96} = 57.02}$	0.001	$\mathbf{F_{7,96} = 49.44}$	0.001	$\mathbf{F_{7,96} = 37.74}$	0.001
Elevation/Forest-use intensity	$\mathbf{F_{16,96} = 4.38}$	0.001	$\mathbf{F_{16,96} = 5.47}$	0.001	$\mathbf{F_{16,96} = 4.91}$	0.001

Table A3. Results of statistical analyses of multiple comparisons of means using Tukey Contrasts. Multiple comparisons are between in tree species richness, Shannon and Simpson diversity using effective number of species, i.e., Hill numbers q = 0, q = 1, and q = 2, respectively in every forest-use intensity and each elevational site. Forest-use intensity levels are old-growth forest (OF), degraded forest (DF) and secondary forest (SF). Bold values are statistically significant at < 0.05.

Elevation (m a.s.l)	**Forest-use intensity**	**Species richness (q = 0)**				**Shannon (q = 1)**				**Simpson (q = 2)**			
		Estimate	**Standard error**	**t-value**	***p*-value**	**Estimate**	**Standard error**	**t-value**	***p*-value**	**Estimate**	**Standard error**	**t-value**	***p*-value**
0	DF vs OF	-0.62	0.54	-1.14	0.51	-0.52	0.51	-1.04	0.57	-0.41	0.46	-0.89	0.65
	SF vs OF	-1.61	0.54	-2.97	**0.03**	-1.51	0.51	-3.00	**0.03**	-1.31	0.46	-2.85	**0.04**
	SF vs DF	-0.99	0.54	-1.83	0.20	-0.99	0.51	-1.96	0.17	-0.90	0.46	-1.96	0.17
500	DF vs OF	-0.15	0.19	-0.754	0.73	-0.20	0.25	-0.79	0.72	-0.08	0.30	-0.28	0.96
	SF vs OF	-0.59	0.19	-3.00	**0.02**	-0.73	0.25	-2.84	**0.04**	-0.60	0.30	-2.00	0.15
	SF vs DF	-0.44	0.19	-2.254	0.10	-0.52	0.25	-2.05	0.14	-0.51	0.30	-1.72	0.24
1000	DF vs OF	0.02	0.23	0.10	0.99	0.48	0.19	2.53	0.06	0.65	0.17	3.71	**0.01**
	SF vs OF	-0.09	0.23	-0.38	0.92	0.18	0.19	0.94	0.63	0.35	0.17	1.97	0.16
	SF vs DF	-0.11	0.23	-0.48	0.88	-0.30	0.19	-1.59	0.29	-0.30	0.17	-1.74	0.23
1500	DF vs OF	-0.29	0.38	-0.76	0.73	-0.67	0.33	-2.01	0.15	-0.70	0.31	-2.29	0.10
	SF vs OF	-1.48	0.38	-3.88	**0.01**	-1.59	0.33	-4.80	**0.001**	-1.44	0.31	-4.71	**0.001**
	SF vs DF	-1.19	0.38	-3.12	**0.02**	-0.93	0.33	-2.79	**0.04**	-0.74	0.31	-2.42	0.08
2000	DF vs OF	0.13	0.35	0.38	0.93	0.37	0.26	1.42	0.36	0.53	0.26	1.99	0.16
	SF vs OF	-0.27	0.35	-0.76	0.74	-0.19	0.26	-0.72	0.76	-0.01	0.26	-0.05	1.00
	SF vs DF	-0.40	0.35	-1.13	0.51	-0.55	0.26	-2.15	0.12	-0.54	0.26	-2.04	0.14
2500	DF vs OF	0.58	0.32	1.79	0.21	0.36	0.28	1.27	0.44	0.24	0.26	0.90	0.65
	SF vs OF	-0.51	0.32	-1.58	0.29	-0.67	0.28	-2.36	0.09	-0.58	0.26	-2.19	0.11
	SF vs DF	-1.09	0.32	-3.38	**0.01**	-1.03	0.28	-3.62	**0.01**	-0.82	0.26	-3.09	**0.02**
3000	DF vs OF	0.10	0.25	0.39	0.92	-0.10	0.21	-0.49	0.88	-0.15	0.18	-0.87	0.67
	SF vs OF	0.02	0.25	0.06	1.00	-0.04	0.21	-0.19	0.98	-0.06	0.18	-0.34	0.94
	SF vs DF	-0.08	0.25	-0.33	0.94	0.06	0.21	0.30	0.95	0.09	0.18	0.53	0.86
3500	DF vs OF	-0.03	0.06	-0.51	0.87	-0.01	0.07	-0.09	1.00	-0.006	0.07	-0.02	1.00
	SF vs OF	0.52	0.06	8.24	**0.001**	0.31	0.07	4.18	**0.003**	0.24	0.07	3.56	**0.01**
	SF vs DF	0.55	0.06	8.75	**0.001**	0.32	0.07	4.26	**0.002**	0.24	0.07	3.58	**0.01**

Table A4. Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) evaluating the effects of elevation and forest-use intensity nested in elevation on tree community composition. Dissimilarity was estimated using incidence-based Jaccard dissimilarity and 999 permutations.

	DF	R^2	F-value	*p*-value
Elevation	**7,96**	**0.2997**	**8.69**	0.001
Elevation/Forest-use intensity	**16,96**	**0.2273**	**2.8829**	0.001

Table A5. Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) evaluating the effects of elevation and forest-use intensity nested in elevation on tree community composition. Dissimilarity was estimated using abundance-based Bray Curtis dissimilarity and 999 permutations.

	DF	R^2	F-value	*p*-value
Elevation	**7,96**	**0.3995**	**14.94**	0.001
Elevation/Forest-use intensity	**16,96**	**0.2337**	**3.82**	0.001

Table A6. Results of statistical analysis of pairwise comparisons between tree community composition estimated using incidence-based Jaccard in every forest-use intensity and per each elevation. Forest-use intensity levels are old-growth forests (OF), degraded forests (DF) and secondary forests (SF). Pairwise comparisons were Bonferroni corrected, we used p-value adjusted, bold values are statistically significant at <0.05.

Elevation (m a.s.l)	**Comparison Forest-use intensity**	**F-value**	**R^2**	***p*-value**	***p*-value adjusted**
0	DF vs OF	1.572143	0.164242	0.073	0.219
0	DF vs SF	2.532803	0.240468	0.007	**0.021**
0	OF vs SF	2.287863	0.222385	0.011	**0.033**
500	DF vs OF	3.980354	0.306644	0.01	**0.03**
500	DF vs SF	3.149622	0.259236	0.013	**0.039**
500	OF vs SF	4.834669	0.376688	0.009	**0.027**
1000	DF vs OF	4.135303	0.340766	0.008	**0.024**
1000	DF vs SF	3.276557	0.290564	0.007	**0.021**
1000	OF vs SF	5.241912	0.395858	0.007	**0.021**
1500	DF vs OF	6.149838	0.434622	0.007	**0.021**
1500	DF vs SF	13.49823	0.627876	0.006	**0.018**
1500	OF vs SF	13.08687	0.620617	0.006	**0.018**
2000	DF vs OF	1.625135	0.168843	0.084	0.252
2000	DF vs SF	2.902745	0.26624	0.036	0.108
2000	OF vs SF	4.451938	0.35753	0.004	**0.012**
2500	DF vs OF	1.813884	0.184828	0.152	0.456
2500	DF vs SF	2.977953	0.271267	0.009	**0.027**
2500	OF vs SF	2.991333	0.272154	0.031	0.093
3000	DF vs OF	3.285182	0.291106	0.059	0.177
3000	DF vs SF	0.722426	0.082824	0.545	1
3000	OF vs SF	5.083685	0.388551	0.006	**0.018**
3500	DF vs OF	1.886943	0.190852	0.224	0.672
3500	DF vs SF	16.81742	0.677646	0.012	**0.036**
3500	OF vs SF	20.04255	0.714719	0.007	**0.042**

Table A7. Results of statistical analysis of pairwise comparisons between tree community composition estimated using abundance-based Bray Curtis in every forest-use intensity and per each elevation. Forest-use intensity levels are old-growth forests (OF), degraded forests (DF) and secondary forests (SF). Pairwise comparisons were Bonferroni corrected, we used p-value adjusted, bold values are statistically significant at <0.05.

