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Carbon sequestration in natural forests and reforestations along an altitudinal gradient in the Andes of Ecuador

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Engineering

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Ghent, May 2016

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Instead of running of, thanking everyone who contributed to the final outcome of this thesis, I would like to start with defining the verb “to acknowledge,” after all this is supposed to be a scientific report. To acknowledge something is to accept or admit the existence or truth of that very something. The truth behind this thesis is, that it is the hard work of a wide spectrum of people. In addition, to acknowledge someone might also simply be to notice someone’s presence (and we did cross a lot of noticeable presences).

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Abstract

In this study carbon (C) stocks of natural tropical forests were assessed along a 2800 m long elevational gradient in the Andes region of North Western Ecuador. Therefore, a monitoring network of 17 permanent sample plots of 40x40m at four different strata (400, 1100, 1900 and 3200 masl) were established along the gradient. Besides diameter and tree height measurements to estimate the aboveground carbon (AGC) stocks, also soil, litter and leaf samples were taken in order to determine soil organic carbon (SOC) stocks and nutrient amounts. The study was extended to a close by reforestation project that ranged from 300 to 2200 masl. However, human disturbances in the latter one were too severe and unaccounted for to attribute any variation of C storage to the elevational gradient and its associated variables like temperature.

The gradient harbours tropical lowland and tropical montane forest which are characterized by very different environmental conditions. Studies concerning tropical forests have mainly focused on lowland forests despite the acknowledged importance of tropical montane forests as refugia in future global warming. Therefore, there is a need for an improved understanding of the dynamics in these ecosystems and the potential they hold.

The main target of this study was to evaluate the drivers behind any potential trend of C storage along the gradient. Both climate and soil properties have singularly been proposed by numerous studies as the dominating driver behind C storage. However, their interdependent nature and the complexity behind ecological processes limits strong conclusions. Therefore, we expected that soil nutrient availability, affected by the decreasing temperature with elevation, is a major driver behind C storage.

In this study the AGC increased with elevation while most studies described a general decrease with elevation. In the soil, bio-available phosphorus (P) increased, but concentrations of both total nitrogen (N) and total P did not show a clear trend with increasing elevation. Probably caused by the important difference of total and bio-available nutrient pools, with the latter being more appropriate to assess C stocks. In addition, the high soil total N at higher altitudes might have been caused by an increased microbial immobilization due to the lower quality of litter material (higher C/N ratio). Foliar concentrations did however show a more consistent trend, with lower N and P concentrations at higher altitudes. These trends might reflect nutrient availability along the gradient, although they are more likely associated with species specific traits which might not only be dictated by soil properties but also by factors such as temperature fluxuations, moist and the efficiency of the photosynthetic apparatus.

Bio-available P probably has an important effect on C storage in the tropical forest which are widely considered to be limited by P. The increase of AGC with elevation might therefore be associated with the increasing bio-available P. This increase of bio-available P has been established in numerous studies which suggest that tropical lowland forests are P limited while montane forest are N limited. In this study, the N available for uptake is probably reduced at higher elevations because of the lower decomposition rates (large amount of litter, low $\delta^{15}\text{N}$ in litter and soil) and the assumed increased microbial immobilization of N with elevation.

Productivity estimations and N mineralization rates might provide additional insights into the nutrient dynamics and effects on plant growth. Hence, long term assessments of elevational gradients hold promise in evaluating ecological processes and their response to different environmental conditions.

Samenvatting

In deze studie werd de koolstof (C) opslag van natuurlijke tropische bossen langsheen een 2800 m lange hoogtegradiënt in de Andes regio van Noordwest Ecuador bepaald. Daarvoor werd een monitoringsnetwerk van 17 permanente staalname plots van 40mx40m op vier verschillende hoogtes (400, 1100, 1900 en 3200 m) opgesteld langsheen de gradiënt. Behalve diameter en boomhoogte metingen om de bovengrondse C-opslag in te schatten, werden er ook bodem-, strooisel- en bladstalen genomen om de bodem C en nutriëntenconcentraties te bepalen. De studie was aanvankelijk gelinkt aan de studie van een naburig herbebossingsproject dat zich situeerde tussen 300 en 2200 m hoogte. De menselijke verstoringen waren echter te groot en onvoorspelbaar om onderbouwde vergelijkingen te maken met de natuurlijke bossen.

De hoogtegradiënt begint met tropisch laagland bos dat overgaat in tropisch gebergte bos. Studies in tropische bossen beperken zich meestal tot laagland bos ondanks het erkende belang van gebergte bos als toekomstige refugia voor de veranderingen van global change. Daarom is er nood aan meer kennis over de dynamieken in deze ecosystemen.

Het belangrijkste doel van deze studie was om de oorzaken achter een potentiële trend van C-opslag langsheen de hoogtegradiënt te identificeren. Zowel klimaat- als bodem karakteristieken zijn afzonderlijk naar voren geschoven als dominante factoren door verschillende studies, maar de onderlinge afhankelijkheid van beide factoren bemoeilijkt de besluitvorming. Daarom verwachten we dat nutriëntenbeschikbaarheid, die wordt beïnvloed door de temperatuurdaling met de stijgende hoogte, een belangrijke factor is voor C-opslag.

In deze studie steeg de bovengrondse C-opslag met stijgende hoogte, terwijl de meeste studies eerder een daling beschreven. In de bodem steeg de bio beschikbare fosfor (P), maar concentraties van totale P en totale stikstof (N) toonden geen uitgesproken trend. Dit kan te wijten zijn aan het belangrijke verschil tussen bio beschikbare en totale nutriënten concentraties wanneer C-opslag wordt geanalyseerd. Onder andere de hoge totale N-concentratie op 3200 m is waarschijnlijk te wijten aan een verhoogde microbiële immobilisatie van N wat op zijn beurt kan verklaard worden door de lagere strooiselkwaliteit op grotere hoogte (hogere C/N-ratio). Bladnutriënten toonden een meer consistente trend met lagere N- en P-concentraties op grotere hoogtes. Deze trends geven mogelijks een betere weergave van de eigenlijke nutriëntenbeschikbaarheid, maar er zijn nog veel andere factoren naast bodem nutriëntenconcentraties die een rol spelen, zoals temperatuur fluctuaties, vocht en fotosynthetische capaciteit.

Bio beschikbare P speelt waarschijnlijk een belangrijke rol in C-opslag van tropische bossen, die algemeen worden bestempeld als P gelimiteerd. De stijgende bovengrondse C-opslag met stijgende hoogte is daarom mogelijks gerelateerd aan de stijgende bio beschikbare P. Deze stijging van bio beschikbare P werd vastgesteld in verschillende studies die suggereerden dat tropische laagland bossen algemeen P gelimiteerd zijn in hun productie terwijl tropische gebergte bossen eerder N gelimiteerd zijn. In deze studie, is de voor planten beschikbare N waarschijnlijk lager op grotere hoogten omwille van een tragere decompositie (meer onverteerd strooisel en een lagere $\delta^{15}\text{N}$ van het strooisel en de bodem) en de veronderstelde verhoogde microbiële immobilisatie van N met stijgende hoogte. Productiviteit inschattingen en kwantificatie van N-mineralisatie kunnen een belangrijke aanvulling zijn voor de evaluatie van nutriëntendynamieken en effecten op plantengroei.

Resumen

Este estudio se ha dedicado a evaluar las reservas de carbono (C) de los bosques tropicales a lo largo de un gradiente de elevación de 2800 m de largo en la región andina del noroeste de Ecuador. Por ello, se estableció una red de monitoreo de 17 parcelas permanentes de muestreo de 40 m x 40 m en cuatro estratos diferentes (400, 1100, 1900 y 3200 m s. n. m.). Además de las mediciones del diámetro y la altura de los árboles para estimar las reservas de carbono superficial (AGC, aboveground carbon), también se tomó muestras de suelo, de residuos y de hojas con el fin de determinar tanto las reservas de carbono orgánico en el suelo (SOC, soil organic carbon) como las cantidades del nutriente. El estudio se extendió hasta un proyecto de reforestación de la cercanía con un rango de altitud entre 300 y 2200 m s. n. m. Sin embargo, las perturbaciones humanas en este último eran demasiado severas y desconocidas como para atribuir cualquier variación del almacenamiento de C al gradiente elevacional y sus variables asociadas tal como la temperatura.

El gradiente alberga bosques tropicales de tierras bajas y de montaña, que se caracterizan por poseer condiciones medioambientales muy diferentes. Los estudios sobre bosques tropicales se han centrado principalmente en los de tierras bajas a pesar de reconocer la importancia de los de montaña como refugios en el futuro calentamiento global. Por consiguiente, es necesario comprender mejor la dinámica en estos ecosistemas y el potencial que contienen.

El objetivo principal de este estudio era evaluar los motores detrás de cualquier tendencia potencial de almacenamiento de C a lo largo del gradiente. Numerosos estudios propusieron especialmente las propiedades del clima y el suelo como los factores dominantes en el almacenamiento de C. Sin embargo, su naturaleza interdependiente y la complejidad detrás de los procesos ecológicos limitan las conclusiones definitivas. Por consiguiente, esperamos que la disponibilidad de nutrientes del suelo, afectada por la disminución de la temperatura con la elevación, sea uno de los principales impulsores del almacenamiento de C.

En este estudio, la AGC aumentó con la elevación, mientras que la mayoría de estudios describieron una disminución general con la elevación. En el suelo, el fósforo biodisponible (P) aumentaba, pero tanto las concentraciones totales de nitrógeno (N) como las concentraciones totales de P no mostraron una tendencia clara con el aumento de la elevación. Esto se debe posiblemente a la diferencia importante de sumideros de nutriente total y biodisponible, siendo este último el más adecuado para evaluar las reservas de C. Adicionalmente, el elevado N total del suelo a altitudes mayores podía haber sido causado por un aumento en la inmovilización microbiana debido al material de desperdicio de calidad inferior (relación C/N mayor). Sin embargo, las agrupaciones foliares mostraron una tendencia más coherente, con concentraciones de N y P más bajas a altitudes superiores. Es posible que estas tendencias sean un reflejo de la disponibilidad de nutrientes a lo largo del gradiente, aunque lo más probable es que estén relacionadas con características propias de la especie, que pueden estar dictadas no solo por las propiedades del suelo sino por factores tales como las fluctuaciones de temperatura, la humedad y la eficacia del mecanismo fotosintético.

Es probable que el P biodisponible tenga un efecto importante en el almacenamiento de C en el bosque tropical, que generalmente se considera como limitado por el P. El incremento del AGC con la elevación puede, por consiguiente, estar asociado con el aumento del P biodisponible. Numerosos estudios han establecido dicho aumento, lo que sugiere que el P se encuentra limitado en los bosques tropicales de tierras bajas, mientras los de montaña tienen el N limitado. En este estudio, el N disponible para captación se encuentra probablemente reducido a elevaciones más altas debido a las tasas de descomposición inferiores (gran cantidad de desperdicios, $\delta^{15}\text{N}$ bajo en la basura y el suelo) y el supuesto incremento de inmovilización microbiana de N con la elevación.

Las estimaciones de productividad y las tasas de mineralización de N pueden proporcionar información adicional sobre la dinámica del nutriente y sus efectos en el crecimiento de las plantas. Por lo que las evaluaciones a largo plazo de los gradientes de elevación prometen valorar los procesos ecológicos y su respuesta a diferentes condiciones medioambientales.

List of abbreviations

AGB: Aboveground biomass; all living biomass above the soil including stem, stump, branches, bark, seeds, and leaves.

AGC: Aboveground carbon

BGB: Belowground biomass; All living biomass of roots

CUE: Carbon use efficiency

CWI: Cloud water interception

DIN: Dissolved inorganic nitrogen

DON: Dissolved organic nitrogen

FWU: Foliar water uptake

g_m : Mesophyll conductance

GPP: Gross primary production

g_s : Stomatal conductance

IPCC: Intergovernmental panel on climate change

LAI: Leaf Area Index

MAP: Mean annual precipitation

masl: meters above sea level

MAT: Mean annual temperature

NEP: Net ecosystem production

NPP: Net primary production

PAR: Photosynthetic active radiation

RAINFOR: Red Amazonica de Inventarios Forestales

REDD: Reducing emissions from deforestation and degradation

SOC: Soil organic carbon

SOM: Soil organic matter: All non-living biomass in the soil

TMCF: Tropical montane cloud forest

VPD: Vapor pressure deficit

WUE: Water use efficiency

Content

- 1 Introduction..... 1
- 2 Literature review 3
 - 2.1 Tropical forests in the global carbon cycle..... 3
 - 2.1.1 The global carbon cycle and the role of tropical forests in this cycle 3
 - 2.1.2 C dynamics in forests..... 3
 - 2.1.3 Assessment of C storage in tropical forests 4
 - 2.1.4 Drivers behind C storage in tropical forests 5
 - 2.2 Nutrients: the drivers of the forest C cycle 6
 - 2.2.1 How do nutrients enter the forest ecosystem? 6
 - 2.2.2 The nutrient cycle within forest ecosystems..... 7
 - 2.2.3 Stable isotopes: a key tool for an improved understanding of forest biogeochemistry. 8
 - 2.3 Taking forest research to a higher level: elevational transects as an open-air laboratory for tropical forest ecology..... 9
 - 2.3.1 Elevational transects and their importance in predicting forest responses to future global change..... 9
 - 2.3.2 Tropical lowland forests versus tropical montane forests 10
 - 2.3.3 C storage along an elevational gradient..... 12
 - 2.3.4 Litter and decomposition 12
 - 2.3.5 C fluxes along an elevational gradient 13
 - 2.3.6 Nutrient fluxes along an elevational gradient..... 13
 - 2.3.7 Nutrient availability 14
- 3 Material and methods..... 15
 - 3.1 Study Area 15
 - 3.1.1 Climate..... 15
 - 3.1.2 Forest description..... 17
 - 3.2 Field protocol..... 19
 - 3.3 Lab protocol..... 21
 - 3.3.1 Soil 21
 - 3.3.2 Litter and leaf material 21
 - 3.4 Analysis..... 22
 - 3.4.1 Surface..... 22
 - 3.4.2 Allometric relations for the natural forests..... 22
 - 3.4.3 Statistics..... 24
- 4 Results 25
 - 4.1 Stand structure..... 25
 - 4.2 C storage..... 26
 - 4.2.1 AGC..... 26

4.2.2	SOC	27
4.3	Soil characteristics	29
4.4	Litter	33
4.5	Leaves	35
4.6	Isotopes	37
5	Discussion	39
5.1	How does the stand structure changes with elevation?	39
5.2	How do the AGC and SOC change with elevation?	39
5.2.1	Limitations of the AGC estimations.....	39
5.2.2	AGC	39
5.2.3	WD	41
5.2.4	SOC	42
5.3	How do nutrient concentrations change with elevation?	42
5.3.1	Soil	42
5.3.2	Soil and litter	42
5.3.3	Soil, litter and leaves	43
5.4	How do the isotopic compositions change with elevation?	46
6	Conclusion	47
7	Annex.....	48
7.1	Case study: a reforestation project in North-Western Ecuador	48
7.1.1	Why a reforestation project in Ecuador?	48
7.1.2	Introduction.....	48
7.1.3	Objectives	49
7.1.4	Material and methods	49
7.1.5	Material and methods	50
7.1.6	Results	51
7.1.7	Discussion	53
7.1.8	Conclusion	55
8	Recommendations for future research	56
9	References.....	57
10	Appendix.....	71
10.1	Maps.....	71
10.2	Recommendations for future field campaigns in natural forests	76
10.2.1	Height measurements	76
10.3	Lab protocol.....	76
10.3.1	Bio-available P soil.....	76
10.3.2	Total P litter	76
10.3.3	Figures	77

10.4	Allometric relations	78
10.5	Figures	79

1 Introduction

Our knowledge of carbon (C) storage and nutrient cycles in tropical forests is not only essential for evaluating the role of tropical ecosystems in the global terrestrial C cycle, but also crucial for the understanding of long term C and nutrient entanglements within tropical forests. Furthermore, as climate change might alter ecosystems' behaviour, predictions on how tropical forests will respond to changing abiotic variables is invaluable. Elevational gradients can fill this knowledge gap on a small time and spatial scale as they are ideal open air laboratories to quantify C storage and nutrient fluxes against a wide range of abiotic variables.

The main focus of research on tropical forests is however confined to the lowland tropical forests, which make up the largest part of tropical forests. In contrast, tropical montane forests are generally understudied although they have been found to serve as important refugia for numerous species and might even be underestimated in terms of their C sequestration potential (Spracklen & Righelato 2014). In addition, identifying the drivers behind carbon sequestration at different altitudes might provide additional insights into the response of lowland and montane tropical forests to disturbances. Temperature has been shown to be strongly correlated with elevation (Lu et al. 2009) and influence a wide range of ecological processes such as decomposition and the associated nutrient availability (Salinas et al. 2011). In addition, nutrient limitation has been shown to affect tropical forests and to shift from P to N limitation with elevation (Moser et al. 2011).

The primary target of this study was therefore to estimate the C storage of tropical forests at different altitudes and to make a link with soil, litter and leaf nutrient concentrations to identify the drivers behind any trend of carbon storage. The studied elevational gradient was located at the North-Western slope of the Ecuadorian Andes, where per stratum four to five permanent sampling plots (PSP) were set up in natural forests at 400, 1100, 1900 and 3200 masl resulting in a total of 17 PSP.

The main question throughout the thesis will be: Is there any trend in AGC with elevation and if so, what are the main drivers behind such a trend? The focus is thereby oriented towards nutrient availability as the main potential driver behind any trend in carbon storage.

Initially the results of the natural forests PSP were to be linked to the evolution of a nearby reforestation project, started in 2013. However, as anthropogenic disturbances were too great and unpredictable, no reliable comparison could be made. The remeasurement of the reforestation project nevertheless allowed the formulation of future recommendations and possibilities, which are described in Annex.

The increase of AGC in the natural forests with elevation in this study is in conflict with the generally proposed hypothesis of lower AGC at higher elevations. The study has however been confronted with some unavoidable build-up of uncertainty. Not only the relatively small number of PSP, their limited size and the unavoidable bias during their set up but also the lack of study area specific allometric relations, which resulted in the predominant use of just one allometric relation, might have given rise to a cumulating over- or underestimation of the AGC. However, left aside the built-up uncertainty during this study, other studies reported high AGC estimations at high altitudes and lower AGC at lower altitudes as well, confirming that our results are not a standalone case. Furthermore, most studies along an elevational gradient were confronted with the same uncertainties. Local variability of the forests per altitude couldn't be assessed accurately due to the small number of PSP and the auto-correlated nature of the often almost neighbouring PSP. It is therefore not possible to conclude the representativeness of the PSP for all forests at these altitudes.

We expected soil nutrient concentrations to be an important driver of any trend in AGC. However, none of the soil properties showed any correlation with the AGC. The expected shift from P to N limitation with elevation was not reflected in the ratio of soil total N over soil total P, which showed an increase instead of a decrease. However, when considering bio-available P instead of total P, soil

N/P did show a decrease. Moreover, also foliar N/P showed a decreasing trend with elevation. This indicates the importance of quantifying bio-available nutrient pools when considering tree growth. The assumed microbial net immobilization of N at the highest altitudes, associated with the lower litter quality, might have resulted in a larger pool of bio-unavailable N. Therefore, direct N mineralization rates might give a better insight into the present N cycling rates than total amounts. Indirect signs of the lower decomposition rates and associated N cycling rates were found in the lower C/N of litter and soil and lower $\delta^{15}\text{N}$ of litter and soil. However, these properties might be more strongly associated with the foliar nutrient concentrations which showed the same trends in nutrient ratios and isotopic composition as in the soil and litter. Hence, this strong interaction between the composition of the plant community and their associated traits and the soil properties is obvious from an evolutionary point of view but it also suggests that forest plant communities might be susceptible to changes in nutrient fluxes.

The underestimation of the AGC at the higher altitude forests might be an extra incentive for the protection of these forests. The increasing atmospheric deposition driven by farming and forest burning, forest clearances for cattle and the expected temperature increase over the coming decades due to climate change, might put these forests in jeopardy. Reforestation projects, like the one described in Annex, could provide a sustainable answer to this problem however.

The thesis starts with an elaborate literature review, providing a basis for the rest of this study. Followed by the material and methods, results, discussion and finally the conclusion.

2 Literature review

2.1 Tropical forests in the global carbon cycle

2.1.1 The global carbon cycle and the role of tropical forests in this cycle

The global carbon (C) cycle consists of three active pools which exchange C. The atmosphere, the oceans and the terrestrial biosphere (Falkowski et al. 2000). Without considering human influences these C pools remain in balance. Nevertheless, human activities during the last 200 years have caused shifts in this equilibrium, resulting in a well described increase of carbon dioxide (CO₂) in the atmosphere as the terrestrial biosphere and oceans only absorb about half of the anthropogenic CO₂ emissions (Schimel et al. 2001; Dixon et al. 1994). The atmosphere and the oceans exchange approximately 90 Gton of C each year in both directions, but the effects of climate change could disturb this equilibrium in the future (Falkowski et al. 2000). The CO₂ solubility (solubility pump) will decrease in the predicted warmer oceans, therefore organic sequestration by phytoplankton (biological pump) will need to be higher (Falkowski et al. 2000). But with the current knowledge it isn't possible to make accurate predictions of this outcome (Falkowski et al. 2000).

In Table 1 the estimated size of the different C pools is given (Falkowski et al. 2000).

Table 1 Size of the different C pools (Gigatons C) and their share of the total non-lithosphere (Ciais et al. 2013; Falkowski et al. 2000). The terrestrial C storage mainly occurs in forests (Falkowski et al. 2000).

C pools	Gigatons C	% of total non-lithosphere	
Atmosphere	830	1.8	
Oceans	38.400	81.3	
	Inorganic	37.400	79.2
	Organic	1.000	2.1
Terrestrial biosphere	2.000	4.2	
	Living biomass	600-1.000	1.8
	Dead biomass	1.200	2.5
Fossil Fuels	4.130	8.7	
Total non-lithosphere	47.250	100	
Lithosphere	75.000.000	1587.3	

The IPCC (Intergovernmental panel on climate change) estimates the amount of annually absorbed C in vegetation and soil to be between 0.9 and 4.3 Gt, with 55 % of the forest C stock located in tropical forests (Pan et al. 2011; Houghton 2005; IPCC 2014). Tropical forests are misleadingly called the lungs of the planet although they act as an important C sink rather than an emitter of CO₂ (Phillips 1998). Recent research nevertheless indicates a weakening of this C sink (Brienen et al. 2015; Pan et al. 2011; Malhi & Grace 2000; Naeem et al. 1996). Additionally, C emissions due to land use change (mainly deforestation), were estimated to be between 0.5 and 2.7 Gt of C per year, which is around 17 % of the total anthropogenic emissions of greenhouse gases (Pan et al. 2011). This deforestation causes a net C emission from tropical forests, despite the C uptake of recovering regrowth forest and growth of intact forest (Pan et al. 2011). Despite the large uncertainty, the importance of protecting forests and preventing further deterioration of forest ecosystems has become more and more evident for both the scientific community and policy-makers (Gibbs et al. 2007). As such, the Kyoto protocol of 1997 approved the grant of carbon credits for reforestation projects while the REDD program (Reducing Emissions from Deforestation and Degradation) stimulated governments to preserve forests.

2.1.2 C dynamics in forests

The C budget of forests can be described by several production terms (Figure 1). Plants take up atmospheric C through photosynthesis, using solar energy, and lose C through respiration. The Gross Primary Production (GPP) is thus the total rate of ecosystem-level C sequestration, while the Net

Primary Production (NPP) is the net rate, which equals the difference between the GPP and the plant or autotrophic respiration. When taking into account the heterotrophic respiration (decomposition of organic material and losses by herbivores) as well, the term Net Ecosystem Production (NEP) is used. Determining the NEP therefore requires differences in C stocks of vegetation and soil over time. However, when approaching the NEP as the net amount of C fixed from the atmosphere into new organic matter while taking into account decomposition, it can also be determined by integrating the incoming and outgoing CO₂ fluxes of the ecosystem. As both approaches don't allow to directly calculate the NEP, field obtained values are actually estimations. Moreover, NEP estimations should include an extensive list of elements; aboveground biomass increment, root increment, litterfall, losses to consumers, volatile and leached organics, dead roots and root exudates (Clark et al. 2001).

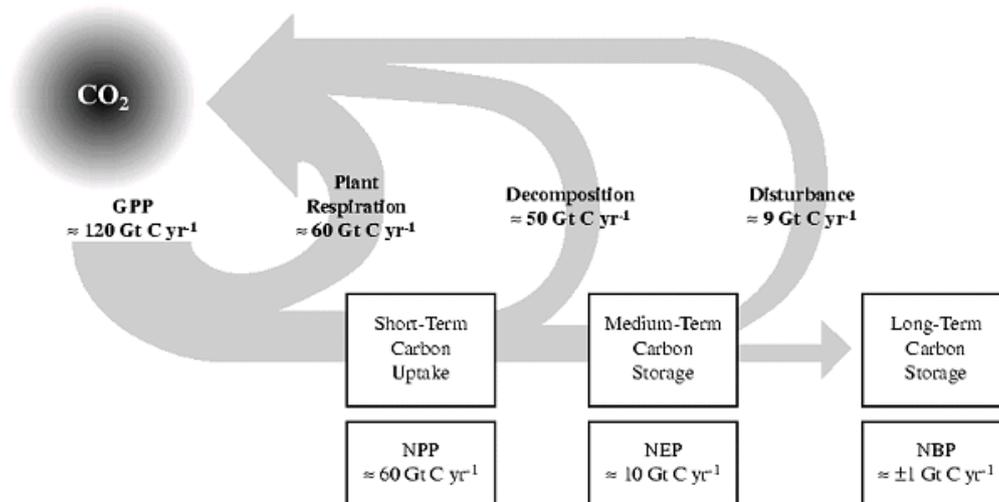


Figure 1 Scheme of global terrestrial C uptake. Plant (autotrophic) respiration releases CO₂ to the atmosphere, reducing GPP to NPP and resulting in short-term C uptake. Decomposition (heterotrophic respiration) of litter and soils in excess of that resulting from disturbance further releases CO₂ to the atmosphere, reducing NPP to NEP and resulting in medium-term C uptake. Disturbance from both natural and anthropogenic sources (e.g., harvest) leads to further release of CO₂ to the atmosphere by additional heterotrophic respiration and combustion-which, in turn, leads to long-term C storage. Adapted from Steffen et al. 1998.

2.1.3 Assessment of C storage in tropical forests

The main C pools of tropical forests are the living biomass of trees, the understory, the dead biomass of wood and litter and soil organic matter. The C storage in the living aboveground biomass (AGB) of trees is the largest pool in tropical forests and therefore the most crucial one for estimation (Table 2). The other C pools can be measured as well, but because of the time consuming nature of these measurements, default factors are widely used (Gibbs et al. 2007). For example, root biomass or belowground biomass (BGB) is usually estimated to be 20% of the AGB (Ramankutty et al. 2007). Field campaigns conducted to obtain forest inventories are tangible approaches of quantification. Through destructive harvesting, allometric equations relate measured attributes such as diameter, height and wood density to biomass. Local equations exist, but pantropical equations have proven to be as accurate as local ones (Chave et al. 2014). Remote sensing analyses combined with ground based inventories allow estimations on a far broader spatial scale. However, compared to other ecosystems, remote sensing of tropical forests has been prone to inaccuracy caused by the C richness and complexity of these ecosystems. Moreover, cloud cover limits the application of visual and infrared instruments.

Table 2 C storage as a percentage of the aboveground biomass (AGB) for tropical forests and for Ecuadorian tropical forests. Belowground biomass (BGB); Coarse woody debris (CWD)

Component	Source	% of AGB of mature forest	% of AGB Forest Ecuador (FAO 2015)
AGB		100	100
Understorey	Brown et al. 1997	< 3	
BGB (roots)	Brown et al. 1982	4-230	25
Litter	Brown et al. 1982	< 5	2
CWD	Delaney et al. 1998	5-40	14

2.1.4 Drivers behind C storage in tropical forests

Although the spatial variation in AGB has been recorded in some clear global patterns, the nature of the ecological drivers behind these patterns remains poorly understood (Baraloto et al. 2011; Malhi et al. 2006; Slik et al. 2010). Strong relationships between stand variables (height, basal area, stem density and wood density) and AGB are to be expected, being obviously inherent to the biomass of individual trees and forest (Chave et al. 2014; Rutishauser et al. 2010). Unlike basal area, height and stem density, the correlation of wood density with aboveground carbon (AGC) is less clear. Although Baker et al. (2004) suggested that the east-west gradient in AGB along the Amazon region was due to the similar gradient of wood density, other researchers contested his results in both the Neotropics and Asia (Stegen et al. 2009; Slik et al. 2010). The higher wood densities in the eastern Amazon were contributed to the slow growing nature of its forests leading to a higher AGB (Baker et al. 2004). Another possible reason for the higher AGB in this area was the higher BA being correlated to the length of the dry season (Malhi et al. 2004). Higher rainfall and shorter dry seasons have been associated with higher AGB in several other researches as well (Chave et al. 2014; Malhi et al. 2006; Quesada et al. 2010; Slik et al. 2010). Although just weakly explaining variations in AGB (Stegen et al. 2011), the effect of climate on AGB has been more consistent than that of soil fertility as both positive and negative effects of N and P concentrations on AGB have been reported (Laurance et al. 1999; DeWalt & Chave 2004; Paoli et al. 2008; Quesada et al. 2010; Quesada et al. 2012; Toledo et al. 2011; Ferry et al. 2012). Positive effects are associated with the increased productivity while the negative effects might be explained by higher turnover rates, leading to reduced standing stocks (Baraloto et al. 2011). Furthermore, as higher physical soil qualities are generally found on more weathered and chemically poorer soils, linking soil characteristics to AGC might be even more complex (Quesada et al. 2010). Quesada suggested a more comprehensive model, shown in Figure 2, taking into account both physical and chemical soil properties (Quesada et al. 2012). Therefore, AGC was determined by both production and turnover rates which are generally related to soil chemical and physical characteristics respectively (Quesada et al. 2012). Bad physical soil properties such as low rooting depth and drainage capacity, give rise to more disturbances and higher turnover rates (Quesada et al. 2009). On these soils, nutrient availability is generally higher allowing higher growth rates and a tendency to more fast growing tree species with shorter life cycles (Quesada et al. 2012). Hence, there is no incentive for trees to invest in more long term structures, and the required support for such structures, benefiting fast growing tree species with lower wood densities (Quesada et al. 2012).

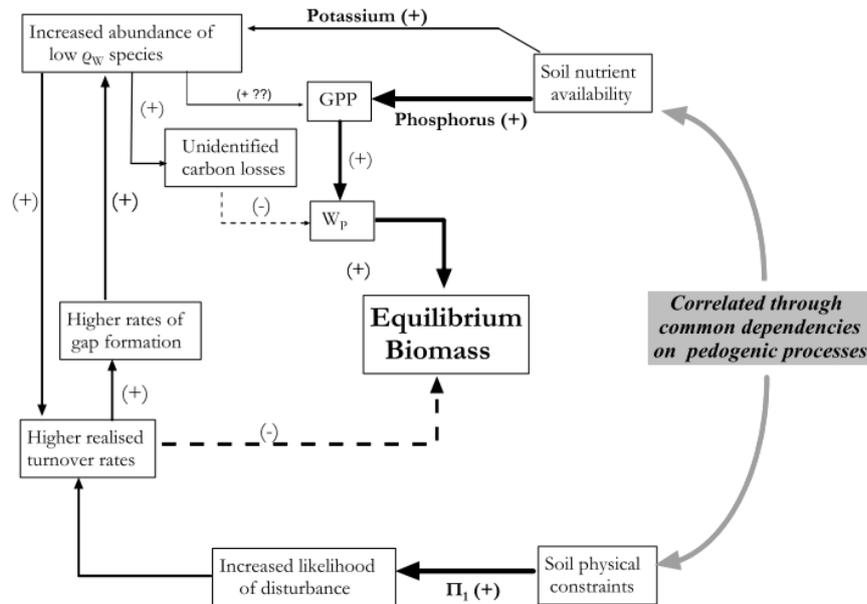


Figure 2 Differential effects of soil nutrients and adverse soil physical conditions on wood production (WP), turnover rates and wood density (ρ_w) of a lowland tropical forest. Both phosphorus (P) and potassium (K) rich soils give rise to higher production rates while physical soil constraints induce higher turnover rates due to a higher frequency of disturbances. Both the turnover and production rate influence the standing forest biomass. Adapted from Quesada et al. 2012.

2.2 Nutrients: the drivers of the forest C cycle

2.2.1 How do nutrients enter the forest ecosystem?

Whittaker describes the rainforest as a forest with “a relatively rich nutrient economy perched on a nutrient-poor substrate (Whittaker 1975).” Although appealing to categorize all forests of the tropics under this denominator, exceptions are omnipresent due to a wide variety of variables, such as climate, species composition, successional state, fertility and as will be discussed in more detail: altitude (Jordan & Herrera 1981; Cleveland et al. 2011a). Compared to boreal and temperate forests, the tropical forests generally have a high nutrient storage in standing biomass and a low forest floor nutrient content. This trend is mainly attributed to the different climate of tropical and boreal and temperate forests (Fernández-Martínez et al. 2014). Nutrients enter ecosystems through atmospheric deposition, weathering or N fixation and leave ecosystems through leaching or denitrification. Plants take up these nutrients and return them to the soil through falling leaves, dead stems and roots. After decomposition of this dead plant tissue, the nutrients are released and made available for uptake by plants, which closes the cycle.

The input itself is low compared to the amount of nutrients within the cycle, only contributing 5 to 30 percent of what trees need. Nevertheless, their continuous flow is important to compensate for nutrients leaving the system.

Weathering is the combination of physical and chemical processes which act upon the chemical structure of minerals, releasing nutrients. The process is slow and depends on temperature, precipitation and the parent material. There is a preferential release of the elements as well, depending on the solubility of the mineral and the tendency to form secondary minerals. In a decreasing order of release, the elements Ca, Na, Mg, K and Fe are brought in the soil solution by weathering. The contribution of weathering is undeniable at the long term, but just a fraction of the direct demand of growing plants, and hence considered a less important input on a shorter timescale.

Atmospheric deposition on the contrary can be a major contribution to ecosystems' nutrient levels and has gained increased interest in the recent decades, because anthropogenic perturbations of the atmosphere have led to an altered rainfall and deposition chemistry. These depositions can be divided into three types; wet, dry and cloud deposition of which the last one is limited to cloud immersed regions, like montane forests. Wet deposition enters forest soils directly through rainfall after canopy passage or after canopy contact. Nutrients which have settled on the canopy as dry deposition can be washed off eventually, but some nutrients (mainly K, Ca and Mg) might be absorbed by the leaves. There is a species specific variation in the chemical composition of this wash off which might be correlated with the occurrence of epiphytes (Cardelús & Mack 2010). The extent of dry deposition depends on wind, atmospheric concentrations of chemical components and canopy composition such as leaf size and area and is considered to be more variable in both quantity and distribution of nutrients. Increased atmospheric deposition in our temperate forests, caused by agricultural and industrial activities, has been a serious constraint on nature conservation targets, because it directly threatens nutrient-poor niches and hence biodiversity. The observed intensification of agriculture in tropical regions might similarly alter nutrient input rates and vegetation communities in the coming future. Especially, the poor mountainous Ecuadorian soils are prone to disturbances by the lingering depositions of sulphur and nitrogen (N) compounds, originating from biomass burning (Fabian et al. 2005; Makowski Giannoni et al. 2014; Boy et al. 2008). Changes here are not limited to increased uptake in leaves, as also changes in the soil microbial community, root biomass, leaf litter and stem growth have been observed (Homeier et al. 2012). A recent study suggests that the extra input isn't followed by an increased leaching of nutrients, as only 10 to 1 % of the applied N and phosphorus (P) fertilization in the Ecuadorian montane forests leached out. The largest part remained within the ecosystem, reflecting the characteristic nutrient limitation of this 'hungry' tropical forest (Wullaert et al. 2010). Finally, biological fixation is considered to be the largest natural input of N, with a relative higher importance in tropical forests on nutrient poor substrates (Reed et al. 2008). The input of free living bacteria is reported to be comparable to that of deposition (Matson et al. 2015) and significantly decreases with higher concentrations of N (Hedin et al. 2009). In disturbed forests on poor soils the effect of N fixers on legumes is therefore greater than on mature forests with a higher soil N content (Barron et al. 2011).

