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Liberation thinning in a tropical mountain forest of Southern Ecuador- Growth response of nine selected timber tree species and functional diversity changes in the forest

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Resumen

Una de las principales características del bosque de montaña tropical es su gran diversidad biológica y el alto grado de amenaza que sufre por los cambios en el uso del suelo, lo que provoca la deforestación y pérdida de hábitat de especies importantes. Por esta y otras razones, se estudió la posibilidad de implementar un tratamiento silvícola o aclareo por liberación, para evaluar el efecto de este tratamiento sobre la diversidad, ya sea que la implementación del aclareo selectivo afecte o no significativamente la diversidad funcional y taxonómica del bosque. Si el incremento de diámetro de los árboles seleccionados y del bosque remanente está influenciado por el raleo selectivo o por otras variables (como variables topográficas) que influyen en el incremento, también evaluamos la dinámica de regeneración natural y la estructura del bosque remanente. También evaluamos si el bosque de montaña tropical en el sureste de Ecuador es homogéneo o existen diferentes tipos de bosque influenciados por gradientes ambientales y altitudinales.

El área de estudio se ubica en la provincia de Zamora Chinchipe al sureste de Ecuador dentro de los límites de la Reserva Biológica San Francisco (RBSF) del Parque Nacional Podocarpus, un área considerada un hotspot de biodiversidad a nivel mundial. En términos geológicos, el área de estudio es parte del terreno de Loja; se compone principalmente de sedimentos metamórficos del Paleozoico y granitos del Triásico. Los suelos de la RBSF pertenecen principalmente al orden de los Inceptisoles, caracterizados por capas orgánicas gruesas, que almacenan grandes contenidos de biomasa y nutrientes. El clima en la cuenca es perhúmedo, con marcados gradientes altitudinales en la temperatura del aire, la humedad y las precipitaciones.

Para el desarrollo de este estudio se seleccionó un área de bosque de 13 ha en la Reserva Biológica de San Francisco (RBSF), ubicada al norte del Parque Nacional Podocarpus (PNP). El área se distribuyó en tres microcuencas denominadas “Quebradas” (Q2 = 5 ha, Q3 = 4 ha, Q5 = 4ha). En estas tres microcuencas árboles plus (o potenciales árboles de cultivo PCT's) de nueve especies arbóreas comercializadas en la región se seleccionaron. Algunos árboles plus fueron liberados de sus competidores, mientras que otros permanecieron en un entorno tranquilo.

En cada microcuenca se delimitaron parcelas de 2500 m^2 (Q2 n = 20; Q3 n = 16; Q5 n = 16), donde se midieron e identificaron todos los árboles ≥ 20 cm DAP, se realizaron cinco inventarios forestales para determinar la dinámica de el bosque. El primer inventario se realizó en 2003. El tiempo entre la primera medición y la segunda medición fue de 2 años (2005), el tiempo entre la segunda y la tercera medición fue de un año (2006). Todos los datos se tomaron de enero de 2003 a abril de 2010. Todos los árboles de inventario se definieron espacialmente y sus datos se combinaron con un modelo digital de terreno (DTM) de muy alta resolución, que se generó en base a un estudio aéreo LiDAR. Los predictores topográficos sirvieron como sustitutos de los factores ambientales, ya que la topografía juega un papel importante para muchos procesos ecológicos en TMF, con efectos reportados sobre el crecimiento de los árboles y la distribución de las especies de árboles.

Para implementar el raleo de liberación en el bosque RBSF, se realizó una inspección visual para determinar el cruce y la superposición de las copas de los competidores de los árboles de nueve especies maderables para luego liberarlos mediante un raleo selectivo. Tres especies se consideran madera valiosa *Tabebuia chrysantha, Podocarpus oleifolius y Cedrela montana*, las otras seis especies *Clusia ducuoides* Engl., *Ficus citrifolia* Mill., *Hieronyma asperifolia* Pax y K. Hoffm., *Hieronyma moritziana* Mull Arg., *Inga acreana* Harms., *Nectandra membranacea* (Sw.) Griseb. se consideran madera de calidad media. La implementación del aclareo selectivo se

realizó entre abril - mayo de 2004. La recolección de muestras botánicas fértiles de los árboles se realizó junto con el primer inventario y en ocasiones posteriores para corroborar o complementar la identificación de ciertas especies no determinadas en el primer inventario.

Se evaluó el crecimiento del diámetro de nueve especies maderables valiosas con respecto a su liberación, para ello se instalaron dendrómetros metálicos que fueron monitoreados durante siete años, los primeros 30 meses corresponden a la primera fase del proyecto forestal incluyendo un período de seis meses antes. de implementación de raleo selectivo. El aumento de diámetro de los árboles restantes se calculó sobre la base de mediciones periódicas durante 10 años, la primera medición al comienzo del experimento y las dos mediciones posteriores (24 meses y 36 meses después), luego las mediciones se realizaron cada dos años.

La cobertura del dosel se estimó en cada una de las 52 parcelas utilizando fotografías hemisféricas y un densitómetro esférico, estos datos se usarán como covariables para el análisis de la dinámica de la regeneración natural. Los datos de precimpitación y temperatura también fueron registrados gracias a las esaciones meteorológicas instaladas en los terrenos de la RBSF y usados como covariables en el análisis de crecimiento diamétrico de las especies liberadas.

La composición florística de cada una de las 52 parcelas se sometió a varios análisis para determinar si existía heterogeneidad. Mediante un modelo de correlación lineal simple entre algunas características del bosque con la altitud de las parcelas se determinó que el área basal ha^{-1}, el número de especies ha^{-1}, el número de árboles ≥ 20 cm DAP ha^{-1} y la apertura del dosel del bosque se correlacionan con la altitud. Luego utilizamos un análisis de correspondencia CCA multivariante canónico que nos permitió determinar qué características influyen significativamente en la separación de las “comunidades” forestales. Corroboramos la separación florística de los grupos mediante un análisis no métrico NMDS multidimensional.

El resultado del análisis de composición florística confirma que la altitud y algunas características a nivel de parcela forman dos grupos o dos tipos de bosques, lo que también encontraron otros investigadores en el área de estudio. El primer tipo de bosque o "Bosque de Valle" se caracteriza por la presencia de *Tabebuia chrysantha* (Jacq.) G. Nicholson, *Cedrela montana* Moritz ex Turcz, *Inga acreana* Harms y *Ficus citrifolia* Mill. Estas especies están involucradas en la aplicación de aclareos selectivos. También existen otras especies como *Cecropia montana* Warb. ex Snethl., *Guarea pterorhachis* Harms y *Heliocarpus americanus* L. que son exclusivos del grupo. El segundo tipo de bosque denominado "bosque de borde" se caracteriza por la presencia de *Podocarpus oleifolius* ex D. Don Lamb., *Hieronyma moritziana* Mull. Arg, *Clusia ducuoides* Engl. que son especies seleccionadas como PCT. Otras especies que caracterizan al grupo son *Purdiaea nutans* Planch., *Graffenrieda emarginata* (Ruiz & Pav.) y *Alchornea grandifolia* Triana y Mull Arg.

Con los datos obtenidos mediante el monitoreo de los dendrómetros instalados y utilizando modelos lineales mixtos generalizados (GLMM), determinamos que todas las especies presentaron un ciclo de crecimiento anual similar debido al clima húmedo de la zona. La precipitación juega un papel secundario porque se produce suficiente lluvia durante todo el año, sin embargo, las variaciones de temperatura son más importantes. Las especies respondieron de manera diferente a la liberación, por lo que podrían clasificarse en tres grupos específicos: crecimiento positivo, crecimiento negativo y sin respuesta a la liberación. A nivel de especies, el aclareo de liberación afectó positivamente solo a dos de las nueve especies liberadas (*Inga acreana* y *Hieronyma asperifolia*) las cuales fueron consideradas como especies de calidad de madera media. Cuatro especies respondieron negativamente al raleo (*Tabebuia chrysantha*, *Cedrela montana*, *Podocarpus oleifolius* y *Nectandra membranaceae*), las dos primeras son de hoja caduca y por lo tanto su crecimiento depende de la temperatura y precipitación de la temporada de crecimiento. El resto de las especies (*Clusia ducuoides*, *Ficus citrifolia* y *Hieronyma moritziana*) no mostraron cambios significativos en el crecimiento en los primeros tres años de seguimiento.

Con la información de los inventarios forestales y las características de la especie, determinamos y utilizamos 6 rasgos funcionales de todas las especies que participaron del estudio para calcular algunos índices de diversidad funcional, estos índices fueron Riqueza Funcional (FRic), Divergencia Funcional (FDiv), uniformidad funcional (FEve), dispersión funcional (FDis) y entropía cuadrática (RoaQ). También calculamos la media ponderada de la comunidad (CWM) y usamos un análisis de Anova de medidas repetidas para analizar la influencia del aclareo (antes - después). Para validar los modelos de cada índice analizado, comparamos cada modelo resultante, aplicando una prueba de bondad (prueba de razón de verosimilitud), descartando predictores no significativos y estableciendo la importancia del resto de factores para mostrar que los modelos no eran demasiado ajustados. Para ello utilizamos el paquete de software lmtest R. además de las características intrínsecas del bosque y la influencia del gradiente altitudinal presente en el área de estudio. Luego de la implementación del aclareo selectivo, solo uno de los índices de Diversidad Funcional determinados (Riqueza Funcional) se vio afectado, los otros índices (FEve, FDis, FDiv, RaoQ) solo fueron influenciados por predictores relacionados con las condiciones ecológicas y características de la comunidad.

Utilizando los datos de ubicación espacial de todos los árboles monitoreados y los modelos digitales del terreno derivados de las imágenes de alta resolución generadas a partir de ellos, se analizó la relación entre la distribución espacial de las especies arbóreas y la topografía utilizando dos técnicas para modelar la distribución de especies con solo presencia : el modelo de máxima entropía (Maxent) y los análisis de factores de nicho ecológico (ENFA), mientras que los efectos relativos del aclareo selectivo y la topografía sobre las tasas de crecimiento a nivel de árboles se analizaron utilizando un modelo lineal de efectos mixtos. Como resultado, determinó que la distribución de varias especies está condicionada principalmente por la topografía en general, la elevación y la posición topográfica en particular. Tanto el modelo de Maxent como el ENFA identificaron el índice de elevación y posición topográfica (TPI) como los principales determinantes para la distribución de la mayoría de las especies arbóreas, mientras que el índice de humedad, el aspecto y la pendiente fueron de menor importancia.

Al combinar los análisis de crecimiento en función de raleo selectivo y predictores topográficos, los resultados mostraron que el incremento anual fue significativamente influenciado por predictores topográficos, las tasas de crecimiento disminuyeron en promedio 0,73 mm año^{-1} por 100 m de incremento de altitud, con respecto a la posición topográfica, los PCT en los bosques del valle tuvieron un aumento anual promedio de 2.02 mm año $^{-1}$ en comparación con 1.04 mm año^{-1} en los bosques de cordilleras. El efecto del tratamiento silvícola en todas las especies fue solo marginalmente significativo, pero su efecto estuvo, sin embargo, dentro del rango, en el extremo inferior de los valores reportados para otros ecosistemas de bosques tropicales (árboles de referencia: 1.35 mm año^{-1}; árboles liberados: 1.60 mm año^{-1}).

En conclusión, podemos observar que las especies que prefieren los sitios abiertos respondieron positivamente a la liberación, mientras que las especies tolerantes a la sombra y las especies con rasgos fenológicos pronunciados como la defoliación respondieron negativamente. El DAP inicial también fue un factor importante para los aumentos de diámetro. Esto se debe a que los árboles de clase I (20 cm a 30 cm DAP) respondieron positivamente al tratamiento, mientras que, para los individuos más grandes o más viejos, las diferencias disminuyeron o se volvieron negativas. También concluimos que el aclareo selectivo a diferentes intensidades afectó levemente la diversidad funcional del bosque. Los índices de DF calculados se basaron en diferentes rasgos de especies, lo que permitió mejorar el conocimiento para diseñar prácticas de manejo sustentable en ecosistemas ecológicamente sensibles y en un contexto de aprovechamiento forestal, la conservación de especies raras o menos abundantes debe ser una prioridad antes de iniciar cualquier actividad forestal.

También podemos notar que, en la distribución espacial y el crecimiento del diámetro, la topografía es un factor clave a nivel general y la elevación y microtopografía a nivel particular. El hecho de que estas características forestales varíen considerablemente en distancias geográficas cortas dentro del TMF subraya la necesidad de que, en lugar de una gestión "amplia", se practique una gestión ambiental a escala fina basada en la zonificación multifuncional. El uso potencialmente eficaz de predictores topográficos en la ordenación forestal sostenible incluye modelos espacialmente explícitos y rendimiento de especies sostenibles. Sin embargo, en la práctica, se necesita más investigación centrada en el modelado predictivo, la mejora de la transferibilidad del modelo y la inclusión de predictores no topográficos (por ejemplo, variables climáticas) para las plantaciones de enriquecimiento y el emparejamiento de sitios y especies en las actividades de reforestación.

Las especies en peligro deben excluirse de la cosecha, la tala y otras actividades forestales. Sin embargo, el manejo forestal sostenible en combinación con la conservación de los ecosistemas debe seguir siendo un objetivo principal para el desarrollo futuro, ya que esto no solo representa ingresos económicos para la población local, sino que también mantiene la funcionalidad del bosque para proporcionar servicios ecosistémicos esenciales.

Abstract

One of the main characteristics of the tropical mountain forest is its great biological diversity and the high degree of threat it suffers from changes in land use, which causes deforestation and loss of habitat for important species. For this and other reasons, we studied the possibility of implementing a silvicultural treatment or release thinning, to evaluate the effect of this treatment on diversity and whether or not the implementation of selective thinning significantly affects the functional and taxonomic diversity of the forest. If the diameter increment of selected trees and remnant forest are influenced by selective thinning or by other variables (such as topographic variables) that influence the increase, we then evaluate the natural regeneration dynamics, and the structure of the remnant forest. We also evaluate whether the tropical mountain forest in southwestern Ecuador is homogeneous or whether there are different types of forest influenced by environmental and altitudinal gradients.

The study area is located in the province of Zamora Chinchipe to the southeast of Ecuador within the limits of the San Francisco Biological Reserve (RBSF) border of the Podocarpus National Park, an area that is considered a biodiversity hotspot worldwide. In geological terms, the study area is part of the Loja terrain; it mainly consists of Paleozoic metamorphic sediments and Triassic granites. The soils in the RBSF mainly belong to the order of Inceptisols, characterized by thick organic layers, which store large contents of biomass and nutrients. The climate in the catchment is per-humid, with marked altitudinal gradients in air temperature, humidity and rainfall.

For the development of this study, a forest area of 13 ha in the Biological Reserve of San Francisco (RBSF), located north of the Podocarpus National Park (PNP) was selected. The area was distributed in three micro catchments called “Quebradas” (Q2 = 5 ha, Q3 = 4 ha, Q5 = 4ha). In these three micro catchments, plus trees (or potential crop trees PCT's) of nine tree species commercialized in the region were selected. Some plus trees were liberated from their competitors whereas others remained in an undisturbed surrounding.

At each micro catchment 2,500 m^2 plots were delimited (Q2 n = 20; Q3 n = 16; Q5 n = 16), where all trees ≥ 20 cm DBH were measured and identified and where forest inventories were carried out five times to determine the dynamics of the forest. The first inventory was carried out in 2003. The time between the first measurement and the second measurement was 2 years (2005) while the time between the second and third measurement was one year (2006). All data were taken from January 2003 – April 2010. All the inventory trees were spatially defined and their data combined with a very high-resolution digital terrain model (DTM), which was generated based on a LiDAR aerial study. The topographic predictors served as surrogates for environmental factors, as topography plays an important role for many ecological processes in TMF, with reported effects on tree growth and the distribution of tree species.

To implement the liberation thinning in the RBSF forest, a visual inspection was carried out to determine the crossing and the crowns overlapping of the competitors of the trees of nine timber species to later release them through selective thinning. Three species are considered valuable wood, including *Tabebuia chrysantha*, *Podocarpus oleifolius* and *Cedrela montana*, while the other six species *Clusia ducuoides* Engl., *Ficus citrifolia* Mill., *Hieronyma asperifolia* Pax and K. Hoffm., *Hieronyma moritziana* Mull Arg., *Inga acreana* Harms., *Nectandra membranacea* (Sw.) Griseb. are considered as medium quality wood. The implementation of selective thinning was carried out between April and May 2004. The collection of fertile botanical samples of the trees was

carried out together with the first inventory and on subsequent occasions to corroborate or to complement certain identity species determined in the first inventory.

The diameter growth of nine valuable timber species was evaluated with respect to their release, and for this, metal dendrometers were installed that were monitored for seven years. The first 30 months correspond to the first phase of the forest project including a six-month period before selective thinning implementation. The diameter increase of the remaining trees was calculated based on periodic measurements over 10 years; the first measurement at the beginning of the experiment, the two subsequent measurements 24 months and 36 months later, and then measurements carried out biannually.

Canopy cover was estimated in each of the 52 plots using hemispherical photographs and a spherical densitometer. These data were used as covariates for the analysis of the dynamics of natural regeneration. The precipitation and temperature data were also recorded in the meteorological stations installed on the RBSF grounds and used as covariates in the analysis of diameter growth of the released species.

The floristic composition of each 52 plots was subjected to several analyses in order to determine if there was heterogeneity. By means of a simple linear correlation model, the correlation of some characteristics of the forest with the altitude a.s.l. of the plots was determined, including the basal area ha^{-1}, the number of species ha^{-1}, the number of trees ≥ 20 cm DBH ha^{-1}, and the forest canopy opening. Then we used a canonical multivariate CCA correspondence analysis that allowed us to determine which characteristics significantly influence the separation of forest “communities”. We could corroborate the floristic separation of the groups by a multidimensional NMDS non-metric analysis.

The result of the floristic composition analysis confirms that altitude and some characteristics at plot level form two floristic groups or two forest types, what was also found by other researchers in the study area. The first forest type or "Valley Forest" is characterized by the presence of *Tabebuia chrysantha* (Jacq.) G. Nicholson, *Cedrela montana* Moritz ex Turcz, *Inga acreana* Harms and *Ficus citrifolia* Mill. These species are involved in the application of selective thinning. There are also other species such as *Cecropia montana* Warb. ex Snethl., *Guarea pterorhachis* Harms and *Heliocarpus americanus* L. which are unique to the group. The second forest type called "edge forest" is characterized by the presence of *Podocarpus oleifolius* ex D. Don Lamb., *Hieronyma moritziana* Mull. Arg, *Clusia ducuoides* Engl. which are species selected as PCT. Other species that characterize the group are *Purdiaea nutans* Planch., *Graffenrieda emarginata* (Ruiz & Pav.) And *Alchornea grandifolia* Triana and Mull Arg.

With the data obtained by monitoring the installed dendrometers and using generalized linear mixed models (GLMM), we determined that all species showed a similar annual cycle due to the humid climate of the area. Precipitation plays a secondary role because sufficient rain occurs throughout the year, however, temperature variations are more important. Species responded differently to release, therefore they could be classified into three specific groups: positive growth, negative growth, and no response to release. At the species level, liberation thinning positively affected only two of the nine released species (*Inga acreana* and *Hieronyma asperifolia*) which were considered as species with medium wood quality. Four species responded negatively to thinning (*Tabebuia chrysantha*, *Cedrela montana*, *Podocarpus oleifolius* and *Nectandra membranaceae*), the first two being deciduous and therefore their growth is dependent upon the temperature and precipitation during the growing season. The rest of the species (*Clusia ducuoides*, *Ficus citrifolia* and *Hieronyma moritziana*) did not show significant changes in growth in the first three years of monitoring.

With the information from the forest inventories and the characteristics of the species, we determined and used 6 functional traits of all the species included in the study to calculate some indices of functional diversity. These indices were Functional Richness (FRic), Functional Divergence (FDiv), Functional uniformity (FEve), Functional dispersion (FDis) and Quadratic entropy (RoaQ). We also calculated the weighted mean of the community (CWM) and used an Anova analyses of repeated measures to analyze the influence of thinning (before - after). To validate the models of each analyzed index, we compared each resulting model, applying a goodness test (likelihood ratio test), discarding non-significant predictors and establishing the importance of the remaining factors to show that the models were not too tight. For this, we used the *lmtest* R software package in addition to the intrinsic characteristics of the forest and the influence of the altitudinal gradient present in the study area. After the implementation of selective thinning, only one of the determined Functional Diversity indices (Functional Richness) was affected, while the other indices (FEve, FDis, FDiv, RaoQ), were only influenced by predictors related to ecological conditions and community characteristics.

Using the spatial location data of all monitored trees and digital terrain models derived from the high resolution images generated from them, the relationship between the spatial distribution of the tree species and the topography was analyzed using two techniques for modeling the distribution of species utilizing presence-only: the maximum entropy model (Maxent) and the analysis of ecological niche factors (ENFA), while, the relative effects of selective thinning and topography on tree-level growth rates were analyzed using a linear mixed-effects model. As a result, it was determined that the distribution of several species is mainly dependent upon the topography in general, the elevation and the topographic position in particular. Both the Maxent model and the ENFA identified the elevation and topographic position index (TPI) as the main determinants for the distribution of most tree species, while humidity index, aspect and slope were only of minor importance.

When combining the analysis of growth as a function of selective thinning and topographic predictors, the results showed that the annual increase was significantly influenced by topographic predictors. Growth rates decreased on average 0.73 mm year^{-1} per 100 m of increase in altitude, with respect to the topographic position, while the PCTs in the valley forests had an average annual increase of 2.02 mm year $^{-1}$ compared to 1.04 mm year^{-1} in the ridge forests. The effect of silvicultural treatment on all species was only marginally significant, but its effect was nevertheless within the range, at the lower end of the values reported for other tropical forest ecosystems (reference trees: 1.35 mm year $^{-1}$; released trees: 1.60 mm year $^{-1}$).

In conclusion, we can note that species that prefer open sites responded positively to the release, while shade-tolerant species and species with pronounced phenological traits such as defoliation responded negatively. The initial DBH was also an important factor for the diameter increases. This is because the class I trees (20 cm to 30 cm DBH) responded positively to the treatment, while, for the larger or older individuals, the differences decreased or became negative. We also conclude that selective thinning at different intensities slightly affected the functional diversity of the forest. The calculated DF indices were based on different species traits, which improved the knowledge for designing sustainable management practices in ecologically sensitive ecosystems and in a context of forest harvesting, where the conservation of rare or less abundant species should be a priority before starting any forestry activity.

We can also note that in spatial distribution and diameter growth, topography is a key factor at a general level and elevation and microtopography at a specific level. The fact that these forest characteristics vary considerably over short geographic distances within the TMF underlines the necessity that instead of "broad" management, a fine-scale environmental management practice should be enacted based on multifunctional zoning. The potentially effective use of topographic predictors in sustainable forest management includes spatially explicit modeling and sustainable species yield. However, in practice, more research focused on predictive modeling is needed, as well as improved model transferability, and the inclusion of non-topographic predictors (e.g. climatic variables) for enrichment plantations along with site-species matching in reforestation activities.

Endangered species should be excluded from harvesting, logging and other forestry activities. However, sustainable forest management in combination with ecosystem conservation should remain a main objective for future development, as this not only represents economic income for the local population, but also keeps the functionality of the forest to provide essential ecosystem services.

Scientific publications

This cumulative thesis is based on the following publications:

I. *Cabrera, O.,* Fries, A., Hildebrandt, P., Günter, S., & Mosandl, R. **2019**. Early growth response of nine timber species to release in a tropical mountain forest of Southern Ecuador. *Forests*, *10*(3), 254. https://doi.org/10.3390/f10030254. See Appendix A.

II. *Cabrera, O*.; Hildebrandt, P.; Stimm, B.; Günter, S.; Fries, A.; Mosandl, R. **2020.** Functional Diversity Changes after Selective Thinning in a Tropical Mountain Forest in Southern Ecuador. *Diversity*, *12*, 256. https://doi.org/10.3390/d12060256. See Appendix B.

III. Kuebler, D., Hildebrandt, P., Guenter, S., Stimm, B., Weber, M., Mosandl, R., Muñoz, J., ***Cabrera, O***., Aguirre, N., Zeilinger, J. & Silva, B. **2016.** Assessing the importance of topographic variables for the spatial distribution of tree species in a tropical mountain forest. *Erdkunde*, 19-47.

IV. Kuebler, D., Hildebrandt, P., Günter, S., Stimm, B., Weber, M., Muñoz, J., ***Cabrera, O***., Zeilinger, J., Silva B. & Mosandl, R. **2020**. Effects of silvicultural treatments and topography on individual tree growth in a tropical mountain forest in Ecuador. *Forest Ecology and Management*, 457, 117726.

The contribution of Omar Cabrera to the publications included in this thesis was as follows:

•**Publication I** (Cabrera et al. 2019) Conceptualization, data collection and organization, data analyses and interpretation, drafting the article and final revision.

•**Publication II** (Cabrera et al. 2020): Conceptualization; data collection and organization; design of methodology; data analyses and interpretation; drafting the article and final revision.

•**Publication III** (Kuebler et al. 2016): Data collection (collection of tree growth data during the first four years of monitoring, spatial location of all trees >20 cm DBH, collection and identification of botanical specimens) and organization; manuscript preparation, drafting the article.

•**Publication IV** (Kuebler et al. 2020): Data collection and organization; field work (implementation of selective thinning,growth experiment implementation), manuscript preparation, drafting the article.

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1. Introduction

Forest ecosystems are complex and require adequate and balanced management (FAO 2003). The current challenge for tropical forests is to adapt the uncontrolled process of wood harvesting and change land use and to promote the sustainable management of forest resources (Putz 1997). To achieve this, forest resource managers must integrate different scientific disciplines, must rely on validated research results, and must be consistent with acceptable environmental standards (Von Gadow et al. 2004).

Tropical forests (TF) cover 7% of the earth's surface, worldwide 28% of dense forests are mountain forests (TMF), TF contain 50% of the world's forest biomass and are considered the most important natural carbon reserves and sinks with respect to future global warming (Saatchi et al. 2011), TMF are one of the most diverse and threatened ecosystems on earth, especially the eastern Andean forests (Myers et al. 2000).

In TF the above ground biomass (AGB) accounts for 70% –90% of the total carbon biomass, mainly stored in the trunks and branches of trees (Sprugel 2002). Furthermore, TF represents 36% of the net primary terrestrial production, which contributes to the regulation of the carbon dioxide (CO2) concentration in the atmosphere (Pan et al. 2011, Malhi & Philips 2004). TMF comprise hydrographic river basins and therefore they are a very important component in the water regime regulation (FAO 2006). Some other functions of these forests are: producing wood and nonwood products, catching and storing precipitations and humidity, maintaining the quality of the water, and also reducing erosion and protecting against landslides and floods.

Therefore, the challenge for foresters and forest management research is to understand the dynamics in tropical forest stands, including the productivity of desired timber species, in order to implement sustainable practices and prevent deforestation and ecosystem destruction (Clark & Clark 1999, Canadell & Schulze 2014) and provide land use concepts that allow a sustainable management and decrease the conversion of natural forests to other land use systems (Knoke et al. 2009).

Sustainable management of natural forests (SFM) could be an important component of these land use concepts and the main idea should be to provide a sustainable yield and to maintain forest biodiversity at the same time. Nevertheless, studies of logging in tropical forests show a variety of effects, from local depletion of valuable species to the increased density of non-commercial species (Bawa & Seidler 1998).

It should be noted that forests are different in terms of structure, biodiversity and their recovery capacity after the intervention is either natural (falling trees, landslides, hurricanes, fires) or planned (thinning, logging, enrichment), one of the functions forest scientists must comply with is to determine changes in forest diversity, structure and function after interventions (Putz 2011).

In this context, forestry without proper planning causes biodiversity loss and alters ecosystem functionality. In the development of sustainable management concepts for TMF, there is a lack of scientific information, e.g. about succession processes after natural disturbances and human interventions and the regeneration of valuable timber trees (Bussman 2005). Another problem is the large number of species, their often uncertain taxonomic identification, and the small number of timber trees and potential crops trees per hectare, which further complicates the implementation of forest management practices (Günter et al. 2012). In fact, general information on the basic ecological processes of the ecosystem is still scarce.

To create a balance between forestry intervention called harvesting or extractive treatments (such as thinning) and the conservation of these ecosystems, sustainable forest management (SFM) actions must be implemented to make use of forest resources and at the same time protect the biodiversity and functionality (Putz et al. 2001, Kusumoto et al. 2014). A main objective of the SFM is the development of sustainable management concepts, such as reduced impact felling (RIL), which establishes cutting cycles or defines a minimum cutting diameter (MCD) to counteract exploitative forest use (Gunter et al. 2006, Edwars et al. 2014, Darrigo et al. 2016).

The ecological problems cited above, are applicables for southern Ecuador, where a large area of TMF at the eastern foothills of the Cordillera Real have been converted into pasture land, agricultural land or secondary forests to meet the economic needs of the local population, producing food, fiber, wood and other goods (Dirzo & Raven 2003, Chazdon R. 2008). The major factors for deforestation, according to Sierra (2013), include cattle ranching and roads construction; factors that are also considered associated with deforestation at the country level, added to the reasons cited by Mosandl et al. (2008), are the basis to consider Ecuador as one of the countries with the highest rate of deforestation in South America.

One of the responses to this problem has been the implementation of intermediate treatments to improve forest productivity, the release of timber trees, eliminating competitors or removing undesirable trees from the forest stand, improving the productivity of promising timber trees or Potential Crop Trees (PCT), from the ecological point of view, the diameter growth of trees is the result of competition for space and resources with other species (Andresen et al. 2005), therefore, it is frequently applied in managed forests for wood production (Frederiksen 2003). The release of competitors is best carried out in boreal forests (Vincent et al. 2009) and alpine forests (Vitali et al. 2016), where implementation results in significant diameter increases but the conditions of structure and diversity are different from those TMF because these forest types have an extraordinarily high species density, although the density of individual species is comparatively low (Adame et al. 2014).

Despite the fact that the concepts and regulations for the use of tropical forest and TMF (here montane forests, a concept that can be adapted to the studied mountain forests) were developed some decades ago (MAE 2000) and contemplate among other guidelines, cutting unwanted trees to enhance the growth of valuable ecological and economic species.

Currently, no scientific evaluations have been made of the possible impacts on taxonomic and functional diversity or on the forest structure because in the tropics, the evaluation is more complex due to the great spatial extent of the different forest ecosystems and their extraordinary high biodiversity (Gibson et al. 2011) product of the rapid change of climatic conditions caused by the local topography and by the altitudinal gradient that structurally and floristically diversify the TMF (Werner & Homeier 2015, Paulick et al. 2017), these conditions limit the growth of species timber, reducing their diameter growth and, therefore, their productivity, due to competition with other plant species.

Since the year 2000, the German Research Foundation, or DFG, (Deutsche Forschungs Gemeinschaft) has funded several studies in the mountainous region of southern Ecuador. It has focussed on the "Functionality of montane tropical rain forests: Biodiversity, Dynamic Processes and Potential Use" (FOR 402) and “Biodiversity and Sustainable Management of a Megadiverse Mountain Ecosystem in South Ecuador” (FOR 816).

From forest management point of view, the project has developed several phases: a first phase which aimed to assess the different forest types within the mountain ecosystem. One key topic of the next phase was the evaluation of different scenarios for controlled intervention by a selective thinning experiment, include the assessment of effects on several groups of organisms like moths, nonvascular plants (mosses, liverworts), lichens and epiphytes and the flow of water and nutrients in the ground and in trees, which was carried out by other working groups. In this framework, the Institute of Silviculture (Technische Universität München) conducted a comprehensive forest inventory in 2003 and installed a silvicultural experiment in order to investigate the effects of selective thinning on diversity, the increment of selected individuals, natural regeneration dynamics, and the structure of the remnant forest.

The purpose of this research is to evaluate the impact of selective thinning over the remnant stand, the influence in the individual growth of trees and the evaluation of the promotion of natural regeneration of valuable species. Finally, with a database that includes ecological and forest assessments, management plans may be established in accordance with legal regulations and to meet the parameters of the use of forests and individual species (Günter & Mosandl 2003).

The hypotheses of the presented study are as follows:

- (H1) The forest area in RBSF belongs to different types of forest influenced by environmental and altitudinal gradients.
- (H2) The implementation of selective thinning in the tropical mountain forest in RBSF does not significantly affect the functional and taxonomic diversity.
- (H3) The diameter increment of potential crop trees and the remaining forest are influenced by selective thinning and topographic variables.

This thesis consists of nine chapters. The first chapter is an introduction wich includes general motivation, delimits the problem, and presents research objectives and hypotheses.

The second chapter offers an overview of the geography and vegetation of Ecuador in general and the Ecuadorian southeast in particular, relevant background information on the state of forest management in Ecuador and specifically the TMF that forms the basis of this thesis. The first two chapters collect information published in articles I-IV (Cabrera et al. 2019, Cabrera et al. 2020, Kuebler et al. 2016 and Kuebler et al. 2020).

The third chapter is a review of the general methodological approach of the ecological-forest experiment where the main climatic, edaphological and vegetation characteristics of the study area are described.

In addition, a review is made of the installation of plots and the acquisition of the data that were used for the scientific publications that make up this dissertation. Another important point of this chapter is that various floristic parameters of the vegetation and their heterogeneity are determined through groups or forests types along the altitudinal gradient.

Chapters IV-VII present a comprehensive synthesis of scientific articles generated over time, mainly about the growth of released timber trees, the influence of selective thinning and the distribution patterns of the species. In addition, it was determined that the topography and altitude are factors that significantly influence the diameter growth of the released trees. Another aspect studied was the impact of selective thinning on the functional diversity of the forest, determining that only functional richness is affected after the implementation of selective thinning.

Chapter VIII analyzes and discusses the results of the previous chapter and frames them in the context of SFM and forestry in the TMF. The ninth chapter provides the general conclusions of the studies that make up this dissertation.

2. Literature review

This chapter presents the characteristics of the natural vegetation in Ecuador focused on TMF in southern Ecuador. Then, the literature on Forest Management in Ecuador and a third part on Deforestation, Conservation and Sustainable Forest Management in tropical mountain forest, which includes an important part on environmental services, forest governance and land tenure (Kuebler et al. 2016; Kuebler et al. 2020 and Weber et al. 2013). The last section describes the silvicultural systems that lead forest management and that could be applicable in the TMF, also refers to the treatment applied in the RBSF forest and selective thinning as a tool to improve the performance of the TMF ensure the continuous supply of the tree stock through the management of natural regeneration.

2.1. Geography and vegetation in Ecuador

Ecuador is a coastal, Andean and Amazonian country (with a total area of 256,370 km^2 following the Peace Agreement with Peru). It is one of the smallest countries in South America, and it has more plant species per unit of area than any other country on the Continent (17,748 documented native species; Neill 2012).

Ecuador is divided into four natural regions 1.) The Pacific coastal region includes the lowlands that extend to the western Andes below 1,000 m of elevation; 2.) The Andean region, including the Andes mountain range over 1,000 m a.s.l., which occupies the central part of the country and is also known as the Sierra; 3.). The lowlands of Amazonian region in the East of the Andes, which includes the bottom eastern flanks under 1,000 m a.s.l.; 4.) The Galápagos Islands, a volcanic archipelago in the Pacific Ocean located 1,000 km to the west of the continent (Neill 2000) (Figure 1).

The coastal region is a strip extended from north to south (20-160 km wide) that is relatively flat except for certain mountain ranges in the North center (0-1,000 m a.s.l.). A relatively low mountain range extends parallel and near the coast by a distance of 350 km from of Esmeraldas city in the North to Guayaquil in the South. The tops of the Coastal mountain range vary between 400 and 600 m of altitude, but some isolated ridges exceed 800 m. The Coastal mountain range is continuous across all its length, and it is known by several names from North to South: Mache, Chindul, Jama, Colonche and Chongón (Neill 2000). In this area, the National Forest Assessment (MAE 2014) refers to three types of climate: Tropical megathermic semi humid weather that is typical of the inside of the coastal region, occupying a large area on the North Coast and disappearing at the level of Guayaquil Gulf. Annual precipitation generally varies between 1,000 and 2,000 mm and is concentrated in a single period, from December to May, being dry the rest of the year. Average temperatures fluctuate around 25 ° C.

Another type of climate is megathermic tropical dry weather located west of the above, it extends to the south of the country influencing the foothills of the Western Cordillera in the province of Loja, between latitudes 0 ° and 4 ° 30 'S. Annual rainfall is between 500 and 1,000 mm, which is collected between December and May. The dry season is very marked and average temperatures are high, i.e. above 24 ° C.

Finally, another type of climate in the coastal region is tropical megathermic semiarid weather. This climate is limited to the peninsula of Santa Elena, San Lorenzo and Arenillas area due to the influence of the Humboldt Sea current. It is very dry, with annual rainfall below 500 mm, which is collected in a single rainy season from January to April and with average temperatures above 23 ° C.

The mountain region or highlands is comprised mainly of the Cordillera Real, the Eastern and Western foothills and the Andean valleys (1,000 – 6,000 m a.s.l.). Most of the Andean cities of Ecuador, including the capital Quito, are located in valleys. In the north and center of Ecuador, the Andes form two different parallel mountain ranges: The Western Cordillera and the Eastern Cordillera; the latter is well-known like the Cordillera Real. Both mountain ranges are crowned by a series of quaternary volcanoes; these volcanic tips exceed the 5,000 m high and are covered by glaciers. The highest volcano is Chimborazo, 6,310 m a.s.l. The most important volcanoes of the western mountain range are from North to South: Chiles (along the border with Colombia), Cotacachi, Pichincha, Illinizas and Chimborazo. The main volcanoes of the Eastern mountain range are Cayambe, Antisana, Cotopaxi, Tungurahua, Altar and Sangay (Neill 2000). In the Andean region, at least two sub-regions can be distinguished: The North- Center region and the South region. Between the eastern and western cordilleras are a series of intermontane valleys, which are separated from one another by a series of high, transverse east-west-trending ridges locally referred to as knots (nudos).

The climate in the Andean region also varies, with the altitude being a factor that greatly influences this variation (MAE 2014). Nival Weather corresponds to average annual temperatures ≤ 0 ° C and above 4500 m a.s.l.

Another climate type is equatorial high mountain weather, which is located about 3,000 m a.s.l. This has fluctuating average temperatures of 8 °C - with variations in maximum and minimum temperatures during the day. The total annual rainfall is irregular, but ranges from 1,000 to 2,000 mm depending on the height and exposure of the slopes.

The next of climate type is equatorial mesothermal semi-humid weather. This is the most frequent inter-zone climate and includes valleys and areas with heights over 3,000 meters. The annual rainfall on two rainy seasons ranges from 500 to 2,000 mm; the annual average temperatures are between 12 and 20 ° C.

Another climate is equatorial mesothermic dry weather, which is typical in the internal valleys of the Andean region. Average annual temperatures fluctuate between 18 - 22 ° C- with very little difference between summer and winter; it has two dry seasons with a very marked difference between June and September. This is separated by two rainy peaks whose annual total does not reach 500 mm.

Finally, the last climate type present in the Andes region of Ecuador is tropical humid megathermic weather, which is considered a climate of transition between the Andean equatorial climates and climates of the coast and Amazon. It covers the outer sides of the two ranges between 1,000 and 2,000 meters approximately. Annual precipitation is strong, generally above 2,000 mm, with some higher values in the lower foothills of the Andes; most of this precipitation is collected in one rainy season. The average temperature varies greatly with altitude but is kept uniform throughout the year.

The south region is not so clearly differentiated into western and eastern cordilleras, but form a more complex pattern of ridges, some of which trend north-south and some east-west. In this region there are no high, quaternary volcanoes; the highest ridges and peaks are barely above 4.000 m a.s.l. (Jørgensen & León-Yánez 1999).

The Amazonian region includes diverse eastern mountain chains (the most important are Cordillera del Cóndor due to its floristic richness and the Cordillera del Cutucú in the North center of the region) and the Amazonian plains (200-3000 m a.s.l. in the East foothills), and they both form the upper zone of the great Amazonian watershed (Romero M. 2001).

In the Amazon region the (MAE 2014) refer to one type called megathermic rainy weather, characterized by an average temperature ≥ 25 ° C and annual rainfall usually above 3,000 mm uniformly distributed throughout the year except for a weak recession between December and February. Besides being the typical climate in this region, this kind of weather affects the north end of the country in the province of Esmeraldas.

The insular region or Galapagos Archipelago is located at approximately 1,000 km from the continent. The group of islands is also known as Archipiélago de Colón. It is formed by 12 bigger islands, many smaller islands and rocky islets, with a total extension of about 8,000 km^2 (Neill 2000).

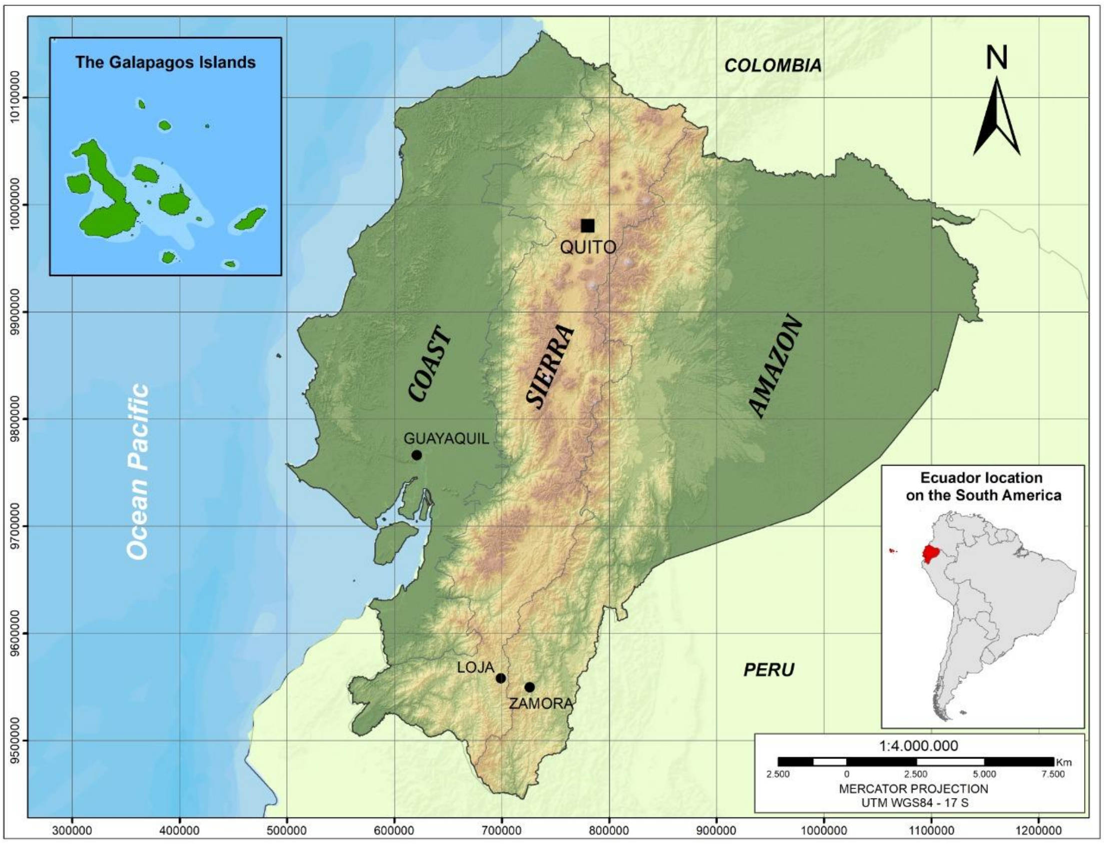


Figure 1. Natural Regions of Ecuador.

The four regions mentioned above possess areas that are covered with natural vegetation. According to Rizzo (2002), forest cover in Ecuador can be classified into four categories: National Systems of Preserved Areas, Protective Forests and Vegetation, Forest State Patrimony and Forest Plantations. These categories are distributed into four natural regions and are located in the various different types of forest; a general ecological classification shows the following types: Wet tropical forest (rain forest), Dry tropical forest, Mangrove swamp forest, and Mountain forest. According to Aguilar & Vlosky (2005), the country also has other types of natural landscapes such as Savannas in the coastal plains and inter Andean plateau, which is locally known as páramo.

A study by Sierra et al. (1999) used a hierarchical model for the description of the types of vegetation and includes a map of all continental Ecuador. These hierarchical levels recognize the difference in the regional floristic compositions within vegetation types and similar physiognomy (Neill 2000).

In the proposed model for continental Ecuador, the authors mentioned above use the regional division of the territory and include the concept of subregions. The coastal is divided into subregion north-central and subregion south. The Andean region or sierra has subregion north-center and subregion south. The Amazon region has north-central subregions, differentiated from the southern region. The hierarchical model divided the regions into sectors, i.e. each region has subregions and these in turn are divided into sectors.

With nesting vegetation physiognomy (Mangrove Forest, Shrubland, Espinar, Savannah, Paramo and Gelidofitia) and other hierarchical criteria such as environmental criteria (dry, wet, fog), the phenological criteria (evergreen, deciduous, semi deciduous) and floristic altitudinal floors (lowland, piemontano, lower montane, montane, upper montane) vegetation determine 62 cover types, 27 on the coast, 24 in the Andes and 11 in the Amazonia.

One of the best studied vegetation types in Ecuador is the lowland rainforest because of its extraordinary biodiversity. Also, several studies describe the structure, composition and forest dynamics in the Ecuadorian Amazonian region. Valencia et al. (1994), for instance, registered in one-hectare plot of the Ecuadorian Amazonian region 1,561 trees ≥ 5 cm dbh (diameter at breast height), 473 species, 187 genera and 54 families. Of these, 693 individuals, 307 species, 138 genera and 46 families were ≥ 10 cm dbh. Valencia et al. (2004) mapped and identified all the trees ≥ 1 cm dbh in a 25-ha plot. *Matisia sp.* and *Rinorea sp*. dominated the forest numerously, and the most important canopy species were *Iriartea deltoidea* and *Eschweilera coriaceae*.

Other vegetation type studies about floristic composition and stand dynamics have been developed in the Andean Region, for instance: Valencia & Jorgensen (1992) sampled in one-hectare plot 1058 trees ≥ 5 cm dbh from 32 different species. The most common species were *Miconia theazans*, *Piper andreanum* and *Miconia pustulata*. Madsen & Ollgaard (1994) also sampled one-hectare plot at 2,900 m a.s.l. (non-ridge forest) where they found 75 species and another hectare plot in the same area (ridge forest) where they found 90 species. There are structural differences that are expressed in basal area/ha between the two plots (44 m^2 vs. 15 m^2). In both plots, the most important families were Clusiaceae, Cunoniaceae, Melastomataceae, Myrsinaceae and Ternstroemiacea. Valencia et al. (1995) measured in one-hectare plot at 2,200 m altitude all trees ≥ 5 cm dbh, and found 55 species and 1,622 individuals with a total basal area of 45 m^2. The understory was dominated by *Geonoma undata* and Lauraceae, which was the family with more species. Sánchez & Rosales (2002) monitored after five years the plot measured by Madsen & Ollgaard (1994) and denominated as "non ridge forest". Mortality in this period was 499 individuals but 469 new individuals were incorporated in nine years. Melastomataceae, Rubiaceae and Lauraceae excelled at the family level. *Weinmannia glabra*, *Gordonia fruticosa* and *Ilex* sp. reached the highest value of importance at the species level.

According to Valencia et al. (1999), there is a "montane cloud forest" in southeastern Ecuador. This is also known by Balslev and Ollgaard (2002) as "Evergreen Montane Forest". Homeier et al. (2010), afirm wich four types of forest can be distinguished by combining different types of classification approaches, for example Paulsch (2002) studied structural parameters; Homeier (2004) the floristic trees composition; Parolly and Kurschner (2005) the species composition of bryophytes and Homeier et al. (2008) making a synopsis of previous studies. In forest type I, located on the lower slopes and valleys at 2200 m, we can find largest trees where the canopy reaches 25-30 m tall, i.e. with emergent trees up to 35 m. The genera with the most species are *Miconia* (Melastomataceae), *Ocotea* ssp., *Persea* ssp., (Lauraceae), *Ficus* ssp. (Moraceae) and *Inga* ssp. (Mimosaceae). The forest type II is close to upper slopes and ridges between 1900 and 2100 m asl.; here the floristic composition of trees and the forest canopy is totally different. Few trees reach 15 m in height; some common taxa are *Alzatea verticillata* Ruiz & Pav (Alzateaceae) *Graffenrieda emarginata* Triana (Melastomataceae), *Podocarpus oleifolius* D. Don (Podocarpaceae) and various Lauraceae. Forest types III and IV typically occur between 2100 m and 2250 m asl respectively. In the first forest, it is common to find *Clusia cf. ducuoides* Engl. (Clusiaceae), *Alchornea grandiflora* Mull. Arg (Euphorbiaceae), *Licaria subsessilis* van der Werff (Lauraceae), *Eschweilera sessilis* AC Sm. (Lecythidaceae) and *Graffenrieda emarginata* Triana (Melastomataceae). The second forest type is exclusively dominated by *Purdiaea nutans* Planch. (Cyrillaceae).

2.2 Forest Management in Ecuador

Ecuador has about 3.4 million hectares suitable for timber harvest (Barrantes et al. 2001), according to the forestry census developed in 2002 by MAG (Ministerio de Agricultura y Ganadería) and SICA (Servicio de Informacion Agropecuaria). This area has about 3.9 million ha and according to FAO (2005) and ITTO (2004) about 3 million hectares. Most of this productive land tenure as proposed by FAO (2006) is in the hands of various indigenous nationalities, although minorities control nearly 50% of the total territory covered with native forest, excluding protected areas under custody of the Ecuadorian State.

Palacios (1993) qualified the Sustainable Forest Management (SFM) as incipient in Ecuador. Since then, many activities at the state and private level have been developed to achieve sustainability in forest use and forest management. Since 1999, especially in Ecuador, forest management systems for economic and ecological timber production are a goal but not a reality (Finegan 1997). Sustainable forest management practices like low impact harvest, cutting cycle or changes in the minimum diameter cut (MDC) can reduce the forest damage and improve the biodiversity conservation (Günter et al. 2006).

Even though experiences of sustainable forest management have been reported in the neighbouring countries (Yanesha in Perú, Chimanes in Bolivia and Cartón in Colombia) some reasons that are forest related can be quoted to have limited the process of sustainable management in Ecuador: the high tree species diversity in general and a few species that can be utilized (< 5 % of native tree species), which in these cases is a limiting factor instead of an opportunity for development, plus the low volume per hectare, the lack of knowledge about dynamics, ecology and regeneration of species (Palacios & Jaramillo 2001), but also the little interest of the forests owners about investing into an activity that economically is less feasible than almost any other activity in agriculture or farming (Palacios 1993).

Another SFM experience was implemented in Awá territories (northwestern Ecuador) in 21 communities, this initiative included a forest inventory and timber harvesting in 1980 ha and a core area reserve 17,000 ha of more than 300,000 ha comprising the Awa territory. The implementation of a forest management project was done by the owners who were advised by the Ministry of Environment in 2001. It approved the first plan for the usage and marketing, of wood. Aerial cables were used to pull logs from the river and transport timber to the market. This process showed that the yield was 45% more profitable than selling roundwood to intermediaries. From that first moment, forest owners followed the guidelines to achieve forest certification and seek international markets that purchase certified wood.

In Morona Santiago province (southern Ecuador), the Amazonian Forest Service was created through the execution of an agroforestry project funded by GTZ-DED-CREA since 1992. In 2001, it obtained legal status and the main objective has been to provide technical assistance in implementing plans to harvest timber at medium and large scale. It also offers services for forest regency (a phase in which a forester endorses the volume of species harvested in usage plans, which consists in the articles of the existing forestry regulations), directed tree felling and the use of a framework to improve harvesting logs in the forest (Gatter y Romero 2005).

Another aspect in recent years is that silvicultural efforts in the country have been focused on reforestation with exotic species on small scale projects of social forestry like DFC (Desarrollo Forestal Comunal), PROBONA (Programa de Bosques Nativos Andinos), CARE, CESA (Central Ecuatoriana de Servicios Agricolas) and others including medium and large scale with long term contracts (PROFAFOR-**PRO**GRAMA **FA**CES DE **FOR**ESTACION).

Few experiences have been developed in reforestation plans with native species in areas with different succession stages and within plantations of exotic species such as pine (*Pinus* sp.) and eucalyptus (*Eucalyptus* sp.). One example was developed by Aguirre (2007), which experimentally performed planting tests with exotic and native species in different abandoned types of environments; one of its outstanding results with respect to the behavior of native species is documented for two pioneer species such as *Alnus acuminata* and *Heliocarpus americanus*, which reach survival and growth rates comparable to those exotic species used for reforestation programs in Ecuador.

Another remarkable result was obtained in an enrichment test of monospecific pine (*Pinus* spp) plantations, i.e. in which two species of cedar (*Cedrela montana* and *C. odorata*) showed better survival rates in gaps, while the growth of diameter and height was better in *Alnus acuminata* and *Piptocoma discolor*.

Other valuable experiences of reforestation in the Amazon ecosystems was done by Sucumbios Forestry Program (PROFORS) during the period from 1988 to 1999 established 2000 hectares of reforestation, and the Fundacion Jatun Sacha who have monitored the performance in plantations since 1990 of about 90 typical species from the region (Revelo and Palacios 2005) forest. Likewise, in the coastal zone forest commercial plantations have been developed, which are mainly supported by private initiatives using species such as “Teca” (*Tectona grandis*), “Balsa” (*Ochroma pyramidalis*) and “Laurel” (*Cordia alliodora*). Most of these plantations are located in the provinces of Los Rios, Guayas and Esmeraldas (Aguirre 2007).

The effort made by Jatun Sacha Foundation via **SUBIR** (Sustainable Use of Biological Resources) project that worked in the Chocó Area (Borbón and Playa de Oro communities) and the Amazonian region from 1992 to 2003, developed economic incentives for the conservation and management of this area. These incentives (for US $ 6 millions) were executed by CARE Ecuador with the support of the United States for International Development, (USAID Ecuador) and with the partnership of foundations such as EcoCiencia and Jatun Sacha, Wildlife Conservation Society, the Ecuadorian Environmental Ministry and other institutions. The project sought the sustainable development of biological resources in Ecuador's northwest region conservation and development, fair trade, and legal wood harvested from SFM zones, training local people in technical and legal security for management of around 20,000 ha of ancestral lands.

Currently, the government through state programs like Socio Bosque (subsidy payment for forest conservation at community and individual level), the National Forest Restoration Plan 2014-2017 promoted by the Ministry of Environment and the incentive program for reforestation with commercial purposes by the Ministry of Agriculture where it is considers cost per hectare of plantation and a list of 19 species (11 native and 8 introduced) that the landowner or community owner can choose for starting the process of reforestation. These have a much important programs that mentioned in previous paragraphs with respect to entities and forest activities and conservation.

According to La Fuente (2013), a new model of forest governance began to be implemented in mid-1999, where the medium-term objective was to establish in Ecuador Sustainable Forest Management. However, despite creating a number of tools at the regional and national level like Outsourced National Forest Control System (SNTCF in Spanish) with two operating levels, the Vigilancia Verde (checkpoints nationwide fix and mobile stations where the mobilization of wood is recorded) and the Forestry Regency formed by professionals which support the process of forest utilization and mobilization guides, there were some weaknesses in the control and monitoring of criteria and indicators of forest sustainability in the country (Günter et al. 2012).

2.3 Deforestation, Conservation and Sustainable Forest Management in the tropical mountain forest.

Globally, Neotropical montane forests represent one of the most diverse ecosystems in the world. The forests in the eastern Andes are one of the biodiversity hotspots (Myers et al. 2000), and in addition they are among the most threatened ecosystems and transformed more quickly; currently mountain forests in this area are occupying small areas and are highly fragmented (Kapelle and Brown 2001).

By a specific deforestation analyses in southern Ecuador Tapia et al. (2015) recognize the original vegetation cover of the area decreased by 46% (1976-2008) and the period in which there were more deforestation is the decade of the 90s, which was a recurring pattern nationwide. Mosandl et al. (2008) refer to factors that promote deforestation statewide agree that agricultural activities such as raising cattle and access to inaccessible areas by roads and secondary roads have high deforestation rates. Blaser et al. (2011) includes the above factors: the oil and timber exploration and a body of laws and unclear regulations, which have been made over the last decade, Ecuador suffers one of the highest rates of deforestation on the continent.

According to Goerner et al. (2007) and Tejedor Garavito et al. (2012), logging overexploitation and agricultural activities cause deforestation and fragmentation of montane forest. Very big plantations (oil palms, cacao, and bananas) drive the deforestation patterns in the north of Ecuador, while in southern region, according to Sierra (2013), opening roads for connecting the andean Region with the Amazonia is a very important historical factor to understand the deforestation process since the opening of these roads causes a disorderly colonization and deforestation with adverse effects on the conservation of diversity (Tapia et al. 2015).

The process of timber harvest at the big enterprises level (through the forestry concessions), communal forests and small producers in their own farms is transformed generally is a process where forest resources are lost with selective logging, usually with anti-technical practices of valuable wood species (Palacios 2007), so the natural forest becomes degraded and converted into areas for cattle pastures with tolerated trees, which in the best case is maintained during 4 - 8 years and is finally transformed into an low productive pastures area invaded by *Pteridium arachnoideum* an agressive and invasive fern has a developed system of rhizomes that after burning regenerate very large leaves that completely cover the canopy and makes it virtually impossible for other species recolonize pastures, making them totally unproductive (Beck et al. 2008).

Biodiversity loss by the above reasons could be one of the weaknesses in implementing forestry programs, whether small or large scale, although von Gadow et al. (2004) accept that forest management is a major support for the conservation of diverse forest ecosystems and in many cases improve economic productivity of forests, while Bawa and Seidler (1998) find that the loss of biodiversity depends on the intensity of the harvest (especially in the number of logs harvested per unit area) and the care taken during the extraction process.

In our country, Ebeling and Yasue (2009), in contrast to Gullison (2003) and compared with Bolivia, determined that for almost all indicators evaluated for the effectiveness of conservation based on timber markets in the tropics, Ecuador does not reach the minimum standards. This is somewhat worrisome because internationally it was believed that certification was a significant step towards conservation, a fact that now involves certain conditions for implementation and that Ecuador does not apply.

2.3.1 Ecosystem Services

The importance of TMF is recognized worldwide, the presence of emblematic species of flora and fauna highlight their value. According to Blaser (2011), a large percentage of the forests are used directly or indirectly by indigenous populations, while around 850,000 people (4.9% of the total population) depend directly on the forests for their livelihood. The wide coverage of services that TMFs offer are differentiated by the ethnic groups or social groups to which the population belongs, for rural populations they are important providers of non-timber forest products (NTFP) with at least 589 species of multiple uses (Blaser 2011, Kübler 2020) while for another important sector of the population it still provides wood and associated forest products, although the majority comes from lowland tropical forests, a percentage comes from TMF. One of the most important services of the TMF is the provisioning and hydrological regulation in addition to the prevention of wind and water erosion, services that are of particular importance and are provided by the TMF (Kübler 2020).

2.3.2 Forest Governance and Land tenure

As mentioned in point 2.2 Ecuador has approximately 3.4 million hectares of natural forest of a productive type and around 3.9 million hectares under some protection regime, according to Kuebler (2020) one of the forms of protection of these areas that the Ecuadorian state to implement are the so-called Protected Areas. Through the National System of Protected Areas (SNAP for its acronym in Spanish) a management model has been implemented that includes a well differentiated status of forest tenure within this system, the first and that most territory includes is the Heritage of state natural areas (PANE for its acronym in Spanish), municipal protected areas run by decentralized local governments, community protected areas and private protected areas (Weber et al. 2013). Technically, the protection of all areas is in charge of the Ministry of the Environment (MAE), although in many cases, the protection and management of the 48 protected areas that exist so far are shared with institutions and private owners (Weber et al. 2013). Bringing together protected areas around a common objective has also been an effective strategy for conservation, in this case the protected areas that provide environmental services, especially of a water type, have been of vital importance for the production of water for human consumption and for generation of energy in large hydroelectric projects (MAE 2018; Weber et al. 2013), finally, the economic reward for forest conservation has also been a program that has allowed in recent years to conserve around 1.6 million hectares of land and forests in general, this program called Socio Bosque allows to date to conserve a series of important ecosystems for the conservation of Ecuadorian biodiversity (Kuebler 2020).

2.4 Rules for Timber Harvesting in Ecuador

Since 1981, Ecuador has applied the Forestry and Conservation of Natural Areas and Wildlife Law with guidelines valid until the end of the 90s (MAE 2000). Afterwards, the Sustainable Forestry Development Strategy for Ecuador (MAE 2000) was developed in which the forestry section of MAG and INEFAN (Ecuadorian Forestry Institute of Natural Areas and Wildlife) merged to create the Ministry of Environment (MAE), which is responsible for most of forestry activities, including SFM and the replenishment of forest resources used by society.

Towards the end of 1999, a new Forestry Law was proposed, which was intended to be a framework for sustainable forest development in the country, but finally this law was not discussed for its approval by the corresponding institution.

To face this situation, the Ecuadorian Government emitted an executive decree in April 2000 to reform the Application to the Law of Forestry and Conservation of Natural Areas and Wildlife Rules (MAE 2000). As an innovation within this decree the basic principles of SFM were incorporated with the consequent regulation of land use planning and management based on indicators and criteria involving society in the management decisions and the declaration of the native forest as a highly vulnerable ecosystem.

Since 2000 the activities of forest control have been accompanied by personnel of the Armed Forces and National Police along with five NGO´s (Fundacion Natura, FEPP, Fundacion Maquipucuna, COMAFORS and CARE Ecuador). The fundamental aim is to control the transportation between forests and markets (Añazco et al. 2010).

At the police checkpoint, verification of the guidelines for transport and timber trade is done. According to the regulation 038/2004 issued by the MAE in 2004, guides for mobilizations are made by forest regents (trained specifically for this evaluation) that also provide logging licenses. This process permitted the usage of the same license for mobilization for different logging licenses, allowing around 50% of the total market to come from illegal timber harvest without the corresponding permission (MAE 2004).

