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Geomorphology and Altitude Effects on the Diversity and Structure of the Vanishing Montane Forest of Southern Ecuador

Omar Cabrera ^{1,*} , Ángel Benítez ¹, Nixon Cumbicus ¹, Carlos Naranjo ¹ , Pablo Ramón ¹ , Fani Tinitana ¹  and Adrián Escudero ²

¹ Departamento de Ciencias Biológicas, Universidad Técnica Particular de Loja, San Cayetano Alto s/n, Loja 1101608, Ecuador; arbenitez@utpl.edu.ec (Á.B.); nlcumbicus@utpl.edu.ec (N.C.); cjnaranjo@utpl.edu.ec (C.N.); paramon@utpl.edu.ec (P.R.); ftinitana@utpl.edu.ec (F.T.)

² Departamento de Biología & Geología, Área de Biodiversidad y Conservación, ESCET, Universidad Rey Juan Carlos, Móstoles, E-28933 Madrid, Spain; adrian.escudero@urjc.es

* Correspondence: hocabrera@utpl.edu.ec; Tel.: +00-593-7-370-1444

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Abstract: (1) **Background:** Neotropical montane forests represent one of the most diverse world ecosystems; however, they are also among the most threatened ones mostly due to deforestation. Our main goal is to classify and clarify the forest types based on the changes in basal area (BA), tree density, and species composition of montane forests in Southern Ecuador, and to determine the influence of critical environmental and geomorphological factors. (2) **Methods:** One hundred thirty-two temporary plots of 400 m² were installed in homogeneous and well-conserved forest stands. We identified and measured all trees >10 cm diameter breast height (DBH). We modeled species diversity (Fisher's alpha) change in relation to climatic, altitudinal, and geomorphological gradients using GLM and Kruskal-Wallis analyses. The change in composition was determined using cluster analyses (BIOENV analysis followed by a LINKTREE procedure). Non-metric multidimensional scaling (NMDS) was used to analyze changes across climatic and geomorphological gradients. Finally, we used a SIMPER analysis to identify the species that contributed most to the floristic dissimilarity among the identified altitudinal forests types. (3) **Results:** The floristic groups were determined by altitude, temperature, and isothermality, but also some geomorphological variables and lithology were used. Plots located in low hills have higher alpha diversity compared to the high hills and dissected mountains. (4) **Conclusions:** Altitude is the most important factor responsible for the division of structural and floristic groups. In addition, those plots located on the whitish tuff have higher alpha value diversity compared with plots in andesitic tuffs. Precipitation on the wettest quarter (>839 mm) and isothermality (>90.5) are the most relevant climatic factors driving the floristic classification.

Keywords: Alpha diversity; beta diversity; diversity patterns; altitudinal gradients; geomorphology; Ecuador; mountain forests

1. Introduction

Neotropical montane forests represent one of the most diverse ecosystems in the world and very rich biodiversity hotspots [1]. Unfortunately, they are also included among the most threatened, especially in those in which deforestation is reaching high rates [2]. In this sense, those located in the Northern Range of Andes Mountains are considered as a conservation priority worldwide [3].

In Ecuador, montane tropical forests are counted among the most endangered ecosystems [4], with a tiny fraction of their historical range remaining (<7%), showing 24% of the total coverage,

19% less over a period of approximately 35 years [5,6]. Surprisingly, and in spite of the valuable ecosystem services they provide, such as water provisioning and biodiversity, information on their critical ecological determinants is still limited [7]. Ecuadorian montane forests remnants are confined to zones where agricultural practices are limited and, logically, they are very difficult to access on steep slopes [8,9]. Some basic questions related to their response to environmental gradients such as altitude, a well-known surrogate of foreseeable climate variation, remain open to discussion.

Several studies have described the variation along altitudinal gradients of these forests in the Andes, but a consensus is far from being achieved with respect to the forest classification. For instance, Van de Hammen [10], synthesizing the work done by geobotanists in Ecuador [11–15], proposed the following forest classification: 0–1000 m, tropical lowland forest; 1000–2300 m, sub-Andean Forest (also known as lower montane); 2300–3500 m, Andean Forest (or upper montane) and from 3500 to 3900, high-Andean Forest.

Lately, Ulloa & Jorgensen [16] considered that the 2300–3500 m elevation which constitutes the natural distribution limit for an important group of tree families, genera, and species is too extensive, and consequently, they proposed two additional categories: Sub-Andean and Andean Forests, respectively. Although sub-Andean Forests have their own floristic composition; some of the genera thriving there, such as *Acnistus*, *Pavonia*, *Vismia*, *Markea*, and other subandine genera are able to reach higher altitudes entering into the genuine Andean forests. From their perspective, Andean Forests range from a strip of woody vegetation that is located between 2400–2600 m altitude up to 3400–3800 m, and are better represented on the outer slopes of the Eastern Cordillera where trees that can reach up to 25 m high are covered by dense vegetation epiphytic mosses, bromeliads, ferns, lichens, liverworts, etc. They would constitute the genuine montane forests in the country. At higher altitudes of 3400–3800 m, Andean forest gives way to the High-Andean Forest and paramo.

