LIANA ABUNDANCE AND FUNCTIONAL DIVERSITY ALONG AN ALTITUDINAL GRADIENT IN NORTHERN ECUADOR

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Abbreviations

a.s.l.: Above sea level

AGB: Aboveground biomass

BA: Basal area

CWM: Community weighted mean

DBH: Diameter at breast height

ENSO: El Niño Southern Oscillation

FAO: Food and Agricultural Organisation of the United States

FDis: Functional dispersion

FDiv: Functional divergence

FEve: Functional evenness

FRic: Functional Richness

LCC: Mass-based leaf carbon content

LES: Leaf economic spectrum

LNC: Mass-based leaf nitrogen content

LPC: Mass-based leaf phosphorus content

MAP: Mean annual precipitation

MAT: Mean annual temperature

MCF: Mindo Cloud forest Foundation

MST: Minimum spanning tree

Ntot: Total nitrogen content

Pbio-av: Bioavailable phosphorus

PC: Principal component

PCA: Principal component analysis

PSP: Permanent sample plot

Ptot: Total phosphorus content

SLA: Specific leaf area

TMCF: Tropical montane cloud forest

VPD: Vapor pressure deficit

WUE: Water use efficiency

Summary

During the last decades, an increase in liana abundance and biomass in Neotropical forests has been noted (Phillips *et al.*, 2002a; Schnitzer and Bongers, 2011). Lianas are an important component of tropical forests, contributing a lot to its structure and biodiversity (Gentry, 1991; Chave *et al.,* 2001), but, more specifically liana competition also impacts tree mortality, growth, and diversity, among others (Schnitzer and Bongers, 2002; van der Heijden *et al.,* 2015). Lianas therefore affect the carbon balance and dynamics and thus changes in the liana community are of particular interest (van der Heijden *et al.,* 2013, 2015).

The main target of this study was to investigate the shift in liana community structure and functional identity along an altitudinal gradient. Such an elevational gradient is an ideal setup, as on a small spatial scale, changes in abiotic and biotic factors can be linked with the changing vegetation. In particular, in this thesis we investigated lianas (diameter ≥ 2 cm) along an altitudinal gradient (400 m a.s.l.-3,200 m a.s.l.) established on the western slope of the Andes in northern Ecuador. All 17 permanent sample plots (40 x 40 m) are located in natural undisturbed old-growth tropical lowland or montane forest divided over four different altitudes. The relationship between the liana community structure (liana diameter distribution, density, AGB and BA) and the altitude was explored, to find out if we could observe a shift in liana community structure with elevation. Additionally, also changes in liana species diversity, functional diversity and leaf traits (SLA, LNC, LPC, LCC, $\delta^{13}C$, $\delta^{15}N$, C:P, C:N and N:P) along the altitudinal gradient were studied. Finally, a comparison was made between the leaf traits of lianas and co-occurring trees to examine if both growth forms utilize the same functional niche or show functional dissimilarities.

Average liana diameter decreases significantly with increasing altitude probably driven by a reduction in temperature. Liana density peaks at 1,900 m a.s.l. but does not show a trend across the different strata. Hence, we can detect a marginal significant decrease in liana AGB and BA. In general, we cannot report a very strong influence of soil fertility on liana density or AGB, only the soil C:N ratio shows a significant negative correlation with liana diameter, liana AGB and liana BA. Not all liana species were identified but almost all species are site-specific and only two species occur in more than one stratum. Further every altitude is dominated by different families. This turnover of species along the altitudinal gradient was also reflected in a change in functional leaf traits. There is a clear shift from the quick return end of the leaf economic spectrum towards a slower return on investment up higher in the mountain chain, with a significant decrease in the CWM of SLA, LPC, $\delta^{15}N$ and LNC and a significant increase in LCC. This changing strategy is a consequence of a shift towards harsher conditions. Namely, a decrease in temperature, precipitation and soil nutrients availability, forces the lianas to switch towards a more conservative strategy. The same trends are also noticed in the leaves of the trees in the same plots but these trees tend to have lower values for SLA, LNC and LPC compared to the lianas. This indicates a dissimilarity in functional niche between the two growth forms whereby lianas are able to maintain a better resource acquisition and growth rate in comparison with the co-occurring trees. Furthermore, no reduction in niche space for lianas is found across the gradient, as deduced from functional diversity indices, while this was the case for the co-occurring trees.

Samenvatting

De voorbije decennia is er een toename in densiteit en biomassa van lianen waargenomen in tropische bossen in de Neotropen (Phillips *et al.*, 2002a; Schnitzer en Bongers, 2011). Lianen zijn belangrijke componenten van deze bossen, sterk bijdragend aan hun structuur en biodiversiteit (Gentry, 1991; Chave *et al.,* 2001), maar toch moet deze trend nauwlettend opgevolgd worden omwille van de competitie tussen lianen en bomen. Er is een impact op onder andere boom mortaliteit, groei en diversiteit (Schnitzer en Bongers, 2002; van der Heijden *et al.,* 2015). Zo zal ook de koolstofbalans en - dynamiek worden beïnvloed (van der Heijden *et al.,* 2013, 2015).

Het voornaamste doel van deze thesis is het onderzoeken van veranderingen in het voorkomen en in de functionele identiteit van lianen langsheen een hoogtegradiënt. Hoogtegradiënten zijn de ideale proefopzet om op een kleine afstand het effect van veranderende abiotische en biotische factoren te kunnen linken met wijzigingen in de vegetatie. In deze thesis worden lianen (diameter ≥ 2 cm) onderzocht langsheen een hoogtegradiënt (400-3200 m boven zeeniveau) op de westerflank van het Andesgebergte in het noorden van Ecuador. Alle 17 permanente proefvlakken (40 x 40 m) zijn gelegen in natuurlijk, onverstoord bos, behorend tot het tropisch laaglandregenwoud of bergnevelwoud, verdeeld over vier hoogtes. De relatie tussen de diameter, densiteit, AGB en BA van de lianen en de hoogte wordt onderzocht om eventuele trends te ontdekken. Vervolgens wordt ook gekeken naar veranderingen in soortenrijkdom, functionele diversiteit en bladkenmerken (SLA, LNC, LPC, LCC, δ^{13}C, δ^{15}N, C:P, C:N en N:P) van lianen langsheen de gradiënt. Uiteindelijk wordt ook een vergelijking gemaakt tussen de bladkenmerken van lianen en bomen om na te gaan of deze twee groeivormen dezelfde functionele niche bezetten of eerder functioneel verschillend zijn.

Langsheen de gradiënt daalt de gemiddelde diameter van de lianen significant met de hoogte, waarschijnlijk een gevolg van de dalende temperatuur. De densiteit is het grootst op een hoogte van 1900 meter maar vertoont geen significante verschillen met de andere strata. Hieruit volgend kunnen we een zwak dalende trend in AGB en BA waarnemen met stijgende hoogte. Over het algemeen kunnen we geen sterke invloed van bodemnutriënten op de densiteit en AGB van de lianen opmerken, enkel de verhouding C:N van de bodem is gecorreleerd met de diameter, AGB en BA van lianen. Niet alle individuen werden geïdentificeerd maar de meeste soorten komen enkel voor in 1 stratum, slechts 2 soorten vormen hierop een uitzondering. Verder wordt iedere hoogte ook gedomineerd door andere families. Deze turnover wordt ook gereflecteerd in een verandering in bladkenmerken. Er is een duidelijk daling waarneembaar van het *quick return end* van het LES naar een *slower return on investment* hogerop in de bergen, met een significante daling in CWM van de SLA, LPC, LNC en δ^{15}N en een significante stijging in LCC. Deze verandering in strategie is het gevolg van een overgang naar extremere omstandigheden. Namelijk een daling in temperatuur, neerslag en nutriënten beschikbaarheid dwingen de lianen over te schakelen naar een meer conservatieve strategie. Dezelfde trend is ook opgemerkt in de bladkenmerken van bomen in dezelfde proefvlakken, hoewel de gemiddelde waarden voor de SLA, LNC en LPC wel lager zijn voor de bomen in vergelijking met de lianen. Dit wijst op het gebruik van een verschillende functionele niche voor beide groeivormen waarbij de lianen over het algemeen efficiënter nutriënten kunnen opnemen en een betere groei kunnen behouden. Verder is ook geen reductie waargenomen in functionele niche voor de lianen langsheen de gradiënt terwijl dit wel zo is voor de bomen.

1. Introduction

Woody vines or lianas are plants that root in the soil and use other plants, mostly trees, to grow towards the canopy. They are structural parasites making use of a host tree to reach better light levels (Schnitzer and Bongers, 2002). These lianas are an important life form in tropical forests. They profoundly contribute to biodiversity by representing 25-35% of the woody species diversity in tropical forests (Chave *et al.,* 2001; Schnitzer *et al.,* 2012). Furthermore, lianas play a significant role in the carbon sequestration and stock by encompassing approximately 10-40% of the woody stems (Gentry, 1991; Chave *et al.,* 2001) and even up to 40% of the leaves present in the forest can be assigned to the lianas (Putz, 1984a).

Although lianas are an important component of the ecosystem, they can severely impact carbon forest dynamics too. Once established in the upper canopy they shade the leaves of their hosts (Zhu and Cao, 2009), thereby creating severe aboveground competition with trees for light. Additionally, lianas have particularly deep rooting systems (Restom and Nepstad, 2004), invoking strong belowground competition for nutrients and water. This strong competition from lianas reduces the growth of trees and is responsible for a higher risk of tree mortality (Putz, 1984a; reviewed by Schnitzer and Bongers, 2002; Ingwell *et al.,* 2010). Furthermore, tree recruitment, fecundity and tree diversity can also be affected (van der Heijden *et al.,* 2015). In this way lianas are able to influence the carbon sequestration in tropical forests (van der Heijden *et al.,* 2013, 2015). According to Pan *et al.* (2011) 55% of the carbon stored in forests is attributed to the tropics and thus changes in the dynamics and productivity of these forests may have consequences for global CO_2 levels (van der Heijden *et al.,* 2013).

The impact of lianas on the forest carbon balance can potentially increase, with a rise in liana density and biomass recorded in Central and South America (Phillips *et al.*, 2002a; Schnitzer and Bongers, 2011). Possible drivers of this increase are human disturbance, higher evapotranspirative demand and a rise in atmospheric CO_2 (Schnitzer and Bongers, 2002, 2011). Lianas seem to profit from these situations because of their efficient water use and multiple ways of reproduction (Schnitzer, 2005). Furthermore, they invest less biomass in their stem (Schnitzer *et al.,* 2000) and can produce more leaves with a low investment cost (van der Sande *et al.,* 2013). Lianas are therefore causing more pressure on the forests (Schnitzer and Bongers, 2002) and they will possibly acquire the ability to spread towards higher altitudes and latitudes (Jiménez-Castillo *et al.,* 2007).

Within this dissertation, a first liana census was carried out in 17 permanent sample plots in northern Ecuador. These plots are situated in four strata along an altitudinal gradient (400-3,200 m above sea level (a.s.l.)) on the western slope of the Andes. Elevational transects are an invaluable source of information in the investigation of climate change. On a small spatial scale, changing abiotic factors can be studied and they can be linked with the surrounding vegetation (Körner, 2007). Especially the gradual shift in temperature serves as an indicator of climate change. The purpose of this study is twofold. The first part is to investigate if there is a shift in liana community structure variables such as liana density, diameter distribution, basal area and aboveground biomass along the elevational transect. Based on recent literature on lianas along altitudinal gradients (Parthasarathy *et al.,* 2004; Fadrique and Homeier, 2016) we expect to see a decrease in liana diameter, density and biomass as temperature decreases higher in the Andes. Namely, lianas are sensitive to freezing induced embolism which limits also their latitudinal dispersion (Schnitzer and Bongers, 2002; Jiménez-Castillo *et al.,* 2007). The second part of the study focusses on changes in species richness and functional diversity along the same gradient. Also here we assume to find a drop in diversity with increasing altitude because of a shift towards harsher growth conditions (van der Heijden and Phillips, 2009a; DeWalt *et al.,* 2015). Leaf traits of lianas, namely the specific leaf area (SLA), mass-based leaf carbon content

(LCC), mass-based leaf nitrogen content (LNC), mass-based leaf phosphorus content (LPC), stable carbon isotope composition (δ^{13}C), stable nitrogen isotope composition (δ^{15}N) and the derived traits, more specifically the carbon to nitrogen ratio (C:N), carbon to phosphorus ratio (C:P) and nitrogen to phosphorus ratio (N:P), are compared along the gradient and linked with the leaf traits of co-occurring trees to determine possible differences in functional niche. We except to find differences in trait values and thus also different resource acquisition strategies for both growth forms whereby lianas are situated at the quick return end of the leaf economic spectrum (LES) (Wright *et al.,* 2004; Zhu and Cao, 2010; Asner and Martin, 2015).

2. Literature review

2.1. Global distribution of vegetation

More than 200 years ago, von Humbolt and Bonpland (1805) illustrated that the global vegetation distribution was related to the climate and in 1900 Köppen presented the first quantitative climate classification by using plants as indicators of the climate. Climatic variables such as temperature and precipitation have been linked to vegetation types (Woodward and Wiliams, 1987), but also to productivity, biomass and leaf area (Chapin *et al.,* 2002). More recently, the Food and Agriculture Organisation (FAO) divided the world in ecological zones defined as 'areas with relatively homogenous natural vegetation, similar in physiognomy'. These zones match almost completely with the climate zones of Köppen-Trewartha (Trewartha and Horn, 1980). Except for the mountains, their definitions vary along the five major domains: tropical, subtropical, temperate, boreal and polar (Simons, 2001; FAO, 2012; Supplementary Figure S1 & Table S1).

The distribution is mainly determined by two main climatic variables: temperature and precipitation. Temperature declines polewards, limiting the distribution of plants. A vital threshold value is the annual minimum temperature (Woodward and Williams, 1987). A minimum temperature between 0 and 10°C is dangerous for plants that aren't cold resistant (Levitt, 1980). When the temperature drops below -15°C, a lot of broadleaved evergreen plant species will die (Levitt, 1980). Broadleaved forests usually occur in places with a positive mean annual temperature. In contrast needle leaved species are mostly found where the mean annual temperature is around 0°C. Areas with highly negative mean annual temperatures contain shrub or tundra vegetation (Sakai, 1978; Churkina and Running, 1998).

Water is a second factor that is useful when explaining the global distribution of the vegetation. However, the total amount of rainfall isn't sufficient. The amount of precipitation must be improved by taking into account water loss through transpiration and evaporation (Woodward and Williams, 1987; Neilson, 1995). Evapotranspiration increases with a decrease in latitude as a result of the rising temperature (Müller, 1982). Also, runoff and drainage towards deeper layers limit the water availability (Woodward and Williams, 1987; Nielson, 1995). Depending on the place on Earth rainfall may be strongly seasonal linked, so possibly the vegetation has to cope with varying amounts of usable water throughout the year (Stephenson, 1990).

Though, temperature or precipitation alone is not enough. It is important that both water and energy are available at the same time to provide good growing conditions. The mixed effect of temperature and water can declare the distribution of the vegetation (Stephenson, 1990). The actual evapotranspiration is therefore restricted by energy or water availability and has a positive relation with the net primary production (Lieth, 1975, 1976). When there is a shortage of water, actual evapotranspiration does not reach the potential evapotranspiration (Thornthwaite and Mather, 1955; Stephenson, 1990). A reduction in usable water for the plants causes a decrease in leaf mass and thus a change from trees to shrubs and further to herbs or even desert vegetation (Schulze, 1982).

It is evident that other factors such as competition, pathogens and anthropogenic influences play a role in the distribution of the vegetation. However, on a global scale similarities in biomes occurring in regions with the same climatic water balance are prominent (Stephenson, 1990).

2.1.1. The tropics

The tropics are roughly situated between the Tropic of Capricorn and the Tropic of Cancer (Geldenhuys, 1994). This area accounts for ≈ 44% of the total forested area (Keenan *et al.,* 2015) and contains ≈ 55% (471 ± 93 Pg C) of the total forest C stock (861 ± 66 Pg C) (Pan *et al.,* 2011). In tropical

forests, ≈ 56% of the stored C is located in biomass and ≈ 32% is situated in the soil (Pan *et al.,* 2011). Furthermore, tropical forests are currently acting as an important C sink (Lewis *et al.,* 2009; Pan *et al.,* 2011). However, according to Brienen *et al.* (2015) this sink effect is declining as a result of a reduction in the net biomass increase. This is the consequence of a higher mortality rate combined with the levelling off of the increase in growth rate (Brienen *et al.,* 2015). Further the sink effect is threatened by important sources of C emissions such as the high deforestation and forest degradation rates in the tropics, causing variability in the sink effect (Cramer, 2004; Pan *et al.,* 2011). Between 2000 and 2007 C emissions in the tropics were little higher than C sequestration by intact and regrowth forests, resulting in the tropical forests as a C source instead of a sink (Pan *et al.,* 2011).

Furthermore, the biodiversity found in the tropics is overwhelming (Dirzo and Raven, 2003) but species richness decreases fast towards the poles (Dirzo and Raven, 2003; Slik *et al.,* 2015). Estimations of Slik *et al.* (2015) suggest the presence of at least 40,000–53,000 tree species in the tropics. While temperate Europe counts only 124 different tree species (Slik *et al.,* 2015).

Tropical forests can be subdivided in different regions, dependent on the amount of precipitation and its seasonality, such as tropical moist and dry forests (FAO, 2012). These regions are all characterized by a variation in species diversity with lowland wet tropical forests holding the highest species richness (Gentry, 1982, 1992). Namely, the diversity of an area in the tropics is positively correlated with the annual rainfall and negatively with the seasonality of rainfall (Clinebell *et al.,* 1995). Specifically, forests with a high rainfall and low seasonality are very productive and they have a high turnover rate. This dynamic reduces homogeneity and provides an opportunity for an even higher species richness (Phillips *et al.,* 1994). At last, when taking into account rainfall, the nutrient balance of the soil is less essential for explaining species diversity in tropical forests. This is mainly because of the correlation between precipitation and soil nutrients. A low amount of nutrients is found in forests with a high rain regime through leaching. Furthermore, in tropical forests there is a fast rate of degradation of organic matter such as leaves and therefore nutrients are quickly taken up by the vegetation. This makes soil quality less important for species richness predictions in tropical forests (Clinebell *et al.,* 1995). This doesn't mean soil nutrients can be neglected when studying the vegetation.

2.1.2. Tropical montane cloud forest

Tropical montane forests are less frequently studied than lowland tropical forests (Spracklen and Righelato, 2014). One of the types of forest found at higher altitudes around the equator is tropical montane cloud forest (TMCF). Characteristic of this ecosystem is the frequent presence of clouds and fog. They are typically situated at 2,000-3,500 metres, although this is not always the case. For example, closer to the coast and on isolated mountain peaks clouds are more often found at an elevation of 1,000 m (Bubb *et al.,* 2004). The occurrence of similar vegetation types and thus more or less similar conditions at different elevations is a consequence of the mass elevation effect. On larger mountains, clouds are formed at higher altitudes because of a larger uptake of solar radiation and a slower release of long wave radiation through the huge mass of the mountain and thus a slower decrease in temperature with increasing altitude (Bruijnzeel *et al.,* 2011; Jarvis and Mulligan, 2011). TMCFs yearly receive 500-6,000 mm of rain, potentially seasonally bound (Bubb *et al.,* 2004). The solar radiation is reduced in these forests because of the interference with the cloud cover, also causing a reduction in vapour pressure deficit (VPD) (Gotsch *et al.,* 2016) and evapotranspiration (Bruijnzeel *et al.,* 2011). Furthermore, cloud immersion provides an extra source of water for the vegetation by direct interception from the clouds (Hu and Riveros-Iregui, 2016). This source of water is especially important during the drier seasons and for the variety of epiphytes (Nadkarni and Solano, 2002), which can comprise up to 25% of the plant species in this type of forest (Foster, 2001).

In Asia, 2.7% of the tropical forested area is TMCF, in the Americas this is only 1.1% and in Africa it is even less: 0.8% (Bruijnzeel *et al.,* 2011). Even though TMCFs only occupy small areas in the world, the ecosystem is very valuable in terms of fauna and flora. It captures a high degree of endemism and biodiversity (Hu and Riveros-Iregui, 2016). For example, the forests on the eastern flank of the Andes harbour 63% of its endemic mammals (Mares, 1992) and approximately 32% of the endemic frogs, birds and mammals of Peru only lives in the cloud forests (Leo, 1995). Some of the remarkable species of TMCFs are tree ferns (Stadtmüller, 1987) and the mountain gorilla (*Gorilla beringei beringei*) (Doumenge *et al.,* 1995) but also a great variety of epiphytes, mosses and lichens seem to flourish well in this ecosystem (Doumenge *et al.,* 1995). Additionally, TMCFs are an important source of water (Bubb *et al.,* 2004). They function as a watershed by capturing water directly on the leaves or the water can primarily condense on branches or on the stem and subsequently be transported towards the ground (Doumenge *et al.,* 1995; Ewing *et al.,* 2009). So, during the dry seasons, rivers and streams coming from a TMCF are more stable (Bubb *et al.,* 2004). Just like other forested mountains TMCFs help controlling water quality and prevent soil erosion as well (Doumenge *et al.,* 1995; Bubb *et al.,* 2004).

2.2. Global trends in density and diversity of lianas

Tropical forests are not only a hotspot for fauna (Dirzo and Raven, 2003) or tree diversity (Slik *et al.,* 2015) but also the place on Earth were lianas prosper well. The abundance and species richness of lianas differ here regionally along a gradient of precipitation, disturbance, soil characteristics and altitude as discussed in the following subsections (DeWalt *et al.,* 2015). Moreover, patterns in liana density and diversity have been found across continents. According to Gentry (1991) liana density peaks in Africa. DeWalt *et al.* (2015) confirms this high liana density in Africa (more than twice the average density of Asian forests) but also found an equivalent liana density in the Neotropics (DeWalt *et al.,* 2015). Liana species richness is the highest in African and South American sites (Gentry, 1991; DeWalt *et al.,* 2015). Also within continents, regions can differ significantly in liana density and diversity (Table 1). The average values are sometimes difficult to compare as researchers take into account different minimum threshold values for their census. For liana abundance, the highest values are found in Ethiopia and Bolivia. Likewise, species richness is the highest in Africa and the America's.

Although liana density may be high in the tropics, most of the lianas are small and only a few lianas reach high diameters (Laurance *et al.,* 2014; Ewango *et al.,* 2015). In the census of Vivek and Parthasarathy (2014), even 79.2% of the lianas had a diameter between 1 and 3 cm. Also striking is the decrease in weight of lianas towards the poles from 25% of woody plant species (Gentry, 1991) to 10% going from tropical to temperate forests (Gentry, 1991; Jiménez-Castillo *et al.,* 2007). The rate of this decline is much faster than those of shrubs, herbs and trees (Gentry, 1991). Compared to the northern hemisphere, liana density is higher in temperate forests south of the equator (Gentry, 1991).

Table 1: Average liana abundance (ha^{-1}) and species richness (ha^{-1}) across different regions

Author	Region	Liana abundance (ha^{-1})	Species richness (ha^{-1})
CENTRAL AMERICA			
Schnitzer *et al.* (2012)	Panama	1,350 (≥ 1 cm diameter)	75
Mascaro *et al.* (2004)	Costa Rica	1,493 (≥ 0.2cm diameter)	/
SOUTH AMERICA			
Romero-Saltos (2011)	Ecuador	1,600 (≥ 1 cm diameter)	180
Laurance *et al.* (2001)	Brazil	400 (≥ 2 cm diameter)	/
Alves *et al.* (2012)	Brazil	573 (≥ 1 cm diameter)	/
Pérez-Salicrup *et al.* (2001)	Bolivia	2,471 (≥ 2 cm diameter)	51
ASIA			
Vivek and Parthasarathy (2014)	India	924 (≥ 1 cm diameter)	23
Reddy and Parthasarathy (2003)	India	827 (≥ 1 cm diameter)	27
Lu *et al.* (2009)	China	153 (≥ 2 cm diameter)	44
Cai *et al.* (2009a)	China	3,407 (≥ 1 cm diameter)	/
DeWalt *et al.* (2006)	Borneo	1,348 (≥ 0.5 cm diameter)	/
AFRICA			
Senbeta *et al.* (2005)	Ethiopia	3,569 (≥ 2 cm diameter)	/
Ewango (2010)	Congo	750 (≥ 2 cm diameter)	64
Thomas *et al.* (2015)	Cameroon	547 (≥ 1 cm diameter)	/

Just as for liana density, liana species diversity is very low in temperate forests and diversity is also lower in temperate forests in the northern hemisphere compared to temperate forests in the southern hemisphere (Gentry, 1991). In the tropical forests liana species diversity also differs greatly across regions, with most of the liana species being site-specific and occurring in small amounts (Ibarra-Manriquez and Martinez-Ramos, 2002; Parthasarathy *et al.,* 2004). For instance, in the census of Parthasarathy *et al.* (2004) 57% of the species had 30 or less individuals. But regularly, it happens that one specific liana species dominates the community, such as *Strychos lenticellata* (21% of the abundancy) in the investigation of Vivek and Parthasarathy (2014), *Maripa panamensis* (11%) in the investigation of DeWalt *et al.* (2000) and *Moutabea aculeate* (17%) in the research of Mascaro *et al.* (2004), among others. The high abundancy presumably arises from a high ecological plasticity. For instance, *Strychos lenticellata* can flourish in shade and light rich environments and reaches the canopy by twinning or as a tendril climber (Vivek and Parthasarathy, 2014).

2.2.1. **Factors influencing global liana distribution**

2.2.1.1. Temperature

The latitudinal distribution of lianas is especially limited by the cold intolerance of their wide and large xylem vessels (Schnitzer and Bongers, 2002; Jiménez-Castillo *et al.,* 2007). This type of vessel is inclined to suffer easily from cavitation (Gentry, 1991; Schnitzer and Bongers, 2002; van der Sande *et al.,* 2013). Hereby the vessel loses its conductivity because of air bubbles (Ewers, 1985). Lianas that do live in temperate climates are adapted to freezing temperatures by using high positive root pressure (Ewers *et al.,* 1991), drainage of the vessels before winter (Sperry *et al.,* 1987) or by the production of new xylem in the spring (Tibbets and Ewers, 2000).

2.2.1.2. Soil nutrients

The relationship between liana density and soil characteristics is not that clear. Gentry (1991) stated that the liana density was higher on nutrient rich soils. Although this relationship is unclear according to Balfour and Bond (1993) and van der Heijden and Phillips (2008), also the results of DeWalt and Chave (2004) do not support this assumption.

2.2.1.3. Mean annual precipitation and seasonality

Lianas, with their large and wide vessels, are sensitive to drought-induced embolism (Zhu and Cao, 2009). But their specific vascular system can also give them an advantage during drier periods and can explain the higher abundance of lianas in seasonal forests (Schnitzer and Bongers, 2011; Chen *et al.,* 2015). First of all, the wide vessels provide a high hydraulic conductivity (van der Sande *et al.,* 2013). For every increase in radius of the vessel, the water flow increases to the fourth power (Tyree and Ewers, 1991). Secondly, lianas have a high proportion of sapwood to heartwood (Tyree and Ewers, 1996), and thus a higher amount of conductive wood (Gartner and Meinzer, 2005). Thirdly, small amount of water can be stored in unlignified parenchymatous cells during the night and are used throughout the day (Ewers *et al.,* 1991). This also reduces the chance of embolism as a result of water stress (Tyree and Ewers, 1996). Moreover, at the start of the dry season lianas use water close to the surface but later in the season they change towards deeper water layers (Andrade *et al.,* 2005). Hereby the lianas use larger quantities of deep soil water than the surrounding trees do during the dry season (Chen *et al.,* 2015), thus also their deep rooting system provides a competitive advantage in dry periods (Tyree and Ewers, 1996; Restom and Nepstad, 2004; Schnitzer, 2005). Additionally, during the dry season, most of the lianas reduce their daily mean sap flux density stronger than the trees in the same area and also their daily water consumption decreases (Chen *et al.,* 2015). This denotes a good stomatal control. Specifically, in this study, it was shown that lianas started to photosynthesize early in the morning and closed their stomata before those of the trees. Thus, they reduce their water loss while maintaining high rates of carbon fixation compared to trees that were more active during the hot middays with high VPDs (Chen *et al.,* 2015).