2.2.2 The nutrient cycle within forest ecosystems

The cycle of nutrients within the ecosystem is known as the biogeochemical cycle which involves the fluxes between trees and soil, with N and P as the two major nutrients. N circulates in a relatively open cycle under natural conditions in tropical forests (Schulze 2000) and strongly underpins the forest C cycle (Yang et al. 2011; Schulze 2000). Plants generally take up N under inorganic form (nitrate or ammonium) and release organic N forms through litter decomposition. Bacteria, fungi and soil fauna mineralize organic N and release ammonium which can be taken up by plants or which can be further processed to nitrate by nitrifying microorganisms (Schulze 2000). Mycorrhizae however are able to breakdown proteins (organic) and most likely contribute to the direct uptake of these organic amino acids by plants (Janos 1980; Fogel 1980). The recycling efficiency of tropical forests in terms of N are comparable to those of temperate forests, but use of P is considered to be more efficient in tropical forests due to the higher number of P deficient soils (Vitousek 1984; Davidson et al. 2007; Townsend et al. 2007). Chemical weathering in tropical soils releases aluminium and iron sesquioxides which have a considerable anion exchange capacity in the acid to neutral tropical soils, resulting in an almost irreversibly immobilization of P. Moreover, unlike the important atmospheric input of N, P enters the ecosystem only through weathering of minerals (Dieter et al. 2010), resulting in a declining availability of P with soil age. Therefore, researchers have looked for correlations between production and bio-available P with conflicting results (Herbert & Fownes 1995; Paoli et al. 2008). Total P on the other hand might have a stronger link with production on the long term than initially thought (Quesada et

al. 2012; Cleveland et al. 2011b) as microbial activity in tropical regions is generally higher than in temperate regions (McGlynn et al. 2007; Smith et al. 2015; Cleveland et al. 2004).

2.2.3 Stable isotopes: a key tool for an improved understanding of forest biogeochemistry

Before evaluating the use of stable isotopes in ecosystem analysis, a brief explanation of the notation is in order. Stable isotope compositions of N and C are generally described in δ notation and expressed in per mil (‰) (Craine et al. 2015).

$$\delta^{15}\text{N} = \frac{\left(\frac{^{15}\text{N}}{^{14}\text{N}}\right)_{\text{sample}}}{\left(\frac{^{15}\text{N}}{^{14}\text{N}}\right)_{\text{standard}}} - 1 \quad \delta^{13}\text{C} = \frac{\left(\frac{^{13}\text{C}}{^{12}\text{C}}\right)_{\text{sample}}}{\left(\frac{^{13}\text{C}}{^{12}\text{C}}\right)_{\text{standard}}} - 1$$

Where $(^{15}\text{N}/^{14}\text{N})_{\text{sample}}$ is the N isotopic composition of a sample and $(^{15}\text{N}/^{14}\text{N})_{\text{standard}}$ is the N isotopic composition of the standard material (Craine et al. 2015). For N this standard is atmospheric molecular N, which by convention is set 0 ‰ (Craine et al. 2015). While for C the standard is Pee Dee Belemnite (PDB) (Craine et al. 2015).

The ratio of ^{15}N and ^{14}N varies in the biosphere due to isotope fractionation in transformation processes such as mineralization, nitrification and denitrification, plant and mycorrhizal N uptake and redistribution of N within trees (Callesen et al. 2013; Högberg 1996). This feature allows us to identify N sources and fluxes within an ecosystem (Delwiche and Steyn 1970; Craine et al. 2015). The considered excessive nature of N within tropical forests compared to temperate forests suggests that this nutrient circulates in a more open circle in the tropical forests (Callesen et al. 2013; Martinelli et al. 1999; Boeckx et al. 2005). Ecosystems with a high N load are generally enriched in ^{15}N because N leaves the system mainly as dissolved inorganic nitrogen (DIN ; NO_3^- , NH_4^+) being poorer in ^{15}N than dissolved organic nitrogen (DON) which is the dominant form of N loss in systems with a low total N load (Högberg 1996; Högberg & Johannisson 1993; Robinson 2001; Boeckx et al. 2005). In addition, this distinction has been proposed as a potential method to track N mineralization as researchers described positive correlations with $\delta^{15}\text{N}$ (Dijkstra et al. 2008). Secondly, a recent study suggested that when C availability, and thus C/N, is low, soil microbial biomass preferably excretes N with low $\delta^{15}\text{N}$, resulting in an enrichment of ^{15}N in N rich ecosystems (Dijkstra et al. 2008). Therefore, the incorporation of microbial biomass in decomposing litter and SOM might add to the enrichment of these two latter pools (Dijkstra et al. 2008).

In low N ecosystems, $\delta^{15}\text{N}$ in the litter layer is relatively low, but in the soil there is a pronounced increase of $\delta^{15}\text{N}$ with depth (Hobbie & Högberg 2012) as decomposition processes become a more dominant influence on soil $\delta^{15}\text{N}$ in deeper layers (Baisden et al. 2002; Natelhoffer & Fry 1988). Moreover, the increasing age of SOM with depth (Craine et al. 2015), has been associated with a higher degree of microbial processing as C/N shows a decline with depth (Craine et al. 2015). However, in high N ecosystems the change in $\delta^{15}\text{N}$ with soil depth is less obvious because of the larger amount of N outflow and the reduced importance of mycorrhizae in the overall system (Hobbie & Högberg 2012).

When plants take up N in N rich environments they have the luxury to discriminate against the larger ^{15}N and predominantly incorporate ^{14}N . However, many factors might cause some pronounced variation in foliar $\delta^{15}\text{N}$. Mycorrhizae, for example have a preferential retention of ^{15}N and a preferential transfer of ^{14}N to host plants (Högberg et al. 2011; Craine et al. 2009). This means that in N rich ecosystems, with lowered importance of mycorrhizae, plants will be less facilitated by mycorrhizae to take up ^{14}N . In addition, fractionations during reduction of NO_3^- to NO_2^- to NH_4^+ and the subsequently incorporation of N into amino acids might enrich cytoplasmic inorganic N pools with ^{15}N (Needoba et al. 2004). Other influencing factors explaining the variation in foliar $\delta^{15}\text{N}$ might be differences in fixation, depth and N form of uptake and use of depositional N (Craine et al.

2015). Nevertheless, in general, researchers found a positive correlation between nutrient availability and foliar $\delta^{15}\text{N}$ during both fertilization experiments (Choi et al. 2005) and experiments that make use of natural fertility gradients (Craine et al. 2009).

The difference between plant and soil $\delta^{15}\text{N}$ is known as the enrichment factor, assuming that enriching processes begin with SOM and end at canopy level (Craine et al. 2015). Globally, plant material is depleted in ^{15}N compared to SOM (Craine et al. 2009) probably because of soil microbial enrichment, mycorrhizal influences and the predominant non-mineral depleted origin of inorganic N (Craine et al. 2015). However, the importance of each aspect needs further research (Craine et al. 2015). Moreover, the high variability in $\delta^{15}\text{N}$ associated with a wide spectrum of influencing factors such as depositional N input, particle size and N fixation, limit the straightforward use of enrichment factors for nutrient availability research (Craine et al. 2015).

Finally, climate, more specifically mean annual temperature (MAT) and mean annual precipitation (MAP) seem positively and negatively correlated with $\delta^{15}\text{N}$ respectively, in both leaves and soil (Amundson 2003; Craine et al. 2009). Furthermore, Amundson et al. 2003 found similar patterns in foliar and soil $\delta^{15}\text{N}$ for different climates (Amundson 2003). However, Craine et al. 2015 suggested that other covarying factors were predominant and that correlations between $\delta^{15}\text{N}$ and climate were only considerable within certain ranges (Craine et al. 2015). There was for example no relation between MAT lower than 9.8°C and soil $\delta^{15}\text{N}$ (Craine et al. 2015). Furthermore, after taking into account SOC and clay concentrations, $\delta^{15}\text{N}$ of SOM didn't show any correlation with MAT or MAP (Craine et al. 2015).

C isotope signatures on the other hand might give an indication of water use efficiencies (WUE) which can be described as the ratio of CO_2 accumulation to transpiration or stomatal conductance (g_s) (Seibt et al. 2008; Cernusak et al. 2008). This g_s can be described as the rate at which CO_2 enters or water vapour exits through the stomata of a leaf (Farquhar & Sharkey 1982). $\delta^{13}\text{C}$ is generally lower in plant material than in the atmosphere, indicating a discrimination of the heavier ^{13}C in plants during photosynthesis (Marshall & Zhang Jianwei 1994). This discrimination depends on the ratio between CO_2 concentration inside the leaf and atmospheric CO_2 concentration (C_i/C_a) which is linked to the photosynthetic demand for CO_2 and g_s (Farquhar et al. 1989). An increase in C assimilation or decrease in g_s results in an increased WUE and reduced leaf CO_2 concentration. The lower C_i/C_a ratio leads to a less pronounced discrimination of ^{13}C and therefore plant material with higher $\delta^{13}\text{C}$ probably has a higher WUE (Moghaddam et al. 2013). However, some aspects might limit the use of $\delta^{13}\text{C}$ to estimate WUE. Seibt (Seibt et al. 2008), reported that photosynthetic ^{13}C discrimination is more sensitive to the ratio of chloroplast to ambient CO_2 concentration (C_c/C_a) than to C_i/C_a , invoking the importance of the mesophyll conductance (g_m) on $\delta^{13}\text{C}$, with g_m being defined as the CO_2 transfer conductance from the intercellular airspaces of the leaf into the chloroplast (Bernacchi et al. 2002; Flexas et al. 2008). Moreover, as WUE depends on evaporative demand and g_s , while photosynthetic ^{13}C discrimination depends mainly on g_s and g_m , both can vary independently (Seibt et al. 2008; Farquhar & Sharkey 1982). For example, environmental conditions might influence $\delta^{13}\text{C}$ on a short time scale as plants respond to altered humidity and temperature, by adjusting g_s (Seibt et al. 2008). But also, long term changes can influence $\delta^{13}\text{C}$ as leaf structures might be altered as a response to drought, giving rise to a different g_m (Seibt et al. 2008).

2.3 Taking forest research to a higher level: elevational transects as an open-air laboratory for tropical forest ecology

2.3.1 Elevational transects and their importance in predicting forest responses to future global change

Although tropical forests have some major influences on global patterns of C storage and biodiversity they are relatively understudied (Malhi et al. 2010). Moreover, as the limited amount of data is mostly confined to the warm, wet lowlands, the great spatial variation in different tropical biomes remains

mainly unaccounted for (Malhi et al. 2010). Environmental gradients within the vast tropical region can significantly advance our understanding of ecosystem functioning. Hence elevational transects and their associated zonation of climate and plant communities, are ideal to fill this gap on a relatively small spatial scale (Körner 2007; Malhi et al. 2010). On the upper range of such elevational gradients the poorly studied tropical montane forests (TMF) are found, which are often considered simple upslope extensions of lowland tropical forests (Bubb et al. 2004). However, these forests are characterized by a very high biodiversity and variety of microclimates, able to support the migratory species in their upward flee from global change to montane refugia (Dodson & Gentry 1991; Rull 2009). The tropical Andean Biodiversity Hotspot is estimated to harbor one sixth of all plant species in less than 1 % of the land earth surface (Myers et al. 2000). Besides the relatively small spatial scale, there remain some other advantages of using elevational over latitudinal gradients. In tropical elevational transects, dormant seasons triggered by lower temperatures are rarely found, which avoids the entanglement of temperature seasonality with other variables such as productivity (Körner 2007; Malhi et al. 2010). Moreover, disturbances of human nature are more likely to be identified as such along the smaller elevational transects than over the large distances of latitudinal ones (Malhi et al. 2010). Finally, as tropical ecosystems are probably more susceptible to temperature changes because of less pronounced fluctuations during their evolution, their responses might give a clearer answer on the effects of future global change (Lu et al. 2009).

2.3.2 Tropical lowland forests versus tropical montane forests

In Ecuador many different ecosystems are present but most of them are under pressure of human disturbances, such as deforestation, forest degradation, cattle raising and oil (region of Yasuni) and copper exploitation (region of Intag). Because of the immense diversity of this relatively small country and the limits of this preliminary study our focus remains within the borders of North Western Ecuador, delineated by the Andes in the west and the sea in the east. The vegetation zones change from the lowest coasts to the highest peaks of the Andes, with lowland (“tierras bajas”) from 0 to 300 m, foothill (“piemontano”) from 300 to 1300 m, low montane (“montano bajo”) from 1300 to 1800 m, montane (“montano”) from 1800 to 3000 and higher montane zones (“montano alto”) from 3000 to 3400 m (Sierra 1999). These altitudinal limits are different for east and west, north and south Ecuador, and even within these zones variation does exist, meaning that the limit of a vegetation type in the north for example can be 300 or 400 m lower in the south. Therefore, to make a distinction of the ecosystems in the specific study area a floristic approach was considered, which is nowadays used in all of Ecuador (Sierra 1999; Ministerio del Ambiente 2013). One of the reasons for the occurrence of similar vegetation types at different altitudes is the Massenerhebung or mountain mass elevation effect, being the driving force behind the occurrence of tropical montane cloud forests (TMCF) at lower altitudes on isolated peaks than on large, massif mountains (Bruijnzeel & Hamilton 2000; Bruijnzeel et al. 1993). Higher temperatures are afforded by the greater sheer mass of larger mountains due to a larger uptake of solar radiation and a slower release of longwave radiation, resulting into more upward cloud formation (Bruijnzeel et al. 2011; Aldrich et al. 1997; Jarvis et al. 2011). The occurrence of certain mountainous ecotones seems to be related to the amount of fog they receive, with frequent fog in lower montane forests and very frequent to almost persistent fog in upper montane forests (Grubb 1971; Oliveira et al. 2014). Besides changing meteorological conditions, soil characteristics such as, altitudinal increases of SOM, accompanied by the more frequent presence of mor humus and moss layers’ at higher altitudes, correlate with the altitudinal floristic zonation as well (Ashton 2003; Quesada et al. 2010). Despite the undeniable influence of climate on soil, also topography and substrate might have some underestimated contributions in dividing the different ecotones (Ashton 2003).

In general, tropical montane forests differ in many ways from lowland tropical forests (Table 3). Both in structure (low tree height, small and tough leaves, low leaf area index (LAI), high amount of roots,

different species compositions and low diversity) and in functioning (low productivity and low nutrient cycling rates) (Malhi et al. 2010). Reasons for these changes could be: periodic drought stress (despite the cloud cover), water saturated soil and decreased soil respiration (especially in stony and shallow soils), low temperatures and radiation, lower photosynthetic activity, limited nutrient supply and uptake, strong winds and the presence of phenolic components and aluminum (Bruijnzeel et al. 1998; Bruijnzeel 2010).

The tall (25-45m), often buttressed trees of the three storied lowland rainforest are gradually displaced by the lower trees of the two storied lower montane forest (Hamilton et al. 1995). This changing tree structure is accompanied by the increased number of epiphytes such as ferns and orchids and the decrease of woody climbers, which were abundant in the lowland. Higher up, the lower montane forests give way to a new formation; upper montane forest with trees being generally more short statured (2-20m), mossy and immersed in dense cloud described as a “persistent, frequent or seasonal cloud cover at the vegetation level (Grubb 1977).” However, difficulties regarding quantification of horizontal precipitation and duration of cloud cover have led to controversy, especially when making the distinction between simple montane and cloud montane rainforest (Hostettler 2002). This cloud cover influences the interaction with the atmosphere through reduced solar radiation and vapor deficit, canopy wetting and suppressing of evapotranspiration. This has a direct effect on some of the forest properties; leaves become smaller and harder, stems get covered almost entirely by liverworts, mosses and epiphytes while the trees themselves show a stunted, gnarled growth and palms are replaced by bamboo as dominant undergrowth species. The glistening wet stems in the morning sun has given rise to the terms elfin or fairy forest (Bruijnzeel et al. 2000). The majority of these tropical montane cloud forests (TMCF) are found along the Andean Cordillera which runs through the entire country (Aldrich et al. 1997). Although these forests are characterized by a very high endemism (Frahm et al. 1991; Jankowski et al. 2007) and important watershed protection function (Bruijnzeel et al. 1993; Bruijnzeel 2001; Oliveira et al. 2014; Stadtmuller et al. 1990), their existence is threatened by anthropogenic activities. Only 4 % of the forests along the western slope remains (Dodson & Gentry 1991). The hydrological importance of TMCF is coupled to its erosion prevention (Sidle et al. 2006) and extensive cloud cover resulting in increased streamflow volumes through additional inputs of cloud water interception (CWI) and reduced evapotranspiration (Bruijnzeel et al. 2011; Gomez-Peralta et al. 2008). The share of CWI in the total moisture content a forest receives might range between 15 and 100 % of the precipitation, depending on altitude, exposition and whether the conditions are humid or dry (L. A. Bruijnzeel, F. N. Scatena 2011). During the dry season the contribution of CWI might even be double that of the wet season (Holder 2004). Moreover, the reduced transpiration caused by the decreases of vapor pressure deficit (VPD) and incoming photosynthetic active radiation (PAR), associated with the lower temperature and higher cloud cover at higher altitudes, might reduce water losses to the atmosphere (Berry & Smith 2012; Gotsch et al. 2014; Reinhardt & Smith 2008). Annual evapotranspiration rates decrease from 1350 mm to 300 mm with increasing altitude, mainly due to the increased fog cover (Grubb & Whitmore 1966; Jarvis & Mulligan 2011). The prevalent water film which is formed on the leaves, might suppress transpiration even further (Letts & Mulligan 2005) but might also strengthen another input known as direct foliar water uptake (FWU) (Eller et al. 2013; Goldsmith et al. 2012). Recent studies have confirmed the importance of FWU in TMCF water fluxes and its influence on survival rates and leaf traits (Eller et al. 2013; Goldsmith et al. 2012).

Table 3 Summary of forest characteristics along an elevational gradient (Sierra 1999). The leaf size decreases with elevation from mesophyll to notophyll and finally microphyll leaves. Lianas are typical woody climbers.

Formation	Lowland evergreen forest	Evergreen lower montane forest	Evergreen upper montane forest
Canopy height	24-45 m	15-33 m	1.5-18 m
Number of canopy strata	3	2	1
Leaf size-class	mesophyll	notophyll	microphyll
Buttresses	frequent and large	uncommon or small	Usually absent
Cauliflory	Frequent	rare	absent
Woody climbers	abundant	usually none	none
Bole climbers	often abundant	frequent to abundant	very few
Vascular epiphytes	Frequent	abundant	frequent
Non-vascular epiphytes	occasional	Occasional to abundant	Often abundant

2.3.3 C storage along an elevational gradient

The total C stock itself does generally not show any elevational gradient, but the allocation of C to aboveground features have been found to reduce in favour of belowground elements (Leuschner et al. 2007; Moser et al. 2011; Malhi et al. 2006). Moreover, decreasing temperature in lowland tropical moist forest, being a variable inherently associated to elevational gradients, has been shown to induce the transition from forests with a large biomass and small detritus stock to forests with a small biomass and high detritus stock, without any significant difference in total C stock (Raich et al. 2006).

Although contested by some (Girardin et al. 2010) a decrease in AGB has been established in numerous studies (Moser et al. 2011; Aiba & Kitayama 1999; Harris et al. 2008). The decrease of AGB has been attributed to a reduced C canopy gain caused by a lower LAI and photosynthetic activity, which in turn might be caused by lower temperatures, N limitation and cloud cover resulting in lower insolation (Moser et al. 2011; Moser et al. 2007; Bruijnzeel et al. 2013; Zach et al. 2010). The C canopy gain determines the C source strength of the forest, while the merismatic activity of a forest determines the C sink strength. Although appealing to attribute the reduction of the AGB directly to reduced temperature and the associated reduced merismatic activity, it conflicts with the increase of BGB (Moser et al. 2011; Zach et al. 2010). Cloud cover and its associated reduction of insolation could therefore have a greater influence on biomass production than temperature.

2.3.4 Litter and decomposition

Litterfall is an important aspect of the annual production with around 30 % of the NPP in tropical forests (Aragão et al. 2009). Although accumulated layers of litter thicken with increasing elevation due to the declining decay of organic material, the annual litterfall itself decreases (Silver 1998; Raich et al. 1997; Moser et al. 2011; Arnold et al. 2009; Grubb 1977; Wolf et al. 2011; Tanner et al. 1998). Fertilization experiments proved the importance of nutrient availability, which revealed an increased productivity with increased amounts of N supply (Adamek et al. 2009; Wright et al. 2011). Nevertheless, similar experiments making use of natural soil richness gradients showed more contrasting results, probably caused by the transition of different functional groups along the elevational gradient (Santiago & Mulkey 2005). Ectomycorrhizal (EM) communities with higher N efficiency might outcompete arbuscular mycorrhizal (AM) communities at higher altitudes where N becomes more limiting, resulting in a gradual shift of functional groups with elevation (Phillips et al. 2013; McGuire et al. 2010). Besides a production element and therefore part of the C cycle, litter layers play a crucial role in supplying and storing nutrients (Vitousek 1984). With increasing elevation decay declines caused by lower temperature (Salinas et al. 2011; He et al. 2009). But also soil moisture, humus properties and litter quality play an important role (Couteaux et al. 1995). In wet lowland rainforest the latter two are most constraining because of optimal temperature and moisture conditions (Tanner et al. 1998). The lower quality of litter at higher elevations is simultaneously an indicator of nutrient poor environments and an amplifier of the low nutrient status; higher C/N and

C/P ratios result in slower decompositions and a slower and smaller release of nutrients (Vitousek 1984). Besides C nutrients ratios, phenolic substances might influence decomposition rates as well. Bruijnzeel and Veneklaas (1998) attributed the higher concentrations of phenolic components in leaves of TMCF to the higher irradiance of UV-B through the reflection of lower clouds (Bruijnzeel & Veneklaas 1998; Hamilton et al. 1995). These phenolic components protect leaves from the harmful radiation but reduce decomposition and might have toxic effects on plant growth, potentially explaining the stunted growth of trees from TMCF.

2.3.5 C fluxes along an elevational gradient

The carbon use efficiency (CUE) is described as the ratio of NPP over GPP, or the fraction of C fixed that is stored in the biomass (Girardin et al. 2013). On a global scale, CUE of terrestrial ecosystems, seem to increase with increasing altitude and latitude and decreasing precipitation and temperature (Zhang et al. 2009). But comparisons between lowland and montane forest suggest a similar CUE because of the parallel decrease of NPP and GPP with increasing altitude (Girardin et al. 2013; van de Weg et al. 2014; Aiba & Kitayama 1999; Girardin et al. 2010; Raich et al. 1997). Nevertheless, poor estimations of transfer through root exudates and to mycorrhizal communities might have a considerable impact on these results (Malhi et al. 2011). Typical CUE values for old growth tropical forests range between 0.3 and 0.5. Hence between 70 and 50 % of the C initially assimilated as biomass is released rapidly into the atmosphere through autotrophic respiration (Chambers et al. 2000; Giardina et al. 2003; Malhi et al. 2011; Malhi et al. 2009; Girardin et al. 2013). The CUE along the elevation gradient makes a shift from aboveground and belowground features, probably caused by the earlier mentioned shift in C allocation. In Southern Ecuador, along an elevational gradient from 1000 to 3000 masl, stem CUE decreased from 0.46 to 0.16 and root CUE increased from 0.17 to 0.55 (Zach et al. 2010). The ratio of growth respiration over total respiration showed a similar trend for both the stem and root aspect (Zach et al. 2010; Robertson et al. 2010; Harris et al. 2008). Although temperature shows the most consistent decrease with elevation, other variables than temperature might be the real direct drivers behind the changing CUE and respiration rates. For example, stomatal conductance of forests at high altitudes shows a significant sensitivity to photosynthetic active radiation (PAR) and vapor pressure deficits (VPD), as a response to relatively quickly changing cloud cover and the associated variability of both PAR and VPD (Motzer et al. 2005). Moreover, the lower carbon source strength of the canopy and its influence on the CUE might be masked by the covariance of the more predictable and quantifiable temperature values. The combination of these factors, which might not vary continuously with altitude, might explain the less pronounced variation of autotrophic respiration along the elevation gradient, compared to the heterotrophic respiration (Robertson et al. 2010). The latter one is mainly determined by temperature, which is strongly correlated with elevation. Furthermore, this more pronounced temperature sensitivity of heterotrophic respiration explains the slower decay of litter at higher sites (Zimmermann et al. 2009; Salinas et al. 2011).

2.3.6 Nutrient fluxes along an elevational gradient

Nutrients might be limiting growth in ecosystems when the demand of plant communities is higher than the supply. In practice, nutrient limitation in tropical forests is recognized when additions of a certain element increase productivity (Vitousek et al. 2010). N and P are known to be limiting in terrestrial ecosystems (Vitousek & Sanford 1986; Tanner et al. 1998), but lowland tropical forests are generally more P limited (Cleveland et al. 2011b), while highland forests are more N limited (Fisher et al. 2013; Tanner et al. 1998; Graefe et al. 2010; Soethe et al. 2008; Nottingham et al. 2015). The montane forest soils are geologically young and therefore retrogradation of P is less advanced than in older, more weathered soils of the lowlands (Lambers et al. 2008; Walker & Syers 1976). This induces a higher amount of bio-available P in montane forests. The youthfulness of these montane soils is also contributed to a higher frequency of landslides and a slower decomposition and weathering caused by the lower temperatures (Salinas et al. 2011). In contrast, P uptake by trees on strongly weathered soils from lowland forests is mainly regulated by the rate of recycling P from litter and the turnover rate of other organic components (Johnson et al. 2003; Vincent et al. 2010; Foster & Bhatti 2006). This

weathering driven retrogradation of P is the most well-known and probably most important factor along altitudinal gradients explaining P limitation. Nevertheless, other factors such as soil barriers which prevent access to P, parent materials with low amounts of P and anthropogenic changes which will rather increase amounts of elements other than P, might have an influence (Vitousek et al. 2010). In lowland forest there is less N limitation due to fast plant turnover and decomposition. In comparison to P, N accumulates over time and has a much more open cycle. This means that N limitation might be mitigated by atmospheric deposition. Another mitigating factor might be the increasing temperature attributed to climate change, which results in higher mineralization rates and the associated higher release of N in the soil (Salinas et al. 2011). The increased N limitation with altitude is related to higher foliar C/N and lower N/P ratios (Koerselman & Meuleman 1996) and the storage of N in accumulating litter material, being unavailable for plant uptake (Grubb 1977; Fisher et al. 2013). Both N mineralization and net nitrification decrease with elevation while the microbial immobilization of N increases, suggesting decreasing N cycling rates (Hart, Stephen C, Stark, J.M., Davidson, E.A., Firestone 1994; Arnold et al. 2009; Wolf et al. 2011; Grubb 1977; Marrs et al. 1988). In addition, Mooshammer et al. (2014) suggested that microbial communities regulate their nitrogen use efficiency (NUE) in response to C and N limitation, resulting in higher and lower N mineralization respectively (Mooshammer et al. 2014; Sterner & Elser 2002). Finally, $\delta^{15}\text{N}$, reflecting the long term characteristics of the soil N cycle, seems to decrease with elevation which is also an indication for lower N cycling rates at higher altitudes (Arnold et al. 2009). The relative enrichment of $\delta^{15}\text{N}$ in ecosystems with higher N cycling is due to increased share of nitrification and denitrification and the associated isotopic fractionation (Arnold et al. 2009).

2.3.7 Nutrient availability

The potential of forests to store extra amounts of C as a response to the predicted increase of CO_2 levels (Clark 2004) will depend partially on their capacity to utilize nutrients efficiently and flexible (Joseph Wright 2013; Cernusak et al. 2013; Reich & Hobbie 2012; Reich et al. 2006; Reich et al. 2014). Tropical trees generally have lower foliar N and P concentrations than temperate forest, probably because of lower P availability and higher growth rates, requiring higher nutrient use efficiencies (Lovelock et al. 2007). The lower foliar P concentrations are more pronounced, even to that extent that foliar N/P values are larger in tropical trees than in temperate and boreal trees (McGroddy et al. 2004). Foliar nutrient concentrations in tropical trees have been used in several studies to estimate nutrient limitation of tree productivity (Tanner et al. 1998; Vitousek 1984; Soethe et al. 2008; Hiremath & Ewel 2001). But, several studies have already indicated that the low flexibility in foliar N/P values of individual trees might limit its response to changes in nutrient availability (Hessen et al. 2004; Sterner & Elser 2002; Sistla & Schimel 2012). Foliar N is generally more associated with specific species traits rather than soil fertility compared to P (Townsend et al. 2007). N in leaves is mainly incorporated in structural amino acids (Chapin et al. 1990), while P is generally stored in labile, non-structural components (Bialeski 1973). Moreover, lower foliar N concentrations in moist and herbivore rich environments have been attributed to the lower risk on fungi infestation (Edwards 1982) and herbivore damage (Fine et al. 2013). Finally, tropical trees have a higher and more variable P resorption than N resorption (Yuan & Chen 2009; Killingbeck 1996) which is probably associated with the lower P availability of tropical soils (Alvarez-Clare & Brooks 2013) and the high variability of soil fertility itself (Quesada et al. 2010). Therefore, both species composition of plant communities and nutrient availability of the concerned soils might influence foliar nutrient concentrations (Mayor et al. 2014). Some researchers have reported strong correlations between soil fertility and foliar nutrient concentrations along an elevation gradient (Soethe et al. 2008; Tanner et al. 1998). These elevational gradients are characterized by strong changes in environmental conditions and topographic features, resulting in clear transitions of plant communities and soil conditions. The entanglement of nutrient availability, taxonomic diversity and other co-varying factors such as light and moist, limits the use of foliar nutrient concentrations for accurate productivity estimations (Townsend et al. 2007; Vitousek et al. 2010), but on the other hand adds to the understanding of the ecology of plant communities and their linkage with the environment.

3 Material and methods

3.1 Study Area

The studied natural forests were located in the provinces Pichincha and Imbabura of North Western Ecuador at altitudes ranging from 400 up to 3200 masl (Figure A 5). These forests were described using the system of classification for continental Ecuador (Ministerio del Ambiente, Ecuador, 2013), the available maps (Figure A 1) and the field descriptions. All natural plots were located in the range where tropical montane cloud forests might occur as can be seen in (Figure A 3). Despite the established importance of cloud cover on tree growth, no reliable estimations of its contribution could be made. The soils at all four altitudes can be described as Andosols according to the FAO classification (Figure A 4). These are soils with good water retention, low bulk density, sandy to loamy texture and high susceptibility to erosion (López et al. 2002). The parent material at the different locations is described in Table 4. The natural forests in Ecuador have been facing human pressures for decades. Also the signs of disturbances just outside the measurement plots were hard to miss and raised questions about the pristine nature of the fragmented forest areas themselves. This can be seen in Figure A 6, which visualizes the different land covers and land uses of the study area.

Table 4 Description of the parent material at the different altitudes. P_{ST}: Pleistocene (2.85 Ma – 11.7 ka), K_S: late Cretaceous (65-100 Ma), g: intrusive. Fanglomerates are a type of conglomerate consisting of heterogeneous rock fragments of all sizes deposited in an alluvial fan. Redbeds volcanics are sedimentary rocks of volcanic origin, that are predominantly red in color due to the presence of ferric oxides (Gardi et al. 2015).

Altitude (masl)	Origin	Material
400	P _{ST}	Lahars, fanglomerates, ash/mud flows
1100		
1900	K _S	Redbed volcanics
3200	G	Granitic/acid

3.1.1 Climate

There is not much climatic knowledge regarding the Andean slopes (Rollenbeck et al. 2006). Moreover, climate, for example the rain distribution, is different on the western and eastern slope (Garreaud 2009). Arid and cold conditions dominate the coast side and extend into the western slope of the Andes (Garreaud 2009). The dry season runs from July to November (Rollenbeck et al. 2006), as can be seen in Figure 3.

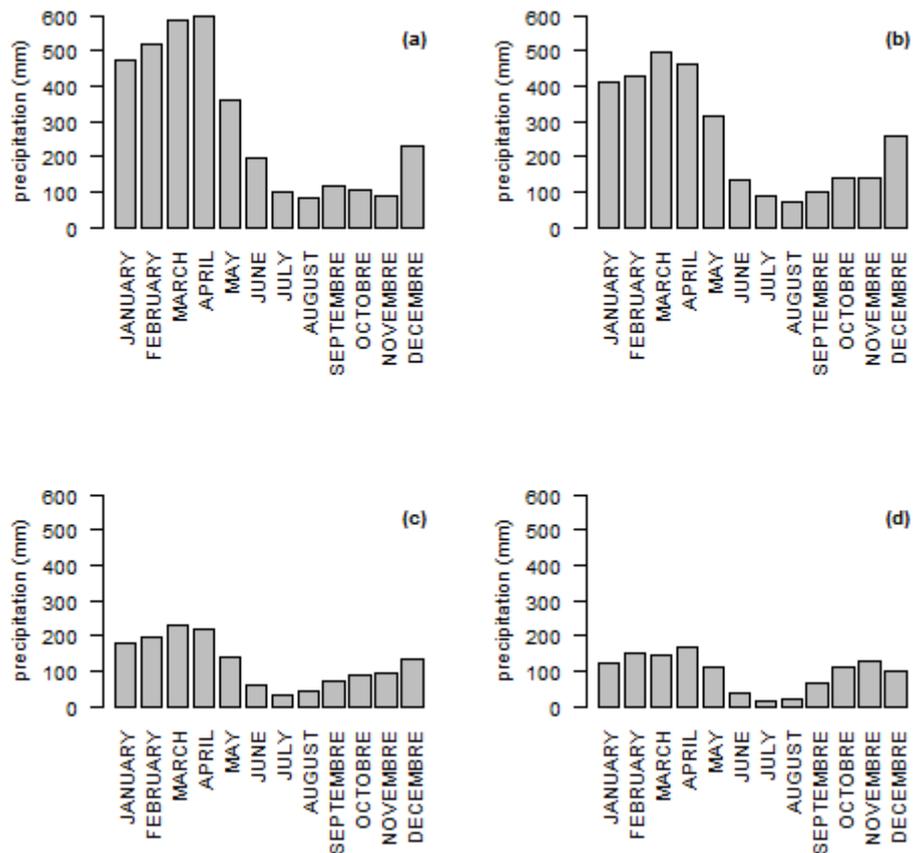


Figure 3 Average monthly precipitation. (a) at 400 masl (b) at 1100 masl (c) at 1900 masl (d) at 3200 masl. The average monthly precipitation was obtained from the Worldclim dataset (Hijmans et al. 2005; Worldclim) with a spatial resolution of 1 km². It should be noted that climatic variables in montane areas are difficult to model (Garreaud 2009) and unaccounted local variances caused by horizontal precipitation, cloud cover and winds might have a serious impact on water availability (Bruijnzeel & Veneklaas 1998; Killeen et al. 2007; Bendix et al. 2006).

Data from meteorological stations in Northern West Ecuador ranging from 400 to 3200 masl was extracted from temperature maps (INAMHI) (Figure 4). The mean annual temperature measured from 1981 to 2010 against the altitude resulted in a good linear fit ($R^2 = 0.933$) with temperature decreasing 0.48°C with every 100 m of rising altitude. Because local temperature measurements of our plots were missing these estimations were used. We were not able to determine a similar relationship for precipitation because of the greater variance with altitude (Girardin et al. 2013; Körner 2007). The average monthly precipitation was obtained from the Worldclim dataset with a spatial resolution of 1 km². To validate our temperature estimations, they were compared with data from Worldclim which was similar for the lowland rainforest but significantly smaller for the forests higher-up. Estimations of the other climatic variables (Table 5) were made after consulting INAMHI, the ministry of environment of Ecuador and the Worldclim database.