In 2001 by Ministerial Agreement 131 issued the Standards for sustainable forest management for timber harvesting. This first rules in Chapter 3, Article 10, quote: For purposes of logging, trees registered in the census shall be classified on the basis of the following criteria: "Tree to remove which DBH is equal or greater than 30 cm and less than MCD (minimum cutting diameter) that it has not been listed as a tree for logging or banding to encourage the development of one or more trees or future use of reserves. Eliminated trees may be extracted from the forest. Not so the trees removed by “banding", wich defines the trees to be thinned when logging. Also in the article 11 of the same law it indicates that the intensity of extraction for short or banding shall not in any case exceed 10% of the volume to take advantage.

Furthermore, on December 21st of 2000 the Ministry of Environment emitted the Norms for Sustainable Forest Management and Timber Utilization in Ecuador (MAE 2001). After that, in 2004, the following Ministerial Agreements (MAE 2004) were subscribed to rule the forestry affairs:

- Norms for Administrative Proceedings to authorize Timber Utilization and Logging. Norm 037 (MAE 2004).
- Norms for the System of Forestry Regency. Norm 038 (MAE 2004).
- Norms for Sustainable Forest Management for Timber Utilization in Humid Forests. Norm 039 (MAE 2004).
- Norm for Sustainable Management of Andean Forest (MAE 2004).

According to this procedure there are two norms about harvesting timber in the Andean forest and the Tropical rain forest (MAE 2004). Technical specifications enclose a list of conditioned species and values of minimum cut diameter (MCD). Our study area includes four conditioned species in the normative for a Tropical rain forest (*Cedrela* spp. *Tabebuia* ssp. and all species of the family Podocarpaceae).

The aforementioned standard with other rules of forest conservation and forest management norms were unified in 2003 in Unified Text of Secondary Environmental Legislation (TULAS by acronym in Spanish). The following legal instrument with which the State account for the standardization of the management and use of forests are the rules to the sustainable management of Andean forests (MAE 2006), unspecified whether repealing or not the old rules, the elements to verify the implementation of silvicultural treatments mentioned in Chapter VI, Article 21 says: "The basal area (BA) removed or damaged by the use and / or the application of silvicultural treatments must not exceed 40% of total BA according to the inventory" while Article 22 says:" The application of different silvicultural treatments use to favor the development of desirable trees, will be under the respective plan approved by the authority ", i.e. that the implementation of silvicultural treatments in the second regulation is carried out at the discretion of the management plan, and not that there will be regulations or any tools to assess the intensity thinning, and in response to the forest or the monetary cost of implementation of silvicultural treatment.

The Ecuadorian State, through the MAE, takes control at different stages of logging and transport of timber and various products different of wood. For this process there are rules. The procedure starts showing the ownership of the property where the logging is carried out; the next step is to perform a management plan that includes a zoning and land use types in the farm. When the property covers more than 50 hectares and the volume of timber is high should implement a PAFSU (sustainable forestry plan), or if the property is small, it must implement a PAFSI (Simplified Forest Harvesting Plan). However, Ecuador does not have a large commercial forest industry. This may be linked to logging permits being short-term in nature, as well as difficult access to forest areas (Kuebler 2020; Global Forest Atlas 2019).

In both cases there are technical specifications (indicating the intensity of forest inventory the minimum cutting diameter of the species and the minimum width of forest roads for the transport of logs) must also be met. The difference is that the first plan is "large scale" and implemented in a period of not less than two years, while the second plan is a smaller scale and time of application is not to exceed one year.

All efforts for the development of sustainable forest management practices in Ecuador focus on different issues related to the harvesting of forests, ecosystem services and forest plantations, but silvicultural experiments evaluating the effectiveness of selective thinning for timber production in natural mountain forests have not been made or at least not been published until this date. The standard analyzed here is mainly focused on forest exploitation and minimally on management (Weber et al 2013).

As previously mentioned, the only silvicultural intervention that is contemplated in the Ecuadorian forest regulations is the extraction of unwanted trees with the aim of increasing the economic value of the forests, although the results of this activity have not been reported since its implementation, it is Silvicultural activities need to be considered a priority for better management of productive forests. Characteristics and attributes of timber species are in many cases completely unknown except for the most commercialized, for example, knowledge about the distribution of tree species is a requirement for the development of scientifically proven foerstal management techniques, therefore, recent advances in species distribution modeling show promise in FMT restocking and enrichment (Kuebler 2020).

2.5 Silviculture in the tropics focused on TMF and silvicultural treatments to improve the timber production in tropical forests.

Theoretically, the general forestry objective is to improve the performance and sustainability of forests through forest management activities that include protective actions such as reduced impact logging, extension of the cutting cycles and the opening of the canopy to promote the density of timber species, actions that have been implemented and monitored over decades and that have been specifically tested in various forest types, demonstrating that sustainability over time may be possible.

However, at present, forests are not only considered as suppliers of wood, but are also considered important sources of environmental services such as the production and regulation of water and supplier of non-wood forest products (NFTP) considered important above all for indigenous peoples living around forests. In our forestry-ecological experiment we focused mainly on determining whether the diemetric growth of timber trees through the implementation of a release thinning is greater than the diameter growth without any intervention.

Four silvicultural systems are recognized worldwide, to frame the treatment implemented in the RBSF forests, Kuebler (2020) refers to the concepts and scope of each silvicultural system, also refers to a much-needed separation to understand the actions of each one, the first two systems are applicable to different and diverse natural forests, while the last two are thought to act in monospecific or mixed plantations (Savill 2004).

The first system called Selection or polycyclic system is based on short cutting cycles, small disturbances distributed throughout the forest, thus also allowing conditions for the establishment of regeneration. Forest types characterized by shade-tolerant, slower-growing canopy trees, as well as small and frequent disturbance regimes, are well suited for these systems (Ashton and Hall 2011). The Shelterwood or monocyclic system includes successive regeneration fellings in the canopy and upper floors to promote advanced regeneration, once regeneration is established the remaining trees are felled to release regeneration as a single cohort in a relatively uniform way (Ashton and Hall 2011; Savill 2004). These systems tend to give rise to stands of uniform age (Savill, 2004). The Shelterwood System is appropriate for forest types that are characterized by shade intolerant canopy trees and are driven by strong episodic disturbance regimes (Ashton and Hall 2011).

The following two silvicultural systems Clear Cutting System and Coppice System are mainly implemented in forest plantations in the tropics. The first system refers to the implementation of plantations after all the available stock has been cut down in a single shift, it is the predominant system for the installation of wood-producing plantations (Kuebler 2020). Finally, the Coppice system is implemented in plantations that have been harvested and whose stumps or roots re-sprout being managed as coppice shoots. In the tropics, plantation shoots have been used for the production of pulpwood (for example from Eucalyptus ssp.) and fuelwood (for example from *Leucaena leucocephala*) (Kuebler 2020).

In the tropics according to Putz (2004) and Kuebler (2020) two types of silvicultural treatments focused on wood production can be identified, Treatments to increase the stock of timber trees and treatments to improve tree growth.

The first of the mentioned treatments (improve the stocking) is implemented to ensure adequate natural regeneration of timber species, mainly for future harvests. First, the presence of seed trees well adapted to the environment is essential to implement this treatment because the seeds of these trees will probably adapt better to the environment and to the forest substrate, contrary to the artificial regeneration brought from other sites. Second, activities to promote natural regeneration produce less impact on the forest and Third, promoting natural regeneration is less expensive than implementing artificial regeneration (Kuebler 2020, Putz 2004).

The success of implementing this treatment lies in the ecological and silvicultural knowledge of the forest, to guarantee the regeneration of commercial species, without causing unnecessary damage to the forest, it is also important to determine the succession status of seedlings, saplings and reserve trees of commercial species. It is imperative to analyze species with little natural regeneration in order to promote seed collection and seedling production and establishment (Ashton and Halley 2011). Enrichment planting uses artificial regeneration to promote desired species in secondary forest areas or degraded areas. In the tropics, it is predominantly applied in secondary and overexploited forests where natural regeneration is insufficient (Zimmerman and Kormos 2012).

The second major approach or general treatment (to improve the growth of timber trees) involves analyzing the competition for light, living space and nutrients, the premise is that by increasing the availability of light and soil resources, growth can be improved, the quality and health of the remaining trees (Wadsworth and Zweede 2006).

Thinning is a tool that allows controlling competition for resources by reducing the number of trees in a given area, it can be implemented throughout the forest or around trees for future harvest (FTC, here in this work we refer to the FCT as potential crop Trees or PCT). In the tropics, the implementation of release thinning (here selective thinning) has become one of the most widely applied silvicultural treatments that have obtained the best results in terms of diameter growth of timber trees (Kuebler 2020). Selective thinning increases the access of released trees to light and water resources, one of the advantages of selective thinning is that it influences the trees closest to the PCT, leaving areas of the stand without intervention, avoiding unnecessary disturbances, making it silvicultural and economically viable. (Putz 2004, Kuebler 2020).

Selective thinning to improve forest productivity, such as the release or removal of competitors from timber trees, were implemented some decades ago, including implementation in tropical countries (Wadsworth 2000, Peña-Clarós et al. 2008, Frederiksen and Putz 2003). The process, in which undesirable species and other competitors near the timber species are eliminated, helps to improve their productivity, because diameter growth is a result of competition for space and resources with other species (Andresen et al. 2005). This silvicultural treatment allows a diameter increase in trees (Lampretch 1990, Kammesheidt et al. 2003, Wadsworth and Zweede 2006) and therefore is frequently applied in managed forests for timber production (Frederiksen y Putz 2003).

Release from competitors is best developed in boreal forests (Vincent et al. 2009) and alpine forests (Vitali et al. 2016), where implementation results in significant diameter increases. Also, in neotropical countries (e.g., Puerto Rico, Nigeria, Guyana, Sarawak and Brazil) this technique has been implemented successfully in managed forests (Wadsworth and Zweede 2006, Peña-Clarós et al. 2008). However, in natural tropical forests, the release from competitors around the desired timber species is poorly investigated thus far, because these forest types present an extraordinarily high species density, even though the density of individual species is comparatively low (Adame et al. 2014). This generally leads to the decelerated diameter growth of tropical forest trees (Vlam et al. 2014), but growth rates vary significantly between species, depending on their growth habit (early-, mid- or late-successional), age, phenological traits and climatic conditions (Pélissier & Pascal 2000, Da Silva et al. 2002).

In some tropical regions, e.g., Africa (Burkina Faso, Cameroon) and Asia (India, Indonesia), silvicultural treatments, such as selective thinning, have been applied for more than a century (Wadsworth 1997). This practice, which aims at the minimizing of impacts on the integrity of natural forests and improving the productivity, was recently implemented in Ecuador. The treatment consists of eliminating species of low commercial value, which are competitors for valuable timber species. This practice is based on the theory that the growth rates of trees are directly related to the quantity of received sunlight and nutrient availability, and for this reason, all undesired or competitor trees around the valuable timber species are removed to obtain adequate lighting and to enhance nutrient availability (Dawkins 1955, Louman et al. 2001). Regarding the impact of selective thinning on functional diversity, we highlight the work carried out by de Avila et al. (2018), and on the structure of the forest, the work of Yguel et al. (2019); both works conclude on the importance of assessing thinning and the impact it has on the forest's richness.

In particular, the selective thinning planned in the RBSF TMF, although it was not certified by FSC, to implement it, minimum rules for reduced impact logging (directed fall) were met, so we consider that this silvicultural treatment should not be considered as achievable for the entire TMF. The lack of knowledge about the response of stands to silvicultural treatments means that these are poorly managed, according to Kuebler (2020) to better understand silvicultural treatments one must start by understanding the impact of these at the individual level (released trees) and a Once you have a clear idea of these effects, you can develop your own silvicultural system for TMFs that combines individual treatments in different forests with different characteristics. Since 2003, the forestry experiment that was implemented and that is analyzed here from various approaches analyses the impact of selective thinning on tree growth (Günter et al. 2008) and according to Kuebler (2020) this experiment continues to the present day being the only one on the impact of silvicultural treatments in the TMF.

3. General characteristics of the Research Area and general methodological framework of the Forest Experiment

This chapter characterizes the study area into several biophysical aspects, highlights its strategic location within one of high biodiversity areas in the world, as well as a summary of the climatic conditions of the study area that are the drivers of biodiversity in the area.

The data acquisition protocol is described in detail since this experiment served as a basis not only for measuring the effect of selective thinning on the diversity and growth of released trees, but also to monitor the effect of selective thinning upon various taxonomic groups as well as the effect it produces in the soil and in natural regeneration.

This work is the product of a 10-year multidisciplinary forestry monitoring experiment. Data, as well as the results, not only served to make the two main publications (Cabrera et al. 2019 and Cabrera et al. 2020) the basis of this report, but they have also served for other important works where they highlight the importance of the ecological-forestry experiment that was implemented and that will be strictly cited to complete the scope of the multidisciplinary research that was carried out in the TMF of the RBSF such as seen by Kuebler et al. (2016) and Kuebler et al. (2020).

3.1 Description of the study site

The study was carried out in the Reserva Biologica San Francisco (RBSF) 03°58′ S, 79°04′ W; 1850 m a.s.l. (Ohl & Bussman 2004), located to the North of Podocarpus National Park (PNP) in Southern Ecuador. RBSF is situated within the eastern cordillera of the Andes (Brehm et al. 2003). This area is located geographically among the Loja and Zamora-Chinchipe provinces (Figure 2).

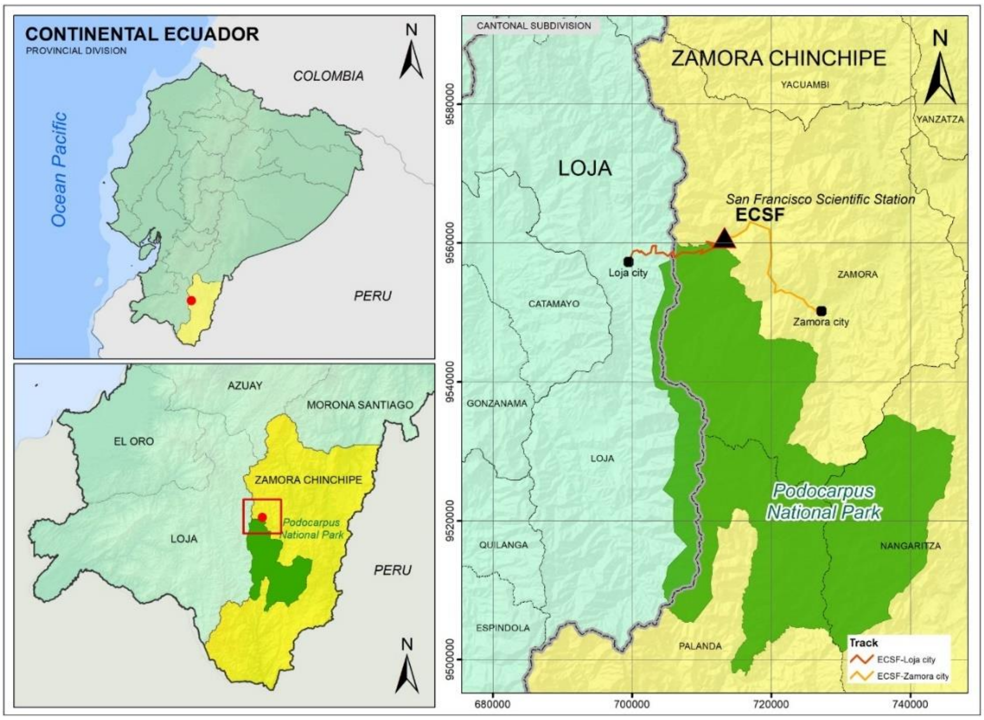


Figure 2. Location of Reserva Biologica San Francisco and Podocarpus National Park

In geological terms, the study area is part of the Loja terrain; it mainly consists of Paleozoic metamorphic sediments and Triassic granites. The entire site is immersed in the “Chiguinda” unit, which is built up of quartzite, metamorphic limestone, graphitic slates and phyllites (Litherland et al. 1994; Goller 2004). Paulsch (2002) suggests that continuous mountain rising provokes high differentiation in the relief where slopes have 60º steepness. The sheer, inclined ground combined with the high amount of precipitation results in waterlogged soils leading to frequent landslides (Merkl 2002). According to Beck et al. (2008), the area where RBSF is established shows the following characteristics (Table 1).

Table 1. Geomorphologic characteristics of RBSF (Beck et al. 2008).

CHARACTERISTICS	DESCRIPTION
Physiographic Province:	Real Cordillera of the Andes (Eastern Cordillera)
Sub – Province:	Cordillera of Sabanilla and Tzunatza
Great Landscape:	Fluvial erosional structural relief
Landscape:	Medium and low mountains branched on paleozoic metamorphics and triasic migmatites. V-shaped valleys indicate the occurrence of schist and phyllites.
Sub-Landscape:	Steep slopes (0-50% inclination), very steep slopes (> 50% inclination).
Geological Process:	Erosion in furrows, landslides and solifluxion
Lithology:	Metamorphic rocks built by cuarcites, phylites
Geological formation:	Chiguinda (Paleozoic semipelites) - Sabanilla Unity (ortho- and paragneisses).

The soils in the RBSF mainly belong to the order of Inceptisols. At the lower parts of the slopes, Dystrudepts are more frequent, whereas at the upper parts Humaquepts and Petraquepts dominate the area (Schrumpf et al. 2001). According to Wilcke et al. (2008), the soils in mountain forests are characterized by thick organic layers, which store large contents of biomass and nutrients. However, the thickness of the organic layer depends mainly on two factors: altitude and slope gradient. At higher elevations, the temperatures are lower and therefore the degradation of the material is decelerated, leading to an accumulation of the organic matter (Martinson et al. 2013). At steep slopes, the organic layer is generally thinner due to enhanced soil erosion processes, which transport the material to the lower and less inclined parts, where the organic matter is sedimented. These processes also affect the chemical properties of the soils, making the availability of nutrients for plants highly heterogeneous (Bendix et al. 2013).

The climate in the catchment is per-humid, with marked altitudinal gradients in air temperature, humidity and rainfall (Fries et al. 2014). The annual mean air temperature ranges from 19.4 °C at the valley bottom to 9.4 °C at the highest mountain tops. However, the average diurnal temperature amplitude is lowest inside dense forest stands compared to the other vegetation units present in the study area (pasture and paramo), because the canopy layer shelters the air inside the forest against daily irradiance and nocturnal outgoing radiation (Fries et al. 2009). Furthermore, the air inside the tropical mountain forest is generally saturated, because dense canopies hinder the exchange of the air inside the forest with the free atmosphere, while the soils inside the forest stands are commonly saturated (Fries et al. 2012).

The distribution of rainfall is linked to altitude, due to orographic precipitation formation (Fries et al. 2014). The average annual rainfall amounts vary between 2300 mm at the valley bottom and 6700 mm at the mountain tops. These annual rainfall amounts include both rain and fog precipitation, because both clouds and fog deposit water directly onto the vegetation, and therefore both must be considered as a relevant available water input from the atmosphere (Bendix et al. 2009). The seasonal rainfall distribution shows a clear annual cycle with the main rainy season between May and September (austral winter) and a relative dry season between November and February (austral summer) (Fries et al. 2014).

Sierra et al. (1999) describes the study area as being two natural formations denominated by mountain rainforest between 1800 - 2800 m a.s.l. and high mountain evergreen forest between 2800 - 3100 m a.s.l. These formations are distributed along the Real Cordillera de los Andes. The most characteristic and frequent tree families are Melastomataceae, Rubiaceae, Lauraceae and Euphorbiaceae, which reach a height of 25 m (Homeier 2004). Based on the structural parameters, Paulsch (2002) found seven types of natural forest in the RBSF. Detailed botanical description of species composition and zonation is given by Bussmann (2001), where vegetation in the RBSF has been grouped into four forest formations: low mountain forest (1800 - 2150 m a.s.l.), high mountain forest (2150 - 2650 m a.s.l.), Jalca (subalpine forest, Ceja Andina, 2650 - 3000 m a.s.l.) and Páramo (2700 - 3150 m a.s.l.). These last two plant communities of Jalca and Páramo are found in interrelationship close to the tree line. Homeier & Breckle (2002) found that the RBSF forest presents a high floristic diversity as a transition zone between mountain forest and rainforest; 182 tree species (> 5 cm dbh) were registered in 15 plots (400 m^2 each plot), where the most important botanical families were Lauraceae (21 species), Melastomataceae (16 species) and Euphorbiaceae (11 species).

The natural vegetation in the RBSF is an evergreen tropical mountain forest, which covers the slopes from the valley bottom up to the tree line at ∼2700 m a.s.l. (Curatola et al. 2015). The forest can be divided into evergreen lower montane forests (up to 2100–2200 m a.s.l.) and upper montane forests, up to the tree line. Above ∼2700 m, a shrub-dominated sub-paramo prevails, where small patches of Elfin forest, the so-called Ceja Andina, dominate the landscape (Homeier et al. 2013). Both types of montane forest can be subdivided into a lower slope (ravine) forest and an upper slope (ridge) forest (Werner & Homeier 2015, Paulick et al. 2017). The ravine forests are characterized by lower stem density, but simultaneously by greater basal areas (tree diameters) and higher canopies when compared to the ridge forests, where lesser tree species are also present. The difference in forest structure is mainly due to the climatic conditions and prevailing soil types (Moser et al. 2011, Dislitch & Huth 2012).

3.2 Data Collection

All data were collected in the RBSF forest from January 2003 to December 2006 in a first phase and 2007-2010 in a second phase. The implementation of selective thinning was conducted from April to May 2004; large trees were inventoried three times: the first time in 2003, the second in 2005 and the third in 2006. The collection of fertile tree samples was held together with the first inventory and on subsequent occasions to corroborate or to complement certain species determined in the initial inventory.

3.2.1 Forest Inventory

Before forest census was developed, a preliminary inventory was carried out by following “transects” along the creeks in some watersheds in the RBSF. Ten plots of 400 m^2 were established with a determined distance (Günter

& Mosandl 2003). Results showed that at least 50 moderate and highly valuable trees ≥ 20 cm dbh were found in one hectare. 35 out of these 50 trees presented profitable and healthy trunks to be considered as trees of higher economic potential. The next step was to establish 50m x 50m permanent plots in three different watersheds of the RBSF, which are named as Q2 - Q3 - Q5. The first survey was conducted between April and June 2003 (Table 2). The total and commercial height of all trees (in meters) were measured and the shapes of the logs were categorized (good = straight, regular= Cracks along the trunk, bad = forks in the trunk). Other forest inventories were performed three times to determine the dynamics of the stand. The time between the first measurement and the second measurement was 2 years (2005), while the time between the second and third measurement was one year (2006).

Table 2. Evaluated Parameters for timber species and all species of trees and natural regeneration in RBSF Forest.

PARAMETERS	**Big and Medium Trees (5.1 - > 20 cm dbh)**	
	VALUABLE SPECIES	**ALL SPECIES**
Taxonomic Identification	**X**	**X**
DBH	**X**	**X**
Total and Commercial Height	**X**	**X**
Social Position	**X**	
Monthly Growth	**X**	
Mechanical Damage	**X**	**X**
Trunk Shape	**X**	

PARAMETERS	**Regeneration (0.1-5cm drc*)**	
	VALUABLE SPECIES	**ALL SPECIES**
Taxonomic Identification	**X**	**X**
Diameter root collar	**X**	**X**
Total Height	**X**	**X**
Mechanical Damage (in stem and foliage)	**X**	**X**
Trunk Shape	**X**	**X**

*diameter root collar

3.2.2 Selective Thinning

The proposed selective thinning consists of releasing high quality individuals selected (considered as Potential Crop Trees, PCT´s) of nine valuable species. The species of PCTs are: *Tabebuia chrysantha* (Jacq.) G. Nicholson “Guayacán”; *Cedrela montana* Turcz. “Cedro de montaña”; *Inga acreana* Harms. “Guabillo”, *Hyeronima asperifolia* Pax & K. Hoffm. “Motilon”, *Hyeronima moritziana* Mull Arg., “Motilon”, *Podocarpus oleifolius* D. Don ex Lamb. “Romerillo”, *Nectandra membranacea* (Sw.) Griseb. “Canelo”, *Clusia ducoides* Engl. “Duco” and *Ficus subandina* Dugand “Higuerón”. The selective thinning was applied from June to July 2004.

To determine the competitor from each of the nine individual timber species or PCT (Potential Crop Tree), all plots were visited. After a visual inspection of the superposition of the crowns of the PCT, the competitor tree was labeled with plastic tape. The shape and quality of the stem and the social position of the crown were evaluated for each PCT (Figure 3). The area of the tree was measured by projecting two axes. The area affected by the trunk and crown of the felled trees was measured directly on the ground, while also assuming the rectangular area of impact over the forest floor.

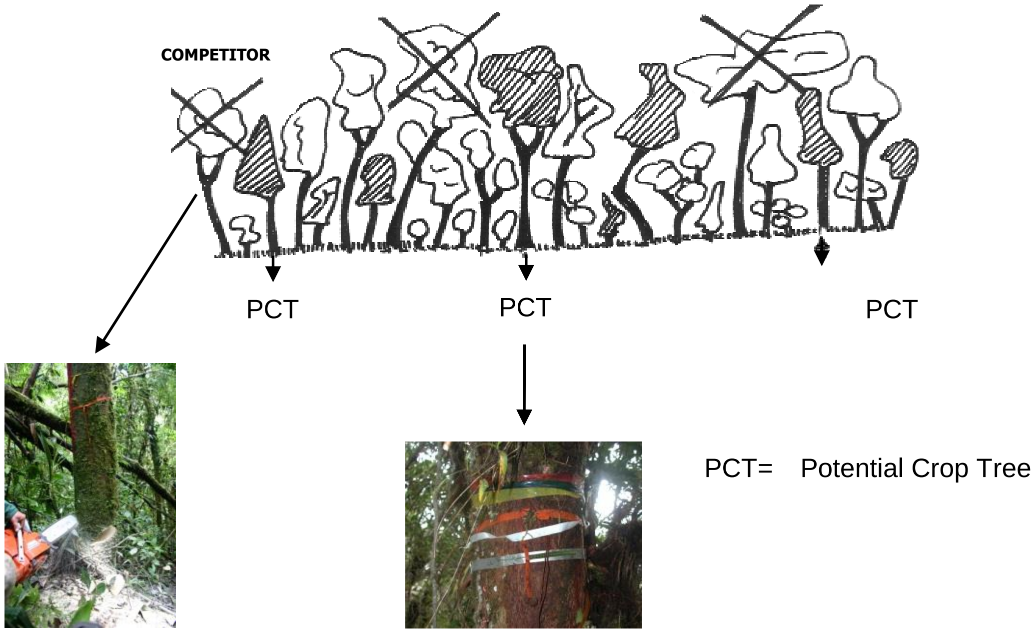
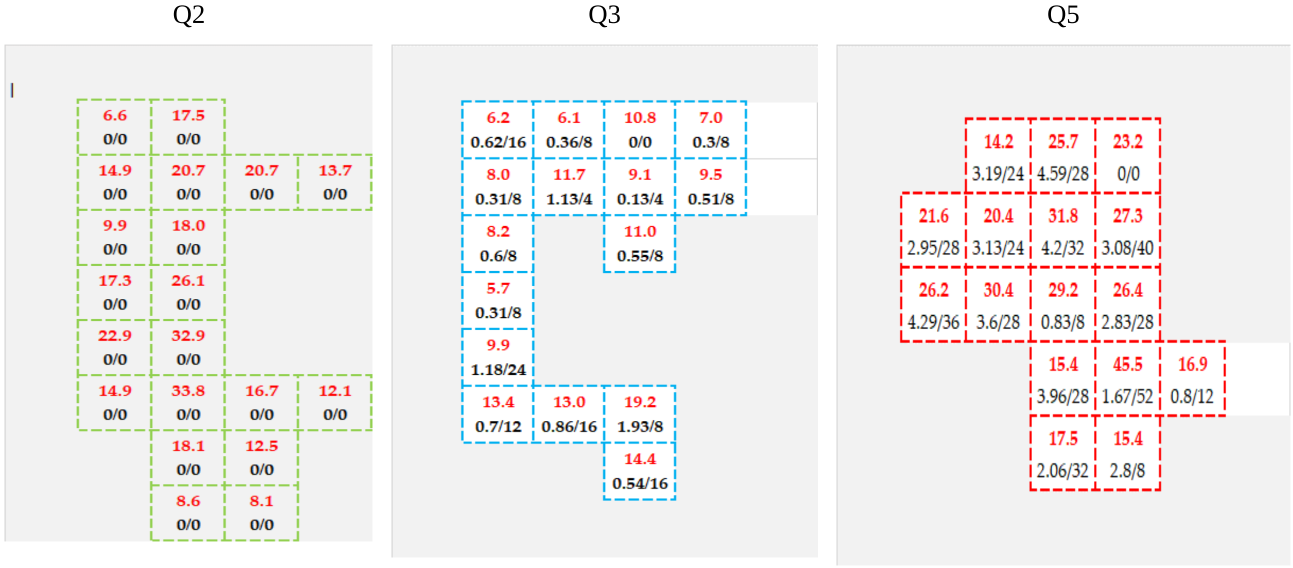


Figure 3. Scheme of selective thinning applied. Valuable tree species are marked with black crowns. Defective timber tree species were measured only, not released.

Of 52 plots installed, 22 served as control (20 in Q2 and one plot in every other block) without any forestry intervention, and in the other 30 plots, selective thinning was applied at different intensities. Values of basal areas extracted were grouped in ranges (Figure 4).



Q2

6.6 0/0	17.5 0/0		
14.9 0/0	20.7 0/0	20.7 0/0	13.7 0/0
9.9 0/0	18.0 0/0		
17.3 0/0	26.1 0/0		
22.9 0/0	32.9 0/0		
14.9 0/0	33.8 0/0	16.7 0/0	12.1 0/0
	18.1 0/0	12.5 0/0	
	8.6 0/0	8.1 0/0	

Q3

6.2 0.62/16	6.1 0.36/8	10.8 0/0	7.0 0.3/8
8.0 0.31/8	11.7 1.13/4	9.1 0.13/4	9.5 0.51/8
8.2 0.6/8		11.0 0.55/8	
5.7 0.31/8			
9.9 1.18/24			
13.4 0.7/12	13.0 0.86/16	19.2 1.93/8	
		14.4 0.54/16	

Q5

	14.2 3.19/24	25.7 4.59/28	23.2 0/0	
21.6 2.95/28	20.4 3.13/24	31.8 4.2/32	27.3 3.08/40	
26.2 4.29/36	30.4 3.6/28	29.2 0.83/8	26.4 2.83/28	
		15.4 3.96/28	45.5 1.67/52	16.9 0.8/12
		17.5 2.06/32	15.4 2.8/8	

Figure 4. Scheme of sample plots in Q2, Q3 and Q5. The numbers in red show the basal area/ha of each plot and the numbers in black show the basal area extracted (m²/ha) / number of individuals extracted (N/ha)**.**

The tree logging intensity corresponded to extract a mean of 2.9 $m^2 ha^{-1}$ (±1.1) or 13.5% of the basal area in Q5, and a mean of 0.62 m^2 ha^{-1} (± 0.29) or 10.2% in Q3.

3.2.3 Morphological and taxonomical descriptions and Silvicultural characteristics of Potential Crop Trees species

To implement selective thinning in the RBSF forest, individuals from nine timber species were chosen to eliminate the competitors. Three species are considered valuable timber (*Tabebuia chrysantha*, *Podocarpus oleifolius* and *Cedrela montana*), while the other six species are considered of medium quality wood. All sampled individuals were grouped into the same diameter classes mentioned in the chapter on methodology. Here we are referring to the individuals of the diameter Class III = 20.1- 30 cm dbh, Class IV = 30.1- 40 cm dbh, Class V = 40.1- 50 cm dbh and class VI ≥ 50.1 cm dbh.

a. Podocarpus oleifolius D. **Don ex Lamb.**

Synonyms: This species does not have synonyms.

Description: Trees up to 30 m tall; sometimes bushes. Leaves are spirally arranged, alternate, opposite or subopposite, linear or ovate, leathery, flat, entire, uninervias, midrib conspicuous, attenuated at the base, sessile or shortly petiolate without stipules. The strobilus is axillary or terminal, sessile or pedunculated. The male cones are cylindrical. Female cones solitary or terminal fertile bracts. Seeds drupaceous fused to epimaceo, becoming leathery or fleshy. Epigeal germination, seeds with two cotyledons.

Geographic distribution: In Ecuador *Podocarpus oleifolius* is distributed in the provinces of Azuay, Bolivar, Imbabura, Loja, Morona Santiago, Pichincha, Sucumbios and Zamora Chinchipe. This species is considered in danger of extinction in many sites in Latin America such as Bolivia (Meneses y Beck 2005), Colombia (Galindo et al. 2003) and Ecuador (Galvez et al. 2003; Loján 1992; Hofstede et al. 1998; Castillo y Castro 1999; Rios y Rios 2000) due to over exploitation for several years. In RBSF, a population is found distributed mainly in Q3 catchment.

Forest type: According to Bussman (2005), this species is part of the high mountain forests or “bosques montanos altos” in the community of *Purdiaea nutans* Planch. where a great amount of natural regeneration is found, even though it can also be found sporadically in the stripe of the low mountain forests or “bosques montanos bajos” (community of *Ocotea - Nectandra*) where regeneration is poor or almost null. And Galvez et al. (2003) suggest this species can be found in the stripes of mountain cloud forest or “bosque de neblina montano”, which is part of the community Romerillales of *Podocarpus oleifolius* with *Gaiadendron punctatum*.

Uses: The wood of *Podocarpus oleifolius*, is prized for its quality construction of furniture, doors, flooring, framing, windows, aerial structures, interior and exterior carpentry, plywood and moldings (Lojan 1992, which means that there is a high demand (Galvez et al. 2003).

b. Tabebuia chrysantha **(Jacq.) G. Nicholson**

Synonyms: *Bignonia chrysantha* Jacq., *Tabebuia rufescens* J. R. Johnst., *Tecoma chrysantha*.

Description: Trees up to 35 m tall and 60 cm dbh; scarce and thick branches, irregular, rounded crown. Palmately compound, opposite, with 5 leaves - 7 leaflets, margins entire, apex acuminate, base obtuse, flowers are campanulate, in groups of terminal inflorescences (panicles) of light yellow color (pers. Obs.). The fruit is a cylindrical capsule of 15 – 47 cm of lenght and 0.8 – 1.4 cm of width. It can be propagated by seeds or stakes; it grows in slopes with poor, dry and arid soils (Loján 1992).

Geographic distribution: In Loja and Zamora Chinchipe Provinces, it can even be found at 2000 m a.s.l in RBSF. Its geographical distribution occurs to the south of Loja and El Oro provinces; it grows in the lowlands of Catamayo, Macará and Puyango watersheds. The altitude for this species ranges from 0 to 1,000 m a.sl.
Forest type: The species is found in "montane rain forest" and "premontane rain forest."

Uses: The wood of this species is listed as one of the hardest and heaviest in the neotropics, with a specific weight between 0.95 and 1.2 g/cm^3. It is used in the construction of furniture, coachwork, flats, industrial use fine crafts, assemblers and tool handles.

***c. Cedrela montana* Moritz ex Turcz.**

Synonims: *Cedrela bogotensis* Triana & Planchón, *C. mexicana* Roem, *C. subandina* Cuatrec.

Description: Trees to 35 m tall, with alternate, compound leaves, between 20 - 55 cm long, with 8-13 pairs of opposite leaflets or subopposite, apex acuminate, base rounded to cordate, sometimes uneven, with entire margins, petiole swollen basally. Inflorescence is terminal or subterminal, glabrous or with scattered soft pubescence; unisexual flowers. The fruits are a woody capsule, ovoid to ellipsoid and pendulum, dehiscent with 5 woody valves. The species is used as fine wood used for construction, furniture and fence posts.

Geographic distribution: In Ecuador *Cedrela montana* is in Azuay, Bolivar, Carchi, Chimborazo, Cotopaxi, Imbabura, Loja, Napo, Pichincha and Tungurahua. *Cedrela montana* grows at elevations between 1,600 and 2,800 m a.s.l., with an average annual temperature ranging between 10 and 20 ºC and annual precipitation of 500 to 2,000 mm.

Forest type: *Cedrela montana* is in Ecuador in montane cloud forest and humid montane forest, between 1,800–3,000 m asl and 500 to 1,000 mm of rain. It also grows in the mountain belt with annual rainfall between 1,000 and 2,000 mm. (Sierra et al. 1999).

Uses: Generally, the genus *Cedrela* is highly appreciated in carpentry, for exteriors and interiors and especially for furniture due to its color, grain, and workability. Characterized by its hardness and high durability, the wood is also used for plywood, cigar boxes, naval construction, racing boats, musical instruments and as chips in construction. It is also used to make artistic carvings (Nieto y Rodriguez 1993).

***d. Clusia ducuoides* Engl.**

Synonyms: This species does not have synonyms.

Description: Trees 12-15 m tall, leaves simple, oblong, rounded apex, secondary rib inconspicuous, little milky latex (Pers. ob.), presence of wading roots.

Geographic distribution: In Ecuador, it can be found in Azuay, Cañar, Imbabura, Loja, Napo, Pastaza y Zamora Chinchipe (Jorgensen y León Yánez 1999). According to Gustafsson (2002), the distribution in altitude of *Clusia* ducuoides Engl. ranges from 500 to 3.500 m a.s.l.

Forest type: Gustafsson (2002) affirms that the genus Clusia is an important component in the mountain forests; the maximum diversity at the level of species also occurs in these forests.

Uses: The species of this genus are used for water resistant timber and therefore are used for roofs and buried pieces of wood.

***e. Ficus citrifolia* Mill.**

Synonyms: This species does not have synonyms.

Description: The genus Ficus has 56 species in Ecuador. There are mostly trees or hemiepiphytes, some riparian. They have simple leaves, conical terminal stipule, and the presence of white latex (Gentry 1993).

Geographic distribution: In Ecuador it can found in Azuay, Bolivar, El Oro, Guayas, Loja, Los Rios and Zamora Chinchipe.

Forest type: According to Sierra et al. (1999) this species can be found in wet forests of both foothills, in denomined "Bosques siempreverdes piemontanos," the genre has a wider distribution.

Uses: There is not much information about this species in particular; the genus itself is not even included in The Flora of Ecuador for Moraceae (Berg 2009). The species was previously studied in a work about the phytochemistry of plant species in the Loja Province, a hexano type compound was obtained, with a resulting sesquiterpene lactone (Ordoñez et al. 2006).

***f. Hyeronima asperifolia* Pax & K. Hoffm.**

Synonyms: *Hyeronima sararita* Cuatrec. (Jorgensen y León Yánez 1999).

Description: They are usually trees, up to 12-15 m tall and stem diameters up to 50-60 cm dbh (Lojan 1992).

Geographic distribution: It is distributed from southern Mexico to Panama, extending into the Caribbean and South America from Colombia to Peru. In Ecuador, it can be found in the Provinces of Carchi, Imbabura, Azuay, Bolívar, Chimborazo, Loja and Zamora Chinchipe (Loján 1992).

Forest type: This species occurs in the montane rain forest; it ranges from 2,200 to 2,800 m a.s.l.

Uses: Timber is used for furniture, bodyworks, tools, floors, sculptures and family buildings. The fruits are edible, and feed birds and squirrels which help its dispersion. Moreover, the demand of seedlings for reforestation is increasing, the species can be established either in pure form or mixed with other species; however, it is recommended for the enrichment in gaps after selective cutting of mature trees (Cuamacáz and Tipaz 1995).

***g. Hyeronima moritziana* Mull Arg.**

Synonyms: *Hyeronima macrocarpa var. moritziana* Mull Arg., *Hyeronima nevadensis* Cuatrec. (Jorgensen y León Yánez 1999).

Description: Trees 15-20 m tall, usually coated with yellow lepidote indumentum hairs. Leaves coriaceous, oblong-lanceolate, ribbed arched towards the margin (broquidodromas). Leaves alternate to semi opposite; pale yellowish color when juvenile. The species have drupaceous fruit (Pers. obs.).

Geographic distribution: In Ecuador, it can be found in Carchi, Esmeraldas, Imbabura, Loja and Zamora Chinchipe.

Forest type: This species is found in the "Bosques húmedos piemontanos", "Bosques húmedos montanos" and the "Bosques siempreverdes de neblina montanos".

Uses: Although no specific information for the species is available, it is well known that some of these species in the genus are used because of the quality of wood for furniture and construction, and some of these species have edible fruits (Loján 1992).

There is no specific information about Hyeronima moritziana, its ecological behavior or main uses, e.g. about medicinal or pharmacological uses. On a generic level, Ecuador has six species of *Hyeronima* (Ulloa and Jorgensen 1993), widely distributed from lowland forests of the Amazon to the Andes. The latest review of the Flora of Ecuador (Jorgensen and León Yanez 1999) suggests the presence of 10 species.

h. Inga acreana Harms.

Synonyms: This species does not have synonyms.

Description: Trees 15-25 m tall, sometimes with small buttresses, compound leaves usually with 4 pairs of leaflets, elliptic leaves without pubescence, leaf nectaries shortly stipitate, flowers arranged in a short spike, fruit a legume, pendula, flattened (Pennington & Revelo 1997).

Geographic distribution: In Ecuador *Inga acreana* Harms is distributed in Zamora Chinchipe, Morona Santiago, Napo and Pastaza provinces. It is a common tree in the rainforests at low altitudes and low mountain zones over lightly flooding sites, up to 800 - 1,200 m of altitude (Pennington and Revelo 1997). The species is frequent in places of secondary vegetation along road sides and it is able to compete with the secondary vegetation (Pennington, 1997).

Forest type: According to Pennington and Revelo (1997), *Inga acreana* found in tropical moist forest in humid foothill forests.

Uses: It is recognized that Inga acreana plays an important role in agroforestry systems which are designed for degraded acidic soils (Pennington 1997). The wood is used for struts and formwork (De la Torre et al. 2008).

i. Nectandra membranacea (Sw.) Griseb.

Synonyms: *Laurus membranacea* Sw. (Jorgensen y León Yánez 1999).

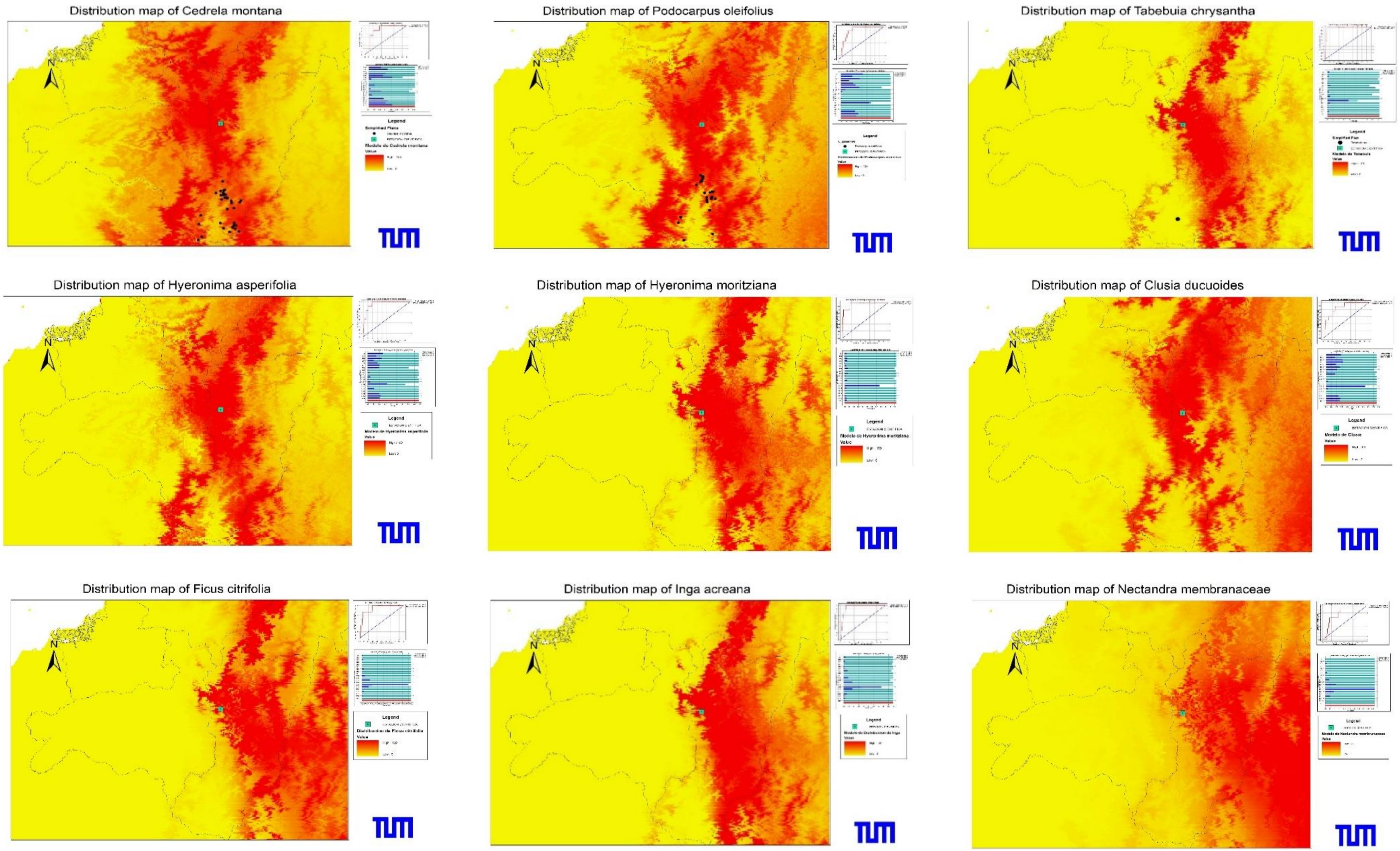
Description: Medium size trees of up to 15 - 20 m height and up to 40 - 50 cm dbh, with cylindric stem and wide crown, young branches with brown hairs**.** The timber is used in house building, doors, windows frames, floors, boxes and firewood. Its fruits feed birds, squirrels and tucans (Cuamacás y Tipaz 1995).

Geographic distribution: In Ecuador, the species is located between 1600 and 3300 m a.s.l., and has been found in the provinces of Carchi, Imbabura, Pichincha, Chimborazo, Bolivar, Cañar, Azuay, Loja, Zamora Chinchipe and Napo (Cuamacás and Tipaz 1995).

Forest type: It can be found in the life zone "cloud forest," with an average temperature of 17 ° C and an average rainfall of 2,800 mm (Cuamacás and Tipaz 1995).

Uses: The wood is used for construction of houses, forming, packaging and construction of canoes and furniture (De la Torre et al. 2008).

As can be seen in the previous descriptions, the species are typical of the TMF and, as can be seen in Figure 5, the potential distribution maps of the species show that the study area is optimal for their presence.



Distribution map of Cedrela montana

Distribution map of Podocarpus oleifolius

Distribution map of Tabebuia chrysantha

Distribution map of Hyeronima asperifolia

Distribution map of Hyeronima moritziana

Distribution map of Clusia ducuoides

Distribution map of Ficus citrifolia

Distribution map of Inga acreana

Distribution map of Nectandra membranaceae

Figure 5. Potential distribution of the nine-timber species monitored in the study, note the wide distribution of some species throughout the provinces of Zamora Chinchipe and Morona Santiago, which widens the range of implementation of the forest management project.

3.3 Data Analysis

3.3.1 Structural and Floristic Parameters

This section describes how the structure and floristic composition of the forest were monitored, along with the natural regeneration of individuals, including both small and large trees. They were divided into diameter classes, Class I encompassing all trees ranging from 0.1-5 cm dbh (natural regeneration) and class II 5.1-20 cm dbh (small trees). The big trees were divided in classes with a range of 10 cm, Class III 20.1 to 30 cm dbh, Class IV of 30.1 to 40 cm dbh, Class V 40.1 to 50 cm dbh and Class VI > 50 cm dbh.

To characterize the initial forest state in RBSF and to have a starting point for future assessments after the implementation of selective thinning at different intensities and to analyze what parameters will change in the forest, structural and floristic parameters were calculated using the following equations (equations 1-5) (Aguirre et al. 2003; Cerón 1993; Madsen and Øllgaard 1994; Madsen 1991; Finol 1976; Galindo et al. 2003; Mori and Boom 1983, Magurran 1988).

$$\text{Relative Density (RD)} = \left(\frac{\text{Individuals per specie}}{\text{Total individuals in the plot}}\right) * 100 \qquad \text{Equation 1}$$

$$\text{Relative Dominance(RDm)} = \left(\frac{\text{Basal area per specie}}{\text{Total Basal Area in the plot}}\right) * 100 \qquad \text{Equation 2}$$

$$\text{Relative Diversity(RDi)} = \left(\frac{\text{\#species per Family}}{\text{Total species}}\right) * 100 \qquad \text{Equation 3}$$

$$\text{Importance Value Index(IVI)} = (\text{Relative density} + \text{Relative Dominance}) \qquad \text{Equation 4}$$

$$\text{Shanon} - \text{Wiener Index } (\text{H}') = -\sum_{i=1}^{S} p_i \ln p_i \qquad \text{Equation 5}$$

S= number of species (richness)

Pi= proportion of individuals of species i respect to total individuals (ie relative abundance of the species) n_1/N.

ni= number of individuals of the species

N= number of all individuals of all species

n_1= number of individuals of the species i

N= number of all the individuals of all the species

3.3.2 Factors that influence the forest grouping

To asses whether there is a significant correlation between the number of trees ha^{-1}, basal area ha-1, dbh ha-^{1}, canopy openness and diversity in terms of the Shannon Index and altitudinal gradient, the Spearman correlation coefficient was used. If the correlation is significant ($r \geq 0.4$; $\boldsymbol{p} \leq 0.05$), structure is influenced by altitude and composition of forest RBSF, determining two or more floristic groups.

Canonical Correspondence analyses (CCA) was used to test whether the same parameters analysed in correlation analysis influenced the grouping (based on species abundance) of floristic sample plots distributed on the three blocks. This analysis is a multivariate technique that allows representing low-dimensional geometric space proximity between a set of objects influenced by a series of predictor variables. The lambda value corresponds to the eigenvalue of each extracted variable in each axis of the array. F - ratio is a statistic that is calculated using the trace or the sum of all the eigenvalues and the p value that indicate the significance of variables ($p \leq 0.05$). Normally the CCA involves two matrices: the matrix of dependent variables (e.g. a matrix of sites x species) and the matrix of independent variables (e.g. a matrix of environmental variables). The relationship between the two matrices is done by means of multivariate regression techniques (Cayuela 2010). Parameters were: elevation (m a.s.l.), number of trees ha^{-1}, basal area ha^{-1}, canopy openness (%), dbh average, and species richness (total number ha^{-1}).

3.4. General results: floristic arrangement, structure and composition of the determined forest types

Globally, tropical mountain forests (TMF) are considered the most diverse ecosystems in the world. In Ecuador, it is estimated that the total number of species is between 18.000 to 22.000 which positions it as one of the most diverse in the world, with a large number of endemic species restricted to develop among middle elevations (900-3000 m) and along the Andes (Valencia 1995). Despite the global importance of TMF, in Ecuador they are also the most threatened. The latest reports indicate that in Ecuador, up until 2005, has lost nearly 51% of its forest area, with a deforestation rate of 1.7%, equivalent to 198 000 ha, all attributed mainly to the change in land use (Mosandl and Gunter 2008).

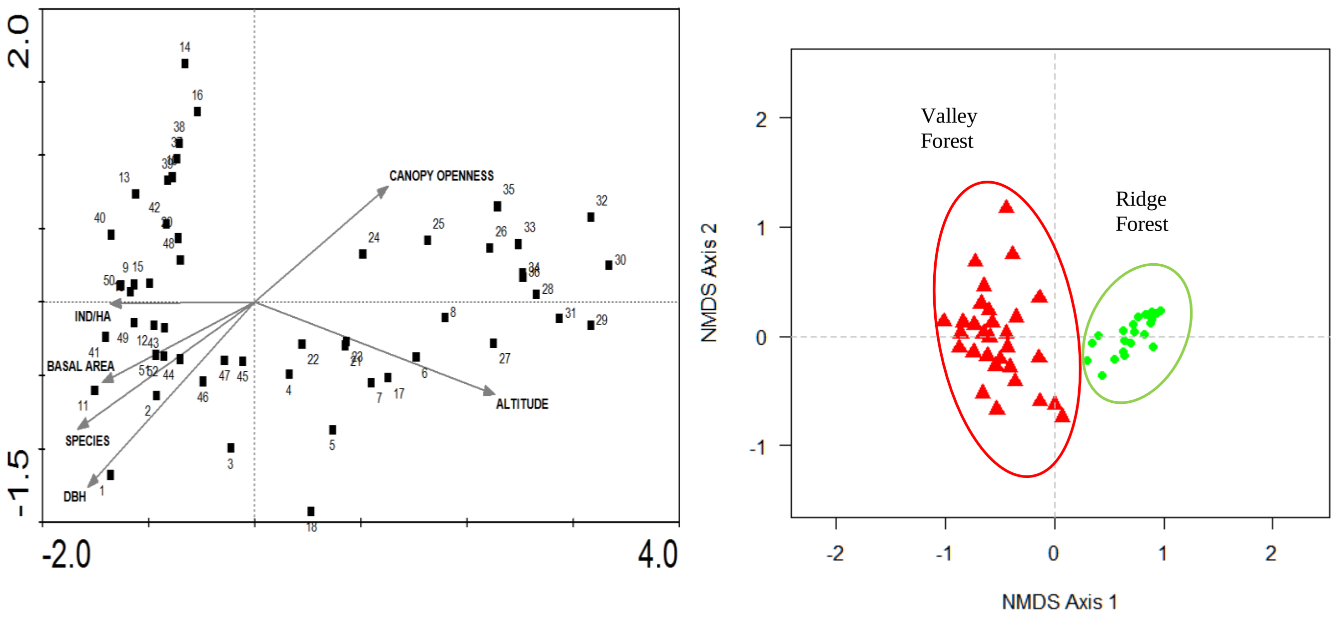
The RBSF Forest is located within one of the hotspots of biodiversity in the world (Myers 2000). The area has an unusually high taxonomic diversity of vascular plants and bryophytes, while another taxonomic group with high diversity are the geometrid moths (in the area > 1000 species) as observed by Brehm *et al.* 2005, as demonstrated by topographic heterogeneity and altitudinal gradient area (Homeier 2008; Bussman 2002) with consequent soil settlement. As well, and according to Richter *et al.* (2003), this high diversity is the result of complex interactions between biotic and abiotic local and regional level.

In the classification of the RBSF forest, Bussman (2005) refers to four differentiated vegetation types. The zoning proposal includes the lower mountain forest corresponding to the *Alzateetalia verticillatae* Order (Bussman 2003). The upper mountain forest is part of the forest zoning Biological Reserve San Francisco corresponding to the *Purdiaeaetalia nutantis* Order (Bussman 2003). Structurally Forest Reserve San Francisco Biologica presents changes mainly from the influence of the altitudinal gradient (Homeier 2009).

3.4.1 Floristic arrangement

Based on plots' floristic similarity among three sampling sites and a strong correlation with various attributes of forest (basal area ha^{-1}, canopy openness, trees ha^{-1} and alpha diversity) with an altitudinal gradient, two types of forest were determined, clearly different in structure and species composition. The spatial distribution of sample plots in altitudinal gradient implies a change in the structure and diversity of each of the plots. Structural groups were defined based on a correlation between altitude and the different attributes of each of the study plots.

After Canonical Correspondence Analysis (CCA), two groups of plots corresponding to the above floristic groups were determined. The biplot (Figure 6) shows the considerable influence of altitude (gradient), basal area and number of individuals per hectare for clustering of the sample plots. In smaller proportion, species diversity (expressed as Shannon index) and canopy openness are also contributing factors that determine the grouping of plots. The analysis of the values of the canonical axes explained 18.1% of variance of data on species and 84% of its relationship with environmental variables (Table 3).


A) CCA

B) NMDS

Figure 6. Biplot showing the ordination of 52 sample plots, blue and red lines show the grouping and the vectors indicate the variables that mostly influence the grouping.

The variables that influence the grouping combine intrinsic characteristics of each forest type and altitudinal gradient. This indicates that the structural and floristic characteristics are the result of the influence of the altitudinal gradient and all environmental variables correlated to this (temperature environmental, precipitation, wind, soil, etc.). The separation allows us to plan the intensity of thinning, since the structure and composition of each forest is a factor that determines the implementation of thinning.

Table 3. CCA model p-values for each variable used.

Variable	**Var.N**	**LambdaA**	***p***	***F*- ratio**
Altitude	4	0.61	**0.001***	7.09
Dbh	7	0.24	**0.001***	3.01
Species	3	0.15	**0.001***	1.76
individuals/ha	2	0.14	**0.030***	1.75
Canopy Openness	8	0.11	**0.044***	1.38
Basal Area	1	0.08	0.279	1.09

The graphs show a strong correlation between altitude and variable characteristics of each plot (Figure 7). The basal area decreases as altitude increases, and at 1900 m a.s.l, basal area can reach 44 m^2 per hectare (includes only the trees > 20 cm dbh). In the plots at 2,100 m a.s.l basal area reaches values of 5 to 14 m^2 per hectare. The same applies to the number of individuals and diversity of the sampled sites. This confirms the trends found in tropical mountain forests, which means that as altitude increases, the diversity of tree species decreases. Canopy openness is higher with the increasing altitude of the plots.

The first group called **"Valley Forest"** from now on throughout the document is characterized by the presence of *Tabebuia chrysantha* (Jacq.) G. Nicholson, *Cedrela montana* Moritz ex Turcz., *Inga acreana* Harms., and *Ficus citrifolia* Mill. These species are involved in the application of selective thinning. There are also other species such as *Cecropia montana* Warb. ex Snethl., *Guarea pterorhachis* Harms and *Heliocarpus americanus* L. that are present in the group and are unique to the group.

The second group called **"Ridge Forest"** from now on throughout the paper, is characterized by the presence of *Podocarpus oleifolius* D. Don ex Lamb., *Hyeronima moritziana* Mull. Arg, *Clusia ducuoides* Engl. which are species selected as PCT. Other species that characterize the group are *Purdiaea nutans* Planch., *Graffenrieda emarginata* (Ruiz & Pav.) and *Alchornea grandifolia* Triana & Mull Arg.

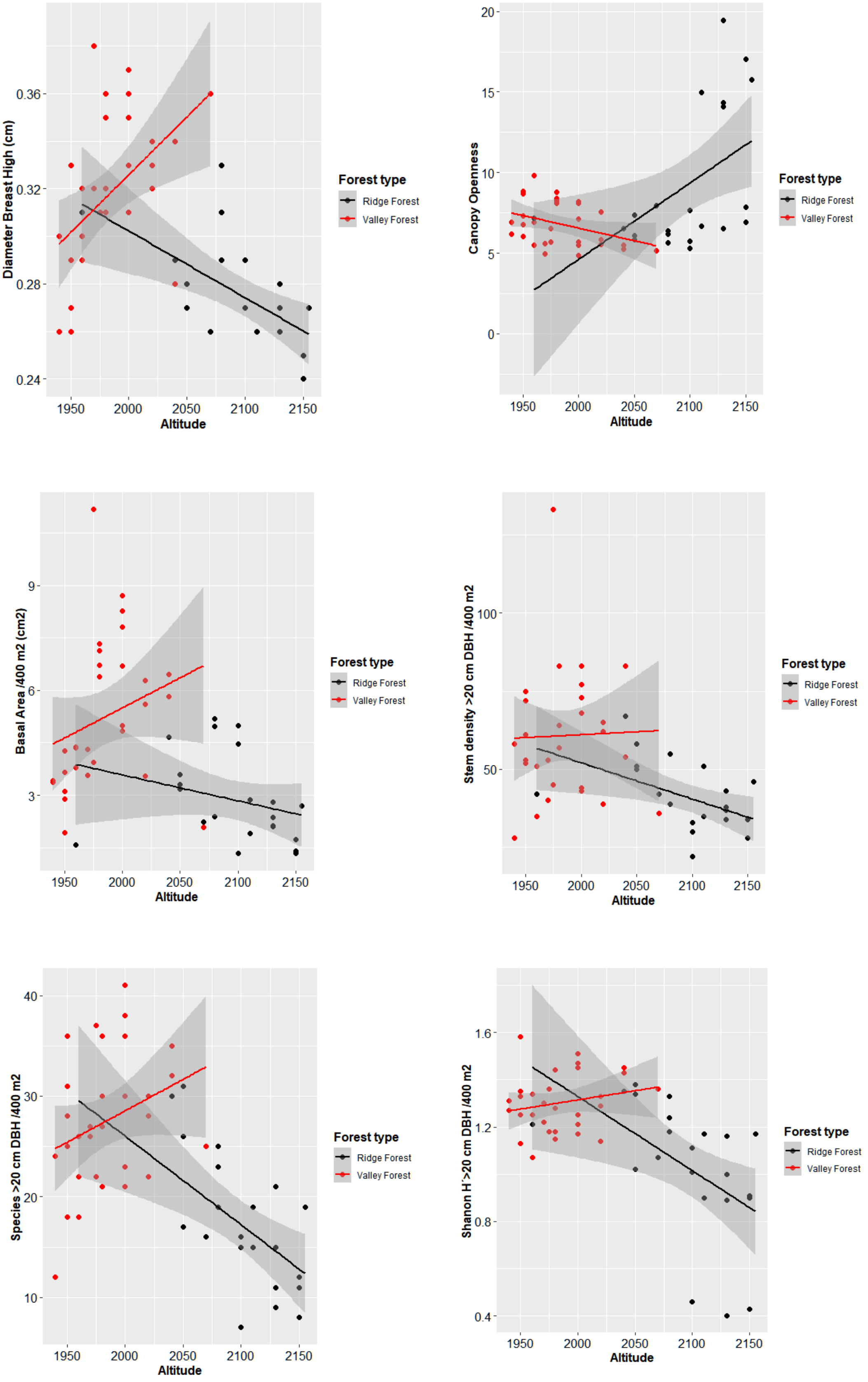


Figure 7. Changes of diversity and structure in altitudinal gradient. Significant correlations (*p* <0.05) are shown in regression line. For all tests n = 52 plots.

