FACULTEIT
BIO-INGENIEURSWETENSCHAPPEN

FUNCTIONAL DIVERSITY IN NATURAL FORESTS ALONG AN ELEVATIONAL TRANSECT IN NORTHERN ECUADOR

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The promotors, The author,

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ACKNOWLEDGEMENTS

Dear reader,

I proudly present this dissertation as the result of a year of hard labour. The work that lies in front of you would not have existed were it not for the support of some people I would like to thank here.

First of all I want to thank my promotors prof. dr. ir. Hans Verbeeck and dr. ir. Marijn Bauters for giving me the opportunity to participate in this fascinating research project. Together with my tutor ir. Miro Demol they provided indispensable advice and feedback throughout the year, for which I'm very grateful. Furthermore I want to thank Debbie Eraly from BOS+ for her warm welcome in Quito and prof. Selene Baez for her support during the planning of the field campaign and the rest of our time in Ecuador.

This is also the right place to thank my thesis buddy Sebastiaan Van den Meerssche. His marvelous cooking skills, and his slightly mangled attempts to describe the created dishes in Spanglish, provided me and the whole field team with high quality entertainment during our stay. Even when we were already in the process of writing our dissertations, he always remained his jolly self and kept our spirits high, which I really appreciated.

Moreover I would like to thank Germán Toasa, a passionate botanist whose knowledge of the Ecuadorian flora is truly exceptional, and his assistent Stephanie. Germán, gracias por ser nuestro guía y apoyar nuestro trabajo de campo. Sin usted, este estudio no sería lo que es hoy. Stephanie, I will always remember how you galloped effortlessly through the Ecuadorian mountains carrying the bloody tree pruner.
A big thanks to Eva and Emma for their help in the field and back in Belgium. I'd also like to thank everyone from the Mindo Cloud Forest Foundation who helped us both in the field and with logistics: María José, Germanía, Roberto, Fausto and Niko. Qué os vaya bien!

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My parents and Titus get a deserved special mention for always believing in me.

Tine Bommarez,

June 2020.

PREAMBLE COVID-19

A field campaign was conducted during the summer of 2019 in Ecuador to remeasure tree diameters in permanent sample plots and collect leaf, wood and soil samples. The plan was to analyse the chemical composition of these samples during the second semester of the academic year 2019-2020. Due to the emerging threat of COVID-19, Ghent University closed all its laboratories for non-essential research. This halted further sample analyses in the lab. Hence, the planned analyses were only partially carried out. The chemical composition of soil samples was not analysed, whereas leaf samples were only partly analysed. This dissertation was finished on the basis of results that were already available.

This preamble was drawn up in mutual consent between the student and the supervisors and was approved by all of them.

CONTENTS

ABBREVIATIONS

a.s.l.	Above sea level
AGB	Above-ground biomass
BA	Basal area
C:N	Carbon to nitrogen ratio
CWM	Community-weighted mean
DBH	Diameter at breast height
FAO	Food and Agricultural Organisation of the United Nations
FD	Functional diversity
FDis	Functional dispersion
FDiv	Functional divergence
FEve	Functional evenness
FRic	Functional richness
HRF	Hierarchical-response framework
iWUE	Intrinsic water-use efficiency
LA	Leaf area
LCC	Mass-based leaf carbon content
LES	Leaf economics spectrum
LME	Linear mixed effects
LNC	Mass-based leaf nitrogen content
MAP	Mean annual precipitation
MAT	Mean annual temperature
MCF	Mindo Cloud forest Foundation
MST	Minimum spanning tree
POM	Point of measurement
PSP	Permanent sample plot
SES	Structural economics spectrum
SLA	Specific leaf area
TMCF	Tropical montane cloud forest
TMF	Tropical montane forest
WD	Wood density
WES	Wood economics spectrum
WUE	Water-use efficiency
δ^{13}C	Stable isotope composition of carbon
δ^{15}N	Stable isotope composition of nitrogen
ΔAGB	Above-ground biomass increment
ΔDBH	Diameter increment

SUMMARY

Research questions The aim of this study was to investigate both forest taxonomic and functional diversity patterns along an elevational transect in northwestern Ecuador. Five research questions were addressed. (1) Does an increase in altitude change the floristic properties of tropical montane forest? (2) Does elevation influence functional diversity of tropical montane forests? (3) How does elevation influence the functional trait patterns observed along the transect? (4) For a given altitude, do functional trait values of newly sprouted trees or dead trees diverge from those of the rest of the trees? (5) Which functional traits are predictive for individual tree growth?

Location This study was conducted along an elevational transect on the western flank of the Ecuadorian Andes. The transect consists of 19 permanent sample plots (PSPs) dispersed among five altitudinal clusters, ranging from 400 to 3200 m a.s.l. The PSPs are located in the provinces of Pichincha and Imbabura.

Methods All trees with a diameter at breast height exceeding 10 cm were inventoried. Leaf and wood samples were collected for the 80% most dominant species and analysed. For each altitudinal cluster, the community-weighted means of functional traits, the taxonomic and functional diversity metrics were calculated and the results were inspected for elevational patterns. Finally, possible correlations between functional traits and individual tree growth were investigated with linear mixed effects models.

Results We identified 1838 stems from 211 unique tree species, belonging to 147 genera and 63 families. Tree species turnover with altitude was high. Altitude therefore had a clear effect on taxonomic diversity. Functional traits also appeared to be strongly correlated with elevation. Functional diversity was, unlike taxonomic diversity and functional traits, weakly related to altitude. A higher abundance of tree species with a conservative strategy was encountered at high altitude. The functional trait values of dead trees and recruits did not diverge from the trait values of the rest of the trees. Finally, wood density was predictive for individual tree growth.

Conclusion The tree species in the tropical montane forest of northwestern Ecuador are highly specialized and have adapted to the environment in which they occur. This is evidenced by the taxonomic diversity and the differences in functional characteristics of tree species along the transect. We draw attention to the threat that climate change poses to these specialised species.

SAMENVATTING

Onderzoeksvragen Het doel van deze studie was om de taxonomische en functionele diversiteit te bestuderen van natuurlijke bossen gelegen langs een hoogtetransect in Ecuador. Er werd geprobeerd om de volgende onderzoeksvragen te beantwoorden. (1) Heeft hoogteligging een invloed op de floristische eigenschappen van tropisch bergregenwoud? (2) Heeft hoogteligging een invloed op de functionele diversiteit in tropisch bergregenwoud? (3) Hoe beïnvloedt hoogteligging de functionele eigenschappen van bomen langs het transect? (4) Verschillen de functionele eigenschappen van dode bomen of recruten op een gegeven hoogte ten opzichte van de meerderheid van de bomen op diezelfde hoogte? (5) Welke functionele eigenschappen zijn gecorreleerd met individuele boomgroei?

Locatie De studie werd uitgevoerd langs een hoogtetransect op de westflank van de Ecuadoraanse Andes. Het transect is opgebouwd uit 19 permanente proefvlakken, verdeeld over vijf strata die in hoogte variëren van 400 tot 3200 meter boven zeeniveau. De proefvlakken bevinden zich in de provincies Pichincha en Imbabura.

Werkwijze In elk proefvlak werden bomen met een diameter op borsthoogte groter dan 10 cm opgemeten en gedetermineerd. Bovendien werden zowel blad- als houtstalen verzameld van de 80% meest dominante soorten. Na de veldcampagne werden deze stalen geanaliseerd. Op basis van de resultaten werden voor elk stratum taxonomische en functionele diversiteitsmaten berekend. Daarnaast werden de gemiddelde waarden van functionele eigenschappen berekend per proefvlak, gewogen voor het grondvlak van elke boomsoort. Er werd nagegaan of deze resultaten gelinkt zijn aan hoogteligging. Ten slotte werden de verbanden tussen functionele eigenschappen en boomgroei onderzocht met behulp van Mixed Effects modellen.

Resultaten Er werden 1838 individuen gemeten en gedetermineerd. In totaal ging het om 211 unieke boomsoorten, die op hun beurt behoorden tot 147 genera en 63 families. Geen enkele boomsoort kwam op elke hoogte voor en slechts 30% van de boomsoorten kwam op meer dan één hoogte voor. Hoogteligging had dus een duidelijk effect op taxonomische diversiteit. Ook functionele eigenschappen bleken sterk gecorreleerd te zijn met hoogte. Functionele diversiteit wordt daarentegen in mindere mate beïnvloed door de hoogteligging. De functionele eigenschappen van dode bomen en nieuwe recruten verschilden niet merkwaardig van deze van de rest van de staande bomen. Tot slot werd vastgesteld dat houtdensiteit een goede predictor is voor individuele boomgroei.

Conclusies De boomsoorten in het tropisch bergregenwoud van noordwest Ecuador hebben zich in sterke mate gespecialiseerd en zijn aangepast aan de omgeving waarin ze voorkomen. Dat blijkt uit de taxonomische diversiteit en de verschillen in functionele eigenschappen van boomsoorten langs het transect. We wijzen op de dreiging die klimaatverandering voor deze gespecialiseerde soorten vormt.

RESUMEN

Enfoque de la Investigación El objetivo de este estudio fue conocer la diversidad taxonómica y funcional de los bosques naturales situados a lo largo de un transecto altitudinal en el noroeste del Ecuador. Se intentó responder a las siguientes preguntas de investigación. (1) ¿Afectan las variaciones altitudinales a las propiedades florísticas de los bosques nativos? 2) ¿Afecta la altitud a la diversidad funcional de los bosques nativos? 3) ¿Cómo afecta la altitud a las características funcionales de los árboles a lo largo del transecto? 4) ¿A una altura determinada, difieren las características funcionales de los árboles muertos o reclutas al compararlos con el resto de los árboles? 5) ¿Qué características funcionales están correlacionadas con el crecimiento individual de los árboles?

Localización El estudio se llevó a cabo a lo largo de un transecto altitudinal en el flanco occidental de los Andes. El transecto se compone de 19 parcelas permanentes divididas en cinco estratos que van desde los 400 a los 3200 metros de altura. Los lugares de muestreo se encuentran en las provincias de Pichincha e Imbabura.

Metodología En cada parcela se midieron y identificaron los árboles con un diámetro a la altura del pecho superior a 10 cm. Además, se recogieron muestras de hojas y madera del 80% de las especies más dominantes. Después, estas muestras fueron analizadas en el laboratorio. Para cada grupo altitudinal se calculó la media ponderada de los rasgos functionales a nivel de comunidad, así como la diversidad taxonómica y funcional. Se comprobó si estos promedios están vinculados a la altitud. Por último, se investigó la relación entre las características funcionales y el crecimiento de los árboles mediante modelos de efectos mixtos.

Resultados Se identificaron 1838 árboles. En total se identificaron 211 especies de árboles, que a su vez pertenecen a 147 géneros y 63 familias, encontrando ninguna especies en cada estrato. El recambio de especies entre estratos es realmente alto, ya que solo el 30% de las especies de árboles se encontraron en más de un estrato. Por lo tanto, la altitud tuvo un claro efecto en la diversidad taxonómica. Las características funcionales también parecen estar fuertemente correlacionadas con la altitud. La diversidad funcional, por otra parte, está influida en menor medida por la altitud. Las características funcionales de los árboles muertos y los nuevos reclutas no diferían notablemente de las del resto de los árboles en pie. Finalmente, se encontró que la densidad de la madera es un buen predictor del crecimiento individual de los árboles.

Conclusiones Las especies de árboles de la selva tropical del noroeste del Ecuador están altamente especializadas y adaptadas al medioambiente en el que se encuentran. Esto se pone de manifiesto en la diversidad taxonómica y las diferencias en las características funcionales de las especies a lo largo del transecto. Hacemos un llamado de atención acerca de la amenaza que el cambio climático supone para estas especies especializadas.

CHAPTER 1

INTRODUCTION

Forests cover approximately 30% of the Earth's surface (FAO and UNEP, 2020). They deliver ecosystem services indispensable for human well-being such as provision of fresh water, food and timber production and climate regulation (Millennium Ecosystem Assessment, 2005). Moreover, tropical forests are highly important for the conservation of global biodiversity (Dirzo, 2001). The study area of this research is located on the western flank of the Andes in northwestern Ecuador. This country is in the top ten countries with most tree species in the world (Beech et al., 2017). The western Andean forests are of utmost importance for biodiversity conservation, as they harbour many species with narrow geographic distributions.

Unfortunately, forests worldwide are subjected to pressures originating from global change and antropogenic disturbances. In 2010, the provinces of Pichincha and Imbabura had a combined area of 902 000 km^2 of natural forests, which is roughly 65 % of their land area. By 2018, they lost 1414 ha of natural forest, which is the equivalent of 509 000 tons of emitted CO_2 (Global Forest Watch, 2020a,b). Further tree cover loss in this region would result in additional loss of stocked carbon and disproportionate loss of forest-dependent species (Hill et al., 2019).

Mapping species distributions and estimating carbon storage in these forests can raise awareness on the importance of conserving these forests and halt further degradation and deforestation. For this purpose, an altitudinal transect of permanent sample plots ranging from 400 tot 3200 meters above sea level was set up in 2011 in northern Ecuador, allowing scientific research in the framework of a reforestation project conducted by BOS+ and Mindo Cloud Forest Foundation and financed by the Belgian company Telenet. The plots are located in tropical montane forest (TMF), in both reforested as well as undisturbed areas. This experimental set-up allows the study of both reforested sites and the natural climax situation. The project is being scientifically monitored by a cooperation between Escuela Politécnica Nacional, Quito, and Ghent University. Previous studies along this transect have rendered interesting insights in terms of tree and liana carbon storage and diversity (Bauters, M., 2013; Strubbe, M., 2013; Demol, M., 2016; Bruneel, S., 2016; Meeussen, C., 2017; Thierens, E., 2017; Pauwels, J., 2018).

The objectives of this field campaign were multiple. First, the demographic rates in TMF was investigated. Comparing the data from the first inventory in 2015 with the new data for plots at a particular altitude allowed us to study vegetation dynamics (growth, recruitment and mortality) for the first time in this unique transect. Moreover, we tried to detect evolutions in the size of the carbon stock. This research topic was further elaborated upon in the parallel thesis by Sebastiaan Van den Meerssche.

We formulate five research questions to target in this thesis:

1. Does an increase in altitude change the floristic properties of tropical montane forest?
2. Does elevation influence the functional diversity of tropical montane forests?
3. How does elevation influence the functional trait patterns observed along the transect?
4. For a given altitude, do functional trait values of newly sprouted trees or dead trees diverge from the properties of the rest of the standing trees?
5. Which functional traits are predictive for individual tree growth?

For the purpose of answering the aforementioned research questions, leaf and wood samples were collected in the forest reserves along the elevational transect. In addition, we enhanced the precision of tree species determination with the aid of a local botanist.

This work consists of seven chapters. Chapter 2 provides a concise overview of the existing literature related to the topic. In Chapter 3, a detailed explanation of the procedures used during the field work and lab analysis can be found. Chapter 4 summarizes the obtained results, which are being discussed further in Chapter 5. In Chapter 6, the main conclusions of this research are given. We end with Chapter 7, containing some brief suggestions for further research along the transect.

CHAPTER 2

LITERATURE REVIEW

Tropical forests occur roughly between the tropics of Cancer and Capricorn and are characterised by year-round high temperatures (Dirzo, 2001). As moist tropics harbour an estimated 50% of the global species richness, these ecosystems are extremely important for the conservation of biodiversity (Dirzo and Raven, 2003). The tropical forest is an umbrella concept harbouring many types of forests. There is no such thing as "the tropical forest". Different types of tropical forests were categorised according to gradients in for example moisture or seasonality (Montagnini and Jordan, 2005).

2.1 Tropical montane forests

A classification suggested by Foster (2001) relies on changes in elevation. While ascending a tropical mountain, forest ecosystems shift from lowland rainforest to lower montane rainforest and subsequent to upper montane rainforest. In presence of frequent cloudcover a peculiar subtype of tropical montane forest can occur, named tropical montane cloud forest (TMCF). Many definitions for TMCF circulate highlighting different features of this forest type. Hamilton et al. (1995) emphasise the difference in stand structure compared to tropical lowland rainforest: trees are smaller and more stunted, stem density is higher and epiphytes become more abundant with altitude, as opposed to lianas (Figure 2.1).

In large inland mountain ranges like the Andes, TMCF is typically found between 2000 and 3500 meters above sea level (m a.s.l.), but it can be found as low as 500-1000 m on isolated peaks or closer to sea (Hamilton et al., 1995). This phenomenon is known as the *mass elevation effect*: on smaller mountains the cloud-base is formed at a lower altitude than on large mountain masses because of the lower uptake of solar radiation and higher humidity levels on small mountains in coastal areas (Bruijnzeel et al., 1993; Flenley, 1995). In 2000, about 1.4% of the world’s tropical forests ($\approx$ 215 000 km^2) was estimated to be TMCF with roughly 40% located in the Americas (Bruijnzeel et al., 2011b). Maps of global TMCF distribution are produced by combining global forest cover assessments with global elevation data and regionally specific altitudinal limits of cloud forests (Bubb et al., 2004; Bruijnzeel et al., 2011a). The most recent maps estimate the TMCF distribution using data obtained through remote sensing (Figure 2.2) (Wilson and Jetz, 2016).

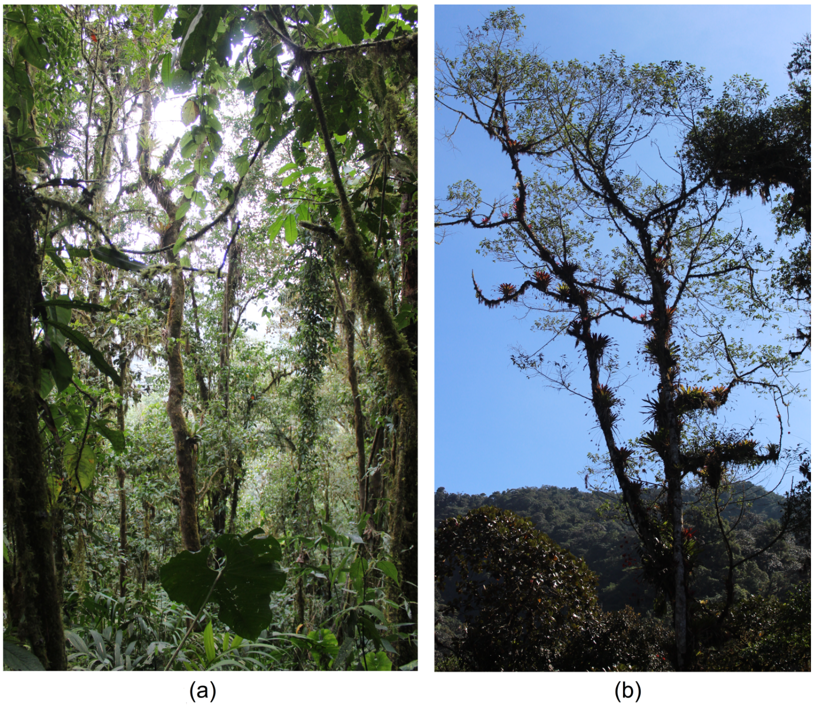

Figure 2.1: Tropical montane cloud forest in the ecologicale reserve *El Cedral* (Ecuador). The stand structure is characterised by (a) persistent cloud cover, small and stunted trees and (b) numerous epiphytes. Photographs taken by author in August 2019.

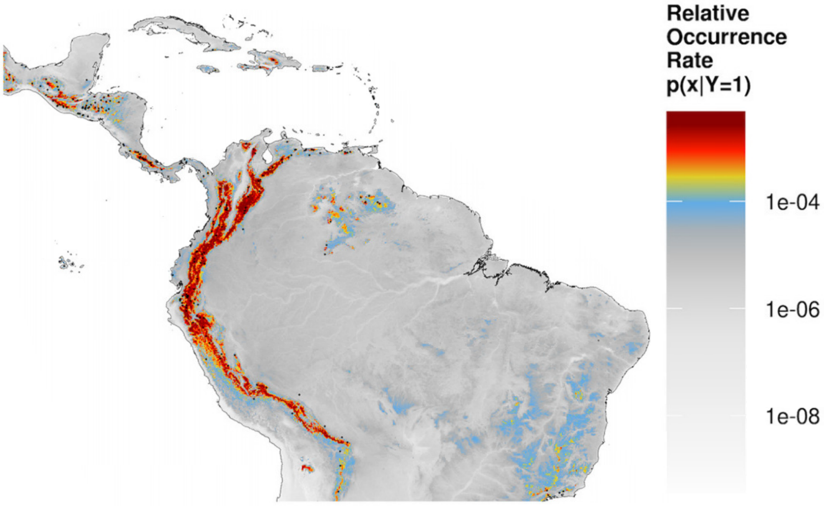

Figure 2.2: Distribution of tropical montane cloud forest in South and Central America. The color of a region reflects the local probability of the occurence of tropical montane cloud forest in a quadrat of 1 km^2. The relative occurence rate of tropical montane cloud forest was esimated using a model of Fithian and Hastie (2013) combined with 529 known cloud forest locations (marked as black points), cloud and elevation metrics. Locations of known cloud forest were obtained from the Tropical Montane Cloud Forest Sites database maintained by the United Nations Environment Program. Remotely sensed cloud cover data were obtained from the MODIS satellite mission. Figure adopted from Wilson and Jetz (2016).

Persistent presence of clouds or fog is the main identifier for TMCF. This frequent fog alters the microclimate drastically by reducing incoming solar radiation and vapor pressure deficit on the one hand and increasing the proportion of diffuse light on the other hand (Letts and Mulligan, 2005; Bruijnzeel et al., 2011a). Together with a lower temperature, orographic rainfall patterns and higher wind speeds typical for mountaneous regions, these factors shape the unique environmental conditions in which TMCF thrives (Gotsch et al., 2016). Over the course of evolution, tree species in TMCF have adapted their ecological strategy to the prevailing microclimate. Stomatal conductance (g_S) and carbon assimilation rates (A) in these trees are lower than in lowland rainforest trees. Moreover, trees in TMCF tend to have higher water-use efficiency (WUE) and lose less water through transpiration (Hamilton et al., 1995; Rosado et al., 2016). In addition, the leaves of some tree species are capable of intercepting cloud water, an important feature known as "cloud stripping" (Figure 2.3) (Bruijnzeel and Proctor, 1995).

