UNIVERSIDAD DE INVESTIGACIÓN DE TECNOLOGÍA EXPERIMENTAL YACHAY

Escuela de Ciencias Biológicas e Ingeniería

TÍTULO: Relaciones espaciales entre lianas y árboles en el Parque Nacional Yasuní

TITLE: Spatial relations between lianas and trees in Yasuni National Park

Trabajo de integración curricular presentado como requisito para la obtención del título de Biólogo

Autor / Author:
Franz Alexander Chandi Villarroel

Tutor / Advisor:
Hugo Romero-Saltos, Ph.D.

Urcuquí, junio de 2022

Urcuquí, 13 de mayo de 2022

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CARRERA DE BIOLOGÍA
ACTA DE DEFENSA No. UITEY-BIO-2022-00016-AD

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AGRADECIMIENTOS

Mi más grande y sincero agradecimiento va dedicado a mis padres, Manuel y Ricardina, por darme la mejor educación de valores en casa que cualquier hijo podría pedir. Su amor y cariño constante disolvió el estrés generado durante mi educación en la Universidad Yachay Tech y el desarrollo de la presente investigación científica. Recordaré a mis compañeros de clase por haber hecho de mi estancia en la universidad una época inolvidable de mi vida, así como a los profesores de Yachay Tech por brindarme una educación personalizada y servir como ejemplo para mi desarrollo como persona e investigador científico.

Agradezco al Dr. Hugo Romero, mi tutor, por su guía en el desarrollo de la presente investigación científica y por darme la oportunidad de analizar sus datos de lianas, colectados en 2008, en una parcela rectangular de 20 m × 500 m en la parcela de 50 hectáreas (ha) del proyecto "Dinámica del Bosque de Yasuní" (PDBY). El PDBY es dirigido por el Dr. Renato Valencia, profesor de la PUCE, a quien también agradezco por compartir los datos de los diferentes censos de árboles en el PDBY, que iniciaron en 1995. Los datos del PDBY no existirían sin la dedicación constante de su equipo de taxónomos y mapeadores, con quienes quedo también indirectamente en deuda. En particular, quiero expresar mi agradecimiento a M.Sc. Consuelo Hernández, profesora de la PUCE y responsable de la base de datos del PDBY, quien proveyó los datos de árboles que eran necesarios para los análisis de esta tesis.

Franz Alexander Chandi Villarroel

ABSTRACT

Different non-stationary Poisson models were developed in order to search for the most optimal models to explain the spatial distribution of lianas based on the spatial distributions of tree taxa (as covariates). The data used come from liana and tree censuses conducted in 2008 and 2002−2003, respectively, in an area of 20 m × 500 m (1 ha) in the permanent vegetation plot of 50 ha in Yasuní National Park. Independent analyses were performed at the taxonomic level of tree species, genera and families, and also with different diameter classes of both lianas and trees. To assess the effect of different diameter classes on the quality of a model, different diameter classes for lianas (≥1.0, ≥1.5, ≥2.0 y ≥2.5 cm) and trees (≥1.0, ≥2.0, ≥3.0, ≥4.0, ≥5.0, ≥6.0, ≥7.0, ≥8.0, ≥9.0 y ≥10.0 cm) were combined in different models, resulting in 40 models per taxonomic level (total 120 models). Each model was evaluated by two indices that measure model performance: the Nash-Sutcliffe Efficiency (NSE) and the Akaike Information Criterion (AIC). In addition, a Spearman correlation was used to assess to what extent the results of a model can be correlated with liana prevalence data as observed in the field and reported in the literature (18 studies between 1984 and 2020). To select the most optimal model from the 40 models run for each taxonomic level of trees, the level of significance of the ρ coefficient of the Spearman correlation was used as a criterion. At the species level, Spearman correlations were not significant because only a few Yasuní tree species were found with liana prevalence data reported in the literature. At the genus level, the models of the tree diameter class ≥7 cm were the only that produced highly significant correlations, in particular the model that resulted when the diameter class of lianas ≥1 cm was considered ($\rho = 0.718$, $P = 0.017$). At the family level, the model with the most significant correlation was the one for the diameter class of trees ≥7 cm and the diameter class of lianas ≥2 cm ($\rho = 0.628$, $P = 0.006$). In these two models, selected for their resemblance to real liana prevalence data, estimates of the parameter θ_t, designated as $\hat{\theta}_t$, were calculated for each tree taxon and their statistical significance under H_0: $\theta_t = 0$ was assessed. This estimate indicates whether a taxon shows a tendency to be or not surrounded by lianas ($\hat{\theta}_t < 0$ to indicate relative absence of lianas nearby the individuals of the tree taxon, and $\hat{\theta}_t > 0$ to indicate association of the individuals of the tree taxon with lianas). The anatomical characteristics of those taxa with a $\hat{\theta}_t$ significantly different from zero were evaluated in order to explain the possible ecological mechanisms behind the statistical results. In general, it was observed that those tree taxa with $\hat{\theta}_t < 0$ (statistically significant) do indeed display liana-deterring characteristics, while those tree taxa with $\hat{\theta}_t > 0$ (statistically significant) do indeed display features that may facilitate liana colonization.

Key words: Poisson model, spatial distribution, lianas, trees, liana prevalence, Yasuní

RESUMEN

Se desarrollaron diferentes modelos espaciales de Poisson no estacionarios con el fin de buscar los modelos más óptimos que expliquen la distribución espacial de lianas en base a las distribuciones espaciales de taxones de árboles (como covariables). Los datos utilizados provienen de los censos de lianas y árboles realizados en 2008 y 2002−2003, respectivamente, en un área de 20 m × 500 m (1 ha) en la parcela permanente de vegetación de 50 ha en el Parque Nacional Yasuní. Se realizaron análisis independientes a nivel taxonómico de especies, géneros y familias de árboles, y también con diferentes clases diamétricas tanto de lianas como de árboles. Para evaluar el efecto de diferentes clases diamétricas sobre la calidad de un modelo, se combinaron diferentes clases diamétricas para lianas (≥1.0, ≥1.5, ≥2.0 y ≥2.5 cm), y para árboles (≥1.0, ≥2.0, ≥3.0, ≥4.0, ≥5.0, ≥6.0, ≥7.0, ≥8.0, ≥9.0 y ≥10.0 cm), dando como resultado 40 modelos por nivel taxonómico (total 120 modelos). Cada modelo fue evaluado por dos índices que miden su desempeño: la Eficiencia de Nash-Sutcliffe (NSE, por sus siglas en inglés) y el Criterio de Información de Akaike (AIC, por sus siglas en inglés). Además, se utilizó una correlación de Spearman para evaluar hasta qué punto los resultados de un modelo pueden correlacionarse con los datos reales de prevalencia de lianas reportados en la literatura (18 estudios entre 1984 y 2020). Para escoger el modelo más óptimo de entre los 40 modelos corridos por cada nivel taxonómico de árboles, se utilizó como criterio el nivel de significancia del coeficiente ρ de la correlación de Spearman. A nivel de especie, las correlaciones de Spearman no fueron significativas porque solo se encontraron pocas especies de árboles de Yasuní con datos de prevalencia de lianas reportados en la literatura. A nivel de género, los modelos de la clase diamétrica de árboles ≥7 cm fueron los únicos que produjeron correlaciones altamente significativas, en particular el modelo que resultó cuando la clase diamétrica de lianas ≥1 cm fue considerada ($\rho = 0.718$, $P = 0.017$). A nivel de familia, el modelo con la correlación más altamente significativa fue el de la clase diamétrica de árboles ≥7 cm y la clase diamétrica de lianas ≥2 cm ($\rho = 0.628$, $P = 0.006$). En estos dos modelos, seleccionados por su cercanía a los datos reales de prevalencia de lianas, se calcularon los estimados del parámetro θ_t, denominado $\hat{\theta}_t$, para cada taxón de árboles y su significancia estadística bajo la H_0: $\theta_t = 0$. Este estimado indica si un taxón muestra tendencia a estar o no rodeado de lianas ($\hat{\theta}_t<0$ para indicar relativa ausencia de lianas cerca de los individuos del taxón del árbol, y $\hat{\theta}_t>0$ para indicar asociación con lianas de los individuos del taxón del árbol). Las características anatómicas de aquellos taxones con un $\hat{\theta}_t$ significativamente diferente de cero fueron evaluadas con el fin de explicar los posibles mecanismos ecológicos detrás de los resultados estadísticos. En general, se observó que aquellos taxones de árboles con $\hat{\theta}_t<0$ (estadísticamente significativos) en efecto muestran características de disuasión de lianas, mientras que aquellos taxones de árboles con $\hat{\theta}_t>0$ (estadísticamente significativos) en efecto muestran características que pueden facilitar la colonización de lianas.

Palabras clave: modelo de Poisson, distribución espacial, lianas, árboles, prevalencia de lianas, Yasuní

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1. INTRODUCTION

In this study, using the historical data generated by Romero-Saltos et al. (2008 liana census; unpublished data) and Valencia et al. (tree census; Valencia et al., 2004), I will attempt to model the spatial distribution of lianas using the spatial distribution of trees in a 20 m × 500 m rectangular plot located in the 50-hectare (ha) Yasuní Forest Dynamics Plot (YFDP). The general postulate I am proposing is that the local interpolated density of trees (tree rooting points per unit area) could potentially be a good predictor of the interpolated local density of lianas (liana rooting points per unit area). Specifically, I will use spatial statistics to assess to what extent the local density of relatively adult lianas could be predicted by the positions of relatively adult trees, taking into account tree taxonomic identities (at species, genus, or family levels), as explanatory variables. Therefore, I am asking what tree taxa can better explain the observed spatial distribution of lianas. Those tree taxa that show, according to the models, a significant positive or negative influence on the presence of lianas, will then be counterbalanced against field observations on the level of liana prevalence[1] reported for such tree taxa (or related taxa) in the literature.

1.1. Lianas in Amazonian Ecuador

At least 47 families, 130 genera and 350 species of lianas have been found in Yasuní while also having a high density like most low-disturbance neotropical forests (Burnham & Romero-Saltos, 2014). Nabe-Nielsen (2001), in Yasuní National Park, found a liana diversity higher than the expected based on its number of individuals, although he argued that the lower density was related to the lack of treefall disturbances in his study area. Romero-Saltos et al. (2001) found that both tree and liana diversity and density followed the same diversity trend across broad vegetation types, namely, diversity was higher in terra firme forests, intermediate in floodplain forests, and lowest in swamp forests. This pattern was mainly explained by the marked differences on soil properties among these vegetation types, although it was uncertain if similar directional changes of diversity and density of lianas and trees would also hold up among habitats within terra firme forests. Studies within the terra firme forest of the YFDP showed that liana and tree diversity, as measured by species richness and Fisher's alpha

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[1] In this study, I will use the term "liana prevalence" to refer to the proportion of trees with lianas in a community (see Muller-Landau & Visser, 2019). Some studies use the term "liana infestation", but such term has a connotation that is not always applicable: under certain circumstances, it can be interpreted as a high amount of liana load on a tree, causing negative effects on tree fitness; however, in practice, this may be basically non-existent for trees with low liana loads, or for trees that, from an ecological or evolutionary perspective, deal well with liana presence on their trunks or in their canopy.

diversity index, followed the same trend of being higher in valley habitat than in ridge habitat; however, liana and tree density showed opposite trends: liana density was higher in valley while tree density was higher in ridge (Romero-Saltos, 2011; Valencia et al., 2004).

In the Sumaco Biosphere Reserve, northeastern Ecuador, Homeier et al. (2010) found that liana density had a non-significant negative correlation with tree density (trees with DBH ≥10 cm) but a significant positive correlation with tree basal area and mean tree diameter; moreover, liana density and basal area showed no consistent pattern with the large-scale altitudinal gradient (500–2000 m). The only liana characteristic found to be correlated with altitude was mean liana diameter, except that mean stem diameter was similar between liana samples at 500 and 1000 m altitude, and only after 1500 m, mean liana diameter started to be significantly smaller. They also found that liana basal area had a significant positive correlation with canopy cover.

1.2. Lianas versus trees

1.2.1. Competition or parasitism?

The interaction between lianas and trees is more complex than simple competition for sunlight or soil nutrients—they also compete for regeneration opportunities in the understory or canopy gaps (Schnitzer & Carson, 2010). The liana-tree interaction has been reframed to structural parasitism (Ewers et al., 2015) rather than competition as the liana-tree interaction is seen as a positive-negative one (Muller-Landau & Pacala, 2020; Stewart & Schnitzer, 2017). Lianas exploit the expensive support structure made by trees to reach the sunlight available in the forest canopy; in this way, lianas can allocate more energy in photosynthetic rather than supportive tissue. The impact may include a higher weight load on the host tree that may increase its diameter/height ratio (Stewart & Schnitzer, 2017), reduce light availability, and change the leaf and branch area index (Sánchez-Azofeifa et al., 2009; Schnitzer & Bongers, 2002). These and other effects can result in lower tree recruitment, growth, reproduction, survival and diversity (Álvarez-Cansino et al., 2015; Kainer et al., 2014; Martínez-Izquierdo et al., 2016; Schnitzer et al., 2014). On the other hand, lianas might have some benefits on trees such as an increased soil quality as a result of their higher leaf litter, mutualism with nitrogen fixers, and horizontal transportation of nutrients (Tang et al., 2012)—interestingly, they could even function as lighting rods due to their higher electric conductivity (Gora et al., 2017).

1.2.2. Liana avoidance strategies

Many tree characteristics have been hypothesized to reduce the odds of having lianas. Some characteristics can avoid liana colonization[2] from the ground, such as the presence of buttress roots which increase soil area occupancy—thus potentially limiting the density of trees and lianas growing nearby—and may act as physical barriers for liana seedlings, which in turn would need to spend more energy on growth before being able to reach the tree stem (Black & Harper, 1979). However, the buttress hypothesis was falsified in a Brazilian tropical wet forest study (Boom & Mori, 1982). Certain bark characteristics, like smooth or exfoliating bark, do not provide a suitable climbing surface or facilitate the dislodge of lianas from its host (Putz, 1984; Talley et al., 1996). Rapid stem thickening reduce the timeframe that lianas have to climb trees while they still have small enough stem diameters, but this only protects trees from lianas with climbing mechanisms that rely on surrounding a tree stem (by twining [circumnutation], by tendrils, or by twining branches)—this rapid growth strategy would not protect trees from root climbers or lianas with adhesive tendrils (Putz, 1984). Spiny tree stems were hypothesized by Putz (1984) to damage lianas during tree oscillation; however, his experimental test of swaying spiny trees manually more than 100 times showed no damage to the entwined lianas, thus falsifying the hypothesis.

From a statistical perspective, the reports that a given tree characteristic does not reduce the chance of liana colonization does not necessarily mean that the characteristic being tested does not exert absolutely any effect. In fact, Sfair et al. (2016) demonstrated that having two or more characteristics associated to liana avoidance is more effective than having a single characteristic. In addition, it is important to realize that the tree characteristics mentioned above are meant to avoid liana invasion from the ground—i.e., they do not avoid liana colonization of the tree canopy from adjacent trees (Boom & Mori, 1982; Putz, 1980). Indeed, some liana deterring characteristics are mechanistically independent of liana colonization from the ground. For example, stem flexibility could allow trees to oscillate at higher angles and break or dislodge lianas during movement (Putz, 1984). Large simple or compound leaves, if used as support by lianas, could also help to get rid of lianas when they are shed (Putz, 1984). Trees with tall branch-free trunks/boles could also avoid lateral invasion of lianas, as lianas from adjacent shorter trees probably cannot easily reach their elevated branches (Putz, 1984).

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[2] In this study, I will use the term "liana colonization" to refer to the process itself by which a liana gets hold of a tree and start to climb it. It should not be confused with the terms "liana prevalence" or "liana infestation" (see previous footnote). Let's also note that many lianas actually reach the canopy of a tree not by climbing on the tree, but rather by using other lianas as support! (H. Romero-Saltos, pers. comm.).

Some other tree characteristics are indirect predictors of liana colonization or liana density. For example, Sfair et al. (2016) demonstrated that tree height was positively correlated with liana colonization in three sites in southeastern Brazil—probably an age effect because most tall trees certainly were also old, and therefore had more time to be colonized by lianas. Also, Putz (1984) realized that certain pioneer trees (early colonizers of disturbed areas) tend to possess liana-proofing characteristics, although, paradoxically, many liana species are also pioneers of disturbed habitats, where they tend to become abundant. Supporting the observations by Putz, Clark & Clark (1990) found that the pioneer tree species *Cecropia obtusifolia* and *C. insignis* had no lianas nor hemiepiphytes. Carse et al. (2000) similarly found that *Cecropia concolor*, despite being a common species in Las Trancas (eastern Bolivia), had low liana prevalence. Therefore, it can be concluded that *Cecropia* and other early tree colonizers tend to possess some liana deterring characteristics such as stem flexibility, long branch-free boles and long leaves that are shed frequently (Carse et al., 2000). These traits are also observed in palms, which along with spines (if present), could help them to avoid lianas (Pérez-Salicrup et al., 2001). Yet, again paradoxically, Pérez-Salicrup et al. (2001) found that liana density was positively associated with palm distribution in Santa Cruz, Bolivia. In conclusion, it seems that liana prevalence patterns strongly depend on the spatial scale analyzed: an analysis conducted at the individual(species)-level can show patterns that are very different, or even contradict, patterns observed when the analysis is conducted at the community-level.

2. OBJECTIVES

This study has the following the following objectives:

1. To model the spatial distribution of lianas using the spatial distribution of trees as explanatory variables in a 20 m × 500 m rectangular plot located inside the 50-ha Yasuní Forest Dynamics Plot (YFDP), using a Poisson process modeling approach that takes into account tree taxonomic levels (species, genus or family) and different tree and liana diameter classes.
2. To assess how accurate the predicted liana counts in the different models resemble the observed liana counts, using common statistical indices to assess model performance (quality).
3. To contrast the results of the different models with published liana prevalence on different tree taxa (field-based empirical data), at different taxonomic levels (species, genus or family).

3. METHODS

3.1. Study area and data availability

In 1995, a 50-hectare (ha) forest plot (1000 m × 500 m) in Yasuní National Park (0° 41′ 0.5″ S, 76° 23′ 58.9″ W, at the plot center) was established as the largest long-term study site in Ecuador's Amazon basin dedicated to the study of plant ecology, particularly demographic processes (Pérez et al., 2014). This immense forest plot is known as the "Yasuní Forest Dynamics Plot" (YFDP), and is located close to the Yasuní Scientific Research Station (YRS), managed by the Pontificia Universidad Católica del Ecuador (PUCE). The plot has an altitudinal range of 215 to 248 m; mean annual rainfall is ~3000 mm; and mean monthly temperature is ~25 °C (Pérez et al., 2014). The YFDP belongs to the network of large-scale forest plots located in different sites around the world, known as ForestGEO (Davies et al., 2021).

