# UNIVERSIDAD TECNOLÓGICA INDOAMÉRICA

## DIRECCIÓN DE POSGRADO

## MAESTRÍA EN BIODIVERSIDAD Y CAMBIO CLIMÁTICO

**TEMA**:

# CONSECUENCIAS DEL PAISAJE LOCAL EN LA REGENERACIÓN NATURAL EN PARCELAS DE RESTAURACIÓN DE BOSQUE EN LOS ANDES TROPICALES PARA MEDIR LA RESILIENCIA DE LOS BOSQUES A LA INFLUENCIA ANTRÓPICA

Trabajo de investigación previo a la obtención del título de Magister en Biodiversidad y Cambio Climático

**Autor(a)**

Tamargo López, Eva

**Tutor(a)**

PhD. Báez Jácome, Selene Báez

AMBATO (QUITO) – ECUADOR

2021

# UNIVERSIDAD TECNOLÓGICA INDOAMÉRICA

## DIRECCIÓN DE POSGRADO

### MAESTRÍA EN BIODIVERSIDAD Y CAMBIO CLIMÁTICO

**THEME**:

---

# CONSEQUENCES OF LOCAL LANDSCAPE IN NATURAL REGENERATION IN FOREST RESTORATION PLOTS IN THE TROPICAL ANDES TO MEASURE THE RESILIENCE OF FORESTS TO ANTHROPIC INFLUENCE

---

Trabajo de investigación previo a la obtención del título de Magister en Biodiversidad y Cambio Climático

**Autor(a)**

Tamargo López, Eva

**Tutor(a)**

PhD. Báez Jácome, Vera Selene

QUITO – ECUADOR

2021

# AUTORIZACIÓN POR PARTE DEL AUTOR PARA LA CONSULTA, REPRODUCCIÓN PARCIAL O TOTAL, Y PUBLICACIÓN ELECTRÓNICA DEL TRABAJO DE TÍTULACIÓN

Yo, Eva Tamargo López, declaro ser autora del Trabajo de Investigación con el nombre "Consecuencias del paisaje local en la regeneración natural en parcelas de restauración de bosque en los Andes Tropicales para medir la resiliencia de los bosques a la influencia antrópica", como requisito para optar al grado de máster en Biodiversidad y Cambio Climático y autorizo al Sistema de Bibliotecas de la Universidad Tecnológica Indoamérica, para que con fines netamente académicos divulgue esta obra a través del Repositorio Digital Institucional (RDI-UTI).

Los usuarios del RDI-UTI podrán consultar el contenido de este trabajo en las redes de información del país y del exterior, con las cuales la Universidad tenga convenios. La Universidad Tecnológica Indoamérica no se hace responsable por el plagio o copia del contenido parcial o total de este trabajo.

Del mismo modo, acepto que los Derechos de Autor, Morales y Patrimoniales, sobre esta obra, serán compartidos entre mi persona y la Universidad Tecnológica Indoamérica, y que no tramitaré la publicación de esta obra en ningún otro medio, sin autorización expresa de la misma. En caso de que exista el potencial de generación de beneficios económicos o patentes, producto de este trabajo, acepto que se deberán firmar convenios específicos adicionales, donde se acuerden los términos de adjudicación de dichos beneficios.

Para constancia de esta autorización, en la ciudad de Quito, a los 31 días del mes de octubre de 2020, firmo conforme:

Autora: Eva Tamargo López

Eva Tamargo
Firma: ……………………….
Número de Cédula:1759388729
Dirección: Pichincha, Quito, Parroquia, Barrio.
Correo Electrónico: eva.tamargo@hotmail.es
Teléfono: +593999899549

# APROBACIÓN DEL TUTOR

En mi calidad de Tutora del Trabajo de Titulación “CONSECUENCIAS DEL PAISAJE LOCAL EN LA REGENERACIÓN NATURAL EN PARCELAS DE RESTAURACIÓN DE BOSQUE EN LOS ANDES TROPICALES PARA MEDIR LA RESILIENCIA DE LOS BOSQUES A LA INFLUENCIA ANTRÓPICA.”
presentado por Eva Tamargo López, para optar por el Título Máster en Biodiversidad y Cambio Climático,

CERTIFICO

Que dicho trabajo de investigación ha sido revisado en todas sus partes y considero que reúne los requisitos y méritos suficientes para ser sometido a la presentación pública y evaluación por parte del Tribunal Examinador que se designe.

Quito, 4 de marzo del 2021

Selene Báez
………………………………….
PhD. Báez Jácome, Vera Selene

# DECLARACIÓN DE AUTENTICIDAD

Quien suscribe, declaro que los contenidos y los resultados obtenidos en el presente trabajo de investigación, como requerimiento previo para la obtención del Título de "Consecuencias del paisaje local en la regeneración natural en parcelas de restauración de bosque en los Andes Tropicales para medir la resiliencia de los bosques a la influencia antrópica", son absolutamente originales, auténticos y personales y de exclusiva responsabilidad legal y académica del autor

Quito, 31 de marzo del 2021

Eva Tamargo
…………………………………

Eva Tamargo López

1759388729

# APROBACIÓN TRIBUNAL

El trabajo de Titulación, ha sido revisado, aprobado y autorizada su impresión y empastado, sobre el Tema: CONSECUENCIAS DEL PAISAJE LOCAL EN LA REGENERACIÓN NATURAL EN PARCELAS DE RESTAURACIÓN DE BOSQUE EN LOS ANDES TROPICALES PARA MEDIR LA RESILIENCIA DE LOS BOSQUES A LA INFLUENCIA ANTRÓPICA, previo a la obtención del Título de máster, reúne los requisitos de fondo y forma para que la estudiante pueda presentarse a la sustentación del trabajo de titulación.

Quito, 28 de mayo de 2021

…………………………………………….

Nora Helena Oleas Gallo

PRESIDENTE DEL
TRIBUNAL

Laura

…………………………………………….

Laura Inés Salazar Cotugno
VOCAL

Selene Báez

…………………………………………….

Vera Selene Báez Jácome
VOCAL

# DEDICATORIA

Le dedico esta tesis a Leo, mi esposo, que con paciencia y amor me acompañó en todo este proceso. También al resto de mi familia, mis hermanas, Inés y Cintia, y mis padres, Rafa y Victoria, que me dieron los ánimos y me impulsaron para continuar hasta el final.

# AGRADECIMIENTO

Me gustaría agradecer en primer lugar a Selene Báez, que, además de darme esta oportunidad, me ha guiado con paciencia desde el comienzo de la tesis, haciendo que la culminación de la misma sea posible. Agradezco también a Marijn Bauters y a Xavier Haro, los cuales hicieron posible las partes más imposibles de esta tesis. A Feno, por aguantar mis constantes dudas de estadística. A todas las personas que me ayudaron en el campo, especialmente a Paola, sin la cual las salidas de campo habrían sido interminables, y que me ha ayudado a respetar la vida de los helechos, incluso en contra de mi voluntad. A Hans Verbeeck y Mike Perring, Debbie Eraly y Brian Krohnke como parte de BOS+ y MCF, Sarah Wilson, y todas las personas que han aportado su granito de arena para dar forma a este proyecto. Le agradezco también a la Escuela Politécnica Nacional y a la Universidad Tecnológica de Indoamérica, así como al financiamiento del proyecto COFOREC (VLIR-OUS, Bélgica), y a la Universidad de Gante, Bélgica, por acogerme temporalmente y hacer mis incomprensibles datos un poco más comprensibles. Por último, le agradezco al Ministerio del ambiente por concederme el permiso 025-2019-IC-FLO-DNB/MA.

## CONTENTS ÍNDEX

## CHAPTER I

## CHAPTER II

## CHAPTER III

## CHAPTER IV

## CHAPTER V

# TABLES INDEX

# FIGURES INDEX

## UNIVERSIDAD TECNOLÓGICA INDOAMÉRICA
## DIRECCION DE POSGRAGO
## MAESTRIA EN BIODIVERSIDAD Y CAMBIO CLIMÁTICO

## TEMA: CONSECUENCIAS DEL PAISAJE LOCAL EN LA REGENERACIÓN NATURAL EN PARCELAS DE RESTAURACIÓN DE BOSQUE EN LOS ANDES TROPICALES PARA MEDIR LA RESILIENCIA DE LOS BOSQUES A LA INFLUENCIA ANTRÓPICA

**AUTORA: Eva, Tamargo López**

**TUTORA: PhD. Vera Selene, Báez Jácome**

## RESUMEN EJECUTIVO

Tras la tala completa de un bosque, la regeneración de especies nativas de árboles puede estar determinado por factores tanto a escala local como de paisaje. La estructura del paisaje puede influenciar a las tasas de recuperación del bosque, aportando semillas, sobre todo por dispersión animal, desde bosques primarios o secundarios hasta las áreas en restauración. El clima también afecta a las dinámicas de los bosques montanos: las tasas de recambio de árboles y la productividad primaria decrecen con bajas temperaturas. Presentamos una selección bayesiana de modelos (LASSO) para nuestro set de variables predictoras (agrupados en comunidad de árboles adultos, cobertura de paisaje y clima) para nuestras variables de respuesta (riqueza y abundancia de plántulas, en general y dispersadas por zoocoría). En el norte de Ecuador, en bosques secundarios tropicales activamente reforestados, hemos encontrado una gran influencia de los árboles plantados en el reclutamiento de juveniles, lo cual podría indicar que una plantación de árboles rica podría ser una buena elección como acción de restauración para este tipo de ecosistemas. Nuestros datos también mostraron un efecto positivo de la heterogeneidad del paisaje en la abundancia de árboles jóvenes, los cuales también se ven negativamente afectados por la estacionalidad de precipitación. Podríamos pensar que sería adecuado centrar los esfuerzos de restauración activa en regiones donde el estrés hídrico sea elevado.

**DESCRIPTORES: Andes, reforestación, biodiversidad, configuración del paisaje, Ecuador**

# UNIVERSIDAD TECNOLÓGICA INDOAMÉRICA

## DIRECCION DE POSGRAGO

## MAESTRIA EN BIODIVERSIDAD Y CAMBIO CLIMÁTICO

# THEME: CONSEQUENCES OF LOCAL LANDSCAPE ON NATURAL REGENERATION IN FOREST RESTORATION PLOTS IN THE TROPICAL ANDES TO MEASURE THE RESILIENCE OF FORESTS TO ANTHROPIC INFLUENCE

**AUTHOR: Eva, Tamargo López**

**TUTOR: PhD. Vera Selene, Báez Jácome**

## ABSTRACT

After the complete clearing of a forest, the regeneration of native tree species can be determined by factors at both the local and landscape scales. Landscape structure can influence forest recovery rates, providing seeds, especially by animal dispersal, from primary or secondary forests to areas under restoration. Climate also affects the dynamics of montane forests: tree replacement rates and primary productivity decrease with low temperatures. We present a Bayesian selection of models (LASSO) for our set of predictor variables (grouped in community of adult trees, landscape cover and climate) for our response variables (richness and abundance of seedlings, in general and dispersed by zoocory). In northern Ecuador, in actively reforested tropical secondary forests, we have found a great influence of planted trees on the recruitment of juveniles, which could indicate that a rich tree plantation could be a good choice as a restoration action for this type of ecosystems. Our data also showed a positive effect of landscape heterogeneity on the abundance of young trees, which are also negatively affected by the seasonality of precipitation. We might think that it would be appropriate to focus active restoration efforts in regions where water stress will be high.

**KEYWORDS: Andes, reforestation, biodiversity, landscape configuration, Ecuador**

**Translated by:**

**MSc. Lorena Espinosa F.**

# **CHAPTER I:** INTRODUCTION

Following high rates of forest conversion, restoring forests on former pastures or agricultural lands is becoming a key land-use dynamic across the tropics (Chazdon, 2008). The success or benefits of active restoration are highly debated: while some researches have not found acceptable level of species diversity in reforested terrains (Philipson et al., 2020), other studies support instead active interventions as a regeneration mechanism that plays an important role in catalyzing forest recovery, contributing to the species diversity (Bremer & Farley, 2010), and enhancing aboveground carbon density recovery by 50% per decade (Philipson et al., 2020). Forest plantations create numerous benefits such as improving the abundance of understory native vegetation, when compared with abandoned grasslands with herbaceous dominance (Cusack & Montagnini, 2004). Likewise, forest cover diminishes soil erosion and prevent fires, facilitating the establishment of native species (Lee et al., 2005). However, natural (or passive) regeneration is often considered a good mechanism for restore forest and ecosystem functions. It has been found that passive regenerated forests shows a higher vegetal diversity and a better forest structure (Sansevero et al., 2017).

Active forest restoration seems particularly important in areas that have been degraded to pastures (Shimamoto et al., 2018), and especially so in tropical montane ecosystems where introduced species of grasses have led to arrested succession (Catterall, 2016; Shono et al., 2006; Wilson & Rhemtulla, 2018). However, understanding the factors that drive biodiversity recovery in these actively restored areas is critical to design appropriate restoration practices. At local scales, tree diversity recovery can be constrained by a combination of factors: predation of seeds and saplings, competition with grasses and other non-woody vegetation, abundance of remnant trees and stumps, soil degradation and microclimate (Guariguata & Ostertag, 2001). As such, tree planting is expected to enhance diversity recovery by attracting seed dispersers and creating a more favorable local microenvironment for newly established trees (Holl et al., 2020). Yet, in these areas, tree diversity recovery may depend on landscape configuration, including natural forest cover and fragmentation, that determines distance to seed sources (Corbin et al., 2015). In consequence, both local and landscape factors need to be considered to infer their relative importance as drivers of biodiversity recovery.

Yet in restoration activities it is critical to consider the landscape features (Molin et al., 2018), our understanding of the importance of landscape on communities restoration and ecosystem functions is still limited (Reid et al., 2014). Distance or proportion of forest remnants is one of the main biophysical drivers of forest regeneration by improving the seed bank density and species richness (Cubiña & Mitchell Aide, 2001; Miazaki Toledo et al., 2018; Molin et al., 2018; Vellend, 2003). Not only distance, but also landscape structure can influence forest regeneration, provoking the unevenly distribution of natural regeneration on mosaic landscapes (Arroyo-Rodríguez et al., 2017), or slowing the process, as in fragmented areas (Uriarte et al., 2016). In tropical natural forests seed dispersal is a critical component of tree diversity recovery, as it maintains tree populations viable (Beckman & Rogers, 2013; Caughlin et al., 2014). But in fragmented areas, vertebrate dispersers may not contribute substantially to long distance dispersion (Melo et al., 2010), resulting in tree species loss (Babweteera & Brown, 2009; Brodie et al., 2009). The presence of seed dispersers can be regulated by the closeness of the edge of natural forests (Da Silva et al., 1996; Hardwick et al., 2004), and by landscape connectivity, which can contribute to species colonization and reduce mortality (Damschen et al., 2019).