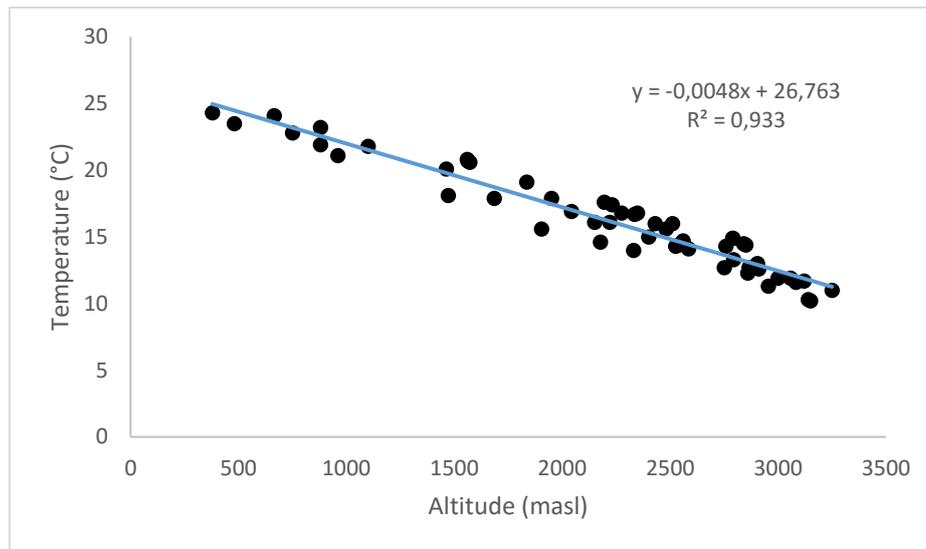


Figure 4 Air temperature in function of altitude for North-Western Ecuador using data from INAMHI (INAMHI)

Table 5 Climatic variables of the studied natural forests (INAMHI; Worldclim; Hijmans et al. 2005). MAT stands for mean annual temperature and MAP stands for mean annual precipitation.

Altitude (masl)	MAT (°C)	MAP (mm)	Solar Irradiance (Wh m ⁻² day ⁻¹)
400	24.81	3447	4415
1110	21.64	3047	4228
1900	17.78	1492	3830
3200	11.32	1181	3618

3.1.2 Forest description

3.1.2.1 Rio Silance (400 masl)

The plots at 400 masl were all located within the Rio Silanche Bird Sanctuary (Mindó Cloud Forest foundation, MCF), a lowland to hilly evergreen rainforest (“bosque siempreverde de tierras bajas del Choco Ecuatorial” and “bosque siempreverde piemontano de Cordillera Occidental de los Andes”) (Ministerio del Ambiente 2013) in the Pichincha province. MAT was 24.81 °C and MAP was around 3450 mm. The canopy consisted of multiple layers of vegetation and large emergent trees. The most dominant tree species were *Pouruma sp.*, *Protium sp.*, *Guarea sp.* and *Ceiba sp.*. Palm trees such as *Wettinia quinaria* and *Iriartea deltoidea* were abundant as well. Some tree ferns were present. The area around the reserve suffered from intense agricultural practices. At the northern border, forest recently had been cut to provide space for banana plantations while at the western border cattle was grazing.

3.1.2.2 Milpe (1100 masl)

The plots at 1100 masl were all located within the Milpe Bird Sanctuary (MCF), a hilly evergreen rainforest (Ministerio del Ambiente 2013) in the Pichincha province. MAT was 21.64 °C and MAP was around 3047 mm. The most dominant tree species were *Andira sp.*, *Otoba gordonifolia*, *Rinorea sp.*, *Ficus sp.*, *Tovomita weddelliana*, *Inga sp.* and *Eugenia sp.*. Palm trees were almost absent. The reserve contained forest which was considered natural although some parts were clearly of recent age and still

recovering. The plots were set up in the zone which was considered natural while further upslope of the plots, there were signs of grazing and deforestation.

3.1.2.3 Maquipucuna (1900 masl)

The plots at 1900 masl were all located within the Maquipucuna reserve, a lower montane evergreen rainforest (“bosque siempreverde montano bajo de Cordillera Occidental de los Andes”) (Sierra 1999; Ministerio del Ambiente 2013) in the Pichincha province. MAT was 17.78 °C and MAP was around 1500 mm. The Maquipucuna Reserve consists of more than 6000 ha, with an altitudinal range from 1000 to 2800 masl, of which more than 80 % is considered to be pristine. The rest consists of secondary forest, pastures and small farms (Tian et al. 2007). The recorded plant diversity ranges up to 2000 species (Webster 2007). The most dominant tree species were *Nectandra sp.*, *Otoba gordonifolia*, *Ruagea sp.*, *Cecropia sp.*, *Critoniopsis sp.*, and *Miconia sp.*. The almost closed forest canopy is formed by tall evergreen trees. The litter layer on the forest floor stays continuously wet and leaves of understory plants are often covered with mosses. Araceae are the predominant epiphytic plants. (Stephenson et al. 2004).

3.1.2.4 Puranquí, Intag (3200 masl)

The plots at 3200 masl were all located within a montane evergreen rainforest (“bosque siempreverde montano alto de Cordillera Occidental de los Andes” (Sierra 1999; Ministerio del Ambiente 2013)) of the Intag region in the Imbabura province. MAT was 11.32 °C and MAP was around 1200 mm. The relatively low (10-15 m) but broad trees grow irregularly and often in a tilted, almost horizontal fashion and form branches from the base. The tree species *Freziera canescens* contributes to more than 70 % of the AGB. Other dominant species were *Weinmannia pinnata*, *Clusia sp.*, *Gordonia fruticosa*, *Oreopanax sp.* and *Clethra sp.* The forest itself resembles an isolated island with abrupt borders of treeless Paramo. Keeping the human disturbances of the lower strata in mind, the sharp delineation seemed the work of farmers and the relentless grazing of their cattle. But significantly different soil types and characteristics of similar forest-versus-Paramo patches suggest a possible coexistence of these two ecosystems for millennia (Nierop et al. 2007). Nevertheless, the intact nature of this forest ecosystem and its neighbouring Paramo remains presumptive, as cows were present, forest fires were burning in the horizon and some 200 m below, forests were cleared and degraded.



Figure 5 From left to right: The forest at 400 masl, 1100 masl, 1900 masl and 3200 masl.

3.2 Field protocol

This protocol is mainly based on the rainfor protocol, a widely used guide to make comparison with other research more convenient, in combination with earlier protocols designed for the Andes region in specific (Condesan 2013). The primary objective of this field campaign was to determine the carbon stocks in undisturbed forest. By choosing plots on different altitudes, we tried to determine altitudinal gradients in ecological processes. We established and measured 4 to 5 PSP in 4 altitudinal strata.

3.2.1.1 Phase one: Selection of sites

In undisturbed forest, PSP were established with dimensions of 40x40m. In each of the 4 strata (Rio Silance at 400 masl, Milpe at 1100 masl, Maquipucuna at 1900 masl and Puranquí (Intag) at 3200 masl). 4 to 5 plots were randomly sampled. However, the desired randomness wasn't always attainable, because of different considerations we had to keep in mind. Soil homogeneity within one plot, accessibility, no disturbances by human or landslides, closed canopies without major treefalls and moderately steep slopes (10-30°) (Salinas et al. 2011). The condition of closed canopies, was assumed to be related to mature forests. Nevertheless, natural disturbances such as landslides do occur in mature forests as well and by avoiding this natural dynamic, there is a risk of overestimation of the forest aboveground biomass.

3.2.1.2 Phase two: Permanent Monitoring plot establishment

The main axes of the plots were oriented north-south and east-west and the centre point was registered with a GPS. The plots were square formed. Squares have a lower edge/area ratio, which gives less decision problems concerning edge trees. For the undisturbed plots, the size of 40x40m was chosen. This is smaller than recommended, but in previous field campaigns it proved that larger plots

are not efficient and practical because of extreme topography and the lack of visibility in the forest in this region (Bauters 2013). The internal as well as the external boundaries of the plots were delineated with 20 meters' segments. The slope of each border was determined every 10m with the forestry pro, which resulted in 32 slope measurements per plot. The borders were recalculated using the slope to find the planimetric border length. The centre of each plot was marked with a plastic tube. The borders were marked with small poles made of young trees outside the plot. After the first corner was marked we walked off the border in a straight line. After twenty meters walking this imaginary border another pole was planted. After another twenty meters the second corner was marked with another pole. This procedure was repeated for the remaining three sides. Finally, we connected the centre of the plot to each pole other than those at the corners. These poles were 20 m away from at least one of the corners. However, often the distance between the poles and the corners was not 20 m, which had to be taken into account for the calculations.

3.2.1.3 Phase three: Marking, measuring and counting of trees and other vegetation

The marking of the trees was done with numeration tags. For this the tag was nailed in the stem at 1.60 m, or 0.30 meters above the measuring point. The tagging was done on the same side of the tree for every subplot which helped to visualize the subplot delineation lines. A tree was included in the plot if >50% of the root system was inside the plot. Trees that looked dead or dying were checked by looking at the cambium. Dead or dying trees weren't measured. Multiple-stemmed trees were tagged only on the largest stem at 1.30 m height. Fallen trees were checked carefully to see if they were still alive. They were tagged 1.60 m from the tree base. Each liana stem that was >10 cm diameter at any point within 2.5 m of the ground, even if <10 cm at 1.30 m was tagged and measured.

Diameters were measured at 1.3 m height (diameter at breast height (DBH) at point of measurement (POM)). If 1.3 m wasn't used as the POM to avoid buttresses or deformities the height of measurement was recorded. The reference height was not the vertical height above the ground, but the straight line distance along the trunk, even if it was leaning or bent. When measuring, the tape was passed under any vines or roots on the stem and was then moved back and forth to clean the POM of loose bark and debris. Hemi-epiphytes, or lianas that closely hugged the stem were lifted, not cut. If the tree was buttressed at 1.3 m, the stem was measured 50 cm above the top of the buttress. The height of POM was recorded. If the tree had a major stem deformity at 1.3 m height, then 2 cm below the deformity was measured. POM height was recorded as well. The diameter at breast height (DBH) was always calculated on the uphill side of the tree, and trees that had fallen or were leaning were always measured at 1.3 m length along the side of the stem furthest of the ground. All stems of trees with multiple stems were measured if these were greater than 10 cm at 1.3 m. We ignored understory trees and shrubs, and standing or lying dead trunks (Wilcke et al. 2005). We included any liana or hemi-epiphyte that reached 10cm diameter at any point along the stem between 0 and 2.5m above the ground.

Tree heights were measured, to establish plot level diameter/height relationships for accurate modelling of tree-by-tree volumes for each plot. The aim was to characterize the 'ideal' height/diameter curve as determined by climatic and edaphic conditions and not to be confused by the influence of damaged trees. The laser of the forestry pro can be fired vertically into the crown from several points directly below the crown of the tree and height recorded as the height of the observer plus the distance of the furthest return for the laser. An advantage of laser range finders is that it is impossible to overestimate the height of independent tall crowns and measurements are faster than with the traditional hypsometers. Nevertheless, some disadvantage became obvious in the field as well. The minimum distance between the point of measurement and the device was 10 meter, therefore it wasn't possible to remain underneath trees which were smaller than 10 m. Measurements had to occur further away from the tree and because of the distinctive slopes this increased the error

of measurement. The laser didn't work under very misty conditions which are to be expected in cloud forests. Under these circumstances less advanced, more user dependable equipment such as the traditional hypsometers could be preferred. Moreover, there isn't much difference in accuracy between measuring 90 or 20 % of the tree heights (see 10.2.1).

3.2.1.4 Phase four: Soil sampling

The samples were collected per plot at the standardized depths of 0-5cm, 5-10cm, 10-20cm, 20-30cm, 30-50cm and 50-100cm and stored in zip locks. Soil bulk density was recorded using an Eijkelkamp soil sampling ring. Bulk densities were initially taken at several depths to account for vertical variance. This method was nevertheless very time consuming and was therefore abandoned, instead bulk densities were measured between 5 and 10 cm, presuming a higher contribution of the upper layers in terms of carbon and nutrients. This bulk density was then used for the entire soil column. The deeper layers generally have a higher bulk density, but possible real trends are masked by high variances within one measurement location and between the several measurement locations of the same stratum (Figure A 9). The objective was to make a comparison along an altitudinal gradient, therefore bulk densities should be comparable in the way they were obtained. The bulk density of the forest at 1100 masl (measurements were initially only at 30 cm) was therefore considered as the average of A1 and A3, which were comparable soils and only depths of 0-5 cm were considered for further analysis (Figure A 9). 5 samples per plot were randomly taken. 4 in the center of each subplot and one in the center of the plot. Per plot mixed samples were made of every depth, resulting in 6 samples per plot and 24 to 30 for every stratum. The litter was sampled by setting up 3 to 4 random squares of 25 X 25 cm in every plot and removing all the litter in this area. The litter was then stored in zip locks and dried.

3.3 Lab protocol

3.3.1 Soil

The soil samples were dried for minimal 2 days at 60 °C. Afterwards they were mixed. We sieved all samples at 2 mm but some unsieved soil was processed as well to analyse the impact of sieving. Big aggregates were grinded manually before passing them through the sieve. Roots, leaves and stones were manually removed. The samples were grinded using a bullet grinder for 2 minutes at 260 tpm. All samples were sieved but some non-sieved material was analysed as well (Figure A 10).

For the analysis of N, C and its isotopes, a continuous flow analyser was used. All individual samples were measured which included depth measurements in intervals of 0-5, 5-10, 10-20, 20-30, 30-50 and >50 cm of depth, over 4-5 plots in each of the four strata. For the measurement of the exchangeable cations, P concentrations (both bio-available and total) and Al concentrations, mixed samples were used. These samples included the interval between 0-30 cm of depth for each plot, resulting in one sample per plot.

AEM strips were used to extract bio-available P from soil using HCl and concentrations were measured using spectrophotometry at a wavelength of 650 nm. Soil pH was measured for two different solutions, demineralized water and 1 M KCL. The soil-solution volume ratio was 1/5. A pH electrode was used and pH was recorded after stabilization. Total P was measured after destruction in acid. A barium chloride (BaCl) extraction was used to measure the concentrations of exchangeable cations. Atomic absorption spectroscopy was used to measure the concentration of calcium (Ca), magnesium (Mg), sodium (Na), potassium (K) and aluminium (Al) (p 76).

3.3.2 Litter and leaf material

Litter material was dried for minimal two days at 60°C and afterwards grinded using a bullet grinder for 2 minutes at 260 tpm. For the analysis of N, C and its isotopes, a continuous flow analyser was used. All litter samples were tested on total P concentrations. After ashing and dissolving in HCl, total P was measured using the continuous flow analyser (method No. G-103-93 Rev. 2). Comparable analyses

were used for the leaves, which are described more into depth in the thesis of Miro Demol (Demol 2016).

3.4 Analysis

3.4.1 Surface

Planimetric surfaces were calculated and used to describe the variables per surface unit. The 40x40m plot was subdivided in 20x20m subplots. When setting up the plot and delineating the subplots we tried to approach a square form, which was unattainable in an area characterized by steep slopes. Nevertheless, it was possible to make an approximation of the area as all the lengths of the subplot sides were known and all the outer angles could be considered to be 90°. Every side was first corrected separately for the slope by multiplying the length with the cosine of the slope. In Figure 6 a subplot is shown with the measured lengths and angle of 90°.

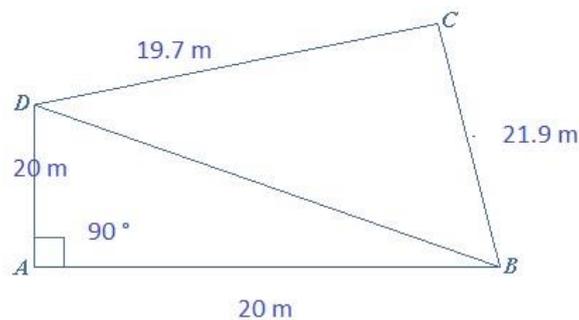


Figure 6 Example of a left-corner subplot of a PSP. The outer angle was considered to be 90° and all the sides of the subplot were known.

The length of the diagonal and surface of the triangle ABD are easily calculated. For the surface measurement of the triangle BCD first the perimeter (p) of this triangle is measured. Then the surface can be calculated as:

$$\text{Area of } BCD = \sqrt{p * (p - DC) * (p - BC) * (p - BD)}$$

The area of the quadrilateral is the sum of the both triangles. All investigated components are quantified in function of the planimetric surface (p^*) unless indicated otherwise (e^*).

3.4.2 Allometric relations for the natural forests

Allometric model construction is based on regressing a dependent variable (i.e. AGB), against one or several independent variables. First, diameter and height measurements were used to setup height-diameter relationships. Nonlinear least-square estimates of the parameters of seventeen published relationships were made using the measured height and diameters (Bates & Watts 1988; Huang et al. 1992; Scaranello et al. 2012; Brown et al. 1989; Banin et al. 2012; Feldpausch et al. 2011; Feldpausch et al. 2012) (Table A 1). The best relationship for each plot was determined based on the Akaike Information Criterion (AIC) and used to estimate the lacking height values for the remaining trees (Hu 1987). 150 of the 1362 (11%) measured trees lacked height measurements. Broken trees, tree ferns and lianas were excluded from the relationship.

Wood densities were assigned to each tree based on tree species determination. Because of the immense diversity of the Ecuadorian forests not all trees species could be determined. The trees with determinations at species or genus level were assigned a density which was derived from the DRYAD database. In contrast to the genus level means, which give reliable approximations of the undetermined species level, within-family densities show a high variability in wood density (Chave et

al. 2006). Therefore, both trees with determinations at family level and trees without determination were assigned a plot averaged density.

Chave et al. (2014) described a pan-tropical allometric relation for tropical forests with DBH, tree height and wood density as variables. In earlier studies Chave made a distinction between wet, moist and dry forest stands. In wet forests evapotranspiration exceeds precipitation for less than one month, which is the case for lowland rainforests with precipitation of more than 3500 mm and montane cloud forests. Moist forests receive between 1500 and 3500 mm, while dry forests receive less than 1500 mm. The first stratum is definitely a wet forest and, based on precipitation only, the two forests at mid altitude and the forest at the highest altitude are moist and dry forests respectively. But the difficulty of defining cloud forests as such makes the distinction less clear as all four strata are possible cloud forests (Figure A 3) (Chave et al. 2005), therefore the pantropical relation of Chave et al. (2014) was preferred. In Table 6 the considered and used allometric equations are summarized. AGC was assumed to be 50 % of the AGB, as is commonly assumed in similar research (Brown & Lugo 1982).

Table 6 Allometric equations used to calculate the aboveground biomass. AGB stands for aboveground biomass in ton ha^{-1} ; AGC stands for aboveground carbon in ton C ha^{-1} ; WD stands for wood density in g cm^{-3} ; DBH stands for diameter at breast height in cm; H stands for tree height in m. Given are the literature source, the equation and the forest type for which the equation is intended.

Source	Allometric equation	Forest type
Chave et al. 2014	$AGB_{tree} = 0.0673 * (WD * DBH^2 * H)^{0.976}$	Tropical forest
Chave et al. 2005	$AGB_{tree} = \exp(-2.817 + 0.916 * \ln(WD * H * DBH^2))$	Dry forest
Chave et al. 2005	$AGB_{tree} = \exp(-2.977 + \ln(WD * H * DBH^2))$	Moist forest
Chave et al. 2005	$AGB_{tree} = \exp(-2.557 + 0.940 * \ln(WD * H * DBH^2))$	Wet forest
Beets et al. 2012	$AGC_{fern} = 0.0027 * DBH^2 * H$	Tree ferns, tropical forest
Saldarriaga et al. 1988	$AGB_{palm} = \exp(-6.3789 - 0.877 * \ln(DBH^{-2}) + 2.151 * \ln(H))$	Palms, tropical forest
Nenninger 2006	$AGB_{tree} = 0.07 * DBH^{2.417}$	Montane forest
Perez 2010	$AGB_{tree} = (-0.967735 + 0.64874 * DBH)^2$	Montane forest
Chamorro et al. 2012	$AGB_{tree} = 0.87754 * (DBH^2 * H)^{0.65358}$	Montane forest
Feldpausch et al. 2012	$AGB_{tree} = \exp(-2.9205 + 0.9894 * \ln(WD * H * DBH^2))$	Tropical forest

The pan-tropical relation of Chave has proven to be of comparable accuracy with local equations. It isn't possible to assess the uncertainty of this equation for our dataset because of lacking biomass values. Therefore, absolute values should be analyzed with care. Moreover, the continuous changing tree structure along the elevation gradient could cause stronger under or overestimations with elevation, resulting in a misunderstanding of the trend of the AGB. An allometric relation specifically designed for montane forests could reveal the importance of this shift in tree structure from low to higher altitude, but there are not many available, left alone for the Andes region or Ecuador (UN-REDD 2013). We found some studies which attained allometric relations for montane forest in Columbia, Venezuela, Peru and Ecuador (Perez 2010; FAO 1975; Nenninger 2006) but none was satisfying to use for our conditions.

Nevertheless, the dominance of *Freziera canescens* in the highest stratum and the unique architecture of this tree (Goodman et al. 2014) (low thick stem with early branching) could justify the use of a specific allometric relationship like the one of Chamorro et al. (2012). Sadly, this equation was designed for 13 dispersed trees within a narrow range of small diameters.

Other equations determined in the montane forests of the Andes region could provide additional insights into species specific allometries of montane forest trees by comparing them with the pantropical relationship of Chave et al. (2014) and other allometric relationships that were mainly based on lowland forest data. Sadly, the datasets behind these local equations are not always

exchanged within the scientific community and remain standalone studies within local reserves. These studies could fill the gap of lacking accurate biomass estimations because there are several weaknesses associated with the completeness, documentation and communication of allometric equations in montane forests. Uncertain biome description, lack of background information about the setup, missing definitions of variables and wrong species determinations all contribute to uncertainty which could be avoided. Nevertheless, there have been some efforts to collect and describe allometric relations, such as the database of GlobAllomeTree.

In this study, a distinction was made between trees, palm trees and tree ferns. Palm trees and tree ferns have unique structures and characteristics and were therefore submitted to specific allometric relations (Rich 1987). The allometric relationship of Saldarragia et al. (1988) was used for palm trees and the relationship of Beets et al. (2012) was used for tree ferns.

3.4.3 Statistics

For the statistical analysis R was used (R Core Team 2014). Kruskal-Wallis tests (K-W) were used to test whether samples originated from the same distribution. The significance of differences between the strata were tested using a subsequent Mann–Whitney two-sample test (U-test; mctp package in R). Different letters indicate significant differences between the four strata ($p=0.05$). Averages of the researched variables are given in tables together with their standard error. Finally, Pearson correlation coefficients were determined (Becker et al. 1988). Correlations were rejected at $p=0.05$ unless stated otherwise.

4 Results

4.1 Stand structure

The average basal area per tree and the total basal area of the different strata increased a 1.7 and 2 fold respectively from the lowest to the highest stand while the tree height and slenderness decreased both 1.5 fold and canopy height decreased 1.2 fold from the lowest to the highest stand (Figure 7). Stem density did not show a continuous trend with altitude and varied strongly among plots of the same strata (Figure 7).

Table 7 gives the average values of the above mentioned variables at each altitude. The slenderness of a tree was defined as the ratio of tree height over DBH.

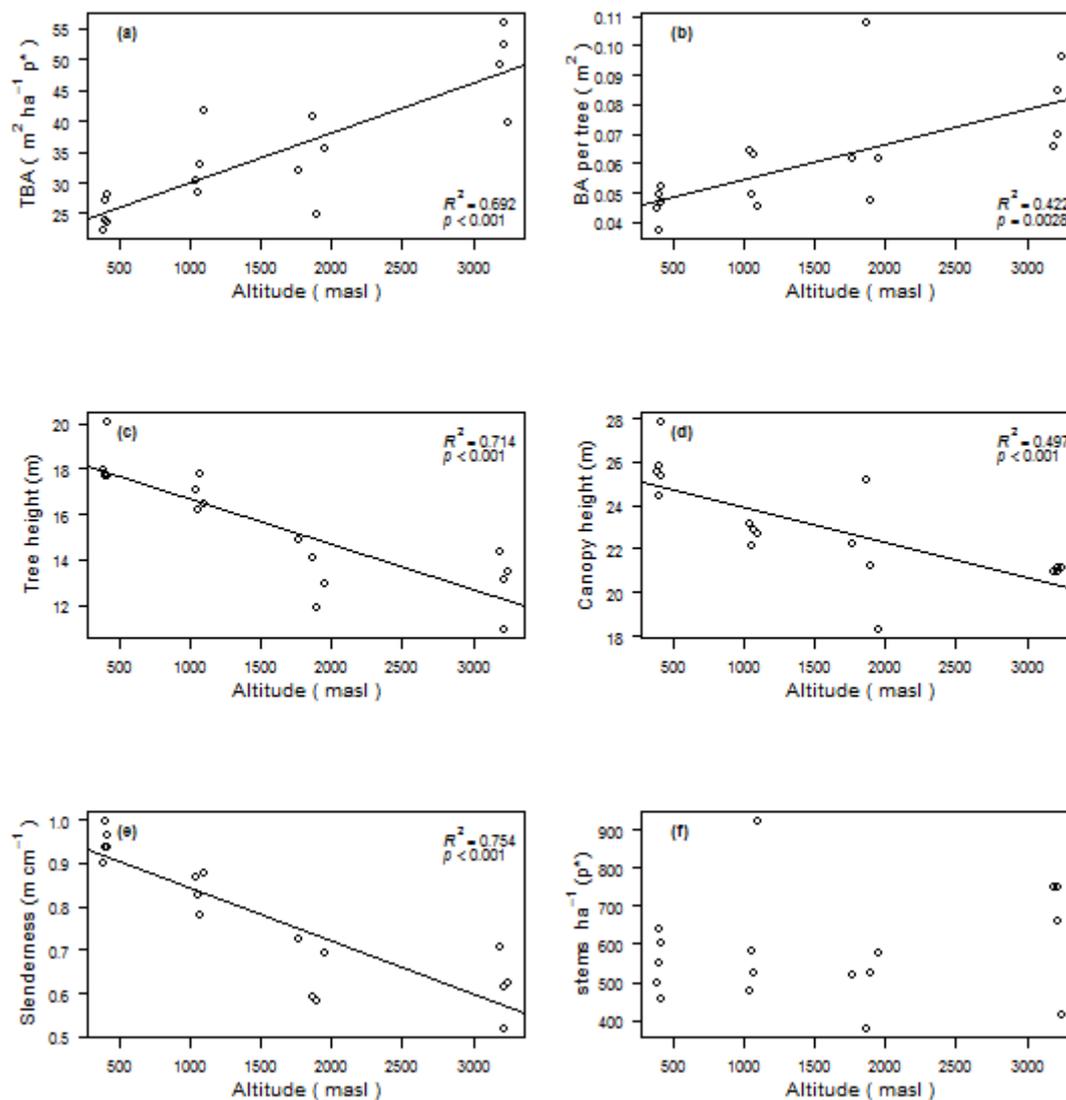


Figure 7 Stand structure variables of the forests in function of altitude. p^* stands for planimetric surface. (a) Total basal area (TBA) in $\text{m}^2 \text{ha}^{-1} \text{p}^*$; (b) Basal area per tree (BA) in m^2 , (c) Tree height in m; (d) The 90 percentile of tree height as an approximation of canopy height in m; (e) Slenderness which is calculated as tree height over diameter in m cm^{-1} ; (f) Stems $\text{ha}^{-1} \text{p}^*$. Linear regressions were visualized and R^2 values were given when $p < 0.05$.

Table 7 Stand structure variables (mean \pm 1SE) of the forests at different altitudes. Different letters indicate significant differences between the four strata ($p=0.05$).

Altitude (masl)	400	1100	1900	3200
Average total basal area (m ² ha ⁻¹)	25.00 (a) ±3.14	33.42 (bc) ±9.38	33.23 (abc) ±10.75	49.35 (bc) ±11.04
Average basal area per tree (m ²)	0.046 (a) ±0.0059	0.053 (a) ±0.0076	0.068 (ab) ±0.014	0.077 (b) ±0.011
Average tree height (m)	18.25 (a) ±1.28	16.85 (b) ±1.14	13.47 (c) ±2.07	12.95 (c) ±2.28
Canopy height (m)	25.77 (a) ±1.58	22.71 (b) ±0.67	21.73 (abc) ±4.53	21.02 (c) ±0.17
Slenderness (m cm ⁻¹)	0.9461 ±0.0459	0.8380 ±0.0707	0.6479 ±0.1146	0.6149 ±0.1207
Stem density (trees ha ⁻¹)	549 (a) ±93	625 (a) ±324	500 (a) ±136	644 (a) ±253

4.2 C storage

4.2.1 AGC

Using the allometric equations of Chave et al. (2014) for trees, Saldarragia et al (1988) for palm trees and Beets et al. 2012 for tree ferns (Table 6) there seems to be an increase in AGC, though not significant for the entire range and with exception of the plots at 1900 masl (Figure 8 and Table 8).

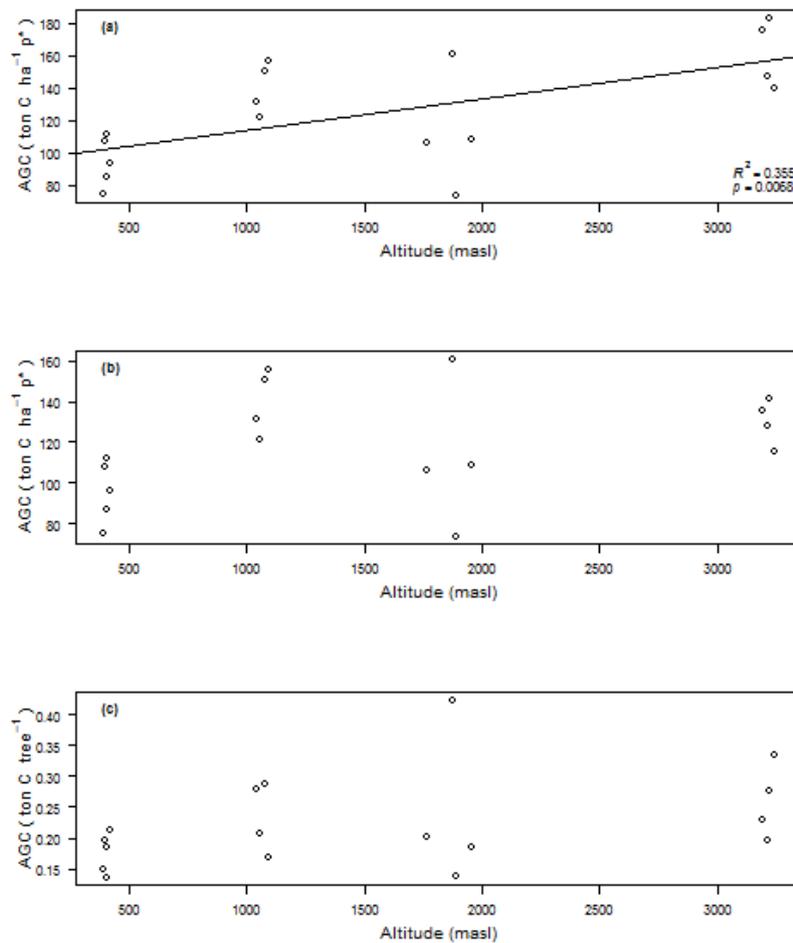


Figure 8 Aboveground carbon (AGC) in $\text{ton C ha}^{-1} \text{p}^*$ in function of altitude (masl). p^* stands for planimetric surface. AGC was assumed to be 50 % of the aboveground biomass (AGB), as is commonly assumed in similar research. (a) AGC in $\text{ton C ha}^{-1} \text{p}^*$. The allometric relation of Chave et al. (2014) was used to estimate carbon storage of the trees, Saldarraga et al. (1988) for the palms and Beets et al. (2012) for the tree ferns; (b) AGC in $\text{ton C ha}^{-1} \text{p}^*$. The allometric relation of Chave et al. (2014) was used for the trees with exception of the trees at 3200 masl for which the equation of Chamorro et al. (2012) was used. Saldarraga et al. (1988) was used for the palms and Beets et al. (2012) for the tree ferns; (c) AGC in ton C tree^{-1} , estimated with the same allometric equations as in (a). Linear regressions were visualized and R^2 values were given when $p < 0.05$.

Table 8 Aboveground carbon (AGC) in $\text{ton C ha}^{-1} \text{p}^*$ (mean \pm 1SE) at the different altitudes (masl). p^* stands for planimetric surface. Different letters indicate significant differences between the four strata ($p=0.05$). The literature sources of the used allometric equations is given.

Altitude (masl)	400	1100	1900	3200	Literature source
Mean AGC ($\text{ton C ha}^{-1} \text{p}^*$)	95.52 (a) ± 18.88	139.44 (b) ± 25.43	112.14 (ab) ± 57.71	161.04 (b) ± 33.83	(Chave et al. 2014; Saldarraga et al. 1988; Beets et al. 2012)
Mean AGC ($\text{ton C ha}^{-1} \text{p}^*$)	95.26 (a) ± 18.88	139.44 (b) ± 25.43	112.14 (ab) ± 57.71	130.10 (b) ± 17.73	(Chave et al. 2014; Saldarraga et al. 1988; Beets et al. 2012; Chamorro et al. 2012)
Mean AGC ($\text{ton C ha}^{-1} \text{p}^*$)	87.71 (a) ± 17.38	127.78 (b) ± 23.33	102.74 (ab) ± 54.42	147.48 (b) ± 31.22	(Feldpausch et al. 2012; Saldarraga et al. 1988; Beets et al. 2012)
AGC per tree (ton C)	0.17 (a) ± 0.039	0.23 (a) ± 0.090	0.24 (a) ± 0.20	0.25 (a) ± 0.081	(Chave et al. 2014; Saldarraga et al. 1988; Beets et al. 2012)

4.2.2 SOC

C concentrations in the soil were only significantly higher at the highest altitude both on a mass and land area base (Figure 10 and Table 9). The SOC values in ton ha^{-1} were questionable high (Figure A

14), even for volcanic soils. This was probably caused by inadequate soil bulk density measurements. On a mass base SOC values from 400 to 1900 masl ranged between 0.06 to 0.08 g g⁻¹ while at 3200 masl SOC was more than 2-fold higher with values up to 0.17 g g⁻¹.

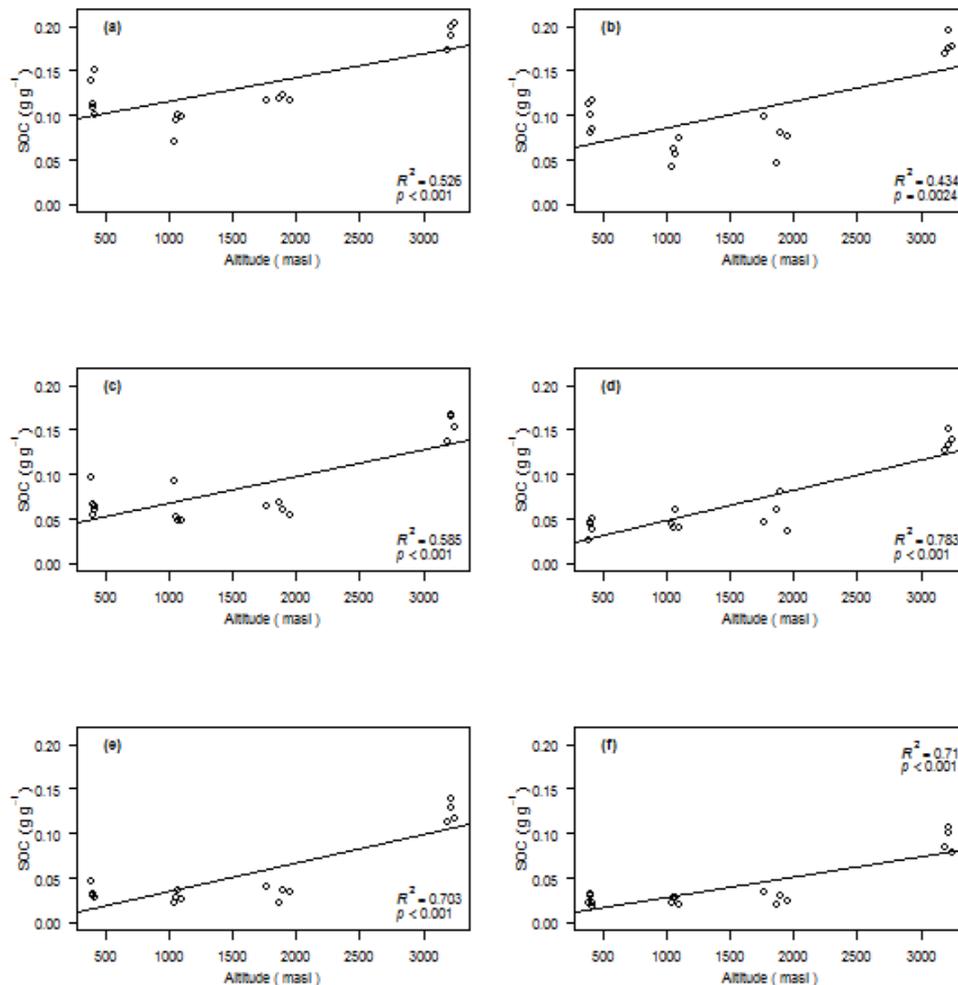


Figure 9 Altitudinal patterns of soil organic carbon (SOC) in g g⁻¹ at different soil depths. (a) 0-5 cm soil depth, (b) 5-10 cm, (c) 10-20 cm, (d) 20-30 cm, (e) 30-50 cm, (f) >50 cm. Linear regressions were visualized and R² values were given when p<0.05.