In the 50-ha YFDP, Dr. Renato Valencia, professor at PUCE, and his collaborators have censused, tagged, measured (diameter at breast height - DBH) and spatially mapped thousands of trees with a diameter at breast height (DBH) ≥1 cm every five to six years, registering during every census the new trees (recruits) as well as dead trees, while also taxonomically identifying as many trees as possible (Pérez et al., 2014). Throughout the years, these and other associated data have served generously to the scientific community: a Google Scholar search gives more than 2300 scientific documents that make reference to the YFDP, directly or indirectly. For the purpose of this study, I used the tree census data compiled for the period of 2002 to 2003, i.e., the tree census period just before the period when the liana census analyzed in this study occurred (2008; see below).

For the purpose of this study, an area of 20 m× 500 m was selected within the 50-ha YFDP. This area is delimited by the following (x;y) coordinates: (140;0) (160;0) (140;500) and (160;500) (**Figure 1**). The lianas in this area were sampled from January to April 2008 by Dr. Hugo Romero-Saltos and his collaborators, who censused, tagged, measured (diameter) and spatially mapped all lianas with diameter ≥1 cm (note that, because of the convoluted growth form that some lianas present, the point of diameter measurement in lianas is not always taken at breast height; see Romero-Saltos 2011, Romero-Saltos et al. 2014). In the internal geographic system of the 50-ha YFDP, which is based on 20 m × 20 m quadrats, this rectangular area corresponds to "column 7". Such liana census was actually the second of this area (the first was in November 2005–August 2006). Most lianas were identified to the species level. Primary (main) and secondary rooting points and stem paths of all lianas from ground level to an approximate height of 2 m were mapped by hand, using the mapping method and graphical coding for lianas described by Romero-Saltos et al. (2014). The scale used for hand mapping was a 10 m × 10 m subquadrat (determined by what can be fitted in an A4 paper sheet).

Because the distribution of lianas at the borders of the censused area might be influenced by trees just outside of this area, in order to model the spatial distribution of lianas, I decided to slightly increase the width of the tree census area by 10 m, i.e. a 40 m × 500 m rectangular plot. Thus, the area of the tree census was delimited by the following (x;y) coordinates: (130;0) (170;0) (130;500) and (170;500) (**Figure 1**).

The detailed description of the structure of the tree and liana communities in the study area falls out of the scope of the present study. In any case, I show a brief description that summarizes the main community structure patterns for the trees and lianas in the 20 m × 500 m plot in **Appendix A**. The general, most important, patterns related to the community structure of trees and lianas in the 50-ha YFDP have already been described by Valencia et al. (2004) and Romero-Saltos (2011), respectively.

3.2. Georeferencing liana points

The scanned maps of all 10 m × 10 m quadrats were previously assembled into larger maps using GIMP software (The GIMP Development Team, 2019) by Hugo Romero's team and I loaded these maps into a geographic information system: QGIS (QGIS Development Team, 2021). Within QGIS, I georeferenced the primary (main) and secondary rooting points of all lianas based on the scanned maps. Each liana rooting point was uniquely identified with the liana tag, along with a code to indicate the rooting point number. I used the ID column of the resulting layer of liana rooting points to merge with the census database containing the taxonomical, size (diameter) and growth status of each liana (climbing, free-standing, or other). A scanned sample map of a 10 m × 10 m area showing how lianas were mapped by hand in the field is shown in **Figure 2**.

3.3. Preparing and filtering data for analyses

I exported the QGIS layer of primary rooting points, containing their coordinates (x;y), into a csv (comma-separated) file, which was then loaded into R (R Core Team, 2020), using the RStudio interface (RStudio Team, 2021). I also loaded the tree dataset, which already contained coordinates (x;y) for every tree, along with species identity and diameter data into R. Given that some family taxonomical names have changed during the last decade (e.g., see APG IV, 2016), I updated the taxonomic information using the databases of GBIF (*Global*

Biodiversity Information Facility; GBIF, 2021) and ITIS (*Integrated Taxonomic Information System*; Chamberlain et al., 2021; ITIS, 2021).

Because it is not known how the past and/or present distribution of trees is affecting the establishment (spatial distribution) of lianas, or viceversa, and because in the YFDP there is no empirical historical data about how a variety of ecological factors (such as plant age, size, growth form, architecture, liana climbing mechanisms, abiotic variables, ...) are affecting how trees and lianas interact (see Putz, 1984), I took the following conservative decisions in order to select the datasets to be analyzed:

(1) I did not use the oldest available tree census data from 1995–1999, and I neither used the 2007–2009 tree census data obtained during the time the lianas were censused (2008); I used the data in-between these two censuses (the tree census data from 2002–2003). In addition, I excluded from the analyses the relatively rare tree taxa with less than 30 individuals (an arbitrary threshold). This decision was taken because tree taxa (at the family, genera or species level) with a small number of individuals are probably not good predictors because, for rare taxa, a correlation between lianas and trees may occur just by chance.

(2) I only modeled the distribution of climbing lianas, because non-climbing lianas might have a different response to the spatial distribution of trees. In other words, free-standing lianas (which look like young trees), or fallen lianas that were still creeping, were excluded from the analyses. In addition, I just used the locations of the primary (main) rooting points of the lianas. Note that a liana has always only one primary rooting point, but could have several secondary rooting points along its stem, especially if it is a creeping liana.

(3) I decided to assess the impact that different tree and liana sizes may have on model performance. Small trees and lianas were progressively excluded from the analyses by creating subsets of lianas and trees with different diameter classes. The tree diameter classes (TDC) used were defined by the sequence of ≥1.0 to ≥10 cm in steps of 1 cm (ten tree diameter classes), while the liana diameter classes (LDC) used were ≥1.0, ≥1.5, ≥2.0, and ≥2.5 cm (four liana diameter classes). The rationale behind this assessment was that small trees may often represent relatively young individuals which probably have not had enough “time” to influence the spatial distribution of lianas. In addition, small lianas may not accurately reflect their preferred habitat (in other words, only lianas that are born in their preferred habitat would grow to a large size). An independent model was generated for each combination of tree and liana diameter classes, to give a total of 40 models (10×4 diameter classes) for each of the three analyzed taxonomic levels: species, genera, and families (total = 120 models).

3.4. Modeling liana spatial distribution

3.4.1. Models generation

I assume that the observed point pattern (spatial distribution) of lianas is a Poisson point process, where liana rooting points are independent of each other. This means that if the study area is divided into pixels, the presence/absence of a liana rooting point(s) in one pixel would not influence the presence/absence values in other pixels (Baddeley et al., 2015). This independence principle however may not be always applicable for lianas because, if a liana climbs one tree, it becomes easier for other lianas to climb the same tree (Pinard & Putz, 1994).

A Poisson process is thoroughly described by its intensity function $\lambda(u)$. In spatial statistics, intensity is defined as the expected number of points per unit area; indeed, the integral of the intensity function around a region equals the expected number of points inside that area (Baddeley et al., 2015). Each plant has its own intensity function that depends on many biotic and abiotic factors. Related taxonomic groups like trees of the same species, genus or family, or plants with the same ecological role or functional group (like climbing lianas), might have similar intensity functions. If lianas tend to be around certain tree taxonomic groups, then the spatial distribution of lianas could be potentially explained by the spatial distribution of trees. This raises the question of which tree taxa explain most of the variation of the liana intensity function (see Objectives section).

The observed liana point pattern (the response variable) is modeled using the point intensities of each taxonomic identity (covariate) at the taxonomic levels of either species, genera, or families of trees as explanatory variables, using the function "ppm" (point process model) of the "spatstat" package in R (Baddeley et al., 2015). This R function requires a trend formula (parameter Q) specifying the logarithm of the intensity of the response variable. For this study, I set the parameter Q as '~.' which indicates an additive model with a main effect for each covariate, resulting in the following trend formula:

$$\lambda_l(u) = \exp\left(\theta_0 + \sum_{t=1}^{N} \theta_t * Z_t(u)\right) \qquad \text{(Equation 1)}$$

where $\lambda_l(u)$ is the predicted point intensity of the response variable l (lianas point pattern) at location u ($u \in \mathbb{R}^2$), θ_0 (intercept) is the expected logarithmic intensity for a location u in which all covariates $Z_t(u)$ equal zero, θ_t is the weight of the covariate $Z_t(u)$, and $Z_t(u)$ is the intensity function of the tree taxon t and is effectively the value of the covariate at location u (for an example on how coefficients can be interpreted, see Results and Discussion). The "ppm" R function returns an estimate of the parameter θ_t, designated as $\hat{\theta}_t$, along with the standard error (±1 SE) and the results of a Z-test for each covariate (i.e., a Z-score showing how many standard deviations the coefficient is different from zero, along with its statistical significance). Exact P-values were calculated from the Z-scores using the R function “dnorm”.

To calculate the point intensity function for each tree taxa t, $\lambda_t(u)$, which act as a covariate $Z_t(u)$, I used the “density” function of the “spatstat” package in R (Baddeley et al., 2015). This R function computes a kernel smoothed intensity function of a given point pattern, and has a built-in edge correction such that the point intensity at the borders is estimated as if the point pattern would continue outside the boundaries of the study area. Moreover, this R function requires a sigma (σ) value which, in practical terms, determines the range of influence of each point on the resulting estimated intensity function (see Baddeley et al., 2015). The R “density” function simply places bivariate normal distributions centered on each point of a given point pattern, with a standard deviation equal to sigma. It also adds up all normal distributions into a single output layer. The function that produces the bivariate Gaussian distribution $G(x,y)$ is (Fisher et al., 1997):

$$G(x,y) = \frac{1}{2\pi\sigma^2} e^{-\frac{x^2+y^2}{2\sigma^2}} \qquad \text{(Equation 2)}$$

Although a bivariate normal distribution is non-zero everywhere, in order to simplify the calculation, it is assumed to be zero after three standard deviations away from the center (Fisher et al., 1997). The area under the curve of a normal distribution is equal to 1, so if the standard deviation (sigma parameter) increases, the bell-shape curve flattens, and the peak of the curve lowers. A standard deviation of 1 results in a peak value of 0.16 at the center of the bivariate normal distribution, while a standard deviation of 10 results in a peak value of 0.0016.

In order to understand the behavior of the “density” function in R, I created a point pattern consisting of two points separated by 30 units, and estimated its point intensity function by using either the “density” function in R, or by manually placing two Gaussian distributions centered at each point. Both methods produced the same output (**Figure 3**).

As explained above (see **Figure 1**), trees censused within 10 meters around column 7 (an area of 40×500 m) were included in the point intensity estimation, in order to increase the accuracy at the borders of the study area (20×500 m). This decision was taken despite the fact that we only need the intensity function $\lambda(u)$ of each tree taxon inside the 20×500 m area, and even when the “density” function in R already has a built-in edge correction, as explained above.

If no sigma value is explicitly given to the “density” R function, the default value for the sigma parameter is arbitrarily calculated as 1/8 of the shortest side of the bounding box enclosing the point pattern (Baddeley et al., 2021). Because in this study the size of the bounding box is 40×500 m, the default sigma value is 40/8 = 5. However, given that the size of the bounding area in this study is several magnitudes higher than the size of a typical tree, the "density" R function with a sigma of 5 produces a point intensity that only represents the immediate local surroundings of trees. On the other hand, a sigma value of 15 produces a point intensity that is too smoothed and might mark regions that, biologically speaking, fall outside the influence of trees. Considering these two extremes, I settled with a sigma value of 10 because it produces a point intensity that more realistically represents the local region in which trees tend to grow (their local preferred habitat), in the scale of this study. The example below with *Piper* trees (**Figure 4**) graphically shows how this decision of a sigma value of 10 was well justified.

3.4.2. Assessing model performance

As explained above, a different model was fitted for every combination of tree taxonomic levels (species, genus and family levels) and diameter classes (of both trees and lianas), for a total of 120 models. Once a model was fitted, the model performance (quality) was tested by dividing the study area into 20×20 m quadrats, counting the lianas inside each quadrat (O_i) (using the "quadratcount" function of the "spatstat" package in R; Baddeley et al., 2015) and comparing it with the predicted counts of lianas for such quadrat (P_i) as calculated by the model (using the "predict" function). To assess how accurate the predicted counts resemble the observed counts, I applied two statistical indices: the Nash-Sutcliffe Efficiency (NSE) and the Akaike Information Criterion (AIC).

The Nash-Sutcliffe Efficiency (NSE) is a normalized goodness-of-fit index that is calculated as:

$$NSE = 1 - \frac{\sum(O_i - P_i)^2}{\sum(O_i - \bar{O})^2} \qquad \text{(Equation 3)}$$

The value of the NSE index can range from $-\infty$ to 1, where 1 indicates a perfect fit, 0 indicates that the mean of the observed counts is as good a predictor as the model, and negative values indicate that the mean of the observed counts is a better predictor than the model (Ritter & Muñoz-Carpena, 2013).

Because high NSE indices cannot distinguish between good models and overfitted models (models with too many degrees of freedom), I also used the Akaike Information Criterion (AIC) to assess a model performance. The AIC is calculated using the "AIC" R function, which has the formula:

$$AIC = -2 * \log(L) + k * penalty \qquad \text{(Equation 4)}$$

where L is the maximized likelihood (a measure of goodness-of-fit) of the model, and $penalty$ is a measure of model complexity weighed by k (default = 2). Therefore, the lower the AIC the better the model quality. For a Poisson process model, $penalty$ is equal to the number of fitted parameters, i.e. the number of covariates plus one for the intercept. In this study, recall that a covariate $Z_t(u)$ is the point intensity of a given taxonomic identity.

3.4.3. Comparison of model predictions to published liana prevalence data

Another way to assess a model is by comparing the results of the model with liana prevalence (i.e., the proportion of trees with lianas, in a given tree taxon; sensu Muller-Landau & Visser, 2019), as reported in the published literature. In this study, I used as references two reports of liana prevalence: the dataset compiled by Muller-Landau & Visser (2019) which comprises 17 studies (including theirs) from 1984 to 2018; and the dataset by Reis et al. (2020). The site information of these 18 studies is shown in **Appendix B**. To correctly match the taxonomy in these 18 studies with the present study, I updated the family and genera names using the GBIF and ITIS databases (GBIF, 2021; Chamberlain et al., 2021; ITIS, 2021).

"Average" liana prevalence for each tree species across all published studies was estimated as an index using the following formula:

$$\bar{P_i} = \frac{\sum_{t=1}^{19} N_{i,t} * P_{i,t}}{\sum_{t=1}^{19} N_{i,t}} \qquad \text{(Equation 5)}$$

where $\bar{P_i}$ is the "average" prevalence in species i, $N_{i,s}$ is the number of trees of species i whose liana prevalence was measured in the study t, and $P_{i,t}$ is the proportion of trees of the species i whose prevalence was measured in the study t. Because it is an additive formula, note that the numerator is the number of trees of species i with lianas, and the denominator is the sample size for species i, across all studies.

In a similar fashion, to calculate the "average" liana prevalence for each genus ($\bar{P_j}$), two methods could be applied:

(i) A modified Equation 5 where species i is replaced by a genus j:

$$\bar{P_j} = \frac{\sum_{t=1}^{19} N_{j,t} * P_{j,t}}{\sum_{t=1}^{19} N_{j,t}} \qquad \text{(Equation 6)}$$

where $\bar{P_j}$ is the "average" liana prevalence in genus j, $N_{j,t}$ is the number of trees of genus j whose liana prevalence was measured in the study t, and $P_{j,t}$ is the proportion of trees of the genus j whose prevalence was measured in the study t.

(ii) An average of the liana prevalence values (calculated using Equation 5) of all species belonging to genus j:

$$\bar{P}_j = \frac{\sum_{i=1}^{S} \bar{P}_i}{S} \qquad \text{(Equation 7)}$$

where $\bar{P}_j$ is the average liana prevalence in genus j, S is the number of species in genus j present in the compiled dataset, and $\bar{P}_i$ is the average prevalence of each species i, within a given genus j.

Method ***(i)*** (Equation 6) has the problem that the average prevalence for each genus will be affected by species with high sample size (number of trees), while method ***(ii)*** (Equation 7) solves this bias by giving equal weight for each species. Therefore, I applied method ***(ii)*** in order to calculate the average liana prevalence for each genus. Using a similar reasoning, the average liana prevalence for each family was calculated as:

$$\bar{P}_k = \frac{\sum_{j=1}^{G} \bar{P}_j}{G} \qquad \text{(Equation 8)}$$

where $\bar{P}_k$ is the average liana prevalence in family k, G is the number of genera in family k present in the compiled dataset, and $\bar{P}_j$ is the average prevalence of each genus j, within a given family k.

The results of each model were compared with the literature using the Spearman rank correlation. For each model, the Spearman coefficient ρ assessed the relation between the Z-scores (from the model) and the average liana prevalence associated to each taxon (from Equations 5, 7, and 8, above). This analysis was separately carried out for each combination of tree and liana diameter classes, as defined above (see "Preparing and filtering data for analyses"). Evidently, I excluded from this analysis those taxa in Yasuní with no liana prevalence reports in the literature. For each ρ calculated, a P-value was also estimated to assess statistical significance. It is expected to see higher ρ coefficients at high TDCs since only three of the 18 studies used to calculate average liana prevalence values included trees with DBH <10 cm (**Appendix B**).

Because it is impractical to show the fitted estimates $\hat{\theta}_t$ of each covariate $Z_t(u)$ (point intensity of the taxonomic identity t) for every one of the 120 models run, in the Results and Discussion section, I only show the $\hat{\theta}_t$ and Z values of one model per taxonomic level: those "best" models having the Spearman ρ with the lowest P-values. In this study, given its ecological/observational context, I am applying an arbitrary α = 0.15 (Type 1 error rate) to decide statistical significance. This relatively high α level would increase the β error rate, but such error would not be considered a serious error in the context of this ecological study. In addition, for the “best” models selected in the basis of their resemblance to real liana prevalence data, as collected in the field, I show how the observed (*y*) vs. predicted (*x*) liana density (*y*-*x* scatter plot) would look for all 20 m × 20 m quadrats (25 quadrats in the one hectare studied). Note that these “best” models also have associated NSE and AIC values, but they may not necessarily be those with the best fit (i.e., with the highest NSE, or the lowest AIC).