3.4.2 Structural parameters of Floristic Groups

As a result of the grouping of the plots in Valley Forest, the diversity of the group is represented by 141 species, which belong to 51 families. The most diverse family is Lauraceae with 17 species and 12.06% of Relative Diversity, followed by Moraceae with 13 species (9.22%), Euphorbiaceae with 10 species (7.09%), Rubiaceae with 10 species (7.09%), Melastomataceae with 9 species (6.38%), Meliaceae with 9 species (6.38%), Cecropiaceae with 4 species (2.84%), Mimosaceae with 4 species (2.84%), Myrtaceae with 4 species (2.84%), and Aquifoliaceae with 3 species (2.13%). Other families (41) have of one to three species with values 2.13- 0.71% of relative diversity.

The species with the highest Relative Density value is *Cecropia montana* Warb. ex Snethl. with 10.52%, followed by *Tabebuia chrysantha* (Jacq.) G. Nicholson (4.82%), *Guarea pterorhachis* Harms (4.46%), *Cecropia gabrielis* Cuatrec (4.15%), *Heliocarpus americanus* L. (3, 63%), *Hyeronima asperifolia* Pax & K. Hoffm. (3.42%), *Sapium glandulosum* (L.) Morong (3.27%), *Miconia quadripora* Wurdack (3.11%), *Inga acreana* Harms. (2.64%), and *Nectandra membranacea* (Sw.) Griseb. (2.54%). The remaining species have values of 2.44-0.05% relative density.

The species with the highest value of Relative Dominance is *Cecropia montana* Warb. ex Snethl. 15.04%, followed by *Tabebuia chrysantha* (Jacq.) G. Nicholson (13.53%), *Guarea pterorhachis* Harms (10.54%), *Hyeronima asperifolia* Pax & K. Hoffm. (7.54%), *Piptocoma discolor* (Kunth) Pruski (6.63%), *Heliocarpus americanus* L. (6.13%), *Cecropia gabrielis* Cuatrec. (5.58%), *Tapirira obtusa* (Benth.) D.J. Mitch. (5.57%), *Miconia quadripora* Wurdack (4.61%), and *Sapium glandulosum* (L.) Morong (4.58%). The remaining species have values of 3.57 - 0.05% Relative Dominance.

In Ridge Forest, diversity is represented by 86 species belonging to 51 families. The most diverse family is Lauraceae with 23 species and 27.7% of Relative Diversity, followed by Euphorbiaceae with 7 species (8.4%), Rubiaceae with 5 species (6%), Melastomataceae and Myrtaceae with 4 species (4.8%), Clusiaceae and Cunnoniaceae with 3 species (3,6%), Aquifoliaceae, Arecaceae, Asteraceae, Meliaceae, Mimosaceae, Moraceae, Myrsinaceae, Sapindaceae, and Sapotaceae with 2 species (2,4%). The remaining families (16) have 1 species and 1.2 % of Relative Diversity.

The species with the highest value of Relative Density is Alchornea grandiflora Mull Arg. (11.95%), followed by *Alzatea verticillata* Ruiz & Pav. (10.67%), *Clusia ducoides* Engl. (10.44%), *Graffenrieda emarginata* (Ruiz & Pav.) Triana (7.77%), *Purdiaea nutans* Planch (5.57%), *Hyeronima moritziana* (Müll. Arg.) Pax & K. Hoffm (3.83 %), *Podocarpus oleifollius* ex D. Don Lamb. (3.71%), *Tapirira obtusa* (Benth.) D.J. Mitch. (3.36%), *Myrcia* sp. (3.25%), *Dictyocaryum lamarckianum* (Mart.) H. Wendl. (2.67%), *Naucleopsis glabra* sprucei ex Pittier (2.2%), *Persea ferruginea* Kunth (1.86%), *Alchornea pearcei* Britton, *Clusia elliptica* Kunth, *Nectandra* sp. (1.74%), *Vismia tomentosa* Ruiz & Pav. (1.62%), *Ocotea* sp.1 and *Persea* sp. (1.51%), *Myrcianthes myrsinoides* (Kunth) Faucet and *Myrsine coriacea* (Sw.) R. Br. Ex Roem. & Schult (1.39%), *Hyeronima asperifolia* Pax & K. Hoffm. (1.28%), *Ladenbergia stenocarpa* (Lamb.) Klotzsch, *Matayba inelegans* Spruce ex Radlk., and *Nectandra membranacea* (Sw.) Griseb. (1.16%). The remaining species (58) have values between 0.93-0.12% of Relative Density.

In Ridge Forest the species with major values of Relative Dominance are *Alzatea verticillata* Ruiz & Pav. (15.03%), followed by *Alchornea grandiflora* Mull Arg. (13.37%), *Clusia ducoides* Engl. (10.06%), *Purdiaea nutans* Planch (5.45%), *Graffenrieda emarginata* (Ruiz & Pav.) Triana (5.37%), *Podocarpus oleifolius* ex D. Don Lamb. (4.23%), *Tapirira obtusa* (Benth.) D.J. Mitch. (3.86%), *Hyeronima moritziana* (Müll. Arg.) Pax & K. Hoffm (3.52%), *Alchornea pearcei* Britton (2.65%), and *Myrcia* sp. (2.35%). The remaining species (76) have values between 2.27 - 0.06% of relative dominance.

The Ridge Forest has a total of 54.3 m^{2} of basal area with an average of 10.3 ± 3.1 m^{2}ha^{-1}, while the Velley Forest has a total of 168.7 m^{2} with an average of 21.8 ± 7.9 m^{2}ha^{-1}, counted from trees of only > 20 cm dbh.

In the Ridge Forest there are a total of 862 individuals > 20 cm dbh and an average of 164, 2 ± 35.3 trees ha^{-1}. In the Valley Forest there are a total of 1933 individuals> 20 cm dbh and an average of 248.8 ± 81.4 trees ha^{-1}.

The Ridge Forets has a total basal area of 3.47 m^{2} in the 5.1-20 cm dbh trees and an average of 11.5 ± 3.9 m^{2} ha^{-1}. The Valley Forest has a total basal area of 3.7 m^{2} in the 5.1-20 cm dbh trees and an average of 8.8 ± 3.8 m^{2} ha^{-1}. In the Ridge Forest there are a total of 443 individuals from 5.1-20 cm dbh, with an average of 1,464 ± 461.8 trees ha^{-1}. In the Valley Forest there are a total of 392 individuals from 5.1-20 cm dbh, with an average of 906.8 ± 383 ind./ha. In the Ridge Forest there are 482.2 ± 5.8 individuals in the second diameter class (5.1-20 cm DBH) while in the Valley Forest there are 449.01 ± 8.24 individuals. In the largest diameter class (> 60 cm dbh) the Ridge Forest has 1.8 ± 5.5 individuals and the Valley Forest 8.8 ± 8.24 individuals. The figures below show the distributions of individuals in all diameter classes in the two Forests types (Figure 8).

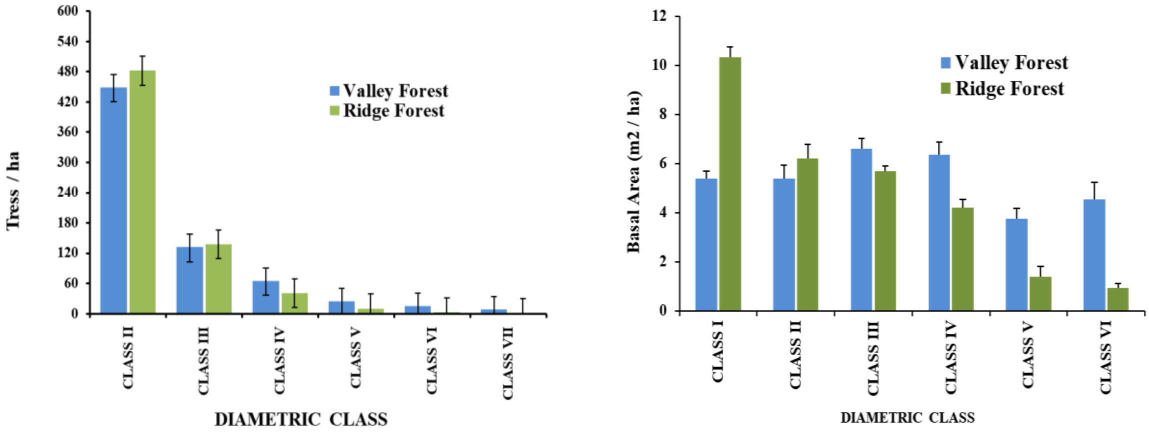


Figure 8. Average basal area ha-1 and trees ha-1 by diameter classes on each forests type.

The structural difference between two floristic groups is low but most evident in the first two diameter classes: In the Ridge Forest there are more individuals per hectare in the first two classes, while in the Valley Forest there are more individuals per hectare in the higher diameter classes.

In Valley Forest there are more trees in larger diameter classes, allowing for harvest with higher intensity. In Ridge Forest, the small number of large trees suggests lower harvest intensity, where the large number of small individuals and the structure of natural regeneration is a typical feature of these forests at this altitude (Bussman 2005).

Regarding the higher number of individuals in lower diameter classes, the Ridge Forest contains higher basal area values in these classes than the other group (Figure 9).

The diameter distributions of trees in RBSF indicate that the trees are distributed in large quantities in smaller diameter classes and the numbers decrease in a negative, exponential way for higher diameter classes. This kind of distribution is representing a plenter structure which is typical for natural forests.

In each group there are unique species that can only be found in their respective groups. In the Valley Forest there are 87 exclusive species representing 47.5% of the total species identified in the study (Table 4).

Table 4. Ecological parameters of Valley Forest exclusive species.

SPECIES	RELATIVE DENSITY	RELATIVE DOMINANCE	IMPORTANCE VALUE INDEX
Saurauia bullosa Wawrd	0.098	0.063	0.381
Saurauia cf. Peruviana	0.049	0.025	0.184
Actinidiaceae	**0.147**	**0.088**	**0.565**
Mauria heterophylla Kunth in H.B.K	1.771	3.383	7.462
Anacardiaceae	**1.771**	**3.383**	**7.462**
Rollinia andicola Mass & Westra	0.295	0.195	1.15
Annonaceae	**0.295**	**0.195**	**1.15**
Ilex amboroica Loes.	0.098	0.104	0.423
Aquifoliaceae	**0.098**	**0.104**	**0.423**
Dendropanax sp.	0.148	0.068	0.545
Schefflera sp.	0.295	0.218	1.172
Araliaceae	**0.443**	**0.286**	**1.718**
Piptocoma discolor (Kunth) Pruski	2.459	3.771	7.989
Critoniopsis sp.	0.639	0.494	1.903
Critoniopsis floribunda (Kunth) H. Rob.	0.049	0.039	0.198
Asteraceae	**3.148**	**4.304**	**10.08**
Tabebuia chrysantha (Jacq.) G.Nicholson	4.722	7.752	15.55
Bignoniaceae	**4.722**	**7.752**	**15.55**
Spirotheca rimbachii Cuatrec.	0.197	0.22	0.747
Bombacaceae	**0.197**	**0.22**	**0.747**
Viburnum pichinchense Benth	0.787	0.385	2.051
Caprifoliaceae	**0.787**	**0.385**	**2.051**
Cecropia angustifolia Trecul	9.887	8.522	21.59
Cecropia andina Cuatrec.	3.935	3.192	8.665
Cecropia montana Warb. ex Snethl.	0.492	0.402	1.223
Pourouma cf. Montana	0.148	0.622	0.989
Cecropiaceae	**14.461**	**12.737**	**32.4**
Tovomita weddeliana Triana & Planch.	0.049	0.023	0.182
Clusiaceae	**0.049**	**0.023**	**0.182**
Weinmannia auriculifera Hieron	0.049	0.04	0.199
Cunnoniaceae	**0.049**	**0.04**	**0.199**
Alchornea glandulosa Poepp. & Endl.	0.344	0.923	1.817
Alchornea latifolia Sw.	0.049	0.036	0.195
Aparisthmium cordatum (A. Juss.) Baill.	0.443	0.538	1.86
Hyeronima oblonga (Tul.) Müll. Arg.	0.098	0.193	0.511
Sapium glandulosum (L.) Morong	3.099	2.589	7.776
Euphorbiaceae	**4.033**	**4.279**	**12.15**
Casearia obovalis Poepp. Ex. Griseb.	0.197	0.155	0.791
Flacourtiaceae	**0.197**	**0.155**	**0.791**
Escallonia paniculata (Ruiz & Pav.) Roem. & Schult.	0.148	0.147	0.404
Glossulariaceae	**0.148**	**0.147**	**0.404**

Discophora sp.	0.049	0.028	0.188
Icacinaceae	**0.049**	**0.028**	**0.188**
Beilschmedia sp.	0.197	0.094	0.731
Lauraceae	**0.197**	**0.094**	**0.731**
Talauma sp.	0.541	0.685	2.215
Magnoliaceae	**0.541**	**0.685**	**2.215**
Byrsonima homeieri W. M. Anderson	0.049	0.024	0.184
Malphigiaceae	**0.049**	**0.024**	**0.184**
Meriania hexamera Sprague	1.279	0.965	3.563
Miconia crecribullata Wurdack	1.181	0.684	3.073
Miconia obscura (Bonpl.) Naudin	0.295	0.172	0.907
Miconia theaezans (Bonpl.) Cogn.	0.148	0.068	0.545
Tibouchina lepidota (Bonpl.) Baill.	0.098	0.048	0.256
Melastomataceae	**3.001**	**1.937**	**8.344**
Guarea pterorhachis Harms	4.23	6.032	12.57
Cedrela montana Moritz ex Turcz.	2.312	1.848	6.248
Guarea kunthiana A. Juss.	1.476	1.787	5.13
Guarea subandina W. Palacios	0.246	0.111	0.686
Meliaceae	**8.264**	**9.778**	**24.63**
Inga acreana Harms.	2.509	1.396	6.432
Inga extra-nodis T.D. Penn.	0.443	0.254	1.576
Mimosaceae	**2.952**	**1.65**	**8.008**
Siparuna aspera (Ruiz & Pav.) A. DC.	0.246	0.134	0.71
Mollinedia sp.	0.049	0.03	0.189
Monimiaceae	**0.295**	**0.164**	**0.898**
Ficus citrifolia Mill.	1.082	1.913	4.314
Ficus pertusa L.f.	0.59	1.663	3.242
Morus insignis Bureau	0.738	0.59	2.537
Pseudolmedia rigida (Kp. K.) Cuatr.	0.197	0.231	0.867
Ficus tonduzii Standl.	0.148	0.175	0.653
Ficus sp.	0.049	0.074	0.233
Helicostylis tovarensis (Klotzch & H. Karst.) C. C. Berg	0.049	0.045	0.204
Ficus maxima Mill.	0.049	0.028	0.187
Ficus trapezicola Dugand	0.049	0.021	0.18
Moraceae	**2.951**	**4.74**	**12.41**
Virola sp.	0.049	0.123	0.282
Myristicaceae	**0.049**	**0.123**	**0.282**
Geissanthus andinus Mez.	0.049	0.033	0.192
Myrsinaceae	**0.049**	**0.033**	**0.192**
Guapira sp.	1.722	1.584	4.295
Nyctaginaceae	**1.722**	**1.584**	**4.295**
Heisteria sp. Nov.	0.197	0.216	0.852
Olacaceae	**0.197**	**0.216**	**0.852**
Piper marequitense C. DC.	0.148	0.072	0.549

Piperaceae	**0.148**	**0.072**	**0.549**
Prumnopitys montana (Humb. & Bonpl. Ex Will.)	0.344	0.264	1.047
Podocarpaceae	**0.344**	**0.264**	**1.047**
Prunus debilis Koehne	0.59	0.423	2.112
Prunus opaca (Benth.) Walp.	0.098	0.111	0.429
Rosaceae	**0.689**	**0.533**	**2.541**
Alibertia sp.	0.394	0.832	1.885
Elaeagia karstenii Standley	0.197	0.135	0.771
Isertia laevis (Triana) B.M. Boom	0.689	0.496	1.624
Palicourea stenosepala	0.148	0.063	0.54
Psychotria sp.	0.197	0.096	0.622
Rubiaceae	**1.625**	**1.622**	**5.442**
Allophylus cf. Floribundus	1.082	0.784	3.295
Cupania sp.	0.049	0.031	0.19
Sapindaceae	**1.131**	**0.815**	**3.485**
Pouteria austin-smithii (Standl.) Cronquist	0.443	0.749	2.181
Sapotaceae	**1.771**	**1.618**	**5.916**
Solanum cf. sycophanta Dunal	0.443	0.42	1.632
Solanaceae	**0.443**	**0.42**	**1.632**
Turpinia occidentalis (Sw.) G. Don	0.935	0.826	3.19
Staphyleaceae	**0.935**	**0.826**	**3.19**
Symplocos cf reflexa A. DC.	0.049	0.03	0.189
Symplocaceae	**0.148**	**0.118**	**0.596**
Theaceae sp.	0.049	0.021	0.18
Theaceae	**0.049**	**0.021**	**0.18**
Daphnopsis sp.	0.049	0.019	0.179
Thymeliaceae	**0.049**	**0.019**	**0.179**
Heliocarpus americanus L.	3.443	3.476	8.898
Tiliaceae	**3.443**	**3.476**	**8.898**
Myriocarpa stipitata Benth.	0.049	0.03	0.189
Urticaceae	**0.049**	**0.03**	**0.189**
Aegiphylla sp.	0.098	0.065	0.383
Verbenaceae	**0.098**	**0.065**	**0.383**
Leonia sp.	0.295	0.221	1.066
Violaceae	**0.295**	**0.221**	**1.066**

Twelve unique species that represent 6.6% of the total species identified were found in the Ridge Forest (Table 5). The remaining 84 species (45.9% of species identified) occur in both floristic groups (Table 6).

Table 5. Ecological parameters of exclusive species into Ridge Forest.

SPECIES	RELATIVE DENSITY	RELATIVE DOMINANCE	IMPORTANCE VALUE INDEX
Dictyocaryum lamarckianum (Mart.) H. Wendl.	3.542	2.153	8.756
Arecaceae	**3.542**	**2.153**	**8.756**
Weinmannia glabra L.f.	0.136	0.133	0.609
Weinmannia sorbifolia Kunth	0.136	0.079	0.556
Cunnoniaceae	**0.272**	**0.212**	**1.165**
Purdiaea nutans Planch	6.403	6.138	16.283
Cyrillaceae	**6.403**	**6.138**	**16.283**
Alchornea triplinervia (Spreng.) Mull. Arg.	0.136	0.093	0.569
Euphorbiaceae	**0.136**	**0.093**	**0.569**
Licaria subsessilis	0.545	0.344	1.91
Ocotea aciphylla (Ness) Mez	0.545	0.326	1.551
Ocotea sp.2	0.272	0.223	0.836
Ocotea sp.4	1.09	0.846	3.637
Persea caerulea (Ruiz y Pav.) Mez	0.136	0.082	0.559
Persea sp.5	0.409	0.503	1.592
Lauraceae	**2.997**	**2.324**	**10.085**
Myrsine andina (Mez) Pipoly	0.136	0.133	0.609
Myrsinaceae	**0.136**	**0.133**	**0.609**

Hyeronima asperifolia Pax & K. Hoffm and ***Nectandra membranacea*** (Sw.) Griseb are either in two determined groups and are considered as generalist species.

Table 6. Ecological parameters of common species in both Valley and Ridge Forests.

	VALLEY FOREST			RIDGE FOREST		
SPECIES	**RELATIVE DENSITY**	**RELATIVE DOMINANCE**	**IMPORTANCE VALUE INDEX**	**RELATIVE DENSITY**	**RELATIVE DOMINANCE**	**IMPORTANCE VALUE INDEX**
Tapirira guianensis	0.05	0.05	0.21	3.68	3.98	11.4
Anacardiaceae	**1.82**	**3.43**	**7.67**	**3.68**	**3.98**	**11.4**
Ilex hippocrateoides	0.15	0.11	0.59	0.27	0.22	1.17
Aquifoliaceae	**0.25**	**0.22**	**1.01**	**0.27**	**0.22**	**1.17**
Hedyosmum guodotianum	0.2	0.16	0.8	0.14	0.07	0.54
Chlorantaceae	**0.2**	**0.16**	**0.8**	**0.14**	**0.07**	**0.54**
Clethra revoluta	0.64	0.52	2.26	0.95	1.45	4.1
Clethraceae	**0.64**	**0.52**	**2.26**	**0.95**	**1.45**	**4.1**
Clusia ducuoides	0.89	0.79	2.34	12.67	12.54	31.33
Vismia tomentosa	0.34	0.18	0.85	1.23	1.07	4.34
Clusiaceae	**1.28**	**0.99**	**3.37**	**13.9**	**13.6**	**35.66**
Cyathea caracasana	1.28	0.65	3.13	0.27	0.15	0.76
Cyatheaceae	**1.28**	**0.65**	**3.13**	**0.27**	**0.15**	**0.76**
Alchornea grandiflora	0.98	0.84	2.6	15.4	17.48	39.34
Hyeronima asperifolia	3.39	4.32	10.35	1.09	0.99	4.12
Hyeronima duquei	0.25	0.11	0.91	0.41	0.34	1.77
Hyeronima moritziana	0.94	0.59	2.4	3.82	3.59	11.49
Euphorbiaceae	**5.56**	**5.86**	**16.26**	**20.71**	**22.4**	**56.72**
Aniba muca	0.54	0.42	1.73	0.14	0.24	0.71
Aniba sp.	0.25	0.2	0.89	0.27	0.18	1.13
Endlicheria oreocola	1.33	1.45	4.98	0.27	0.23	1.18
Endlicheria sericea	1.08	0.66	3.28	0.27	0.39	1.35
Lauraceae sp.	1.08	1.1	3.72	0.95	0.78	3.43

Nectandra lineatifolia	2.21	1.9	6.53	2.18	2.28	7.18
Nectandra membranacea	2.46	1.9	6.23	1.09	0.71	3.84
Nectandra sp.3	0.05	0.02	0.18	0.14	0.14	0.61
Nectandra subullata	0.44	0.53	1.74	0.68	0.91	2.61
Ocotea benthamiana	0.05	0.02	0.18	0.27	0.37	1.32
Ocotea sp.1	0.89	0.79	2.77	0.27	0.14	0.75
Persea ferruginea	0.39	0.31	1.36	2.59	2.56	8.89
Persea sp.4	0.69	0.7	2.16	0.41	0.58	1.67
Persea subcordata	0.1	0.07	0.39	0.27	0.13	1.09
Lauraceae	**11.56**	**10.06**	**36.13**	**9.81**	**9.62**	**35.75**
Eschweilera sessilis	0.39	0.42	1.58	0.14	0.07	0.55
Lecythidaceae	**0.39**	**0.42**	**1.58**	**0.14**	**0.07**	**0.55**
Alzatea verticillata	0.89	1.21	2.86	10.9	16.14	32.82
Lythraceae	**0.89**	**1.21**	**2.86**	**10.9**	**16.14**	**32.82**
Graffenrieda emarginata	1.33	0.8	3	7.63	5.29	18.36
Meriania sp. nov.	3.2	2.8	8.42	0.27	0.21	1.16
Miconia punctata	0.1	0.07	0.39	0.14	0.11	0.58
Miconia tinifolia	0.05	0.02	0.18	0.14	0.07	0.54
Melastomataceae	**4.67**	**3.69**	**11.99**	**8.17**	**5.67**	**20.65**
Ruagea glabra	2.21	2.42	6.72	0.14	0.13	0.6
Meliaceae	**2.21**	**2.42**	**6.72**	**0.14**	**0.13**	**0.6**
Inga striata	1.53	1.1	4.16	0.41	0.33	1.76
Abarema killipii	0.05	0.03	0.19	0.55	0.34	2.24
Mimosaceae	**1.57**	**1.12**	**4.35**	**0.95**	**0.66**	**4**
Naucleopsis sp.nov	1.13	0.84	3.07	2.32	2.17	6.86
Ficus cuatrecasana	0.39	1.04	2.2	0.14	0.23	0.71
Moraceae	**1.53**	**1.88**	**5.27**	**2.45**	**2.4**	**7.57**
Myrsine coriacea	0.59	0.47	1.93	1.5	1.84	5.72
Myrsinaceae	**0.59**	**0.47**	**1.93**	**1.5**	**1.84**	**5.72**

Calyptranthes cf purchela	0.1	0.05	0.37	1.36	0.99	5.07
Calyptranthes sp.	0.15	0.2	0.68	0.14	0.09	0.57
Eugenia sp.	0.64	0.55	2.07	0.27	0.2	0.81
Myrcia sp.	0.44	0.32	1.64	3.41	2.45	10.61
Myrtaceae	**1.33**	**1.12**	**4.75**	**5.18**	**3.73**	**17.07**
Podocarpus oleifollius	0.74	0.73	2.02	3	3.32	10.73
Podocarpaceae	**0.74**	**0.73**	**2.02**	**3**	**3.32**	**10.73**
Roupala montana	0.2	0.19	0.83	0.14	0.15	0.62
Proteaceae	**0.2**	**0.19**	**0.83**	**0.14**	**0.15**	**0.62**
Elaeagia utilis	1.87	2.12	6.07	0.41	0.3	1.73
Faramea coerulescens	0.05	0.02	0.18	0.14	0.07	0.54
Ladenbergia stenocarpa	0.15	0.08	0.56	1.09	0.69	3.48
Rubiacea sp.	0.05	0.02	0.18	0.14	0.07	0.55
Stilpnophyllum oellgaardii	0.05	0.02	0.18	0.14	0.28	0.76
Rubiaceae	**2.16**	**2.26**	**7.17**	**1.36**	**1.05**	**4.79**
Meliosma sp.	0.54	0.55	1.97	0.68	0.85	2.9
Sabiaceae	**0.54**	**0.55**	**1.97**	**0.68**	**0.85**	**2.9**
Matayba inelegans	0.34	0.27	1.27	0.95	0.63	3.62
Sapindaceae	**0.34**	**0.27**	**1.27**	**0.95**	**0.63**	**3.62**
Micropholis guyanensis	1.23	0.82	3.37	0.27	0.24	0.85
Chrysophyllum lanatum	0.1	0.05	0.37	0.14	0.08	0.55
Sapotaceae	**1.33**	**0.87**	**3.74**	**0.41**	**0.31**	**1.4**
Symplocos coriaceae	0.1	0.09	0.41	0.14	0.07	0.55
Symplocaceae	**0.15**	**0.12**	**0.6**	**0.14**	**0.07**	**0.55**

3.5 Discussion

The forest-ecological experiment carried out shows that the implementation of selective thinning in order to increase the diameter of some timber individuals, and potentially timber species numbers, is possible in the tropical mountain forest where climatic conditions are adverse and great biodiversity within the forest creates unfriendly circumstances for these types of activities.

Despite the fact that forest exploitation in the area has been carried out for years, the harvesting process is nontechnical and unmonitored with respect to the consequences of exploitation. The lack of statistics on the mechanical-physical impact caused by harvesting large trees on the remaining forest, and the effect on the remaining stand, opens up very large possibilities that with a research protocol implemented based on this research, the harvesting process can be technified to improve the performance of species.

Forest management as a conservation tool focuses on the long-term maintenance of forest yield rates, and with the improvement in yield, the product of selective thinning can prevent deforestation, according to Tapia et al. (2015) is an area that during the last decade has suffered one of the highest rates of deforestation in Ecuador.

3.5.1 Diversity and floristic groups

Globally, Tropical Mountain Forests (TMF) are considered the most diverse ecosystems in the world. The last map representing the global diversity of vascular plant species (Kier et al. 2005), emphasizes the areas of tropical mountain forest as the most important hot spots of the world.

In Ecuador, it is estimated that the total number of species is between 18.000 and 22.000, which positions it as one of the most diverse areas in the world. There is a large number of endemic species restricted to develop among middle elevations (900-3000 m) along the Andes (Valencia et al. 1995). Despite the global importance of TMF in Ecuador, they are also the most threatened. The latest reports indicate that up to 2005, 51% of the forest area was being lost - with a deforestation rate of 1.7%, which is equivalent to 198 000 ha. This was mainly attributed to the change in land use (Mosandl et al. 2008).

The RBSF Forest is within one of the hotspots of biodiversity in the world (Myers et al. 2000). The area has an unusually high taxonomic diversity of vascular plants (Homeier 2008) and bryophytes (Gradstein et al. 2008). This high diversity is the result of complex interactions between biotic and abiotic, local and regional level factors.

The TMF on the eastern slope of the Cordillera, south of the Andes in RBSF according to Bussman (2005), is classified into two types: montane forests (up to 2100 m) and high montane forests (up to 2750 m). In addition, four differentiated vegetation types are identified. The zoning proposal includes the lower mountain forest corresponding to Alzateetalia verticillatae Order (Bussman 2003), where the “Valley Forest” was studied.

The high mountain forest is located in the upper part of the RBSF and can be homologated in the Purdiaeaetalia nutantis Order determined by Bussman (2003), which includes the "Ridge Forest" as determined in this study.

For both floristic groups, the microclimatic and topographic conditions of the area cause the species to find suitable sites and share habitat preferences, the analysis of Klüber et al. (2016) explains how several species included in the floristic groups have habitat and topographic preferences, an argument that also reinforces the grouping of the species present in the forest of the RBSF.

Structurally the RBSF forest presents changes mainly due to the influence of the altitudinal gradient (Homeier et al. 2010). The two aforementioned floristic groups are structurally different, which also involves changes in forest management perspectives.

In the plots at lower elevations, the height of the trees reaches 12 to 16 meters, while in the plots at higher elevations, the tree height ranges from 6 to 8 meters. The total basal area of the plots decreases with altitude, as seen in lower plots with an average 21.6 m^2ha^{-1} (± 0.24); in the plots at higher altitudes the average basal area reaches 10.02m^2ha^{-1} (± 0.18).

One of the objectives of this work is to show that in the tropical mountain forest, which is one of the most diverse and threatened in the country and in the world, some woody species respond favorably to forest planned intervention (liberation) with an emphasis on traditional uses of the forest and the damage caused by intervention being insignificant.

The process of thinning implemented here does not imply the use of wood in an immediate way, but a treatment to increase the yield of commercial timber; it is an opportunity to verify that the process can be replicated at the farm level and at the level of community forests. This process generates a big question; how to protect intervening? The starting point is clearly thorough expanding knowledge of the forest, including variables that are rarely taken into account in forest planning and processes that result in highly invasive intervention and do not guarantee the conservation of the ecosystem as such. It is clear that conservation involves diversity at all levels, but also includes ecosystems or ecological processes at various levels (Noss 1990, Galindo 2000).

Natural forests ensure diversity and ecosystem processes, but the "managed landscapes" are those with a high level of social responsibility and a solid ecological basis implemented in the process of management and harvesting, maintaining where possible ecological dynamics, and at the same time promoting practices that restore the structure, composition and function of the landscape and the forest (Opdam et al. 1995; Rice and Ward 1996).

3.5.2 Changes in the floristic composition.

To assess changes in the structure and species composition, we evaluated the impact immediately after applying selective thinning. The Simpson index was calculated, which is a measure of dominance. When the index value increases, diversity decreases, i.e. the index overestimates the most abundant species to the detriment of total species richness.

Benitez et al. (2004) assessed changes in species composition, calculating the index of Margalef and Shanon-Wiever, preharvest (1994) and post-harvest (1997) for all trees over 10 cm dbh, comparing the application of traditional methods with the application of planned operation methods. They found that with increasing the magnitude of the damage to the remaining forest (traditional method), species diversity decreases.

Hall et al. (2003) evaluated changes in the species composition and structure of a logged forest with selective logging for six months and eighteen years in an area of Central Africa. They also took as a reference a non-intervened area of the same forest type. As a result, significant differences (p <0.05) of the low number of small trees (2.5 to 10 cm dbh) in the forest harvested 18 years prior also demonstrated significant differences between the largest number of species in the ecological guild "shade tolerant"included in the undisturbed forest, against the low number of individuals in the forest harvested 18 years previously.

Gutierrez-Granados et al. (2011) found in harvested sites a reduction of species of smaller diameter (10 cm dbh) compared to unlogged sites. Likewise Berry et al. (2008) found significant differences at the level of total species richness in trees up to 10 cm dbh among harvested sites versus sites without intervention, while diversity was not affected significantly in medium and large trees. However, in our study, no significant differences were found in the floristic composition of natural regeneration. There is a significant difference between the regeneration in the gaps and the regeneration within the forest, as in the works mentioned above, where the presence of fast growing or light tolerant species such as *Heliocarpus americanus* and some species of palms of the genus Geonoma, make the difference with natural regeneration species within the forest, which are tolerant to shade (Hall et al. 2003).

In Ecuador there is no scientific evidence to show the effect of selective logging or thinning on forest floristic richness. In South America, Ochoa (1998) shows the impact of harvesting activities on community trees. In other continents where tropical rainforests exist (Asia and Africa), where the implementation of silvicultural systems of use and management have over 100 years of history, there is evidence of the degradation of areas subject to logging and traditional land uses. More scientific evidence is needed to promote selective thinning as a sustainable and biodiversity-conserv system. (Mo et al. 2011).

Whereas the total diversity of trees is vital for the abundance of total forest diversity, this diversity varies significantly due to changes in habitat and the level of intervention (Huang et al. 2003), showing that in the tropical mountain forest, with the experiment implemented in the first 36 months of evaluation, no significant differences between the total species richness of trees was found, before and after selective thinning. According to Putz et al. (2012), assessing the impact of forestry practices (in this particular case timber harvest) is more complicated than for example assessing carbon storage and forest productivity based on the growth of individuals.

One element that is considered relevant before implementing selective thinning is to analyze the floristic composition of the original stand and not to affect species with fewer individuals. This is accomplished with a careful analysis of the trees to be released and the population status of the competitors. If individuals of species that have few representatives are cut, the total diversity decreases, but if individuals of species with many representatives are removed, the total diversity is maintained or increased depending on the number of species and the number of individuals per species. Our data show that in any thinning intensity, there are significant differences between the initial state and the final state of the forest (in the stratum of trees> 20 cm dbh).

According to Benitez et al. (2004), comparing two logging methods indicates that in applying traditional methods, the diversity indices tend to decrease, while applying the planned exploitation techniques indicated, diversity tends to increase or at least is maintained. Although the experiment conducted here is not considered logging, planned thinning would address the possibility for cutting the individuals of the species with the largest number of representatives. Although the spatial distribution of trees in the forest does not always match the needs of the producer, which is a very heterogeneous pattern in which the individuals of the species are identified as competitors, they will not always include in the species with more representatives. Removing individuals from the species with only one representative does not mean that we remove the stand, but probably within the forest there exist other individuals who are part of the total diversity of the forest.

In all selective thinning intensities in the "Valley Forest," competitors were eliminated belonging to 44 species (33% of certain species) and two unique individuals were extracted (1.7% of certain species): *Virola* sp. (Myristicaceae) and *Chrysophyllum lanatum* (Sapotaceae).

Within "Ridge Forest" in all thinning intensities individuals of 13 species were extracted (19% of all species determined for the group) and two unique individuals of *Alchornea triplinervia* (Euphorbiaceae) and *Persea subcordata* (Lauraceae) were extracted as well. In this floristic group individuals of 2 species were removed (2.9% of total identified) who had an individual tree.

Although most studies refer to the impact of harvesting but not to thinning, certain similarities can be considered. Selective, low impact harvesting affects forest composition (Jackson et al. 2002; Baraloto et al. 2012; Pereira et al. 2002). However, the intervention is considered one of the factors that regulates not only the floristic composition of the forest, but also regulates the structure, thus allowing the light produced by falling trees to allow for the entry of new individuls. The "lost" species percentage (loss of stand sampled since surely species are present in the forest with other individuals outside the boundaries of the plots studied) are relatively small compared with the losses caused by natural events such as hurricanes (unlikely in mountainous areas), landslides (very common in the area) or forest fires (anthropogenic or natural).

Although total tree diversity is vital for the presence of total forest diversity, this diversity varies significantly due to changes in habitat and the level of intervention. Huang et al. (2003) show that in tropical mountain forests with experiments implemented in the first 36 months of evaluation, no significant differences were observed between the total richness of tree species, that is, before and after selective thinning. According to Putz et al. (2012), assessing the impact of forestry on forest diversity (especially by timber extraction) is more complicated than, for example, assessing carbon storage and forest productivity as a function of individual growth.

4. Early growth response of nine timber species to Release in a Tropical Mountain Forest of Southern Ecuador (Publication I, Cabrera et al. 2019).

4.1. Methods

4.1.1 Data Collection

After the installation of the plots as mentioned in section 3.2.1 of this document, a total of 448 PCT individuals were identified, of which 197 individuals were selected for release (section 3.2.2) and 251 were left in their natural environment as a reference (control trees) to compare the effect of the silvicultural treatment to natural conditions. In Q5, eight of the nine PCT species were present, with exception of *Clusia ducuoides*, whereas in Q3, *Ficus citrifolia* and *Inga acreana* were absent and only one individual of *Cedrela montana* was found. The plots in Q2 included all of the selected PCT species, with several individuals (Table 7).

Table 7. Released potential crop trees (PCTs) and reference trees (R) that were monitored in the RBSF.

Species	Q5 PCT	Q5 R	Q3 PCT	Q3 R	Q2 R	Total PCT´s	Total R
Cedrela montana	20	14	0	1	7	20	22
Podocarpus oleifolius	1	0	12	7	10	13	17
Tabebuia chrysantha	46	14	0	2	25	46	41
Ficus citrifolia	4	3	0	0	13	4	16
Nectandra membranacea	9	8	5	1	27	14	36
Hyeronima asperifolia	27	10	1	1	15	28	26
Hyeronima moritziana	3	0	16	10	11	19	21

Clusia ducuoides	0	0	37	37	14	37	51
Inga acreana	16	5	0	0	16	16	21
					Total	**197**	**251**
						448	

By means of their initial DBH, the individual trees were grouped into four diameter classes (class I = 20.1–30 cm DBH, class II = 30.1–40 cm DBH, class III = 40.1–50 cm DBH, and class IV ≥ 50.1 cm DBH). Afterwards, the treatment was defined (release or control) and the monitoring periods (monthly) were established, taking into consideration the general climatic conditions (Table 8).

Table 8. Variables analyzed and the factors included in the applied GLMM model.

Analyzed Variables	Description	Factor
Diameter Class	Diameter class of the released and reference trees	Class I: 20.1–30 cm DBH Class II: 30.1–40 cm DBH Class III: 40.1–50 cm DBH Class IV: >50 cm DBH
Treatments	Removed competitors	Released
	Non-removed competitors	Reference
Period	Time between initial measurement drive by climatic seasons	Period I: 12 months Period II: 24 months Period III: 36 months
Precipitation	Accumulated monthly precipitation	mm/month
Temperature	Monthly average temperature	°C/month

To determine the competitors of the selected PCT trees, all plots were visited and the tree form, crown diameter and social position within the forest stand, as well as stem quality, were analyzed and evaluated. All detected competitors were labeled with plastic tape and removed during a campaign between April and May of 2004. The release included mainly competitor trees, which were cut using the method of directional falling to avoid additional damage to the ecosystem (Peña-Claros et al. 2008). Furthermore, no herbicides were applied to the stumps to guarantee the development of species collectivity in their natural environment without alterations or contaminations.

The determined trees as competitors that were cut and the percentage that these represent with respect to the total number of individuals of the species determined in the forest inventory are shown below (Table 9).

Table 9. Removed trees by species and percentage with respect to the total of individuals inventoried in primary montane forest of RBSF.

Montane Forest RBSF			
Species	**Cut**	**Total**	**%**
Chrysophyllum lanatum	1	1	100
Virola sp.	1	1	100
Alchornea triplinervia	1	1	100

Persea subcordata	1	1	100
Prunus huantensis	3	4	75.0
Symplocos coriaceae	1	2	50.0
Vismia tomentosa	1	2	50.0
Cinnamomum sp.	1	2	50.0
Guarea grandifolia	2	5	40.0
Persea sp.1	2	5	40.0
Aparisthmium cordatum	1	3	33.3
Clethra revoluta	1	3	33.3
Miconia obscura	1	3	33.3
Viburnum pichinchense	2	6	33.3
Aniba hostmannian	1	4	25.0
Psychotria sp.	1	4	25.0
Vismia tomentosa	3	12	25.0
Talauma sp.	2	9	22.2
Myrsine coriacea	1	5	20.0
Schefflera sp.	1	5	20.0
Elaeagia utili	5	28	17.9
Piptocoma discolor	5	28	17.9
Turpinia occidentali	3	17	17.6
Cyathea caracasana	1	6	16.7
Genipa americana	1	6	16.7
Naucleopsis glabra	1	6	16.7
Solanum oblongifolium	1	6	16.7
Hyeronima duquei	1	6	16.7
Inga striata	4	26	15.4
Persea ferruginea	2	13	15.4
Tapirira obtusa	1	7	14.3
Miconia quadripora	5	38	13.2
Cecropia angustifolia	19	146	13.0
Morus insignis	1	8	12.5
Nectandra lineatifolia	3	16	18.8
Heliocarpus americanus	6	52	11.5
Eschweleira sp.	1	9	11.1
Matayba inelegans	2	10	20.0
Sapium glandulosum	5	46	10.9
Trichilia maynasiana	2	21	9.5
Nectandra reticulata	2	11	18.2
Naucleopsis glabra	1	12	8.3
Myrcia sp.	2	28	7.1
Guarea pterorhachis	3	44	6.8
Nectandra lineatifolia	1	16	6.3
Tapirira obtusa	2	16	12.5
Alchornea grandiflora	7	112	6.3
Cecropia andina	4	67	6.0
Hyeronima asperifolia	3	55	5.5

Nectandra membranacea	1	22	4.5
Trichilia maynasiana	1	22	4.5
Guapira sp.	2	27	7.4
Inga acreana	3	33	9.1
Alzatea verticillata	3	67	4.5
Cedrela sp.	1	38	2.6
Graffenrieda emarginata	3	46	6.5
Tabebuia chrysantha	1	67	1.5
Clusia ducoides	1	95	1.1
	138	**1352**	**23.2**

4.1.2 Data Analyses

The diameter increment of all trees was calculated using the initial DBH measurement made in the first inventory. Control trees and PCT's (see paragraph 3.2.2.1) were installed dendrometers, which were monitored for 36 months once every month. This process was planned to make a comparison between monitoring periods (annual) and between the intensity of thinning.

Diameter increment of PCT´s and remnant trees was calculated with the equation 8:

$$D_i = \frac{D_1 - D_0}{t} \qquad \text{Equation 8}$$

D_i= Diameter increase (cm/year)
D_o= dbh (cm) at beginning (first inventory)
D_1= dbh (cm) at the end (final)
t= time (years) between measurements

The diameter increment of the remaining trees was calculated based on three measurements, the first at starting the experiment (D_0) and the two subsequent measurements (12 months and 24 months after). For PCT's the first measurement is also the first measurement of the first inventory and monthly monitoring dendrometers gives the monthly increase applying featured above-mentioned equation.

To test whether the categorical and continuous variables monitored (intensity of selective thinning, diameter class tree, monitoring period, precipitation and temperature) influence the variability of diameter increment of trees of nine timber species and the remaining forest, the lmer function was used (linear mixed model) using the LMER4 statistical package of R 3.2.0 (R Development Core Team 2015). To adjust the model, the function Anova of CAR package was used. We used mixed models that combine explanatory categorical variables (variables without numerical value, in this case, the diameter classes, treatment) and give an effect of "random" type, in this particular case the repeated measurements throughout time (period). The response variable (in this case the diameter increment) are compared with data obtained temporarily measuring the same tree, what we commonly call pseudoreplication, in the mixed models at least one explanatory categorical variable is incorporated where they add the response data (Seaone 2014).

4.2 Results

The diameter increase evaluation of released trees indicates that species respond differently to treatment compared to reference trees. The selected timber species responded differently to release respective to their reference trees (Table 11). Therefore, the species analyzed were separated into three groups (positive response, negative response and no response to release).

4.2.1 Positive response

The species that responded positively to release were *Inga acreana* and *Hyeronima asperifolia*, which had a greater diameter increment than their reference trees.

Inga acreana showed a mean growth of 1.13 cm ± 0.72 (standard deviation) over the whole study period, whereas the control trees showed an increment of only 0.56 cm ± 0.47. The diameter growth of the released trees was not continuous, in which the lowest increment was measured during the first year (1.01 cm ± 0.81), which afterwards increased to 1.16 cm ± 0.61 (second year) and finally to 1.22 cm ± 0.78 (third year). For the control trees, a more constant growth was observed, but also with the lowest increment during the first year. This may be due to the initiation time of the investigation (June, austral winter), when precipitation generally peaks but the lowest temperatures are typically observed. Furthermore, temperatures were lowest in June 2004, directly after the release, compared to the following years, which may have influenced the diameter growth of all species. In general, the highest DBH increments for all species were observed at the beginning of the year (austral summer), when temperatures are highest and enough water is available (Figures 9).

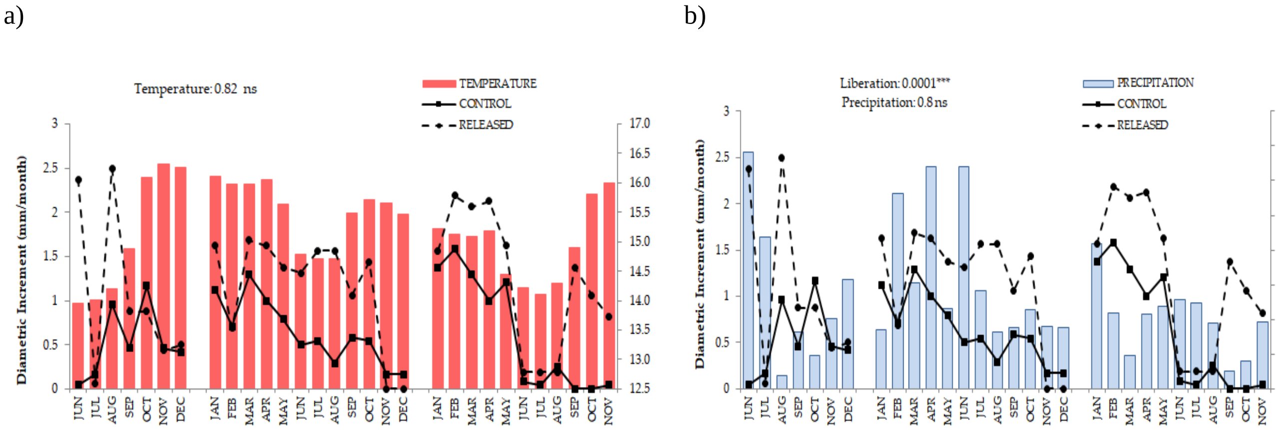


Figure 9. Diameter increase (ordinate axis in mm month^{-1}) by period (on the abscissa axe shown three periods) of *Inga acreana*, respective to **a.)** mean monthly temperature (secondary ordinate axe in °C) and **b.)** monthly accumulated precipitation (secondary ordinate axe in mm month^{-1}).

The released trees of *Hyeronima asperifolia* showed a mean growth of 0.63 cm ± 0.64 over the whole study period, whereas the control trees only had an increase of 0.35 cm ± 0.36 (Table 11). Similar to *Inga acreana*, the diameter growth of *Hyeronima asperifolia* increased during the observation period, which resulted in the highest increment of growth during the third year (0.76 cm ± 0.53). However, the diameter class of the released trees was also important, because smaller trees showed higher DBH increments (Table 11). For *Inga acreana*, increments were exclusively observed in class I (diameter: 20.1 cm - 30 cm), whereas *Hyeronima asperifolia* showed increments in all classes, but showed higher values for classes I–III. As shown in Table 11, the enhanced diameter growth of both species was principally caused by the treatment (release), but also the temperature and precipitation (Figure 10). The diameter class had significant influence for *Hyeronima asperifolia*.

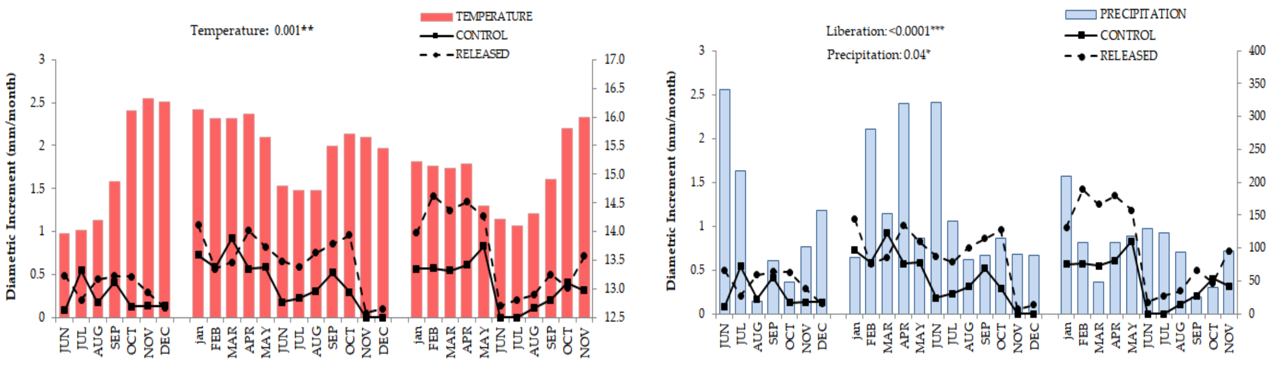

a) b)

Figure 10. Diameter increase (ordinate axis in mm month^{-1}) by period (on the abscissa axe shown three periods) of *Hyeronima asperifolia*, respective to **a.)** mean monthly temperature (secondary ordinate axe in °C) and **b.)** monthly accumulated precipitation (secondary ordinate axe in mm month^{-1}).

Despite being a perhumid area, there are seasons when the humidity decreases, this being one of the processes in many species: phenological processes such as flowering and fruiting. In the analyses of growth, we include temperature, it turned out, the temperature has a more immediate influence than precipitation, as rainwater is usually stored for relatively long periods in soil and is consumed by the plants according to their need while the temperature is fluctuating and directly influences the plants, in this specific case, the increase in diameter of the released trees coincides with increasing temperature.

In summary, both species showed higher diameter growth compared to their control trees during the entire study period, which illustrates the expected effects of release, namely improvements in light and nutrient availability, leading to faster DBH growth.

4.2.2 Negative response

The species with negative responses to release were *Cedrela montana*, *Tabebuia chrysantha*, *Podocarpus oleifolius* and *Nectandra membranacea*. All these species showed significantly lower diameter growth respective to their control trees, especially during the second and third year after release (Table 11).

The species with the most significant differences in the group was *Cedrela montana* (1.16 cm ± 1.21 vs. 0.87 cm ± 1.24), the diameter increment of *Cedrela montana* in released trees and the reference trees presents a similar pattern. Both in the second period, a bigger increase is observed in both diameter classes, but it is not significantly different compared to other periods or when comparing treatments.

In *Cedrela montana* defoliation process is associated with the end of the wettest time and the start of the coldest season lasts approximately 3 months (although the fluctuation is just 1.5 ° C in the season), The growth trend, regardless of whether they were released or not, declines significantly. There is a marked trend throughout the year and the release of individuals apparently affected more this growth process. In the first monitoring year, ther was a negative responds to release: the same pattern is observed over the first three years and as we said above, if the growth of the species is associated with the seasonality of precipitation and temperature, thinning will not affect positively the species that have destrinctive seasonality in their physiological processes because individuals are beginning their foliacion stage, they turn all their energy to this process, inhibiting in a certain way the growth, regardless of whether or not they are released from their competitors (Figure 11).

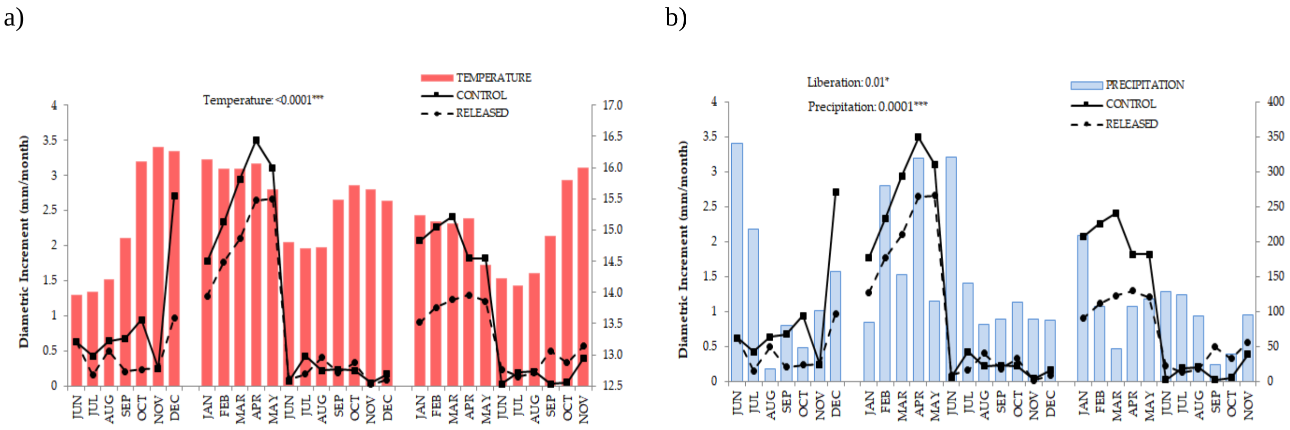
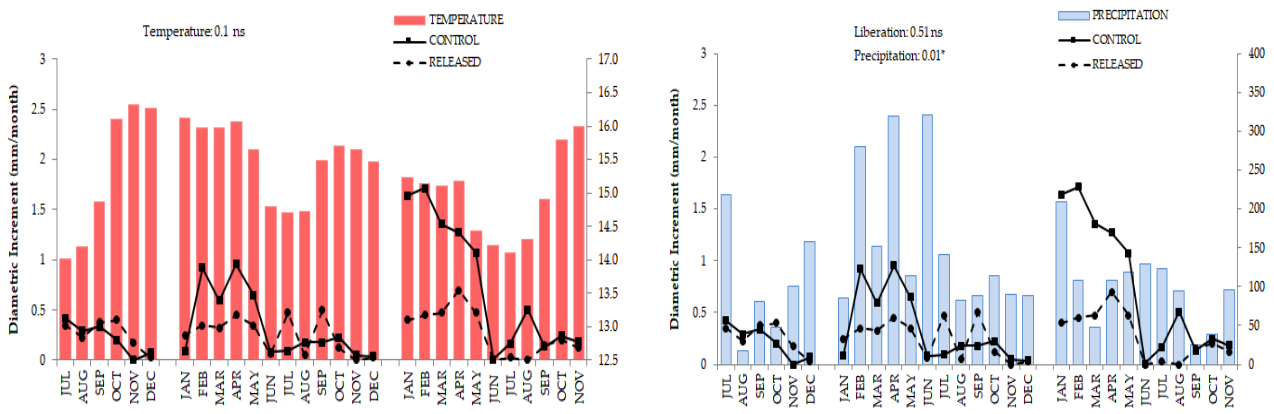


Figure 11. Diameter increase (ordinate axis in mm month^{-1}) by period (on the abscissa axe shown three periods) of *Cedrela montana*, respective to **a.)** mean monthly temperature (secondary ordinate axe in °C) and **b.)** monthly accumulated precipitation (secondary ordinate axe in mm month^{-1}).

In *Nectandra membranacea* increment is higher in control trees than in released trees (0.44 cm ± 0.62 vs. 0.26 cm ± 0.32). This is because light and nutrient availability are not the main factors for their DBH increment, what is more important are their growth habits and phenological traits, besides temperature and precipitation. However, like the two species which responded positively to release, the highest DBH increments were observed for diameter classes I–III.

Relased trees of *Nectandra membranacea* show a higher diameter increment in relation to reference trees. Released trees of diameter class I show more diameter increment than individuals of class II. In reference trees in year one and two, the trees of diameter class II show more diameter increment. Liberation influences the diameter increment but the difference is not significant.

In *Nectandra membranacea*, released trees grow less than the control trees in the first period, immediately after releasing the trees, there is a certain rise in trees released. In the following monitored periods growth more than the released trees. Precipitation is a factor that significantly influences the dynamics of growth of the trees of this species, unlike the temperature that has no significance in the model. In the initial period from January to June is where the trees grow in both treatments. In the second semester, growth is lower (Figure 12).



a)

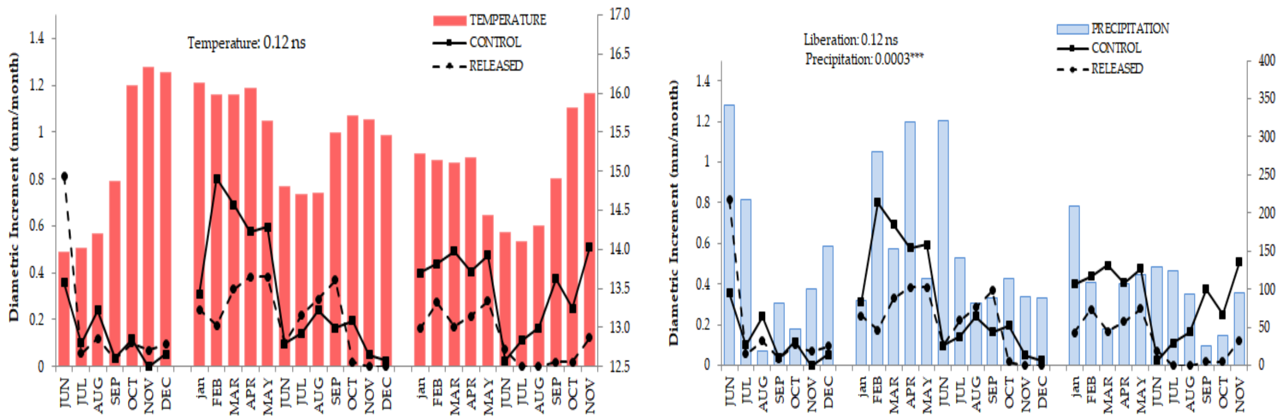
b)

Figure 12. Diameter increase (ordinate axis in mm month^{-1}) by period (on the abscissa axe shown three periods) of *Nectandra membranacea*, respective to **a.)** mean monthly temperature (secondary ordinate axe in °C) and **b.)** monthly accumulated precipitation (secondary ordinate axe in mm month^{-1}).

Diameter increase of the liberated trees in relation to reference trees is no significant Ch = 2.38; ***p*** = 0.1222. The increase is higher in reference trees. There are significant differences in diameter increments between different diameter classes evaluated Ch = 2.65; ***p*** = 2.4e-08. The precipitation significantly influences the diameter increment Ch= 1.39; ***p***= 0.0003, temperature is not significant Ch= 1.1; ***p***= 0.2. The interaction between treatment and diameter classes is not significant Ch = 4.01, ***p*** = 0.39. The interaction between treatment and precipitation is not significant Ch= 1.8; ***p***= 0.16. Finally, the interaction between diameter class and precipitation is signicant Ch= 1.3; p= 0.0037.

The diameter increment of *Tabebuia chrysantha* is evident in trees released from the diameter class I in the first year after release. The growth of this group of individuals decreases during the following two periods. In control trees these "peaks" of increase were not observed. In individuals of the first diameter class, the diameter increment increases during the three periods.

In *Tabebuia chrysantha* the release does not fulfill an important role in the growth of the trees and the recurring pattern of growth *Tabebuia chrysantha* is linked to the presence of precipitation (Figure 13).



a)

b)

Figure 13. Diameter increase (ordinate axis in mm month^{-1}) by period (on the abscissa axe shown three periods) of *Tabebuia chrysantha*, respective to **a.)** mean monthly temperature (secondary ordinate axe in °C) and **b.)** monthly accumulated precipitation (secondary ordinate axe in mm month^{-1}).

Analyses of diameter increment of *Podocarpus oleifolius* shows that the implementation of selective thinning favorably affects individuals of this species, although the increase is not enough to make statistically significant differences between the individuals released and the reference individuals. The interaction between period and treatment is not significant and treatment with the diameter class is not significant.

The evaluation of diameter increment when comparing the effect of PCT´s liberation with respect to reference individuals do not show significant differences Ch= 8.7, ***p***=0,833. After 36 months of implementation of selective thinning, the size of released trees expressed by the diameter class is a factor that positively affects the growth of released individuals Ch=8.7; ***p***= 0.012. The precipitation does not significantly influence the diameter increment Ch= 0.1; ***p***= 0.74, temperature is not significant Ch= 0.73; ***p***=0.9. The interaction between Treatment and Diameter Class is not significant Ch= 1.6; ***p***= 0.44. The interaction between Treatment and precipitation is not significant Ch= 0.33; ***p***= 0.56. Finally, the interaction between Diameter Class and precipitacion is not significant Ch= 0.06; *p*= 0.96.

In *Podocarpus oleifolius* the precipitation and release do not produce a significant effect on growth, the opposite occurs, i.e. control trees grow more than trees released. The diameter growth peaks which belong to the trees released, did not differ significantly in the overall average. The statistical model shows significant differences in terms of size (diameter class) of trees released (***p*** = 0.01*), but the interaction between treatment and diameter class is not significant, meaning that the release has a different answer depending on the initial diameter of the tree, but does not produce a significant positive effect (Figure 14).

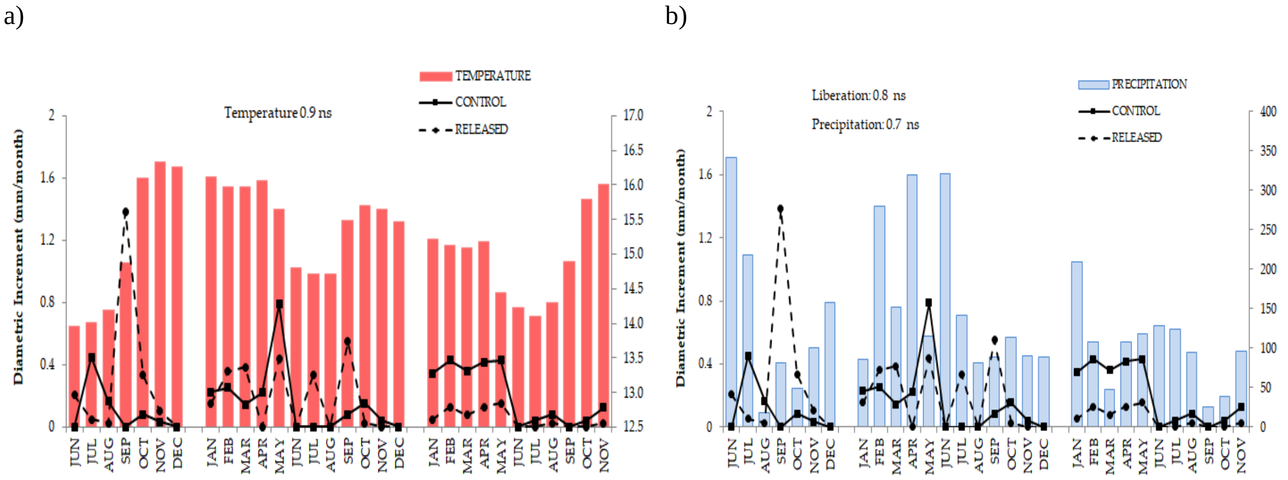


Figure 14. Diameter increase (ordinate axis in mm month^{-1}) by period (on the abscissa axe shown three periods) of *Podocarpus oleifolius*, respective to **a.)** mean monthly temperature (secondary ordinate axe in °C) and **b.)** monthly accumulated precipitation (secondary ordinate axe in mm month^{-1}).