Elevation (m a.s.l)	**Comparison Forest-use intensity**	**F-value**	**R^2**	***p*-value**	***p*-value adjusted**
0	DF vs OF	1.572143	0.164242	0.06	0.11
0	DF vs SF	2.532803	0.240468	0.01	**0.0275**
0	OF vs SF	2.287863	0.222385	0.007	**0.0275**
500	DF vs OF	3.256349	0.28929	0.039	0.117
500	DF vs SF	2.64077	0.248175	0.023	0.069
500	OF vs SF	4.834669	0.376688	0.008	**0.024**
1000	DF vs OF	4.135303	0.340766	0.013	**0.039**
1000	DF vs SF	3.276557	0.290564	0.012	**0.036**
1000	OF vs SF	5.241912	0.395858	0.015	**0.045**
1500	DF vs OF	6.149838	0.434622	0.006	**0.018**
1500	DF vs SF	13.49823	0.627876	0.008	**0.024**
1500	OF vs SF	13.08687	0.620617	0.007	**0.021**
2000	DF vs OF	1.625135	0.168843	0.082	0.246
2000	DF vs SF	2.902745	0.26624	0.019	0.057
2000	OF vs SF	4.451938	0.35753	0.008	**0.024**
2500	DF vs OF	1.819823	0.185321	0.154	0.462
2500	DF vs SF	2.977953	0.271267	0.009	**0.027**
2500	OF vs SF	3.001878	0.272851	0.029	0.087
3000	DF vs OF	3.285182	0.291106	0.044	0.132
3000	DF vs SF	0.722426	0.082824	0.586	1
3000	OF vs SF	5.083685	0.388551	0.008	**0.024**
3500	DF vs OF	1.886943	0.190852	0.231	0.693
3500	DF vs SF	16.81742	0.677646	0.009	**0.027**
3500	OF vs SF	20.04255	0.714719	0.012	**0.036**

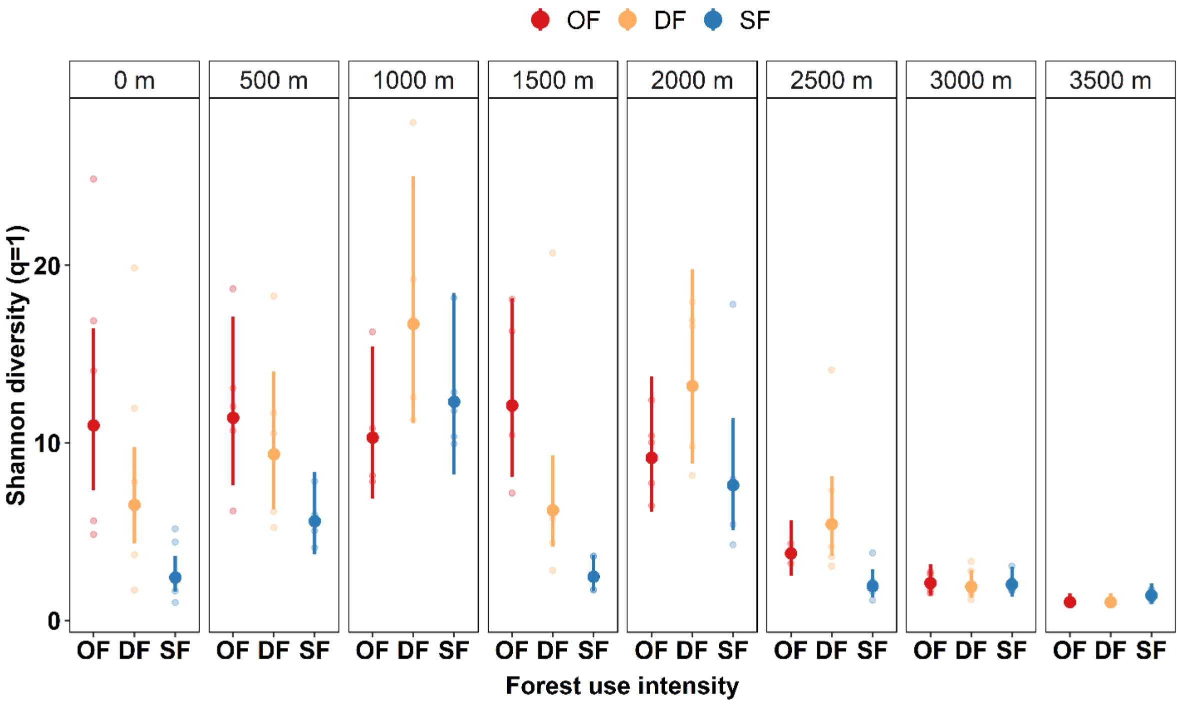

Figure A1. Shannon diversity (Hill number = 1) along the elevation gradient and different levels of forest use intensity (n = 120 plots). Shannon diversity was significantly affected by elevation (F7,96 = 49.4, p-value < 0.001) and forest-use intensity within elevation (F16, 96 = 5.47, p-value <0.001; Supplementary table 2). Bold points are predicted means from the nested ANOVA (lines are 95 % confidence intervals). Light points are plot-level values. Forest-use intensity levels are old-growth forest (OF, red), degraded forest (DF, yellow) and secondary forest (SF, blue).

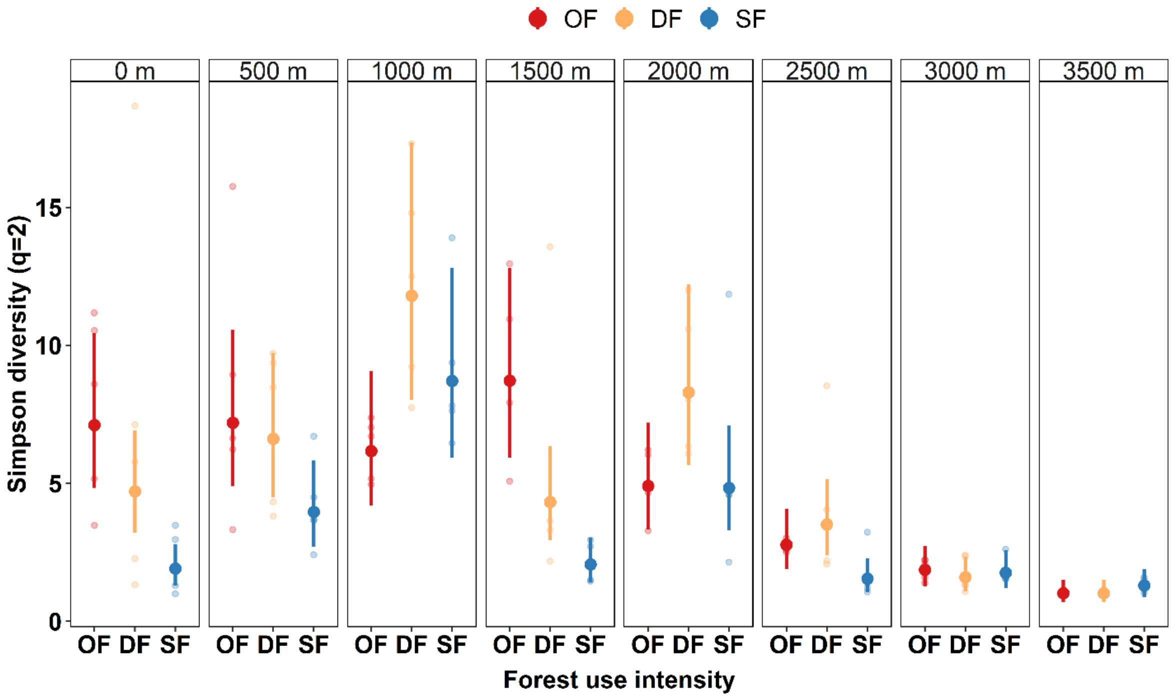

Figure A2. Simpson diversity (Hill number = 2) along the elevation gradient and different levels of forest use intensity (n = 120 plots). Simpson diversity was significantly affected by elevation ($F_{7,96}$ = 37.74, *p*-value < 0.001) and forest-use intensity within elevation ($F_{16, 96}$ = 4.91, *p*-value <0.001; Supplementary table 2). Bold points are predicted means from the nested ANOVA (lines are 95 % confidence intervals). Light points are plot-level values. Forest-use intensity levels are old-growth forest (OF, red), degraded forest (DF, yellow) and secondary forest (SF, blue).