4. RESULTS AND DISCUSSION

For each of the 120 models run (which result from the combination of different tree and liana diameter classes, at different taxonomic levels), **Appendix C** shows the values of the model performance indices (NSE, AIC), **Appendix D** shows the number of covariates and the number of tree and liana individuals used in the models, and **Tables 1–3** shows the Spearman correlation results (ρ coefficients, P-values, and number of comparisons).

4.1. Models performance according to NSE and AIC

In general, the NSE indices (**Appendix C: Tables C1–C3**) show higher prediction performance with lower tree diameter classes (TDCs) as it was expected because more covariates were included (**Appendix D: Tables D1–D3**) and therefore the model had more degrees of freedom to be adjusted. To evaluate if the increase in NSE values justified the addition of more covariates (taxa), the AIC values were compared (**Appendix C: Tables C4–C6**). The AIC indices show a relatively small decrease (improvement of model quality) with the decrease of TDC (i.e., the increase of more covariates). However, the way the AIC is calculated (Equation 4) does not take into account the addition or subtraction of tree individuals in the same tree taxa that is used as covariate, at different TDCs. Therefore, the higher model performance observed in lower TDCs, both for NSE and AIC, could not necessarily be interpreted as a real trend, but could simply be the result of model overfitting, given the large number of covariates (number of taxa) in the Yasuní forest. On the other hand, compared to what was observed with TDC, the values of the AIC indices showed a higher relative decrease as the liana diameter class (LDC) increased. This is because the model, as LDCs increase, has to explain the distribution of less liana points, while the AIC formula (Equation 4) is not penalizing the decrease of liana individuals in the response variable l (lianas point pattern).

4.2. Selecting the best models that resemble published liana prevalence data

4.2.1. Spearman correlation results

The Spearman correlation results (**Table 1−3**) showed that at higher TDC, Spearman coefficients ρ increased, thus reflecting a better agreement between the results of a model and the reported liana prevalence data. The models with the lowest significant P-values of the Spearman correlations were observed in the TDC ≥7 cm. In the Yasuní data sample analyzed here, higher TDCs evidently excluded more taxa (fewer taxa had ≥30 individuals), and the number of comparisons available for the correlation were reduced. Thus, if more individuals of large trees (DBH ≥10 cm) were sampled, the correlation with lowest P-value could be found at a TDC higher than ≥7 cm, given that most field data of liana prevalence that are being used to fit the models came from trees with a DBH ≥10 cm (**Appendix B**).

Regarding the effect of LDCs, the results differed between genera and families. For genera, the lower significant P-value (0.013) was observed in the LDC ≥1 cm (**Table 2**), while for families, the lower significant P-value (0.006) was observed in the LDC ≥2 cm (**Table 3**), although both occurred in TDC ≥7 cm, as explained above. The ρ coefficients for both genera and families were around 0.6–0.7, which are relatively high given the ecological context of this study. Note that the strength of the correlations can be affected by the behavior of each taxon within a given taxonomic level. For example, different genera of the same family showing opposite trends with regard to their liana prevalence, would certainly lower the ρ coefficient and the correlation significance for such family.

4.2.2. $\hat{\theta}_t$ estimates of the best selected models

In practice, the estimate of the parameter θ_t, referred as $\hat{\theta}_t$, provides information about the strength of the spatial relation between lianas and a given tree taxon: *a negative value means that the tree taxon tends to reduce the number of surrounding lianas, while a positive value means that the tree taxon tends to increase the number of surrounding lianas*. A value of zero would mean a completely neutral effect of the tree taxon on the spatial distribution of lianas. These spatial relations, as described by $\hat{\theta}_t$, could be statistically significant or not, given the null hypothesis of $\theta_t = 0$. In other words, given an α=0.15, we can conclude from the Z-scores and associated P-values whether or not $\hat{\theta}_t$ is significantly different from zero. The $\hat{\theta}_t$ estimates of the models with the most highly significant Spearman correlations at the genus and family taxonomic levels (red rectangles in **Tables 2** and **3**) are shown in **Tables 4** and **5**, respectively. No models were selected at the species level (**Table 1**) because Spearman correlations at that taxonomic level had very low number of comparisons (only 2–8 tree species).

4.2.3. A discussion on the taxa with $\hat{\theta}_t$ estimates significantly different from zero

In **Tables 4** and **5**, the taxa with statistically significant (at an α=0.15) $\hat{\theta}_t$ estimates are shaded. As explained above, a negative $\hat{\theta}_t$ estimate of a tree taxon means that it tends to be surrounded by a low number of lianas, while a positive $\hat{\theta}_t$ estimate of a tree taxon means that it tends to be surrounded by a high number of lianas.

In **Table 4**, *Matisia, Eugenia, Iriartea* and *Siparuna* showed statistically significant negative $\hat{\theta}_t$ estimates. This is not unexpected because the species in these genera share some liana deterring characteristics. The long clear bole of *Matisia cordata*, in addition to its relatively large buttresses, may provide less structural support for lianas, making it difficult for lianas to reach the main stem and the high branches; on the other hand, its rough bark could provide a suitable climbing surface for some liana species (Humboldt et al., 1808; Williams, 1936). Liana deterring characteristics also have been observed in *M. obliquifolia*, which has smooth bark, a long clear bole, although no buttresses (observations from labels of herbarium specimens: W. S. Alverson No. 2115 and G. P. Cooper No. 435). In Serra do Japi, Brazil, Villanueva-Bonilla et al. (2017) assessed trunk traits in six *Eugenia* spp. (among other Myrtaceae), and found out that four of them have exfoliating bark and three of them have smooth bark; these characteristics evidently would help to detach lianas from the trunk (Putz 1984, Talley et al. 1996). *Iriartea deltoidea* can have up to 100 stilt roots with sharp spines, which might prevent liana infestation from the ground, similarly to large buttresses; as many palms, *I. deltoidea* also has an unbranched main stem (branch free bole) with smooth bark, and long leaves at the top of the trunk which are continuously shed, thus possibly shedding lianas along with them (Henderson, 1990). *Siparuna* spp. have smooth or slightly furrowed thin bark, occasionally finely defoliating (Renner & Hausner, 2005). The latex or exudate from *S. decipiens* and *S. pachyantha*, traditionally used to treat snakebites and small wounds (Renner & Hausner, 2005), shows irritating properties, which I propose could potentially damage young liana stems as well.

In contrast, the genera with positive $\hat{\theta}_t$ estimates significantly different from zero (i.e., with a high number of surrounding lianas) were *Brownea, Pseudolmedia,* and *Zygia*. *Brownea grandiceps* is a slow growing tree with a dense crown and long evergreen leaves (Russell et al., 2003); these characteristics may provide good structural support to lianas, while also giving them sufficient time to reach the canopy as the tree grows. It is interesting to note that even though *Pseudolmedia* had a significantly positive coefficient, some species in this genus have liana deterring characteristics: for example, long branch-free boles of up to 20 meters have been observed in *P. laevigata* and *P. laevis* (Gutiérrez et al., 2002; Williams, 1936), and smooth to somewhat rough bark has been observed in *P. oxyphyllaria* (observations from labels of herbarium specimens: B. Hammel et al. No. 16646, P. K. Harmon No. 45, and N. Zamora & H. G. Michael No. 1557); however, these characteristics can not prevent liana infestation from adjacent trees, or when the trees were young and small. *Zygia* spp. are slender, multi-stemmed arborescent shrubs or trees with long and short leaves (Barneby & Grimes, 1998); these architectural characteristics can provide suitable structural support for lianas, even though the bark of *Zygia* spp. tends to be smooth or flaking (Barneby & Grimes, 1998)—certainly not the ideal climbing surface. Although there is no data on the vegetative phenology of branch shedding in all these genera, I would expect them to shed branches at a relatively low rate, because they are not pioneering trees nor they have low wood density.

In **Table 5**, the families with negative $\hat{\theta}_t$ estimates significantly different from zero (i.e., with a low number of surrounding lianas) were Urticaceae and Myristicaceae. The many *Cecropia* species in the Urticaceae family are all pioneer fast-growing trees, have long branch-free boles, have huge umbrella-shaped leaves that shed at a fast rate, and often have associations with *Azteca* ants; all these characteristics should reduce the timeframe available for lianas to reach the canopy before the tree gets too tall, while also trimming back approaching vines with the help of ants (Condit et al., 2010; Lok et al., 2010). Also in Urticaceae, the genus *Pourouma* shares similar characteristics with *Cecropia*: long branch-free boles, huge leaves, ant associations, and preference to forest openings (Condit et al., 2010; Fonseca, 1999). Note that these genera were not included as covariates in the analysis at genus level (**Table 4**) because they had, at a TDC ≥7 cm, a density of <30 individuals (probably due to the lack of large disturbed areas in the study area). However, when these genera combined into the Urticaceae family, the family was above the threshold abundance defined for this study (≥30 individuals) and thus it was included as a covariate. Regarding Myristicaceae trees, which often tend to have thin bark that breaks off easily, it has been observed that branches, which grow in groups perpendicularly from the main stem and at equal intervals up the trunk, tend to break and shed easily (Condit et al., 2010); this means that lianas could be shed with the falling branches and would have to climb the main stem again to reach the next set of branches, which are higher up towards the canopy.

On the other hand, the families with statistically significant positive $\hat{\theta}_t$ estimates were Nyctaginaceae, Fabaceae and Annonaceae. In the study area, Nyctaginaceae was composed by the genera *Guapira* and *Neea*. Although not present in Yasuní, *G. standleyana* has non-exfoliating bark and a strongly ribbed and fluted trunk, while *G. discolor* may sometimes present a multi-stemmed trunk and a low-branching crown with irregular spreading (Condit et al., 2010; Nelson et al., 2014); these characteristics should provide good structural support for lianas, even though *Guapira* trees tend to have smooth bark. *Neea* are tall shrubs or small to medium-sized trees with round or spreading crowns, some with small buttresses (e.g., *Neea floribunda*) or smooth bark (e.g., *Neea parviflora*) (Williams, 1936); the low stature of *Neea* trees may facilitate their liana colonization. Regarding Fabaceae, the most common genera after applying the density filter of ≥30 individuals, were *Inga*, *Zygia*, *Brownea*, and *Macrolobium* (with 104, 63, 46 and 43 individuals, respectively; **Table 4**). *Zygia* and *Brownea* were already discussed above. *Inga* has no or poorly developed buttresses (Leon, 1966) and sometimes shows the classical mimosaceous umbrella-like dense branching pattern, or a branching pattern that is generally profuse and irregular; these characteristics should provide good structural support for lianas. With regard to *Macrolobium*, depending on the species, one may encounter a mix of liana-deterring and liana-facilitation characteristics. For example, *M. bifolium* is a deciduous medium-height tree (5–18 m) with a large, dense, roundish crown, but the bole can be unbranched for more than half its height (Fern, 2021); this would provide both good and bad structural support for lianas, depending on the size of the tree when a liana colonized it. Regarding Annonaceae, trees in this family tend to have a branch distribution similar to Myristicaceae, i.e. perpendicular to the trunk and regularly spaced. However, unlike Myristicaceae, Annonaceae has bark that is tough and difficult to break (Condit et al., 2010). In the study area, at a TDC ≥7 cm and density ≥30 individuals at the family level, the most common genera of Annonaceae were *Guatteria* and *Duguetia* (with 16 and 14 individuals, respectively). Species of *Guatteria* can vary from short to very tall trees, but most have relatively slender trunks that may be prone to be circumnutated by lianas (Maas et al., 2015). *Duguetia* trees tend to be of low stature, with a spreading crown branching at low heights (Williams, 1936); these characteristics probably help lianas to climb and hang onto them more permanently.

In conclusion, in general, the tree taxa with negative and statistically significant $\hat{\theta}_t$ have certain liana deterring characteristics, while the tree taxa with positive and statistically significant $\hat{\theta}_t$ tend not to have such characteristics. In fact, the tree taxa with positive $\hat{\theta}_t$ tend to have suitable trunks for climbing, with branches at low heights forming dense crowns (high trellis availability). Note that most taxonomic descriptions mainly focus on foliar and floral traits, but give scarce information on architectural and bark characteristics. Yet, these tree characteristics may be relevant to assess the potential for liana load. Although hard to find in the literature, such tree characteristics may certainly be captured in the field by a trained observer.

4.2.4. How to predict liana density using the $\hat{\boldsymbol{\theta}}_t$ estimate

An important application of the $\hat{\theta}_t$ estimates from the model is that they can be used to estimate the local point intensity of lianas, given the influence of different tree taxa, at a given local spatial scale. I hereby elaborate on a simple example using the data from **Table 4** at the genus level. In that Table, the basal liana point intensity (i.e., the point intensity of lianas at any location before taking into account the presence of any tree) is estimated by the model as $e^{-Intercept} = e^{-1.72} = 0.18$ lianas/m^2 or 1 liana/5.58 m^2. If we take, for example, the tree genus *Brownea*, the liana point intensity will change as a function of the value of the *Brownea* tree point intensity. Because a sigma of 10 was used to calculate all tree point intensities, each tree point can raise up to 0.0016 units of the intensity function (the maximum value takes place on top of the point itself). Imagine that in a location u in the forest, there is a tree of the *Brownea* genus; in this location, the predicted liana point intensity could have at least a value of:

$$e^{-Intercept+\hat{\theta}_{Brownea}*Z_{Brownea}(u)} = e^{-1.72+102.37*0.0016} = 0.21 \text{ lianas/m}^2 \text{ (1 liana/4.74 m}^2\text{)}$$

Note that if more *Brownea* trees were around location u, the calculated liana density would increase. Imagine now that there is a forest area with one tree of *Brownea* and one tree of *Pseudolmedia*. Assuming, to simplify (unrealistically), that both trees are located in the same location u, the liana point intensity would be equal to:

$$e^{-Intercept+\theta_{Brownea}*Z_{Brownea}(u)+\theta_{Pseudolmedia}*Z_{Pseudolmedia}(u)} =$$

$$e^{-1.72+102.37*0.0016+117.37*0.0016} = 0.25 \text{ lianas/m}^2 \text{ (1 liana/3.93 m}^2\text{)}.$$

In a similar fashion, for a given area of the forest, we can estimate the local liana density as a function of increasingly more tree taxa (i.e., by including the effect of more tree covariates). This model-based estimation of local liana density is used in the next section to compare the observed vs. predicted density of lianas, at the spatial scale of the 20 m × 20 m quadrats in the study area of 20 m × 500 m, for those models that best resembled the liana prevalence data, as reported by the literature.

4.2.5. Observed vs. predicted liana density in the selected models

For those models that best resembled published liana prevalence field data, I reconstructed, using the $\hat{\theta}_t$ estimates from the models above (red rectangles in **Tables 2** and **3**), the liana point intensities using the point intensities of tree taxa, for every 20 m × 20 m quadrat in the 20 m × 500 m study area. **Figures 5** and **6** show the observed vs. predicted liana density using tree genera and tree families as covariates, respectively. Each point in the scatter plots (also known as calibration plots, in the context of model fitting) represent one of the 20 m × 20 m quadrats (total 25 quadrats). The blue equation and blue line represent the linear regression adjusted to the points. How well the *y*=*x* line (black line) fits the observed vs predicted points is indicated by the NSE index (Moriasi et al., 2007). The closer the points are to the *y*=*x* line, the better is the model prediction.

Figures 5 and **6** show that the quadrats 13−20 (green points; i.e., the area between *y* = 240 m and *y* = 400 m in the study area; see **Figure 1**) have, on average, a higher liana density than the other quadrats (red points). Because this group of quadrats is continuous in space, it is reasonable to assume that there might be one or more spatial covariates acting on these quadrats but not on others, effecting an increase in liana density. Factors that may be causing this pattern are unknown and could be as varied as disturbance intensity, abundance of tree taxa susceptible to liana load (or lack of tree taxa unsusceptible), different soil properties, among others. Some of these potential factors could be related to the spatial distribution of different tree taxa. Including them in future analyses as new, uncorrelated, covariates could increase the model quality to explain the local spatial distribution of lianas.

5. CONCLUSIONS

- From the 120 Poisson models fitted to the spatial distribution of lianas using the spatial distribution of trees, the two models that best resembled (statistically speaking) published liana prevalence data were the ones using a liana diameter class (LDC) $\geq$1 cm at the genus level (ρ=0.718, P=0.017) and a LDC $\geq$2 cm at the family level (ρ=0.628, P=0.006), both with a tree diameter class (TDC) $\geq$7 cm (**Tables 2** and **3**).
- The anatomical descriptions of those tree taxa with $\hat{\theta}_t$ estimates significantly different from zero (**Tables 4** and **5**) are congruent with the sign of the estimate: those taxa with negative $\hat{\theta}_t$ have liana-deterring characteristics, while those taxa with positive $\hat{\theta}_t$ tend not to have such characteristics, and even have trunks suitable for climbing with branches starting at low heights and dense crowns.
- The calibration plots (**Figures 5** and **6**) showed that eight spatially contiguous quadrats had higher liana density than the other quadrats, which implies that there might be other spatial covariates inducing higher liana density in those quadrats. Ecological factors associated to these putative covariates may include disturbance intensity or soil properties; if these covariates are uncorrelated with the spatial distribution of tree taxa, including them in future analyses should increase the model performance or quality.
- Future studies should assess whether the best models calibrated in this study can be used to successfully extrapolate liana density in areas of the 50-ha Yasuní Forest Dynamics Plot where trees have been censused but not lianas, as a way to test the usefulness and real-life accuracy of the models.

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7. TABLES

Table 1. Spearman correlation ***between*** the Z-scores of a model that used tree SPECIES as covariates ***and*** the average liana prevalence in such tree species, for different combinations of tree and liana diameter classes. Only species with ≥30 individuals were included in the analyses.