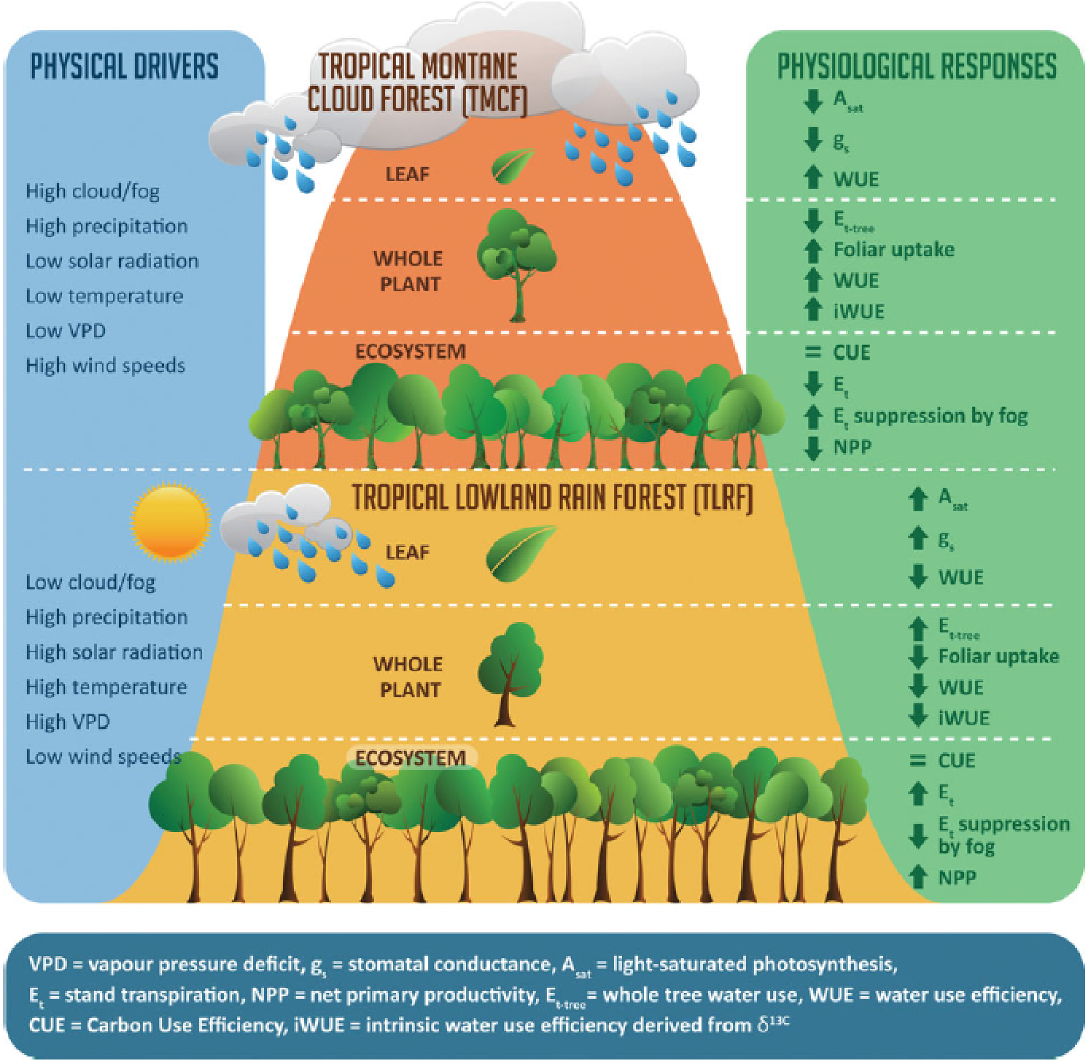

Figure 2.3: A comparison of the environmental drivers in tropical montane cloud forest (TMCF) versus tropical lowland rain forest. The physiological responses of the vegetation at leaf, whole plant and ecosystem level are depicted for both types of tropical forests. Figure adopted from Gotsch et al. (2016).

2.2 Impact of global change on tropical montane forests

Forests face multiple threats of anthropogenic origin. Many uncertainties remain as to how forests will respond to the combined pressure of deforestation, forest degradation and climate change in the long-term. This section elaborates upon the nature of these pressures and looks forward to what the future might hold for tropical montane forests.

2.2.1 Deforestation and forest degradation

Forests, especially tropical forests, are subjected to rapid deforestation rates. The area of land covered by forests has decreased dramatically over the last decades. In the period between 1990 and 2015 approximately three percent of the world's total forest area was lost (Keenan et al., 2015). Deforestation rates have been slowing down over recent years but remain nonetheless disturbingly high, especially in tropical countries (Table 2.1) (Keenan et al., 2015; FAO and UNEP, 2020). Historically, Andean cloud forests occupied ≈ 60 000 km^2, but more than half of this area has been cleared over time (Mulligan, 2010).

The main driver for deforestation in Latin America is agriculture, both on commercial and local scale (Hosonuma et al., 2012). In Ecuador land use changes for human settlements and pasture have resulted in heavy deforestation of the Andean cloud forests (Wunder, 1996). Nowadays fragmented patches of TMCF or varying sizes can be found throughout a landscape matrix of other land uses (Scatena et al., 2010). By no means does this imply that remaining patches are in pristine condition, because in certain areas timber logging causes latent degradation of the forest ecosystem (Hosonuma et al., 2012). The extreme topography associated with tropical montane forests has provided temporary salvation for the remnant patches so far. Their limited accessibility and low population density resulted in a lower fragmentation than in tropical lowland forests (FAO and UNEP, 2020). However, the effects of climate change lie just around the corner. . .

Table 2.1: Trends in natural forest area. Forest area per region per year in 10^6 ha (FAO, 2015).

Region	1990	2000	2005	2010	2015
Ecuador	14.6	13.7	13.3	12.9	12.5
Neotropics	957.8	914.3	890.8	873.1	862.3
World	4128.3	4055.6	4032.7	4015.7	3999.1

2.2.2 Climate change

Forests play a vital role in the global carbon cycle, because they act as a net carbon sink, storing $(2.4 \pm 0.4) \times 10^{15}$ g carbon per year (Pan et al., 2011). This allows them to partially buffer the increase in atmospheric CO_2. However, the natural buffer capacity of the world's oceans and forests to store CO_2 cannot keep up with the rate at which this greenhouse gas is being emitted. The atmospheric CO_2 concentration has now reached a staggering 414 ppm (Tans and Keeling (2020)). As a result of this rise, 2019 was the second warmest year in a 140-year record and was marked by extreme precipitation and drought events across the world (NOAA National Centers for Environmental Information, 2020). Forests suffer from these changes: carbon stocks are sensitive to the daytime maximum temperature and precipitation in the driest quarter (Sullivan et al., 2020). Higher temperatures and more intensive droughts cause increased tree mortality in Amazonia, which results in a lowered capacity to store carbon. Indeed, carbon sink strength of these tropical forests appears to have declined since the 1990s (Hubau et al., 2020).

What exact impact climate change will have on tropical montane forests is still unclear; however, it is very likely that these forests will be hit harder than lowland forests. Montane ecosystems are thought to be more vulnerable to climate change and are likely to be the first regions to be affected by it. Tropical montane forests, for example, harbour many endemic species with narrow geographic and thermal ranges, which therefore face a high risk of extinction (Perez et al., 2016; Hill et al., 2019). TMF can therefore be regarded as an “early indicator of climate change" (Spehn et al., 2006).

The projected changes in atmospheric conditions will lead to an increased evaporative demand. This may affect the water cycle of the ecosystem through increased water losses by evapotranspiration (Gotsch et al., 2016). One could argue that the increased atmospheric CO_2 concentration might positively affect photosynthetic rates and lead to a higher WUE and ecosystem productivity (Franks et al., 2013). However, warming-induced drought stress is expected to dampen this CO_2 fertilization effect through increased tree mortality in lowland as well as in altitudinal forests (Gómez-Guerrero et al., 2013; Hubau et al., 2020). Moreover, Bauters et al. (2020) found evidence for a decrease in intrinsic water-use efficiency (iWUE) in trees of the Congo basin caused by rising temperatures over the course of decades, countering the expected increase in iWUE as a consequence of the CO_2 fertilization effect.

2.2.3 Ecosystem response

As stated in the previous sections, climate change is expected to have a profound impact on tropical montane forests. We differentiate between the short-term effects and long-term effects climate change will have on TMF (Figure 2.4).

Species are expected to migrate poleward and upward due to global temperature rise. The median rate at which species shift to higher elevations is estimated at 11.0 meters per decade. The shift rates vary greatly between species and are influenced by the prevailing microclimate (Chen et al., 2011). Species on cooler, poleward-facing slopes might survive despite high average regional temperature changes. On the other hand, species experiencing intolerable microclimatic extremes can go locally extinct in spite of moderate background climate change (Suggitt et al., 2011). The response of tropical forests to climate change remains understudied in comparison with the response of boreal or temperate forests (Feeley et al., 2015).

A straightforward approach to detect upward species migration is to study changes in altitudinal distribution of mountain vegetation over time. Moret et al. (2019) resurveyed the vegatation on Mt. Antisana, Ecuador and compared with Alexander von Humboldt's *Tableau Physique* denoting the altitudinal ranges of Mt. Antisana's vegetation in beginning of the 19th century. The comparison revealed an altitudinal shift of $\approx$ 250 meters over 215 years. These upward elevational shifts provide insight into the speed at which climate warming affects the vegetation in mountain ecosystems (Steinbauer et al., 2018). The examined species did not respond uniformly to warming with some being able to follow climate change rates and others lagging behind (Moret et al., 2019). This type of comparative studies is rather rare because it requires a time series of accurate species distribution data. Therefore this approach is not widely applicable in the tropics (Feeley et al., 2015).

The aforementioned method is insufficiently applicable. There is a need for alternative approaches based on more-readily available data. Approaches based on taxonomic or functional changes in a tree community offers an alternative for estimating the response of montane forests to climate change (Steinbauer et al., 2018). Prior to the immigration of species from lower-lying altitudes, abundances of the locally present species will shift towards a greater abundance of species able to tolerate the temperature rise (Smith et al., 2009). Hence, focusing on shifting species abundances provides an opportunity for estimating the response of ecosystems to climate change within a shorter timeframe than the one used by Moret et al. (2019) in their study on species migration.

Fadrique et al. (2018) conducted one of the few available studies on the response of tropical Andean forests to climate change, using an approach based on the thermal optima of tree species. This study encountered evidence for a directional shift in species composition and relative species abundances in Andean forests over time. Species composition has shifted towards higher relative abundances of species from lower, warmer elevations, a phenomenon known as *thermophilization* (Gottfried et al., 2012). This trend is widely observed throughout Andean montane forests, yet the rate of compositional change varies across elevations (Fadrique et al., 2018).

The variation in compositional change rates can be explained by various factors. First, warming rates are not uniform but vary on a local scale. Microclimate can weaken or strengthen the impact of the background warming rate (Suggitt et al., 2011). Second, ecotones like the cloud formation zone pose a barrier to species migration. The cloud-base ecotone plays a pivotal role in determining several microclimatic variables such as temperature, precipitation, light availability (Rapp and Silman, 2012; Letts and Mulligan, 2005). Tree communities around ecotones are dominated by specialist species. TMCF falls into this category of specialised tree communities. It may be harder for non-specialised species of lower altitudes to colonise these ecotonal forests and equally hard for specialist species to colonise zones higher uphill, further away from the ecotone (Foster, 2001). Third, thermophilization rates can be limited by biotic interactions. Belowground linkages between plants and soil (a)biota may partially explain why mountain vegetation lags behind climate warming rates (Hagedorn et al., 2019). To predict how tropical forests will respond to climate change in the long term, it is of key importance gain a better understanding of how environmental controls influence their ecological functioning (Aparecido et al., 2018).

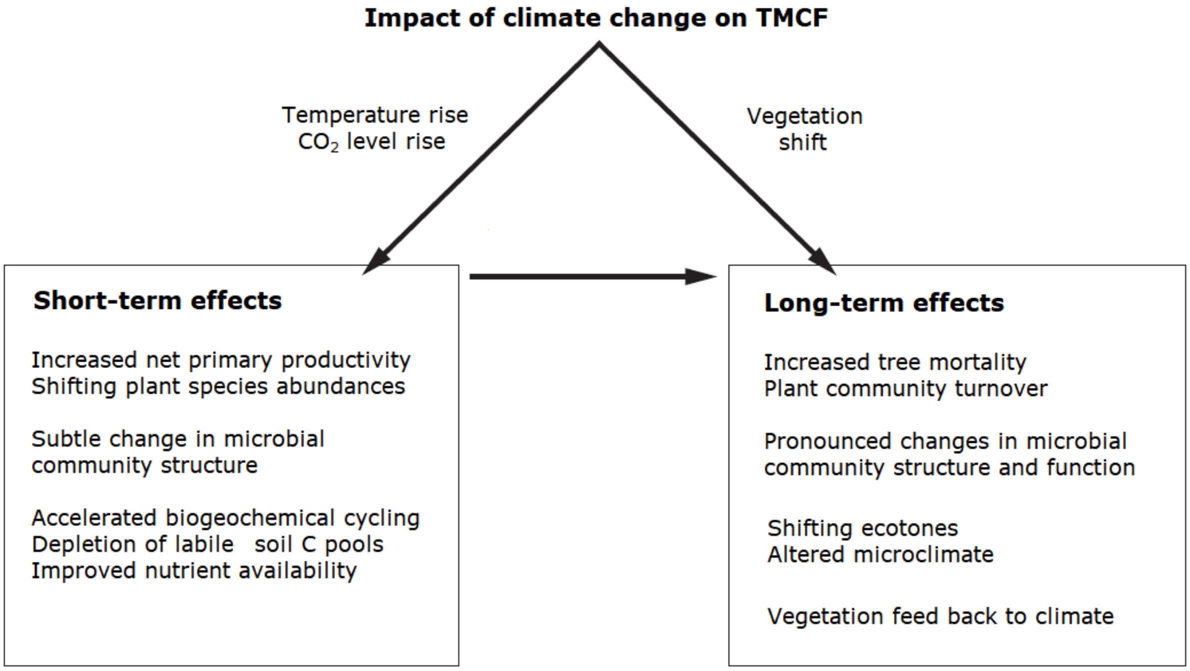

Figure 2.4: Expected short- and long-term impacts of climate change on TMCF. Figure was edited from Hagedorn et al. (2019) and contains general information on the impact of climate change on all mountain ecosystems (Hagedorn et al., 2019), as well as specific additional information on the expected impact on TMCF (Hubau et al., 2020; Suggitt et al., 2011).

The unusually high concentration of endemic species found in TMCF is the consequence of interlinked factors. The steep topographic gradients in mountainous regions give rise to a small-scale mosaic of different habitats in which the upper limit of lowland tree species and lower limit of montane species creates a species-rich interface. Together with the additional moisture gradient caused by the transition from humid lowlands to the drier interandean highlands, these factors gave rise to an explosive speciation, resulting in an unseen number of endemic species (Gentry, 1992; Foster, 2001; Homeier et al., 2010).

2.3 Elevational transect studies

In ecosystem research, elevational transects provide a unique opportunity to quantify long-term ecosystem shifts as a response to changes in environmental conditions (Malhi et al., 2010). Altitudinal gradients can be regarded as "space-for-time" substitutions when trying to understand the impact of climate change on ecosystems (Hagedorn et al., 2019). The underlying assumption is that the spatial differences between ecosystems along an elevational transect are the result of long-term adaptation to the local conditions (Humboldt and Bonpland, 1805).

The steep environmental gradients over a short spatial distance represent an exciting research opportunity, because many environmental factors change while ascending a mountain. The most unambiguous shift with increasing altitude is a decrease in air temperature. Per kilometer gain in altitude the average air temperature drops by $\approx 5.5^{\circ}$C (Barry, 1981). Atmospheric pressure also declines with altitude. One could argue that the decrease in partial pressure of carbon dioxide reduces photosynthesis at higher altitudes (Gale, 1972). However, an increased carboxylation capacity and adapted leaf structure might partially counteract this phenomenon (Cordell et al., 1998). Under cloudless skies both radiation and the fraction of UV-B light are higher at high altitudes (Körner, 2007). It is difficult to generalise radiation patterns in TMCF along altitudinal gradients because clouds alter light quantity and quality (Reinhardt et al., 2010). Other environmental variables like relative humidity, precipitation and wind velocity may or may not increase with altitude depending on the region.

The shifts in environmental gradients when ascending a mountain are similar to the patterns observed with increasing latitude. However, setting up elevational transect studies in the tropics has the advantage of a lack of seasonal changes, which do have to be taken into account in large-scale latitudinal transects (Körner, 2007). Despite the existing knowledge on shifting physical drivers with altitude, it remains hard to distil a general altitude-related trend in biological phenomena such as productivity or plant functional traits. Distinct geophysical drivers covary along a single altitudinal transect, and therefore it is difficult to attribute perceived trends to a single environmental variable (Körner, 2007).

Although caution is advised when interpreting the results obtained through an elevational transect study, this experimental set-up still provides unique opportunities to study the effect of environmental factors on plant morphology, speciation, physiological responses and ecosystem functioning.

2.4 Functional traits

Our study site is located in the Biodiversity Hotspot of western Ecuador. Approximately 9000 plant species can be found here, of which 25% are endemic to this region (Myers et al., 2000). Ecologists that are trying to make sense of this wide diversity and understand the driving mechanisms behind it, are increasingly focusing on an approach based on plant functional traits instead of taxonomy (Levine, 2016). Plant functional traits are defined as the *'morphological, anatomical, physiological, biochemical and phenological characteristics of plants'* (Violle et al., 2007). They are linked to the ecological strategy of a plant and can be defined at the level of an individual organ (leaf, stem) or at whole-plant level (Levine, 2016; Violle et al., 2007). An example of such a functional trait is adult plant height. This trait corresponds with a plant's ability to capture light and disperse its seeds, but these benefits come at a construction and maintenance cost (Falster and Westoby, 2003). The plant realm is filled with these so-called *ecological trade-offs*, many of which can be quantified by means of functional traits.

The popularity of trait-based research has skyrocketed over the last two decades, resulting in an improved availability of plant trait data. The TRY initiative was founded in 2007 as an attempt to compile a global plant trait database (Kattge et al., 2011). As of July 2019, the TRY database comprised over 11.5 million trait records of 280,000 plant taxa for more than 2000 traits (Kattge et al., 2020). The existence of such vast databases has led to the construction of so-called *Plant Economics Spectra*.

2.4.1 Plant Economics Spectra

Ecologists discovered that only certain trait combinations are viable, implying a correlation between various traits. Hence, plants can be positioned along a reduced number of axes of variation. Throughout the last two decades, scientist have tried to capture these viable trait combinations in so-called *spectra*, reflecting ecological trade-offs. Wright et al. (2004) was the first to suggest the *Leaf Economics Spectrum* (LES): a framework in which leaf functional traits are positioned along one single axis, ranging from plants with a quick to slow return on investment. A detailed description of central leaf traits and their placement in the LES is available in Demol, M. (2016). When producing woody tissue, plants face similar trade-offs. Chave et al. (2009) considers wood density (WD) as a central trait in the framework of the *Wood Economics Spectrum* (WES). The axis ranging from low to high WD represents conflicting demands in terms of biomechanical support, water transport and storage of nutrients.

The *spectrum of plant form and function* as proposed by Díaz et al. (2016) was introduced as a two dimensional global spectrum with LES as one dimension and plant (organ) size as the second. Six traits are thought to capture the essence of plant form and function (Table 2.2).

Table 2.2: Six key functional traits according to Díaz et al. (2016) and commonly used abbreviations respectively. Their ecological meaning is briefly explained in terms of trade-offs. The unit of measurements used in this thesis are given for every functional trait.

Functional trait	Abbreviation	Ecological meaning	Unit
Adult plant height	H	Trade-off between usage of light resources and the construction costs of wood and risk of breakage	m
Wood density	WD	Trade-off between mechanical strength, hydraulic safety and construction costs	g cm^{-3}
Leaf area	LA	Trade-off between light interception and leaf energy and water balance	cm^2
Specific leaf area	SLA	Trade-off between carbon gain through photosynthesis and leaf longevity	cm^2 g^{-1}
Nitrogen content per unit leaf mass	N_{mass}	Trade-off between the photosynthetic potential and the costs of acquiring nitrogen	mg g^{-1}
Seed mass	SM	Trade-off between seedling survival and colonisation ability in space and time	mg

The recent technological advancement in techniques such as airborne laser-guided hyperspectral imaging or terrestrial laser scanning are opening up new perspectives for large-scale mapping of functional trait diversity (Asner et al., 2017b). Verbeeck et al. (2019) pleads for the construction of a *Structural Economics Spectrum* (SES) reflecting canopy structure properties from data obtained through terrestrial laser scanning. The incorporation of SES, LES and WES could potentially lead to the creation of a *Global Plant Economics Spectrum*.

2.5 Functional diversity

The link between plant diversity and ecosystem functioning is not straightforward. The number of taxonomic tree species in a tropical forest does not necessarily determine its ecological functioning (Díaz, S. and Cabido, M., 2001). Moreover, species diversity in the tropics is often inadequately mapped (Feeley et al., 2015). To close the gap between taxonomic diversity and ecosystem functioning, the concept of *functional diversity* (FD) was introduced. FD relates to the values and range of species functional traits. It correlates more strongly with ecosystem processes and ecosystem resilience to climate change than species richness does, hence the interest in quantifying FD through various metrics (Folke et al., 2004; Hooper et al., 2005).

We restrict ourselves to the use of four indices to quantify functional diversity within the scope of this thesis, each capturing a different aspect of FD: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis). The former three indices were proposed by Mason et al. (2005) and further elaborated by Villéger et al. (2008), the latter was proposed by Laliberté and Legendre (2010). All four indices are independent and can handle relative abundances and multiple, continuous traits (Villéger et al., 2008; Laliberté and Legendre, 2010). The use of these indices results in a minimal loss of information, as opposed to dividing species into functional groups. Grouping species with continuous trait values into a discrete number of functional groups results in significant information loss (Wright et al., 2006).

As visualised in figure 2.5, functional richness measures the amount the trait space occupied by the species within a community (Mason et al., 2005). FRic is calculated as the minimum convex hull volume which includes all species and is a metric for habitat filtering. It is a measure for the whole of successful strategies among coexisting species in a certain environment (Cornwell et al., 2006).