The altitudinal classification of the forest implies leaving aside several other attributes that influence their composition and structure such as soil types, light availability, dynamics, species turnover, inter- and intra-specific competition, and natural and anthropogenic disturbances. Proposing a solid classification is a priority in Ecuador in order to minimize the high rates of deforestation the country suffers [17].

In parallel, Sierra [18] suggested a completely different classification which has become to be the most used and probably the current reference classification standard in the country. In what they called the sub-region South of Ecuador, eight types of forest vegetation were proposed; four present in the Western mountains influenced by the dry climate of the Pacific zone, namely humid montane scrub (2000–3000 m), montane dry scrub (1400–2500 m), semi-deciduous lower montane forest (1100–1500 m), and montane cloud forest (1500–2900 m), and four in the Eastern mountain range (with a critical Amazonian influence), the lower montane evergreen forest (1300–1800 m), montane cloud forest (1800–2800 m), upper montane evergreen forest (2800–3100 m), and humid scrub lower montane (1200–1800 m).

Such a complex picture needs clarification, especially in the case of the montane forests of Southern Ecuador. This is a critical point due to their outstanding diversity probably being linked to a very complex geology and patent influence of the Tumbesian region (an important point inside of the Hot Spot called Tumbes-Chocó-Magdalena), which actively comes from Northern Peru [19], and also especially for their critical conservation status consequences of severe fragmentation and degradation. As a result, to determine the patterns of diversity variation of montane forests of Southern Ecuador and their main ecological drivers [20,21], it is a priority challenge to guarantee their management, restoration, and conservation. A syntaxonomical classification of these Southern Ecuadorian forests has recently been proposed by different studies [19,21–23], but their work is confined to the Eastern most cordillera forests in the region. As a consequence, information on these types of forests at a broad regional scale is lacking.

Our main objective is to determine the variability in the structure and floristic composition of montane forests in Southern Ecuador and how this is linked to geomorphological and climatic factors,

including altitude, which has been one of the factors that have influenced the classification of montane forests for several decades in Ecuador.

2. Materials and Methods

2.1. Study Area

The study was conducted in the province of Loja, located in Southern Ecuador, and the sampling area covered approximately 6000 km², confirmed by a mosaic of remnants of forests of different sizes embedded in territories dedicated to livestock and agriculture. The distances between plots in each sampling site vary from 1 km (Espíndola) to 0.1 km (Cajanuma, canton Loja). This site is part of a protected area and belongs to a large forest > 500 ha (Podocarpus National Park). Plots are distributed between 2300–2900 m. (Figure 1).

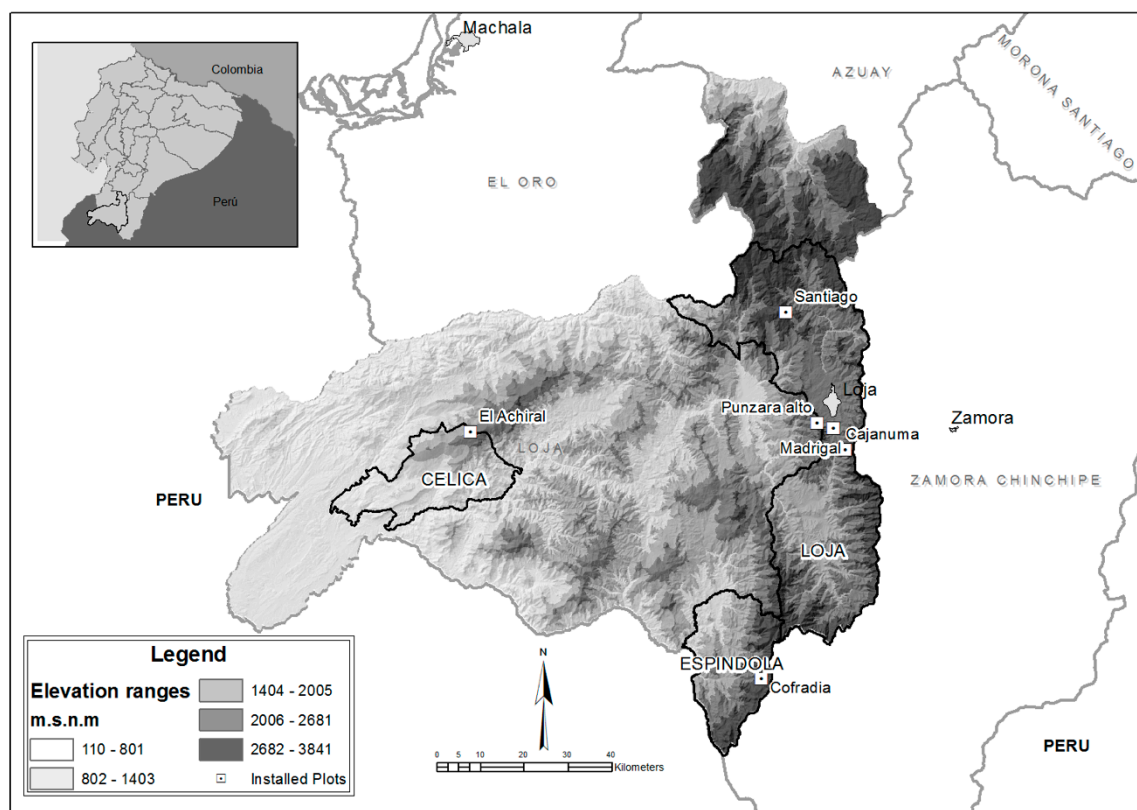


Figure 1. Map location of sampling plots.