In general, the abundance of lianas depends on mean annual rainfall (a negative correlation) and seasonality (a positive correlation) (Schnitzer, 2005), representing the exact opposite pattern of vascular plants (Gentry, 1982).

2.2.2. Factors influencing global liana species richness

Different correlations are found for species richness. When using a pantropical liana dataset, DeWalt *et al.* (2015) found no relationship between dry season length and species richness. Diversity was highest around 4,000 mm rain in a year and decreased when mean annual precipitation decreased or increased. This was only a marginal significant correlation (DeWalt *et al.,* 2015). Van der Heijden and Phillips (2009a) also investigated the link between species richness and mean annual precipitation on the one hand and dry season length on the other hand, but this only in the Neotropics. There was a linear positive correlation with mean annual precipitation and a negative one with the length of the dry season. The differences might be the result of the small and narrow areas sampled for the Neotropical dataset or the limited number of plots in the global liana database (DeWalt *et al.,* 2015).

2.3. Altitudinal gradient

When rising from sea level to higher altitudes several environmental conditions change (Körner, 2007). More specifically the atmospheric pressure, temperature and clear-sky turbidity are variables dependent on the altitude a.s.l. (Körner, 2007).

For every kilometre gain in elevation the air temperature decreases with 5.5°C (Barry, 1992). Because of a decrease in temperature the air is not capable of holding the same amounts of moisture as lower levels. So, evaporation will be slower through the lower VPD. There will be a decrease in actual evapotranspiration and a reduction in the deficit of the water balance (Stephenson, 1990). Furthermore, with a decrease in temperature and thus lower mineralization rates the net primary productivity along an altitudinal transect declines (Girardin *et al.,* 2010).

In general, there is also a decrease of ≈ 11% of the atmospheric pressure per increase of a kilometre, also the partial pressure of CO_2 and O_2 declines. At a fixed temperature, a decrease in pressure causes an increase in gas exchange as a result of fewer collisions between the particles. But there is actually a decrease in temperature with rising altitude, causing a decline of gas (O_2 and CO_2) exchange in the leaves of plants (Körner, 2007). The facilitated gas exchange is further diminished by the fact that 70-80% of the resistance of the exchange of CO_2 between air and leaves takes place in the liquid phase and probably a higher efficiency in CO_2 fixation at higher elevation levels too (Körner *et al.,* 1991). Thus, the rise in velocity of molecular gas diffusion expected with a pressure drop is counteracted by a slower velocity through the reduced temperature at higher altitudes (Körner, 2007).

Solar radiation increases and so does UV-B with altitude. However, this is only the case when the sky is clear, and this trend is interfered by clouds and fog (Körner, 2007). The increase is a consequence of the shorter pathway covered by the radiation and thus a reduced chance of scattering and absorption (Blumthaler *et al.,* 1997).

Other factors such as wind, precipitation and geology don't show a universal representative trend with altitude. There may be some local trends along a transect but those can't be generalized as 'altitude phenomena' (Körner, 2007). Lauscher (1976) investigated rainfall at different latitudinal gradients. Around the equator (0-10°) precipitation seems to decrease with altitude but at other latitudes different patterns occur (Figure 1). Furthermore, mountainous areas are generally less windy than plains because of their sheltering effect. More specifically, mountains in the tropics would have a very quiet wind regime (Lauscher, 1977). Though it would be ideal to eliminate regional factors such as moisture and wind along an elevation transect, this is seldom the case and this makes it even harder to compare results on a global scale (Körner, 2007).
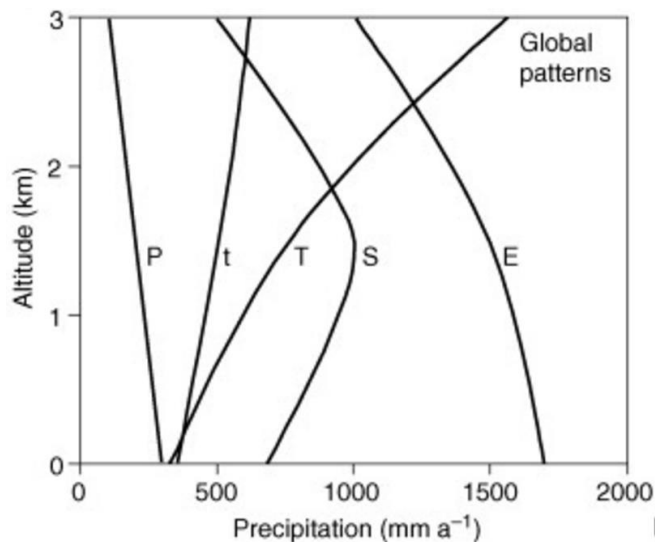
Figure 1: A global typology of altitudinal trends in precipitation. E, equatorial (0–10° latitude); S, subtropical (10–30° latitude); t, transition (30–40° latitude); T, temperate (40–60° latitude); and P, polar (Greenland). Modified, with permission, from Lauscher (1976).

2.3.1. **Vegetation along an altitudinal transect in the tropics**

By changing environmental conditions the vegetation changes too, determined by both the altitude as local factors such as land use (Spehn *et al.,* 2006) or precipitation (Körner, 2007). As reviewed by Willig *et al.* (2003), biological diversity is higher close to sea level and decreases with increasing altitude. According to Gentry (1982, 1992) woody plant species richness declines fast with rising altitude, this upwards of 1,500 metres, below this altitude species diversity stays similar. Further also species composition alters with altitude. The proportion of woody species occupied by lianas drops with increasing elevation while mainly shrubs take over (Jiménez-Castillo *et al.,* 2007).

Next to species composition and diversity, notable changes are also found for aboveground biomass and productivity of the vegetation in montane forests. There is a decline of the growth (Tanner *et al.,* 1998) and maximum height of the trees over an altitudinal gradient (Aiba and Kitayama, 1999; Leuschner *et al.,* 2007) and the climatic treeline is situated at places with an annual mean temperature between 5 and 9°C during the growth season (Körner and Paulsen, 2004; Bader *et al.,* 2007). Low night temperatures and high solar radiation during the day are potentially the two mechanisms limiting tree growth above the treeline (Bader *et al.,* 2007). Although there is a decrease in stature and aboveground biomass (Girardin *et al.,* 2010) there is no change in the total C stock along an altitudinal transect, because of a shift towards higher amount of C in the belowground stock (soil and root biomass) (Girardin *et al.,* 2010; Moser *et al.,* 2011). Both fine and coarse root biomass increase with elevation (Leuschner *et al.,* 2007).

Actually, not only the temperature hinders the growth of vegetation at higher altitudes (Moser *et al.,* 2011) but also nutrient availability (Girardin *et al.,* 2010) limits the aboveground biomass and productivity (Tanner *et al.,* 1998) in montane forests. This is the consequence of a decrease in litterfall mass at high altitudes and thus lower availability of N, P and often Ca, Mg and K (Tanner *et al.,* 1998). Further a reduced mineralization and thus a limited cation exchange capacity complicates the growth (Wilcke *et al.,* 2008). According to Wolf *et al.* (2011) a decrease in N with elevation is not uncommon in the tropics. This is also confirmed by Wilcke *et al.* (2008) in Ecuador. Fisher *et al.* (2013) performed a fertilising experiment in the Andes in Peru which revealed that P was limiting in lowland Amazonia and that N was a constraint at low and at higher altitudes. Moser *et al.* (2011) found a similar trend, a

shift from P towards N limitation with altitude. The gradients in soil nutrients are reflected in the nutrient composition of the leaves. There is a decrease in foliar nitrogen (van de Weg *et al.,* 2009) and also leaf N:P ratios decrease with increasing elevation (Fisher *et al.,* 2013). Furthermore, leaf characteristics modify along an elevation transect, the leaf area (Aiba and Kitayama, 1999) and SLA (van de Weg *et al.*, 2009) decline.

2.3.2.Lianas along an elevational transect

Studies of lianas along an elevational transect show different patterns (Parthasarathy *et al.,* 2004; Homeier *et al.,* 2010; Alves *et al.,* 2012; Fadrique and Homeier, 2016). This may be a consequence of the diversity of approaches used for collecting data and all the distinct environmental factors influencing the spread and growth of lianas (Pérez-Salicrup *et al.,* 2001).

A negative correlation between liana diameter and altitude is found by Homeier *et al.* (2010) in northeastern Ecuador (500-2,000 m a.s.l.), by Fadrique and Homeier (2016) in southern Ecuador (1,000-3,000 m a.s.l.), by Alves *et al.* (2012) in Brazil (0-1,000 m a.s.l.) and Heaney and Proctor (1990) in Costa Rica (100-2,600 m a.s.l.). Large lianas are rare and can only be found at lower altitudes, for example, no lianas > 10 cm diameter were found in montane forests (1,000 m) in Brazil (Alves *et al.,* 2012) and no lianas > 6 cm were found in upper montane forests (3,000 m) in Ecuador (Fadrique and Homeier, 2016).

Furthermore, the relationship between liana density and altitude is studied by Fadrique and Homeier (2016), similar to the diameter reduction there is a pattern of decreasing density with increasing altitude. These findings confirm the same trend as found by Parthasarathy *et al.* (2004) in India but don't match with the data collected by Homeier *et al.* (2010). According to the last one there is no significant shift in liana abundance and a peak in density at 2,000 m (Homeier *et al.,* 2010).

Thirdly, also liana aboveground biomass is negatively correlated with the elevation (Alves *et al.,* 2012; Fadrique and Homeier, 2016) more specifically a decline of 0.18 Mg/ha per rise of 100 m (Fadrique and Homeier, 2016). Especially the large lianas, found at lower altitude (Alves *et al.,* 2012; Fadrique and Homeier, 2016), contribute a lot to the total aboveground biomass (Alves *et al.,* 2012). In Brazil 26-35% of the liana aboveground biomass at lower elevational levels was derived from lianas with a diameter > 10 cm (Alves *et al.,* 2012).

Strongly linked with liana diameter, density and biomass is liana basal area which also declines as altitude increases (Parthasarathy *et al.,* 2004). However, according to Homeier *et al.* (2010) there is no significant shift in liana basal area along a 500 to 2,000 metre transect.

Finally, liana species diversity falls with increasing altitude (Gentry, 1991; Schnitzer and Bongers, 2002; Jiménez-Castillo *et al.,* 2007). However, Parthasarathy *et al.* (2004) found the highest species richness halfway the altitudinal transect. Further most liana species are site-specific and thus species composition changes along the gradient (Parthasarathy *et al.,* 2004). In the census of Parthasarathy *et al.* (2004) in India 69% of the species were only found at one of the five investigated altitudes and none of the species occurred at all of the five strata (Parthasarathy *et al.,* 2004).

2.3.3.Factors controlling lianas along elevational gradients

Along an altitudinal transect the temperature probably determines the liana density (Fadrique and Homeier, 2016). The minimum temperature is an important factor because, as mentioned before, lianas have a susceptible vascular system that also limits the latitudinal distribution of the lianas. (Ewers, 1985; Parthasarathy *et al.,* 2004; Jiménez-Castillo *et al.,* 2007).

Still, it is difficult to pinpoint which factors cause the variations in liana abundance and biomass because not only the elevation and thereby a reduction in temperature (Fadrique and Homeier, 2016), but also other environmental factors such as stand age (DeWalt *et al.,* 2000), soil fertility, rain regime and water availability (Parthasarathy *et al.,* 2004) and canopy disturbance have their impact (Alves *et al.,* 2012).

A poor soil fertility reflected by high C:N ratios and a thick organic layer, typical at higher altitudes (Tanner *et al.,* 1998), has a negative effect on liana biomass (Fadrique and Homeier, 2016). A higher soil pH and more exchangeable Ca and Mg, often found at lower altitudes, are reasons for an increase in liana biomass (Fadrique and Homeier, 2016). Other researchers as Phillips *et al.* (2005) or van der Heijden and Phillips (2008) question the influence of soil fertility and found no relationship at all. They suggest to look at the amount of host trees as another factor controlling liana abundance and liana aboveground biomass. However, Alves *et al.* (2012) and Vivek and Parthasarathy (2014) only found a weak relationship therein.

Large trees at higher altitude carry fewer and smaller lianas than the ones with the same diameter at lower elevation levels (Homeier *et al.,* 2010; Fadrique and Homeier, 2016), probably resulting from a decrease in liana density and diameter with altitude. But liana infestation is also controlled by the diameter of the host (Fadrique and Homeier, 2016). The larger a tree, the less sensitive it becomes for liana infestation. Trunk infestation by lianas from the ground is restricted by a maximum host diameter and thus a lower support availability (Putz, 1984b; Nabe-Nielsen, 2001). But trees with a large diameter are more likely to support at least one liana and carry often more lianas (Nabe-Nielsen, 2001; Fadrique and Homeier, 2016). Namely, older trees have had more time to gather lianas and here, new lianas can use the already existing ones to reach the canopy (Pérez-Salicrup *et al.,* 2001). Further also infestation through the crown of neighbouring trees is possible (Putz, 1984b). Maliza and Grau (2006) also found a higher infestation grade and liana load in larger trees but they also noticed a decrease in liana loads when host trees were lager than 80 cm diameter. A process that is also described by Schnitzer (personal communication): large trees may shed their lianas or the lianas are pulled out the tree when neighbouring trees die. Once liana free the chance of a new infestation, restricted by the large diameter, is negligible.

In the liana census of Alves *et al.* (2012) along an altitudinal transect in Brazil, forest structure including canopy height and support structures didn't show a strong relationship with the liana biomass and abundance. At least the current forest structure of the tropical Atlantic forest in Brazil wasn't good enough to forecast the liana biomass and abundance. Temperature and disturbance seemed better factors for explaining the variation in biomass and abundance (Alves *et al.,* 2012).

2.4. Changing environment

The last century our world is developing fast. Due to an increase in anthropogenic greenhouse gasses and changes in land use / land cover, specifically deforestation and forest degradation (Wright, 2005), the chemical composition of our atmosphere changes and there is global warming (Hardy, 2003; Malhi and Wright, 2004). Focussing on tropical forests, there are a lot of pressures that influence the structure and dynamics of the forest and its species (Wright, 2005; Schnitzer and Bongers, 2011).

2.4.1. Climate change

Since the 19th century, CO_2 levels in our atmosphere augmented with 30% (Wright, 2005). In February 2017, the global CO_2 concentration amounted 405.75 ppm (Earth System Research Laboratory), in 1997 this was only 363 ppm (Laurance *et al.,* 2014; Earth System Research Laboratory). This increase is

driven by deforestation and the burning of fossil fuels (Malhi and Grace, 2000). Approximately since 1976, there has been an increase in temperature of 0.26 ± 0.05°C every ten years in tropical regions (Malhi and Wright, 2004). The same pattern is actually observed all around the globe (IPCC, 2002). Between 1960 and 1998, there was also a decrease in rainfall of 1.0 ± 0.8% in the tropics every ten years. This trend is the most distinct in northern Africa followed by Asia (Malhi and Wright, 2004). In the Neotropics droughts as a consequence of El Niño are more frequent (Dunbar, 2000; Tudhope *et al.,* 2001). El Niño is a rise in the temperature of the surface sea water of the equatorial Pacific Ocean and a fluctuation in the atmospheric pressure above the equatorial Pacific (Malhi and Wright, 2004) called the Southern Oscillation (Trenberth, 1997). Together they form El Niño-Southern Oscillation (ENSO). Along the west coast of South America, countries such as Ecuador and Peru, receive more rain than normally during an ENSO (Rodbell *et al.,* 1999), while in the Amazon the opposite happens (Asner *et al.,* 2000; Williamson *et al.,* 2000).

Mountainous forested areas in the tropics follow the same trend of increasing temperature and decreasing precipitation. Also, the cloud cover attenuates at these higher altitudes probably resulting from a rise in altitude of cloud formation (Still *et al.,* 1999).

2.4.2. Changing tropical forests

The global 4 128 million hectares of forests in 1990 has been diminished to 3 999 million hectares in 2015 (FAO, 2015). During the last two decades of the twentieth century deforestation rates were especially very high in the tropics (Ramankutty and Foley, 1999; Supplementary Figure S2). Between 2000 and 2010 yearly 7 million hectares of forest disappeared in the tropics, almost 40% of the deforestation in the tropics and the subtropics is for conversion towards commercial agriculture land and about 33% for subsistence agriculture (FAO, 2016). Also in the cloud forests, conversion for agricultural use is most common. But also deforestation for cattle ranching or even drug cultivation was reported in TMCFs (Bubb *et al.,* 2004). In general, the rates of deforestation have declined from a yearly net forest loss of 0.13% in the early nineties to a net annual decrease of 0.08% between 2010 and 2015 (FAO, 2015).

Deforestation doesn't only lead to a reduced amount of forest but also to more and smaller patches of forest and a higher amount of edges, a process which is called fragmentation (Wright, 2005; Schnitzer and Bongers, 2011). Only a small part of the cleared area will be transformed into secondary forest. These forests normally comprise other and fewer species than the primary forests (Chazdon, 2003; Lugo and Helmer, 2004), losing a lot of the original plant diversity (Brooks *et al.,* 2002).

Forest degradation also takes place because of illegal hunting and logging. Poachers influence the species composition of a forest and thus alter the mechanisms that provide the coexistence of thousands of species in tropical forests (Wright, 2003). For instance, by killing the dispersal agents of some trees such as large birds or mammals the dispersal distance of seed-bearing trees is drastically reduced (Wright *et al.,* 2000; Wright, 2003). Now, this process favours trees counting on wind dispersal or dispersal by small birds or bats (Wright *et al.,* 2007). Also lianas, which mostly rely on anemochory in the Neotropics (Chazdon *et al.,* 2003) are taking advantage of this situation (Wright *et al.,* 2007). Species composition is further altered by the logging of trees. These proceedings guide towards a change in species composition, forests with less valuable wood (Ferry Slik *et al.,* 2002) and forests with more gaps giving new opportunities to pioneer species and lianas (Putz 1984a; Schnitzer *et al.,* 2000, 2004).

Also global climate change influences the forests in the tropics (Wright, 2005). Productivity increases as a consequence of a higher CO_2 fertilization, which leads towards a higher tree turnover rate, measured as an increase in tree mortality and recruitment (Phillips and Gentry, 1994; Lewis *et al.,*

2004; Phillips *et al.,* 2004). Under higher CO_2 concentration fecundity is also higher, resulting from both an earlier maturation as an increased carbon allocation to reproduction (LaDeau and Clark, 2001). Furthermore aboveground biomass and stem density increase (Phillips *et al.,* 2002b; Lewis *et al.,* 2004). Although, according to a recent paper there is a decline in the net rate of aboveground biomass increment because of a stagnation in productivity increment and an increase in mortality (Brienen *et al.,* 2015). Finally, also lianas seem to gain in weight (Phillips *et al.,* 2002a; Chazdon, 2003; Lugo and Helmer, 2004; Schnitzer and Bongers, 2011), as discussed below.

Nogués-Bravo *et al.* (2007) forecast that in the 21st century mountains at higher latitudes are more vulnerable to climate change than mountains situated around the equator because of a higher increase in temperature in the northern hemisphere compared to mountain systems in temperate or tropical areas. This will not only affect species richness and species composition but can for example also cause problems with water resources (Nogués-Bravo *et al.,* 2007). However, Deutsch *et al.* (2008) predict that especially biodiversity in the tropics may be endangered by global warming. Species here are living in an environment close to the optimum temperature and are not that resistant to thermal fluctuations as species in temperate or boreal regions (Deutsch *et al.,* 2008). Also TMCFs and the typical species associated with these forests are very vulnerable for climate change (Nadkarni and Solano, 2002). Next to changes in temperature and rainfall, they lose an important source of water with the rise in cloud cover to higher altitudes (Still *et al.,* 1999) and there is thus a rise in altitude of their optimal habitat conditions. When the vegetation belt rises to higher altitudes on a mountain, there is a reduction in available surface area because of the cone shape of the mountain (Funnell and Parish, 2005). Furthermore, cloud forests are often already situated at the top of the mountains and thus unable to expand uphill while losing their optimal climate conditions (Bubb *et al.,* 2004). A decrease in the necessary water availability, provided by mist or clouds, during the dry season may be fatal for organisms living here (Loope and Giambelluca, 1989; Nadkarni and Solano, 2002), especially for epiphytes (Nadkarni and Solano, 2002). After conducting a transplant experiment, Nadkarni and Solano (2002) predict a reduction in growth and leaf production for the epiphytes in addition to a higher mortality.

2.4.3. Liana proliferation

Currently, there is a widespread increase in liana abundance and biomass of both large and small lianas in Neotropical forests (Phillips *et al.,* 2002a; Ingwell *et al.,* 2010; Schnitzer and Bongers, 2011; Schnitzer *et al.,* 2012). In the census of Schnitzer *et al.* (2012), in Panama, there was an increase of 75% in small lianas (≥ 1 cm diameter) and for large lianas (≥ 5 cm diameter) an increase of almost 140% over a period of 30 years. In the Amazon Laurance *et al.* (2014) found an annual increase in liana density of 1.00% ± 0.88% between 1999 and 2012 mainly with an increase in small lianas (2-3 cm diameter). For temperate and subtropical forests the results aren't that clear (Schnitzer and Bongers, 2011), but Gallagher *et al.* (2010) warn for increases in liana biomass and abundance of invasive lianas. Provisionally an increase in lianas in African, Australian or Asian forests hasn't been noticed yet (Schnitzer and Bongers, 2011), with several studies showing no change of even a decline (Caballé and Martin, 2001; Ewango, 2010). More information and more studies are necessary to confirm this contrast and to detect the possible drivers (Schnitzer and Bongers, 2011). Liana proliferation arises from a variety of factors as described below.

2.4.3.1.   Factors causing liana proliferation

Biological and anthropogenic disturbance

Disturbance can refer to biological or anthropogenic disturbance. The first one includes events such as treefall, caused by storms, hurricanes or natural tree mortality. Since 1950 there has been an increase

in forest turnover of tropical forests and this process has been accelerating since 1980 (Phillips and Gentry, 1994). Subsequently, lianas can easily exploit the free space through clonal recruitment after falling from the canopy (Schnitzer and Bongers, 2011; Yorke *et al.,* 2013), this is aided by the fact that more than 90% of the lianas survives the fall of their host tree (Putz, 1984a). They are not only able to re-root and grow back to the canopy but often produce multiple liana stems (Putz, 1984a; Schnitzer *et al.,* 2004) which may separate later and become independent lianas (Schnitzer *et al.,* 2006). Furthermore, they can grow horizontally on the soil and re-root in gaps with better light conditions (Schnitzer and Bongers, 2011; Yorke *et al.,* 2013) or they can develop through seeds or seedlings present in the gaps (Putz, 1984a; Schnitzer *et al.,* 2000). The variety of mechanisms gives the lianas an advantage compared to trees that usually regenerate through seeds or seedlings. Definitely clonality benefits lianas to survive severe disturbances and to proliferate afterwards (Cornelissen *et al.,* 2003; Yorke *et al.,* 2013). Proliferation is aided by the fact that lianas don't invest as much biomass in their stem as trees do and therefore they are able to grow quickly towards the canopy (Schnitzer *et al.,* 2000). Lianas themselves are responsible for a higher tree mortality and thereby positively affect this whole process (Ingwell *et al.,* 2010).

Also anthropogenic disturbances including logging, fragmentation and land use change cause problems. The created gaps or edges with higher light availability are the ideal place for liana growth (Putz, 1984a; Schnitzer *et al.,* 2000; Laurance *et al.,* 2009). Next to forest degradation, the formation of new, young forests also generates perfect circumstances for liana establishment because of the support for the climbers and the high light availability (Madeira *et al.,* 2009). Following the disturbance there is not only an increase in abundance but also in liana species richness (Laurance *et al.,* 2001). As mentioned before, hunting provides a benefit to species with wind dispersal (Wright *et al.,* 2007). The majority of the lianas in the Neotropics uses this strategy for the spread of their seeds and so they profit from this form of disturbance too (Gentry, 1983).

Elevated CO_2 concentrations in the atmosphere

Higher amounts of CO_2 in the atmosphere can have a positive effect on the growth and fecundity of lianas (Körner, 2009). This has been shown for lianas in temperate forests such as English ivy *(Hedera Helix)* (Zotz *et al.,* 2006) which seem to benefit more from elevated CO_2 concentrations than trees (Belote *et al.,* 2003). Because of the higher leaf to stem ratio of lianas and their higher specific leaf area and efficient use of nitrogen and phosphorus during photosynthesis, they are able to react faster on the elevated CO_2 levels than trees (Zhu and Cao, 2010). In addition, the general increase in forest productivity results in a higher tree mortality. Forest turnover will rise and lead to an increase in gaps, again creating opportunistic environments for lianas (Putz 1984a; Schnitzer *et al.,* 2000, 2004; Laurance *et al.,* 2009; Schnitzer and Carson, 2010). However, other authors such as Marvin *et al.* (2015) did not notice a significant difference between liana and tree response under elevated CO_2 conditions.

Changing rainfall patterns

Lianas seem to profit from a reduction in rainfall amounts (reviewed by Schnitzer and Bongers, 2011). The lianas are less sensitive to water stress because they have a high water use efficiency whereby they still have a good growth rate in comparison to the surrounding vegetation during the dry season (Schnitzer, 2005). According to Schnitzer (2005), lianas grow seven times more during the dry season than trees in a seasonal forest in Panama, while during the wet season this is only two times more. This is aided by the higher osmotic adjustment in liana leaves, contributing to turgor maintenance, during the dry season compared to co-occurring trees (Maréchaux *et al.,* 2017). Meanwhile, there are fewer clouds, a reduced canopy cover and so a higher light availability which gives the lianas an even higher advantage in the seasonal forests (Graham *et al.,* 2003). Moreover, lianas don't seem to suffer

as much as trees from leaf fall during the dry season. Some species are even capable of producing fresh leaves (Putz and Windsor, 1987). Those have a more efficient photosynthesis (Wright and van Schaik, 1994) and are less frequently eaten in the dry season because of a lower herbivore abundance (Coley, 1983). In addition, tree mortality and forest turnover will be higher as a result of drought (Philips *et al.,* 2009). This together with the fact that liana proliferation is higher after disturbance will not only lead to an increase in lianas, but lianas will probably also move more uphill and towards higher latitudes (Jiménez- Castillo *et al.,* 2007).

2.4.3.2.   Effects of liana proliferation

This general increase in lianas in the Neotropics will reduce the growth of the trees (van der Heijden and Phillips, 2009b) and cause more tree mortality driven by the competition for light, nutrients and water (Schnitzer and Bongers, 2002; Ingwell *et al.,* 2010). Further, by putting more pressure on the crown, stem and roots they will cause deformations of the trees (Putz and Mooney, 1991). The presence of lianas would cause a reduction of up to 18% of the biomass of the forest (Schnitzer *et al.,* 2014). Eventually this will lead to a loss of carbon uptake (van der Heijden *et al.,* 2013). This has been demonstrated through a large-scale liana removal experiment, comparing liana free forest with adjacent unmanipulated forest. Here it is shown that canopy productivity of the forests decreases with 14% when lianas are removed, but the productivity of wood rises with 64.5% (van der Heijden *et al.,* 2015). Van der Heijden *et al.* (2015) even suggest that liana free forests accumulate 76% more biomass than other tropical forests with lianas. Furthermore, with an increase in lianas there is a change from investment in woody biomass to leaves which have a shorter carbon residence time (van der Heijden *et al.,* 2015). Thus, liana increment will not be sufficient to compensate for the decrease in biomass accumulation in trees (van der Heijden *et al.,* 2015) and the C stock in tropical forests will be affected negatively (van de Heijden *et al.,* 2013).

Climate change and an increase in lianas can also cause a shift in tree species composition. Especially the recruitment and growth of shade-tolerant, non-pioneer species will be affected (Schnitzer *et al.,* 2000; Schnitzer and Bongers, 2002; van der Heijden *et al.,* 2008; Schnitzer and Carson, 2010). Shade-tolerant trees have a slower growth rate and generally a higher amount of branches to intercept more light what makes them more vulnerable for liana infestation (Schnitzer *et al.,* 2000). There will be a shift oriented towards more fast-growing trees that are buffered against severe liana infestation because of their fast height growth, large leaves and non-branching stems (Putz, 1984b). Fast growing species generally have a lower wood density and thus the alteration in species composition will influence the carbon balance too (van der Heijden and Phillips, 2009b). Additionally, a change in tree species will also influence the competition of trees mutually and thus affect carbon forest dynamics (Schnitzer and Bongers, 2002).