Locally, lack of seed dispersal is the principal factor limiting forest recovery, followed by low germination and seed survival. Seed survival and germination can be low in secondary forests (Toledo-Aceves et al., 2021), majorly for pasture grasses competition (Holl,K. D et al., 2000; Rojas-Botero et al., 2020). These factors can be minimized in the presence of grown trees, which shadow the grasses, apport new seeds, ameliorate soil conditions and create a microclimate suitable for seedlings (Holl, et al., 2000). Forest structure and species composition changes along elevation gradients in montane forest. Elevational gradients are closely correlated with temperature and total precipitation, and this climate factor affects strongly mountain forests dynamics: rates of tree turnover and primary productivity decrease with lower temperatures (Báez et al., 2015; Leuschner et al., 2013; Stephenson & Van Mantgem, 2005), and have a strong effect on recovery of species composition on abandoned pastures (Aide et al., 1996). Precipitation also alter montane forest dynamics, but its influence is less clear (Báez et al. 2015). Extreme values on precipitation can have negative effects on plant production and recruitment, especially during early forest succession (Anderson-Teixeira et al., 2013; Schuur & Matson, 2001; Uriarte et al., 2016).

It has been proved that nucleation, or artificially simulate natural colonization patches during succession, when supported by tree plantation, could improve the functionality of the restored forest (Rojas-Botero et al., 2020). Thus, understanding the relative importance of local vs. landscape variation on the rates of recovery of degraded areas is critical to develop forest restoration guidelines and policies.

In this study we evaluated the influence of local factors and landscape configuration in the natural regeneration of tree saplings along an elevation gradient of ~2000 masl in montane tropical forests of Ecuador. We analyzed the effect of landscape configuration and plot-scale local conditions on the richness, abundance and dispersal syndrome of natural regenerated trees in six sites of actively reforested forest. The study's general objective is to identify the influence of landscape, local forest structure and climate in the natural regeneration of tropical forests in Northwest- Ecuador. Understanding natural regeneration as abundance and species richness of saplings. Specifically, we aim to identify if local tree richness increase abundance and richness of sapling at local level. To estimate if regional forest proportion and landscape structure increase abundance and richness of sapling at local scale and analyze whether climate can influence abundance and richness of saplings in restored areas.

The following specific research questions are addressed in this study

1) Do local conditions related to tree structure and diversity in forest restoration areas affect tree diversity recovery?

2) How do landscape conditions influence the success of tree biodiversity recovery in reforestation areas?

3) How does climate affect biodiversity recovery in reforested areas along an elevation gradient in tropical montane forests?

We tested the following hypothesis:

H1. Plots with higher abundance and diversity of trees will have higher abundance and diversity of naturally recruited woody young trees.

H2. Larger proportion of natural forest in the area increases the abundance and species richness of woody young trees in restored forests, particularly of species dispersed by animals.

H3. Biodiversity recovery is higher in montane forests with higher environmental temperature and lower precipitation seasonality.

# **CHAPTER II:** METHODS

## Study Area

This study was conducted in the North-Western Andean slopes of Ecuador. We sampled six reforestation areas that encompass about 346 ha in a gradient between 300 and 2300 masl of elevation (Figure 1), including lowland moist forest, lower evergreen montane forest, and evergreen upper montane forest (Ministerio del Ambiente del Ecuador, 2012). In our restoration areas, tree planting took place between 2011 and 2012, using native (e.g., *Alnus acuminata*, *Critoniopsis occidentalis*) and exotic (e.g., *Alnus nepalensis)* species of trees. These are used in forest restoration projects because their fast growth reduces light incidence to lower forest strata and reduces the growth of established grasses (e.g., *Setaria* spp.) planted for cattle ranching, and thus are expected to enhance the rates of natural tree ingrowth.

### *Forest plots: tree and sapling communities and species dispersal syndromes*

We revisited the six restoration sites after seven to nine years since trees were planted (in 2019) and established a total of 128 circular permanent plots with a ratio of 8 m (0.201ha) at varying distances from natural forests (mean 20 plots per site, min= 14, max=32). In our monitoring plots, we evaluated the abundance and diversity of the tree and the sapling communities. The ‘tree community’ included all individual stems ≥5 cm DBH at 1.30 m height that were planted during forest restoration. The ‘sampling community’, on the other hand, included all woody species measuring ≥ 50 cm height not reaching 5 cm of DBH, that colonized the reforestation plots after forest restoration took place. Therefore, we measured the DBH of trees ≥5 cm DHB and the height of saplings. Botanical samples taken for taxonomic identifications were deposited at Herbarium QCA in Quito, Ecuador.

We used taxonomic descriptions and other published literature to obtain information on species dispersal syndromes. We classified our species in two broad categories of seed dispersal: zoochory or other type that included anemochory, hydrochory, barochory, autochory (Appendix 1).

### *Landscape: land cover and landscape structure*

We used Sentinel-2 satellite imagery to classify the entire landscape of the forest restoration areas into forest, agriculture, water, exposed soil, and urban areas. No images free of cloud and associated cloud-shadow were available for the study area for dates were vegetation sampling was conducted, so we masked out clouds from all images between January 2019 and April 2020 using the Sentinel-2 QA and Cirrus bands. We then created a single composite using the median value of each pixel.

Training data for classification analysis were obtained using field inventories, available data from the Ecuadorian Ministry of Environment and high-resolution imagery from Google Earth. Forest training data were derived from surveyed data, areas inside nature reserves and areas that were recently protected under the Socio Bosque conservation initiative (de Koning et al., 2011).

We used Random Forest (RF) as a classification approach (Breiman, 2001); RF has been successfully used to classify complex landscapes in the humid and dry tropics (Fagan et al., 2015; Haro-Carrión & Southworth, 2018; Sesnie et al., 2010). Predictors for the RF classification included six Sentinel-2 bands, four band ratios, two vegetation indices, and five image transformations (Appendix 2). All remote sensing classification analyses were performed using the Google Earth Engine (GEE) platform with the default RF parameters.

Once obtained the classification results, this classification was lightly refined only for the location at the lowest elevation (Suamox), with that purpose, extra sampling points were added. This adjustment was necessary because of the variability in vegetation communities due to difference in altitude and distance to the other locations. The initial model was conserved for every other location, due to its best accuracy values and, generally, it represented better the field observation expectations.

We obtained eleven landscape predictors from the produced land-cover map: percentages of land use (i.e., agriculture, native forest, restored forest, soil, urban and water). We obtained percent coverage of native forest land-cover class, within a 200-m buffer around each vegetation plot. The area of the buffer was selected based on the findings of Souza et al. (2014), Rezende et al. (2015) and Toledo et al. (2018, 2020), which found neighborhood effect in regenerating forests in distances of up to 200 m. Additionally, we found 200 m consistent with dispersion information available for our study area.

To account for different land-cover configurations -how pixels of each land-cover type are distributed within the 200 m buffer area of each forest plot- we calculated various landscape indices including: contagion, PLADJ, Shape Index, Core and Number of patches (Li & Reynolds, 1993; Riiters et al., 1996) (Appendix 3). Predictors were calculated using package SDMTools (VanDerWal et al., 2014 in R, and the code detailed in Fletcher et al., 2019). For further statistical analyses we chose ‘Contagion’ as our measure of fragmentation because this index measures aggregation among different types of vegetation cover. ‘Contagion’ is defined as the probability of finding an i cover pixel adjacent to an j cover pixel. Thus, high contagion values indicate high land cover heterogeneity.

*Climatic conditions*

We used the Chelsa extrapolated climate database (Karger et al., 2017, 2020), to obtain our climatic variables, since it has a high resolution and gives a better representation of the climate in tropical mountains. We extracted various climatic parameters for our study sites, including mean annual temperature (MAT, bio_1), mean annual precipitation (MAP, bio_12), precipitation seasonality (PS, bio_15), and precipitation of the driest quarter of the year (PDQ, bio_17). Precipitation seasonality is calculated as a coefficient of variation $(bio15 = (\sqrt{\frac{1}{11}\sum_{i=1}^{12} p_i - (\sum_{i=1}^{12} p_i/12))^2})/(\sum_{i=1}^{12} p_i)/12)$ (being p the monthly precipitation amount) and estimates the change in monthly precipitation over the year, and precipitation of the driest quarter of the year is the mean monthly precipitation amount of the driest quarter (3 consecutive months).

## Data analysis

### *Sapling diversity across six forest restoration sites*

We first built species accumulation curves to evaluate whether our sampling effort was adequate to capture substantial variation in our study sites. We developed our species accumulation plots using rarefied species diversity. Rarefaction is a statistical tool that assess species richness for a given number of samples. Plotting the rarefaction curves allows to represent the number of species as a function of the number of samples, and this permit to determinate the sampling effort. Furthermore, to understand variation in sapling species composition among our study sites, we used Multivariate *Non-Metric Multidimensional Scaling* (NMDS), with bray-curtis distances. This ordination technique allows comparing and visualizing changes in species composition across plant communities. We first checked the fit of our data for the NMDS, with a Shepard plot, that presents the dispersion of the data around the regression. All analyses were developed using the “vegan” package (Oksanen et al., 2020) in R statistical software (R Foundation for Statistical Computing, Vienna, AT, version R.4.0.2.).

### *Local tree community, landscape and climatic effects on sapling diversity*

We used a least absolute shrinkage and selection operator regression (LASSO) in a Bayesian statistical framework to explore how the sapling community was affected by the 1) local tree community, 2) configuration of the surrounding landscape in an area of 200 m, and 3) climatic variation. LASSO regression is a regularization method that sets to zero estimates of predictor variables that have minimal effects on the statistical model. Once these variables with negligible effects are identified in an initial statistical analysis, they are eliminated, and the model is fit again using non-regularization priors. Then the posterior distributions of the predictors can be interpreted as effect sizes (Bauters et al., 2021; Piironen & Vehtari, 2017).

For each of our final models, we calculated marginal and conditional $R^2$ values. Marginal $R^2$ is proportion of variance explained by fixed factors, while conditional $R^2$

indicates the variance explained by both fixed and random factors together (Nakagawa & Schielzeth, 2013). All statistical analysis were conducted in the R statistical software (R Foundation for Statistical Computing, Vienna, AT, version R.4.0.2.) with the packages "brms" (Bürkner, 2018), "ggplot2" (Wickham, 2016), "sjPlot" (Lüdecke, 2021) and "sjstats" (Lüdecke, 2021).

We selected a subset of variables with correlation coefficients <0.70 to be included as model predictors. For example, tree basal area and species richness had a low correlation coefficient and both were included in our models (Appendix 4a-c). On the other hand, elevation was highly negatively correlated with mean annual temperature (MAT) and mean total annual precipitation (TAP), we selected elevation to capture variation on the two other variables. Precipitation seasonality was not correlated to elevation and thus it was the only climatic variable to account for water stress to plants that was included in our models. Similarly, Contagion and PLADJ were highly correlated, thus we selected Contagion as an index of landscape fragmentation. Contagion and climatic variables were not correlated. Other landscape variables represented a small fraction of the landscape and therefore were not considered as predictors for statistical modelling.

In consequence, our LASSO regressions estimated the abundance and richness of the sapling community, and abundance and richness of saplings dispersed by zoochory, for a total of four regression analyses. The full models included as additive fixed factors the following standardized variables: tree basal area (sum of the basal area of trees in a plot), tree species richness, % forest cover, fragmentation index, elevation and precipitation seasonality; and site as a random effect. We run an additional set of models including plantation age to account for a possible effect of time since plantation on sapling recruitment (results not shown), but the age predictor was regularized to zero, and therefore it was deleted from the final models. This was expected, since we sampled similar aging terrains, from seven to nine years since the tree plantation.

## **CHAPTER III:** RESULTS

In the 128 permanent plots we found 1149 individual trees, in 149 tree species, in 89 genera, and 42 taxonomic families. The overall tree mean DBH was 12 cm (min=5, max=49.66), varying from a mean of 7.67 to 15.34 cm DBH among restoration sites (Table 1). At plot scale, tree basal area had a mean of 0.14 (min=0, max=0.616), and varied from 0.01 to 0.24 $cm^2$ across sites.

### *Sapling diversity across six forest restoration sites*

We recorded 2895 individual saplings that were classified in 224 morphospecies, 120 genera and 52 taxonomic families. According to location, sapling abundance varied from a mean of 3.85 to 34.75 individuals per plot, with an overall mean of 23.60 sapling per plot (Table 1). Among restoration sites, sampling species richness varied from 1.68 to 11.07 per plot, with a mean of six species per plot per reforestation site (Table 1).

The results of the species accumulation curves indicated that our sampling effort was adequate to capture variation in species composition in each of our six study sites (Appendix 5). It also indicated large differences rarefied in sapling species diversity among our sites. Our NMDS analyses also indicated that the sapling community, representing natural ingrowth, was substantially different among the six forest regeneration sites (Figure 2).

### *Local tree community vs. landscape effects on sapling diversity recovery*

The results of the LASSO regression indicated that total abundance of saplings and abundance of animal dispersed saplings were affected in the same way by the local, landscape, and climatic factors. In both analyses, plot scale tree basal area played a minor role, as the estimate of this variable was shrunk to zero in the regularization analyses (Figure 3, Appendix 6). For both types of sapling abundance, species richness of trees had the strongest positive effect, followed by fragmentation. On the contrary, precipitation seasonality and forest cover, both had negative effects on the total and zoochory dispersed abundance of saplings. In the models examining sapling abundance fixed factors explained almost 50% of the variation (marginal $R^2$= 0.47), and random factors did not add substantially to the explanatory power of the models (conditional $R^2$= 0.48).

Sapling species richness was affected by a narrower subset of predictors compared to sapling abundance (Figure 3, Appendix 7). Sapling species richness (total and for zoochory dispersed species) was positively affected by the species richness of the tree community in the sampling plot (local factor). Percentage forest cover, however, had a negative effect on total sapling diversity. The models examining sapling species richness explained almost 60% of the total variation (conditional $R^2$ =0.60), due to the random factors, that, in this case, added explanatory power in both models (species richness marginal $R^2$= 0.36; species richness (zoochory) marginal $R^2$= 0.13). According to their dispersal mechanism, trees influence in different ways the sapling community. In our analyses, tree abundance and species richness of trees dispersed by zoochory had statistically significant and positive effects on sapling abundance and species richness (Fig 4). This result did not hold for trees with other dispersal syndromes, although tree species richness did have a positive effect on sapling species richness (Fig 4). Sapling abundance regressions captured 20% of the variation ($R^2$=0.20), while sapling species richness explained almost 50% (Figure 3).

## **CHAPTER IV:** DISCUSSION

Our study suggests that the local tree community, landscape configuration, and environmental variation related to precipitation seasonality affected woody biodiversity recovery in restored tropical montane forests. The species richness of the trees planted during forest restoration practices had the most consistent positive effect on sapling abundance and species richness. In our study areas, the sapling community established in restoration plots via dispersal or self-seeding

### Planted trees richness drives plant community recovery

Tree species richness was the main factor enhancing the abundance and species richness of saplings established after forest restoration (Figure 3, Appendix 6 and 7). This pattern was stronger for species dispersed by zoochory, but it held for the sapling community as a whole and for species non-zoochorial dispersal syndromes (Figure 4). Higher sapling abundance in more species rich restored plots may be related to 1) self-seeding of established trees contributed to increase the sapling species richness (Hardwick et al., 2004), and 2) higher species richness resulted in resources that attracted frugivore species that also acted as seed dispersers, which diversified the seed bank and eventually enhanced sapling diversity (Guevara & Laborde, 1993; Li et al., 2020).