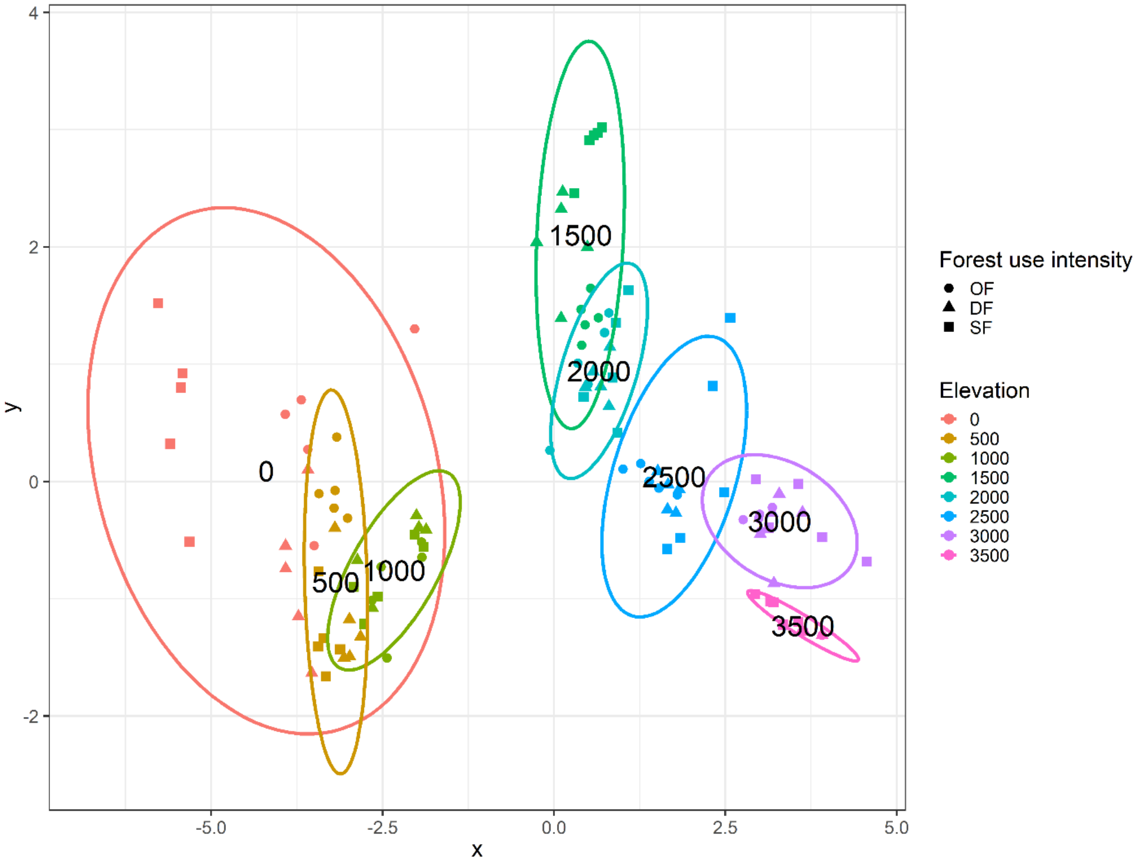

Figure A3. Tree community composition along eight elevational sites and three different forest-use intensity levels. Non-metric multidimensional scaling (NMDS) based on Bray Curtis dissimilarity (n = 5 plots per forest-use intensity within elevation), ellipses show the range of each elevation site. Forest-use intensity levels are old-growth forest (OF, circles), degraded forest (DF, triangles) and secondary forest (SF, squares).

6.2 Appendix B-supporting information for chapter 2

Supporting information

Monge-González, M.L. et al. 2020. Interactive effects of land-use intensity and elevation reduce functional redundancy of tropical tree communities.

Supplementary Methods

Study region

The study region encompasses a range of environmental conditions (Gómez-Díaz et al., 2017), from tropical-dry climate in the lowlands (mean annual temperature (MAT): 26-21 °C, mean annual precipitation (MAP): 1222-1331 mm), over temperate-humid at mid-elevations (MAT: 14-19 °C; MAP: 2952-1435 mm), to a cold, dry high-elevation climate (MAT: 9 °C; MAP: 708 mm) (SMN, 2019; Soto-Esparza & Giddings-Berger, 2011). For a more detailed description of the study region see Monge-González et al., (2020) or study design and forest-use intensity definitions see Gómez-Díaz et al. (2017).

Trait measurements and imputation.

We chose traits because they capture variation in plant growth and function (Díaz et al., 2016), and are likely to respond to changes in land-use intensity and climate. For example, maximum tree height is related with a species' capacity to capture light and seed dispersal (Díaz et al., 2016). Wood density is related with mechanical support, and the selected leaf traits with leaf energy and water balance, mechanical strength, and photosynthesis (Díaz et al., 2016.

Traits were measured following standardized measurement protocols (Chave, 2005; Pérez-Harguindeguy et al., 2016). We determined maximum tree height for each species following King et al. (2006) by first classifying the trees into three groups: 1) species with more than 20 individuals, 2) species with between 5-19 individuals, and 3) species with less than five individuals. For the first group, we calculated maximum tree height as the mean of the tallest three individuals. For the second group, we calculated maximum tree height as the mean of the tallest two individuals; and for the third group, we used the height of the tallest individual (King et al., 2006).

We collected wood samples for 131 species and leaf samples for 144 species using an increment borer and the water-displacement method. We selected 1 to 3 tree individuals per species and collected 5 to 10 leaves per individual, and collected 1 to 3 wood samples per tree. We calculated leaf area using WinFOLIA (Version 2016b Pro, Regent Instruments Canada, 2016). For chlorophyll concentration, we used a SPAD-502 chlorophyll meter (Spectrum Technologies, Plainfield, IL, USA) and converted measurements to chlorophyll concentration using the formula by Coste et al. (2010).

Because we were not able to collect traits for all species in our plots, we obtained wood density values for 44 species from the Botanical Information and Ecology Network (BIEN) database (Enquist, Condit, Peet, Schildhauer, & Thiers, 2016). For 16 species for which species-level data were not available, we calculated the genus-level average for wood density, a trait that is phylogenetically highly conserved (Chave et al., 2006). We then performed phylogenetic trait imputation for species with missing leaf traits following Penone et al. (2014). To this end, we first constructed a phylogeny using the molecular phylogeny of Smith and Brown (2018), conservatively binding species using dating information from congeners in the tree with the '*congeneric.merge*' function in the package '*pez*' (Pearse et al., 2015). We used the random forest algorithm with the function '*missForest*' in the '*missForest*' package (Stekhoven & Buehlmann, 2012) and phylogenetic eigenvectors (Penone et al., 2014). We tested the impact on the imputation error of using different numbers of phylogenetic eigenvectors (n = 1 – 30) and selected the number of phylogenetic eigenvectors that minimized the imputation error for each trait. In total, we imputed leaf trait values for 21% of all species (39 of 184), which is below the recommended threshold of 30% (Penone et al., 2014).