Functional evenness can be computed as the counterpart of taxonomic evenness indices. FEve describes the uniformity of the distribution in the trait space and is calculated by means of a mimimum spanning tree. This is the tree linking all points in the trait space which minimises the sum of the branch lengths (Figure 2.5). FEve is maximal when the abundance of trait values in the trait space is uniform. A more uniform distribution of trait values could imply increased complementarity between species and result in a better use of resources (Mouillot et al., 2005).

Functional divergence captures to which degree the most abundant species occur at the extremities of the trait space. FDiv is calculated as the mean distance between the species and the trait space's centre of gravity (Figure 2.5). If many abundant species lay far off-centred, FDiv will be high. A high value for FDiv indicates a high degree of niche differentiation, suggesting lower resource competition (Mason et al., 2005; Villéger et al., 2008).

An additional FD index is called functional dispersion. FDis is the mean distance in the multidimensional trait space of individual species to the centroid of all species (Figure 2.6). FDis considers relative species abundances and is unaffected by the number of species in a community, which gives this metric an advantage over the aforementioned FD metrics (Laliberté and Legendre, 2010).

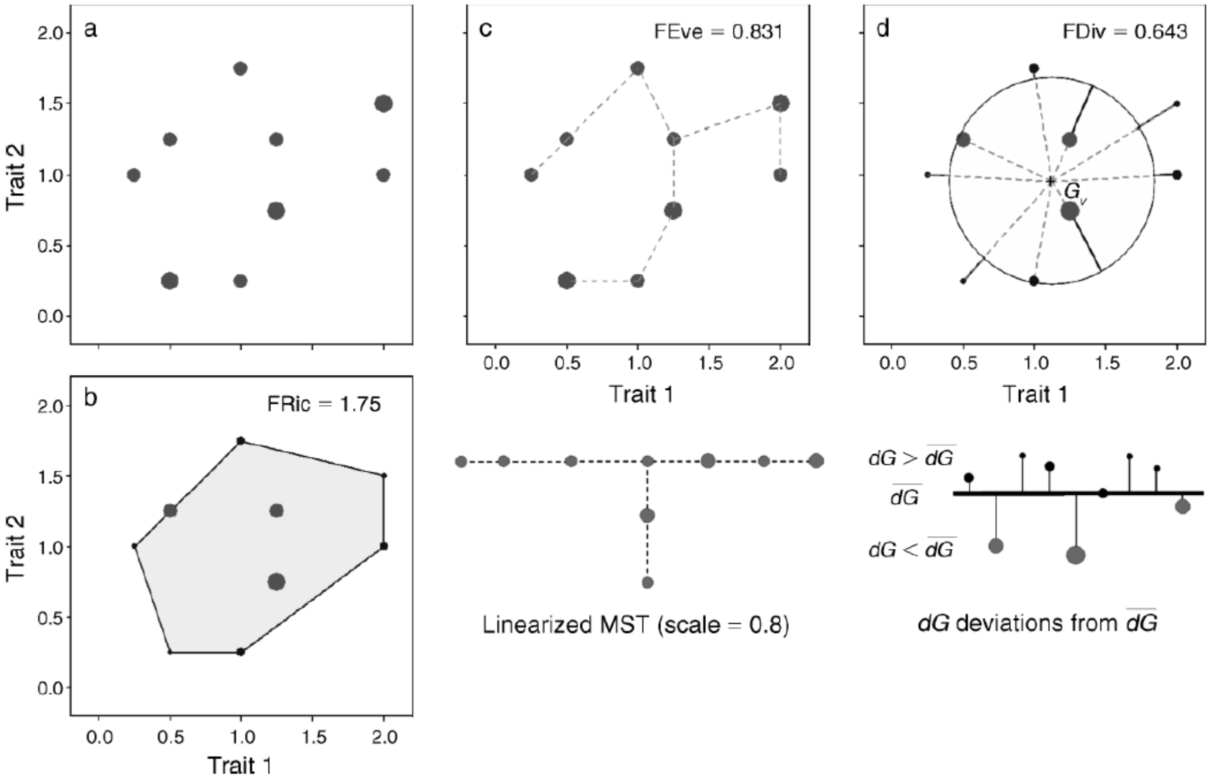

Figure 2.5: Summary of the calculation three functional diversity indices: functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv). (a) Representation of nine species within a two-dimensional trait space. The dots indicate the position of the species within the trait space according to their trait values. Dot size is proportional to species abundancy. (b) FRic is measured by the minimum convex hull volume including all inventoried species. In this example FRic is represented by the grey-coloured area. (c) The minimum spanning tree (MST) linking all species in the trait space is used as basis for calculating FEve. FEve measures the regularity of points and abundancies along the MST. The linearised MST is shown below panel c. (d) FDiv is measured as the mean distance between species and the trait space's centre of gravity (G_V), weighted by their abundance. Figure adopted from Villéger et al. (2008).

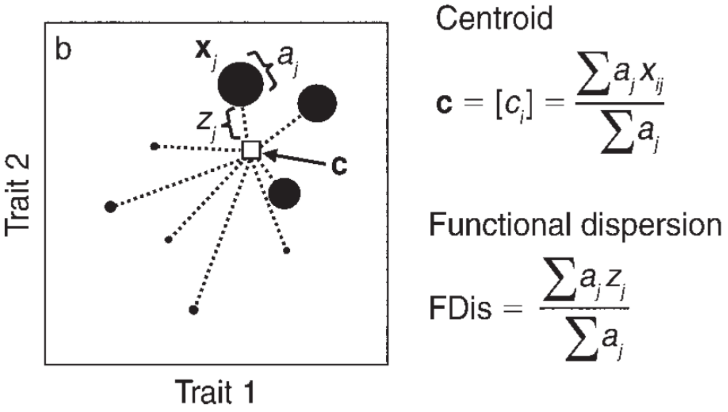

Figure 2.6: Visualisation of the functional dispersion (FDis) calculation. Eight species are represented by dots in a two-dimensional trait space. The dot size is proportional to the relative species abundancy. Vector **c** is the centroid of all species and z_j is the distance of species j to centroid **c**. FDis is calculated as the mean of all distances z_j, weighted by the relative abundance a_j of each species j. Figure adopted from Laliberté and Legendre (2010).

2.6 Stable isotope compositions

In the 1930s, it was discovered that stable isotopes, including ^{13}C and ^{15}N, are abundant in the natural world. Their natural abundance can be expressed as a ratio, standardizing for the natural abundancy of the stable isotope in a reference material. The reference materials used in this study are Vienna Pee Dee Belemnite and atmospheric N_2 for determination of the stable carbon and nitrogen isotope composition respectively. The formulas used for the calculation of the stable isotope composition of a given sample are:

$$\delta^{13}C = \frac{(^{13}\mathrm{C}\ /\ ^{12}\mathrm{C})_{sample}}{(^{13}\mathrm{C}\ /\ ^{12}\mathrm{C})_{reference}} - 1$$

$$\delta^{15}N = \frac{(^{15}\mathrm{N}\ /\ ^{14}\mathrm{N})_{sample}}{(^{15}\mathrm{N}\ /\ ^{14}\mathrm{N})_{reference}} - 1$$

Natural abundances of the stable carbon and nitrogen isotopes can be used to assess biogeochemical and ecological processes. The drivers behind δ^{13}C and δ^{15}N have been intensively studied over the last couple of decades. The photosynthetic pathway exerts an important influence on the δ^{13}C found in leafy tissue. Three major groups of plants with distinct photosynthetic pathways are being distinguished: C3, C4 and CAM (Crassulacean Acid Metabolism) plants. C3 plants include, among others, all arborescent life forms and use RuBisCo (ribulose biphosphate carboxylase oxygenase) as their most prominent carbon fixating enzyme in the Calvin cycle. RuBisCo discriminates against the heavy carbon isotope. PEP (phosphoenolpyruvate) carboxylase, the most prominent carbon fixating enzyme in C4 plants, exhibits this discrimination to a much lower extent (Farquhar, 1983).

The C3 pathway operates in $\approx$ 85% of all plant species, including tropical trees (Ehleringer et al., 1997). Other factors besides the plant's photosynthetic machinery influence carbon isotope discrimination. δ^{13}C is also influenced by the ratio of intercellular versus ambient partial pressures of CO_2, soil moisture levels, temperature, light regimes and precipitation, among other factors. All of these environmental factors act upon the stomatal conductance and the CO_2 assimilation rate of the leaf (Farquhar et al., 1989a; Körner et al., 1991). Water is lost through the stomata during photosynthesis, hence a correlation exists between δ^{13}C and the intrinsic water-use efficiency of the plant (Farquhar and Richards, 1984). The less negative δ^{13}C, the greater iWUE (Farquhar et al., 1989b). The combined influence of environmental factors may explain why δ^{13}C increases with rising altitude (Körner et al., 1991). This trend seems to depend on the plant life form as well. The effect of altitude on δ^{13}C for example seems more pronounced in trees than in lianas (Meeussen, C., 2017).

Foliar nitrogen isotope ratios (δ^{15}N) can provide insights into the nitrogen cycling across ecosystems. δ^{15}N is negatively correlated with mean annual precipitation (MAP) and positively correlated with mean annual temperature (MAT) and nitrogen availability (Craine et al., 2009). Under most conditions, δ^{15}N is a good proxy for the readily available nitrogen in the system, under the form of NO_3^-, NH_4^+ or dissolved organic nitrogen (Marshall et al., 2007). δ^{15}N also exhibits a decrease with elevation. Bauters et al. (2017) suggests this indicates a shift toward more nitrogen-conservative species at higher altitudes in ecosystems with a more conservative nitrogen cycle.

CHAPTER 3

MATERIALS AND METHODS

In this chapter, the geographical and environmental characteristics of the study site are discussed, followed by a description of the protocol employed for remeasurement of plots. Hereafter the procedure for sampling leaf and wood specimens and their analysis is explained. Finally, we discuss the statistical processing of the obtained data.

3.1 Study area

Seven clusters of reforested permanent sample plots (PSPs) in different altitudinal strata were established by Bauters, M. (2013). These PSPs are located in northern Ecuador on the western Andean flank in the provinces of Pichincha and Imbabura (Figure 3.1). Earlier work by Bauters, M. (2013); Bruneel, S. (2016); Demol, M. (2016) aimed to delineate undisturbed forest at the same altitudes, with the purpose of comparing the reforested sites with the natural climax situation in terms of carbon storage and functional diversity. In 2018, the first resurvey of the PSPs in natural forest was done by the botanist Nicanor Mejía. This resurvey took place in close cooperation with professor Selene Báez, affiliated with Escuela Politécnica Nacional in Quito. In 2019, our team conducted a second resurvey (Table 3.1).

Each cluster consists of at least three square forest plots with a dimension of 40 by 40 m. The square shape has a lower edge:area ratio than other shapes, this results in less decision problems concerning edge trees than for rectangular PSPs (Phillips et al., 2002). Every plot was subdivided into four subplots of 20 by 20 m. The plot size of 0.16 ha is smaller than the recommended 1 ha by RAINFOR, but has proven to be more feasible in the scope of this research project (Bauters, M., 2013). Multiple smaller plots are more suitable for this study given the steep slopes in TMCF and the smaller chance to include human disturbances. Indicators of human disturbance are among others trails, logged trees and cattle tracks.

The study features forest ecosystems along a 2800 m elevation gradient. Across this transect, clusters of PSPs at five altitudinal strata were delineated. The lower limit of the transect comprises tropical lowland rainforest (stratum 1), the intermediate strata (strata 2, 3 and 4) encompass TMCF and the upper stratum (stratum 5) features TMCF near the treeline. Higher up the vegetation shifts to páramo grasslands.

Stratum 1 - Río Silanche Bird Sanctuary This reserve comprises 100 ha of Chocó-lowland Rainforest at 400 m a.s.l., located in the province of Pichincha, Ecuador. It is owned by the Mindo Cloudforest Foundation (MCF), a local non-governmental organization with the mission of conserving biodiversity on the western Andean flank. The reserve is part of a bigger reserve network that is currently made up out of five individual reserves (Mindo Cloudforest Foundation, 2019b). The surrounding landscape matrix mainly consists out of farmland for oil palm and cacao production (Meeussen, C., 2017). The most common tree species are *Pourouma bicolor*, *Wettinia quinaria* and *Cecropia insignis*. The high abundance of *P. bicolor* indicates that this reserve likely consists of secondary forest (G. Toasa, personal communication, August 2019).

Stratum 2 - Milpe Bird Sanctuary This 100-hectare reserve is also owned by MCF and consists of Chocó-Andean foothills rainforest in the Pichincha province, at an elevation of 1100 m a.s.l. The Milpe and Río Silanche Bird Sanctuaries are home to an incredible amount of endemic birds, like the iconic Chocó toucan (Mindo Cloudforest Foundation, 2019a). This stratum has the highest tree species diversity. The most common tree species are *Otoba gordoniifolia*, *Stephanopodium angulatum* and *Ocotea* sp.

Stratum 3 - Maquipucuna Cloud Forest Reserve The PSPs in the Maquipucuna Cloud Forest Reserve were set up at an elevation of 1900 m a.s.l. in the centre of the 6500-hectare reserve. Their remote location and closed canopy suggests the ecosystem here is truly primary cloud forest (Demol, M., 2016; Bruneel, S., 2016). A well-known inhabitant of this protected area is the Andean spectacled bear (*Tremarctor ornatus*) (Maquipucuna Reserve, 2019). *Stylogyne ambigua*, *Cyathea caracasana* and *Cecropia herthae* were the dominant tree species in this stratum.

Stratum 4 - El Cedral Ecological Reserve The ecological reserve El Cedral is located in Nanegal, near the valley of Yunguilla (Calacalí), Pichincha, Ecuador. It comprises 72 ha of primary cloud forest between 2200 m a.s.l. and 2500 m a.s.l. The surrounding landscape consists of natural forests. The owner of the reserve is Germán Toasa, a dedicated botanist who guided us during the field campaign in the summer of 2019. The most abundant tree species in this stratum are *Beilschmiedia tovarensis*, *Chrysochlamys colombiana* and *Weinmannia* sp.

Stratum 5 - Puranquí Community Forest The Puranquí Community Forest is located in the valley of Intag in the province of Imbabura. Four PSPs were established just below the tree line, at an altitude of 3200 m a.s.l. The forests in this region are threatened by bushfires (often lit on purpose) and illegal mining activities. Presence of grazing cattle was also noted near the PSPs. Given the close presence of the village and cattle, it is unlikely that the PSPs in this stratum comprise primary forest. Highly dominant tree species were *Freziera canescens*, *Oreopanax* sp. and *Clethra* sp.

Table 3.1: General information on the strata established for this study. For each stratum the elevation in meters above sea level is displayed, as well as the number of permanent sample plots, the year of establishment and the years of remeasurement.

Stratum	Name	Elevation	Nr. of PSPs	Establishment	Resurvey	
1	*Río Silanche*	400	4	2015	2018	2019
2	*Milpe*	1100	4	2015	2018	2019
3	*Maquipucuna*	1900	4	2015	2018	2019
4	*El Cedral*	2400	3	2015	2018	-
5	*Puranquí*	3200	4	2015	-	2019

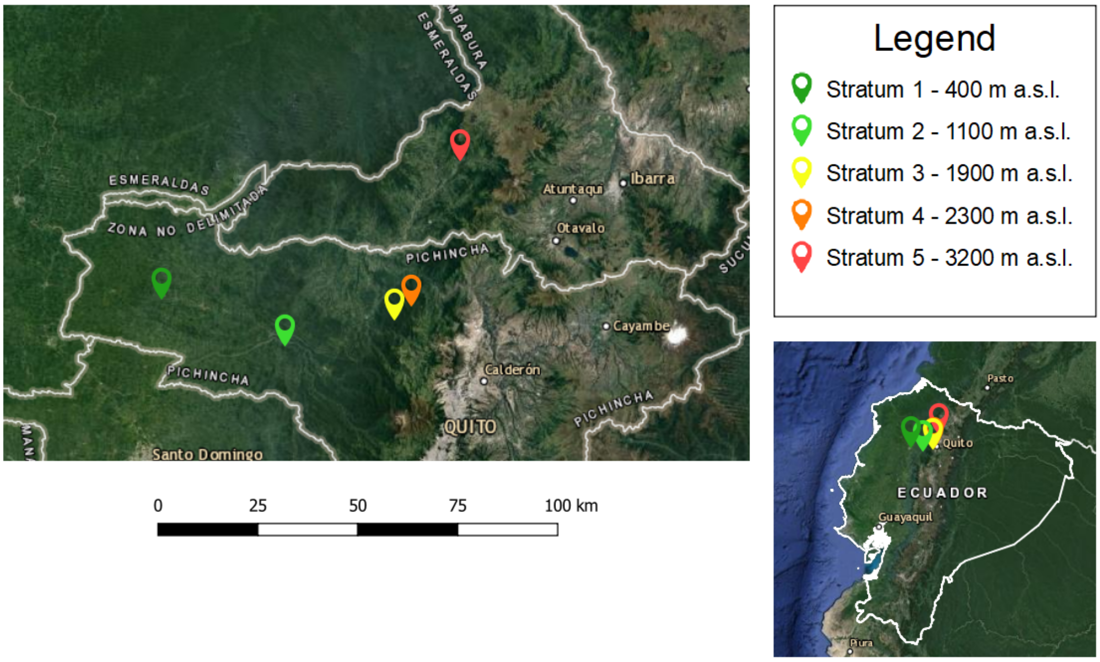

Figure 3.1: Location of the study sites. The right picture indicates that the strata can be found in northern Ecuador on the western Andean flank. The location of the different strata is depicted on the left figure, showing that strata 1 to 4 are located in the province of Pichincha. Stratum 5 on the contrary is located in the province of Imbabura.

Table 3.2: Climatic characteristics include mean annual temperature (MAT), mean annual precipitation (MAP), solar radiation (E), water vapor pressure (P_w), average wind velocity (V_{wind}). Climatic data with a resolution of 1 km^2 was retrieved from the WorldClim database version 2.1 (Fick and Hijmans, 2017).

	Stratum 1	Stratum 2	Stratum 3	Stratum 4	Stratum 5
Latitude (N)	0.1473	0.0356	0.0968	0.1155	0.4497
Longitude (W)	79.1425	78.8665	78.6228	78.5724	78.4708
No. of PSPs	4	4	4	3	4
Plot size (ha)	0.16	0.16	0.16	0.36	0.16
Altitude (m a.s.l.)	394 - 420	1041 - 1098	1764 - 1953	2220 - 2521	3191 - 3241
MAT (°C)	23.8	20.0	17.6	15.9	11.0
MAP (mm)	3447	3050	1560	1391	1205
E (kJ m^{-2} day^{-1})	12051	13377	15518	15627	15716
P_w (kPa)	2.58	2.09	1.69	1.40	1.10
V_{wind} (m s^{-1})	1.28	1.60	1.94	2.31	2.70
Soil type	andisol	andisol	andisol	andisol	andisol

The decline in mean annual temperature is strongly correlated with altitude. Many other ecological drivers covary: mean annual precipitation and water vapor pressure (P_w) decline with altitude, whereas wind velocity (V_{wind}) and incoming solar radiation (E) [1] increase. The soil type for all strata is andisol (Bruneel, S., 2016).

3.2 Recensus of permanent sample plots

The methodology for this resurvey was based on the RAINFOR protocol (Phillips et al., 2002).

Delineating permanent sample plots

In the period of July to September 2019, the previously established PSPs were resurveyed. The GPS coordinates of previous field notes were used to navigate to the plot centre. The plot corners were marked with bright painted PVC tubes during the first resurvey in 2018. This was helpful during the delineation of the inner and outer plot borders. Attention was payed whether there were no tagged trees excluded or untagged trees included while stringing and whether trees near inner plot borders were included in the right subplot.

Tree tagging

Certain tree species reacted negatively to the nailing of numeration tags during previous field campaigns, so a fine, bright coloured rope was used to tie the tags to the trees instead. The tags were tied to the tree at a height of approximately 30 cm above the point of measurement (POM). New recruits with a diameter at breast height (DBH) larger than or equal to 10 cm were tagged. During every field campaign a distinct tag colour is used. Some trees had lost their tag over the years. In this case, the previous tag number was figured out based on information on diameter and tree species. Subsequently, these trees were given a new tag and the new tag number was carefully linked to the old. Trees that could not be found were assumed to be dead.

Diameter measurement and marking of trees

The standard POM was at a reference height of 1.3 m. To define the POM in the field, a pole marked at 1.3 m was pushed firmly into the soil at the downhill side of the tree. The reference height was measured as the straight-line distance along the trunk, not as the vertical height above the ground (Figure 3.2). Sometimes the POM differed from this reference height, in order to avoid deformities or buttresses. In this case, the height of the alternative POM was recorded. The POM was marked on the stem with bright spray paint. Certain special cases we handled as follows:

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[1] Solar radiation (E) is assumed to increase with rising altitude. The values represented for E in Table 3.2 are daily averages under the condition of cloudless skies. Given that cloud cover plays a central role in tropical montane cloud forests, the level of solar radiation actually reaching the forest floor may be altered strongly as a consequence of persistent cloud cover.

- The cambium of leafless trees was slashed to clarify whether these trees were still alive.
- Although the RAINFOR protocol advises to only tag the largest stem of multiple-stemmed trees, we tagged every stem and noted carefully which tag numbers belonged to the same tree. This approach leaves less room for discussion when comparing diameters between distinct resurveys.
- Since the survey of Bruneel, S. (2016) and Demol, M. (2016) pointed out that only four lianas with a DBH > 10 cm were present within the PSPs, their contribution to the overall carbon storage was considered as negligible in comparison to the contribution of trees. Hence, no liana diameters were measured. For more detailed info on lianas along the transect see Meeussen, C. (2017).

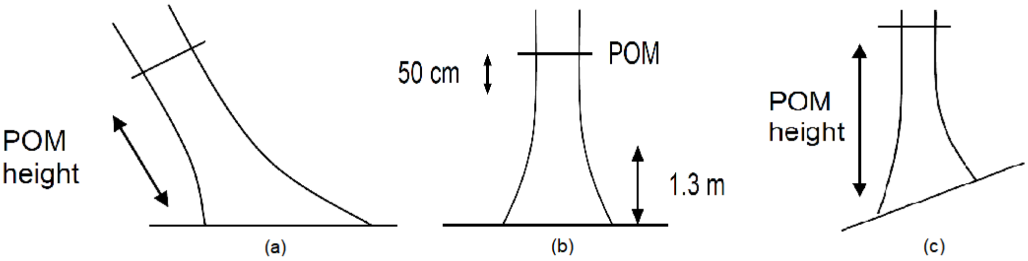


Figure 3.2: In certain cases, the reference height of 1.3 m cannot be used as the point of measurement in order to avoid deformities. (a) In leaning trees, 1.3 m length is measured along the side of the stem closest to the ground. (b) If the tree is buttressed at 1.3 m, the stem is measured 50 cm above the top of the buttress. (c) The point of measurement is determined at the downhill side of trees on a slope. Adopted from Phillips et al. (2002).