2.2. Sampling Design

One hundred thirty-two plots of 400 m² were installed following a hierarchical approach. They were organized into three districts (Celica, Espíndola, and Loja), with 6 sample sites (3 in Loja, 1 in Celica and 1 in Espíndola), 44 localities, and three plots for each of the localities (Supplementary Table S1). According to Homeier [24], this area is adequate for surveying trees for comparative purposes in this type of ecosystem. In each plot, the DBH of the trees ≥ 10 cm was measured, and each individual was identified. The identification of the species was carried out in the field. For the species that could not be identified in the field, a botanical sample was collected for later identification in the Herbarium. Vouchers were included in HUTPL, LOJA, QCA, and QCNE. We followed the catalog of the vascular plants of Ecuador for the nomenclature of the species [25]. Also used the update of the flora of Ecuador [26] and the MOBOT page TROPICOS (www.tropicos.org). To characterize the

montane forests of different localities, structural and floristic parameters were calculated using the equations proposed by Madsen & Øllgaard [7] and Magurran [27].

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

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

Nineteen climate variables available in Worldclim (<http://www.worldclim.org>; the size of the pixel covers 30 arcseconds or approximately one square kilometer) were used [28]. We also included some additional variables such as the physiographic province, the orogenic geological-landscape, and the lithology of each sector where the plots settle (Supplementary Table S2). The sets of variables were analyzed independently to isolate the effect on diversity and composition, i.e., climate and geomorphological variables versus diversity. Principal component methods are also used for selecting subsets of independent variables for the regression models [29]. The first few components (Supplementary Table S3) were used as predictors in the regression [30,31]. The 19 climatic variables that showed correlation were discarded automatically, leaving 9 main variables (Supplementary Table S4). They were used in principal component analyses (PCA) using the function of R “prcomp” (R Core Team). Finally, we chose the PCA values of the first two main components (Supplementary Table S5).

2.3. Statistical Analysis

2.3.1. Taxonomic Diversity

In this study, we combine PCA and the generalized linear models (GLM) to obtain predictive models for Fisher’s alpha diversity calculated at the plot level with other climate variables (rainfall, isothermality, etc.) as predictors. The new variables from PCA are suitable to use as predictors in a regression equation since they remove possible effects of multicollinearity.

To model the total tree diversity (Shannon Index) and evenness, generalized linear models (GLM) were used [32]. The Kruskal-Wallis one-way analysis-of-variance by rank test (H test) was used to determine whether alpha diversity is affected by geomorphological category (physiographic province, great landscape, landscape, and lithology) levels. The basal area was calculated for all trees of each species. To determine differences between the values of the dasometric and floristic variables of each community type (see below), we performed an ANOVA using the aov function. To adjust the model of each of the tests we used the Tukey’s test using the tukey.test function in the software R [33]. When the resulting value of $p \leq 0.05$, the difference is significant.

2.3.2. Composition

We used a cluster analysis (complete linkage) to classify all the floristic inventories taken in each plot by using the Bray-Curtis distance as a measure of similarity and transforming the density data (square root) to normalize them. This clustering structure was tested using a profile similarity permutation test (SIMPROF procedure) and a similarity percentage analysis. We used SIMPER similarity percentage analysis to know which species are responsible for the similarity/dissimilarity between floristic groups.

To identify the environmental and geological variables that underlie this classification, we labeled each sample with the environmental variable thresholds obtained after a BIOENV analysis followed by a LINKTREE procedure. These analyses were undertaken using the PRIMER v6 software [34]. Non-metric multidimensional scaling (NMDS) was performed to visualize the main environmental and geomorphological factors that influence the grouping of these forest communities. To calculate the resemblance matrix between plots, the Bray–Curtis dissimilarity distance was used. The results were plotted in an NMDS ordination diagram. Values of species abundance, basal area, trees density, and environmental and geomorphological variables were fitted onto the first two axes of the NMDS

ordination. Squared correlation coefficients (r^2) and empirical p -values (p) were calculated for these linear fittings. Ordination was performed with the package ‘vegan’ [35] in R software [33].

3. Results

3.1. Alpha Diversity

In the one hundred thirty-two plots analyzed and 4343 individuals sampled, 164 species belonging to 52 botanical families were determined. The five most diverse families were Melastomataceae with 11 species (6.7% of all species); Rubiaceae with 10 species (6.1%) and Asteraceae, Lauraceae and Cunoniaceae with nine species each (5.5%). There were 22 families that possess a single species (0.6%). Families like Lauraceae, with 502 individuals (11.6%), followed by Melastomataceae with 368 (8.5%) and Clusiaceae with 367 (8.49%), are the most representative families. There were 10 families that have 100–200 individuals (2.5–5.5%); and 24 families had between 10 and 100 individuals (0.3–2.4%). We also detected 14 rare families with 2–9 individuals (0.09–0.2%). The analysis of the composition of the transects resulted in four clearly defined floristic groups. The values of relative diversity and relative dominance of each of them are shown in Tables 1 and 2.