Supplementary Results

Table B1. Quality estimates of functional space. In bold the number of dimensions and the metric used to compute functional distance.

Mean squared deviation	Distances	
Dimensions	Gower	Euclidean
2	**0.0038**	**1.35**
3	**0.0021**	**0.7588**
4	**0.0010**	**0.3732**
5	0.0004	**0.1347**
6	**0.00034**	**0.034**
7	**0.0002**	

Table B2. Results of the analysis of variance (ANOVA) for the models evaluating the effects of elevation and forest-use intensity nested in elevation on functional diversity, functional redundancy using effective number of species i.e., Hill numbers q = 0, 1, and 2.
Bold values are statistically significant.

Variable	**Elevation**			**Elevation/Forest-use intensity**		
	DF	**F value**	***p*-value**	**DF**	**F value**	***p*-value**
Functional diversity (q=0)	7,87	25.76	**9.81** $^{e-19}$	16,87	1.68	**6.55** $^{e-02}$
Functional diversity (q=1)	7,87	21.39	**1.67** $^{e-16}$	16,87	2.16	**1.20** $^{e-02}$
Functional diversity (q=2)	7,87	18.96	**3.80** $^{e-15}$	16,87	2.27	**7.90** $^{e-03}$
Functional redundancy (q=0)	7,87	43.36	**9.59** $^{e-26}$	16,87	5.88	**1.81** $^{e-08}$
Functional redundancy (q=1)	7,87	28.03	**8.47** $^{e-20}$	16,87	5.94	**1.44** $^{e-08}$
Functional redundancy (q=2)	7,87	19.79	**1.27** $^{e-15}$	16,87	4.61	**1.36** $^{e-06}$

Table B3. Results of standardized major axis (SMA) regression analysis. Regressions are between biomass and functional diversity using effective number of species, i.e., Hill numbers q = 0, 1, and 2, in every elevational site. Bold values are statistically significant.

	Functional diversity								
	q = 0			**q = 1**			**q = 2**		
Elevation (m a.s.l)	**R^2 (*p*-value)**	**Intercept (low, high)**	**Slope (low, high)**	**R^2 (*p*-value)**	**Intercept (low, high)**	**Slope (low, high)**	**R^2 (*p*-value)**	**Intercept (low, high)**	**Slope (low, high)**
0	**0.37** **(0.015)**	-0.14 (-0.44, 0.16)	0.32 (0.20, 0.50)	**0.36** **(0.017)**	-0.22 (-0.53, 0.08)	0.31 (0.20, 0.50)	**0.33** **(0.022)**	-0.27 (-0.59, 0.04)	0.32 (0.20, 0.51)
500	0.0018 (0.90)	-0.21 (-0.77, 0.34)	0.32 (0.16, 0.65)	0.014 (0.72)	1.27 (0.62, 1.91)	-0.38 (-0.75, -0.19)	0.02 (0.62)	1.30 (0.59, 2.01)	-0.41 (-0.83, -0.20)
1000	0.0024 (0.88)	1.40 (0.75, 2.06)	-0.44 (-0.88, -0.22)	0.04 (0.54)	1.31 (0.69, 1.94)	-0.43 (-0.85, -0.21)	0.072 (0.42)	1.23 (0.65, 1.82)	-0.41 (-0.80, -0.20)
1500	0.23 (0.06)	1.54 (0.90, 2.17)	-0.49 (-0.81, -0.29)	**0.33** **(0.02)**	1.52 (0.92, 2.12)	-0.50 (-0.81, -0.31)	**0.35** **(0.019)**	1.52 (0.91, 2.13)	-0.51 (-0.82, -0.32)
2000	**0.32** **(0.027)**	-0.18 (-0.50, 0.13)	0.29 (0.18, 0.47)	0.19 (0.10)	-0.22 (-0.56, 0.11)	0.28 (0.17,0.47)	0.14 (0.16)	-0.24 (-0.59, 0.09)	0.28 (0.16, 0.48)
2500	0.0014 (0.89)	-0.45 (-0.99, 0.08)	0.35 (0.19, 0.63)	0.0006 (0.93)	-0.97 (-1.74, -0.19)	0.51 (0.28,0.92)	0.0039 (0.83)	1.41 (0.64, 2.18)	-0.50 (-0.91, -0.27)
3000	0.15 (0.15)	-0.25 (-0.52,0.017)	0.23 (0.13, 0.39)	0.16 (0.13)	-0.17 (-0.37, 0.022)	0.17 (0.10, 0.29)	0.20 (0.088)	-0.15 (-0.32, 0.014)	0.15 (0.09, 0.25)
3500	**0.42** **(0.008)**	0.76 (0.43, 1.08)	-0.27 (-0.43, -0.17)	**0.37** **(0.015)**	0.69 (0.38, 1.00)	-0.25 (-0.40, -0.16)	**0.33** **(0.02)**	0.64 (0.34, 0.94)	-0.23 (-0.38, -0.14)

Table B4. Results of standardized major axis (SMA) regression analysis. Regressions between biomass with functional redundancy using effective number of species, i.e., Hill numbers q = 0, 1, and 2, in every elevational site. Bold values are statistically significant.

	Functional redundancy								
	q = 0			**q = 1**			**q = 2**		
Elevation (m a.s.l)	**R^2 (*p*-value)**	**Intercept (low, high)**	**Slope (low, high)**	**R^2 (*p*-value)**	**Intercept (low, high)**	**Slope (low, high)**	**R^2 (*p*-value)**	**Intercept (low, high)**	**Slope (low, high)**
0	**0.43** **(0.007)**	-8.98 (-14.78, -3.19)	6.36 (4.11, 9.86)	**0.42** **(0.008)**	-7.35 (-11.93, -2.77)	5.00 (3.22, 7.77)	**0.41** **(0.01)**	-5.77 (-9.35, -2.19)	3.86 (2.47, 6.02)
500	0.18 (0.18)	-21.87 (-40.86, -2.89)	12.27 (6.50, 23.19)	0.025 (0.64)	-17.78 (-33.75, -1.81)	9.42 (4.73, 18.76)	0.015 (0.71)	18.69 (6.35, 31.03)	-7.24 (-14.46, -3.62)
1000	0.0026 (0.88)	-2.31 (-10.26, 5.64)	5.38 (2.68, 10.79)	0.24 (0.12)	15.35 (8.49, 21.75)	-5.01 (-9.27, -2.70)	**0.36** **(0.04)**	15.37 (8.59, 22.15)	-5.77 (-10.21, -3.26)
1500	**0.26** **(0.048)**	46.47 (25.96, 66.99)	-16.45 (-26.91, -10.05)	**0.37** **(0.015)**	38.43 (22.00, 54.86)	-14.22 (-22.49, -8.99)	**0.39** **(0.01)**	29.66 (17.10, 42.21)	-11.07 (-17.38, -7.06)
2000	0.24 (0.062)	-5.51 (-13.37, 2.34)	6.87 (4.16, 11.33)	0.15 (0.14)	-7.17 (-14.01, -0.34)	5.66 (3.35,9.58)	0.07 (0.33)	-6.12 (-11.57, -0.67)	4.29 (2.47, 7.43)
2500	0.016 (0.66)	-14.49 (-25.76, -3.23)	7.48 (4,15, 13.49)	0.07 (0.35)	-6.11 (-10.61, -1.60)	3.08 (1.73, 5.47)	0.13 (0.18)	-4.01 (-6.77, -1.25)	1.96 (1.12, 3.41)
3000	0.018 (0.62)	-1.93 (-3.96, 0.09)	1.63 (0.92, 2.86)	0.17 (0.12)	-1.23 (-2.31, -0.16)	0.94 (0.56, 1.59)	**0.25** **(0.05)**	-1.02 (-1.80, -0.24)	0.72 (0.44, 1.19)
3500	**0.55** **(0.001)**	7.06 (4.43, 9.69)	-2.55 (-3.77, -1.72)	**0.44** **(0.006)**	1.79 (1.04, 2.55)	-0.65 (-1.01, -0.42)	**0.26** **(0.05)**	1.22 (0.62, 1.82)	-0.45 (-0.74, -0.27)

Table B5. Results of standardized major axis (SMA) regression analysis. Regressions are between stems density (ha-1) with functional diversity, using effective number of species, i.e., Hill numbers q = 0, 1, and 2, in every elevational site. Bold values are statistically significant.

