Peer-reviewed version available at *Diversity* **2019**, *11*, 196; doi:10.3390/d11100196

Article

Forest Diversity and Structure in the Amazonian Mountains Ranges of Southeastern Ecuador

Wilson Quizhpe [1,*] Ángel Benitez [2], Jesús Muñoz [3], Klever Cuenca [1], Hernán Uvidia [1], Isau Huamantupa [4] and Omar Cabrera [2,*]

[1] Departamento de Ciencias de la Vida, Universidad Estatal Amazónica sede El Pangui, El Pangui, Zamora-Chinchipe, Ecuador.
[2] Departamento of Ciencias Biológicas, Universidad Técnica Particular de Loja, San Cayetano Alto s/n, Loja, Ecuador.
Correspondence: hocabrera@utpl.edu.ec
Tel.: +00-593-7-370-1444
[3] Real Jardín Botánico de Madrid, Plaza de Murillo, 2, 28014 Madrid, España.
[4] Herbario CUZ, Universidad Nacional de San Antonio Abad del Cusco (UNSAAC). Prolongación Av. De la Cultura 733, Cusco.

Abstract:

1) Background: We analyzed the size structure, richness and diversity in eight permanent forest plots in the upper limit of the great Amazon basin located in the Ecuadorian parts of Cordilleras del Cóndor and Cutucú. Our hypothesis was that not all the forests of the eastern mountain ranges are homogeneous in characteristics, but rather present differences in their structure, richness and floristic diversity. In order to test this, our main objective was to classify the types of forests based on characteristics in diametric structure and species composition of the Amazonian forests of the eastern cordilleras in southern Ecuador, and also to determine the influence of critical edaphic-environmental and geomorphological factors. **2) Methods:** Eight one-hectare permanent plots were installed in homogeneous and well-conserved forest stands. Four plots were located in the province of Zamora Chinchipe and four in the province of Morona Santiago. We identified and measured all trees> 10 cm at diameter breast height. For each plot, soil samples were taken, along with environmental and slope data. The multidimensional non-metric adjusted scaling (NMDS) was used to evaluate changes in climatic and geomorphological gradients. The relationship between the composition of the species at the plot level and the edaphoclimatic variables was tested using a canonical correspondence analysis (CCA). Finally, we modeled the change in species diversity (Fisher's alpha) in relation to the climatic gradients, altitudinal and geomorphological using a GLMM**. 3) Results:** Overall, we identified 517 species belonging to 76 families. We determined the existence of two different types of forest, the first one named *Terra Firme*, characterized by the presence of a larger number of species and individuals per plot, compared to the second type of forest, called *Tepuy* or Sandstones forest. Species richness was negatively correlated with soil phosphorus content and pH, mean annual temperature, annual precipitation and altitude. The CCA analysis showed differences in the species composition between the *Terra Firme* and Sandstone forests. The climatic seasonality and the concentration of cations in the soil influence the diversity of the Amazon forest communities of the southeastern cordilleras. The forests of *Terra Firme*, which are settled in more stable and nutrient-rich climatic areas, were more diverse. Sandstone forests are poor in nutrients and develop in areas with stronger seasonality.

Keywords: alpha diversity; canonical correspondence; NMDS; Sandstones Forests; *Terra firme* Forests

---

1. Introduction

Peer-reviewed version available at *Diversity* **2019**, *11*, 196; doi:10.3390/d11100196

Ecuador is considered one of the 17 mega-diverse countries of the world [1], the diversity of plants throughout its territory being a consequence of distribution patterns and geodynamic processes which have been studied during the last decades. The Ecuadorian Amazon is widely known for its great diversity of plants and animals, there have been determined peaks of diversity worldwide recognized [2,3]. Regretfully, anthropic pressure determined by changes in land use and deforestation make it one of the most endangered ecosystems and therefore a priority for conservation [4].

In the last decades, the forests of the Ecuadorian Amazon have been subjected to high rates of deforestation, resulting in modified environmental conditions at a local and regional scale (higher temperatures, changes in precipitation regimes, increased CO2 concentrations), and the fragmentation of these habitats [5]. These ecosystems harbor one of the highest concentrations of vascular plant species [6], but the majority of the studies are limited to the floristic diversity of these ecosystems [7,8]. For example, Silva et al. 2010 [9] omitted the influence that environmental, geomorphologic and soil factors might have on plant diversity. Some authors have pointed out that species richness decreases at higher elevations, and that this reduction is associated with factors such as precipitation, seasonality, soil fertility and topography [10-12]. Others pointed out that climatic variables (e.g., annual rainfall quantity) are not good estimators of richness [13].

In Ecuador, two mountain ranges border the great Amazonian basin at its western limit - Cordillera del Cóndor and the Cutucú. These two Cordilleras are located in the southeastern part of Ecuador, on its border with Peru, being the largest in the country, after the main mountain range of the Andes. They are characterized by having white sandstones plateaus with an acidic nature, similar to those of the northeastern mountains of South America, typical of the Precambrian shield of the Guianas. Additionally, they are located in close vicinity to the Huancabamba depression, the lowest point of the Andes. As a result, the clouds that form on the western slope slide through this depression, and then deposit their moisture load on these ridges, pushed by the prevailing easterly winds [14].

Previous studies conducted in Cordillera del Cóndor [8,14] have revealed a high floristic richness, similar in magnitude to other areas of the Neotropics. Along the Condor and Cutucú mountain ranges there are several small sandstone islands, where countless species endemic to this type of environment grow. These areas show geological characteristics similar to those of the Venezuelan Guyana massif, and their vegetation presents specific characters and adaptations [8].

It is estimated that the flora of the Cordillera del Cóndor exceeds 4,000 species of vascular plants and of 300-400 species of bryophytes [8]. Studies conducted both in Ecuador and Peru document a high species richness; in the case of species above 10 cm DBH, with the average density is of 253 to 300 species per hectare (Phillips et al., 1994 [11-13, 18,19]. Although the flora and vegetation of some specific sites in the Cutucú and Cóndor mountain ranges is known in detail [15-17], no studies have been carried out regarding the factors that determine the richness and diversity in these mountain ranges,

In this context, the main objective of this study was to determine the forest types from the cordilleras of southeastern Ecuador and to determine which environmental factors affect the diversity and structure of these forests. For this, we proposed two questions: (1) Is the forest of the eastern mountain ranges of southern Ecuador homogeneous? and (2) What edapho- climatic or other factors influence the richness, structure and floristic composition of these forests?

2. Methods

2.1 Study area

The study was carried out in eight localities of the Amazonian forests of the Cóndor and Cutucú mountain ranges, in the southeast of Ecuador, located between 700 - 1,650 m, in the provinces of Morona Santiago in the towns of Wusui (plots 5and 6) and Koankos (plots 7,8) and Zamora Chinchipe in the localities of Nangaritza (plots 1,2) and Wawaime (plots 3 and 4) (Figure 1).