4.2.3 Null Response

The species that did not show significant responses to release (neither positive nor negative) were *Hyeronima moritziana*, *Clusia ducuoides* and *Ficus citrifolia*, which indicates that other factors have a greater influence on the diameter growth of these species.

The diameter growth of *Hyeronima moritziana* (0.12 cm ± 0.23 vs. 0.17 cm ± 0.22) and Clusia ducuoides (0.10 cm ± 0.16 vs. 0.10 cm ± 0.21) was generally low (released trees and control trees) over the complete study period, but with generally the highest DBH increments during the third year (Figure 15).

Released trees show no significant difference in the diameter increment with respect to the reference trees Ch = 1.68; ***p*** = 0.19. By comparing the diameter increment of trees with respect to the diameter classes, there are no significant differences between classes Ch = 2.3; ***p*** = 0.302. The precipitation does not significantly influen the diameter increment Ch= 0.001; ***p***= 0.97, temperature is not significant Ch= 01; ***p***= 0.9. The interaction between the treatment and diameter classes is not significant. The differences in the diameter increment F = 0.07; ***p*** = 0.78. The interaction between treatments and precipitation is not significant Ch= 0.34; ***p***= 0.55. The interaction between diameter class and precipitation is not significant Ch= 0.64; ***p***= 0.72.

In *Hyeronima moritziana* as well as in the above species, neither liberation nor the precipitation and temperature have significance when analyzing the difference in diameter growth of trees. There are no significant differences in diameter growth between control trees vs. trees released, nor do growth peaks match the seasonality of precipitation or temperature behavior shown in some of the studied species.

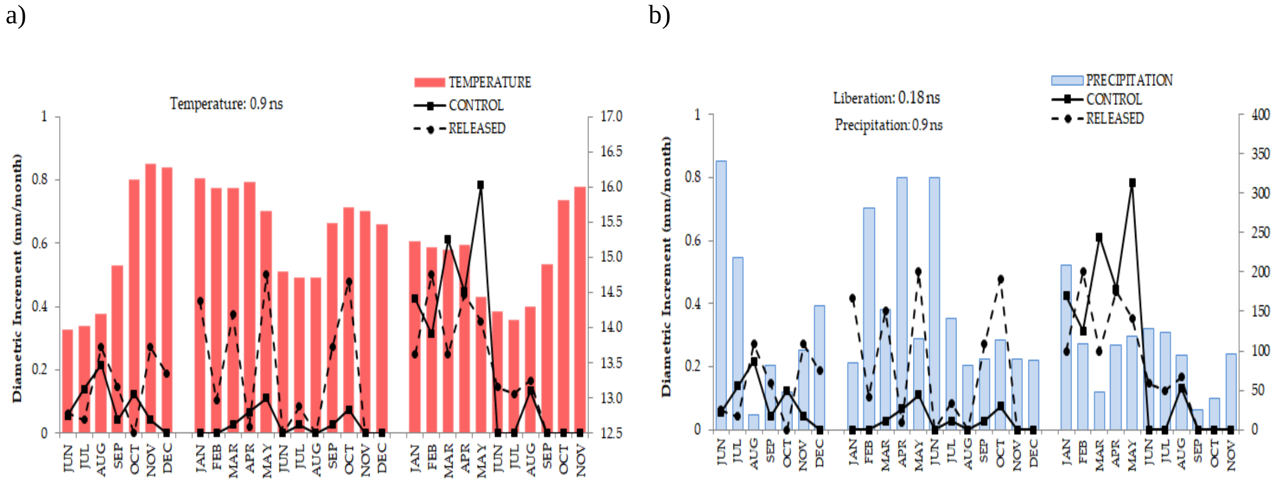


Figure 15. Diameter increase (ordinate axis in mm month^{-1}) by period (on the abscissa axe shown three periods) of *Hyeronima moritziana*, respective to **a.)** mean monthly temperature (secondary ordinate axe in °C) and **b.)** monthly accumulated precipitation (secondary ordinate axe in mm month^{-1}).

In contrast, *Ficus citrifolia* (1.11 cm ± 1.04 vs. 1.09 cm ± 1.22) showed higher DBH increments during first two study years, which can be related to the prevailing climate conditions, because mean monthly temperatures as well as precipitation amounts were higher then, when compared to the third year (Figures 16). This is confirmed in Table 10, where temperature and precipitation are seen to show significant influence on the diameter growth of *Ficus citrifolia* but are secondary for the other two species (Table 12). Respective to the diameter classes, the three species had the highest increments in class I and class II.

The release of *Ficus citrifolia* trees does not influence the diameter increment of them There are no significant differences between reference and released trees Ch= 0.006; ***p*** = 0.93. The precipitation significantly influences the diameter increment Ch= 10.2; ***p***= 0.001, temperature show significance Ch= 2.3; ***p***= 0.003. The interaction between liberation and diameter classes shows no significant difference Ch = 0.11; ***p***= 0.73. The interaction between liberation and precipitation is not significant Ch= 0.16; ***p***= 0.68. Finally, the interaction between Diameter class and precipitation is not significant Ch= 2.08; ***p***= 0.14.

In *Ficus citrifolia* there are differences in diameter increment between trees released and reference trees, but it is not significant. In trees released, the diameter increment increases progressively in all three monitoring periods, while in the reference tree diameter increment values decreased in the three periods. In the first two periods, the control trees have the highest average growth, while in the last monitoring period; it coincided with the seasonality of temperature and precipitation. Trees released show a blunting growth, which is not significant with respect to the total for the period (Figure 16).

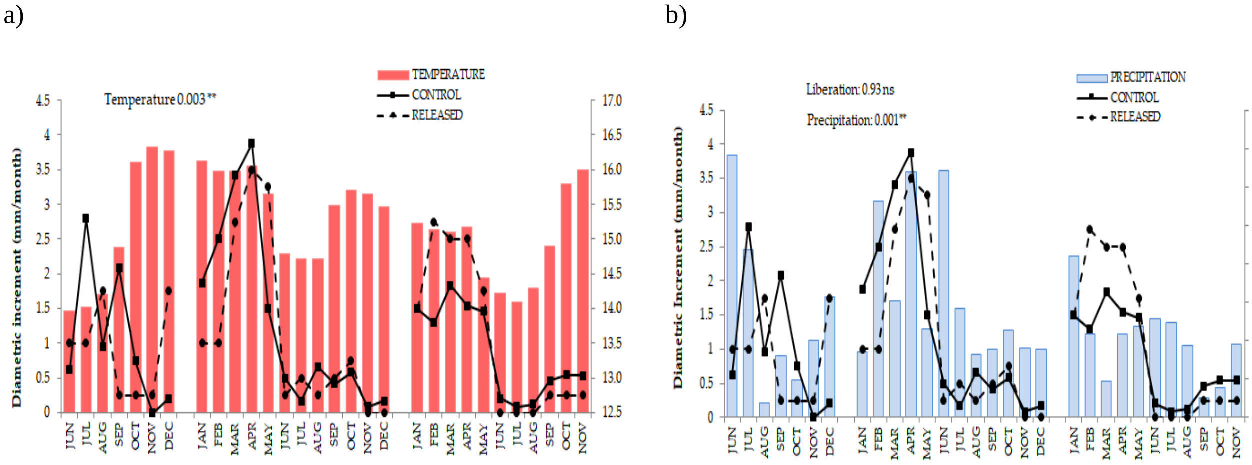


Figure 16. Diameter increase (ordinate axis in mm year^{-1}) by period (on the abscissa axe shown three periods) of *Ficus citrifolia*, respective to **a.)** mean monthly temperature (secondary ordinate axe in °C) and **b.)** monthly accumulated precipitation (secondary ordinate axe in mm month^{-1}).

The diameter increment of *Clusia ducuoides* shows no significant differences between released trees and the control trees Ch= 0.02; ***p*** = 0.86. Neither is there significant differences when comparing the diameter increment of trees belonging two diameter classes evaluated Ch = 2.31; ***p*** = 0.3069. Neither precipitation Ch = 0.7; ***p*** = 0.9, or temperature Ch = 0.34, ***p*** = 0.2, have significance in the model. The interaction between Treatment and Diameter Classes shows no significant difference Ch = 0.90; ***p*** = 0.63. In the interaction between treatment and precipitation, it was not observed that diameter increment presented significant differences Ch = 0.11; ***p*** = 0.72. Finally, the interaction between Diameter class and precipitation is not significant Ch= 2.2; ***p***= 0.32 (Figure 17).

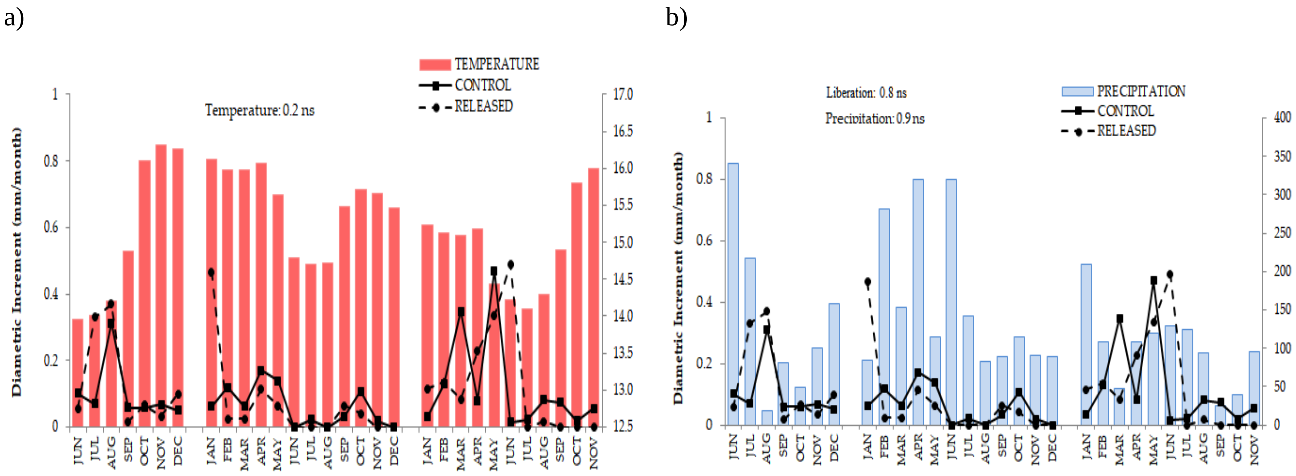


Figure 17. Diameter increase (ordinate axis in mm month^{-1}) by period (on the abscissa axe shown three periods) of *Clusia ducuoides*, respective to a) mean monthly temperature (secondary ordinate axe in °C) and b) monthly accumulated precipitation (secondary ordinate axe in mm month^{-1}).

Table 10. Values of diameter increase (cm) per period and the diameter classes of the nine selected timber species.

Species	**Periods**	**Class 1**		**Class 2**		**Class 3**		**Class 4**	
		Control	**Released**	**Control**	**Released**	**Control**	**Released**	**Control**	**Released**
Inga acreana	1	0.43	1.01	0	0	0	0	0	0
Hyeronima asperifolia		0.48	0.45	0.15	0.43	0.15	0.78	0.04	0.1
Cedrela montana		1.01	0.81	1.39	0.47	1.36	1.5	0	0
Tabebuia chrysantha		0.28	0.72	0.14	0.11	0.15	0.07	0.08	0.23
Nectandra membranacea		0.16	0.34	0.27	0.17	0.31	0.17	0	0
Podocarpus oleifolius		0.17	0.12	0.07	0.02	0.03	0.42	0	0
Ficus subandina		1.0	0.88	1.24	1.25	0	0	0	0
Clusia ducuoides		0.13	0.15	0.06	0.08	0.13	0.08	0	0
Hyeronima moritziana		0.12	0.18	0.11	0.06	0	0	0	0
Inga acreana	2	0.64	1.16	0	0	0	0	0	0
Hyeronima asperifolia		0.45	0.73	0.43	0.67	0.35	0.83	0	0.46
Cedrela montana		1.2	0.96	1.31	0.65	1.25	1.33	0	0
Tabebuia chrysantha		0.37	0.44	0.32	0.12	0.19	0.14	0.42	0.13
Nectandra membranacea		0.35	0.41	0.2	0.08	0.46	0.08	0	0
Podocarpus oleifolius		0.08	0.1	0.06	0.04	0.33	0.42	0	0
Ficus subandina		1.35	0.96	1.27	1.33	0	0	0	0
Clusia ducuoides		0.07	0.06	0.11	0.05	0	0.08	0	0
Hyeronima moritziana		0.05	0.25	0.03	0.13	0	0	0	0
Inga acreana	3	0.63	1.22	0	0	0	0	0	0
Hyeronima asperifolia		0.49	0.82	0.2	0.78	0.44	0.86	0	0.57
Cedrela montana		0.99	0.74	1.06	0.64	1	0.73	0	0
Tabebuia chrysantha		0.47	0.09	0.16	0.15	0.1	0.06	0.59	0.18
Nectandra membranacea		0.37	0.5	0.56	0.05	1.34	0.05	0	0

Podocarpus oleifolius	0.11	0.16	0.2	0	0.3	0	0	0
Ficus subandina	0.86	1.18	0.88	0.95	0	0	0	0
Clusia ducuoides	0.13	0.15	0.09	0.05	0.14	0.18	0	0
Hyeronima moritziana	0.3	0.2	0.17	0.2	0	0	0	0

Class I = 20.1–30 cm, class II = 30.1–40 cm, class III = 40.1–50 cm, class IV ≥ 50.1 cm.

Table 11. *P*-values of the variables and the interactions that influence the variability of the diameter increase (GLMM). Significant values (p ≤ 0.05) are highlighted in bold.

Species	Release		Precipitation		Temperature		Diameter Class		Release x Diameter Class		Release x Precipitation		Release x Temperature		Diameter Class x Precipitation		Diameter Class x Temperature	
	Ch	**p**	**Ch**	**p**	**Ch**	**p**	**Ch**	**p**	**Ch**	**p**	**Ch**	**p**	**Ch**	**p**	**Ch**	**p**	**Ch**	**p**
Inga acreana	14.9	**≤0.0001**	0.05	0.81	0.05	0.83	—	—	—	—	0.18	0.66	0.99	0.31	—	—	—	—
Hyeronima asperifolia	33.5	**≤0.0001**	4.1	**0.04**	9.8	**0.001**	16.7	**0.0008**	5.01	0.08	0.0	0.99	0.27	0.6	0.42	0.9	3.5	0.31
Cedrela montana	6.2	**0.01**	15.1	**≤0.0001**	31.9	**≤0.0001**	4.9	0.08	1.5	0.21	1.01	0.31	2.3	0.12	4.5	0.1	5.9	**0.05**
Tabebuia chrysantha	2.3	0.12	13.5	**0.0002**	1.74	0.18	26.3	**≤0.0001**	4.04	0.39	1.9	0.16	0.39	0.52	13.5	**0.003**	0.62	0.88
Podocarpus oleifolius	0.04	0.83	0.09	0.75	0.009	0.92	8.6	**0.01**	1.6	0.5	0.34	0.6	0.2	0.65	0.07	0.96	0.89	0.64
Nectandra membranacea	5.5	**0.01**	14.9	**≤0.0001**	31.8	**≤0.0001**	1.4	0.49	0.12	0.72	2.7	0.9	3.5	0.06	0.2	0.9	2.7	0.2
Clusia ducuoides	0.02	0.86	0.0004	0.98	1.3	0.24	2.4	0.3	0.91	0.63	0.09	0.76	1.1	0.3	2.2	0.33	4.7	0.09
Hyeronima moritziana	1.7	0.19	0.0008	0.98	0.0006	0.98	2.4	0.3	0.07	0.79	0.45	0.5	3.4	**0.05**	0.64	0.72	0.0002	0.99
Ficus citrifolia	0.007	0.93	10.1	**0.001**	8.8	**0.002**	0.46	0.49	0.12	0.72	0.19	0.65	0.17	0.67	1.9	0.16	3.3	0.06

4.3 Discussion

Historically the growth of trees has been modeled based on different classification criteria. The most common have been the taxonomic affinity, ecological guild they belong to the species and similar growth dynamics patterns, even different statistical approaches (Adame et al. 2014) and different models to interpret the growth and performance of plantations and different tropical forest types (Vanclay 1994). Natural tropical forests of Ecuador have been monitored for several decades (Neill 2000). Remeasurement is continuous over time - given only the influence of climatic factors affecting the entire forest. Monitoring of forest growth and particular species based on experimentation such as adding nutrients to the soil (Homeier 2008) or release of trees as in this experiment (Günter et al. 2008) are topics that provide knowledge about the effects of activities forestry and effectiveness when implementing experimentally.

In our study, we separate the 9 species, monitored in three groups. The first group consists of species that have responded positively to the release (*Inga acreana* and *Hyeronima asperifolia*). In species like *Cedrela montana*, *Nectandra membranacea*, *Podocarpus oleifolius,* and *Tabebuia chrysantha*, the individuals that served as control grew more than liberated individuals, despite there are differences between the diameter classes of liberated trees. The last group of species (*Hyeronima moritziana*, *Clusia ducuoides* and *Ficus citrifolia*) responded neutrally to thinning.

Inga acreana and *Hyeronima asperifolia* respond positively to thinning. For *Inga acreana*, the difference between treatments is obvious. The species of genus Inga are considered as medium-sized and shade intolerant according to Palacios (2004), while according to Adame et al. (2014), some species of the genus are considered shade intolerant or moderately shade tolerant

In *Hyeronima asperifolia* the response of trees to liberation is positive. Wadsworth and Zweede (2006) refer to the release based on a thinning, which is a valid method for increasing the growth and yield of selected trees. Likewise, Günter et al. (2008), when referring to the first year of monitoring nine timber species, shows data where Hyeronima asperifolia has an interesting early response, although the difference between the thinned trees and trees of control is not significant at the time.

In *Hyeronima asperifolia,* the reference trees that grew more are Class III 20-30 cm dbh, while the trees that grew released were larger Class V (40-50 cm dbh), according to de Graaf et al. (1999). What happens with the trees of timber species after implementing various treatments (including refining and selective harvesting) is that trees released are those with the greatest increase (0.39 and 0.71 cm / yr) and (0.47 cm / year 0.86 cm / year) in another period. Having released the trees creates better conditions of light, resulting in a diameter increase, Pereira da Silva et al. (2002) in the Brazilian Amazon found that there are significant differences in diameter growth of larger trees, an event also supported by Clark and Clark (1999) which determines the pattern of growth by diameter is strongly dependent on the size of the tree.

In the next group of species released trees grow less than the trees control, i.e. the release of the trees produced an inhibitory effect on diameter growth. King et al. (2005) developed a hypothesis which states that the variation in the diameter growth of trees of certain species are related to two factors, the first is the amount of light intercepted by the tree and the second is the density of the wood, specifically expected an inverse relationship between growth and wood density of the species studied The result of his research was that he found that the correlation was higher between wood density and growth that the correlation between growth and the amount of light was intercepted. The three species with market value are in this group, the four species have hard and dense wood; *Tabebuia chrysantha* and *Cedrela montana* have defoliation.

5. Functional Diversity Changes after Selective Thinning in a Tropical Mountain Forest in Southern Ecuador (Publication II, Cabrera et al. 2020).

5.1 Methods

5.1.1 Data Collection

The methods described here were used for publication II (Cabrera et al. 2020) where a more detailed description of them can be found. First, the following traits were selected to determine the functional diversity changes in this tropical mountain ecosystem after applying selective thinning: **(1)** Wood density (WD) (Zanne et al. 2009, Chave et al. 2009, MAE 2014, Palacios 2004); **(2)** Average diameter (DBH); **(3)** Growth (annual diameter increase); **(4)** Leaf Type; **(5)** Ecological Guild (Chave et al. 2009, Palacios 2004); **(6)** Dispersion syndrome (Table 6). Functional traits allow the analyses of the diversity and structure of the community (Chave et al. 2009), in contrast to conservative features, which are related to reproduction and succession.

WD was selected because this trait is connected to several aspects of plant ecology, including growth rate, carbon allocation strategy, structural stability, resistance to diseases or pests, and primary production (Homeier et al. 2010, Zanne et al. 2009, Osazuwa et al. 2015), while the average DBH and growth are directly related to the silvicultural treatment applied. Leaf type is a functional trait which has been used to predict the growth of tropical trees (dos Santos et al. 2020) and which reflect adaptations that allow plants to live under various environmental conditions (Wang et al. 2017). Here, we include the type of leaf in the FD analyses, as a way to indicate the plant's strategy to acquire and redistribute nutrients for growth (Osazuwa et al. 2015). According to Xu et al. (2009), there are differences between the species that have compound leaf and simple leaf species, so these categories can be assumed to have slow and fast metabolic rates, respectively. The simple leaves are easier to manufacture than the compound leaves, but this is compensated by the duration being the same, that is, a longer useful life of the compound leaves for the benefit of the plant. As a conservative trait (reproduction and succession, which are intrinsic to each individual species), the ecological guild or type of succession was used. The last trait, "Dispersal syndrome", is closely related to the relative abundance of species (Jara-Guerrero et al. 2011). In wet tropical forests that exhibit a large aggregation of specific trees at scales ranging from a few meters to a few hundred meters, the dominant syndrome is zoochory (Seidler y Plotkin 2006), while in the tropical dry forests, the dominant syndrome is the anemochory, which also leads to certain specific distribution patterns (Jara-Guerrero et al. 2011), although barochory is also a more frequent syndrome in dry forests than in wet tropical forests (Cortéz-Flores et al. 2019). The implementation of selective thinning could cause changes in the forest structure by changing the dominant dispersal syndrome, reducing the individuals that belong to each species.

Table 12. Functional (conservatives and acquisitive) traits, including categories, units and codes used to calculate FD and CWM.

Functional Trait	Type	Categories	Unit	Code
Wood density	Acquisitive	-	g cm^3	WD
Stem Density	Acquisitive	-	cm	DBH
Diameter growth	Acquisitive	-	cm year^{-1}	G
Leaf type	Acquisitive	Simple		LT
		Compound		
Ecological guild	Conservative	Shade tolerant		ST
		Light Tolerant		LT
		Partial light Tolerant		PLT
		Partial Shade Tolerant		PST
Dispersion syndrome	Conservative	Anemochory		AN
		Zoochory		ZOC
		Barochory		BAR

WD data for all tree species involved in the study were provided by the local RBSF database (TMF Database). In the event that a species was not listed, the data were acquired from the Global Wood Density Database (https://datadryad.org/), particularly as a subset for the Latin American region (Zanne et al. 2009, Jara-Guerrero et al. 2011), or in ICRAF's free and accessible database (functional attributes and the ecological database, http://db.worldagroforestry.org/wd). The monthly diameter growth was controlled by dendrometers fixed on each PCT tree (Gunter et al. 2008). For all tree species, the growth was determined by three general forest inventories carried out at 18 and 36 months after implementing the permanent plots. The stem density was determined by counting all individuals of a species before and after selective thinning. The leaf type was identified directly after botanical collections and observations in the field, while the ecological guild and the dispersion syndrome of each üspecies were determined using attributes and ecological characteristics as described by Palacios (2004) and Jara-Guerrero et al. (2011).

5.1.2 Data Analises

To determine the functional diversity (FD) multi-trait indices and CWM for this TMF after selective thinning, the FD package was used (Laliberte et al. 2010) and the following indices were included:

Functional Richness (FRic), which represents the amount of space occupied by a community, independent from the relative abundances of the species (Mason et al. 2013).

Functional Divergence (FDiv), measures how species of a community diverge in their distance from the center of gravity in the functional space, and determines the relative abundance of a species within its functional range, (Mason et al. 2013, Villéger et al. 2008). FDiv provides additional information for FRic, because this index indicates which species has the most extreme feature combinations (i.e., specialized species), and which ones are generalist (Mouchet et al. 2010).

Functional Evenness (FEve), quantifies the regularity of how species abundances are distributed within their functional range, by correlating abundance with average distance between different species (Zanne et al. 2009). FEve can be related to the uniformity of species (Pielou's J) and the FDiv because it determines if the extent of functional distances between the species is regular (Biswas & Mallik 2010).

Functional Dispersion (FDis), gives the mean distance of an individual species relative to the centroid of the community, which depicts its mean distance relative to all species in the community, and therefore, accounts for relative abundances of a species.

Rao Quadratic Entropy (RaoQ), correlates the abundances of different species (Botta-Dukat 2005) to improve the FD index. An adverse property of RaoQ is that its value may decrease if species richness increases, because abundances and dissimilarity between the species are considered. Therefore, the introduction or loss of species in a community increases or decreases the species abundance, but, at the same time, may reduce the dissimilarity between the species.

Community weighted mean (CWM), represents the sum of each species trait value weighted by its relative abundance in the community (Lavorel et al. 2008). To characterize the community structure from a functional point of view, we used the community weighted mean, which is calculated combining the species abundance with the trait values of the given species (Ricotta y Moretti 2011). This describes the trait averages over a community (Bello et al. 2007) and reflects the dominant trait in a given community (Viollé et al. 2007, Garnier et al. 2004, Leps et al. 2006).

To relate the FD indices and the CWM to the predictors, we used multivariate linear mixed modelling (LMM) with random nested intercepts. For each index or CWM, the fixed effects were the altitude, the relative removed basal area, the number of trees ha^{-1}, the initial basal area, and the initial species number, whereas the random effects were the plot membership nested in the "quebrada". All the previously mentioned predictors are directly related to the selective thinning, except altitude, which is a natural distribution gradient but often considered by other authors (Paulsch 2002, Homeier et al. 2010) because of its importance for analyzing forest composition and structure.

To perform the LMM analyses, the NLME package of R was used (Bates et al. 2007), in which the explanatory categorical factors were combined to calculate random values for the repeated measurements throughout time (before–after). As fixed factors, we used all the predictors inherent to structural and ecological forest conditions before and after the selective thinning (period and treatment) and as a random variable, we used the membership to nested sampling. To validate the models of each analyzed index, we compare each resulting model, applying a goodness test (likelihood ratio test), discarding non-significant predictors and establishing the importance of the remaining factors to prove that the models were not over fitted. For this, we used the "lmtest" package of R software (Hothorn et al. 2019).

5.2 Results

After applying the linear mixed model (LMM), we found that the variations of the different indices that compose the FD of studied TMF is not produced exclusively by the implementation of selective thinning, but also by the distribution of the TMF along the altitudinal gradient, which implies different structural and diversity conditions.

The FRic variability was significantly influenced by the implementation of selective thinning, while the predictors related to habitat characteristics and altitudinal gradient did not show significant effect. Functional uniformity (FEve) was not significantly affected by any predictor. FDis was significantly influenced by predictors related to selective thinning and natural conditions of the forest. FDis and RaoQ were influenced by predictors related to natural conditions of the forest, while the predictors related to the implementation of treatment did not significantly influence these indices (Table 13).

Table 13. Linear mixed models (LMM) of Functional Diversity indices as a function of stem density (stem ha^{-1}), total species, thinning intensity, altitude, treatment, period, treatment: period (fixed effects) and of plot membership nested in sample site (intercept random effects), and likelihood ratio tests (LRT). FEve was not affected by any predictor.

Predictors	**Functional Richness: FRic**		**Functional Diversity: FDiv**		**Functional Dispersion: FDis**		**Rao Quadratic Entropy: RaoQ**	
	LTR *p* Value <0.001		**LTR *p* Value <0.001**		**LTR *p* Value <0.001**		**LRT *p* Value 0.01**	
	Coeff	***p*-Value**	**Coeff**	***p*-Value**	**Coeff**	***p*-Value**	**Coeff**	***p*-Value**
(Intercept)	−1.08	**<.0001**	8.6	**<.0001**	4.3	**<.0001**	2.06	**<.0001**
Stem density							5.2	**0.02**
Total Species								
Thinning Intensity	2.47	**0.0182**	4.04	**0.004**				
Altitude			−7.31	**0.001**	12.9	**0.005**	14.4	**0.0002**
Treatment								
Period	−7.3	**<.0001**						
Treatment: Period	−1.89	**0.0270**						

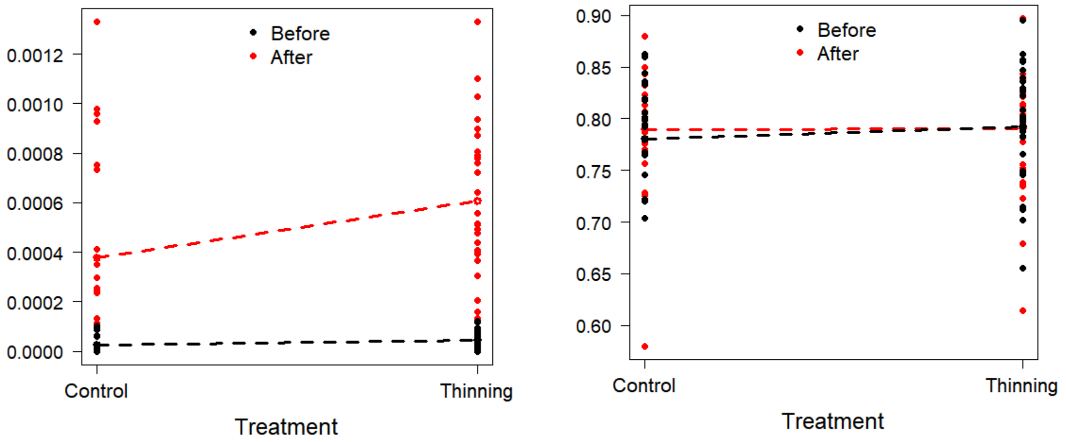
The ANOVA results comparing the values of the FD indices before and after the implementation of selective thinning indicate that significant differences were evident only for FRic (Table 14, Figure 19a), whereas the other indices (FDis, FEve, FDiv and RaoQ) were less sensitive to the implementation of selective thinning and more susceptible to changes in the natural conditions of the TMF (Table 14, Figure 18 b–e).

Table 14. Functional diversity indices (mean ± SD), including the F-statistic values respective to the effect of thinning. Functional indices were calculated based on the six traits described in Table 1.

INDEX	**Before**	**After**	**Coeff**	**F *p*-Value**
Functional Richness (FRic)	0.000025 ±0.000003	0.0005 ± 0.00003	−9.03	**<.0001**
Functional Evenness (FEve)	0.786 ± 0.061	0.791 ± 0.058	−0.26	0.7902
Functional Divergence (FDiv)	0.835± 0.041	0.838 ± 0.047	−0.41	0.6793
Functional Dispersion (FDis)	0.251 ± 0.022	0.263 ± 0.023	0.23	0.3246
Quadratic Entropy (RaoQ)	0.0696 ± 0.011	0.0691 ± 0.012	0.11	0.8919

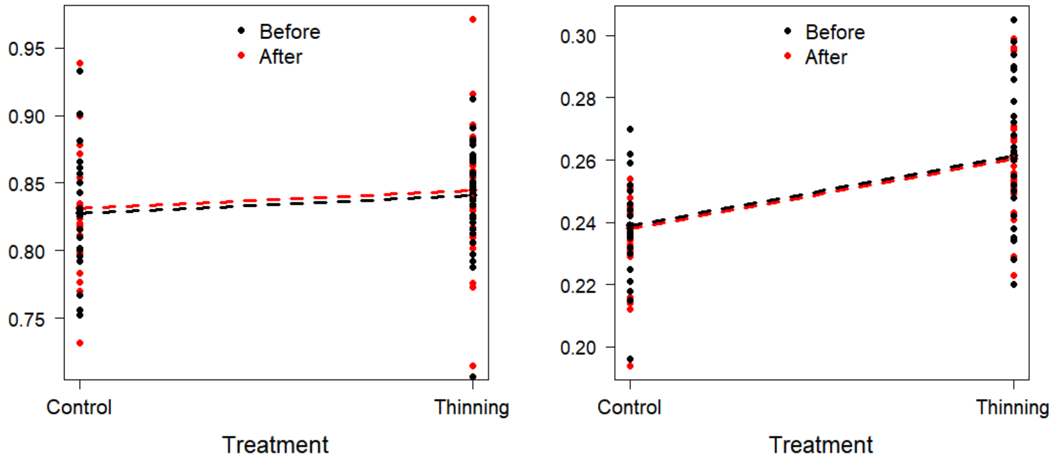
(**a**) FRic

(**b**) FEve



(**c**) FDiv

(**d**) FDis



(**e**) RaoQ

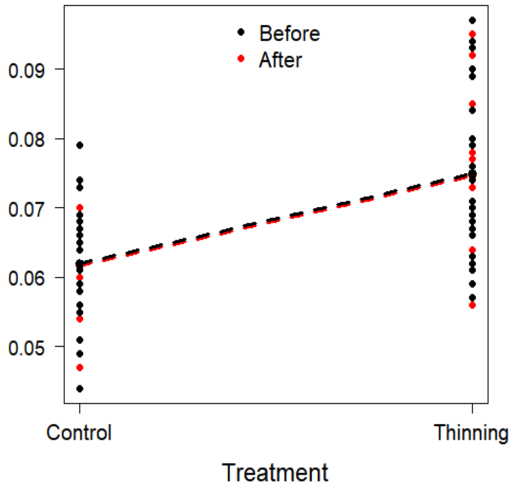


Figure 18. Effects of thinning on functional diversity indices (*n* = 52) before and after implementation of selective thinning. (**a**) Functional Richness (FRic), (**b**) Functional evenness (FEve), (**c**) Functional divergence (FDiv), (**d**) Functional dispersion (FDis) and (**e**) Rao Quadratic entropy (RaoQ). Details of analyses of variance among control and thinned plots are given in Table 3.

The CWM values of the dominant trait in each of the sampled plots had different responses to the intervention. The frequency (trees after thinning of more important species in each plot) of certain species was affected by the extracted basal area and changed significantly after thinning was implemented; however, the initial number of species is also a predictor that significantly influences PCT frequency variability. Regarding growth, the implementation of selective thinning significantly affects the variability of the trait, although some predictors such as the number of species, the number of trees per hectare and the altitude gradient are also significant in the variability of the trait. Regarding the initial DBH, only the number of trees/ha^{-1} exerts significant influence on the trait (Table 15).

Table 15. Linear mixed models (LMM) of Community weighted mean CWM of potential crop trees frequency (FREQUENCY), diameter growth (GROWTH) and initial diameter at breast height (DBH) as a function of stem density (trees ha^{-1}), total species, thinning intensity, altitude, treatment, and plot membership nested in sample site (intercept random effects), and likelihood ratio tests (LRT).

Predictors	**FREQUENCY**		**GROWTH**		**DBH**	
	LRT *p* Value 0.01		**LRT *p* Value <0.0001**		**LRT *p* Value 0.01**	
	Coeff	***p*-Value**	**Coeff**	***p*-Value**	**Coeff**	***p*-Value**
Stem density			1.89	**0.002**	1.04	**0.004**
Total Species	1.8	**<.0001**				
Thinning Intensity	3.47	**<.0001**				
Altitude			−0.98	**0.003**	−2.43	**0.002**
Treatment	1.5	**<.0001**				

5.3 Discussion

An important step before applying selective thinning, as shown in this study, is the analyses of the floristic composition of the original forest in an attempt to conserve the extraordinary biodiversity. However, a carefully planned silvicultural method can allow, at the same time, to increase the growth rates of the desired species and, subsequently, the extraction of resources for the economic development of the local population (Costa et al. 2003, Bawa y Seidler 1998).

Therefore, individual tree species must be carefully analyzed to determine their economic or ecological value. If tree species with a limited number of individuals are cut, the diversity, and consequently, the functionality of the ecosystem may be affected, although during this investigation, not only individuals of abundant species were eliminated but also species with few representatives.

As shown in this study, if these preconditions are respected, selective thinning intensity does not cause significant changes in the forest ecosystem. Furthermore, the results suggest that the applied strategy makes the studied TMF more productive, especially in terms of growth, because the loss of taxonomic and functional diversity is minimal. The forest still serves as a conservation area, providing all of its ecosystem services; therefore, selective logging could also be a useful tool for biodiversity conservation and sustainable forest management (Lohbeck et al. 2013, de Avila et al. 2015).

Selective thinning also causes greater gaps within the forest stand, which changes the ecosystem conditions as a result of canopy openness. However, natural tree fall has the same effects, although gaps are generally less frequent. As Gunter et al. (2008) found in the same TMF, Arctiidae moth communities were affected by both, selective thinning and natural tree fall, during the first year, whereas monocotyledonous and dicotyledonous vascular epiphytes did not show significant changes in structure or composition. Nevertheless, these impacts might be different in ravine forest or ridge forest parts (Noske et al. 2008, Werner 2011), due to the different forest structure (Gunter et al. 2008).

Plant traits are indicators of diversity, functionality and community composition (Mouchet et al. 2010), which are generally used to determine environmental changes over time or to understand natural successional processes. However, the selective thinning applied in this study adds another gradient of use, because the removed individuals belong to certain undesired species, which might affect the functional composition of the forest community. Therefore, to analyze changes of FD indices in this TMF regarding selective thinning, the used traits are mainly related to resource acquirement, because these allow one to evaluate if species exploit the available resources quickly, which generally occurs during periods of abundance at sites with sufficient water availability (López-Iglesias et al. 2014).

To assess the impacts of silvicultural interventions into an ecosystem and its functioning, all interactive components must be combined to obtain serial robust numerical indices (Wadsworth 1997), which can be provided by the FD. FD implies more than number of species and diversity, because multiple traits are considered, such as species dispersion syndromes, leaf functional characteristics, etc. Therefore, FD is an important attribute to analyze the response of a forest community to environmental changes. However, if only richness and diversity of species is evaluated to analyze the impact of forestry interventions, the generated information is still insufficient to understand the natural process of forest ecosystems (Benítez et al. 2018).

In agreement with Baroloto et al. (2012), some FD indices showed significant changes after thinning, especially those related to the predictors that include thinning, but not those related to the altitude gradient, since this does not imply a pronounced effect on the communities or alteration in ecosystem processes. In general, functional diversity varies significantly as a result of changes in the forest community, as well as with the level of intervention; however, the total richness of the tree species may not change significantly due to the applied treatment (Huang et al. 2003). As Putz et al. (2012) indicated, the impact of forestry, especially logging, is more destructive with respect to carbon storage, but if growth rates increase forest productivity, carbon storage can be compensated.

Curzon et al. (2017) concluded that in the temperate forests, functional diversity remains stable over the years after major disturbances like thinning or logging. By comparing the results in the temperate forests with our results in tropical montane forests, they both agree that neither produce significant changes in functional or taxonomic diversity shortly after the disturbance.

The Functional Divergence (FDiv) was influenced by the extracted basal area (slimming intensity) and altitude, which means that no clear influence of the intervention respective to the variability of this index could be demonstrated. The FDis and RaoQ indices were only influenced by the number of trees, which is a natural condition of the forest ecosystems and depends on various environmental factors (Moser et al. 2011, Dislich & Huth 2012, Cabrera et al. 2019, Paulsch 2002, Homeier et al. 2010).

The abundance and the initial DBH were less affected by intensity of the selective thinning applied, while the growth was improved due to changes in the initial conditions, mainly concerning availability of light and nutrients (Moser et al. 2011). However, the community shows significant changes when comparing thinned plots and control plots and the specific role of each species could not be determined—such effects include succession changes, reproduction and interactions with other species. However, the experiment was executed within a natural reserve and no long-term treatment was applied to analyze larger scale logging regimes, such as a forest concession. Furthermore, the evaluation period was relatively short, and for this reason, changes in growth rates of remaining trees and modifications in species composition, such as reduction in shade-tolerant species, could not be analyzed. This also includes the effects on other important organism groups, such as epiphytes, orchids, mosses, ferns or insects, which should be the objective for further investigations.

In summary, selective thinning did not significantly alter the functionality of this TMF compared to the natural ecosystem (control plots). The FD was almost unchanged, which is the most critical point when applying a sustainable forest treatment. Future studies should focus on the links between biodiversity and ecosystem services (Mori et al. 2017), and long-term field monitoring is necessary (Gunter et al. 2008).

6. Assessing the importance of topographic variables for the spatial distribution of tree species in a tropical mountain forest (Publication III, Kuebler et al. 2016).

6.1 Methods

6.1.1 Data collection

In this section we summarize the methods used in publication III (Kuebler et al. 2016) to determine the topographic factors that influence the spatial distribution of the 16 most frequent tree species in the tropical mountain forest of the RBSF. The chosen forest species have between 55-196 individuals and represent 49% of the total abundance and 52% of the total basal area of the study area.

Species distribution modeling is based on the concept issued by Hutchinson (1957) which assumes that species only occur where environmental conditions are favorable, that is, the distribution of species is linked to an n-dimensional structure constituted by environmental factors.

A comprehensive and very detailed analyses of the concepts and scope of the species distribution models can be found in Kuebler et al. (2016) however in this document we highlight the most important processes of the two models used to evaluate the distribution of the species in the TMF of the RBSF.

6.1.1.1 Maximum Entropy Models (Maxent)

The first method used to model the distribution of species was MAXENT maximum entropy model, which is a machine learning technique that adjusts to a probability distribution of species occurrence with environmental layers throughout a specific study area.

The MAXENT analyses was carried out using the Maxent software (V 3.3.3k) (Phillips et al. 2006) in addition R software package “Dismo” (Hijmans et al. 2013) was used. According to Kuebler et al. (2016) this software was used because it showed good performance in comparison with other algorithms for the spatial distribution model

(SDM) of only presence, but also allows inferring the importance of environmental variables in the distribution of species.

6.1.1.2 ENFA

The second method to model the distribution of species is the Ecological Niche Factor Analyses (ENFA) which applies a very suitable method to determine the importance of environmental variables for the characterization of the ecological niche of a given species (Basile et al. 2008, Kuebler et al. 2016).

Methodologically, ENFA works as a principal component analyses (PCA) reducing the n-environmental variables introduced as predictors of occurrence, to a small number of orthogonal factors in which the first factor listed, called "marginality" contains and describes the environmental conditions. preferred, among the whole set of possible conditions. The ENFA model was run using the R package "adehabitat" (Calenge 2006).

6.1.2 Data Analyses

We analyse the influence of topographic factors on the spatial distribution of forest species since topography and its associated microvariables play an important role in many ecological processes in TMF in general (for example, Baldeck et al. 2013; Takyu et al. 2002), and in the RBSF in particular (for example, Ließ et al. 2011; Oesker et al. 2008, Kuebler et. al 2016).

For model evaluation, two criteria were used: the independent area of the threshold under the curve (AUC) of the receiver operating characteristic (ROC) (Fielding and Bell 1997) and the threshold-dependent real skills statistics (TSS) (Allouche et al. 2006) in this work we evaluate the final models created based on the total data set, different permutations to rule out whether the final models are products of chance and models product of partitions of the data divided at random k-times (Fielding and Bell 1997).

Using multiple metrics is important because each metric assesses a different aspect of predictive performance (Elith and Graham 2009). Despite using a k-fold data partitioning technique for some of these metrics, the full available data was used to create the final models (Fielding and Bell 1997, Kuebler 2020).

To evaluate the factors that influence the spatial species distribution, a digital terrain model (DTM) obtained based on a digital LIDAR sensor with a resolution of 1m was used. The derived topographic variables were calculated using the free software SAGAGIS and the R software package "Rsaga". One of the aspects to consider was the sensitivity of the modeled areas to the edge effect and for this, a 1km zone was expanded around the areas of the plots of the silvicultural experiment, and then it was delimited with the polygons of the installed plots, in this way this error was minimized when obtaining the variables (Kuebler 2020). The generated variables that were considered important for the analyses are: elevation, topographic position index (TPI), aspect, SAGA humidity index (WI) and slope. Another resource used to model the distribution of species is the location of all the trees with more than 20 cm DP, in the permanent plots referred to in section 3.2.1 of this document. Two models were evaluated, the Maxima entropy (Maxent) and the Ecological Niche Factor Analyses (ENFA), the evaluation of both models is detailed in Kuebler et al. (2016).

6.1.2.1 Maxent

The most used method to evaluate the MAXENT models is the AUC, which was basically created to evaluate the species distribution models (SDM) based on the presence and absence of the species, however, it can be used for presence-only techniques, because plotting the sensitivity against a random sample of background locations is sufficient to define a ROC curve (Wiley et al. 2003; Phillips et al. 2006, Kuebler et al. 2016).

Rather than expressing only the ability of the model to discriminate between suitable and unsuitable habitat for the species, as is the case with presence / absence methods, the AUC now also evaluates the probability that a chosen presence site will randomly ranked above a previously randomized site (Phillips et al. 2006, Kuebler et al. 2016).

6.1.2.2 ENFA

As in the previous method, the evaluation of the ENFA has been carried out only with presence metrics provided by the AUC method, a situation that has been criticized by several authors (Lobo et al. 2008; Jiménez-Valverde 2012). Therefore, to evaluate the ENFA model, we additionally calculated the threshold-dependent real ability statistic (TSS), which is similar to the generalized Kappa statistic, but less dependent on the prevalence of the modeled species (Allouche et al. 2006). Is defined as:

TSS = sensitivity + specificity - 1

where sensitivity is defined as the proportion of observed presences correctly predicted as presences, and specificity is the proportion of observed absences that are correctly predicted as absences (Allouche et al. 2006, Kuebler et al. 2016). TSS values <0.2 can be considered poor, 0.2 to 0.6 as fair to moderate, and> 0.6 as good (Landis and Koch 1977).

To calculate the TSS, continuous habitat predictions must be transformed into a binary presence-absence format. For the analyses referred to here, we calculated a threshold score for each permutation according to the method based on maximizing the sum of sensitivity and specificity (Max SSS), which is equivalent to maximizing the TSS (Liu et al. 2013, Kuebler 2020).

6.2 Results

In this section we show that the distribution of species based on topographic and environmental factors corroborate and strengthen the physiognomic classification of FMT. These results refer in full to those published in Kuebler et al. (2016), where you can find general details.

One of the main findings of this study determined that species distribution is influenced by elevation and TPI, while the wetness SAGA index and the slope have marginal importance. The evaluation of both distribution models (Jacknife in Maxent and absolute marginality in ENFA showed that TPI and elevation were decisive for the distribution of tree species.

Another important result were the prediction maps of habitat suitability based on the Maxent and Enfa distribution models, these maps (Kuebler et al. 2016) show the preference of some species for habitats located at lower elevations and in valleys, while other species prefer higher elevations and ridges.

Species distribution and the potential of habitats corroborate the presence of two types of forest based on the elevation and the physiography of the terrain. Homeier et al. (2010) and the results of this work in section 4.1 found that in the study area there are two types of forest, each characterized by its composition and structure and now determined by the distribution of characteristic species.

Of modeled species *Cedrela montana* (characteristic species of ***Tabebuia-Cedrela*** group in this work and of Forest Type II in Homeier et al. 2010) and *Clusia ducuoides* (characteristic species of ***Podocarpus-Clusia*** group in this work and of Forest Type I in Homeier et al. 2010) present characteristic distribution patterns for each one, *Cedrela* and associated species with the floristic group that it represents prefer habitats located at lower elevations and valleys while *Clusia* and associated species with its group prefer higher habitats in ridges, and as presented in the floristic classification, in the distribution maps there are species that do not show a preference for either of the two habitats and are found in both forest types indistinctly.

6.3 Discussion

The discussion focuses on three important points 1) Limitations of the study, 2) Aspects of the species distribution models and 3) The interpretation of the importance of the individual topographic variables. In general, we accept as a restriction of the study that the presence and absence data set of the studied species represent a small subset of the complete range of environmental conditions where the species are found, according to Raes (2012) this corresponds to “an artificially restricted geographic space”, several implications of this restriction have been identified by previous studies on SDM, which can also be applied to our results.

1) The first aspect of the discussion refers to the limitations of the study, the evaluation curves of the models were possibly affected by restricted environmental ranges, with stronger effects towards the upper and lower extremes (Thuiller et al. 2004). In areas with great climatic variability such as the one in which we developed our study, the prediction of habitat suitability should not be carried out in areas beyond the range of environmental conditions with which the models were calibrated (Sánchez-Fernández et al. 2011; Thuiller et. al. 2004). Third, like habitat suitability, the importance of topographic variables cannot be extrapolated beyond the range of environmental conditions. This is especially true for species with a wide distribution range, both in dry and humid forests (Volland-Voigt et al. 2011). In our study area, several species show a clear preference for negative TPI values, which correspond to valleys. However, this does not allow us to infer preferences for topographic positions of this species in other regions of its range of distribution. It is important to acknowledge the aforementioned points, but they do not conflict with the main objectives of this study, which focus on the local scale.

Another dilemma that addresses the discussion about the limitations of the study refers to two ecological theories that limit the validity of the use of SDM in forest communities with multiple species, the niche theory and the neutralist theory, the first (Hutchinson 1957) postulates that different tree species specialize in different habitats, where they are competitively dominant and relatively more abundant, the neutralist theory (Hubbell 2001) instead proposes that dispersal limitations and stochastic processes drive species composition, and that the differentiation of niches only plays a limited role for the coexistence of species.

When constructing the SDM, the spatial patterns caused by neutral processes could be erroneously interpreted as niche processes, if these patterns are correlated with environmental variables. Some authors in their respective studies (Queenborough et al. 2007; Valencia et al. 2004; Getzin et al. 2014) limited the scope of the niche theory in the maintenance of species diversity in tropical forests on small scales, however , many other studies found only little evidence for this hypothesis and concluded that niche processes played a predominant role in the distribution of tree species at local scales in tropical forests (Gunatilleke et al. 2006; Chuyong et al. 2011; Yamada et al. al. 2010; Itoh et al. 2003; John et al. 2007; Jones et al. 2008).

When considering mainly the inclusion of topographic variables, especially in the areas where this study was developed, the terrain conditions are so heterogeneous and cause various types of forest, the SDM processes are mainly the product of niche processes, being congruent with previous studies in our study area (Bussmann 2003; Homeier et al. 2008; Homeier et al. 2010) in which the significant influence of the topographic gradient on the occurrence of various types of forest was confirmed, therefore, it seems It is acceptable to assume that species distribution patterns in our study area are mainly caused by niche processes, and that the use of SDM is justified for our study area.

2) The second aspect of the discussion focuses on the evaluation of the SDM. The evaluation criteria show two different behaviors and showed low values for the distribution models of certain species, in the cross validation with random data partitioning, the AUC values indicated that 6 Maxent models and 5 ENFA models could be considered deficient or random, while using TSS 15 of the 16 models performed moderately to efficiently. Similarly, all of the final ENFA models and 15 of the 16 final Maxent models performed significantly better than the null models.

From the ecological point of view, the distribution patterns of the species confirm the belonging of the species to the forest types determined in previous works (Homeier et al. 2008; Homeier et al. 2010). The previous results were obtained in the same study area (RBSF), but using independent sampling plots and different methods, however, having used more than one method for the evaluation of the SDM performance criteria compensates for the reduced area. of study and the relevance of the species to previously established distribution patterns in the determined forest types.

Comparing the MAXENT and ENFA models, the models for most species were more robust using the first method, this is consistent with the findings of previous studies (Hermosilla et al. 2011; Elith et al. 2006), where Maxent showed better performances than other SDM algorithms. One of the reasons for this would be that Maxent fits models with different classes of characteristics (linear, product, quadratic, hinge, threshold, and categorical, Phillips and Dudík 2008), while ENFA only fits linear relationships (Hirzel et al. 2002).

Likewise, another factor that somewhat limited the scope of the study was spatial autocorrelation, a variable that should be excluded or included in the SDM. It is excluded if it constitutes a "spurious" spatial correlation that in many cases is produced by a biased or insufficient sampling, while the "real" spatial autocorrelation should be included in the models because it represents the ecological conditions of distribution of the species (such as the dispersal process) and the habitat conditions (such as soil conditions) in which they are actually distributed. These reasons show that, at least in our study, a reduction in model performance when spatially separated data partitions are used for cross-validation should not necessarily mean that models without a spatial autocorrelation correction are falsely inflated.

3) Finally, the third aspect of the discussion focuses on the interpretation of the topographic variables within the SDM. In our particular case in both models (MAXENT, ENFA), elevation plays an important role in the construction of each of them on a local scale, elevation whose predominant influence on the distribution of species

at intermediate and large scales is well established in Phytogeography (Humboldt and Bonpland 1805; Gentry 1988), was also reported as important at small scales in tropical forests (Lieberman et al. 1985; Wang et al. 2009; Lan et al. 2009; Ledo et al. 2 013).

Although elevation does not act directly on the distribution of species, it has an indirect influence on physiological processes of plants and directly on climatic factors, in the study area the temperature varies -0.52 ° C / 100 m of elevation, which translates into approx. 1.56 ° C difference between the lowest part and the highest part in the study area (Fries et al. 2009), the average annual precipitation increases by 250 mm / 100 m (corresponding to a difference of 750 mm between the sites lowest and highest) and fog input increases by 40 mm / 100 m (corresponding to a difference of 120 mm between the lowest and highest sites) (Rollenbeck 2006). Likewise, the increase in elevation results in a decrease in soil fertility and a decrease in N availability (Tanner et al. 1998) was confirmed for RBSF (Wilcke et al. 2008; Wolf et al. 2011). Furthermore, in our study area, mineral soil depth decreases, organic layer thickness and pH increase, and soil texture becomes thicker at the A horizon with increasing elevation (Wilcke et al. 2008; Liess et al. 2011; Wolf et al. 2011). The difference in the values of the variables in the gradient allows us to understand the influence and importance of elevation in the distribution of species and why we consider it in the SDM.

Another important topographic variable in the SDM construction was the TPI, which, like elevation, indirectly influences, creating a variety of microhabitats that result in forest types. Previous work carried out in the same study area (Homeier et al. 2008) makes reference that different types of forest can be found in the valleys and on the ridges and the continuous values of the TPI express the position of each site in a topographic gradient that it goes from the valleys to the middle slopes. to ridges (Guisan et al. 1999) and is also consistent with previous work (Takyu et al. 2002; Webb et al. 1999; Queenborough et al. 2007; Valencia et al. 2004; Lan et al. 2009; Wang et al. al. 2009; Chuyong et al. 2011) where they determine that topography influences the composition of tropical forests.

The differences in structure and composition of the forests located in the different topographic positions were mainly caused by frequent alterations in the mountain ranges, which were more exposed to chronic and catastrophic wind events than the valleys (Webb et al. 2009), in our area Of study in the ridges, the trees are smaller in height and the relationship between this and DBH is also lower, a fact that supports the previous hypothesis and would occur as a response or adaptation to continuous exposure to the wind. However, the dynamics is higher in valleys than in ridges (Homeier et al. 2010), suggesting that factors related to topography other than wind exposure play a more important role for the distribution of species.

In the valleys, in areas that are periodically flooded, the trees develop the relatively superficial root system, which exposes large trees to being more susceptible to falls (Ashton et al. 2011), while, in the areas of ridges, the trees develop their root system in order to anchor the individual to the ground in a deep way. Other factors influenced by the topographic position in the RBSF are the amount of humus in the soil, the acidity and the nutrients that are lower in the ridges than in the bottom of the valley, likewise, the transfer of water and the removal of minerals. they are most evident on ridges or continuous landslides (Wilcke et al. 2011; Wolf et al. 2011).

Finally, Werner and Homeier (2015) argue that habitat heterogeneity along the topographic gradient from valleys to ridges is caused by a combination of the factors mentioned above and is maintained through a nutrient-driven feedback loop and mediated by plants.

7. Effects of silvicultural treatments and topography on individual tree growth in a tropical mountain forest in Ecuador (Publication IV, Kuebler et al. 2020).

7.1 Methods

7.1.1 Data collection

In this section we summarize the methods used in publication IV (Kuebler et al. 2020) to determine to what extent the topography and the silvicultural treatment implemented influence the individual diameter growth of the trees of the tropical mountain forest in southern Ecuador. We predicted that growth rates between species 1) would show a positive response to silvicultural treatment, and 2) would decrease with increasing elevation and along the gradient from the valleys to the ridges.

As in the previous section, the results of the forestry experiment installed in 2003 were taken as a basis (Sections 3.2.1 and 3.2.2 of this document), we called the silvicultural treatment as release thinning or improvement thinning and the spatial position of each of the trees in the forest inventory.

The diameter growth of the trees was measured by monitoring artisanal steel band dendrometers installed in each PCT at breast height (1.30 m above the ground) or on buttresses or other irregularities, if there were following a protocol previously established. Dendrometers were placed 6 months before silvicultural interventions, because newly installed dendrometers often underestimate radial growth (Pélissier and Pascal 2000). The data used for this study consist of monthly growth records between June 2004 (that is, when silvicultural treatments were applied) and April 2010. For each tree we calculate periodic annual increases (PAI) in DBH during the total time period as the response variable in our statistical analyses.

Likewise, to build the evaluation model, three predictors were chosen at the tree level, their initial DBH, the elevation and the topographic position index (the details of the calculation of this index can be found in Kuebler et al. 2016 and in Kuebler 2020) , in the study area, the two abiotic type predictors related to the terrain have a great influence on the variation in growth between species (Bräuning et al. 2008) and are the most influential microtopographic metrics that determine the spatial distribution of the species arboreal on a fine scale (Kuebler et al. 2016).

The digital terrain model (DTM) was used in both Kuebler et al. 2016 and Kuebler et al. 2020, with a resolution of 1m, from an aerial LIDAR survey (Silva et al. 2015) from which the topographic position index (TPI) was derived, where if a given pixel is in a lower valley / slope, this is expressed with negative TPI values, a mean slope is expressed around zero TPI values and a higher peak / slope (positive TPI values) compared to surrounding pixels (Guisan et al. 1999).

7.1.2 Data Analyses

According to Kuebler et al. (2020), all the data were fit into a single Linear Mixed Model (LMM) in an iterative construction process, looking for which model best describes the empirical data (Zuur, 2009). The Akaike information criterion (AIC) was used for the construction of models, and the likelihood ratio tests. No systematic model selection method was used, because all predictors have a theoretical justification for their inclusion. Instead, only models that included all predictors were considered (Whittingham et al. 2006). The models were fitted using the lme4 package (Bates et al., 2015) in the R statistical environment (R Core Team, 2018).

The final LMM with the optimal fixed effects structure and random effects structure was (Kuebler 2020):

$$\ln(\mathrm{PAI}isp + 1) = \beta 0 + \beta 1 \times \mathrm{Treatment}isp + \beta 2 \times \mathrm{Elevation}isp + \beta 3 \times \mathrm{TPI}isp + \beta 4 \times \mathrm{DBH}isp + \mu 0s + \mu 1s \times \mathrm{Treatment}isp + \mu 2p + \varepsilon isp$$

Where:

- $\mathrm{PAI}isp$ is the response variable indicating the value of DBH growth per year. It was transformed using the natural logarithm of (PAI + 1) to reduce non-normality of residuals and heteroscedasticity.
- $\mathrm{Treatment}isp$ indicates the silvicultural treatment with dummy coding (reference level = 0, released level = 1).
- $\mathrm{Elevation}isp$, $\mathrm{TPI}isp$ and $\mathrm{initialDBH}isp$ are the respective values of the continuous predictors. Two-way interactions between predictors did not lead to a better model performance and were therefore not included. The continuous predictors were scaled by centring them on 0 and dividing them by two times their standard deviation (SD).
- $\mu 0s$ denotes a random intercept for species s to account for interspecific difference in growth rates (Bräuning et al., 2008).
- $\mu 1s \times \mathrm{Treatment}isp$ denotes random slopes for the effect of treatment on species s to account for interspecific differences of responses to the silvicultural treatment (Günter et al. 2008).
- $\mu 2p$ denotes a random intercept for each experimental plot p to account for heterogeneity across plots within the RBSF.

The models for each species were evaluated using the standard model of validation plots for LMM (Zuur, 2009): fitted values against residuals for the entire model, a normal QQ plot, model residuals against all predictors, and adjusted values against to residues for each species (Kuebler 2020). The entire process of validation of the EPI response model for each species is explained in Kuebler (2020) in section 3.2.

7.2 Results

In this section we summarize the results obtained by Kuebler et al. (2020), however, in order not to be redundant with Kuebler 2020, our approach reviews the results exclusively of the interaction between silvicultural treatment and topography, without delving into the statistical analyses that is important but that in a detailed and precise way is found in Kuebler (2020).

The implementation of release thinning means better conditions of space, light and resources for the released trees. The environmental, territorial conditions on a small and large scale of the TMF make up heterogeneous conditions in which species must establish themselves. According to Kuebler et al. (2020), the implementation of thinning only showed a marginal effect with respect to diameter growth, that is, there was no significant difference in diameter growth between the reference trees and the released trees (1.35 mm y^{-1} vs. 1.60 mm y^{-1}, respectively).

Another factor that conditioned the growth of trees was the position on the ground, with the topographic gradient, the PCTs in the valleys have a PAI average of 2.02 mm y^{-1} in the valleys compared to 1.04 mm y^{-1}in ridges.

Elevation also plays an important role in tree growth, in this specific case, growth rate decreases an average of 0.73 mm y^{-1} for every 100 m increase in elevation. All the results obtained show that the PAI is not only influenced by the release of PCTs, but also encompasses a series of factors that demonstrate how complex it is to obtain positive results, especially in TMFs.

7.3 Discussion

The approach used for this work combines tree growth data and microtopography data generated through remote systems with high resolution images, this allowed us to analyze how the abiotic characteristics of the microsite in the field influence growth. of the released trees.

Two of the main variables that significantly affected the PAI were elevation and topographic position, while release had a marginal effect, however, the results obtained indicate a certain potential for the application of these silvicultural treatments, although they can be displaced by the effects of the environmental gradient and the heterogeneity of tree growth.