Table 1. Families with more species of the total determined (relative diversity) in the four determined floristic groups (NMDS) of the montane forest in our study.

| Groups | Families | # Species | Relative Diversity |
|--------|-----------------|-----------|--------------------|
| I | MELASTOMATACEAE | 10 | 9.01 |
| | LAURACEAE | 8 | 7.21 |
| | ASTERACEAE | 6 | 5.41 |
| | CUNNONIACEAE | 6 | 5.41 |
| | RUBIACEAE | 6 | 5.41 |
| II | AQUIFOLIACEAE | 6 | 9.38 |
| | MELASTOMATACEAE | 6 | 9.38 |
| | CUNNONIACEAE | 5 | 7.81 |
| | LAURACEAE | 5 | 7.81 |
| | SYMPLOCACEAE | 5 | 7.81 |
| III | AQUIFOLIACEAE | 6 | 9.38 |
| | MELASTOMATACEAE | 6 | 9.38 |
| | CUNNONIACEAE | 5 | 7.81 |
| | LAURACEAE | 5 | 7.81 |
| | SYMPLOCACEAE | 5 | 7.81 |
| IV | LAURACEAE | 6 | 11.11 |
| | EUPHORBIACEAE | 5 | 9.26 |
| | MYRTACEAE | 4 | 7.41 |
| | ASTERACEAE | 3 | 5.56 |
| | MELASTOMATACEAE | 3 | 5.56 |

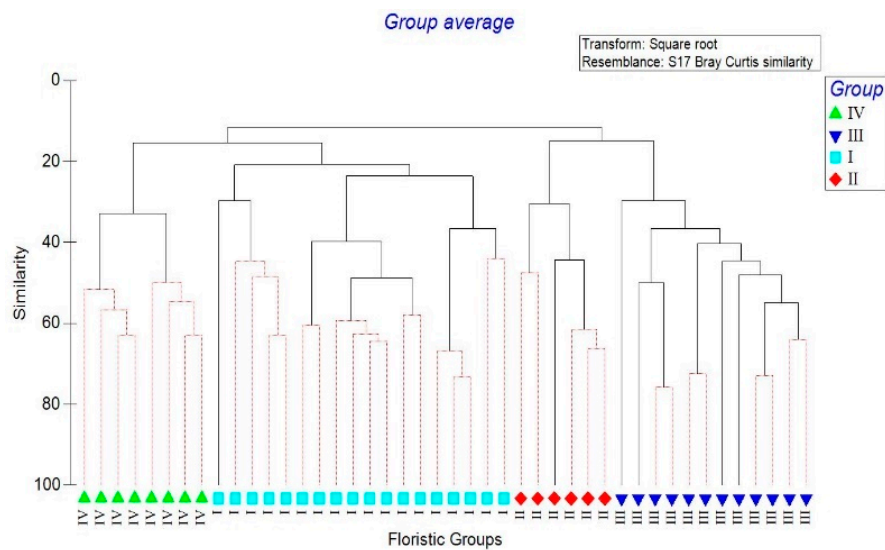
The total basal area of the sampled individuals reached 157.7 m². Lauraceae had the highest basal area 19.1 m² (12.1% of the total), followed by Podocarpaceae with 16.6 m² (10.5%), Clusiaceae with 13.2 m² (8.5%), and Cunoniaceae with 10.8 m² (6.8%). There were twenty-four families with basal areas between 1–10 m² (0.6–5.6%) and other 24 families with areas of 0.1–1 m² (0.2 to 0.6%). In each floristic group, there are species with the highest value of the basal area. Some species are characteristic for all groups, and other species are exclusive to each group (Table 2).

Table 2. Species with greater basal area in each floristic group.

| Groups | Species | Basal Area (m ²) | Relative Dominance |
|--------|---|------------------------------|--------------------|
| I | <i>Schefflera ferruginea</i> (Kunth) Harms | 4 | 8.1 |
| | <i>Critoniopsis pycnantha</i> (Benth.) H. Rob. | 2.5 | 5.1 |
| | <i>Oreopanax eriocephalus</i> Harms | 2.2 | 4.5 |
| | <i>Nectandra reticulata</i> (Ruiz & Pav.) Mez | 2.2 | 4.5 |
| | <i>Clusia alata</i> Triana & Planch. | 1.6 | 3.3 |
| II | <i>Prumnopitys montana</i> (Humb. & Bonpl.) Laub. | 1.8 | 8.6 |
| | <i>Persea ferruginea</i> Kunth | 1.4 | 6.4 |
| | <i>Clusia alata</i> Triana & Planch. | 1.3 | 6.2 |
| | <i>Gordonia fruticosa</i> (Schrad.) H. Keng. | 1.3 | 6 |
| | <i>Weinmannia ovata</i> Cav. | 1.3 | 5.9 |
| III | <i>Podocarpus oleifolius</i> D. Don ex Lamb. | 10.1 | 17.4 |
| | <i>Clusia alata</i> Triana & Planch. | 4.1 | 7.1 |
| | <i>Persea ferruginea</i> Kunth | 3.7 | 6.3 |
| | <i>Citronella</i> sp. | 3.5 | 6 |
| | <i>Podocarpus sprucei</i> Parlatore | 3.4 | 5.9 |
| IV | <i>Guarea kunthiana</i> A. Juss. | 2.6 | 8.8 |
| | <i>Miconia jahnii</i> Pittier | 2.3 | 7.9 |
| | <i>Endlicheria</i> sp. | 2.1 | 7 |
| | <i>Nectandra laurel</i> Ness | 1.8 | 6.1 |
| | <i>Myrcianthes discolor</i> (Kunth) McVaugh. | 1.8 | 6 |