As a result, there will be less carbon accumulation, and so atmospheric CO_2 will increase even more. This will only fasten the process of global warming (van der Heijden *et al.,* 2015). It is not just the carbon stock that will be affected but also the water balance by the ability of lianas to reach deeper groundwater layers during the dry season (Schnitzer *et al.,* 2000). Furthermore, the nutrient dynamics will be impacted as well (Schnitzer *et al.,* 2012). More specifically, lianas frequently possess more nitrogen (Kusumoto and Enoki 2008) and phosphorus (Cai and Bongers, 2007) in their leaves than trees and can redistribute nutrients far in the forest due to their wide ranging root system (Schnitzer *et al.,* 2000, 2012).

2.5. Biological diversity

Ecosystems are under pressure as a consequence of diversity loss by invasive species, forest degradation and deforestation, among others (Wright, 2005). How the ecosystem processes and services will react on the decrease in diversity is still uncertain (Chapin *et al.,* 2000).

Diversity includes species diversity and functional diversity. Species diversity or species richness is the amount of different species related to a site (Gotelli and Colwell, 2011). On the other hand, there is functional diversity which can be subdivided in functional richness and functional composition. Functional richness encompasses the variety of functional traits occurring in a system (Diaz and Cabido, 2001). The traits tell something more about the function of the organism in the community (Petchey and Gaston, 2006), about how species are adapted morphologically, phenologically and physiologically to fit in the environment (Gallagher and Leishman, 2012a). Functional composition is a measure of the presence and relative abundance of traits. Additionally, species with similar key functional traits can be grouped together in a functional type (Diaz and Cabido, 2001).

Functional diversity, but particularly functional composition, has a strong association with ecosystem processes and can provide more insight into ecosystem functioning compared to species richness (Tilman *et al.,* 1997; Diaz and Cabido, 2001). Two processes drive the variation in traits in a system. The first, habitat filtering is the process whereby species disappear from unfitting areas. Only the species with the most appropriate traits will be able to maintain their position, leading to convergence in trait values (Weiher *et al.,* 1998). The second and opposite process is limiting similarity. Heterogeneity causes a better deviation of finite resources and so species with distinct traits can survive next to each other (Schoener, 1974). The functioning of the ecosystem will be influenced severely by changes in functional types (Tilman *et al.,* 1997). Namely, the variety in functional types plays a major role in long-term ecosystem stability by providing a buffer to changes in the environment as climate change (Diaz and Cabido, 2001).

2.5.1. Liana functional traits

Functional traits are the relevant characteristics of a species, with a meaningful role in its performance (McGill *et al.,* 2006). Lianas differ functionally from trees and other growth forms and so they fulfil other functions in the systems (Wright *et al.,* 2004; Sanchez-Azofeifa *et al.,* 2009; Collins *et al.,* 2016). Hereafter some of the most essential traits of lianas and their function will be discussed together with the differences in traits between lianas and co-occurring trees. This is followed by an overview of liana trait variation around the globe.

2.5.1.1. Seeds, flowers and fruits

The seeds of lianas are in general smaller than those of trees (Gallagher and Leishman, 2012b). The seed mass of plants is an indicator of the resources available for the seedling to survive and develop. This is certainly of importance when establishing in shady or dry environments. Further, small seeds are usually produced in bigger amounts and dispersed over longer distances compared to large seeds (Cornelissen *et al.,* 2003).

Besides the distance and the ultimate point of establishment, also the mode of dispersal depends on the seed mass (Cornelissen *et al.,* 2003). Anemochory is most common with small seeds (Hughes *et al.,* 1994) and thus also a prominent dispersal strategy for lianas (Chazdon *et al.,* 2003; Bongers *et al.,* 2005; Senbeta *et al.,* 2005). By using this strategy, seeds can be distributed over long distances towards gaps in the forest (Gallagher and Leishman, 2012a). This method of dispersal may also be valuable during the dry season when there is almost no rainfall and stronger winds (Schnitzer, 2005).

However, in the census of Parthasarathy *et al.* (2004) and Vivek and Parthasarathy (2014) both in India, the majority of the species was animal dispersed. This strategy was especially important in evergreen forests (Parthasarathy *et al.,* 2004). Vivek and Parthasarathy (2014) reported that 63.6% of the liana individuals was animal dispersed, followed by 33.8% of the individuals dispersed by the wind. Different dispersal methods may originate from differences in seasonality and the amount of precipitation, where the number of species relying on zoochory is greater in wetter areas (Gentry 1982, 1991).

Vivek and Parthasarathy (2014) also investigated flower and fruit traits in Indian forests. In the former category, more lianas possessed conspicuous flowers compared to inconspicuous flowers. In the latter category, fleshy-fruited was more common than dry-fruited, with the berry the most dominant in the fleshy-fruited group and the follicles for the dry-fruited species (Vivek and Parthasarathy, 2014).

2.5.1.2. Leaf traits

Leaf traits are important ecological proxies. Plants use nutrients and the energy of the sun to produce photosynthetic surface. Leaves at their turn are necessary to provide photosynthetic products for metabolism, growth or to re-invest in the construction of new leaves. This procedure differs between plant species (Wright *et al.,* 2004). The leaf economic spectrum (LES) proposed by Wright *et al.* (2004) handles the variety in velocity of the return on investment of dry mass and nutrients in the leaves. In this continuous spectrum, species with a quick return on investment are situated at one side and the ones with a slow return on the other side. These last ones are species with a low nutrient concentration in the leaves and low rates of respiration and photosynthesis. Additionally, they have a long leaf lifetime and a low specific leaf area (SLA; photosynthetic active area divided by dry mass) (Wright *et al.,* 2004). SLA tells something more about how much is invested in photosynthetic surface.

So, a low SLA refers to a species with a thick leaf and/or dense tissue (Wright *et al.,* 2004) and prognosticates a long leaf lifespan (Coley, 1983; Wright and Westoby, 2002). A low SLA and thus a thick leaf may indicate a longer diffusion pathway for the light towards the chloroplasts and so slower rates of photosynthesis and less carbon assimilation for a giving N status. Or the reduced photosynthesis could also be a consequence of a higher internal shading of the chloroplasts in the leaves (Parkhurst, 1994; Green and Kruger, 2001; Wright *et al.,* 2001).

A low SLA was also linked with lower nutrient concentrations (Wright *et al.,* 2004). Leaf nitrogen concentration (LNC) and leaf phosphorus concentration (LPC) are two important components for photosynthesis. Nitrogen is necessary for the production of molecules as RuBisCO (Ribulose-1,5-bisphosphate carboxylase/oxygenase) (Lambers *et al.,* 1998; Reich *et al.,* 2007; Gallagher and Leishman, 2012b) and is indeed positively correlated with the SLA (Reich *et al.,* 2007; Gallagher and Leishman, 2012b). Phosphorus as a component of adenosine triphosphate (ATP), lipid membranes and nucleic acids is also essential for plant functioning. It is taken up from the soil and cannot be filtered from the air as is possible for other nutrient such as nitrogen (Wright *et al.,* 2004).

When comparing the leaves of trees and lianas, lianas have a higher SLA than trees (Cai *et al.,* 2009b; Zhu and Cao, 2010; Gallagher and Leishman, 2012b; Collins *et al.,* 2016). Accordingly, Gallagher and Leishman (2012b) discovered that the nitrogen content of the leaves is higher for lianas than trees in littoral rainforest vegetation in Australia. The same trend is noticed in seasonal tropical forests in southwestern China (Zhu and Cao, 2009). In addition, lianas have a higher turnover rate (Avalos *et al.,* 2007) and thus a shorter leaf life span (Zhu and Cao, 2010). Finally, they also have a higher photosynthetic rate (Zhu and Cao, 2009, 2010). This combination of liana traits shows that lianas are situated at the quick return end of LES (Zhu and Cao, 2010; Gallagher and Leishman, 2012b). Conversely, trees occur along the entire range of the LES with pioneer trees most similar to lianas.

Shade tolerant trees more commonly use the strategy of maintenance of the acquired resources (Wright *et al.,* 2004).

2.5.1.3. Climbing mechanism

Lianas are climbers and use specific strategies to reach the canopy. Different climbing mechanisms have been identified: twiners, tendril climbers, root climbers, scramblers, grapnel-like climbers and hook climbers (Putz, 1984a; Parthasarathy *et al.,* 2004). Twiners wrap themselves around the host, mainstem-twiners use their stem while branch-twiners make use of leaf-bearing branches to twine around the present support (Laurance *et al.,* 2001). Tendril climbers ascend with the help of modified leaves, petioles or stems (DeWalt *et al.,* 2000; Gallagher and Leishman, 2012a). Scramblers don't have special modifications, they just rely on the external support of their host (Putz, 1984a). Further, stem nodes may produce roots that attach to imperfections of the host tree or cling to the host by glandular secretions (Putz, 1984a). When the stem outgrowths are hooked or like a grapnel and used to lean on the host, the climber is called a hook climber (Gallagher and Leishman, 2012a) or grapnel-like climber respectively (Putz and Chai, 1987). Straight outgrowths are called spines (Gallagher and Leishman, 2012a).

Different climbing mechanisms occur in different forests, depending on the available external support of the host trees and the distance towards the canopy (Kelly, 1985). All climbing strategies have a specific place in the forest where they flourish well. For instance, species defined as tendril climbers seem to profit from disturbance. They prefer hosts with smaller stems, forest edges or forest in the early stages of succession (DeWalt *et al.,* 2000). Also twiners prefer small diameter host trees (Putz and Chai, 1987). Climbing strategies can also be dependent on regional and local environments. For example, most of the liana species in the censuses in India were twiners and twining is also the most dominant strategy here (Parthasarathy *et al.,* 2004; Vivek and Parthasarathy, 2014). Though in dry evergreen forests the tendril climbers gained more weight compared to the areas with a wetter climate (Parthasarathy *et al.,* 2004). Senbeta *et al.* (2005) who studied lianas in Afromontane rainforests located in Ethiopia also determined a higher dominancy of twiners. In China, Yuan *et al.* (2009) found more individuals using the root climbing strategy.

2.5.1.4. Wood traits

As mentioned before lianas have large and wide vessels (Schnitzer and Bongers, 2002) which reduce the resistance to water flow and thus lead towards a high conductivity (Chave *et al.,* 2009). High growth rates are also possible because of a low construction cost of the stem. Lianas rely on the present structures in the forest and don't need to invest much in their own mechanical strength (van der Sande *et al.,* 2013). Further, lianas have a higher proportion of sapwood (Baas *et al.,* 2004), a lower sapwood density compared to trees (Zhu and Cao, 2009) and a low wood density (Putz, 1983). According to Putz (1983) liana wood density varied between 0.31-0.95 g/cm^3. A mean liana wood density of 0,40 g/cm^3 was found by Putz (1990) in Panama.

Although less information is available on wood traits in comparison with leaf traits, they should form a similar continuous spectrum called the 'wood economic spectrum' (Chave *et al.,* 2009). Here, just like in the 'leaf economic spectrum', there is a trade-off between the different functions of wood like mechanical support, transport of water and nutrients and the storage of resources (Chave *et al.,* 2009). Wood density is the main wood trait used and can be considered as a measure of carbon investment (Chave *et al.,* 2009). Species with a lower wood density such as lianas often have thin fibre walls (Pratt *et al.,* 2007) and thus a lot of space for conduits which favour the transport of water but reduce the resistance to cavitation (Baas *et al.,* 2004; Chave *et al.,* 2009). Further, resulting from a trade-off

between transport safety and water storage they are able to store more water (Pratt *et al.,* 2007). Finally, there is also a positive correlation between transport safety and xylem density and thus mechanical stability, leading towards a lower mechanical stability for species with a low wood density (Pratt *et al.,* 2007; Poorter, 2008).

2.5.1.5.   Root traits

Compared to trees, lianas have a higher specific root length, root branching intensity and higher root nitrogen and phosphorus concentrations (Collins *et al.,* 2016). Root tissue density is lower in the fine roots of lianas than in those of trees (Collins *et al.,* 2016). Although more studies are necessary to confirm these results for a higher liana species diversity and different forest types (Collins *et al.,* 2016). These characteristics indicate a rapid resource acquisition (Collins *et al.,* 2016) and a fast turnover rate (Eissenstat *et al.,* 2000) of the fine roots of lianas, just as for their leaves (Collins *et al.,* 2016). Confirmed by multiple authors is the deep rooting system of lianas (Restom and Nepstad, 2004; Andrade *et al.,* 2005; Schnitzer, 2005; van der Sande *et al.,* 2013).

2.5.1.6.   Biogeographical variation in liana traits

A pantropical analysis comparing traits of climbing plants (lianas, vines and scramblers) showed distinct trait differences across biogeographical zones (Africa, America, Asia and Australasia) (Gallagher and Leishman, 2012a). In South and Central America, the leaf area was higher compared to the other continents. Unfortunately, Africa and Southeast Asia were only represented by a small amount of available data (Gallagher and Leishman, 2012a). The Americas also differed in function of their climbing mechanism. Tendril climbers were more common. Furthermore, dispersal agents as wind and water were more predominant in America than in other study areas (Gallagher and Leishman, 2012a).

Differences in climbing species between the Americas and Africa could be attributed to high phylogenetic clustering probably because of the isolation of the continents by the oceans. The number of genera in taxonomic families in America is much higher than in Africa (Gallagher and Leishman, 2012a). So the difference in increasing liana abundance in some regions across the world may be determined by a phylogenetic component (Schnitzer and Bongers, 2011) or a difference in trait characteristics (Gallagher and Leishman, 2012a). It is possible that the species in America react heavier on the drivers of liana proliferation or the ones more abundant in Africa don't respond so strongly (Gallagher and Leishman, 2012a).

2.5.1.7.   Latitudinal variation in liana traits

Gallagher and Leishman (2012a) also studied the variation in traits of climbers (lianas, vines and scramblers) along a latitudinal and climatic gradient. They found a significant correlation between SLA, leaf size, seed mass and latitude. These three traits also correlate with the mean annual temperature and rainfall. There was no pattern found between latitude and climbing mechanism or dispersal mode.

Firstly, the SLA of climbing plants decreases towards the equator, i.e. leaf thickness increases. This pattern was solely based on data from temperate Australia and tropical South America (Gallagher and Leishman, 2012a), so the result should be interpreted with caution because it only covers a small biogeographical area.

Secondly, there is a significant negative correlation between latitude and the leaf area of climbing plants. At a latitude of 40-50° the average leaf area was approximately half of the average leaf area around the equator (Gallagher and Leishman, 2012a). Although explanatory power of the trend was low, resulting from the high variation in leaf area within a region (Gallagher and Leishman, 2012a). There is still some discussion about the drivers of this variation in leaf area. Some possible reasons are

proposed, including maximization of their ability to intercept light (Falster and Westoby, 2003), to suffer less from herbivory (Moles and Westoby, 2000), as a strategy to lose less water (Parkhurst and Loucks, 1972) or as a mechanism to optimize the temperature of the leaf and so the photosynthesis (Vogel, 2009).

Thirdly, climbers with a higher seed mass are more common close to the equator. Seed mass augments with 0.95 mg if the latitude decreases with one degree. However, latitude can only explain a small portion of this trend and so does rainfall. Growth form is more determinative and mean annual temperature can also explain more of the variation than the latitude (Gallagher and Leishman, 2012a). However, no trend is found in dispersal mechanism. Overall, dispersal by animals is more frequent towards the temperate areas than in the tropics. However, this pattern was not significant (Gallagher and Leishman, 2012a).

The most dominant climbing mechanism is twining, followed by tendril climbers. Climbing mechanism doesn't show a pattern with latitudinal distribution (Gallagher and Leishman, 2012a). Because of the heterogeneity in forests a lot of variation in climbing mechanism has already been found within the forest (Bongers *et al.,* 2005; Gallagher and Leishman, 2012a). Heterogeneity offers an opportunity to establish different climbing mechanisms because every strategy requires other conditions (DeWalt *et al.,* 2000).

3. Material and Methods

3.1. Study area and plot description

In August and September 2016, liana inventorization and data collection occurred in 17 permanent sample plots (PSP) in old-growth tropical lowland and montane forests in the provinces Pichincha and Imbabura, northern Ecuador. These plots are situated along an altitudinal gradient on the western slope of the Andes (400-3,200 m a.s.l.) (Figure 2), covering four different strata which each contain four or five plots similar in elevation (Table 2 and Supplementary Figure S3). All plots were established during a previous field campaign (summer 2015) and consist of old-growth natural tropical montane cloud forest in absence of human disturbance. The plots are 40 by 40 m and the centre is marked with a PVC tube. The main axes of the plots are oriented north-south and east-west and the plots are all square formed. All the soils of the four strata are classified as Andosols according to the 'World Reference Base for Soil Resources' (IUSS Working Group, 2014; Bruneel, 2016). Andosols are dark soils developed in volcanic ejecta. They possess a good water retention capacity and have a low bulk density. Unfortunately, they are susceptible to erosion and disturbances (Arnalds, 2008). Furthermore, Bruneel (2016) investigated the soil nutrients concentration in the permanent sample plots (Table 3, Supplementary Figures S4, S5, S6 and S7) and showed that Mg, K and Al concentrations increase significantly along the gradient ($p = 0.04$, $p < 0.001$ and $p < 0.001$ respectively) while Ca and Na do not show a significant trend (Table 3). The total nitrogen (Ntot) concentration of the upper 30 cm of the soil increases with increasing altitude ($p = 0.013$) (Figure S4) similar as the bioavailable phosphorus (Pbio-av) concentration ($p < 0.01$) (Figure S5). However, the total phosphorus (Ptot) concentration stays more or less constant along the elevational gradient (Figure S5). N:Ptot increases with altitude ($p < 0.01$), while this is not the case for N:Pbio-av (Figures S6 and S7). Climatic data, such as the mean annual precipitation (MAP) and mean annual temperature (MAT) were extracted from the WorldClim database (with a resolution of 1 km^2) and are available for every stratum in Table 4 (Hijmans *et al.*, 2005; WorldClim). Next to a decrease in temperature with rising altitude, there is also a decrease in precipitation along the altitudinal gradient.
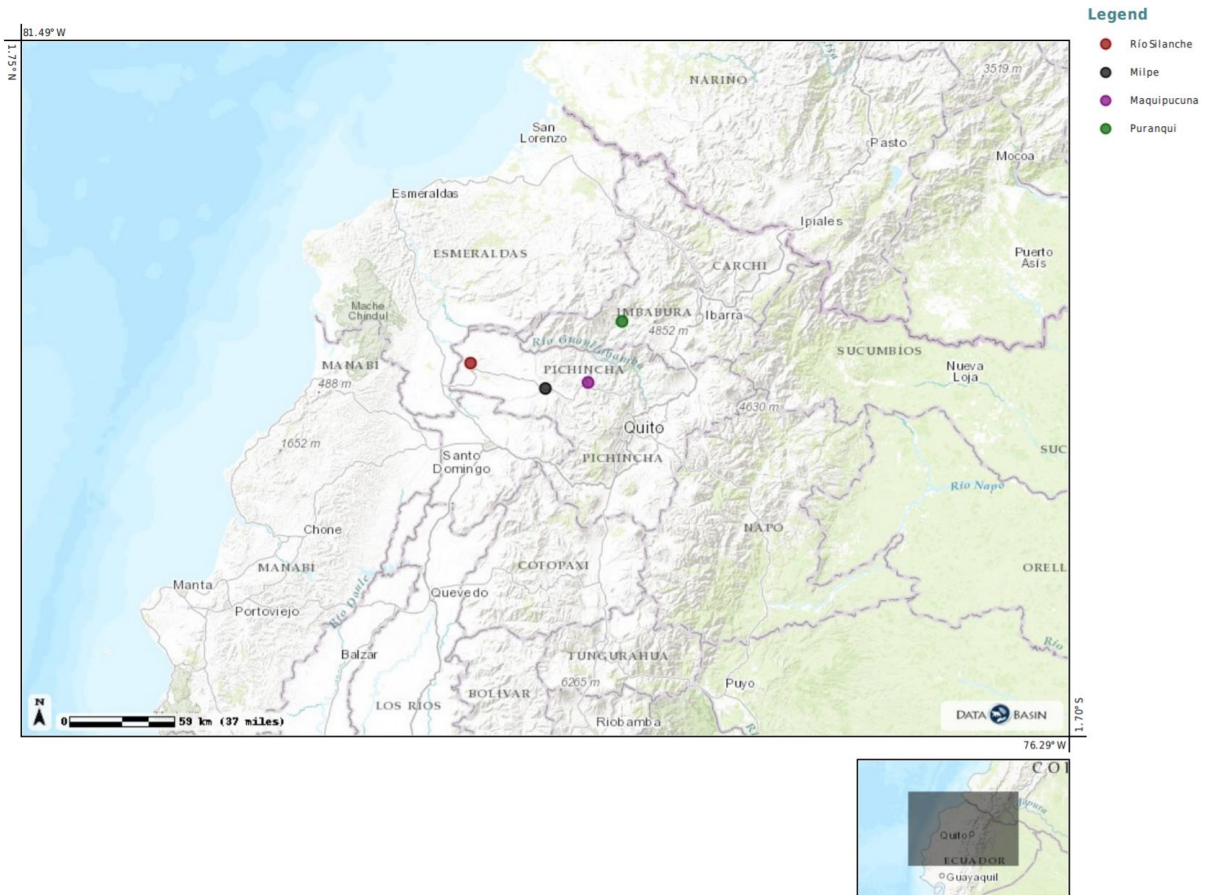
Figure 2: Visualisation of the different locations of the strata (represented by dots on the map). From left to right: Rio Silanche 400 m a.s.l. (brown), Milpe 1,100 m a.s.l. (black), Maquipucuna 1,900 m a.s.l. (purple) and Puranqui 3,200 m a.s.l. (green) (Created on databasin.org).

Table 2: Overview of the different strata, their names, altitude and the number of permanent sample plots.

Stratum	Name of the reserve	Altitude (m) a.s.l.	Number of plots
Stratum 1	Rio Silanche Bird Sanctuary	400	5
Stratum 2	Milpe Bird Sanctuary	1,100	4
Stratum 3	Maquipucuna Cloud Forest Reserve	1,900	4
Stratum 4	Puranqui Community Forest	3,200	4

Table 3: Soil properties (mean of the upper 30 cm of the soil ± 1SE) along the altitudinal gradient: total nitrogen (Ntot), bioavailable phosphorus (Pbio-av), total phosphorus (Ptot), magnesium (Mg), potassium (K), calcium (Ca), sodium (Na), aluminium (Al), stable nitrogen isotope composition ($\delta^{15}N$) and stable carbon isotope composition ($\delta^{13}C$) (Bruneel, 2016).

	Stratum 1	Stratum 2	Stratum 3	Stratum 4
Ntot (g kg^{-1})	6.78 ± 0.57[a]	5.02 ± 0.70[b]	5.56 ± 1.00[b]	8.88 ± 0.71[c]
Pbio-av (mg kg^{-1})	0.24 ± 0.37[a]	1.30 ± 1.44[b]	10.33 ± 1.53[c]	6.70 ± 3.95[d]
Ptot (mg kg^{-1})	931.64 ± 157.15[a]	619.75 ± 258.27[b]	665.41 ± 157.47[bc]	787.73 ± 6.84[c]
Mg (mg kg^{-1})	32.18 ± 5.55[a]	36.01 ± 21.18[a]	126.61 ± 114.49[b]	85.19 ± 34.44[b]
K (mg kg^{-1})	67.82 ± 17.12[a]	41.24 ± 12.98[b]	82.46 ± 32.50[a]	136.07 ± 48.59[c]
Ca (mg kg^{-1})	181.14 ± 45.05[a]	273.94 ± 130.74[a]	1010.22 ± 828.56[b]	310.26 ± 236.23[ab]
Na (mg kg^{-1})	31.55 ± 28.94[a]	12.15 ± 1.84[b]	17.58 ± 6.73[ab]	23.66 ± 4.91[a]
Al (mg kg^{-1})	30.04 ± 8.65[a]	34.80 ± 15.45[a]	34.90 ± 26.01[a]	170.95 ± 42.26[b]
δ^{15}N (‰)	6.65 ± 0.35[a]	4.39 ± 0.93[b]	3.68 ± 0.48[c]	3.35 ± 0.44[c]
δ^{13}C (‰)	-27.17 ± 0.27[a]	-27.64 ± 0.10[b]	-27.16 ± 0.61[a]	-24.23 ± 0.70[c]

Table 4: Mean annual temperature (MAT) (°C), minimum temperature of the coldest month (°C), mean annual precipitation (MAP) (mm), precipitation of the wettest month (mm) and precipitation of the driest month (mm) for the different strata (average data for 1960-1990) (Hijmans *et al.,* 2005; WorldClim).

Stratum	MAT (°C)	Min. temperature coldest month (°C)	MAP (mm)	Precipitation wettest month (mm)	Precipitation driest month (mm)
Stratum 1	23.8	18.8	3447	597	85
Stratum 2	20.0	14.7	3034	495	73
Stratum 3	17.4	10.9	1492	241	36
Stratum 4	11.2	4.9	1181	173	15

Rio Silanche

The lowest stratum, 400 m a.s.l., counts 5 permanent sample plots located in the Rio Silanche Bird Sanctuary. This nature reserve consists of 100 ha of protected Chocó lowland rainforest and is situated in a hilly lowland forest in the Pichincha province. It is part of a network of reserves owned by the Mindo Cloud forest Foundation (MCF), a non-profit conservation organisation. The forest is protected since 2005 but the surrounded area was converted into farmland for the production of oil palm and cacao. Further, also mining is common in the region. The forest consists of multiple vegetation layers and the most common tree species are *Pouruma sp., Protium sp.* and *Ceiba sp*. Also palm trees seem to flourish in this forest (Demol, 2016).

Milpe Bird Sanctuary

At 1,100 m a.s.l. 4 permanent sample plots were established in the Milpe Bird Sanctuary, a 100 ha Chocó-Andean foothill reserve in the province Pichincha. Since 2004 also this nature reserve is preserved by the MCF. According to Demol (2016) who investigated tree species diversity, this stratum was the most divers. *Otoba gordonifolia* was the most dominant tree and the Myristicaceae, Moraceae and Lauraceae the most important families, weighted on basal area (Demol, 2016).

Maquipucuna Cloud Forest Reserve

Four more plots are situated at an altitude of 1,900 m a.s.l. in the centre of the Maquipucuna Cloud Forest reserve. This reserve consists of lower and upper montane cloud forest and above 1,500 m the forest has a persistent cloud cover (Svenning and Balslev, 1998). Protection of the area started already in 1988. The reserve is famous for its population of spectacled bears (*Tremarctos ornatus*), feeding on wild avocadoes (*Nectandra spp.*) that grow in the lower parts of the forest (Castellanos, 2011). Dominant species in the area include *Cecropia sp., Otoba gordonifolia* and *Critoniopsis sp.* (Demol, 2016).

Puranqui Community Forest

The last 4 permanent sample plots are positioned at 3,200 m a.s.l. in the Puranqui Community Forest in the Intag Zone, province Imbabura. The plots are situated just below the treeline which forms the border with Páramo grassland more uphill. The canopy of the forest is low and the trees are irregularly shaped and grow often crooked or almost horizontal. Tree species persistent in this forest are *Freziera canescnens, Weinmannia pinnata* and *Clusia sp.* (Demol, 2016). Cows were grazing only a few hundred metres below the permanent sample plots and signs of their presence were noticed around the plots. This may question the undisturbed state of the forest.

3.2. Data acquisition

The permanent sample plots were relocated and plot boundaries were delimited with ropes. To simplify data acquisition the plots were subdivided in 4 subplots of 20 x 20 m according to the main axes of the plot.