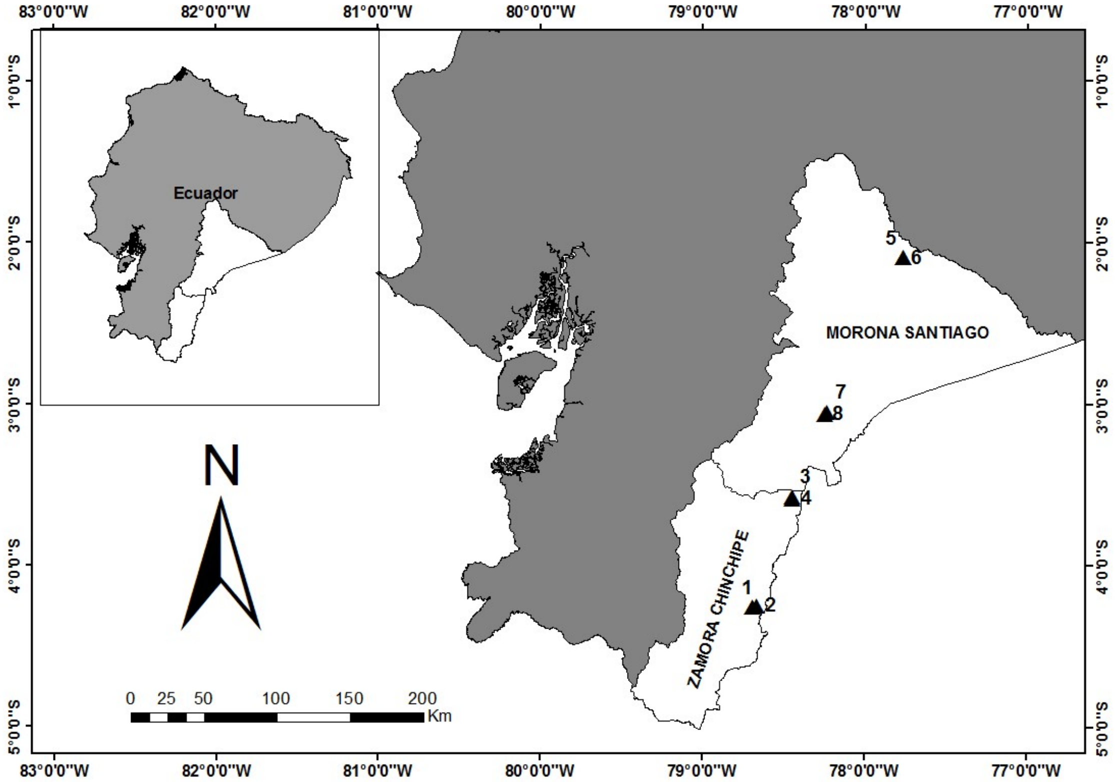

Figure 1. Location of the sampling plots

2.2. Plot installation

In each locality, two permanent one hectare-plots were established. Each of these 8 plots was subdivided into 25 subplots of 20 × 20 m. For each subplot, the geographical position, elevation and slope data were recorded. All individuals equal to or greater than 10 cm in diameter at breast height (DBH) were sampled. This is a standardized methodology that has been applied in other regions of the Neotropics, including Ecuador [20-22].

The collected plants were identified in the Herbarium QCNE and LOJA. For the nomenclature of the species, the catalogs of the flora of Ecuador and Peru were used [23-25]. The similarity between each pair of plots was calculated using the abundance of each species per plot.

To characterize the forests of different localities, structural and floristic parameters were calculated using the equations proposed by [26-28].

Peer-reviewed version available at *Diversity* **2019**, *11*, 196; doi:10.3390/d11100196

$$\text{Relative Diversity(RD)} = \left(\frac{\text{species per Family}}{\text{Total species}}\right) * 100$$

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

2.3 Climatic and Edaphic variables

From each plot, soil samples were collected from the four extremes and one from the center; the five samples were then homogenized and conserved for later analysis. All the laboratory analyzes were performed in AGROBIOLAB (Quito) with standardized protocols for each variable analyzed. The edaphic-climatic variables used were: Hydrogen potential (pH), Electrical conductivity (EC), Organic matter (MO), Aluminum plus hydrogen (AL + H), Boron (B), Calcium (Ca), Cation exchange capacity (CICE), Copper (Cu), Iron (Fe), Potassium (K), Magnesium (Mg), Manganese (Mn), Sodium (Na), Total nitrogen (NH4), Phosphorus (P), Sulfur (SO4), Zinc (Zn).

The bioclimatic data were extracted from Worldclim [29]. The climatic variables that we used were Average annual temperature, Isothermality, Seasonality of Temperature, Annual range of Temperature, Annual total precipitation, Precipitation of the driest month, Seasonality of precipitation, Precipitation of the warmest quarter, and terrain variables like elevation and slope.

2.6 Statistical Analysis

All analyzes were performed using software R 2.14.0. The total species richness was modeled using a Generalized Mixed Linear Models (GLMM) [30]. Using the function glm of software R [31], a saturated model was constructed with the 14 explanatory variables cited above. The relationship between the composition of species and the measured edapho-climatic variables was analyzed by canonical correspondence analysis [32]. Preliminarily the analysis of indirect canonical correspondence (DCA) indicated that the values of standard deviation [33,34], a canonical correspondence analysis (CCA) was performed. Using the step () function, the optimal model based on the AIC (Akaike Information Criterion) statistic was constructed [35,36]. The variance inflation factor (VIF) was calculated to eliminate redundant variables in the final model, considering VIF > 20 the threshold from which a variable was considered highly correlated with the others in the model.

We performed a fitted non-metric multidimensional scaling analysis (NMDS), in which the variables identified in the CCA were used to interpret the ordering. For the CCA and NMDS analyzes, the abundance values were transformed using Hellinger distance, in order to avoid an exaggerated influence of the rare species [37]; the NMDS was calculated using the Euclidean distance. The CCA and NMDS analyzes were done using the "vegan" package [38]. We used SIMPER similarity percentage analysis to know which species are responsible for the similarity/dissimilarity between floristic groups using the same package.