	Functional diversity								
	q = 0			**q = 1**			**q = 2**		
Elevation (m a.s.l)	**R^2 (*p*-value)**	**Intercept (low, high)**	**Slope (low, high)**	**R^2 (*p*-value)**	**Intercept (low, high)**	**Slope (low, high)**	**R^2 (*p*-value)**	**Intercept (low, high)**	**Slope (low, high)**
0	**0.44** **(0.006)**	-1.30 (-2.10, -0.50)	0.69 (0.44, 1.06)	**0.29** **(0.03)**	-1.38 (-2.28, -0.48)	0.68 (0.42,1.11)	**0.25** **(0.05)**	-1.44 (-2.38, -0.51)	0.69 (0.42, 1.14)
500	0.18 (0.18)	-0.65 (-1.45, 0.14)	0.40 (0.21, 0.76)	0.003 (0.85)	1.78 (0.74, 2.81)	-0.47 (-0.94, -0.23)	0.03 (0.59)	1.86 (0.74,2.98)	-0.51 (-1.02, -0.26)
1000	0.12 (0.28)	2.90 (1.24, 4.56)	-0.79 (-1.53, -0.41)	0.22 (0.14)	2.78 (1.25,4.32)	-0.78 (-1.46, -0.41)	0.25 (0.11)	2.63 (1.20, 4.06)	-0.74 (-1.37, -0.40)
1500	0.049 (0.42)	2.60 (1.27, 3.92)	-0.74 (-1.29, -0.42)	0.16 (0.13)	2.61 (1.33, 3.88)	-0.75 (-1.28, -0.44)	0.17 (0.11)	2.63 (1.34, 3.91)	-0.77 (-1.30, -0.45)
2000	0.09 (0.27)	3.53 (1.77, 5.29)	-1.01 (-1.75, -0.58)	0.18 (0.11)	3.34 (1.74, 4.95)	-0.97 (-1.63, -0.58)	0.20 (0.08)	3.28 (1.72,4.85)	-0.96 (-1.61, -0.57)
2500	**0.32** **(0.034)**	-1.24 (-2.09, -0.39)	0.54 (0.33, 0.89)	0.019 (0.63)	-2.11 (-3.58, -0.63)	0.78 (0.43, 1.41)	0.002 (0.87)	-2.13 (-3.60, -0.66)	0.77 (0.43, 1.40)
3000	0.08 (0.30)	1.94 (0.95, 2.93)	-0.60 (-1.05, -0.35)	0.23 (0.06)	1.44 (0.77, 2.11)	-0.45 (-0.74, -0.27)	0.20 (0.08)	1.27 (0.67, 1.87)	-0.39 (-0.66, -0.23)
3500	**0.44** **(0.006)**	-0.82 (-1.21, -0.43)	0.28 (0.18, 0.44)	**0.44** **(0.006)**	-0.75 (-1.11, -0.39)	0.26 (0.16, 0.40)	**0.43** **(0.007)**	-0.71 (-1.04, -0.37)	0.24 (0.15,0.37)

Table B6. Results of standardized major axis (SMA) regression analysis. Regressions are between stems with functional redundancy, using effective number of species, i.e., Hill numbers q = 0, 1, and 2, in every elevational site. Bold values are statistically significant.

	Functional redundancy								
	q = 0			**q = 1**			**q = 2**		
Elevation (m a.s.l)	**R^2 (*p*-value)**	**Intercept (low, high)**	**Slope (low, high)**	**R^2 (*p*-value)**	**Intercept, (low, high)**	**Slope (low, high)**	**R^2 (*p*-value)**	**Intercept, (low, high)**	**Slope (low, high)**
0	**0.43** **(0.007)**	-32.12 (-48.12, -16.11)	13.72 (8.88, 21.21)	**0.35** **(0.01)**	-25.54 (-39.07 -12.02)	10.79 (6.78, 17.19)	**0.28** **(0.04)**	-19.80 (-30.75, -8.85)	8.32 (5.11, 13.54)
500	0.075 (0.41)	-38.40 (-70.58, -6.21)	15,20 (7.75, 29.79)	0.001 (0.91)	-30.46 (-56.15, -4.77)	11.66 (5.81,23.39)	0.001 (0.91)	28.43 (8.69,48.18)	-8.96 (-17.97, -4.46)
1000	0.08 (0.38)	-20.61 (-41.33, 0.108)	9.73 (4.98, 19.01)	0.066 (0.44)	32.38 (12.90, 51.86)	-9.05 (-17.80, -4.60)	0.14 (0.25)	35.00 (13.49, 56.51)	-10.43 (-20.01, -5.44)
1500	0.22 (0.07)	81.71 (42.05, 121.37)	-24.58 (-40.76,-14.82)	**0.33** **(0.02)**	68.89 (37.15,100.63)	-21.25 (-34.03, -13.27)	**0.32** **(0.02)**	53.39 (28.50, 78.28)	-16.55 (-26.59,-10.30)
2000	0.021 (0.60)	-61.83 (-104.02, -19.64)	23.46 (13.36,41.18)	0.07 (0.30)	63.66 (29.92, 97.40)	-19.35 (-33.44, -11.19)	0.19 (0.10)	47.53 (23.60, 71.45)	-14.65 (-24.53, -8.75)
2500	0.17 (0.13)	-31.16 (-50.91, -11.41)	11.52 (6.69, 19.84)	0.015 (0.66)	15.52 (6.61,24.43)	-4.75 (-8.56, -2.63)	0.18 (0.12)	9.74 (4.60, 14.88)	-3.02 (-5.18, -1.76)
3000	0.0004 (0.94)	13.36 (6.14, 20.57)	-4.24 (-7.48, -2.40)	2.38^{e-05} (0.98)	7.63 (3.44,11.81)	-2.45 (-4.34, -1.39)	0.017 (0.63)	-4.89 (-8.06, -1.71)	1.88 (1.07, 3.30)
3500	**0.33** **(0.024)**	-7.44 (-11.36, -3.53)	2.61 (1.63, 4.19)	**0.46** **(0.005)**	-1.93 (-2.84, -1.03)	0.67 (0.44,1.03)	**0.40** **(0.010)**	-1.36 (-2.02, -0.70)	0.46 (0.29, 0.72)

Table B7. Results of standardized major axis (SMA) regression analysis. Regressions are between biomass with species diversity using effective number of species, i.e. Hill numbers q = 0, 1, and 2, in every elevational site. Bold values are statistically significant.