The pattern of growth decline with elevation has been previously reported (Clark et al. 2015; Homeier et al. 2010; Sherman et al. 2012), but the effect size in our study was larger than in other studies. There are many potential explanations among which the most indicated for our study area refers to the marked altitudinal gradient of the forests in which the silvicultural treatment was implemented, the species composition changes from the most productive forest type I at higher elevations. low to less productive forest types II at higher elevations (Homeier et al. 2010), this change partly explains the decrease in PAI with elevation (Bräuning et al. 2008). Despite the congruwence of our results with those reported previously, a “species” effect was noted, that is, the variability of the growth of PCTs of the same species that are more similar than the growth rates of PCTs of different species.

The best linear unbiased predictions (BLUP) suggest that the PAI of species linked to type II forest was lower than species linked to type I forest, although there were species included in type I forest that grew less than all species. All this randomness in the PAI predictions of species were controlled in the iterative models that were not finally published, but the elevation values shown in these models were greater than those that we finally obtained in the adapted model, this suggests that the strong response from EPI to elevation is due not only to changing species composition due to transitions of forest types, but also to other factors.

For similar geographic scales, the explanation of the influence of the TPI on the PAI has been partly explained by the difference in the floristic composition of the forests in the different topographic positions, with fast-growing species distributed in the valleys and slow-growing species in ridges (Homeier et al. 2010, Liu et al. 2014).

However, the intraspecific differences of the PAI influenced by the TPI may have other explanations, especially those created by microtopography and its influence on biotic and abiotic characteristics, for example, in comparison with valleys and lower slopes, ridges and upper slopes. are characterized by higher humus concentrations, lower pH and fewer nutrients (Wilcke et al., 2011; Wolf et al., 2011), lower litter decomposition (Werner and Homeier, 2015), and a drop-in litter less abundant and rich in nutrients (Oesker et al., 2008). As we determined in the previous work, the topographic variables are significant predictors of the PAI, however much of the variability of the PAI was not explained by the fixed effects of the model but by the effect of the plot, this makes us suppose that the variables Microtopographies did not capture all the growth variability caused by the strong environmental heterogeneity within the study area.

In general, it can be said that the effect of the silvicultural treatment had little explanatory power when modeling the EPI, not the topographic and elevation predictors, however, a true zero treatment effect would explain that the silvicultural treatment did not reach the conventional threshold level of statistical significance.

It should be noted that there was variation in the effect of treatment on EPI between species, with a negative effect in some cases (Cabrera et al. 2019), these differences between species probably explain in part the absence of statistical significance of silvicultural treatment at the level of population (ie across all species), fitting a species-specific model would likely have increased the explanatory power of the treatment effect for some species. Despite the low significance of the treatment effect, the growth rates are in line with other studies in tropical forests (Le Bec et al., 2015; Ruger et al., 2011).

We assume that the unexplained variability of growth between trees caused a large overlap in growth responses, which in turn reduced the statistical power of our analyses. Consequently, the probability of detecting statistical significance of a potential effect of silvicultural treatment could have been low.

With an increase of 18.5% (0.25 mm a-1) that corresponds to the difference between the released trees and the reference trees, our results differ somewhat from those obtained in lowland tropical forests, where the percentage increases. in growth rates after silvicultural treatments, for example, 22-27% (Villegas et al. 2009), 50-60% (Peña-Claros et al. 2008), 13-28% (Souza et al. 2015) and 19-24% (Vatraz et al. 2016). Although the implementation conditions differ somewhat and the ecosystems are also different, they still allow a moderate comparison with our results, therefore, the percentage increase in PAI due to silvicultural treatment in our study seems to be within the range, but at the lower end. of the reported values of tropical forests.

The results obtained refer to a population level, being necessary to refer to Günter et al. (2008) and Cabrera et al. (2019) for an analysis of the approach at the species level of the results obtained in the application of silvicultural treatment. Only here will we refer to a single important timber species such as Cedrela montana that presents in the two cited works, considerably lower growth rates for the released trees compared to the reference trees, our statistical model suggests that there is only a minor difference between the reference trees and those released, this apparent contradiction would have an answer in the analyses of the growth rings (in 38 of the 41 trees analyzed) that during 27 years (1976-2003) that is, before the application of the treatment, the growth variability was also high, so we accept this same pattern to explain that the implementation of the treatment did not have a significant opsitive impact on growth. Given that tree growth in tropical forests tends to self-correlate over time (Brienen et al. 2006; Dionisio et al. 2018), the differences probably persisted after the application of silvicultural treatment. Unlike Günter et al. (2008) and Cabrera et al. (2019), our statistical model controlled for environmental heterogeneity and, in doing so, also considered some of the pre-treatment growth differences between the reference and released groups.

8. Synthesis

This synthesis briefly addresses how each of the articles included in this dissertation respond to its hypotheses and finally how it contributes to sustainable forest management of the TMF. This work was planned to know the response of valuable timber forest species to a silvicultural treatment that consisted of releasing potential trees (PCT) from their competitors and evaluating the long-term effect, at the species and ecosystem level and evaluating the impact on the functional diversity of the forest.

8.1 TMF heterogeneity and species distribution patterns

Several studies carried out determined that more than one type of forest can be found in the RBSF. Bussman (2005) studied the effects that the altitudinal gradient and the associated environmental factors produced on the vegetation along the mountains through a hierarchical analysis of the vegetation cover and the floristic composition. This phytogeographic study demonstrated the presence of several types of forest and floristic communities. This heterogeneity of the forest in our study area was corroborated by several authors (Paulsch 2002, Homeier et al. 2010) who determined at least two types of forests based on their productivity, structure and floristic composition (this work in sections 3.4 and 3.5; Homeier et al. 2010).

Another factor that determined the heterogeneity of TMF refers to the species distribution. Kuebler et al. 2016 determined the distribution patterns of the 16 most frequent species determined in a forest inventory installed in three micro-basins within the RBSF. They determined the distribution patterns of these species, being mainly the topographic factors (directly) and the gradient effects (indirect) that mainly influence their distribution.

For this Kuebler et al. 2016 (Publication III) used two processes; the first called maximum entropy (MAXENT) and one known as Ecological Niche Factor Analyses (ENFA). In addition, the prediction maps of habitat suitability for each species were carried out, emphasizing the presence of two groups of species associated with the presence of the types of forest called in this work "Valley Forest" with higher scores for habitat suitability on lower elevations in valleys and “Ridge Forest"that preferred higher elevations and ridges.

Structurally, the determined forests present significant differences with regards to particular parameters. In the plots located in "Valley Forest" tree height reaches 12 to 20 meters while in the plots at higher elevations in the "Ridge Forest," tree height ranges from 6 to 8 meters. The total basal area decreases with altitude, where in lower elevation plots the average basal area was 21.6 m^2 ha^{-1} (± 0.24); in the plots at higher altitudes the average basal area reaches 10.02 m^2 ha^{-1} (± 0.18). The difference is evident and in this diverse context both in species and in forest types, the forest experiment was implemented to understand the background response of some tree species to a planned silvicultural intervention.

8.2 Growth of released species and influence of topographic factors.

In this section we analyse the growth of released species (Publication I, Cabrera et al. 2019) and the combination of selective thinning with topographic factors (Publication IV, Kuebler et al 2020). Reference is made to two approaches, the first from a forestry point of view and the second from an ecological forestry approach, both complementary in the search for the most convenient actions when planning the sustainable management of the TMF.

8.2.1 Growth Response of Nine Timber Species to Release in a TMF of southern Ecuador

The effect of the release on the PCTs' growth was analyzed at the species level. We were able to determine different responses to treatment in each of the species studied. The species which prefer open sites responded positively to release, while shade tolerant species and species with pronounced phenological traits responded negatively. The initial DBH was also an important factor for diameter increases. This is because trees of diameter class I (20 cm to 30 cm DBH) responded positively to the treatment, whereas for bigger or older individuals, the differences decreased or became negative.

We differentiate three species groups. The first group that responded positively to the release in this group are *Inga acreana* and *Hyeronima asperifolia*. *Inga acreana* showed a mean annual growth of 1.13 cm ± 0.72 (standard deviation) over the whole study period, whereas the control trees showed an annual increment of only 0.56 cm ± 0.47. Diameter growth of the released trees was not continuous, in which the lowest increment was measured during the first year (1.01 cm ± 0.81).

Released trees of *Hieronyma asperifolia* showed a mean annual growth of 0.63 cm ± 0.64 over the whole study period, whereas the control trees only had an increase of 0.35 cm ± 0.36. Similar to *Inga acreana,* the diameter growth of *Hyeronima asperifolia* increased during the observation period, which resulted in the highest increment of growth during the third year (0.76 cm ± 0.53).

Species with negative responses to release were *Cedrela montana*, *Tabebuia chrysantha*, *Podocarpus oleifolius* and *Nectandra membranacea*. All species showed significantly lower diameter growth respective to their control trees, especially during the second and third year after release.

The species with the most significant differences in the group was *Cedrela montana* (1.16 cm ± 1.21 vs. 0.87 cm ± 1.24), where diameter increment in released trees and the reference trees presents a similar pattern. A bigger increase is observed in both diameter classes, both taken in the second period, but it is not significantly different compared to other periods and when comparing treatments. The diameter increment of control trees of *Nectandra membranacea* is higher than the increment of released trees (0.44 cm ± 0.62 vs. 0.26 cm ± 0.32).

Analysis of diameter increment of *Podocarpus oleifolius* shows that the implementation of selective thinning favorably affects individuals of this species, although the increase is not enough to make statistically significant differences between the individuals released and the reference individuals. The diameter increment of *Tabebuia chrysantha* is evident in trees released from the diameter class I in the first year after release. The growth of this group of individuals decreases during the following two periods.

The species group that did not show any effect on growth by release is made up of *Hyeronima moritziana*, *Clusia ducuoides* and *Ficus citrifolia*. Apparently, factors other than liberation have an influence on the diametric growth of these species. The diametric growth of *Hyeronima moritziana* (0.12 cm ± 0.23 vs. 0.17 cm ± 0.22) and *Clusia ducuoides* (0.10 cm ± 0.16 vs. 0.10 cm ± 0.21) was generally low (released trees and control trees) over the complete study period, but with generally the highest DBH increments during the third year. In contrast, *Ficus citrifolia* (1.11 cm ± 1.04 vs. 1.09 cm ± 1.22) showed higher DBH increments during the first two years.

When relating growth to climatic factors in the positive response group (specifically precipitation and temperature), the influence of temperature is clearly noted, and despite the fact that its fluctuation is relatively small (1.5 °C) throughout the year, the increase in diameter of the released trees coincides with the increase in temperature. However, the value does not reach an important level of significance when analyzing the growth process.

In the first year of monitoring, all species responded negatively to the release. As we said above, if the growth of the species is associated with the seasonality of precipitation and temperature, thinning will not positively affect the species that have pronounced seasonality in their physiological processes because individuals are beginning their foliation stage, where they turn all their energy to this process, inhibiting in a certain way the diametric growth, regardless of whether or not they are released from their competitors.

All of the selected species showed a similar annual cycle respective to their diameter increase. Generally, growth was observed during the austral summer period, specifically between December and April, when temperatures are highest and sufficient water is available. During austral winter (June to September), most of the species reduced or suspended their growth because of the lower temperatures during this period. Therefore, due to the per-humid climate in the RBSF, precipitation is secondary for diameter growth, because sufficient rainfall occurs during the year which is then stored in the soil, where water is consequently always available for the plants. What is more important are the small temperature variations between austral summer and austral winter, which are generally used by the plants to begin their phenological processes.

Finally, the initial DBH of the trees (diameter classes) was found to be an important factor for the success of the treatment. Trees of class I (20 cm to 30 cm DBH) generally responded positively to the treatment, whereas for bigger or older individuals, the differences between the released and control trees decreased or became negative.

8.2.2 Effects of Silvicultural treatments and topography on individual tree growth

The present study investigated the relative effects of silvicultural treatments and topography on growth rates at the tree level in a TMF. In this section we will analyze how the silvicultural treatment (release thinning) interacts with the strong topographic gradients in the study area. Unlike the previous study that focused clearly on the response of trees to silvicultural treatment, this approach seeks to determine the influence of topographic factors in addition to silvicultural intervention.

The Annual Periodic Increase (PAI) in DBH six years after the silvicultural treatment was used as our outcome variable. As topographic predictors we used elevation and a topographic position index. To control for the by-species growth variability we included random intercepts for species and random slopes for the effect of treatment on species in our model.

One of the premises that have been developed over many years and have been included in our work is the fact that tree growth decreases as altitude increases (Clark et al. 2015; Homeier et al. 2010; Sherman et al. 2012), but the effect size in our study was larger than in other studies.

Over the altitudinal range of the silvicultural experiment the species composition shifts from the productive lower forest (type I or Valley Forest in this dissertation) to the higher, less productice forest (type II or Ridge forest in this dissertation). This would explain to some extent the decrease in PAI with elevation (Bräuning et al. 2008).

Are our results in line with this explanation? A moderately high SD of the random intercept across species in our results indicates that there is indeed a substantial species effect, with growth rates of PCTs from the same species being more similar than growth rates of PCTs from different species.

Based on Homeier et al. (2008), we can link all eight species in our study to either Forest type I or II. Species linked to Forest type II (*Clusia ducuoides, Hyeronima moritziana and Podocarpus oleifolius*) have a lower PAI than species linked to Forest type I (*Cedrela montana*, *Hyeronima asperifolia*, *Inga acreana* and *Nectandra membranacea*). The two species of the Valley Forest *Inga acreana* and *Hieronyma asperifolia* are furthermore the species with a positive response to release thinning (Cabrera et al. 2019).

The elevation indirectly affects other factors that also possibly play an important role in the decrease of the PAI rates. For example, increasing elevation has been related to an average annual fall rate of -0.52 K / 100 m (Fries et al., 2009); an increase in mean annual precipitation and fog entry by 250 mm/100 m and 40 mm/100 m, respectively (Rollenbeck, 2006); a decrease in soil fertility, N availability, soil depth minerals and an increase in the thickness of the organic layer and pH (Ließ et al., 2011; Ließ, 2011; Wilcke et al., 2009; Wolf et al. 2011). Abiotic and biotic differences due to microtopographic variations are large in our study area: compared to valleys and lower slopes, ridges and upper slopes are characterized by higher humus concentrations, lower pH and fewer nutrients (Wilcke et al. al. 2011; Wolf et al. 2011), lower litter decomposition (Werner and Homeier 2015), and a less abundant and nutrient-rich fall (Oesker et al. 2008).

The results obtained have theoretical support from other similar studies in the same place of study (Homeier et al., 2010) or in other TMF where several results indicate that they did not find significant differences between valleys and lower slopes (Bellingham and Tanner, 2000), or higher growth rates on the ridges compared to the lower slopes (Herwitz and Young 1994).

All the aforementioned allows us to assert that the topographic variables (Elevation and TPI) are strong when grouping the abiotic conditions of the study area, however the experimental plots explained a considerable amount of the variability of the PAI that was not explained by fixed effects. Therefore, the microtopographic variables did not capture all the growth variability caused by the strong environmental heterogeneity within the study area.

8.3 Functional diversity changes in the tropical mountain forest after the implementation of selective thinning

Selective thinning has been implemented in tropical forests in regions such as Asia and Africa for more than a century, however in Ecuador it has recently been implemented.

The treatment consists of eliminating species of low commercial value that are competitors of more valuable species. This practice is based on the theory that tree growth rates are directly related to the amount of sunlight received and the availability of nutrients, and for this reason, all unwanted or competing trees around valuable timber species are removed to obtain adequate lighting and improve nutrient availability (Dawkins 1955, Louman et al. 2001).

To determine if the implementation of release thinning affects the functional diversity of TMF in the RBSF, we calculated and monitored the variability of six indices of functional diversity before and after applying the silvicultural treatment. The following indices were included:

- Functional Richness (FRic), which represents the amount of space occupied by a community, independent from the relative abundances of the species (Mason et al. 2013).

- Functional Divergence (FDiv) measures how species of a community diverge in their distance from the center of gravity in the functional space, and determines the relative abundance of a species within its functional range, (Mason et al. 2013, Villéger et al. 2008). FDiv provides additional information for FRic, because this index indicates which species has the most extreme feature combinations (i.e., specialized species), and which ones are generalist (Mouchet et al. 2010).

- Functional Evenness (FEve) quantifies the regularity of how species abundances are distributed within their functional range, by correlating abundance with average distance between different species (Zanne et al. 2009). FEve can be related to the uniformity of species (Pielou's J) and the FDiv because it determines if the extent of functional distances between the species is regular (Biswas and Mallik 2010).

- Functional Dispersion (FDis) gives the mean distance of an individual species relative to the centroid of the community, which depicts its mean distance relative to all species in the community, and therefore, accounts for relative abundances of a species.

- Rao Quadratic Entropy (RaoQ) correlates the abundances of different species (Botta- Dukat 2005) to improve the FD index. An adverse property of RaoQ is that its value may decrease if species richness increases, because abundances and dissimilarity between the species are considered.

- Community weighted mean (CWM) represents the sum of each species trait value weighted by its relative abundance in the community (Lavorel et al. 2008). To characterize the community structure from a functional point of view, we used the community weighted mean, which is calculated combining the species abundance with the trait values of the given species (Ricotta and Moretti 2011). This describes the trait averages over a community (Bello et al. 2007) and reflects the dominant trait in a given community (Violle et al. 2007, Garnier et al 2004, leps et al. 2006).

The functional diversity indices monitored were calculated based on the following traits of the species: wood density, stem density, diameter growth, type of leaf, ecological union and dispersal syndrome, the first four being acquisitive traits while the rest they are conservative (Cabrera et al. 2020).

It is necessary to note that many authors consider that functional diversity is closely linked to the functionality of ecosystems, the most diverse ecosystems generally maintaining the ecosystemic functions of each one. However, the impact of silvicultural treatments is a critical point of disagreement between conservationists and foresters because a reduction in diversity (for example, timber extraction by thinning) could result in a loss of functionality (Biswas and Mallik 2010).

This is demonstrated by other studies (Baraloto et al. 2012; Clark and Covey 2012), which indicate that the functionality of the ecosystem is altered due to the loss of species, even if there were no significant changes in taxonomic diversity. However, Chaudhary et al. 2016 clarifies that these traditional approaches must be reviewed, because the impacts of silvicultural treatments cannot only be limited to the relative loss of species.

With the collected data, this work investigated the response of the TMF to selective thinning in southern Ecuador and evaluated the impact of selective thinning on the diametric growth of the released species, the diversity and functionality of the forest and answered the following question: Does selective thinning imply the loss of functional diversity of the natural forest?

The initial hypothesis was that selective thinning significantly affects functional diversity, due to the loss of species that naturally constitute the forest community. To do this, the changes in the acquisitive and conservative traits of the species were analyzed and related to the intensity of thinning.

Regarding the diversity of the forest, in selective thinning implementation the maximum impact was the loss of the only individuals registered in the inventory of four species: *Virola* sp. (Myristicaceae), *Chrysophyllum lanatum* T.D. Penn (Sapotaceae), *Alchornea triplinervia* (Spreng.) Mull. Arg. (Euphorbiaceae) and *Persea subcordata* (Ruiz and Pav.) Nees (Lauraceae). In total, extracted species belonged to 30 families, in which nine species were of Lauraceae; six species of Euphorbiaceae; five species of Meliaceae; three species of Clusiaceae, Melastomataceae, Moraceae and Rubiaceae; and where two species of Cecropiaceae and Mimosaceae were cut.

At the structural level, the percentage of tree extraction with respect to the total number of individuals per species ranged between 1.5 and 100%, with an average value of 23.2%, and at the basal area it resulted in an average stem extraction of 18.8 ± 12.1 (SD) ha^{-1}, with a minimum of 4 trees ha^{-1} and a maximum of 56 trees ha^{-1}. The basal area extracted was on average 1.8 ± $1.4m^2$ ha^{-1} (SD), and the most intensive extraction was 4.8 m^2 ha^{-1}.

Regarding the impact of selective thinning on the functional diversity indices, we found that the variations of the different indices that make up the FD of the studied TMF are not produced exclusively by the implementation of selective thinning, but also by the distribution of the TMF along the altitudinal gradient, which implies different structural and diversity conditions.

The indices that were significantly influenced by the implementation of thinning were FRic (Functional Richness) and FDis (Functional Dispersion), the rest of the indices being influenced by predictors related to the natural conditions of the forest, while the predictors related to the implementation of the treatment were not significantly influenced by these indices. Functional uniformity (FEve) was not significantly affected by any predictor.

We were able to determine that the changes in functional diversity and community composition after the implementation of selective thinning are minimal. In four of the six functional diversity indices evaluated, silvicultural intervention does not have significant effects, which indicates that a planned intervention allows for conserving the functionality and diversity of the forest, allowing it to serve as a conservation area, providing all its ecosystem services; therefore, selective logging could also be a useful tool for biodiversity conservation and sustainable forest management (Lohbeck et al. 2013, De Avila et al. 2015).

Another relevant aspect found in our research refers to the use of acquisitive traits of the species in the evaluation of functional diversity, traits that are closely linked to the implementation of thinning that in theory influences, for example, the growth of trees and in stem density which translates into resources for forest owners.

9. Conclusions

This study provides several important points focused on sustainable forest management in Ecuador, especially the TMF of southern Ecuador. Our results converge on some criteria that allow us to manage biodiversity among montane forests, which are fragile and increasingly threatened by changes in land use, overexploitation and deforestation due to extensive livestock farming.

The diversity of the TMF at the species and community level is corroborated when in a relatively small area we determine at least two types of forests with species characteristic of each one and with an easily identifiable structure in the field. This allows for proposing management guidelines for each type of forest, since each responds differently to the implementation of silvicultural treatments. The response at the species level is also documented here.

The floristic structure and composition of the “Valley Forest” and the “Ridge Forest” are coupled to more widely distributed floristic formations such as the Order Alzateetalia verticillatae and Purdiaeaetalia nutantis respectively, as determined by Bussman (2003), which validates the floristic analysis carried out in our study area, by the coincidence of indicator species of each floristic association.

With regards to the silvicultural treatment (release from competitors) that was applied to nine timber species resulted in different individual responses. In general, species which preferred open sites responded positively to release, whereas shade tolerant species responded negatively. Tree species which are light- and shade-tolerant did not show any changes respective to diameter growth. Furthermore, the two species with defoliation (seasonality) responded negatively, which may be due to the time of release (June, during austral winter), which occurred during the time new leaves are built.

All selected species showed a similar annual cycle respective to their diameter increase. Generally, growth was observed during the austral summer period, specifically between December and April, when temperatures are highest and sufficient water is available. During austral winter (June to September), most of the species reduced or suspended their growth because of the lower temperatures during this period. Therefore, due to the per-humid climate in the RBSF, precipitation is secondary for diameter growth, because enough rainfall occurs during the year which is then stored in the soil, where water is consequently always available for the plants. What is more important are the small temperature variations between austral summer and austral winter, which are generally used by the plants to begin their phenological processes.

Finally, the initial DBH of the trees was found to be an important factor for the success of the treatment. Trees of class I (20 cm to 30 cm DBH) generally responded positively to the treatment, whereas for bigger or older individuals, the differences between the released and control trees decreased or became negative. This means that improved light conditions as well as nutrient availability are specifically beneficial for younger trees, which still compete for space and nutrients. Older trees are established within their ecosystem and generally grow slower, which explains why release did not increase their competitive abilities. Therefore, the release of trees in natural tropical mountain forests is only practical for younger trees, which are still competing for light and nutrients.

Impact of selective thinning on functional diversity

Selective thinning was carried out at different intensities, which slightly affected the forest FD. The calculated FD indices were based on different characteristics of the species, which improved the knowledge to design sustainable forest management practices in ecologically sensitive ecosystems. However, significant changes in DF were expected for all traits and predictors, because forest composition, stand heterogeneity, and climatic conditions in a TMF are especially challenging. As the findings of this study showed, the intensity of the treatment did not have a significant effect on the changes in FD within the community, either because of the short time between the implementation of the thinning and the measurements or because of the composition of the eliminated individuals.

In the context of logging, the conservation of rare or less abundant species should be a priority before starting any forestry activity. Endangered species should be excluded from harvesting processes, logging and other forestry activities. Nonetheless, a sustainable forest management in combination with ecosystem conservation should remain a main objective for future development, because this not only guarantees an economic income for the local population, but also ensures the functionality of the forest stand to provide essential ecosystem services.

Finally, with respect to the verification of the hypotheses raised at the beginning of the work, indeed the RBSF forest is heterogeneous and at least two types of forest can be found to be influenced by the altitudinal gradient and its associated environmental variables (H1). We also verified that the implementation of release thinning does not significantly affect the taxonomic and functional diversity of the forest in RBSF (H2). Diametric growth in certain species is influenced by selective thinning and by the topography of the land and its correlated environmental variables (H3).

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10. Annexes

forests

Article

Early Growth Response of Nine Timber Species to Release in a Tropical Mountain Forest of Southern Ecuador

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Abstract: Research Highlights: This study determined that treatment "release from competitors" causes different reactions in selected timber species respective to diametrical growth, in which the initial size of the tree (diametric class) is important. Also, the growth habit and phenological traits (defoliation) of the species must be considered, which may have an influence on growth after release. **Background and Objectives:** The objective of the study was to analyze the diametric growth of nine timber species after their release to answer the following questions: (i) Can the diametric growth of the selected timber species be increased by release? (ii) Does the release cause different responses among the tree species? (iii) Are other factors important, such as the initial diameter at breast height (DBH) or the general climate conditions? **Materials and Methods:** Four-hundred and eighty-eight trees belonging to nine timber species were selected and monitored over a three-year period. Release was applied to 197 trees, whereas 251 trees served as control trees to evaluate the response of diametrical growth. To determine the response of the trees, a linear mixed model (GLMM, R package: LMER4) was used, which was adjusted by a one-way ANOVA test. **Results:** All species showed a similar annual cycle respective to diametric increases, which is due to the per-humid climate in the area. Precipitation is secondary for the diametric growth because sufficient rainfall occurs throughout year. What is more important, however, are variations in temperature. However, the species responded differently to release. This is because the initial DBH and growth habit are more important factors. Therefore, the species could be classified into three specific groups: Positive, negative and no response to release. **Conclusions:** Species which prefer open sites responded positively to release, while shade tolerant species and species with pronounced phenological traits responded negatively. The initial DBH was also an important factor for diametric increases. This is because trees of class I (20 cm to 30 cm DBH) responded positively to the treatment, whereas for bigger or older individuals, the differences decreased or became negative.

Keywords: climate conditions; diametric growths; growth habit; initial DBH; tree competition

1. Introduction

During the last few decades, deforestation and land degradation in tropical forests have been studied extensively, due to their role in the global carbon cycle and climate system [1,2], as well as because of their importance in ecosystem services [3]. Tropical forests cover 7% of the earth's surface but contain 50% of the global forest biomass, and therefore are the most important natural carbon stocks and sinks regarding future global warming [4]. The above ground biomass (AGB) accounts for 70%–90% of the total carbon biomass, mainly stored in the trunks and branches of trees [5]. Furthermore, tropical forests represent 36% of the net primary terrestrial production, which contributes to the regulation of the carbon dioxide (CO_2) concentration in the atmosphere [2,6]. Therefore, the challenge for foresters is to understand the dynamics in tropical forest stands, including the productivity of desired timber species, in order to implement sustainable practices and prevent deforestation and ecosystem destruction [7,8].

Intermediate treatments to improve forest productivity, such as the release or removal of competitors from timber trees, were implemented some decades ago, including implementation in tropical countries [9–11]. The process, in which undesirable species and other competitors near the timber species are eliminated, helps to improve their productivity, because diametric growth is a result of competition for space and resources with other species [12]. This silvicultural treatment allows a diametric increase in trees [13–15] and therefore is frequently applied in managed forests for timber production [11]. Release from competitors is best developed in boreal forests [16] and alpine forests [17], where implementation results in significant diametric increases. Also, in neotropical countries (e.g., Puerto Rico, Nigeria, Guyana, Sarawak and Brazil) this technique has been implemented successfully in managed forests [10,15]. However, in natural tropical forests, the release from competitors around the desired timber species is poorly investigated thus far, because these forest types present an extraordinarily high species density, even though the density of individual species is comparatively low [18]. This generally leads to the decelerated diameter growth of tropical forest trees [19], but growth rates vary significantly between species, depending on their growth habit (early-, mid- or late-successional), age, phenological traits and climatic conditions [20,21].

Timber harvesting in natural tropical forests may have a similar effect to release [22], but the remaining trees often suffer considerable impacts, which can only be minimized by applying directed fall techniques [23]. Nonetheless, an enhanced diametric growth of desirable timber species in natural tropical forests may lead to sustainable forest management if the collectivity of the ecosystems involved are not affected [24]. The same is valid for tropical mountain forests (>1500 m a.s.l.), which have been recognized as being indispensable for all environmental services, such as water production and storage, as well as for water regulation [25], besides their extraordinarily high biodiversity [3]. The high biodiversity of tropical mountain forests is a result of rapidly changing climate conditions caused by the local topography. Generally, air temperature decreases towards higher elevations, but precipitation amounts increase, resulting in fast changing environmental conditions [26–28]. The altitudinal gradients diversify both structurally and floristically the tropical mountain forest [29,30], but also limit the growth of timber species, reducing their diametric growth and therefore their productivity, due to competition with other plant species.

Knowledge on the behavior of timber species within tropical mountain forests respective to release is still lacking, but this silvicultural treatment can promote sustainable natural forest management without ecosystem destruction. In Ecuador, this intermediate treatment was recently implemented, but the effects must be still evaluated. Hence, the objective of this work is to analyze the radial incrementation of nine timber species in a tropical mountain forest in southern Ecuador after their release (removal of competitors). This research aims to answer the following questions: (i) Can the diametric growth of the selected timber species be increased by release? (ii) Does release cause different responses in the tree species? (iii) Are other factors important, such as the initial DBH, seasonality or general climate conditions? To determine the response of the trees, a linear mixed model (GLMM, R package: LMER4) was applied.

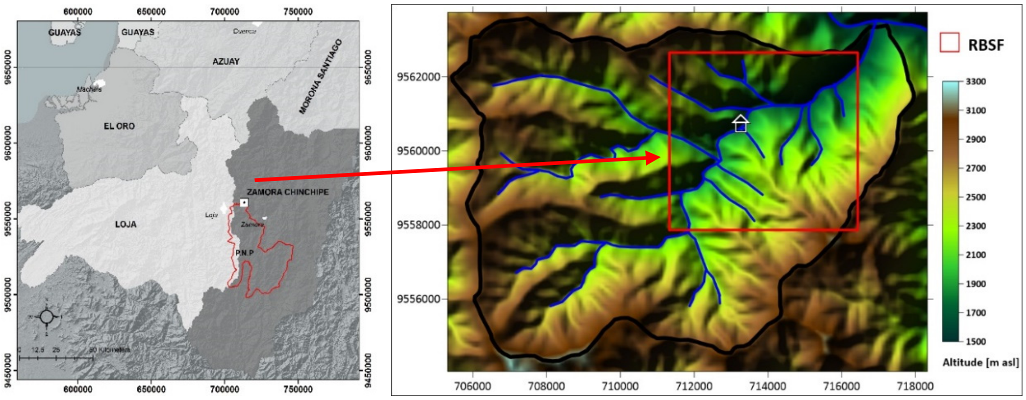
2. Materials and Methods

2.1. Study Area

The study was executed in the primary tropical mountain forest of the "Reserva Biológica San Francisco" (RBSF, 1850 m a.s.l., [31]), located at the eastern escarpment of the south Ecuadorian Andes. The elevation of the catchment [32], which drains into the Amazon Basin, ranges from ∼1700 m a.s.l. at the valley bottom to ∼3200 m a.s.l. at the highest mountain peaks (Figure 1). The natural vegetation in the RBSF is an evergreen tropical mountain forest, which covers the slopes from the valley bottom up to the tree line at ∼2700 m a.s.l. [33]. The forest can be divided into evergreen lower montane forests (up to 2100–2200 m a.s.l.) and upper montane forests, up to the tree line. Above ∼2700 m, a shrub-dominated sub-paramo prevails, where small patches of Elfin forest, the so-called Ceja Andina, dominate the landscape [34]. Both types of montane forest can be subdivided into a lower slope (ravine) forest and an upper slope (ridge) forest [29,30]. The ravine forests are characterized by lower stem density, but simultaneously by greater basal areas (tree diameters) and higher canopies when compared to the ridge forests, where lesser tree species are also present. The difference in forest structure is mainly due to the climatic conditions and prevailing soil types [28,35].

The climate in the catchment is per-humid, with marked altitudinal gradients in air temperature, humidity and rainfall [36]. The annual mean air temperature ranges from 19.4 °C at the valley bottom to 9.4 °C at the highest mountain tops. However, the average diurnal temperature amplitude is lowest inside dense forest stands compared to the other vegetation units present in the study area (pasture and paramo), because the canopy layer shelters the air inside the forest against daily irradiance and nocturnal outgoing radiation [37]. Furthermore, the air inside the tropical mountain forest is generally saturated, because dense canopies hinder the exchange of the air inside the forest with the free atmosphere, while the soils inside the forest stands are commonly saturated [38].

The distribution of rainfall is linked to altitude, due to orographic precipitation formation [36]. The average annual rainfall amounts vary between 2300 mm at the valley bottom and 6700 mm at the mountain tops. These annual rainfall amounts include both rain and fog precipitation, because both clouds and fog deposit water directly onto the vegetation, and therefore both must be considered as a relevant available water input from the atmosphere [26]. The seasonal rainfall distribution shows a clear annual cycle with the main rainy season between May and September (austral winter) and a relative dry season between November and February (austral summer) [36].



(**A**) (**B**)

Figure 1. Location of the study site at the border of the Podocarpus National Park (P.N.P., **A**) and a digital elevation model (UTM 17S) of the San Francisco catchment, including the Reserva Biológica San Francisco (RBSF) area (**B**).

The soils in the RBSF mainly belong to the order of Inceptisols. At the lower parts of the slopes, Dystrudepts are more frequent, whereas at the upper parts Humaquepts and Petraquepts dominate the area [39]. According to Wilcke et al. [40], the soils in mountain forests are characterized by thick organic layers, which store large contents of biomass and nutrients. However, the thickness of the organic layer depends mainly on two factors: The altitude and the slope gradient. At higher elevations, the temperatures are lower and therefore the degradation of the material is decelerated, leading to an accumulation of the organic matter [41]. At steep slopes, the organic layer is generally thinner due to enhanced soil erosion processes, which transport the material to the lower and less inclined parts, where the organic matter is sedimented. These processes also affect the chemical properties of the soils, making the availability of nutrients for plants highly heterogeneous [25].

2.2. Experimental Design

Over the past few decades, several permanent plots have been monitored in a natural tropical mountain forest in southern Ecuador, where the growth of different tree species has been analyzed along with observations of the behavior of the trees, respective to the addition of nutrients [34]. Other studies monitored the DBH increment of the different tree species to estimate the AGB and annual biomass production, as well as the influence of climate factors on the trees at different altitudes [29,35] and alterations of the climate conditions due to deforestation [37,38]. As part of a long-term monitoring forestry project, in January 2003, 52 plots of 2500 m^2 each were installed inside the tropical mountain forest of the RBSF. The plots were located in three different gullies (quebradas) at different altitudes: Quebrada 2 (Q2, 20 plots), quebrada 3 (Q3, 16 plots) and quebrada 5 (Q5, 16 plots). After the plot installation, a forest inventory was carried out and all trees with a DBH greater than 20 cm were marked, as recommended by [42], to analyze the growth of the forest trees. Afterwards, botanical samples were collected and identified taxonomically in the herbarium LOJA.

For the release, only high-quality trees were selected, called "potential crop trees" (PCTs), including nine timber species, because the silvicultural treatment applied here tends to promote sustainable forest management without ecosystem destruction. A PCT is a commercial species with a diameter at breast height (DBH) larger than 20 cm, with a good stem shape and concurrent health [43]. The PCT species selected for this study were: *Tabebuia chrysantha* (Jacq.) G. Nicholson; *Cedrela montana* Turcz.; *Inga acreana* Harms., *Hyeronima asperifolia* Pax & K. Hoffm., *Hyeronima moritziana* Mull Arg., *Podocarpus oleifolius* D. Don ex Lamb., *Nectandra membranacea* (Sw.) Griseb., Dugand. Three of these species are considered to be valuable timbers, namely *Tabebuia chrysantha*, *Podocarpus oleifolius* and *Cedrela montana*, whereas the other six are classified as medium quality timbers. *Tabebuia chrysantha*, *Podocarpus oleifolius and Nectandra membranacea* are hard wood trees of late-succession. *Tabebuia chrysantha* has rings and pores which are easily visible. *Cedrela montana* is a semi-hard wood tree of mid-succession with visible rings and pores. *Inga acreana*, *Hyeronima asperifolia and Hyeronima moritziana* are also semi-hard wood trees of mid-succession, but do not present rings. *Clusia ducoides* and *Ficus subandina* are soft wood trees of early to mid-succession without rings [44].

In the installed plots, a total of 448 PCT individuals were identified, of which 197 individuals were selected for release and 251 were left in their natural environment as a reference (control trees) to compare the effect of the silvicultural treatment to natural conditions. In Q5, eight of the nine PCT species were present, with exception of *Clusia ducuoides*, whereas in Q3, *Ficus citrifolia* and *Inga acreana* were absent and only one individual of *Cedrela montana* was found. The plots in Q2 included all of the selected PCT species, with several individuals (Table 1).

Table 1. Released potential crop trees (PCTs) and reference trees (R) that were monitored in the different gullies (Quebradas: Q2, Q3 and Q5).

Species	Q5 PCT	Q5 R	Q3 PCT	Q3 R	Q2 R	Total PCT's	Total R
Cedrela montana	20	14	0	1	7	20	22
Podocarpus oleifolius	1	0	12	7	10	13	17
Tabebuia chrysantha	46	14	0	2	25	46	41
Ficus citrifolia	4	3	0	0	13	4	16

Table 1. *Cont.*

Species	Q5 PCT	Q5 R	Q3 PCT	Q3 R	Q2 R	Total PCT's	Total R
Nectandra membranacea	9	8	5	1	27	14	36
Hyeronima asperifolia	27	10	1	1	15	28	26
Hyeronima moritziana	3	0	16	10	11	19	21
Clusia ducuoides	0	0	37	37	14	37	51
Inga acreana	16	5	0	0	16	16	21
					Total	**197**	**251**
						448	

By means of their initial DBH, the individual trees were grouped into four diametric classes (class I = 20.1–30.0 cm DBH, class II = 30.1–40.0 cm DBH, class III = 40.1–50.0 cm DBH, and class IV ≥ 50.1 cm DBH). Afterwards, the treatment was defined (release or control) and the monitoring periods (monthly) were established, taking into consideration the general climatic conditions (Table 2).

Table 2. Variables analyzed and the factors included in the applied GLMM model.

Analyzed Variables	Description	Factor
Diameter Class	Diametric class of the released and reference trees	Class I: 20.1–30.0 cm DBH Class II: 30.1–40.0 cm DBH Class III: 40.1–50.0 cm DBH Class IV: >50.0 cm DBH
Treatments	Removed competitors	Released
	Non-removed competitors	Reference
Period	Time between initial measurement drive by climatic seasons	Period I: 12 months Period II: 24 months Period III: 36 months
Precipitation	Accumulated monthly precipitation	mm/month
Temperature	Monthly average temperature	°C/month

2.3. *Silvicultural Treatment*

As mentioned before (Section 1), release consists of the removal of competitors to improve space and increase the availability of nutrient for the desired species [12,43]. This treatment is based on the theory that the growth rates of trees are directly related to the quantity of sunlight received. Therefore, all other trees and undesirable species or competitors around the desired timber species are removed to obtain adequate lighting and to enhance nutrient availability [45,46] (Figure 2). To determine the competitors of the selected PCT trees, all plots were visited and the tree form, crown diameter and social position within the forest stand, as well as stem quality, were analyzed and evaluated. All detected competitors were labeled with plastic tape and removed during a campaign between April and May of 2004. The release included mainly competitor trees, which were cut using the method of directional falling to avoid additional damage to the ecosystem [10]. Furthermore, no herbicides were applied to the stumps to guarantee the development of species collectivity in their natural environment without alterations or contaminations.

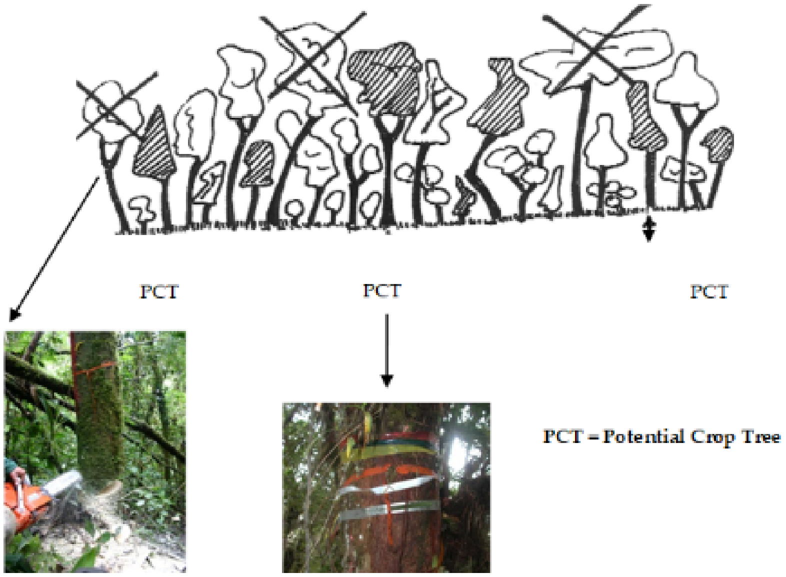


Figure 2. Implementation scheme of the applied silviculture treatment with photos during the campaign (May 2004, place: Q5).

2.4. Data Analysis

To evaluate individuals in the nine selected PCT species, the monthly diameter increase of each tree was measured. The trees were monitored for 36 months and the DBH measurements of each recording, compared to the initial value as well as to the previous data, were used to analyze the effect of liberation on the individual tree species over time. Therefore, metallic dendrometers were used, fixed to the PCTs and control trees, besides specific labels for each tree species and their respective diameter class (Figure 2). Furthermore, to improve the analysis, additional the DBH data of the selected species were included, provided by other studies which estimated AGB and the annual biomass production in the RBSF [34,47].

The diametric increase of the PCTs and reference trees were calculated by means of the equation proposed by [21]. The diametric increase (Di [cm/month]) can be determined as the difference between the initial diameter (Do [cm]) and the subsequent DBH measurement (D1 [cm]), divided by the time between the field campaigns (which is monthly here). The equation was applied to all selected trees after their initial DBH measurement, indicating the monthly DBH increase of each tree. Then, all of the individual monthly results were averaged to obtain the mean increase for each species, considering their specific diametric class. Finally, the average monthly DBH increases were used to calculate mean annual values as well as a value for the entire study period (36 months).

The homoscedasticity of the results was checked by means of the Levene's test [48]. Their normality was checked with the Shapiro–Wilk test [49] using the software R, version 3.2.0 [50]. If significant differences in diameter growth between the PCTs and the reference trees were found, considering the different diametric classes, an exploratory T-test (using the software R) was executed, whereas an independent Tukey test (Tukey HSD function, using the software R) was applied if significant differences between the monitoring periods were determined. Both tests were accepted with p-values ≤ 0.05, meaning that the results were statistically significant.

To check whether the initial DBH (diametric classes) or other factors, like seasonality or climate conditions, determine the diameter growth of the selected timber species, a linear mixed model (GLMM, R package: LMER4) was applied. The linear mixed model combines explanatory categorical factors like diameter class, treatment or climate conditions, and provides a "random" variable for the repeated measurements throughout time (period). To adjust the linear mixed model, a one-way ANOVA test was executed and accepted with p-value ≤ 0.05.

3. Results

The selected timber species responded differently to release respective to their reference trees (Table 3). Therefore, the species analyzed were separated into three groups (positive response, negative response and no response to release).

3.1. Positive Response to Release

The species that responded positively to release were *Inga acreana* and *Hyeronima asperifolia*, which had a greater diametric increment than their reference trees. *Inga acreana* showed a mean growth of 1.13 cm ± 0.72 (standard deviation) over the whole study period, whereas the control trees showed an increment of only 0.56 cm ± 0.47. The diametric growth of the released trees was not continuous, in which the lowest increment was measured during the first year (1.01 cm ± 0.81), which afterwards increased to 1.16 cm ± 0.61 (second year) and finally to 1.22 cm ± 0.78 (third year). For the reference trees, a more constant growth was observed, but also with the lowest increment during the first year. This may be due to the initiation time of the investigation (June, austral winter), when precipitation generally peaks but the lowest temperatures are typically observed [36,37]. Furthermore, temperatures were lowest in June 2004, directly after the release, compared to the following years, which may have influenced the diametric growth of all species. In general, the highest DBH increments for all species were observed at the beginning of the year (austral summer), when temperatures are highest and enough water is available (Figures 3 and 4).

The released trees of *Hyeronima asperifolia* showed a mean growth of 0.63 cm ± 0.64 over the whole study period, whereas the control trees only had an increase of 0.35 cm ± 0.36 (Table 3). Similar to *Inga acreana*, the diametric growth of *Hyeronima asperifolia* increased during the observation period, which resulted in the highest increment of growth during the third year (0.76 cm ± 0.53). However, the diametric class of the released trees was also important, because smaller trees showed higher DBH increments (Table 4). For *Inga acreana,* increments were exclusively observed in class I (diameter: 20.1 cm to 30.0 cm), whereas *Hyeronima asperifolia* showed increments in all classes, but showed higher values for classes I–III. As shown in Table 5, the enhanced diametric growth of both species was principally caused by the treatment (release), but also the temperature (Figure 3) and precipitation (Figure 4). The diametric class had significant influence for *Hyeronima asperifolia*.

In summary, both species showed higher diametric growth compared to their control trees during the entire study period, which illustrates the expected effects of release, namely improvements in light and nutrient availability, leading to faster DBH growth.

3.2. Negative Response to Release

The species with negative responses to release were *Cedrela montana*, *Tabebuia chrysantha*, *Podocarpus oleifolius* and *Nectandra membranacea*. All of these species showed significantly lower diametric growth respective to their control trees, especially during the second and third year after release (Table 3). The species with the most significant differences were *Cedrela montana* (1.16 cm ± 1.21 vs. 0.87 cm ± 1.24), followed by *Nectandra membranacea* (0.44 cm ± 0.62 vs. 0.26 cm ± 0.32). This is because light and nutrient availability are not the main factors for their DBH increments, what is more important are their growth habits and phenological traits, besides temperature and precipitation (Table 5). However, like the two species which responded positively to release, the highest DBH increments were observed for diametric classes I–III. Only *Tabebuia chrysantha* showed small increments in class IV (diameter over 50 cm) over the whole study period (Table 4).

Table 3. Average annual diameter increase, including standard deviation (SD). Values highlighted (bold) are statistically significant ($p \leq 0.05$).

Species	**Treatment**				**Treatment × Period**											
	Control		**Released**		**I**				**II**				**III**			
					Control		**Released**		**Control**		**Released**		**Control**		**Released**	
	$\bar{x}$	**SD**	$\bar{x}$	**SD**	$\bar{x}$	**SD**	$\bar{x}$	**Sd**	$\bar{x}$	**SD**	$\bar{x}$	**SD**	$\bar{x}$	**SD**	$\bar{x}$	**SD**
Inga acreana	0.56	0.47	**1.13**	0.72	0.43	0.36	**1.01**	0.81	0.64	0.36	**1.16**	0.61	0.63	0.66	**1.22**	0.78
Hyeronima asperifolia	0.35	0.36	**0.62**	0.54	0.26	0.34	**0.44**	0.58	0.41	0.39	**0.67**	0.46	0.38	0.34	**0.76**	0.53
Cedrela montana	**1.16**	1.21	0.87	1.24	**1.20**	1.23	0.93	1.38	**1.25**	1.02	0.98	1.55	**1.03**	1.32	0.70	0.63
Tabebuia chrysantha	**0.27**	0.34	0.21	0.41	0.16	0.21	**0.28**	0.62	**0.32**	0.32	0.21	0.28	**0.33**	0.45	0.12	0.15
Podocarpus oleifolius	**0.15**	0.26	0.14	0.46	0.09	0.19	**0.19**	0.68	0.16	0.32	**0.19**	0.35	**0.21**	0.26	0.05	0.13
Nectandra membranacea	**0.44**	0.62	0.26	0.32	**0.25**	0.30	0.26	0.28	**0.34**	0.43	0.25	0.30	**0.76**	0.90	0.27	0.38
Clusia ducuoides	0.10	0.16	0.10	0.21	0.11	0.15	0.10	0.15	0.06	0.10	0.07	0.18	0.12	0.20	0.13	0.29
Hyeronima moritziana	0.12	0.23	0.17	0.22	0.10	0.20	0.12	0.16	0.03	0.06	0.19	0.27	0.25	0.31	0.20	0.20
Ficus citrifolia	1.11	1.04	1.09	1.22	1.12	0.92	1.06	1.21	1.31	1.37	1.15	1.32	0.87	0.69	1.07	1.18

Table 4. Values of diametric increase (cm) per period and the diametric classes of the nine selected timber species.

Species	**Periods**	**Class 1**		**Class 2**		**Class 3**		**Class 4**	
		Control	**Released**	**Control**	**Released**	**Control**	**Released**	**Control**	**Released**
Inga acreana	1	0.43	1.01	0	0	0	0	0	0
Hyeronima asperifolia		0.48	0.45	0.15	0.43	0.15	0.78	0.04	0.1
Cedrela montana		1.01	0.81	1.39	0.47	1.36	1.5	0	0
Tabebuia chrysantha		0.28	0.72	0.14	0.11	0.15	0.07	0.08	0.23
Nectandra membranacea		0.16	0.34	0.27	0.17	0.31	0.17	0	0
Podocarpus oleifolius		0.17	0.12	0.07	0.02	0.03	0.42	0	0
Ficus subandina		1.00	0.88	1.24	1.25	0	0	0	0
Clusia ducuoides		0.13	0.15	0.06	0.08	0.13	0.08	0	0
Hyeronima moritziana		0.12	0.18	0.11	0.06	0	0	0	0
Inga acreana	2	0.64	1.16	0	0	0	0	0	0
Hyeronima asperifolia		0.45	0.73	0.43	0.67	0.35	0.83	0	0.46
Cedrela montana		1.20	0.96	1.31	0.65	1.25	1.33	0	0
Tabebuia chrysantha		0.37	0.44	0.32	0.12	0.19	0.14	0.42	0.13
Nectandra membranacea		0.35	0.41	0.20	0.08	0.46	0.08	0	0
Podocarpus oleifolius		0.08	0.10	0.06	0.04	0.33	0.42	0	0
Ficus subandina		1.35	0.96	1.27	1.33	0	0	0	0
Clusia ducuoides		0.07	0.06	0.11	0.05	0	0.08	0	0
Hyeronima moritziana		0.05	0.25	0.03	0.13	0	0	0	0

Table 4. *Cont.*

Species	Periods	Class 1		Class 2		Class 3		Class 4	
		Control	Released	Control	Released	Control	Released	Control	Released
Inga acreana	3	0.63	1.22	0	0	0	0	0	0
Hyeronima asperifolia		0.49	0.82	0.20	0.78	0.44	0.86	0	0.57
Cedrela montana		0.99	0.74	1.06	0.64	1	0.73	0	0
Tabebuia chrysantha		0.47	0.09	0.16	0.15	0.10	0.06	0.59	0.18
Nectandra membranacea		0.37	0.50	0.56	0.05	1.34	0.05	0	0
Podocarpus oleifolius		0.11	0.16	0.20	0	0.30	0	0	0
Ficus subandina		0.86	1.18	0.88	0.95	0	0	0	0
Clusia ducuoides		0.13	0.15	0.09	0.05	0.14	0.18	0	0
Hyeronima moritziana		0.30	0.20	0.17	0.20	0	0	0	0

Class I = 20.1–30 cm, class II = 30.1–40 cm, class III = 40.1–50 cm, class IV $\geq$ 50.1 cm.

Table 5. *P*-values of the variables and the interactions that influence the variability of the diametric increase (GLMM). Significant values ($p \leq 0.05$) are highlighted in bold.

Species	Release		Precipitation		Temperature		Diametric Class		Release × Diametric Class		Release × Precipitation		Release × Temperature		Diametric Class × Precipitation		Diametric Class × Temperature	
	Ch	p	Ch	p	Ch	p	Ch	p	Ch	p	Ch	p	Ch	p	Ch	p	Ch	p
Inga acreana	14.9	**$\leq$0.0001**	0.05	0.81	0.05	0.83	–	–	–	–	0.18	0.66	0.99	0.31	–	–	–	–
Hyeronima asperifolia	33.5	**$\leq$0.0001**	4.1	**0.04**	9.8	**0.001**	16.7	**0.0008**	5.01	0.08	0.0	0.99	0.27	0.6	0.42	0.9	3.5	0.31
Cedrela montana	6.2	**0.01**	15.1	**$\leq$0.0001**	31.9	**$\leq$0.0001**	4.9	0.08	1.5	0.21	1.01	0.31	2.3	0.12	4.5	0.1	5.9	**0.05**
Tabebuia chrysantha	2.3	0.12	13.5	**0.0002**	1.74	0.18	26.3	**$\leq$0.0001**	4.04	0.39	1.9	0.16	0.39	0.52	13.5	**0.003**	0.62	0.88
Podocarpus oleifolius	0.04	0.83	0.09	0.75	0.009	0.92	8.6	**0.01**	1.6	0.5	0.34	0.6	0.2	0.65	0.07	0.96	0.89	0.64
Nectandra membranacea	5.5	**0.01**	14.9	**$\leq$0.0001**	31.8	**$\leq$0.0001**	1.4	0.49	0.12	0.72	2.7	0.9	3.5	0.06	0.2	0.9	2.7	0.2
Clusia ducuoides	0.02	0.86	0.0004	0.98	1.3	0.24	2.4	0.3	0.91	0.63	0.09	0.76	1.1	0.3	2.2	0.33	4.7	0.09
Hyeronima moritziana	1.7	0.19	0.0008	0.98	0.0006	0.98	2.4	0.3	0.07	0.79	0.45	0.5	3.4	**0.05**	0.64	0.72	0.0002	0.99
Ficus citrifolia	0.007	0.93	10.1	**0.001**	8.8	**0.002**	0.46	0.49	0.12	0.72	0.19	0.65	0.17	0.67	1.9	0.16	3.3	0.06

3.3. Null Response to Release

The species that did not show significant responses to release (neither positive nor negative) were *Hyeronima moritziana*, *Clusia ducuoides* and *Ficus citrifolia*, which indicates that other factors have a greater influence on the diametric growth of these species. The diametric growth of *Hyeronima moritziana* (0.12 cm ± 0.23 vs. 0.17 cm ± 0.22) and *Clusia ducuoides* (0.10 cm ± 0.16 vs. 0.10 cm ± 0.21) was generally low (released trees and control trees) over the complete study period, but with generally the highest DBH increments during the third year. In contrast, *Ficus citrifolia* (1.11 cm ± 1.04 vs. 1.09 cm ± 1.22) showed higher DBH increments during the first two years of the study, which can be related to the prevailing climate conditions, because mean monthly temperatures as well as precipitation amounts were higher then, when compared to the third year (Figures 3 and 4). This is confirmed in Table 5, where temperature and precipitation are seen to show significant influence on the diametric growth of *Ficus citrifolia* but are secondary for the other two species (Table 5). Respective to the diametric classes, the three species had the highest increments in class I and class II. Only *Clusia ducuoides* showed small DBH increments in class III (Table 4).

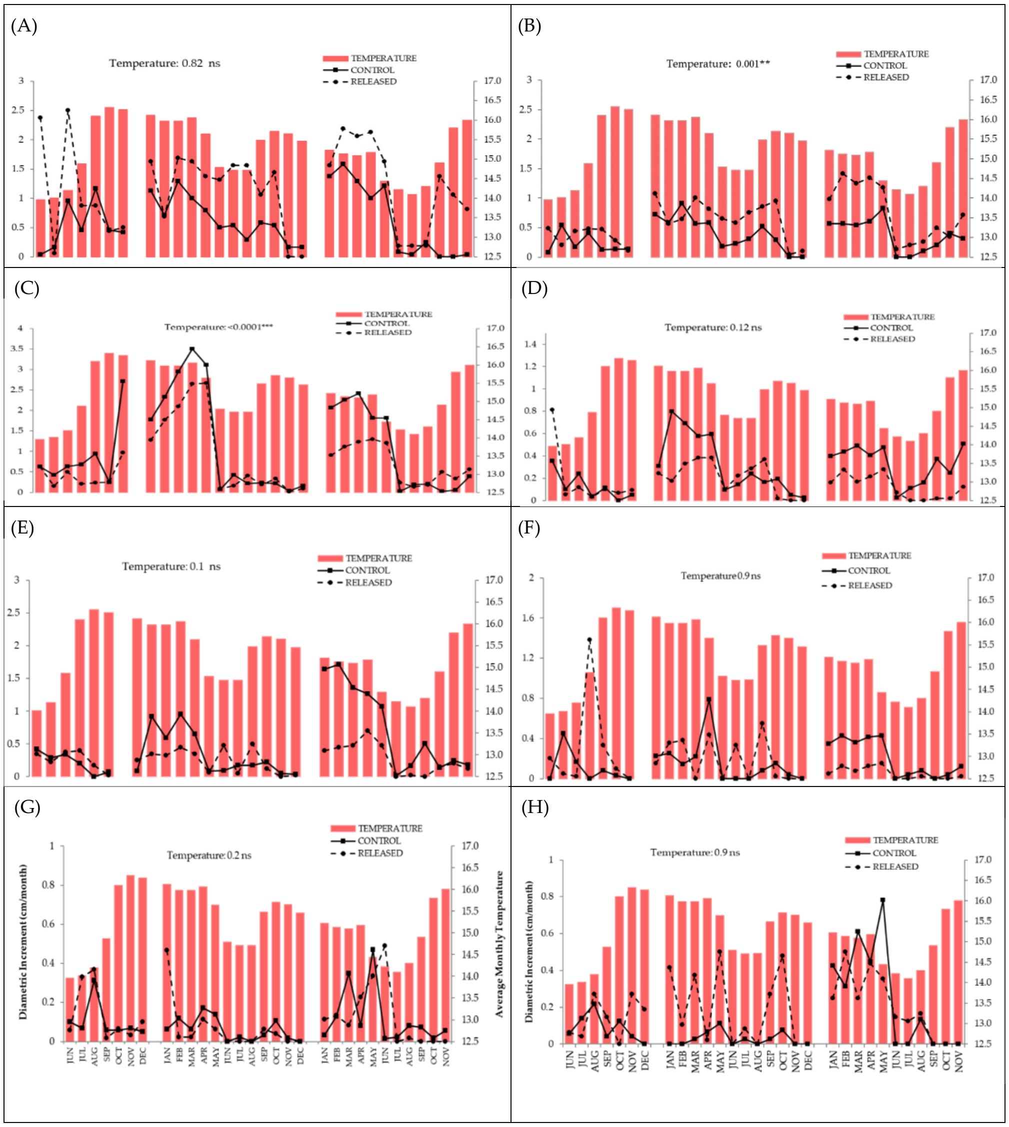


Figure 3. *Cont.*

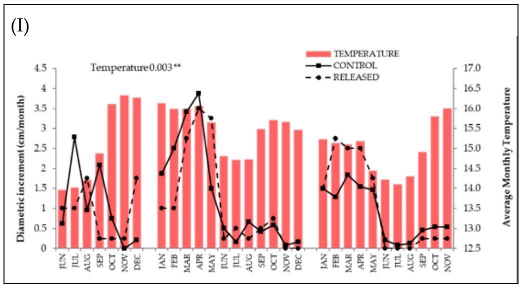


Figure 3. Diameter increase, by period, respective to the mean monthly temperature. (**A**) *Inga acreana*, (**B**) *Hyeronima asperifolia*, (**C**) *Cedrela montana*, (**D**) *Tabebuia chrysantha*, (**E**) *Nectandra membranaceae*, (**F**) *Podocarpus oleifolius*, (**G**) *Clusia ducuoides*, (**H**) *Hyeronima moritziana*, (**I**) *Ficus citrifolia*.