3. Results

3.1 Alpha Diversity and forest structure

A total of 5771 trees > 10 cm DBH were sampled, belonging to 76 families and 517 species. The most diverse family is Fabaceae with 51 species (Relative Diversity RD = 9.9%), followed by Rubiaceae (40 ssp, 7.7%), Euphorbiaceae and Lauraceae with 36 ssp. (7%), Moraceae with 27 ssp. (5.2%), Sapotaceae with 19 ssp. (3.7%), Clusiaceae and Melastomataceae with 18 ssp. (3.5%), Myristicaceae

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 17 September 2019 doi:10.20944/preprints201909.0177.v1

Peer-reviewed version available at *Diversity* **2019**, *11*, 196; doi:10.3390/d11100196

with 15 ssp (2.9%), Burseraceae and Cecropiaceae with 14 ssp (2.7%), Annonaceae and Myrtaceae with 13 ssp. (2.5%), Flacourtiaceae (11 ssp 2.1%) and Sapindaceae with 10 ssp (1.9%). The rest of the 55 families have between 1 and 10 species (0.2-1.7%) (Supplementary Table S1).

The total basal area of the sampled trees reached 185.4 m^2. The family with the highest value of the basal area is Myristicaceae with 17.6 m^2 (9.59% of the total), followed by Moraceae with 15.8 m^2 (8.52%), Sapotaceae with 14.53 m^2 (7.84%), Fabaceae with 12.1 m^2 (6.52%), Euphorbiaceae with 11.9 m^2 (6.44%), Arecaceae 11.9 m^2 (6.41%), Rubiaceae with 10.7 m^2 (5.8%) and Lauraceae with 10.1 m^2 (5.4%). There were 23 families that had between 1- 8 m^2 (0.61-4%), while the rest of families had lower values (0.1-0.53%).

The five species with the highest basal area were *Chrysophyllum sanguineolentum* with 10.5 m^2 (5.7% of Relative dominance), followed by *Otoba glycycarpa* with 9.1 m^2 (4.9%), *Pseudolmedia laevigata* with 4.9 m^2 (2.7%), *Chimarrhis hookeri* with 4.7 m^2 (2.5%) and *Wettinia maynensis* with 4.5 m^2 (2.4%)

The five species with the highest number of individuals were *Wettinia maynensis* (Arecaceae) with 321 (5.6% of the total measured individuals), followed by *Chrysophyllum sanguineolentum* with 260 individuals (4.5%), *Pseudolmedia laevigata* with 175 (3.03%), *Euterpe catinga* with 158 individuals (2.7%) and *Alchornea grandiflora* with 142 individuals (2.5%). There were 179 species (3%) that were represented by a single individual.

3.2 *Species Turnover*

The fitted NMDS analysis shows a clear separation into two groups of plots The first group, that we choose to name *Terra Firme* Forest (TF) was formed by the plots 1-3-5-7. The second group, *Tepuy* forest or White Sandstones forest (UY), was formed by the plots 2-4-6-8 (Figure 2). All the soil variables that were included in the fitted NMDS analysis significantly influenced the grouping of the plots, although with a low correlation is relatively low. On the other hand, phosphorus (P) and iron (Fe) had no significant influence on the formation of the two groups. Regarding the climatic variables, the average annual temperature and precipitation had a significant influence, altitude was also a factor contributing significantly in the grouping (Table 1).

In TF forests are characterized by a greater number of individuals and a greater number of species per unit area, (3,009 DAP individuals ≥ 10 cm were recorded in an area of 40,000 m^2 with an average of 151 species per hectare), compared to the Tepuy forests (2,651 individuals and an average of 89 species).

Table 1. Factors and vectors that significantly influenced the grouping of the forest plots of the eastern mountain ranges of southern Ecuador

Vectors				
Soil	**NMDS1**	**NMDS2**	***r*²**	***P*-value**
K	-0.3582	-0.9336	0.13	**0.001*****
B	0.2160	0.9764	0.13	**0.001*****
pH	-0.2344	-0.9721	0.10	**0.001*****
Mg	-0.2496	-0.9684	0.09	**0.002****
Mn	-0.1163	-0.9932	0.08	**0.001*****
NH4	0.1225	0.9925	0.07	**0.003****

Ca	-0.3771	-0.9262	0.07	**0.003****
Cu	-0.1009	-0.9949	0.07	**0.004****
Zn	-0.2935	-0.9560	0.06	**0.003****
M.O	0.1225	0.9925	0.06	**0.05.**
Na	-0.1816	-0.9834	0.04	**0.023***
Climatic	**NMDS1**	**NMDS2**	***r*²**	***P*-value**
Aat	0.4554	-0.8903	0.05	**0.009****
Pe	0.9169	-0.3990	0.03	**0.048***
Terrain	**NMDS1**	**NMDS2**	***r*²**	***P*-value**
Altitude	0.1486	0.9889	0.11	**0.001*****

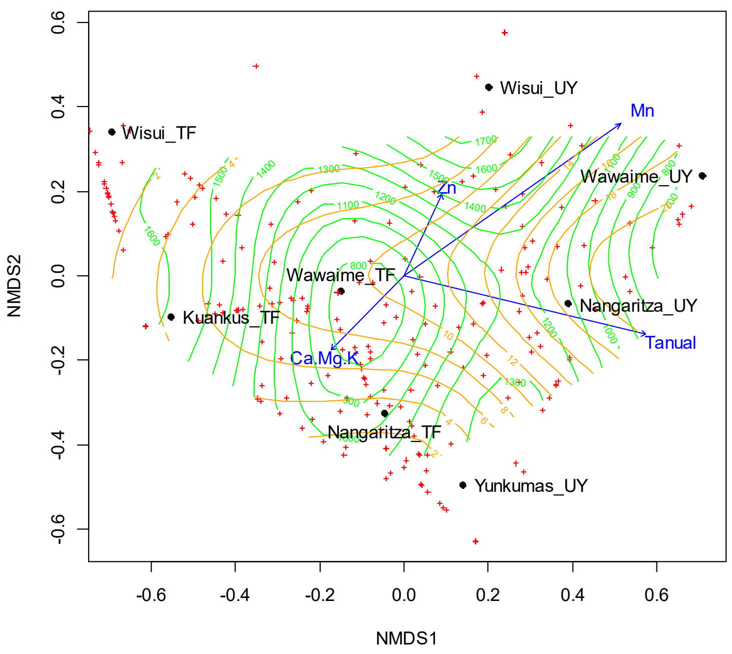

Figure 2. NMDS Analysis shows the differentiation between the TF and UY plots, the green surface represents the elevation, and the orange SO4.

The TF plots were more diverse than the plots in UY forest. TF forests also had a larger volume, except in Nangaritza (UY), which showed a greater volume than the corresponding TF forest from the same sector, and also a greater volume than the rest of the forests of the same formation (Table 2). In each forest, the ecologically dominant species was determined, a list of the three most important species from each of the sampled sites can be found in the Supplementary Table S2.

Table 2. Descriptive values of the attributes of the forests in each plots.