	Species diversity								
	q = 0			**q = 1**			**q = 2**		
Elevation (m a.s.l)	**R^2 *p*-value**	**Intercept (low, high)**	**Slope (low, high)**	**R^2 *p*-value**	**Intercept (low, high)**	**Slope (low, high)**	**R^2 *p*-value**	**Intercept (low, high)**	**Slope (low, high)**
0	**0.64** **(0.0002)**	-0.37 (-0.78, 0.03)	0.57 (0.40, 0.81)	**0.57** **(0.001)**	-0.55 (-1.02, -0.08)	0.59 (0.40,0.87)	**0.51** **(0.002)**	-0.60 (-1.08, -0.11)	0.58 (0.38,0.86)
500	0.19 (0.17)	-0.30 (-1.15, 0.55)	0.55 (0.29, 1.04)	0.007 (0.80)	-0.88 (-2.13, 0.36)	-0.72 (0.36, 1.45)	0.02 (0.63)	2.47 (1.09,3.84)	-0.81 (-1.61, -0.40)
1000	1.88^{e-05} (0.98)	1.50 (1.17, 1.84)	-0.22 (-0.45, -0.11)	0.18 (0.18)	1.63 (1.15, 2.11)	-0.36 (-0.68, -0.19)	0.27 (0.09)	1.75 (1.15, 2.35)	-0.47 (-0.87, -0.26)
1500	0.21 (0.08)	3.35 (2.04, 4.66)	-1.01 (-1.68, -0.61)	**0.32** **(0.026)**	3.78 (2.25, 5.31)	-1.27 (-2.04 -0.79)	**0.34** **(0.021)**	3.62 (2.15, 5.10)	-1.25 (-1.99, -0.78)
2000	**0.30** **(0.032)**	0.38 (0.03, 0.73)	0.32 (0.19, 0.51)	0.23 (0.068)	-0.05 (-0.54, 0.42)	0.42 (0.25, 0.69)	0.14 (0.15)	-0.30 (-0.87, 0.26)	0.47 (0.27,0.79)
2500	0.042 (0.47)	-1.03 (-2.13, 0.06)	0.74 (0.41, 1.33)	0.06 (0.39)	-1.44 (-2.62, -0.27)	0.79 (0.44, 1.41)	0.04 (0.45)	-1.39 (-2.47, -0.32)	0.72 (0.40, 1.29)
3000	0.07 (0.33)	-0.188 (-0.57, 0.20)	0.32 (0.18, 0.56)	**0.28** **(0.03)**	-0.23 (-0.53, 0.05)	0.27 (0.17, 0.45)	**0.37** **(0.01)**	-0.24 (-0.49,-0.00064)	0.25 (0.15,0.40)
3500	**0.66** **(0.0002)**	2.23 (1.51, 2.95)	-0.80 (-1.12, -0.57)	**0.45** **(0.005)**	1.17 (0.68, 1.65)	-0.42 (-0.65, -0.27)	**0.33** **(0.023)**	0.97 (0.52, 1.43)	-0.36 (-0.57, -0.22)

Table B8. Results of standardized major axis (SMA) regression analysis. Regressions are between stems density (ha-1) and species diversity using effective number of species, i.e. Hill numbers q = 0, 1, and 2, in every elevational site. Bold values are statistically significant.

	Species diversity								
	q = 0			**q = 1**			**q = 2**		
Elevation (m a.s.l)	**R^2 (*p*-value)**	**Intercept (low, high)**	**Slope (low, high)**	**R^2 (*p*-value)**	**Intercept, (low, high)**	**Slope (low, high)**	**R^2 (*p*-value)**	**Intercept (low, high)**	**Slope (low, high)**
0	**0.62** **(0.0004)**	-2.45 (-3.63, -1.27)	1.23 (0.86, 1.76)	**0.43** **(0.007)**	-2.72 (-4.22, -1.21)	1.28 (0.83, 1.99)	**0.35** **(0.01)**	-2.71 (-4.27, -1.15)	1.25 (0.78,1.98)
500	0.13 (0.26)	-1.05 (-2.45, 0.35)	0.68 (0.35,1.32)	0.001 (0.92)	3.39 (1.40, 5.37)	-0.90 (-1.80, -0.44)	0.020 (0.67)	3.56 (1.37,5.75)	-1.00 (-2.00, -0.50)
1000	0.00017 (0.96)	-0.14 (-1.06, 0.77)	0.41 (0.20, 0.82)	0.13 (0.26)	2.86 (1.50,4.21)	-0.65 (-1.25, -0.34)	0.18 (0.19)	3.37 (1.63, 5.12)	-0.86 (-1.63, -0.45)
1500	0.14 (0.16)	5.53 (2.95, 8.10)	-1.51 (-2.57, -0.89)	0.24 (0.058)	6.51 (3.49, 9.54)	-1.90 (-3.13, -1.15)	0.24 (0.06)	6.30 (3.32, 9.28)	-1.87 (-3.08, -1.13)
2000	1.20^{e-05} (0.99)	4.39 (2.39, 6.38)	-1.09 (-1.93, -0.62)	0.11 (0.21)	5.21 (2.75, 7.68)	-1.44 (-2.46, -0.84)	0.19 (0.09)	5.58 (2.96,8.19)	-1.60 (-2.68, -0.96)
2500	0.19 (0.11)	-2.69 (-4.63, -0.74)	1.14 (0.66, 1.96)	0.0004 (0.94)	4.14 (1.82, 6.46)	-1.22 (-2.22, -0.67)	0.03 (0.50)	3.69 (1.62, 5.76)	-1.11 (-2.00, -0.62)
3000	0.012 (0.69)	2.84 (1.42, 4.27)	-0.84 (-1.48, -0.47)	0.03 (0.48)	2.37 (1.16,3.57)	-0.72 (-1.26, -0.41)	0.01 (0.66)	2.11 (1.00,3.22)	-0.65 (-1.15, -0.37)
3500	**0.39** **(0.01)**	-2.32 (-3.49, -1.15)	0.82 (0.52, 1.29)	**0.46** **(0.0047)**	-1.25 (-1.84, -0.67)	0.43 (0.28, 0.66)	**0.44** **(0.006)**	-1.07 (-1.58, -0.56)	0.37 (0.24,0.57)

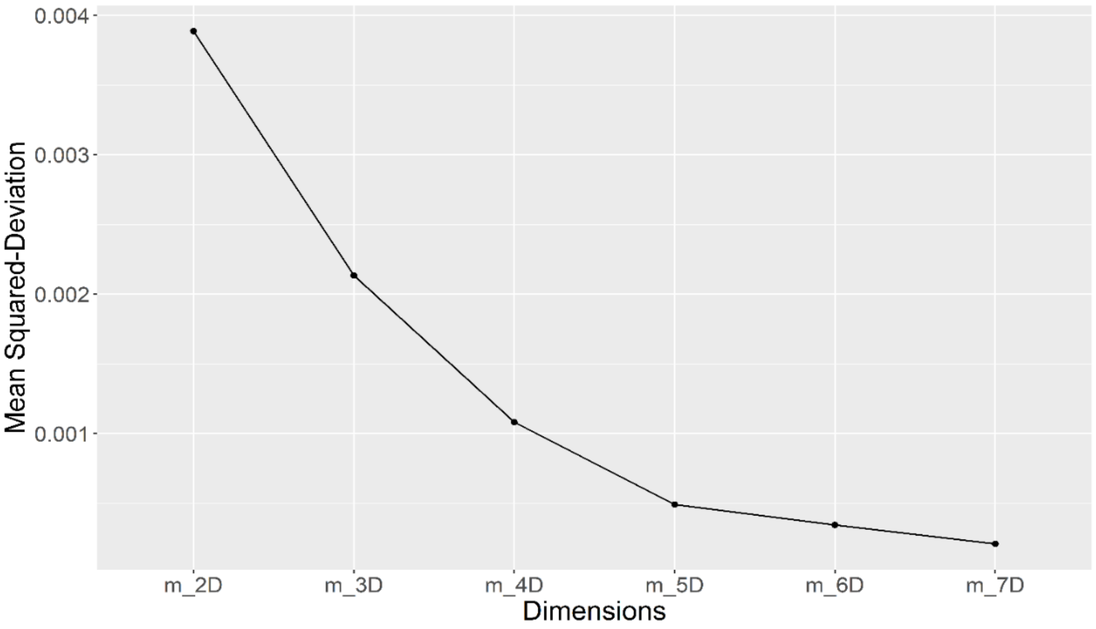

Figure B1. Quality of functional multidimensional functional spaces. Points represent standard deviation values of the mean squared deviation.