3.2. Species Turnover

The classification based on the SIMPROF test (with permutations) provides four groups (Figure 2). In each cluster node, the percentage of each species which contributes to the differentiation with other nodes was identified. The species that mostly contributed to the dissimilarity between the groups (by SIMPER) were *Podocarpus oleifolius*, and *Podocarpus sprucei*, which are typical species of humid montane forests (Group IV). For *Guarea kunthiana*, A. Juss characterized the floristic Group IV, and the abundance of this species in this group is significant enough to separate it from the rest of the floristic groups. Other species that define the floristic dissimilarity of the groups are *Cupania cinerea* (Poepp.), *Ilex andicola* Loes, *Weinmannia ovata* (Cav.), and *Gordonia ourcese* (Schrad.) (H. Keng, Table 3). Floristic groups were also strongly influenced by environmental variables and altitude. Groups I and IV are separated from the other groups by altitude (>2700 m). They, in turn, are separated by the influence of the wettest quarter (>839 mm). On the other node, floristic Groups II and III are separated by isothermality (>90.5) representing a high oscillation between the average temperature during the day (Table 4).



Group I: Santiago, Madrigal—Punzara Center-North; Group II: Cajanuma—Center-South;
Group III: Cofradia—South; Group IV: Achiral—West

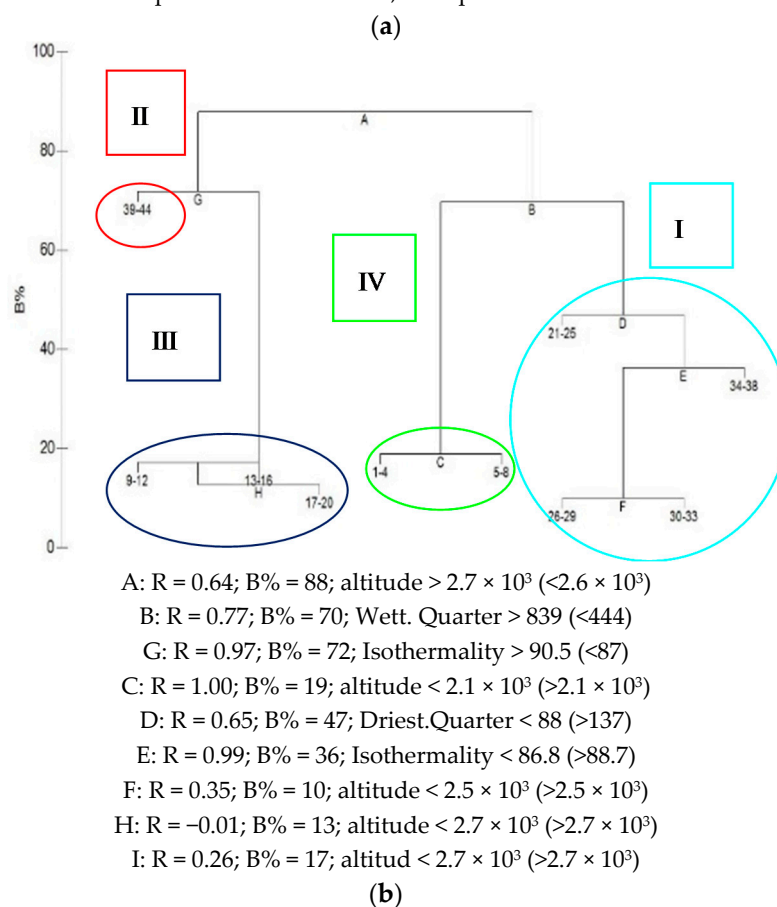


Figure 2. (a) Cluster based on floristic similarity using the Bray-Curtis measure (SIMPROF) and (b) Dendrogram (LINKTREE) grouping plots based on environment variables and the altitude of montane forests in Southern Ecuador. Use of the same color represents the same floristic group.