Tree height measurement

The understory in nearly every stratum was very dense. Since the Nikon Forestry Pro uses a laser beam to measure tree height, its use is restricted to those trees with an uninterrupted view between the observer's eye and the stem basis and between the observer's eye and highest point of the tree's crown. In practice, finding such trees was a highly time-consuming process. Therefore no tree heights were measured, instead DBH-height relationships determined in earlier work were used (Bauters, M., 2013; Bruneel, S., 2016; Demol, M., 2016).

Species identification

Trees were identified by the botanist Germán Toasa. To observe the leaves and flowers of a tagged tree, a camera with a powerful optical zoom was used. Fallen leaves, fruits or flowers and the smell of the slashed bark provided additional clues. When an individual could not be identified in the field, a botanical leaf sample was made to allow identification afterwards. In case the tree species could not be determined, the genus was recorded. Herbarium specimens were deposited at Escuela Politécnica Nacional, Quito, Ecuador.

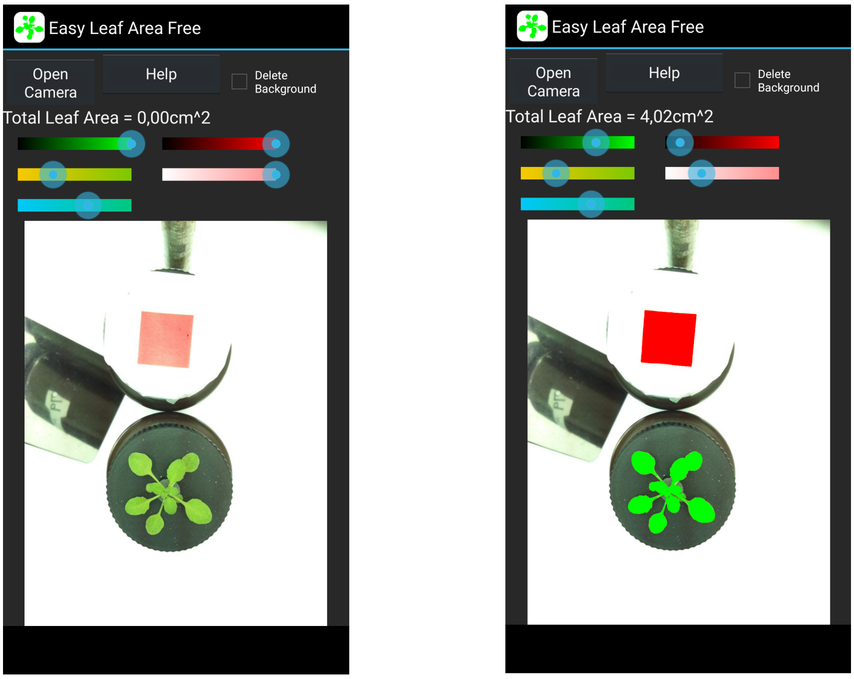
3.3 Leaf sampling and analysis

For every plot we composed a list of the cumulative basal area for all occurring tree species, ranked from most to least abundant. To get an accurate representation of leaf traits on plot level the most dominant tree species that make up a large proportion of the basal area were sampled. Tree species were ordered on the basis of the percentage of the basal area they represented on plot level. We aimed at sampling leaves of the most abundant tree species making up 80 % of the total basal area of each plot.

Leaf samples were collected with a telescopic tree pruner with a maximum length of twelve meter. If possible at least three individuals per species were sampled, preferably trees in different diameter classes. The collected leaves originate from the middle or the lower sections of the trees. It was not possible to collect sun leaves originating from a section of the tree higher than the length of the tree pruner. From each tree a sub-sample of five leaves within a range of different ages was taken (excluding juvenile, sick and dying leaves). The leaf samples were oven-dried at 70°C for at least 48h to avoid contamination by funghi.

Leaf area (LA) was determined of fresh leaves with the aid of the application *Easy Leaf Area*, developed at Department of Plant Sciences of the University of California by Easlon and Bloom (2014). This is a free, open source software designed with the purpose of enabling rapid LA measurements in the field. LA can be determined by means of photographing the leaf with a red reference square of two by two cm (Figure 3.3). The LA is then calculated using the RGB value of each pixel to identify the leaf in each picture. The accuracy of this method is very high even with the common camera of a phone, but the user must be careful to avoid perspective and lens distortion (Easlon and Bloom, 2014). We determined the LA (petiole included) on the same day as the samples were collected using a smartphone camera. Directly after collecting the sampled leaves are the greenest. Over time they turn brown and shrink which makes it more difficult to distinguish the leaf pixels from the red scale pixels. The application *Easy Leaf Area* is able to process multiple leaves of one sample at a time. The cumulative LA of every sample was noted.

The dried leaf samples were weighed using a precision balance with a readability down to 0.1 g to obtain the cumulative dry weight (M_{dry}) of all leaves making up one leaf sample. Specific Leaf Area (SLA) was calculated by dividing LA of all sampled leaves per individual by their summed M_{dry}: $SLA = \frac{LA}{M_{dry}}$.
After determining SLA, the samples were ground into a fine powder using a Retsch ZM-200 centrifugal mill at sieving pore diameter of 0.2 mm. Thereafter, all chemical analyses were conducted at the Isotope Bioscience Laboratory (ISOFYS) at Ghent University. To determine mass-based leaf nitrogen (LNC) and carbon content (LCC) 2.70-3.30 mg of each sample was analysed using an elemental analyser (Automated Nitrogen Carbon Analyser; ANCA-SL, SerCon, UK), interfaced with an isotope ratios mass spectrometer (IRMS; 20-20, SerCon, UK). In total, 260 leaf samples were sent for analyses of LCC, LNC, leaf nitrogen and carbon stable isotope composition.



Total Leaf Area = 0,00cm^2

Total Leaf Area = 4,02cm^2

(a) (b)

Figure 3.3: Usage of the application Easy Leaf Area. (a) Tap 'Open Camera' and take a picture of the leaf and the red scale area. Both should be at the same distance from the camera and parallel to the camera. (b) By moving the sliders leaf and scale identification are adjusted and a value for the leaf area is obtained. Pixels identified as leaf pixels are recoloured pure green and scale pixels are recoloured pure red for visual confirmation (Easlon and Bloom, 2014). (Easy Leaf Area license Copyright © 2012, 2013, University of California. All rights reserved.)

3.4 Wood sampling and analysis

We collected wood samples of tree species that had not been sampled for wood during previous inventories. In total 59 wood samples covering 47 tree species were taken using an increment borer with a core diameter of 5.15 mm (Haglöf, Långsele, Sweden). All wood cores were taken at breast height (1.3 - 1.4 m) of trees standing outside of the PSPs. It is important to not damage the trees standing inside of the plot, because this might disturb natural mortality rates. We aimed for a drilling depth slightly longer than the tree's radius. However, this drilling depth could not be achieved in individuals with very hard wood to avoid breaking the auger. We followed the instructions of Grissino-Mayer (2003) when coring the tree and extracting the core (Figure 3.4). If possible, multiple individuals of the same tree species were sampled so the variability of wood specific gravity between individuals could be determined. For 11 out of the 47 sampled tree species we were able to collect two or more samples. The wood cores were stored in paper straws and dried for 48h at a temperature of 103°C to drive off all free and bound water (Williamson and Wiemann, 2010).

Specific Gravity (G_b) of wood is an important ecological trait that is calculated as the oven dry mass (M_{dry}) of a wood sample divided by its green volume (V_{green}), relative to the density of water (value used for ρ_{water} is 1 g/cm^3): $G_b = \frac{M_{dry}}{V_{green}} \cdot \rho_{water}$ (Williamson and Wiemann, 2010).

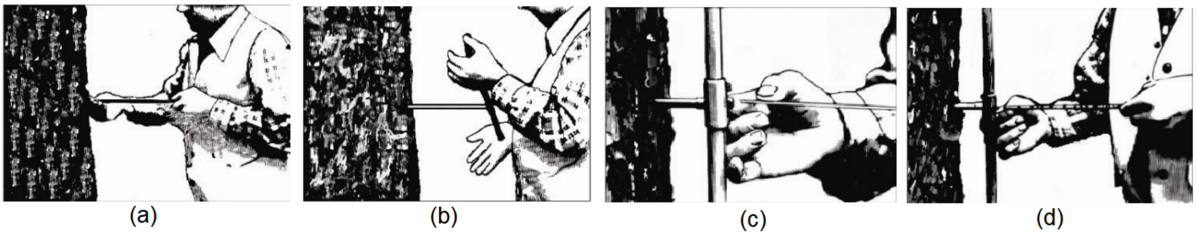


Figure 3.4: Instructions for collecting wood samples. (a) Place the tip of the borer in an angle of 90° at the appropriate boring height. Grasp the shaft of the auger with one hand and hold the handle center with the other. (b) Apply inward pressure to help the auger tip penetrate the outer bark. Keep applying this pressure while rotating the increment borer until the threads engage and the auger tip enters the tree. (c) Slide the extractor into the auger and turn the handles counter-clockwise for two turns. (d) Pull the extracor cap gently until the core breaks free (Grissino-Mayer, 2003). Figure adopted from Chave (2005).

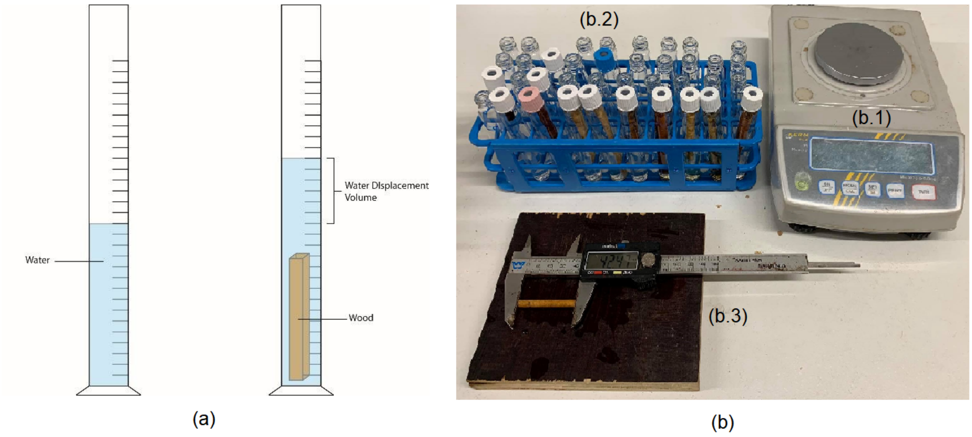


Figure 3.5: Two methods for assessing the volume of increment cores. (a) Experimental set-up for the water displacement method. The green volume of the wood core is measured by immersing the wood sample in a container of water. The volume of the sample is then equal to the weight of the displaced water, since water has a density of 1 g/cm^3 (Chave, 2005). Figure adopted from Hossain et al. (2017). (b) Our experimental set-up for determining wood density. (b.1) M_{dry} is determined using a balance with a readability of 1 mg. (b.2) Wood samples are submersed in water for 48 h. The rehydrated wood core has a volume that is not significantly different than the original V_{green} (Schüller et al., 2013). (b.3) The length of the rehydrated wood core is measured geometrically with a digital caliper.

M_{dry} was determined using a balance with a readability of 1 mg. A frequently used method to determine V_{green} of wood cores is the water displacement method (Figure 3.5). However, we chose to measure V_{green} geometrically instead of using the water displacement method. The reason for this is the fact that the wood cores shrink significantly after extraction in both in the radial and axial direction, which results in a biased G_b measurement when using the water displacement method (Schüller et al., 2013). The alternative is measuring the length of a rehydrated wood sample geometrically with a digital caliper (Figure 3.5). This measurement is a good approximation for the length of the freshly collected wood sample. The green volume is calculated using this length and the uniform sample diameter of 5.15 mm (identical to the diameter of the increment borer). Green volumes calculated in this way are believed to be a more reliable approximation of the true green volume (Schüller et al., 2013). Finally, we acknowledge that wood density varies from in radial and axial direction, but did not account for this variation, nor did we account for compaction caused by the auger tip.

3.5 Statistical analysis

The data analysis was performed using R (version 3.6.3), an open source software programme (RStudio Team, 2019).

3.5.1 Taxonomic diversity

All plant species names were standardised with the aid of the R package *taxonstand* (Cayuela et al., 2019). Taxonomic authorities for all species referred to in this thesis are available from the Plant List (www.theplantlist.org).

Five taxonomic diversity metrics were calculated to assess the species richness and composition of permanent sample plots using the R package *vegan*: species richness, rarefied species richness, Shannon diversity index, Simpson diversity index and Pielou's evenness index (Oksanen et al., 2019; Shannon and Weaver, 1963; Simpson, 1949; Pielou, 1966). The comparison of species richness between plots of different dimensions is misleading, as this measurement does not take into account the larger number of observed trees associated with the altered plot size. Rarefaction methods standardise species richness for a given sample size and facilitate the comparison of species richness between plots in different strata. In this master thesis, the rarefied species richness was calculated for every plot using the lowest observed stem density (47, stratum 1 plot 4) (Gotelli and Colwell, 2001).

To compare the floristic composition the pairwise Bray-Curtis dissimilarity between strata was calculated (Bray and Curtis, 1957). The general formula for calculating the Bray-Curtis dissimilarity between stratum x and y is as follows:

$$BC_{xy} = \frac{\sum_{j=1}^{J} |n_{xj} - n_{yj}|}{\sum_{j=1}^{J} n_{xj} + n_{yj}} \tag{3.1}$$

with n_{xj} the number of counts for species j in stratum x. This measure takes on values between 0 (completely identical strata) and 1 (completely disjoint strata). The contribution of species j to the overall dissimilarity is weighted by its relative abundance. Because the computation involves summing the absolute difference between species counts, an underlying assumption of the Bray-Curtis measure is that the strata have an equal sample size. This is not the case in our dataset so the dissimilarity between strata was overestimated due to the fact that a part of the difference between two strata can be explained by the difference in sample size (Ricotta and Podani, 2017).

3.5.2 Community-weighted means of functional traits

Community-weighted means (CWM) of several functional traits were calculated on a plot basis, weighted for basal area (BA). CWMs are available for WD, SLA, C:N, mass-based leaf nitrogen content (LNC), stable isotope composition of carbon (δ^{13}C) and the stable isotope composition of nitrogen (δ^{15}N). The BA-weighted means for every trait were calculated using the formula proposed by Asner et al. (2017a):

$$\overline{x_w} = \frac{\sum_{i=1}^{N} W_i x_i}{\sum_{i=1}^{N} x_i} \tag{3.2}$$

with x_w being the BA-weighted mean for the trait, x_i is the mean trait values for species i and W_i is the basal area of species i relative to the total BA of the plot. For the calculation of CWMs of SLA, C:N, LNC, δ^{13}C and δ^{15}N the only functional trait values used were the ones obtained through in the field campaign of 2019. Given the low number of wood samples taken, the values for WD were supplemented with data from Global Wood Density Database using the R package `biomass` (Chave et al., 2009; Rejou-Mechain et al., 2017).

3.5.3 Functional diversity

The four functional diversity indices were calculated using the FD package (Laliberté et al., 2014): functional richness, functional evenness, functional divergence and functional dispersion. It is advised to limit the number of functional traits used to calculate FD indices and stick to a handful of traits with as low a correlation as possible (Mason et al., 2005; Villéger et al., 2008; Laliberté and Legendre, 2010). Hence, the FD indices were calculated at plot level taking into account values for three functional traits: wood density (WD), specific leaf area (SLA) and carbon to nitrogen ratio (C:N). Before testing for significant differences, the assumption of homoskedasticity was checked with Bartlett's test (Arsham and Lovric, 2011). In case of sufficient equality of variances, we tested for significant differences in FD indices for altitude with the Kruskal-Wallis test (Breslow, 1970). Dunn's test with a Bonferroni correction was used to make post hoc pairwise comparisons (Dunn, 1964).

3.5.4 Functional trait signature of recruits and dead trees

Hereafter all trees included in the initial survey in 2015 and/or the resurvey were divided into three different categories in order to investigate possible differences in CWMs for functional traits per category. These categories are:

- Dead trees: trees deceased in the period between the census of 2015 and the resurvey.
- Survivors: trees included in the first census of 2015 and marked as alive during the resurvey of 2019.
- Recruits: trees sprouted after the first census in 2015 and hence included for the first time in the resurvey.

The same procedure was followed in the calculations of the CWMs per plot per category as described in the previous section. Since it was impossible to collect leaf or wood samples from dead trees, and undesirable to collect leaf or wood samples from recruits (as these may vary from the leaves of an adult tree), we used the following procedure to attribute trait values to these two categories.

If we collected leaf and wood samples for tree species x, we were able to determine functional trait values for this particular species. Hence, we assigned the functional trait values obtained for a survivor of tree species x to all individuals belonging to species x in the category of dead trees or new recruits as well. We repeated this step until the functional trait values for all sampled tree species were extrapolated to individuals belonging to the same tree species within the categories of dead trees or recruits. This procedure relies on the assumption that intraspecific trait variability is, generally spoken, smaller than interspecific trait variability (Kattge et al., 2011).

3.5.5 Modeling tree growth with functional traits

Finally we investigated the relationship between functional traits and tree growth through modeling. Because our observations are nested within a hierarchical structure of strata and plots, we could not use simple linear models. To account for the variation in diameter increment (ΔDBH) explained by the subgroup a tree is in, we opted for the use of linear mixed effects models. This model structure enabled us to control for the non-independence of the diameter observations (Gałecki and Burzykowski, 2013).

For this purpose the R package `lme4` was used (Bates et al., 2015). The variable ΔDBH is the response variable chosen to represent tree growth. Both DBH and ΔDBH were log transformed because of their positively skewed distribution. *Altitude*, *trait value* and DBH are the variables of interest to explain the variance in diameter increment and hence treated as fixed effects. Their interaction term was left out in all models because this factor was never significant. We wanted to account for the variability in ΔDBH caused by the experimental set-up. Therefore the random structure included the nested random effects *cluster* and *plot* as random intercepts. No random slope was assigned.

In total, four models were constructed, each focusing on the effect of a single functional trait on ΔDBH. Extending the reasoning of the Leaf and Wood Economics Spectra, we hypothesize a negative correlation between WD and ΔDBH and between C:N and ΔDBH on the on hand, and a positive correlation between SLA and ΔDBH and between LNC and ΔDBH on the other hand (Wright et al., 2004; Chave et al., 2009). The following model structures were used:

$$log_{10}(\Delta DBH) = Altitude + WD + log_{10}(DBH) + (1|Cluster/Plot)$$

$$log_{10}(\Delta DBH) = Altitude + SLA + log_{10}(DBH) + (1|Cluster/Plot)$$

$$log_{10}(\Delta DBH) = Altitude + LNC + log_{10}(DBH) + (1|Cluster/Plot)$$

$$log_{10}(\Delta DBH) = Altitude + C : N + log_{10}(DBH) + (1|Cluster/Plot)$$

Model residuals were checked to ensure the assumption of homoskedasticity was met by visual inspection of the residual plots, the Q-Q plots and the residual histograms.

CHAPTER 4

RESULTS

In this chapter we present some general characteristics of the altitudinal strata. We then discuss the findings on taxonomic diversity, followed by the results on functional diversity and functional traits. We conclude with the outcomes of the linear mixed effects models.

4.1 Stratum characteristics

Table 4.1 gives an overview of the general stand characteristics of each stratum. The number of tree species, genera and families were calculated based on the living trees in the most recent survey. Tree identifications were made at three taxonomic ranks: species, genus and family. The majority of the encountered trees could be determined up to species level (Table 4.2). The share of individuals that was determined up to species level has increased since the first inventory from 30% to 94.5% (Bruneel, S., 2016; Demol, M., 2016). A minority of the encountered trees were determined up to genus (3.4%) and family level (0.1%). Two percent of the individuals could not be identified.

To collect a representative amount of leaf samples, we aimed at sampling all tree species making up 80% of the basal area of each plot. Due to time constraints, this sampling percentage was not obtained in every plot. The eventual sampling percentages varied between 38% and 97 % (Figure B.2). Only in strata 4 and 5 this lower limit was exceeded (coverage percentage of over 90% for every plot). In stratum 1 and 2 a coverage percentage of roughly 65% was attained. No samples were collected in stratum 3 due to the yearly migration of the Andean spectacled bear in the Maquipucuna Cloud Forest Reserve at the time of the field campaign.

Table 4.1: Stand characteristics of the different strata in this study. For basal area (BA) and above-ground biomass (ABG) calculations, see Van den Meerssche, S. (2020).

	Stratum 1	Stratum 2	Stratum 3	Stratum 4	Stratum 5
Census interval (years)	4	4	4	3	4
No. of total trees (DBH > 10 cm)	263	334	250	661	330
No. of dead trees (since 2015)	86	76	69	92	55
No. of recruits (since 2015)	23	63	27	87	25
No. of tree species	59	76	64	65	25
No. of genera	49	57	55	52	23
No. of families	24	32	34	30	18
BA (m^2 ha^{-1})	17.7 ± 3.1	21.7 ± 8.44	23.3 ± 3.1	45.2 ± 14.3	34.8 ± 2.05
AGB (ton ha^{-1})	122.5 ± 14.3	174.9 ± 62.4	156.3 ± 31.3	296.7 ± 138.1	226.8 ± 37.8

Table 4.2: Level of tree species determination for the inventory of 2019. For every stratum, the number of individuals determined up to species, genus and family level is available, as well as the number of trees that could not be determined.