Liana Diameter Class (LDC) (cm)	**Tree Diameter Class (TDC) (cm)**									
	≥1	**≥2**	**≥3**	**≥4**	**≥5**	**≥6**	**≥7**	**≥8**	**≥9**	**≥10**
≥1	-0.619 (0.115) 8	-0.257 (0.658) 6	0.000 (1.000) 4	0.400 (0.750) 4	0.800 (0.333) 4	1.000 (0.333) 3	-0.500 (1.000) 3	1.000 (0.333) 3	0.500 (1.000) 3	1.000 (1.000) 2
≥1.5	-0.762 (0.037) 8	-0.771 (0.103) 6	0.000 (1.000) 4	0.400 (0.750) 4	0.800 (0.333) 4	0.500 (1.000) 3	0.500 (1.000) 3	0.500 (1.000) 3	0.500 (1.000) 3	1.000 (1.000) 2
≥2	-0.548 (0.171) 8	-0.600 (0.242) 6	0.000 (1.000) 4	0.400 (0.750) 4	0.400 (0.750) 4	0.500 (1.000) 3	0.500 (1.000) 3	0.500 (1.000) 3	1.000 (0.333) 3	1.000 (1.000) 2
≥2.5	-0.595 (0.132) 8	-0.600 (0.242) 6	0.400 (0.750) 4	0.400 (0.750) 4	0.200 (0.917) 4	0.500 (1.000) 3	1.000 (0.333) 3	0.500 (1.000) 3	1.000 (0.333) 3	1.000 (1.000) 2

Legend:

ρ coefficient
(P-value)
Number of comparisons

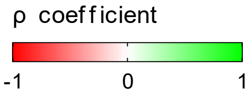


Table 2. Spearman correlation ***between*** the Z-scores of a model that used tree GENERA as covariates ***and*** the average liana prevalence in such tree genera, for different combinations of tree and liana diameter ranges. Only genera with ≥30 individuals were included in the analyses. The model with the most significant Spearman correlation (lowest P-value) is framed by a red rectangle.

Liana Diameter Class (LDC) (cm)	**Tree Diameter Class (TDC) (cm)**									
	≥1	**≥2**	**≥3**	**≥4**	**≥5**	**≥6**	**≥7**	**≥8**	**≥9**	**≥10**
≥1	0.199 (0.253) 35	0.012 (0.951) 30	-0.188 (0.357) 26	-0.161 (0.484) 21	0.191 (0.418) 20	0.311 (0.209) 18	0.718 (0.017) 11	0.500 (0.216) 8	0.393 (0.396) 7	0.200 (0.714) 6
≥1.5	0.153 (0.380) 35	-0.240 (0.201) 30	-0.312 (0.121) 26	-0.279 (0.219) 21	0.156 (0.509) 20	0.317 (0.200) 18	0.627 (0.044) 11	0.119 (0.793) 8	-0.071 (0.906) 7	0.143 (0.803) 6
≥2	0.022 (0.901) 35	-0.107 (0.571) 30	-0.282 (0.162) 26	-0.210 (0.358) 21	0.244 (0.299) 20	0.348 (0.158) 18	0.327 (0.327) 11	0.190 (0.665) 8	0.000 (1.000) 7	0.257 (0.658) 6
≥2.5	-0.024 (0.893) 35	-0.262 (0.162) 30	-0.124 (0.544) 26	-0.209 (0.361) 21	0.310 (0.183) 20	0.286 (0.249) 18	0.382 (0.248) 11	0.119 (0.793) 8	0.214 (0.662) 7	0.543 (0.297) 6

Legend:

ρ coefficient
(P-value)
Number of comparisons

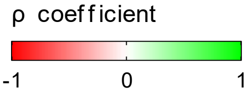


Table 3. Spearman correlation ***between*** the Z-scores of a model that used tree FAMILIES as covariates ***and*** the average liana prevalence in such tree families, for different combinations of tree and liana diameter ranges. Only families with ≥30 individuals were included in the analyses. The model with the most significant Spearman correlation (lowest P-value) is framed by a red rectangle.

Liana Diameter Class (LDC) (cm)	**Tree Diameter Class (TDC) (cm)**									
	≥1	**≥2**	**≥3**	**≥4**	**≥5**	**≥6**	**≥7**	**≥8**	**≥9**	**≥10**
≥1	-0.016 (0.923) 38	0.108 (0.582) 28	0.185 (0.375) 25	0.062 (0.789) 21	0.171 (0.456) 21	0.144 (0.531) 21	0.391 (0.109) 18	0.176 (0.512) 16	0.189 (0.498) 15	0.346 (0.247) 13
≥1.5	-0.147 (0.377) 38	-0.425 (0.025) 28	-0.042 (0.844) 25	0.095 (0.682) 21	0.118 (0.609) 21	0.261 (0.252) 21	0.329 (0.182) 18	0.247 (0.355) 16	0.111 (0.695) 15	0.308 (0.306) 13
≥2	-0.342 (0.036) 38	-0.175 (0.371) 28	0.088 (0.673) 25	0.101 (0.661) 21	0.129 (0.577) 21	0.265 (0.245) 21	0.628 (0.006) 18	0.594 (0.017) 16	0.436 (0.106) 15	0.593 (0.036) 13
≥2.5	-0.300 (0.068) 38	-0.325 (0.092) 28	-0.012 (0.955) 25	0.170 (0.459) 21	0.161 (0.484) 21	0.287 (0.206) 21	0.492 (0.040) 18	0.494 (0.054) 16	0.514 (0.052) 15	0.533 (0.064) 13

Legend:

ρ coefficient
(P-value)
Number of comparisons

ρ coefficient

-1 0 1

Table 4. $\hat{\theta}_t$ estimates (±1 standard error, SE) for the model that best resembled published liana prevalence data using the spatial distribution of tree GENERA as covariates: the model with LDC ≥1 cm and TDC ≥7 cm (red rectangle in **Table 2**). Genera with <30 individuals were excluded from the analyses. $z_t(u)$ is the point intensity of the taxonomic identity t. Taxonomic identities (genera) are sorted by Z-scores, from lowest to highest. Shaded cells mean statistical significance at an α = 0.15, as arbitrarily set in this study.

Tree taxonomic identity *t* of the covariate $Z_t(u)$	**$\hat{\theta}_t$ (±1 SE)**	**Z-score**	**P-value**	**No. tree individuals in 40 m × 500 m area used to calculate each covariate $Z_t(u)$**	**Average liana prevalence from published data (see Equation 7)**	**No. tree individuals analyzed from published data**
(Intercept)	***-1.72 (±0.24)***	***-7.164***	***<0.001***	-	-	-
Matisia (Malvaceae)	-47.63 (±15.51)	-3.070	0.004	126	0.38	16
Eugenia (Myrtaceae)	-116.69 (±40.99)	-2.846	0.007	30	0.50	447
Iriartea (Arecaceae)	-24.94 (±8.85)	-2.818	0.008	162	0.03	440
Siparuna (Monimiaceae)	-30.35 (±21.68)	-1.400	0.150	58	0.56	75
Protium (Burseraceae)	-30.22 (±22.36)	-1.351	0.160	54	-	-
Aparisthmium (Euphorbiaceae)	-9.70 (±7.26)	-1.337	0.163	30	-	-
Eschweilera (Lecythidaceae)	-25.75 (±23.01)	-1.119	0.213	86	0.65	31
Pouteria (Sapotaceae)	-20.86 (±34.31)	-0.608	0.332	36	0.72	228
Gustavia (Lecythidaceae)	-5.81 (±34.49)	-0.168	0.393	37	0.64	209
Guarea (Meliaceae)	2.53 (±17.50)	0.144	0.395	58	0.82	223
Neea (Nyctaginaceae)	15.49 (±26.41)	0.587	0.336	39	0.79	97
Macrolobium (Fabaceae)	14.23 (±17.76)	0.801	0.289	46	-	-
Inga (Fabaceae)	14.77 (±10.93)	1.351	0.160	104	0.76	27
Zygia (Fabaceae)	29.75 (±19.74)	1.507	0.128	43	-	-
Pseudolmedia (Moraceae)	117.37 (±32.85)	3.573	0.001	33	0.57	330
Brownea (Fabaceae)	102.37 (±25.77)	3.973	<0.001	63	-	-

Table 5. $\hat{\theta}_t$ estimates (±1 standard error, SE) for the model that best resembled published liana prevalence data using the spatial distribution of tree FAMILIES as covariates: the model with LDC ≥2 cm and TDC ≥7 cm (red rectangle in **Table 3**). Families with <30 individuals were excluded from the analyses. $Z_t(u)$ is the point intensity of the taxonomic identity t. Taxonomic identities (families) are sorted by Z-scores, from lowest to highest. Shaded cells mean statistical significance at an α = 0.15, as arbitrarily set in this study.

Tree taxonomic identity *t* of the covariate $Z_t(u)$	**$\hat{\theta}_t$ (±1 SE)**	**Z-score**	**P-value**	**No. tree individuals in 40 m × 500 m area used to calculate each covariate $Z_t(u)$**	**Average liana prevalence from published data (see Equation 8)**	**No. tree individuals analyzed from published data**
(Intercept)	***-4.39 (±0.67)***	***-6.584***	***<0.001***	-	-	-
Urticaceae	-83.83 (±31.67)	-2.647	0.012	46	0.45	1065
Myristicaceae	-46.81 (±25.76)	-1.817	0.077	63	0.52	1026
Arecaceae	-15.65 (±16.43)	-0.953	0.253	200	0.20	961
Monimiaceae	-22.94 (±34.78)	-0.660	0.321	59	0.50	109
Malvaceae	-1.84 (±20.08)	-0.091	0.397	210	0.56	882
Violaceae	8.39 (±40.88)	0.205	0.391	40	0.58	98
Moraceae	8.71 (±25.44)	0.342	0.376	125	0.58	1188
Lauraceae	13.56 (±26.65)	0.509	0.351	113	0.44	491
Myrtaceae	31.32 (±48.34)	0.648	0.323	41	0.47	1934
Sapotaceae	30.95 (±41.97)	0.737	0.304	61	0.69	2951
Euphorbiaceae	10.84 (±11.39)	0.951	0.254	100	0.58	1626
Meliaceae	25.21 (±24.53)	1.027	0.235	95	0.66	1668
Lecythidaceae	27.78 (±23.66)	1.174	0.200	140	0.61	259
Burseraceae	35.40 (±30.15)	1.174	0.200	80	0.69	764
Rubiaceae	56.21 (±40.98)	1.372	0.156	42	0.61	497
Nyctaginaceae	72.66 (±31.45)	2.310	0.028	46	0.72	275
Fabaceae	35.14 (±11.25)	3.124	0.003	314	0.63	2498
Annonaceae	168.75 (±43.88)	3.845	<0.001	44	0.51	2147

8. FIGURES

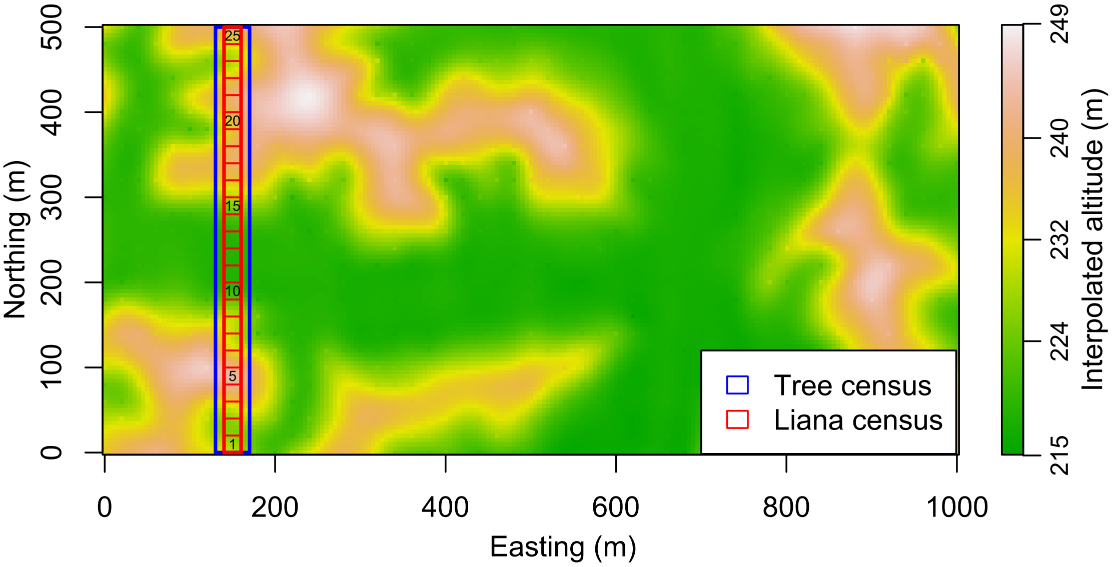


Figure 1. Areas of the tree census (blue rectangle: 40 m × 500 m) and liana census (red rectangle: 20×500 m) used in this study, located within the 50-ha Yasuní Forest Dynamics Plot (YFDP) (1000 m × 500 m). Altitude was interpolated from 1326 altitudinal measurements evenly spaced across the YFDP, using ordinary kriging. The area of the liana census was divided into 20×20 m quadrats, enumerated from 1 to 25 (south to north). The performance of the model to predict liana distribution based on tree distribution was assessed at the level of each quadrat (see calibration plots in **Figures 5** and **6**).

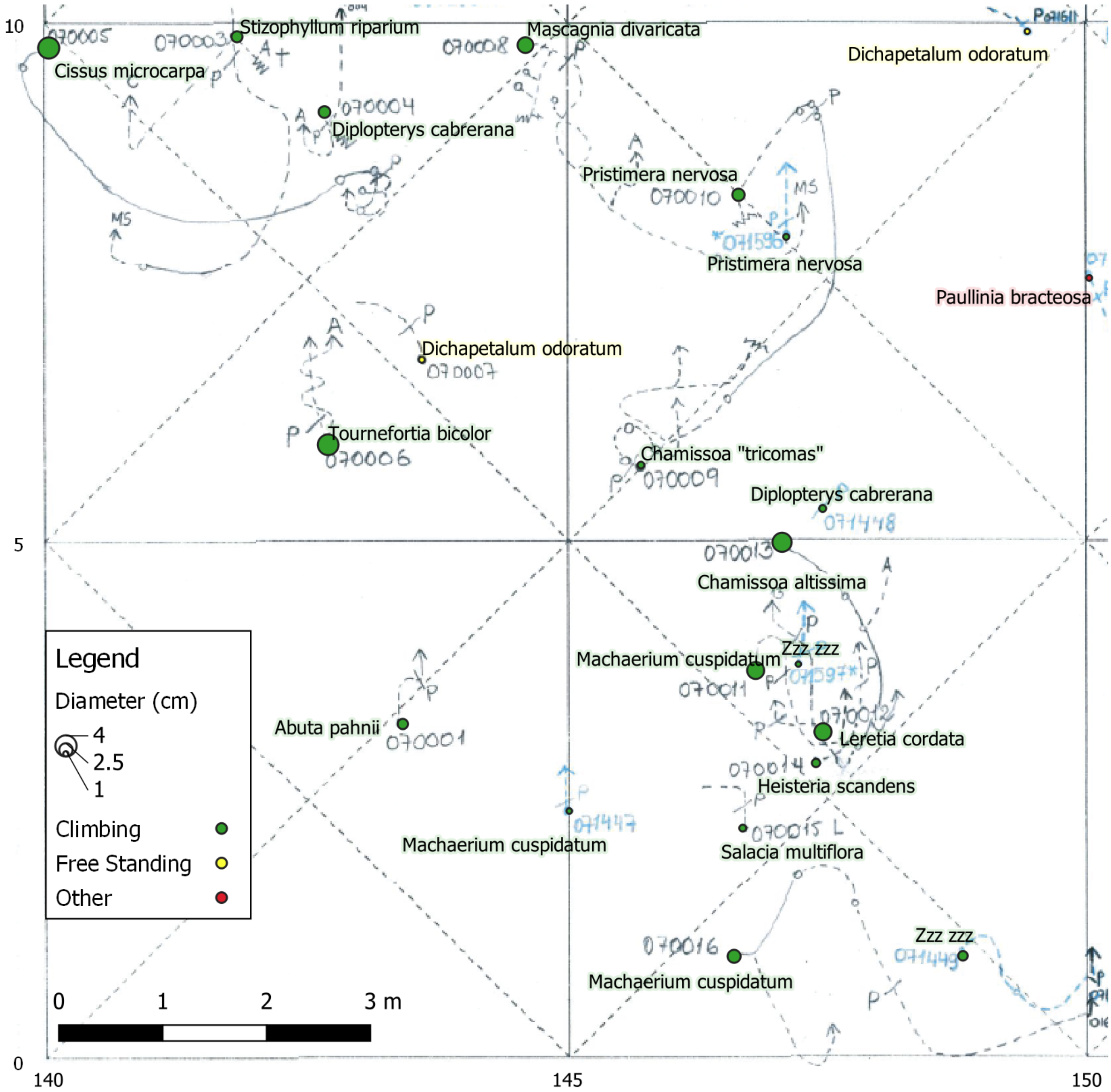


Figure 2. Example of georeferenced layer of primary rooting points of lianas, placed on top of the scanned map, in a 10 m × 10 m quadrat. The diameter of a rooting point circle represents the diameter of the liana.