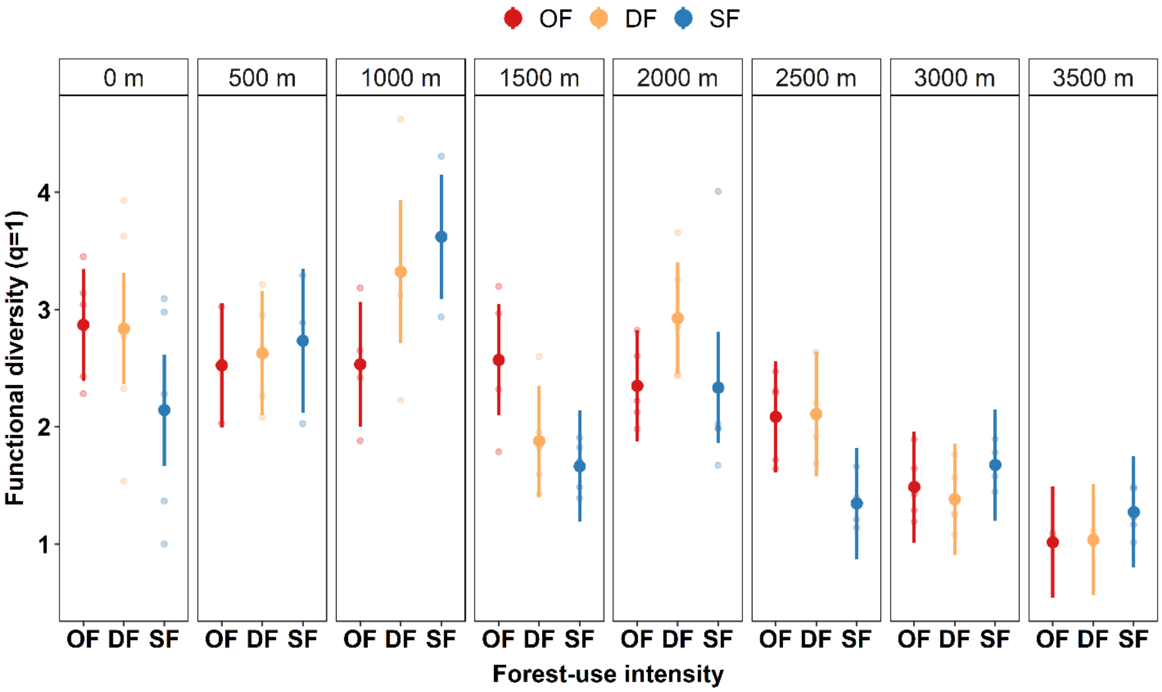

Figure B2. Functional diversity (q = 1) along the elevation gradient and different levels of forest-use intensity (n = 111 plots). Functional diversity was significantly affected by elevation ($F_{7,87}$ = 21.39, *p*-value= 1.67^{e-16}) and forest-use intensity within elevation ($F_{16, 87}$ = 2.16, *p*-value = 1.20^{e-02}; Table B2). Bold points are predicted means from the nested ANOVA (lines are 95 % confidence intervals). Light points are plot-level values. Forest-use intensity levels are old-growth forest (OF), degraded forest (DF) and secondary forest (SF).

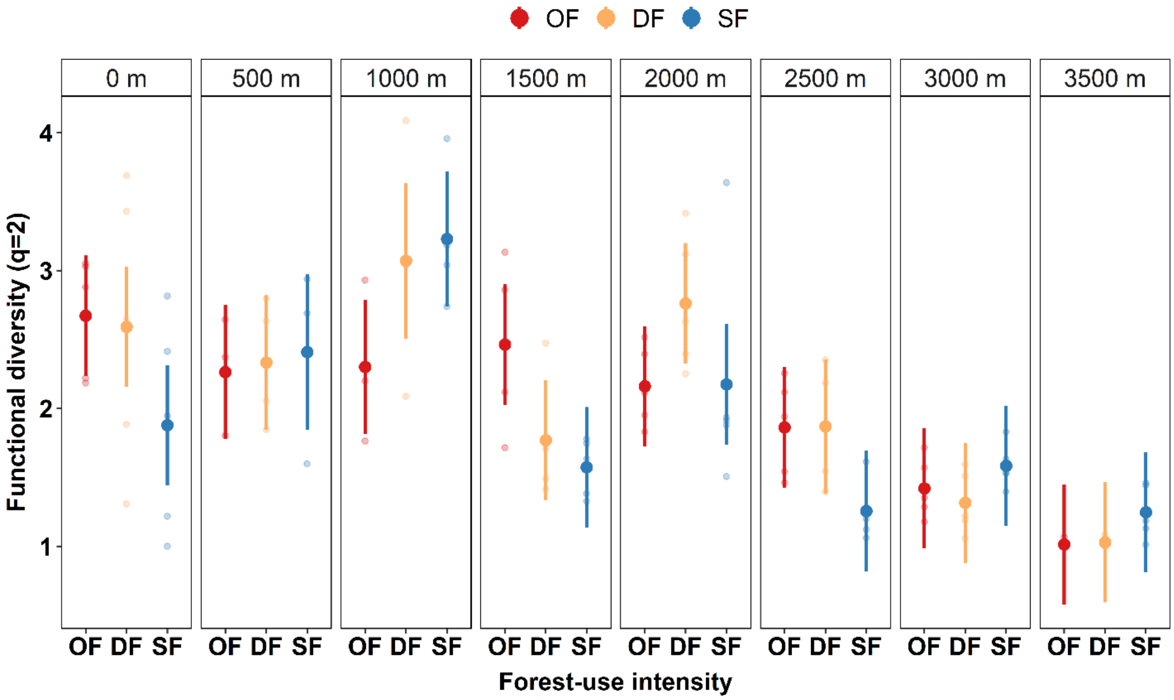

Figure B3. Functional diversity (q = 2) along the elevation gradient and different levels of forest use intensity (n = 111 plots). Functional diversity was significantly affected by elevation ($F_{7,87}$ = 18.96, *p*-value= 3.80 $^{e-15}$) and forest-use intensity within elevation ($F_{16,\,87}$ = 2.27, *p*-value = 7.90 $^{e-03}$; Table B2). Bold points are predicted means from the nested ANOVA (lines are 95 % confidence intervals). Light points are plot-level values. Forest-use intensity levels are old-growth forest (OF), degraded forest (DF) and secondary forest (SF).