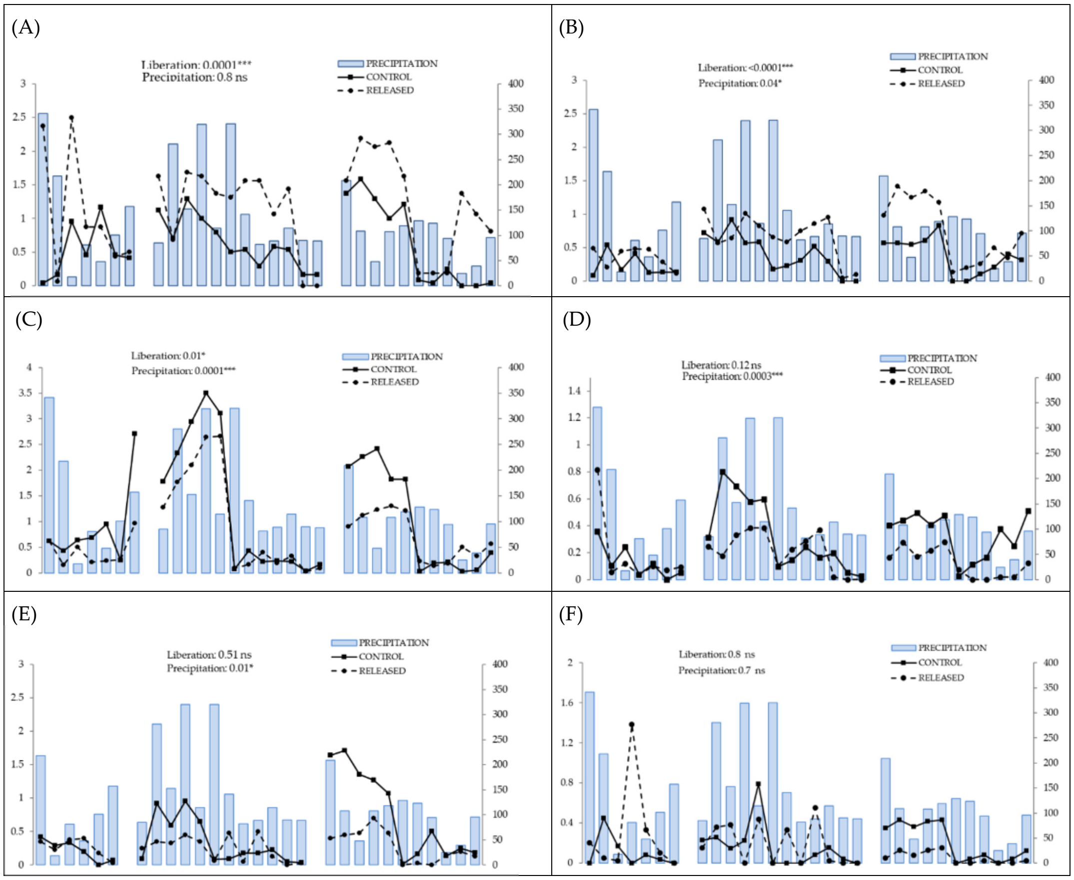


Figure 4. *Cont.*

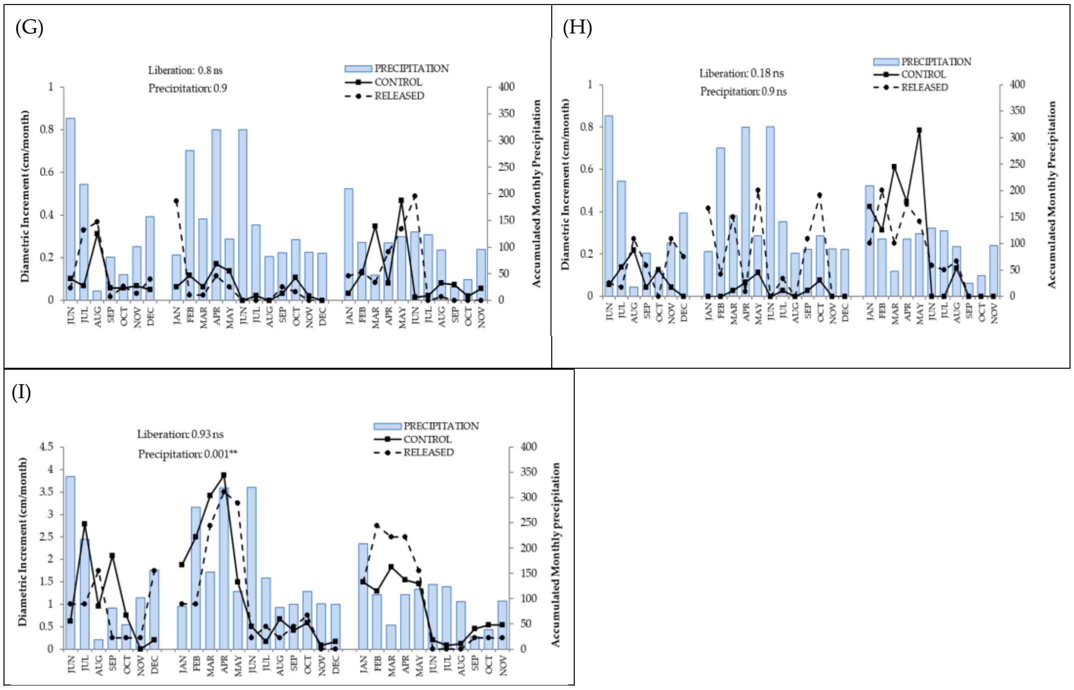


Figure 4. Diametric increase, by period, respective to monthly precipitation. (**A**) *Inga acreana*, (**B**) *Hyeronima asperifolia*, (**C**) *Cedrela montana*, (**D**) *Tabebuia chrysantha*, (**E**) *Nectandra membranaceae*, (**F**) *Podocarpus oleifolius*, (**G**) *Clusia ducuoides*, (**H**) *Hyeronima moritziana*, (**I**) *Ficus citrifolia*.

4. Discussion

The nine selected timber species responded differently to the release because their growth habits, initial DBH (diametric class) and phenological traits, which determined the success of the treatment. Historically, tree growth has been modeled based on different classification criteria, in which the most common criterion are taxonomic affinity, ecological guild and growth dynamics [18,51]. The growth and dynamics of natural tropical forests in Ecuador have been monitored for decades by means of continuous measurements over time [52]. However, the main focus of this work has been determining the influence of climatic factors and ecosystem services, due to the high deforestation rates observed in Ecuador [53,54], but not silvicultural treatments, such as the release from competitors. Monitoring the diametric growth of certain species by adding nutrients to the soil [34] or analyzing the DBH increment, respective to climatic conditions [29,35], are topics that provide knowledge about forest dynamics, but do not contribute to sustainable forest management.

Although the study area corresponds to a natural tropical mountain zone, where marked altitudinal gradients in temperature and precipitation exist [36,37], provoking different physiological responses in the species [55], climate conditions were secondary due to the pre-humid tropical climate in the study area. The relative dry season is formed between austral winter and austral summer (October/November), which is used by many species for phenological processes such as flowering and fruiting [36]. All of the selected PCT species showed a similar annual cycle respective to diametric growth, which was mainly triggered by the slightly higher temperatures during the austral summer period. This also holds true for the species *Cedrela montana* and *Tabebuia chrysantha*, which interrupt their cambial activity, simulating a dormancy period (defoliation), similar to tree species in temperate climatic regions [56], leading to the formation of growth rings.

The released trees of the individual species were separated into three groups based on their diametric class and individual response. The first group consisted of species which responded positively to the release (*Inga acreana* and *Hyeronima asperifolia*), whereas the second group included species which responded negatively (*Cedrela montana*, *Nectandra membranacea*, *Podocarpus oleifolius* and

Tabebuia chrysantha), while the third group of species were those that responded neutrally (*Hyeronima moritziana, Clusia ducuoides* and *Ficus citrifolia*).

The members of the species of genus Inga are generally medium-sized and shade intolerant [57], but some species are only moderately shade tolerant [18]. However, *Inga acreana* grows in relatively open sites, where release improves the environmental conditions and consequently diameter growth [23,58,59]. Nonetheless, as the present study found, this is only valid for smaller individuals (20–30 cm, class I) because larger diameter classes did not show any significant increments.

Hyeronima asperifolia also responded positively to release, which was also stated in [23], which additionally found an interesting early response for this species. However, the early response could not be confirmed by the present study because significant differences between the released and control trees were higher at the end of the observation period (Table 3). Respective to the diametric classes, the highest increments were calculated for classes I–III, whereas class IV only showed small increases for the released trees (Table 4). The differences in growth between the diametric classes were stated in previous studies [7,21], which indicate that diametric growth is strongly dependent on the size of the tree, in which larger trees generally show lower increments. By analyzing the climate conditions (Figures 3 and 4), it is evident that *Hyeronima asperifolia* reduces or suspends growing in June (austral winter) when precipitation amounts are at their highest but temperatures are at their lowest. This behavior was also found in other species in the RBSF area [58], because rainwater is usually stored in the soil and is available for the plants for longer periods or during the whole year. The diametric growth generally occurs during austral summer, when highest temperatures are observed, confirming that temperature variations control the phenological processes and growth rates of the different species in the study area.

The next group of species showed a negative response to the treatment, which means that release produced an inverse effect, as was expected respective to diameter growth. As [60] indicated, variations in the diameter growth of certain species are related to two factors: First, the amount of light intercepted by the tree and second, the density of the wood. Therefore, an inverse relationship between growth and wood density can be assumed, which is confirmed by this study, because the four species of this group have hard and dense wood. Additionally, *Cedrela montana* and *Tabebuia chrysantha* exhibit defoliation, which also affects their diametric growth [55].

Cedrela montana is a slow-growing deciduous species which forms growth rings in its trunk and has defoliation [61], which is associated with austral winter, when temperature is lowest. Although the seasonal temperature fluctuations are only around 1.5 °C in the study area, other studies have confirmed that temperature is significantly correlated to diametrical growth [42]. The highest diametric increases are observed during the warm season (austral summer), whereas growth is reduced or suspended during the cold season (austral winter). This overall trend matches with the growth rates found in this study. However, the reason for the negative response of *Cedrela montana* may be the time of release (June), because normally the trees begin with the process of leaf change and flower production [42]. Release generated changed light conditions, which may have interrupted the natural phenological cycle of the species. This is confirmed by [23], which also found a negative response to release for *Cedrela montana*, concluding that the negative response is due to the species' marked phenological traits and physiological processes.

Tabebuia chrysantha is also a deciduous species [42] whose defoliation time coincides with *Cedrela montana*, starting in June (austral winter). According to [62], *Tabebuia chrysantha* shows very low diametric increments during austral winter, when the production of new leaves and flowers begins. This is because the tree needs all of its available resources to progress through these physiological stages. Therefore, the time of release for this study may have affected this species, however, the growth rates were similar to the control trees during the first year of observation (Figures 3 and 4). This leads to the assumption that the change in light conditions has also affected the released trees over the following years, because this species prefers shaded sites [57]. Observing Table 4, the control trees showed notably higher diametric increases during years 2 and 3, especially during the austral summer periods.

The negative response of *Podocarpus oleifolius* cannot be explained by the time of release nor the general climate conditions. This is because temperature and precipitation did not produce a significant effect on growth for this species (Table 5). Therefore, the change in light conditions may have affected this species too. However, as the results of the applied statistical model indicated (Table 5), significant differences between released trees and control trees were only found in terms of size (diameter class; $p = 0.01$). As shown in Table 4, *Podocarpus oleifolius* only presented small increments for classes I–III, in which the released trees in class I showed a generally higher diametric growth than the control trees, whereas the control trees had higher increments than the released trees in class II. Class III showed the highest diametric growth rates for both the control and released trees, especially during the first two years of observation. However, during the third year, the released class III trees did not show any increment, explaining the overall trend for the released trees being negative. Therefore, the applied silvicultural treatment was only useful for smaller or younger trees, where their diametric growth was enhanced due to the improved light conditions. For bigger or older trees this factor is secondary. The generally low growth rates of *Podocarpus oleifolius* were also observed in [63], where an average annual growth of 1.7 mm in Costa Rica was calculated. However, the present study only obtained an annual average growth of 0.21 mm, which is confirmed by [34], which investigated *Podocarpus oleifolius* in the RBSF area.

Additionally, for *Nectandra membranacea*, the effect of release was negative. The diametric growth of this species was related to the treatment and the climatic conditions (temperature and precipitation, Table 5), as *Podocarpus oleifolius* and *Nectandra membranacea* showed clear variation in growth between diametric classes (Table 4). Young and small trees (typically class I) reacted positively to release. This is because their diametric increment is higher when compared to the control trees. Nonetheless, in classes II and III, the diametric growths of the released trees were notably lower than the control trees, resulting in a negative response. The negative response of *Nectandra membranacea* was also found in [23], which indicated that light conditions are important for younger trees, but if the tree is established in the ecosystem, other factors such as nutrient availability are more important. Furthermore, too much light may increase plant transpiration and therefore more water is necessary, which may reduce diametric growth.

Ficus citrifolia, *Clusia ducuoides* and *Hyeronima moritziana* showed no response to the treatment, which means that no differences in diametric growth between the released and control trees were found. These species are tolerant to shade and light, and as such, no effect was obtained. However, within the timber species studied, the highest increments were measured for diametric classes I and II (smaller and younger trees), whereas in class III, the increments were strongly reduced, and in class IV they were absent or insignificant (Table 4).

The present investigation, as with most growth studies, was based on traditional forest inventory practices, including diameter measurements and applying a linear model (here, we applied GLMM, R package: LMER4). However, as [64] suggested, to get a better resolution of the growth response of species and individual trees, non-linear models should also be examined. Hence, individual tree variability, as well as the tree's specific location within the ecosystem can be considered in the models. These variables could improve the understanding of the growth response of individual trees after this intermediate treatment [65]. Furthermore, tree-ring series should be analyzed, because they provide more accurate estimations of radial growth than inventory data and allow reconstruction at a fine scale [66]. However, tropical forest trees generally do not form rings, which limits analyses to specific species, however in boreal or alpine forests, where all tree species have growth-rings, this factor should be included. Consequently, developing future studies using this approach can improve the resolution of the growth pattern of trees within forest stands.

5. Conclusions

The silvicultural treatment (release from competitors) that was applied to nine timber species in a natural tropical mountain forest in southern Ecuador resulted in different individual responses.

In general, species which preferred open sites responded positively to release, whereas shade tolerant species responded negatively. Tree species which are light- and shade-tolerant did not show any changes respective to diametric growth. Furthermore, the two species with defoliation (seasonality) responded negatively, which may be due to the time of release (June, during austral winter), which occurred during the time new leaves are built.

All of the selected species showed a similar annual cycle respective to their diametric increase. Generally, growth was observed during the austral summer period, specifically between December and April, when temperatures are highest and sufficient water is available. During austral winter (June to September), most of the species reduced or suspended their growth because of the lower temperatures during this period. Therefore, due to the per-humid climate in the RBSF, precipitation is secondary for diametric growth, because enough rainfall occurs during the year which is then stored in the soil, where water is consequently always available for the plants. What is more important are the small temperature variations between austral summer and austral winter, which are generally used by the plants to begin their phenological processes.

Finally, the initial DBH of the trees (diametric classes) was found to be an important factor for the success of the treatment. Trees of class I (20 cm to 30 cm DBH) generally responded positively to the treatment, whereas for bigger or older individuals, the differences between the released and control trees decreased or became negative. This means that improved light conditions as well as nutrient availability are specifically beneficial for younger trees, which still compete for space and nutrients. Older trees are established within their ecosystem and generally grow slower, which explains why release did not increase their competitive abilities. Therefore, the release of trees in natural tropical mountain forests is only practical for younger trees, which are still competing for light and nutrients.

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Functional Diversity Changes after Selective Thinning in a Tropical Mountain Forest in Southern Ecuador

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Abstract: Background: The impact of selective thinning on forest diversity has been extensively studied in temperate and boreal regions. However, in the tropics, knowledge is still poor regarding the impacts of this silvicultural treatment on functional diversity, especially in tropical mountain forests, which are considered to be highly biodiverse ecosystems and also endangered by human activities. By evaluating the changes on functional diversity by using different indicators, hypothesizing that selective thinning significantly affects (directly or indirectly) tropical mountain forests, this work promotes sustainable ecosystem use. **Methods:** A total of 52 permanent plots of 2500 m^2 each were installed in a primary mountain forest in the San Francisco Biological Reserve to assess the impact of this silvicultural treatment. Selective thinning can be defined as a controlled process, in which trees that compete with ecologically and/or valuable timber species are progressively removed to stimulate the development of profitable ones, called potential crop trees (PCT). In doing so, the best specimens remain in the forest stand until their final harvest. After PCT selection, 30 plots were chosen for the intervention, while 22 plots served as control plots. The thinning intensity fluctuated between 4 and 56 trees ha^{-1} (average 18.8 ± 12.1 stems ha^{-1}). Functional Diversity (FD) indices, including the community weighted mean (CWM), were determined based on six traits using the FD package implemented in R software. The difference between initial and final conditions of functional richness (FRic), functional divergence (FDiv), functional evenness (FEve), functional dispersion (FDis), and Rao quadratic entropy (RaoQ) was modeled using linear mixed models (LMM). As fixed factors, we used all the predictors inherent to structural and ecological forest conditions before and after the selective thinning and as a random variable, we used the membership to nested sampling units. **Results:** Functional Richness (FRic) showed significant changes after selective thinning, the other indexes (FEve, FDis, FDiv, RaoQ) were only influenced by predictors related to ecological conditions and characteristics of the community.

Keywords: forest management; intermediate treatments; mountain rain forest composition; species richness; tree species loss

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1. Introduction

Although natural tropical mountain forests (TMF) are highly valuable because of their biological richness and the provision of essential ecosystem services, they are disappearing at alarming rates [1], which is mainly due to anthropogenic land use changes [2–5]. This also holds true for southern Ecuador, where a large area of the natural TMF at the eastern foothills of the Cordillera Real have been converted into pasture land, agricultural land or secondary forests to meet the economic needs of the local population, producing food, fiber, wood and other goods [6,7]. According to Carreño-Rocabado et al. [8], land use change is one of the main drivers for biodiversity loss, which also seriously affects ecosystem functions and services. However, intensity, type and frequency of disturbance must also be considered as factors that influence the functionality of ecosystems [9,10].

In this context, forestry without proper planning causes loss of biodiversity and alters ecosystem functionality. To create a balance between exploitation and conservation of these ecosystems, sustainable forest management (SFM) must be implemented to make use of forest resources, while, at the same time, protecting the biodiversity [11,12]. One main aim of SFM is the development of sustainable management concepts, such as reduced impact logging (RIL), which establishes cutting cycles or defines a minimum cutting diameter (MCD) to counteract exploitative forest use [13–15].

In some tropical regions, e.g., Africa (Burkina Faso, Cameroon) and Asia (India, Indonesia), silvicultural treatments, such as selective thinning, have been applied for more than a century [16]. This practice, which aims at the minimizing of impacts on the integrity of natural forests and improving the productivity, was recently implemented in Ecuador. The treatment consists of eliminating species of low commercial value, which are competitors for valuable timber species. This practice is based on the theory that the growth rates of trees are directly related to the quantity of received sunlight and nutrient availability, and for this reason, all undesired or competitor trees around the valuable timber species are removed to obtain adequate lighting and to enhance nutrient availability [17,18]. Regarding the impact of selective thinning on functional diversity, we highlight the work carried out by de Avila et al. [19], and on the structure of the forest, the work of Yguel et al. [20]; both works conclude on the importance of assessing thinning and the impact it has on the forest's richness. Existing forestry studies generally focus on documentation of timber species and their production [21], on the yield of agroforestry plantations [22], on reforestation methods with native or exotic species [23,24], as well as on payment schemes for forest ecosystem services [25–28]. Furthermore, information respective to the effects of tree removal in natural tropical forest stands, in terms of richness and diversity, is still scarce. Nonetheless, this knowledge is necessary to understand the natural processes and dynamics of these ecosystems in the follow-up of man-made disturbances.

Regulation concepts respective to the exploitation of natural tropical forests in Ecuador were developed some decades ago [29], which also included practices to cut undesired trees to enhance the growth of ecological and economical valuable species. However, no scientific assessments to evaluate the possible impacts of thinning on forest structure or diversity in these ecosystems have been made so far. The available literature focuses on forest types in the temperate and boreal zones [30,31], because in the tropics, the evaluation is more complex due to the large spatial extension of the different forest ecosystems and their extraordinary high biodiversity [5]. This also includes TMF, where the effects of silvicultural interventions and their impacts on taxonomic or functional diversity have not been evaluated yet.

In general, the Functional Diversity (FD) of an ecosystem is defined by multiple indicators, which include species characteristics, climatic gradients and water availability [32]. However, for a long time, species richness was the most widely used metric to assess ecosystem functionality, because it is assumed that a higher number of species within a forest community indicates a healthy and functional ecosystem [33]. This is not always true, because species richness also depends on forest type [34,35], which is why functional diversity can not only be analyzed in natural communities, but also in intervened communities. If measurable biological characteristics are directly related to ecological functions, the functional strategies of the species within a forest community can be described using functional features; that is, measurable biological characteristics related to ecological functions [20]. According to Violle et al. [33], functional traits can be monitored at different levels of organization (ecosystem, community, species or population), in which the number and type of traits vary according to the size of the species present, as well as in terms of forest taxonomic diversity.

However, the improvement of nutrients availability in forest soils also enhances growth but only for species with acquisitive traits (e.g., diametric growth, carbon storage), because species with functional conservative traits (e.g., number of stomata per cm^2, dispersion syndrome) need adequate light [36]. These indicators must be adjusted with respect to the studied ecosystem and the specific silvicultural treatment applied [37].

Therefore, selective thinning should not only improve forest production of all desired tree species, but also obviate over fertilization, which might also have negative effects on the provided ecosystem services for the local and regional population [38–40]. Nonetheless, the impact that silvicultural treatments produce is a critical point of disagreement between conservationists and foresters because a reduction in diversity (e.g., timber extraction by thinning) might result in a loss of functionality [41]. This is shown by other studies [42,43], which indicate that ecosystem functionality is altered due to the loss of species, even if no significant changes in taxonomic diversity occurred. However, as Chaudhary et al. [44] clarified, these traditional approaches must be revised, because the impacts of silvicultural treatments can not only be limited to the relative loss of species. Unfortunately, only a few studies respective to impacts of selective thinning on diversity and forest structure, as well as on its effectiveness, have been published so far.

In this study, the response of TMF to selective thinning in southern Ecuador was investigated. The objective of the study was to evaluate the impact of selective thinning on the growth, diversity and functionality of the forest, and to answer the following question: Does species loss due to the implementation of selective thinning imply the loss of functional diversity of the natural stand?

The hypothesis tested was that selective thinning significantly affects functional diversity, due to the loss of species that naturally constitute the forest community. To this end, changes in the acquisitive and conservative traits of the species were analyzed and related to the intensity of thinning.

2. Materials and Methods

2.1. Study Area

The study was carried out in the primary TMF of the "Reserva Biológica San Francisco" (RBSF; 3°58′ S, 79°04′ W) [45], located on the eastern escarpment of the Ecuadorian Andes, within the San Francisco River watershed, which drains into the Amazon Basin [46]. Elevations range from ~1700 m a.s.l. at the valley bottom to ~3200 m a.s.l at the highest mountain peak, the Cerro del Consuelo.

The type of natural vegetation is evergreen TMF, which covers the slopes from the valley bottom up to the tree line at approximately 2700 m a.s.l [47]. The forest can be classified as lower montane forest (up to 2200 m a.s.l) and upper montane forest (from 2200 m a.s.l up to the tree line). These two forest types can be subdivided into ravine and ridge forest [48], in which ravine forest is characterized by bigger trees respective to basal areas and canopy heights, but by lower stem density, compared to ridge forests, where also less tree species are observed. Differences in forest structure are mainly due to climatic conditions, topography and prevailing soil types [49,50]. A more detailed description of the biophysical conditions and forest types in the study area can be found in Cabrera et al. [51], Paulsch [52] and Homeier et al. [53].

2.2. Plot Installation

Fifty-two permanent field plots of 2500 m^2 each were installed in RBSF area within three gullies or micro-watersheds (Q = quebradas) in the lower montane forest at different altitudes (1860–2140 m a.s.l.). The plots were installed where the forest presented better conservation state and the presence of timber and ecologically important species was confirmed. Specifically, 16 plots were implemented in Q3 and in Q5, whereas 20 plots were created in Q2 (Figure 1). Respective to the forest type, all plots in Q5 belong to ravine forest, whereas all plots in Q3 are ridge forest. The plots in Q2 are mixed, which means that 6 plots belong to ridge forest, while the rest belongs to ravine forest. This results in a total of 30 plots belonging to ravine forest and 22 plots belonging to ridge forest (Supplementary Materials Figure S1). As reference or control plots, where no thinning activities were realized, one plot in Q3 and one in Q5 (K-plot; see Figure 1) and all plots in Q2 were chosen to obtain a balanced number of control plots for the ravine and ridge forest parts. For analysis, the two forest types were not separated because the full pool of valuable timber species were analyzed.

After plot installation, forest inventory was executed, in which a total of 2797 trees were found with a diameter at breast height (DBH) greater than 20.0 cm. These trees were labeled, and botanical samples were taken for their subsequent taxonomical identification at the LOJA Herbarium.

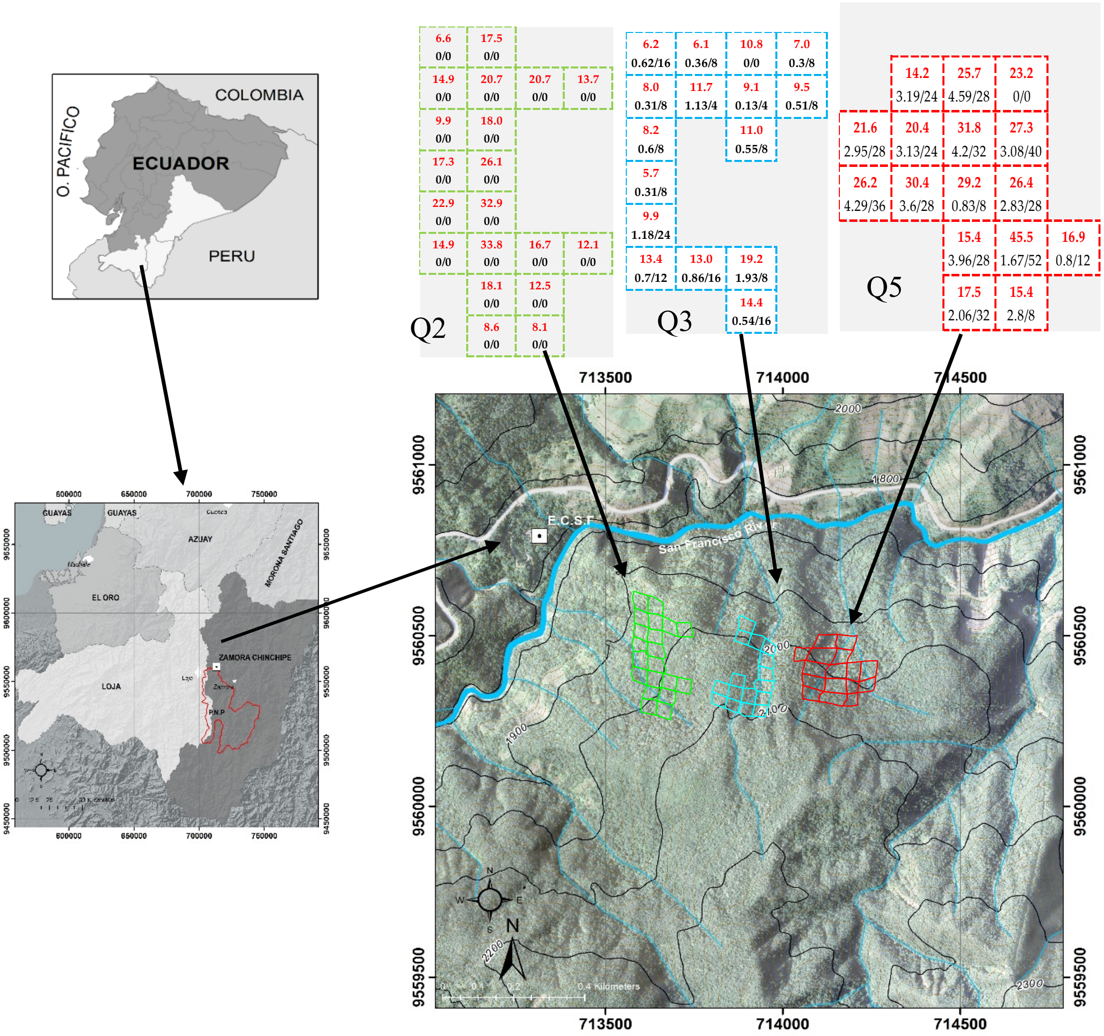


Figure 1. Location of the study area and plot distribution in the RBSF. The red numbers indicate total basal area ha^{-1}, other numbers in the squared plots indicate mean values of extracted basal area and the number of extracted trees (basal Area extracted/extracted trees ha^{-1}). All plots in Q2 (green block), as well as the K-plots in Q3 (blue block) and Q5 (red block), are control plots without intervention (i.e., no selective thinning).

2.3. Selective Thinning and Intensity

Selective thinning consists of the elimination of competitors in order to improve light conditions and nutrient availability for desired timber species or other species which fulfill an important ecological role in the ecosystem (potential crop trees, PCT) [54,55]. To implement this silvicultural treatment, first, the PCTs inside each plot were identified (Supplementary Materials Table S2). As de Graaf et al. [55] defined, a commercial PCT species should have a DBH greater than 30 cm, with a healthy stem and good wood quality. In this study, ecologically important species were considered for which the DBH threshold was reduced to ≥20 cm to receive a better representation of PCT distribution and species frequency for this TMF.

After PCT selection, the strongest competitors for each PCT were identified. As an indication for competition degree, stem or crown overlap of the competitive specimens were determined, since they can limit the growth of the PCTs (light and nutrient availability). The subsequent removal of competitors by thinning included all tree species with DBH greater than 20.0 cm (total number: $n = 138$), with the exception of trees which belonged to rare species. All competitor trees were cut using the method of directional felling to minimize damages for the remaining forest stand [56]. The selective thinning was executed 18 months after the initial forest inventory, and during this period, the natural diametric growth of the PCTs was monitored using metal dendrometers [51]. Functional diversity analyses of the thinned and control plots were carried out one year and two years after the silvicultural treatment.

2.4. Assessing Impact of Selective Thinning on Functional Diversity

For the present research, the following traits were selected to determine the functional changes in this tropical mountain ecosystem after applying selective thinning: (1) Wood density (WD) [57–60]; (2) Average diameter (DBH); (3) Growth (annual diametric increase); (4) Type of leaf; (5) Ecological Guild [58,60]; (6) Dispersion syndrome (Table 1). Functional traits allow the analysis of the diversity and structure of the community [58], in contrast to conservative features, which are related to reproduction and succession.

WD was selected because this trait is connected to several aspects of plant ecology, including growth rate, carbon allocation strategy, structural stability, resistance to diseases or pests, and primary production [53,57,61], while the average DBH and growth are directly related to the silvicultural treatment applied. Leaf type is a functional trait which has been used to predict the growth of tropical trees [62] and which reflect adaptations that allow plants to live under various environmental conditions [63]. Here, we include the type of leaf in the FD analysis, as a way to indicate the plant's strategy to acquire and redistribute nutrients for growth [61]. According to Xu et al. [64], there are differences between the species that have compound leaf and simple leaf species, so these categories can be assumed to have slow and fast metabolic rates, respectively. The simple leaves are easier to manufacture than the compound leaves, but this is compensated by the duration being the same, that is, a longer useful life of the compound leaves for the benefit of the plant. As a conservative trait (reproduction and succession, which are intrinsic to each individual species), the ecological guild or type of succession was used. The last trait, "Dispersal syndrome", is closely related to the relative abundance of species [65]. In wet tropical forests that exhibit a large aggregation of specific trees at scales ranging from a few meters to a few hundred meters, the dominant syndrome is zoochory [66], while in the tropical dry forests, the dominant syndrome is the anemochory, which also leads to certain specific distribution patterns [65], although barochory is also a more frequent syndrome in dry forests than in wet tropical forests [67]. The implementation of selective thinning could cause changes in the forest structure by changing the dominant dispersal syndrome, reducing the individuals that belong to each species.

Table 1. Functional (conservatives and acquisitive) traits, including categories, units and codes used to calculate FD and CWM.

Functional Trait	Type	Categories	Unit	Code
Wood density	Acquisitive	-	g cm^3	WD
Stem Density	Acquisitive	-	cm	DBH
Diametric growth	Acquisitive	-	cm $year^{-1}$	G
Leaf type	Acquisitive	Simple Compound		LT
Ecological guild	Conservative	Shade tolerant Light Tolerant Partial light Tolerant Partial Shade Tolerant		ST LT PLT PST
Dispersion syndrome	Conservative	Anemochory Zoochory Barochory		AN ZOC BAR

2.5. Data Acquisition

WD data for all tree species involved in the study were provided by the local RBSF database (TMF Database). In the event that a species was not listed, the data were acquired from the Global Wood Density Database (https://datadryad.org/), particularly as a subset for the Latin American region [57,65], or in ICRAF's free and accessible database (functional attributes and the ecological database, http://db.worldagroforestry.org/wd). The monthly diametric growth was controlled by dendrometers fixed on each PCT tree [68]. For all tree species, the growth was determined by three general forest inventories carried out at 18 and 36 months after implementing the permanent plots. The stem density was determined by counting all individuals of a species before and after selective thinning. The leaf type was identified directly after botanical collections and observations in the field, while the ecological guild and the dispersion syndrome of each species were determined using attributes and ecological characteristics as described by Palacios et al. [60] and Jara et al. [65].

2.6. Statistical Analysis

To determine the functional diversity (FD) multi-trait indices and CWM for this TMF after selective thinning, the FD package was used [69] and the following indices were included:

- Functional Richness (FRic), which represents the amount of space occupied by a community, independent from the relative abundances of the species [70].
- Functional Divergence (FDiv) measures how species of a community diverge in their distance from the center of gravity in the functional space, and determines the relative abundance of a species within its functional range, [70,71]. FDiv provides additional information for FRic, because this index indicates which species has the most extreme feature combinations (i.e., specialized species), and which ones are generalist [72].
- Functional Evenness (FEve) quantifies the regularity of how species abundances are distributed within their functional range, by correlating abundance with average distance between different species [57]. FEve can be related to the uniformity of species (Pielou's J) and the FDiv because it determines if the extent of functional distances between the species is regular [41].
- Functional Dispersion (FDis) gives the mean distance of an individual species relative to the centroid of the community, which depicts its mean distance relative to all species in the community, and therefore, accounts for relative abundances of a species.
- Rao Quadratic Entropy (RaoQ) correlates the abundances of different species [73] to improve the FD index. An adverse property of RaoQ is that its value may decrease if species richness

increases, because abundances and dissimilarity between the species are considered. Therefore, the introduction or loss of species in a community increases or decreases the species abundance, but, at the same time, may reduce the dissimilarity between the species.

- Community weighted mean (CWM) represents the sum of each species trait value weighted by its relative abundance in the community [74]. To characterize the community structure from a functional point of view, we used the community weighted mean, which is calculated combining the species abundance with the trait values of the given species [75]. This describes the trait averages over a community [76] and reflects the dominant trait in a given community [33,77,78].

To relate the FD indices and the CWM to the predictors, we used multivariate linear mixed modelling (LMM) with random nested intercepts. For each index or CWM, the fixed effects were the altitude, the relative removed basal area, the number of trees ha^{-1}, the initial basal area, and the initial species number, whereas the random effects were the plot membership nested in the "quebrada". All the previously mentioned predictors are directly related to the selective thinning, except altitude, which is a natural distribution gradient but often considered by other authors [52,53] because of its importance for analyzing forest composition and structure.

To perform the LMM analysis, the NLME package of R was used [79], in which the explanatory categorical factors were combined to calculate random values for the repeated measurements throughout time (before–after). As fixed factors, we used all the predictors inherent to structural and ecological forest conditions before and after the selective thinning (period and treatment) and as a random variable, we used the membership to nested sampling. To validate the models of each analyzed index, we compare each resulting model, applying a goodness test (likelihood ratio test), discarding non-significant predictors and establishing the importance of the remaining factors to prove that the models were not over fitted. For this, we used the lmtest package of R software [80].

3. Results

3.1. Selective Thinning and Structure

In the 30 thinned plots (Q3 and Q5), the percentage of tree extraction with respect to the total number of individuals per species ranged from 1.5–100%, with an average value of 23.2%. Species with high extraction intensity were: *Prunus huantensis* Pilg (75%), *Symplocos coriaceae* A. DC. (50%), *Vismia tomentosa* (Ruiz and Pav.) (50%), *Cinnamomum* sp. (50%), *Persea subcordata* (50%); (Supplementary Materials Table S3). This resulted in an average stem extraction of 18.8 ± 12.1 (SD) ha^{-1}, with a minimum of 4 trees ha^{-1} and a maximum of 56 trees ha^{-1}. The basal area extracted was on average 1.8 ± 1.4 m^2 ha^{-1} (SD), and the most intensive extraction was 4.8 m^2 ha^{-1}.

During the thinning campaign, several species were registered (Supplementary Table S2), particularly *Virola* sp. (Myristicaceae), *Chrysophyllum lanatum* T.D. Penn (Sapotaceae), *Alchornea triplinervia* (Spreng.) Mull. Arg. (Euphorbiaceae) and *Persea subcordata* (Ruiz and Pav.) Nees (Lauraceae) that were affected, eliminating the only representative individual in the floristic inventory (100%), which may influence the calculation of the FD.

Overall, the extracted species belonged to 30 families, in which nine species of Lauraceae; six species of Euphorbiaceae; five species of Meliaceae; three species of Clusiaceae, Melastomataceae, Moraceae and Rubiaceae; and two species of Cecropiaceae and Mimosaceae were removed.

3.2. Floristic Composition

The plant diversity in the studied TMF is represented by 174 species, which belong to 53 botany families. The families with the most species richness are Lauraceae with 27 species, representing 15.5% of the relative diversity of the forest; this is followed by Moraceae with 16 species (9.2%), Rubiaceae with 12 species (6.9%), Euphorbiaceae with 11 species (6.3%), Melastomataceae with 10 species (5.7%), Meliaceae with 9 species (5.2%), Cecropiaceae with 7 species (4%), Clusiaceae and Myrtaceae with 5 species (2.9%), Asteraceae, Cunnoniaceae as well as Mimosaceae were represented with 4 species

(2.3%), and Anacardiaceae, Aquifoliaceae, Myrsinaceae, Rosaceae, Sapindaceae as well as Sapotaceae with 3 species (1.7%). The remaining families (35) had only 1–2 species, representing 0.6–1.1% of relative diversity.

3.3. Changes in Functional Diversity

Applying the linear mixed model (LMM), we found that the variations of the different indices that compose the FD of studied TMF is not produced exclusively by the implementation of selective thinning, but also by the distribution of the TMF along the altitudinal gradient, which implies different structural and diversity conditions.

The FRic variability was significantly influenced by the implementation of selective thinning, while the predictors related to habitat characteristics and altitudinal gradient did not show significant effect. Functional uniformity (FEve) was not significantly affected by any predictor. FDis was significantly influenced by predictors related to selective thinning and natural conditions of the forest. FDis and RaoQ were influenced by predictors related to natural conditions of the forest, while the predictors related to the implementation of treatment did not significantly influence this indices (Table 2).

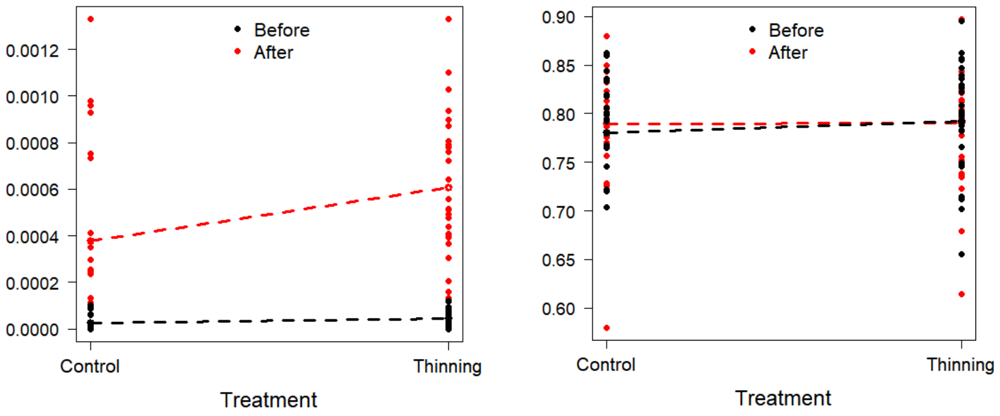
Table 2. Linear mixed models (LMM) of Functional Diversity indices as a function of stem density (stem ha^{-1}), total species, thinning intensity, altitude, treatment, period, treatment:period (fixed effects) and of plot membership nested in sample site (intercept random effects), and likelihood ratio tests (LRT). FEve was not affected by any predictor.

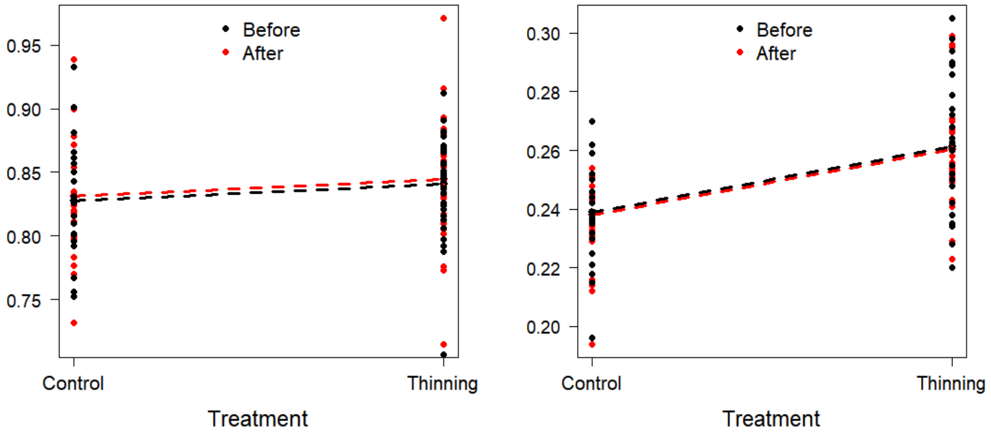
Predictors	**Functional Richness: FRic LTR *p* Value <0.001**		**Functional Diversity: FDiv LTR *p* Value <0.001**		**Functional Dispersion: FDis LTR *p* Value <0.001**		**Rao Quadratic Entropy: RaoQ LRT *p* Value 0.01**	
	Coeff	***p*-Value**	**Coeff**	***p*-Value**	**Coeff**	***p*-Value**	**Coeff**	***p*-Value**
(Intercept)	−1.08	**<0001**	8.6	**<0001**	4.3	**<0001**	2.06	**<0001**
Stem density							5.2	**0.02**
Total Species								
Thinning Intensity	2.47	**0.0182**	4.04	**0.004**				
Altitude			−7.31	**0.001**	12.9	**0.005**	14.4	**0.0002**
Treatment								
Period	−7.3	**<0001**						
Treatment: Period	−1.89	**0.0270**						

The ANOVA results comparing the values of the FD indices before and after the implementation of selective thinning indicate that significant differences were evident only for FRic (Table 3, Figure 2a), whereas the other indices (FDis, FEve, FDiv and RaoQ) were less sensitive to the implementation of selective thinning and more susceptible to changes in the natural conditions of the TMF (Table 3, Figure 2b–e).

Table 3. Functional diversity indices (mean ± SD), including the F-statistic values respective to the effect of thinning. Functional indices were calculated based on the six traits described in Table 1.

INDEX	**Before**	**After**	**Coeff**	**F *p*-Value**
Functional Richness (FRic)	0.000025 ± 0.000003	0.0005 ± 0.00003	−9.03	**<0001**
Functional Evenness (FEve)	0.786 ± 0.061	0.791 ± 0.058	−0.26	0.7902
Functional Divergence (FDiv)	0.835 ± 0.041	0.838 ± 0.047	−0.41	0.6793
Functional Dispersion (FDis)	0.251 ± 0.022	0.263 ± 0.023	0.23	0.3246
Quadratic Entropy (RaoQ)	0.0696 ± 0.011	0.0691 ± 0.012	0.11	0.8919


(**a**) FRic (**b**) FEve


(**c**) FDiv (**d**) FDis

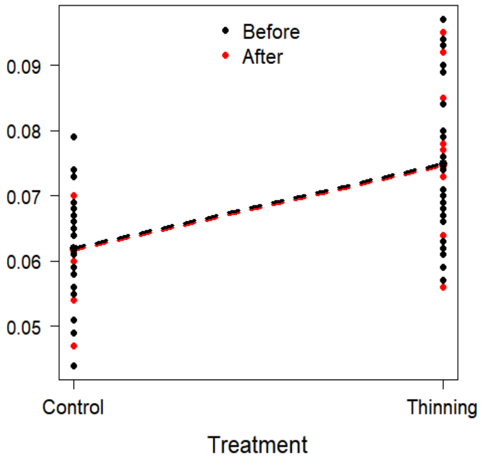

(**e**) RaoQ

Figure 2. Effects of thinning on functional diversity indices ($n = 52$) before and after implementation of selective thinning. (**a**) Functional Richness (FRic), (**b**) Functional evenness (FEve), (**c**) Functional divergence (FDiv), (**d**) Functional dispersion (FDis) and (**e**) Rao Quadratic entropy (RaoQ). Details of analyses of variance among control and thinned plots are given in Table 3.

The CWM values of the dominant trait in each of the sampled plots had different responses to the intervention. The frequency (trees after thinning of more important species in each plot) of certain species was affected by the extracted basal area and changed significantly after thinning was implemented; however, the initial number of species is also a predictor that significantly influences PCT frequency variability. Regarding growth, the implementation of selective thinning significantly affects the variability of the trait, although some predictors such as the number of species, the number of trees per hectare and the altitude gradient are also significant in the variability of the trait. Regarding the initial DBH, only the number of trees/ha^{-1} exerts significant influence on the trait (Table 4).

Table 4. Linear mixed models (LMM) of Community weighted mean CWM of potential crop trees frequency (FREQUENCY), diametric growth (GROWTH) and initial diameter at breast height (DBH) as a function of stem density (trees ha^{-1}), total species, thinning intensity, altitude, treatment, and plot membership nested in sample site (intercept random effects), and likelihood ratio tests (LRT).

Predictors	**FREQUENCY**		**GROWTH**		**DBH**	
	LRT *p* Value 0.01		**LRT *p* Value <0.0001**		**LRT *p* Value 0.01**	
	Coeff	***p*-Value**	**Coeff**	***p*-Value**	**Coeff**	***p*-Value**
Stem density			1.89	**0.002**	1.04	**0.004**
Total Species	1.8	**<0001**				
Thinning Intensity	3.47	**<0001**				
Altitude			−0.98	**0.003**	−2.43	**0.002**
Treatment	1.5	**<0001**				

4. Discussion

An important step before applying selective thinning, as shown in this study, is the analysis of the floristic composition of the original forest in an attempt to conserve the extraordinary biodiversity. However, a carefully planned silvicultural method can allow, at the same time, to increase the growth rates of the desired species and, subsequently, the extraction of resources for the economic development of the local population [81,82].

Therefore, individual tree species must be carefully analyzed to determine their economic or ecological value. If tree species with a limited number of individuals are cut, the diversity, and consequently, the functionality of the ecosystem may be affected, although during this investigation, not only individuals of abundant species were eliminated but also species with few representatives.

As shown in this study, if these preconditions are respected, selective thinning intensity does not cause significant changes in the forest ecosystem. Furthermore, the results suggest that the applied strategy makes the studied TMF more productive, especially in terms of growth, because the loss of taxonomic and functional diversity is minimal. The forest still serves as a conservation area, providing all of its ecosystem services; therefore, selective logging could also be a useful tool for biodiversity conservation and sustainable forest management [83,84].

Selective thinning also causes greater gaps within the forest stand, which changes the ecosystem conditions as a result of canopy openness. However, natural tree fall has the same effects, although gaps are generally less frequent. As Gunter et al. [68] found in the same TMF, Arctiidae moth communities were affected by both, selective thinning and natural tree fall, during the first year, whereas monocotyledonous and dicotyledonous vascular epiphytes did not show significant changes in structure or composition. Nevertheless, these impacts might be different in ravine forest or ridge forest parts [85,86], due to the different forest structure [68].

Plant traits are indicators of diversity, functionality and community composition [72], which are generally used to determine environmental changes over time or to understand natural successional processes. However, the selective thinning applied in this study adds another gradient of use, because the removed individuals belong to certain undesired species, which might affect the functional composition of the forest community. Therefore, to analyze changes of FD indices in this TMF regarding selective thinning, the used traits are mainly related to resource acquirement, because these allow one to evaluate if species exploit the available resources quickly, which generally occurs during periods of abundance at sites with sufficient water availability [87].

To assess the impacts of silvicultural interventions into an ecosystem and its functioning, all interactive components must be combined to obtain serial robust numerical indices [16], which can be provided by the FD. FD implies more than number of species and diversity, because multiple traits are considered, such as species dispersion syndromes, leaf functional characteristics, etc. Therefore, FD is an important attribute to analyze the response of a forest community to environmental changes. However, if only richness and diversity of species is evaluated to analyze the impact of forestry interventions, the generated information is still insufficient to understand the natural process of forest ecosystems [2,88].

In agreement with Baroloto et al. [42], some FD indices showed significant changes after thinning (Table 3), especially those related to the predictors that include thinning, but not those related to the altitude gradient, since this does not imply a pronounced effect on the communities or alteration in ecosystem processes. In general, functional diversity varies significantly as a result of changes in the forest community, as well as with the level of intervention; however, the total richness of the tree species may not change significantly due to the applied treatment [89]. As Putz et al. [90] indicated, the impact of forestry, especially logging, is more destructive with respect to carbon storage, but if growth rates increase forest productivity, carbon storage can be compensated.

Curzon et al. [91] concluded that in the temperate forests, functional diversity remains stable over the years after major disturbances like thinning or logging. By comparing the results in the temperate forests with our results in tropical montane forests, they both agree that neither produce significant changes in functional or taxonomic diversity shortly after the disturbance.

The Functional Divergence (FDiv) was influenced by the extracted basal area (slimming intensity) and altitude, which means that no clear influence of the intervention respective to the variability of this index could be demonstrated. The FDis and RaoQ indices were only influenced by the number of trees, which is a natural condition of the forest ecosystems and depends on various environmental factors [49–53].

The abundance and the initial DBH were less affected by intensity of the selective thinning applied, while the growth was improved due to changes in the initial conditions, mainly concerning availability of light and nutrients [49]. However, the community shows significant changes when comparing thinned plots and control plots and the specific role of each species could not be determined—such effects include succession changes, reproduction and interactions with other species. However, the experiment was executed within a natural reserve and no long-term treatment was applied to analyze larger scale logging regimes, such as a forest concession. Furthermore, the evaluation period was relatively short, and for this reason, changes in growth rates of remaining trees and modifications in species composition, such as reduction in shade-tolerant species, could not be analyzed. This also includes the effects on other important organism groups, such as epiphytes, orchids, mosses, ferns or insects, which should be the objective for further investigations.

In summary, selective thinning did not significantly alter the functionality of this TMF compared to the natural ecosystem (control plots). The DF was almost unchanged, which is the most critical point when applying a sustainable forest treatment. Future studies should focus on the links between biodiversity and ecosystem services [92], and long-term field monitoring is necessary [68].

5. Conclusions

In a neotropical TMF in southern Ecuador, selective thinning was performed at different intensities, which only slightly affected the FD of the forest. The calculated FD indices were based on different species traits, which improved the knowledge for designing sustainable management practices in ecologically sensitive ecosystem.

However, significant FD changes for all traits and predictors are not expectable, because to determine the ecosystem composition, the homogeneity of a forest stand, and the climatic conditions, especially in a TMF, is especially challenging. As the findings of this study showed, intensity of the treatment had no significant effect on FD changes in the community, whether the time span between the measurements, nor the eliminated individuals.

In the context of logging, the conservation of rare or less abundant species should be a priority before starting any forestry activity. Endangered species should be excluded from harvesting processes, logging and other forestry activities. Nonetheless, a sustainable forest management in combination with ecosystem conservation should remain a main objective for future development, because this not only guarantees the economic income for the local population, but also ensures the functionality of the forest stand to provide essential ecosystem services.

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/12/6/256/s1, Figure S1: Plots distribution in two forests types, the location of plot K that served as a control is shown in addition to the Q2 plots, Table S2: PCT´s list and individuals released and control, Table S3: Individuals by species removed and percentage with respect to the total of individuals inventoried in primary montane forest of RBSF.

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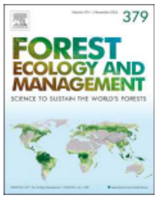

Effects of silvicultural treatments and topography on individual tree growth in a tropical mountain forest in Ecuador

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ABSTRACT

Few studies have analysed the effect of silvicultural treatments on tree growth in tropical montane forests (TMF). These forests have strong topographic gradients, which influence growth rates and can potentially interact with silvicultural treatments. The present study investigated the relative effects of silvicultural treatments and topography on growth rates at the tree level in a TMF.

For this, we combined two distinct data sources: (1) field data from a silvicultural experiment in the Andes of southern Ecuador where liberation thinnings, i.e. the removal of the strongest crown competitors, were applied to potential crop trees (PCT) in 2004; and (2) topographic variables obtained from a high-resolution digital terrain model created from an airborne LIDAR survey. We fitted all data in a single linear mixed-effect model. Based on monitoring data from 174 released and 200 reference PCTs of 8 timber species, we calculated periodic annual increment (PAI) in DBH 6 years after the silvicultural treatment as our outcome variable. As topographic predictors, we used elevation and a topographic position index. To control for the by-species growth variability we included random intercepts for species and random slopes for the effect of treatment on species in our model.

PAI was significantly influenced by the topographic predictors. Over the elevational gradient, growth rates declined on average by 0.73 mm a^{-1} per 100 m increase in elevation. For the topographic position, PCTs in valleys had an average PAI of 2.02 mm a^{-1} compared to 1.04 mm a^{-1} on ridges. The effect of the silvicultural treatment across all species was only marginally significant, but its effect size was nevertheless within the range, but at the lower end of values reported for other tropical forest ecosystems (reference trees: 1.35 mm a^{-1}; released trees: 1.60 mm a^{-1}). Between species, baseline growth rates as well as the treatment effect varied considerably. Best linear unbiased predictions of species effects suggested that 5 species responded positively to the silvicultural treatment, whereas 3 species showed no treatment effect. Overall, tree growth varied substantially as indicated by the large residual variance that remained unaccounted for in the model.

Our findings indicate that positive effects of silvicultural treatments in TMF are likely to exist, but that they are possibly obfuscated by strong topographical gradients and large between-tree growth variability. Overall, our results suggest that "broad-brush" management prescriptions are not suited for sustainable forest management of TMF. Instead, granular and spatially explicit prescriptions that take the strong impact of topography on diameter growth as well as species-specific responses to silvicultural treatments into account should be favoured.

1. Introduction

Andean tropical montane forests (TMF) are an epicentre of global biodiversity and endemism (Jenkins et al., 2013; Myers et al., 2000), but at the same time threatened by ongoing deforestation and forest fragmentation. TMF have been converted mainly to pasture used to raise cattle in extensive grazing systems (Tapia-Armijos et al., 2015). This has resulted in a large loss of biodiversity (Peters et al., 2010) and

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ecosystem services (Weber et al., 2013). As is the case in many areas across the tropics, deforestation has been mainly driven by other types of land use being more economically viable than natural forests (Geist and Lambin, 2002; Hosonuma et al., 2012). Sustainable forest management (SFM) could provide higher economic value to standing forests and therefore be a viable financial alternative to forest conversion (Putz et al., 2008), especially when combined with carbon offset schemes such as REDD+ (Nasi et al., 2011).

Silvicultural interventions to maintain or improve long-term natural forest productivity should be an integral part of SFM (Günter et al., 2012). Experiences in tropical lowland and premontane forest ecosystems have shown that growth rates of potential crop trees (PCT) can be increased by applying silvicultural treatments such as liberation thinning (e.g. Maître, 1990; Sist and Abdurachman, 1998; Wadsworth and Zweede, 2006; Peña-Claros et al., 2008; Villegas et al. 2009; de Avila et al., 2017). To develop locally adapted silvicultural management systems, ecological knowledge of tree species and especially reliable data about the impact of silvicultural treatments on tree growth are necessary (Pereira de Carvalho et al., 2004). This aspect remains understudied in TMF, as most studies about the impact of silvicultural treatments have focused on tropical lowland forests.

Tree growth in tropical forests is highly variable due to multiple sources of variability, such as local abiotic site characteristics and biotic interactions (Le Bec et al., 2015; Pretzsch, 2009). This is especially true for TMF, which are characterized by strong environmental and topographic gradients on small scales (Beck et al., 2008). The influence of these microtopographic gradients on tree growth seems to be high, but still poorly understood (Bräuning et al., 2008; Homeier et al., 2010). This poses a challenge for silviculture in TMF, as it is not enough to merely know that tree growth changes with topography. Instead, management planning requires quantitative estimates for the magnitude of change across gradients as well as knowledge about species-specific responses to topography. Further, microtopography should be controlled for when studying the impact of silvicultural treatments on tree growth in TMF. Otherwise, there is a risk that growth variation due to these gradients might be falsely attributed to silvicultural treatments. Yet, studies focussing on silvicultural treatments in TMF rarely included information about topographic gradients in their analysis (but see Ashton et al., 2011). Studies that focussed on the relationship between tree growth and abiotic site characteristics in TMF, on the other hand, usually have not been in the context of silvicultural experiments (e.g. Clark et al., 2015; Homeier et al., 2010; Le Bec et al., 2015; Rapp et al., 2012; Sherman et al., 2012; Yanez-Espinosa et al., 2006).

In the present study, we focused on the impacts of silvicultural treatments and small-scale abiotic site characteristics on tree growth in a TMF. For this, we used a dataset from a natural forest management experiment that was installed in 2004 in southern Ecuador (Günter et al., 2008). As proxies for small-scale site conditions, we used microtopographic variables obtained from a high-resolution digital terrain model (Silva et al., 2015). To our knowledge, the combination of ground-based tree growth data from silvicultural experiments with high-resolution remote sensing data has never been carried out in TMF research.

Our specific objectives were to quantify how diameter growth rates of potential crop trees (PCTs) are impacted by 1) liberation thinning and 2) elevation and topographic position. We aimed to provide estimates for these objectives across all species as well as on the species-level. We predicted that growth rates across species would 1) show a positive response to the silvicultural treatment, and 2) decrease with increasing elevation and along the gradient from valleys to ridges.

2. Methods

2.1. Study region

Data in this study stem from a natural forest management experiment established in the privately owned Reserva Biologica San Francisco (RBSF, 3° 58′S, 79° 04′W) on the eastern slope of the Cordillera El Consuelo in the Andes of southern Ecuador. The altitude of the experiment is 1850–2150 m asl. Mean annual precipitation at 1952 m asl amounts to 2100 mm and annual temperature averages 15 °C. The site is characterized by steep environmental gradients and a high topographical heterogeneity, which defines its floristic composition and forest structure (Homeier et al., 2010). For the altitudinal range of the experiment, Homeier et al. (2008) distinguished three main forest types: Forest type I, the tallest and most speciose forest, grows in major ravines and gentle lower slopes on altitudes below 2200 m asl. The canopy in this forest type reaches 25–30 m, with some emergents reaching up to 35 m. Forest type II can be found on upper slopes and ridges between 1900 and 2100 m asl, with a canopy height of 15 m. In forest type III, found between 2100 and 2250 m asl, the trees usually do not surpass 12 m. For a comprehensive description of the geology, climate, flora, and fauna of the RBSF, we refer to Beck et al. (2008).

2.2. Silvicultural experiment and growth data

For the silvicultural experiment, 52 experimental plots with an area of 0.25 ha each were installed in 2003 in visibly undisturbed natural forest in the RBSF (Günter et al., 2008). The total size of the experimental plots on the ground was 13 ha, which corresponds to 11.1 ha in projected map view. The plots were located in three adjacent microcatchments named MC2, MC3 and MC5, with sample areas of 5, 4 and 4 ha on the ground, respectively. All trees with diameter at breast height (DBH) ≥ 20 cm were measured for DBH, mapped and identified to species level. The exact location of individual trees was calculated based on ca. 5.000 trigonometric measures between trees as well as ca. 150 trigonometric measures between trees and 53 reference points which had been registered with a differential GNSS (Trimble GPS Pathfinder Pro).

In 2004, a total of 449 PCTs from a pool of 9 different species were selected. These species were *Cedrela montana*, *Clusia ducuoides*, *Ficus citrifolia*, *Handroanthus chrysanthus, Hyeronima asperifolia*, *Hyeronima moritziana*, *Inga acreana*, *Nectandra membranacea* and *Podocarpus oleifolius*. They were selected based on their (potential) commercial value and, where possible, additional ecological and/or medicinal importance. Criteria for the selection of individual trees as PCTs were a straight butt log, single leading stem, small branches and no defects.

Subsequently, a silvicultural treatment was applied to 205 PCTs in a campaign between April and May 2004. For this, we first determined the strongest competitor in the upper canopy of each selected PCT based on tree form, crown diameter and social position within the forest stand. These competitors were then removed using directional felling to minimize damage to the residual stands. Such a treatment has been named liberation thinning or improvement felling (Guariguata, 1999; Günter et al., 2008; Wadsworth and Zweede, 2006). A total of 244 PCTs in MC2, MC3 and MC5 remained as reference trees without silvicultural treatment (Table 1). In the original design of the experiment, different treatment intensities were applied in the microcatchments; MC2 served as reference area without any treatment and MC3 and MC5 as areas of moderate and intense improvement fellings, respectively, in order to study the influence of treatment intensities on water fluxes on the catchment level (Wilcke et al., 2009). For individual PCTs, however, the liberation effect was comparable between MC3 and MC5 since the strongest competitor was removed for each PCT. As we focused on the individual tree level, and not the stand level, we did not differentiate between treatment intensity and only use “reference” and “released” as factor levels for the silvicultural treatment.

Home-made steel band dendrometer were installed on each PCT at breast height (1.30 m above ground) or above buttresses or other irregularities, if present. The dendrometer were fitted 6 months prior to the silvicultural interventions, because newly installed dendrometers often underestimate radial growth (Pélissier and Pascal, 2000). The

Table 1

Overview of treatment intensity and removed basal area (adapted from Günter et al. (2008)). Basal area (BA) values represent all trees and palms with DBH ≥ 20 cm).

	MC2	MC3	MC5
Size (ha)	5	4	4
PCTs	136	133	180
Released PCTs	–	76	129
Reference PCTs	136	57	51
Pre-treatment BA (m^2/ha)	17.4 (± 1.7)	10.3 (± 0.8)	24.3 (± 1.8)
Removed trees/ha	–	18	32
Removed BA/ha (m^2/ha)	–	0.62 (± 0.16)	2.5 (± 0.64)
Ratio of removed BA/ha to pre-treatment BA/ha (in %)	–	6.0%	10.3%

dataset for this study consists of monthly registrations of growth between June 2004 (i.e. when silvicultural treatments were applied) and April 2010. For each tree, we calculated periodic annual increments (PAI) in DBH over the total time period as the outcome variable in our statistical analysis.

We removed the following PCTs from our analysis:

- Reference trees with less than 20 m from an improvement felling (n = 13), because their growth might have been impacted by the silvicultural treatment.
- All trees of *Ficus citrifolia* (n = 20), because only 4 PCTs had been released for this species and our random slope linear mixed effect modelling approach (see Section 2.3.2) is susceptible to groups containing few data (Harrison et al., 2018).
- All PCTs that have died over the monitoring period (n = 17).

This resulted in a total of 399 PCTs included in our study. For trees with DBH ≥ 20 cm, the 8 studied species in this paper comprised 18.8% of the total number of trees and 19.6% of the total basal area per hectare of the initial forest stand. For all PCTs in this study, the location, species and applied silvicultural treatment are shown in Fig. A1 and Table 2.