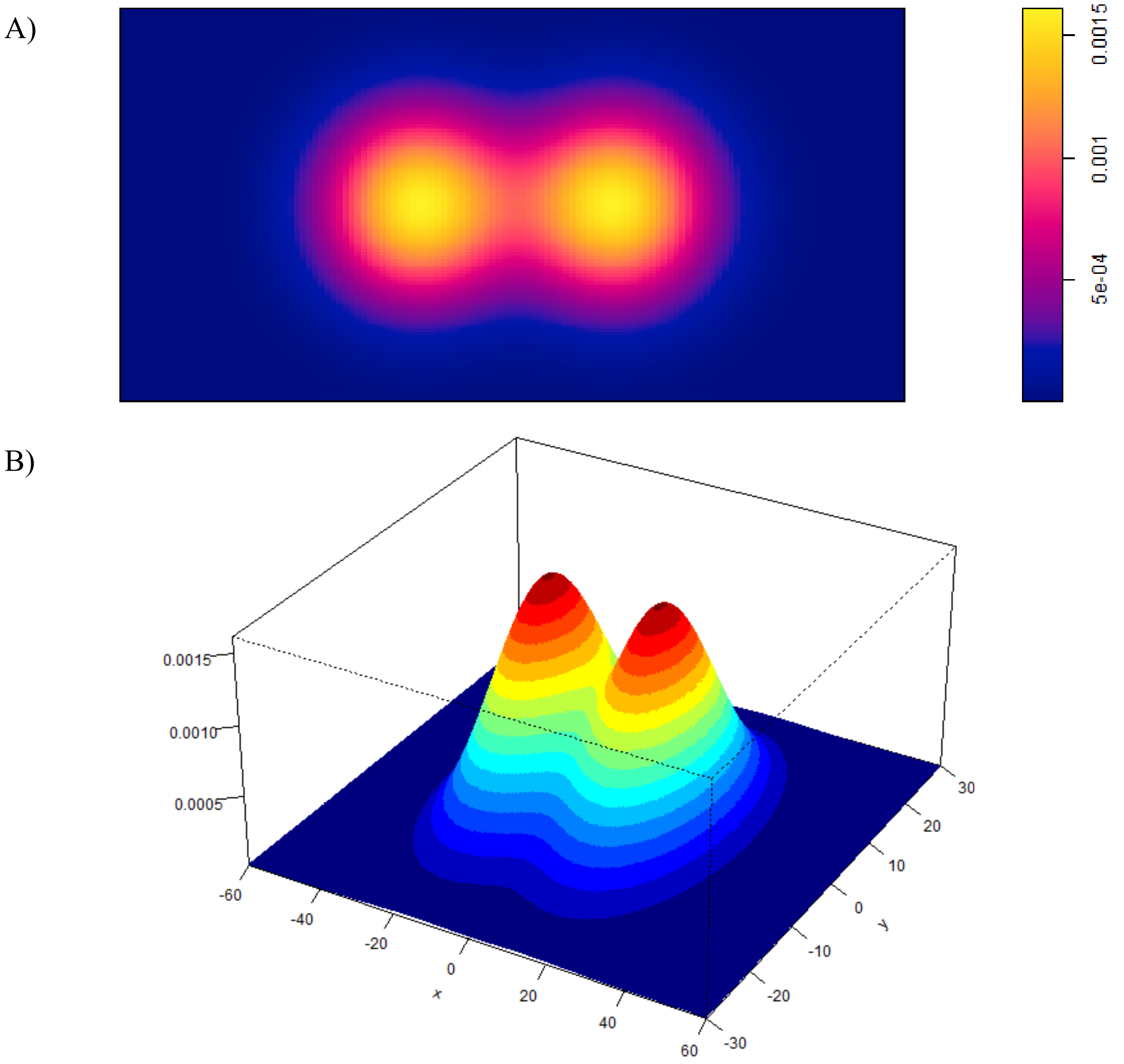


Figure 3. Comparison of the point density for the point pattern composed of the points (-15;0), and (15;0) estimated by: A) the density function of the "spatstat" package in R, and B) manually placing two normal distributions centered at each point of the point pattern. Both methods produce essentially the same output.

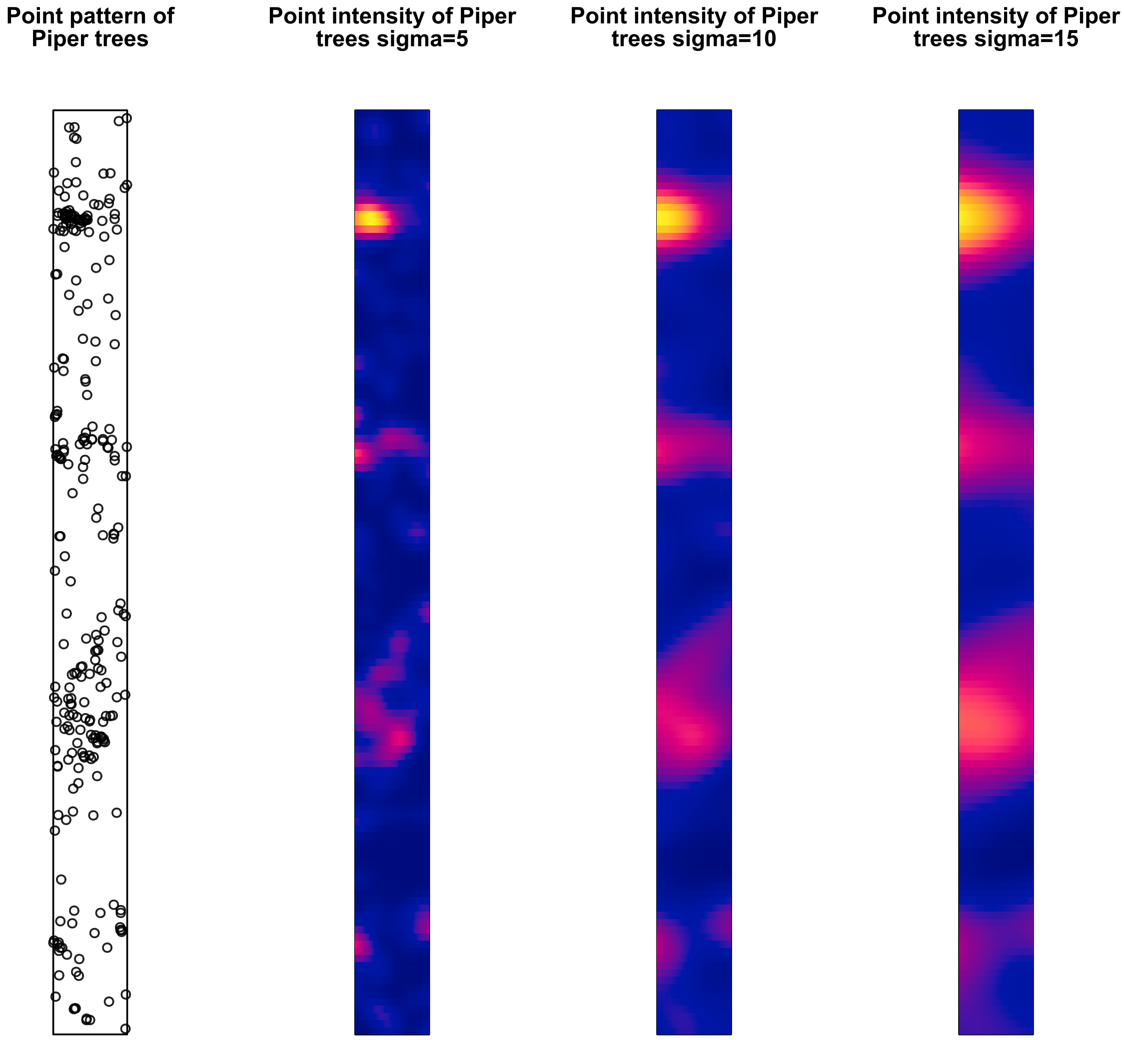


Figure 4. Point pattern of *Piper* trees (left) and its corresponding intensity functions with sigmas 5, 10, and 15. The "density" function in R with a sigma of 5 produces a point intensity that represents the immediate local surroundings of *Piper* trees, while a sigma of 10 produces a point intensity that better represents the community region in which *Piper* tends to grow. A sigma of 15 produces a point intensity that is too smoothed and might color regions outside the region of influence of *Piper* trees, biologically speaking. For this study, I decided to use a sigma of 10. Colors represent different scales for each point intensity layer.

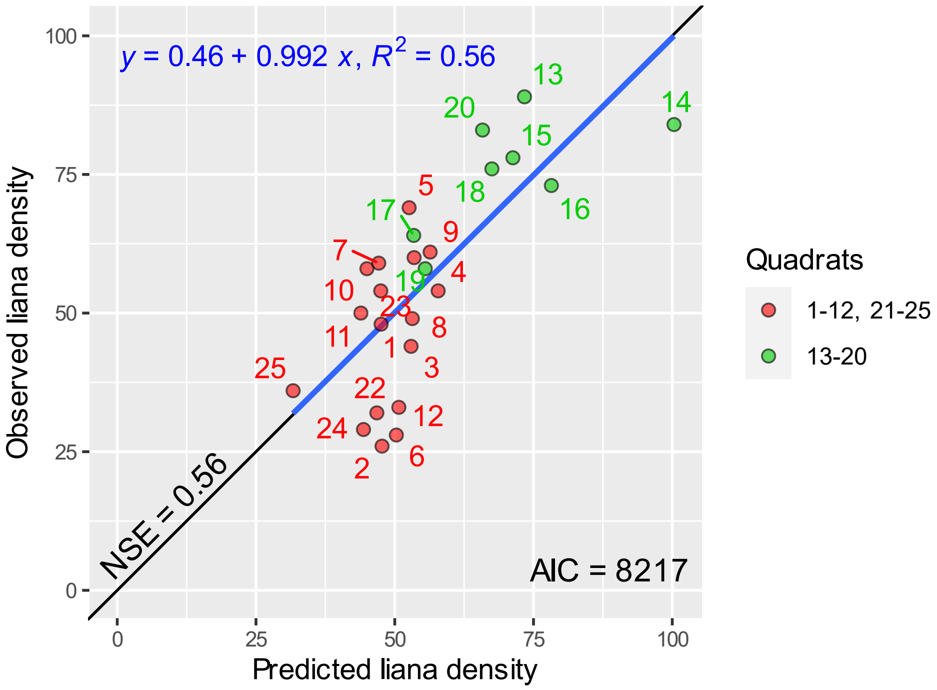


Figure 5. Calibration plot for the model that explains the spatial distribution of lianas ≥1 cm using tree GENERA (DBH ≥7 cm) as covariates (see **Table 4** for the list of covariates). Numbers next to each point are the quadrat names, from 1 to 25 (see **Figure 1**). The quadrats were separated into two groups (red and green dots) based on their observed liana density values. The black line is the *y*=*x* line, while the blue line is the best-fit line.

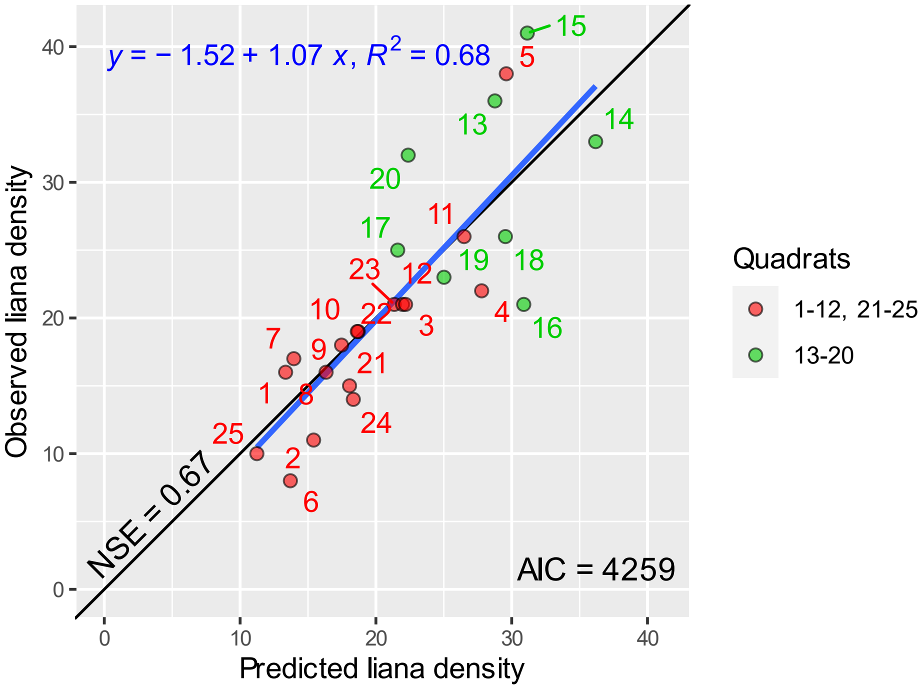


Figure 6. Calibration plot (observed vs. predicted liana density) for the model that explains the spatial distribution of lianas ≥2 cm using tree FAMILIES (DBH ≥7 cm) as covariates (see **Table 5** for the list of covariates). Numbers next to each point are the quadrat names, from 1 to 25 (see **Figure 1**). The quadrats were separated into two groups (red and green dots) based on their observed liana density values. The black line is the *y*=*x* line, while the blue line is the best-fit line.

9. APPENDICES

Appendix A. Brief description of the community structure of lianas and trees in the study area: 20×500 m area (column 07) in the 50-ha Yasuní Forest Dynamics Plot.

By: Hugo Romero-Saltos[1]*, Renato Valencia*[2]*, Consuelo Hernández*[2]*, Franz Chandi*[1]
[1] *Universidad Yachay Tech, Escuela de Ciencias Biológicas e Ingeniería, 100115 Urcuquí, Ecuador*
[2] *Pontificia Universidad Católica del Ecuador, Escuela de Ciencias Biológicas, 17-01-21-84 Quito, Ecuador*

The study area corresponds to a rectangular plot of 20 m × 500 m, known as "column 07" in the 50-ha Yasuní Forest Dynamics Plot (YFDP). This area was divided in 25 quadrats (20×20 m each). Each quadrat was categorized as ridge or valley habitat based on the quadrat's mean altitude; following Romero-Saltos (2011), if mean altitude of a quadrat is ≥227.2 m, it was classified as ridge habitat. This thesis used the data of all lianas with diameter ≥1 cm and all trees with diameter at breast height (DBH) ≥1 cm, censused in 2008 and 2002–2003, respectively.

Size distribution

Figure A1 shows the distributions of relative abundance by diameter classes (10 mm intervals for lianas, and 4 cm for trees) in the ridge and valley habitats. Relative abundance distributions did not differ significantly in the liana community (Kolmogorov-Smirnov test: D=0.363, P=0.2) neither in the tree community (Kolmogorov-Smirnov test: D=0.235, P=0.734).

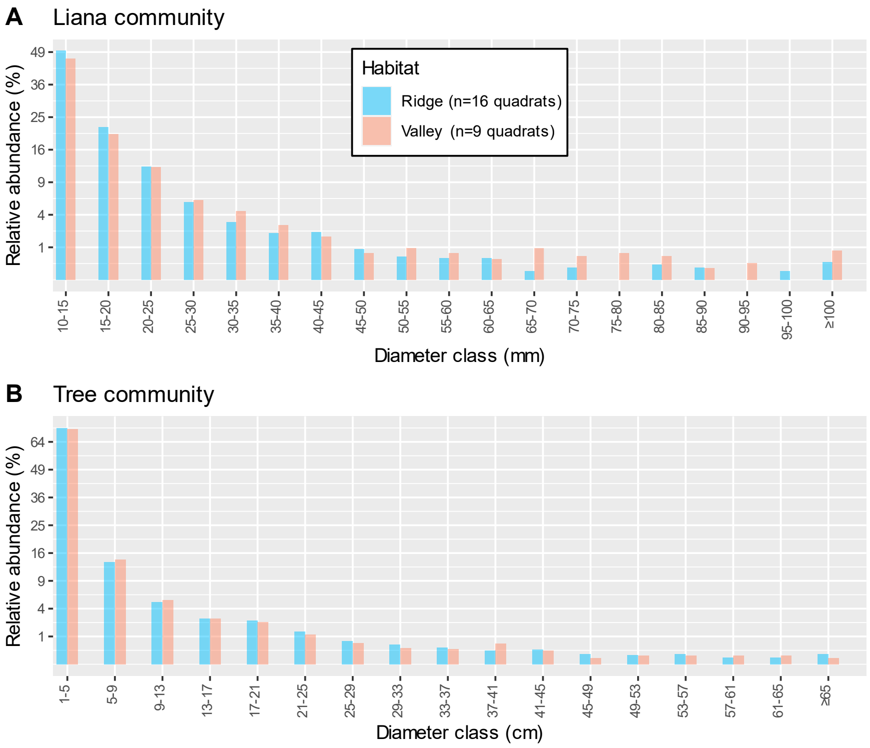


Figure A1. Relative abundance per diameter class of (A) lianas and (B) trees censused in a 20 m × 500 m area in the Yasuní Forest Dynamics Plot. The scale in the *y*-axis is square root transformed to facilitate visualization of small proportions.

Rank-abundance plots

Whittaker rank-abundance plots for the liana and tree communities (**Figure A2**) were adjusted using the Lognormal and Mandelbrot models. Formulas and fitted parameters of these models are described in **Tables A1** and **A2**, respectively. According to AIC, the liana community was best described by the Lognormal model, while the tree community was best described by the Mandelbrot model.

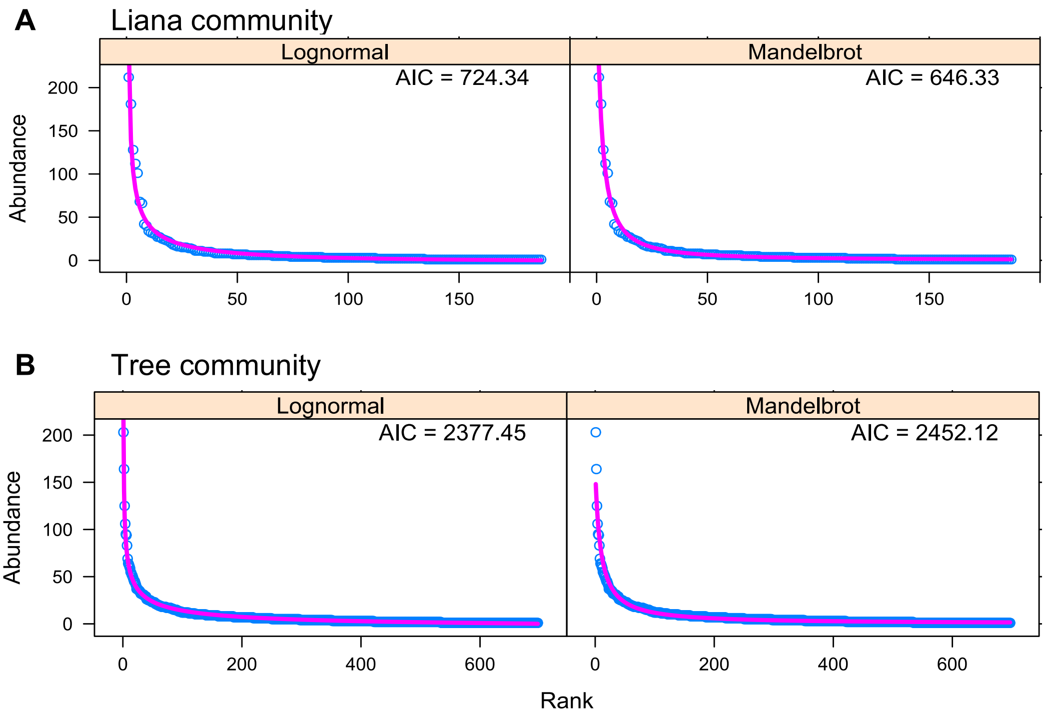


Figure A2. Fitted rank-abundance plots using the Lognormal and Mandelbrot models for the (A) liana community and (B) tree community censused in a 20 m × 500 m area in the Yasuní Forest Dynamics Plot. AIC = Aikake Information Criterion.

Table A1. Formulas to fit a rank-abundance plot using the Lognormal and Mandelbrot models (Oksanen et al., 2020).