Table 3. Floristic dissimilarity values between groups and species that contribute with their presence and abundance to the floristic difference.

| Groups IV & III | | Average Dissimilarity = 95.40 | | | | |
|--|-----------|-------------------------------|---------|---------|----------|--------|
| Species | Group IV | Group III | Av.Diss | Diss/SD | Contrib% | Cum. % |
| | Av.Abund | Av.Abund | | | | |
| <i>Podocarpus oleifolius</i> D. Don ex Lamb. | 0 | 3.06 | 3.65 | 2.98 | 3.83 | 3.83 |
| <i>Miconia jahnii</i> Pittier | 2.98 | 0.14 | 3.41 | 2.66 | 3.58 | 7.41 |
| <i>Guarea kunthiana</i> A. Juss. | 2.62 | 0 | 3.1 | 2.51 | 3.24 | 10.65 |
| <i>Clusia latipes</i> Triana & Planch. | 0 | 2.19 | 2.61 | 1.71 | 2.74 | 13.39 |
| <i>Aniba muca</i> (Ruiz&Pav) Mez | 2.25 | 0.22 | 2.59 | 1.4 | 2.72 | 16.11 |
| Groups IV & I | | Average dissimilarity = 84.56 | | | | |
| Species | Group IV | Group I | Av.Diss | Diss/SD | Contrib% | Cum. % |
| | Av.Abund | Av.Abund | | | | |
| <i>Guarea kunthiana</i> A. Juss. | 2.62 | 0.21 | 2.85 | 1.96 | 3.37 | 3.37 |
| <i>Miconia jahnii</i> Pittier | 2.98 | 1.15 | 2.43 | 1.35 | 2.87 | 6.25 |
| <i>Aniba muca</i> (Ruiz&Pav) Mez | 2.25 | 0.57 | 2.39 | 1.27 | 2.82 | 9.07 |
| <i>Cupania cinerea</i> Poepp. | 1.72 | 0 | 2.13 | 0.88 | 2.52 | 11.6 |
| <i>Nectandra laurel</i> Ness | 1.65 | 0.9 | 1.87 | 1.09 | 2.21 | 13.8 |
| Groups III & I | | Average dissimilarity = 86.22 | | | | |
| Species | Group III | Group I | Av.Diss | Diss/SD | Contrib% | Cum. % |
| | Av.Abund | Av.Abund | | | | |
| <i>Podocarpus oleifolius</i> D. Don ex Lamb. | 3.06 | 0.22 | 3.35 | 2.25 | 3.88 | 3.88 |
| <i>Clusia latipes</i> Triana & Planch. | 2.19 | 0.23 | 2.36 | 1.48 | 2.74 | 6.62 |
| <i>Ilex andicola</i> Loes | 2.09 | 0.11 | 2.35 | 1.61 | 2.72 | 9.34 |
| <i>Podocarpus sprucei</i> Parlatore | 1.98 | 0 | 2.28 | 2.15 | 2.64 | 11.99 |
| <i>Citronella</i> sp. | 1.93 | 0 | 2.18 | 1.18 | 2.53 | 14.51 |
| Groups IV & II | | Average dissimilarity = 91.53 | | | | |
| Species | Group IV | Group II | Av.Diss | Diss/SD | Contrib% | Cum. % |
| | Av.Abund | Av.Abund | | | | |
| <i>Weinmannia ovata</i> Cav. | 0 | 2.75 | 2.83 | 1.59 | 3.09 | 3.09 |
| <i>Guarea kunthiana</i> A. Juss. | 2.62 | 0 | 2.76 | 2.39 | 3.01 | 6.1 |
| <i>Aniba muca</i> (Ruiz&Pav) Mez | 2.25 | 0 | 2.39 | 1.4 | 2.61 | 8.72 |
| <i>Persea ferruginea</i> Kunth | 0 | 2.2 | 2.31 | 1.22 | 2.53 | 11.24 |
| <i>Gordonia fruticosa</i> | 0 | 2.19 | 2.24 | 2.25 | 2.45 | 13.69 |
| Groups III & II | | Average dissimilarity = 85.12 | | | | |
| Species | Group III | Group II | Av.Diss | Diss/SD | Contrib% | Cum. % |
| | Av.Abund | Av.Abund | | | | |
| <i>Weinmannia ovata</i> Cav. | 0 | 2.75 | 2.79 | 1.59 | 3.28 | 3.28 |
| <i>Miconia jahnii</i> Pittier | 0.14 | 2.61 | 2.55 | 1.9 | 2.99 | 6.27 |
| <i>Gordonia fruticosa</i> | 0 | 2.19 | 2.21 | 2.25 | 2.6 | 8.87 |
| <i>Clusia alata</i> Triana & Planch. | 1.64 | 2.07 | 2.18 | 1.31 | 2.57 | 11.43 |
| <i>Ilex andicola</i> Loes | 2.09 | 0 | 2.18 | 1.7 | 2.56 | 13.99 |
| Groups I & II | | Average dissimilarity = 85.28 | | | | |
| Species | Group I | Group II | Av.Diss | Diss/SD | Contrib% | Cum. % |
| | Av.Abund | Av.Abund | | | | |
| <i>Weinmannia ovata</i> Cav. | 0 | 2.75 | 2.76 | 1.54 | 3.23 | 3.23 |
| <i>Gordonia fruticosa</i> (Schrاد.)H.Keng | 0 | 2.19 | 2.18 | 2.15 | 2.56 | 5.79 |
| <i>Clusia alata</i> Triana & Planch. | 1.11 | 2.07 | 2.1 | 1.15 | 2.46 | 8.25 |
| <i>Weinmannia elliptica</i> Kunth | 0.06 | 2.07 | 2.01 | 1.51 | 2.36 | 10.61 |
| <i>Miconia jahnii</i> Pittier | 1.15 | 2.61 | 1.99 | 1.44 | 2.33 | 12.94 |