Plot	**Families**	**Genera**	**Species**	**Trees/ha**	**Shanon**	**Basal Area/ha**	**Volume /ha**
Nangaritza TF I	39	81	121	670	3.99	21.35	266.20
Wawaime TF II	41	90	135	948	4.02	34.65	438.24
Wisui TF III	45	100	155	643	4.3	36.02	594.45
Kuankos TF IV	43	106	191	748	3.93	36.01	469.88
Nangaritza UY I	39	61	80	478	3.92	22.74	294.39
Wawaime UYII	24	33	50	445	2.8	9.12	54.54

Peer-reviewed version available at *Diversity* **2019**, *11*, 196; doi:10.3390/d11100196

Wisui UY III	35	68	87	985	3.5	21.06	171.92
Kuankos UY IV	38	74	138	743	3.5	12.79	123.29

The species richness showed a negative correlation with the annual average temperature, phosphorus, pH, annual precipitation and altitude; that means that species richness decreases as the elevation increases. Richness was higher in the TF foresy compared to UY forest, where the soil and environmental characteristics were different. Only the calcium concentration shows a positive relationship with the species richness (Table 3).

Table 3. Results of mixed generalized models of total species richness. Coef = coefficient of variation in the model; SD = standard deviation; *P* = significance of the model (p <0.05).

Variable	**Coef.**	***SE***	***t*-value**	***P***
Intercept	146.42	26.92	5.43	**<0.0001*****
Calcium	1.24	0.2321	5.34	**<0.0001*****
Annual Average Temperature	2.15	0.6984	-3.09	**0.002****
Phosphorus	-1.07	0.1289	-8.35	**<0.0001*****
pH	-6.7	2.05	-3.26	**0.001****
Annual Precipitation	0.0093	0.0022	-4.13	**<0.0001*****
Altitude	0.0093	0.0051	-4.58	**<0.0001*****

Regarding the diametric structure of the forests, the TF plots have significantly more individuals in the first four diametric classes (10-40 cm DBH) than the UY forest plots, except in Wuisui and Kuankus, where the UY plots had more individuals of the first diametric class. The trees of the last two diametric classes (50 -> 50 cm DBH) disappear in the UY forests, except in the town of Wuisui, where one individual belonging to the diametric class VI was present (Figure 3).

Table 4. Number of individuals in the determined diametric classes, in each locality and in each type of forest, bold values show significant differences.

Site/Plot		**CLASS I**		**CLASS II**		**CLASS III**		**CLASS IV**		**CLASS V**		**CLASS VI**	
	Df	**Chi-sq**	***p***	**Chi-sq**	***p***	**Chi-sq**	***p***	**Chi-sq**	***p***	**Chi-sq**	***p***	**Chi-sq**	***p***
Nangaritza Nangaritza	1	3.8	**0.05***	17.8	**< 0.001*****	7.2	**0.007****	0.94	0.33 ns	n/a	n/a	n/a	n/a
Wawaime Wawaime	1	31.5	**< 0.001*****	29.7	**< 0.001*****	25.9	**< 0.001*****	10.7	**0.001*****	3.12	0.08 ns	n/a	n/a
Wisui Wisui	1	30.7	**< 0.001*****	10.3	**0.001*****	22.6	**< 0.001*****	8.2	**0.004****	9.3	**0.003****	0.35	0.55 ns
Kuankos Kuankos	1	3.7	**0.05***	13.6	**< 0.001*****	12.9	**< 0.001*****	13.7	**< 0.001*****	3.1	0.07 ns	3.1	0.07 ns

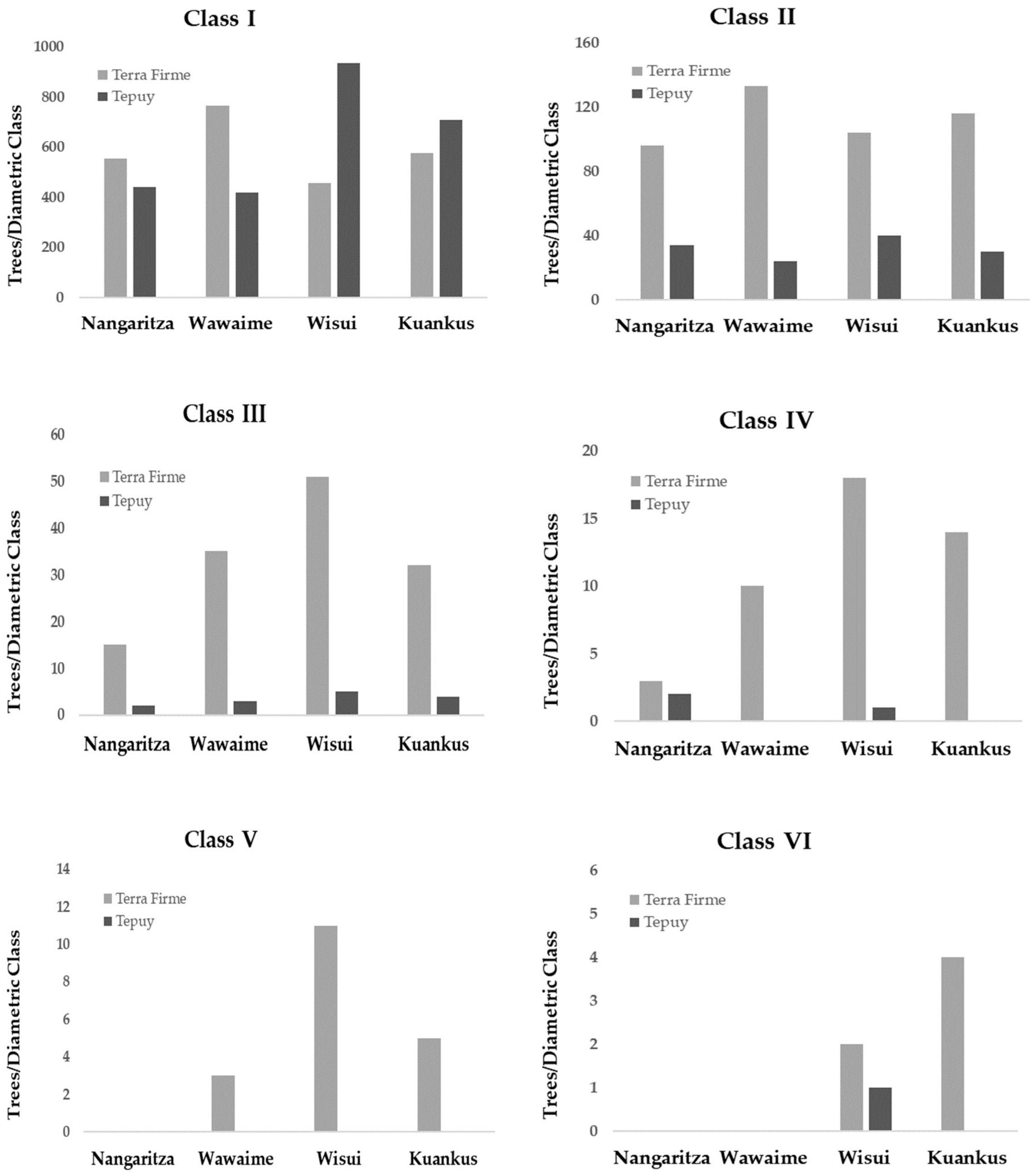

Figure 3. Total number of trees in each diametric class, by sampling site and type of forest.