Table 9 Soil organic carbon (SOC) in g g⁻¹ of the upper 30 cm of soil (mean ± 1SE) in function of altitude (masl). Different letters indicate significant differences between the four strata (p=0.05).

Altitude (masl)	400	1100	1900	3200
SOC (g g ⁻¹)	0.073 (a)	0.061 (a)	0.072 (a)	0.16 (b)
	±0.0091	±0.0059	±0.012	±0.017

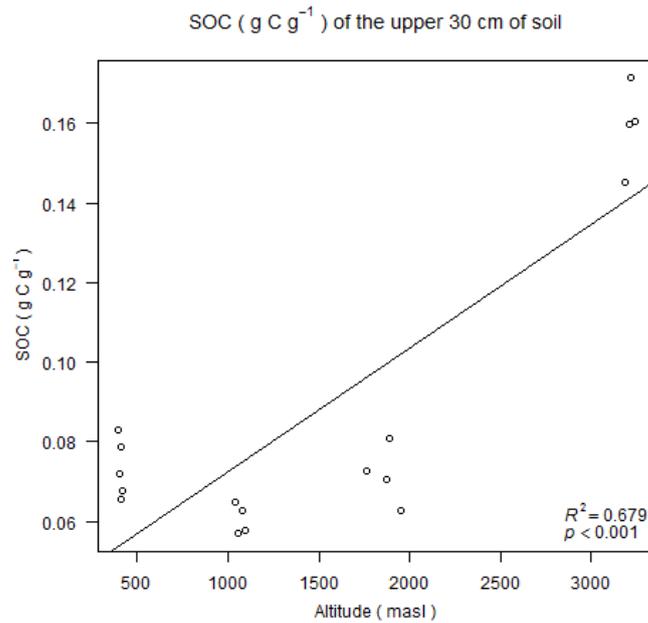


Figure 10 Soil organic carbon (SOC) in g⁻¹ of the upper 30 cm of soil in function of altitude. The linear regression was visualized and the R² value was given as p<0.05.

4.3 Soil characteristics

In the upper 10 cm of soil, total N concentrations reached a significant minimum at mid-altitude (1100-1900 masl), while the lowest (400 masl) and highest (3200 masl) altitude shared a comparable high amount of N (Figure 11). In the deeper layers these concentrations decreased more rapidly at the mid- and lower altitude compared to the highest altitude. Resulting in a significant lower N concentration at the deeper soil layers (>20 cm) from 400 to 1900 masl compared to the N concentrations at the highest stratum. In these deeper soil layers there was no significant change in N from 400 to 1900 masl

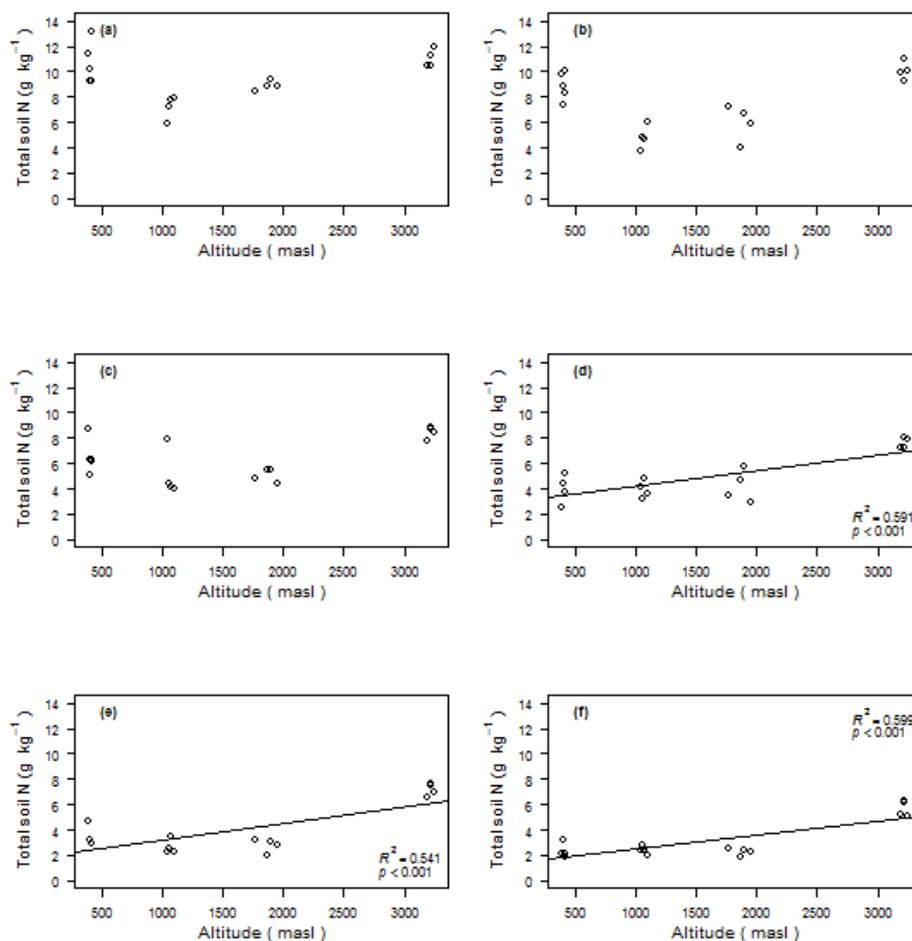


Figure 11 Altitudinal patterns in soil total N concentrations in g kg⁻¹ at different soil depths. (a) 0-5 cm soil depth, (b) 5-10 cm, (c) 10-20 cm, (d) 20-30 cm, (e) 30-50 cm, (f) >50 cm. Linear regressions were visualized and R² values were given when p < 0.05.

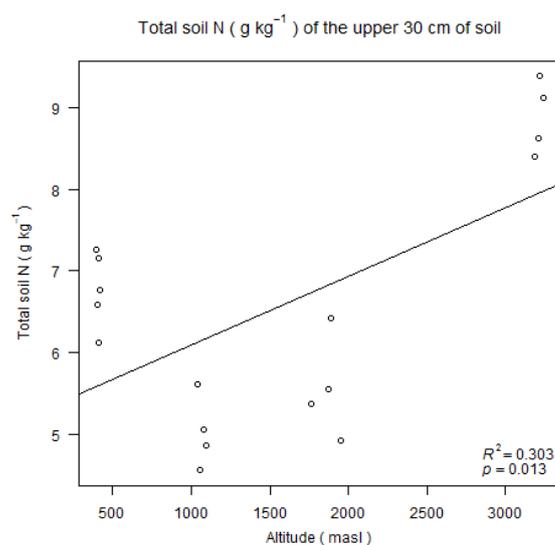


Figure 12 Soil total N in g kg⁻¹ of the upper 30 cm of soil in function of altitude. The linear regression was visualized and the R² value was given as p < 0.05.

The bio-available P concentration and ratio of bio-available P to total P increased drastically from 400 m to 1900 masl after which it decreased less pronounced towards the highest stratum (Figure 13). Total P showed a slightly similar trend as to N for the range of 400 to 1900 masl but didn't increase that drastically at the highest stratum, moreover, concentrations at the highest stratum were significantly lower than those at 400 masl. There were no significant correlations between N and the different P pools. But N/P ratios seemed to increase with elevation due to the stronger decrease of N compared to P from 400 to 1900 masl (Figure 23 and Figure A 19).

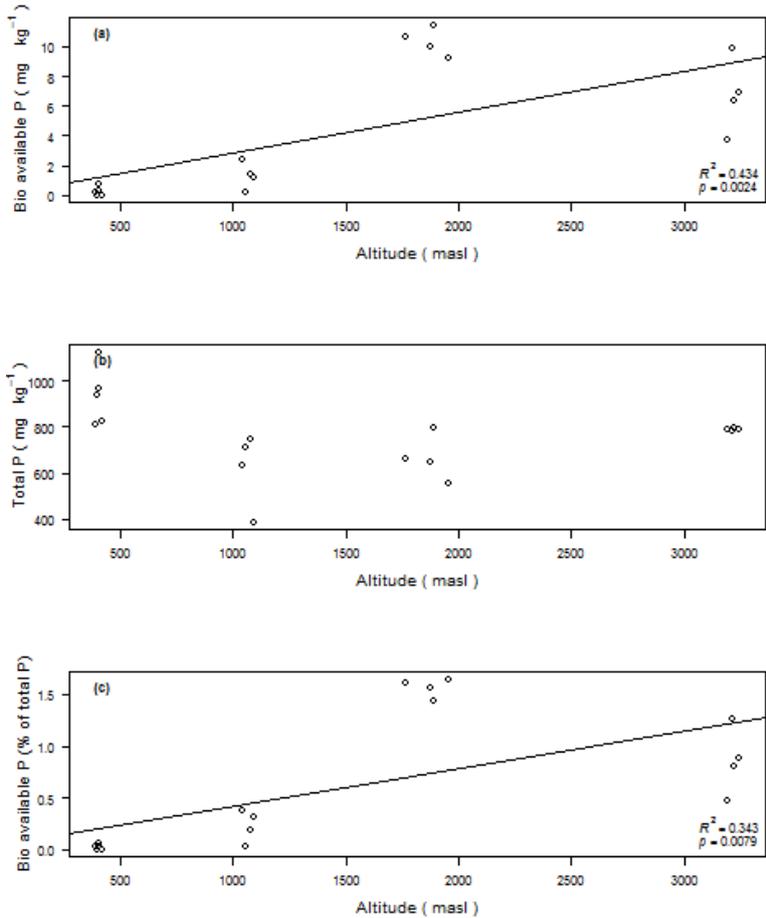


Figure 13 Altitudinal patterns of different P pools. (a) Bio-available P in mg kg⁻¹ for the upper 30 cm of soil; (b) Total P in mg kg⁻¹ for the upper 30 cm of soil; (c) The percentage of bio-available over total P for the upper 30 cm of soil. Linear regressions were visualized and R² values were given when p<0.05.

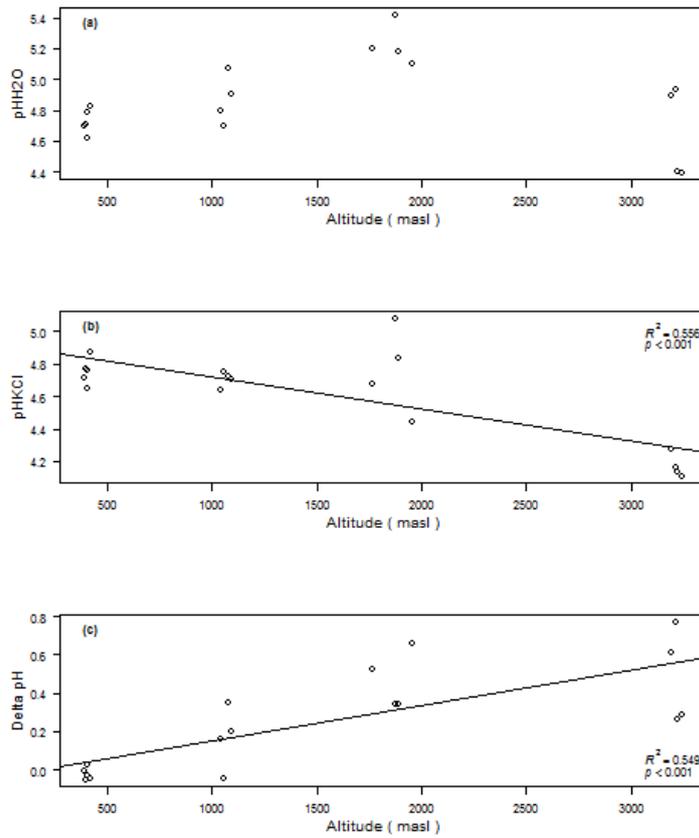


Figure 14 Altitudinal patterns in soil pH. (a) pH-H₂O of the upper 30 cm of soil; (b) pH-KCl of the upper 30 cm of soil; (c) Difference between pH-H₂O and pH-KCl of the upper 30 cm of soil. Linear regressions were visualized and R² values were given when p<0.05.

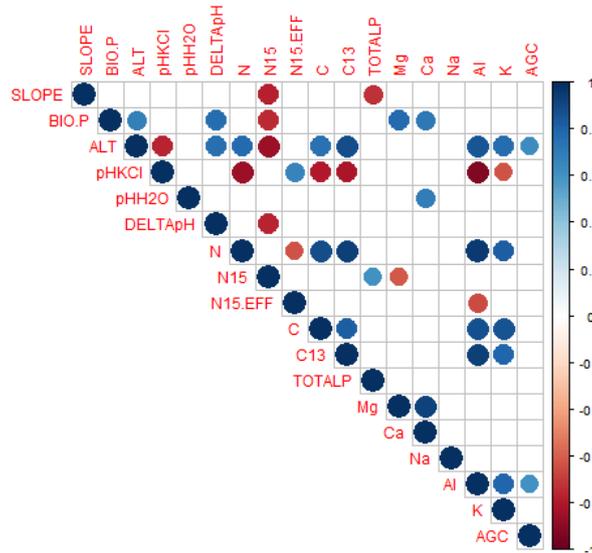


Figure 15 Pearson correlation table of soil properties of the upper 30 cm of soil. Correlations that weren't significant were left out ($p < 0.01$) and soil variables that didn't show any correlation with other variables were left out entirely. BIO.P is the bio-available P, ALT is altitude, DELTApH is the difference between pH-H₂O and pHKCl, N15 is $\delta^{15}N$, N15EFF is the difference between litter $\delta^{15}N$ and soil $\delta^{15}N$ at a depth of 0-5 cm, C13 is $\delta^{13}C$ and AGC is the aboveground carbon.

Table 10 Soil properties (mean \pm 1SE) at different altitudes. Different letters indicate significant differences between the five study plots ($p=0.05$). Bio P stands for bio-available P.

Altitude (masl)	400	1100	1900	3200
Total N (g kg ⁻¹)	6.78 (a) ± 0.57	5.02 (b) ± 0.70	5.56 (b) ± 1.00	8.88 (c) ± 0.71
Bio P (mg kg ⁻¹)	0.24 (a) ± 0.366	1.30 (b) ± 1.44	10.33 (c) ± 1.53	6.70 (d) ± 3.95
Total P (mg kg ⁻¹)	931.64 (a) ± 157.15	619.75 (b) ± 258.27	665.41 (bc) ± 157.47	787.73 (c) ± 6.839
pH-H ₂ O	4.73 (a) ± 0.10	4.87 (a) ± 0.25	5.23 (b) ± 0.22	4.65 (a) ± 0.47
pH-KCl	4.75 (a) ± 0.10	4.70 (a) ± 0.074	4.76 (a) ± 0.43	4.17 (b) ± 0.12
pH-H ₂ O minus pH-KCl	-0.024 (a) ± 0.040	0.16 (ab) ± 0.26	0.47 (b) ± 0.025	0.48 (b) ± 0.40
Mg (mg kg ⁻¹)	32.18 (a) ± 5.55	36.01 (a) ± 21.18	126.61 (b) ± 114.49	85.19 (b) ± 34.44
K (mg kg ⁻¹)	67.82 (a) ± 17.12	41.24 (b) ± 12.98	82.46 (a) ± 32.50	136.07 (c) ± 48.59
Ca (mg kg ⁻¹)	181.14 (a) ± 45.05	273.94 (a) ± 130.74	1010.22 (b) ± 828.56	310.26 (ab) ± 236.23
Na (mg kg ⁻¹)	31.55 (a) ± 28.94	12.15 (b) ± 1.84	17.58 (ab) ± 6.73	23.66 (a) ± 4.91
Al (mg kg ⁻¹)	30.04 (a) ± 8.65	34.80 (a) ± 15.45	34.90 (a) ± 26.01	170.95 (b) ± 42.26

4.4 Litter

The mass of litter seemed positively correlated with altitude but only the highest stratum had a significantly higher amount of litter (Figure 16, Figure 18). The C/N ratio of the litter increased along the gradient with exception of the range between 1100 and 1900 masl (Figure 17). Although not as significant also C/P showed a positive correlation with altitude (Figure 18). C/P and C/N were positively correlated as were N/P and C/P but there was no significant correlation for N/P and C/N. C, N and P were highly correlated with each other on an area base. All nutrients showed a positive correlation with altitude on a land area basis but only C maintained the correlation on a mass base, N and P on the other hand, declined or were negatively correlated with elevation.

Table 11 Litter properties (mean \pm 1SE) at different altitudes. Different letters indicate significant differences between the five study plots ($p=0.05$). The concentrations were given in g g⁻¹ and in kg ha⁻¹ planimetric land surface. The amounts of litter C, N and P in kg ha⁻¹ were estimated based on the nutrient concentrations in g g⁻¹ and the litter mass in kg ha⁻¹.

Altitude (masl)	400	1100	1900	3200
Litter mass (ton ha ⁻¹)	7.98 (a) ± 1.65	6.92 (a) ± 7.39	9.90 (a) ± 3.92	17.51 (b) ± 5.26
C (g g ⁻¹)	0.32 (a) ± 0.073	0.38 (a) ± 0.076	0.36 (a) ± 0.059	0.44 (b) ± 0.067
N (g g ⁻¹)	0.020 (a) ± 0.0023	0.021 (a) ± 0.0038	0.019 (a) ± 0.0018	0.015 (b) ± 0.0030
P (mg g ⁻¹)	0.93 (a) ± 0.11	0.82 (ab) ± 0.17	0.96 (a) ± 0.12	0.69 (b) ± 0.083
C (kg ha ⁻¹)	2634.40 (a) ± 968.38	2421.29 (a) ± 2016.26	3627.13 (a) ± 1642.56	7618.62 (b) ± 3058.95
N (kg ha ⁻¹)	169.32 (a) ± 49.75	140.86 (a) ± 129.77	191.12 (ab) ± 75.83	263.32 (b) ± 105.08
P (kg ha ⁻¹)	7.62 (a) ± 1.55	6.09 (a) ± 7.13	9.45 (ab) ± 2.77	11.96 (b) ± 3.41

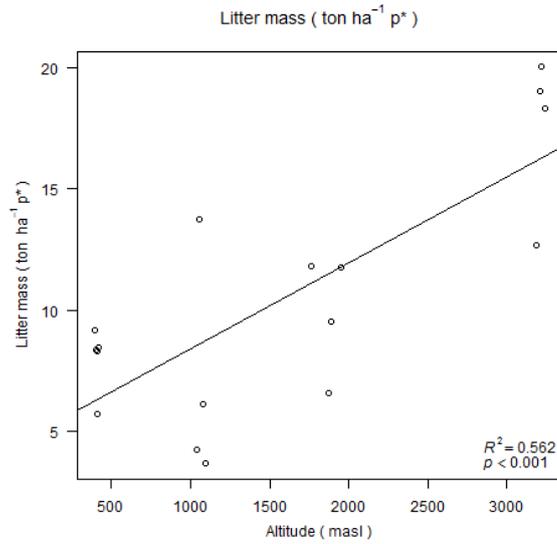


Figure 16 Litter mass (ton ha^{-1}) in function of altitude. p^* stands for planimetric surface. The linear regression was visualized and the R^2 value was given as $p < 0.05$.

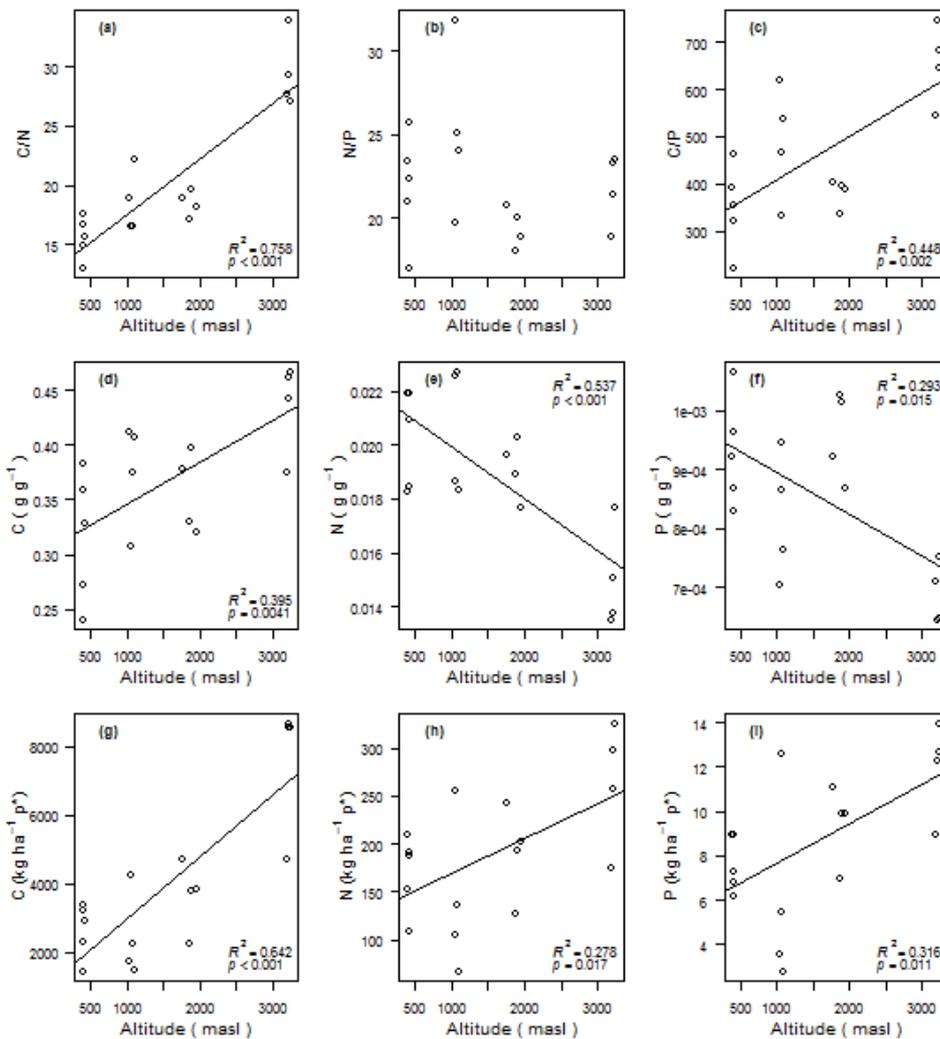


Figure 17 Altitudinal patterns in C, N and P concentrations of the litter. p^* stands for planimetric surface. (a) Litter C/N, (b) N/P and (c) C/P ratios were calculated on a mass base. Litter C, N and P are given in g g^{-1} (d,e,f) and in $\text{kg ha}^{-1} p^*$ taking into account the mass of litter per surface area (g,h,i). Linear regressions were visualized and R^2 values were given when $p < 0.05$.

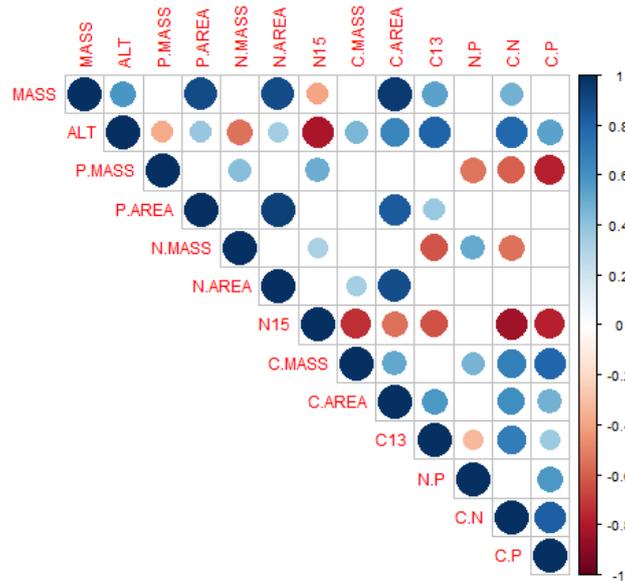


Figure 18 Pearson correlation table of litter properties. Correlations that weren't significant were left out ($p < 0.01$) and soil variables that didn't show any correlation with other variables were left out entirely. MASS is the litter mass, ALT is altitude, P.MASS and P.AREA are the P concentrations on a litter mass base and on a planimetric land surface base respectively. C.MASS and C.AREA are the C concentrations on a litter mass base and on a planimetric land surface base respectively. N.MASS and N.AREA are the N concentrations on a litter mass base and on a planimetric land surface base respectively. N15 and C13 are the $\delta^{15}N$ and $\delta^{13}C$ of the litter on a litter mass base. N.P, C.N and C.P are the nutrient ratios of the litter area on a mass base.

4.5 Leaves

In Table 12 the foliar nutrient concentrations are given on a leaf mass base ($g\ g^{-1}$) and leaf area base ($mg\ cm^{-2}$). The decrease in foliar N and P are more significant than the increase of C with elevation. Both C/P and C/N show an increasing trend while N/P shows a decreasing trend with elevation. The SLA showed a decreasing trend, resulting in an increasing trend of foliar N and P on a leaf area base.

Table 12 Community weighted means (basal area) of foliar C, N and P concentrations on a mass and leaf area base (mean \pm 1SE) (Demol 2016). Different letters indicate significant differences between the five study plots ($p = 0.05$).

Altitude (masl)	400	1100	1900	3200
C	0.44 (a)	0.44 (ab)	0.44 (a)	0.48 (b)
($g\ g^{-1}$)	± 0.0018	± 0.024	± 0.015	± 0.0070
N	0.027 (a)	0.025 (ab)	0.020 (b)	0.010 (c)
($g\ g^{-1}$)	± 0.0025	± 0.0045	± 0.0026	± 0.0013
P	1.30 (a)	1.44 (b)	1.30 (ab)	0.65 (c)
($mg\ g^{-1}$)	± 0.11	± 0.13	± 0.19	± 0.052
SLA	142.38	152.19	114.13	50.84
($cm^2\ g^{-1}$)	± 7.91	± 21.85	± 6.13	± 9.09
C	3.1	2.9	3.9	9.5
($mg\ cm^{-2}$)	± 0.17	± 0.40	± 0.33	± 1.7
N	0.19 (a)	0.16 (b)	0.18 (ab)	0.20 (a)
($mg\ cm^{-2}$)	± 0.025	± 0.0075	± 0.029	± 0.0098
P	0.0091 (a)	0.0095 (a)	0.011 (b)	0.013 (b)
($mg\ cm^{-2}$)	± 0.0011	± 0.00053	± 0.0021	± 0.0012

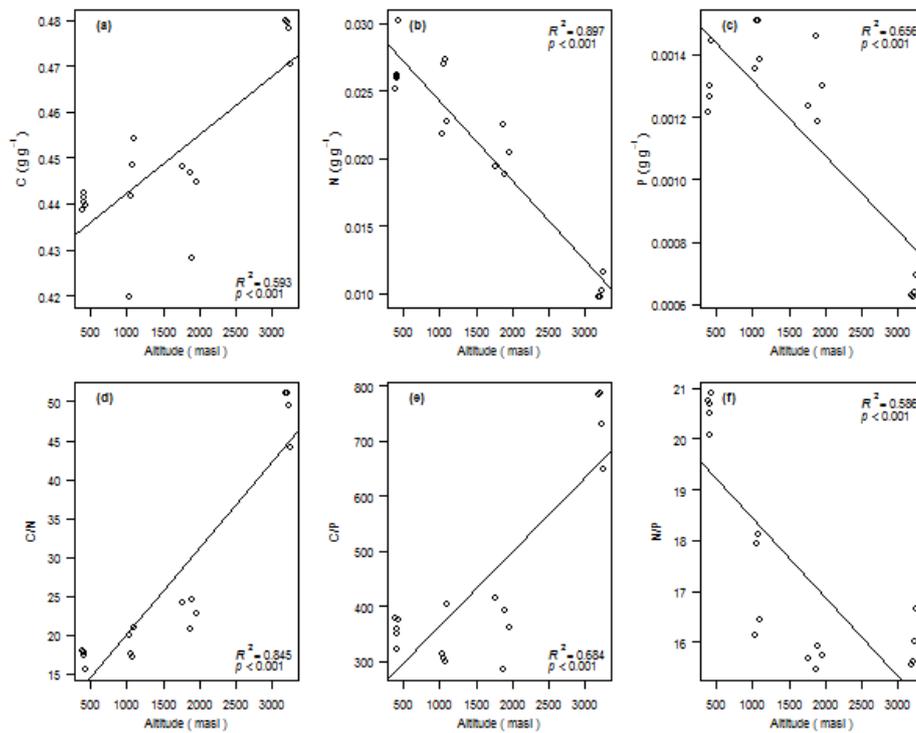


Figure 19 Foliar nutrient concentrations and ratios. (a,b,c) Foliar C, N and P concentrations in $g\ g^{-1}$ (d,e,f) Foliar C/N, C/P and N/P ratios on a mass base in function of altitude (Demol 2016). Linear regressions were visualized and R^2 values were given when $p < 0.05$.

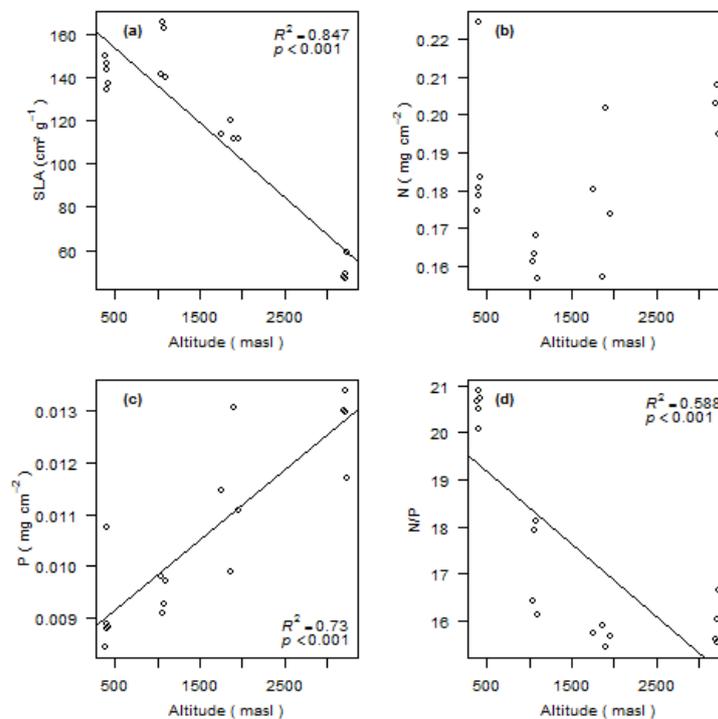


Figure 20 Foliar nutrient concentrations and nutrient ratios on a leaf area base in function of altitude (Demol 2016). (a) specific leaf area (SLA) in $cm^2\ g^{-1}$ (b,c) foliar N and P concentration in $g\ cm^{-2}$ (d) foliar N/P. Linear regressions were visualized and R^2 values were given when $p < 0.05$.

4.6 Isotopes

The highest stratum was significantly enriched in foliar, litter and soil C13 compared to the three lower strata, while the lowest stratum was significantly enriched in foliar, litter and soil N15 (Figure 21 and Table 13). There is a continuous decrease and increase of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ respectively throughout the different depths (Figure A 28). The comparison of the leaves, litter and soil in terms of isotopic composition suggest comparable trends. For the soil a depth average of the upper 30 cm was taken. $\delta^{15}\text{N}$ declined in all three pools with altitude but this decrease is most pronounced in the leaves and least in the soil. $\delta^{13}\text{C}$ increased in all three pools with altitude but this increase is most pronounced in the soil and least in the leaves.

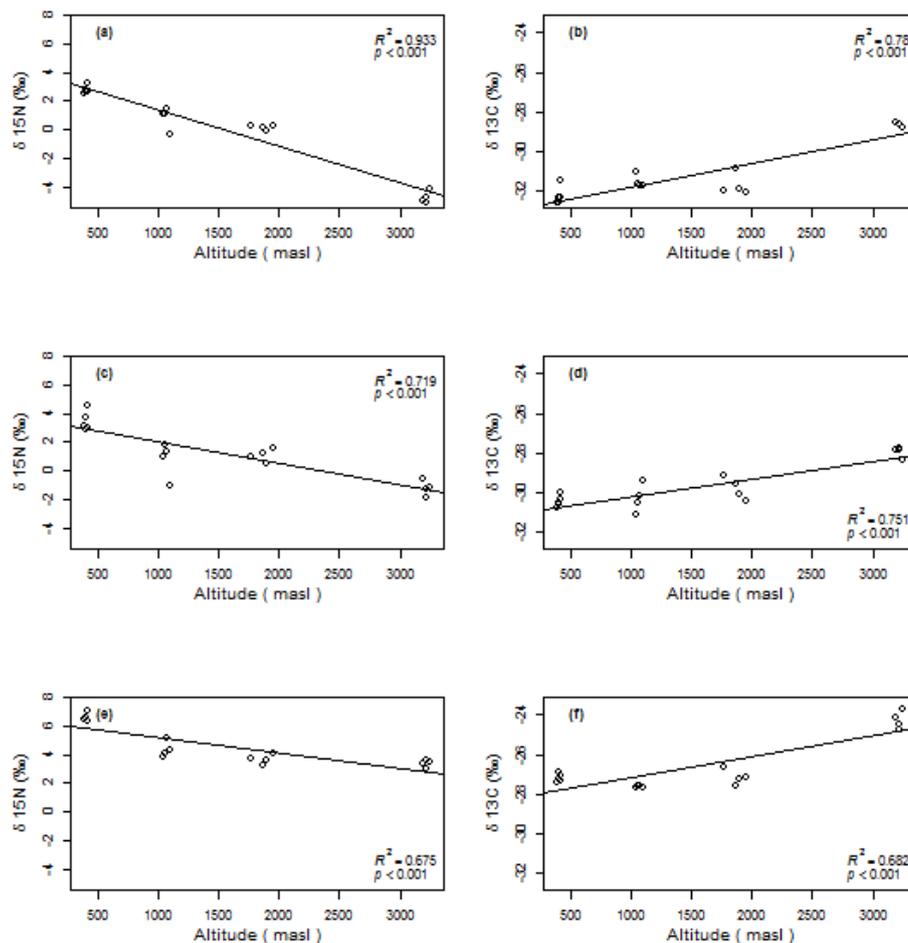


Figure 21 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of the leaves, litter and soil (upper 30 cm) in ‰. (a) foliar $\delta^{15}\text{N}$ in ‰ (b) foliar $\delta^{13}\text{C}$ in ‰ (c) litter $\delta^{15}\text{N}$ in ‰ (d) litter $\delta^{13}\text{C}$ in ‰ (e) soil $\delta^{15}\text{N}$ in ‰ (f) soil $\delta^{13}\text{C}$ in ‰ Linear regressions were visualized and R^2 values were given when $p < 0.05$.

Table 13 Stable isotope composition (mean \pm 1SE) at different altitudes for leaves, litter and soil. Different letters indicate significant differences between the five study plots ($p=0.05$).