The arrangement of the plots clearly indicates an influence of environmental and geomorphologic factors for ordination (Figure 3). Samples of montane forest in Southern Ecuador form four groups: Group I (North–center) consists of the plots on Santiago, Madrigal-Punzara; Group II is comprised of Cajanuma plots (South-central); Group III Cofradía plots (South) and Group IV Achiral plots (West) are also included.

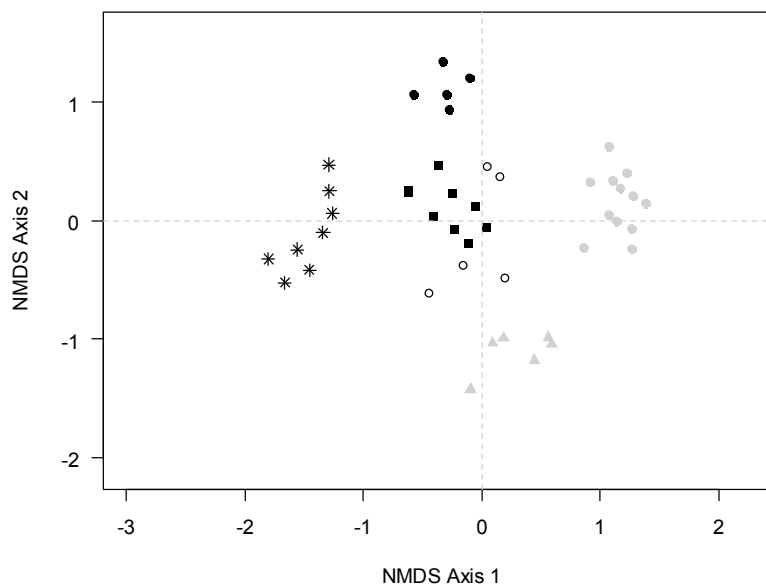


Figure 3. Non-metric multidimensional scaling analysis of species composition for the samples (plots) in the studied montane rain forests. Santiago forest (white circle), Punzara forest (black circle), and Madrigal forest (black square) conform to Group I. Cajanuma forests (gray triangle) represent Group II, Cofradia forests (gray circle) represent Group III, and Achiral forests (star) conform to Group IV.

Altitude showed a significant and strong correlation with the NMDS ordination axes, while seasonal temperature and isothermality showed weaker correlations (Table 4). Consistently, altitude, geologic landscape, and lithology factors were relevant predictors of this plant diversity (Table 4). The dissimilarity values indicated high variability of the composition, although there are species that grow indifferently in all groups as *Miconia jhanii*, *Meliosma arenosa*, *Ilex rupicola*, and *Meriania tomentosa*. We determine 14 families that occur in the four floristic groups. In each group, tree density and relative dominance of the families change along the altitudinal gradient.

Table 4. Significant variables affecting the grouping of montane forest in Southern Ecuador.

| Vectors | | | | |
|-------------------------------|---------|--------|--------|------------|
| | NMDS1 | NMDS2 | r^2 | p -Value |
| Altitude | 0.882 | −0.469 | 0.7101 | <0.0001 |
| Temperature Season | 0.730 | −0.686 | 0.1713 | 0.0199 |
| Isothermality | 0.467 | 0.884 | 0.2462 | 0.0059 |
| Factors | | | | |
| West Cordillera | −1.458 | −0.105 | 0.3924 | <0.0001 |
| East Cordillera | 0.324 | 0.023 | | |
| Physiographic province | | | | |
| Denudative | 0.5856 | 0.128 | 0.2474 | <0.0001 |
| Fluvial Erosional | −0.488 | −0.106 | | |
| Great landscape | | | | |
| Low Hills | −0.2503 | 0.093 | | |
| High Hills | 0.7127 | 0.436 | | |
| High Mountain | 0.2963 | −1.111 | 0.7057 | <0.0001 |
| Low Mountain | −0.0453 | −0.131 | | |
| Dissected Mountain | −1.458 | −0.105 | | |
| Landscape | | | | |
| Andesitic collade | 1.142 | 0.151 | | |
| Intrusive | −0.045 | −0.131 | 0.6351 | <0.0001 |
| Metamorphic | 0.016 | −0.096 | | |
| Andesitic Tuffs | −1.458 | −0.105 | | |
| Whitish Tuffs | −0.250 | 0.093 | | |
| Litology | | | | |

3.3. Modeling the Diversity

Principal components (PC1 and PC2) significantly influence the variability of the alpha diversity expressed in the Shannon Index (Table 5). Variables and values included in each component are shown in Supplementary Table S3, and the cumulative values of each component are shown in Supplementary Table S5.