The mechanisms through which higher tree species richness could enhance the abundance of saplings are less clear (Fig 3, Appendix 6). But this pattern is clear in our study, where we found that the tree species richness regression line is above the 1-1 line, meaning that each tree species supposes a recruitment of 16 sapling individuals and 4 sapling species.  This is a consistent positive effect of tree diversity on the potential of regeneration of tree species in reforested areas, indicating the benefits of a rich and abundant plantation for forest restoration in montane tropical forests.

## Landscape configuration effects on plant community recovery

Our analyses indicated that landscape configuration had unexpected effects on the recovery of the sapling community. Forest plots surrounded by areas with higher fragmentation index values had higher abundance of saplings in general, and also of saplings dispersed by zoochory (Figure 3, Appendix 6). This positive effect of fragmentation on woody sapling abundance in reforestation plots may be related to a higher diversity of seed dispersers adapted to different environments ranging from natural and secondary forests to agricultural and urban environments. In addition, the 200 m buffer areas where our landscape metrics were taken, habitat fragmentation may not impose large barriers for movements of small mammals and birds, which are likely the most important seed dispersers in the area (Holbrook, 2011). Furthermore, the positive effect of fragmentation on sapling abundance in our restored areas may be due to the overall acceptable conservation status of our study areas, as natural forest cover is present in the buffer areas of 98% of the forest surveyed plots. In very degraded landscapes with limited and isolated areas with natural vegetation, seed dispersers would need to move over large distances to reach seed sources; there a positive effect of fragmentation may not occur.

It was unexpected to find a negative effect of native forest cover for sapling abundance (total and dispersed by zoochory) and total sapling species richness (Figure 3, Appendices 6 and 7). This finding contradicts other studies, where natural forest is essential for forest regeneration (Cubiña & Mitchell Aide, 2001; Molin et al., 2018; Vellend, 2003) and that even remnant trees and tree fences can act as seed source to recovering forests (Rojas-Botero et al., 2020; Schlawin & Zahawi, 2008). Certain studies, however, have found that proportion of mature forests does not have large positive effects on seedlings diversity and abundance (Aide et al., 1996; Toledo-Aceves et al., 2021). In our study, it is possible that the effects of the local tree community were much stronger than positive influences on sapling recovery, possibly masking any positive effects of natural forest cover on woody saplings. It is also possible that certain interactions between the restored tree community and the proportion of forest cover are needed to have a positive effect of natural forests on natural ingrowth. For example, in our study sites, certain areas reforested with fast-growth tree species had understory conditions that did not seem appropriate for sapling recovery due to low light incidence in the forest ground and understory. In these conditions it is possible that seed inputs from natural forests surrounding these areas did not result in an overall positive effect on the sapling community. On the other hand, other sites with low natural forest cover in the buffer areas had high sapling regeneration, probably due to self-seeding, and possibly to seed inputs from trees left in pastures to provide shadow to cattle.

### Water stress is a modulator of sapling recovery in tropical montane forests

We found a negative effect of precipitation seasonality on the abundance of saplings community and also saplings dispersed by zoochory (Figure 3, Appendix 6). Previous studies have found a negative effect of long-dry seasons in tree communities of tropical forests, specially, in early stages of the succession (Uriarte et al., 2016; Vieira et al., 2004). Drought is also associated to tree mortality (ref). Thus, these results suggest that water stress limits the potential of biodiversity recovery in tropical montane forests, and therefore, more seasonal areas would require more concentrated efforts to restore forest vegetation.

### Different pathways in forest succession

Our results indicated that our forest restoration areas included a great variety of natural regenerated species. Our sampling effort was somewhat adequate to capture natural regenerated species recovery, but toward lower elevations, much effort is needed to record the diversity to adequate levels (Appendix 5). These patterns are somewhat expected for highly diverse forests, where the species pool is extremely high and different across altitudinal and elevation gradients. We found that the regenerating species community is site-specific, as shown in the NMDs figure, implying that each site is colonized by different species of trees. Santa Rosa, Piedras Negras and La Yumbada showed proximity in the plot (Figure 1) since they are similar locations, they are geographically close and have similar elevation in comparison with the rest of locations. Each of the other location, Suamox, Mundo Nuevo and El Cristal, are located in a different province, and present a specific ecosystem type. Other studies have found this same difference in species composition between regenerating forests (Poorter et al., 2019; Wilson & Rhemtulla, 2016).

In forest restoration, tree seedling establishment is an important indicator of success. Even if timing regeneration can be variable (Meli et al., 2017; Rozendaal et al., 2019), active restoration can enhance seedlings communities in comparison with passive regeneration (Rojas-Botero et al., 2020; Toledo-Aceves et al., 2021), yet this not necessarily means a higher recruitment rate when comparing active and passive restoration (Toledo-Aceves et al., 2021). Tree planting can also increase the richness and abundance of late successional and syn-zoochorous seedling species in late stages (Toledo-Aceves et al., 2021). Our study contributes to improve the knowledge of landscape effects in tropical forest, landscape characteristics, as forest cover and fragmentation can impact the local biodiversity in anthropic landscapes and has to be taken into account when prioritizing restoration projects investments (Gardner et al., 2012).

We conclude that restoration practices have a strong relevance on forest regeneration. We think that a highly diverse plantation, with native species, can enhance the succession rate for species and functional diversity, allowing also a recuperation of faunal diversity, even if the landscape it is not a strong ally. It is important too to be able to predict which parental trees will contribute more to seed rain in these forests, for a better restoration planning (Hardwick et al., 2004). But, also, we stand that, the biggest restoration efforts should be placed on areas where the local tree richness is low, and the precipitation seasonality is strong. It is important to understand the complexity of secondary forests, as they are ecosystems affect by multiple factors and hazard processes, which make their study a complex task, as those multiple factor can show dependencies and collinearities that makes their comprehension complicated.

# **CHAPTER V:** CONCLUSIONS AND RECOMMENDATIONS

## *Conclusions*

This study indicates that active restoration techniques can be important for natural biodiversity recovery in tropical montane forests. Local conditions determined by the restored forests are critical determinants of the rates of biodiversity recovery through natural ingrowth, since we found a consistent positive effect of tree diversity on the potential of regeneration of tree species in reforested areas. Thus, indicating the benefits of a rich and abundant plantation for forest restoration in montane tropical forests, especially when the plantation includes trees dispersed by zoochory syndromes.

It is important to understand and predict which parental trees will contribute more to seed rain in these forests, for a better restoration planning (Hardwick et al., 2004). But, also, we stand that, the biggest restoration efforts should be placed on areas where the local tree richness is low, and the precipitation seasonality is strong. It is important to understand the complexity of secondary forests, as they are ecosystems affect by multiple factors and hazard processes, which make their study a complex task.

## *Recommendations*

Further investigations are required. It would be important to augment the buffer extension, so more landscape matrix is captured and analyzed, to have a more regional comprehension of landscape effects on succession, and not only the local environment is investigated. It would also be interesting to test the effect of landscape in these same regions, when no active restoration has been carried, to test whether landscape effects will increase.

## CITED LITERATURE

Aide, T. M., Zimmerman, J. K., Rosario, M., & Marcano, H. (1996). Forest Recovery in Abandoned Cattle Pastures Along an Elevational Gradient in Northeastern Puerto Rico. *Biotropica*, *28*(4), 537–548. https://doi.org/10.2307/2389095

Anderson-Teixeira, K. J., Miller, A. D., Mohan, J. E., Hudiburg, T. W., Duval, B. D., & DeLucia, E. H. (2013). Altered dynamics of forest recovery under a changing climate. *Global Change Biology*, *19*(7), 2001–2021. https://doi.org/10.1111/gcb.12194

Arroyo-Rodríguez, V., Melo, F. P. L., Martínez-Ramos, M., Bongers, F., Chazdon, R. L., Meave, J. A., Norden, N., Santos, B. A., Leal, I. R., & Tabarelli, M. (2017). Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. *Biological Reviews*, *92*(1), 326–340. https://doi.org/10.1111/brv.12231

Babweteera, F., & Brown, N. (2009). Can remnant frugivore species effectively disperse tree seeds in secondary tropical rain forests? *Biodiversity and Conservation*, *18*(6), 1611–1627. https://doi.org/10.1007/s10531-008-9546-6

Báez, S., Malizia, A., Carilla, J., Blundo, C., Aguilar, M., Aguirre, N., Aquirre, Z., Álvarez, E., Cuesta, F., Duque, Á., Farfán-Ríos, W., García-Cabrera, K., Grau, R., Homeier, J., Linares-Palomino, R., Malizia, L. R., Cruz, O. M., Osinaga, O., Phillips, O. L., … Feeley, K. J. (2015). Large-scale patterns of turnover and basal area change in Andean forests. *PLoS ONE*, *10*(5), 1–14. https://doi.org/10.1371/journal.pone.0126594

Bauters, M., Moonen, P., Summerauer, L., Doetterl, S., Wasner, D., Griepentrog, M., Mumbanza, F. M., Kearsley, E., Ewango, C., Boyemba, F., Six, J., Muys, B., Verbist, B., Boeckx, P., & Verheyen, K. (2021). Soil Nutrient Depletion and Tree Functional Composition Shift Following Repeated Clearing in Secondary Forests of the Congo Basin. *Ecosystems*. https://doi.org/10.1007/s10021-020-00593-6

Beckman, N. G., & Rogers, H. S. (2013). Consequences of seed dispersal for plant recruitment in tropical forests: Interactions within the seedscape. *Biotropica*, *45*(6), 666–681. https://doi.org/10.1111/btp.12071

Breiman, L. (2001). Random forests. *Machine Learning*, *45*, 5–32. https://doi.org/10.1201/9780429469275-8

Bremer, L. L., & Farley, K. A. (2010). Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. *Biodiversity and Conservation*, *19*(14), 3893–3915. https://doi.org/10.1007/s10531-010-9936-4

Brodie, J. F., Helmy, O. E., Brockelman, W. Y., & Maron, J. L. (2009). Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. *Ecological Applications*, *19*(4), 854–863. https://doi.org/10.1890/08-0955.1

Catterall, C. P. (2016). Roles of non-native species in large-scale regeneration of moist tropical forests on anthropogenic grassland. *Biotropica*, *48*(6), 809–824.

Caughlin, T. T., Ferguson, J. M., Lichstein, J. W., Zuidema, P. A., Bunyavejchewin, S., & Levey, D. J. (2014). Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages. *Proceedings of the Royal Society B: Biological Sciences*, *282*. https://doi.org/10.1098/rspb.2014.2095

Chazdon, R. L. (2008). Beyond deforestation: Restoring forests and ecosystem services on degraded lands. *Science*, *320*(5882), 1458–1460. https://doi.org/10.1126/science.1155365

Corbin, J. D., Robinson, G. R., Hafkemeyer, L. M., & Handel, S. N. (2015). A long-term evaluation of applied nucleation as a strategy to facilitate forest restoration. *Ecological Applications*, *26*(1), 150527150908005. https://doi.org/10.1890/15-0075.1

Cubiña, A., & Mitchell Aide, T. (2001). The Effect of Distance from Forest Edge on Seed Rain and Soil Seed Bank in a Tropical Pasture. *Biotropica*, *33*(2), 260–267. https://doi.org/10.1646/0006-3606(2001)033[0260:teodff]2.0.co;2

Cusack, D., & Montagnini, F. (2004). The role of native species plantations in recovery of understory woody diversity in degraded pasturelands of Costa Rica. *Forest Ecology and Management*, *188*(1–3), 1–15. https://doi.org/10.1016/S0378-1127(03)00302-5

Da Silva, J. M. C., Uhl, C., & Murray, G. (1996). Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. *Conservation Biology*, *10*(2), 491–503. https://doi.org/10.1046/j.1523-1739.1996.10020491.x

Damschen, E. I., Brudvig, L. A., Burt, M. A., Fletcher, R. J., Haddad, N. M., Levey, D. J., Orrock, J. L., Resasco, J., & Tewksbury, J. J. (2019). Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment. *Science*, *365*(6460), 1478–1480. https://doi.org/10.1126/science.aax8992

Fagan, M. E., DeFries, R. S., Sesnie, S. E., Arroyo-Mora, J. P., Soto, C., Singh, A., Townsend, P. A., & Chazdon, R. L. (2015). Mapping species composition of forests and tree plantations in northeastern Costa Rica with an integration of hyperspectral and multitemporal landsat imagery. *Remote Sensing*, *7*(5), 5660–5696. https://doi.org/10.3390/rs70505660

Guariguata, M. R., & Ostertag, R. (2001). Neotropical secondary forest succession: Changes in structural and functional characteristics. *Forest Ecology and Management*, *148*(1–3), 185–206. https://doi.org/10.1016/S0378-1127(00)00535-1

Hardwick, K., Healey, J. R., Elliott, S., & Blakesley, D. (2004). Research needs for restoring seasonal tropical forests in Thailand: accelerated natural regeneration. *New Forests*, *27*(3), 285–302. https://doi.org/10.1023/b:nefo.0000022228.08887.d2

Haro-Carrión, X., & Southworth, J. (2018). Understanding land cover change in a fragmented forest landscape in a biodiversity hotspot of coastal Ecuador. *Remote Sensing*, *10*(12), 1–21. https://doi.org/10.3390/rs10121980

Holbrook, K. M. (2011). Home range and movement patterns of toucans: Implications for seed dispersal. *Biotropica*, *43*(3), 357–364.

https://doi.org/10.1111/j.1744-7429.2010.00710.x

Holl,K. D, Loik,M. E, Lin,E. H.V, & Samuels,I. A. (2000). Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restoration Ecology*, *8*(4), 339–349.