Altitude (masl)	400	1100	1900	3200
$\delta^{13}\text{C}$ leaves	-32.27 (a) ± 0.36	-31.54 (a) ± 1.12	-31.70 (a) ± 0.92	-28.65 (b) ± 0.42
$\delta^{13}\text{C}$ litter	-30.46 (a) ± 0.36	-30.30 (a) ± 1.12	-29.82 (a) ± 0.92	-27.95 (b) ± 0.42
$\delta^{13}\text{C}$ soil	-27.17 (a) ± 0.27	-27.64 (b) ± 0.099	-27.16 (a) ± 0.61	-24.23 (c) ± 0.70
$\delta^{15}\text{N}$ leaves	2.77 (a) ± 0.37	0.82 (b) ± 1.30	0.15 (b) ± 0.23	-4.80 (c) ± 0.63
$\delta^{15}\text{N}$ litter	3.49 (a) ± 0.86	0.76 (b) ± 2.00	1.06 (b) ± 0.73	-1.26 (c) ± 0.86
$\delta^{15}\text{N}$ soil	6.65 (a) ± 0.35	4.39 (b) ± 0.93	3.68 (c) ± 0.48	3.35 (c) ± 0.44

5 Discussion

5.1 How does the stand structure changes with elevation?

Because of the strong correlation between altitude and temperature, the decrease in tree height and canopy height is probably due to the adverse direct effects of low temperature on plant metabolism and the more indirect effects on nutrient availability, causing a shift from AGB to BGB (Moser et al. 2008; Lieberman et al. 1996; Raich et al. 1997; Baez et al. 2015; Culmsee et al. 2010; Fisher et al. 2013). Nevertheless, extreme conditions more frequently found in mountainous areas such as water logging, drought, strong winds and increased UV-B radiation may influence these results as well. Total basal area increased with altitude (Figure 7), which was confirmed by some researchers (Aiba & Kitayama 1999; Lieberman et al. 1996) but contested by others (Leuschner et al. 2007; Raich et al. 1997; Moser et al. 2008; Clark et al. 2015; Girardin et al. 2013). Both Moser et al. (2011) and Clark et al. (2015) observed a decrease of the total basal area until a certain altitude, after which the total basal area increased, caused by a significant larger stem density at the higher altitudes that compensated for the lower basal area per tree. In the Ecuadorian Andes, Unger et al. (2012) described a similar structure on an individual tree basis, with smaller but broader trees at higher altitudes. Besides being an indicator of climatic and environmental conditions, this varying tree structure might have some practical implications for the estimation of the aboveground biomass through allometric relationships. These relationships link structural variables, mainly DBH and tree height, to AGB in order to make an estimation of the AGB through relatively easy measurements. However, these relationships are often bond to certain study areas and even widely validated relationships such as those described by Chave et al. (2014) cannot grasp all the present variability (Girardin et al. 2010). Therefore, the pronounced continuously changing tree architecture along this elevational gradient might be a serious obstacle because of the lack of appropriate and adequate relationships. Clark et al. (2015) did not even make an estimation of the AGB along a 2700 m long elevational transect in Costa Rica, because of the unknown accuracy of these estimates. The AGB estimates of our 2800 m long elevational transect should also be approached as estimates of unknown accuracy based on allometric relations of DBH and tree height to biomass rather than AGB measurements.

5.2 How do the AGC and SOC change with elevation?

5.2.1 Limitations of the AGC estimations

The pantropical allometric relation of Chave et al. (2014) was established using mainly tropical lowland forest data and has already led to overestimations of biomass in TMF (Girardin et al. 2010). Moreover, numerous studies have described a trend of shifting C allocation from the AGB to the roots or BGB (Leuschner et al. 2007; Moser et al. 2010) which is not accounted for in allometric relationships (Leuschner et al. 2007). Besides, multi-stemmed trees were increasingly abundant with altitude, which might result in a cumulating under or overestimation with elevation. Finally, the pronounced stunted trees at 3200 masl had very low stem heights relative to the total tree height, which might result in another overestimation when using only total tree height. Unfortunately, the observed trend of decreasing stem height with elevation could not be confirmed as no measurements were made. Tree architecture changes frequently with elevation, but whether single species allometries shift is generally not known (Clark & Kellner 2012). As sound allometric relations for TMF are still lacking we decided to use the, well-verified less specific, equation of Chave et al. 2014 (400 to 1900 masl) (Alves et al. 2010; Unger et al. 2012) in combination with the, more specific less-verified, equation of Chamorro et al. 2012 (3200 masl) for mountainous, almost single species, stands.

5.2.2 AGC

AGC didn't show the expected decrease with elevation (Moser et al. 2011; Raich et al. 1997; Girardin et al. 2010; Kitayama & Aiba 2002; Leuschner et al. 2007; Marshall et al. 2012; Kitayama & Mueller-Dombois 1994) (Figure 8), instead it showed a rather discontinuous increase with values ranging from 95 to 145 ton C ha⁻¹ for respectively the lowest and highest stratum. Therefore, elevation and more

specifically the abiotic variables strongly correlated with elevation like temperature, might not be the most important factors to explain variation in AGC. In many cases no relationships were found between AGC and elevation (Culmsee et al. 2010; Unger et al. 2012; Girardin et al. 2014) probably due to regional differences in soil characteristics, precipitation patterns, temperature regimes, topography and functional attributes within tree communities (Moser et al. 2011; Malhi et al. 2002; Slik et al. 2010; Raich et al. 2006; Mascaro et al. 2011; Baker et al. 2004). As accurate estimates of temperature and precipitation were not available, their influence on AGC remains presumptive. However their clear continuous decrease with elevation conflicts with the relatively high AGC values at higher altitudes (Clark et al. 2013). Nevertheless, lacking correlation of AGC with climate was found in similar altitudinal research as well (Slik et al. 2010; Leuschner et al. 2007; Spracklen & Righelato 2014). When applying the species specific equation of Chamorro et al. (2012), next to those of Chave et al. (2014), Saldarragia et al. (1988) and Beets et al. (2012) the AGC of the highest altitude decreased from 156 to 123 ton C ha⁻¹. The significant reduction was mainly found in the larger trees, which might indicate an underestimation rather than an improved estimation due to the smaller range of diameters for which this equation was initially intended.

In Figure 22 the data of this thesis was combined with that of other researchers in Ecuador. Unger et al. (2012) studied the AGC on a transect from 500 to 2000 masl in North-Eastern Ecuador, Leuschner et al. (2007) from 1000 to 3000 masl and Hofstede et al. (1999) from 2300 to 2800 masl in Southern Ecuador and Fehse et al. (2002) in the Polyopsis forest of North-Western Ecuador at 3600 masl. Although both Leuschner et al., Unger et al. and Hofstede et al. described a decrease of AGC with altitude in Ecuador, this was not the case for our results. However, the very high AGC at 3200 masl was comparable with that found in two mature Polyopsis and Alnus forests in Ecuador (Fehse et al. 2002). The high variability of the forest at 1900 masl is probably caused by local dynamics. The plot with the highest AGC also had the highest basal area per tree because of an enormous *Ruagea gordonifolia* with a basal area of 1.00 m² in the middle of the plot (Figure 7). The plot with the lowest AGC and basal area per tree had some fallen trees within its boundaries and standing trees which were young and small. Moreover, one other plot showed some clear signs of recent landslides. Haagen (2011), found AGC to be 125.7 ± 49.2 ton C ha⁻¹ in the same study area at 1976 masl which is in the same range of our estimation of AGC being 112.14 ± 57.71 ton C ha⁻¹. Despite the relatively high AGC and biodiversity at 1100 masl, there had not been any inventarisations yet. In the study area at 400 masl on the other hand, Bauters et al. (2013) estimated AGC as 98.2 ton C ha⁻¹ which is close to our estimation of 95.26 ± 18.88 ton C ha⁻¹. Although different allometric relationships were used by Bauters et al. (2013) (relationship of Chave et al. 2005) and Haagen (2011) (relationship of Brown et al. 1997), the obtained estimations were comparable to those of this study (relationship of Chave et al. 2014).

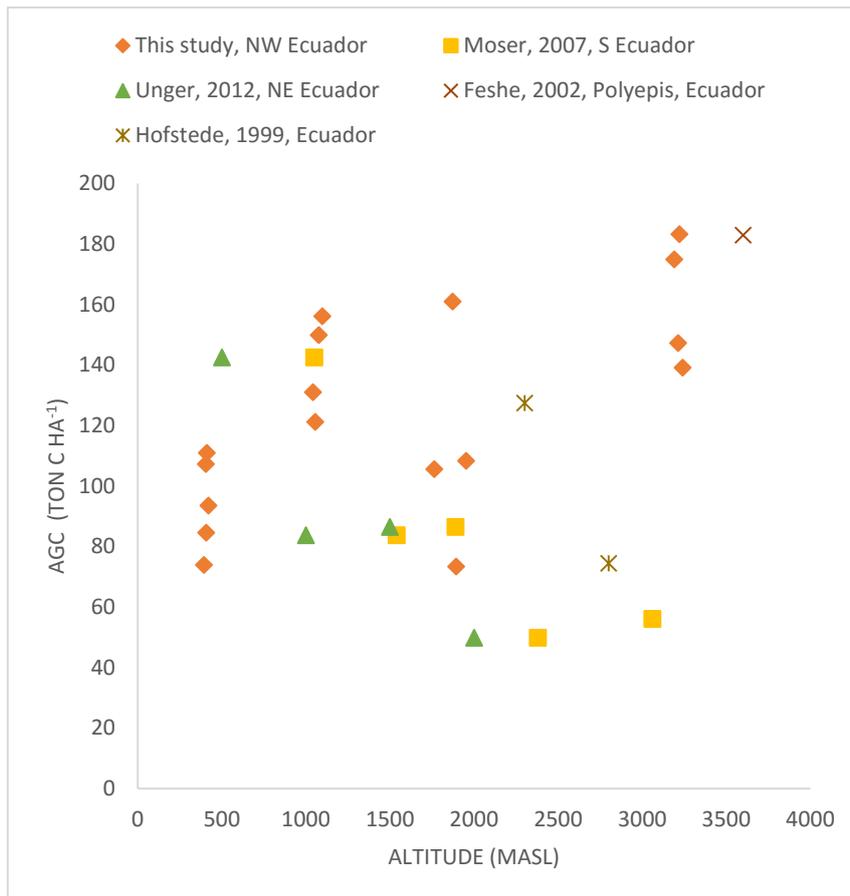


Figure 22 Aboveground carbon (AGC) in ton C ha⁻¹ in function of altitude in Ecuador for different studies (Unger et al. 2012; Hofstede, R., Aguirre 1999; Leuschner et al. 2007; Fehse et al. 2002). AGC for this study was estimated based on the allometric relationships of Chave et al. 2014, Saldarraga et al. 1988 and Beets et al. 2012.

An important note for this study is that it is confined to carbon stock measurements only. This implies that productivity as such was not assessed, while this is more likely to show a clear trend along the transect. The majority of studies reported a decrease of the aboveground net primary production (ANPP) with elevation (Kitayama & Aiba 2002; van de Weg et al. 2014; Girardin et al. 2010) and significantly lower aboveground gross primary production (AGPP) at cloud immersed TMCF (van de Weg et al. 2014) next to the already mentioned decrease of AGC. The main reason behind this reduced productivity is probably the interacting effect of temperature and nutrient availability. As reduced temperatures give rise to lower decomposition rates and lower N cycling rates. However, Clark et al. (2015) found that the forest above-ground biomass residence time increased substantially with elevation and that at a TMCF at 2830 masl, basal area increment was comparable to that of lower tropical forests, caused by the higher stem density offsetting the lower basal area increment per tree.

5.2.3 WD

WD showed a positive correlation with AGC (Figure A 13). However, this positive correlation is probably caused by using wood-density-based allometric equations as no correlation was found between WD and AGC calculated with the relation of Brown et al. (1989) for moist forests, which lacks a WD input. Moreover, although Baker et al. (2004) attributed spatial patterns in AGC in the Amazon region to WD, other researchers contested his results and found no simple relationship between WD and AGC (Stegen et al. 2009; Strubbe 2013; Quesada et al. 2012). Finally, Chave described a decrease of WD with altitude from 0.652 g cm⁻³ for non-montane and 0.599 g cm⁻³ for montane tree species (Chave et al. 2006). Lowest wood densities were however found at the lowest altitude and averages over the different altitudes ranged between 0.5 and 0.6 g cm⁻³.

5.2.4 SOC

SOC was exceptionally high at every altitude (0.06-0.08 g g⁻¹), but at 3200 masl, concentrations were over two times those of the lower altitudes (Figure 10). The reduced temperature at higher elevations should disfavour decomposition and therefore increase SOC (Dieleman et al. 2013; Girardin et al. 2010), but with exception of the highest altitude, increases of SOC were discontinuous and nonsignificant. Nevertheless, leaf litter accumulation, being also an indicator of decomposition rates, showed a comparable discontinuous increase with elevation (Figure 16). Another climatic variable, changing with elevation, is cloud cover (Nair et al. 2008). Although strongly variable, frequencies and magnitude of cloud cover seem to cumulate between 2000 and 3000 masl (Bendix et al. 2006; Bendix et al. 2006; Bruijnzeel et al. 2011). The increasingly high SOC and amount of litter from 1100 to 3200 masl might partially be caused by the reduced insolation, higher soil moisture and concentration of phenolic components caused by intense cloud covering (Bruijnzeel et al. 2013). Arnold et al. (2009) described a decrease of SOC with elevation in the same study area, but within a narrower range (between 400 and 1500 masl). He attributed the increase of coarser soil particles with elevation to the younger soils at higher elevations which might be constraining SOC accumulation at these altitudes. In Southern Ecuador SOC has been found to increase from 1000 to 3000 masl (Wilcke et al. 2002; Moser et al. 2007) although contrasting results have been observed in the same study area (Soethe et al. 2008). At the lower altitudinal range (<1500 masl), soil development might be dominating the accumulation of SOM over temperature, while the opposite might be true for the higher altitudinal range (>1500 masl) resulting in a minimum at mid-altitude where both aspects are important. As texture determinations are missing in this study, this explanation remains presumptive. The slower decomposition at higher altitudes might be deduced with more certainty from the increasing C/N and C/P ratios in the soil, litter and leaves (Figure 23) (Soethe et al. 2008; Chave et al. 2009). Moreover, as observed climatic and topographic (Figure A 12) aspects of the elevational gradient don't explain the trend in SOC and AGC, nutrient availability might do so.

5.3 How do nutrient concentrations change with elevation?

5.3.1 Soil

Variations in chemical soil properties of tropical regions tend to correlate with parent material and soil age (Quesada et al. 2011). The parent material at 3200 masl is made up of igneous rocks and is comparable in composition to the granitic Guiana Shield (FAO 2015). The latter area has been subjected to weathering for thousands of years, resulting in significant leaching of bases and the accumulation of aluminium sesquioxides (FAO 2015). However, weathering in the Andes region is of a more recent age, as soils are relatively young due to substantial tectonic movements (FAO 2015). These dynamics have given rise to a wide variety of parent materials in Ecuador as the igneous material in the centre of the mountain gradually makes place for increasingly sedimentary material along the slopes (FAO 2015). Moreover, a recent study has indicated that the different soil compositions between the western and eastern side of the Andes, are mainly associated with changes in parent material (Buytaert et al. 2003). Besides parent material, also volcanos might have an important influence on soil formation (Hall et al. 2008) as andic soil properties seem to diminish with increasing distance from volcanos (Buytaert et al. 2007; Buytaert et al. 2003). The relatively isolated location of the forest at 3200 masl, in combination with the vicinity of a number of volcanos such as the Cuichocho and Imbabura (Hall et al. 2008) and the intrusive nature of the parent material (FAO 2015), might all add to the distinct nutrient concentrations found at this altitude, which will be described in the next section.

5.3.2 Soil and litter

Soil total N was highest in the forest at 3200 masl, followed by the forest at 400 masl and lowest at mid-altitude from 1100 masl to 1900 masl (Figure 12). The relatively high N concentrations at 400 masl are to be expected, as soil $\delta^{15}\text{N}$, being related to N cycling rates, is significantly higher than at the higher altitudes (Figure A 27). Additionally, the high N concentrations are limited to the upper soil

layers and after a certain depth the N levels become comparable to the values found at 1100 and 1900 masl (Figure 11), suggesting that N is processed and taken up before it can be transported downward into deeper layers. The high N concentrations in the upper soil, litter and leaves at this lowest altitude, suggest that no N limitation occurs (Figure A 19).

Although soil N is even higher at 3200 masl than at 400 masl, foliar and litter N are significantly lower, suggesting that only a small fraction of the soil N is taken up by the trees at this altitude (Figure A 19) (Fisher et al. 2013; Wullaert et al. 2010; Homeier et al. 2012). This might have numerous reasons such as impeded uptake due to unfavourable soil conditions or anthropogenic disturbances. A more practical reason for the exceptionally high soil N concentrations could be inadequate distinction between the organic and mineral layer during sampling. However, leaving out the upper 10 cm of soil reduced the N concentrations from 400 to 1900 masl to a comparable level, while N concentrations remained significantly larger for the highest altitude at all depths, indicating that large amounts of N were consistent over the entire profile (Figure 11). Moreover, comparable results of low uptake/input ratios have been described in other TMCF based on rainfall chemistry, atmospheric deposition and nutrient uptake (Bruijnzeel 1989; Bruijnzeel et al. 1993; Tanner 1985; Tanner 1980; Pizarro 1985). Another reason might be the unaccounted importance of the different N pools when solely using total N in different climates. Microbial transformations might render N unavailable for trees and therefore N mineralization rate might be a better indication for N availability (Silver 1994; Nottingham et al. 2015). Moreover, as the C/N ratio of litter material increased with elevation, microbial communities will lower their CUE and increase their NUE, resulting in higher N immobilization and lower N mineralization rates (Mooshammer et al. 2014). In doing so, soils might act as potential N sequestration pools, considering that most SOM in mineral soils is composed of microbial processed organic material (Hedin et al. 2003; Chao & Balsler 2010; Gleixner 2013; Mooshammer et al. 2014). Immobilization of soil C and N might be deduced from the comparison with foliar C and N, as the continuous C increase and N decrease in the leaves are different from the trends of the soil concentrations (Figure A 19). In addition, both soil C and N show a strong correlation (Figure 15), possibly because microbial communities need a more fixed amount of C versus N to align with their internal C/N composition (Xu et al. 2013; Buchkowski et al. 2015). However, there should be a turning point at which the ecosystem switches from C to N limitation. This threshold elemental ratio of C/N ($TER_{C/N}$) in litter has been considered to range between 20 and 25, based on studies that measured the transition from net N immobilization to net N mineralization during decomposition (Mooshammer et al. 2014). The averaged C/N of litter gradually increased with altitude from 15 to 20 until 1900 masl and then steeply rose until a value of approximately 30 was reached at 3200 masl (Figure 17), suggesting that N limitation became more important with altitude and that between 1900 and 3200 masl a transition to net N immobilization took place. Furthermore, these lower rates of N mineralization can also be deduced from the decreasing $\delta^{15}N$ in leaves, litter and soil with elevation (Figure 21).

Bio-available P increased significantly from 400 to 1900 masl while total P decreased slightly over the same altitudinal range (Figure 13). The higher bio-available P might be attributed to the younger soils at higher altitudes due to smaller timescale in which P could become unavailable by complexation. The decrease of bio-available P at 3200 masl might be caused by the very high Al (Figure A 17) and SOC concentrations and low pH (Figure 14) at this altitude, responsible for the formation of insoluble aluminium phosphates.

5.3.3 Soil, litter and leaves

Both foliar N and P showed a decreasing trend with elevation in this study (Figure 19) (Demol 2016). Soethe described a similar decrease in foliar N between 1900 and 3000 masl from 21.7 to 11.3 mg g⁻¹ in Southern Ecuador (Soethe et al. 2008). Although foliar P concentrations were a twofold larger than those of this study, the rate of decrease was comparable to our results. At 400, 1100 and 1900 masl both the N and P concentrations were in the ranges of nutrient sufficiency for tropical trees while they rather suggested nutrient deficiency at 3200 masl (Bergmann 1993; Vitousek et al. 1995; Tanner et al.

1990; Drechsel & Zech 1991). Moreover C/N and C/P from 400 to 1900 masl for both leaves and litter were all lower than the values obtained by McGroddy in nutrient limited tropical lowland (C/N of 30 and C/P of 950), suggesting that at these altitudes both N and P concentrations were sufficient for tree growth (McGroddy et al. 2004).

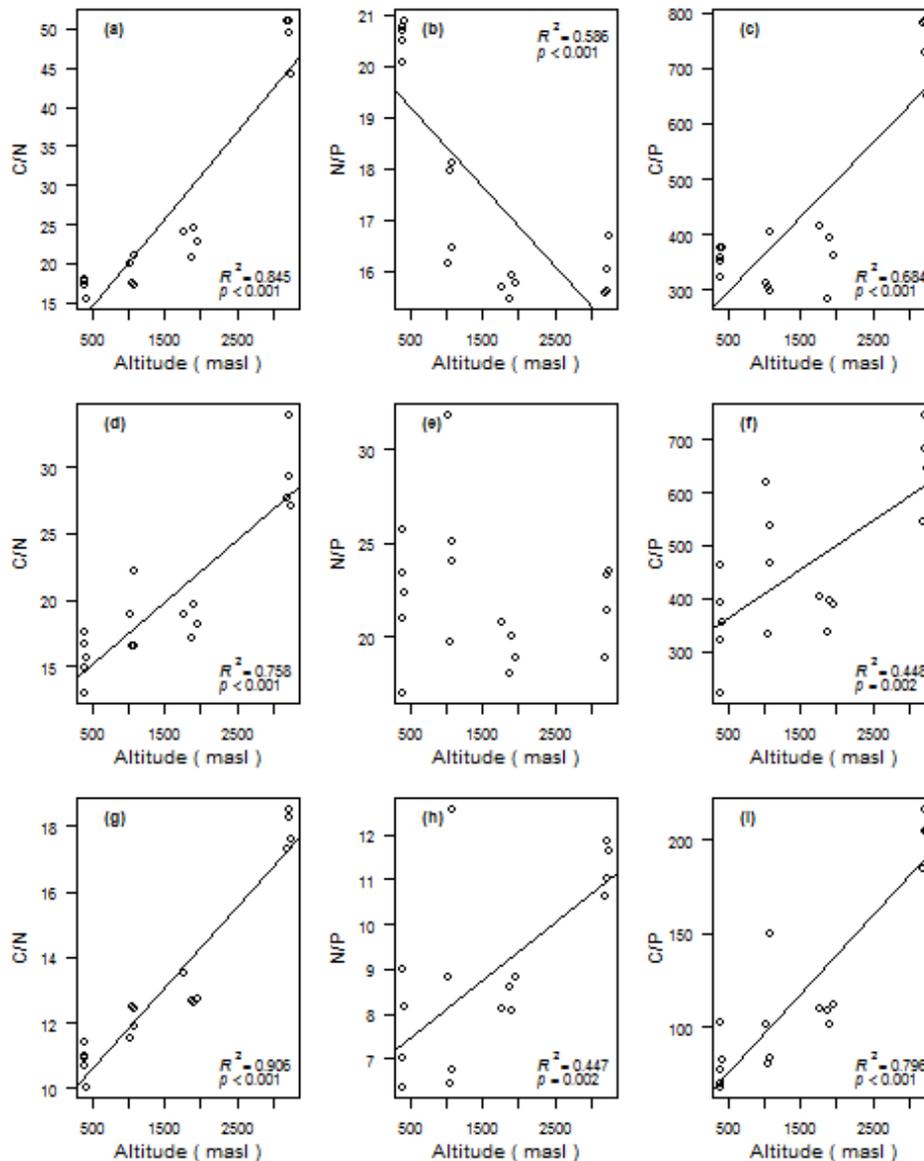


Figure 23 Nutrient ratios of leaves (a,b,c), litter (d,e,f) and soil (g,h,i) in function of altitude. The increase of C/N with altitude became less pronounced from leaves to litter to soil with respectively a 3-, 2- and 1.2- fold increase from lowest to highest altitude. Linear regressions were visualized and R^2 values were given when $p < 0.05$.

Leaves at higher altitudes generally have a lower specific leaf area (SLA; ratio of leaf area to dry mass), because of thicker and more xeromorphic leaves (Moser et al. 2007). In response to cold and moist conditions tree species might increase the cell wall thickness of their leaves, which implies lower foliar N concentration in order to minimize the risk of fungi infestations (Edwards & Grubb 1982). SLA did decrease with elevation (Demol 2016) and resulted in apparently equal foliar N amounts on a leaf area basis along the gradient and even a slight increase of foliar P on a leaf area basis (Figure 20), which might have been the result of adaptations of tree species and communities to the change of environmental conditions and nutrient dynamics with elevation (Kitayama & Aiba 2002; Vitousek et al. 1992). At lower temperatures, trees require larger amounts of rubisco for a similar leaf area to sustain

similar photosynthetic rates (Terashima et al. 1995), therefore trees need larger amounts of N (essential part of rubisco) (van de Weg et al. 2012; Reich & Walters 1994) and P (influences rubisco regeneration rate) (Parry et al. 2008) on a leaf area base to cope with the colder conditions of the higher altitudes.

Tree diversity decreased discontinuously with altitude (Figure A 29) and at 3200 masl the forest was for 74 % of the AGC dominated by one species (*Freziera canescens*) (Figure A 33). It is possible that the nutrient concentrations in the mixed samples reflected foliar nutrient concentrations of the dominant species rather than stand-specific foliar compositions. Leaving *F. canescens* out of the data reduced the C/N values from 50 to 35 at 3200 masl, but despite the considerable reduction, C/N values at this altitude remained high compared to the lower altitudes. Another way to assess the importance of the tree species community in foliar composition is to focus on species which occur on different altitudes. The combination of the high species diversity and the clearly different species compositions along the gradient (Demol 2016) limited the dataset to just one suitable species (*Otoba gordonifolia*), which was increasingly dominant from 400 to 1100 and 1900 masl. Although not significant, foliar C/P seemed to decrease with altitude, but for C/N no trend was found (Figure A 24). Moreover, differences within one stratum were often greater than those between the strata at different altitudes. In addition, the decreasing dominance of the tree species with altitude might be related to a shift towards the outer ranges of its species-specific optimal habitat, resulting in a lower growth rate caused by this less fitting environment (Janzen 1967).

Nevertheless, evaluating the ratio of N to P might still reveal possible nutrient limitations, being a better indicator than considering the nutrients individually (Koerselman & Meuleman 1996). Foliar community weighted N/P seemed to decrease from 400 to 1900 masl (Figure 23) suggesting more of a tendency towards P limitation at the lower and more N limitation at the higher altitudes. The increasing foliar N/P from 1900 to 3200 masl might be caused by the unique environmental features of the forest discussed earlier. The foliar N/P of *O. gordonifolia* also showed a weak decrease from 400 to 1900 masl, confirming the possible nutrient limitation shift from lower to higher altitudes. McGroddy defined tropical lowlands as P limited with foliar N/P values of approximately 20, which is comparable to the N/P values at 400 masl suggesting P limitation at this altitude, while at higher altitudes N limitation becomes more important as is confirmed by Soethe in the Southern Ecuadorian mountains (McGroddy et al. 2004; Soethe et al. 2008). Furthermore, community weighted foliar N/P is always lower than litter N/P suggesting that more N is locked away in litter or that P is resorbed more efficiently (Figure 23) (McGroddy et al. 2004; Yuan & Chen 2009) than N before leaf abscission. This difference seems to decrease from 400 to 1900 masl which might indicate lower N mineralization rates at higher altitudes. In addition, the low amount of nutrients in the litter on a mass base seem to be compensated significantly by the higher amount of litter, resulting in a higher nutrient concentration of the litter on a land area base at 3200 masl (Figure 17). Finally, soil N/P seems to increase with elevation when using total P (Figure 23) but decrease when using bio-available soil P as denominator (Figure A 25). Moreover, the latter soil ratio also showed a weak positive correlation with foliar N/P (Figure A 18) which is to be expected as nutrient limitation will probably affect an entire ecosystem. Therefore, Nottingham et al. (2015) suggested that also microbial communities are constrained by P limitation in the lowlands and N in the highlands. This is in line with our earlier presumptions of a microbial limitation shift from C to N with elevation. P limitation of microbial communities in lowland forests has been deduced from the increased litterfall production, microbial biomass and decomposition in response to P fertilization (Nottingham et al. 2015). The strong linkage between plant and soil microbial communities, will probably magnify the shift in nutrient limitation through leaf production, litterfall and decomposition. The lower productivity at the higher altitudes (Girardin et al. 2010) in combination with the already low foliar N/P ratios (van de Weg et al. 2014), might further slowdown decomposition and the amount of bioavailable N.

5.4 How do the isotopic compositions change with elevation?

$\delta^{15}\text{N}$ increased from leaves to soil, with intermediary values for the litter (Figure 21). Although no continuous trend of the difference between leaves and soil was found, the difference was significantly higher at 3200 masl than at the lower altitudes. This might be caused by the expected net microbial immobilization of N at this altitude and the associated $\delta^{15}\text{N}$ enrichment of SOM. The significant decrease of foliar $\delta^{15}\text{N}$ with elevation further suggests decreasing N availability. Furthermore, it is shown that $\delta^{15}\text{N}$ decreases as decay slows down (Connin et al. 2001). Hence, the associated significant $\delta^{15}\text{N}$ reduction of litter material and SOM with elevation is in line with the above mentioned finding that N mineralization and litter decomposition is lower at higher altitudes, resulting in lower N availability. Additionally, $\delta^{15}\text{N}$ showed a pronounced increase with depth (Figure A 28), which is probably due to an increased microbial processing at larger depths. This might also be deduced from the decreasing soil C/N with soil depth. With increasing soil depth C/N becomes increasingly optimal for microbial communities indicating increased microbial processing. $\delta^{15}\text{N}$ of leaves, litter and soil showed an apparent positive correlation with temperature and therefore $\delta^{15}\text{N}$ also showed a negative correlation with elevation as the first one was estimated from the latter one. However, no account was made of the different possible interdependent variables such as SOC and soil N, which have been shown to limit the correlation with MAT to certain intervals or even entirely (Craine et al. 2009). $\delta^{15}\text{N}$ has also been found to correlate negatively with precipitation, suggesting that moisture input increased with elevation rather than decrease (Craine et al. 2009). However, because of the limited accuracy of the precipitation data and the unaccounted fog input, no substantiated conclusions of correlation with precipitation could be made.

Foliar $\delta^{13}\text{C}$ was significantly higher at 3200 masl, which might be an indication of higher WUEs at this altitude. However, $\delta^{13}\text{C}$ might correlate with a variety of abiotic and biotic factors changing with elevation such as soil moisture, temperature, atmospheric CO_2 concentrations (Terashima et al. 1995) and leaf morphology. In addition, the significant higher $\delta^{13}\text{C}$ at 3200 masl was also recognized in the litter and soil, which is more likely caused by the internal processes of the trees rather than specific litter and soil processes. $\delta^{13}\text{C}$ values are often used as a proxy for WUE. However, along the transects, the site conditions and species compositions change dramatically, and hence the $\delta^{13}\text{C}$ values should be interpreted in a more complex framework. Hence the increased $\delta^{13}\text{C}$ might also be associated with an increased photosynthetic capacity at the higher elevations, observed in other studies (Wittich et al. 2012; Bresson et al. 2009). Hence the observation of increasing $\delta^{13}\text{C}$ might be simply linked to the changing leaf morphology/strategy along the transect. Additionally, the lower atmospheric pressure and lower partial pressure of CO_2 at higher elevations might result into lower leaf internal CO_2 concentrations, inducing a weaker discrimination against ^{13}C , and hence a relative increase of $\delta^{13}\text{C}$ with altitude. As these covarying factors are interdependent and not easily assessed independently, statements regarding WUE or photosynthetic capacity from this dataset remain presumptive.

6 Conclusion

The increase of AGC with elevation in this study is in conflict with the generally proposed hypothesis of lower AGC at higher elevations. The study has however been confronted with some unavoidable build-up of uncertainty. Not only the relatively small number of PSP, their limited size and the unavoidable bias during their set up but also the lack of study area specific allometric relations, which resulted in the predominant use of just one allometric relation, might have given rise to a cumulating over- or underestimation of the AGC. However, left aside the built-up uncertainty during this study, other studies reported high AGC estimations at high altitudes and lower AGC at lower altitudes as well, confirming that our results are not a standalone case. Furthermore, most studies along an elevational gradient were confronted with the same uncertainties. Local variability of the forests per altitude could not be assessed accurately due to the small number of PSP and the auto-correlated nature of the often almost neighbouring PSP. It is therefore not possible to conclude the representativeness of the PSP for all forests at these altitudes.

We expected soil nutrient concentrations to be an important driver of any trend in AGC. However, none of the soil properties showed strong correlations with the AGC. Bio-available P did increase significantly with elevation and considering the widely assumed P limitation of tropical forests, this might nevertheless be an important driver behind carbon storage. The expected shift from P to N limitation with elevation was not reflected in the increasing ratio of soil total N over soil total P. However, when considering bio-available P instead of total P, soil N/P did show a decrease and also foliar N/P showed a decreasing trend with elevation. Bio-available nutrient pools and to a lesser extent foliar nutrient concentrations are better linked to nutrient availability of soils. Hence, nutrient limitation might have shifted from P to N limitation with elevation. For example, the microbial net immobilization of total N at the highest altitudes might have been associated with the lower litter quality, resulting in a larger pool of bio-unavailable N. Therefore, direct N mineralization rates might give a better insight into the present N cycling rates than total amounts. Indirect signs of the lower decomposition rates and associated N cycling rates were found in the lower C/N of litter and soil and lower $\delta^{15}\text{N}$ of litter and soil. However, these properties might be more strongly associated with the foliar nutrient concentrations which showed the same trends in nutrient ratios and isotopic composition as in the soil and litter. Hence, this strong interaction between the composition of the plant community and their associated traits and the soil properties is obvious from an evolutionary point of view but it also suggests that forest plant communities might be susceptible to changes in nutrient fluxes.

The underestimation of the AGC at the higher altitude forests might be an extra incentive to ensure their protection. The increasing atmospheric deposition driven by farming and forest burning, forest clearances for cattle and the expected temperature increase over the coming decades due to future global change, might put these forests in jeopardy. Reforestation projects, like the one described in Annex on p 48, could provide a sustainable answer to this problem however.

7 Annex

7.1 Case study: a reforestation project in North-Western Ecuador

7.1.1 Why a reforestation project in Ecuador?

Tropical forests are widely considered to harbor the most extensive collections of terrestrial biodiversity and have been attributed a pivotal role in mitigating climate change. However, their existence is threatened by increasing forest degradation, deforestation and global change. In the period 2010-2015 both Africa and South-America had the highest net annual loss of tropical forests of 2 and 2.8 million hectares respectively. Ecuador, in specific, had the second highest rate of deforestation of the continent with an estimated 74000 ha per year. Human impact in Ecuador has caused the decline of the total forest area from 14.631 to 12.548 million ha for the period 1990-2015 corresponding with an annual loss of 0.6% (FAO 2015) (Table 14). Nowadays 50.5 % of the land is covered by forest, although it is assumed that originally 90 % of the land was forest (FAO 2015; Bruijnzeel et al. 2011). 0.4% of the current forest area is reforested and it has shown an annual increase of 0.9% from 1990 to 2015 (FAO 2015). However, when looking at the periods 2000-2010 and 2010-2015 annual rates were -1 and -1.7 respectively, suggesting that the reforestation investment of the period 1990-2000 (annual growth rate of 4.7%) is gradually being nullified (FAO 2015). Moreover, instead of making use of the wide range of tree species and their extensive spectrum of growth conditions (Ecuador is one of the 17 megadiverse countries of the world (FAO 2006) where 1 km² contains around 1250 plant species), more than 90% of all forest plantations in 2005 consisted of exotic species, primarily *Eucalyptus* and *Pinus* (FAO 2006). The reason why to prefer well studied exotic species over well adapted local species, is purely economical and short term oriented, without any ecological considerations. However, using local species instead of exotic species doesn't necessarily leads to low production rates. *Alnus acuminata* for example might be able to compete in growth with exotic species (Gunter et al. 2009; Cavelier 1995). Moreover, reforestation might add a significant surplus to small scale tropical farmers, when making use of less productive "wastelands." Knoke et al. (2009), estimated that deforestation could be reduced 65 % and that incomes could increase 45% in the study area of the Podocarpus National Park of Southern Ecuador. So, if research on reforestation with native species is still poor (Brandbyge & Nielsen 1986), simple natural regeneration could be an overlooked easy solution. However, due to the low speed of recovery on often burned (Hamilton et al. 1995) and degraded lands and the insufficient species composition, natural regeneration might not be successful at all (Aguirre et al. 2011; Gunter et al. 2007).