Every living climbing liana with an average diameter larger or equal to 2 cm was included in this inventory and received a plastic tag with a number. A diameter cut-off of 2 cm was selected as it is the suggested minimum diameter for investigations of abundance and diversity of canopy lianas (Kurzel *et al.,* 2006). (Hemi-) epiphytes, rattans, other climbing palms and climbing Poaceae (e.g. bamboos) were excluded. Inclusion or exclusion of a liana was further based on its last rooting point. Only lianas with a final rooting point in the plot before ascending to the canopy were tagged and measured. The diameter of all lianas (≥ 2 cm diameter) was determined based on the protocol of Gerwing *et al.* (2006) and the supplemental protocol of Schnitzer *et al.* (2008). The measurement protocol can be found in the appendix (Supplementary Figure S8). Mostly diameter measurements were at a reference height of 130 cm from the last rooting point of the liana. This was not measured as a vertical height but measured along the stem of the liana. If the point of measurement deviated from the standard point (based on the measurement protocol) this was carefully written down. Further the point of measurement was indicated with a strip of orange painting on the liana stem. This renders the ability to measure at the same height in potential future censuses. Finally, the number of the main host tree,

tagged during the previous field campaign, was noted together with the main host status, the rooting type of the liana and the status of the liana.

Species identification of the lianas was done by a local Ecuadorian botany student (Lenin Nicanor Mejía Pazos). Identification was mainly based on stem and leaf characteristics. If determination in the field was not possible, leaves were collected to compare with available dried plant material (herbarium of Universidad Técnica del Norte, Ibarra Ecuador). Unfortunately, determination of all lianas was impossible, and several individuals remain unknown (n = 65 with n = 31, n = 17, n = 15 and n = 2 in stratum 1, stratum 2, stratum 3 and stratum 4 respectively), while others were identified up to family (n = 33) or genus level (n = 327).

For further data processing, also information gathered during previous field campaign was used. In the summer of 2015 Stijn Bruneel and Miro Demol established the PSPs. They measured tree diameters at breast height (DBH at 130 cm) for every living tree exceeding a threshold value of 10 cm DBH. Trees were included when more than 50% of the rooting system fell into the PSP. With a Nikon Forestry Pro also tree height measurements were conducted. In total 1,395 trees were tagged and measured. Furthermore leaf traits of 178 individual trees, or 82 different tree species, were sampled and analysed for leaf area (LA), specific leaf area (SLA), leaf dry mass (LM), carbon isotope ratio (δ^{13}C), nitrogen isotope ratio (δ^{15}N), mass-based leaf carbon content (LCC), mass-based leaf nitrogen content (LNC), mass-based leaf phosphorus content (LPC) and for the ratios carbon to nitrogen (C:N), carbon to phosphorus (C:P) and nitrogen to phosphorus (N:P). Further also the leaf carbon content on area basis (LCCa), leaf nitrogen content on area basis (LNCa) and leaf phosphorus content on area basis (LPCa) were calculated by dividing respectively the LCC, LNC and LPC by the SLA (Demol, 2016). Furthermore, wood density (WD), tree height (H) and an estimation of mature tree height for every species calculated as the 90% percentile of the tree heights recorded for a certain species, were determined. Finally, soil samples were taking at the standardized depths of 0-5 cm, 5-10 cm, 10-20 cm, 20-30 cm, 30-50 cm and 50-100 cm. Five samples were taken for every plot and mixed samples were made for every depth to determine the pH, soil bulk density, soil N, C, P and Al concentrations, exchangeable cations and isotope compositions (Bruneel, 2016).

3.3. Leaf sampling and analysis

Liana leaf samples were taken to investigate the variation in functional leaf traits along the altitudinal gradient. The goal was to sample 3 individuals per species per stratum. In some strata this threshold was not reached particularly because the canopy was too high to collect liana leaves even with a tree pruner of 12 metre but also because of a lack in repetition in the occurrence of the species. When possible a sub-sample of 10 leaves was taken for every individual selected liana. In total, 89 individuals were sampled with 17, 17, 25 and 30 individuals from the lowest to the highest altitude. The leaves were transported in plastic bags and dried between newspapers as soon as possible. After being pressed overnight, an image was taken while the leaf was levelled out under a Plexiglas and leaf area was determined using ImagJ (from the US National Institutes of Health; http://www.nih.gov/). Subsequently the leaves were taken to the Universidad Técnica del Norte in Ibarra to complete the drying process with hot air. When the leaves were dry, they were transported to Belgium for further analysis. In Belgium, when necessary, they were dried once again in the ovens of Ghent University at 60 degrees Celsius to avoid deterioration by fungi.

Per individual liana the collected leaves were weighted to determine the dry weight of the samples. Specific leaf area (SLA) was determined as leaf area over dry weight. Thereafter the leaves were

pulverized with a Retsch ZM-200 centrifugal mill at sieving pore of 0.2 mm. After each pulverization, the machine was carefully cleaned to avoid contamination. Subsequently, chemical analyses were conducted at the Isotope Bioscience Laboratory (ISOFYS) at Ghent University. For the determination of the mass-based leaf carbon (LCC) and leaf nitrogen (LNC) concentrations in the leaves, 0.35-0.65 mg of the sample was analysed with an elemental analyser: the ANCA-SL (Automated Nitrogen Carbon Analyser - Solids and Liquids) interfaced with a SerCon 20-22 IRMS (SysCon electronics). As references sorghum flour and wheat flour were used. Further isotope values were determined, for carbon calibrated to IAEA-CH-6 and for nitrogen to IAEA-N-1.

Also the mass-based leaf phosphorus concentration (LPC) was determined for every sample, based on the Chapman and Pratt (1961) procedure. Approximately 0.5 g of the sample was weighed and the exact weight was recorded. The samples were incinerated for 5 hours in a porcelain cup at a temperature of 550°C and 5 mL of 2 M HCl was added to dissolve the ashes. Subsequently, the samples were diluted with MilliQ water up to a volume of 25 mL and reposed for 30 minutes after shaking. The solutions were poured through a phosphorus-free filter whereby the first drops of the filtrate were discarded. Finally, the phosphorus concentrations were determined with the Bran Luebbe AA3 auto-analyser.

3.4. Statistical analysis

Analysis of the data was executed in R (version 3.3.3), an open source software program (R Core Team, 2017).

In total 688 lianas were tagged and included in the liana community structure analyses. Liana diameter and basal area (BA) were available directly from field measurements. Liana aboveground biomass (AGB) estimations were obtained using the formula described in Schnitzer *et al.* (2006):

$$AGB = exp\big(-1.484 + 2.657 ln(D)\big)$$

Liana aboveground oven-dry weight (AGB) is expressed in kg and D stands for the diameter of the liana in cm measured 130 cm above its last rooting point. Plot-level liana AGB was determined by summation of all lianas. Regressions were made to investigate how liana diameter, density, biomass and basal area fluctuate in function of the altitude. Significant differences across the strata were tested with a Kruskal-Wallis test and subsequently with a Mann-Whitney U test (Hollander *et al.,* 2013) and Pearson correlations were computed to investigate the link between liana community structure variables and environmental factors.

For species-specific analyses, all unknown liana species (65 individuals) were removed from the dataset. Species richness and other indices such as the Simpson diversity index (Simpson, 1949), Shannon diversity index (Shannon and Weaver, 1963), alpha diversity (Whittaker, 1972) and Pielou's evenness (Pielou, 1966) were computed using the R package 'vegan' (Oksanen *et al.,* 2017). Because comparing species richness along plots with a different sample size is not recommended, the rarefied species richness was calculated as well, also with the R package 'vegan' (Oksanen *et al.,* 2017). Rarefaction allows comparison of different plots by standardizing them by the lowest amount of observed species (Gotelli and Colwell, 2001).

Thereafter 9 liana leaf traits were analysed: specific leaf area (SLA), mass-based leaf carbon content (LCC), mass-based leaf nitrogen content (LNC), mass-based leaf phosphorus content (LPC), leaf carbon to nitrogen ratio (C:N), leaf carbon to phosphorus ratio (C:P), leaf nitrogen to phosphorus ratio (N:P), the stable carbon isotope composition ($\delta^{13}C$) and the stable nitrogen isotope composition ($\delta^{15}N$). For every trait the community weighted mean (CWM), weighted on basal area, was calculated at plot-level

and linear regressions were performed to detect possible shifts in ecological strategy with elevation. Significant differences across the strata were tested with a Kruskal-Wallis test, followed by a Mann-Whitney U test (Hollander *et al.,* 2013). Subsequently a principal component analysis (PCA) was carried out with the 9 liana leaf traits to determine the links between the different traits and the major axis of variation. For this the different traits were scaled to a unit standard variation and a mean of zero. Only the principal components with an eigenvalue more than 1 were retained. Boxplots of the principal components (PC) were constructed to visualize possible trends with elevation.

Next, liana functional diversity indices were determined in order to quantify the distribution of the traits along the elevation gradient. Four indicators of functional diversity were selected as proposed by Mason *et al.* (2005) and Villéger *et al.* (2008): functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis). As detailed in Figure 3, functional richness describes the occupation of the trait space by the inventoried species. Functional evenness is a measure of the uniformity in the distribution of the species in the trait space. Functional divergence comprises the deviation of the most general species from the average trait values, thus the distance from the centre of the functional space (Figure 3) (Mason *et al.,* 2005; Villéger *et al.,* 2008). The last indicator, functional dispersion, is the average distance of species, weighted by abundance, from the centroid of all species present in the community (Figure 4) (Laliberté and Legendre, 2010). These functional diversity indices were determined taking into account the 9 liana leaf traits that were available. We also compared the results with the functional diversity indices of the co-occurring trees. Unfortunately, we were unable to do the calculations for liana functional diversity with the same traits as used for the trees because we didn't possess all traits. Calculating liana functional diversity indices with the most compatible traits rendered the same significant trends as when using all 9 liana leaf traits. Calculations were performed using the R package 'FD' (Laliberté *et al.,* 2014). Before analysis N:P, C:P, C:N, SLA, LPC and LNC were log transformed because of their right skewed distribution and δ^{13}C because of its left skewed distribution. Pearson correlations were executed to identify important associations between the different traits.

Finally, the functional community structure of the forests, i.e. including both lianas and trees, was investigated. Boxplots were constructed to compare liana and tree leaf traits along the gradient and to investigate possible dissimilarities in functional niche between both growth forms. To test for significant differences a Kruskal-Wallis test and subsequently a Mann-Whitney U test was used (Hollander *et al.,* 2013). This was followed by a PCA combining all liana and tree traits to determine the covariation among the traits. For the PCA the different traits were scaled to a unit standard variation and a mean of zero. Only the principal components with an eigenvalue more than 1 were retained. Prior to analysis all the traits with a skewed distribution were log transformed. Additionally, Pearson correlations between liana and tree leaf traits and soil properties were computed in order to better understand the functional distinctiveness, found between the two growth forms.
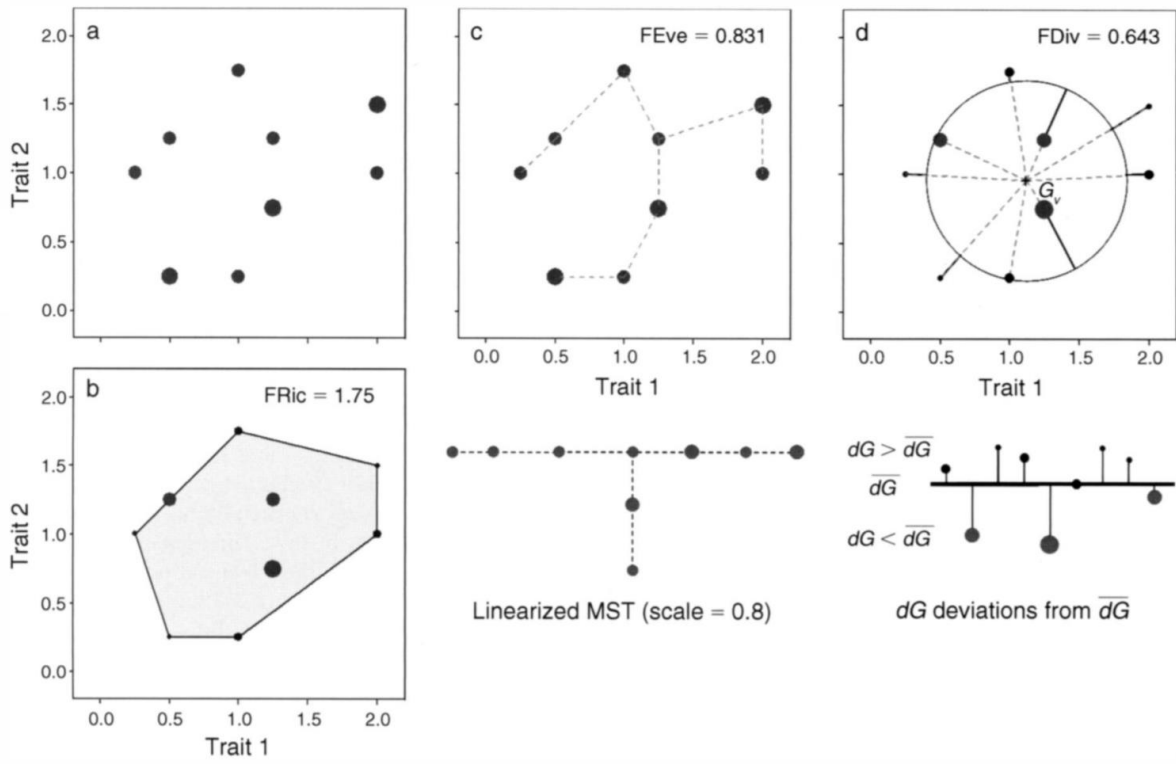
Figure 3: Overview of the determination of three functional diversity indices: functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) based on two traits and nine species. Panel a: The different dots represent the nine species plotted according to their traits values. The size of the dots is a measure of the species abundance. Panel b: A convex hull is plotted. The area or volume, coloured in grey, describes the functional richness. It correspondents to the smallest area necessary to comprise all the species. Panel c: Functional evenness is based on the regularity in distance and abundance of the species along a minimum spanning tree (MST) which links the points. The MST is also plotted stretched right below panel c. Panel d: Representation of the centre of gravity (Gv) of all the species and the mean distance towards the centre (black circle). The lines between the mean distance and the points are a visualisation of the deviation of the points from the mean (also plotted below the box). Functional divergence will increase when there are more species with a high abundance lying outside the circle (Villéger *et al.,* 2008).
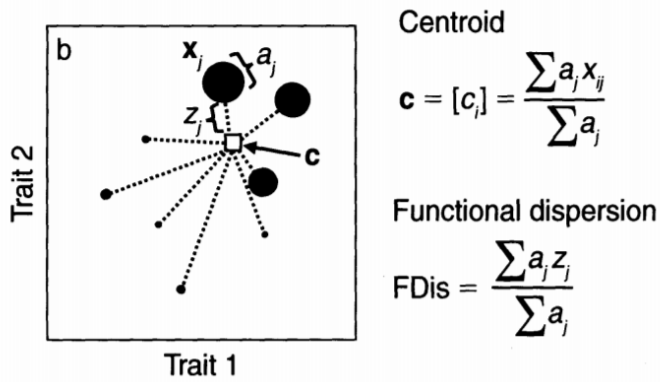
Figure 4: Visualisation of the calculation of functional dispersion (FDis). The different species (n = 8) are represented by dots and plotted according to their trait values. The size of the dots is a measure of the abundance of the species. Xj is the position of species j, aj the abundance of species j and zj the distance of the species towards the centroid. The centroid is the average value of trait i weighted by the abundances of the species. Subsequently functional dispersion is calculated using the distances of the species toward the centroid weighted by abundance (Laliberté and Legendre, 2010).

4. Results

4.1. Liana community structure

The first part of the analysis focusses on the gathering of information about liana community structure variation along the altitudinal gradient. Liana community structure analysis includes data about density, diameter, basal area and aboveground biomass of 688 individuals. Stem density is similar across the strata (p = 0.58) (Table 5, Figure 5) and the abundance peaks (non-significantly) at an altitude of 1,900 m a.s.l. The highest liana density is detected in plot 3 in stratum 3, namely 88 lianas on a surface of 1,600 m^2. With only 11 lianas on the same surface area, plot 2 in stratum 4 has the lowest liana abundance. Size density distributions across the different strata (Figure 6) show an overall high frequency of lianas in the smallest diameter class 2-3 cm (48.5% of all tagged individuals), followed by a strong decrease in liana abundance in the subsequent diameter classes. Large lianas are very scarce, only a very limited number of lianas is situated in the higher diameter classes. Lianas with a diameter bigger than 12 cm are only found in the lowest stratum, where they even reach diameters of 20 cm. The percentage of lianas with a diameter equal or more than 4 cm decreases along the gradient: 32.5%, 24.1%, 21.2% and 11.9% for stratum 1, stratum 2, stratum 3 and stratum 4 respectively. Thus, thicker lianas are more common in the lowest strata. Significant decreases with altitude are found in liana diameter (p < 0.001), liana basal area (p < 0.01) and liana aboveground biomass (p < 0.01) of individual lianas (Figure 5). Total liana basal area and total aboveground liana biomass also decrease from the lowest to the highest stratum although this reduction in basal area and biomass is only marginally significant (p = 0.093 and p = 0.051 respectively) (Figure 5).

Table 5: Liana community structure variables and their standard deviations across the altitudinal gradient: stratum 1 (400 m a.s.l.), stratum 2 (1,100 m a.s.l.), stratum 3 (1,900 m a.s.l.) and stratum 4 (3,200 m a.s.l.). Significant differences across the strata (p = 0.05) are shown as different letters.

	Stratum 1	Stratum 2	Stratum 3	Stratum 4
Altitude (m) a.s.l.	400	1,100	1,900	3,200
n of PSPs	5	4	4	4
Tree density (ha^{-1})*	549 ± 93[a]	625 ± 324[a]	500 ± 136[a]	644 ± 253[a]
Mean BA per tree (m^2)*	0.046 ± 0.01[a]	0.053 ± 0.01[a]	0.068 ± 0.01[ab]	0.077 ± 0.01[b]
Mean tree height (m)*	18.25 ± 1.28[a]	16.85 ± 1.14[b]	13.47 ± 2.07[c]	12.95 ± 2.28[c]
Liana density (ha^{-1})	257.5 ± 108.7[a]	214.1 ± 130.2[a]	368.8 ± 160.6[a]	170.3 ± 98.5[a]
Mean liana diameter (cm)	3.9 ± 0.3[a]	3.4 ± 0.2[ab]	3.3 ± 0.2[b]	3.1 ± 0.3[b]
Mean liana BA (cm^2)	15.0 ± 3.1[a]	10.5 ± 0.9[ab]	9.9 ± 1.9[b]	8.5 ± 2.2[b]
Total liana BA (m^2 ha^{-1})	0.4 ± 0.2[a]	0.2 ± 0.1[a]	0.4 ± 0.2[a]	0.1 ± 0.1[a]
Mean liana AGB (kg biomass)	14.8 ± 5.1[a]	8.0 ± 0.9[ab]	7.6 ± 2.6[b]	6.1 ± 2.3[b]
Total liana AGB (ton biomass ha^{-1})	4.1 ± 2.2[a]	1.7 ± 0.9[a]	3.1 ± 2.5[a]	1.0 ± 0.5[a]

*data obtained from Bruneel (2016)

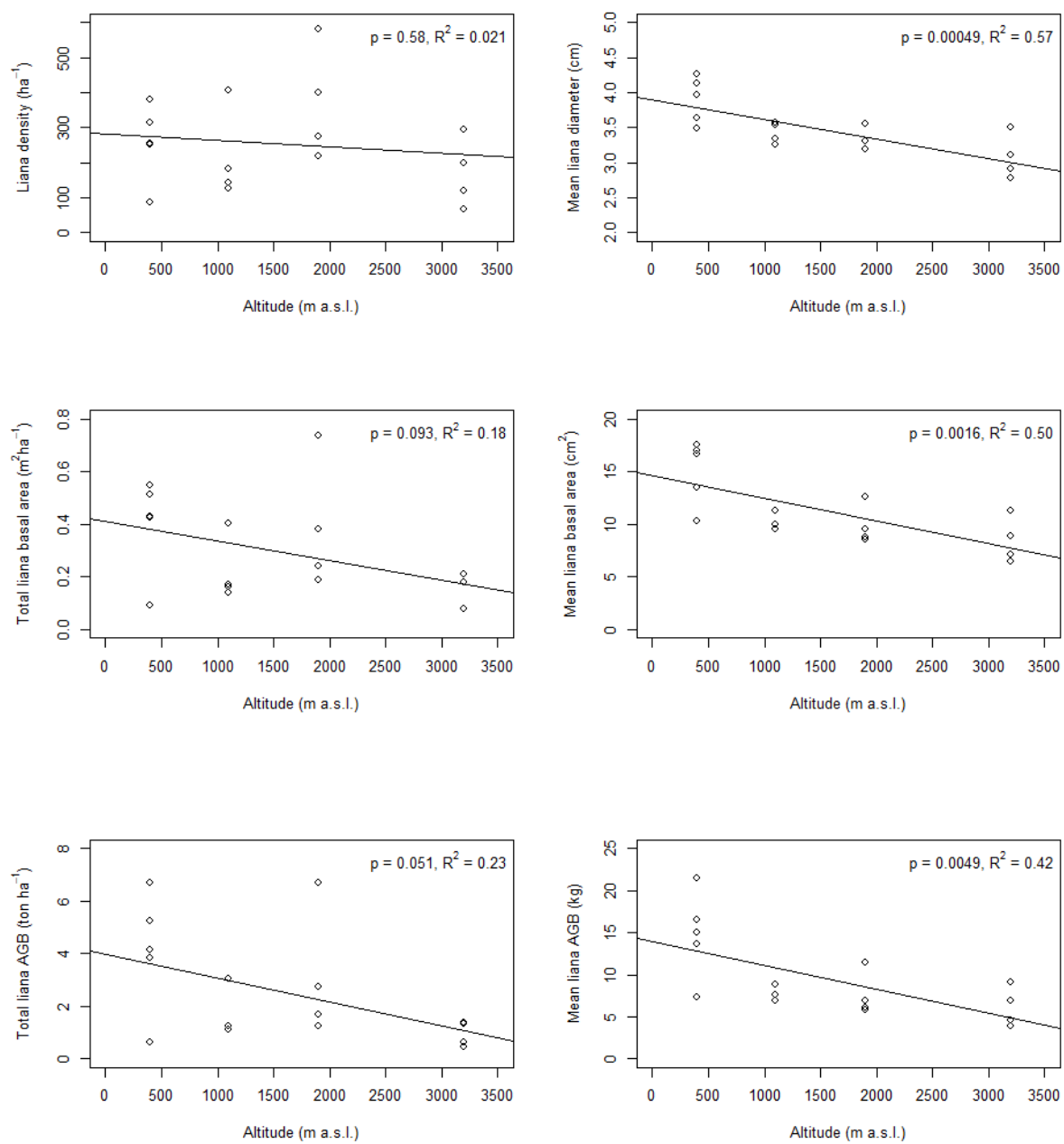*Figure 5:* Linear regressions of liana community structure variables in function of the altitude. From the upper left to the bottom right: liana density (ha^{-1}), mean liana diameter (cm), total liana basal area (cm^2 ha^{-1}), mean liana basal area (cm^2), total liana aboveground biomass (ton ha^{-1}) and mean liana aboveground biomass (kg). P values and R^2 values were added for every graph.
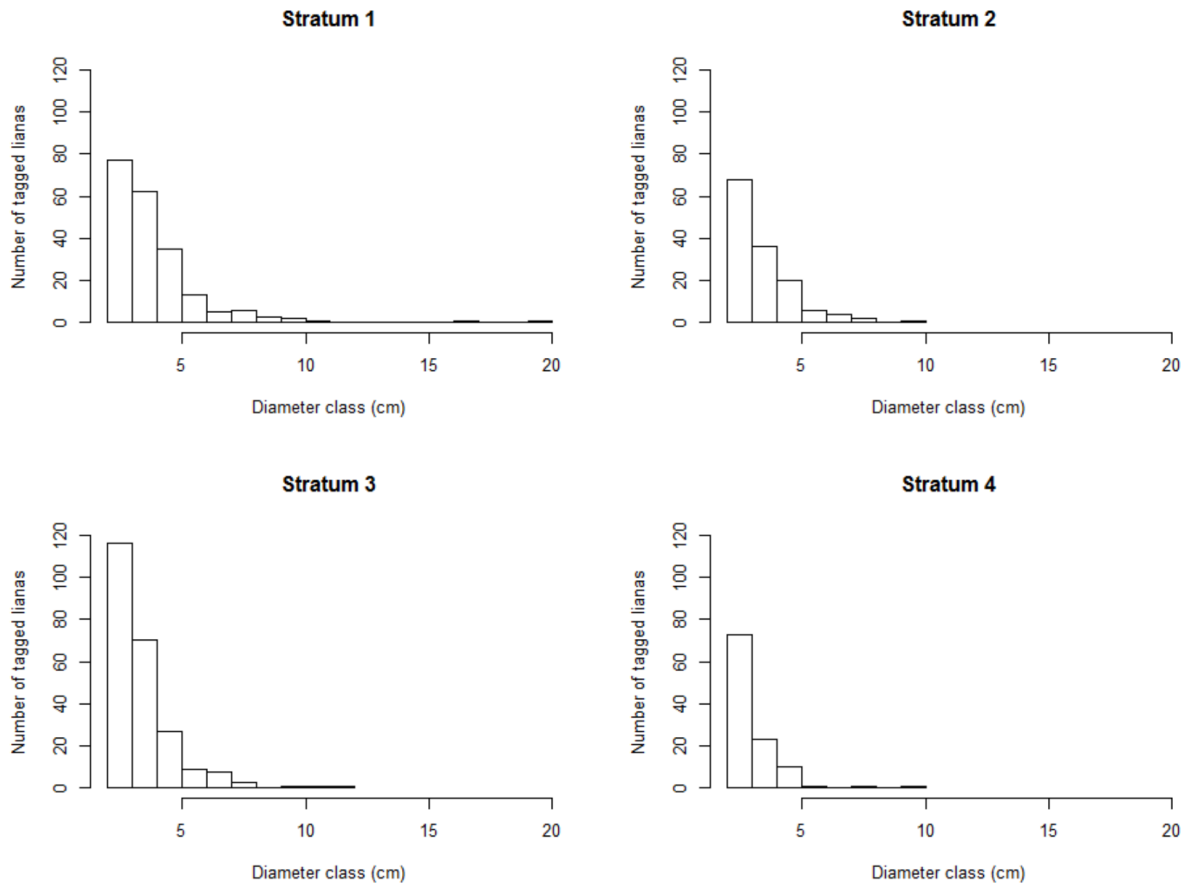
Figure 6: Size density distributions (bin size 1 cm) across the four strata. Upper left panel: Stratum 1 (n = 206). Upper right panel: Stratum 2 (n = 137). Bottom left panel: Stratum 3 (n = 236). Bottom right panel: Stratum 4 (n = 109).

Pearson correlations between liana community structure variables and environmental factors such as soil properties, MAT, MAP, tree BA and tree density were computed (Supplementary Table S2). MAT and tree BA are significantly correlated with liana diameter ($p < 0.001$ for MAT and $p < 0.05$ for tree BA) and liana AGB ($p < 0.05$ for both), the correlation with MAT is a positive one and the correlation with tree BA is a negative one. Also the soil C:N ratio is negatively correlated with liana community structure variables, more specifically liana diameter ($p < 0.01$), liana AGB ($p < 0.05$) and liana BA ($p < 0.05$). Extra positive correlations were found between liana diameter and canopy height ($p < 0.05$), MAP ($p < 0.01$) and δ^{15}N ($p < 0.001$). A negative correlation between liana diameter and δ^{13}C ($p < 0.05$) was found as well.

4.2. Liana species diversity and functional diversity

4.2.1. Taxonomic diversity

From all tagged lianas (n = 688), 65 individuals stayed unidentified. Only the resulting 623 lianas were included in diversity analyses. Several individuals have been identified as belonging to the same species, although species-level classification and nomenclature is currently lacking. Of these, 5 species groups were classified up to family level and 40 up to genus level. The remaining 263 individuals were fully identified belonging to 13 different species. In total 58 different liana species were distinguished covering 23 different families and 36 distinct genera. Determination of the species was the hardest in

stratum 1 where 31 individuals were left unidentified, in the following strata this were respectively 17, 15 and 2 individuals (Supplementary Table S3).