Holl, K. D., Reid, J. L., Cole, R. J., Oviedo-Brenes, F., Rosales, J. A., & Zahawi, R. A. (2020). Applied nucleation facilitates tropical forest recovery: Lessons learned from a 15-year study. In *Journal of Applied Ecology* (Vol. 57, Issue 12). https://doi.org/10.1111/1365-2664.13684

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. ., Linder, H. P., & Kessler, M. (2020). Data from: Climatologies at high resolution for the earth’s land surface areas. *Dryad Digital Repository*. https://doi.org/http://dx.doi.org/doi:10.5061/dryad.kd1d4

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, P., & Kessler, M. (2017). Climatologies at high resolution for the Earth land surface areas. *Scientific Data*, *4*(170122). https://doi.org/https://doi.org/10.1038/sdata.2017.122

Leuschner, C., Zach, A., Moser, G., Homeier, J., Graefe, S., Hertel, D., Wittich, B., Soethe, N., Iost, S., Röderstein, M., Horna, V., & Wolf, K. (2013). The Carbon Balance of Tropical Mountain Forests Along an Altitudinal Transect. In J. Bendix, E. Beck, A. Bräuning, F. Makeschin, R. Mosandl, S. Scheu, & W. Wilcke (Eds.), *Ecosystem Services, Biodiversity and Environmental Change in a Tropical Mountain Ecosystem of South Ecuador* (221st ed., pp. 117–139). Springer. https://doi.org/10.1007/978-3-642-38137-9_10

Li, H., & Reynolds, J. F. (1993). A new contagion index to quantify spatial patterns of landscapes. *Landscape Ecology*, *8*(3), 155–162. https://doi.org/10.1007/BF00125347

Meli, P., Holl, K. D., Benayas, J. M. R., Jones, H. P., Jones, P. C., Montoya, D., & Mateos, D. M. (2017). A global review of past land use, climate, and active vs. passive restoration effects on forest recovery. *PLoS ONE*, *12*(2), 1–17. https://doi.org/10.1371/journal.pone.0171368

Melo, F. P. L., Martínez-Salas, E., Benítez-Malvido, J., & Ceballos, G. (2010). Forest fragmentation reduces recruitment of large-seeded tree species in a Semi-deciduous tropical forest of Southern Mexico. *Journal of Tropical Ecology*, *26*(1), 35–43. https://doi.org/: 10.1017/S026646 74099904 3 5

Miazaki Toledo, R., Ferreira Santos, R., Baeten, L., Perring, M. P., & Verheyen, K. (2018). Soil properties and neighboring forest cover affect aboveground biomass and functional composition during tropical forest restoration. *Applied Vegetation Science*, *21*(2), 179–189. https://doi.org/10.1111/avsc.12363

Ministerio del Ambiente del Ecuador. (2012). Sistema de clasificación de los Ecosistemas del Ecuador Continental. In *Subsecretaría de Patrimonio Natural* (p. 186). https://www.ambiente.gob.ec/wp-content/uploads/downloads/2012/09/LEYENDA-ECOSISTEMAS_ECUADOR_2.pdf

Molin, P. G., Brancalion, P. H. S., Chazdon, R., Frosini, S., & Ferraz, D. B. (2018). A landscape approach for cost- • effective large-scale forest restoration. *Journal of*

*Applied Ecology*, *January*, 1–12. https://doi.org/10.1111/1365-2664.13263

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Philipson, C. D., Cutler, M. E. J., Brodric, P. G., Asne, G. P., Boy, D. S., Costa, P. M., Fiddes, J., Food, G. M., Van Der Heijden, G. M. F., Ledo, A., Lincol, P. R., Margrov, J. A., Marti, R. E., Milne, S., Pinar, M. A., Reynolds, G., Snoep, M., Tangki, H., Wai, Y. S., … Burslem, D. F. R. P. (2020). Active restoration accelerates the carbon recovery of human-modified tropical forests. *Science*, *369*(6505), 838–841. https://doi.org/10.1126/science.aay4490

Piironen, J., & Vehtari, A. (2017). Sparsity information and regularization in the horseshoe and other shrinkage priors. *Electronic Journal of Statistics*, *11*(2), 5018–5051. https://doi.org/10.1214/17-EJS1337SI

Poorter, L., Rozendaal, D. M. A., Bongers, F., de Almeida-Cortez, J. S., Almeyda Zambrano, A. M., Álvarez, F. S., Andrade, J. L., Villa, L. F. A., Balvanera, P., Becknell, J. M., Bentos, T. V., Bhaskar, R., Boukili, V., Brancalion, P. H. S., Broadbent, E. N., César, R. G., Chave, J., Chazdon, R. L., Colletta, G. D., … Westoby, M. (2019). Wet and dry tropical forests show opposite successional pathways in wood density but converge over time. *Nature Ecology and Evolution*, *3*, 928–934. https://doi.org/10.1038/s41559-019-0882-6

Reid, J. L., Mendenhall, C. D., Rosales, J. A., Zahawi, R. A., & Holl, K. D. (2014). Landscape context mediates avian habitat choice in tropical forest restoration. *PLoS ONE*, *9*(3). https://doi.org/10.1371/journal.pone.0090573

Rojas-Botero, S., Solorza-Bejarano, J., Kollmann, J., & Teixeira, L. H. (2020). Nucleation increases understory species and functional diversity in early tropical forest restoration. *Ecological Engineering*, *158*(August), 106031. https://doi.org/10.1016/j.ecoleng.2020.106031

Rozendaal, D. M. A., Bongers, F., Aide, T. M., Alvarez-dávila, E., Ascarrunz, N., Balvanera, P., Becknell, J. M., Bentos, T. V, Brancalion, P. H. S., Cabral, G. A. L., Calvo-rodriguez, S., Chave, J., César, R. G., Chazdon, R. L., Condit, R., Dallinga, J. S., Almeida-cortez, J. S. De, Jong, B. De, Oliveira, A. De, … Schwartz, N. B. (2019). Biodiversity recovery of Neotropical secondary forests. *Science Advances*, *5*(3). https://doi.org/10.1126/sciadv.aau3114

Sansevero, J. B. B., Chazdon, R. L., Crouzeilles, R., Monteiro, L., Iribarrem, A., Lindenmayer, D. B., Ferreira, M. S., Latawiec, A. E., & Strassburg, B. B. N. (2017). Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. *Science Advances*, *3*(11), e1701345. https://doi.org/10.1126/sciadv.1701345

Schlawin, J. R., & Zahawi, R. A. (2008). “Nucleating” succession in recovering neotropical wet forests: The legacy of remnant trees. *Journal of Vegetation Science*, *19*(4), 485–492. https://doi.org/10.3170/2008-8-18387

Schuur, E. A., & Matson, P. A. (2001). Net primary productivity and nutrient cycling across a mesic to wet precipitation gradient in Hawaiian montane forest. *Oecologia*, *128*(3), 431–442. https://doi.org/10.1007/s004420100671

Sesnie, S. E., Finegan, B., Gessler, P. E., Smith, A. M. S., Zayra, R. B., & Thessler,

S. (2010). The multispectral separability of Costa Rican rainforest types with support vector machines and Random Forest decision trees. *International Journal of Remote Sensing*, *31*(11), 2885–2909. https://doi.org/10.1080/01431160903140803

Shimamoto, C. Y., Padial, A. A., Da Rosa, C. M., & Marques, M. C. M. (2018). Restoration of ecosystem services in tropical forests: A global meta-analysis. *PLoS ONE*, *13*(12), 1–16. https://doi.org/10.1371/journal.pone.0208523

Shono, K., Davies, S. J., & Kheng, C. Y. (2006). Regeneration of native plant species in restored forests on degraded lands in Singapore. *Forest Ecology and Management*, *237*(1–3), 574–582. https://doi.org/10.1016/j.foreco.2006.10.003

Stephenson, N. L., & Van Mantgem, P. J. (2005). Forest turnover rates follow global and regional patterns of productivity. *Ecology Letters*, *8*(5), 524–531. https://doi.org/10.1111/j.1461-0248.2005.00746.x

Toledo-Aceves, T., Trujillo-Miranda, A. L., & López-Barrera, F. (2021). Tree regeneration in active and passive cloud forest restoration: Functional groups and timber species. *Forest Ecology and Management*, *489*(August 2020). https://doi.org/10.1016/j.foreco.2021.119050

Uriarte, M., Schwartz, N., Powers, J. S., Marín-Spiotta, E., Liao, W., & Werden, L. K. (2016). Impacts of climate variability on tree demography in second growth tropical forests: the importance of regional context for predicting successional trajectories. *Biotropica*, *48*(6), 780–797. https://doi.org/10.1111/btp.12380

Vellend, M. (2003). Habitat loss inhibits recovery of plant diversity as forests regrow. *Ecology*, *84*(5), 1158–1164. https://doi.org/10.1890/0012-9658(2003)084[1158:HLIROP]2.0.CO;2

Vieira, S., de Camargo, P. B., Selhorst, D., da Silva, R., Hutyra, L., Chambers, J. Q., Brown, I. F., Higuchi, N., dos Santos, J., Wofsy, S. C., Trumbore, S. E., & Martinelli, L. A. (2004). Forest structure and carbon dynamics in Amazonian tropical rain forests. *Oecologia*, *140*(3), 468–479. https://doi.org/10.1007/s00442-004-1598-z

W. S. Lee, E., Hau, B., & Corlett, R. (2005). Natural regeneration in exotic tree plantations in Hong Kong, China. *Forest Ecology and Management*, *212*, 358–366.

Wilson, S. J., & Rhemtulla, J. M. (2016). Acceleration and novelty: Community restoration speeds recovery and transforms species composition in Andean cloud forest. *Ecological Applications*, *26*(1), 203–218. https://doi.org/10.1890/14-2129.1/suppinfo

Wilson, S. J., & Rhemtulla, J. M. (2018). Small montane cloud forest fragments are important for conserving tree diversity in the Ecuadorian Andes. *Biotropica*, *50*(4), 586–597. https://doi.org/10.1111/btp.12542

# TABLES

*Table 1. Climatic, landscape and local conditions of the six forest restoration areas in North Western Ecuador considered in this study; MAT (mean annual temperature), TAP (total mean annual precipitation).*

| Location | Mean altitude (masl) | Plots | MAT | TAP | Precipitation driest quarter | Precipitation seasonality | % native forest cover | Contagion | Individual trees per plot | Species of trees per plot | Tree mean DBH per plot | Basal area trees per plot | Saplings per plot | Species of saplings per plot |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Suamox | 345.52 | 29 | 22.70 | 2584.42 | 207.31 | 63.04 | 17.26 | 35.07 | 17.33 | 7.93 | 13.16 | 0.23 | 31.47 | 11.07 |
| El Cristal | 1338.20 | 20 | 19.46 | 2388.21 | 325.75 | 32.74 | 21.62 | 29.95 | 3.55 | 1.75 | 8.61 | 0.02 | 34.75 | 8.50 |
| Mundo Nuevo | 1406.64 | 14 | 14.63 | 1684.45 | 199.91 | 33.16 | 7.04 | 64.86 | 2.07 | 0.64 | 7.67 | 0.01 | 23.07 | 1.93 |
| Piedras Negras | 1539.21 | 14 | 16.43 | 1954.95 | 188.14 | 48.80 | 61.12 | 52.57 | 11.35 | 4.82 | 15.18 | 0.24 | 25.71 | 7.76 |
| La Yumbada | 1878.64 | 14 | 17.21 | 1985.95 | 198.53 | 48.22 | 38.09 | 37.07 | 10.13 | 3.50 | 15.34 | 0.20 | 22.75 | 5.44 |
| Santa Rosa | 2182.00 | 32 | 15.94 | 1874.87 | 181.19 | 47.93 | 50.67 | 44.10 | 5.23 | 2.00 | 14.21 | 0.11 | 3.85 | 1.68 |
| Mean | 1448.37 | 20.50 | 17.73 | 2078.81 | 216.81 | 45.65 | 32.63 | 43.94 | 8.28 | 3.44 | 12.36 | 0.14 | 23.60 | 6.06 |
| SD | 626.38 | 8.14 | 2.92 | 338.36 | 54.16 | 11.37 | 20.88 | 12.91 | 5.74 | 2.64 | 3.37 | 0.10 | 10.79 | 3.76 |

# FIGURES

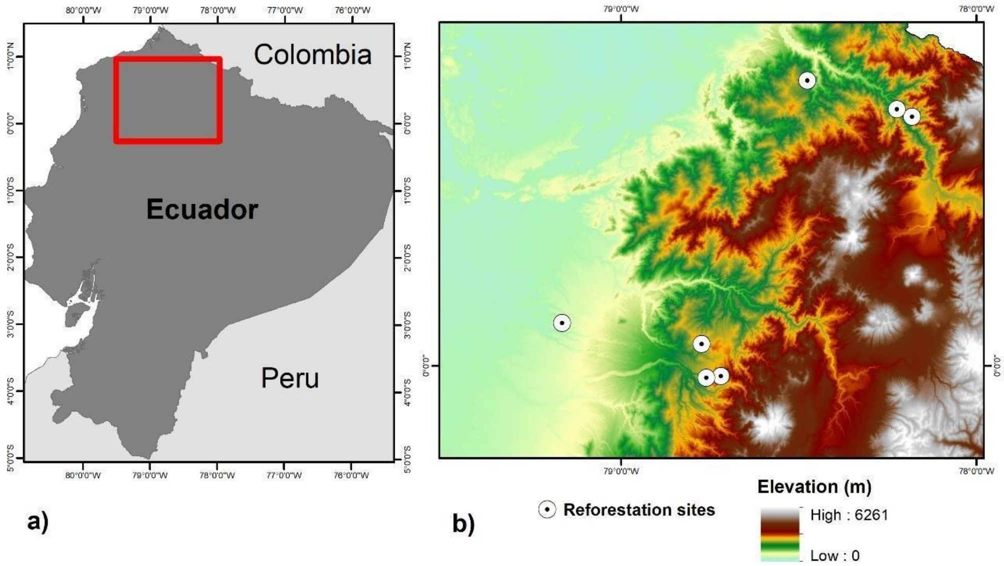


*Figure 1. Map of the study area in North-West Ecuador. White points are the locations of the study, placed in Pichincha and Imbabura. Darkest colors indicate higher elevations.*