Table 14 Forest area and annual change rates between 1990 and 2015 in Ecuador. A distinction was made between primary forest, natural regeneration and planted forests (FAO 2015).

	Prim. forest	Nat. reg.	Planted	Total
Forest area 2015 (10 ³ ha)	12467	26	55	12548
% of forest area 2015	99.4%	0.2%	0.4%	100%
Annual change rate (1990-2015)	-0.6%	-2.8%	+0.9%	-0.6%

7.1.2 Introduction

The target of the reforestation project was to store 62727 ton C over 500 ha in the biomass of planted trees from 2015 to 2041 on property of different private owners. This means that approximately 2318 ton C needs to be sequestered every year considering linear growth. Supported by BOS+ in assignment by Telenet the works were conducted by local workers of MCF (Mindó Cloud Forest Foundation). The trees were planted between 2013 and 2014 and should remain untouched for the coming 30 years. A range of 85 different local species were used.

7.1.3 Objectives

The objective of the field campaign was to make an estimation of the aboveground carbon storage present at the moment of inventarisation. Therefore, tree height, root collar diameter (RCD) and diameter at breast height (DBH) were measured and tree species were determined. Afterwards, these measurements were used in existing allometric relations to estimate the aboveground biomass and carbon storage of the project area.

7.1.4 Material and methods

7.1.4.1 Study Area

The reforested areas were located in four provinces (Pichincha, Imbabura, Carchi and Esmeraldas) as can be seen in Figure 24 and Figure 25. A more detailed description of the environmental conditions can be found in Table 15. Two clusters can be distinguished, the Pichincha cluster in the South (1,2,3) and the Imbabura cluster in the North (4,5,6,7).

Table 15 Site description of the reforestation project (INAMHI n.d.; Bauters 2013)

Province	Strat.	Area (ha)	Altitude (masl)	Natural habitat	MAT (°C)	P (mm)	SOC (%)	Soil type
Pichincha	1	29	2200	Mountain rainforest	15	2750	1.92	Aluandic Andosol
	2	39	1600	Subtropical rainforest	18	2750	2.18	Aluandic Andosol
	3	43	300	Lowland rainforest	21	2750	4.4	Aluandic Andosol
Imbabura	4	21	1750	Dry forest with seasonal rains	18	750	0.33	Haplic Andosol
	5	135.5	1100	Subtropical rainforest with long dry season	18	1500	1.93	Vertic Andosol
Carchi	6	98	1400	Subtropical rainforest with long dry season	25	2550		
Esmeraldas	7	69	1300	Subtropical rainforest				

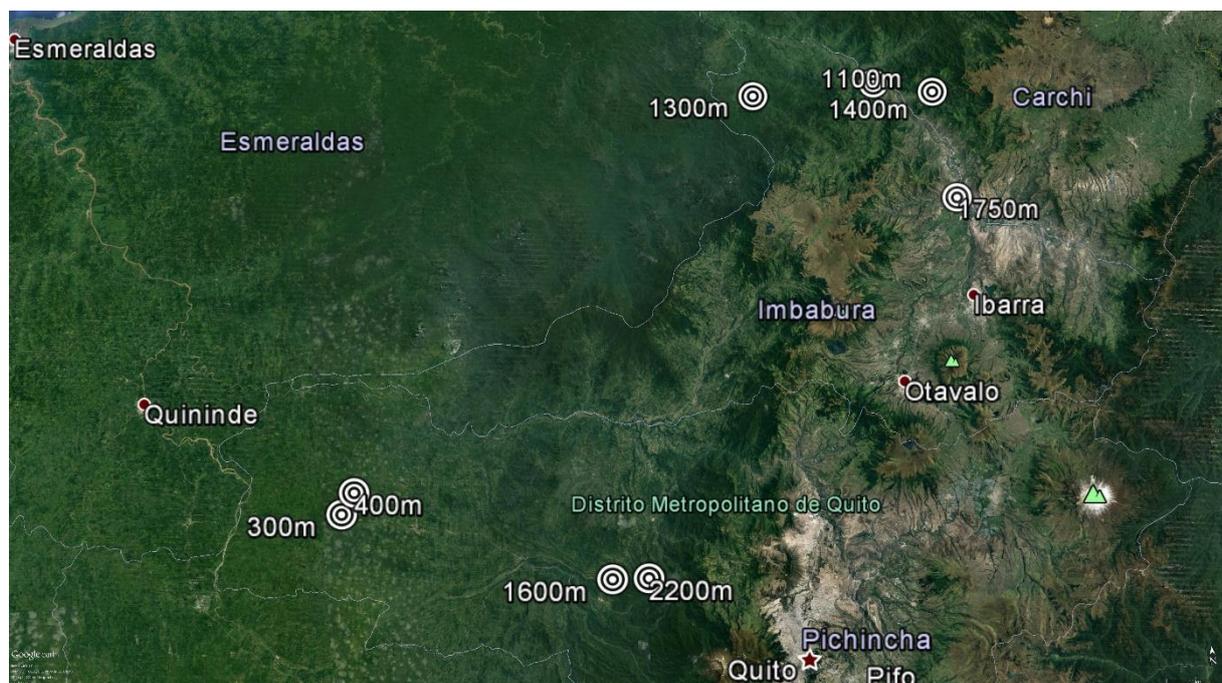


Figure 24 Location of the different reforestation areas depicted by their altitude.

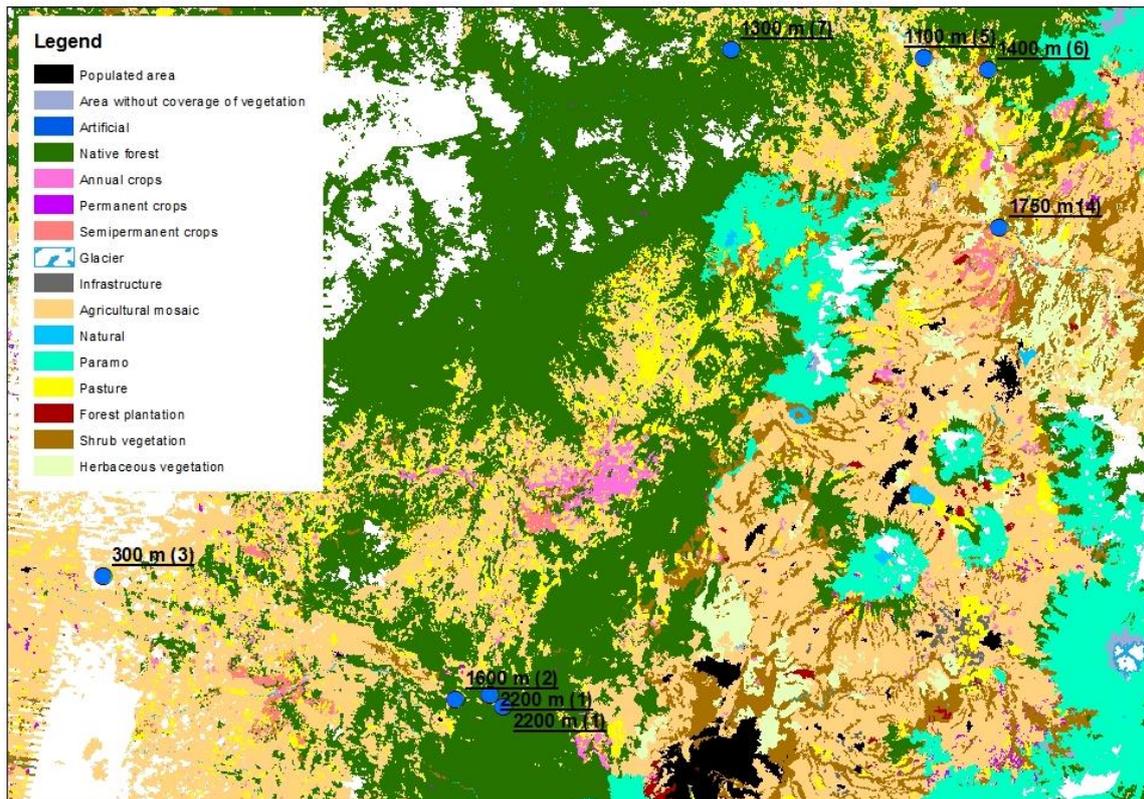


Figure 25 Location of the different reforestation areas, depicted as “Altitude (number of stratum).” The different land covers are described by their color code.

7.1.5 Material and methods

7.1.5.1 Fieldwork

The 41 inventoried PSPs (8 in S3, 6 in S5, 4 in S7, 5 in S6, 8 in S2, 4 in S4, 10 in S1) of the planted forest were already selected and established in the previous field campaigns (Bauters 2013; Strubbe 2013). The density of trees planted was approximately 1000 trees per ha. Considering that the circular plots for the inventory have 8 m of radius, the area of the circular plot is 201 m² which means approximately 20 trees inside each circular plot. The elevation and coordinates of the center of each established plot was available for relocation. When finding the landmark which indicates the center (mostly a tube) the borders were delineated using a rope.

The measurements were comparable to those of natural forest but because of the relative small dimensions, RCD (Root Collar Diameter) was measured as well. The trees were divided in planted or natural regeneration based on their location and attributes. This allowed to estimate the survival, recruitment and mortality of the trees. For the identification of the trees local workers were addressed. But despite their efforts many trees remained unidentified.

Secondary forest differs in many ways from primary forest. Therefore, allometric relations set up based on primary forests to estimate the C amount of secondary forest result in an error. Allometric relations which contain (in order of lesser importance) diameter at breast height (DBH), wood density (WD) and height (H) have proven to be the most efficient for secondary forests (Nelson et al. 1999).

7.1.5.2 Analysis

To estimate the amount of aboveground C stored, the method of the previous reforestation campaign was used (Soria 2014). First, a relationship between DBH and RCD was established for trees taller than 1.3 m, which allowed the prediction of DBH based on RCD for the remaining trees (trees smaller than

1.3m). Afterwards, the predicted or measured DBH was used as an independent variable to predict the AGB from a variety of published relationships (Table 16). The AGB estimation from tree to strata level based on plot inventories involved three steps as described for the earlier remeasurement campaigns (Van Breugel et al. 2011) (1) the estimation of individual tree biomass, (2) the summation of individual tree AGB to estimate plot AGB, and (3) the calculation of an across-plot average to yield a strata-level estimate (Soria 2014).

The current allometric models are mainly developed for mature trees. Research shows that these models don't cover the dynamics associated with trees in the sapling stage because young rainforest trees invest more in leaves and branches than in stem growth. As there were no allometric relations available for young mixed forests stands, we used the same equations as the once used in the previous field campaign (Soria 2014), summarized in Table 16.

Table 16 Allometric equations used for the reforestation project. Description of the intended forest type, region and diameter range.

$AGB_{tree} (kg) =$	Forest type	Region	DBH (cm)	Literature source
$\exp(-2.489 + 2.43 * \ln(DBH))$	Young secondary forest	Malaysia	0.11-28.7	(Kenzo et al. 2010)
$\exp(-2.207 + 2.62 * \ln(DBH) + \ln(WD))$	Young secondary forest	Indonesia	7.6-48.1	(Ketterings et al. 2001)
$\exp(-1.97 + 2.413 * \ln(DBH))$	Young secondary forest	Central Amazon	1.2-28.6	(Nelson et al. 1999)
$1.087 * \exp(-2.232 + 2.422 * \ln(DBH))$	Young secondary forest	Colombia	0.9-40	(Sierra et al. 2007)
$0.0673 * (WD * DBH^2 * H)^{0.976}$	Mature forest	Pantropical	>5	(Chave et al. 2014)

7.1.6 Results

Some results indicate that tropical regrowth forests are stronger C sinks than the intact forests due to rapid biomass accumulation under succession, but these estimates are poorly validated because of sparse data (Pan et al. 2011). We encountered different difficulties, which flow from the lack of basic knowledge of reforested areas. First, existing allometric relations generally use DBH instead of RCD as the primary variable (Nogueira et al. 2008). 840 of the 1278 trees were less than 1m30, which means they hadn't a DBH to measure at all. A prediction of this "non-existing DBH" was made by fitting a linear regression based on RCD Figure 26. Destructive measurements would have proven a great asset in establishing more accurate local equations using RCD instead of DBH (Ribeiro et al. 2014; Fitzgerald 1983). However, other simple methods exist to estimate the biomass of small trees, such as the visual obstruction method (Fleming 2014).

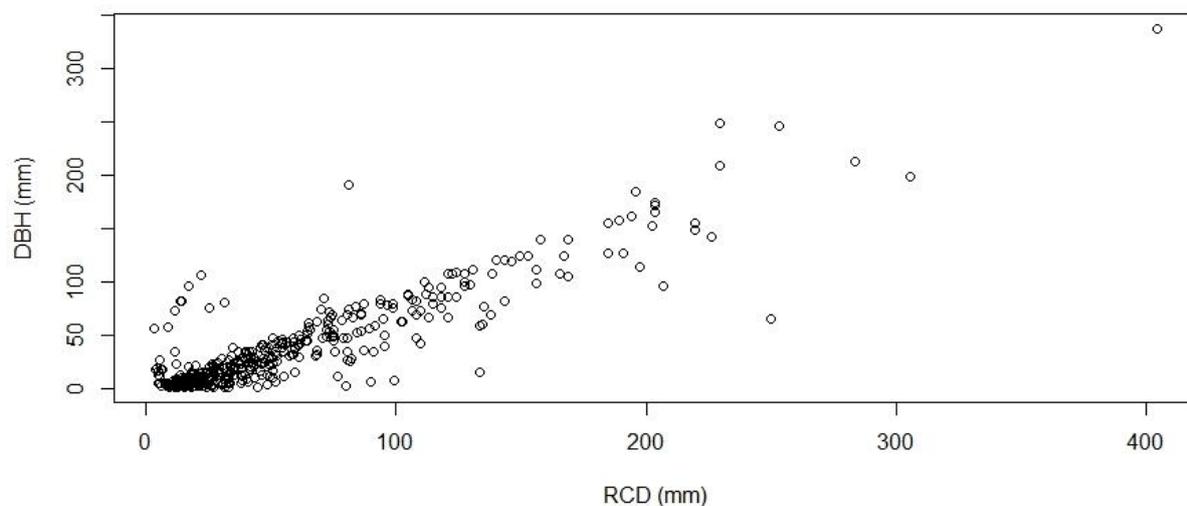


Figure 26 Linear fit of the DBH in function of the RCD for 435 trees in 41 plots. The relationship that was found was $DBH=0.7452 \cdot RCD-3.4677$ ($R^2=0.81$)

In Table 17 AGC ($\text{ton C ha}^{-1} e^*$ with e^* standing for earth surface) are calculated using the different allometric equations. However, as areas of the different locations were calculated as earth surfaces (e^*), neglecting the slopes will result in an underestimation ranging from 2 to 14% dependent on the location. In Table 18 AGC for the entire area are given. To calculate the amount of C from biomass, a factor 0.5 was used as was done for the natural forests (Brown 1997).

Table 17 C storage ($\text{ton C ha}^{-1} e^*$) in the different reforestation areas. e^* stands for earth surface.

Stratum	3	5	7	6	2	4	1
Altitude (masl)	300	1100	1300	1400	1600	1750	2200
Area (ha)	43	135.5	69	98	39	24	29
Kenzo et al.	7.26	0.073	0.51	0.14	8.92	0.50	1.94
2010	± 4.41	± 0.089	± 1.69	± 0.19	± 3.90	± 0.28	± 1.00
Ketterings et al.	6.02	0.055	0.42	0.099	8.28	0.49	1.86
2001	± 4.04	± 0.073	± 1.56	± 0.15	± 4.17	± 0.37	± 1.08
Nelson et al.	11.69	0.12	0.84	0.22	14.29	0.82	3.13
1999	± 7.03	± 0.15	± 2.74	± 0.31	± 6.21	± 0.46	± 1.62
Sierra et al.	10.00	0.10	0.71	0.19	12.26	0.69	2.67
2007	± 6.05	± 0.13	± 2.34	± 0.27	± 5.35	± 0.39	± 1.39
Chave et al.	7.081	0.019	0.087	0.094	7.91	0.18	1.42
2014	± 4.29	± 0.012	± 0.19	± 0.18	± 4.01	± 0.33	± 0.84
Target 2015-2016							21.32
SOC (ton C/ha)	197.27	130.08			255.09	20.12	79.88

Table 18 C storage (ton C) in the different reforested areas. When taking into account the measured slopes, the AGC for the entire area using the equation of Nelson et al (1999), increases with 37.97 ton C or 3%.

Stratum	3	5	7	6	2	4	1	Total	
Altitude (masl)	300	1100	1300	1400	1600	1750	2200		
Area (ha)	43	135.5	69	98	39	24	29	437.5	
AGC (ton C)	Kenzo et al. 2010	312.00	9.92	35.43	13.52	348.70	11.93	56.22	786.71
	Ketterings et al. 2001	258.74	7.49	32.50	9.75	323.05	11.87	54.08	697.47
	Nelson et al. 1999	502.47	16.59	57.63	22.22	557.38	19.79	90.78	1266.86
	Sierra et al. 2007	429.84	13.91	49.04	18.81	477.99	16.67	77.55	1083.80
	Chave et al. 2014	304.51	2.57	6.00	9.19	308.67	4.26	41.15	676.36
	Target 2015-2016								9329
	SO C (ton C)	8482.61	17625.84			9948.51	482.88	2316.52	38856.35

7.1.7 Discussion

Using the prevailing equations, our C estimations are significantly smaller than the target for the period 2015-2016. Furthermore, the equation of Chave has been found to consistently overestimate AGB of smaller diameter classes (Girardin et al. 2010). However, left aside the many uncertainties that piled up along the way in the calculations, socio-economic aspects seemed the limiting factor in the reforestation project. Trees had been cut and cows were grazing on land that was proclaimed to be safeguarded from such disturbances. Therefore, the initial plan to commit this thesis to the reforestation project had to be adjusted.

The future prospects to make assessments of biodiversity might be pre-evaluated already from the amount of different tree species. Some species seem to grow very well, and become dominating over other species. *Aliso* or *Alnus* is the dominant tree in over half of the plots and just 9 species take in 72 % of the total AGC. 18 % of the AGC was taken by undetermined species. *Aliso*, having a good growth, reduces diversity through competition with other tree species and allelopathic exudates (Cavelier 1995). *Alnus* is a promising tree in reforestation projects when only focused on C storage but when diversity becomes important its distribution needs to be kept in check. *Alnus nepalensis* is moreover an exotic species that originates from the Himalayan mountains, unlike the local *A. acuminata* that was planted as well during the project. In addition, the importance of choosing well adapted species is quite clear as approximately 55 % of the planted trees in 2013 died by 2015 (Ferreri 2015).

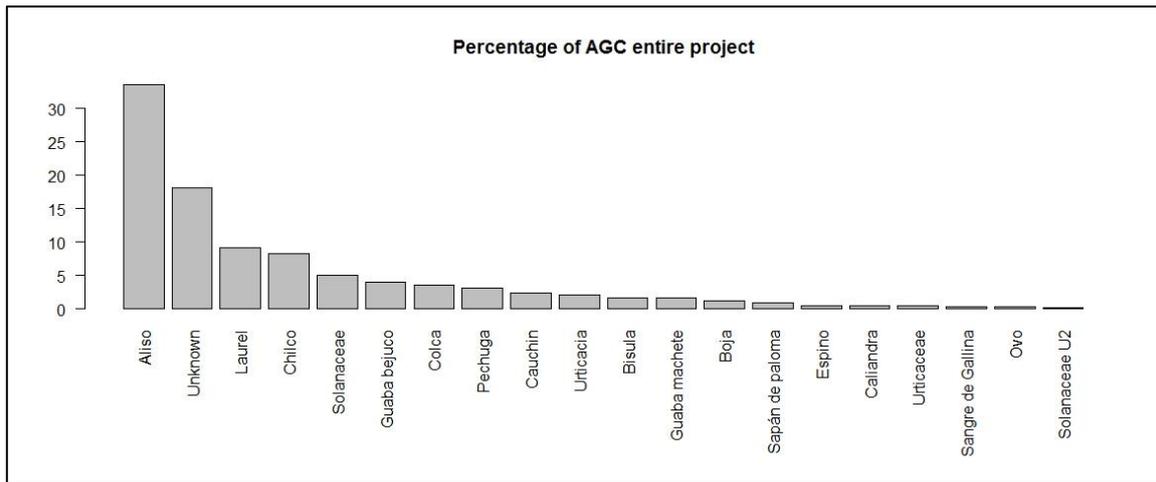


Figure 27 Percentage of each species based on the aboveground carbon (AGC) of the entire project. A wide range of different species that weren't distinguished from one another, are covered by the term "Unknown"

Stratum 4 is subjected to arid seasons therefore windbreaks of the exotic *Casuarina* (Figure 28) were planted and irrigated regularly. After measuring these trees, assuming a planting distance of 3 m and extrapolating to the total area of stratum 4, values ranging from 74 to 121 ton AGC were calculated. While the estimated AGC of the stratum without accounting for the windbreaks ranged only from 4.3 to 19.8 ton C. Because of the irrigation the *Casuarina* trees enjoyed it is hard to assess the toughness of these species against that of the other planted tree species, which lacked irrigation. Nevertheless, it is obvious that the conditions of this stratum aren't ideal for tree growth of unirrigated local tree species. Using exotic species may look promising in terms of growth on the short term, but on the long term a trade off or even a loss of ecosystem services might be the case. Planting pines on the grasslands of the Paramo in Ecuador for example, resulted in a loss of soil C, N and water retention capacity (Farley 2007). Nevertheless, afforestation of degraded grasslands have been reported to give rise to a significant increase of SOC (Lal 2005).



Figure 28 *Casuarina* as wind break

7.1.8 Conclusion

The increasing AGC with elevation in the natural forests in combination with the increasing number of economically marginal lands at high altitudes (Fehse et al. 2002), holds potential for future reforestation projects. However, as this reforestation project has shown, such projects are mainly limited by socio-economic aspects and the feasibility of future endeavors will depend on how local people are involved. Investigating which species compositions will yield the most in terms of biodiversity and C sequestration, is not possible and will have no benefit if local communities aren't convinced of the added value.

8 Recommendations for future research

Appropriate allometric relationships have proven to be invaluable for accurate estimations of AGC. Furthermore, the increasing amount of multi-stemmed trees at higher altitudes in combination with the overall stunted architecture of these trees, should be taken into account when establishing or choosing allometric relations.

No tree growth estimations could be made as this field campaign tagged and measured the trees for the first time. Knowledge about the tree growth might however reveal a better correlation with nutrient contents than did the AGC. In addition, tree growth rates might also be beneficial to evaluate the feasibility of reforestation projects at certain altitudes, as quick forest establishments are generally preferred. In addition, litter fall experiments might provide important additional insights through leaf productivity. These tree growth measurements and litterfall experiments can be linked to fertilization experiments to, analyse responses of these variables on increased nutrient availability.

To analyse nutrient cycles, fluxes instead of concentrations hold much more promise. N mineralization rates and C respiration rates provide more clear insights into ecological processes than standing C stocks.

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10 Appendix

10.1 Maps

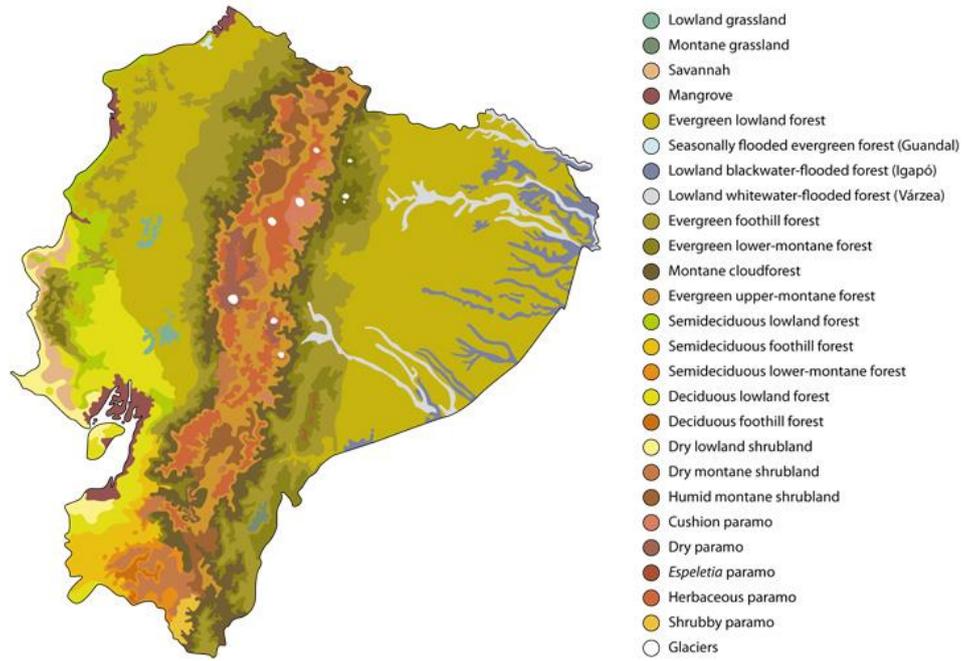


Figure A 1 Vegetation types in Ecuador according to Sierra (Sierra 1999)



Figure A 2 Location of the natural forest strata, depicted by their corresponding altitude.

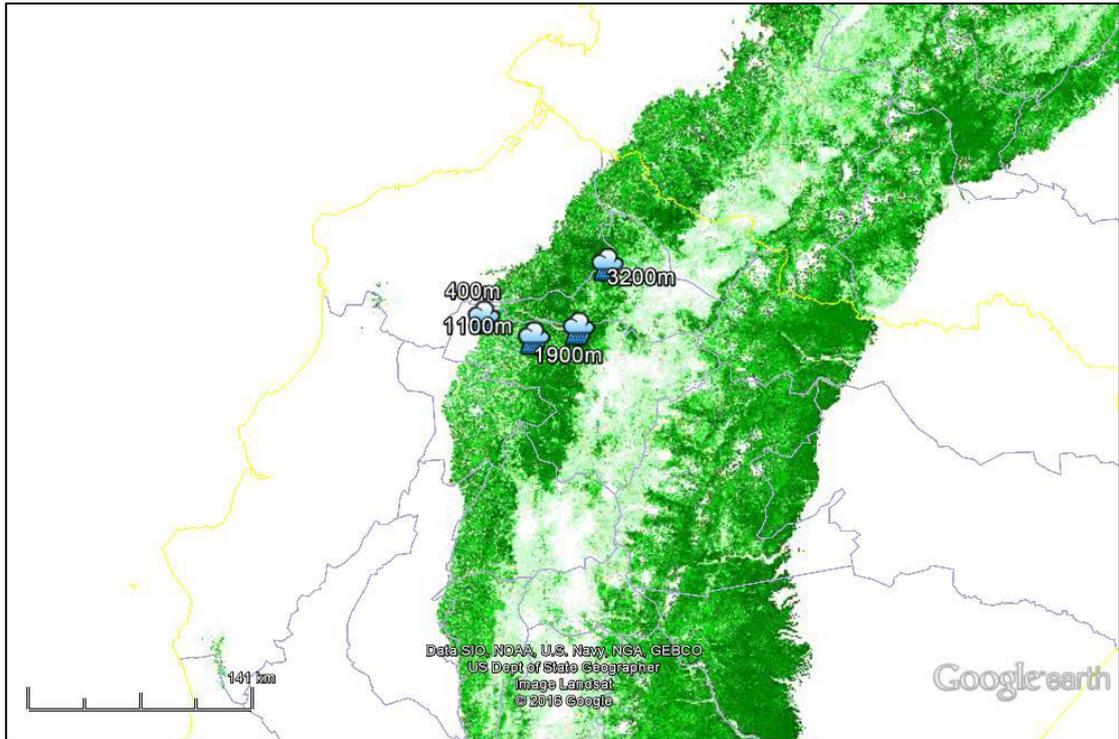


Figure A 3 Map of tropical montane cloud forests (in green) in the Northern Andes region, with an accuracy of 1 km², and visualization of the different forest locations (Aldrich et al. 1997; Mulligan & Burke 2005; Wutrich 2006).

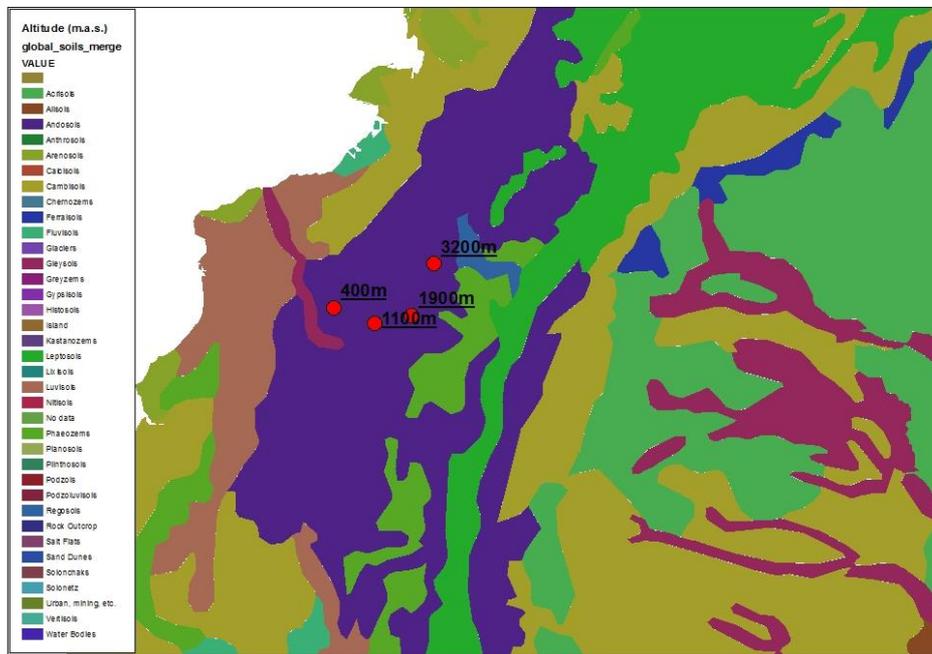


Figure A 4 Soil classification of the study area, according to the FAO. Visualization of the different forest locations. Modified from FAO.

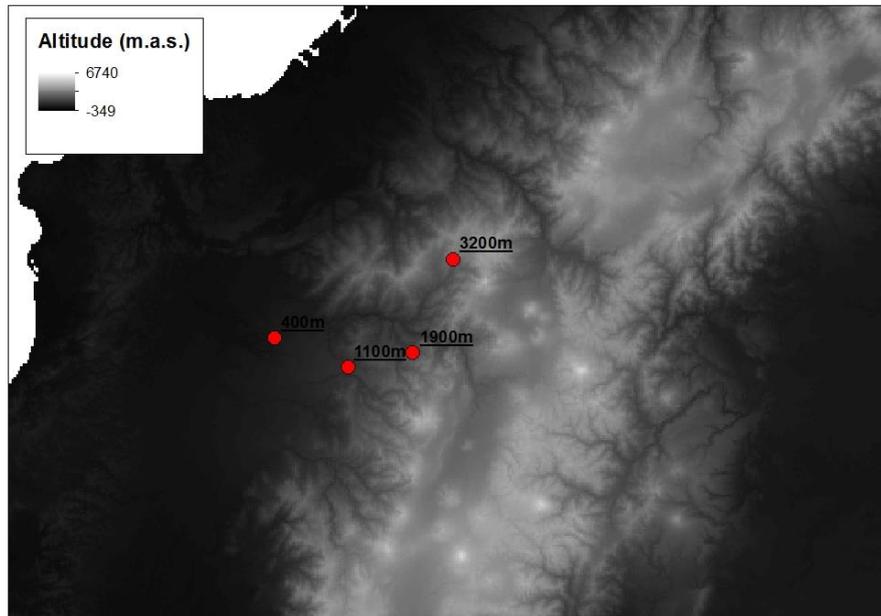


Figure A 5 Digital elevation model of the study area with visualization of the different forests locations. Accuracy of 1 km². Modified from Worldclim (Hijmans et al. 2005; Worldclim).

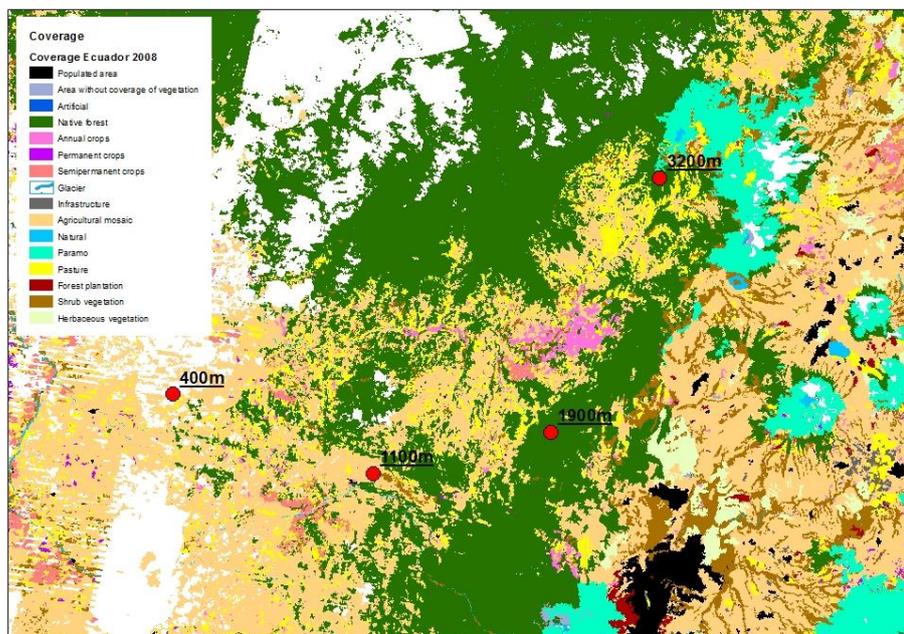


Figure A 6 Land coverage in the study area with visualization of the different forests locations. Accuracy of 1 km². Modified from Patrimonio ambiente, Ecuador (Ministerio del ambiente, Ecuador).