The SIMPER analysis shows that the plots of the same province and forest type have greater similarity than the plots of the same forest located in another province (Table 5). There are also species which are characteristic of each plot, contributing to the dissimilarity between the plots. The list of the species and their percentage of contribution to the dissimilarity between each forest can be found in the Supplementary Table S3.

Table 5. Dissimilarity values between the different types and sampling areas

PLOTS	Average dissimilarity
UY I - TF III	**99.87**
TF III - UY IV	**99.86**

UY I - TF IV	**99.75**
TF III - UY III	**99.75**
TF I - TF III	**99.3**
TF IV - UY IV	**99.06**
UY I - UY IV	**99.02**
TF I - UY III	**98.94**
UY I - UY III	**98.81**
TF I - TF IV	**98.55**
UY I - TF II	**98.29**
TF I - UY II	**97.53**
TF I - UY I	**97.4**
TF II - TY III	**97.24**
TF II - TF III	**96.65**
TF III - TF IV	**96.58**
TF II - UY II	**96.49**
TF II - TF IV	**95.5**
TF II - UY IV	**95.3**
UY I - UY II	**93.92**
TF I - UY IV	**93.34**
TF I - TF II	**87.54**

The canonical ordering analysis (CCA) shows that the eigenvalues associated with the restricted axes (EV1 = 0.8342; EV2 = 0.6893) are greater than those associated with the unrestricted ones (EV1 = 0.4869; EV2 = 0.4519), so the use CCA is appropriate in this case, although the variance explained by the model is low (Table 6).

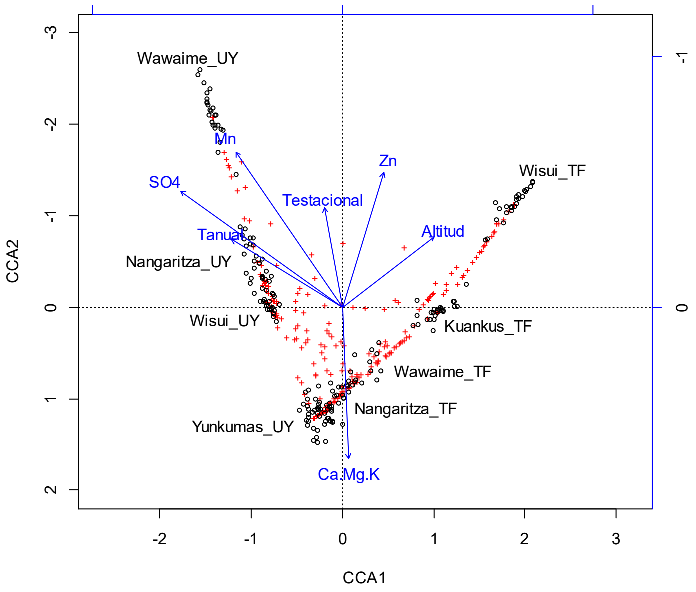

Figura 4. CCA ordination showing grouping at subplot level. N = 200 subplots of 400 m².

Tabla 6. Summary of the CCA model.

	Inertia	Explained Variance		
		Model	Axis 1	Axis 2
Total	33.8	1.0		
~ Tannual + So4 + Ca.Mg.K + Mn + Altitude + Tseasonallity + Zn	4.01	11.87%	2.40%	1.98%
Unconstrained	29.76	88.13%		

4. Discussion

Our results show that the forests from the Cóndor and Cutucú mountain ranges group into two distinct forest types, the *Terra Firme* forest and the Sandstones or *Tepuy* forest, and the differentiation is due to climatic, environmental, topographic and edaphic factors.

Condit et al. 1996 [39] point out the close relationship that exists between abundance and richness: given the same area, a habitat with a larger number of individuals should contain more species than one with a smaller number of individuals. Similar studies conducted in Ecuador and Peru document between 253 to 300 species of DBH ≥ 10 cm per hectare [3,40], which agrees with our results and refutes the claim that lowland Amazonian forests would be richer than the forests found along the base of the Andes mountain range, which in turn should be richer in grasses, shrubs and epiphytes [41].

The ecologically important species were also different between the two types of forest: in the TF forest, the best represented species were *Chrysophyllum sanguineolentum*, *Otoba glycycarpa* and *Wettinia maynensis*, while in the UY forests the most abundant and frequent species was *Alchornea grandiflora*. In forests similar to those studied here, Huamantupa 2009 [42] found that the five most abundant species were: *Iriartea deltoidea*, *Pseudolmedia laevis*, *Otoba glycycarpa*, *Astrocaryum murumuru* and *Leonia glycicarpa*. Other studies in Amazonian forests of Ecuador, Peru and Colombia mentioned Lecythidaceae, Myristicaceae, Arecaceae and Moraceae as dominating this type of ecosystem [9,12,40,43].

The diversity pattern in our study areas was very similar to that found in other Amazonian forests. Other authors, such as [13,44], noted that forests on white sands have a low diversity compared to forests of *Terra Firme*. In our study, the presence of a greater number of species in TF forests was mainly due to edaphic factors. In different ecosystems (Lowland and Montane Forests), species diversity and tree height decrease as altitude increases [10,45-48], which agrees with our observations. In addition, factors such as increased precipitation, lack of seasonality in temperature and natural fertility of soils have been considered determinants in the number of species that certain system is able to sustain [10,49].

Other factors we found to negatively affect the species richness were the level of pH and the concentrations of phosphorus and calcium in the soil. Studies in other ecosystems indicate that the availability of nutrients in the soil is an important factor affecting the richness of tree species [46,48,50]. Our results indicate a similar pattern occurs in the two studied ecosystems, where the wealth in UY forests is reduced due to soils with high levels of homogeneity, acidic pH and poor nutrients. A high richness of arboreal species is related to high levels of soil heterogeneity [51,52].

Peer-reviewed version available at *Diversity* **2019**, *11*, 196; doi:10.3390/d11100196

In addition to edaphic factors, it is assumed that the reduction of tree species in UY forests is due to stressful climatic conditions, such as strong winds, water deficiency, steep slopes and large rock masses. However, it has been observed that, in other tropical ecosystems, species richness increases in places with high to moderate slopes [24,46,53]. Finally, Escudero 1996 [54] notes that rocky outcrops could significantly reduce the space available for tree species to establish.