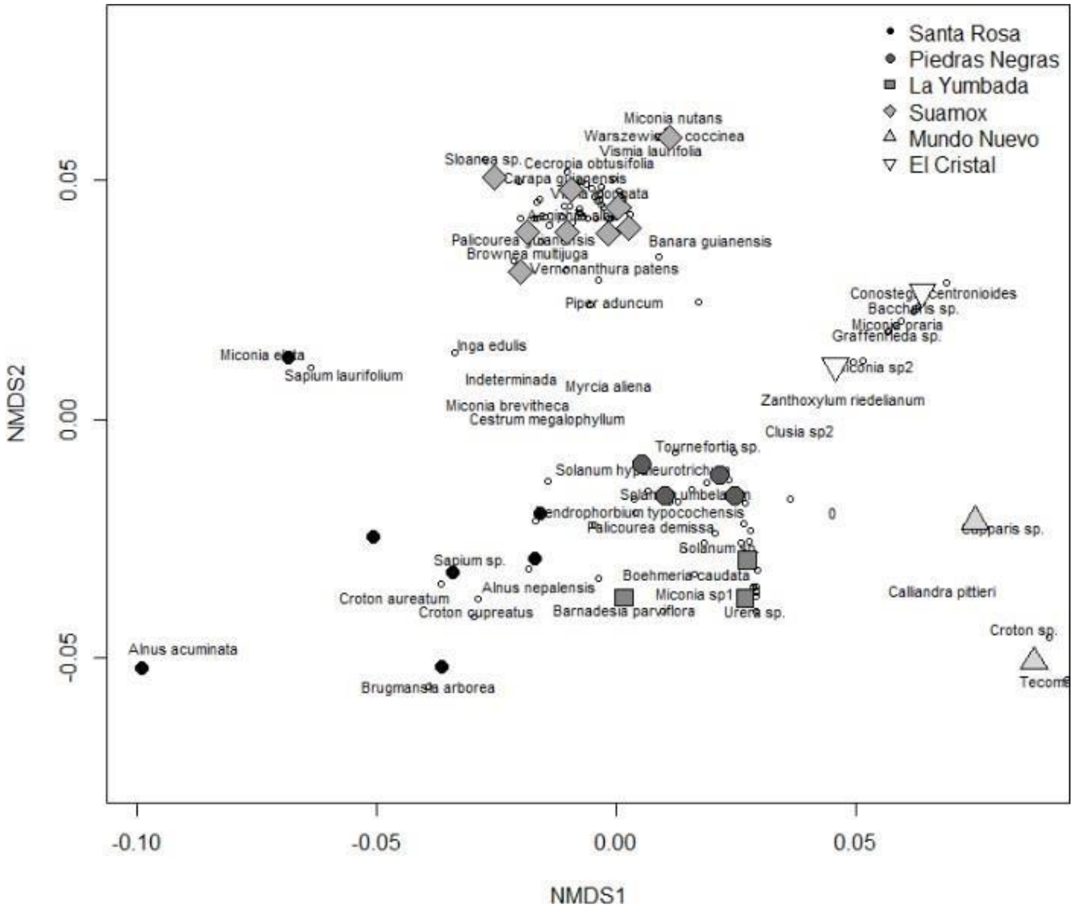


*Figure 2. NMDS representation of species communities along the six locations of the study. Each polygon represents a different terrain in the location, distance among polygons indicates the difference among the species community composition. Santa Rosa, Piedras Negras and La Yumbada show proximity since are the most similar locations, they are geographically close and have similar elevation in comparison with the rest of locations. Suamox, Mundo Nuevo and El Cristal are located in a different province, and present a specific ecosystem type.*

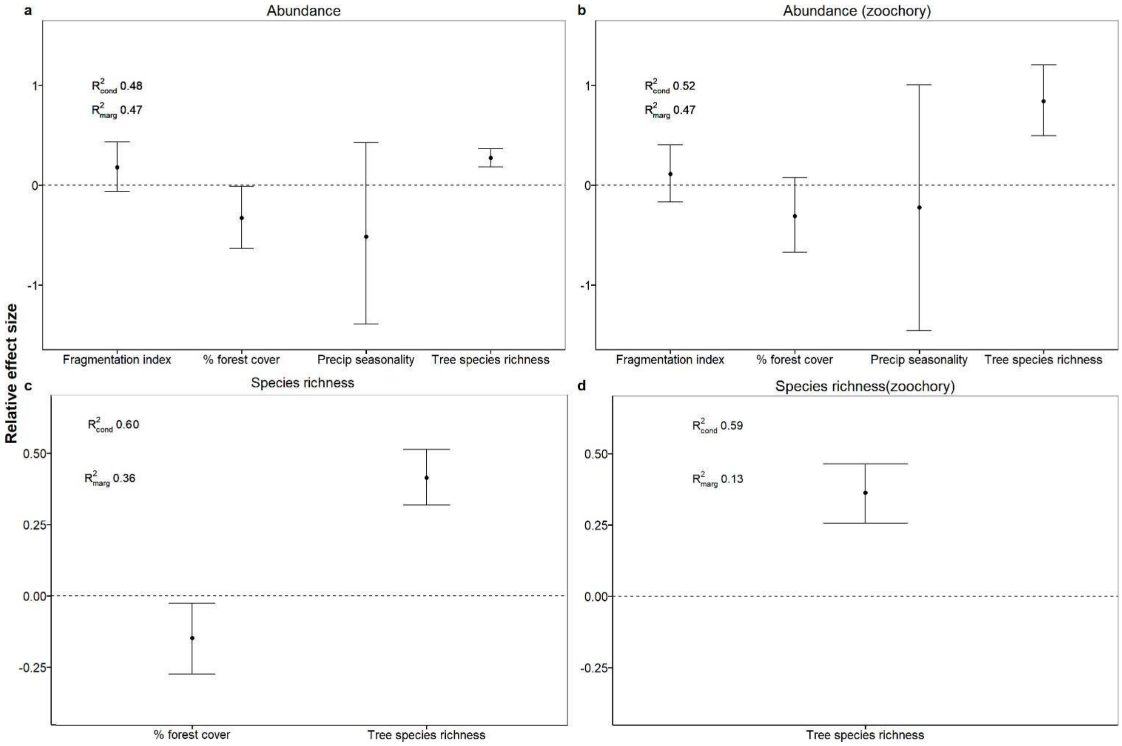


*Figure 3. Relative effect size of the predictors kept after the LASSO filtering for each response variable a) Abundance of natural regenerated trees, b) richness of natural regenerated trees, c) number of individuals of trees dispersed by zoochory on natural regenerated communities and d) number of species of trees dispersed by zoochory on natural regenerated communities. The error bars indicate the credible interval, when these bars cross the zero line, the predictor has no significative effect on the response variable. Full models available in Appendices 6 and 7.*

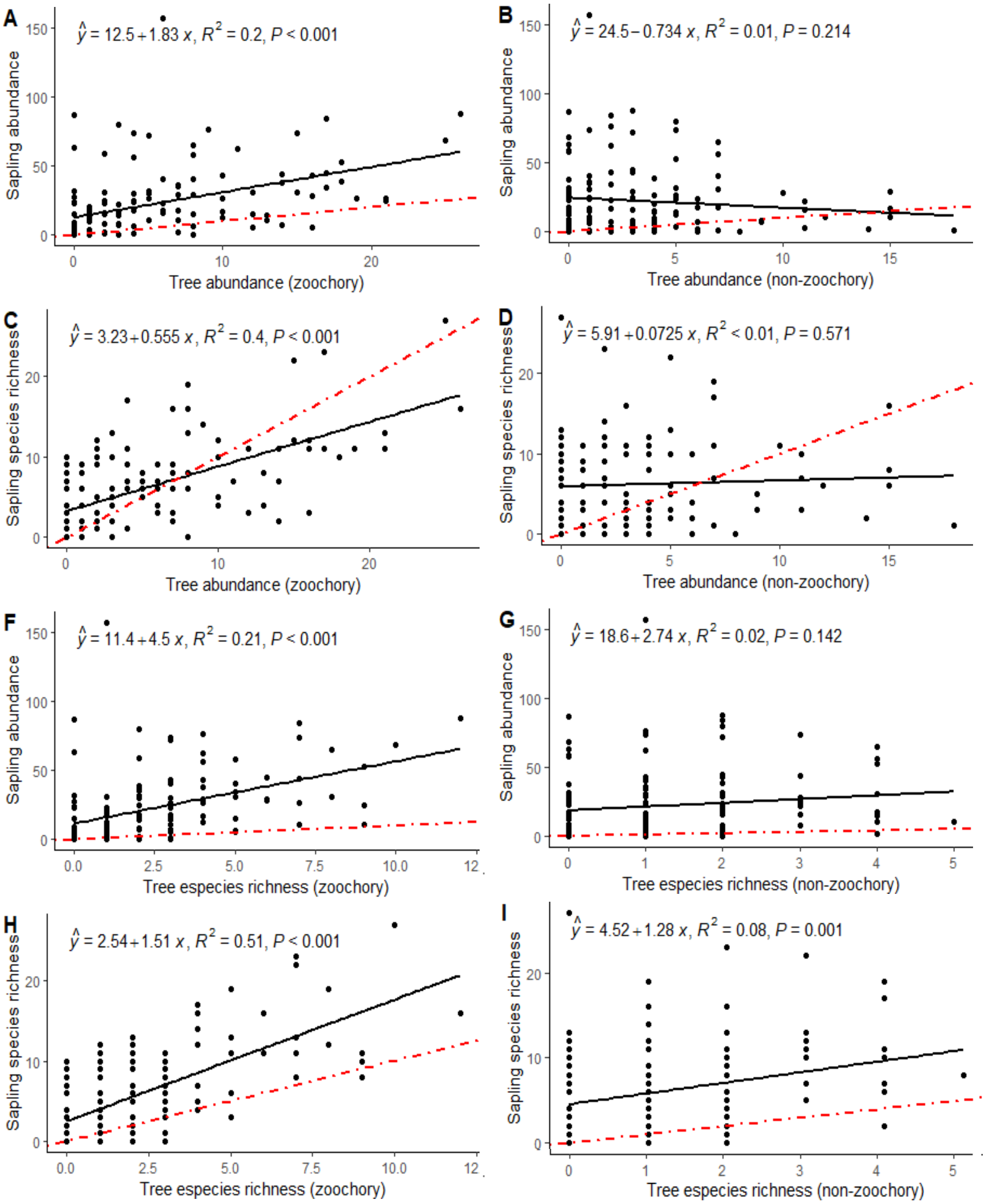


*Figure 4. Abundance and species richness of saplings as a function of the abundance and species richness of planted trees considering their dispersal syndrome. Data from 128 forest plots established in restored tropical montane forests. The dotted line indicates 1-1 relationship between x and y axis.*

# APPENDIX

Appendix 1. Dispersal syndrom of 203 species of trees and shrubs distributed in 128 plots in restoration areas in NW Ecuador.

| Genera/Species | Dispersal category | Ressource |
|---|---|---|
| *Acalypha sp.* | Zoochory | (Aguilar Cevallos, 2018; Estrada & Fleming, 2012; Sandor, 2012) |
| *Aegiphila alba* | Zoochory | (Gomez et al., 2013) |
| *Alchornea glandulosa* | Zoochory | (Aguilar Cevallos, 2018) |
| *Alchornea latifolia* | Zoochory | (Gomez et al., 2013) |
| *Alnus acuminata* | Other | (Gomez et al., 2013) |
| *Alnus nepalensis* | Other | (Sandor, 2012) |
| *Alnus sp.* | Other | (Gomez et al., 2013) |
| *Anacardium excelsum* | Zoochory | (Wilson & Rhemtulla, 2016) |
| *Annona cf muricata* | Zoochory | (Wilson & Rhemtulla, 2016) |
| *Annona mucosa* | Zoochory | (Wilson & Rhemtulla, 2016) |
| *Annona muricata* | Zoochory | (Beckman & Muller-Landau, 2011) |
| *Annona sp.* | Zoochory | (Gomez et al., 2013) |
| *Ardisia colombiana* | Zoochory | (Gomez et al., 2013) |
| *Baccharis brachylaenoides* | Other | (Sandor, 2012) |
| *Baccharis cf nitida* | Other | (Anderson et al., 2009) |
| *Baccharis latifolia* | Other | (Gomez et al., 2013) |
| *Baccharis trinervis* | Other | (Gomez et al., 2013) |
| *Bactris corossilla* | Zoochory | (Link & Stevenson, 2004) |
| *Banara guianensis* | Zoochory | (Gomez et al., 2013) |
| *Barnadesia parviflora* | Other | (Gomez et al., 2013) |
| *Beilschmiedia costaricensis* | Zoochory | (Gomez et al., 2013) |
| *Beilschmiedia sp.* | Zoochory | (Gomez et al., 2013) |
| *Bocconia fructescens* | Zoochory | (Gomez et al., 2013) |
| *Bocconia integrifolia* | Zoochory | (Gomez et al., 2013) |
| *Boehmeria caudata* | Zoochory | (Nepstad et al., 1996; Uhl et al., 1988) |
| *Brownea multijuga* | NA | |
| *Brunellia pauciflora* | NA | |
| *Calliandra pittieri* | NA | |
| *Capparis sp.* | Zoochory | (Gomez et al., 2013) |
| *Carapa guianensis* | Zoochory | (Gomez et al., 2013) |
| *Carapa megistocarpa* | Zoochory | (Gomez et al., 2013) |
| *Castilla elastica* | Zoochory | (Gomez et al., 2013) |

| | | |
|---|---|---|
| *Cecropia obtusifolia* | Zoochory | (Gomez et al., 2013) |
| *Cecropia sp.* | Zoochory | (Ledo et al., 2012) |
| *Cecropia sp1* | Zoochory | (Ledo et al., 2012) |
| *Cedrela* | Other | (Gomez et al., 2013) |
| *Cedrela nebulosa* | Other | (Das Chagas E Silva & Soares-Silva, 2000; Ledo et al., 2012) |
| *Cedrela odorata* | Other | (Gomez et al., 2013) |
| *Ceiba sp.* | Other | (Gomez et al., 2013) |
| *Cestrum megalophyllum* | Zoochory | (Gomez et al., 2013) |
| *Chrysophyllum cainito* | Zoochory | (Wilson & Rhemtulla, 2016) |
| *Chrysophyllum imperiale* | Zoochory | (Gomez et al., 2013) |
| *Citharexylum cf kunthianum* | Other | (Gomez et al., 2013) |
| *Citrus limonum* | Zoochory | (Aguilar Cevallos, 2018), Sarah |
| *Clarisia biflora* | Zoochory | (Gomez et al., 2013) |
| *Clarisia racemosa* | Zoochory | (Scotti-Saintagne et al., 2012) |
| *Clavija sp.* | Zoochory | (Gomez et al., 2013) |
| *Clibadium cf surinamense* | Other | (Aguilar Cevallos, 2018) |
| *Clusia sp.* | Zoochory | (Aguilar Cevallos, 2018) |
| *Clusia sp1* | Zoochory | (Aguilar Cevallos, 2018) |
| *Clusia sp2* | Zoochory | (Aguilar Cevallos, 2018) |
| *Clusia sp3* | Zoochory | (Aguilar Cevallos, 2018) |
| *Clusia sp4* | Zoochory | (Aguilar Cevallos, 2018) |
| *Clusia weberbaueri* | Zoochory | (Aguilar Cevallos, 2018) |
| *Cojoba arborea* | Zoochory | (Gomez et al., 2013) |
| *Conostegia centronioides* | Zoochory | (Aguilar Cevallos, 2018) |
| *Cordia alliodora* | Other | (Gomez et al., 2013) |
| *Critoniopsis occidentalis* | Other | (Gomez et al., 2013) |
| *Critoniopsis sp.* | Other | (Gomez et al., 2013; James et al., 1998; Lamb. A. F. A., 1968) |
| *Croton aureatum* | Other | (Wilson & Rhemtulla, 2016) |
| *Croton cupreatus* | Other | (Augspurger, 1984) |
| *Croton flocosus* | Other | (Adler, 1995; Parker et al., 2010; Van Der Pijl, 1957; Wilson & Rhemtulla, 2016) |
| *Croton sp.* | Other | (Adler, 1995; Parker et al., 2010; Van Der Pijl, 1957; Wilson & Rhemtulla, 2016) |
| *Croton sp1* | Other | (Adler, 1995; Parker et al., 2010; Van Der Pijl, 1957; Wilson & Rhemtulla, 2016) |
| *Croton sp2* | Other | (Adler, 1995; Parker et al., 2010; Van Der Pijl, 1957; Wilson & Rhemtulla, 2016) |
| *Cupania sp.* | Zoochory | (Gomez et al., 2013) |