Around 1.4% of the monthly growth measurements had been flagged as doubtful in the database, for instance because of disturbed or replaced dendrometer bands. To deal with this, we first decomposed the cumulative growth time series into monthly growth values and then removed the doubtful measurements. Subsequently, we substituted the removed growth values with the mean growth of all non-missing months of the respective PCT. Finally, we reconstructed cumulative growth time series using the substituted growth values. We assume that this approach introduced no bias because replaced values were roughly evenly spread across species and treatment levels.

2.3. *Data analysis*

To quantify the relative impacts of silvicultural treatments and small-scale abiotic site characteristics on tree growth, we used individual trees as the independent sampling units of observation and fitted all data in a single linear mixed-effect model (LMM; Zuur, 2009). LMMs have been successfully used to model tree growth following silvicultural interventions in tropical forests (Lussetti et al., 2019; Ruslandi et al., 2017).

Table 2

Overview of released and reference PCTs included in the study.

Species	Reference	Released	Total
Cedrela montana	20	21	41
Clusia ducuoides	40	34	74
Handroanthus chrysanthus	35	44	79
Hyeronima asperifolia	24	27	51
Hyeronima moritziana	19	19	38
Inga acreana	18	14	32
Nectandra membranacea	34	17	51
Podocarpus oleifolius	16	17	33
Total	206	193	399

2.3.1. *Selection of predictors*

Aside from the silvicultural treatment, we selected three predictors at the tree level with a strong a priori justification based on their theoretical ecological relevance and reported effects on PAI (e.g. Clark et al., 2015; Rapp et al., 2012; Le Bec et al., 2015; Ruslandi et al., 2017). The first predictor was the initial DBH, as measured before the application of the silvicultural treatment. The other two predictors were proxies for small-scale abiotic site characteristics: elevation and a topographic position index (TPI). In our study area, these two predictors have an impact on intraspecies growth variation (Bräuning et al., 2008) and are the most influential microtopographic metrics determining the spatial distribution of tree species at a fine scale (Kübler et al., 2016). We used a digital terrain model (DTM) with a resolution of 1 m created from an airborne LIDAR survey (Fig. A2; Silva et al., 2015). Based on this DTM raster, we derived a TPI which expresses whether a given pixel is in a valley/lower slope (negative values of TPI), midslope (values around zero of TPI) or ridge/upper slope (positive values of TPI) compared to surrounding pixels (Fig. A2; Guisan et al., 1999). The TPI is scale-dependent; for its calculation, a moving circular window is used, whose size can be varied. In a pre-analysis, we assessed different sizes ranging from 50 to 400 m for plausibility and retained a TPI with a moving window of 100 m radius. We then extracted the respective values for the spatial locations of each PCT from the DTM and TPI rasters.

2.3.2. *Modelling PAI growth*

We applied an iterative model building process to determine which model best describes our empirical data and present here the final LMM with the optimal fixed effects structure and random effects structure (Zuur, 2009). Model building was guided by a comparison of alternative models based on Akaike information criterion (AIC) and likelihood ratio tests (LRT) as selection criteria. We used the maximum likelihood method (ML) to calculate AIC values during model building, whereas the final model was fitted using restricted maximum likelihood (Zuur, 2009). As all selected predictors have a theoretical justification for their inclusion, we refrained from employing a systematic stepwise model selection method and instead only considered models including all predictors (Whittingham et al., 2006). All models were fitted using package lme4 (Bates et al., 2015) in the R statistical environment (R Core Team, 2018).

The final model presented in this study is:

$$\begin{aligned}\ln(\mathrm{PAI}_{isp}+1) &= \beta_0+\beta_1\times \mathrm{Treatment}_{isp}+\beta_2\times \mathrm{Elevation}_{isp}+\beta_3\times \mathrm{TPI}_{isp}+\beta_4\\ &\quad \times \mathrm{DBH}_{isp}+\mu_{0s}+\mu_{1s}\times \mathrm{Treatment}_{isp}+\mu_{2p}+\varepsilon_{isp}\end{aligned} \quad (1)$$

The response variable PAI_{isp} indicates the value of DBH growth per year of PCT i (i = 1, ⋯,399) of species s on experimental plot p. As model assumptions of normality of residuals and homogeneity of variance were not met, we explored three transformations of PAI that are frequently used when modelling tree growth (Lhotka and Loewenstein, 2011): Natural logarithm of PAI, natural logarithm of (PAI + 1) and square root of PAI. The transformation $\ln(\mathrm{PAI}_{isp}+1)$ substantially reduced non-normality of residuals and heteroscedasticity and was therefore used for the subsequent model development.

In the fixed part of the model, $\mathrm{Treatment}_{isp}$ indicates the silvicultural treatment with dummy coding (reference level = 0, released level = 1). The continuous predictors $\mathrm{Elevation}_{isp}$, TPI_{isp} and $\mathrm{initialDBH}_{isp}$ are the respective values of elevation, topographic position index and initial DBH of the i-th PCT. During model building, we examined all possible two-way interactions between predictors. None lead to a better model performance (based on AIC and LRTs) and we therefore didn't include them in our final model. We scaled all continuous predictors by centring them on 0 and dividing them by two times their standard deviation (SD) to directly compare the relative strength of influence between the three scaled continuous predictors and the (binary) treatment predictor (Gelman, 2008).

In the random-effects structure of the model, we fitted three random effects. To control for the by-species growth variability, and therefore generalize our results to a wider context, we included two species effects as random effects: Random intercepts μ_{0s} for species s and random slopes $\mu_{1s} \times \text{Treatment}_{isp}$ for the effect of treatment on species s. This allowed us to fit all growth data in a single model, as the random intercept term accounted for interspecific difference in growth rates (Bräuning et al., 2008) and the random slope for interspecific differences of responses to the silvicultural treatment (Günter et al., 2008). We fitted the model allowing for correlation and different variances between random intercepts and random slopes (Bates et al., 2015). We further fitted a random intercept μ_{2p} for each experimental plot p to account for heterogeneity across plots within the RBSF.

We didn't include other random slopes in our final model. By doing so, we assume that the effect of treatment is constant across experimental sites and that the effects of elevation, TPI and initial DBH on PAI are invariant across species and experimental plots.

2.3.3. *Model validation and analysis of model outcomes*

The final model was assessed based on the following standard model validation plots for LMM (Zuur, 2009): fitted values vs residuals for the entire model, a normal Q-Q plot, model residuals versus all predictors and fitted values versus residuals for each species.

To inform about the significance of fixed effect, we computed 50% and 95% likelihood profile confidence intervals on variance-covariance and fixed effects parameters of our final model (Bates et al., 2015). Following Shenkin et al. (2015), we use two levels of evidence against the null hypothesis that the coefficient of a fixed effect is zero. If the confidence limits of a fixed effect coefficient do not contain zero at the 95% confidence level, we consider this effect as significant. If the 95% confidence interval includes zero but the 50% confidence interval does not, we describe such an effect as marginally significant.

To visualize effect sizes at the population level (i.e. when all random effects are set to zero), we computed predicted PAI responses for each fixed effect while leaving all other fixed effects constant at their respective observed mean value. We further derived 95% confidence intervals for these predictions using parametric bootstrapping (number of simulations = 2000), with each simulation generating new values of both the random effects and residual error (Bates et al., 2015). For easier interpretation, we back-transformed predicted PAI and confidence intervals from the ln(1 + x)-scale back to their original scale using a "ratio estimator" correction factor to avoid bias (Snowdon, 1991):

$$\widehat{PAI}' = (e^{\widehat{PAI}} - 1) \times CF \tag{2}$$

where $\widehat{PAI}'$ is the predicted back-transformed value of PAI after correcting log transformation bias, $\widehat{PAI}$ the prediction of the final LMM in the log-scale, and CF the correction factor.

We calculated CF as follows:

$$CF = \frac{\overline{PAI}}{e^{\overline{\widehat{PAI}}} - 1} \tag{3}$$

where $\overline{PAI}$ is the arithmetic sample mean of untransformed PAI and $e^{\overline{\widehat{PAI}}} - 1$ the mean of the uncorrected back-transformed predicted PAI values.

We then plotted each fixed effect in its original scale against back-transformed predicted PAI. To improve the interpretability of the TPI plot, we classified the continuous TPI values into five discrete slope position classes (valley, lower slope, middle slope, upper slope and ridge) according to Weiss (2001).

To test whether the inclusion of random intercepts and random slopes improved our model fit, we used likelihood ratio test statistics (LRT; Zuur, 2009). For random intercepts, we compared a model with only random intercepts to a model with neither random intercepts nor random slopes. For random slopes, we compared the final model to a model containing only random intercepts.

For species-specific predictions of PAI of reference PCTs (random intercepts) and of the effect of treatment on PAI (random slopes), we present best linear unbiased predictions (BLUPs) for the within-species coefficients of the random effects. Prediction intervals at the 95%-level for BLUPs were calculated based on conditional variance-covariance matrices of the random effects (Pinheiro and Bates, 2000). For better interpretability, we back-transformed predictions and associated prediction intervals using the "ratio estimator" correction factor CF.

3. Results

3.1. *Descriptive statistics*

Mean PAI across all PCTs was 1.54 mm a^{-1} (95% CI [1.37, 1.71]). Fig. 1 indicates that the initial DBH of PCTs had no strong trend on DBH growth. Elevation and TPI on the other hand appeared to have a

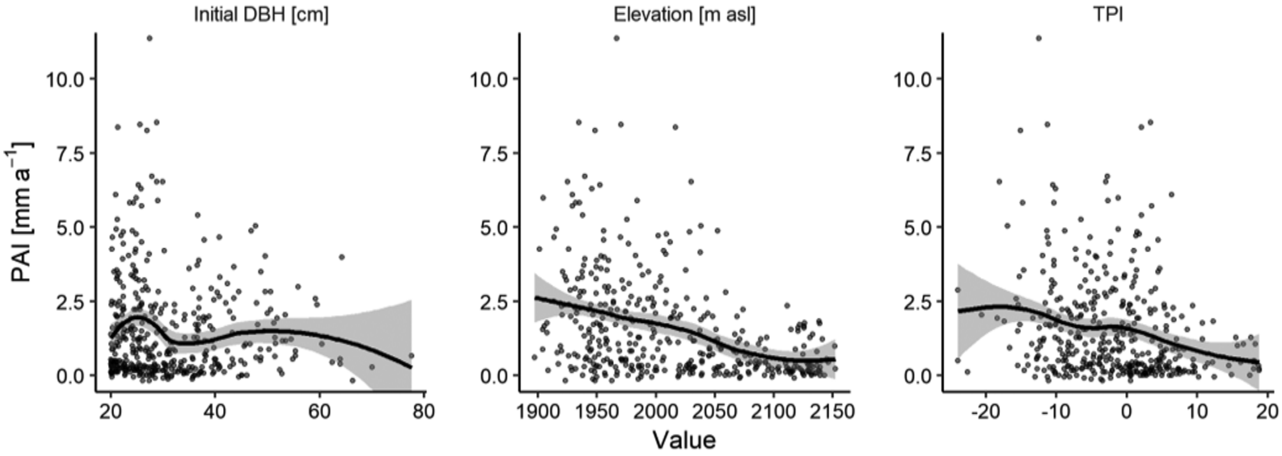

Fig. 1. The relation between PAI and initial DBH (left panel), elevation (middle panel) und TPI (right panel). Black lines and grey areas show locally weighted regressions and their standard error bounds, respectively.

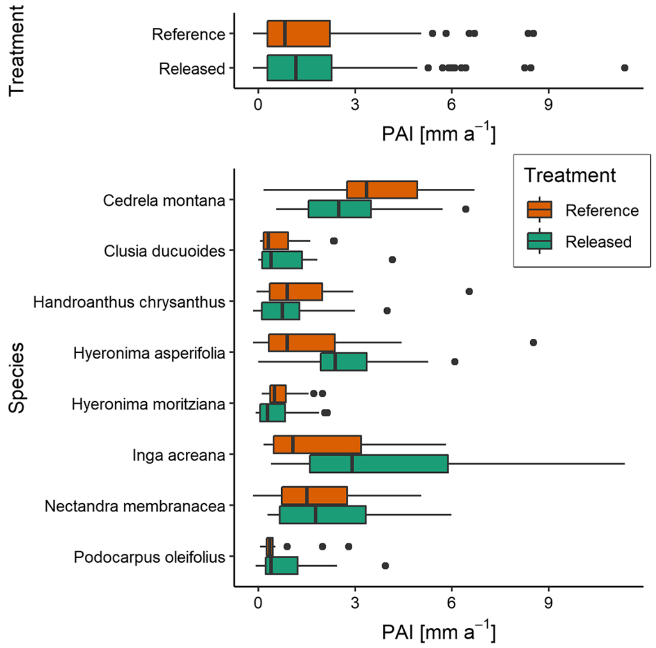

Fig. 2. Box plots of PAI of reference and released PCTs across all species (top panel) and for each individual species (bottom panel).

decreasing trend, i.e. DBH growth decreased with increasing elevation and increasing TPI (high values of TPI correspond to ridges/upper slopes). Overall, released PCTs seemed to have higher PAI than reference PCTs (Fig. 2, top). Between species, PAI for reference trees as well as the effect of treatment on PAI varied considerably (Fig. 2, bottom).

3.2. Model outcomes

Model validation graphs for the final LMM revealed no violations of model assumptions (Fig. A3 in supplementary materials). Model residuals appeared to be normally and homogeneously distributed and no trends in residuals vs predictor variables could be observed. Multicollinearity was not an issue, as correlation between fixed effects was low (Table A1 in supplementary information).

Figs. 3 and 4 provide information about the fixed effect structure of the final model. We back-transformed fixed effect predictors and PAI in Fig. 4 to original scales after calculating population-level predictions.

The intercept of fixed effects, i.e. the estimated value of PAI when all fixed effects were set to 0, was significantly different from zero and amounted to 0.74 (95% CI [0.57, 0.92]) in the ln(1 + x)-scale (Fig. 3) and 1.35 mm a^{-1} (95% CI [0.94, 1.85]) back-transformed to the original scale.

The effect of elevation on PAI was significant, as its 95% confidence interval does not include zero (Fig. 3). PCTs at higher altitudes had their PAI decreased by 0.38 (95% CI [0.56, 0.22]) in the ln(1 + x)-scale for an increase of two SD in elevation. Fig. 4 presents back-transformed predictions for PAI across all random effects over the range of elevation while all other fixed effects were held constant at their mean values. PAI decreased from 2.49 mm a^{-1} at 1897 m asl to 0.62 mm a^{-1} at 2152 m asl, corresponding to an average decrease of 0.73 mm a^{-1} per 100 m increase in elevation.

TPI was a significant predictor, too, with an increase of two SD of TPI leading to a decrease in PAI of 0.13 (95% CI [0.25, 0.01]) in the ln (1 + x)-scale (Fig. 3). Back-transformed predicted PAI for minimum TPI (valleys) and maximum TPI (ridges) under standardized conditions were 2.02 mm a^{-1} and 1.04 mm a^{-1}, respectively (Fig. 4).

Silvicultural treatment showed a moderate effect size in the expected direction, with released PCTs having their PAI increased by 0.09 (95% CI [−0.10, 0.28]) in the ln(1 + x)-scale compared to reference PCTs. Under standardized conditions, predicted PAI at the population-level was 1.35 mm a^{-1} for reference trees and 1.60 mm a^{-1} for released trees (Fig. 4). The effect of silvicultural treatment was only marginally significant (Fig. 3).

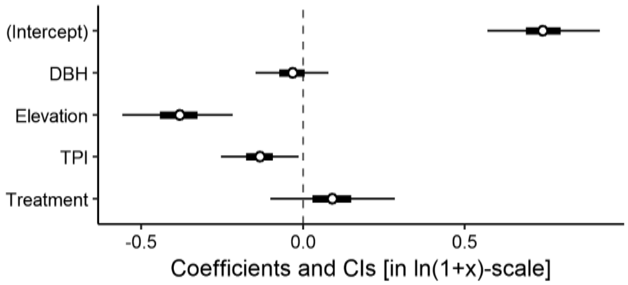

Fig. 3. Parameter estimates for the fixed effect structure of the final LMM. The centre dots show coefficients for the effect of predictors on PAI (in the ln (1 + x)-transformed scale). The 50% and 95% confidence intervals of coefficients are indicated by thick horizontal lines and thinner, wider horizontal lines, respectively. The vertical dashed grey line marks the null value.

The initial DBH at the beginning of the experiment was not a significant predictor (Fig. 3). For a two SD increase in initial DBH, PAI decreases by 0.03 (95% CI [−0.08, 0.15]) in the ln(1 + x)-scale. Over the range of initial DBH from 20 cm to 78 cm, PAI was predicted to decrease from 1.52 mm a^{-1} to 1.29 mm a^{-1} (Fig. 4).

Table 3 informs about the random effect structure of the final model. LRTs indicated that a model without any random effects was outperformed by a model with only random intercepts for experimental plots (L = 5.52, df = 1, p = 0.02), which in turn was outperformed by a model with random intercepts for experimental plots and species (L = 34.64, df = 1, p < 0.001). The final model with random slopes for the effect of treatment on species as well as the two random intercepts performed best (L = 7.80, df = 2, p = 0.02).

Variances of the three random effects, i.e. the unexplained variation in PAI due to each random effect after controlling for the fixed effects, had similar magnitudes; the SD of the variability of the intercept across experimental plots, intercept across species and slope for the effect of treatment across species was 0.13 (95% CI [0.02, 0.21]), 0.21 (95% CI [0.08, 0.38]) and 0.21 (95% CI [0.07, 0.40]), respectively. The estimated residual variance, i.e. variation in PAI that remained unaccounted for in the model, was considerably higher (SD = 0.46 (95% CI [0.42, 0.49])).

The correlation between random intercepts and slopes was −0.16 (95% CI [−0.79, 0.97]). This suggests that species with a lower intercept (i.e. lower growth rates of reference PCTs) had a higher slope (i.e. a more positive reaction to the silvicultural treatment), and vice versa. However, this model outcome is uncertain due to the large confidence interval.

Fig. 5 presents BLUPs and prediction intervals for species-specific intercepts and slopes for treatment. *Cedrela montana* had by far the highest PAI when all fixed effects were zero, while *Handroanthus chrysanthus*, *Hyeronima moritziana* and *Podocarpus oleifolius* showed the lowest PAI. The highest positive treatment effects were predicted for *Hyeronima asperifolia* and *Inga acreana*, followed by lower positive effects for *Clusia ducuoides, Podocarpus oleifolius* and *Nectandra membranacea*. Three species (*Cedrela montana*, *Handroanthus chrysanthus* and *Hyeronima moritziana*) had a slightly negative predicted treatment effect. Overall, uncertainties of the species-specific treatment effect were high, with the prediction interval of only two species not crossing the zero line.

4. Discussion

In this study, we quantified to what extent improvement fellings and small-scale abiotic site characteristics affected diameter growth of PCTs

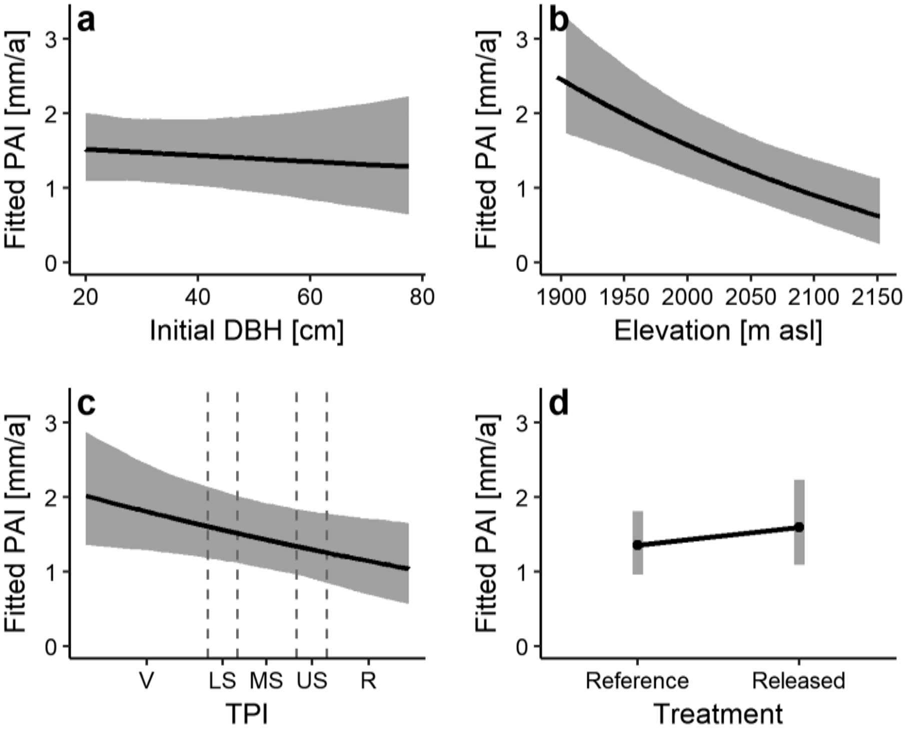

Fig. 4. Prediction of PAI responses over the observed range of each fixed effect while leaving all other fixed effects constant at their mean value. Random effects were set to zero. Grey areas around the black line shows the 95% confidence intervals based on parametric bootstrapping. PAI and fixed effects were back-transformed to their original scales after computation of predictions. TPI values (c) were classified into V (valley), LS (lower slope), MS (middle slope), US (upper slope) and R (ridge) according to Weiss (2001).

in a TMF. Using a novel approach that combined field data from a silvicultural experiment and microtopographic variables derived from high-resolution remote sensing data allowed us to disentangle these effects. PAI was significantly influenced by elevation and topographic position, with growth rates declining strongly over the gradient from lower elevations and valleys to higher elevations and ridges. In contrast, the applied silvicultural treatment was only marginally significant, but nevertheless showed a moderate positive effect size. Our study indicates that in TMF, potential positive effects of silvicultural treatments likely exist but are possibly obfuscated by strong environmental gradients and high between-tree growth heterogeneity.

4.1. Effect of topographic variables

A decline of diameter growth with elevation has been reported for many TMF (Clark et al., 2015; Homeier et al., 2010; Sherman et al., 2012), but the effect size in our study was larger than in other studies. There are multiple potential explanations for this.

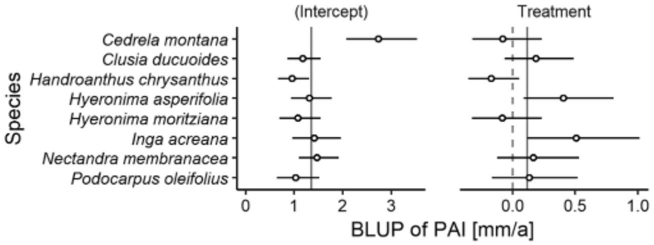

Fig. 5. Back-transformed BLUPs of species-specific intercepts (left) and slopes of treatment (right). Horizontal lines show the 95% prediction interval. Solid vertical grey lines show the estimated fixed coefficients across all species, i.e. the estimated PAI when all fixed effects as well as the treatment effect were zero (left) and the estimated change in PAI due to the silvicultural treatment (right). The vertical dashed grey line (right) marks a zero treatment effect.

Over the altitudinal range of the silvicultural experiment, species composition shifts from the more productive Forest type I at lower elevations to less productive Forest types II and III at higher elevations (Homeier et al., 2010). This shift has been reported to explain in part the decrease in PAI with elevation (Bräuning et al., 2008). Are our results in line with this explanation? A moderately high SD of the random intercept across species in our results indicates that there is indeed a substantial species effect, with growth rates of PCTs from the same species being more similar than growth rates of PCTs from different species. Based on Homeier et al. (2008), we can link all eight species in our study to either Forest type I or II/III. BLUPs for the random intercept of species (Fig. 5) suggest that PAI of species linked to Forest type II and III (*Clusia ducuoides*, *Hyeronima moritziana* and *Podocarpus oleifolius*) were lower than PAI of species linked to Forest type I (*Cedrela montana*, *Hyeronima asperifolia*, *Inga acreana* and *Nectandra membranacea*). However, *Handroanthus chrysanthus*, also typical for Forest type I, showed the lowest growth rates of all species. Further, species-specific PAI predictions were uncertain and, except for *Cedrela montana*,

Table 3
Results for the random effect structure of the final LMM. SD = standard deviation for each variance component and the 95% confidence interval; AIC = AIC for models with 1) random intercepts for experimental plots, 2) random intercepts for experimental plots and species, 3) random slopes of treatment on species and both random intercepts; AIC for the model without random effects was 610.8; L and p-value = likelihood ratio test statistics; Correlation = correlation between the random intercept and slopes for species.

Random parts	SD	AIC	L	p-value	Correlation
Intercepts (experimental plots)	0.13 [0.02, 0.21]	607.3	5.52	0.02	
Intercepts (species)	0.21 [0.08, 0.38]	574.6	34.64	< 0.001	−0.16 [−0.79, 0.97]
Slopes (treatment on species)	0.21 [0.07, 0.40]	570.8	7.80	0.02	
Residual	0.46 [0.42, 0.49]				

showed only small overall differences between species. Additionally, we controlled for growth rate differences between species in our model by allowing random intercepts for species. Unpublished models without species effects, which we explored during the iterative model building process, had considerably larger effect sizes for elevation than our final model. Our findings therefore suggest that the strong response of PAI to elevation is not only caused by shifting species composition due to forest type transitions, but also other factors.

Over the altitudinal range of the silvicultural experiment, increasing elevation has been linked to an annual average lapse rate of -0.52 K/100 m (Fries et al., 2009); an increase of average annual precipitation and fog input by 250 mm/100 m and 40 mm/100 m, respectively (Rollenbeck, 2006); a decrease in soil fertility, N availability, mineral soil depth and an increase of the thickness of the organic layer and pH (Ließ et al., 2011; Ließ, 2011; Wilcke et al., 2009; Wolf et al., 2011). It is likely that a combination of these environmental changes causes the large decline of PAI with elevation in our study.

The strong decline of PAI over the gradient from valleys to ridges is in line with some reports from previous studies in TMF (Homeier et al., 2010), whereas other studies found no significant difference in growth rates between valleys and lower slopes (Bellingham and Tanner, 2000), or higher growth rates on ridges compared to lower slopes (Herwitz and Young, 1994). For spatial scales similar to the one in our study, the effect of TPI on PAI has been partly explained by differences in species compositions between different topographic positions, with valleys harbouring fast-growing species and ridges slow-growing species (Liu et al., 2014). This was also reported for our study area (Homeier et al., 2010). However, as interspecific differences in growth rates were accounted for in our model, other factors can probably explain the strong effect of TPI on PAI. Abiotic and biotic differences due to microtopographic variations are large in our study area: Compared to valleys and lower slopes, ridges and upper slopes are characterized by higher humus concentrations, lower pH and less nutrients (Wilcke et al., 2011; Wolf et al., 2011), lower leaf litter decomposition (Werner and Homeier, 2015), and less abundant and nutrient-rich throughfall (Oesker et al., 2008). These differences between topographic positions can be partly explained by frequent landslides and the resulting removal of mineral soil on ridges (Vorpahl et al., 2012).

Elevation and TPI being strong and significant predictors for PAI supports their use as proxies for the local abiotic environment. Yet, experimental plots explained a considerable amount of the variability of PAI that was not explained by the fixed effects. Hence, microtopographic variables did not capture all growth variability caused by the strong environmental heterogeneity within the study area.

4.2. *Effect of silvicultural treatment*

Our findings may appear contradictory at first: There was only weak evidence to reject the null hypothesis of a zero effect of the silvicultural treatment, but the point estimate for the effect of the silvicultural treatment on PAI seemed nevertheless non-negligible. Here, we discuss both these findings.

A true zero treatment effect would explain the silvicultural treatment not reaching the conventional threshold level of statistical significance. However, absence of evidence is not evidence of absence; there are multiple alternative explanations for the weak explanatory power of the silvicultural treatment. First, the treatment effect on PAI varied between species, with a slightly negative effect predicted for three of the eight analysed species (Fig. 5). These interspecies differences likely explain in part the absence of statistical significance of the silvicultural treatment at the population level (i.e. across all species). Fitting a specific model for each species would probably have increased the explanatory power of the treatment effect for some species.

Second, elevation and TPI had larger coefficients than the silvicultural treatment (Fig. 3). These large topographic effects likely have a high associated growth variability, which in turn might have obfuscated potential treatment effects in our statistical analysis.

Third, the variability in PAI unexplained by the fixed effects that is due to between-tree differences is large. This is in line with other studies about tree growth in tropical forests (Le Bec et al., 2015; Ruger et al., 2011). We assume that the unexplained between-tree growth variability caused a large overlap in growth responses, which in turn lowered the statistical power of our analysis. Consequently, the probability of detecting statistical significance of a potential effect of the silvicultural treatment might have been low.

Our model suggests that the predicted PAI for reference and released trees was 1.35 mm a^{-1} and 1.60 mm a^{-1}, respectively. This corresponds to a treatment effect of 0.25 mm a^{-1} or a percentage increase of 18.5%. In tropical lowland forests, percentage increases in growth rates after silvicultural treatments were e.g. 22–27% (Villegas et al., 2009), 50–60% (Peña-Claros et al., 2008), 13–28% (Souza et al., 2015) and 19–24% (Vatraz et al., 2016). While these reports differed in terms of the applied silvicultural treatments and studied forest ecosystems (often including already exploited stands), they still allow for an approximate comparison with our findings. Hence, the percentage increase of PAI due to the silvicultural treatment in our study seems to be within the range, but at the lower end of reported values from tropical forests.

As the focus of our study was on the population level, we refer to Günter et al. (2008) and Cabrera et al. (2019) for an in-depth analysis and discussion of species-level responses to the silvicultural treatments in our study area. Here, we limit our consideration to *Cedrela montana*. For this species, Günter et al. (2008) and Cabrera et al. (2019) reported considerably lower growth rates for released trees compared to reference trees. While this is in line with our raw data (Fig. 2), our statistical model suggests that there is only a minor difference between reference and released trees. What is the reason for this seemingly contradictory finding? Long-term growth data for *Cedrela montana* from tree ring analyses of 38 of the total of 41 PCTs used in the silvicultural experiment (Spannl et al., 2012) give a possible answer to this question. Between 1976 and 2003, i.e. before the application of the silvicultural treatment, the mean growth rate for the reference group was considerably higher than for the released group ($PAI_{reference} = 2.31$ mm a^{-1}, $PAI_{released} = 1.43$ mm a^{-1}). These pre-treatment differences in growth rates between the reference and released group existed by chance, probably due to the large between-tree growth variability and environmental heterogeneity in our study area. As tree growth in tropical forests tends to be autocorrelated in time (Brienen et al., 2006; Dionisio et al., 2018), the differences likely persisted after the application of the silvicultural treatment. Unlike Günter et al. (2008) and Cabrera et al. (2019), our statistical model controlled for environmental heterogeneity, and by doing so also accounted for some of the pre-treatment growth differences between the reference and released groups.

4.3. *Implications*

What do our results mean for the sustainable management of TMF?

First, we showed that the magnitude of the overall impact of liberation thinnings on PCTs was within the range of values reported from other tropical forest ecosystems. This, in conjunction with results from an earlier study that showed that the silvicultural treatment had only minor ecological impacts on the remaining stand in the study area (Günter et al., 2008), suggests that silvicultural interventions have potential in the sustainable management of TMF. On the other hand, the effect of the silvicultural treatment being on the lower end of reported values raises the question of the economic viability of liberation thinnings, especially in view of the higher costs for timber extraction in TMF (Günter, 2011). Future studies should focus on this aspect as it is likely to influence whether silvicultural treatments will be adapted by forest managers or not.

Second, responses to the liberation thinning varied between species, which suggests that an indiscriminate application across the whole stand is not advisable. Instead, the silvicultural treatment should only be applied to those species that responded positively. However, as predictions of species-specific treatment effects had high uncertainties in our study, further research is required for reliable recommendations on the species level.

Third, the impact of microtopography and related ecological processes on diameter growth seems to be stronger than the impact of silvicultural treatments in TMF. Additionally, microtopographic variables also heavily influence biomass stocks (González-Jaramillo et al., 2018; Homeier et al., 2010) and species composition (Homeier et al., 2010; Kübler et al., 2016). This shows that fundamental forest characteristics can vary considerably within short geographic distances in TMF, and that in consequence, “broad-brush” management is not suited under these conditions. Instead, management prescriptions should be granular and spatially explicit at a fine scale to take elevation and microtopographic variation into account (e.g. similar to a shelterwood system for forests comprising ridge-valley topography in Sri Lanka (Ashton et al., 2011)). High-resolution terrain data, which becomes increasingly available and affordable, could provide valuable input to such a management system. However, despite these opportunities related to technical innovation, field methods have to be adapted to enable small holders and foresters in developing countries to make suitable management decisions also under difficult field conditions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117726.

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ASSESSING THE IMPORTANCE OF TOPOGRAPHIC VARIABLES FOR THE SPATIAL DISTRIBUTION OF TREE SPECIES IN A TROPICAL MOUNTAIN FOREST

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Summary: Availability and improved access to high-resolution digital terrain models (DTM) enables new approaches for the analysis of spatially explicit biological data. In this study, the spatial distribution of 16 tree species in a tropical mountain rain forest in South Ecuador and its relationship with topographic variables was evaluated at a fine-scale ecological level using two presence-only species distribution modelling techniques: The maximum entropy model (Maxent) and the ecological niche factor analysis (ENFA). Spatially explicit tree data stem from long-term forest monitoring plots in three microcatchments with a total area of 11.1 ha. Topographic variables were derived from a high-resolution DTM. Model performance was assessed by the true skill statistic (TSS) and area under curve (AUC) of the receiver operator characteristic (ROC), using both a k-fold approach and null-models. Performance varied among species and techniques, but generally Maxent models showed better performance than ENFA models. Furthermore, the ecological plausibility of the models was confirmed by comparing them with a previously established forest type classification. Among the explanatory topographic variables, elevation and a Topographic Position Index (TPI) appear as the main determinants for the distribution of most of the tree species. This study demonstrates that even on a small scale, the use of presence-only species distribution modelling techniques is a viable option for modelling suitable habitat for tree species in tropical mountain rain forests, indicating suitability for supporting stand-level planning and site-species matching techniques for natural forest management.

Zusammenfassung: Die zunehmende Verfügbarkeit von hochauflösenden digitalen Geländemodellen ermöglicht neue Ansätze zur Analyse von räumlich expliziten biologischen Daten. In dieser Studie haben wir die räumliche Verteilung von 16 Baumarten und deren Zusammenhang mit topographischen Variablen auf einer feinskaligen ökologischen Ebene in einem tropischen Bergregenwald in Südecuador evaluiert. Dafür haben wir zwei auf Präsenzdaten basierende Techniken zur Habitatmodellierung angewandt: Die Maximum-Entropie Methode (Maxent) und „Ecological Niche Factor Analysis“ (ENFA). Räumlich explizite Baumdaten stammen aus Langzeitbeobachtungsflächen von drei kleinen Wassereinzugsgebieten mit einer Fläche von 11.1 ha. Topographische Variablen wurden aus einem hochauflösenden digitalen Geländemodel abgeleitet. Zur Bewertung der Modelle wurden die True Skill Statistic (TSS) und die Fläche unterhalb der Kurve der Receiver Operating Characteristic (ROC) für sowohl k-fache Kreuzvalidierungen als auch Null-Modelle berechnet. Die Güte der Modelle hat zwischen den beiden Techniken und verschiedenen Arten variiert, aber generell schnitten Maxent-Modelle besser als ENFA-Modelle ab. Des Weiteren haben wir die ökologische Plausibilität der Modelle überprüft, indem wir sie mit einer bereits bestehenden Waldtypenklassifizierung verglichen haben. Unter den erklärenden topographischen Variablen scheinen die Höhe über dem Meeresspiegel und ein Topographischer Positions Index (TPI) die bestimmenden Faktoren für die Verteilung der meisten Baumarten zu sein. Diese Studie belegt, dass selbst auf kleinen Skalen auf Präsenzdaten basierende Techniken zur Habitatmodellierung angewandt werden können, um geeignete Habitate für Baumarten in tropischen Bergregenwäldern abzubilden. Dies deutet darauf hin, dass diese Techniken zur Unterstützung von Planungen auf Bestandesebene und zur Auswahl von geeigneten Standorten für Baumarten im Rahmen der Bewirtschaftung von Naturwäldern geeignet sind.

Keywords: Montane forest, species distribution modelling, Maxent, ENFA, biogeography, Ecuador

1 Introduction

For land use and conservation planning and sustainable forest management, accurate information about tree species distribution and its ecological drivers on different spatial scales is essential. While there is a long research history for temperate forests about the relationship between the distribution of tree species and environmental variables (Ellenberg 2009; Burns and Honkala 1990a, 1990b), the knowledge about this subject is scarce for tropical forests. This holds especially true for the Andean tropical montane forest, which is an epicenter of global biodiversity and endemism (Myers et al. 2000), yet still one of the least-studied tropical regions on the planet (Pitman et al. 2011).

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Only few studies have previously analyzed the relationship between environmental variables and species distribution in steep tropical mountain forests at local scales (Svenning et al. 2009; Jones et al. 2011; Aiba et al. 2004; Homeier et al. 2010; Ledo et al. 2013; Fagua et al. 2013; Baldeck et al. 2013). In these studies, topographic variables (e.g. elevation, aspect) were used as proxies for environmental factors such as light availability, micro-climate or edaphic conditions, which have a direct effect on plant growth. The studies generally used a spatial resolution of at least 10–20 m for both topographic and species data (but see Ledo et al. 2013), and a discrete habitat type classification to represent topography (but see Baldeck et al. 2013), which means that gradual microtopographic habitat changes were not taken into account.

In this study, we use species distribution modelling (SDM) (Guisan and Thuiller 2005) to assess the importance of topographic variables for the distribution of the 16 most abundant tree species in a 11.1–ha sample plot in a tropical mountain forest in southern Ecuador. SDM, a growing field in ecological biogeographical research, biodiversity conservation, and ecosystem management (Elith et al. 2006), is rarely used at a very fine scale and in a small study area, which is probably linked to the scarcity of high-resolution environmental variables and datasets as well as species information at those fine scales (Khatchikian et al. 2011). Although SDM is generally used for predictive modelling of species environmental requirements, numerous examples exist where those methods were used to infer the importance of environmental factors for the distribution of species (e.g. Wollan et al. 2008; Lausch et al. 2011; Hermosilla et al. 2011; Vedel-Sørensen et al. 2013; Cauwer et al. 2014). SDM allows for the consideration of gradual microtopographic habitat changes because species occurrences and continuous topographic variables can be used without any prior spatial aggregation or habitat type classification.

The main objectives of the study were to investigate the performance of two commonly used SDM algorithms (Ecological Niche Factor Analysis (ENFA) and Maxent) to model the distribution of tree species at a very fine scale, and subsequently, to assess the importance of different topographic variables for the spatial distribution of tree species.

2 Methods

2.1 Study area

Our study site is located within the privately owned Reserva Biológica San Francisco (RBSF, 3°58'S, 79°04'W), on the eastern slope of the Cordillera El Consuelo in the Andes of southern Ecuador. The RBSF has an altitude of 1800–3150 m asl and lies along the road between the towns Loja and Zamora in the Zamora-Chinchipe Province, bordering on the North of the Podocarpus National Park. The altitude of our study site is 1850–2150 m asl. Mean annual precipitation at 1952 m amounts to 2100 mm and annual temperature averages 15 °C. The site is characterized by steep environmental gradients and a strong topographical heterogeneity, which in turn strongly defines the floristic composition and forest structure (Homeier et al. 2010). For a comprehensive description of the geology, climate, flora, and fauna of the RBSF, we refer to Beck et al. (2008a).

2.2 Tree dataset

Our tree dataset stems from permanent study plots, which were installed for a silvicultural forest management experiment and first measured in 2003 (Günter et al. 2008). The size of the experimental plots on the ground is 13 ha, which corresponds to 11.1 ha in projected map view. The plots are subdivided between three microcatchments, have areas of 5, 4 and 4 ha on the ground, and a maximal distance of 870 m between farthest points (east–west direction, projected map view).

All trees on these sample plots with a diameter at breast height (DBH) ≥ 20 cm were measured for DBH, mapped, individually labeled, and identified to species level. Trees with DBH < 20 cm were not assessed on the whole sample plot area, but on smaller subplots, and are therefore not included in this study. We included the 16 most abundant species, with total occurrences in the sampling plots ranging from 55–196 trees for each species, corresponding to 4.95–17.66 trees/ha. The included tree species represent 49 % of abundance and 52 % of basal area of all trees in the sampling plots (Tab. 1). Figure A-1 shows the distribution of all trees with DBH ≥ 20 cm of those species.

For the elevation range of the permanent study plots, Homeier (2008) distinguished three main forest types in the RBSF based on the combination

Tab. 1: Characteristics of the 16 species included in the analysis. The assignment of each tree species to a forest types is based on Homeier (2008). The altitudinal ranges of species are based on all available occurrence data in Ecuador in the Global Biodiversity Information Facility (GBIF)

Species	Species code	N	Abundance [N / ha]	Basal area [m^2 / ha]	Forest type	Altitudinal range in Ecuador [m asl]
Alchornea grandiflora Müll. Arg.	Alchgran	123	11.13	3.22	II, III	900–2300
Alzatea verticillata Ruiz & Pav.	Alzavert	93	8.42	3.43	II, III	1200–2250
Cecropia andina Cuatrec.	Cecrandi	81	7.33	2.12	I	1540–2400
Cecropia angustifolia Trécul	Cecrangu	194	17.55	5.32	I	0–2300
Cedrela montana Moritz ex Turcz.	Cedrmont	55	4.98	1.39		1400–3200
Clusia ducuoides Engl.	Clusducu	96	8.69	2.27	II, III	250–3030
Graffenrieda emarginata (Ruiz & Pav.) Triana	Grafemar	86	7.78	1.50	I, II, III	1120–2900
Guarea kunthiana A. Juss.	Guarkunt	109	9.86	4.95	I	80–3100
Heliocarpus americanus L.	Heliamer	73	6.61	2.26	I	50–2615
Hyeronima asperifolia Pax & K. Hoffm.	Hyeraspe	82	7.42	3.28	I	1.8–3000
Meriania franciscana C. Ulloa & Homeier	Merifran	68	6.15	1.83	I	1890–2500
Nectandra lineatifolia (Ruiz & Pav.) Mez	Nectline	60	5.43	1.64	I, II	200–3000
Nectandra membranacea (Sw.) Griseb.	Nectmemb	75	6.79	1.67	I	80–2900
Sapium glandulosum (L.) Morong	Sapiglan	63	5.70	1.80	I	30–2150
Tabebuia chrysantha G. Nicholson	Tabechry	97	8.78	5.36	I	0–1800
Tapirira guianensis Aubl.	Tapiguia	63	5.70	2.84	I	2–1800

of different vegetation classification approaches. Forest type I, the tallest and most speciose forest, grows in major ravines and gentle lower slopes on altitudes below 2200 m asl. The canopy in this forest type reaches 25–30 m, with some emergents reaching up to 35 m. Common trees of this forest type include *Piptocoma discolor* (Asteraceae), *Tabebuia chrysantha* (Bignoniaceae), *Hyeronima asperifolia* and *Sapium glandulosum* (Euphorbiaceae), *Nectandra linneatifolia* and *N. membranacea* (Lauraceae), *Meriania* sp., *Miconia punctata* and other *Miconia* spp (Melastomataceae), *Inga* spp (Mimosaceae), *Morus insignis*, *Naucleopsis glabra*, and *Ficus* spp (Moraceae), *Prumnopitys montana* (Podocarpaceae), *Micropholis guyanensis* (Sapotaceae) and *Heliocarpus americanus* (Tiliaceae). After the formation of gaps, distinct succession phases can be observed in forest type I, with fast-growing pioneer species (e.g. *Piptocoma discolor*, *Cecropia andina*, *Heliocarpus americanus*) being subsequently replaced by late-successional species and long-lived pioneers such as *Tabebuia chrysantha* and *Cedrela* sp. (Homeier and Breckle 2008).

Forest type II can be found on upper slopes and ridges between 1900–2100 m asl, with a canopy height of 15 m. This forest type, characterized by a thick humus layer, is dominated by the frequent tree species *Alzatea verticillata* (Alzateaceae), *Dictyocaryum lamarckianum* and *Wettinia aequatorialis* (Arecaceae), *Weinmannia pinnata*, *W. sorbifolia* and *W. spruceana* (Cunoniaceae), *Abarema killipii* (Fabaceae), *Hyeronima moritzinana* (Euphorbiaceae), *Ocotea aciphylla* (Lauraceae), *Graffenrieda emarginata* and *Miconia calophylla* (Melastomataceae), *Podocarpus oleifolius* (Podocarpaceae) and *Matayba inelegans* (Sapindaceae). In contrast to forest type I, early and late successional phases show a very similar species composition in forest type II (Homeier and Breckle 2008).

In forest type III, found between 2100 and 2250 m asl, the trees usually do not surpass 12 m. Characteristic tree species include *Hedyosmum translucidum* (Chloranthaceae), *Clusia* cf *ducuoides*, *Clusia* spp and *Tovomita weddeliana* (Clusiaceae), *Weinmannia haenkeana* and *W. ovata* (Cunoniaceae), *Purdiaea nutans* (Clethraceae), *Alchornea grandiflora*

(Euphorbiaceae), *Endlicheria oreocola*, *Licaria subsessilis*, *Ocotea benthamiana* and *Persea subcordata* (Lauraceae), *Eschweilera sessilis* (Lecythidaceae), *Graffenrieda emarginata* (Melatomataceae), *Calyptranthes pulchella* and *Myrcia* sp. (both Myrtaceae) and *Podocarpus oleifolius* (Podocarpaceae).

2.3 Topographic variables

The modelled area in this study corresponds to the area of the permanent sample plots. In order to define the habitat characteristics of those plots, we derived topographic variables based on a digital terrain model (DTM) with a spatial resolution of 1 m (covering 132267 raster data cells), which was created with data from an airborne LIDAR sensor. Derived topographic variables were calculated using the open source software SAGA GIS (SAGA Development Team 2008) and the R-package "RSAGA" (Brenning 2008). In order to avoid edge effects, variables were first calculated over a larger extent and subsequently, a mask of the permanent sample plots was applied.

Both SDM algorithms used in this study (see Section 2.4) are considered to be relatively robust against multicollinearity between predictors (Hirzel et al. 2002; Elith et al. 2011). However, while model performance might not be affected by collinearity, model interpretation can be hindered and Maxent tends to overfit models (Elith et al. 2011). In order to prevent this, we examined cross-correlations between potential topographic variables in a preliminary analysis. Only variables with pairwise Pearson correlations coefficients of $r \leq 0.45$ were retained for the modelling process (Tab. A-1). Based on assumed ecological relevance for tree species distribution, we included the following variables in the final models: Elevation, slope, aspect, SAGA Wetness Index (WI) and Topographic Position Index (TPI) (Fig. A-2).

For the calculation of slope and aspect, we used a 2nd degree polynomial fit. Slope is an indicator of the intensity of gravitational and disturbance processes acting upon vegetation, which play an important role in our study area (Muenchow et al. 2012; Vorpahl et al. 2012). Mean slope on the permanent sample plots was 31.2°, with the first and third quartiles being 25.8° and 36.6°, respectively.

Aspect, an inherent circular variable, was converted into two separate continuous variables denominated northness and eastness by using the sine and cosine transformations, respectively. They quantify the degree to which the aspect is north and east. As our study plots are located on a northern flank, values for northness are mostly positive towards one, with little variation between plots. Northness was therefore not included in the analysis. Eastness, on the other hand, was included, because it varies between plots and has an ecological importance as prevalent wind direction and climate influence is usually in an east-west gradient in the RBSF (Rollenbeck 2006).

Soil moisture is an important factor structuring local pattern of species distributions (Pélissier et al. 2002). To account for this, we calculated the SAGA Wetness Index, which represents relative local soil moisture availability. It is calculated similarly to the more commonly used Topographic Wetness Index, but is based on a modified catchment area calculation (Böhner et al. 2002).

Former studies showed a strong influence of topography on both biotic and abiotic factors in our study area (Wilcke et al. 2011; Homeier et al. 2010; Werner et al. 2012; Vorpahl et al. 2012; Svenning et al. 2009). Therefore, we calculated a TPI (Guisan et al. 1999), ranging from positive values expressing ridges and upper slopes to negative values describing valleys and lower slopes. The TPI is scale-dependent; for its calculation, a moving circular window is used, whose size can be varied. In a pre-analysis, we assessed a range of different sizes for plausibility and retained a TPI with a moving window of 100 m radius.

Available spatial explicit data about environmental conditions, such as precipitation (e.g. Fries et al. 2014), temperature, soil properties and landslide risk, proved to be too coarse to be included in the present study. In Section 4.3, we therefore discuss how individual topographic variables relate to environmental conditions in our study area.

2.4 Species distribution modelling

SDM is based on the niche concept defined by Hutchinson (1957), which assumes that species can persist in only a limited range of environmental conditions. According to this concept, the distribution of species is linked to an n-dimensional structure that is made up of different environmental factors. Models estimate the niche space occupied by species by linking species occurrences with environmental layers in a given study extent (Franklin and Miller 2009). However, how exactly SDM relates to the niche concept is currently discussed in an ongoing debate (Elith and Leathwick 2009; Jiménez-Valverde et al. 2008; Soberón 2010; Araújo and

Guisan 2006). In our study, we followed Jiménez-Valverde et al. (2008) and considered that different modelling methods predict a gradient of potential–realized distributions, where potential distribution refers to the places where a species could live and realized distribution to the places where a species actually lives.

Generally, SDM algorithms can be classified as either presence-absence or presence-only models (Elith et al. 2006). Having a complete tree census, absence data for a given species could be simulated for the modeled area based on the occurrence data, e.g. by randomly assigning an arbitrary number of pixels with a minimal distance to all occurrence points of that species as absence points. However, it would be difficult to distinguish between absences where species are absent because environmental conditions at a site are not suitable ("true absences" sensu Hirzel and Le Lay (2008), "environmental absences" sensu Lobo et al. (2010)) and absences where a species might not be present on an environmentally suitable site due to dispersal limitations, biotic interactions, historic events and demographic stochasticity ("fallacious absences" sensu Hirzel and Le Lay (2008), "contingent absences" sensu Lobo et al. (2010)). We assume that this is especially true at local scales and in species-rich ecosystems (Willis and Whittaker 2002) and for large organisms such as trees (Jones et al. 2008). We therefore used presence-only techniques for our analyses (Hirzel and Le Lay 2008; Jiménez-Valverde et al. 2008).

In recent years, a number of factors relating to data quality has been identified that might reduce the performance of presence-only techniques. In this section we will mention how these factors relate to data from a complete tree census at a local scale, which has rarely been analyzed with SDM (but see Hengl et al. 2009). Such data has certain particularities in comparison with other datasets commonly used for SDM.

Spatial autocorrelation, a pattern in which observations are related to one another by the geographic distance between the observation (Legendre and Fortin 1989), is present in virtually all spatially explicit ecological datasets (Lennon 2000). Although it can artificially inflate validation measures for models (Veloz 2009; Merckx et al. 2011; Segurado et al. 2006), most studies using SDM do not directly account for the effects of spatial dependence (Dormann et al. 2007; Elith and Leathwick 2009). Contrary to SDM algorithms for presence/absence data (Dormann et al. 2007; Crase et al. 2012), little work has focused on methods for taking into account the spatial autocorrelation of occurrences for presence-only algorithms (Veloz 2009). We addressed this issue in our model evaluation technique (see Section 3.1.3) and in the discussion (see Section 4.2.3).

Geographical sampling bias can occur when some (usually easily accessible) areas are sampled more than others and can severely diminish model quality (Phillips et al. 2009; Syfert et al. 2013). We acknowledge that our data only represents a small part of the true range of environmental conditions in which the tree species occur. However, we believe that no geographical sampling bias exists within our modeled area, because sampling intensity is equal for each site during a full tree census. Therefore, we applied no method for dealing with geographical sampling bias during the model building process.

2.4.1 Maxent

Maxent is a machine-learning technique that fits a probability distribution of species occurrence with environmental layers over the entire study area (Peterson 2006). We selected Maxent for our analysis because it showed not only a good model performance in comparison to other presence-only SDM algorithms (Elith et al. 2006; Hernandez et al. 2008; Wisz et al. 2008; Pearson et al. 2007), but also allows to infer the importance of environmental variables for species distribution (Elith et al. 2011).

Maxent default configuration is to allow selecting from a range of functional forms ("feature types") to describe the relationship between the probability of occurrence and an environmental variable. Those functional forms are linear, product, quadratic, hinge, threshold and categorical (Elith et al. 2011). According to Syfert et al. (2013), we fitted models with the default auto feature option and compared them with models fitted with simple functional forms, excluding hinge, threshold and categorical features (results not published). The models fitted with simple functional forms performed similarly to those with auto features, but seemed ecologically more sensible and much less prone to overfitting, without unrealistically steep slopes and abrupt changes. Therefore, we report models fitted without hinge, threshold and categorical features in this paper.

Maxent uses random background samples for the model fitting process. The intention of those samples is not to pretend that a species is absent at the selected sites, but to provide a sample of the set of conditions available in the modeled area (Phillips et al. 2009). We created 10,000 random samples within the modeled area with the R-package "dismo" (Hijmans et al. 2013), which were also used during the evaluation of model performance (see Section 2.5). As pointed out beforehand, we assumed that no geographical sample bias exists in the model area and therefore, an unweighted and completely random creation of background samples was justified (Elith et al. 2011).

Other settings of Maxent were left on default; convergence threshold (0.00001), maximum iterations (1,000), and regularization multiplier (r = 1). Maxent analysis was carried out using Maxent software (Version 3.3.3k, Phillips et al. 2006) and R-package "dismo" (Hijmans et al. 2013).

The importance of each topographic variable was assessed for each species with a jackknife test that builds several models using the same occurrence data, but a different set of predictor variables. At first, models for each species were created excluding one variable each run and then, models were run with only one variable at a time. Finally, the regularized training gain of those different models and models created with all predictor variables were compared for each species.

We further examined response curves for each species showing how logistic output (probability of presence) varies over the complete range of each topographic variable when creating a model using only the corresponding variable (Phillips et al. 2006).

2.4.2 Ecological Niche Factor Analysis (ENFA)

The ENFA compares the ecological conditions of sites where a species occurs with conditions of the entire study area (Hirzel et al. 2002). We chose the ENFA for our analysis because it is well suited for determining the importance of environmental variables for the characterization of the ecological niche of a given species (Basille et al. 2008).

The ENFA, conceptually similar to a principal component analysis, reduces the environmental variables introduced as predictors to a small number of orthogonal factors. The first factor, termed "marginality", contains the most information and describes the preference of a given species for specific environmental conditions among the whole set of possible conditions. Negative and positive coefficients for each environmental variable indicate that the species prefers lower and higher values than the mean of the study area respectively (Basille et al. 2008). The absolute value of the marginality expresses the ecological importance of the habitat factor for the species (Hirzel et al. 2002). The ENFA was carried out using the R-package "adehabitat" (Calenge 2006).

2.5 Evaluation of model performance

We assessed the performance of the produced models using two evaluation criteria: the threshold-independent area under the curve (AUC) of the receiver operating characteristic (ROC) (Fielding and Bell 1997) and the threshold-dependent true skill statistics (TSS) (Allouche et al. 2006). These metrics were calculated for (i) final models (created with the complete available dataset), (ii) different permutations of null-models to test if the final models differ significantly from what would be expected by chance alone (Raes and Steege 2007), (iii) randomly split k-fold cross validation data partitions (Fielding and Bell 1997), and (iv) spatially separated data partitions to examine the effect of spatial autocorrelation on model performance (Veloz 2009). The methods applied for data partitioning and randomization (ii–iv) are described in the Appendix. Additionally, our results were compared with those of previous work about tree species characteristics in our study area (Homeier et al. 2010; Homeier et al. 2008).

The use of multiple metrics is important, because each metric evaluates a different aspect of predictive performance (Elith and Graham 2009). Despite using a k-fold data partitioning technique for some of those metrics, the complete available data were used to create the final models (Fielding and Bell 1997).

2.5.1 AUC

The AUC is a common metric in presence-only SDM (Merckx et al. 2011). It was initially used for presence/absence techniques, but can be employed for presence-only techniques as well, because plotting sensitivity against a random sample of background locations is sufficient to define an ROC curve (Wiley et al. 2003; Phillips et al. 2006). However, rather than expressing the ability of the model to discriminate between suitable and unsuitable habitat, as it is the case with presence/absence methods, the AUC is now the probability that a randomly chosen presence site is ranked above a random background site (Phillips et al. 2006).

Whereas values of the AUC range from 0.5 (random prediction) to 1 (perfect accuracy) when used with presence/absence data, the maximum achievable AUC is less than 1 for presence-only data (Wiley et al. 2003). The threshold of the AUC for more informative than random or good models varies according to different sources and ranges from 0.6–0.85 (Merckx et al. 2011). In this study, we interpreted values of the AUC of 0.6–0.7 as poor, 0.7–0.8 as average, 0.8–0.9 as good, and 0.9–1 as excellent (Merckx et al. 2011).

The same 10,000 random background points previously created for the Maxent models were used as pseudo-absences for the calculation of the AUC.

2.5.2 TSS

Although widely (and often exclusively) used for the evaluation of presence-only models (Merckx et al. 2011), the reliability of the AUC as the only quality metric for model evaluation has been challenged in recent years (Lobo et al. 2008; Jiménez-Valverde 2012). Therefore, we additionally calculated the threshold-dependent true skill statistic (TSS), which is similar to the widespread Kappa statistic, but less dependent on the prevalence of the modelled species (Allouche et al. 2006). It is defined as

$$TSS = sensitivity + specifity - 1$$

where sensitivity is the proportion of observed presences that are correctly predicted as presences, and specificity is the proportion of observed absences that are correctly predicted as absences (Allouche et al. 2006). Values of TSS < 0.2 can be considered as poor, 0.2–0.6 as fair to moderate and >0.6 as good (Landis and Koch 1977).

In order to calculate the TSS, the continuous habitat predictions have to be transformed into a binary format. As the intensity of mapped predictions vary between different model algorithms, threshold selection should be objective and not rely on arbitrary values (Elith and Graham 2009). For our analysis, we calculated a threshold score for each permutation according to the method based on maximizing the sum of sensitivity and specificity (Max SSS), which is equivalent to maximizing the TSS (Liu et al. 2013).

2.5.3 Comparison with existing knowledge

While model evaluation in SDM mainly focuses on predictive performance, it is also important to evaluate the ecological realism of models (Franklin and Miller 2009). To accomplish this, we compared our models with results previously obtained by Homeier and Breckle (2008) and Homeier et al. (2010). Those authors described three different forest types in the elevation range of our permanent sample plots (see Section 2.2 for a short description of these types) and assigned each species to one or multiple forest types (see Tab. S1 in the Supporting Information of Homeier et al. 2010). We performed a hierarchical cluster analysis based on the marginality factor of the ENFA for each species and each topographic variable in order to define different groups of tree species. We then assessed if these cluster groups agreed with the previously defined forest types (Homeier et al. 2008). Subsequently, we explored for each species to what extent the grouping based on ENFA models concurred with the classification of Homeier et al. (2010).

3 Results

3.1 Evaluation of model performances

Figure 1 summarizes the results of the different quantitative evaluation metrics for the 16 species and for the average across all species.

3.1.1 Significance of final models

For null-models, the average AUC score of all one-sided 95 % confidence intervals across all quantity ranges of randomly sampled locations was 0.62 for Maxent and 0.58 for ENFA models (red squares in panel aa and ab, Fig. 1). AUC scores across all species of the final models averaged to 0.76 for Maxent (ranging from 0.61 to 0.90) and 0.74 (0.65–0.80) for ENFA (blue triangles in panel aa and ab, Fig. 1). For 15 of the 16 species, AUC scores of the final models for Maxent were higher than the 95 % confidence interval of the respective null-models. Only *Nectandra lineatifolia* performed significantly worse than the respective null-models (panel ay, Fig. 1). The final ENFA models of all 16 species showed significantly higher AUC values than the respective null-models.