Model	Model Formula	Variables
Lognormal	$a_r = \exp\,(log(\mu) + log(\sigma)\,\mathrm{n})$	μ is the mean, σ is the standard deviation, n is a nuisance parameter (a normal deviate) of the log-normal distribution fitted to the observed data
Mandelbrot	$a_r = Nc(r + \beta)^\gamma$	The parameter β is added to the Zipf model and p_1 changes to a meaningless constant c

Table A2. Fitted parameters of the rank-abundance plots using the Lognormal and Mandelbrot models, for the liana and the tree communities censused in a 20 m × 500 m area in the Yasuní Forest Dynamics Plot. AIC = Aikake Information Criterion.

Community	Model	Parameter 1	Parameter 2	Parameter 3	AIC
Lianas	Lognormal	$\log(\mu)$=1.133	$\log(\sigma)$=1.580		724.340
	Mandelbrot	β=0.664	γ=-1.336	c=2.671	646.330
Trees	Lognormal	$log(\mu) = 1.266$	$\log(\sigma) = 1.289$		2377.455
	Mandelbrot	$\beta = 0.354$	$\gamma = -1.092$	$c = 9.812$	2452.119

Density of individuals, species density and Fisher´s alpha

In **Table A3**, the community(ies) of lianas and trees with diameter ≥1 cm were described using the following descriptors: mean density of individuals (N), mean species density (S, defined as No. species / area), and mean Fisher's alpha (α) diversity index. Except for density of individuals (N), these descriptors were calculated excluding the unidentified individuals (152 unidentified lianas and 11 unidentified trees). According to t-tests, density of individuals and species density were not significantly different between the ridge and valley, for both lianas and trees. On the other hand, Fisher's alpha was significantly higher in the valley than in the ridge for trees, but not for lianas.

Table A3 Means (±1 SD, standard deviation) of density of individuals, species density, and Fisher's alpha per 20 m × 20 m quadrat for the ridge (n=16 quadrats) and valley (n=9 quadrats) habitats, for lianas and trees with diameter ≥1 cm censused in a 20 m × 500 m area in the Yasuní Forest Dynamics Plot.

Community	**Descriptor**	**16 Ridge quadrats (20 m × 20 m quadrats)**	**9 Valley quadrats (20 m × 20 m quadrats)**	**t (P-value)**
Liana community	Density of individuals (N)	84.75 (±22.234)	81.778 (±33.026)	0.241 (0.814)
	Species density (S)	32.75 (±6.894)	33.222 (±11.122)	-0.116 (0.910)
	Fisher's alpha (α)	22.463 (±7.201)	27.261 (±9.346)	-1.333 (0.205)
Tree community	Density of individuals (N)	226.938 (±34.171)	223.556 (±49.092)	0.183 (0.858)
	Species density (S)	126.75 (±17.067)	133.556 (±20.433)	-0.847 (0.411)
	Fisher's alpha (α)	120.641 (±20.45)	145.227 (±20.751)	-2.858 (0.011)

Rarefaction of species richness

Rarefaction (species accumulation) curves for species richness (defined as the number of species as a function of the number of individuals, i.e. No. species / No. individuals) was calculated for the ridge and valley habitats, using Chao's et al. (2014) method based on Hill numbers, using the R package "iNEXT" (Hsieh et al., 2020). 84% confidence intervals (CI) were used for the comparison between habitats, because 84% CI correspond to a type I error probability of 0.05 in this type of analyses (Payton et al., 2003). The liana community from the valley had significantly higher species richness than the ridge, but for the tree community there was no significant difference between ridge and valley (**Figure A3**). This diversity pattern for trees contradicts the pattern shown above with the Fisher´s α diversity index, which showed that trees were more diverse in valley than in ridge (**Table A3**).

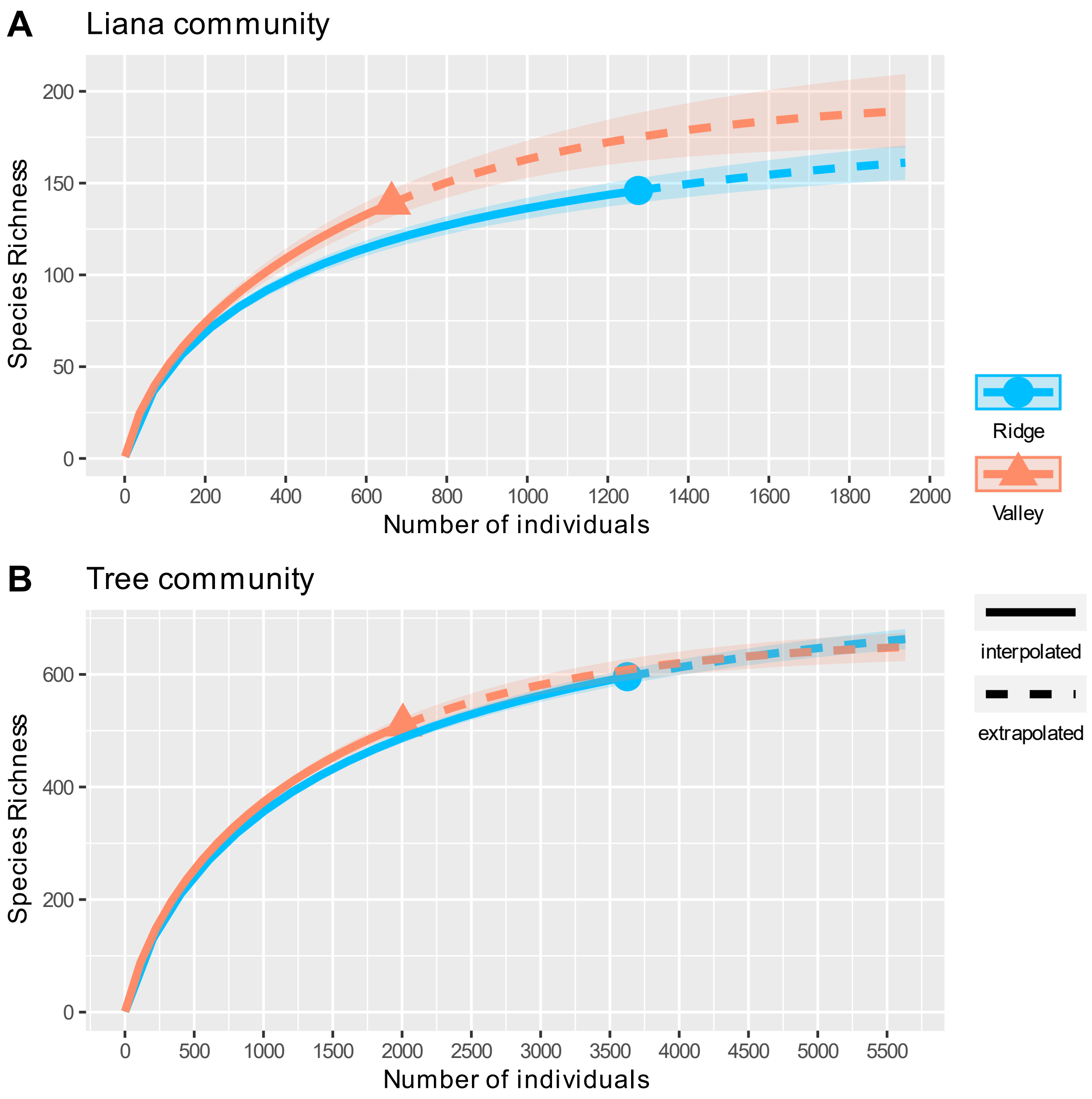


Figure A3. Species richness rarefaction curves for (A) lianas and (B) trees censused in a 20 m × 500 m area in the Yasuní Forest Dynamics Plot. Shaded areas represent confidence intervals at 84%.

Non-metric multidimensional scaling (NMDS) of the liana and tree communities

To capture the overall variation in community structure of lianas and trees in the 20 m × 500 m study area, we conducted Non-metric Multidimensional Scaling (NMDS) ordinations using species abundance data in each of the 20 m × 20 m quadrats. In addition, the community descriptors (density of individuals N, species density S, and Fisher's α; see **Table A3**) were represented onto the NMDS graphs as vectors, along with Altitude (a gradient). Independent NMDS analyses were conducted for lianas and trees (**Figure A4**). Lianas and trees showed similar ordination patterns. The density (N) vector tended to be positively correlated with the Altitude vector (both point to a similar direction), while Fisher's α tended to be negatively correlated with Altitude. For the liana community, species density (S) appears to be positively correlated with Altitude, but this somehow contradicts the findings of the rarefaction curve for lianas (**Figure A3**), although in there we used rarefacted species richness as the response variable, not species density.

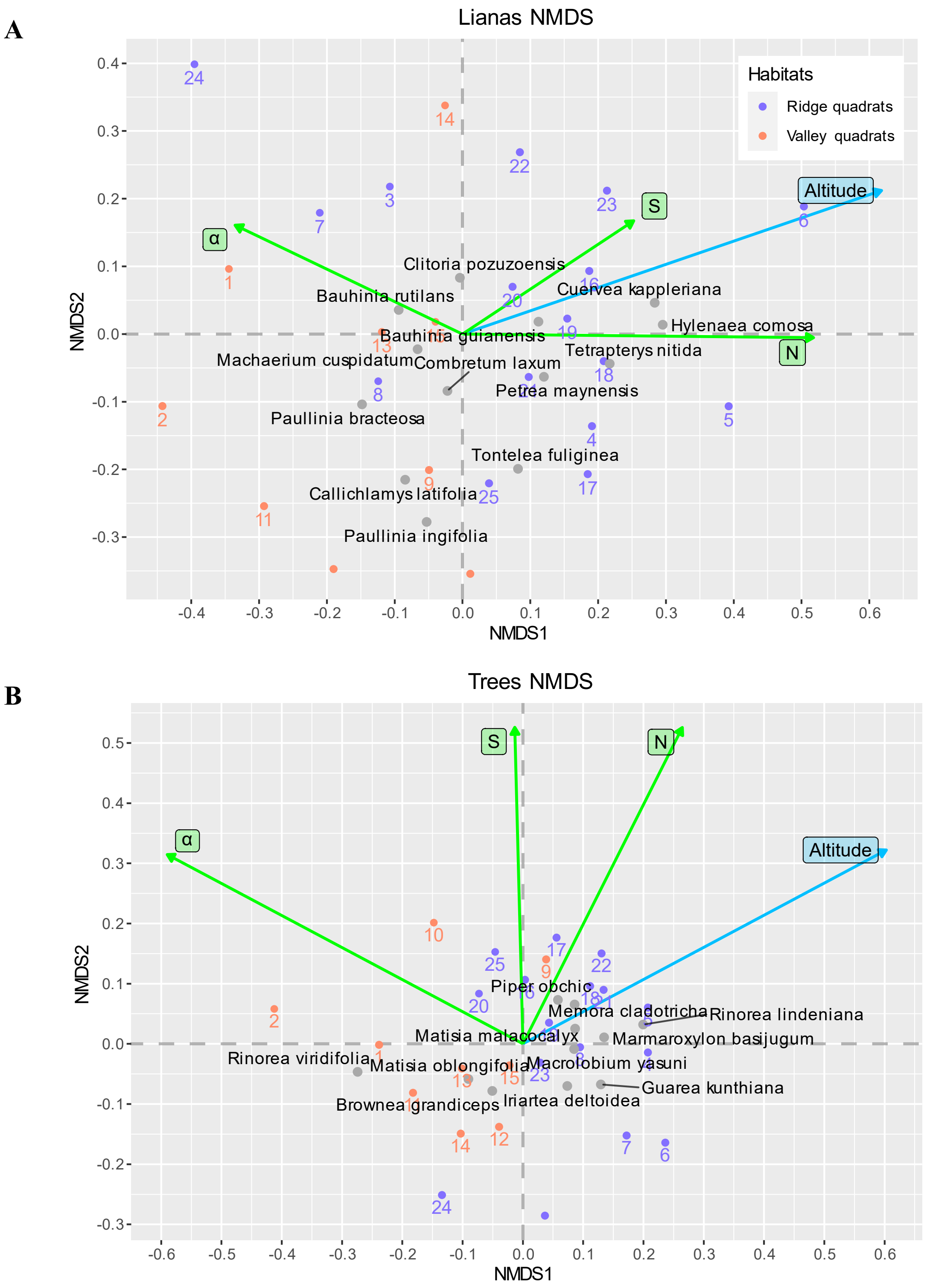


Figure A4. NMDS analyses representing the variation in community structure of (A) lianas and (B) trees censused in a 20 m × 500 m area in the Yasuní Forest Dynamics Plot. Points represent quadrats (with ID number according to **Figure 1**) and the most common species of lianas (≥30 individuals) and trees (≥60 individuals). Tendency vectors represent the community descriptors of density of individuals N, species density S, and Fisher's α.

Appendix B. Site information of the 18 studies used to calculate the average liana prevalence per taxonomic tree identity, at the species, genus, and family levels (modified from Muller-Landau & Visser, 2019). DBH = diameter at breast height. GBH = girth (circumference) at breast height.

Country	Site	Forest type	Years data collected	Tree size	Liana size	Reference
Bolivia	Agroindustria Forestal La Chonta timber concession in the Provice of Guarayos, Department of Santa Cruz	Subtropical humid forest	2001	DBH ≥10 cm	DBH ≥2 cm	Alvira, D., F. E. Putz, and T. S. Fredericksen. 2004. Liana loads and post-logging liana densities after liana cutting in a lowland forest in Bolivia. Forest Ecology And Management 190:73-86.
Argentina	Northern Argentina (258580S, 548130W)	Logged subtropical semideciduous forest	2000	DBH ≥10 cm	DBH ≥1 cm	Campanello, P. I., M. Villagra, J. F. Garibaldi, L. J. Ritter, J. J. Araujo, and G. Goldstein. 2012. Liana abundance, tree crown infestation, and tree regeneration ten years after liana cutting in a subtropical forest. Forest Ecology And Management 284:213-221.
Malaysia	Danum Valley	Virgin lowland diperocarp forest	1987-1989	GBH ≥30 cm	DBH ≥2 cm	Campbell, E. J. F., and D. M. Newbery. 1993. Ecological relationships between lianas and trees in lowland rain-forest in Sabah, East Malaysia. Journal Of Tropical Ecology 9:469-490.
Chile	Valdivian forest	Southern temperate rain forest	2007-2008	Height ≥1.5 m	Height ≥1.3 m	Carrasco-Urra, F., and E. Gianoli. 2009. Abundance of climbing plants in a southern temperate rain forest: host tree characteristics or light availability? Journal Of Vegetation Science 20:1155-1162.
Bolivia	Las Trancas, Lomerio region	Dry subtropical forest	1995	DBH ≥20 cm	Not mentioned	Carse, L. E., T. S. Fredericksen, and J. C. Licona. 2000. Liana tree species associations in a Bolivian dry forest. Tropical Ecology 41:1-10.
Costa Rica	La Selva	Primary wet tropical forest	1987-1988	DBH ≥10 cm	Not mentioned	Clark, D. B., and D. A. Clark. 1990. Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. Journal Of Tropical Ecology 6:321-331.

Country	Site	Forest type	Years data collected	Tree size	Liana size	Reference
United States	Southern Lake Michigan lake plain	Old secondary temperate forest	Not mentioned	DBH ≥5 or ≥10 cm, depending on vegetation type	All lianas physically climbing	Leicht-Young, S. A., N. B. Pavlovic, K. J. Frohnapple, and R. Grundel. 2010. Liana habitat and host preferences in northern temperate forests. Forest Ecology And Management 260:1467-1477.
Argentina	Parque Sierra de San Javier, Tucuman	Subtopical montane forest	2003	DBH ≥10 cm	DBH ≥2 cm	Malizia, A., and H. R. Grau. 2006. Liana-host tree associations in a subtropical montane forest of north-western Argentina. Journal Of Tropical Ecology 22:331-339.
United States	Southwestern Ohio	Mature temperate floodplain forest	2007-2008	DBH ≥10 cm	Height ≥1.3 m	Milks, J. R., J. Hibbard, and T. P. Rooney. 2017. Exfoliating bark does not protect Platanus occidentalis from root-climbing lianas. Northeastern Naturalist 24:520-525.
Panama	Barro Colorado Island	Lowland moist tropical forest	1996-2005	DBH ≥10 cm	Discrete proportions of liana coverage	Muller-Landau, H.C. & Visser, M.D. In press. How do lianas and vines influence competitive differences and niche differences among tree species? Concepts and a case study in a tropical forest Journal Of Ecology.
India	Varagalaiar, Anamalais, Indira Gandhi National Park and Wildlife Sanctuary, Combatore district, Tamil Nadu	Seasonal moist lowland forest	1999	DBH ≥30 cm	DBH ≥1 cm	Muthuramkumar, S., and N. Parthasarathy. 2001. Tree-liana relationships in a tropical evergreen forest at Varagalaiar, Anamalais, Western Ghats, India. Journal Of Tropical Ecology 17:395-409.
Bolivia	Oquiriquia timber concession	Lowland dry to moist tropical forest liana forest	1995	DBH ≥10 cm	DBH ≥2 cm	Perez-Salicrup, D. R., V. L. Sork, and F. E. Putz. 2001. Lianas and trees in a liana forest of Amazonian Bolivia. Biotropica 33:34-47.
Panama	Barro Colorado Island	Lowland moist tropical forest	Not mentioned	DBH ≥20 cm	Not mentioned	Putz, F. E. 1984. How trees avoid and shed lianas. Biotropica 16:19-23.
Brazil	27 forests of southern Amazonia	Tropical forests	2010-2016	DBH ≥10 cm	Discrete proportions of liana coverage	Reis, SM, Marimon, BS, Morandi, PS, et al. 2020. Causes and consequences of liana infestation in southern Amazonia. J Ecol. 108: 2184– 2197.
Puerto Rico	El Verde	Subtropical wet forest	2001-2002	DBH ≥10 cm	DBH ≥1 cm	Rice, K., N. Brokaw, and J. Thompson. 2004. Liana abundance in a Puerto Rican forest. Forest Ecology And Management 190:33-41.