| | | |
|---|---|---|
| *Cupania cinerea* | Zoochory | (Wilson & Rhemtulla, 2016) |
| *Delostoma integrifolium* | Other | (Sandor, 2012) |
| *Dendropanax macrophyllus* | Zoochory | (Aguilar Cevallos, 2018) |
| *Dendrophorbium typocochensis* | NA | |
| *Dussia lehmannii* | NA | |
| *Elaeagia sp.* | Other | (Gomez et al., 2013) |
| *Erythrina edulis* | Zoochory | (Gomez et al., 2013) |
| *Erythrina megistophylla* | Zoochory | (Gomez et al., 2013) |
| *Erythrina sp.* | Zoochory | (Gomez et al., 2013) |
| *Eschweilera* | Zoochory | (Aguilar Cevallos, 2018; Wilson & Rhemtulla, 2016) |
| *Eschweilera pittieri* | Zoochory | (Aguilar Cevallos, 2018; Wilson & Rhemtulla, 2016) |
| *Eschweilera sp1* | Zoochory | (Aguilar Cevallos, 2018; Wilson & Rhemtulla, 2016) |
| *Euphorbia lechera* | NA | |
| *Ficus americana* | Zoochory | (Aguilar Cevallos, 2018; Wilson & Rhemtulla, 2016) |
| *Ficus brevibracteata* | Zoochory | (Aguilar Cevallos, 2018; Wilson & Rhemtulla, 2016) |
| *Ficus cervantesiana* | Zoochory | (Aguilar Cevallos, 2018; Wilson & Rhemtulla, 2016) |
| *Ficus tonduzii* | Zoochory | (Aguilar Cevallos, 2018; Wilson & Rhemtulla, 2016) |
| *Freziera sp1* | Zoochory | (Aguilar Cevallos, 2018; Wilson & Rhemtulla, 2016) |
| *Garcinia madruno* | Zoochory | (Gomez et al., 2013) |
| *Geissanthus* | Zoochory | (Aguilar Cevallos, 2018; Wilson & Rhemtulla, 2016) |
| *Graffenrieda cucullata* | Other | (Gomez et al., 2013) |
| *Grias neuberthii* | Zoochory | (de la Peña-Domene et al., 2016) |
| *Guarea kunthiana* | Zoochory | (Gomez et al., 2013) |
| *Hedyosmum cuatrecazanum* | Zoochory | (Gomez et al., 2013) |
| *Heliconia sp.* | NA | |
| *Heliocarpus americanus* | Other | (Gomez et al., 2013) |
| *Hieronyma fendleri* | Zoochory | Sarah, (Gomez et al., 2013) |
| *Huberodendron patinoi* | Other | (Gomez et al., 2013) |
| *Indeterminada* | NA | |
| *Inga cf acuminata* | Zoochory | (Wilson & Rhemtulla, 2016) |
| *Inga cf alata/ cf striata* | Zoochory | (Wilson & Rhemtulla, 2016) |
| *Inga cf striata* | Zoochory | (Wilson & Rhemtulla, 2016) |
| *Inga edulis* | Zoochory | (Wilson & Rhemtulla, 2016) |

| | | |
|---|---|---|
| *Inga marginata* | Zoochory | (Wilson & Rhemtulla, 2016) |
| *Inga oerstediana* | Zoochory | (Wilson & Rhemtulla, 2016) |
| *Inga sp.* | Zoochory | (Gomez et al., 2013) |
| *Inga spectabilis* | Zoochory | (Gomez et al., 2013) |
| *Inga vera* | Zoochory | (Gomez et al., 2013) |
| *Iriartea deltoidea* | Zoochory | (Gomez et al., 2013) |
| *Juglans neotropica* | Zoochory | (Jara-Guerrero, 2014) |
| *Leucaena leucocephala* | NA | |
| *Licania duniflora* | Zoochory | (Kominami et al., 2003) |
| *Meriania maxima* | Other | (Gomez et al., 2013) |
| *Miconia aeruginosa* | Zoochory | (Gomez et al., 2013) |
| *Miconia brachycalix* | Zoochory | (Gomez et al., 2013) |
| *Miconia brevitheca* | Zoochory | (Buitrón-Jurado & Ramírez, 2014) |
| *Miconia centrodesma* | Zoochory | (Gomez et al., 2013) |
| *Miconia cf brachycalyx* | Zoochory | (Gomez et al., 2013) |
| *Miconia elata* | Zoochory | (Aguilar Cevallos, 2018) |
| *Miconia lasiocalyx* | Zoochory | (Gomez et al., 2013) |
| *Miconia nutans* | Zoochory | (Aguilar Cevallos, 2018) |
| *Miconia oraria* | Zoochory | (Gomez et al., 2013) |
| *Miconia reducens* | Zoochory | (Gomez et al., 2013) |
| *Miconia sp1* | Zoochory | (Gomez et al., 2013) |
| *Miconia sp2* | Zoochory | (Gomez et al., 2013) |
| *Miconia sp3* | Zoochory | (Gomez et al., 2013) |
| *Miconia theaezans* | Zoochory | (Aguilar Cevallos, 2018; Reys et al., 2009; Wilson & Rhemtulla, 2016) |
| *Miconia tomentosa* | Zoochory | (Gomez et al., 2013) |
| *Minquartia guianensis* | Zoochory | (Gomez et al., 2013) |
| *Monnina pseudopilosa* | NA | |
| *Myrcia aliena* | Zoochory | (Gomez et al., 2013) |
| *Myrcia fallax* | Zoochory | (Gomez et al., 2013) |
| *Myrcia sp.* | Zoochory | (Gomez et al., 2013) |
| *Myrsine coriacea* | Zoochory | (Sandor, 2012) |
| *NA* | NA | |
| *Nectandra acutifolia* | Zoochory | (Gomez et al., 2013) |
| *Nectandra subbullata* | Zoochory | (Gomez et al., 2013) |
| *Ochroma pyramidale* | Other | (Gomez et al., 2013) |
| *Ocotea cernua* | Zoochory | (Gomez et al., 2013) |
| *Ocotea insularis* | Zoochory | (Gomez et al., 2013) |

| | | |
|---|---|---|
| *Oreopanax sp.* | Zoochory | (Aguilar Cevallos, 2018; Wilson & Rhemtulla, 2016) |
| *Ossaea micrantha* | Zoochory | (Gomez et al., 2013) |
| *Pachira patinoi* | Zoochory | (Buitrón-Jurado & Ramírez, 2014) |
| *Palicourea cf chimbaracensis/cf acanthaceae* | Zoochory | (Gomez et al., 2013) |
| *Palicourea demissa* | Zoochory | (Gomez et al., 2013) |
| *Palicourea guianensis* | Zoochory | (Stimm et al., 2008) |
| *Persea pseudofasciculata* | Zoochory | (Gomez et al., 2013) |
| *Piper aduncum* | Zoochory | (Buitrón-Jurado & Ramírez, 2014; Gomez et al., 2013; Wilson & Rhemtulla, 2016) |
| *Piper sp.* | Zoochory | (Gomez et al., 2013) |
| *Piptocoma discolor* | Other | (Gomez et al., 2013) |
| *Pourouma bicolor* | Zoochory | (Aguilar Cevallos, 2018; Reys et al., 2009; Wilson & Rhemtulla, 2016) |
| *Pouteria* | Zoochory | (Gomez et al., 2013) |
| *Pouteria capacifolia* | Zoochory | (Aguilar Cevallos, 2018; Reys et al., 2009; Wilson & Rhemtulla, 2016) |
| *Protium sagotianum* | Zoochory | (Gomez et al., 2013) |
| *Pseudolmedia rigida* | NA | |
| *Psidium guajava* | Zoochory | (Gomez et al., 2013) |
| *Pterocarpus cf rohrii* | Other | (Wilson & Rhemtulla, 2016) |
| *Randia cf armata* | Zoochory | (Sandor, 2012) |
| *Randia sp.* | Zoochory | (Aguilar Cevallos, 2018; Reys et al., 2009; Wilson & Rhemtulla, 2016) |
| *Roupala cf montana* | Other | (Gomez et al., 2013) |
| *Sapium laurifolium* | Zoochory | (Aguilar Cevallos, 2018; Reys et al., 2009; Wilson & Rhemtulla, 2016) |
| *Sapium sp.* | Zoochory | (Gomez et al., 2013) |
| *Saurauia pseudostrigillosa* | Zoochory | (Gomez et al., 2013) |
| *Schefflera sp1* | Zoochory | (Sandor, 2012) |
| *Schefflera sp2* | Zoochory | (Sandor, 2012) |
| *Schefflera sphaerocoma* | Zoochory | (Stimm et al., 2008) |
| *Schizolobium parahibum* | Other | (Gomez et al., 2013) |
| *Simira cordifolia* | Zoochory | (Parrotta, 1999) |
| *Siparuna descipiens* | Zoochory | (Gomez et al., 2013) |
| *Siparuna piloso-lepidota* | Zoochory | (Gomez et al., 2013) |
| *Solanum aphyodendron* | Zoochory | (Gomez et al., 2013) |
| *Solanum barbulatum* | Zoochory | (Calderón-Sáenz & Mendoza-Cifuentes, 2000) |
| *Solanum cf pensile* | Zoochory | (Gomez et al., 2013) |
| *Solanum hypaleurotrichum* | Zoochory | (Gomez et al., 2013) |

| | | |
|---|---|---|
| *Solanum nudum* | Zoochory | (Gomez et al., 2013) |
| *Solanum sp.* | Zoochory | (Gomez et al., 2013) |
| *Solanum umbelatum* | Zoochory | (Gomez et al., 2013) |
| *Syzygium jambos* | Zoochory | (Sandor, 2012) |
| *Syzygium malaccense* | Zoochory | (Sandor, 2012) |
| *Tapirira guianensis* | Zoochory | (Gomez et al., 2013) |
| *Tecoma stans* | NA | |
| *Tetrorchidium macrophyllum* | Zoochory | (Gomez et al., 2013) |
| *Theobroma cacao* | Zoochory | (Gomez et al., 2013) |
| *Theobroma sp.* | Zoochory | (Gomez et al., 2013) |
| *Thevetia sp.* | NA | |
| *Tibouchina lepidota* | Other | (Wilson & Rhemtulla, 2016) |
| *Tournefortia sp.* | Zoochory | (Gomez et al., 2013) |
| *Trema micrantha* | Zoochory | (Sandor, 2012) |
| *Trichospermum galeottii* | Other | (Gomez et al., 2013) |
| *Urera sp.* | Zoochory | (Gomez et al., 2013) |
| *Verbesina cf arborea* | Other | (Wilson & Rhemtulla, 2016) |
| *Verbesina cf lloensis* | Other | (Wilson & Rhemtulla, 2016) |
| *Verbesina cf. lloensis* | Other | (Wilson & Rhemtulla, 2016) |
| *Vernonanthura patens* | Other | (Aguilar Cevallos, 2018) |
| *Virola calophylla* | Zoochory | (Gomez et al., 2013) |
| *Virola elongata* | Zoochory | (Gomez et al., 2013) |
| *Virola reidii* | Zoochory | (Sandor, 2012) |
| *Vismia baccifera* | Zoochory | (Aguilar Cevallos, 2018; Ledo et al., 2012) |
| *Vismia laurifolia* | Zoochory | (Aguilar Cevallos, 2018; Ledo et al., 2012) |
| *Vismia obtusa* | Zoochory | (Aguilar Cevallos, 2018; Ledo et al., 2012) |
| *Vismia sp.* | Zoochory | (Aguilar Cevallos, 2018; Ledo et al., 2012) |
| *Vismia tomentosa* | Zoochory | (Gomez et al., 2013) |
| *Warszewiczia coccinea* | Other | (Gomez et al., 2013) |
| *Weinmannia balbisiana* | Other | (Buitrón-Jurado & Ramírez, 2014) |
| *Wettinia quinaria* | Zoochory | (Gomez et al., 2013) |
| *Zanthoxylum formicerum* | Zoochory | (Gomez et al., 2013) |
| *Zanthoxylum riedelianum* | Zoochory | (Gomez et al., 2013) |
| *Zapoteca sp.* | Other | (Aguilar Cevallos, 2018; Ledo et al., 2012; Wilson & Rhemtulla, 2016) |

Adler, G. H. (1995). Studies on Neotropical Fauna and Environment Tail Autotomy in the Central American Spiny Rat , Proechimys semispinosus Tail Autotomy in the Central American Spiny Rat , Proechimys semispinosus. *Studies on Neotropical Fauna and Environment, 30*(4), 237–244. https://doi.org/https://doi.org/10.1080/01650529509360962

Aguilar Cevallos, Y. (2018). *Síndromes de dispersión de especies leñosas nativas del Centro Científico Río Palenque, Provincia de Los Ríos, Ecuador*. Universidad de Guayaquil.

Anderson, J. T., Rojas, S. J., & Flecker, A. S. (2009). High-quality seed dispersal by fruit-eating fishes in Amazonian floodplain habitats. *Oecologia*, *161*(2), 279–290. https://doi.org/10.1007/s00442-009-1371-4

Augspurger, C. K. (1984). Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology*, *65*(6), 1705–1712. https://doi.org/10.2307/1937766

Beckman, N. G., & Muller-Landau, H. C. (2011). Linking fruit traits to variation in predispersal vertebrate seed predation, insect seed predation, and pathogen attack. *Ecology*, *92*(11), 2131–2140.