The one-sided 95 % confidence intervals of the TSS scores of the null-models averaged to 0.20 for Maxent and 0.16 for ENFA across all quantity ranges. In comparison, final Maxent models scored an average TSS value of 0.46 (0.23–0.67), while the average value of ENFA models was 0.41 (0.29–0.51). Results

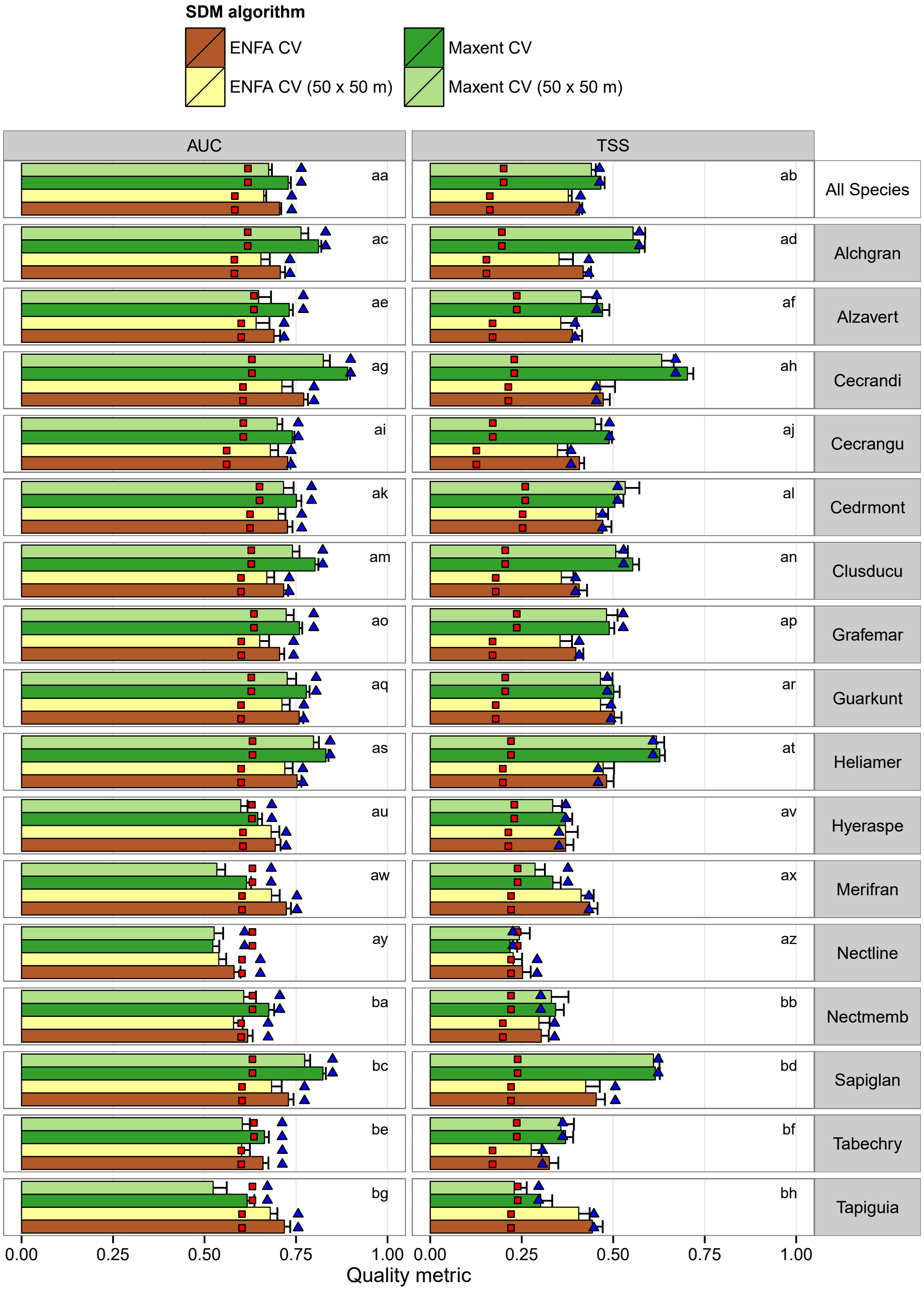


Fig. 1: Model evaluation for each species (ac–bh) and for the mean across all species (aa, ab). Results for AUC and TSS are on the left and right side respectively. ENFA models are indicated by brown bars and Maxent models by green bars. Dark green/brown colors show random data partitioning for cross-validation (CV), while light green/brown colors show cross-validation with spatially separated data partitions (CV 50 x 50 m). Error bars indicate the 0.95 confidence interval. Red squares symbolize the upper 0.95 quantile of the quality metrics for the null-models of the respective quantity range. Blue triangles show the quality metrics of the final models for each species

for individual species showed the same trend as results for the AUC: all final ENFA models and 15 out of 16 Maxent models performed significantly better than the respective null-models. The only species performing worse than the null-model was *Nectandra lineatifolia* (panel az, Fig. 1).

3.1.2 Random data partitioning

For cross validation with random data partitioning, average scores across all species for Maxent models were higher than for ENFA models for both AUC (0.75 *vs.* 0.71, panel aa, Fig. 1) and TSS (0.47 *vs.* 0.41, panel ab, Fig. 1).

The mean of AUC scores for models with random data partitioning (CV, dark green/brown) ranged from 0.54 to 0.87 for Maxent and 0.59 to 0.78 for ENFA. Mean scores for the TSS ranged from 0.18 to 0.68 for Maxent and 0.25 to 0.53 for ENFA.

Applying the classification of Merckx et al. (2011) to the AUC scores, 5 Maxent models can be considered as good, 5 as average, 5 as poor, and one as random. For ENFA, 11 models were average, 4 poor, and one random. Conversely, the classification of TSS scores according to Landis and Koch (1977) indicated that all models performed fairly to moderately for ENFA, and for Maxent, 3 models performed good and 13 fairly to moderately (Fig. 2).

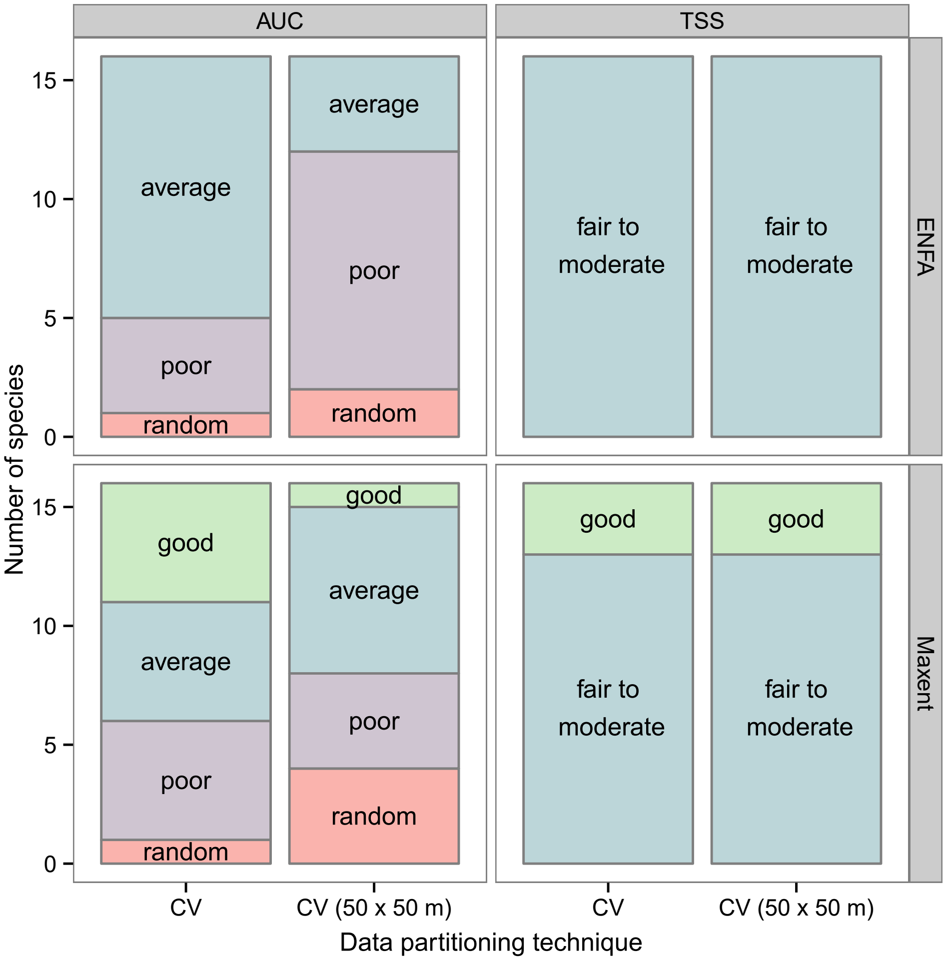


Fig. 2: Summary of the model performance for all 16 species. AUC scores (left) were classified into quality classes (<0.6 random, 0.6–0.7 poor, 0.7–0.8 average, 0.8–0.9 good, 0.9–1 excellent, Merckx et al. 2011). The classification scale of Landis and Koch (1977) was used for TSS scores (right, <0.2 poor, 0.2–0.6 fair to moderate, >0.6 good). Results are shown for SDM algorithms (Maxent and ENFA) and data partitioning techniques (cross-validation with random partitions (CV) and cross-validation with spatially separated partitions (CV 50 x 50 m))

3.1.3 Spatially separated data partitioning

For models with spatially separated data partitions (CV (50 x 50 m), light green/brown, Fig. 1), mean AUC scores of Maxent and ENFA ranged from 0.48 to 0.82 and 0.53 to 0.72 respectively. Mean TSS scores ranged from 0.13 to 0.58 for Maxent and from 0.19 to 0.47 for ENFA. These AUC scores indicated that one Maxent model was good, 7 average, 4 poor, and 4 random, whereas 4 ENFA models were average, 10 poor, and 2 random. Mean TSS scores, on the other hand, indicated 16 fair to moderate models for ENFA, and 3 good and 13 fair to moderate models for Maxent (Fig. 2).

Compared to cross validation with random data partitioning, evaluation metrics for nearly all species were lower for cross validation with spatially separated data partitioning (exception: TSS for *Cedrela montana* and AUC and TSS for *Nectandra lineatifolia*, panel al, ay, and az, Fig. 1). For AUC/ENFA, AUC/Maxent, TSS/ENFA and TSS/Maxent, scores for randomly separated data partitioning were 0.04, 0.05, 0.03, and 0.03 higher than for spatially separated data partitioning, respectively. Furthermore, variation between the 50 model runs for each species, evaluation metric, and data partitioning technique was higher for spatially separated data partitioning compared to random data partitioning (average 0.95 confidence intervals across all species and evaluation metrics was 0.015 and 0.027, respectively).

3.2 Most important variables for characterization of suitable habitat for tree species

The contribution of ecological variables for the distribution of each species according to Maxent and ENFA is compared in figure A-3. These results are based on final models created with the complete dataset. Considering that *Nectandra lineatifolia* performed worse than the null-model in 4 of the 8 presented evaluation metrics, we acknowledged that this species cannot be satisfactorily modeled with our data and excluded it for the final models.

The importance of variables was calculated with two conceptually different methods (see Section 2.4). Therefore, we assumed that figure A-3 should only be assessed visually in order to examine to what extent results of the two SDM algorithms have a similar trend. For most species, the relative importance according to Maxent and ENFA showed a similar pattern (e.g. *Cecropia andina*), whereas few other species, such as *Cedrela montana* or *Meriania franciscana* showed more pronounced differences.

When considering the average across all 16 species, ENFA and Maxent models generally agreed on the importance of each topographic variable for species distribution (Tab. 2). The absolute coefficient of the marginality factor of the ENFA models indicated that the most important variables were elevation (0.70) and TPI (0.41), whereas Wetness Index (0.31), eastness (0.26) and slope (0.17) only had minor importance. Likewise, according to the Maxent jackknife analysis, the most influential variables when used individually ("Gain with only variable") were elevation (0.34) and TPI (0.17), while eastness (0.09), Wetness Index (0.08) and slope (0.03) were less influential.

The jackknife test for Maxent, where each variable was withdrawn in turn ("Gain without variable"), identified elevation (0.34) as the variable that mostly decreased training gain when excluded. Consequently, this variable contained the most information not present in the four remaining variables, which were of lesser importance (0.45–0.48).

Tab. 2: The mean importance of topographic variables across all species according to ENFA and Maxent. The absolute value of marginality of the ENFA describes how far species depart from the mean available conditions in the study area. For Maxent, "Gain with only variable" shows the regularized training gain of models created individually with only one ecological variable compared with models created with all variables, whereas "Gain without variable" compared the regularized training gain of models with one variable excluded compared with models created with all variables. Values in parenthesis indicate the 0.95 confidence interval

Variable	ENFA: Absolute marginality	Maxent: Gain with only variable	Maxent: Gain without variable
Eastness	0.26 (0.15–0.37)	0.09 (0.05–0.13)	0.45 (0.31–0.59)
Elevation	0.70 (0.59–0.81)	0.34 (0.22–0.46)	0.34 (0.22–0.46)
Slope	0.17 (0.11–0.23)	0.03 (0.02–0.04)	0.48 (0.34–0.62)
TPI 100m	0.41 (0.33–0.50)	0.17 (0.10–0.25)	0.46 (0.32–0.59)
Wetness Index	0.31 (0.26–0.37)	0.08 (0.03–0.13)	0.48 (0.34–0.62)

For the two most important topographic variables, elevation and TPI, Maxent response curves were compared to the representations of the niche-environment system in our study area (Fig. 3). Response curves for elevation show a continuous descending or ascending trend for most species, whereas response curves for TPI are characterized by a local maximum for the majority of species.

3.3 Comparison with previous classifications

Three clusters (clustering height of 1.49) were identified with a hierarchical cluster analysis based on the marginality factors of each species and topographic variable (Tab. A-2, Fig. A-4). *Nectandra lineatifolia*, not being significantly different from the null-models, was not included in this cluster analysis.

Group A, consisting only of the species *Tapirira guianensis*, showed a distinct preference for lower values of eastness and higher values of slope. Group B consisted of 10 species, showing a clear preference for lower elevations, valleys (lower coefficients of TPI and higher coefficients of Wetness Index), and (less clearly) for higher coefficients of eastness and slope over the mean of the available conditions in the study area. Group C, composed of 4 species, on the other hand, preferred higher elevation and ridges (higher coefficients for TPI and lower coefficients of Wetness Index), whereas preferences for eastness and slope varied between species of this group. Hence, group B seemed to be equivalent to the definition of forest type I, while group C reflected forest types II and III as defined by Homeier et al. (2008).

The previous assignment of individual species to forest types by Homeier et al. (2010) is well reflected in the groups resulting from the cluster analysis (Tab. A-2). Only three species are not congruent with this assignment; for *Cedrela montana*, no information was provided, *Graffenrieda emarginata* was assigned to all 3 forest types and *Tapirira guianensis* was assigned to an individual cluster group, although Homeier et al. (2010) classified this species as belonging to forest type I.

3.4 Prediction maps of habitat suitability

Maps of habitat suitability for each species were created based on the results for ENFA and Maxent models. For the prediction, the models created with the complete data set for each species were used. The maps (Fig. 4) visually emphasize the cluster groups identified in the previous section. Within the three experimental plots, species of group B generally had higher scores for habitat suitability on lower elevations and in valleys, whereas species of group C preferred higher elevations and ridges.

Further, it can be observed that the predicted habitat suitability score is generally higher for ENFA models than for Maxent models. This is a result of the fact that different model algorithms generate mapped predictions with differing intensities (Elith and Graham 2009). It can be compensated for by using objective methods for threshold selection instead of arbitrary values during the transformation of continuous predictions into discrete classes.

4 Discussion

4.1 Limitations

4.1.1 Subset of the full range of environmental conditions

The tree presence data used for model calibration only represent a very small subset of the full range of environmental conditions of the species, corresponding to "an artificially constrained geographic space" (Raes 2012). Several implications of this restriction have been identified by previous studies about SDM, which may also apply to our results.

First, response curves are possibly influenced by the restricted environmental ranges, with strongest effects towards the upper and lower ends (Thuiller et al. 2004). As mentioned in the methods section, we first fitted Maxent models with hinge and threshold features types, which resulted in unrealistic habitat suitability maps and response curves. Overfitting in the tails of the response curves could be one possible explanation for this. However, by limiting feature types to linear, product and quadratic features, overfitting seemed to have been reduced considerably (Fig. 3). In the case of the ENFA, only linear dependencies within the species niche are fitted (Hirzel et al. 2002). Therefore, we assumed that restricted data only produced a minor effect on the upper and lower environmental ranges for ENFA results.

Second, prediction of habitat suitability should not be realized to areas beyond the range of environmental conditions the models were calibrated with (Sánchez-Fernández et al. 2011; Thuiller et al. 2004). This is especially the case for the region of our study area, which is characterized by consider-

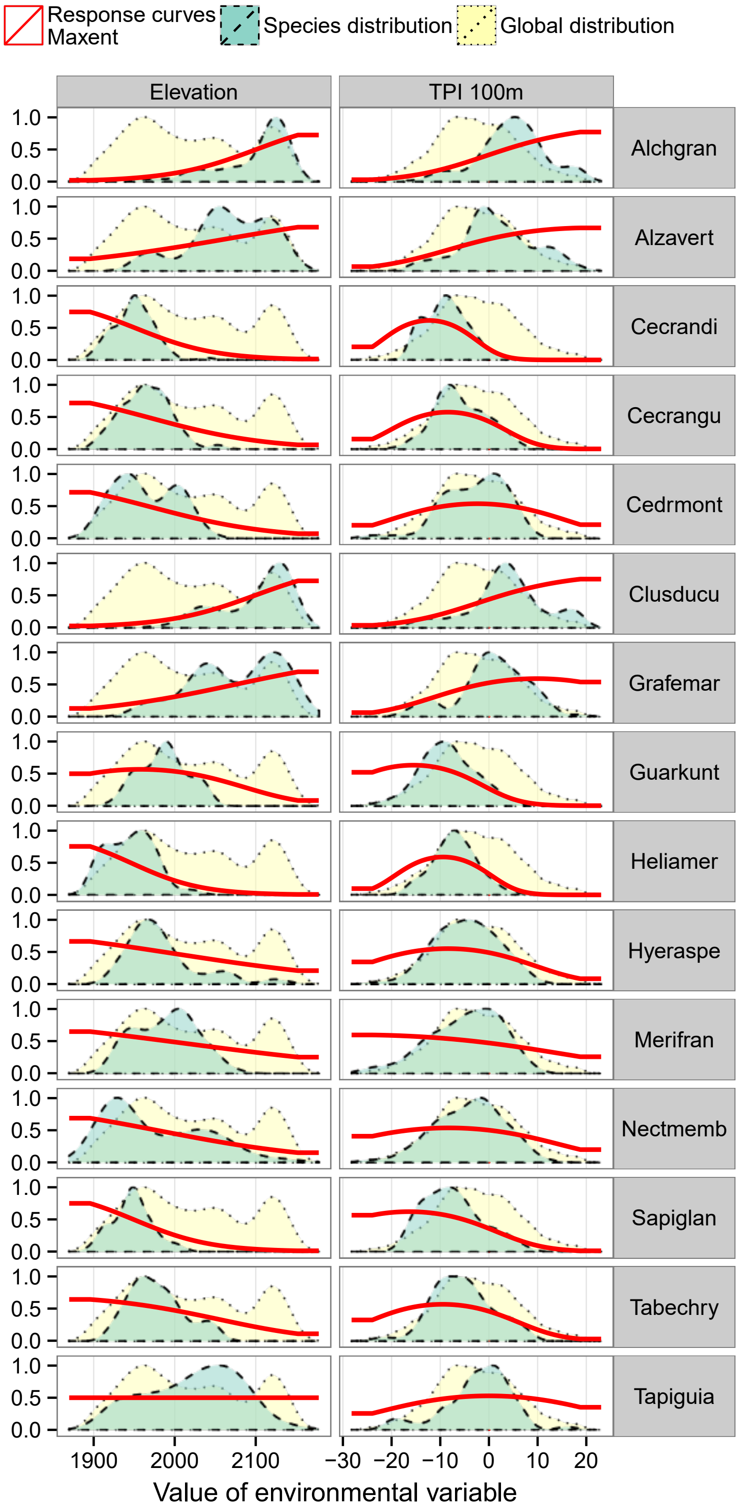


Fig. 3: Response curves for the Maxent models and representation of the niche-environment system in the study area for the two most important variables (elevation and TPI) and 15 species. The distribution of the available topographic variables in the study area ("Global distribution") is compared to the distribution of topographic variables on sites where the species occurs ("Species distribution")

able climatic variability (Rollenbeck 2006) – over a distance of 30 km in east-west direction, Beck et al. (2008b) reported a gradient of mean annual precipitation ranging from 3103 to 1068 mm on equal elevations (1950 m asl). If habitat suitability were to be predicted to a wider area in future studies, it would therefore be highly advisable to include precipitation and other relevant climatic factors as predictor variables (see e.g. Engelbrecht et al. 2007). Furthermore, the resulting habitat suitability maps should be verified with additionally sampled independent test data.

Third, like habitat suitability, the importance of topographic variables cannot be extrapolated beyond the range of environmental conditions either. This is especially true for species with a wide distribution range, such as *Tabebuia chrysantha*, occurring from Northern Mexico to Bolivia and in both dry and humid forests (Volland-Voigt et al. 2011). In our study area, this species shows a clear preference for negative values of TPI (Tab. A-2), which correspond to valleys. However, this does not allow inferring preferences for topographic positions of this species in other regions of its distribution range.

The above-mentioned points are important to acknowledge, but they do not conflict with the main objectives of this study, which are focused on the local scale.

4.1.2 Niche or neutral processes

The focus on the local scale however might result in a different potential problem, which is linked to the ongoing debate in recent decades whether niche or neutral processes are more important for species distribution in multi-species communities. Niche differentiation with respect to resources remains one of the most prominent theories for tropical tree species (Hutchinson 1957). It postulates that different trees species specialize on different habitats, where they are competitively dominant and relatively more abundant. The neutralist theories, on the other hand, propose that dispersal limitations and stochastic processes drive species composition, and that niche differentiation only plays a limited role for species coexistence (Hubbell 2001). In the context of SDM, spatial patterns in species distributions caused by neutral processes might be erroneously interpreted as being caused by niche processes, if those patterns happen to be spatially correlated with environmental variables.

Previous studies about the influence of both processes at local scales in tropical forests reached diverging results. Harms et al. (2001) concluded that niche processes only played a limited role in the maintenance of species diversity, which was partially supported by some studies (Queenborough et al. 2007; Valencia et al. 2004; Getzin et al. 2014). Conversely, numerous other studies only found little evidence for this hypothesis and concluded that niche processes played a predominant role for the distribution of tree species at local scales in tropical forests (Gunatilleke et al. 2006; Chuyong et al. 2011; Yamada et al. 2010; Itoh et al. 2003; John et al. 2007; Jones et al. 2008). Baldeck et al. (2013) and Chang et al. (2013) recently pointed out that most of the studies cited in this paragraph only used environmental variables related to topography, and that by including spatially explicit soil resource variables in addition to topographic variables alone, the variation in the tree community composition in tropical forests explained by the environment greatly increased. They concluded that the role of niche processes may have been underestimated in previous studies.

This indicates that especially in regions characterized by very heterogeneous topographic conditions, such as our study area, niche processes are most important for the distribution of species. This is congruent with previous studies in our study area (Bussmann 2003; Homeier et al. 2008; Homeier et al. 2010), which showed a strong influence of topography on the occurrence of different forest types. Therefore, it seems acceptable to assume that species distribution patterns in our study area are mainly caused by niche processes, and that the use of SDM is justified for our study area.

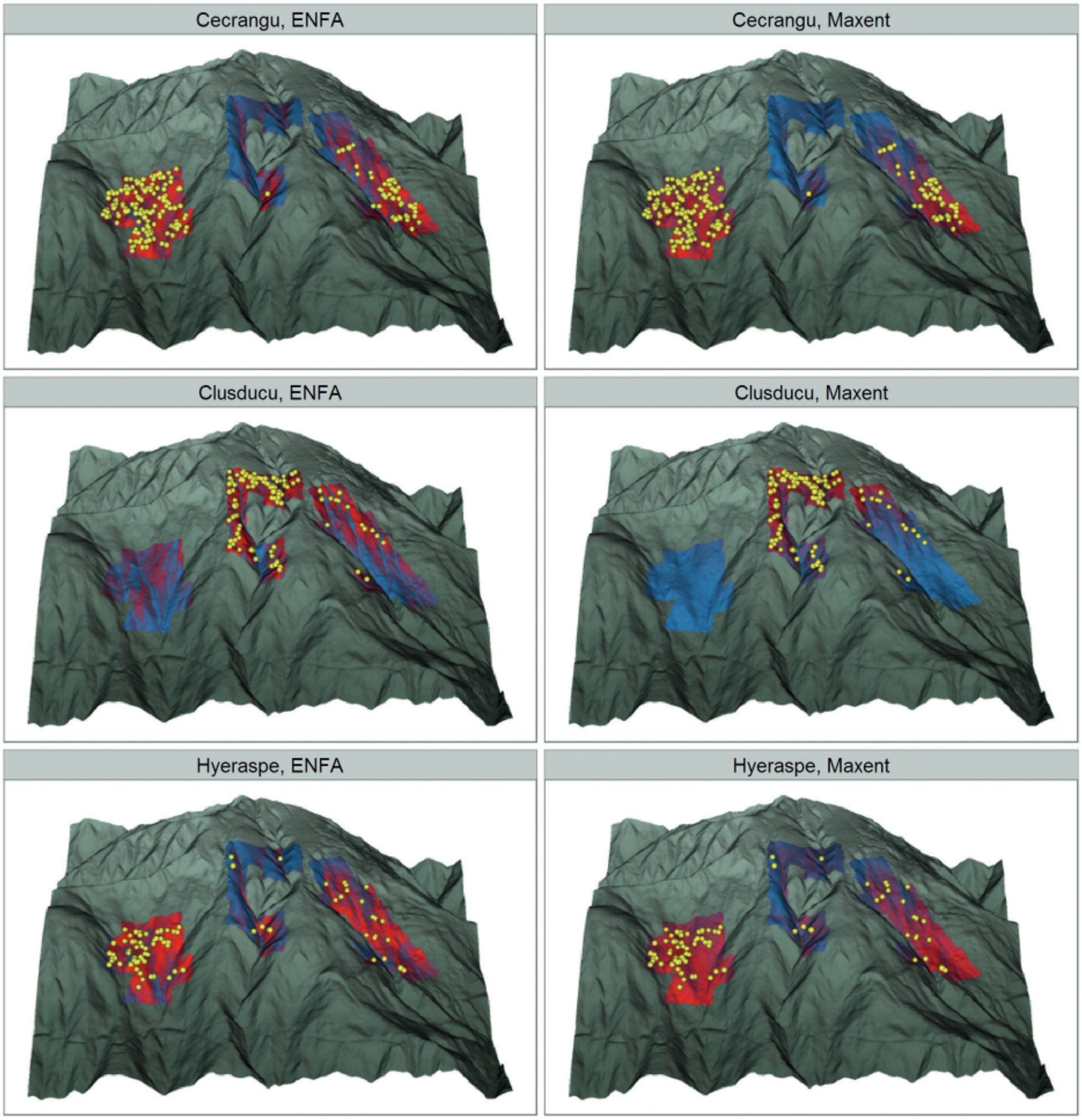
4.2 Aspects of SDM

4.2.1 Model evaluation

AUC values of our models were low for many species. For example, for cross validation with random data partitioning, AUC values indicated that 6 Maxent models and 5 ENFA models could be considered as poor or random. In contrast, according to TSS values, all models performed at least fairly to moderately. Likewise, all final ENFA and 15 out of 16 final Maxent models performed significantly better than the null-models. Additionally, the ecological interpretation of our models was very similar to pre-existent knowledge about forest types and the membership of different tree species to these forest types (Homeier et al. 2008; Homeier et al. 2010). Those previous results were obtained in the same study area (RBSF), but using independent sample plots and different methods.

The relatively low values of the AUC compared to the other quality metrics might be caused by two implications of its use with presence-only models. First, the maximum achievable AUC is no longer 1, but $1 - a/2$, where a is the fraction of the area covered by the species true distribution, which is normally unknown (Wiley et al. 2003; Phillips et al. 2006). Considering that we only used the 16 most common species, values of a may be high, and consequently, the maximum achievable AUC might be low. Second, the AUC depends partly on the total extent of the study area. It increases with larger extents, where environmental conditions differ much from those of the area where the species occurs (Lobo et al. 2008). Our relatively small study area therefore might have contributed to the low values of AUC.

The fact that our models performed well for the majority of species according to the TSS and the comparison with null-models, combined with the fact that the ecological interpretation agreed with previous studies, suggest that AUC underestimated the performance of the models. Our results therefore underline the importance of using more than one performance criterion for the evaluation of SDM (Lobo et al. 2008).



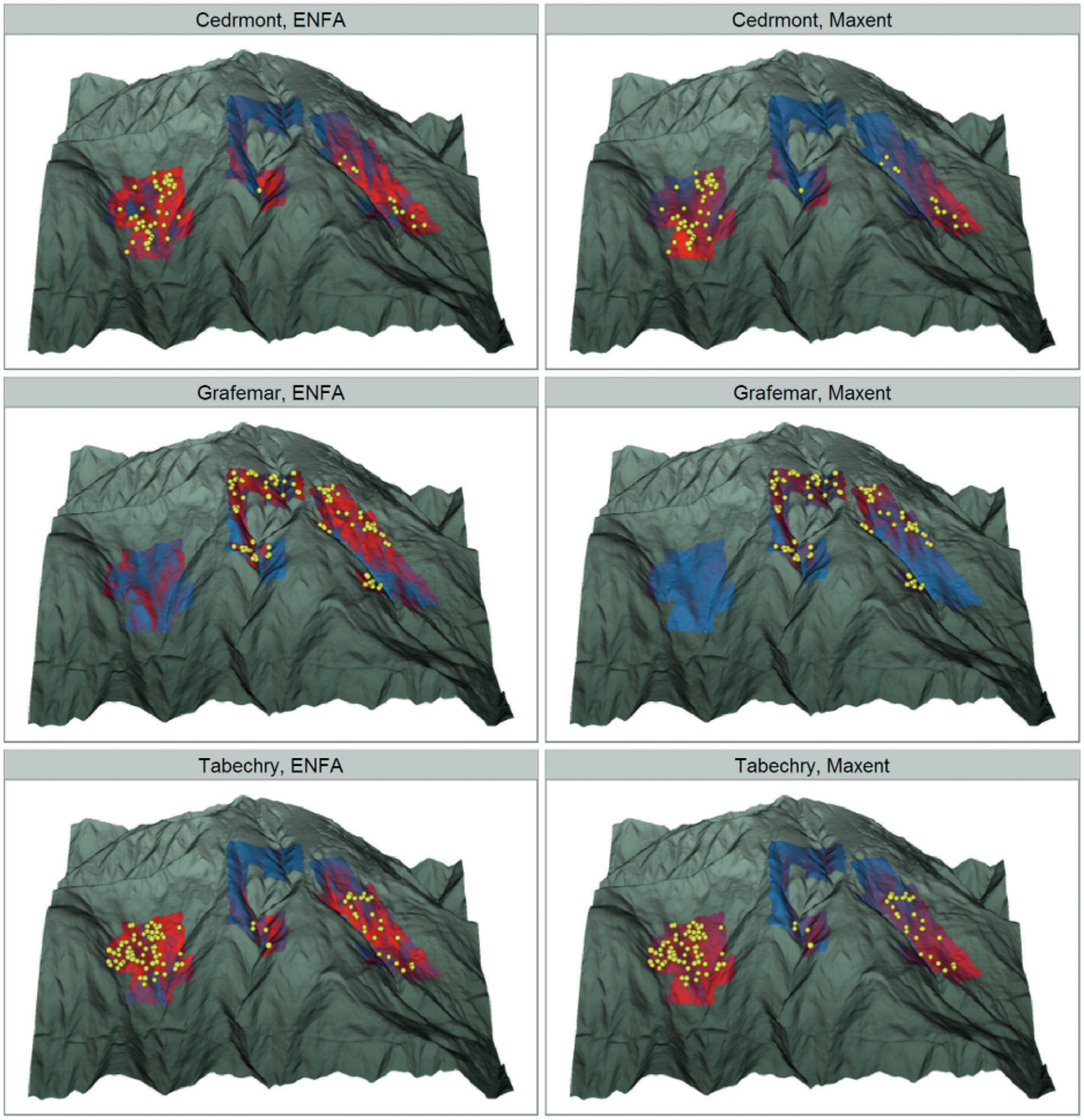


Fig. 4: Habitat suitability maps of 6 trees species from final ENFA and Maxent models. Blue colors indicate unsuitable conditions and red colors suitable conditions. Yellow points show the registered occurrence of each species, which were used for model creation. Species of cluster group B (*Cecropia angustifolia*, *Cedrela montana*, *Hyeronima asperifolia* and *Tabebuia chrysantha*) tend to have areas predicted as suitable in valleys and lower altitudes, whereas areas with high predicted suitability for species of cluster group C (*Clusia ducuoides* and *Graffenrieda emarginata*) are located on ridges and higher altitudes

4.2.2 Comparison between results of ENFA and Maxent

For most species, Maxent models were more robust than ENFA models (exceptions are, e.g., *Meriania franciscana* and *Tapirira guianensis*, Fig. 1). This is congruent with findings from previous studies, where Maxent showed better performances than other SDM algorithms (Hermosilla et al. 2011; Elith et al. 2006). The fact that Maxent fits models with different feature classes (linear, product, quadratic, hinge, threshold and categorical, Phillips and Dudík 2008), whereas ENFA only fits linear relationships (Hirzel et al. 2002), might be an explanation for this. Even though we only allowed linear, product and quadratic features for Maxent (see Section 2.4.1), this algorithm likely fits complex species-environment relationships still better than the ENFA.

In terms of variable importance across all species, the results of both SDM algorithms were very similar. This confirms findings from previous studies that used Maxent and ENFA to analyze the importance of environmental variables (McKinney et al. 2012; Hermosilla et al. 2011).

4.2.3 Effect of spatial autocorrelation on model performance

Model quality metrics were lower for cross validation with spatially separated data partitions compared to randomly separated data partitions (see Section 3.1.3). This could be interpreted as a correction for quality metrics, which may have been falsely inflated due to the presence of spatial autocorrelation in the tree occurrence data (Veloz 2009; Merckx et al. 2011). However, this approach might be overly simplistic in our case for a number of reasons.

First, spatial autocorrelation can be divided into "spurious" autocorrelation, an artefact of experimental design caused for example by biased sampling, and "real" spatial autocorrelation, which corresponds to the actual spatial structure of species distribution. "Spurious" spatial autocorrelation should be removed from the data, whereas no data should be discarded for "real" autocorrelation (Kamino et al. 2012). Having a complete tree census with a sampling intensity of 100 %, we assumed that no spatial sampling bias occurred for the modelled area, and that existing spatial autocorrelation in our occurrence data is therefore "real".

Second, "real" spatial autocorrelation can further be separated into two types of distinct processes: endogenous and exogenous. Endogenous processes are associated directly with the biological occurrence data, while exogenous processes are independent from the occurrence data. For example, tree clustering could be caused by limited ability to disperse away from a parent tree (endogenous process), or by fine-scale variation in soil conditions (exogenous process) (Franklin and Miller 2009). In the context of SDM, spatial autocorrelation in occurrence data could therefore be considered either as noise hindering the analysis of species-habitat association, or as a direct result of species-habitat association.

Third, subsampling presence points in order to ensure that clusters of training data are not excessively clustered around test data reduces spatial autocorrelation (Veloz 2009), but also jettisons information and therefore reduces the predictive performance of models (Lennon 2000; Segurado et al. 2006).

These reasons show that, at least in our study, a reduction of model performance when using spatially separated data partitions for cross validation must not necessarily mean that models without a correction of spatial autocorrelation are falsely inflated.

4.3 Interpretation of the importance of individual topographic variables

4.3.1 Elevation

Elevation, whose predominant influence on species distribution at intermediate and large scales is well established in phytogeography (Humboldt and Bonpland 1805; Gentry 1988), was identified by our study as the most important topographic variable for the distribution of tree species at a local scale. Similar results on small scales in tropical forests were reported previously (Lieberman et al. 1985; Wang et al. 2009; Lan et al. 2009; Ledo et al. 2013). The altitudinal gradient is an indirect factor (no direct effect on species distribution, also known as proxy factors), which correlates with direct factors (physiological effect on plant growth). In terms of climatic direct factors, Fries et al. (2009) reported an annual average lapse rate of -0.52 K/100 m in the study area for the altitudinal range of the permanent sample plots (1850–2150 m asl), which translates to a difference of annual average temperatures of 1.56 K between the lowest and highest sites in the sample plots. Similarly, average annual precipitation increases by 250 mm/100 m (corresponding to a difference of 750 mm between lowest and highest sites) and fog input augments by 40 mm/100 m (corresponding to a difference of 120 mm between lowest and highest sites) (Rollenbeck 2006). While these climatic elevation gradients play an important role for the distribution of tree species, additional ecological gradients related to elevation have to be taken into account. With regards to soil properties, the general trend in tropical mountains that increasing elevation results in decreasing soil fertility and decreased N availability (Tanner et al. 1998) was confirmed for the RBSF (Wilcke et al. 2008; Wolf et al. 2011). Further, in our study area the mineral soil depth decreases, the thickness of the organic layer and pH increase and soil texture becomes coarser in the A horizon with increasing elevation (Wilcke et al. 2008; Liess et al. 2011; Wolf et al. 2011).

These strong gradients of direct factors help to understand why elevation is the most important variable for species distribution, even at small scales. However, disentangling the relative contribution of each of the direct factors linked to elevation is beyond the scope of our study.

4.3.2 TPI

Maxent and ENFA models identified TPI as the second most important variable for the distribution of tree species. This result was expected, because a different forest type can be found on ridges compared to valleys (Homeier et al. 2008), and the continuous values of the TPI express the position of each site on a topographical gradient ranging from valleys to mid-slopes to ridges (Guisan et al. 1999). This is congruent with findings from previous studies examining the influence of topography on forest composition in tropical forests (Takyu et al. 2002; Webb et al. 1999; Queenborough et al. 2007; Valencia et al. 2004; Lan et al. 2009; Wang et al. 2009; Chuyong et al. 2011). Like elevation, the topographic position is an indirect factor having strong effects on direct factors by creating a variety of microhabitats along a topographic gradient. Webb et al. (1999) concluded that differences in forest structure and composition between topographic positions were mainly caused by frequent disturbances on ridges, which were more exposed to chronic and catastrophic wind events than valleys. In our study area, this hypothesis is supported by the fact that trees have lower canopy heights as well as lower height to DBH ratios on ridges compared to valleys (Homeier et al. 2010), which might be an adaptation to exposure to wind. However, tree turnover rates are actually higher in valleys than on ridges in our study area (Homeier et al. 2010), which suggests that factors related to topography other than wind exposure play a more important role for the distribution of tree species. Periodic waterlogging processes in valleys during high rain events may explain higher turnover rates in valleys, because they force trees to have shallow rooting systems, which may result in higher mortality through tree falls (Ashton et al. 2011). Furthermore, ridge-top soils generally have higher humus concentrations and are more acid and poorer in nutrients (especially N) than valley-bottom soils (Wilcke et al. 2011; Wolf et al. 2011). This can be partly explained by lateral transport of water and matter and the removal of mineral soil on ridges caused by landslides, which are mainly controlled by topography in the RBSF (Vorpahl et al. 2012). Additionally, throughfall in valleys is more abundant and nutrient-richer than on ridges (Oesker et al. 2008) and herbivory and leaf litter decomposition is considerably lower on ridges than on valleys (Werner and Homeier 2015). Moreover, ridges are more prone to drought (Bussmann 2003) due to higher solar radiation compared to valleys, although this might be mitigated by the fact that ridges receive more scavenged cloud water than valleys (Homeier et al. 2010).

Werner and Homeier (2015) argue that habitat heterogeneity along the topographical gradient from valleys to ridges is caused by a combination of the above-mentioned factors and maintained through a plant-mediated, nutrient-driven feedback cycle. While fast-growing tree species adapted to aboveground competition (i.e. light) are more competitive in valleys, slow-growing tree species adapted to belowground competition in nutrient-poor soils are more competitive on ridges. These slow-growing species are generally characterized by large investments in long-living foliage with antiherbivore defenses (Coley et al. 1985), which, in combination with mechanically resistant leaves due to increased wind and drought exposure, result in poor litter decomposability. This causes an accumulation of litter and mor humus, which in turn immobilizes basic cations, contributes to soil acidification and further enhances soil nutrient limitations on upper slopes and ridges.

4.3.3 Other topographic variables

Compared to elevation and TPI, the remaining variables played a less important role across all tree species. With regards to slope, results of previous studies (Wang et al. 2009; Baldeck et al. 2013), where this variable showed a higher influence, are not supported by our findings. We explain this by the fact that slope showed a relatively small variation in our sample plots (first and third quartiles 25.8° and 36.6° respectively), and therefore contributed only little to the total variation in environmental conditions. Similarly, aspect (eastness) varied little in our sample plots (first and third quartiles of eastness -0.72 and -0.23 respectively), which may explain its low influence compared to other studies (Wang et al. 2009). The preference of *Tapirira guianensis* for negative values of eastness and positive values of slope might be explained by its ability to sprout from uprooted trees (Negrelle 1995) and the resulting competitive advantage on sites with frequent disturbances.

One possible explanation for the low importance of the Wetness Index for species distribution might be related to its higher spatial variability within our sample plots compared to the other 4 topographic variables, which are smoother and more continuous (Fig. A-2). This seems to be a consequence of the high-resolution DTM, and therefore a Wetness Index calculated based on a coarser DTM might result in a higher importance for species distribution.

5 Conclusion

In this study, we showed that SDM is an adequate tool to analyze the ecological relationships between species and the environment at local scales in tropical forests, as our results about the importance of topographic variables were congruent with previous studies. All topographic predictors used in this study were derived from a high-resolution DTM, which will be increasingly available in the future. This will allow applying SDM-based methods in a wider range of situations and regions. Apart from inference, predictive modelling of species habitat suitability can be used for several applications. Examples include the identification of priority areas for biodiversity conservation, a more efficient planning of field inventories, identification of suitable species and sites for reforestation projects (e.g., restoration with natural species), and pre-selection of possible sites for seed collection. Additionally, when combined with forest inventory data, topographic variables could be used to create high-resolution spatial predictions of forest stand parameters or carbon stocks. Those predictions could then serve as a planning instrument for sustainable forest management and conservation by facilitating the creation of adequate small-scale management units.

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Appendix

Supplementary material

A 1 Data partitioning and randomization

AUC and TSS were calculated for final models (created with the complete dataset) and different models obtained from either null-distributions or k-fold data partitioning.

Null-models were used to test if the final models differ significantly from what would be expected by chance alone (Raes and Steege 2007). For this, presence points were randomly sampled from all locations within the modeled area. Maxent and ENFA models were then fitted to these presence points and the AUC and TSS were calculated for each model. In order to account for differences in the number of occurrences per species, we created null-models for different quantity ranges of randomly sampled locations, which were defined by intervals of 10 (30–39, 40–49, … 190–199). For each quantity range, this process was repeated 100 times. The AUC and TSS values of the final models generated with actual presence data were then compared with those of the null-models of the respective quantity range. If the metrics for the actual presence data was higher than the one-sided 95 % confidence interval of the frequency distribution obtained from the null-models, the actual species model was interpreted as performing significantly better than expected by chance (Raes and Steege 2007).

For each species, we additionally used a fivefold cross-validation, where available presence points were randomly split into five equally sized data partitions. In turn, five different ENFA and Maxent models were then trained with 4/5 of the data, while the withheld 1/5 of the data was used to calculate AUC and TSS values for each model. In order to obtain a more robust estimation of test statistics, we repeated this process 10 times for each species.

At local scales, the distribution of tree species in tropical forests depends not only on environmental factors, but also on dispersal limitations, biotic interactions, historical events and stochastic processes (Svenning et al. 2009; Jones et al. 2011; Harms et al. 2001; Baldeck et al. 2013). All these factors might result in spatial autocorrelation in tree occurrences, which in turn might falsely inflate measures of model performance (Veloz 2009). In order to examine the effect of spatial autocorrelation on model performance, we separated training and test data into spatially separated partitions (Veloz 2009). This was achieved by using a pre-existent system of subplots installed in 2003, subdividing the permanent sample plots into 52 quadrats with dimensions of approximately 50 x 50 m (Günter et al. 2008). Considering that spatial autocorrelation in many tropical forests is strongest at scales < 20 m (Condit et al. 2000), we assumed that the size of the pre-existent subplots of 50 x 50 m was sufficiently large to account for spatial autocorrelation. For each species, subplots were randomly sampled from the study area until the cumulative number of presence points within these subplots exceeded 20 % of the total presence points of the respective species. All presence points within those randomly sampled subplots were assigned to a test group, and the remaining presence points to a training group. ENFA and Maxent models were generated with the training group and test statistics were calculated for the test group. This process was repeated 50 times for each species.

A 2 Supplementary tables and figures

Tab. A-1: Correlation matrix of the topographic variables used for the modelling process. Only variables with absolute values of the Pearson's correlation coefficient r ≤ 0.45 were retained. All correlations are significant

	Eastness	Elevation	Slope	TPI 100 m	Wetness Index
Eastness	1.00				
Elevation	-0.03	1.00			
Slope	0.07	-0.17	1.00		
TPI 100m	-0.03	0.45	-0.21	1.00	
Wetness Index	-0.05	-0.33	-0.26	-0.39	1.00

Tab. A-2: Coefficients of the marginality factor of the ENFA for 15 tree species and 5 topographic variables. Positive coefficients of marginality indicate that the species prefers higher-than-mean values with respect to the study area, while negative values indicate the preference of lower-than-mean values. The column "Cluster group" shows the result from a hierarchical cluster analysis (Fig. A-4). Column "Forest type" lists the forest type(s) each species was assigned to by Homeier et al. (2010)

Species	Eastness	Elevation	Slope	TPI 100 m	Wetness Index	Cluster group	Forest type
Tapiguia	-0.84	0.03	0.46	0.03	-0.27	A	I
Cecrandi	0.29	-0.59	0.16	-0.45	0.58	B	I
Cecrangu	0.15	-0.82	-0.03	-0.42	0.35	B	I
Cedrmont	0.31	-0.92	0.13	-0.08	0.18	B	
Guarkunt	0.34	-0.48	0.21	-0.72	0.30	B	I
Heliamer	0.05	-0.79	-0.17	-0.41	0.43	B	I
Hyeraspe	0.10	-0.83	-0.16	-0.43	0.31	B	I
Merifran	0.11	-0.73	0.43	-0.48	0.22	B	I
Nectmemb	-0.03	-0.92	0.21	-0.29	-0.14	B	I
Sapiglan	0.31	-0.73	0.11	-0.44	0.41	B	I
Tabechry	0.27	-0.79	0.04	-0.47	0.28	B	I
Alchgran	0.12	0.73	-0.29	0.53	-0.30	C	II, III
Alzavert	-0.42	0.66	-0.03	0.56	-0.27	C	II, III
Clusducu	-0.10	0.74	-0.22	0.51	-0.37	C	II, III
Grafemar	-0.49	0.72	0.12	0.38	-0.28	C	I, II, III

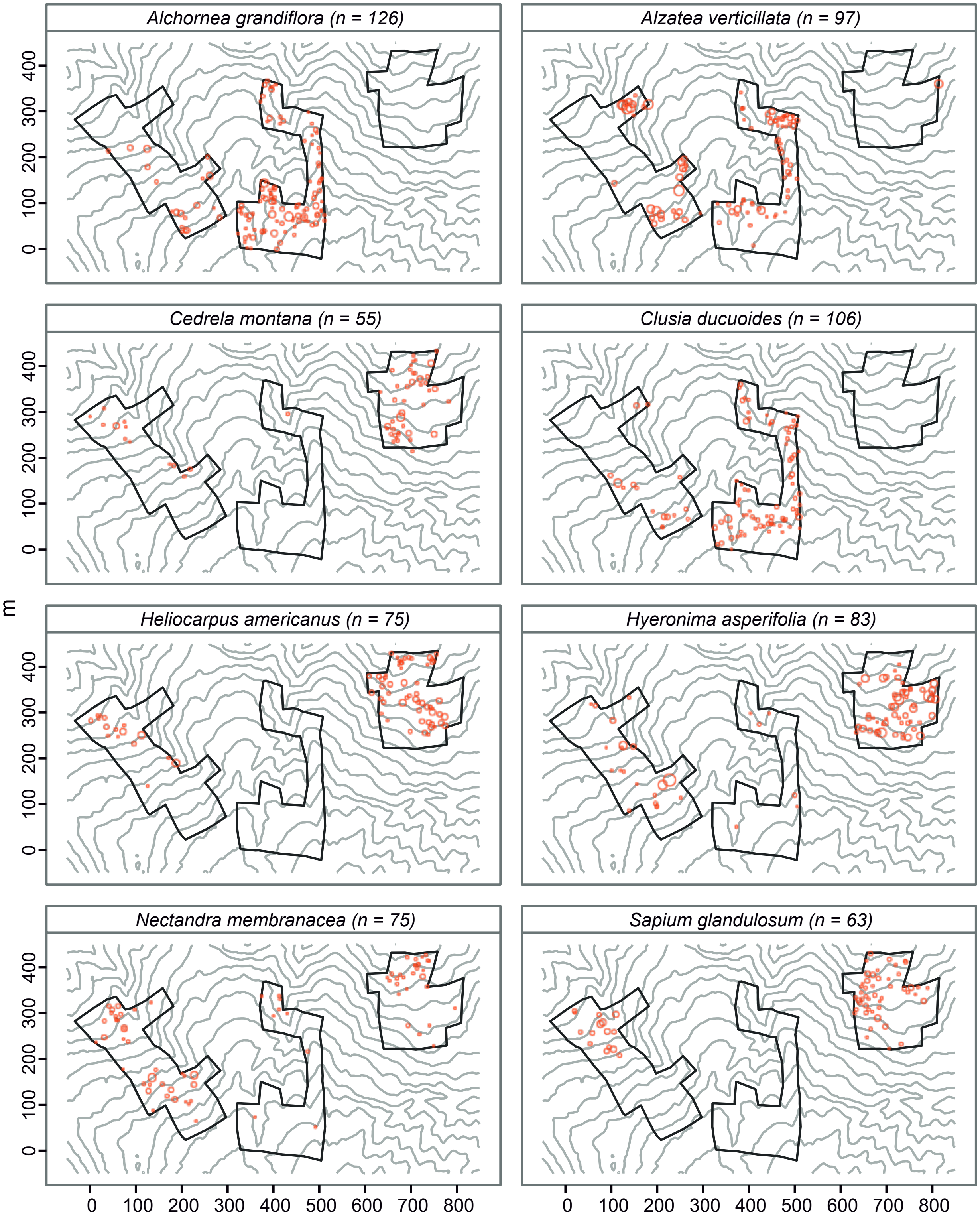
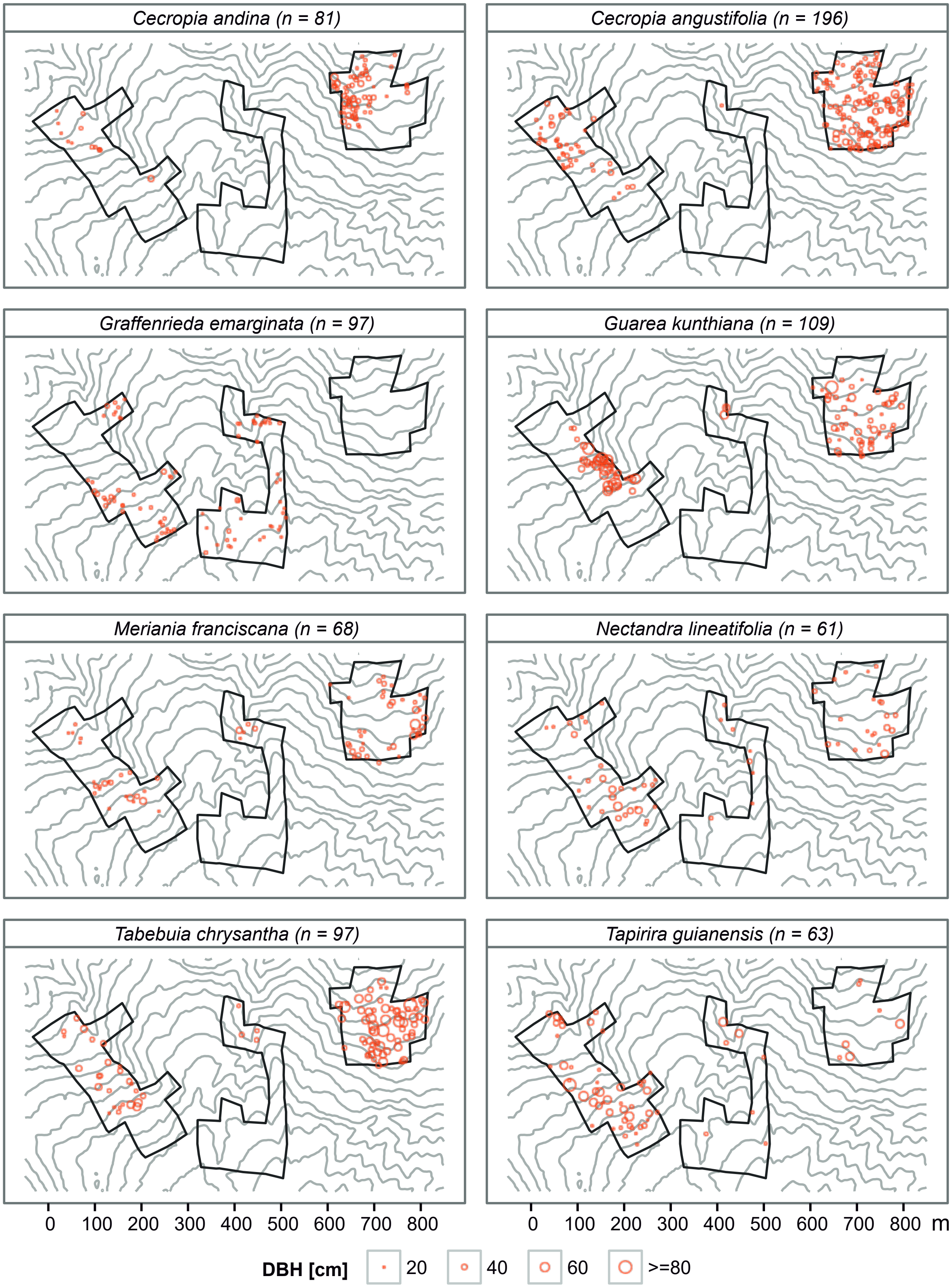


Fig. A-1: Stem distributions of all trees with DBH ≥ 20 cm on the 11.1 ha permanent sample plot in the RBSF for the 16 most abundant tree species. Each red circle represents one tree; the size of the circle shows the DBH of trees. The grey lines are elevation contour lines at 20-m intervals. The black lines are limits of the permanent sample plots


Cecropia andina (n = 81)
Cecropia angustifolia (n = 196)
Graffenrieda emarginata (n = 97)
Guarea kunthiana (n = 109)
Meriania franciscana (n = 68)
Nectandra lineatifolia (n = 61)
Tabebuia chrysantha (n = 97)
Tapirira guianensis (n = 63)
0 100 200 300 400 500 600 700 800
0 100 200 300 400 500 600 700 800 m
DBH [cm]
20
40
60
>=80

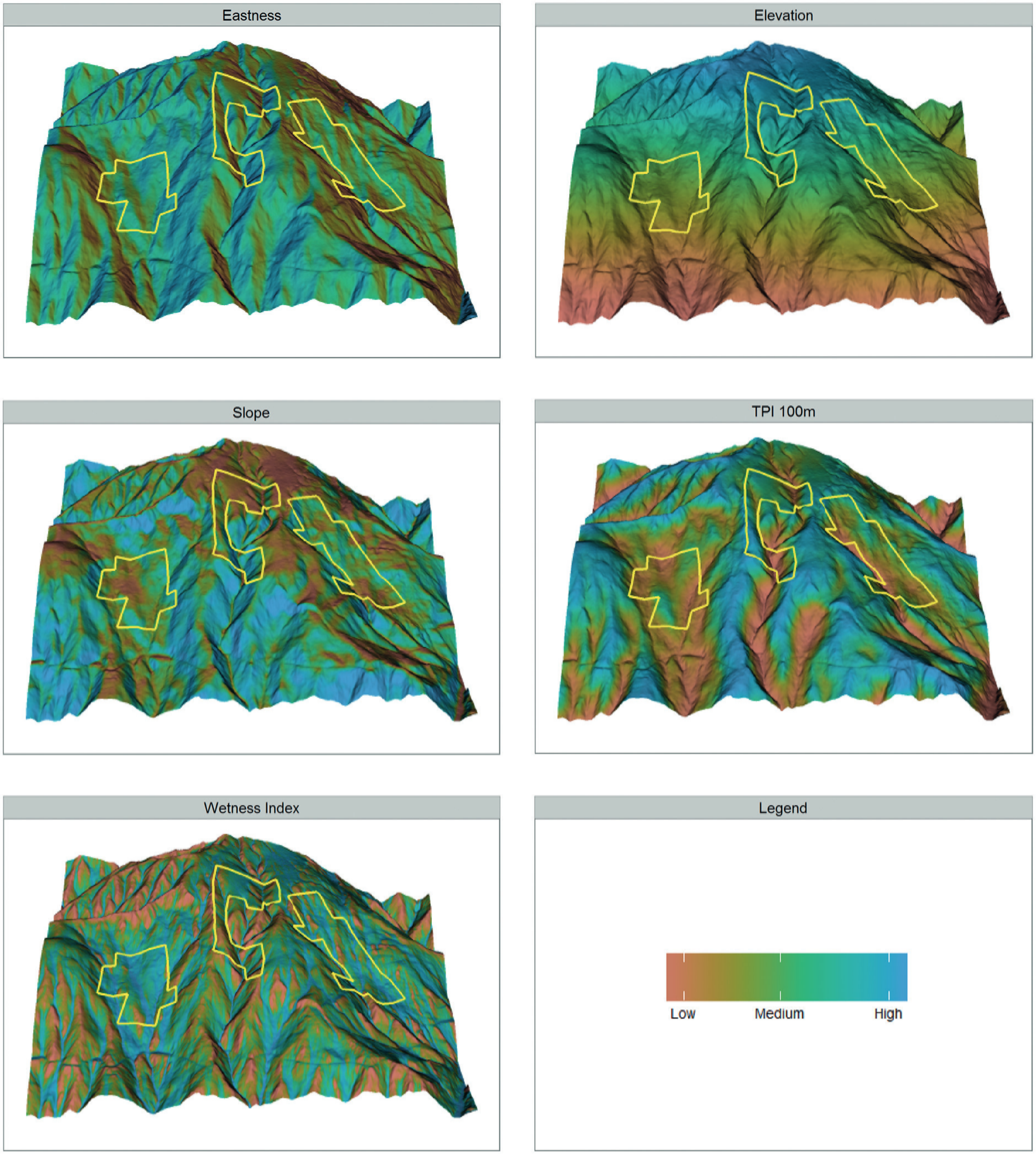


Fig. A-2: Maps of the five topographic variables used for the modelling process. Yellow lines show the position of the permanent sample plots

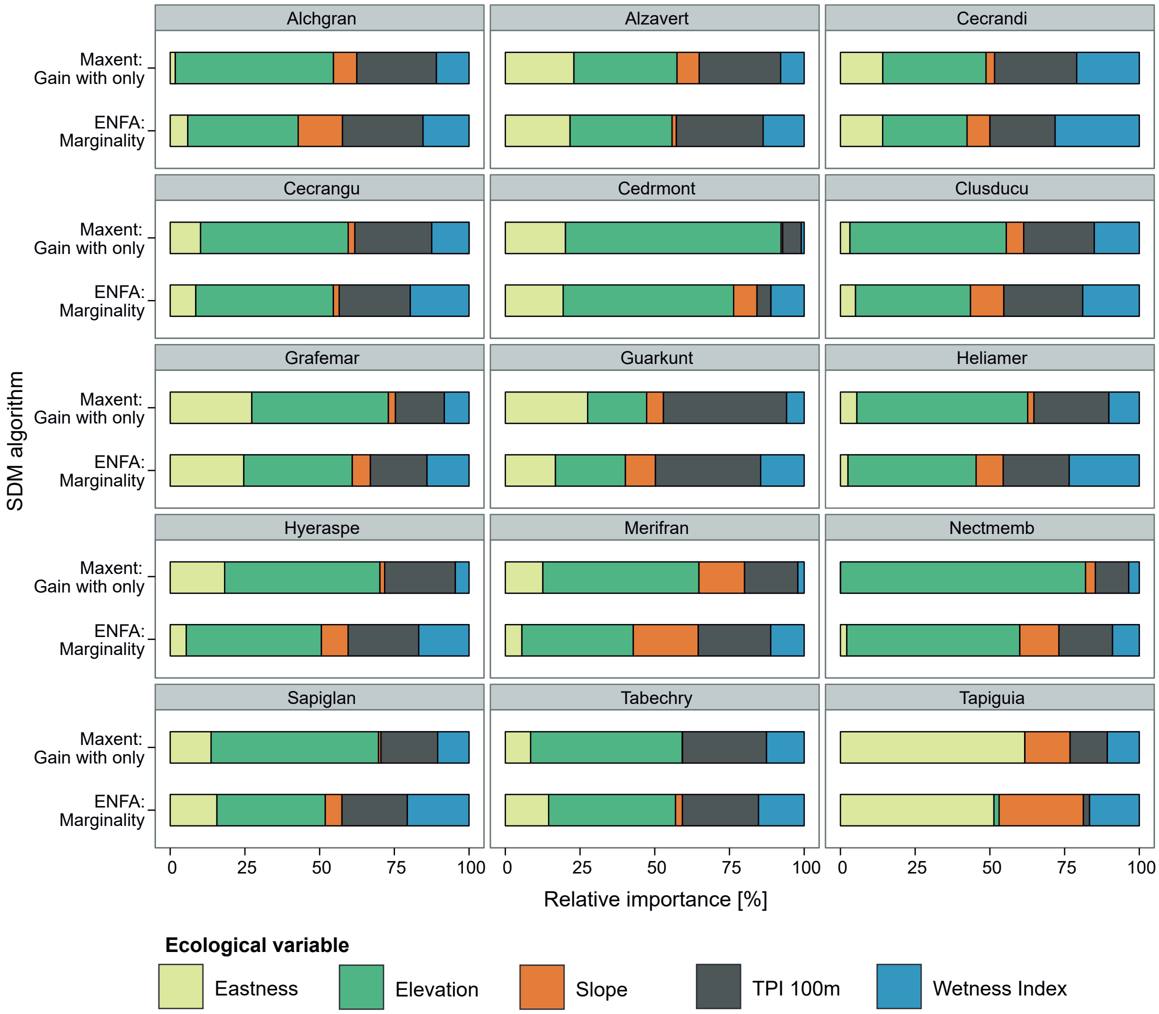


Fig. A-3: Contribution of ecological variables for the distribution of each of the 15 retained species after model evaluation. The upper bar on each panel shows results from the jackknifing test in Maxent, where models were created with only one variable in turn and regularized training gain of these models was subsequently compared with models created with all predictor variables. The lower bar shows absolute values of the marginality factor of the ENFA models. In order to allow a better comparison between Maxent and ENFA models, absolute values for importance were transformed to relative values

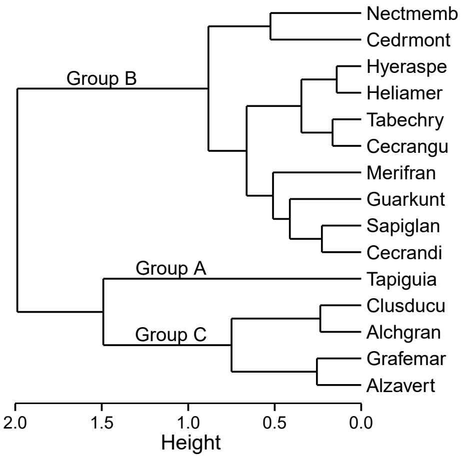


Fig. A-4: Dendrogram of 15 tree species based on the values of the marginality factor of the ENFA for each topographic variable (Tab. A-2). A dissimilarity matrix was calculated using Euclidean distance and subsequently, three groups (Group A, B and C) were identified with the complete linkage method