	Stratum 1	Stratum 2	Stratum 3	Stratum 4	Stratum 5	**Total**	
Species level	247	298	235	643	313	1736	(94.5%)
Genus level	2	24	13	10	14	63	(3.4%)
Family level	1	1	0	0	0	2	(0.1%)
No determination	13	11	2	8	3	37	(2.0%)
	263	334	250	661	330	**1838**	

4.2 Altitudinal trends in taxonomic diversity

To quantify alpha diversity along the transect, several taxonomic metrics were calculated including species richness, rarefied species richness, Shannon and Simpson diversity and Pielou’s evenness. Stratum 2 was the most diverse in terms of total number of unique tree species occurring at the altitude of 1100 m a.s.l. (Table 4.1). The highest non-rarefied species richness on plot level was encountered in stratum 4 (Table 4.3). Rarefied species richness was calculated for the lowest number of observed trees in a plot (47, stratum 1 plot 4). This measurement showed an optimum at the altitude of 1100 m a.s.l. Rarefaction curves for every plot are available in Figure A.7. The Shannon and Simpson diversity indices reached a plateau between stratum 2 and 4. Pielou’s evenness index reaches a minimum at the highest altitude.

Table 4.3: Mean and standard deviation of indicators for taxonomic diversity for the different strata along the elevational gradient. The different indicators used are: species richness, rarefied species richness, Shannon diversity index, Simpson diversity index and Pielou’s evenness index. The rarefied species richness was calculated for a sample size of 47.

	400 m a.s.l.	1100 m a.s.l.	1900 m a.s.l.	2400 m a.s.l.	3200 m a.s.l.
Species richness	26.0 ± 6.1	35.0 ± 8.3	27.8 ± 2.6	41.3 ± 2.5	17.0 ± 0.8
Rarefied species richness	21.1 ± 2.5	25.9 ± 2.9	24.2 ± 1.0	22.0 ± 1.3	13.8 ± 1.3
Shannon diversity index	2.8 ±0.2	3.2 ± 0.2	3.1 ± 0.1	3.1 ± 0.1	2.2 ±0.2
Simpson diversity index	0.91 ±0.01	0.94 ± 0.01	0.94 ± 0.01	0.93 ± 0.01	0.82 ± 0.04
Pielou’s evenness index	0.86 ± 0.02	0.91 ± 0.02	0.93 ± 0.01	0.85 ± 0.04	0.78 ± 0.06

Bray-Curtis dissimilarities calculated between strata were generally high, always exceeding 0.79 (Formula 3.1). This indicates a high species turnover along the transect (Figure 4.1). Dissimilarity in species composition seems to be related to the distance between reserves. The highest dissimilarity was recorded between stratum 1 and 5, with a dissimilarity of almost 1. The dissimilarities between neighbouring strata ranged between 0.80 and 0.90. The lowest dissimilarity (0.79) was recorded between the altitudes of 1900 m a.s.l and 2400 m a.s.l. A more detailed overview including Bray-Curtis dissimilarities between individual plots can be found in Figure A.6.

Figure 4.2 gives an overview of the distribution of all 211 unique tree species (including tree ferns and canopy palms) encountered along the transect. We did not find a single species occurring at every altitude. The most dissimilar strata were the reserves at the extremities of the transect. These two reserve have a complete turnover in species composition over

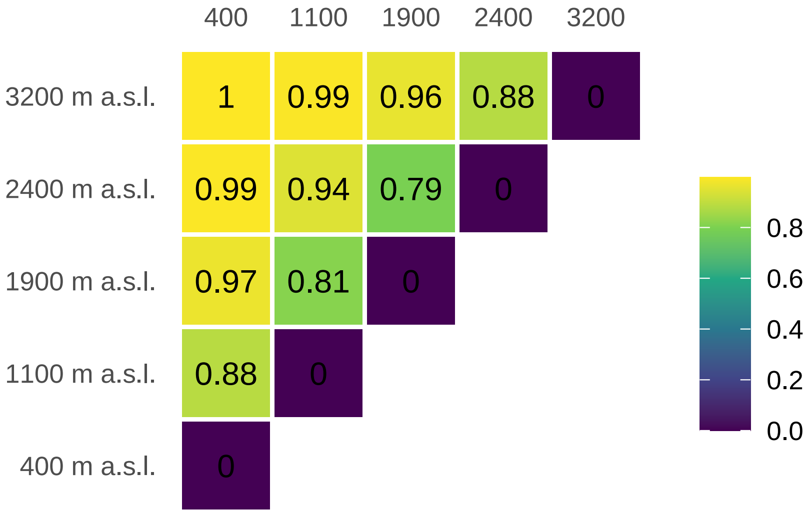


Figure 4.1: Visualisation of the Bray-Curtis dissimilarities between all strata based on tree species composition. The exact value of the Bray-Curtis dissimilarity between two strata is depicted in the corresponding grid cell. The lighter the hue of the grid cell, the bigger the dissimilarity between the two strata.

less than 100 km in a bird's-eye view of distance (Figure 3.1). The two most similar reserves (Maquipucuna and El Cedral) had 24 tree species in common.

The highest absolute number of tree species (79) was found in stratum 2 at 1100 m a.s.l. of which 40 were unique in this stratum while 17 species were also recorded on an altitude of 400 m a.s.l. and 11 species were shared between the altitudes of 1100 and 1900 m a.s.l. Sixty-nine percent of all observed species were unique to one single stratum. Twenty-eight percent of all species were shared between two strata[1]. One tree species, *Miconia clathrantha*, was recorded at all altitudes except for the highest. Figure A.1 to A.5 rank the most common species in every stratum according to aggregated basal area per species.

The degree of unique species per stratum can be expressed on several bases (Figure 4.3). Counting the number of unique species is the most straightforward approach to do this. Another way of showing the degree of endemism per altitude is to express the number of unique species per stratum relative to the total number of species recorded. At an altitude of 3200 m a.s.l. 68% of the tree species were not found in any of the other strata. To gain insight into how abundant these unique species are, the ratio of the aggregated basal area belonging to unique species to the aggregated basal area of the whole stratum was calculated.

---

[1] Some of the tree species occurring in two strata were recorded in non-neighbouring strata. The tree species *Billia rosea* for example was encountered in stratum 2 and 4 but not in stratum 3. We suspect that tree species recorded in non-neighbouring strata also occur at the interlying altitudes, but were not recorded because of the limited sample size.

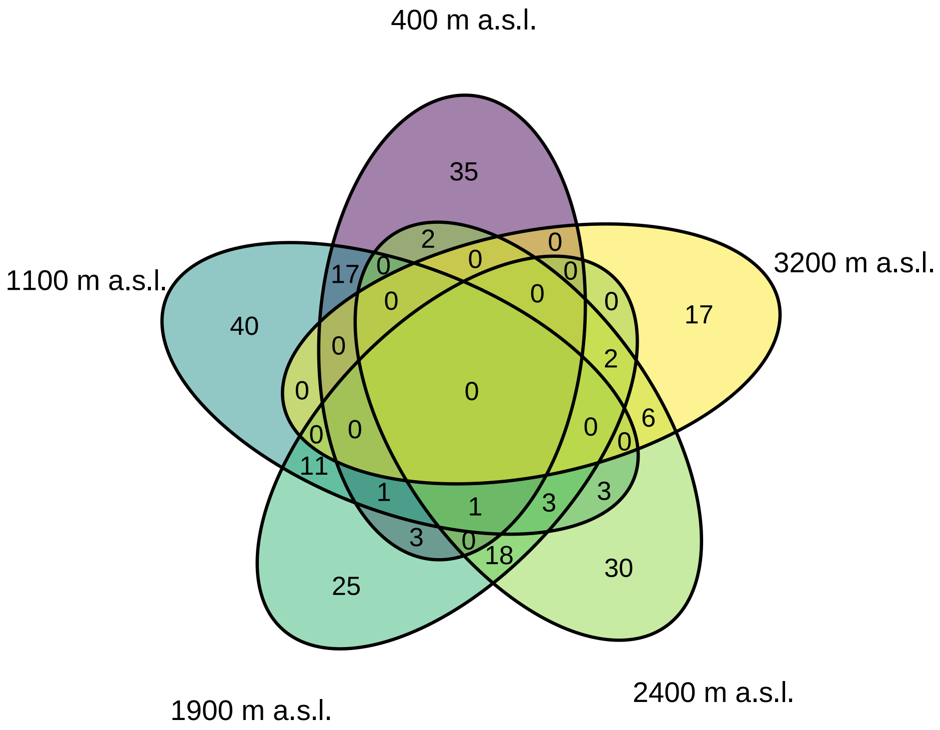


Figure 4.2: Venn diagram representing the number of unique tree species found in each stratum. The intersections of ellipses indicate the number of species found in multiple strata. The resurvey of 2019 (2018 for stratum 4) was used as a reference for this figure.

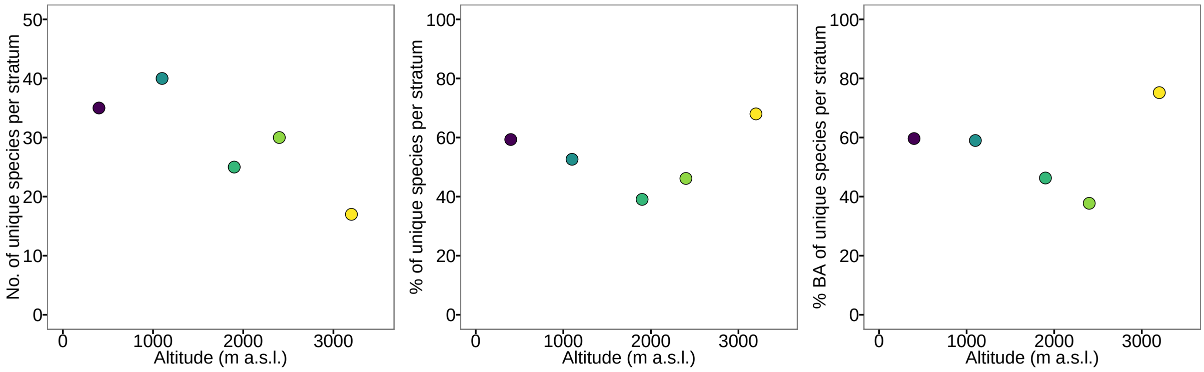


Figure 4.3: Left panel: Number of unique species per stratum as a function of altitude. Middle panel: Percentage of unique species relative to the total number of species per stratum as a function of altitude. Right panel: Percentage of the basal area (BA) per stratum belonging to unique species relative to the total BA per stratum as a function of altitude.

4.3 Altitudinal trends in functional diversity

A graphical representation of the altitudinal trend in the FD indices can be found in Figure 4.4. We did not find significant linear trends in every FD index with altitude, as was the case in earlier work by Demol, M. (2016). FRic peaked at 2400 m a.s.l., followed by the second highest values for FRic in stratum 2. The remaining strata show lower values for FRic, suggesting a stronger clumping of species in the trait space in these strata. FEve seems to decrease with altitude, apart from an outlier in stratum 1. The highest values for FDiv were recorded in stratum 1 and 5. For FDis we observed similar values for strata 1 to 4 with a drop at the highest altitude. This decrease is the only significant linear change with altitude observed for any of the FD indicators (p = 0.03). A summary with the means and standard deviations of the FD indices at every altitude is available in Table 4.4.

Table 4.4: Mean and standard deviation of indicators for functional diversity for the different strata along the elevational gradient. The different indicators used are: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis). Calculations were made making use of functional trait values for specific leaf area (SLA), wood density (WD) and carbon to nitrogen ratio (C:N). The Kruskal-Wallis test for significant differences was only used in case the assumption of homoskedasticity was met. Different letters indicate significant differences between groups (p<0.05).

	400 m a.s.l.	1100 m a.s.l.	1900 m a.s.l.	2400 m a.s.l.	3200 m a.s.l.
FRic	1.9 ± 2.1	6.9 ± 3.3	2.7 ± 1.2	13.8 ± 4.3	2.1 ± 1.3
FEve	0.51 ± 0.28	0.59 ± 0.07	0.54 ± 0.07	0.55 ± 0.04	0.44 ± 0.04
FDiv	0.84 ± 0.08^{a}	0.63 ± 0.03^{b}	0.71 ± 0.07^{ab}	0.60 ± 0.15^{ab}	0.77 ± 0.10^{ab}
FDis	0.82 ± 0.46^{ab}	1.14 ± 0.13^{a}	0.84 ± 0.19^{ab}	1.00 ± 0.25^{ab}	0.35 ± 0.14^{b}

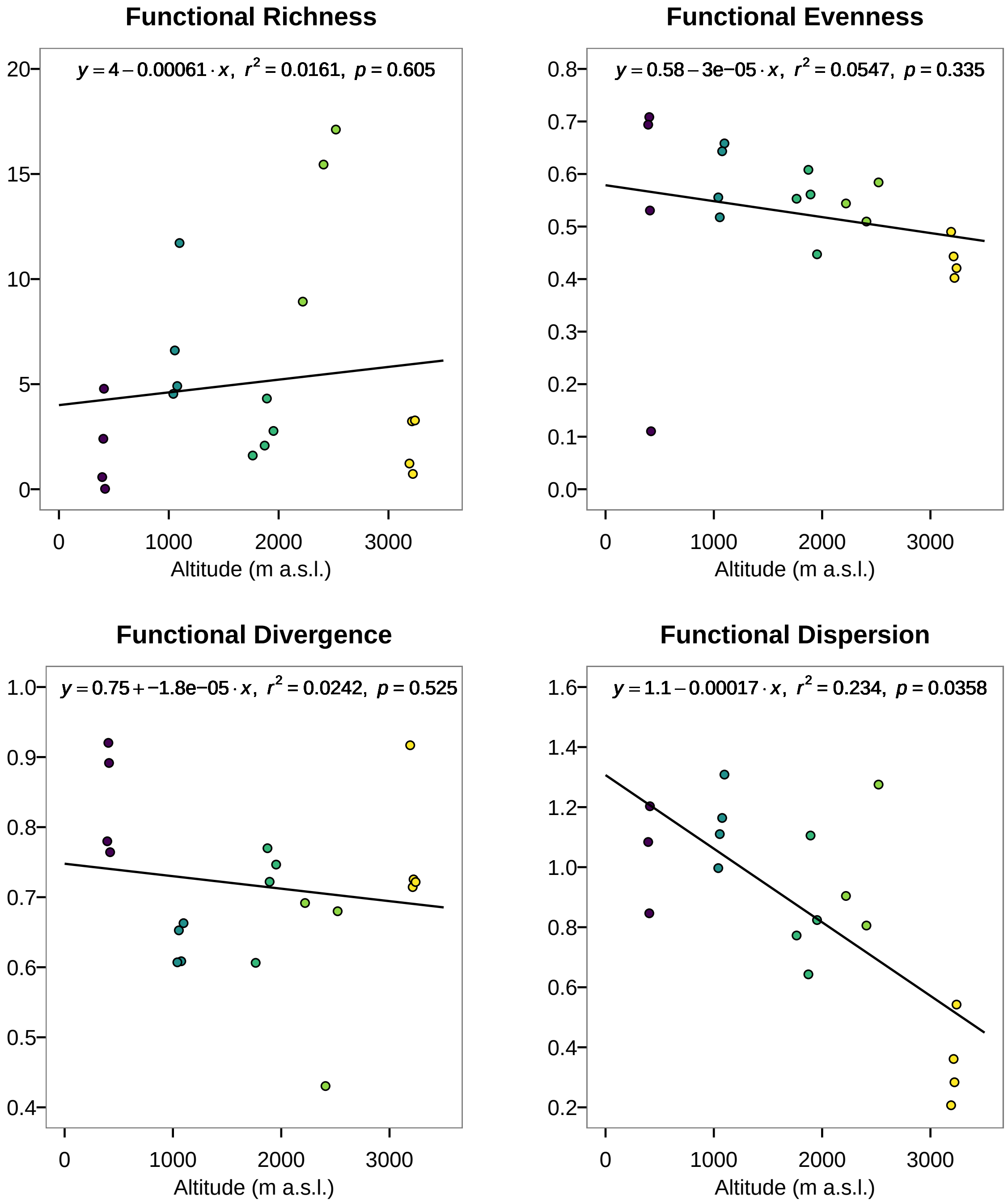


Figure 4.4: Functional diversity (FD) indicators as a function of elevation. The different indicators used are: functional richness, functional evenness, functional divergence and functional dispersion. Calculations were made making use of functional trait values for SLA, WD and C:N. A summary of the FD-indicators can be found in Table 4.4. No dimensionality reduction was required, all three PCoA axes were retained. In total 83 tree species were retained for analysis.

4.4 Altitudinal trends in functional traits

The CWMs of functional traits showed clear trends with altitude (Figure 4.5). Our observations confirm the trends observed in earlier work on the same altitudinal transect (Demol, M., 2016; Bruneel, S., 2016; Bauters et al., 2017). The functional trait values for SLA, LNC and δ^{15}N decrease significantly with altitude (*p*-values of 6.14×10^{-7}, 4.71×10^{-6} and 1.16×10^{-8} respectively). WD, C:N and δ^{13}C on the other hand show significant increases with altitude (*p*-values of 0.028, 8.59×10^{-6} and 1.28×10^{-9} respectively).

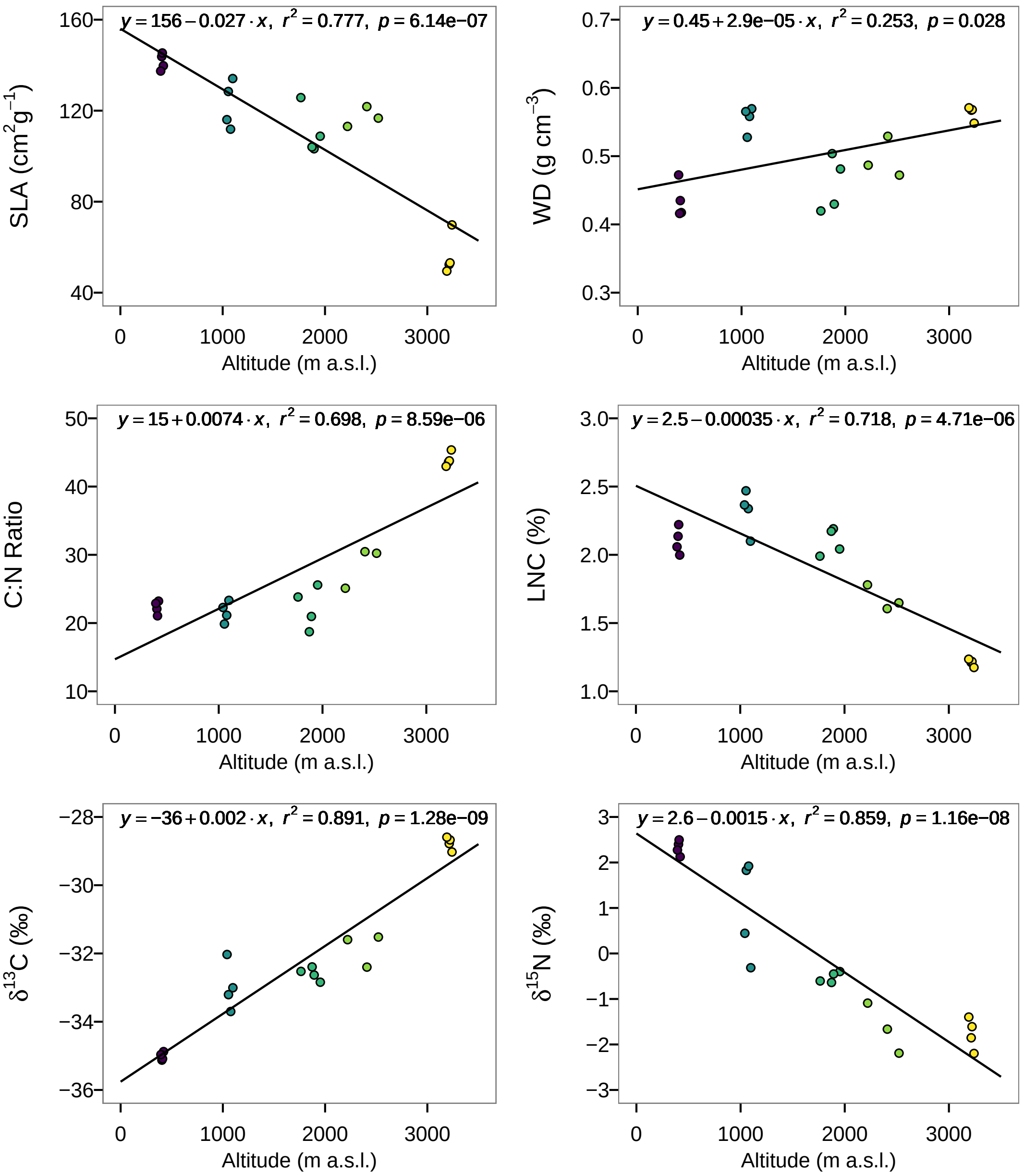


Figure 4.5: Altitudinal trends in community-weighted means (CWM) of trait values. The CWM of 19 permanent sample plots for 6 traits: specific leaf area (SLA), wood density (WD), carbon to nitrogen ratio (C:N), leaf nitrogen content (LNC), stable carbon isotope composition (δ^{13}C) and stable nitrogen isotope composition (δ^{15}N). Trend lines obtained through linear regression were added, as well as R^2 and *p* values.

4.5 Functional trait signature of dead trees and recruits versus survivors

The elevational trends in functional traits for the categories *dead trees*, *survivors* and *recruits* were compared to each other. Wood density (WD) generally increased with altitude for dead trees and survivors. No significant increase in WD was detected for recruited trees (Figure 4.6). The Bartlett test indicated heteroskedasticity for stratum 3 to 5, hence the Kruskal-Wallis test was only executed for stratum 1 and 2. No significant differences between categories for a given altitude were detected for WD (Table 4.5).