Buitrón-Jurado, G., & Ramírez, N. (2014). Dispersal spectra, diaspore size and the importance of endozoochory in the equatorial Andean montane forests. *Flora*, *209*(7), 299–311. https://doi.org/10.1016/j.flora.2014.03.009

Calderón-Sáenz, E., & Mendoza-Cifuentes, H. (2000). Melastomatáceas de los Géneros Axinaea, Blakea, Castratella, Centronia, Killipia, Meriania, Monochaetum, Ossaea y Tibouchina en Colombia. *Biota Colombiana*, *1*(3), 336–357. https://doi.org/0124-5376

da Silva Possette, R. F., Bos Mikich, S., Guenther Hatschbach, G., dos Santos Ribas, O., & Liebsch, D. (2015). Floristic composition and dispersal syndromes in Araucaria Forest remnants in the municipality of Colombo, Paraná state, Brazil. *Check List*, *11*(5), 1771. https://doi.org/10.15560/11.5.1771

Das Chagas E Silva, F., & Soares-Silva, L. H. (2000). Arboreal flora of the Godoy Forest State Park, Londrina, PR. Brazil. *Edinburgh Journal of Botany*, *57*(1), 107–120. https://doi.org/https://doi.org/10.1017/S096042860000007X

de la Peña-Domene, M., Howe, H. F., Cruz-León, E., Jiménez-Rolland, R., Lozano-Huerta, C., & Martínez-Garza, C. (2016). Seed to seedling transitions in successional habitats across a tropical landscape. *Oikos*, *126*(3), 410–419. https://doi.org/10.5061/dryad.4846b

Estrada, A., & Fleming, T. H. (2012). Frugivores and seed dispersal (Springer Science & Business Media (ed.); ilustrada). https://books.google.com.ec/books?id=-rz0CAAAQBAJ&dq=method+of+seed+dispersal+acalypha&hl=es&source=gbs_navlinks_s

Gomez, D. F. C., Stevenson, P. R., Álvarez, E., Aldana, A. M., Umaña, M., Cano, Á., Adarve, J., Benítez, D., Castaño, A., Cogollo, Á., Devia, W., Fernández, F., García, L. M., Melo, O., Peñuela, M. C., Restrepo, Z., Serna, M., Velásquez, O., Velázquez, C., & von Hildebrand, P. (2013). Patrones de frecuencia y abundancia de sistemas de dispersión de plantas en bosques colombianos y su relación con las regiones geográficas del país. *Colombia Forestal*, *16*(1), 33–51. https://doi.org/10.14483/udistrital.jour.colomb.for.2013.1.a03

James, T., Vege, S., Aldrich, P., & Hamrick, J. L. (1998). Mating systems of three tropical dry forest tree species. *Biotropica*, *30*(4), 587–594. https://doi.org/10.1111/j.1744-7429.1998.tb00098.x

Jara-Guerrero, A. (2014). *Ecología de la dispersión de plantas en los bosques secos del suroccidente Ecuatoriano.* Universidad Politécnica de Madrid.

Kominami, Y., Sato, T., Takeshita, K., Manabe, T., Endo, A., & Noma, N. (2003). Classification of bird-dispersed plants by fruiting phenology, fruit size, and growth form in a primary lucidophyllous forest: An analysis, with implications for the conservation of fruit-bird interactions. *Ornithological Science*, *2*(1), 3–23. https://doi.org/10.2326/osj.2.3

Lamb. A. F. A. (1968). *Fast Growing Timber trees of the Lowland Tropics. Cedrela Odorata* (U. of Oxford (ed.)).

Ledo, A., Montes, F., & Condés, S. (2012). Different spatial organisation strategies of woody plant species in a montane cloud forest. *Acta Oecologica*, *38*, 49–57. https://doi.org/10.1016/j.actao.2011.09.003

Leung, G. P. C., Hau, B. C. H., & Corlett, R. T. (2009). Exotic plant invasion in the highly degraded upland landscape of Hong Kong, China. *Biodiversity and Conservation, 18*(1), 191–202. https://doi.org/10.1007/s10531-008-9466-5

Link, A., & Stevenson, P. R. (2004). Fruit dispersal syndromes in animal disseminated plants at Tinigua National Park, Colombia. *Revista Chilena de Historia Natural, 77*(2), 319–334. https://doi.org/10.4067/S0716-078X2004000200010

Nakamoto, A., Kinjo, K., & Izawa, M. (2009). The role of Orii's flying-fox (Pteropus dasymallus inopinatus) as a pollinator and a seed disperser on Okinawa-jima Island, the Ryukyu Archipelago, Japan. *Ecological Research, 24*(2), 405–414. https://doi.org/10.1007/s11284-008-0516-y

Nepstad, D. C., Uhl, C., Pereira, C. A., da Silva, J. M. C., & da Silva, J. M. C. (1996). A Comparative Study of Tree Establishment in Abandoned Pasture and Mature Forest of Eastern Amazonia. *Oikos, 76*(1), 25–39. https://doi.org/10.2307/3545745

Parker, I. M., López, I., Petersen, J. J., Anaya, N., Cubilla-Ríos, L., & Potter, D. (2010). Domestication Syndrome in Caimito (Chrysophyllum cainito L.): Fruit and Seed Characteristics. *Economic Botany, 64*(2), 161–175.

Parrotta, J. A. (1999). Productivity, nutrient cycling, and succession in single- and mixed-species plantations of Casuarina equisetifolia, Eucalyptus robusta, and Leucaena leucocephala in Puerto Rico. *Forest Ecology and Management, 124*(1), 45–77. https://doi.org/10.1016/S0378-1127(99)00049-3

Renner, S. S., & Won, H. (2001). Repeated evolution of dioecy from monoecy in siparunaceae (Laurales). *Systematic Biology, 50*(5), 700–712. https://doi.org/10.1080/106351501753328820

Reys, P., Sabino, J., & Galetti, M. (2009). Frugivory by the fish Brycon hilarii (Characidae) in western Brazil. *Acta Oecológica, 35*(1), 136–141. https://doi.org/10.1016/j.actao.2008.09.007

Russo, S. E. (2003). Responses of dispersal agents to tree and fruit traits in Virola calophylla (Myristicaceae): Implications for selection. *Oecología, 136*(1), 80–87. https://doi.org/10.1007/s00442-003-1239-y

Sandor, M. (2012). Forest Regeneration on the Osa Peninsula, Costa Rica. University of Connecticut.

Scotti-Saintagne, C., Dick, C. W., Caron, H., Vendramin, G. G., Guichoux, E., Buonamici, A., Duret, C., Sire, P., Valencia, R., Lemes, M. R., Gribel, R., & Scotti, I. (2012). Phylogeography of a species complex of lowland Neotropical rain forest trees (Carapa, Meliaceae). *Journal of Biogeography, 40*(4), 676–692. https://doi.org/10.1111/j.1365-2699.2011.02678.x

Soares Bufalo, F., Galetti, M., & Culot, L. (2016). Seed Dispersal by Primates and Implications for the Conservation of a Biodiversity Hotspot, the Atlantic Forest of South America. *International Journal of Primatology, 37*(3), 333–349. https://doi.org/10.1007/s10764-016-9903-3

Stimm, B., Beck, E., Günter, S., Aguirre, N., Cueva, E., Mosandl, R., & Weber, M. (2008). Reforestation of Abandoned Pastures: Seed Ecology of Native Species and Production of Indigenous Plant Material. In E. Beck, J. Bendix, I. Kottke, F. Makeschin, & R. Mosandl (Eds.), *Gradients in a Tropical Mountain Ecosystem of Ecuador. Ecological Studies (Analysis and Synthesis)* (pp. 417–429). Springer, Berlin, Heidelberg. https://doi.org/https://doi.org/10.1007/978-3-540-73526-7_40

Uhl, C., Buschbacher, R., & Serrao, E. A. S. (1988). Abandoned Pastures in Eastern Amazonia. I. Patterns of Plant Succession. *The Journal of Ecology, 76*, 663–681. https://doi.org/10.2307/2260566

Van Der Pijl, L. (1957). The dispersal of plants by bats (Chiropterochory). *Acta Botánica Neerlándica, 6*, 291–315.

Whistler, W. A., & Elevitch, C. R. (2006). Syzygium malaccense ( Malay apple ), ver. 2.1. *Species Profiles for Pacific Island Agroforestry. Permanent Agriculture Resources (PAR)*, 1–13.

Wilson, S. J., & Rhemtulla, J. M. (2016). Acceleration and novelty: Community restoration speeds recovery and transforms species composition in Andean cloud forest. Ecological Applications, 26(1), 203–218. https://doi.org/10.1890/14-2129.1/suppinfo

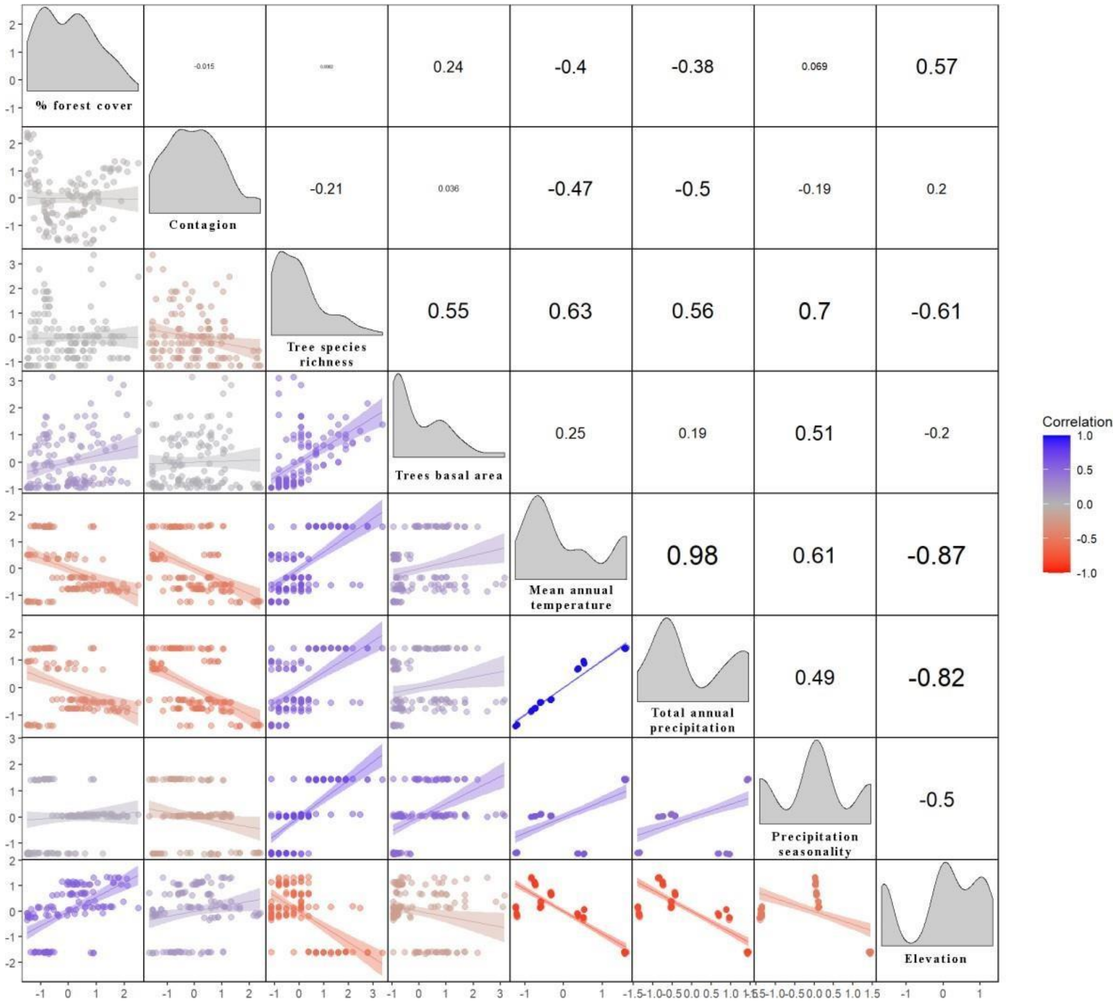
Appendix 2. Variables used for the Random Forest classification of Sentinel II images.

| Variable | Description / Formula |
|---|---|
| Sentinel-2 bands | |
| Blue | B2 (490 nm) |
| Green | B3 (560 nm) |
| Red | B4 (665 nm) |
| NIR | B8 (842 nm) |
| SWIR1 | B11 (1610 nm) |
| SWIR2 | B12 (2190 nm) |
| Simple ratios | |
| NIR / Red | NIR / Red |
| SWIR 1 / Red | SWIR1 / Red |
| SWIR 1 / NIR | SWIR1 / NIR |
| SWIR 1 / SWIR 2 | SWIR1 / SWIR2 |
| Vegetation indices | |
| NDVI | (NIR-Red) / (NIR+Red) |
| SAVI[a] | ((NIR-Red) / (NIR+Red+L))(1+L) |
| Image transformations | |
| VIS123 | Blue + Green + Red |
| MID57 | SWIR1 + SWIR2 |
| TCT 1[b] | $K_1$xBlue + $K_2$xGreen + $K_3$xRed + $K_4$xNIR + $K_5$xSWIR1 + $K_6$xSWIR2 |
| TCT 2[c] | $K_7$xBlue + $K_8$xGreen + $K_9$xRed + $K_{10}$xNIR + $K_{11}$xSWIR1 +$K_{12}$xSWIR2 |
| TCT 3[d] | $K_{13}$xBlue+$K_{14}$xGreen+$K_{15}$xRed+$K_{16}$xNIR+$K_{17}$xSWIR1+$K_{18}$xSWIR2 |

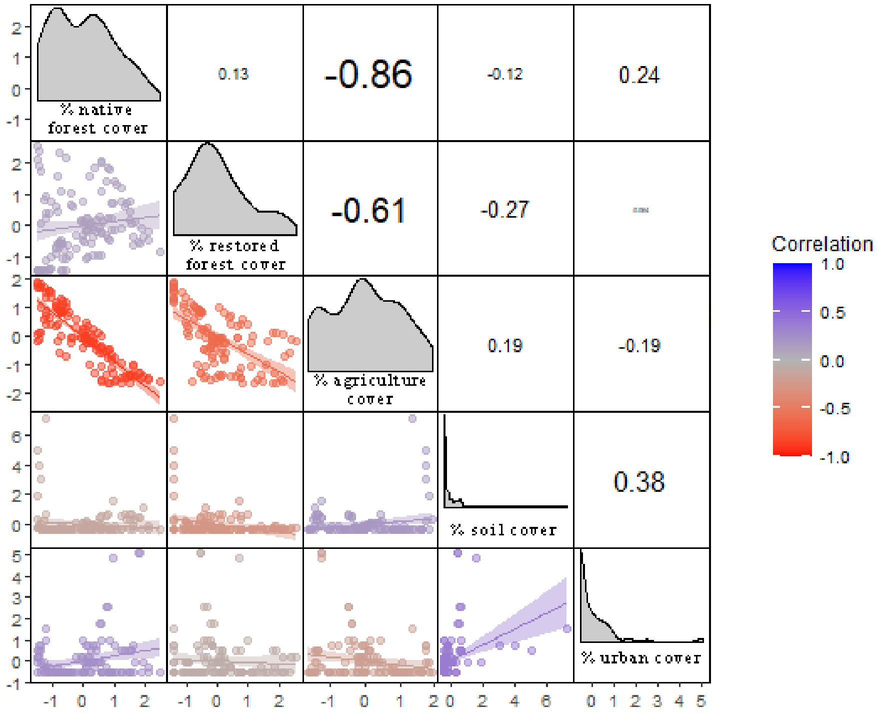
Appendix 3. Land-cover type proportions and landscape configuration metrics in the buffers (200m) around the 128 plots in North Western Ecuador locations. Landscape configuration metrics: Contagion (landscape heterogeneity), PLADJ (landscape continuity), Core (percentage of internal forest), Shape index (edge proportion) and Number of independent patches in the buffer area.