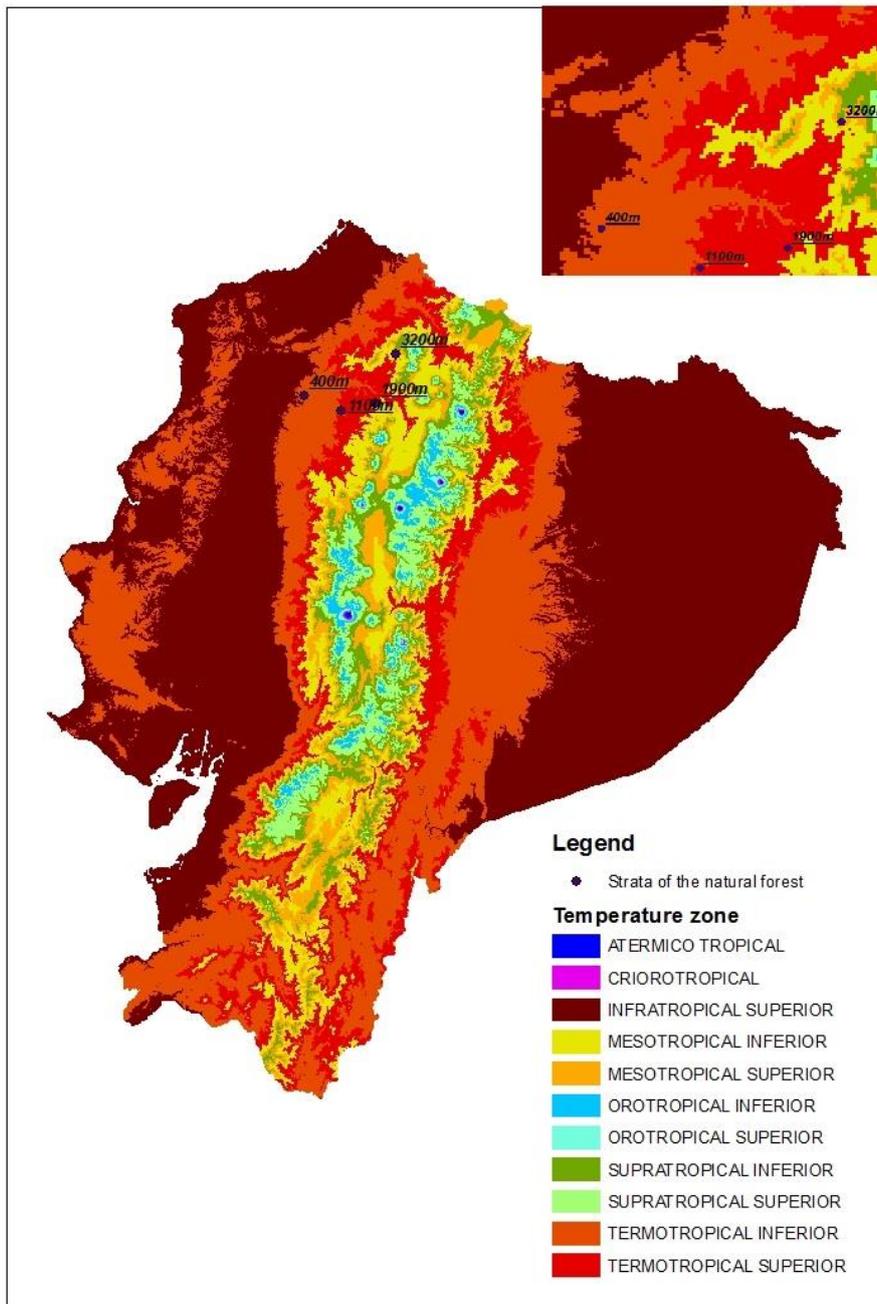


Figure A 7 The temperature types ($I_t = (T+M+m) \cdot 10$) are based on an index which combines information of the maximum (M), minimum (m) and mean annual temperature (T). The information was obtained from INAMHI, MONITOREO DEL PATRIMONIO NATURAL del Ministerio del Ambiente of Ecuador and Worldclim. The stratum at 400 m is located in the termotropical inferior type (I_t : 600-710); the strata at 1100 and 1900 m are located in the termotropical superior type (I_t : 490-600); the stratum at 3200 m is located in the supratropical inferior type (I_t : 240-320) bordering the mesotropical superior type (I_t : 320-405). The accuracy is 1 km² (INAMHI; Worldclim).

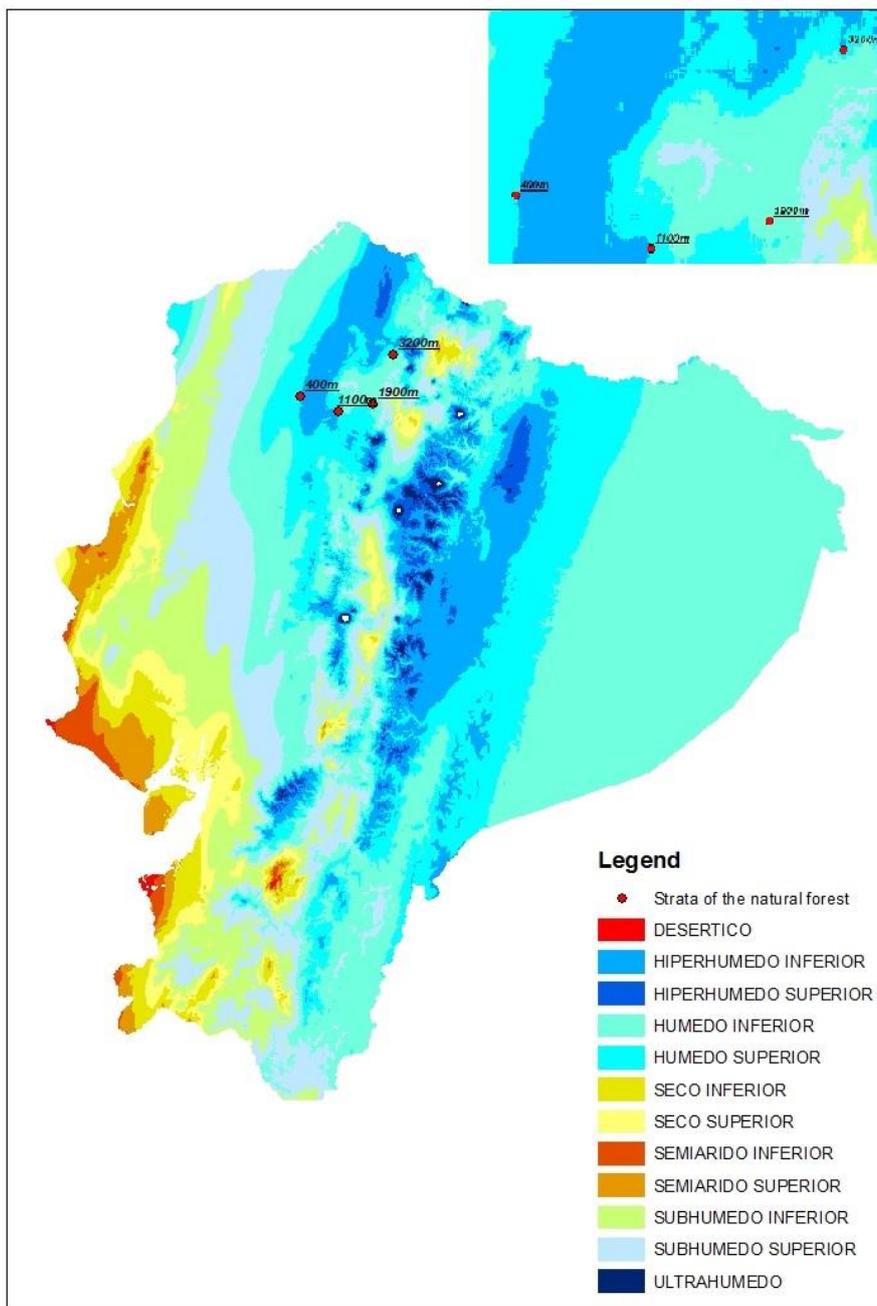


Figure A 8 The precipitation types ($I_0 = (P_p/T_p) * 10$) are based on an index which combines information of the mean annual precipitation (P_p) and mean annual temperature/10 (T_p). The information was obtained from INAMHI, MONITOREO DEL PATRIMONIO NATURAL del Ministerio del Ambiente of Ecuador and Worldclim. The stratum at 400, 1100 and 3200 masl are located in the humedo superior type (I_0 : 9-12) while the stratum at 1900 masl is located in the humedo inferior type (I_0 : 6-9). The accuracy is 1 km² (INAMHI; Worldclim).

10.2 Recommendations for future field campaigns in natural forests

10.2.1 Height measurements

During this field campaign around 90 % of the tree heights were determined. When assuming only 20 % of the trees were measured, what would be the effect compared to measuring 90 % of the trees? Per plot 20 % of the trees with measured heights were randomly chosen and the other tree heights were neglected. A first observation is that almost all models allocated to certain plots were different. However, the averaged deviation of the measured versus the estimated height didn't differ much, with a value of 2.77 m and 3.19 m for the 90 % and the 20 % scenario respectively. This result can be kept in mind for future time restricted field campaigns.

10.3 Lab protocol

10.3.1 Bio-available P soil

AEM strips were used to extract bio-available phosphorus from soil. 30 mL milliQ water was added to 0.5 gram of soil and shaken for 16 hours at room temperature. Afterwards the strips were removed and cleaned with milliQ water. The P retained on the strips was eventually removed by using 20 mL of 0.5 M HCl. These samples were shaken for 22 hours at room temperature. Afterwards the strips were removed and the HCl solution was retained for analysis. Bio-available P concentrations were measured using spectrophotometry. Concentrations were measured relative to those of a standard series ranging from 0 to 0.025 mM. 150 μ L phosphate reagent was added to 1 mL of the retained HCl solution, shaken and left to rest for 30 minutes. Finally, the absorbances were measured at a wavelength of 650 nm.

10.3.2 Total P litter

All litter samples were tested on total P concentrations. Between 0.5 and 1 g of every sample was weighted and afterwards ashed in the oven at 550 °C for 5 hours in porcelain cups. After the samples were cooled down they were dissolved in 5 to 10 mL 2 M HCl for respectively samples of 0.5 and 1 g. These samples were then poured in flasks of 25 or 50 mL, for 0.5 or 1 g samples respectively. MilliQ water was used to make sure all residues of the cups were in the flasks. The flasks were shaken and left to rest for 15 minutes. MilliQ was added until the flasks contained 25 or 50 mL of solution. The flasks were then shaken and allowed to stand for 30 minutes before passing the solution of each flask through a P-free filter. The samples were then analysed using the continuous flow analyzer.

10.3.3 Figures

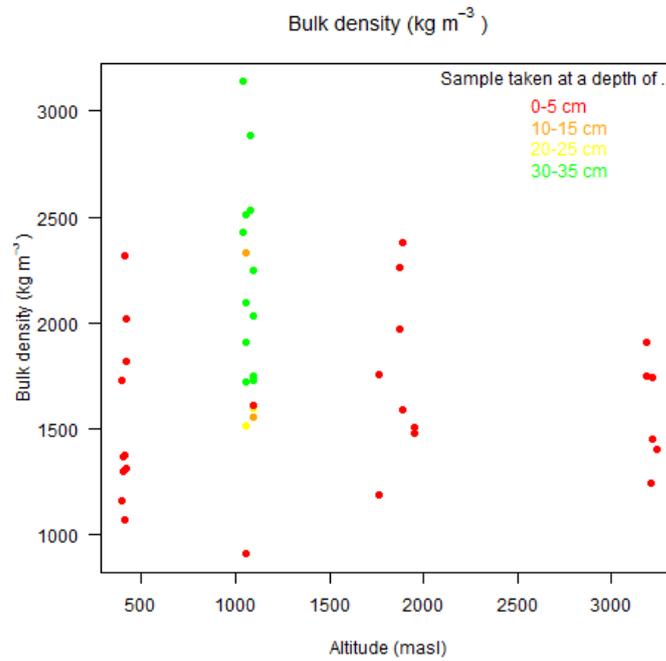


Figure A 9 Soil bulk density (kg m⁻³) in function of altitude. The different colors depict the different depths at which the samples were taken.

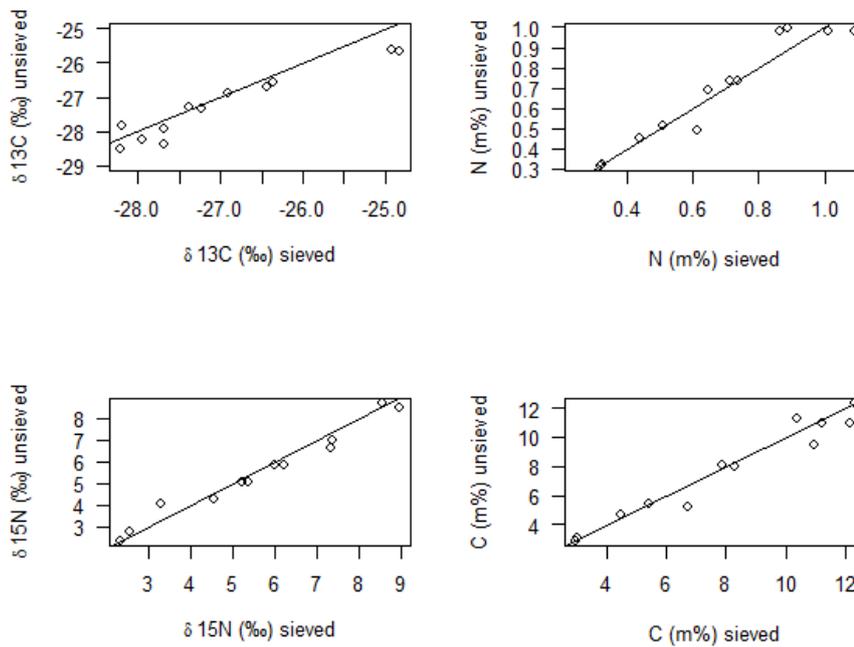


Figure A 10 Sieved versus unsieved soil material for δ¹³C (‰), N (m%), δ¹⁵N (‰) and C (m%). To compare sieved and unsieved samples a Wilcoxon ranked sum test was used ($p < 0.05$). The samples didn't differ in their N, δ¹⁵N and C concentrations, but did differ in their δ¹³C concentrations.

10.4 Allometric relations

Table A 1 List of the checked height-diameter relationships with the literature sources and type of equation. *H* stands for tree height, *DBH* for diameter at breast height and *a*, *b* and *c* are the parameters that were determined for fitting the data to the different relationships.

N°	Formula	type	Source
1	$H = 1.3 + a * (1 - e^{-b*DBH^c})$	Weibull	(Huang et al. 1992)
2	$H = 1.3 + a * (1 - e^{-b*DBH})^c$	Chapman-Richards	
3	$H = 1.3 + a / (1 + b^{-1} + DBH^{-c})$	Modified logistic	
4	$H = 1.3 + a * e^{b/(DBH+c)}$	Exponential	(Scaranello et al. 2012)
5	$H = a * (1 - e^{-b*DBH^c})$	Weibull	
6	$H = a * (1 - e^{-b*DBH})^c$	Chapman-Richards	
7	$H = 1.3 + a / (1 + b * e^{-c*DBH})$	Logistic	
8	$H = a / (1 + b * e^{-c*DBH})$	Logistic	
9	$H = 1.3 + b * e^{a+b/(DBH+1)}$	Exponential	
10	$H = a * e^{-b * e^{-c*DBH}}$	Gompertz	
11	$H = 1.3 + a * DBH / (b + DBH)$	Hyperbolic	(Brown et al. 1989)
12	$H = 1.3 + DBH^2 / (a + b * DBH)^2$	Hyperbolic	
13	$H = 1.3 + a * DBH^b$	Power	
14	$H = a * DBH^b$	Power	
15	$H = e^{a+b*log(DBH)}$	Exponential	
16	$H = a - b * e^{-c*DBH}$	Non-linear exponential	(Feldpausch et al. 2012)
17	$H = a * (1 - e^{-b*DBH})$	Non-linear exponential	(Banin et al. 2012)

Table A 2 Assignment of the best fitting height-diameter relationship to every PSP.

Altitude (masl)	PSP	N° formula
400	1	14
	2	9
	3	16
	4	11
	5	11
1100	1	7
	2	11
	3	11
	4	12
1900	1	7
	2	9
	3	11
	4	7
3200	1	8
	2	9
	3	9
	4	7

10.5 Figures

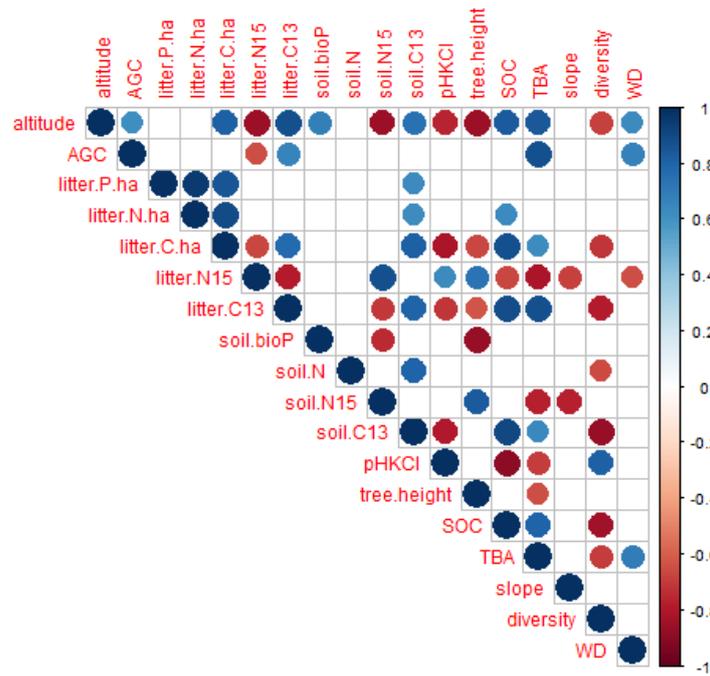


Figure A 11 Correlation table. Correlations with ($p < 0.05$) were left out and variables that didn't show any correlation at this confidence level were rejected. AGC stands for aboveground carbon; litter.P.ha, litter.N.ha and litter.C.ha stand for the litter P, N and C concentrations of the litter on a land surface base; litter.N15 and litter.C13 are the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of the litter on a mass base; soil.bioP, soil.N, soil.N15 and soil.C13 stand for the soil bio-available P concentration, soil total N concentration, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of the upper 30 cm of soil respectively; SOC stands for soil organic carbon; TBA stands for total basal area; diversity stands for tree diversity; WD stands for wood density

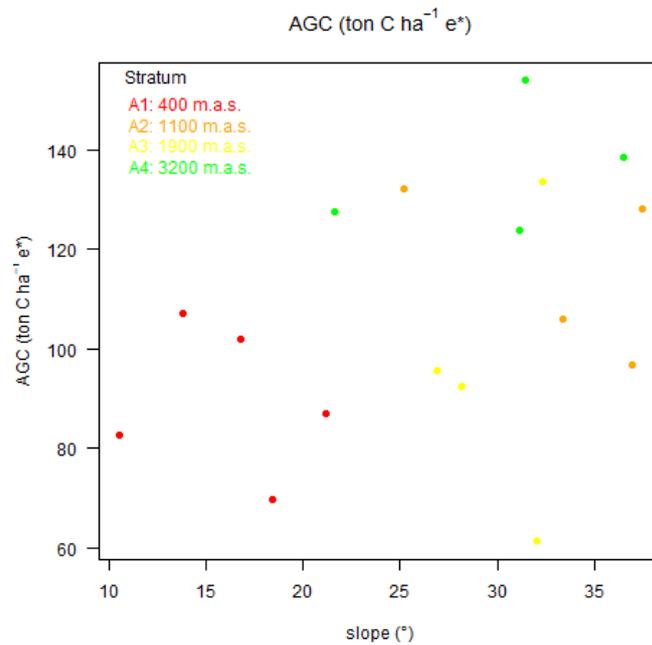


Figure A 12 AGC in $\text{ton C ha}^{-1} \text{e}^*$ in function of slope ($^\circ$). e^* stands for earth surface. The different colors indicate different altitudes. (red) forest at 400 masl (orange) at 1100 masl (yellow) at 1900 masl (green) at 3200 masl.

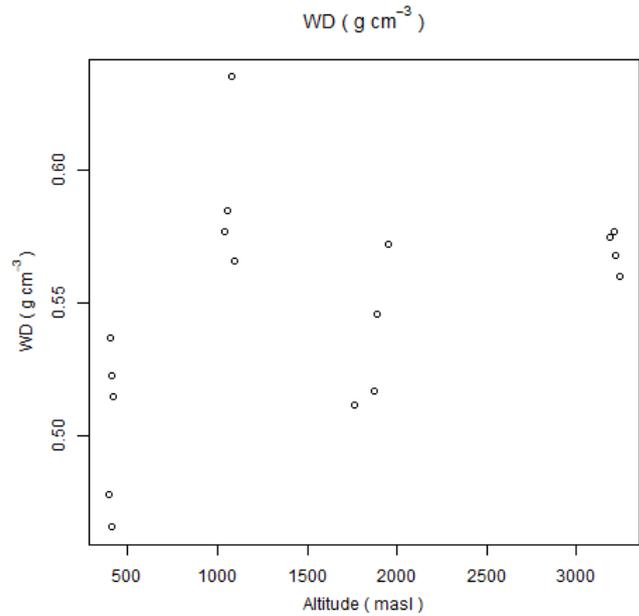


Figure A 13 Wood density (WD) in g cm^{-3} in function of altitude. The community weighted means were based on the basal area. The linear regression was not visualized and the R^2 value was not given as $p > 0.05$. No measurements of WD were made, instead the estimation of WD visualized here, was made using the DRYAD database. Only trees that were determined at species or genus level were used to estimate the average WD per plot.

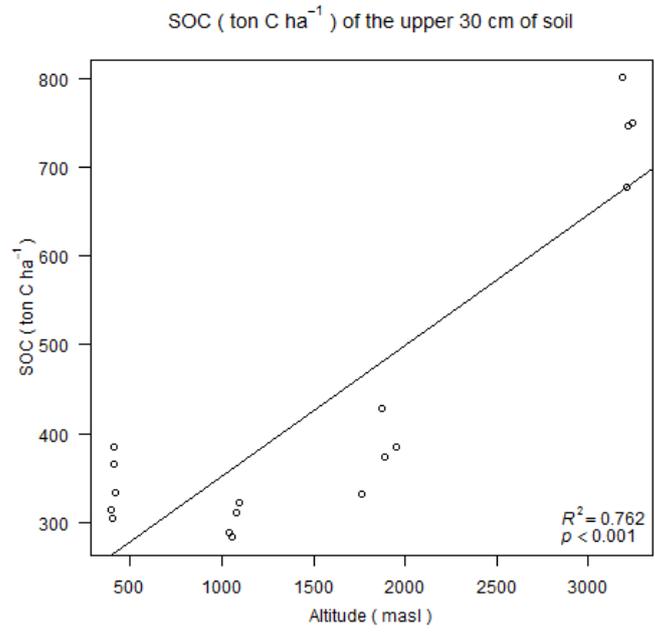


Figure A 14 Altitudinal patterns in soil organic carbon (SOC) in ton C ha^{-1} of the upper 30 cm of soil. The linear regression was visualized and the R^2 value was given as $p < 0.05$.

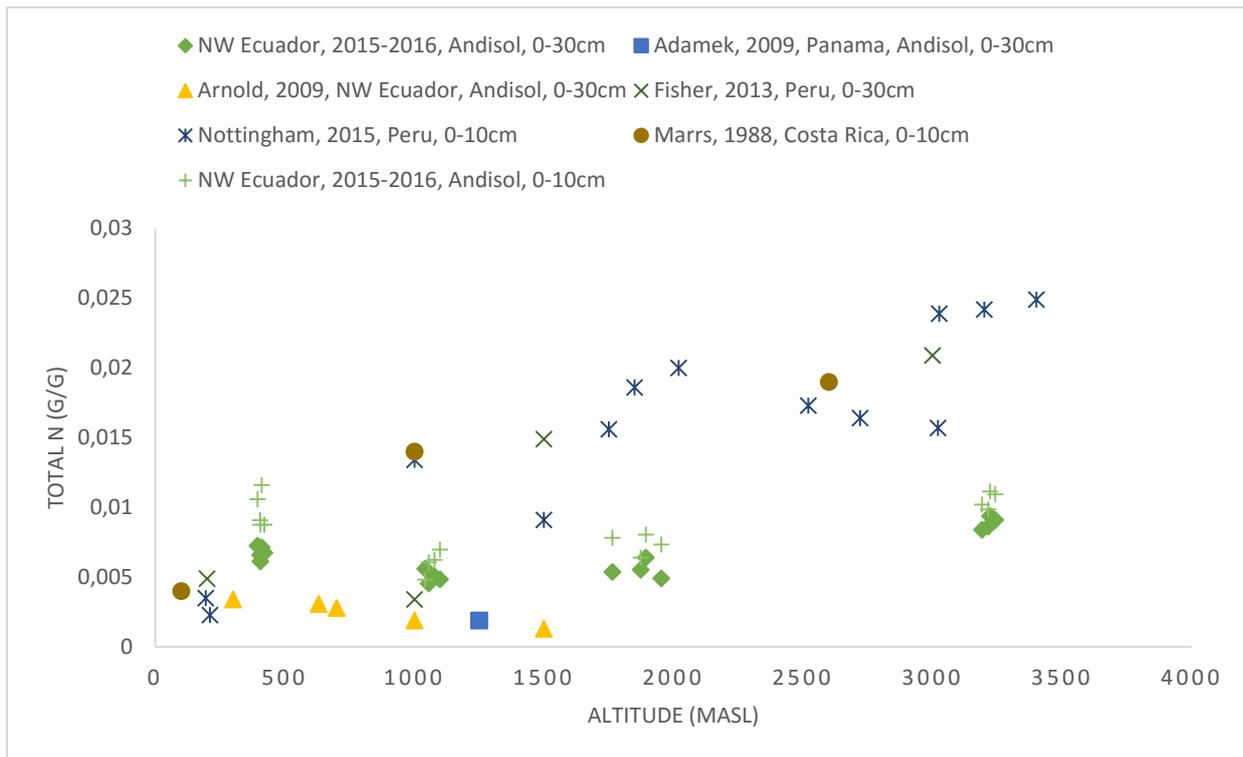


Figure A 15 Total soil N in $g\ g^{-1}$ of different studies in South-America with mentioning of the literature source, country, soil type if given and depth interval.

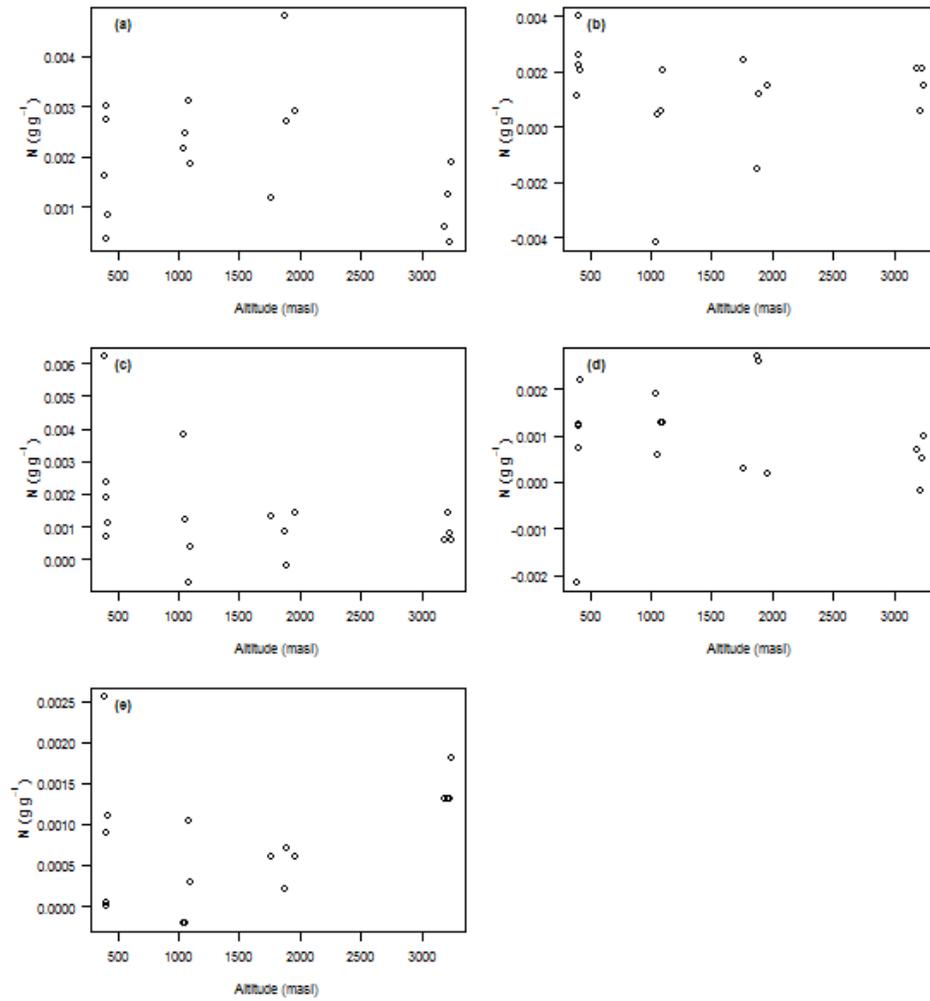


Figure A 16 Soil total N difference between soil depths in g kg^{-1} in function of altitude. (a) difference of soil total N between 2.5 and 7.5 cm of soil depth (b) difference of soil total N between 7.5 and 15 cm of soil depth (c) difference of soil total N between 25 and 15 cm of soil depth (d) difference of soil total N between 40 and 25 cm of soil depth (e) difference of soil total N between >50 and 40 cm of soil depth.

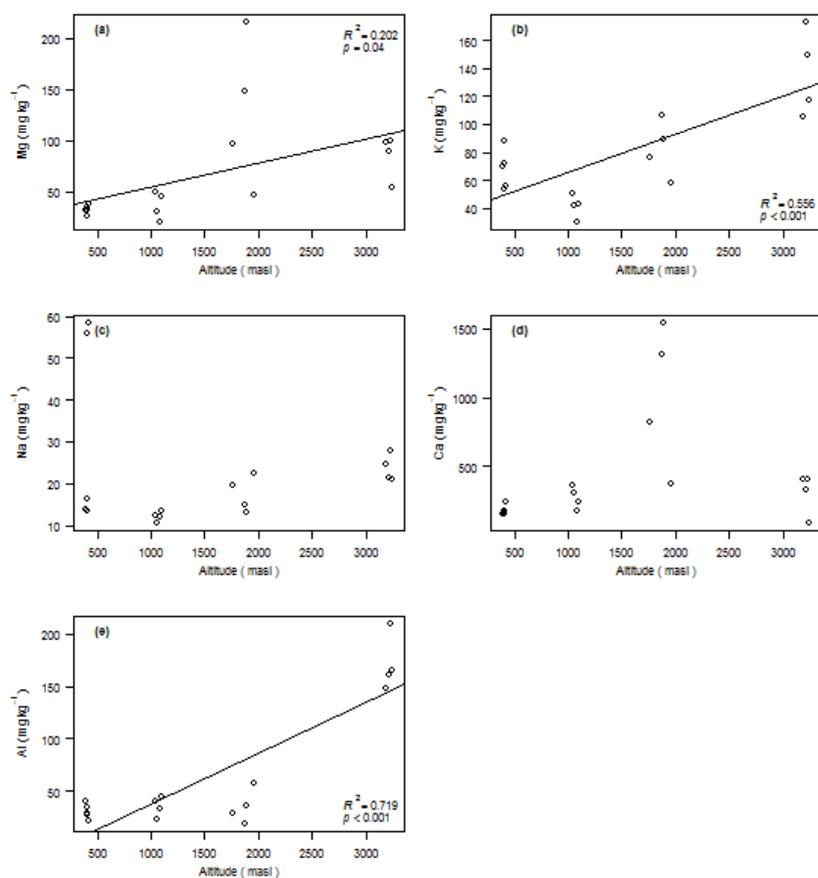


Figure A 17 (a) Mg, (b) K, (c) Na, (d) Ca and (e) Al concentrations in mg kg^{-1} of the upper 30 cm of soil. Mg and Ca concentrations were significantly correlated while the other micronutrients didn't show any significant correlation. Al concentrations were similar at the lower and mid-altitudes but increased more than 3-fold at the highest stratum. Linear regressions were visualized and R^2 values were given when $p < 0.05$.

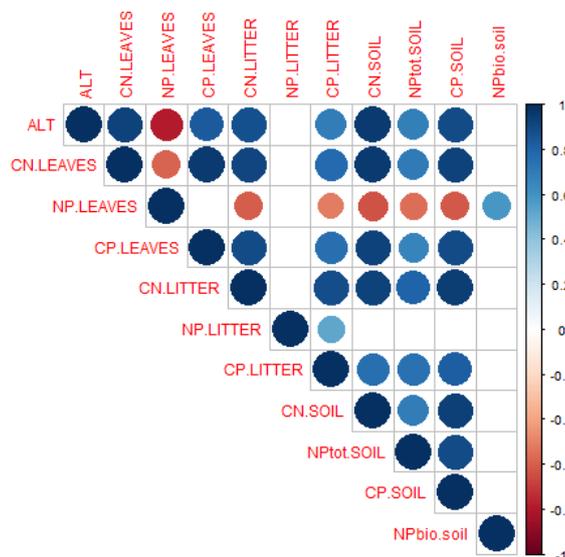


Figure A 18 Correlation table for the nutrient ratios of leaves, litter and soil. Correlations with ($p < 0.05$) were left out and variables that didn't show any correlation at this confidence level were rejected. ALT stand for altitude; CN.LEAVES, CP.LEAVES and NP.LEAVES stand for the C/N, C/P and N/P ratio of the leaves; CN.LITTERS, CP.LITTER and NP.LITTER stands for the C/N, C/P and N/P ratio of the litter; CN.SOIL and CP.SOIL stand for the C/N and C/P ratio based on total P of the soil; NPtot.soil and NP.biosoil stand for the N/P of the soil based on total P and bio-available P.

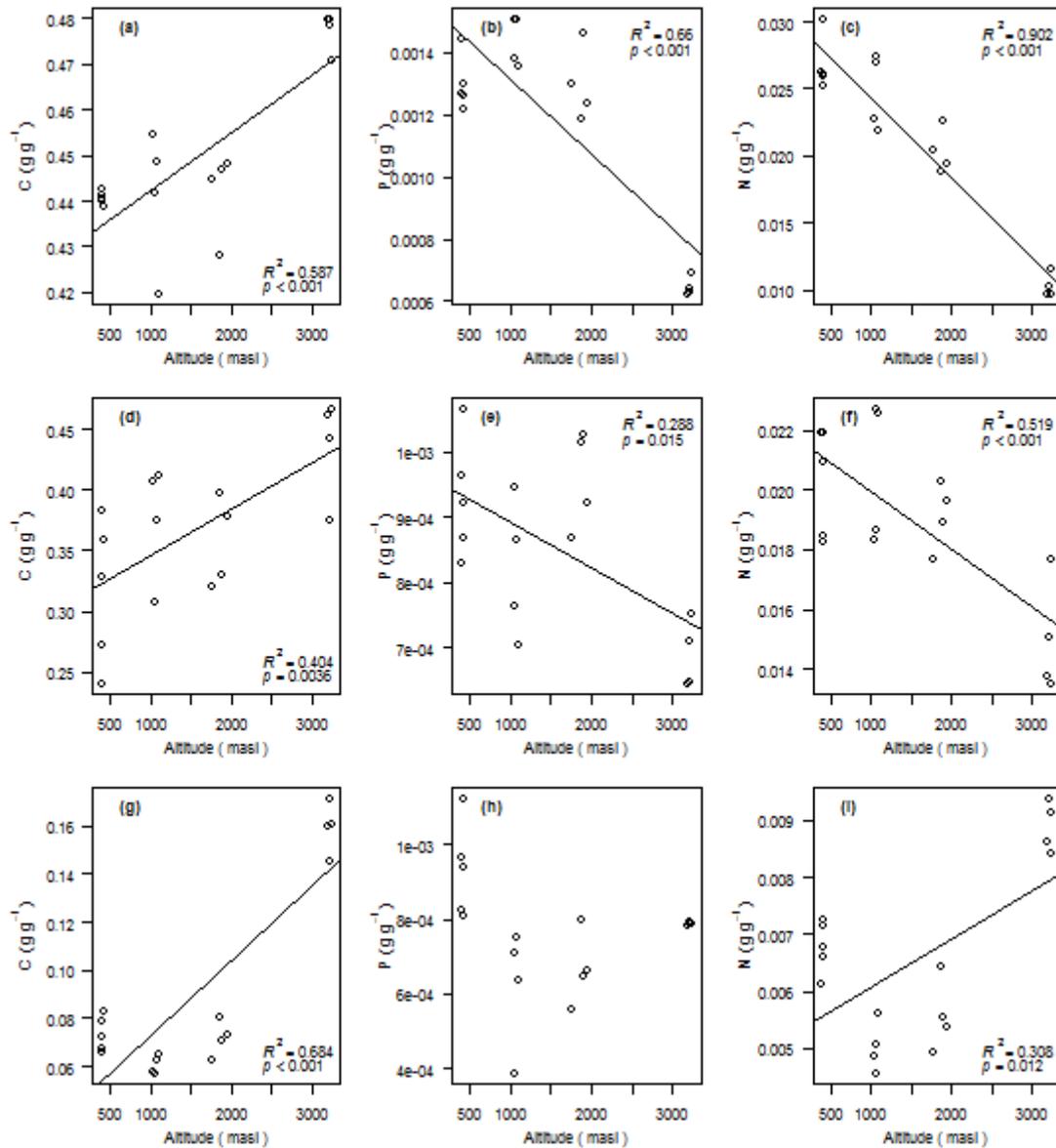


Figure A 19 Nutrient concentrations of the leaves, litter and soil in function of altitude. (a) Foliar C in $g\ g^{-1}$ (b) Foliar P in $g\ g^{-1}$ (c) Foliar N in $g\ g^{-1}$ (d) Litter C in $g\ g^{-1}$ (e) Litter P in $g\ g^{-1}$ (f) Litter N in $g\ g^{-1}$ (g) Soil C in $g\ g^{-1}$ (h) Soil P in $g\ g^{-1}$ (i) Soil N in $g\ g^{-1}$. N concentrations declined in both leaf and litter, with a significant decrease towards the highest altitude. When evaluating the differences of nutrients between leaves, litter and soil. There is a clear decrease with altitude in the difference of leaf N, litter N and soil N. Linear regressions were visualized and R^2 values were given when $p < 0.05$.