The plot species composition was mainly determined by a combination of environmental, topographic and edaphic factors (soil parameters). In our case, altitude, temperature and precipitation explained in large part the observed differences in the composition of species. Similar results have been documented in mountain forests and dry forests, where altitude and variables related to water availability are the main determinants of diversity [48,55]. On the other hand, Poulsen et al. 2006 [56] point out that, at local and regional scale, environmental factors such as altitude, topography and edaphic parameters are the main drivers of the floristic changes of the vegetation. In addition, environmental changes at different scales in the Amazon basin influence the floristic composition and distribution of plant communities [10,57-60].

The pH, concentration of cations, nitrogen, phosphorus, copper and soil organic matter largely explained the changes in the composition of species. As mentioned by Neill 2005 [8], the geological composition of the Cordillera del Cóndor region is key to understanding its floristic composition. This is consistent with similar studies carried out in different tropical ecosystems, where soil parameters play an important role in the determination of species composition [19,61-63]. The differences in the composition of species between the TF and UY plots are mainly due to the fact that the former have a greater amount of nutrients and lower acidity. Homeier et al. 2010 [48] states that there is a significant relationship between tree diversity and soil parameters, such as pH, calcium, nitrogen, phosphorus, magnesium and potassium. This is important since there is a decrease in nutrient content and an increase in acidity of the soil as the altitude increases.

The edapho-environmental conditions that exist in the eastern mountain range are a fundamental to understanding the composition and structure of the Terra Firme (TF) and Tepuy (UY) forests. The conservation of these ecosystems can guarantee the survival of a large number of specialized tree species restricted to these habitats.

Finally, Sollins 1998 [64] states that the availability of phosphorus, potassium, calcium and magnesium influences significantly the composition of species in lowland rainforests. Similar results have been reported in Amazonian forests, where calcium and aluminum have shown a high correlation with the distribution patterns of species at regional and local scales [9, 56, 59,65,66].

In conclusion, the diversity of the communities of tree species in the Amazonian forests would be conditioned by environmental, topographic and edaphic factors. Altitude, geomorphology and soil parameters such as pH, nitrogen, phosphorus and potassium would be responsible for the greatest differences in the composition and species richness of the TF and UY forests. In the latter, the conditions of low amount of nutrients and high acidity of the soil would allow the establishment of species adapted to living on white sands soils, which are poor in nutrients.

Supplementary Materials: Table S1: Values of Relative Diversity and number of species determined in the forests of southeastern Ecuador; Table S2: Structural parameters of the three most ecologically important species recorded in each of the plots analyzed in the Terra Firme and Tepuy Forests. DR Relative Density; Dom

Relative Dominance; IVI, Importance Value Index Table S3: Dissimilarity between forest types and sampling sites, species and abundance values and percentage contribution for dissimilarity are shown.

Author Contributions: Conceptualization, W.Q.; A.B.; J.M., methodology, W.Q. A.B. O.C; writing—original draft preparation, W.Q., A.B., J.M., K.C, H.U, I.H. and O.C.; writing—review and editing W.Q,A.B,O.C.

Funding: This research received no external funding.

Acknowledgments: W.Q; K.C; H.U thanks the Universidad Estatal Amazonica for their support in concluding the manuscript, O.C. and A.B., thanks the UTPL for their support in the culmination of the manuscript. We thank Dr. Diana Szeckely for her help in language revision.

References

1. Shi, H.; Singh, A.; Kant, S.; Zhu, Z. & Waller, E. Integrating habitat status, human population pressure, and protection status into biodiversity conservation priority setting. *Conserv. Biol.* **2005**, *19*, 1273-1285. DOI: 10.1111/j.1523-1739.2005.00225.x.
2. Guevara Andino, J. E., Pitman, N. C., ter Steege, H., Mogollón, H., Ceron, C., Palacios, W., ... & Fine, P. V. Incorporating phylogenetic information for the definition of floristic districts in hyperdiverse Amazon forests: Implications for conservation. *Ecol. Evol.* **2017**, *7*, 9639-9650. DOI: 10.1002/ece3.3481.
3. Valencia, R., Balsley, H., & Paz y Miño, G. High tree alpha diversity in Amazonian Ecuador. *Biodivers. Conserv.* **1994**, *3*, 21-28.
4. Añazco, M., Morales, M., Palacios, W., Vega, E., Cuesta, A. "Sector Forestal Ecuatoriano: Propuestas para una gestión forestal sostenible". Serie Investigación y Sistematización No. 8. 2010, Programa Regional ECOBONA-INTERCOOPERATION. Quito.
5. Malhi, Y., Phillips, O. L., Lloyd, J., Baker, T., Wright, J., Almeida, S., ... & Killeen, T. An international network to monitor the structure, composition and dynamics of Amazonian forests (RAINFOR). *J. Veg. Sci.* **2002**, *13*, 439-450. DOI: 10.1658/1100-9233(2002)013[0439:AINTMT]2.0.CO;2.
6. Dinerstein, E., Olson, D. M., Graham, D. J., Webster, A. L., Pimm, S. A., Bookbinder, M. P. & Ledec, G. A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean. 1995. The World Bank/World Wildlife Fund, Washington, D.C.
7. Duque, A., Cárdenas, D. & Rodríguez, N. Dominancia Florística y Variabilidad Estructural en Bosques de Tierra Firme en el Noroccidente de la Amazonía Colombiana. *Caldasia* **2003**, *25*, 139-152.
8. Neill, D.A. Cordillera del Cóndor: Botanical treasures between the Andes and the Amazon. *Plant Talk* **2005**, *41*, 17-21.
9. Silva, J., Montoya, A., López, D. & Hurtado, H. Variación florística de especies arbóreas a escala local en un bosque de tierra firme en la Amazonia colombiana. *Acta Amazónica* **2010**, *40*, 179-188.
10. Gentry, H. A. Tree species richness of upper Amazonian forests. *Proc. Natl. Acad Sci. U.S.A.* **1988**, *85*, 156-159.
11. Phillips, O. L., Hall, P., Gentry, A.H., Sawyer, S. A. & Vasquez, R. Dynamics and species richness of tropical rain forests. *Proc. Natl. Acad. Sci. U.S.A.* **1994**, *91*, 2805–2809.
12. Valencia, R., Foster, R. B., Villa, G., Condit, R., Svenning, J. C., Hernández, C., Romeleroux, K., Losos, E., Magard, E. & Basley, H. Tree species distributions and local habitat variation in the Amazon: Large forest plot in eastern Ecuador. *J. Ecol.* 2004, *92*, 214–229. DOI: 10.1111/j.0022-0477.2004.00876.x
13. ter Steege, H., Sabatier, D., Casterllanos, H., Van Andel, T., Duivenvoorden, J., De Oliveira, A., Ek, R., Lilwak, R., Maas, P. & Mori, S. An analysis of the floristic composition and diversity of Amazonian forests including those of the Guiana Shield, *J. Trop. Ecol.* **2000**, *16*, 801-828. DOI: 10.1017/S0266467400001735.
14. Schulenberg, T.S. & Awbrey, K. (editors). The Cordillera del Cóndor region of Ecuador and Peru: A biological assessment. 1997, RAP Working Papers 7, 1-231.
15. Ulloa, C., & Neill, D. Phainantha shuariorum (Melastomataceae), una especie nueva de la Cordillera del Cóndor, Ecuador, disyunta de un género guayanés. *Novon* 2006, *16*, 281-285. DOI: 10.3417/1055-3177(2006)16[281:PSMUEN]2.0.CO;2.
16. Guayasamin, J.M, & Bonaccorso, E., Eds. Evaluación Ecológica Rápida de la Biodiversidad de los Tepuyes de la Cuenca Alta del Río Nangaritza, Cordillera del Cóndor, Ecuador. 2011. Conservación Internacional. Quito, Ecuador.