| Location | % native forest cover | % restored forest cover | % agriculture cover | % exposed soil cover | % urban cover | % water cover | Contagion | PLADJ | Core | Shape index | Number of patches |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Suamox | 17.26 | 16.32 | 66.5 | 0.01 | 0.02 | 0 | 35.07 | 82.84 | 0.11 | 4.98 | 15.43 |
| El Cristal | 21.62 | 39.08 | 39.12 | 0.08 | 0.12 | 0 | 29.95 | 81.15 | 0.27 | 4.81 | 9.85 |
| Mundo Nuevo | 7.04 | 0.03 | 91.05 | 1.51 | 0.19 | 0.19 | 64.86 | 95.88 | 0.03 | 1.99 | 3.57 |
| Piedras Negras | 61.12 | 35.32 | 5.14 | 0.41 | 0.24 | 0.14 | 52.57 | 89.96 | 0.73 | 1.92 | 1.94 |
| La Yumbada | 38.09 | 13.28 | 48.62 | 0.12 | 0.19 | 0 | 37.07 | 82.14 | 0.21 | 4.67 | 10.75 |
| Santa Rosa | 50.67 | 18.73 | 30.36 | 0.3 | 0.49 | 0.04 | 44.10 | 82.68 | 0.38 | 4.07 | 7.71 |
| Mean | 32.63 | 20.46 | 46.80 | 0.41 | 0.21 | 0.06 | 43.94 | 85.78 | 0.29 | 3.74 | 8.21 |
| SD | 20.88 | 14.54 | 29.71 | 0.56 | 0.16 | 0.08 | 12.91 | 5.87 | 0.25 | 1.42 | 4.95 |

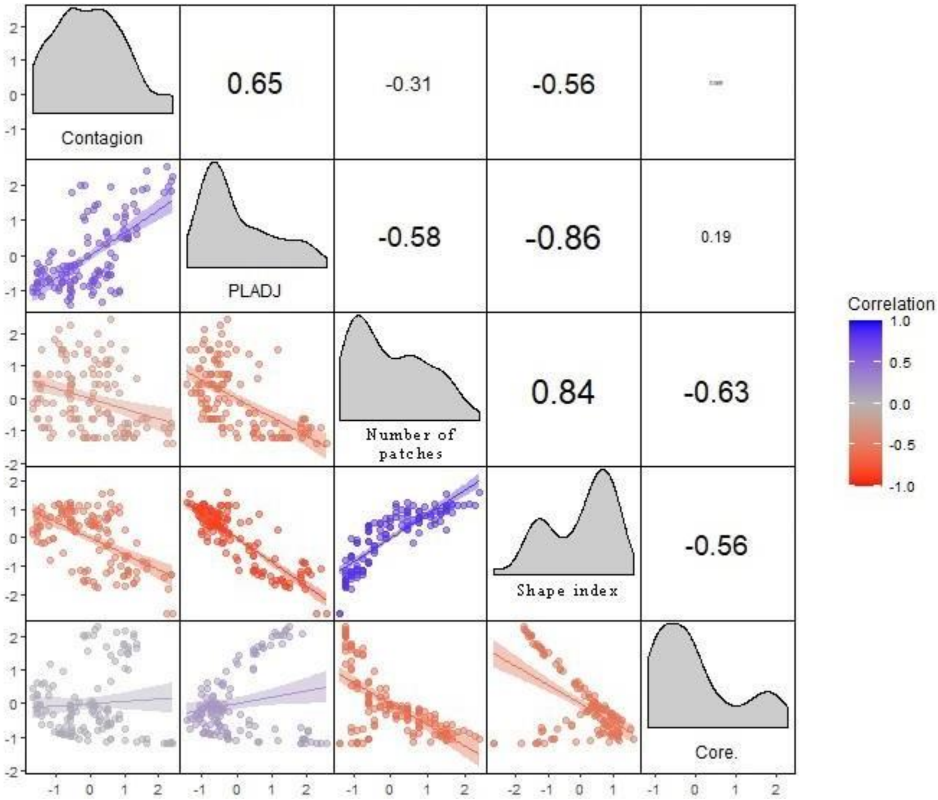
Appendix 4a. Correlation table for predictor variables. Strength of correlations are represented with bigger sized numbers in the upper plot and more intense color in the lower plot, being blue positive correlations and red negative ones. The lower triangle panel shows the linear trend of the data.



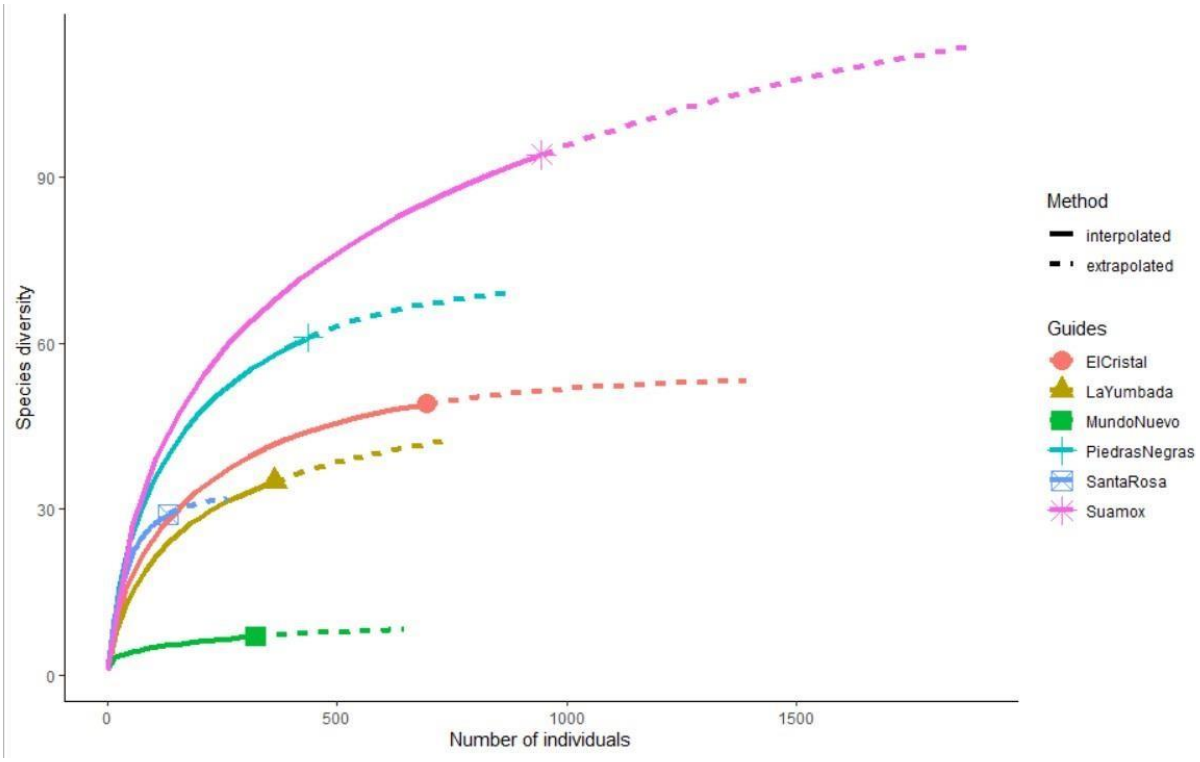
Appendix 4b. Correlation table for landscape cover predictor variables. Strength of correlations are represented with bigger sized numbers in the upper plot and more intense color in the lower plot, being blue positive correlations and red negative ones. The lower triangle panel shows the linear trend of the data.



Appendix 4c. Correlation table for landscape fragmentation predictor variables. Strength of correlations are represented with bigger sized numbers in the upper plot and more intense color in the lower plot, being blue positive correlations and red negative ones. The lower triangle panel shows the linear trend of the data.



Appendix 5. Species accumulation curves on rarefacted saplings species diversity in six forest restoration areas in North-Western Ecuador.



Appendix 6. Full and regularized models for total abundance of saplings, and abundance of saplings dispersed by zoochory. Full models include all predictors whereas regularized models include only the variables with estimates that were not set to zero by the LASSO regression.

| **Full model Sapling abundance (all species)** | **Estimates** | **Est.Error** | **l-95% CI** | **u-95% CI** | **Rhat** | **Bulk_ESS** | **Tail_ESS** |
|---|---|---|---|---|---|---|---|
| **Intercept** | 2.90 | 0.40 | 2.11 | 3.72 | 1 | 1817 | 2352 |
| **Trees basal area** | -0.06 | 0.10 | -0.28 | 0.13 | 1 | 3368 | 3946 |
| **Trees species richness** | 0.83 | 0.17 | 0.50 | 1.17 | 1 | 3802 | 3390 |
| **Elevation** | -0.08 | 0.29 | -0.75 | 0.47 | 1 | 3020 | 3144 |
| **Precipitacion seasonality** | -0.28 | 0.36 | -1.06 | 0.28 | 1 | 1901 | 2649 |
| **% forest cover** | -0.22 | 0.17 | -0.56 | 0.05 | 1 | 3047 | 2881 |
| **Fragmentation index** | 0.15 | 0.13 | -0.06 | 0.40 | 1 | 2942 | 3509 |

| **Regularized model Sapling abundance (all species)** | **Estimates** | **Est.Error** | **l-95% CI** | **u-95% CI** | **Rhat** | **Bulk_ESS** | **Tail_ESS** |
|---|---|---|---|---|---|---|---|
| **Intercept** | 2.97 | 0.47 | 2.00 | 3.93 | 1.01 | 826 | 967 |
| **Trees species richness** | 0.91 | 0.16 | 0.60 | 1.24 | 1 | 4225 | 2985 |
| **Fragmentation index** | 0.19 | 0.14 | -0.08 | 0.45 | 1 | 4079 | 3025 |
| **% forest cover** | -0.34 | 0.16 | -0.65 | -0.03 | 1 | 3176 | 2621 |
| **Precipitation seasonality** | -0.53 | 0.46 | -1.39 | 0.44 | 1 | 1906 | 1764 |

**R2c=0.484, R2m=0.472**

| **Full model Sapling abundance (zoochory)** | **Estimates** | **Est.Error** | **l-95% CI** | **u-95% CI** | **Rhat** | **Bulk_ESS** | **Tail_ESS** |
|---|---|---|---|---|---|---|---|
| **Intercept** | 2.39 | 0.53 | 1.31 | 3.45 | 1 | 1595 | 1804 |
| **Trees basal area** | -0.01 | 0.10 | -0.22 | 0.20 | 1 | 3911 | 4046 |
| **Trees species richness** | 0.73 | 0.19 | 0.34 | 1.09 | 1 | 3595 | 2946 |
| **Elevation** | -0.12 | 0.33 | -0.93 | 0.46 | 1 | 2670 | 3008 |
| **Precipitation seasonality** | -0.07 | 0.31 | -0.81 | 0.54 | 1 | 2499 | 2303 |
| **% forest cover** | -0.17 | 0.17 | -0.53 | 0.09 | 1 | 3260 | 3726 |
| **Fragmentation index** | 0.08 | 0.12 | -0.11 | 0.35 | 1 | 3229 | 3648 |

| Regularized model Sapling abundance (zoochory) | Estimates | Est.Error | l-95% CI | u-95% CI | Rhat | Bulk_ESS | Tail_ESS |
|---|---|---|---|---|---|---|---|
| **Intercept** | 2.42 | 0.48 | 1.42 | 3.35 | 1 | 1044 | 1499 |
| **Trees species richness** | 0.84 | 0.18 | 0.49 | 1.2 | 1 | 3514 | 2620 |
| **Fragmentation index** | 0.12 | 0.15 | -0.17 | 0.42 | 1 | 3615 | 2986 |
| **% forest cover** | -0.32 | 0.19 | -0.7 | 0.05 | 1 | 3055 | 2554 |
| **Precipitation seasonality** | -0.24 | 0.64 | -1.51 | 1.08 | 1 | 1587 | 1794 |

**R2c=0.516, R2m=0.474**

Appendix 7. Full and regularized models for total species richness of saplings, and species richness of saplings dispersed by zoochory. Full models include all predictors whereas regularized models include only the variables with estimates that were not set to zero by the LASSO regression.

| **Full model Sapling species richness** | **Estimates** | **Est.Error** | **l-95% CI** | **u-95% CI** | **Rhat** | **Bulk_ESS** | **Tail_ESS** |
|---|---|---|---|---|---|---|---|
| **Intercept** | 1.63 | 0.34 | 0.95 | 2.32 | 1 | 1394 | 1870 |
| **Trees basal area** | 0 | 0.04 | -0.09 | 0.08 | 1 | 4435 | 3916 |
| **Trees species richness** | 0.39 | 0.05 | 0.29 | 0.5 | 1 | 3632 | 3637 |
| **Elevation** | 0.04 | 0.19 | -0.28 | 0.53 | 1 | 2778 | 2876 |
| **bio15** | 0.06 | 0.22 | -0.28 | 0.59 | 1 | 2327 | 2137 |
| **Forest cover** | -0.14 | 0.08 | -0.29 | 0 | 1 | 2284 | 1523 |
| **Contagion** | -0.06 | 0.05 | -0.17 | 0.02 | 1 | 2636 | 3062 |

| **Regularized model Sapling species richness** | **Estimates** | **Est.Error** | **l-95% CI** | **u-95% CI** | **Rhat** | **Bulk_ESS** | **Tail_ESS** |
|---|---|---|---|---|---|---|---|
| **Intercept** | 1.60 | 0.32 | 0.95 | 2.27 | 1 | 1110 | 1325 |
| **Trees species richness** | 0.41 | 0.05 | 0.32 | 0.51 | 1 | 2391 | 2678 |
| **Forest cover** | -0.15 | 0.06 | -0.27 | -0.02 | 1 | 2126 | 2154 |

**$R^2c=0.596$; $R^2m=0.357$**

| **Full model Sapling species richness (zoochory)** | **Estimates** | **Est.Error** | **l-95% CI** | **u-95% CI** | **Rhat** | **Bulk_ESS** | **Tail_ESS** |
|---|---|---|---|---|---|---|---|
| **Intercept** | 1.14 | 0.47 | 0.18 | 2.11 | 1 | 1338 | 1820 |
| **Trees basal area** | 0.01 | 0.04 | -0.07 | 0.11 | 1 | 4553 | 3862 |
| **Trees species richness** | 0.36 | 0.06 | 0.24 | 0.48 | 1 | 3794 | 3852 |
| **Elevation** | 0 | 0.19 | -0.39 | 0.48 | 1 | 2618 | 2870 |
| **bio15** | 0.07 | 0.24 | -0.28 | 0.68 | 1 | 2332 | 2145 |
| **Forest cover** | -0.06 | 0.07 | -0.22 | 0.04 | 1 | 3141 | 3876 |
| **Contagion** | -0.02 | 0.05 | -0.12 | 0.06 | 1 | 4382 | 4007 |

| Regularized model Sapling species richness (zoochory) | Estimates | Est.Error | l-95% CI | u-95% CI | Rhat | Bulk_ESS | Tail_ESS |
|---|---|---|---|---|---|---|---|
| **Intercept** | 1.11 | 0.49 | 0.10 | 2.00 | 1 | 1063 | 1135 |
| **Trees species richness** | 0.37 | 0.05 | 0.26 | 0.46 | 1 | 1728 | 1992 |

**$R^2c=0.586$, $R^2m=0.133$**