Country	Site	Forest type	Years data collected	Tree size	Liana size	Reference
Peru	Tambopata Nature Reserve	Lowland moist tropical forest	2005-2006	DBH ≥10 cm	Height ≥1.30 m	van der Heijden, G. M. F., J. R. Healey, and O. L. Phillips. 2008. Infestation of trees by lianas in a tropical forest in Amazonian Peru. Journal Of Vegetation Science 19:747-U748.
India	Point Calimere Wildlife Sanctuary	Tropical dry evergreen forest	Not mentioned	GBH ≥10 cm	DBH ≥1 cm	Vivek, P., and N. Parthasarathy. 2017. Patterns of tree-liana interactions: distribution and host preference of lianas in a tropical dry evergreen forest in India. Tropical Ecology 58:591-603.
Malaysia	Pasoh Forest Reserve	Lowland tropical forest	2002	DBH ≥10 cm	Discrete proportions of liana coverage	Wright, S. J., I.-F. Sun, M. Pickering, C. D. Fletcher, and Y.-Y. Chen. 2015. Long-term changes in liana loads and tree dynamics in a Malaysian forest. Ecology 96:2748-2757.

Appendix C. Indices of model performance (NSE, AIC) in each of the 120 models run, for each taxonomic level (species, genus and family).

NSE indices

Table C1. NSE for the models with tree SPECIES as covariates.

Liana Diameter Class (LDC) (cm)	Tree Diameter Class (TDC) (cm)									
	≥1	≥2	≥3	≥4	≥5	≥6	≥7	≥8	≥9	≥10
≥1	0.938	0.865	0.826	0.699	0.522	0.565	0.421	0.249	0.182	0.177
≥1.5	0.762	0.823	0.828	0.614	0.509	0.584	0.435	0.186	0.094	0.110
≥2	0.924	0.821	0.842	0.549	0.469	0.531	0.465	0.137	0.068	0.100
≥2.5	0.410	0.762	0.838	0.501	0.408	0.465	0.429	0.096	0.062	0.082

NSE

Color legend:

-1 0 1

Table C2. NSE for the models with tree GENERA as covariates.

Liana Diameter Class (LDC) (cm)	Tree Diameter Class (TDC) (cm)									
	≥1	≥2	≥3	≥4	≥5	≥6	≥7	≥8	≥9	≥10
≥1	0.933	0.922	0.889	0.856	0.743	0.718	0.558	0.499	0.442	0.314
≥1.5	0.872	0.886	0.789	0.837	0.719	0.696	0.510	0.466	0.438	0.292
≥2	0.947	0.908	0.830	0.807	0.697	0.663	0.553	0.452	0.464	0.402
≥2.5	0.486	0.758	0.790	0.757	0.694	0.706	0.569	0.474	0.486	0.446

NSE

Color legend:

-1 0 1

Table C3. NSE for the models with tree FAMILIES as covariates.

Liana Diameter Class (LDC) (cm)	Tree Diameter Class (TDC) (cm)									
	≥1	≥2	≥3	≥4	≥5	≥6	≥7	≥8	≥9	≥10
≥1	0.742	0.751	0.638	0.708	0.701	0.744	0.697	0.693	0.614	0.505
≥1.5	0.764	0.752	0.618	0.696	0.756	0.736	0.632	0.566	0.593	0.405
≥2	0.773	0.753	0.696	0.684	0.777	0.733	0.673	0.625	0.572	0.495
≥2.5	0.820	0.765	0.690	0.682	0.788	0.772	0.699	0.670	0.666	0.644

NSE

Color legend:

-1 0 1

AIC indices

Table C4. AIC for the models with tree SPECIES as covariates.

Liana Diameter Class (LDC) (cm)	Tree Diameter Class (TDC) (cm)									
	≥1	≥2	≥3	≥4	≥5	≥6	≥7	≥8	≥9	≥10
≥1	8148	8160	8166	8213	8238	8226	8247	8270	8280	8271
≥1.5	5767	5753	5767	5784	5794	5781	5793	5813	5820	5810
≥2	4261	4244	4252	4267	4267	4259	4264	4281	4289	4285
≥2.5	3065	3047	3055	3060	3065	3058	3060	3076	3080	3075

Color legend: AIC 3047 5664 8280

Table C5. AIC for the models with tree GENERA as covariates.

Liana Diameter Class (LDC) (cm)	Tree Diameter Class (TDC) (cm)									
	≥1	≥2	≥3	≥4	≥5	≥6	≥7	≥8	≥9	≥10
≥1	8118	8145	8157	8163	8210	8201	8217	8234	8243	8264
≥1.5	5751	5763	5784	5771	5789	5789	5787	5796	5800	5812
≥2	4252	4254	4257	4256	4274	4266	4269	4264	4261	4267
≥2.5	3038	3047	3056	3054	3067	3050	3053	3053	3049	3048

Color legend: AIC 3038 5651 8264

Table C6. AIC for the models with tree FAMILIES as covariates.

Liana Diameter Class (LDC) (cm)	Tree Diameter Class (TDC) (cm)									
	≥1	≥2	≥3	≥4	≥5	≥6	≥7	≥8	≥9	≥10
≥1	8186	8176	8225	8189	8202	8200	8220	8205	8237	8245
≥1.5	5795	5790	5802	5789	5785	5784	5793	5783	5800	5809
≥2	4286	4278	4267	4255	4245	4251	4259	4248	4273	4274
≥2.5	3071	3055	3047	3052	3049	3045	3050	3039	3057	3051

Color legend: AIC 3039 5642 8245

Appendix D. Number of covariates (number of taxa) and number of tree and liana individuals used in each of the 120 models run, for each taxonomic level (species, genus and family).

Table D1. Number of covariates (TREE SPECIES) and number of tree and liana individuals used in each model.

Liana Diameter Class (LDC) (cm)	**Tree Diameter Class (TDC) (cm)**									
	≥1	**≥2**	**≥3**	**≥4**	**≥5**	**≥6**	**≥7**	**≥8**	**≥9**	**≥10**
≥1	91 6334 1395	46 3210 1395	33 2032 1395	17 1166 1395	12 796 1395	9 576 1395	8 493 1395	6 390 1395	5 328 1395	3 247 1395
≥1.5	91 6334 835	46 3210 835	33 2032 835	17 1166 835	12 796 835	9 576 835	8 493 835	6 390 835	5 328 835	3 247 835
≥2	91 6334 549	46 3210 549	33 2032 549	17 1166 549	12 796 549	9 576 549	8 493 549	6 390 549	5 328 549	3 247 549
≥2.5	91 6334 354	46 3210 354	33 2032 354	17 1166 354	12 796 354	9 576 354	8 493 354	6 390 354	5 328 354	3 247 354

Legend:

N of covariates
N of tree individuals
N of liana individuals

Color legend:

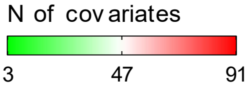


Table D2. Numbers of covariates (TREE GENERA) and number of tree and liana individuals used in each model.

Liana Diameter Class (LDC) (cm)	**Tree Diameter Class (TDC) (cm)**									
	≥1	**≥2**	**≥3**	**≥4**	**≥5**	**≥6**	**≥7**	**≥8**	**≥9**	**≥10**
≥1	78 9336 1395	53 5553 1395	42 3742 1395	32 2611 1395	25 1867 1395	23 1428 1395	16 1005 1395	11 734 1395	9 593 1395	8 499 1395
≥1.5	78 9336 835	53 5553 835	42 3742 835	32 2611 835	25 1867 835	23 1428 835	16 1005 835	11 734 835	9 593 835	8 499 835
≥2	78 9336 549	53 5553 549	42 3742 549	32 2611 549	25 1867 549	23 1428 549	16 1005 549	11 734 549	9 593 549	8 499 549
≥2.5	78 9336 354	53 5553 354	42 3742 354	32 2611 354	25 1867 354	23 1428 354	16 1005 354	11 734 354	9 593 354	8 499 354

Legend:

N of covariates
N of tree individuals
N of liana individuals

Color legend:

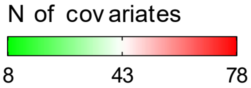


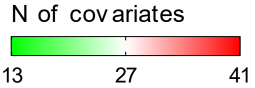
Table D3. Numbers of covariates (TREE FAMILIES) and number of tree and liana individuals used in each model.

Liana Diameter Class (LDC) (cm)	**Tree Diameter Class (TDC) (cm)**									
	≥1	**≥2**	**≥3**	**≥4**	**≥5**	**≥6**	**≥7**	**≥8**	**≥9**	**≥10**
≥1	41 11039 1395	29 6932 1395	25 4924 1395	21 3652 1395	21 2845 1395	21 2279 1395	18 1819 1395	16 1512 1395	15 1297 1395	13 1113 1395
≥1.5	41 11039 835	29 6932 835	25 4924 835	21 3652 835	21 2845 835	21 2279 835	18 1819 835	16 1512 835	15 1297 835	13 1113 835
≥2	41 11039 549	29 6932 549	25 4924 549	21 3652 549	21 2845 549	21 2279 549	18 1819 549	16 1512 549	15 1297 549	13 1113 549
≥2.5	41 11039 354	29 6932 354	25 4924 354	21 3652 354	21 2845 354	21 2279 354	18 1819 354	16 1512 354	15 1297 354	13 1113 354

Legend:

N of covariates
N of tree individuals
N of liana individuals

Color legend:



Appendix E. Code in R used to model the spatial distribution of lianas using the spatial distribution of trees.

The following pages show the R code used not only to conduct the different data analyses, but also to automatically produce the different figures and tables as outputs of the results.

```
#Load libraries
library(tidyr);library(tibble);library(plyr);library(spatstat);library(officer);library(reshape)
library(ggrepel);library(ggpmisc);library(stringr);library(xlsx);library(rstatix)
library(ggtext);library(cowplot);library(grid);library(knitr);library(dplyr);library(sf)
library(flextable);library(officedown);library(iotools);library(raster);library(maptools)
mutate=dplyr::mutate
summarise=dplyr::summarise
#Hide warning messages from r and set default parameters the document visualization
knitr::opts_chunk$set(warning=FALSE,message=FALSE,error=FALSE,echo = TRUE,results='asis',
           fig.cap=TRUE,fig.width=10,fig.height=6,fig.align='center')
set_flextable_defaults(
 font.family = "Arial", font.size = 9,
 theme_fun = "theme_vanilla",digits =3,
 big.mark="", table.layout="autofit")
centeredP <- fp_par(text.align = "center")
figNum<-function(){run_autonum(seq_id = "FigureS", pre_label = "Figure S")}
tabNum<-function(){run_autonum(seq_id = "TableS", pre_label = "Table S")}
addCaptionToFig<-function(fig,label){
 if (class(fig)[1] == 'function'){fig()} else if (is.na(fig)){} else {plot(fig)}
 cat('\n')
 if (is.null(opts_knit$get("rmarkdown.pandoc.to"))) {print(label)}else{
  knit_print_block(block_caption(label=label,style="caption",autonum=figNum()))}
}
addSignif<-function(df){
 add_significance(df,p.col='pval',cutpoints=c(0,0.001,0.01,0.05,1),
          symbols = c("***","**", "*",''),output.col='signif.')
}
#Set the working directory to be the same as the script location
dirname(rstudioapi::getSourceEditorContext()$path) %>% setwd()
```

Code for data loading

Load lianas and trees databases

```
LianaDF <- read.csv("LianaRoots.csv")
TreeDF <- read.csv("Tree Points.csv")
TreeDF <- TreeDF %>%
 #Remove problematic characters from the column specie:
 mutate(specie = gsub('¡|-','',specie))
ClimbingLianas<-LianaDF %>%
 filter(GS == 'c',#Select climbing lianas only
     diameter>=1,#A few interesting lianas with a diameter <1 cm were censed
           #but these are not relevant for this study
     #A couple of censed lianas barely outside the boundaries of the census
     #will be removed as they strictly lie outside the
```

```
    #boundaries of the spatial analysis:
    x>=140,x<=160)
```

There were 2214 liana individuals in the original dataset however, there are only 1395 climbing lianas which are considered for the model training.

Update taxonomic identification of trees

```
updTaxonID<-read.xlsx2("TreeTaxonInfo.xlsx",sheetIndex = 1)
TreeDF<-TreeDF%>%mutate(family=updTaxonID$family[match(family,updTaxonID$oldFam)])
```

Load the literature review data composed by Muller & Visser (2018) about the proportion of trees with lianas (prevalence) per tree species from 18 studies with publishing dates ranging between 1984-2020. This data will be used to compare with the results of this study.

```
litrev<-read.xlsx2("litrevUpdatedTaxon.xlsx",sheetIndex = 1,colClasses=NA) %>%
  dplyr::select(-family) %>% mutate(family=updFam)
#Calculate the average prevalence per taxon group per taxon level
taxonLevels = c('specie','genus','family')
spAvgPrev=litrev %>% mutate(Ninfested=round(prevalence*n)) %>%
  group_by(specie,genus,family) %>% summarise(n=sum(n),Ninfested=sum(Ninfested)) %>%
  mutate(prev=Ninfested/n) %>% mutate(SD=sqrt(prev*(1-prev)/n)) %>% data.frame()
genAvgPrev=spAvgPrev %>% rename(spPrev=prev,spSD=SD) %>% group_by(genus,family) %>%
  summarise(n=sum(n),Ninfested=sum(Ninfested),prev=mean(spPrev),SD=sd(spPrev)) %>% data.fram
e()
famAvgPrev=genAvgPrev %>% rename(genPrev=prev,genSD=SD) %>% group_by(family) %>%
  summarise(n=sum(n),Ninfested=sum(Ninfested),prev=mean(genPrev),SD=sd(genPrev)) %>% data.fr
ame()
avgPrevalence<-list(spAvgPrev,genAvgPrev,famAvgPrev)
names(avgPrevalence)<-taxonLevels
```

Define Bounding boxes for column 7 and for trees used to calculate its point intensities (col7 with 10 meters buffer)

```
col7Window = owin(xrange = c(140,160), yrange = c(0,500))
treesWindow = owin(xrange = c(130,170), yrange = c(0,500))
#Define the quadrats at which to test the model by comparing the observed
#and predicted liana counts
quadrats <- quadrats(col7Window,xbreaks=seq(140,160,20),ybreaks=seq(0,500,20))
```

Plot the study area

```
altitude<-raster("altitude interpolated.grd")
altit.im<-as.im(altitude)
altit.range<-range(altit.im)
NLegendLabels=5
NAltitColors=15
legBreaks=seq(altit.range[1],altit.range[2],diff(altit.range)/(NLegendLabels-1))%>%
  round()
col7=extent(140, 160, 0, 500)
grid<-st_make_grid(col7,n=c(1,25))
grid<-as_Spatial(grid,IDs=paste(1:25))
ids=c(1,seq(5,25,5))
plotStudyArea<-function(){
```

```
  plot(altit.im,axes=TRUE,ann=TRUE,xlab="Easting (m)",ylab="Northing (m)",col=terrain.colors,
      main='',riblab=list(text='Interpolated altitude (m)',padj=0.7),
      ribsep=0.05,ribwid=0.025,
      ribargs=list(cex.axis=0.85,cex.main=1.5,padj=-1,at=legBreaks, labels=legBreaks))
  rect(130,0,170,500,border='blue',lwd=2)
  rect(140,0,160,500,border='red',lwd=2)
  legend(x=700,y=120,legend=c('Tree census','Liana census'),border=c('blue','red'),fill=0)
  plot(grid,add=T,border='red')
  txt.xy<-coordinates(grid[ids])
  text(txt.xy, labels=ids, cex=0.5)
}
svg(filename = 'graficas/Study Area.svg',width=7,height=4.8)
plotStudyArea()
dev.off()
```

```
plotStudyArea()
```

Code to understand the density function

The density function returns the point intensity (PI) of the point pattern (PP) given. To do this, it places Gaussian distributions with a standard deviation equal to the sigma parameter defined at the call of the function or, if the sigma parameter is not defined, the function arbitrarily uses a sigma value that is 1/8 of the shortest side of the point pattern window, which results in a sigma of 5 for the defined trees window. Example of the estimated intensity functions for trees of the piper genus with a sigma of 5, 10 or 15.

```
PiperDF<-TreeDF %>% filter(genus=='Piper')
PiperPP<-as.ppp(PiperDF,W=treesWindow)
plotIntensities<-function(){
  par(mfrow=c(1,4))
  plot(PiperPP,use.marks=FALSE,main='Point pattern of\nPiper trees')
  plot(treesWindow,main='Point intensity of Piper\ntrees sigma=5')
  plot(density(PiperPP),add=TRUE)
  plot(treesWindow,main='Point intensity of Piper\ntrees sigma=10')
  plot(density(PiperPP,sigma=10),add=TRUE)
  plot(treesWindow,main='Point intensity of Piper\ntrees sigma=15')
  plot(density(PiperPP,sigma=15),add=TRUE)
}
svg(filename = 'graficas/compare sigmas.svg')
plotIntensities()
dev.off()
```

```
addCaptionToFig(plotIntensities,'Point pattern of Piper trees (left) and its corresponding intensity functions with sigmas 5, 10, and 15.')
```

the range of influence of a tree point with a sigma of 5 is too local while a sigma of 15 expands that range way too much, therefore a sigma value of 10 is chosen.

```
sigma=10
```

For comparison, a point pattern composed of two points will be used to estimate its point intensity using the density function, and manually placing Gaussian distributions on top of each point and adding up those distributions into a single output layer.

```r
library(GA)
z<-function(x,y){z<-exp(-((x-mux)^2+(y-muy)^2)/(2*(sigma^2)))/(2*pi*sigma^2)}
limx=60;limy=30;sep=15
x <- seq(-limx,limx, length= 500)
y <- seq(-limy,limy, length= 500)
#Gaussian distribution 1:
mux=-sep #mean of x1
muy=0 #mean of y1
f1 <- outer(x,y,z)
##Gaussian distribution 2:
mux=sep #mean of x2
muy=0 #mean of y2
f2 <- outer(x,y,z)
#Add both gaussian distributions:
ft<-f1+f2
png(filename = 'graficas/bivar norm dist sd_10.png',width=8,height=5,
   units='in',res=200)
persp3D(x, y, ft, theta = 30, phi = 30, expand = 0.5,zlab='')
dev.off()

#Using the intended density function of spatstat
w<-owin(c(-limx,limx),c(-limy,limy))
pp<-data.frame(x=c(sep,-sep),y=c(0,0))
samplePP<-as.ppp(pp,W=w)
denscurve<-density(samplePP,sigma=10,edge=F)
svg(filename = 'graficas/intensityTwoPts_sigma_10.svg',width=8,height=5)
plot(denscurve,main=NULL)
dev.off()

compDensFigs<-function(){
  plot(denscurve,main=NULL)
  legend(x='topleft',legend='A',bty='n')
  persp3D(x, y, ft, theta = 30, phi = 30, expand = 0.5,zlab='')
  legend(x='topleft',legend='B',bty='n')
}
addCaptionToFig(compDensFigs,'Comparison of the point intensity calculation methods between a) the density function of the spatstat package, and b) manually placing two normal distributions centered at each point of the point pattern. The point pattern is composed of the points (-15,0), and (15,0).'
)
```

Code for data processing and analyses

A function is defined to model the PI (point intensity) of lianas using the PIs of each tree taxon. The taxon can be at either the species, genus, or family level which is specified by the parameter ‘taxonLvl’ at the call of the function. Because small lianas and trees could produce noise for the model training (since small trees might not had enough time to have an effect in the spatial distribution of lianas, and small lianas might produce a bad representation the preferred liana habitat), liana and tree individuals with diameters smaller than the LTD and TTD parameters are removed. From the remaining individuals, only the tree groups with number of individuals larger or equal than the parameter TNindiv, are used as explanatory variables for the model.