17. Neill, D., & Asanza, M. *Lozania nunkui* (Lacistemataceae), a new species from the sandstone plateaus of the Cordillera del Cóndor in Ecuador and Peru. *Novon* **2012**, *22*, 207-211. DOI: 10.3417/2009021
18. Vásquez, R. & Phillips, O. Allpahuayo: Floristics, Structure, and Dynamics of a High.Diversity Forest in Amazonian Perú. *Annals of the Missouri Botanical Garden* **2000**, *87*, 499-527. DOI: 10.2307/2666143
19. Pitman, N. C. A., Terborgh, J. W., Silman, M. R., Núñez V., Neill, D. A., Ceron, C. E., Palacios, W. A. & Aulestia, M. Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* 2001, *82*, 2101–2117. DOI: 10.1890/0012-9658(2001)082[2101:DADOTS]2.0.CO;2.
20. Dallmeier, F. Long-term monitoring of biological diversity in tropical forest areas - Methods for establishment and inventory of permanent plots. United Nations Educational, 1992, Scientific and Cultural Organization, Paris.
21. Campbell, P., Comiskey, J., Alonso, A., Dallmeier, F., Nuñez, P., Beltran, H., Baldeon, S., Nauray, W., Colina, R.D.L., Acurio, L. & Udvardy, S. (2002) Modified Whittaker plots as an assessment and monitoring tool for vegetation in a lowland tropical rainforest. *Environmental Monitoring and Assessment* **2002**, *76*, 19-41.
22. Condit, R. S., Ashton, M. S., Balslev, H., Brokaw, N. V., Bunyavejchewin, S., Chuyong, G. B., ... & Ewango, C. E. Tropical tree a-diversity: results from a worldwide network of large plots. Biologiske Skrifter.2005.
23. Brako, L. & Zarucchi, J.L. Catálogo de las Angiospermas y Gimnospermas del Perú. *Monographs in Systematic Botany from the Missouri Botanical Garden* **1993**, *45*, xl, 1-1286.
24. Jørgensen, P. & S. León-Yánez (editors). (1999) Catalogue of the Vascular Plants of Ecuador. *Monographs in Systematic Botany from the Missouri Botanical Garden* **1999**, *75*, 1-1181.
25. León-Yánez, S., Valencia, R., Pitman, N., Endara, L., Ulloa, C. & Navarrete, H. (eds.). Libro rojo de las plantas endémicas del Ecuador, 2ª edición. Pontificia Universidad Católica del Ecuador, 2011, Quito.
26. Cabrera, O., Benítez, Á., Cumbicus, N., Naranjo, C., Ramón, P., Tinitana, F., & Escudero, A. Geomorphology and Altitude Effects on the Diversity and Structure of the Vanishing Montane Forest of Southern Ecuador. *Diversity* **2019**, *11*, 32. DOI: 10.3390/d11030032.
27. Madsen, J.E.; Øllgaard, B. Floristic composition, structure, and dynamics of an upper montane rain forest iSouthern Ecuador. *Nord. J. Bot.* **1994**, 14, 403–423.
28. Magurran, A.E. Why diversity? In *Ecological Diversity and Its Measurement*; Springer: Dordrecht, The Netherlands, 1988; pp. 1–5.
29. Hijmans, R.J.; Cameron, S.E.; Parra, J.L.; Jones, P.G.; Jarvis, A. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **2005**, *25*, 1965–1978, DOI:10.1002/joc.1276.
30. Mccullagh, P. & Nelder, J. A. 1989. Generalized linear models (2nd edition). CRC Press/Chapman and Hall, Boca Raton, Florida.
31. R Development Core Team. *A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2013; ISBN 3-900051-07-0.
32. Hill, M.O. & Gauch, H.G. (1980) Detrended correspondence analysis: an improved ordination technique. *Vegetation* **1980**, *42*, 47–58.
33. ter Braak, C.J.F. Canonical correspondence analysis, a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 1986, *67*, 1167–1179. DOI: 10.2307/1938672.
34. Legendre, P., & Anderson, M.J. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecol Monogr* **1999**, *69*, 1–24.
35. Oksanen, J. Constrained Ordination: Tutorial with R and vegan. 2012. Available at: http://cc.oulu.fi/~jarioksa/opetus/metodi/sessio2.pdf (accessed May 31th).
36. Cayuela, L., Golicher, D.J., Rey Benayas, J.M., González-Espinosa, M. & Ramírez-Marcial, N. Fragmentation, disturbance and tree diversity conservation in tropical montane forests. *J Appl. Ecol.* 2006, *43*, 1172-1181. DOI: 10.1111/j.1365-2664.2006.01217.x.
37. Legendre, P., & Gallagher, E.D. Ecologically meaningful transformations for ordination of species data. *Oecologia* **2001**, *129*, 271-280. DOI: 10.1007/s004420100716.
38. Oksanen, J.; Blanchet, F.G.; Kindt, R.; Legendre, P.; Minchin, P.R.; O'Hara, R.B.; Oksanen, M.J. *Package 'vegan'. Community Ecology Package*; Version, 2(9); 2013. Available online: https://cran.r-project.org/web/packages/vegan/vegan.pdf (accessed on 12 October 2018).