Looking at the complete liana database, the most important families are the Asteraceae with a relative abundance of 18.6%, the Ericaceae (17.8%) and the Marcgraviaceae (11.7%). However, the most persistent family alters across the altitudinal transect: in stratum 1 the Asteraceae (46.9%), Bignoniaceae (22.9%) and Fabaceae (9.1%) are the most important families; in stratum 2 the Clusiaceae (26.7%), Sapindaceae (26.7%) and Aquifoliaceae (15.8%) dominate; in stratum 3 the Marcgraviaceae (30.3%), Ericaceae (27.1%) and Rosaceae (8.1%) are the most abundant; and in stratum 4 the Ericaceae (36.4%), Smilaceae (30.8%) and Asteraceae (28.0%) are the most persistent families.

Furthermore, every stratum can be characterised by its most persistent species (Table 6). At every altitude, more than 50% of the lianas belongs to the top 3 most dominant species. But on the other hand, approximately 35% of the species were only found once in the whole census (Supplementary Figure S9). Most of the species are also uniquely linked to one specific stratum. Only 2 species were observed at more than one altitude: *Serjania sp. 1* in Rio Silanche and Milpe (stratum 1 and stratum 2) and *Clusia sp. 1* in Rio Silanche, Milpe and Maquipucuna (corresponding to stratum 1, 2 and 3).

Table 6: The top 3 most persistent liana species for every stratum weighted on abundance (relative abundance) and on basal area (abundance weighted on BA).

Stratum	Species	Relative abundance (%)	Abundance weighted on BA (%)
Stratum 1	*Mikania nigricans (Asteraceae)*	30.9	28.2
	Melloa sp. 1 (Bignoniaceae)	22.9	17.2
	Dalbergia brownei (Fabaceae)	9.1	27.1
Stratum 2	*Serjania sp. 1 (Sapindaceae)*	26.7	28.9
	Ilex sp. 1 (Aquifoliaceae)	15.8	13.9
	Clusia sp. 1 (Clusiaceae)	15.8	17.8
Stratum 3	*Marcgravia brownei (Marcgraviaceae)*	30.3	34.6
	Psammisia aberrans (Ericaceae)	27.1	33.1
	Piper sp. 2 (Piperaceae)	7.7	/
	Rubus robustsus (Rosaceae)	/	4.7
Stratum 4	*Smilax sp. 1 (Smilacaceae)*	30.8	20.2
	Macleania macrantha (Ericaceae)	19.6	26.6
	Psammisia sp. 2 (Ericaceae)	16.8	24.3

For every altitude, the species richness was computed. The highest value on stratum level is found in Maquipucuna (stratum 3), the lowest amount of species is discovered in Puranqui (stratum 4). However, we do not find a significant shift (p = 0.84) in species richness along the gradient (Figure 7 and Supplementary Table S4). Because the absolute number of inventoried species for every plot affects species richness also the rarefied species richness was calculated. Rarefied species richness was computed relative to the lowest amount of tagged and identified lianas on plot level: 10 lianas in plot 2, stratum 4 (Supplementary Table S3). A rarefaction curve can be found in the appendix (Supplementary Figure S10). For most of the plots species richness will certainly increase if the sample

size is enlarged. The average rarefied species richness is the highest in Milpe (stratum 2) followed by Maquipucuna (stratum 3) but also here there is no significant shift (p = 0.90 across the altitudinal gradient (Figure 7 and Supplementary Table S4). Other diversity indices such as the Shannon diversity index, the Simpson diversity index, the alpha diversity index and evenness can be found in Supplementary Table S4, also linear regressions are visualized in the appendix (Supplementary Figure S11). The Shannon diversity index (p = 0.73), Simpson diversity index (p = 0.63), alpha diversity (p = 0.82) and evenness (p = 0.85) do not show a trend along the gradient (Supplementary Table S4 and Figure S11).
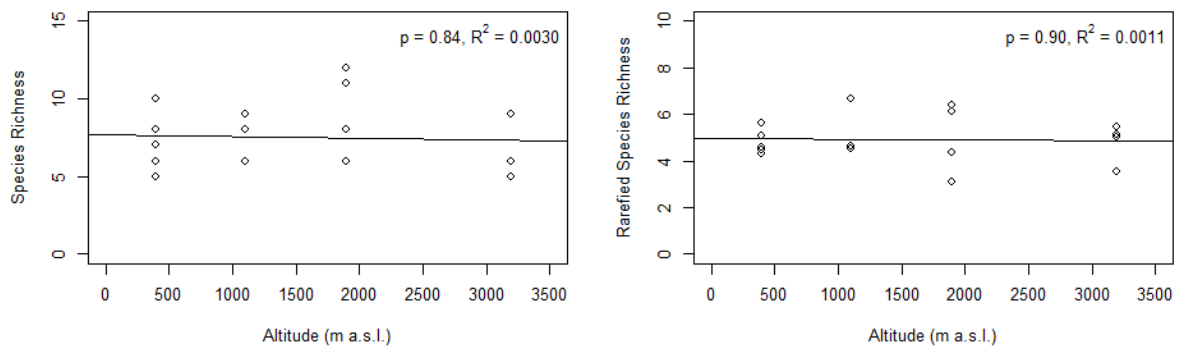
Figure 7: Regression analyses of liana species richness and rarefied species richness along the altitudinal gradient with p values and R² values.

4.2.2. Liana leaf traits

CWMs, weighted on basal area, of the liana leaf traits show important trends along the altitudinal gradient (Figure 8, Supplementary Table S5). For the SLA, LPC, LNC and δ^{15}N a significant decrease is found with altitude, $p < 0.05$, $p < 0.01$, $p < 0.05$ and $p < 0.001$ respectively. For LCC and C:P the opposite trend is found, an increase with altitude ($p < 0.05$ for both). δ^{13}C and the ratios C:N and N:P are also increasing but these regressions are not significant or marginally significant ($p = 0.57$ for δ^{13}C, $p = 0.063$ for C:N and $p = 0.088$ for N:P).
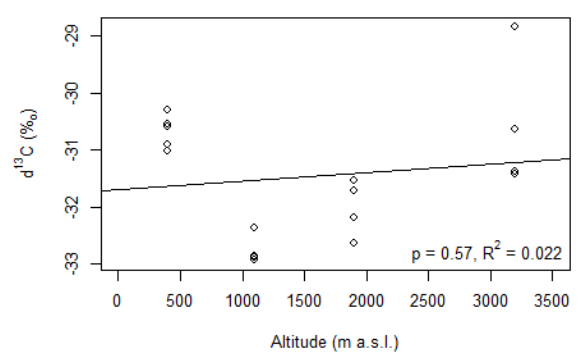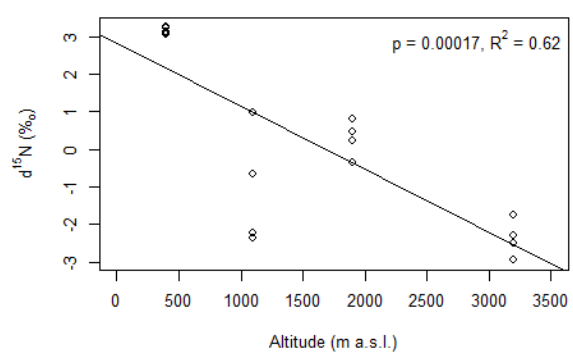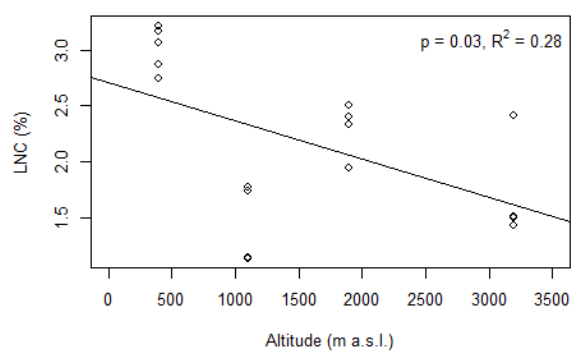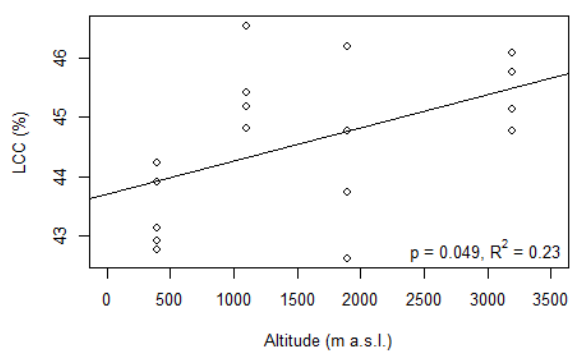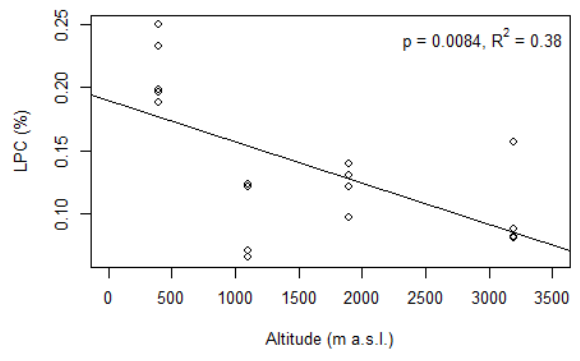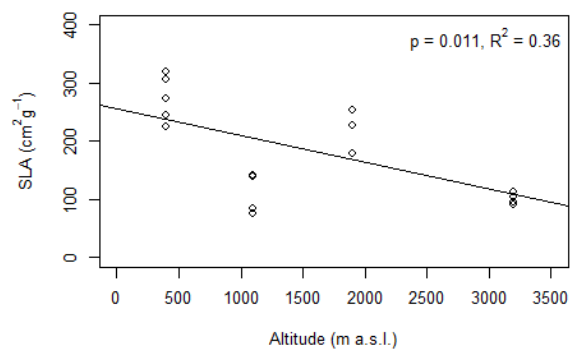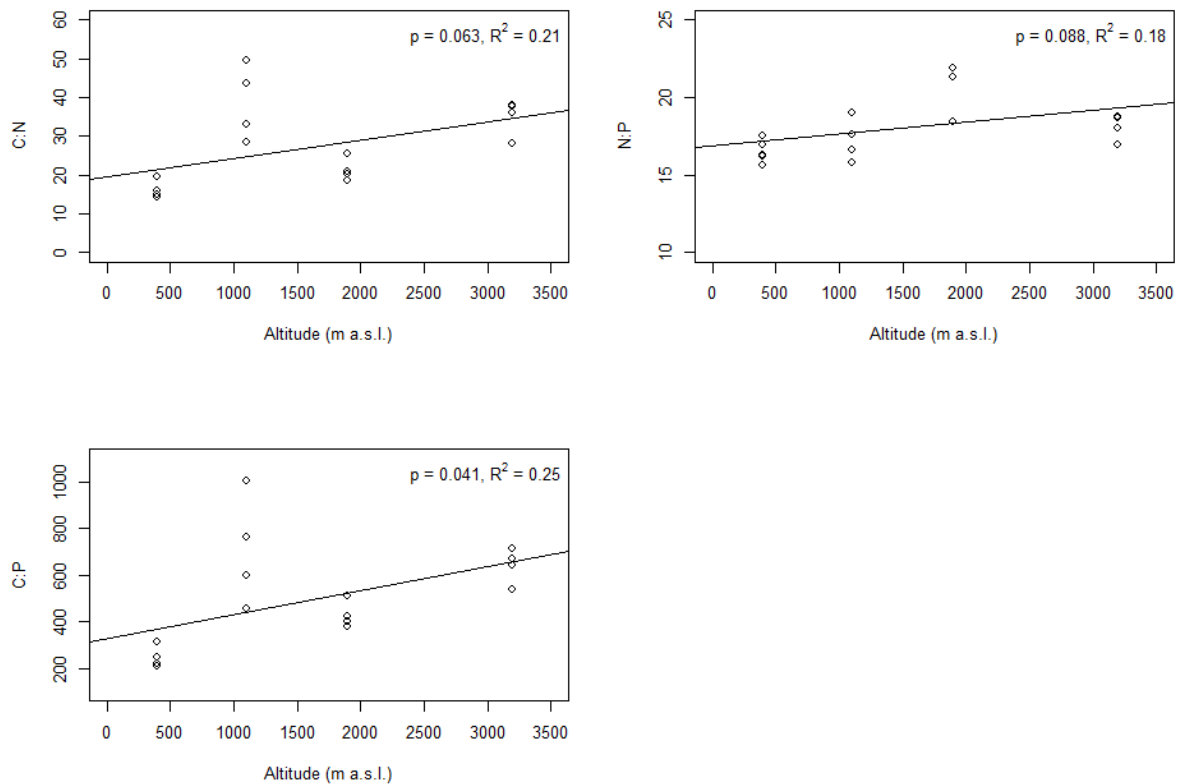
Figure 8: Community weighted means of the specific leaf area (SLA), mass-based leaf nitrogen concentration (LNC), mass-based leaf carbon concentration (LCC), mass-based leaf phosphorus concentration (LPC), the stable isotope compositions of nitrogen (δ^{15} N) and carbon (δ^{13}C), the carbon to nitrogen ratio (C:N), nitrogen to phosphorus ratio (N:P) and carbon to phosphorus ratio (C:P) in function of the altitude. Linear regressions were added together with the p values and R^2 values.

Subsequently the traits were used to execute a principal component analysis (Figure 9 and Table 7). The proportion of variation explained by the first principal component is 59%, the cumulative proportion explained by the first two components amounts 76%. The first axis is positively correlated with the SLA, leaf nitrogen concentration and leaf phosphorus concentration and negatively with the ratios carbon to phosphorus and carbon to nitrogen. The second axis reflects δ^{13}C (a negative correlation) and the ratio of nitrogen to phosphorus (a positive correlation).
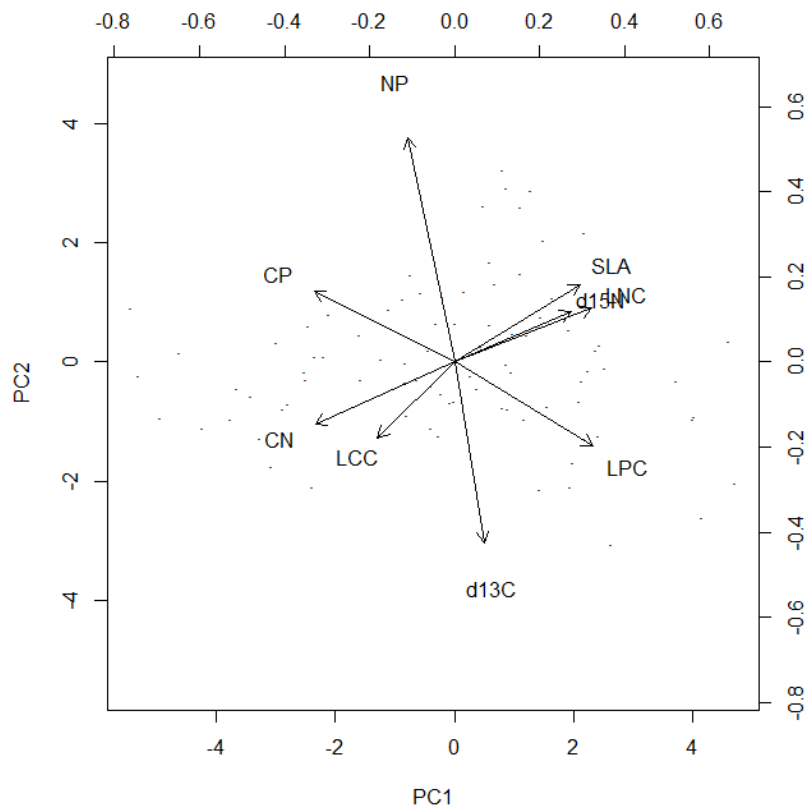
Figure 9: PCA biplot based on the 9 liana leaf traits collected during the fieldwork: the specific leaf area (SLA), mass-based leaf nitrogen content (LNC), mass-based leaf phosphorus content (LPC), mass-based leaf carbon content (LCC), stable carbon isotope composition ($\delta^{13}C$), stable nitrogen isotope composition ($\delta^{15}N$), carbon to nitrogen ratio (C:N), nitrogen to phosphorus ratio (N:P) and carbon to phosphorus ratio (C:P).

Table 7: Summary of the principal component analysis of the 9 different liana leaf traits: mass-based leaf nitrogen content (LNC), mass-based leaf carbon content (LCC), mass-based leaf phosphorus content (LPC), carbon to nitrogen ratio (C:N), nitrogen to phosphorus ratio (N:P), carbon to phosphorus ratio (C:P), stable carbon isotope composition ($\delta^{13}C$), stable nitrogen isotope composition ($\delta^{15}N$) and specific leaf area (SLA). Only principal components with eigenvalues > 1 were retained.

	PC1	PC2
LNC	**0.40**	0.16
LCC	-0.23	-0.22
LPC	**0.41**	-0.25
C:N	**-0.41**	-0.18
N:P	-0.14	**0.66**
C:P	**-0.41**	0.20
$\delta^{13}C$	0.09	**-0.53**
$\delta^{15}N$	0.34	0.14
SLA	**0.37**	0.22
Standard deviation	2.31	1.24
Proportion of variance	0.59	0.17
Cumulative proportion	0.59	0.76

Finally, boxplots of the principal components in function of the altitude were constructed (Figure 10). PC1 decreases significantly along the gradient, except for stratum 2 were the mean value is similar to the average value found in stratum 4. PC2 does not show a distinct trend across the different strata.
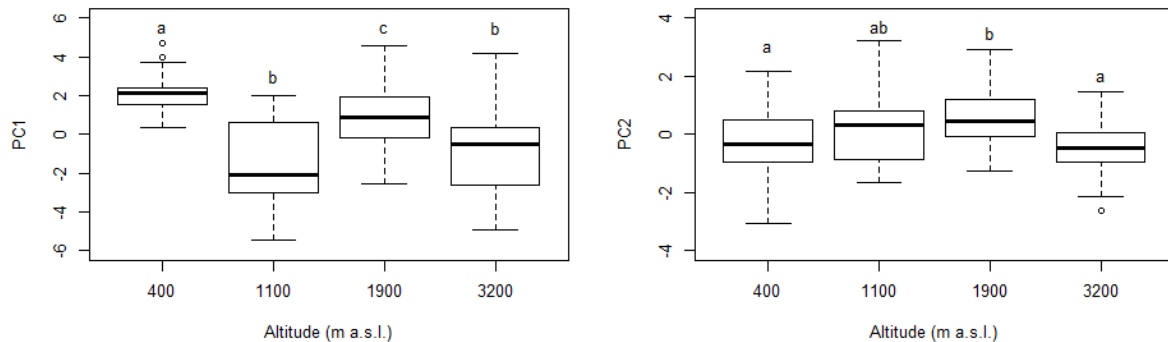
Figure 10: Boxplots of the first and second principal components (PC) in function of the altitude. Significant differences across the strata (p < 0.05) are indicated as different letters.

4.2.3. Functional diversity

Functional diversity was investigated as clarification of the functioning of lianas in the ecosystem and to be able to compare the differences in functional niches between lianas and co-occurring trees. Therefore, 9 different liana leaf traits were used, although they cannot be assessed independently as significant correlations have been found (Supplementary Table S6). Specifically, significant positive correlations were observed between SLA and LNC (p < 0.001), SLA and LPC (p < 0.001), LPC and LNC (p < 0.001), LNC and δ^{15}N (p < 0.001) and C:N and C:P (p < 0.001), while significant negative correlations were found between SLA and C:N (p < 0.001), LNC and C:N (p < 0.001), LNC and C:P (p < 0.001), δ^{15}N and C:N (p < 0.001) and C:P and δ^{15}N (p < 0.001). This was followed by the calculations of the functional diversity indices, weighted on basal area.

Functional divergence (p < 0.01) and dispersion (p < 0.05) increase significantly with altitude. Evenness stays more or less constant along the gradient (p = 0.93) and functional richness increases non-significant (p = 0.16) (Figure 11, Supplementary Table S7).
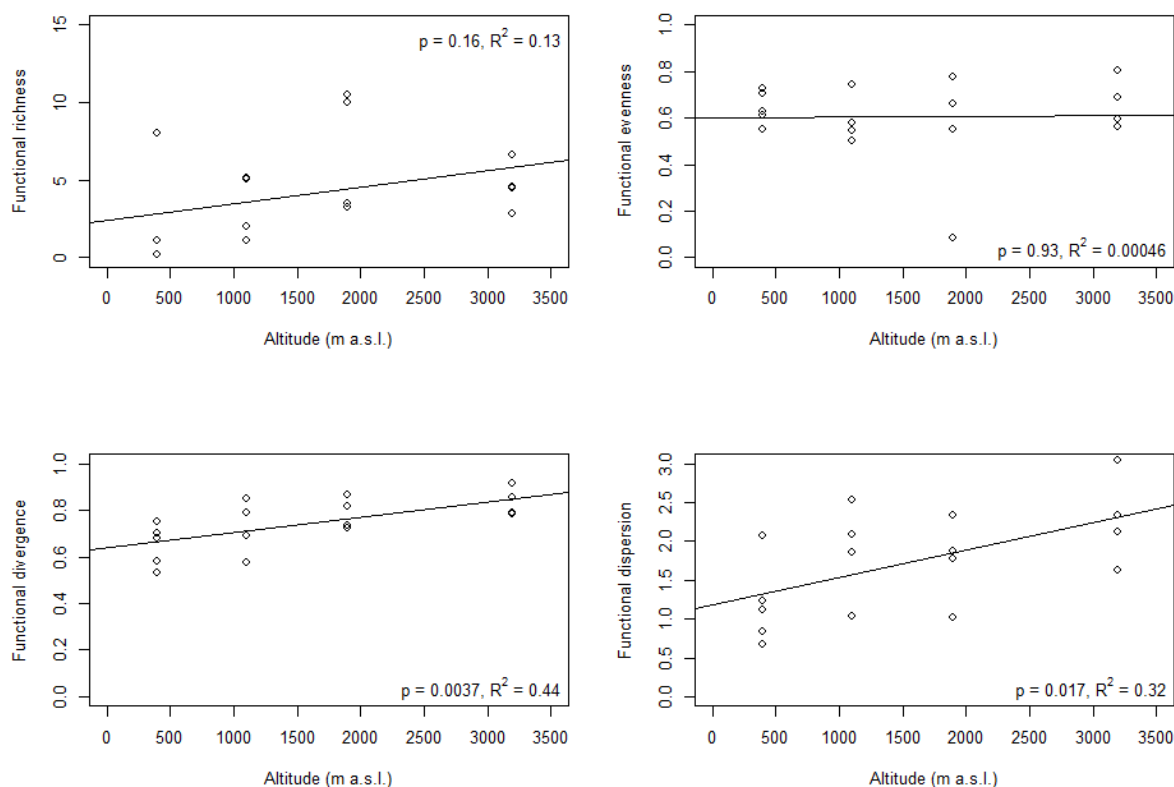
Figure 11: Linear regressions of the functional diversity indicators: functional richness, functional evenness, functional divergence and functional dispersion (including p and R^2 values) along the altitudinal transect.

4.3. Functional community structure

In a last step, the stand level functional community structure is investigated, combining trait information of both lianas and trees. Tree and liana leaf traits were compared along the altitudinal gradient (Figure 12). Most traits show similar trends for both growth forms. SLA, LNC, LPC and $\delta^{15}N$ are decreasing along the altitudinal gradient (SLA: $p < 0.001$ for lianas and $p < 0.01$ for trees; LNC: $p < 0.05$ for lianas and $p < 0.001$ for trees; LPC: $p < 0.01$ for lianas and $p < 0.001$ for trees; $\delta^{15}N$: $p < 0.001$ for both growth forms). $\delta^{13}C$ is increasing along the gradient for tree as well as for lianas ($p < 0.05$ for lianas and $p < 0.001$ for trees). The same trend is noted for C:N and C:P as well, but the increase is only marginally significant for the lianas (C:P: $p < 0.058$ for lianas and $p < 0.001$ for trees; C:N: $p = 0.099$ for lianas and $p < 0.001$ for trees). For the LCC no trend is observed for lianas ($p = 0.619$) and an increase for the trees ($p < 0.05$). Finally, also the ratio nitrogen to phosphorus shows a distinct pattern for lianas compared to trees. There is no significant trend for lianas ($p = 0.19$) while for trees the ratio decreases significantly along the gradient ($p < 0.001$).
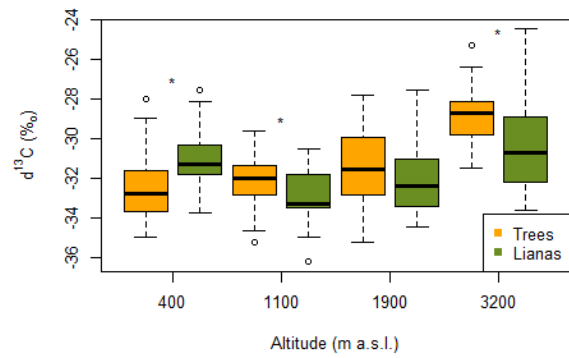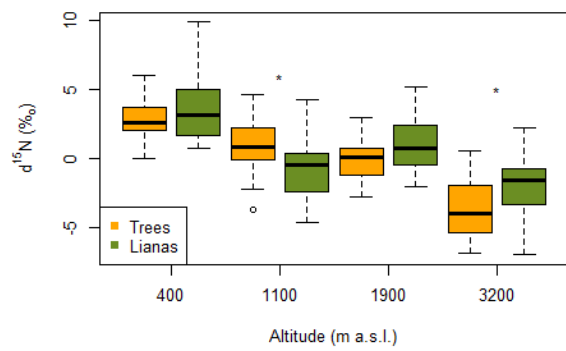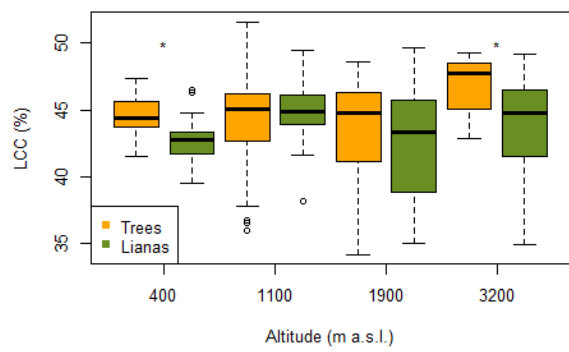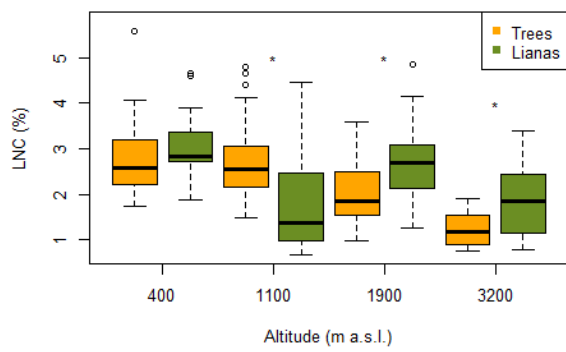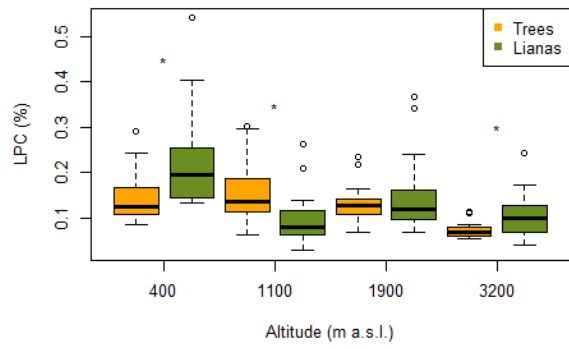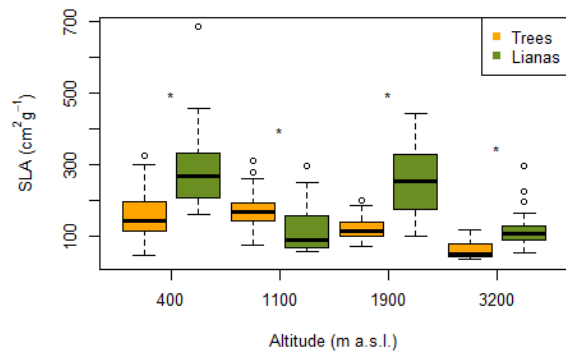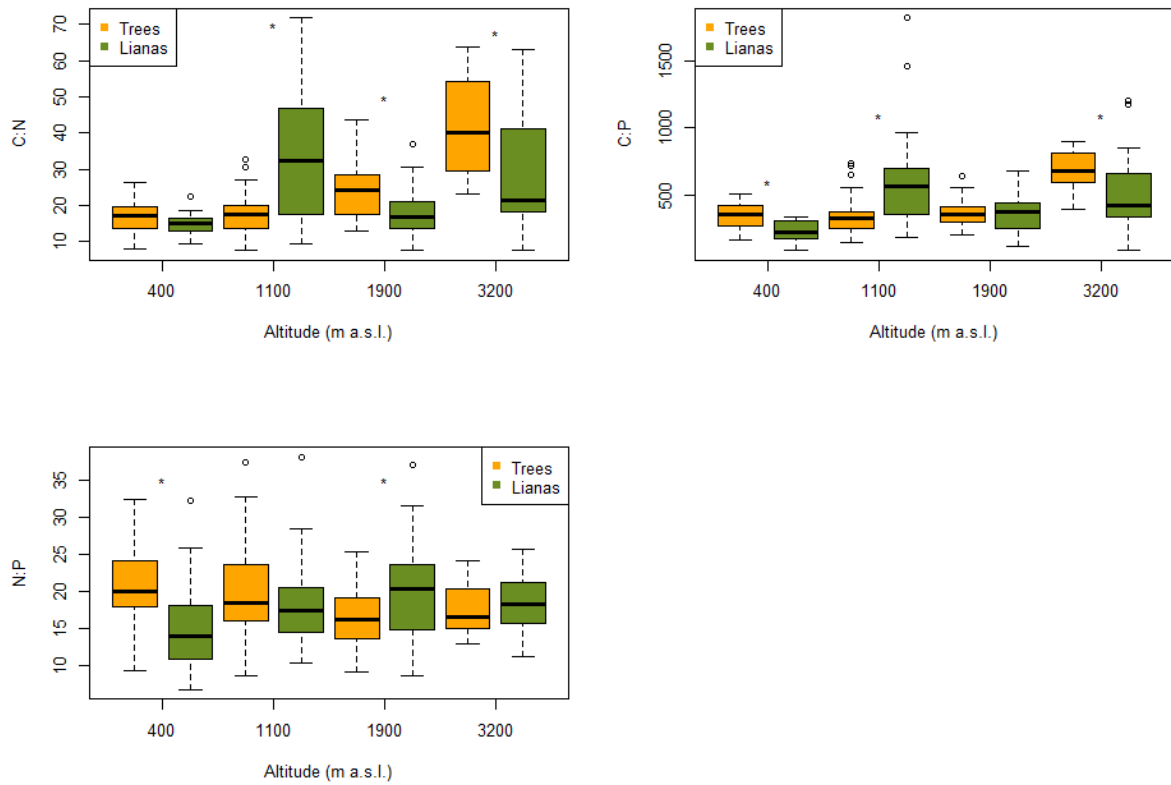
Figure 12: Boxplots of the different traits: specific leaf area (SLA), mass-based leaf phosphorus content (LPC), mass-based leaf nitrogen content (LNC), mass-based leaf carbon content (LCC), stable nitrogen isotope composition (δ^{15}N), stable carbon isotope composition (δ^{13}C), carbon to nitrogen ratio (C:N), carbon to phosphorus ratio (C:P) and nitrogen to phosphorus ratio (N:P) in function of the altitude. The values of the lianas are coloured in green, the values of the trees in orange. The asterisk stands for a significant difference (p < 0.05) between the traits of both growth forms at the same altitude.