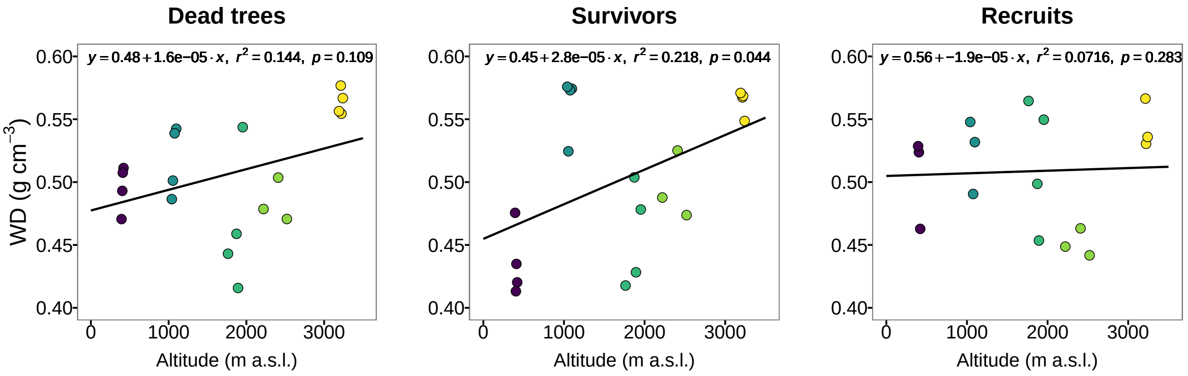


Figure 4.6: A comparison of altitudinal trends for wood density (WD) for dead trees, survivors and recruits. Left panel: community-weighted means (CWM) of WD per plot for trees that have died between the first census in 2015 and the resurvey. Middle panel: CWMs of WD per plot for trees that were included in both surveys. Right panel: CWMs of WD for new recruited trees that were included for the first time in the resurvey. Trend lines obtained through linear regression were added, as well as R^2 and p values. Different colours represent the five altitudinal strata.

Table 4.5: Mean and standard deviation of the wood density per altitude for three different categories: dead trees, survivors and recruits. If the assumption of homoskedasticity was met, significant differences were tested with the Kruskal-Wallis test.

Altitude	Dead trees	Survivors	Recruits	p Bartlett test	p Kruskal-Wallis test
400 m a.s.l.	0.48 ± 0.12	0.47 ± 0.14	0.51 ± 0.11	0.121	0.981
1100 m a.s.l.	0.55 ± 0.14	0.55 ± 0.14	0.57 ± 0.14	0.849	0.306
1900 m a.s.l.	0.49 ± 0.08	0.48 ± 0.13	0.53 ± 0.14	<0.001	-
2400 m a.s.l.	0.47 ± 0.10	0.49 ± 0.10	0.45 ± 0.13	0.002	-
3200 m a.s.l.	0.52 ± 0.09	0.54 ± 0.06	0.53 ± 0.05	<0.001	-

Specific leaf area (SLA) decreased significantly with altitude for both dead trees and survivors. No clear trend was discovered for SLA in recruits (Figure 4.7). The assumption of homoskedasticity was met for strata 2,4 and 5. At the altitudes of 1100 m a.s.l. and 2400 m a.s.l., the SLA of dead trees was significantly lower than the SLA of the survivors. In the highest stratum, recruits had a significantly higher SLA than the survivors (Table 4.6).

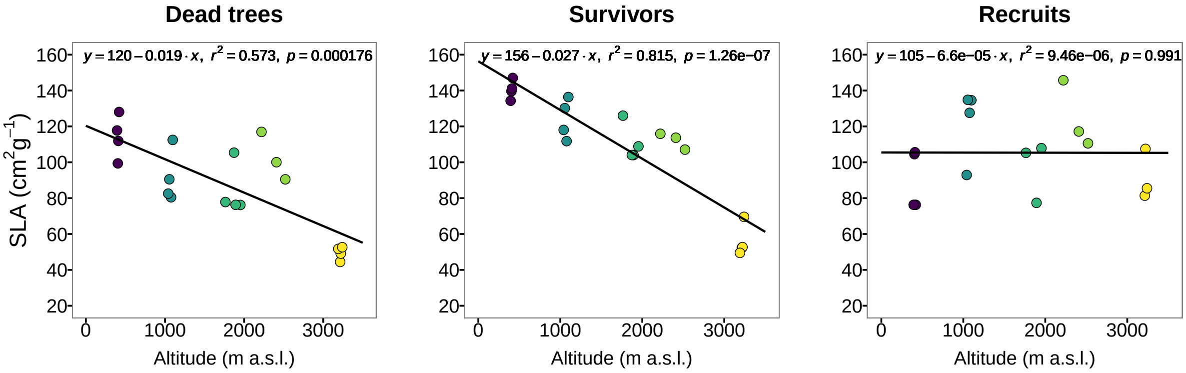


Figure 4.7: A comparison of altitudinal trends for specific leaf area (SLA) for dead trees, survivors and recruits. Left panel: community-weighted means (CWM) of SLA per plot for trees that have died between the first census in 2015 and the resurvey. Middle panel: CWMs of SLA per plot for trees that were included in both surveys. Right panel: CWMs of SLA for new recruited trees that were included for the first time in the resurvey. Trend lines obtained through linear regression were added, as well as R^2 and p values. Different colours represent the five altitudinal strata.

Table 4.6: Mean and standard deviation of the specific leaf area per altitude for three different categories: dead trees, survivors and recruits. If the assumption of homoskedasticity was met, significant differences were tested with the Kruskal-Wallis test. Different letters indicate significant differences between groups (p<0.05).

Altitude	Dead trees	Survivors	Recruits	p Bartlett test	p Kruskal-Wallis test
400 m a.s.l.	107.7 ± 38.0	136.2 ± 37.2	84.2 ± 20.0	0.010	-
1100 m a.s.l.	104.9 ± 37.0^{a}	125.9 ± 43.9^{b}	131.7 ± 47.4^{b}	0.183	<0.001
1900 m a.s.l.	81.3 ± 16.4	119.5 ± 31.3	112.3 ± 35.3	<0.001	-
2400 m a.s.l.	103.4 ± 36.4^{a}	113.7 ± 33.7^{b}	119.3 ± 40.3^{b}	0.098	0.007
3200 m a.s.l.	74.1 ± 31.7^{ab}	66.7 ± 32.0^{a}	91.2 ± 34.3^{b}	0.935	0.027

Carbon to nitrogen ratio (C:N) increases significantly with elevation for dead trees and survivors. We observed in increasing trend for recruits as well, however, this trend was not significant (Figure 4.8). For all strata, the assumption of homoskedasticity was met. The Kruskal-Wallis test pointed out significant differences between categories in every stratum (Table 4.7). In stratum 1, the carbon to nitrogen ratio of dead trees and recruits were significantly higher than for survivors. In stratum 2 and 3, the C:N ratio for dead trees was significantly higher than for survivors. In stratum 4, the C:N ratio for new recruits was significantly lower than for dead trees and survivors. In the highest stratum, the C:N ratio of both dead trees and survivors was significantly lower than for survivors.

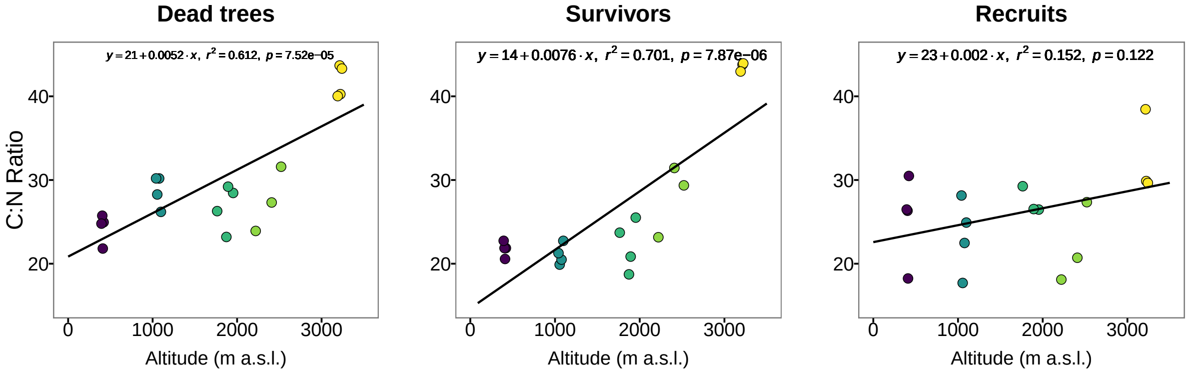


Figure 4.8: A comparison of altitudinal trends for carbon to nitrogen ratio (C:N) for dead trees, survivors and recruits. Left panel: community-weighted means (CWM) of C:N per plot for trees that have died between the first census in 2015 and the resurvey. Middle panel: CWMs of C:N per plot for trees that were included in both surveys. Right panel: CWMs of C:N for new recruited trees that were included for the first time in the resurvey. Trend lines obtained through linear regression were added, as well as R^2 and p values. Different colours represent the five altitudinal strata.

Table 4.7: Mean and standard deviation of the carbon to nitrogen ratio per altitude for three different categories: dead trees, survivors and recruits. If the assumption of homoskedasticity was met, significant differences were tested with the Kruskal-Wallis test. Different letters indicate significant differences between groups (p<0.05).

Altitude	Dead trees	Survivors	Recruits	p Bartlett test	p Kruskal-Wallis test
400 m a.s.l.	25.2 ± 5.6^{a}	21.1 ± 4.3^{b}	28.3 ± 4.9^{a}	0.051	<0.001
1100 m a.s.l.	26.9 ± 5.0^{a}	21.5 ± 5.2^{b}	21.9 ± 6.3^{b}	0.24	<0.001
1900 m a.s.l.	26.5 ± 6.6^{a}	22.6 ± 5.8^{b}	23.8 ± 6.4^{ab}	0.70	0.003
2400 m a.s.l.	27.9 ± 8.7^{a}	26.2 ± 8.1^{a}	23.3 ± 8.0^{b}	0.71	0.001
3200 m a.s.l.	31.5 ± 12.6^{a}	39.1 ± 10.8^{b}	33.5 ± 8.7^{a}	0.17	<0.001

Leaf nitrogen content (LNC) decreased significantly with altitude for all three categories (Figure 4.9). Because of heteroskedasticity for all strata except for stratum 3, only these results were tested for significant differences with the Kruskal-Wallis test (Table 4.8). A post hoc comparison with Dunn's test pointed out that dead trees at 1900 m a.s.l. had a significantly lower leaf nitrogen content than survivors or recruits.

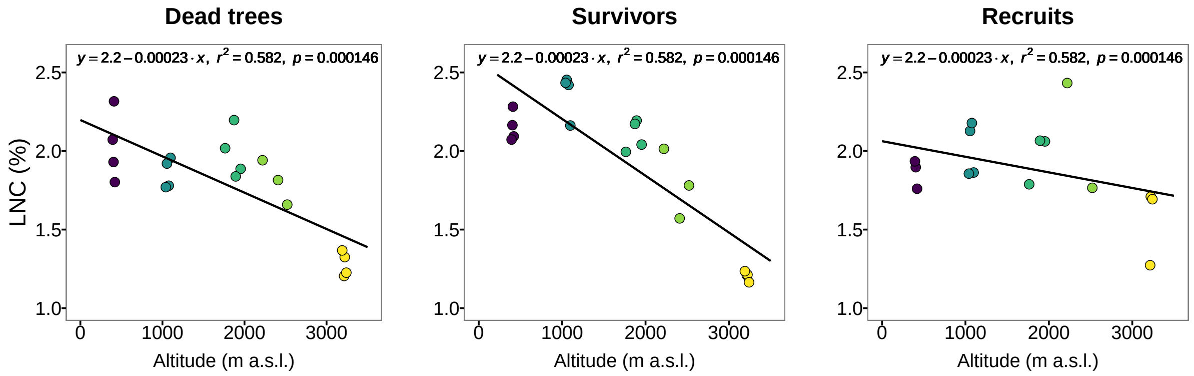


Figure 4.9: A comparison of altitudinal trends for mass-based leaf nitrogen content (LNC) for dead trees, survivors and recruits. Left panel: community-weighted means (CWM) of LNC per plot for trees that have died between the first census in 2015 and the resurvey. Middle panel: CWMs of LNC per plot for trees that were included in both surveys. Right panel: CWMs of LNC for new recruited trees that were included for the first time in the resurvey. Trend lines obtained through linear regression were added, as well as R^2 and p values. Different colours represent the five altitudinal strata.

Table 4.8: Mean and standard deviation of the mass-based leaf nitrogen content (%) per altitude for three different categories: dead trees, survivors and recruits. If the assumption of homoskedasticity was met, significant differences were tested with the Kruskal-Wallis test. Different letters indicate significant differences between groups (p<0.05).

Altitude	Dead trees	Survivors	Recruits	p Bartlett test	p Kruskal-Wallis test
400 m a.s.l.	2.03 ± 0.41	2.21 ± 0.44	1.86 ± 0.25	0.019	-
1100 m a.s.l.	1.95 ± 0.35	2.25 ± 0.53	2.25 ± 0.43	0.003	-
1900 m a.s.l.	2.00 ± 0.41^{a}	2.25 ± 0.58^{b}	2.08 ± 0.47^{b}	0.067	0.020
2400 m a.s.l.	1.81 ± 0.38	1.89 ± 0.50	2.17 ± 0.70	<0.001	-
3200 m a.s.l.	1.84 ± 0.91	1.42 ± 0.58	1.55 ± 0.35	<0.001	-

4.6 Effect of functional traits on tree growth

The estimates for the effects of the fixed effects used in the linear mixed effects models, together with the standard error (SE) and *p*-value are available in table 4.9. The R^2_{marg} and R^2_{cond} are approximations for the amount of variability that can be explained by the fixed effects and the entire model respectively (Nakagawa and Schielzeth, 2013).

Overall the models were able to explain roughly 10% the variance in ΔDBH. Little variance was explained by the fixed effects, resulting in R^2_{marg} between 0.04 and 0.07. The effect of altitude was never significant. The effect of DBH was highly significant for every model. The only functional trait with a significant effect on the response variable ΔDBH was wood density. The direction of this effect is negative: high wood densities are correlated with lower increments in diameter at breast height. The effects of SLA and LNC are negative, whereas the effect of C:N is positive. However, none of these effects were significant.

Table 4.9: Fixed effect estimates of four functional traits for the diameter increment as response variable: wood density (WD; g cm^{-3}), specific leaf area (SLA; cm^2 g^{-1}), carbon to nitrogen ratio (C:N) and leaf nitrogen content (LNC; %). The effect estimate is given for the intercept, altitude (km a.s.l.) DBH and the functional trait, along with the standard error (SE), *P* value, the marginal and the conditional R^2_{adj}. The interaction between altitude and functional trait was not significant in any of the four models, and was hence not retained.

Response	Effect	Estimate	SE	*P* value	R^2_{marg}	R^2_{cond}
ΔDBH (cm)	Intercept	-1.41	0.28	<0.001	0.070	0.100
	WD	-0.58	0.29	0.051		
	Altitude	-0.05	0.07	0.527		
	DBH	0.62	0.07	<0.001		
ΔDBH (cm)	Intercept	-0.86	0.38	0.029	0.042	0.088
	SLA	-0.01	0.01	0.374		
	Altitude	-0.16	0.09	0.150		
	DBH	0.45	0.09	<0.001		
ΔDBH (cm)	Intercept	-0.62	0.39	0.117	0.066	0.123
	LNC	-0.14	0.08	0.072		
	Altitude	-0.22	0.09	0.081		
	DBH	0.48	0.08	<0.001		
ΔDBH(cm)	Intercept	-1.09	0.30	0.002	0.062	0.121
	CN	0.003	0.005	0.563		
	Altitude	-0.20	0.09	0.114		
	DBH	0.49	0.08	<0.001		

CHAPTER 5
DISCUSSION

In this chapter, we discuss the results of this study and compare our findings to the outcomes of other studies. We explore whether these results confirm or contradict some well-known theories in community ecology.

5.1 Altitudinal trends in taxonomic diversity

The tropical Andes is of great interest to community ecologists. Historically, previous studies regarding tropical tree diversity in the Neotropics mainly focused on Amazon ecosystems on the eastern slope of the Andes (Homeier et al., 2010; Arellano and Macía, 2014; Girardin et al., 2014). For the western Andean slope, relatively few studies on tree diversity are available. However, recently this region has been receiving increased attention from scientists (Jiménez Paz, 2016; Myster, 2017; Wilson and Rhemtulla, 2018; Worthy et al., 2019). That said, comparing non-rarefied species richness from other studies in the same region to our findings is problematic. This observation is influenced by plot size, the number of observed stems, the cut-off diameter and the achieved determination accuracy. Therefore we restrict ourselves to the discussion of generally observed trends in species richness with altitude both in this and other studies.

We observed a directional change in alpha diversity with altitude (Table 4.3). Rarefied species richness reached a plateau between the 1100 and 1900 m a.s.l., followed by a small decrease at 2400 m a.s.l. and a steep drop towards the highest stratum. Indeed, tree species diversity near the treeline was remarkably lower than for lower-lying strata. The relative abundance of the most frequent species found in this stratum catches the eye: *Freziera canescens* makes up as much as 60% of the total basal area. Consequently, Pielou's eveness index reached its minimum at this altitude (Figure A.5).

Von Haller (1742) was the first to note a general decrease in species richness of vascular plants with altitude. From then onwards, numerous scientists conducted elevational transect studies throughout the world's mountainous regions, confirming this relationship for the Neotropics as well (Humboldt and Bonpland, 1805; Homeier et al., 2010; Swenson et al., 2011). Recent studies on the floristic properties of tree communities confirm this trend for northwestern Ecuador (Jiménez Paz, 2016; Worthy et al., 2019). It should be noted, however, that the decrease in species richness with altitude is not linear. Our results indicate a plateau in species richness at intermediate altitudes, providing support for the hypothesis of the *mid-elevation diversity bulge* effect as postulated by Lieberman et al. (1996).

Given this non-linear relationship, elevation is not the only driving factor determining tree community composition. In northern Ecuador, tree species distribution varies significantly at a local scale between forest reserves at the same elevation (Wilson and Rhemtulla, 2018). This finding stresses the importance of local topography as another main driver of the extensive speciation in the region (Steinbauer et al., 2016). Indeed, the relationship between species richness and elevation is by no means linear but highly dependent on local conditions (Worthy et al., 2019).

Even though the high-altitude forest harboured the least absolute number of species, the share of species unique to this stratum and the accumulated basal area represented by these unique species was higher than for any of the lower-lying strata (Figure 4.3). Every forest reserve in our transect harboured tree species found in none of the other reserves, suggesting that each forest reserve makes a significant contribution to the overall conservation of tree species in the region (Figure 4.2). The rapid species turnover with altitude was quantified by means of Bray-Curtis dissimilarities between reserves (Figure 4.1). The forests of Maquipucuna and El Cedral (found at 1900 and 2400 m a.s.l. respectively) had only 24 tree species in common. This is an impressive finding, given the fact that the sampling locations were only 6 km away from one another in a bird's-eye view of distance. Another study on tree species turnover in the province of Imbabura confirms the importance of small-scale niche differentiation as a driver of speciation. Jiménez Paz (2016) used finer elevational intervals of approximately 300 meters and discovered beta diversity between this sites remained high.

The reserves at the outer ends of the elevational transect did not share a single tree species[1] (Figure 4.2). Nonetheless, no such rapid turnover is observed at family level (Figure A.8). The families *Clusiaceae*, *Melastomataceae*, *Meliaceae* and *Rubiaceae* were found at every altitude and nineteen more families were shared between three or more strata (Table B.3). These findings support Gentry's hypothesis of *explosive speciation*. Gentry postulated that the high species richness in the tropical Andes is due to relatively late speciation driven by ultrafine niche partitioning. The Andean uplift created microhabitats fostering speciation through the combined influence of slope orientation, local rainshadows and dispersal barriers (Gentry, 1989). Fairly recent speciation (on a geologic time scale) could account for our observation of a large number of detected species within a restricted number of families.

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[1] One tree species, *Miconia clathrantha*, was recorded at all altitudes except for the highest. Although it is theoretically possible for a tree species to span such a broad range of altitudes, we do not exclude the possibility of a tree determination error.

5.2 Altitudinal trends in functional diversity

As indicated in the previous section, the reserves along the altitudinal transect harbour a staggering taxonomic diversity. Species composition surely affects ecological functioning, but traditional taxonomic diversity indices are unable to resolve the question whether taxonomically differing tree communities are functionally similar or not. To gain insight into the ecological functioning of the forest at different altitudes, we assessed several functional diversity indicators.

Functional richness is sensitive to outliers and unable to incorporate relative abundances. Moreover, this metric, as well as functional evenness and functional divergence, depend on the number of species retained for their calculation (Laliberté and Legendre, 2010). Given the weaknesses in our sampling scheme, these properties are highly undesirable (Table B.2). Hence, we restrict ourselves to the in-depth discussion of statistically significant differences for FDiv and FDis, as visualised in figure 5.1.

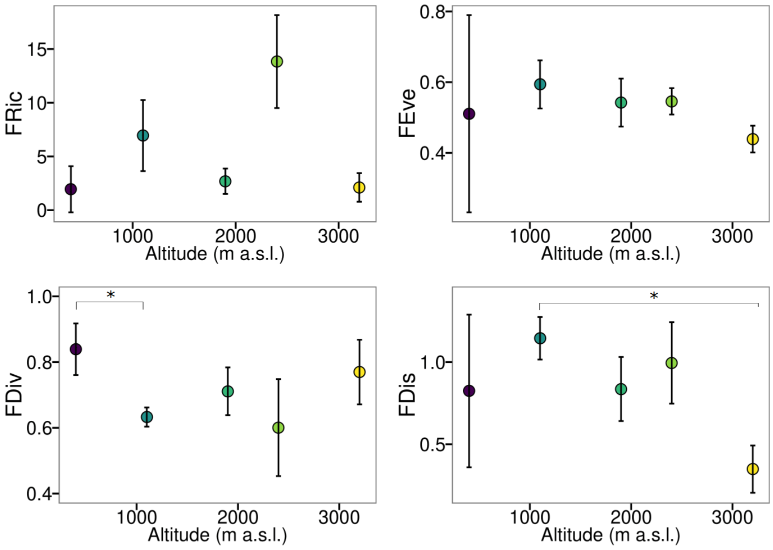

Figure 5.1: Mean values for functional diversity indicators per sampled altitude. The different indicators used are: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis). Errorbars reflect the standard error on every mean. Significant differences (p-value < 0.05) between strata were indicated with an asterix.

We denoted a significant difference in FDiv between stratum 1 and 2. Species with extreme trait values are known to inflate FDiv (Figure 5.2). We attribute the discrepancy in FDiv between these strata to the high abundance of *Pourouma bicolor* at 400 m a.s.l.: this species makes up 30% of the total basal area in stratum 1 (Figure A.1). It has characteristics of a typical *quick return on investment*-species, positioning it at an extremity of the trait space. *Pourouma bicolor* employs an acquisitive strategy: this tree species is characterized by a low wood density and carbon to nitrogen ratio, but a high specific leaf area (WD = 0.31 g cm^{-3}, C:N = 22.9 and SLA = 147 cm^2 g^{-1}). We therefore conclude that *Pourouma bicolor* is the main driver of the inflated FDiv value for stratum 1 compared to stratum 2. Moreover, the high abundance of this tree species suggests this forest reserve consists of secondary forest.