Peer-reviewed version available at *Diversity* **2019**, *11*, 196; doi:10.3390/d11100196

39. Condit, R., Hubbell, S.P., Lafrankie, J. V., Sukumar, R., Manokaran, N., Foster, R. B., & Ashton, P.S. Species-area and species-individual relationships for tropical trees: A comparison of three 50- ha plots. *J. Ecol.* **1996**, *84*, 549-562.
40. Pitman, N. C. A., Terborgh, J. W., Silman, M. R., Núñez V., Neill, D. A., Ceron, C. E., Palacios, W. A. & Aulestia, M. Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* 2001, *82*, 2101–2117. DOI: 10.1890/0012-9658(2001)082[2101:DADOTS]2.0.CO;2.
41. Gentry, A.H. Floristic similarities and differences between Southern Central America and Upper and Central Amazonia. Pp. 141-157 en A. H. Gentry, editor. Four Neotropical Rainforests. 1990. Yale University Press, USA.
42. Huamantupa, I. Análisis de la composición arbórea en los bosques amazónicos de tierra firme en la base de los Andes. Tesis de Maestría, 2009. Universidad Internacional Menéndez Pelayo.
43. Condit, R., Pitman, N., Leigh, E. G., Chave, J., Terborgh, J., Foster, R. B., Nuñez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H., Losos, E. & Hubbell, S. P. Betadiversity in tropical forest trees. *Science* **2002**, *295*, 666–669. DOI: 10.1126/science.1066854.
44. Fine, P.V.A., Villacorta, R., Pitman, N., Mesones, I. & Kembel, W. A Floristic study of the white-sand forests of Peru. *Annals of the Missouri Botanical Garden* **2010**, *97*, 283-305. DOI: 10.3417/2008068.
45. Lieberman, D., Lieberman, M., Peralta, R., & Hartshorn, G. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *J. Ecology*, **1996**, 84, 137–152.
46. Aiba, S., & Kitayama, K. Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant. Ecol.* **1999**, *140*, 139–157.
47. Kessler, M. The elevational gradient of Andean plant endemism: Varying influences of taxon-specific traits and topography at different taxonomic levels. *J. Biogeogr.* 2002, 29, 1159–1165. DOI: 10.1046/j.1365-2699.2002.00773.x.
48. Homeier, J., Breckle, S., Gunter, S., Rollembeck, R., & Leuschner, C. Tree Diversity, Forest Structure and Productivity along Altitudinal and Topographical Gradients in a Species-Rich Ecuadorian Montane Rain Forest. *Biotropica* **2010**, *42*, 140-148. DOI: 10.1111/j.1744-7429.2009.00547.x.
49. Clinebell, R. R.., Phillips, O. L., Gentry, A. H., Stark, N. & Zuuring, H. Prediction of neotropical tree and liana species richness from soil and climatic data. *Biodivers.Conserv.* **1995**, *4*, 56-90.
50. Givnish, T. J. On the causes of gradients in tropical tree diversity. *J. Ecol.* 1999, *87*, 193-210. DOI: 10.1046/j.1365-2745.1999.00333.x.
51. Tilman, D., & Pacala, S. The maintenance of species diversity in plant communities. Species Diversity in Ecological Communities. 1993. University of Chicago Press, Chicago.
52. Rajaniemi, T. K. Explaining productivity-diversity relationships in plants. *Oikos* 2003, 101, 449–457. DOI: 10.1034/j.1600-0706.2003.12128.x.
53. Slik, J. F., Raes, N., Aiba, S. I., Brearley, F. Q., Cannon, C. H., Meijaard, E., ... & Sheil, D. Environmental correlates for tropical tree diversity and distribution patterns in Borneo. *Divers. Distrib.* 2009, 15, 523-532. DOI: 10.1111/j.1472-4642.2009.00557.x.
54. Escudero, A. Community patterns on exposed cliffs in a Mediterranean calcareous mountain. *Vegetation* **1996**, 125, 99–110.
55. Espinosa, C. I., Cabrera, O., Luzuriaga, A. L., & Escudero, A. What factors affect diversity and species composition of endangered Tumbesian dry forests in Southern Ecuador? *Biotropica* **2011**, *43*, 15-22.
56. Poulsen, A.D., Tuomisto, H., Baslev, H. Edaphic and Floristic Variation a 1-ha Plot of Lowland Amazonian Rain Forest. *Biotropica* 2006, 38, 468-478. DOI: 10.1111/j.1744-7429.2006.00168.x.
57. Duivenvoorden, J. F. & Lips, J. M. A land-ecological study of soils, vegetation, and plant diversity in Colombian Amazonia. 1995. Tropenbos Foundation, Wageningen, The Netherlands.
58. Toumisto, H., Ruokolainen, K., Kalliola, R., Linna, A., Danjoy, W. & Rodriguez, M. Dissecting Amazonian biodiversity. *Science* **1995**, *269*, 63-66.
59. Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. Dispersal, environment, and floristic variation of western Amazonian forests. *Science* **2003**, *299*, 241–244. DOI: 10.1126/science.1078037.
60. Duque, A., Sanchez, M., Cavelier, J., & Duivenvoorden, J. F. Different floristic patterns of woody understorey and canopy plants in Colombian Amazonia. *J. Trop. Ecol.* **2002**, *18*, 499-525. DOI: 10.1017/S0266467402002341.

Peer-reviewed version available at *Diversity* **2019**, *11*, 196; doi:10.3390/d11100196

61. Phillips, O. L., Nuñez, P., Vargas, A., Monteagudo, A., Peñacruz, A., Chuspezans, M. E., Galiano, W., Sanchez, M., Yli-Halla, M., & Rose, S. Habitat association among Amazonian tree species: A landscape scale approach. *J. Ecol* **2003**, *91*, 757–775.
62. ter Steege, H., Pitman, N. C. A., Phillips, O. L., Chave, J., Sabatier, D., Duque, A., Molino, J.F., Prevost, M.-F., Spichiger, R., Castellanos, H., Vonhildebrand, P., & Vasquez, R. Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* **2006**, *443*, 444–447.
63. Chytry, M., Danihelka, J., Kubesova, S., Lustyk, P., Ermakov, N., Hajek, M., Hajkova, P., Koci, M., Otypkova, Z., Rolecek, J., Reznickova, M., Smarda, P., Valachovic, M., Popov, D., & Pisut, I. Diversity of forest vegetation across a strong gradient of climatic continentally: Western Sayan Mountains, southern Siberia. *Plant Ecol.* **2008**, *196*, 61–83.
64. Sollins, P. Factors influencing species composition in tropical lowland rain forest: Does soil matter? *Ecology* **1998**, 79, 23-30.
65. Duque, A., Sanchez, M., Cavelier, J., Duivenvoorden, J. F., Mirana, P., Mirana, J. & Mtapi, A. 2001 Relación bosque-ambiente en el Medio Caquetá, Amazonia colombiana. En: Evaluación de recursos vegetales no maderables en la Amazonia noroccidental. Caracterización ambiental (Duivenvoorden, J., Balslev, H., Cavelier, J., Grandez, C., Tuomisto, H., Valencia, R. eds.) pp. 23-30. 2001. IBED, Universiteit van Amsterdam, the Netherlands.
66. Jones, M.M., Tuomisto, H. & Olivas, P.C. Differences in the degree of environmental control on large and small tropical plants: just a sampling effect? *J. Ecol.* **2008**, *96*, 367–377.