Subsequently, a principal component analysis was performed on the combined tree and liana leaf traits (Figure 13 and Table 8). The first axis accounts for 54% of the variation and reflects the LNC and SLA (a positive relationship) and the C:P and C:N ratio (both a negative correlation). The second one explains 19% of the variation and reflects mainly the ratio N:P (a positive correlation).
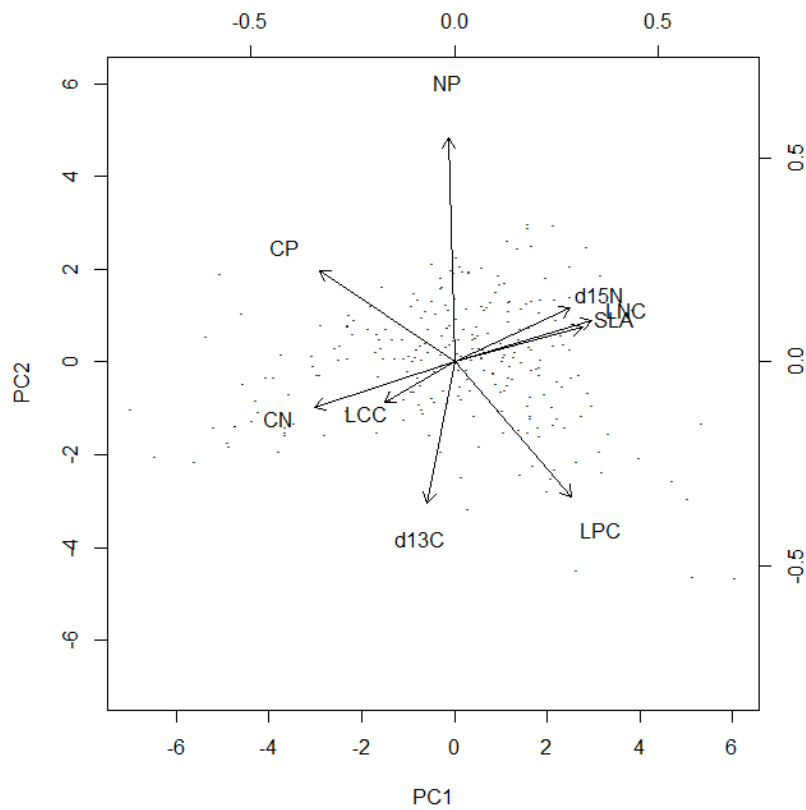
Figure 13: PCA biplot of all common collected leaf traits of lianas and trees: specific leaf area (SLA), mass-based leaf carbon content (LCC), mass-based leaf nitrogen content (LNC), mass-based leaf phosphorus content (LPC), carbon to nitrogen ratio (C:N), carbon to phosphorus ratio (C:P), nitrogen to phosphorus ratio (N:P), stable carbon isotope composition (δ^{13}C) and stable nitrogen isotope composition (δ^{15}N).

Table 8: Summary of the PCA of all common liana and tree leaf traits: specific leaf area (SLA), mass-based leaf carbon content (LCC), mass-based leaf nitrogen content (LNC), mass-based leaf phosphorus content (LPC), carbon to nitrogen ratio (C:N), carbon to phosphorus ratio (C:P), nitrogen to phosphorus ratio (N:P), stable carbon isotope composition (δ^{13}C) and stable nitrogen isotope composition (δ^{15}N). Only the principal components with an eigenvalue > 1 were retained.

	PC1	PC2
SLA	**0.39**	0.11
LPC	0.36	**-0.41**
LNC	**0.42**	0.13
δ^{15}N	0.35	0.17
LCC	-0.22	-0.13
δ^{13}C	-0.08	**-0.43**
C:N	**-0.43**	-0.14
C:P	**-0.42**	0.28
N:P	-0.02	**0.69**
Standard deviation	2.21	1.31
Proportion of variance	0.54	0.19
Cumulative proportion	0.54	0.73

Boxplots of the principal components in function of the altitude were constructed (Figure 14). PC1 of both growth forms decreases with increasing altitude (p < 0.01 for lianas and p < 0.001 for trees) while PC2 does not show a distinct trend for lianas (p = 0.31) but decreases for the trees (p < 0.001). The average values of PC1 are significantly different at every altitude for both growth forms. For PC2 this is also the case except for stratum 2. To end, Pearson correlations of leaf traits and soil properties were calculated (Supplementary Table S8). Strong and significant negative correlations were found between the liana leaf traits SLA, LPC, δ^{15}N and LNC and the soil properties Al, K, N, δ^{13}C, C and C:N. Strong and significant positive correlations were discovered between the same liana leaf traits and soil δ^{15}N and also between liana LCC and δ^{13}C and Al, K, N, δ^{13}C, C and C:N. Tree leaf traits were mainly strongly correlated with soil δ^{15}N and soil C:N.
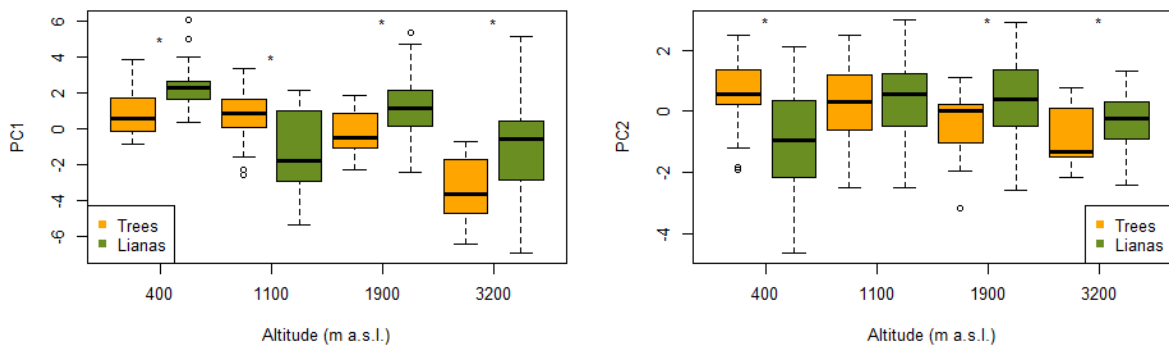
Figure 14: Boxplots of the principal components (PC) in function of the altitude. The asterisk stands for a significant difference (p < 0.05) between the PCs of both growth forms at the same altitude.

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5. Discussion

In this research, we investigated how the liana community structure, diversity and trait composition vary along an altitudinal gradient in northern Ecuador. We have not found a shift in liana density, but there is a significant decrease in liana diameter and a marginally significant decrease in liana biomass and basal area with increasing altitude. No trends are observed for species richness, rarefied species richness or other species diversity indicators. Two measures of functional diversity, namely FDis and FDiv do show an increasing trend with increasing altitude, while no trend is observed for FRic and FEve. For both lianas and trees there is a shift towards a more conservative strategy along the gradient with mostly a significant difference between the two growth forms at each stratum. This study therefore provides important insights as one of the (currently) few studies on lianas along altitudinal gradients (Balfour and Bond, 1993; Parthasarathy *et al.*, 2004; Homeier *et al.*, 2010; Alves *et al.*, 2012; Asner and Martin, 2015; Fadrique and Homeier, 2016).

5.1. Liana community structure along the altitudinal gradient

Liana diameter decreases significantly along the altitudinal gradient. A decrease in liana diameter with elevation is also found in the investigation of Homeier *et al.* (2010) and Fadrique and Homeier (2016). Further, small lianas are more abundant than large lianas. Namely, approximately 50% of the lianas is situated in the diameter class 2-3 cm and also the proportion of small climbers increases with altitude, equivalent to the observations of Homeier *et al.* (2010).

On the contrary, no trend is found in liana stem density along the altitudinal gradient. These results match with the results of the investigation of Homeier *et al.* (2010) where liana density did not show a significant decreasing trend with elevation as previously found by Parthasarathy *et al.* (2004). Later Fadrique and Homeier (2016) found a similar liana density at an altitude of 1,000 m and 2,000 m but a strong decrease in liana density at 3,000 m a.s.l. Although the decrease would not be significant in our case, the average liana density at 3,200 m is only half of the average density at 1,900 m a.s.l. Furthermore, the mean liana density peaks (non-significantly) at an altitude of 1,900 m, a similar elevation as the peak in liana density in the investigation of Homeier *et al.* (2010), namely 2,000 m a.s.l. The average liana density in this census amounts 252 ± 85 individuals (≥ 2 cm diameter) ha^{-1}. A lower value than found in other liana inventories along altitudinal gradients in South America: 573 individuals (≥ 1 cm diameter) ha^{-1} (Alves *et al.*, 2012), 458 lianas (≥ 1 cm diameter) ha^{-1} (Fadrique and Homeier, 2016) and 1,403 lianas (≥ 1 cm diameter) ha^{-1} (Homeier *et al.*, 2010). However, by accounting for the difference in minimum diameter cut-off, values are more or less similar. Specifically, Parthasarathy *et al.* (2004) showed that liana abundance increased by 22% up to 71% when the diameter threshold was lowered from 2 to 1 cm and Burnham (2004) found an increase of 31% when she included lianas with a minimum diameter of 1 cm instead of 2 cm. Furthermore, different environmental conditions, forest types and the disturbance history can contribute to the variation found across sites (Parthasarathy *et al.*, 2004; Alves *et al.*, 2012). We do find a high variation in liana density between the plots, from a minimum of 69 individuals ha^{-1} to a maximum of 581 individuals ha^{-1}. The strong variation at plot level is possibly a consequence of the small plot size combined with the clumped spatial distribution of lianas (Ledo and Schnitzer, 2014). Namely, lianas can reproduce vegetatively and especially after disturbance clonal reproduction occurs in the neighbourhood of a conspecific stem and leads towards a clumped distribution of the lianas and thus a positive density dependence for most of the lianas. Also Alves *et al.* (2012) found a strongly clumped spatial distribution along an altitudinal gradient in Brazil. However, they also suggest to look at the past canopy disturbance as another factor influencing the liana distribution. Unfortunately, we don't possess data

related to past canopy disturbance and although there were signs of disturbance, e.g. treefall, we did not characterise these current gaps.

Several factors are quoted as possible drivers of liana density distribution. Alves *et al.* (2012) propose, as mentioned before, the past canopy disturbance and also the minimum temperature as variables explaining the abundance of lianas. Homeier *et al.* (2010) and Balfour and Bond (1993) prefer to look at the available host structure as a predictor of liana abundance and according to Parthasarathy *et al.* (2004) the forest stature could also influence liana density. Tree density does not change significantly along our gradient but tree height decreases and the trees are further also larger in diameter at the highest altitude (Bruneel, 2016). More specific, total tree basal area increases along the gradient and might drive the variation in liana density as thicker trees are mostly older, have had more time to gather lianas and have a more favourable canopy position (Malizia and Grau, 2006; Homeier *et al.* 2010). However, in our investigation no correlations between liana density and tree density, tree basal area or canopy height were found. Furthermore Homeier *et al.* (2010) also found a positive correlation between liana density and the soil Ca concentration in addition to a negative correlation between liana density and exchangeable Al. Also a great part of the variation in liana abundance was explained by the soil C:N ratio in multiple regression analysis. In this study, soil C:N increases significantly from a value of 12 towards a value of 18 along the transect and indicates a decrease in N availability. Further $\delta^{15}N$ in the soil, litter and the leaves of trees and lianas decreases which denotes a lower rate of N mineralization (Bruneel, 2016). Al is significantly higher in the highest stratum and Ca concentrations in the soil are the highest in the third stratum. However, none of these soil properties correlates significantly with liana density in our liana census and thus results of Homeier *et al.* (2010) cannot be confirmed. Finally, Malizia *et al.* (2010) found a high positive correlation between P and liana abundance. Along the altitudinal gradient, the P concentration in the soil did not show a significant pattern and showed a negative marginally significant correlation (p = 0.09) with the liana abundance in our investigation. The influence of soil nutrients on liana density remains unclear and a major point of discussion as opposing results are found in multiple liana inventories (Putz and Chai, 1987; Laurance *et al.,* 2001; DeWalt and Chave, 2004; van der Heijden and Philips, 2008; Malizia *et al.*, 2010)

Liana abundance is also positively correlated with dry season length and negatively with the mean annual precipitation (Schnitzer, 2005). Precipitation decreases along the altitudinal gradient and could thus benefit the lianas but no correlation was found between those variables. We should keep in mind that the precipitation data was derived from the WorldClim database and is not that accurate for our region with strong variations in topography. The values represent the average rainfall between 1960 and 1990 and do not take into account the strong local variability in the mountainous area as they are not measured in situ. Furthermore, also fog, mist and clouds, important components of tropical cloud forests, may influence the water availability (Bubb *et al.,* 2004). At last, temperature remains the factor most often reported as a driver of a decreasing liana abundance with altitude (Jiménez-Castillo *et al.,* 2007; Alves *et al.,* 2012; Fadrique and Homeier, 2016). This is related to the wide and large vessels of lianas which are vulnerable to embolism caused by freezing temperatures (Ewers, 1985). According to the investigation of Jiménez-Castillo *et al.* (2007) lianas are more temperature sensitive than trees and shrubs as their relative proportion decreases the fastest along an elevational and latitudinal gradient. The temperature along our gradient decreases from a MAT of 23.8°C in the lowest stratum towards a MAT of 11.2°C at the highest altitude but is uncorrelated with liana abundance. The altitudinal gradient and investigated range in precipitation and temperature have not caused a gradient in liana density. But the occurrence of large lianas and the decrease in diameter can be linked with the altitude and decreasing temperature and rainfall. A strong significant correlation is found between liana diameter and abiotic variables strongly linked with the altitude such as MAP and MAT. Further we found also a positive correlation between liana diameter and canopy height and a negative correlation between

liana diameter and tree basal area, soil $\delta^{15}N$ and the soil C:N ratio. Indicating a decrease in diameter because of a reduction in available soil N.

When plotting the average liana basal area and biomass of the different plots, we find a marginally significant decrease in liana biomass and basal area between 400 and 3,200 metre resulting from a decrease in liana diameter but a more or less constant density of lianas. Average liana basal area is identical for stratum 1 and 3 and further there are no significant differences in basal area across the elevational gradient, comparable to the results of Homeier *et al.* (2010). For liana biomass, a similar non-significant trend is also found by Fadrique and Homeier (2016), namely a reduction of 0.18 Mg ha^{-1} with every 100 m gain in elevation. In our census, the biomass decreases with 0.09 Mg ha^{-1} every increase of 100 m but our liana density and biomass were also lower.

5.2. Species diversity along the altitudinal gradient

Species richness does not show a distinct trend across the elevational gradient. However, we must take into account that a fraction of the individuals was not identified, potentially influencing our results. Further, species richness is also limited by our sample size. From the rarefaction curve we can deduce that species richness will increase as sample size increases. Also rarefied species richness and other diversity indices (Shannon diversity, Simpson diversity, alpha diversity and evenness) do not show a trend along the altitudinal gradient. Some authors find a decrease in liana diversity with elevation (Gentry, 1991; Lieberman *et al.,* 1996). Further, in the investigation of Parthasarathy *et al.* (2004) liana diversity decreased along the gradient but was the highest around 600-700 m, probably influenced by the altitude and the canopy height. Although they assume to find other correlations with rainfall and seasonality as well. Indeed, van der Heijden and Phillips (2009a) found a positive correlation between MAP and species richness in the Neotropics. Based on this information we would expect a decrease in richness along our gradient as MAP decreases. However, precipitation data is not completely reliable as we discussed before. Furthermore, we proportionally have more unidentified individuals in the lowest strata of our dataset (15%, 12.4%, 6.4% and 1.8% in stratum 1, stratum 2, stratum 3 and stratum 4 respectively), so we might find a higher species richness in the lower strata but this can't be proved. That we still find a high species richness in the highest stratum is not unusual in Ecuador, even up to 10% of the species here is bound to altitudes beyond 3,000 m a.s.l. and thus still a lot of the Ecuadorian species are found high in the Andes (Balslev, 1988). In 2016, Demol investigated tree species richness in the same permanent sample plots. He found a significantly higher rarefied species richness at 1,100 and 1,900 m a.s.l. Additionally, based on his data we can deduce that lianas are responsible for 16-26,7% of the woody species richness along the altitudinal gradient, which is in line with global liana diversity studies by Gentry (1985, 1991) (19-23%) and Schnitzer *et al.* (2012) (35%).

The majority of the species discovered along the transect are site/stratum specific, with only two species occurring in more than one stratum. This might indicate that the liana species composition is strongly driven by the environment (de Oliveira *et al.,* 2014). The species showing a wider ecological amplitude, namely, *Clusia sp 1* and *Serjania sp 1*, occur in the lower strata, respectively stratum 1, 2 and 3 and stratum 1 and 2. Both species are dominant in stratum 2 but only occur in small amounts in the other strata. This might indicate that stratum 1 and 3 are more or less the outer ranges of their desired habitat. Unfortunately, we could not investigate if these species also showed a significant shift in trait values along the gradient as generally observed (and discussed in the following sections) as we only sampled *Clusia sp 1* in stratum 2 and only had 4 samples of *Serjania sp* 1 (3 in stratum 2 and 1 in stratum 1). The trait values of *Clusia sp 1* do not show strong intra-specific variability and approach the

average trait values of stratum 2 while for *Serjania sp 1* the sample in stratum 1 had an extreme low N content in comparison with the average LNC in stratum 1. Conversely, the samples in stratum 2 had extreme high N concentrations in comparison with the mean LNC in stratum 2. Probably the distribution of a species is co-determined by its functional identity and plasticity in trait values. Although we notice intra-specific variation in trait values, we do not possess enough samples to investigate the amplitude in trait values of the different species. Further, most of the lianas (> 50% in each stratum) belong to the top 3 most abundant species of the stratum while approximately 35% of the species are represented by only one individual along the gradient. This high number of rare liana species could potentially be influenced by the small plot size. However, also Parthasarathy *et al.* (2004) found similar patterns with most of the liana species occurring in low numbers and being site specific along an altitudinal gradient in India. Furthermore, we find that the top ten most abundant species accounts for 58% of the identified individuals, which is more than the 48% found in the census of Schnitzer *et al.* (2012) here also the amount of species represented by 1 individual was lower, namely 5% of all species. So, we have a small number of really dominant species and a high number of rare species, a common pattern in ecology (MgGill *et al.,* 2007).

5.3. Liana functional diversity along the altitudinal gradient

5.3.1. Liana leaf traits

Most of the community weighted means of the different liana leaf traits show a significant shift in average value along the altitudinal gradient. But also between different liana species in the same stratum or even within individuals of the same species, traits can vary strongly. A high variation of traits within a growth form is not unusual and also noticed by Santiago and Wright (2007) and Poorter and Bongers (2006) in co-existing trees. The combinations of traits might lead towards a stable mixture of strategies, a continuum along the leaf economic spectrum (Westoby *et al.,* 2002; Poorter and Bongers, 2006).

The community weighted mean of the specific leaf area decreases significantly along the altitudinal gradient. We found the lowest values in stratum 4, significantly different from those in stratum 1 and 3. So there is a shift along the gradient towards thicker liana leaves (Cornelissen *et al.,* 2003) higher in the Andes. This decrease in SLA is probably resulting from an adaptation of the lianas to the harsher conditions at the higher elevational levels, where it is colder and drier and the soil mineralization rate is reduced. Multiple studies have already shown a lower SLA in areas with a limited precipitation (Niinemets, 2001; Wright *et al.,* 2002; Wright *et al.,* 2005). This decreasing trend in SLA is also observed by Asner and Martin (2015) in the Peruvian Amazon.

The SLA is strongly correlated with the nitrogen and phosphorus concentration in the liana leaves. Such high pairwise correlations between leaf traits are also found worldwide, forming the leaf economic spectrum (Wright *et al.,* 2004). Just as for the SLA, both the community weighted means of LNC and LPC decrease significantly along the gradient. Furthermore, we also find an increase in the CWM of LCC. These are all indications that at higher altitude we enter a less productive area and shift towards a more conservative strategy (Coley *et al.,* 1985; Wright *et al.,* 2004). However, interpretation on nutrient limitation and how this affects the liana community is not that straightforward. The average leaf N:P values, fluctuating between 16.52 and 20.73, indicate that P limitation increases marginally significant with altitude, with the highest leaf N:P values at 1,900 m a.s.l. (Koerselman and Meuleman, 1996; Cornelissen *et al.,* 2003). This is not reflected in the soil nutrients as phosphorus does not show a significant trend along the altitudinal gradient (Bruneel, 2016). Bio-available phosphorus does

increase from 400 to 1,900 m a.s.l but drops at an altitude of 3,200 m a.s.l. (Bruneel, 2016). This decrease and thus also the limited availability of phosphorus for lianas is possibly a consequence of the immobilization of phosphorus in the Andosols, which are known to have a high P retention trough the formation of aluminium phosphates and other secondary minerals (Nanzyo, 2002). Indeed, we see also an increase in the Al concentration along the gradient and find strong negative correlations between Al and the CWM of liana leaf traits such as SLA, LNC and LPC, indicating a negative impact of Al. Also soil N increases along the transect but because of a decrease in the mineralization rate limited by the temperature it is probably not all available for the vegetation (Bruneel, 2016; Moser *et al.* 2011). This can be deduced from the positive correlation between the CWM of liana leaf traits such as SLA, LNC and LPC and soil $\delta^{15}N$ and a decrease in LNC in the liana leaves at higher altitudes. Furthermore, we also find a sharp decrease in liana leaf $\delta^{15}N$, also an indication of a lack in N availability at higher altitudes. Namely, plant material enriched in $\delta^{15}N$ is linked to a high nitrification rate (Pardo *et al.,* 2006). The CWM of liana leaf C:P rises significantly and the CWM of liana leaf C:N rises marginally significant along the gradient, so there is a higher uptake of carbon per unit of phosphorus and per unit of nitrogen higher on the mountain. Reflected in an increase in the CWM of LCC and a decrease in the CWM of LNC and LPC as the nutrients become more limiting. So the decrease in CWM of SLA, LPC and LNC with elevation is probably driven by the nutrient availability of the stratum (Cornelissen *et al.* 2003). The high nutrient concentrations in the leaves in the lower strata are indicators of an efficient resource acquisition, while higher on the mountain species with a lower nutrient concentration are probably able to cope better with the reduced nutrient supply (Wright *et al.,* 2004). A faster turnover would be too costly over here (Reich *et al.,* 2014).

Overall, these shifts in trait values along the altitudinal gradient indicate a shift from the quick return end of the leaf economic spectrum to the slow return on investment strategy at higher altitudes. Namely, liana leaves with a high SLA and high nutrient concentrations in stratum 1 towards leaves with a significant lower SLA and nutrient concentrations at 3,200 m a.s.l. At higher altitudes, there is a higher carbon investment per unit and thus a denser leaf tissue and a longer leaf nutrients resistance time (Westoby *et al.* 2002, Wright *et al.* 2004). So they focus more on survival and defence as high growth rates are probably impeded by environmental restrictions. While the liana species in lower altitudes invest in fast growth comparable to pioneer tree species (Wright *et al.,* 2004; Poorter and Bongers, 2006). Along the gradient there is thus a shift in the liana community composition probably resulting from environmental filtering (Fortunel *et al.,* 2014).

For the CWM of the stable carbon isotope composition, $\delta^{13}C$, no trend along the gradient is observed. $\delta^{13}C$ is a proxy for the water use efficiency (WUE) or the ratio of CO_2 accumulation on stomatal conductance (Farquhar and Richards, 1984). The values of $\delta^{13}C$ coincide with those of Cai *et al.* (2009b) only our sampled range is bit larger but their investigation included only 18 liana species. As no trend is observed we assume a more or less similar WUE across the gradient and no stronger limitations on water supply for lianas at higher altitudes than closer to sea level.