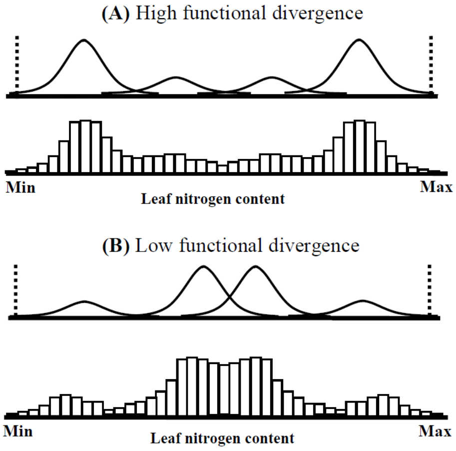

Figure 5.2: Functional divergence. The curves show the distribution of species abundance in the trait space. The trait space used in this example is one dimensional and composed with functional trait values for leaf nitrogen content. The vertical dotted lines indicate the edges of the occupied by the sampled species in the trait space. (A) A community in which the most abundant species occur at the extremities of the occupied trait range will obtain a relatively high value for functional divergence. (B) A community in which the most abundant species occur near the centre of the occupied trait range will obtain a relatively low value for functional divergence. Figure adopted from Mason et al. (2005).

Next, we observed a significant difference in functional dispersion between stratum 2 and 5 (Figure 5.1). The tree community at 3200 m a.s.l. occupies a more narrow range of the trait space than the tree community at 1100 m a.s.l. We intent to explain this observation with the aid of the *habitat filter*-concept as proposed by (Diamond, 1975). Environmental conditions near the treeline are less favourable for plant growth. Trees growing here need to endure high wind speeds, low temperatures and high solar radiation among others. The harsh environmental conditions prevailing at high elevations restrict the range of successful plant strategies in montane forests. The *habitat filter* shaped the high-altitude tree community in such a way that only in a narrow range of the functional trait space is occupied by the prevailing tree species, giving rise to lowered values for FDis in the highest stratum.

Generally spoken, no clear trends in FD indices with altitude were discovered. This leads us to suspect that functional diversity of tropical montane forests is, unlike taxonomic diversity, poorly related to altitude. Apaza-Quevedo et al. (2015) suggested that human-induced edge effects may be partially responsible for the observed functional diversity patterns in tropical montane forests, stressing the importance of forest intactness for its ecological functioning. Forest edges are associated with abrupt changes in (a)biotic conditions (Laurance et al., 2002). Besides an elevational gradient in our experimental set-up, we speculate a concomitant gradient in forest intactness exists along our elevational transect, possibly co-responsible for the observed trends in functional diversity. As previously described in chapter 3, the forest reserves included in this study are embedded in a wider landscape-matrix. The landscape-matrices vary from predominantly farmland (stratum 1 and 5) to predominantly primary forest (stratum 3 and 4). An alternative explication for the observed patterns in functional diversity could be the severity of the human-induced land-use change in the surroundings of each forest reserve.

This study on the altitudinal patterns in functional diversity was conducted at the same sites and with the same sampling design as an earlier study conducted by Demol, M. (2016).

Both studies aimed at sampling the most common species per stratum weighted for basal area. However, we did not find clear altitudinal trends for three out of the four FD indices, which is contradictory to the work of Demol, M. (2016), who found significant linear trends for all four FD indices.

Several factors may lie at the basis of these differing outcomes. First, we calculated FD indices for five altitudinal clusters instead of the original four. A set of three plots was added at 2400 m a.s.l. between the altitudes of 1900 and 3200 m a.s.l. to close the gap in elevation between the existing clusters. As detailed earlier, the functional diversity patterns in this stratum deviate from the expectations we had previous to the study based solely on elevation. This addition negates the previous findings of a linear pattern in functional diversity with altitude. Second, the determination accuracy has improved drastically between the two censuses. Incorrect or incomplete tree determinations may have led to erroneous results in the past. Third, we did not sample in stratum 3 but based or calculations on extrapolated trait values for species occurring in multiple strata. Since we did not obtain the proposed sampling percentage of 80% in this stratum, our results for the FD indices at 1900 m a.s.l. are likely unreliable. Fourth, a different set of functional traits was chosen to calculate FD indices in both studies. Demol, M. (2016) used a set of five traits including SLA, WD, C:N, δ^{13}C and tree height, whereas we used a set of only three traits including SLA, WD and C:N. Last, Demol, M. (2016) retained 81 species for analysis and used a reduced-space representation with a quality of 0.82, whereas we retained 83 species without dimensionality reduction.

Apart from these differences, we acknowledge two other weaknesses in our sampling design. The number of collected wood samples was low compared to the number of leaf samples (Table B.1). Moreover, we mostly sampled one or two individuals per species which is insufficient to assess the role of intraspecific trait variability (de Bello et al., 2011).

5.3 Altitudinal trends in functional traits

The new permanent sample plots at 2400 m a.s.l. included in the study for the first time fit well within the earlier findings on altitudinal trends in functional traits along the same transect (Figure 4.5) (Demol, M., 2016). Linear regressions turned out highly significant for every trait. The trait values for SLA and LNC decreased with altitude, whereas trait values for WD and C:N increased with altitude. Our results point towards a shift from an acquisitive plant strategy (high values for SLA and LNC, but low values for WD and C:N) at lower altitudes towards a conservative strategy (low values for SLA and LNC, but high values for WD and C:N) higher upslope. Hereby we can confirm the conclusion of other research (Apaza-Quevedo et al., 2015; Demol, M., 2016; Bauters et al., 2017). Similar shifts with altitude have been widely observed throughout the tropics (Katabuchi et al., 2012; Asner et al., 2017a).

The stable carbon and nitrogen isotope composition of plants can be used as proxies for community responses to environmental changes. These traits are less suited for the estimation individual ecological strategies employed by tree species. δ^{13}C and δ^{15}N should be interpreted on ecosystem-scale. The observed increase in δ^{13}C with elevation suggests a more conservative water use of high-altitude forests (Figure 4.5). The higher intrinsic water-use efficiency is likely to be an adaptation to the higher radiation and vapor pressure deficits in montane areas. This adaptation was also noted through changes in xylem sap flow in Atlantic rainforest in Brazil (Rosado et al., 2016). Canopy δ^{15}N signatures decreased with elevation, pointing towards a more conservative N cycle at higher elevations (Figure 4.5). This trend was observed across continents in both South American and African forests (Bauters et al., 2017).

The observed patterns in functional traits with altitude hint that linear fit might not be the best possible fit to the observed trends (Figure 5.3). The altitudinal patterns for SLA, C:N, LNC, δ^{13}C and δ^{15}N show a steep in- or decreases at certain altitudes. We reason that when trespassing a certain pivotal altitudes, environmental conditions change drastically resulting in a swift shift in the ecological strategy employed by the vegetation. An example of such a drastic change in environmental conditions is the cloud-base, where among others irradiance, temperature and precipitation regimes are altered. Reducing the elevational intervals by adding additional plots between existing clusters in future research could help confirm or reject this hypothesis.

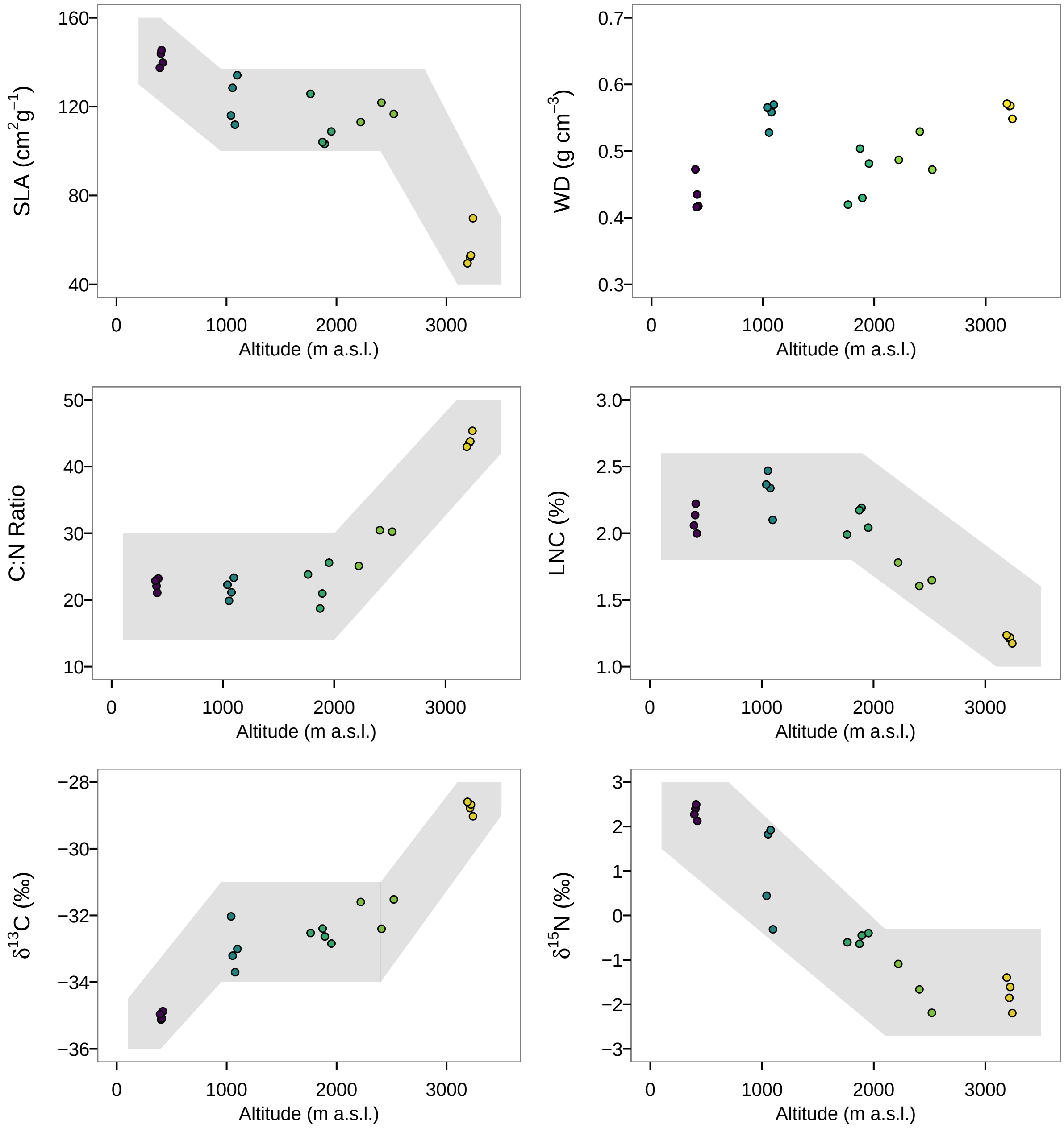

Figure 5.3: Altitudinal trends in community-weighted means (CWM) of trait values. The CWM of 19 permanent sample plots for 6 traits: specific leaf area (SLA), wood density (WD), carbon to nitrogen ratio (C:N), leaf nitrogen content (LNC), stable carbon isotope composition (δ^{13}C) and stable nitrogen isotope composition (δ^{15}N). The shaded areas indicate steep changes in functional trait values.

5.4 Functional trait signature of recruits and dead trees

Chronic pressures such as temperature rise, increased atmospheric CO_2 concentration and atmospheric nitrogen deposition act as an environmental filter on the world's ecosystems. The hierarchical-response framework (HRF) suggests that the response of ecosystems to these pressures is stepwise (Figure 5.4) (Smith et al., 2009).

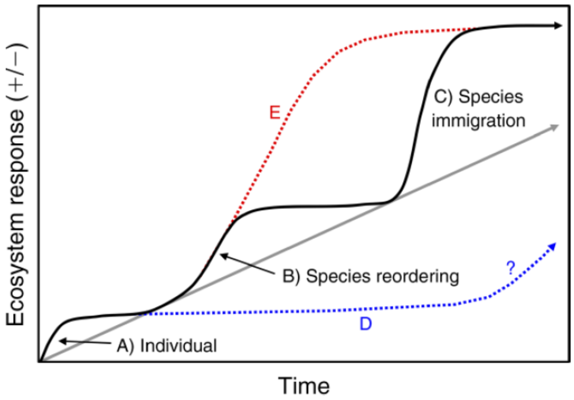

Figure 5.4: The hierarchical-response framework (HRF). (A) Individuals respond relatively rapidly to the exerted pressure (e.g. physiological or metabolic changes, mortality). (B) The abundances of the prevailing species shift because some species are being favoured over others by the changing conditions. (C) New species which are better adapted to the new conditions immigrate into the ecosystem. (D) Ecosystems dominated by long-lived species with slow turnover rates, like tropical forests, may lag behind in their response to changing conditions. Figure adopted from (Smith et al., 2009).

We hypothesized that newly recruited trees using a different ecological strategy than the bulk of the trees, might be better adapted to thrive despite the aforementioned human-induced pressures. Similarly, trees with a particular strategy might suffer more from these changing conditions than others. For this study, we primarily focused on studying step B of the HRF in the forest reserves along the elevational transect. We did this, not by studying shifts in abundances of taxonomic tree species, but through studying shifts in functional trait signatures. Comparing functional trait signatures for dead trees or recruits versus survivors offers a promising track to monitor the response of tropical forests to global change. The research strategy of relating functional traits with (neo)tropical forest dynamics has already been used by some authors, for example to investigated the response of juvenile trees to intensive logging (Hogan et al., 2018).

For the purpose of studying whether or not newly sprouted trees or dead trees have distinct functional trait characteristics from the rest of the standing stock, we compared the functional trait signature for both of these categories to the signature of the bulk of survivors for a given altitude. Wood density revealed no differences between categories, whereas leaf functional traits pointed out some significant differences. We found minor indications that dead trees between the altitudes of 400 and 2400 m a.s.l. could have had a more conservative ecological strategy than the bulk of the survivors (Table 5.1). In some strata dead trees had a higher C:N, lower SLA or lower LNC. In the highest forest reserve a lower than average C:N was observed for dead trees.

Table 5.1: Summary of significant shifts in functional traits for dead trees compared to survivors. An arrow pointing upwards indicates trait values for a particular functional trait were on average higher for dead trees than for survivors; vice versa for arrows pointing downwards.

	400 m a.s.l.	1100 m a.s.l.	1900 m a.s.l.	2400 m a.s.l.	3200 m a.s.l.
WD	-	-	-	-	-
SLA	-	⇓	-	⇓	-
C:N	⇑	⇑	⇑	-	⇓
LNC	-	-	⇓	-	-

The results for the functional trait signature of recruits are inconclusive (Table 5.2). The recurring problem of small sample sizes and heteroskedasticity led to a limited amount of statistically significant shifts in functional traits for new recruits compared to survivors. The only trait with observable shifts in recruits for multiple altitude was C:N ratio (Figure 4.8, Table 4.7). On average, recruits at 400 m a.s.l. had a higher C:N than the survivors, while the opposite was true at 2400 and 3200 m a.s.l. Given the small census interval, the number of recruits and dead trees included in the study was limited. We expect more reliable results and magnified trends from future recensus campaigns, because the current census interval is perhaps too small compared to tree turnover rates in tropical forests to draw correct conclusions (Sheil and Phillip, 1995; Lewis et al., 2004). Further research is needed to confirm or reject the observed trends.

Table 5.2: Summary of significant shifts in functional traits for new recruits compared to survivors. An arrow pointing upwards indicates trait values for a particular functional trait were on average higher for recruited trees than for survivors; vice versa for arrows pointing downwards.

	400 m a.s.l.	1100 m a.s.l.	1900 m a.s.l.	2400 m a.s.l.	3200 m a.s.l.
WD	-	-	-	-	-
SLA	-	-	-	-	⇑
C:N	⇑	-	-	⇓	⇓
LNC	-	-	-	-	-

Our results did not show support for the immigration of tree species originating from lower-lying altitudinal strata into higher-lying forest reserves (Table B.4). Given the existing dispersal barriers, the slow upward migration and slow turnover rates of Andean trees, this result is in line with our expectations (Feeley et al., 2011). We suspect that many so-called newly emerged species actually do occur within the stratum, but were not recorded during the first census because of the limited plot size. Increasing the plot size or the number of plots would enhance the likelihood of discovering species with a lower frequency of occurrence. Moreover, these newly observed species could be due to tree determination errors as the result of a confusion between two tree species belonging to the same genus.

5.5 Patterns in diameter increment in relation to functional traits

Leaf traits appeared to be poor predictors of individual tree growth (Table 4.9). The directions of these effect are counterintuitive from what we would expect when reasoning in the framework of the Leaf Economics Spectrum: acquisitive trait values such as high SLA and LNC were negatively correlated with growth, whereas conservative trait values such as high for C:N were positively correlated with diameter increment (Wright et al., 2004). These trends were however not significant, thus can't be consolidated. This could partially be due to the strong correlation that exists between leaf functional traits and altitude (Figure 4.5).

Of all functional traits tested, only wood density had a significant effect on ΔDBH (Table 4.9). The direction of this effect was negative, corresponding to the prediction of the Wood Economics Spectrum (Chave et al., 2009). High wood densities are correlated with lower diameter increments, reflecting the ecological trade-off trees face when producing woody tissue. King et al. (2006) found the same relationship between wood density and tree growth for lowland tropical forest in Malaysia. Moreover, Poorter et al. (2008) was able to relate high wood density to lower growth rates in Mexican, Bolivian and Panamanian forests as well.

We experienced some difficulties in modeling the relationship between tree growth and functional traits, leading to a couple of insights. First, our experimental set-up is currently not sturdy enough to study the relationship between functional traits and tree growth. Due to the clustering of plots at a certain location, the variable *cluster* needed to be controlled for in the random structure of the linear mixed effects model, lowering the explanatory power of the variable *altitude* in the fixed effects. Second, the measurement error on diameter measurements impeded the detection of a clear relation between growth and functional traits. The point of measurement (POM) was not indicated with spray paint in the first survey of 2015. If the diameter remeasurement was carried out a few centimeters above or below the initial POM, this resulted in a distorted assessment of the diameter increment (ΔDBH). Moreover the time gap between the first census and the recensus was perhaps insufficient to separate growth response from measurement error. These factors resulted in the recording of both negative or excessive ΔDBH measurements (Figure 5.5).

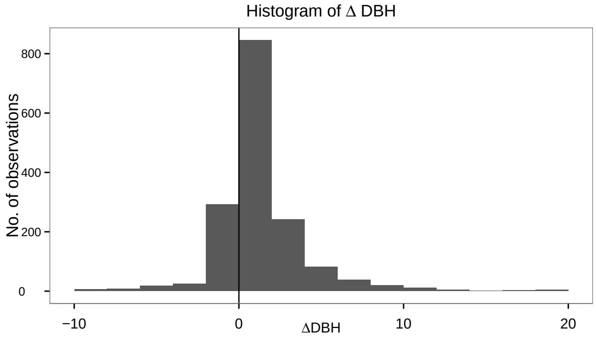

Figure 5.5: Histogram of the increments in diameter at breast height in centimeters recorded between the first census and the recensus.

An alternative is to use community-weighted means of functional traits to model stand-level above-ground biomass productivity (ΔAGB) instead of individual diameter growth. Finegan et al. (2015) investigated this relationship for tropical rainforests in Bolivia, Brazil and Costa Rica. They found support for the hypothesis that CWMs of traits are correlated with ΔAGB. Specific leaf area was their most important predictor for ΔAGB, with a positive correlation between SLA and ΔAGB. Wood density was negatively correlated with ΔAGB, this effect was however not significant. The interval between two censuses used for their study varied between 8 and 11 years. This reinforces our suspicion that intervals of 3 to 4 years between censuses are most likely insufficient to detect correlations between functional traits and ΔAGB.

CHAPTER 6

CONCLUSION

In this concluding chapter we try to answer the research questions as posed in Chapter 1, and review the implication of our results on the future of tropical montane forests.

(1) *Does an increase in altitude change the floristic properties of forests on the western flank of the Ecuadorian Andes?*

Yes, elevation affects the floristic properties of montane forests in the Ecuadorian Andes. Taxonomic diversity metrics indicate that species diversity decreases with elevation. However, the species turnover rate with altitude stresses the contribution of each forest reserve to the overall conservation of Andean tree species.

(2) *Does elevation influence functional diversity of Andean forests?*

Functional diversity is, unlike taxonomic diversity, weakly related to altitude. Other factors, such as forest intactness, may be more strongly correlated with functional diversity patterns along the transect than elevation.

(3) *How does elevation influence the functional trait patterns observed along the transect?*

Functional traits are strongly related to altitude. Tree species with a conservative strategy seem to be relatively more abundant at high altitudes. Moreover, we consider the existence of turnover altitudes along the transect where drastic changes in environmental conditions provoke steep changes in functional trait patterns. Further research could help clarify whether the cloud-base ecotone can be regarded as such a turning point within this transect.

(4) *For a given altitude, do functional trait values of newly sprouted trees or dead trees diverge from those of the rest of the trees?*

We did not find clear diverging patterns in the functional trait signatures between categories. Further research with a larger number of individuals in both categories could reveal whether this was due to the small sample size or to the fact that functional trait signatures between categories do not diverge.

(5) *Which functional traits are predictive for individual tree growth?*

Wood density is predictive for individual tree growth. Higher wood density is correlated with a slower increment in diameter at breast height. Leaf functional traits appeared to be poor predictors of individual tree growth, but reducing the measurement error on diameter measurements could reveal a correlation in future studies.

Our results suggest that tree species in northwestern Ecuador have narrow geographic ranges. Therefore we can state that these species have narrow thermal tolerances and will suffer disproportionately from climate change (Janzen, 1967; Perez et al., 2016). Species that fail to migrate at the pace of global temperature rise face the risk of extinction (Feeley et al., 2012). So far, we found little to no support for changing forest composition as a result of human-induced pressures. This leads us to suspect the rate of adaption and migration is in many cases slower than the rate of global temperature rise (Feeley et al., 2011).

Moreover, the observed patterns in functional traits with altitude let us suspect certain pivotal altitudes exist at which environmental conditions change drastically. The prevailing vegetation is adapted to the environmental conditions at each specific site. The cloud-base could be associated with these pivotal altitudes. Future changes in the location or frequency of cloud formation processes due to climate change could affect tree species which have specialized to thrive in this environment, resulting in further disturbance of tropical montane forest. The whole of these findings indicate that tropical montane forests are especially vulnerable to climate change.