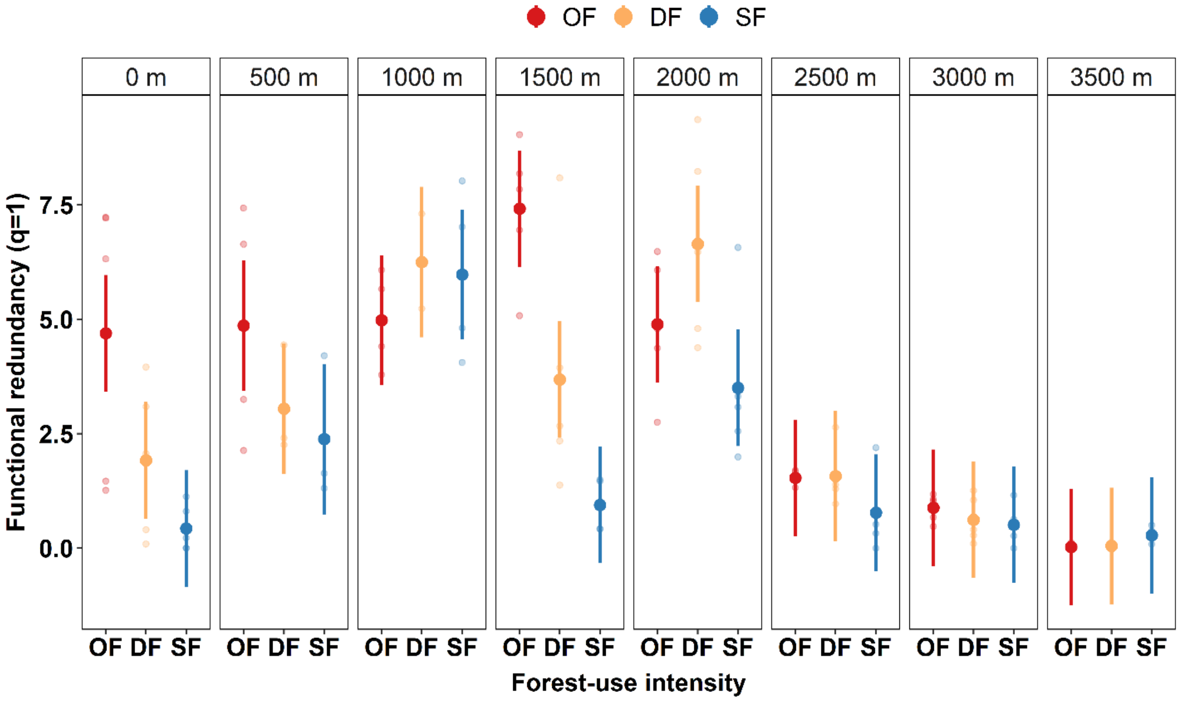

Figure B4. Functional redundancy (q = 1) along the elevation gradient and different levels of forest use intensity (n = 111 plots). Functional redundancy was significantly affected by elevation ($F_{7,87}$ = 28.03, *p*-value =8.47^{e-20}) and forest-use intensity within elevation ($F_{16, 87}$ = 5.94, *p*-value= 1.44 $^{e-08}$). Bold points are predicted means from the nested ANOVA (lines are 95 % confidence intervals). Light points are plot-level values. Forest-use intensity levels are old-growth forest (OF), degraded forest (DF) and secondary forest (SF).

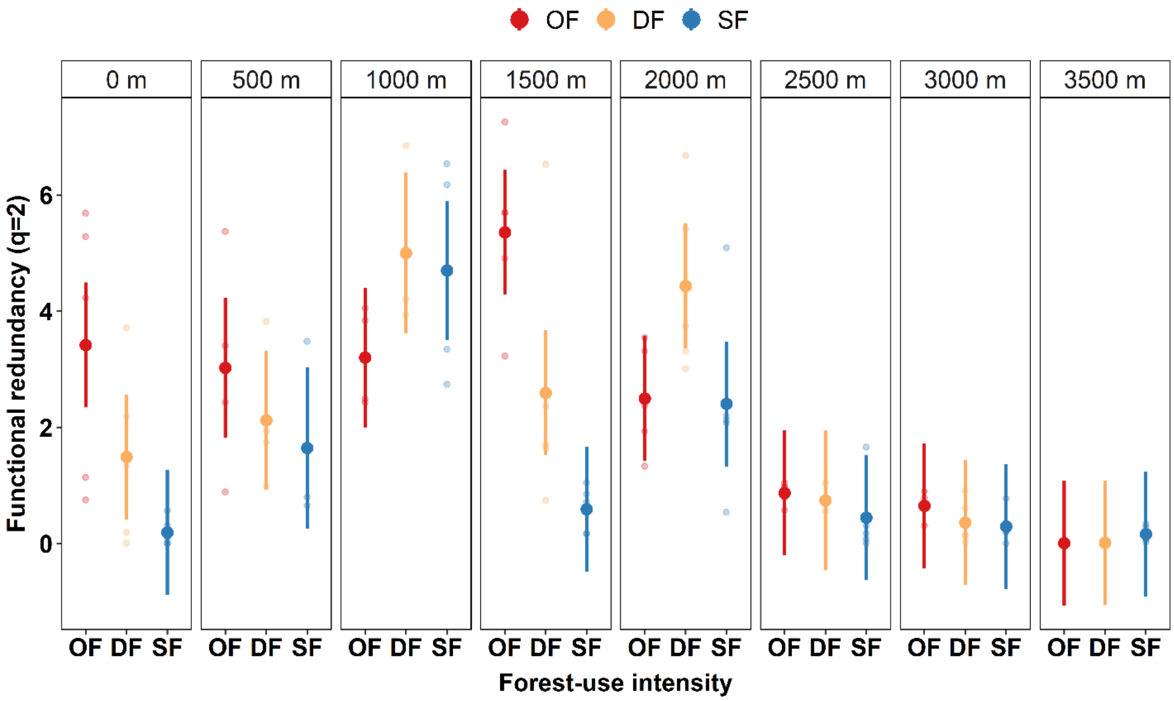

Figure B5. Functional redundancy (q = 2) along the elevation gradient and different levels of forest use intensity (n = 111 plots). Functional redundancy was significantly affected by elevation ($F_{7,87}$ = 19.79, *p*-value =1.27 $^{e-15}$) and forest-use intensity within elevation ($F_{16, 87}$ = 4.61, *p*-value= 1.36 $^{e-06}$). Bold points are predicted means from the nested ANOVA (lines are 95 % confidence intervals). Light points are plot-level values. Forest-use intensity levels are old-growth forest (OF), degraded forest (DF) and secondary forest (SF).

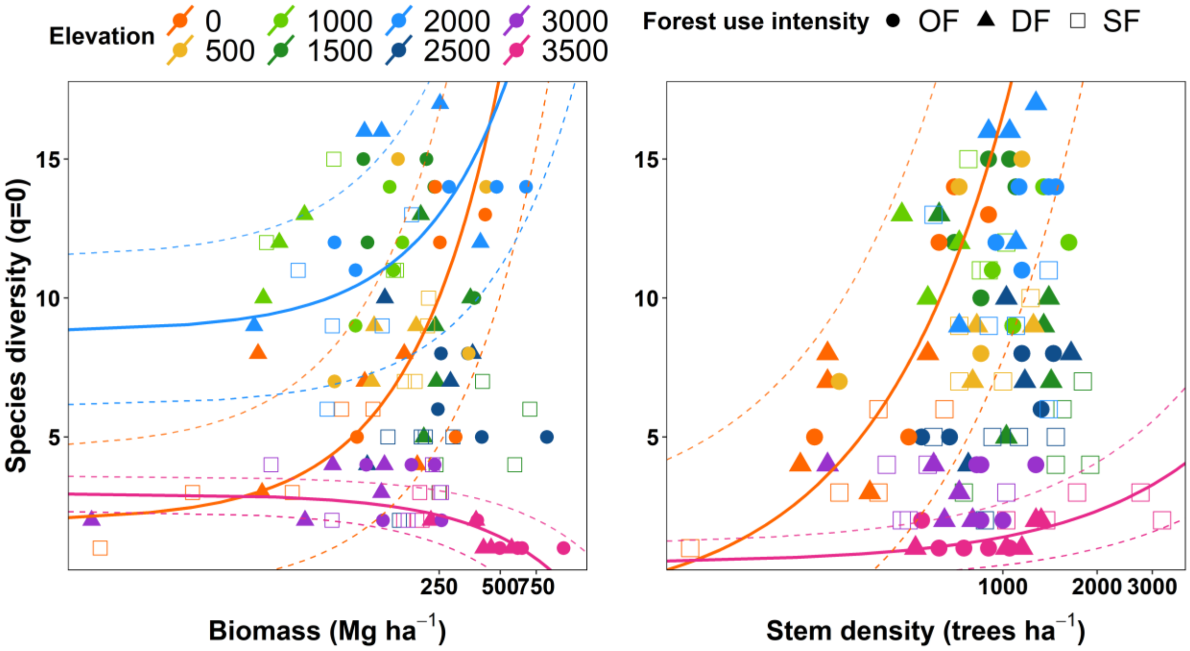

Figure B6. Relationships between species diversity (Hill number q = 0) with biomass and stem density on the log scale, fitted with standardized major axis (SMA) regression. Solid lines represent the regression model and show significant relationships (p-value < 0.05) and dashed lines indicate confidence intervals 95%. Forest-use intensity levels are old-growth forest (OF, circles), degraded forest (DF, triangles) and secondary forest (SF, squares).

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