5.3.2. **Functional diversity**

Investigating shifts in functional diversity indices across the strata informs us on the variability of liana traits occurring and therefore also the occupation of the niche space in these different environments. A first index, functional evenness, does not show a pattern along the altitudinal gradient. So in every stratum we find more or less the same regularity in the abundance distribution across the trait space (Mason *et al.,* 2005). Secondly, functional richness stays more or less constant across the gradient as well. In stratum 3 we have two plots with a higher functional richness, which indicates that the lianas occupy a larger functional niche over here (Villéger *et al.* 2008). This higher variety of traits might result from a higher amount of samples taken in the higher strata in combination with the higher species

richness found in these plots as well (Supplementary Table S3). Species richness can influence functional richness if the extra species fulfil different functions and are not possessing similar traits (Diaz and Cabido, 2001). As there is no significant difference in functional richness across the elevational gradient we might assume that both in the harsh and more favourable conditions in our census the occupation of the functional niche is equal (Westoby *et al.,* 2002). The wide variety of trait values in tougher conditions can be related to microvariation within sites creating different opportunities for different species (Westoby *et al.,* 2002) or might be a consequence of partitioning of resources whereby the different liana species specialize on other resources (Schnitzer and Carson, 2001, 2010). Also disturbance may play a role as it keeps liana density and diversity high (Schnitzer and Carson, 2001; Ledo and Schnitzer, 2014). As no decrease in liana density or species richness is reported along our gradient we might assume that also disturbance has an influence along the transect keeping liana abundance high at higher altitudes. Consequently, if both liana density and species richness are kept high this might also maintain a high functional richness along our gradient. Functional richness might even be underestimated in this census as sample size was small and the amount of rare species probably would increase with increasing sample size. Further we lack samples from a lot of rare and unidentified species as well. Hence, we are not able to make clear assumptions about the trend and the reason behind it. For functional dispersal and divergence there was a significant linear increase across the different strata with the highest values found in stratum 4. An increase in divergence is probably resulting from the extreme trait values of the more abundant species. Indeed, in stratum 4 *Maclenia macrantha* (Ericaceae) had very low values for SLA, LNC and LPC compared to the average values in that stratum determined especially by the two other abundant families (the Asteraceae and the Smilaceae) with high values for SLA, LNC and LPC. Conversely, for the trees along the same gradient functional richness and dispersion decrease with altitude while functional divergence shows a similar trend as for the lianas, an increase with increasing altitude (Demol, 2016). Apparently, the higher altitudes and the associated harsher conditions such as a decrease in MAT, MAP and mineralization rate, seem to affect the functional niche of trees stronger, with a reduction in niche occupation as a result. A possible hypothesis is that the environment is less restrictive for lianas, for instance they are able to cope better with a reduction in precipitation (Schnitzer, 2005) and so they might be able to profit from the vacant niche space. Hence, probably habitat filtering reduces the trait space of trees while lianas are able to increase their trait space as a result of niche differentiation (Schoener, 1974; Weiher *et al.,* 1998)

5.4. Functional community structure of the forest along the altitudinal gradient

Along the altitudinal gradient, for most traits comparable trends are observed for lianas and trees. Moreover, significant differences are found between the growth forms within the same strata, indicating that trees and lianas use different functional niches.

The SLA of both growth forms decreases significantly along the altitudinal gradient. The SLA was significantly higher for lianas compared to trees. These results are in line with the results of Sanchez-Azofeifa *et al.* (2009), Cai *et al.* (2009b), Asner and Martin (2012) and Gallagher and Leishman (2012b). However, stratum 2 shows a divergent pattern, with a higher SLA for the co-occurring trees. As expected (Wright *et al.,* 2004) a similar trend is noticed in the nutrient concentrations of the leaves, a decrease in LNC and LPC with generally higher values for lianas. A higher LPC and LNC in liana leaves compared to co-occurring trees is also found by Zhu and Cao (2009), Asner and Martin (2012) and Gallagher and Leishman (2012b). Again, stratum 2 follows the opposite trend, here LPC and LNC are significantly higher in tree leaves. We suggest some possible reasons for this reversal in trait values in stratum 2. According to Moser *et al.* (2007), soil nitrogen is the most important driver of the LNC. The

drop in liana LNC might result from a decrease in soil $\delta^{15}N$ compared with stratum 1 and a reduction in soil N, indeed total N in the upper 30 cm of the soils would be the lowest in this stratum. Additionally, this nitrogen limitation is also reflected in the C:N ratio, as nitrogen becomes scarcer the ratio C:N rises. C:N is significantly higher in liana leaves compared with tree leaves in stratum 2 and further $\delta^{15}N$ is significantly lower, indicating a higher limitation of N for the lianas. Perhaps more trees possess mechanisms helping them to cope with low nitrogen availability such as N fixation. We could indeed detect that 2 tree species belonging to the Fabaceae occurred in the top ten of the most abundant species in this stratum. However, these results are not in line with the results of the investigation of Asner and Martin (2015), they evinced a higher investment in foliar chemicals for lianas compared to trees if the soil was low in available N. A second assumption is a possible role of potassium and soil $\delta^{13}C$. In stratum 2 potassium and $\delta^{13}C$ concentrations are significantly lower than in the other strata. Further both have a strong, correlation with the liana leaf traits (SLA, LNC, LPC and $\delta^{15}N$) but not with tree leaf traits, further research is necessary to make conclusions. In addition, this apparent reversal in strategy might be the consequence of a higher proportion of pioneer tree species present in this stratum. Pioneer tree species are situated at the quick return end of the LES and thus possess a high SLA and high leaf nutrient concentrations. Furthermore, Asner and Martin (2012) also report that differences in chemical allocation between trees and lianas are influenced by the climate, with the highest differences found above a mean temperature of 25°C and beneath a yearly precipitation of 2,500 mm. So, the reversal in strategy might be partially influenced by the absence of extreme weather conditions in this stratum (temperature is below 25°C and precipitation above 2,500 mm) leading already to a convergence in trait values between the two growth forms and thus maybe in addition to other factors to a conversion in trait values. Finally, also soils containing less rock-derived nutrients as Ca and P could induce a convergence in trait values (Asner and Martin, 2015). The C:P ratio of lianas was significantly higher in this stratum and the ratio N:P was also high for both lianas and trees, signs of phosphorus limitation. This might thus also drive the convergence in trait values. Finally, we also want to add that the trait values calculated for the lianas in stratum 2 are only based on 17 samples, this is certainly not ideal to make strong conclusions.

Hence, it is difficult to make assumptions on the divergence and converge observed in liana and tree leaf traits. But in general, we see a divergence in traits between lianas and trees growing under the same conditions which suggest a different niche occupation. Compared to trees, lianas have generally a higher SLA and nutrient concentrations and thus rely more on the strategy of the quick return on investment while the trees along this gradient tend to be situated at the other side of the spectrum, they use a more conservative strategy. These results are in line with the results of Sanchez-Azofeifa *et al.* (2009), Zhu and Cao (2010) and Collins *et al.* (2016). The trend is also confirmed by the significant differences observed between the PCs of both growth forms. A possible cause of the shift in traits between lianas and co-occurring trees is that lianas don't need to invest so much resources in their structural support and can allocate more nutrients in growth and resource acquisition (Putz, 1983; Ewers *et al.,* 2015).

$\delta^{13}C$ increases significantly along the gradient for trees but not for lianas, so the shift towards a higher WUE is more significant and stronger in trees than lianas. Further the average value of $\delta^{13}C$ per stratum is generally lower for the lianas except in stratum 1. This indicates that lianas don't use water more efficient than trees or would not have an advantage in drier periods, results also encountered by Asner and Martin (2012).

For the nitrogen isotope ratio, $\delta^{15}N$, we find a similar trend for lianas and trees, a significant decrease which indicates a reduction in available N. The ratios C:N and C:P rise along the elevation gradient for

trees and similarly also for lianas (but here the increase is only marginally significant). However, different trends are visualized for the ratio N:P. No significant trend is observed for the lianas while we find a significant decrease for the trees. So, for the trees there is a shift from phosphorus limitation in the lowlands towards nitrogen limitation at higher altitudes, while for lianas phosphorus stays the limiting nutrient. A possible cause of the variation in nutrient limitation can be a different strategy and thus also a different efficiency in the uptake of nutrients as P (Hättenschwiler *et al.,* 2008). Further we also noticed that the CWM of the liana leaf traits (SLA, LNC, LPC, δ^{15}N and N:P) are significantly correlated with the Al concentration in the soil, while this is not the case for the leaf traits of the trees. This might indicate that lianas are more sensitive to the severe effects of Al toxicity and thus suffer harder form the phosphate retention in the soil, leading towards a stronger P limitation for lianas in comparison with trees. Alternatively, trees might possess mechanisms to exclude or detoxify the Al, making them more resistant against aluminium toxicity (Barcélo and Poschenrieder, 2002).

We can assume that lianas and trees use different strategies but for both growth forms we see a clear significant shift in the mean trait values along the altitudinal gradient. So, the whole community changes towards a slower return on investment, a more conservative strategy higher in the mountains probably driven by environmental filtering as temperature, soil fertility and precipitation change along the gradient (Fortunel *et al.,* 2014).

6. Conclusion

The decrease in temperature and precipitation along our gradient impact directly but also indirectly, as a result of a reduction in N mineralization rate and decomposition, the liana community structure and the liana leaf traits. However, it is still difficult to pinpoint which abiotic or biotic factors are responsible for the observed trends along our altitudinal gradient as several complex ecological processes and interactions affect the different variables.

We show a clear decrease in liana diameter and a marginal significant decrease in liana biomass and basal area along the altitudinal gradient, attributed especially to the decrease in temperature in combination with the sensitivity of lianas to freezing induced embolism (Ewers, 1985). Although we also found a significant negative correlation between liana diameter, liana biomass and liana basal area and the soil C:N ratio and a significant positive correlation between liana diameter and soil $\delta^{15}N$, indicating a potential influence of nitrogen limitation. Liana density stays more or less similar across the gradient and we could not detect an influence of soil nutrients or forest stature on the liana abundance. It is possible that disturbance might be a mechanism maintaining liana abundance along the gradient as it is quoted by a lot of authors as a main driver in liana density (Laurance *et al.,* 2001; Schnitzer and Carson, 2001; Schnitzer and Bongers, 2011; Ledo and Schnitzer, 2014), but this couldn't be investigated. Apparently, species richness and other species diversity indicators do not show a trend over the gradient and at the same time the functional niche space occupied by the lianas doesn't decrease along the gradient. This indicates that liana functional richness is not constrained by the environment. On the contrary, tree species richness, functional richness and dispersion decrease along the gradient probably stronger affected by habitat filtering.

Furthermore, we report a significant decrease in the CWM of liana leaf traits such as SLA, LNC, LPC and $\delta^{15}N$ across the gradient and an increase in LCC and C:P. This indicates a shift from a strong resource acquisition strategy to a more conservative strategy and thus a higher investment in the defence of leaf tissue instead of growth. This shift is also noticed in the leaves of the co-occurring trees. The transition is mainly driven by changes in environmental conditions such as a decrease in precipitation, temperature and soil fertility. However, there is still a significant difference in trait values between both growth forms. Liana SLA, LNC, LPC and $\delta^{15}N$ are generally higher in comparison with the average tree leaf trait values representing an occupation of a different functional niche.

In general lianas seem to be less constrained by the changes in soil nutrients, temperature and precipitation along the gradient. This is deduced from the absence of a trend in density, species richness and functional richness along the gradient. All this is further supported by the fact that they are able to sustain a higher SLA, LNC and LPC in their leaves compared to trees at higher altitudes. This gives them the opportunity to maintain a fast growth rate and the ability to take up nutrients more efficiently along the wide ecological range investigated in this census.

This investigation still has a lot of limitations. So, accurate climatic data, definitely for the precipitation, measured in situ could improve our conclusions regarding the changes with altitude. Additionally, information concerning disturbance (past and current) would enable us to make more extended conclusions. The functioning of epiphytes and hemi-epiphytes wasn't included in this thesis but can provide us with some interesting information. Another exciting topic would be to study the growth rates of both lianas and trees (tagged and measured previous summers) to increase our knowledge of the interactions between both growth forms and their correlations with the available soil nutrients. As this is currently one of the few studies of liana traits along an altitudinal gradient, this research can be extended towards more gradients in different countries, hopefully providing us with more information

about why lianas are able to proliferate in the Neotropics. Further, more research is necessary to understand the differences in WUE and nutrient limitation between both growth forms.

7. References

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8. Appendix

Table S1: FAO Global Ecological Zone Framework for 2010 (FAO, 2012).

EZ Level 1 – Domain		EZ Level 2 – Global Ecological Zone		
Name	**Criteria** *(Equivalent to Köppen-Trewartha Climatic groups)*	**Name** *(Reflecting dominant zonal[a] vegetation)*	**Code**	**Criteria** *(Approximate equivalent of Köppen – Trewartha Climatic types, in combination with vegetation physiognomy and one orographic zone within each domain)*
Tropical	All months without frost: in marine areas over 18°C	Tropical rain forest	TAr	Wet: 0 – 3 months dry[b]. When dry period, during winter
		Tropical moist forest	TAwa	Wet/dry: 3 – 5 months dry, during winter
		Tropical dry forest	TAwb	Dry/wet: 5 – 8 months dry, during winter
		Tropical shrubland	TBSh	Semi-Arid: Evaporation > Precipitation
		Tropical desert	TBWh	Arid: All months dry
		Tropical mountain systems	TM	Approximate > 1000 m altitude (local variations)
Subtropical	Eight months or more over 10°C	Subtropical humid forest	SCf	Humid: No dry season
		Subtropical dry forest	SCs	Seasonally Dry: Winter rains, dry summer
		Subtropical steppe	SBSh	Semi-Arid: Evaporation > Precipitation
		Subtropical desert	SBWh	Arid: All months dry
		Subtropical mountain systems	SM	Approximate > 800-1000 m altitude
Temperate	Four to eight months over 10°C	Temperate oceanic forest	TeDo	Oceanic climate: coldest month over 0°C
		Temperate continental forest	TeDc	Continental climate: coldest month under 0°C
		Temperate steppe	TeBSk	Semi-Arid: Evaporation > Precipitation
		Temperate desert	TeBWk	Arid: All months dry
		Temperate mountain systems	TeM	Approximate > 800 m altitude
Boreal	Up to 3 months over 10°C	Boreal coniferous forest	Ba	Vegetation physiognomy: coniferous dense forest dominant
		Boreal tundra woodland	Bb	Vegetation physiognomy: woodland and sparse forest dominant
		Boreal mountain systems	BM	Approximate > 600 m altitude
Polar	All months below 10°C	Polar	P	Same as domain level

[a] Zonal vegetation: resulting from the variation in environmental, i.e. climatic, conditions in a north south direction.

[b] A dry month is defined as the month in which the total of precipitation P expressed in millimeters is equal to or less than twice the mean Temperature in degrees Centigrade.

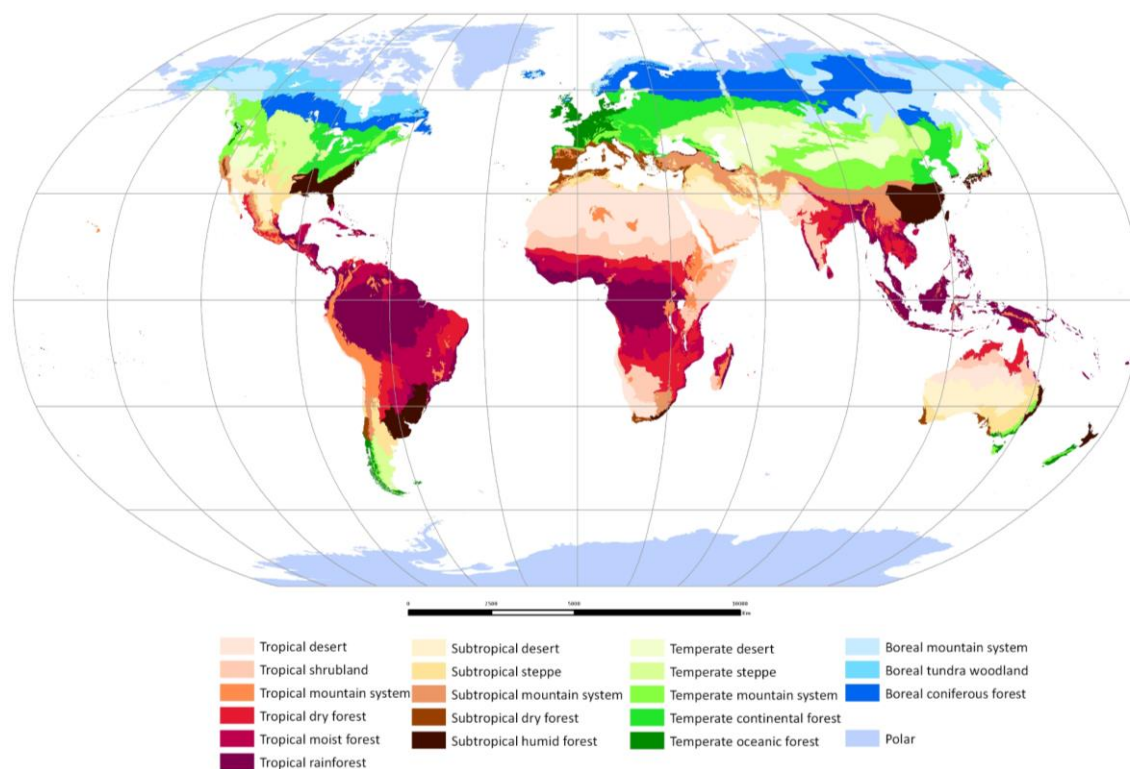*Figure S1:* The 2010 Global Ecological Zones map (FAO, 2012).
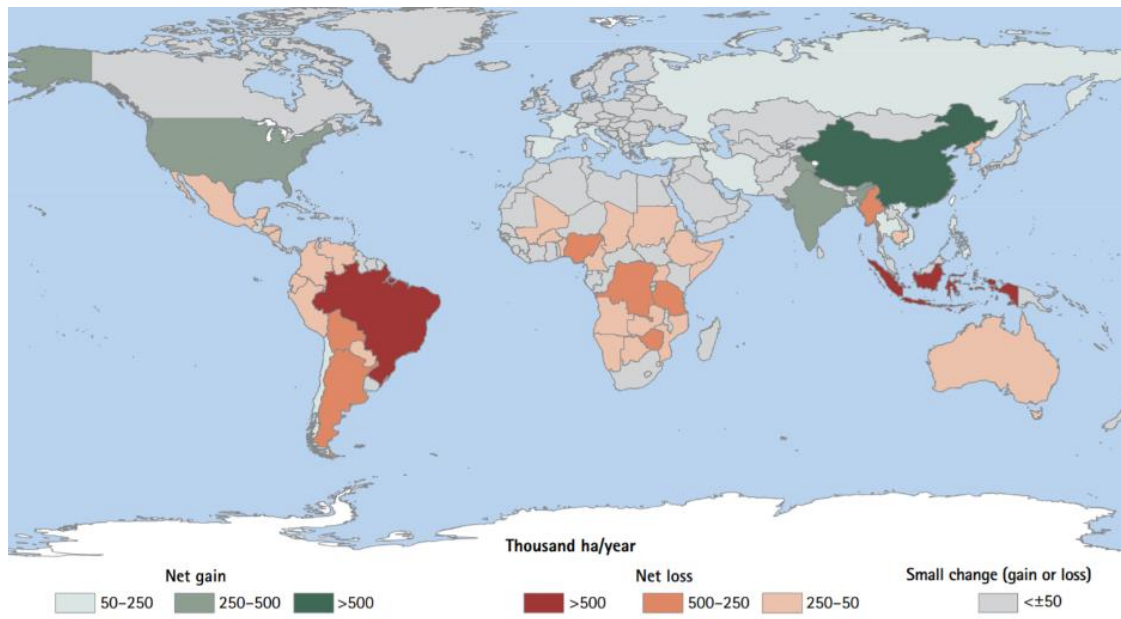
Figure S2: Annual net forest gain/loss in thousand ha/year by country, 1990-2015 (FAO, Global Forest Assessment, 2015).

Figure S3: Impressions of the different strata. Upper left panel: Rio Silanche (400 m a.s.l.). Upper right panel: Milpe (1,100 m a.s.l.). Bottom left panel: Maquipucuna (1,900 m a.s.l.). Bottom right panel: Puranqui (3,200 m a.s.l.).
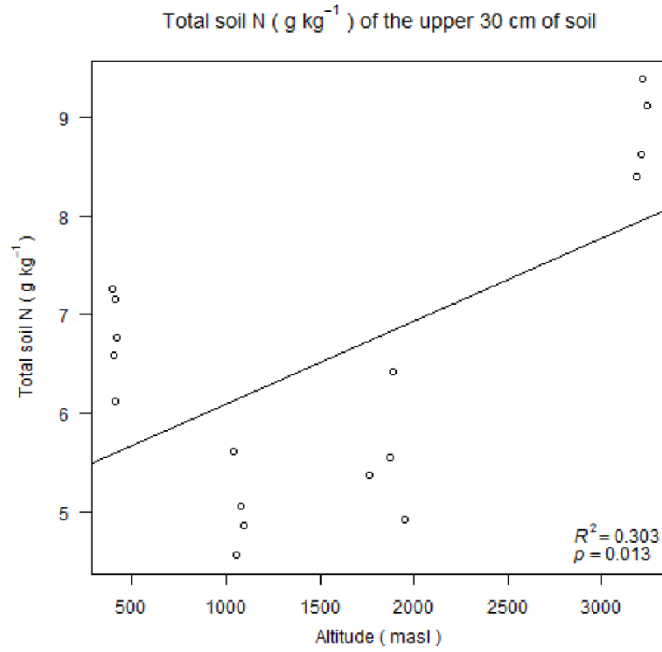
Figure S4: Linear regression of soil total N (g kg^{-1}) of the upper 30 cm of the soil in function of the altitude in m a.s.l. (masl) (Bruneel, 2016).
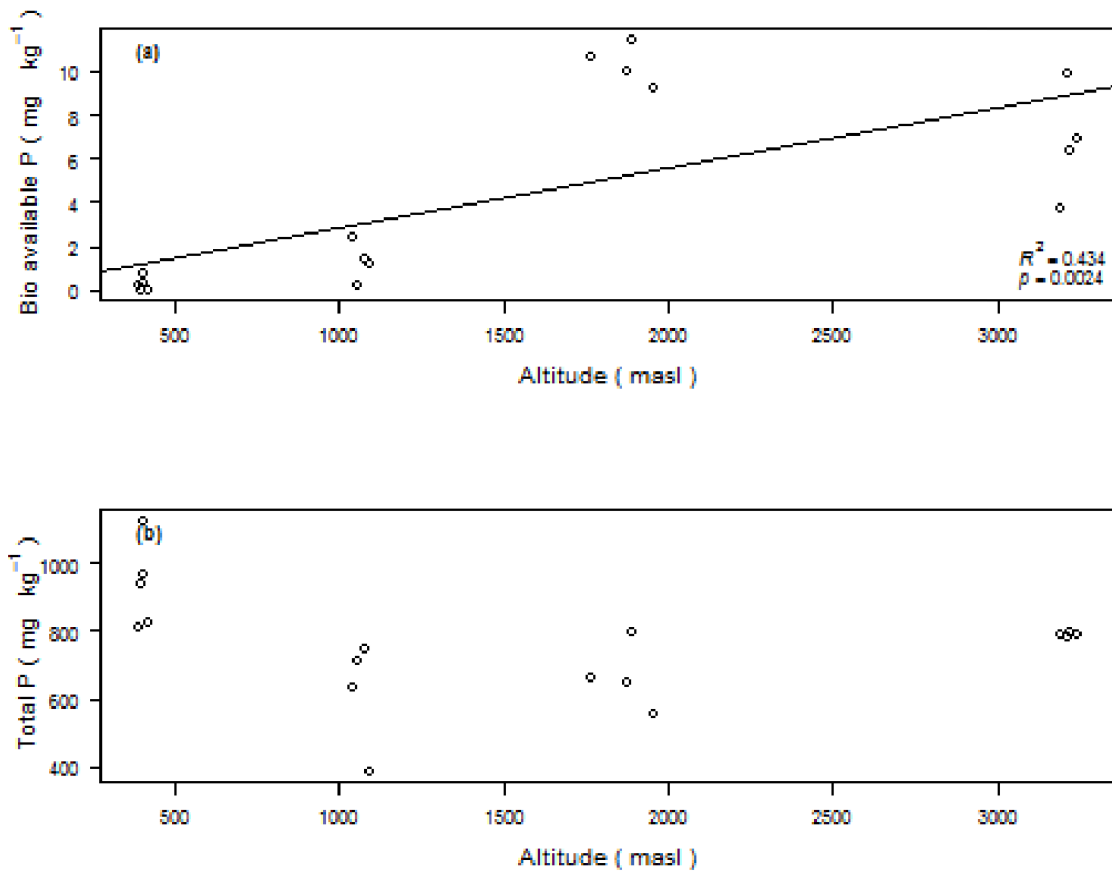
Figure S5: Visualisation of the bioavailable P (mg kg^{-1}) in the upper 30 m of the soil in function of the altitude in m a.s.l. (masl) in panel a and of the total P (mg kg^{-1}) in the upper 30 cm of the soil in function of the altitude in m a.s.l. (masl) in panel b (Bruneel, 2016).
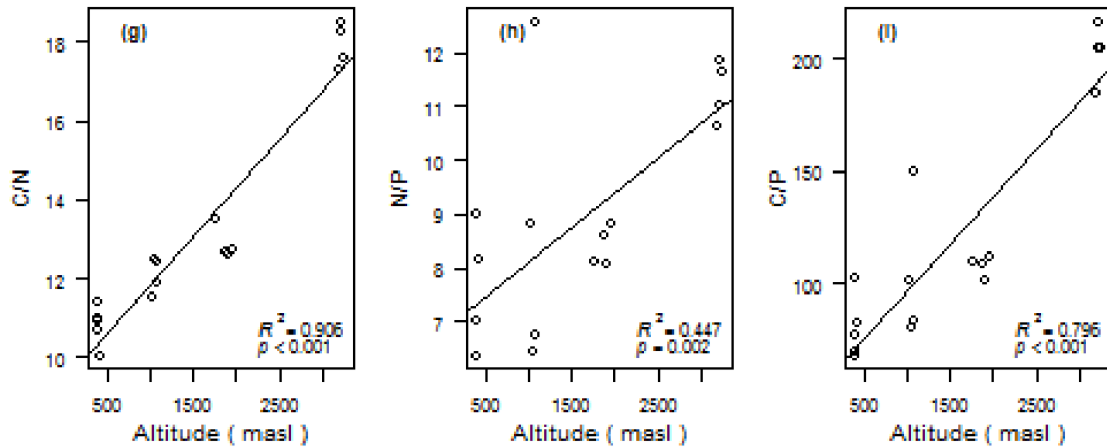
Figure S6: From the right to the left the following linear regressions are plotted: carbon to nitrogen (C:N) in function of the altitude, nitrogen to phosphorus (N:P) in function of the altitude and carbon to phosphorus (C:P) in function of the altitude in m a.s.l (masl). Total phosphorus (Ptot) was used to calculate the ratios (Bruneel, 2016).
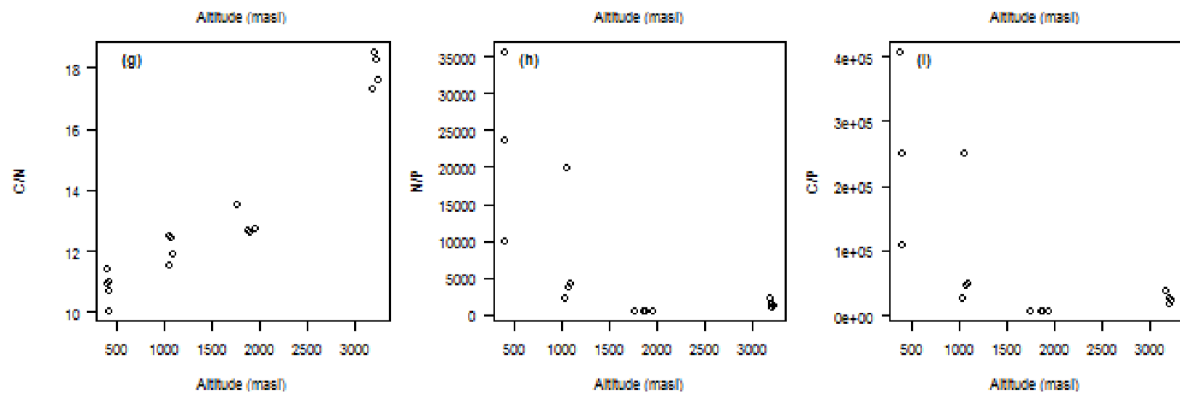
Figure S7: Visualisation of carbon to nitrogen (C:N) in function of the altitude, nitrogen to phosphorus (N:P) in function of the altitude and carbon to phosphorus (C:P) in function of the altitude in m a.s.l (masl). Bio available phosphorus (Pbio-av) was used to calculate the ratios instead of total phosphorus (Bruneel, 2016).
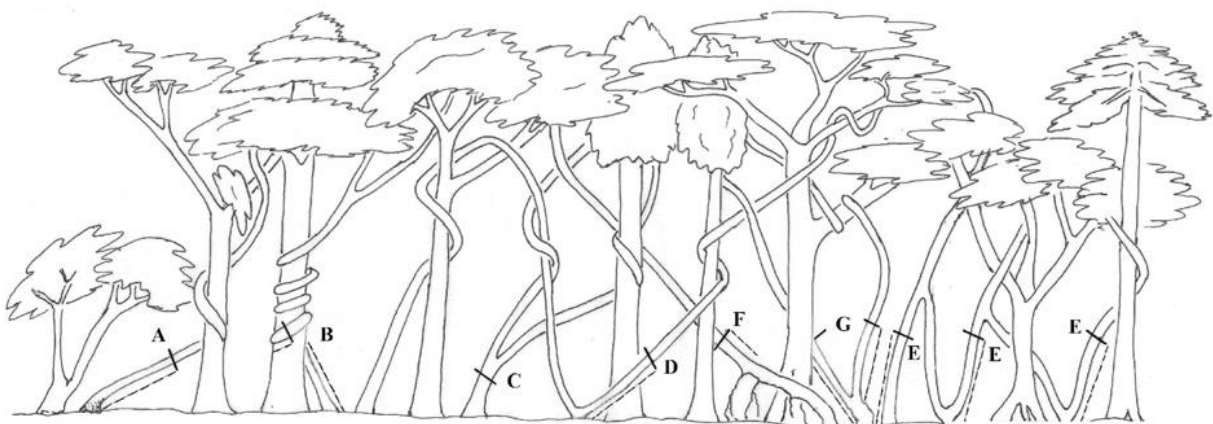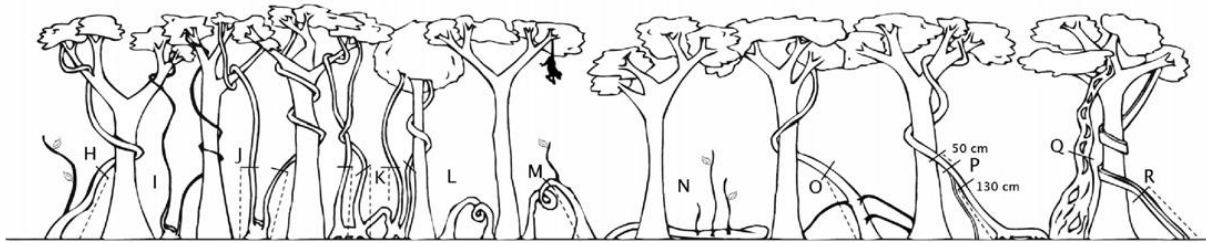
(A) Measure the diameter of all lianas (≥2 cm) 130 cm from the main rooting point at the soil surface.