CHAPTER 7

FUTURE RESEARCH OPPORTUNITIES

Creating a second altitudinal transect with permanent sample plots at the same altitudes as the current transect would be a strong asset to future research. This additional transect would allow the investigation of small-scale variability of the floristic compostion of forest reserves at similar altitudes.

Moreover, an additional transect would facilitate modeling the relationship between functional traits and tree growth. It is advisable to repeat this modeling exercise within a couple of years. Taking into account that diameter measurements inherently display large measurement errors, larger ΔDBH would make it easier to detect a relationship between functional traits and tree growth.

Larger census intervals will increase the sample size of recruits and dead trees. It could be interesting to repeat the analysis of the functional trait signature of these categories in the future, as well as investigating shifting abundances in taxonomic tree species.

Lastly, it would be worthwhile to create additional altitudinal clusters between the existing ones. This could help to identify whether so-called pivotal altitudes exist, and what environmental conditions drive the shifts in functional traits.

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APPENDIX A

APPENDIX FIGURES

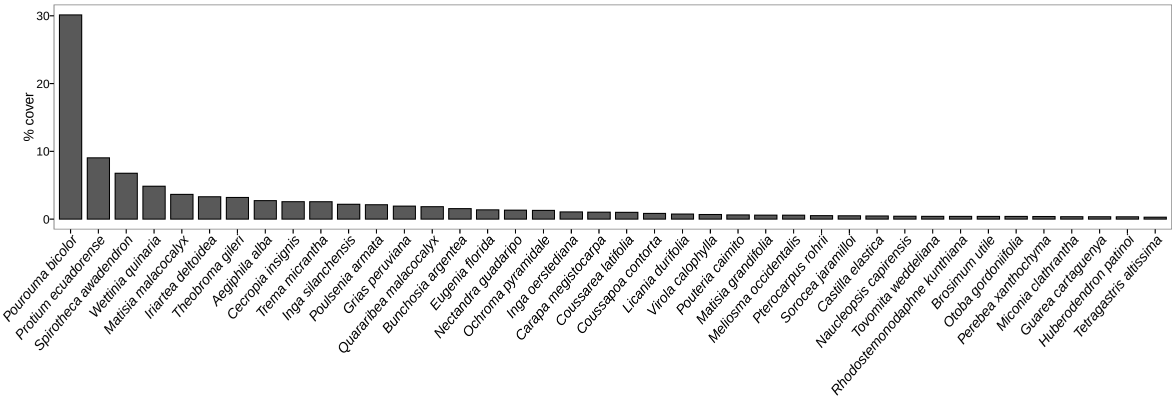

Figure A.1: Histogram ranking the 40 most abundant tree species in stratum 1 from high to low percentage of aggregated basal area per species.

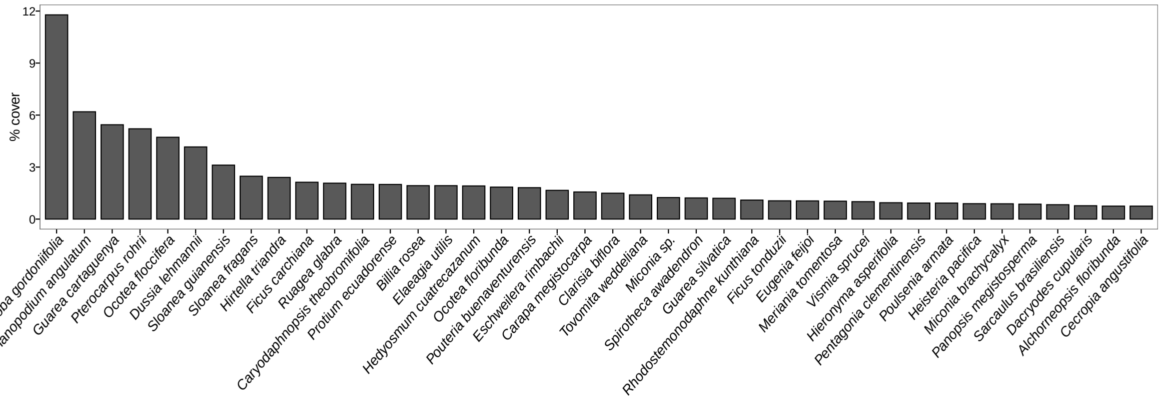

Figure A.2: Histogram ranking the 40 most abundant tree species in stratum 2 from high to low percentage of aggregated basal area per species.

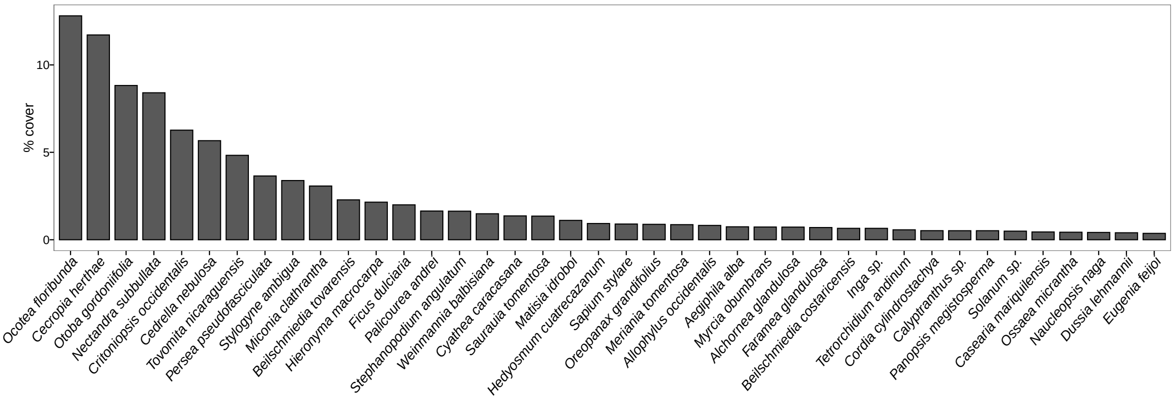

Figure A.3: Histogram ranking the 40 most abundant tree species in stratum 3 from high to low percentage of aggregated basal area per species.

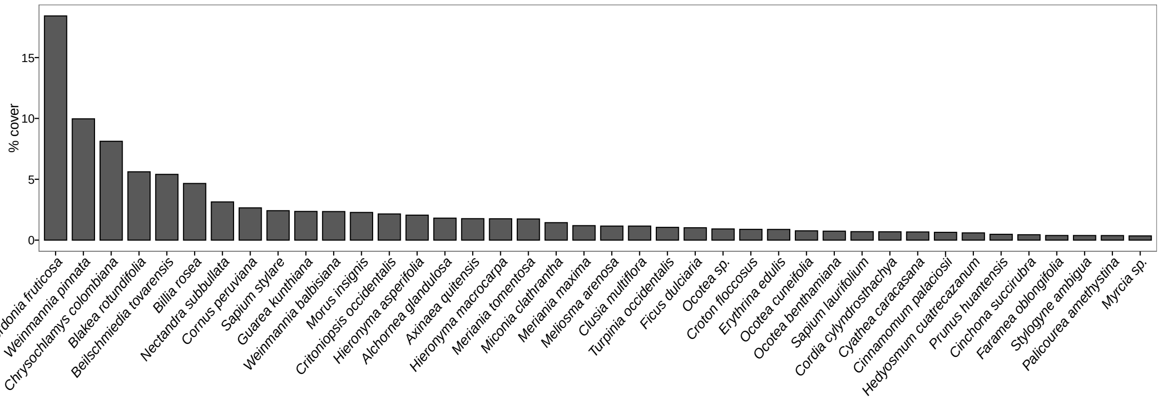

Figure A.4: Histogram ranking the 40 most abundant tree species in stratum 4 from high to low percentage of aggregated basal area per species.

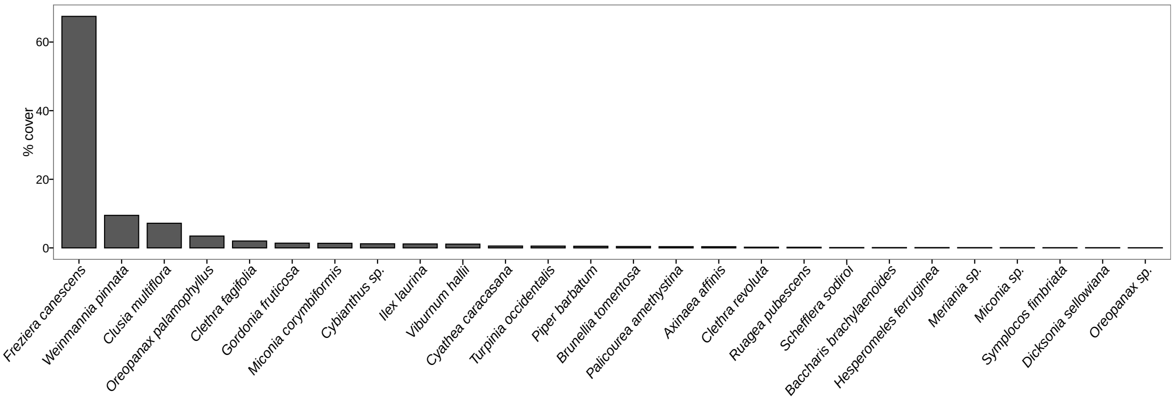

Figure A.5: Histogram ranking all the tree species in stratum 5 from high to low percentage of aggregated basal area per species.

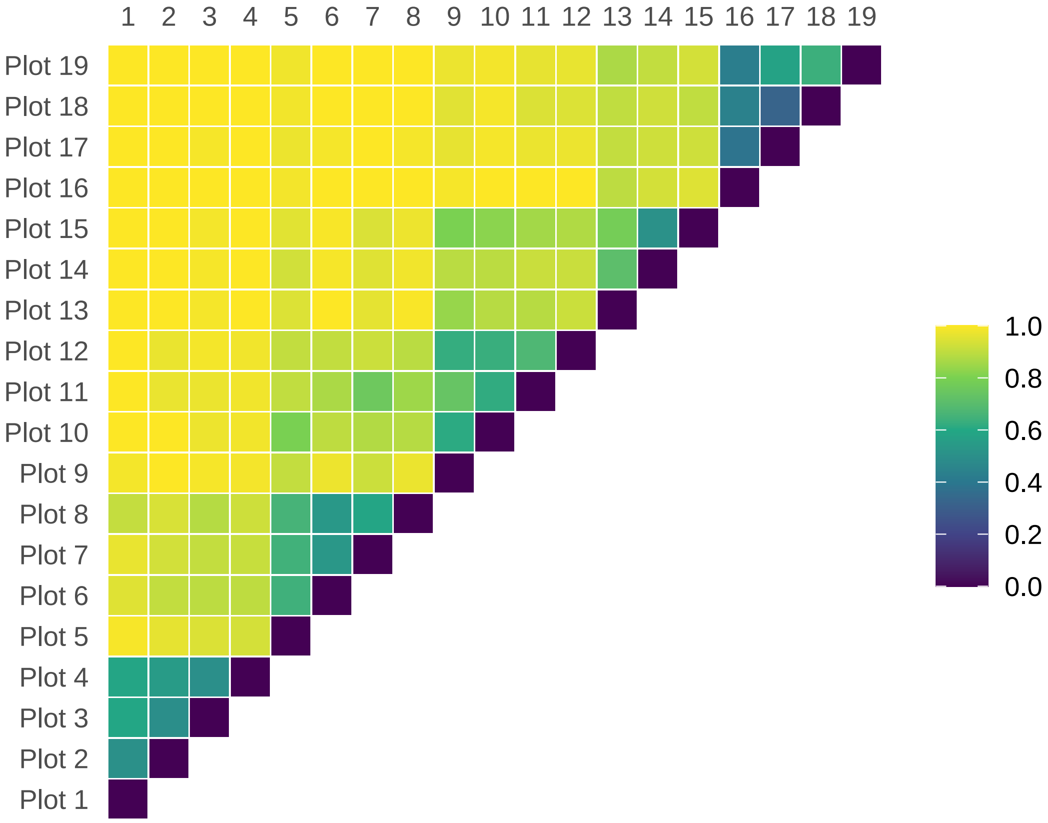

Figure A.6: Visualisation of the Bray-Curtis dissimilarities between all plots based on tree species composition. The lighter the hue, the bigger the dissimilarity between two plots. Stratum 1 consists of plots 1 to 4, stratum 2 consists of plots 5 to 8, stratum 3 consists of plots 9 to 12, stratum 4 of plots 13 to 15 and plots 16 to 19 belong to the highest stratum.

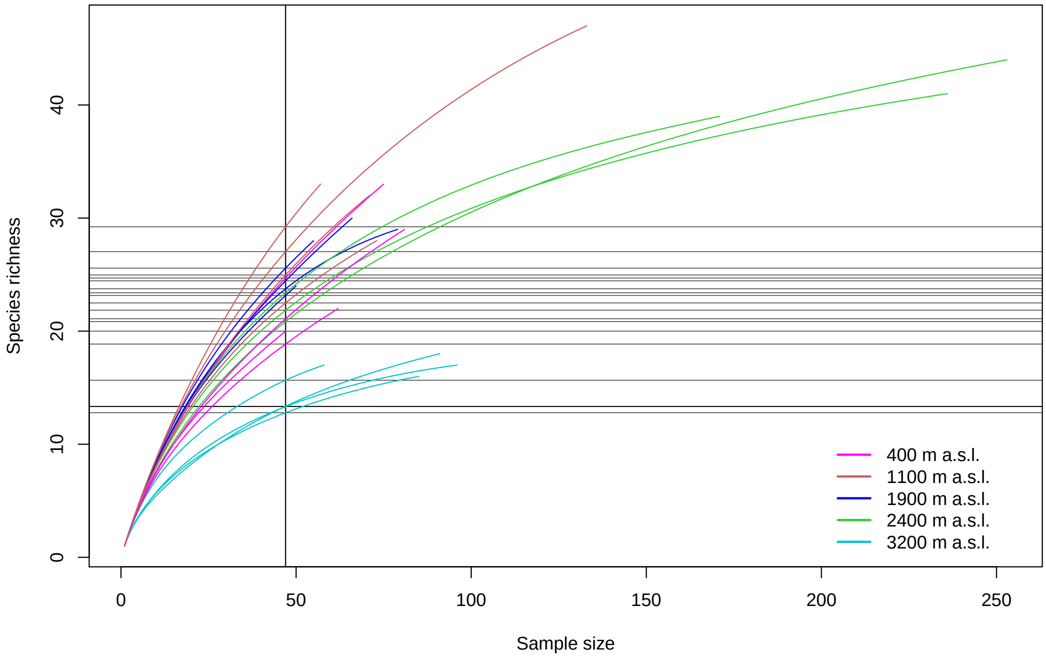

Figure A.7: Rarefaction curves for all 19 plots. The rarefied species number of each plot is the point of intersection between the sample size of 47 and the curve. The endpoint of each curve represents the actual sample size.

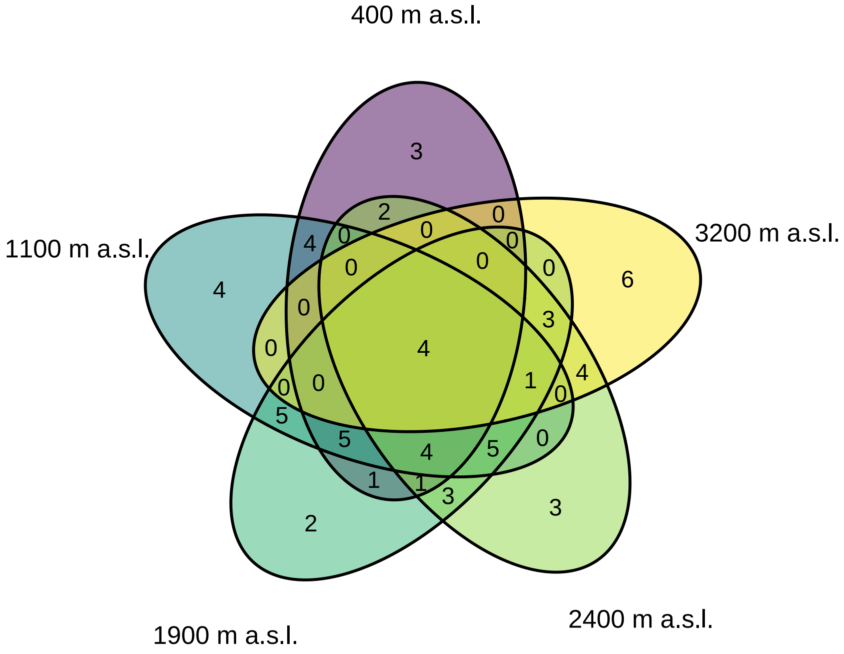

Figure A.8: Venn diagram representing the number of unique families found in each stratum. The intersections of ellipses indicate the number of families found in multiple strata. The resurvey of 2019 (2018 for stratum 4) was used as a reference for this figure.

APPENDIX B

APPENDIX TABLES

Table B.1: Overview of the absolute number of samples for leaves and wood cores per stratum.

Stratum	No. of leaf samples	No. of wood samples
1	32	11
2	96	19
3	0	0
4	115	23
5	14	6

Table B.2: Overview of the sampling percentage obtained in every plot for leaf and wood sampling.

Stratum	Plot	Leaf samples (% BA sampled)	Wood samples (% BA sampled)
1	1	38.4 %	58.2 %
1	2	67.1 %	57.7 %
1	3	66.2 %	40.7 %
1	4	64.8 %	40.7 %
2	5	70.4 %	41.5 %
2	6	60.3 %	26.1 %
2	7	70.7 %	33.0 %
2	8	41.5 %	41.8 %
3	9	0 %	0 %
3	10	0 %	0 %
3	11	0 %	0 %
3	12	0 %	0 %
4	13	92.1 %	52.5 %
4	14	79.6 %	67.8 %
4	15	92.0 %	40.9 %
5	16	95.5 %	15.5 %
5	17	97.5 %	16.9 %
5	18	91.3 %	14.8 %
5	19	95.1 %	42.6 %

Table B.3: Detailed overview of each family that occurred along the transect with the total number of stems counted for each altitudinal cluster of plots. All stems recorded during the first census and/or the re-survey were included.

Family	400 m a.s.l.	1100 m a.s.l.	1900 m a.s.l.	2400 m a.s.l.	3200 m a.s.l.
Actinidiaceae	0	0	3	4	0
Adoxaceae	0	0	0	1	20
Annonaceae	0	2	1	0	0
Apocynaceae	2	0	0	0	0
Aquifoliaceae	0	0	0	0	11
Araliaceae	0	1	2	6	56
Arecaceae	48	0	0	0	0
Boraginaceae	0	0	6	0	0
Brunelliaceae	0	0	0	3	3
Burseraceae	20	8	0	0	0
Cannabaceae	1	0	0	4	0
Capparaceae	0	1	0	0	0
Cardiopteridaceae	0	0	0	3	0
Celastraceae	0	0	0	1	0
Chloranthaceae	0	3	3	5	0
Chrysobalanaceae	2	4	1	0	0
Clethraceae	0	0	0	0	26
Clusiaceae	2	7	12	63	22
Compositae	0	0	13	13	2
Cornaceae	0	0	0	13	0
Cunoniaceae	0	0	3	75	18
Cyatheaceae	0	0	16	18	15
Dichapetalaceae	0	24	3	0	0
Dicksoniaceae	0	0	0	0	1
Ebenaceae	0	0	1	0	0
Elaeocarpaceae	0	11	0	0	0
Erythroxylaceae	0	1	0	0	0
Euphorbiaceae	0	6	9	37	0
Hypericaceae	0	1	0	0	0
Icacinaceae	0	4	1	0	0
Lamiaceae	6	0	3	0	1
Lauraceae	6	42	41	99	0
Lecythidaceae	12	7	1	0	0
Leguminosae	13	22	2	10	0
Malpighiaceae	3	1	0	0	0
Malvaceae	55	7	5	0	0
Melastomataceae	4	25	29	130	14
Meliaceae	8	22	3	19	3
Moraceae	19	14	6	20	0
Myristicaceae	5	55	15	0	0
Myrtaceae	3	10	7	0	0
Olacaceae	0	4	0	0	0
Pentaphylacaceae	0	0	0	0	126
Phyllanthaceae	0	5	5	20	0
Piperaceae	0	0	0	0	19
Primulaceae	0	8	20	13	0
Proteaceae	0	4	1	0	0
Putranjivaceae	1	2	0	0	0
Rosaceae	0	0	3	5	1
Rubiaceae	10	22	33	36	11
Rutaceae	0	1	1	0	0
Sabiaceae	2	0	1	15	0
Salicaceae	0	0	3	4	0
Sapindaceae	0	3	2	37	0
Sapotaceae	4	15	0	0	0
Schlegeliaceae	1	0	0	0	0
Siparunaceae	1	0	0	2	0
Solanaceae	1	0	0	0	0
Staphyleaceae	0	0	0	11	6
Symplocaceae	0	0	0	0	1
Theaceae	0	0	0	28	7
Thymelaeaceae	1	0	0	0	0
Urticaceae	77	4	18	4	0

Table B.4: Taxonomic identity of new recruits belonging to a species not earlier detected among the standing stock during the first census in 2015. Other strata in which these species occur are displayed, together with species of the same genus occurring in the stratum itself.

	Emerging tree species among new recruits	Presence in other strata	Presence of other species of same genus in stratum
Stratum 1	*Guarea macrophylla*	-	-
	Billia rosea	Stratum 4	*Miconia brachycalyx, Miconia clathrantha*
Stratum 2	*Miconia theaezans*	Stratum 4	*Sloanea guianensis, Sloanea fragrans*
	Sloanea pubescens	-	-
	Casearia cajambrensis	-	*Casearia mariquilensis*
	Calatola costaricensis	Stratum 2	-
	Clavija procera	-	-
Stratum 3	*Faramea oblongifolia*	Stratum 4	*Faramea glandulosa*
	Guatteria pittieri	Stratum 2	-
	Nectandra laurei	-	*Nectandra subbullata*
	Zanthoxylum formiciferum	Stratum 2	-
	Ardisia ambigua	Stratum 3	-
Stratum 4	*Gymnosporia gentryi*	-	-
	Viburnum hallii	Stratum 5	-
Stratum 5	*Dicksonia sellowiana*	-	-