To measure the performance of the model, two metrics are used. The NSE, which measures the similarity between the observed and predicted counts of lianas per each quadrat of 20x20, and the spearman correlation between the Z-score of each tree taxon (how many standard deviations the coefficient associated to a tree taxon is away from the intercept coefficient) and the average prevalence of the corresponding tree taxon according to the literature. These metrics along with the model coefficients are returned by the function defined below:

```r
#Function to extract the coefficients of each model and calculate their P-values
extractCoefs<-function(PoissonMdl,taxonLvl,FilteredTrees){
 df<-summary(PoissonMdl)$coefs.SE.CI %>% dplyr::select(-c('Ztest','CI95.lo','CI95.hi'))
 df<-df %>%
  mutate(pval=round(dnorm(Zval),3)) %>% addSignif() %>%
  mutate(N=FilteredTrees$N[match(rownames(df),FilteredTrees[[taxonLvl]])]) %>%
  rownames_to_column(taxonLvl)
 idx<-which(taxonLvl==taxonLevels)
 if (idx<3){
  for (i in (idx+1):3){
   toAdd<-taxonLevels[i]
   df<-mutate(df,{{toAdd}}:=
         TreeDF[[toAdd]][match(df[[taxonLvl]],TreeDF[[taxonLvl]])]) %>%
    relocate(.data[[toAdd]])
  }
 }
 if (taxonLvl=='specie'){
  df<-mutate(df,specie=gsub('_',' ',specie)) %>% dplyr::select(-genus)
 }
 Prev<-avgPrevalence[[taxonLvl]]
 df[c('Prev','N lit.','SD')]<-Prev[match(df[[taxonLvl]],Prev[[taxonLvl]]),
                      c('prev','n','SD')]
 df<-arrange(df,Zval) %>% dplyr::rename('N indiv.'=N) %>%
  mutate(across(c(where(is.numeric),-pval), round, 3))
 return(df)
}
litrevCorr<-function(df){
 with(df,cor.test(Zval,Prev,method="spearman"))
}

MdlTraining <- function(taxonLvl,LTD,TTD,TNindiv,
            MaxTreeDiam=Inf){
 #Select lianas and trees with diameters higher than the threshold diameters
 FilteredLianas<-ClimbingLianas %>%
  filter(diameter>=LTD)
 FilteredTrees<-TreeDF %>%
  filter(diameter>=TTD,diameter<MaxTreeDiam,!grepl("\\(|zz",.data[[taxonLvl]])) %>%
  group_by(.data[[taxonLvl]]) %>% mutate(N=n()) %>%
  filter(N>=TNindiv) %>%
  mutate({{taxonLvl}}:=as.factor(.data[[taxonLvl]]))

 #Transform the dataframes to point pattern objects
 LianasPP<<-as.ppp(FilteredLianas[c('x','y')], W=col7Window)
 TreesPP<-as.ppp(FilteredTrees, W=treesWindow)
```

```r
 #Calculate the point intensity of each tree taxon
 splittedTrees<-split(TreesPP) #Separate trees in point patterns per each taxon
 TreePI<-density(splittedTrees,sigma=sigma)

 #Adjust the Model
 PoissonMdl<-ppm(LianasPP,trend=~.,data=TreePI)
 #Compare the results with the literature review data
 TreeCoefs<-extractCoefs(PoissonMdl,taxonLvl,FilteredTrees)
 coefsInLitRev<-TreeCoefs %>% drop_na(Prev)
 corrLitRev<-litrevCorr(coefsInLitRev)
 pvalLitRev<-corrLitRev$p.value
 corrLitRev<-round(corrLitRev$estimate,3)
 NofComp<-nrow(coefsInLitRev)
 TreeCoefs<-TreeCoefs %>% mutate(pval=paste0(pval,signif.)) %>%
  dplyr::select(-signif.) %>% rename('Z-score'='Zval','P-value'='pval')
 #Count lianas w/ diameters>=LTD inside each quadrat
 ObsLianaCounts<-quadratcount(LianasPP,tess=quadrats)
 names(ObsLianaCounts)<-25:1
 #Predict the liana counts using the model
 PredLianaCounts<-predict(PoissonMdl,window=quadrats,type='count')
 NSE<-1-(sum((ObsLianaCounts-PredLianaCounts)^2))/
  sum((ObsLianaCounts-mean(ObsLianaCounts))^2)
 NSE<-round(NSE,3)
 TreeCoefs[is.na(TreeCoefs)]<-'-'
 colnames(TreeCoefs)[1:2]<-str_to_title(colnames(TreeCoefs)[1:2])
 aic<-round(AIC(PoissonMdl))
 list(NSE=NSE,AIC=aic,corrLitRev=corrLitRev,pvalLitRev=pvalLitRev,NofComp=NofComp,
    NLianaPts=LianasPP$n,NTreePts=TreesPP$n,NCovars=length(TreePI),TreeCoefs=TreeCoefs,
    TTD=TTD,taxonLvl=taxonLvl,Obs=ObsLianaCounts,Pred=PredLianaCounts)
}
#Function to plot the observed counts vs the model predicted counts
plotObsVsExp<-function(Mdl){
 Obs=Mdl$Obs;Pred=Mdl$Pred;taxonLvl=Mdl$taxonLvl;NSE=Mdl$NSE;NCovars=Mdl$NCovars
 TTD=Mdl$TTD
 maxval=max(c(max(Obs),max(Pred)))
 label = textGrob(label=paste('NSE =',NSE),x=0.2,y=0.85,just=c("right", "top"),
          gp=gpar(col = "red",size = 3))
 taxonLvl <- mapvalues(taxonLvl, from=c("specie", "genus", "family"),
             to=c("species", "genera", "families"))
 plot<-ggplot(mapping = aes(y=Obs,x=Pred))+geom_point()+
  geom_abline(intercept=0,slope=1,col='red')+
  geom_smooth(method='lm',formula=y~x)+
  stat_poly_eq(formula = y~x,col='blue',
   aes(label = paste(..eq.label.., ..rr.label.., sep = "~~~")), parse=TRUE)+
  geom_text_repel(mapping = aes(label = rownames(Obs)))+
  annotation_custom(label, xmin = -Inf, xmax = Inf, ymin = -Inf, ymax = Inf)+
  ylab('Observed counts')+xlab('Predicted counts')+
  expand_limits(x = c(0,maxval), y = c(0,maxval))+
  theme(axis.text=element_text(size=8))
```

```
 plotFile<-paste('graficas/GOF Model with trees at the',taxonLvl,'as covariates.svg')
 ggsave(plotFile,plot,width=6,height=3.7)
 plot
}
```

In order to select the liana threshold diameter (LTD) and the tree threshold diameter (TTD), a function is defined which will run the model for different combinations LTD and TTD and extract the NSE, AIC, number of tree taxa used as covariates, Spearman correlation variables (rho coefficient, P-value, number of taxa compared), number of liana and tree individuals included in each model.

```
LianaD<-seq(1,2.5,by=0.5)
TreeD<-1:10
color.gradient <- colorRampPalette(c("red","white",'green'),alpha=0.9)
col.palette<-color.gradient(30)
map2color<-function(x,pal,limits=NULL){
  if(is.null(limits)) limits=range(x)
  pal[findInterval(x,seq(limits[1],limits[2],length.out=length(pal)+1), all.inside=TRUE)]
}

fixedDecimals<-function(n,dec=2){
 sprintf(paste0("%.",dec,"f"),round(n,dec))
}

MdlAssessmentIndexes<-function(taxonLvl,TNindiv){
 Matrix<-matrix(nrow=length(LianaD),ncol=length(TreeD),
          dimnames=list(LianaD=paste0('\U2265',LianaD),TreeD=paste0('\U2265',TreeD)))
 MatrixList<-list(NSE=Matrix,AIC=Matrix,litRevCor=Matrix,NVars=Matrix,taxonLvl=taxonLvl)
 for (lianaD in 1:length(LianaD)){
  for (treeD in 1:length(TreeD)){
   MdlOutput=MdlTraining(taxonLvl,LianaD[lianaD],TreeD[treeD],TNindiv)
   ZPsignif=data.frame(pval=MdlOutput$pvalLitRev) %>% addSignif %>% pull(signif.)
   NSE=fixedDecimals(MdlOutput$NSE,3)
   pvalLitRev=fixedDecimals(MdlOutput$pvalLitRev,3)
   corrLitRev=fixedDecimals(MdlOutput$corrLitRev,3)
   MatrixList$NSE[lianaD,treeD]<-NSE
   MatrixList$AIC[lianaD,treeD]<-MdlOutput$AIC
   MatrixList$litRevCor[lianaD,treeD]<-
    paste(corrLitRev,paste0('(',pvalLitRev,ZPsignif,')'),MdlOutput$NofComp,sep='\n')
   MatrixList$NVars[lianaD,treeD]<-paste(MdlOutput$NCovars,MdlOutput$NTreePts,
                      MdlOutput$NLianaPts,sep='\n')
   print(paste((lianaD-1)*length(TreeD)+treeD,'/',
         length(LianaD)*length(TreeD),'Models done'))
  }
 }
 return(MatrixList)
}
#Function to plot the matrix with color coded cells
setColor<-function(val){
 idx=gsub('\n.*','',val) %>% as.numeric()
 if (idx>1 || idx<(-1)){
  map2color(idx,rev(col.palette),limits=valLims)
```

```
 } else{
  map2color(idx,col.palette,limits=c(-1,1))
 }
}
LRD='Liana Range\nDiameter\n(cm)';TRD='Tree Range Diameter (cm)'
keys=c(LRD,1:10)
plotColorLegend<-function(palette,valLims,id,taxonLvl){
 coef=id
 if (coef=='Spearman correlation'){coef=expression(paste(rho,phantom(x),'coefficient'))}
 forLegend <<- ggplot()+geom_tile(aes(x=1:2,y=1:2,fill=valLims))+
   scale_fill_gradientn(name=coef,colours= palette,limits=valLims,
              breaks=c(valLims,round(mean(valLims))),
              guide="colorbar",na.value="white")+theme(legend.position = 'bottom')+
   guides(fill = guide_colourbar(title.position = "top",title.theme=element_text(size=9),
                   label.theme=element_text(size=8),
                   frame.colour="black",ticks.colour="black",barheight=0.5))
 leg=get_legend(forLegend)
 ggsave(paste0('leg ',paste(id,taxonLvl),'.svg'),leg,width=2,height=1)
}
ColoredTable<-function(Matrix,title,id,taxonLvl){
 ft<-Matrix %>% as.data.frame() %>% rownames_to_column(LRD)
 typology <- data.frame(
  keys = keys,
  what = c(LRD, rep(TRD,10)),
  measure = names(ft),
  stringsAsFactors = FALSE )
 valLims<<-gsub('\n.*','',unlist(ft[-1])) %>% as.numeric() %>% range()
 if (id=='AIC'||id=='N of covariates'){
  print(paste('the range of',id,'are of',paste(valLims,collapse='-')))
  plotColorLegend(rev(col.palette),valLims,id,taxonLvl)
 } else {
  plotColorLegend(col.palette,c(-1,1),id,taxonLvl)
 }
 names(ft)<-keys
 ft<-flextable(ft) %>% set_header_df(mapping=typology, key="keys") %>% merge_h(part = "header")
%>%
  merge_v(j = LRD, part = "header") %>% theme_vanilla() %>% fix_border_issues() %>%
  bold(j=1) %>% bg(j=2:ncol(ft),part='body',bg=setColor) %>% #vline(j=1,border=fp_border(width=2))
%>%
  width(j=1,width=2.25,unit='cm') %>% width(j=2:11,width=rep(1.3,10),unit='cm') %>%
  align(align = "center", part = "all") %>%
  padding(padding.left=1,padding.right=1) %>% set_caption(title,tabNum())
}

plotMatrices<-function(MatrixList){
 taxonLvl=MatrixList$taxonLvl
 taxonLvl <- mapvalues(taxonLvl, from=c("specie", "genus", "family"),
            to=c("species", "genera", "families"))
 titles<-c(paste('NSE for the models with tree',taxonLvl,'as covariates'),
     paste('AIC for the models with tree',taxonLvl,'as covariates'),
```

```
        paste('Spearman correlation variables for the models with tree',taxonLvl,'as covariates'),
        paste('N of covariates / N of tree Pts / N of liana Pts used in each model'))
 ids<-c('NSE','AIC','Spearman correlation','N of covariates')
 heatmaps<-mapply(ColoredTable,MatrixList[1:4],titles,ids,taxonLvl,SIMPLIFY = F)
 return(heatmaps)
}
```

Tree taxon groups with low number of individuals would likely get coefficients with values due to random chance. Therefore a filter is used to select the tree taxon groups with a number of individuals >= threshold number of individuals (TNindiv). The TNindiv is arbitrarily defined as 30. The models presented in the paper will be the ones that produce the highest Spearman correlation at each taxonomic level.

Models using the spatial distribution of tree species as covariates:

```
rawSppIdxs<-MdlAssessmentIndexes(taxonLvl='specie',TNindiv=30) %>% invisible()

ColoredTablesSpp<-plotMatrices(rawSppIdxs)

ColoredTablesSpp$NSE

ColoredTablesSpp$AIC

ColoredTablesSpp$litRevCor

ColoredTablesSpp$NVars
```

The Spearman correlation matrices have volatile values because only a handful of taxon groups are being compared (2 to 8). Therefore the models using tree species as covariates are not shown in the results section.

Models using the spatial distribution of tree genera as covariates:

```
rawGenusIdxs<-MdlAssessmentIndexes(taxonLvl='genus',TNindiv=30) %>% invisible()

ColoredTablesGenus<-plotMatrices(rawGenusIdxs)

ColoredTablesGenus$NSE

ColoredTablesGenus$AIC

ColoredTablesGenus$litRevCor

ColoredTablesGenus$NVars
```

The model with the most significant Spearman correlation at the genus level has the parameters TTD = 7 cm, and LTD = 1 cm.

Models using the spatial distribution of tree familes as covariates:

```
rawFamIdxs<-MdlAssessmentIndexes(taxonLvl='family',TNindiv=30) %>% invisible()

ColoredTablesFams<-plotMatrices(rawFamIdxs)

ColoredTablesFams$NSE

ColoredTablesFams$AIC

ColoredTablesFams$litRevCor

ColoredTablesFams$NVars
```

The model with the most significant Spearman correlation at the family level has the parameters TTD = 7 cm, and LTD = 2 cm.

Code to visualize coefficients and observed vs. predicted liana counts for the selected models

Coefficient tables and calibration plots of the selected models explained by the spatial distribution of tree species, genera, and families, respectively. Model explained by the spatial distribution of tree genera:

```
GenusMdl<-MdlTraining(taxonLvl='genus',LTD=1,TTD=7,TNindiv=30)
GenusMdl$TreeCoefs %>% flextable() %>% merge_v(j="Family") %>% set_caption('Fitted trend coeffi
cients for the model that explains the spatial distribution of lianas \U2265 1 cm using the spatial distr
ibution of tree genera (\U2265 7cm, \U2265 30 individuals) as covariates',tabNum())
```

```
GenusPlot<-plotObsVsExp(GenusMdl)
addCaptionToFig(GenusPlot,'Calibration plot for the Poisson model fitted to the liana PP using the PD
of tree species (dbh \U2265 7 cm) as covariates.')
```

Model explained by the spatial distribution of tree families:

```
FamMdl<-MdlTraining(taxonLvl='family',LTD=2,TTD=7,TNindiv=30)
FamMdl$TreeCoefs %>% flextable() %>% set_caption('Fitted trend coefficients for the model that ex
plains the spatial distribution of lianas \U2265 1 cm using the spatial distribution of tree families (\U2
265 7cm, \U2265 30 individuals) as covariates',tabNum())
```

```
FamPlot<-plotObsVsExp(FamMdl)
addCaptionToFig(FamPlot,'Calibration plot for the Poisson model fitted to the liana PP using the PD o
f tree families (dbh\U2265 7 cm) as covariates.')
```

To test if young palms have a higher Z value rank, a model is generated using only trees with diameters within a range of 1-5 cm DBH.

```
FamMdlSmallTrees<-MdlTraining(taxonLvl='family',LTD=1.69,TTD=1,TNindiv=30,MaxTreeDiam=5)
FamMdlSmallTrees$TreeCoefs %>% flextable() %>% set_caption('Fitted trend coefficients for the mo
del that explains the spatial distribution of lianas ≥2 cm using small trees (1-5 cm DBH) grouped at th
e genus level as covariates,',tabNum())
```

```
df=data.frame(NSE=FamMdlSmallTrees$NSE,AIC=FamMdlSmallTrees$AIC,'N of tree Fams'=FamMdlS
mallTrees$NCovars,
        'p.coefficient'=FamMdlSmallTrees$corrLitRev,'P-value'=FamMdlSmallTrees$pvalLitRev,
        'N of comparisons'=FamMdlSmallTrees$NofComp)
df %>% flextable() %>% set_caption('Coefficients that evaluate the performance of the model using t
he PI of small trees (1-5 cm DBH) grouped at the family level whose PI are used as covariates.',tabNu
m())
```

To finalize, the tables are saved in spreadsheets:

```
coefs7cm<-list(TreeGenera=GenusMdl$TreeCoefs,
            TreeFams=FamMdl$TreeCoefs,SmallDBHTreeFams=FamMdlSmallTrees$TreeCoefs)
openxlsx::write.xlsx(coefs7cm,"Tree Coefs.xlsx",
                overwrite=TRUE)
openxlsx::write.xlsx(avgPrevalence,"Avg Prevalence.xlsx",
                overwrite=TRUE)
```