(B) Measure twining lianas 130 cm from the rooting point, along the stem of the liana.

(C) If lianas branch below 130 cm (but ≥40 cm from the roots, for less than 40 cm see G), measure 20 cm below the branching point.

(D) If lianas loop to the ground and root before ascending into the canopy, ignore the loop and measure 130 cm from the last substantial (cannot be easily dislodged) rooting point along the stem that ascends into the canopy.

(E) If lianas loop to the ground and root (as in D), but the loops have branches that ascend to the canopy, measure each rooted ascending stem of the individual separately and use the multiple stem datasheet.

(F) If lianas have aerial roots >80 cm from the ultimate rooting point of the prostrate stem, measure 50 cm above highest rooted aerial root.

(G) If lianas branch <40 cm from the rooting point, measure each branch of the individual separately at 130 cm above the main rooting point and use the multiple stem datasheet.

(H) Ignore branches < 2 cm diameter and measure the principal stem 130 cm from the roots.

(I) Exclude lianas that branch below 130 cm from the roots if none of the stems are ≥ 2 cm diameter 130 from the roots.

(J) If a branch within 40 cm of the roots, measure each stem (≥ 2 cm) 130 cm from the rooting point. Note that they are branches of a single individual and tag them as multiple stems (see below).

(K) Measure each resprout or branch (≥ 2 cm) 130 cm from the roots of each distinct rooting point. Label the largest stem that ascends towards the canopy as the 'principal stem', and label and map each additional multiple stem uniquely with the tag number followed by a letter.

(L) Exclude "ground-to-ground" lianas, those that do not ascend toward the canopy, but rather loop from one rooting spot to another or that are prostrate on the soil without any resprouts or branches, even if they are ≥ 2 cm diameter.

(M) Include "ground-to-ground" lianas if they have a resprout or branch, even if the branch is < 2 cm diameter. If the branch is < 2 cm, measure the principal stem 130 cm from the roots, ignoring the branch. If the branch is ≥ 2 cm and within 130 cm of the roots, the point of measurement should be on the ascending branch.

(N) Exclude lianas growing prostrate along the soil if they do not have a stem ≥ 2 cm ascending towards the canopy.

(O) Exclude multiple branches that originate within 130 from the main roots if they are smaller than 2 cm in diameter.

(P) Measure 50 cm above the last aerial root if that root is >80 cm from the final rooting location of the stem before the stem ascends to the canopy.

(Q) If the stem is anomalous and not uniform below 130 cm from the roots, measure stem 20 cm above the point where it becomes uniform. If there is no uniform area within reach, measure the stem 130 cm from the roots.

(R) If the stem is flat and wide, include the liana if the mean of its wide and narrow axes is ≥ 2 cm.

! Stems with anomalies (nodes, damage, bulges or stem splitting) at 130 cm should be measured 5 cm below the anomaly.

! If the entire stem is non-uniform and anomalous below 130 cm, measure stem where it becomes uniform. If there is no uniform are, then measure the non-uniform are 130 cm from the rooting point.

! uneven terrain: When measuring on a slope or uneven terrain, measure from the uphill side of the stem.
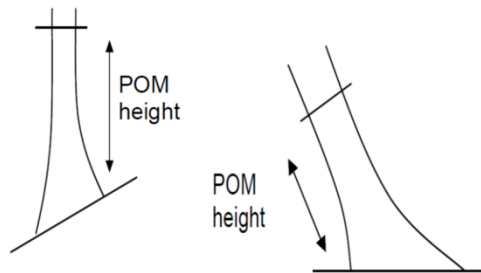
Each stem that is independently rooted and not obviously connected to another climbing stem should be treated as a separate individual. If the stems are connected below the soil surface then we consider them to be independent stems. Further each liana will be categorized as either cylindrical or noncylindrical (flat, elliptical, triangular, irregular,).

CYLINDRICAL:

a. Stems < 5 cm diameter ⬜   use calipers at widest axis at the appropriate point of
                     measurement.

b. Stems > 5 cm diameter ⬜   use diameter tape.

c. If a stem > 5 cm w/calipers but < 5 cm with diameter tape ⬜ use diameter tape.

NONCYLINDRICAL:

Measure diameters along their widest (d1) and narrowest (d2) axes at the appropriate point of measurement. The average size of the two measurements must be ≥ 2 cm to include the liana in the census. Use the geometric mean (diameter = sqrt (d1 *d2)) to estimate basal area (Schnitzer *et al.,* 2006).

$$D = \sqrt{\left(\frac{4 * BA}{PI}\right)}$$

With: D = diameter of the liana at POM

          BA = Basal Area of the liana

Figure S8: Supplementary protocol based on Gerwing *et al.* (2006) and Schnitzer *et al.* (2008) (exceptional points of measurements).

Table S2: Pearson correlation coefficients between liana community structure variable: liana diameter, liana density, liana aboveground biomass (AGB) and liana basal area (liana BA); and environmental factors including number of trees (Ntrees), tree basal area (trees BA), canopy height, mean annual precipitation (MAP), mean annual temperature and the following soil properties (upper 30 cm of the ground): the total phosphorus content (Ptot), magnesium (Mg), calcium (Ca), sodium (Na), aluminium (Al), potassium (K), nitrogen (N), stable nitrogen isotope composition (δ^{15}N), stable carbon isotope composition (δ^{13}C), carbon (C) and the carbon to nitrogen ratio (C:N). Significance: * = p values < 0.05, ** = p values < 0.01 and ***= p values < 0.001.

	Liana diameter (cm)	Liana density (ha^{-1})	Liana AGB (ton biomass ha^{-1})	Liana BA (m^2 ha^{-1})
Ntrees (DBH ≥ 10 cm ha^{-1})	-0.01	-0.03	0.05	0.02
Tree BA (m^2 ha^{-1})	**-0.60***	-0.30	**-0.51***	-0.48
Canopy height (m)	**0.50***	-0.19	0.13	0.06
MAP (mm)	**0.72****	-0.04	0.35	0.26
MAT (°C)	**0.76*****	0.17	**0.50***	0.45
Ptot (mg kg^{-1})	0.34	-0.42	-0.02	-0.16
Mg (mg kg^{-1})	-0.46	0.08	-0.28	-0.18
Ca (mg kg^{-1})	-0.33	0.16	-0.17	-0.06
Na (mg kg^{-1})	-0.04	-0.06	0.04	-0.02
Al (mg kg^{-1})	-0.47	-0.30	-0.40	-0.41
K (mg kg^{-1})	-0.43	-0.30	-0.41	-0.41
N (g kg^{-1})	-0.24	-0.36	-0.30	-0.36
δ^{15}N (‰)	**0.79*****	0.01	0.47	0.36
δ^{13}C (‰)	**-0.53***	-0.24	-0.34	-0.36
C (g kg^{-1})	-0.47	-0.36	-0.44	-0.46
C:N	**-0.63****	-0.31	**-0.52***	**-0.50***

Table S3: Summary of the number of tagged lianas, unidentified lianas and the number of leaf samples for the different plots along the gradient.

Stratum	Plot	Tagged lianas	No determination	Number of collected samples
	1	50	9	2
	2	61	16	3
Stratum 1	3	41	5	3
	4	14	/	2
	5	40	1	7
	1	65	13	8
Stratum 2	2	23	/	4
	3	20	3	3
	4	29	1	2
	1	93	5	5
Stratum 3	2	64	6	4
	3	35	2	3
	4	44	2	13
	1	32	/	17
Stratum 4	2	11	1	1*
	3	19	/	5
	4	47	1	7*

*for 1 sample, there is only information obtained about specific leaf area (SLA) and leaf phosphorus content (LPC), no data available for leaf carbon content (LCC), leaf nitrogen content (LNC), carbon to nitrogen ratio (C:N), stable carbon isotope composition (δ^{13}C), stable nitrogen isotope composition (δ^{15}N), carbon to phosphorus ratio (C:P) and nitrogen to phosphorus ratio (N:P) because the samples got mixed in the autoanalyzer during C/N analysis.
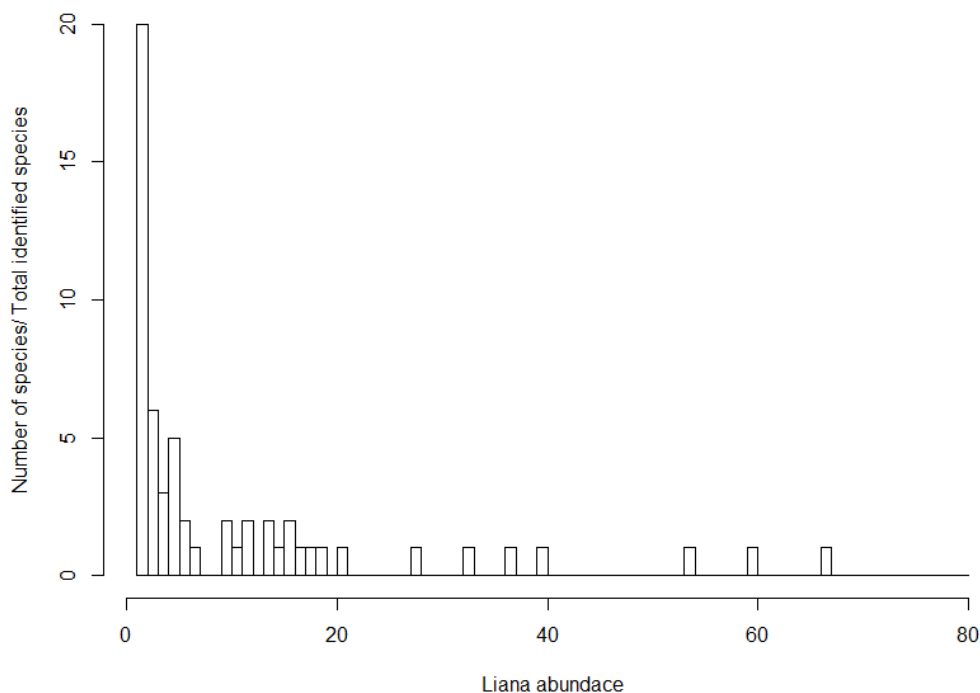

Figure S9: Density distribution of the liana species (n = 58) in function of the abundancy.

Table S4: Indicators of diversity for every altitude along the gradient. The different diversity indicators are: species richness, rarefied species richness, the Shannon diversity index, the Simpson diversity index, alpha diversity and evenness including the standard deviation. Significant differences across the strata ($p < 0.05$) are indicated in the table as different letters.

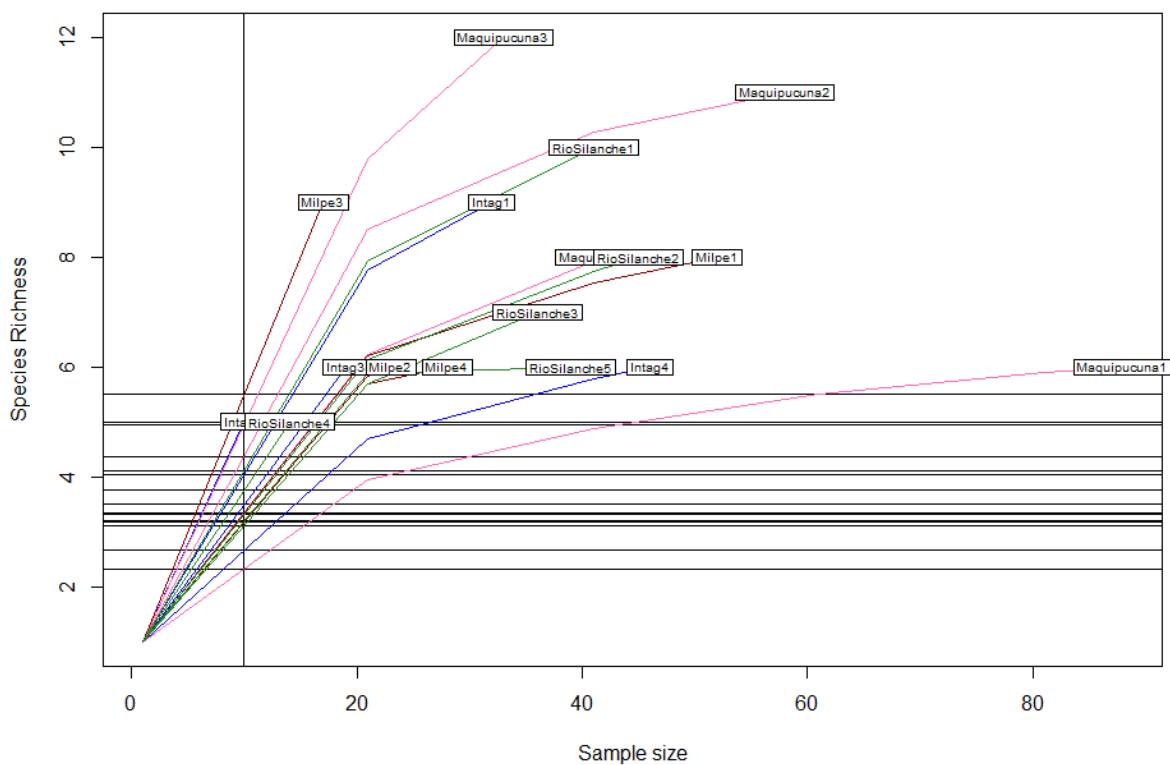|	Stratum 1	Stratum 2	Stratum 3	Stratum 4
Species richness	7.20 ± 1.92^a	7.25 ± 1.50^a	9.25 ± 2.75^a	6.50 ± 1.73^a
Rarefied species richness	4.80 ± 0.53^a	5.11 ± 1.04^a	4.99 ± 1.53^a	4.77 ± 0.86^a
Shannon diversity	1.63 ± 0.21^a	1.69 ± 0.24^a	1.73 ± 0.50^a	1.56 ± 0.28^a
Simpson diversity	0.75 ± 0.06^a	0.77 ± 0.05^a	0.74 ± 0.12^a	0.73 ± 0.10^a
Alpha diversity	2.88 ± 0.82^a	3.84 ± 2.61^a	3.80 ± 2.25^a	3.25 ± 1.06^a
Evenness	0.84 ± 0.09^a	0.86 ± 0.06^a	0.78 ± 0.12^a	0.85 ± 0.14^a

Figure S10: Rarefaction curve: Species richness in function of the number of samples for every plot.
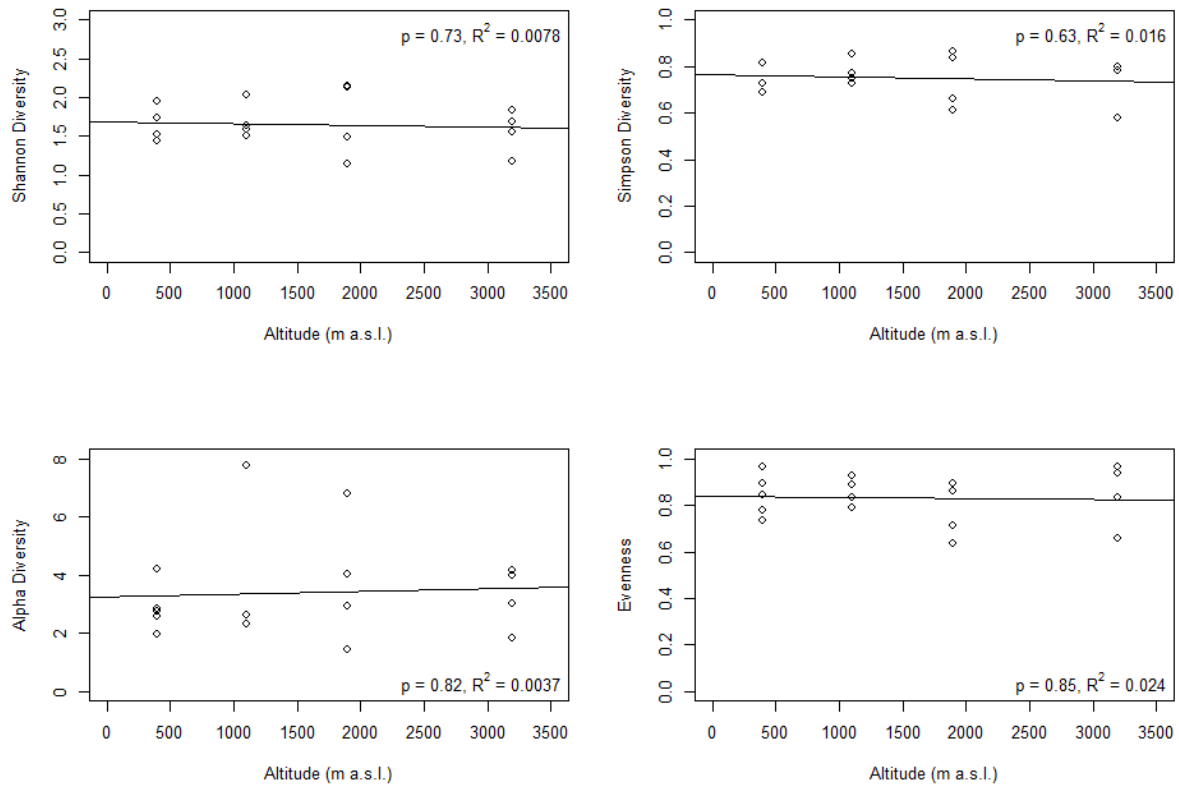
Figure S11: Linear regressions of the Shannon diversity index, Simpson diversity index, alpha diversity and evenness in function of the altitude (p-values and R^2 values are given for each plot).

Table S5: Community weighted means, weighted on abundance, and standard deviations of all traits across the altitudinal transect: including the specific leaf area (SLA), mass-based leaf phosphorus concentration (LPC),mass-based leaf nitrogen concentration (LNC), mass-based leaf carbon concentration (LCC), nitrogen isotope composition ($\delta^{15}N$), carbon isotope composition ($\delta^{13}C$), carbon to nitrogen ratio (C:N), carbon to phosphorus ratio (C:P) and nitrogen to phosphorus ratio (N:P). Significant differences across the strata ($p < 0.05$) are indicated in the table as different letters.

	Stratum 1	Stratum 2	Stratum 3	Stratum 4
SLA (cm^2/g)	273.29 ± 39.67[a]	109.84 ± 34.67[b]	227.82 ± 35.23[a]	100.38 ± 10.16[b]
LPC (%)	0.21 ± 0.03[a]	0.09 ± 0.03[b]	0.12 ± 0.02[b]	0.10 ± 0.04[b]
LNC (%)	3.01 ± 0.20[a]	1.44 ± 0.36[b]	2.29 ± 0.25[c]	1.71 ± 0.47[bc]
LCC (%)	43.38 ± 0.64[a]	45.50 ± 0.75[b]	44.33 ± 1.53[ab]	45.44 ± 0.60[b]
δ^{15}N (‰)	3.15 ± 0.09[a]	-1.07 ± 1.58[bc]	0.28 ±0.49[b]	-2.38 ± 0.50[c]
δ^{13}C (‰)	-30.68 ± 0.29[a]	-32.77 ± 0.27[b]	-32.02 ± 0.50[b]	-30.58 ± 1.21[a]
C:N	15.76 ± 2.19[a]	38.66 ± 9.69[b]	21.31 ± 2.97[c]	34.94 ± 4.61[b]
C:P	247.47 ± 39.62[a]	705.58 ± 234.29[bc]	429.00 ± 58.37[b]	641.42 ± 76.08[c]
N:P	16.52 ± 0.72 [a]	17.25 ± 1.36 [ab]	20.73 ± 1.55 [b]	18.10 ± 0.85 [ab]

Table S6: Pearson correlations between the different liana leaf traits including specific leaf area (SLA), mass-based leaf phosphorus concentration (LPC), mass-based leaf nitrogen concentration (LNC), stable nitrogen isotope composition (δ^{15}N), leaf carbon concentration (LCC), stable carbon isotope composition (δ^{13}C), the carbon to nitrogen ratio (C:N), the carbon to phosphorus ratio (C:P) and the nitrogen to phosphorus ratio (N:P). Significance: * = p values < 0.05, ** = p values < 0.01 and ***= p values < 0.001.

	SLA	LPC	LNC	δ^{15}N	LCC	δ^{13}C	C:N	C:P
LPC	**0.63***							
LNC	**0.75***	**0.75***						
δ^{15}N	**0.55***	**0.55***	**0.68***					
LCC	**-0.32**	**-0.24***	**-0.32**	**-0.34**				
δ^{13}C	0.00	**0.37***	**0.25***	-0.04	0.07			
C:N	**-0.66***	**-0.58***	**-0.83***	**-0.70***	**0.53***	-0.17		
C:P	**-0.56***	**-0.67***	**-0.71***	**-0.66***	**0.51***	**-0.22***	**0.89***	
N:P	0.01	**-0.54***	0.05	-0.09	0.04	**-0.25***	-0.03	**0.36***

Table S7: Functional richness, evenness, divergence and dispersion and their standard deviation along the altitudinal gradient. Significant differences across the strata (p < 0.05) are indicated in the table as different letters.

	Stratum 1	Stratum 2	Stratum 3	Stratum 4
Functional richness	2.14 ± 3.29[a]	3.33 ± 2.08[a]	6.80 ± 3.96[a]	4.61 ± 1.52[a]
Functional evenness	0.64 ± 0.07[a]	0.59 ± 0.10[a]	0.52 ± 0.30[a]	0.66 ± 0.11[a]
Functional divergence	0.65 ± 0.09[a]	0.73 ± 0.12[ab]	0.79 ± 0.07[ab]	0.84 ± 0.06[b]
Functional dispersion	1.18 ± 0.54[a]	1.88 ± 0.63[ab]	1.75 ± 0.54[ab]	2.28 ± 0.59[b]

Table S8: Pearson correlations between the community weighted means of the leaf traits for both lianas and trees and the soil properties (upper 30 cm of the ground) from Bruneel (2016). Leaf traits include specific leaf area (SLA), mass-based leaf phosphorus concentration (LPC), mass-based leaf nitrogen concentration (LNC), mass-based leaf carbon concentration (LCC), stable nitrogen isotope composition ($\delta^{15}N$), stable carbon isotope composition ($\delta^{13}C$), the carbon to nitrogen ratio (C:N), the carbon to phosphorus ratio (C:P) and the nitrogen to phosphorus ratio (N:P) for both lianas and trees. Soil properties (upper 30 cm of the ground) include the total phosphorus content (Ptot), magnesium (Mg), calcium (Ca), sodium (Na), aluminium (Al), potassium (K), nitrogen (N), stable nitrogen isotope composition ($\delta^{15}N$), stable carbon isotope composition ($\delta^{13}C$), carbon (C) and the carbon to nitrogen ratio (C:N). Significance: * = p values < 0.05, ** = p values < 0.01 and ***= p values < 0.001.

	Ptot (mg kg⁻¹)	Mg (mg kg⁻¹)	Ca (mg kg⁻¹)	Na (mg kg⁻¹)	Al (mg kg⁻¹)	K (mg kg⁻¹)	N (g kg⁻¹)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	C (g kg⁻¹)	C:N
LIANAS											
SLA (cm²/g)	0.05	-0.44	-0.12	-0.08	**-0.91***	**-0.87***	**-0.77***	**0.66**	**-0.92***	**-0.92***	**-0.93***
LNC (%)	0.12	-0.46	-0.14	0.13	**-0.90***	**-0.81***	**-0.69**	**0.74***	**-0.87***	**-0.88***	**-0.95***
$\delta^{15}N$ (‰)	0.21	-0.40	-0.09	0.13	**-0.91***	**-0.77***	**-0.65**	**0.78***	**-0.87***	**-0.88***	**-0.97***
LCC (%)	-0.04	0.08	-0.22	0.07	**0.87***	**0.71**	**0.67**	-0.46	**0.87***	**0.85***	**0.89***
$\delta^{13}C$ (‰)	-0.08	0.28	-0.02	0.05	**0.90***	**0.76***	**0.72***	**-0.67**	**0.88***	**0.89***	**0.91***
LPC (%)	-0.17	-0.28	0.09	-0.06	**-0.94***	**-0.84***	**-0.88***	0.45	**-0.94***	**-0.96***	**-0.90***
C:N	0.00	0.34	-0.01	0.00	**0.96***	**0.83***	**0.79***	**-0.63**	**0.94***	**0.96***	**0.97***
N:P	**0.49***	**-0.61**	**-0.49***	0.32	**-0.52***	-0.47	-0.15	**0.95***	-0.47	-0.46	**-0.70**
C:P	0.11	0.23	-0.14	0.07	**0.97***	**0.83***	**0.86***	**-0.50***	**0.96***	**0.98***	**0.94***
TREES											
SLA (cm²/g)	0.38	0.06	0.21	0.22	**-0.57***	-0.19	-0.13	**0.62**	-0.46	-0.44	**-0.63**
LPC (%)	**0.49***	-0.28	-0.22	0.28	-0.37	-0.15	0.11	**0.76***	-0.25	-0.24	**-0.53***
LNC (%)	**0.50***	-0.08	0.00	0.35	-0.39	-0.09	0.09	**0.68**	-0.24	-0.24	**-0.51***
$\delta^{15}N$ (‰)	0.43	-0.24	-0.07	0.33	**-0.63**	-0.38	-0.19	**0.80***	**-0.53***	**-0.54***	**-0.78***
LCC (%)	-0.29	-0.06	-0.19	-0.25	0.44	0.12	0.02	**-0.53***	0.32	0.30	0.49
$\delta^{13}C$ (‰)	**0.59***	-0.03	-0.23	0.38	0.39	**0.54***	**0.75***	0.27	**0.54***	**0.54***	0.27
C:N	-0.37	-0.07	-0.17	-0.34	0.41	0.08	-0.02	**-0.55***	0.28	0.29	**0.51***
C:P	-0.40	0.01	-0.07	-0.35	0.40	0.07	-0.06	**-0.61***	0.28	0.27	**0.52***
N:P	-0.24	**0.56***	**0.60***	-0.04	0.04	0.11	-0.17	**-0.51***	0.09	0.02	0.24