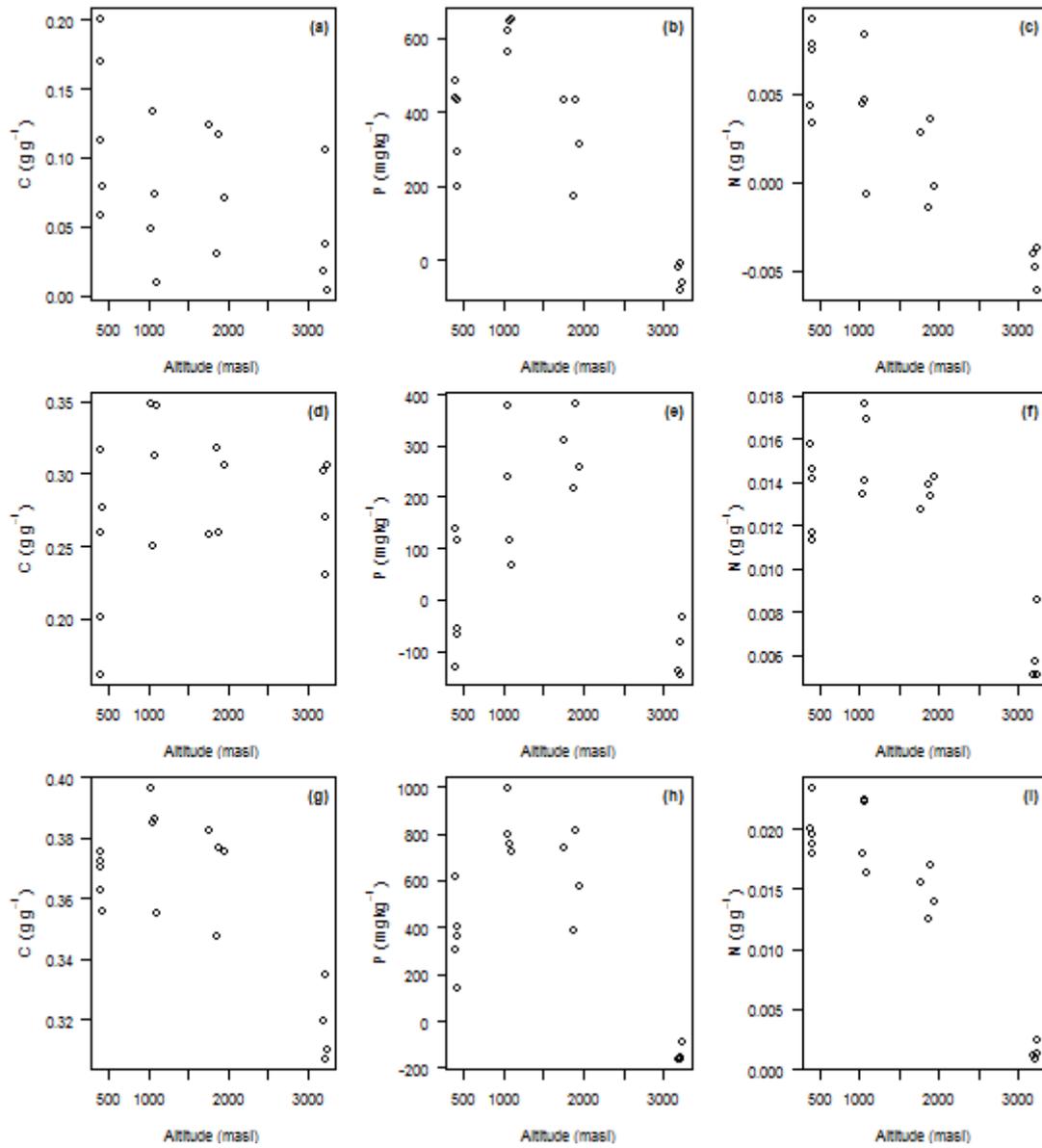


Figure A 20 Nutrient differences between leaves, litter and soil. (a) C differences between leaves to litter ($g\ g^{-1}$) (b) P differences between leaves to litter ($mg\ kg^{-1}$) (c) N differences between leaves to litter ($g\ g^{-1}$) (d) C differences between litter to soil ($g\ g^{-1}$) (e) P differences between litter to soil ($mg\ kg^{-1}$) (f) N differences between litter to soil ($g\ g^{-1}$) (g) C differences between leaves to soil ($g\ g^{-1}$) (h) P differences between leaves to soil ($mg\ kg^{-1}$) (i) N differences between leaves to soil ($g\ g^{-1}$).

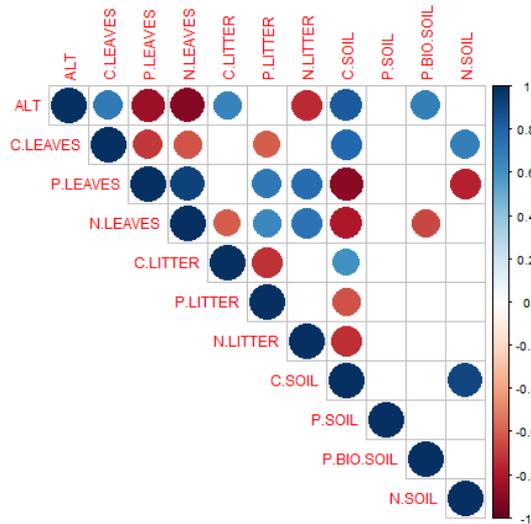


Figure A 21 Correlation table for the nutrient concentrations of leaves, litter and soil ($p < 0.01$). ALT stands for altitude; P.SOIL stands for total P concentration of the soil; P.BIO.SOIL stands for bio-available P concentration of the soil.

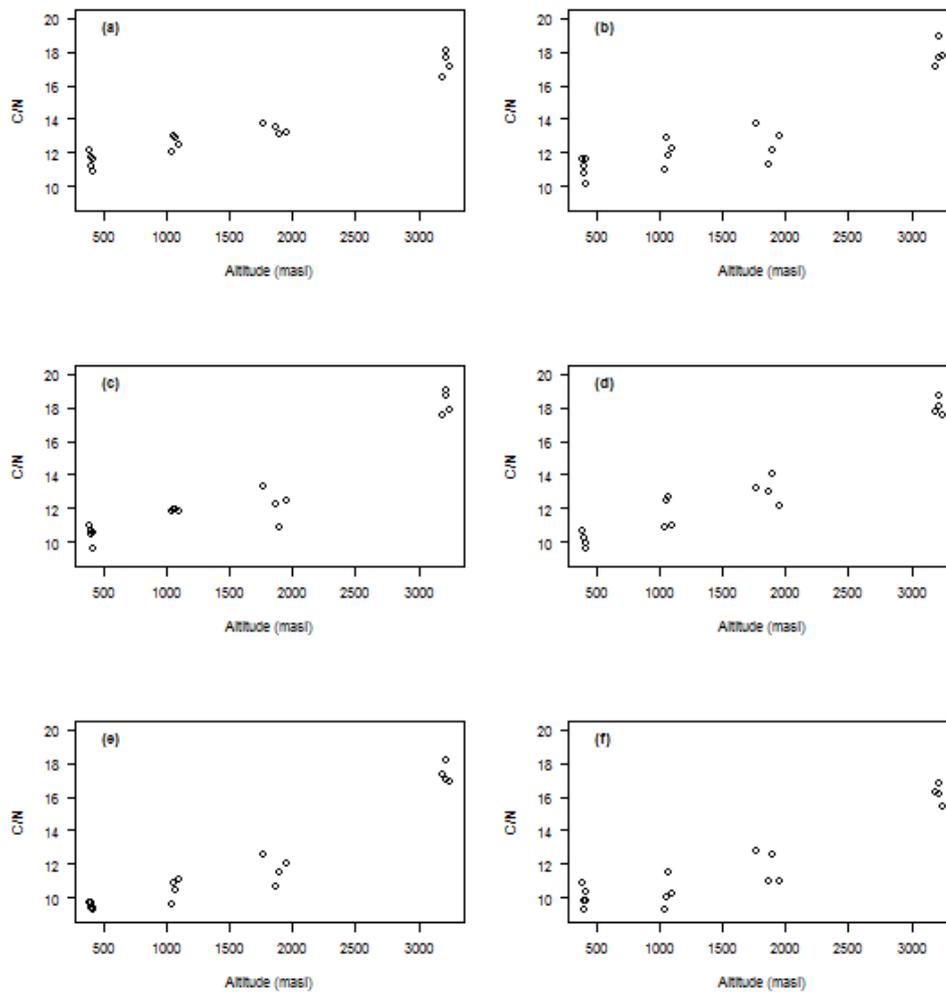


Figure A 22 C/N of the soil at different depths in function of altitude. (a) C/N at 0-5 cm soil depth (b) C/N at 5-10 cm soil depth (c) C/N at 10-20 cm soil depth (d) C/N at 20-30 cm soil depth (e) C/N at 30-50 cm soil depth (f) C/N at >50 cm soil depth.

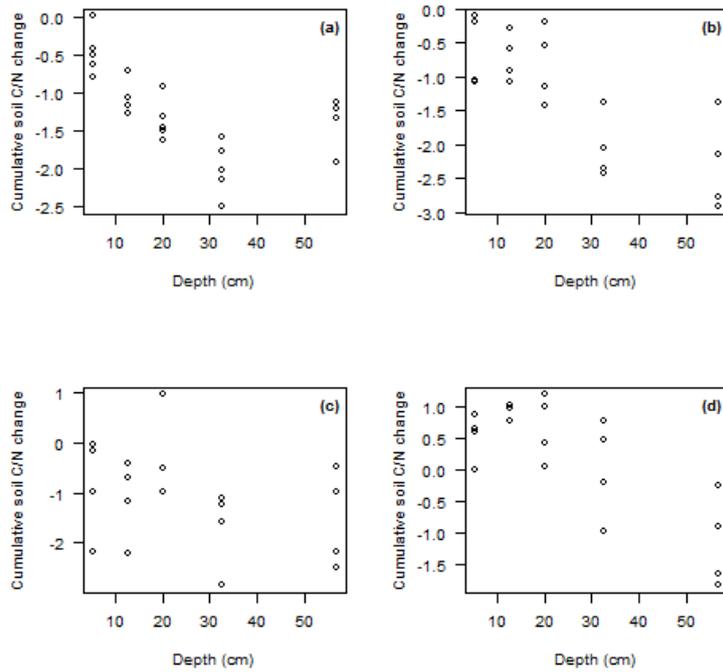


Figure A 23 Cumulative soil C/N change with depth for the different altitudes. First differences between the depths were calculated. For example: the soil C/N ratio at a depth of 7.5 cm minus the soil C/N ratio at a depth of 2.5 cm or the soil C/N ratio at a depth of 15 cm minus the soil C/N at a depth of 7.5 cm. These differences were eventually added together. For example, the y-axis value at 20 cm of depth gives the difference between the soil C/N ratio at a depth of 25 cm minus the soil C/N ratio at a depth of 2.5 cm. (a) at 400 masl (b) at 1100 masl (c) at 1900 masl (d) at 3200 masl.

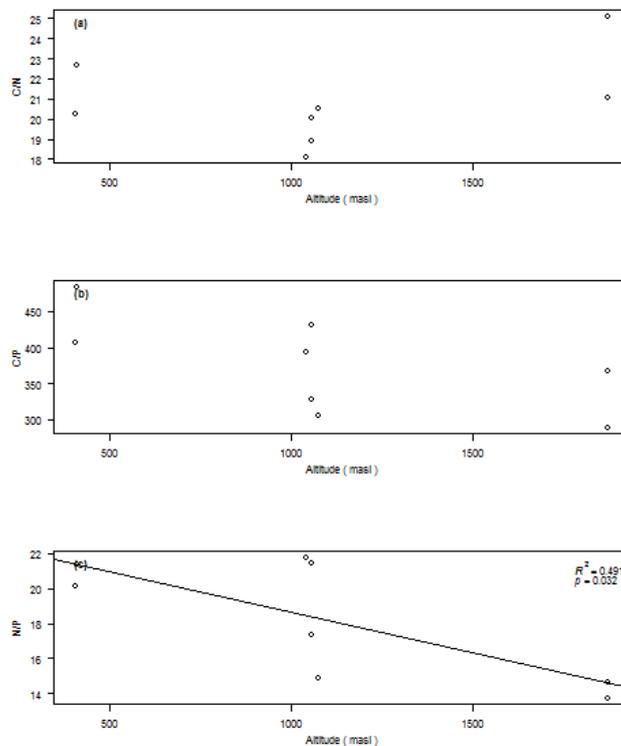


Figure A 24 Foliar nutrient ratios of *Otaba gordonifolia* in function of altitude. (a) C/N (b) C/P (c) N/P. Linear regressions were visualized and R^2 values were given when $p < 0.05$.

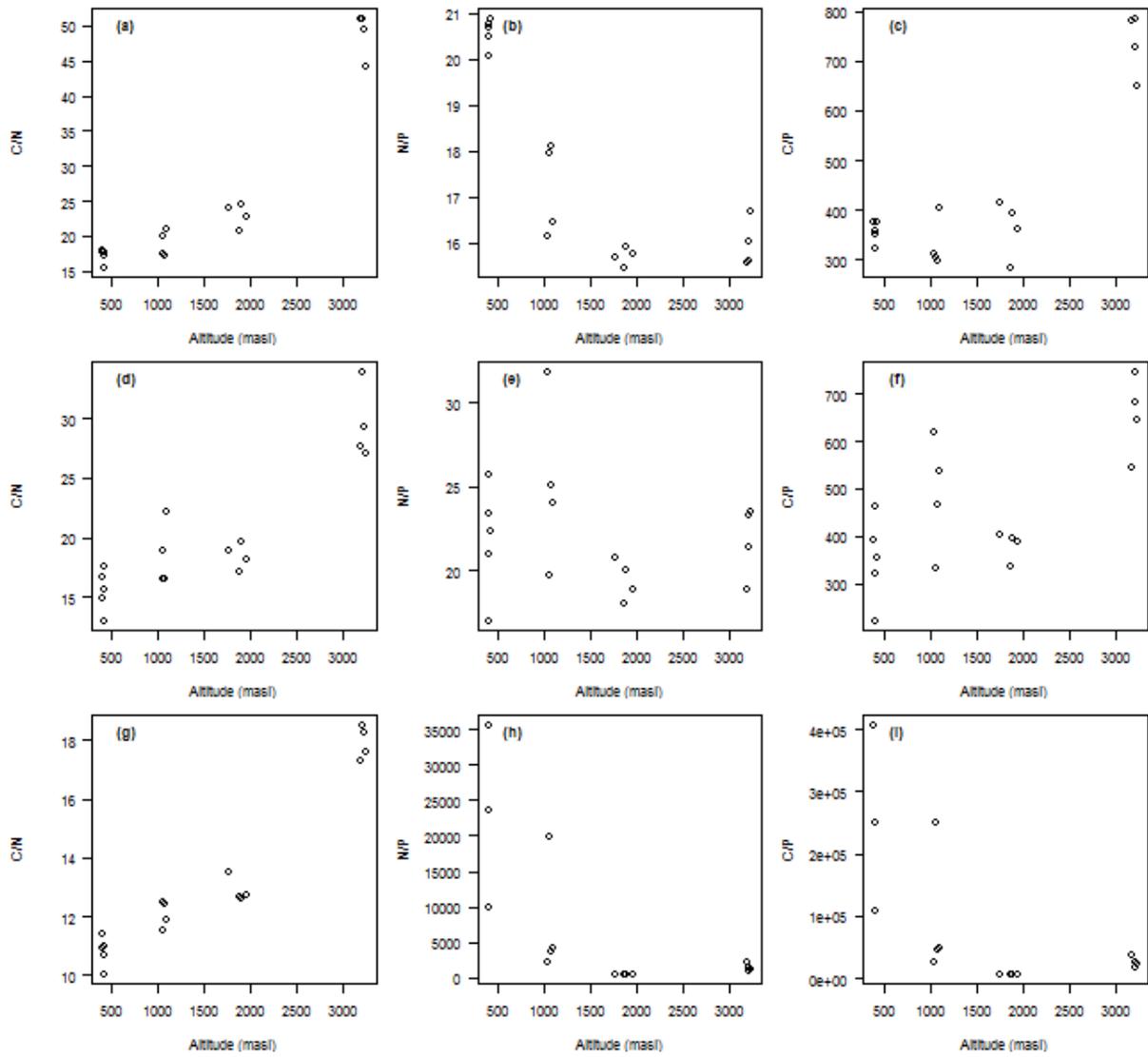


Figure A 25 Nutrient ratios of the leaves, litter and soil in function of altitude. Soil bio-available soil P was used instead of soil total P to calculate soil N/P and C/P. (a) Foliar C/N (b) Foliar N/P (c) Foliar C/P (d) Litter C/N (e) Litter N/P (f) Litter C/P (g) Soil C/P (h) Soil N/P (i) Soil C/P.

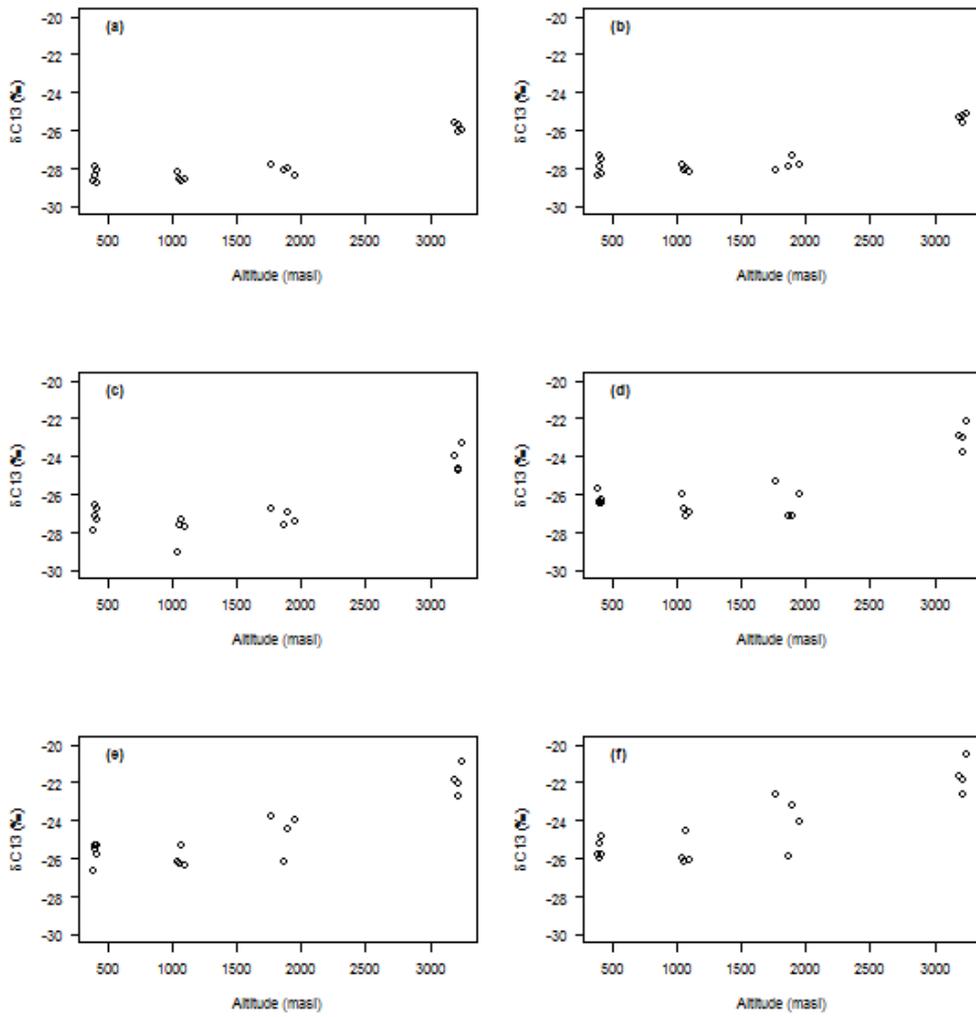


Figure A 26 $\delta C13$ (‰) of the soil at different depths in function of altitude. (a) at 0-5 cm of soil depth (b) at 5-10 cm of soil depth (c) at 10-20 cm of soil depth (a) at 20-30 cm of soil depth (a) at 30-50 cm of soil depth (a) at >50 cm of soil depth.

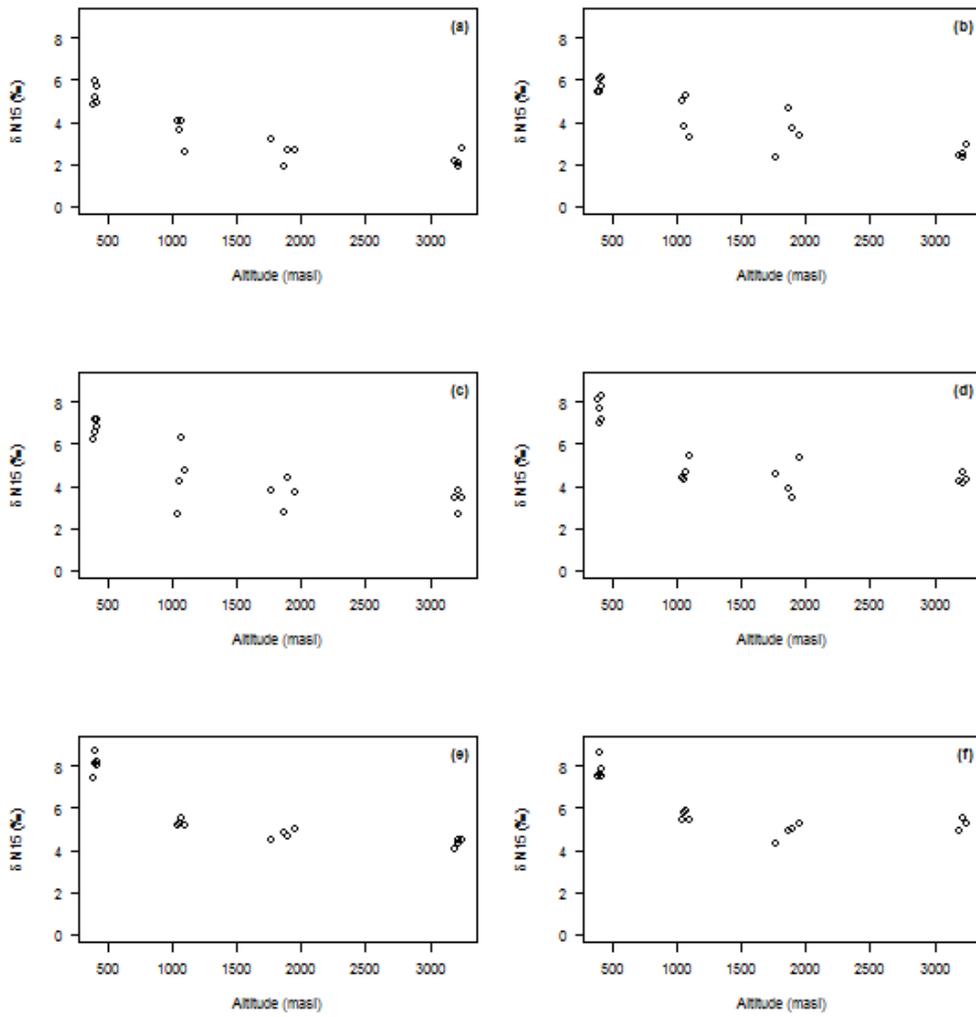


Figure A 27 δN_{15} (‰) of the soil at different depths in function of altitude. (a) at 0-5 cm of soil depth (b) at 5-10 cm of soil depth (c) at 10-20 cm of soil depth (d) at 20-30 cm of soil depth (e) at 30-50 cm of soil depth (f) at >50 cm of soil depth.

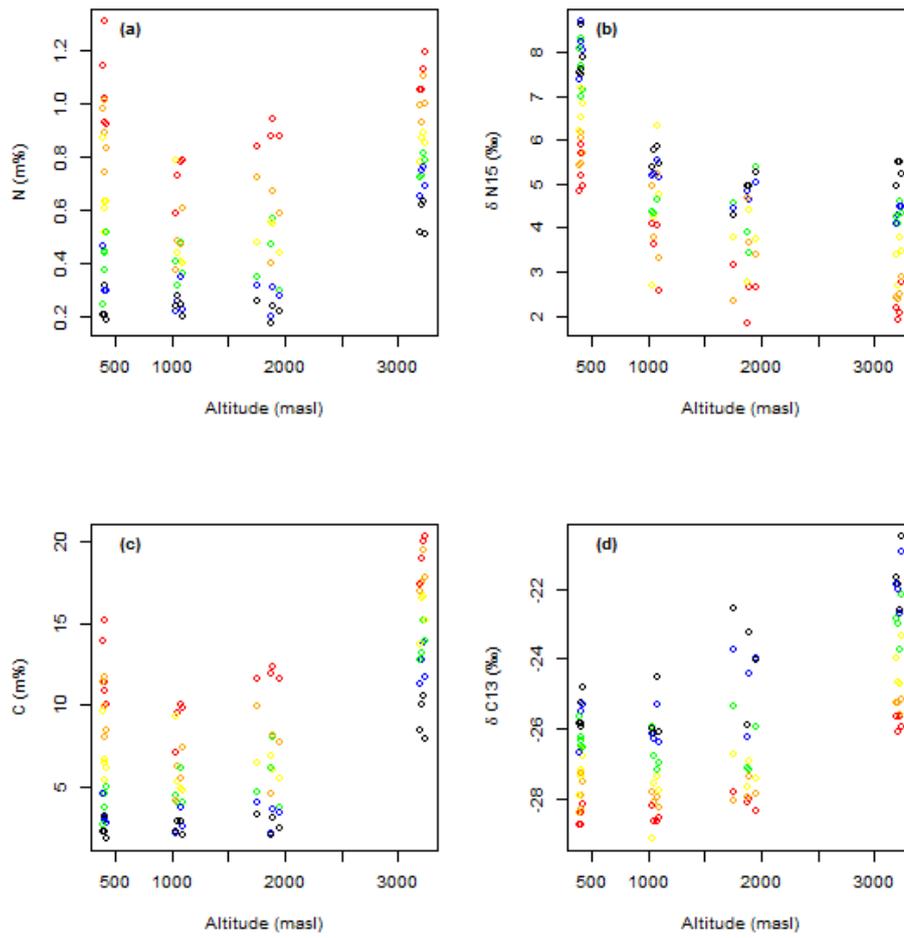


Figure A 28 (a) N (m%), (b) δN_{15} (‰), (c) C (m%) and (d) δC_{13} (‰) at different depths in function of altitude. With increasing depth, the soil organic matter (SOM) becomes increasingly C13 and N15 enriched. (red) 0-5 cm of soil depth (orange) 5-10 cm of soil depth (yellow) 10-20 cm of soil depth (green) 20-30 cm of soil depth (blue) 30-50 cm of soil depth (black) >50 cm of soil depth.

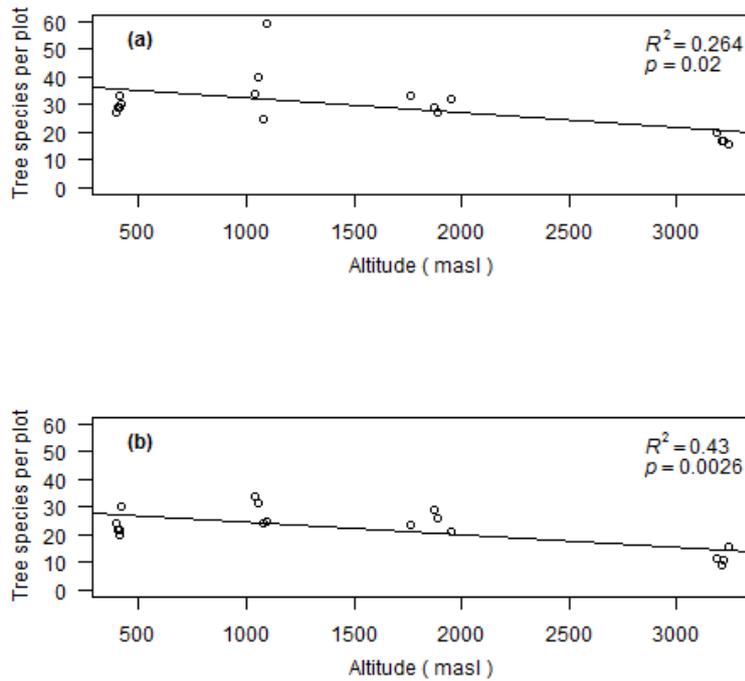


Figure A 29 Tree diversity in tree species per plot. (a) Tree species per plot (b) Tree species per plot based on the rarefaction method. With the individual based rarefaction method, tree diversity for each stratum was based on the plot with the lowest stem density. The number of species in the other plots was interpolated to align with the same density of this lowest stem density plot. Only at the highest altitude, species diversity was significantly lower compared to the lower altitudes. In total, 28 % of the trees were determined at species level, 51 % at genus level, 11 % at family level and 10 % lacked determinations.

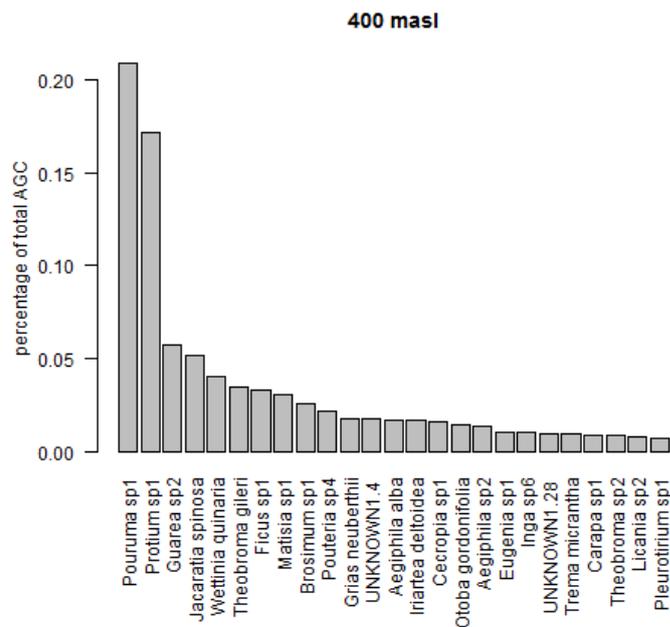


Figure A 30 Share of each species as a percentage of the aboveground carbon (AGC) for the forest at 400 masl.

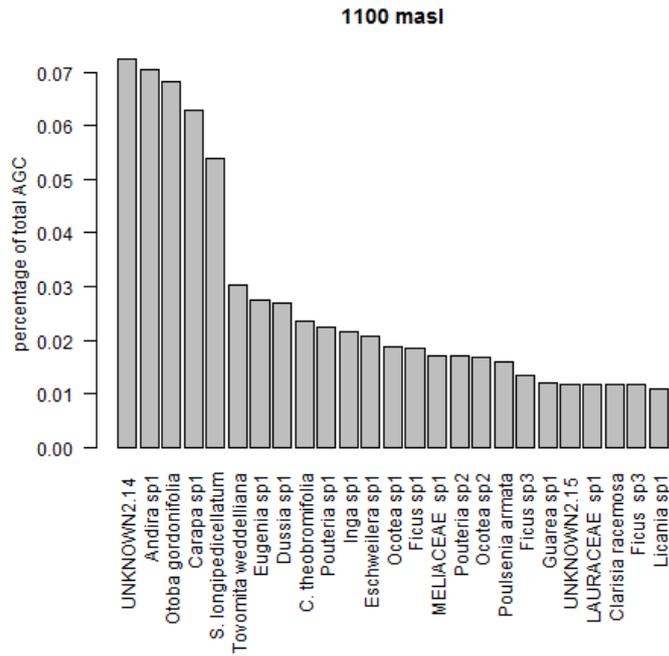


Figure A 31 Share of each species as a percentage of the aboveground carbon (AGC) for the forest at 1100 masl.

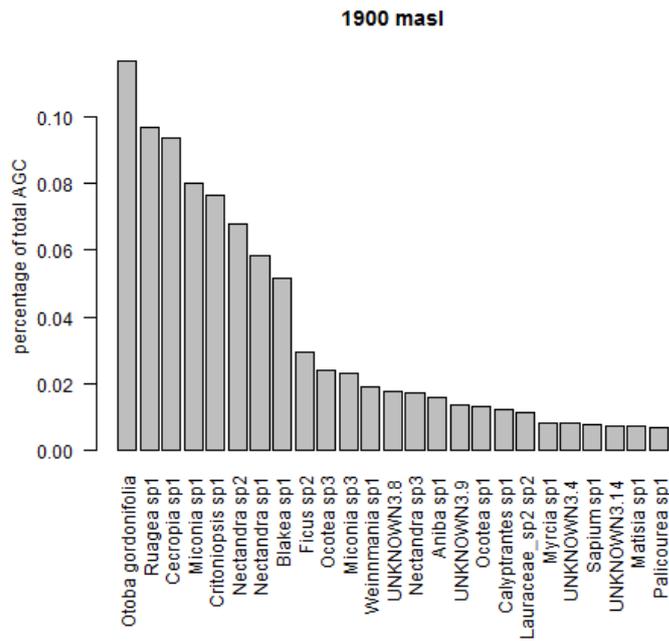


Figure A 32 Share of each species as a percentage of the aboveground carbon (AGC) for the forest at 1900 masl.

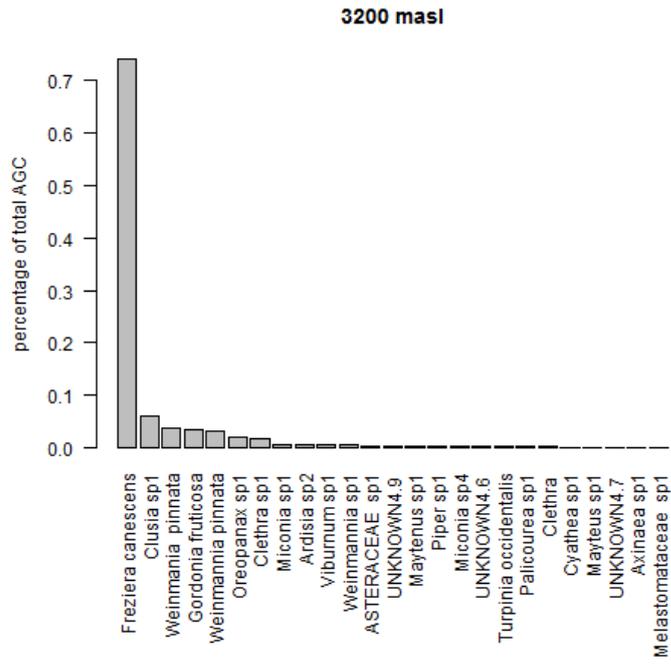


Figure A 33 Share of each species as a percentage of the aboveground carbon (AGC) for the forest at 3200 masl.