Table 5. Generalized linear models of total tree diversity (Shannon Index) with two principal components (PC1 and PC2), respectively.

| MODEL | Estimate | Std. Error | t Value | Pr(> t) |
|-----------|------------|------------|---------|------------|
| Intercept | 0.0085217 | 0.00089 | 9.479 | <0.001 *** |
| PC 1 | −0.0012392 | 0.00028 | −4.294 | <0.001 *** |
| PC 2 | 0.0027677 | 0.00089 | 3.095 | <0.01 * |

Signif. codes: *** 0–0.001; * ≥ 0.01 AIC: 244.85.

There was a highly significant difference between the “Great Landscape” categories and their alpha-diversity (Kruskal-Wallis, degrees of freedom [df] = 4, $\chi^2 = 20.14$, $p < 0.001$). We compared Fisher’s alpha-diversity index between pairs of geomorphologic landscapes, and “low hills” had significantly higher values compared with the values of “high hills and “dissected mountains” (Wilcoxon rank-sum test $W = 126$, $p < 0.01$).

On the other hand, alpha-diversity showed significant differences between “lithology” categories (Kruskal-Wallis, degrees of freedom [df] = 4, $\chi^2 = 23.42$, $p < 0.001$). Then, were compared alpha-diversity values with each level of “lithology”. “Whitish tuffs” showed significantly larger alpha-diversity with respect to “andesitic lavas” (Wilcoxon rank-sum test $W = 96$, $p < 0.001$) and “andesitic tuffs” (Wilcoxon rank-sum test, $W = 64$, $p < 0.01$).

Along the altitudinal gradient, trees of smaller diameters predominate in all groups (I–IV). Structurally montane forest is heterogeneous, and the number of trees of each diametric class showed significant differences (Table 6), especially in the number of trees in the floristic group II (Cajanuma, South-Central position) where it was higher.

Table 6. Structural parameters and diversity of montane forest in Southern Ecuador. The mean value \pm SD is shown; different letters show significant differences ($p \leq 0.05$).

| Parameters | G1 (Santiago-Punzara-Madrigal) | G2 (Cajanuma) | G3 (Cofradía) | G4 (Achiral) |
|---|-----------------------------------|-------------------|------------------|------------------|
| Shannon Diversity Index (/400 m ²) | 28.9 \pm 8.6a | 30 \pm 4.51b | 21.1 \pm 4.3a | 22.8 \pm 2.3a |
| Species Tree Richness/400 m | 2.6 \pm 0.4a | 2.58 \pm 0.22a | 2.44 \pm 0.34a | 2.88 \pm 0.12b |
| Trees/400 m (>10 cm DAP) | 86.1 \pm 28.9a | 127.3 \pm 40.9b | 112 \pm 15.3a | 96.7 \pm 17.9a |
| Basal Area (>10 cm DAP) | 2.7 \pm 0.9a | 3.6 \pm 1.2a | 4.9 \pm 1.8b | 3.7 \pm 0.6a |

4. Discussion

Our results showed significant changes in the floristic diversity, structure, and composition of the species related to the ecological (altitude) and geomorphological gradients (varied lithology and geological landscapes distributed in a relatively small region) in montane tropical forests. Historically, it is recognized that the elevation of the Andes produced the occurrence of particular environments such as our region, with a great diversity of geological landscapes (mountains dissected, high mountains and low mountains, high and low hills) and becoming a unique region with a huge presence of environmental heterogeneity and complex distribution patterns of diversity and ecosystems [36]. This is one of the reasons behind the adaptation and speciation processes found in tropical zones,

mainly being found within the mountain forests found in the tropical Andes and considered as the world center of diversity [37–39].

Geomorphological factors related to lithology were the most relevant predictors of alpha diversity of tropical montane forests. Similarly, several studies have confirmed the trend of tropical forests in general, and particularly the mountain forests distribute their species richness driven to certain environmental and topographic gradients [40,41]. Worldwide, mountainous regions show abrupt climate gradients over short distances. The most renowned world centers of diverse vascular plants are found in the mountainous regions of the tropics and sub-humid tropics; these areas have high geodiversity characterized by heterogeneous geology (different lithology) and a high diversity of soils types (a result of the diversity of rocks that make up the region's lithosphere).

According to Rafiqpoor et al. [42], diversity of the physical environment promotes ecological specialization, and complex ecological landscapes offer greater potential for allopatric speciation. Homeier et al. [41] determined a high correlation between soil nutrients and tree diversity as being related to the availability of these elements (Ca, Mg and pH) which determine or affect corresponding species richness. In addition, the seasonality of precipitation (driest quarter–wettest quarter) appears to be an important factor when defining patterns of diversity and distribution of some species. The tropics are particularly sensitive to the duration of dry periods, particularly species with shallow roots as shrubs and small trees [43]. Similar patterns occur in other latitudes of the planet. For example, alpha diversity decreases as seasonality increases along a latitudinal gradient in tropical areas of India [44].

Theories of distribution patterns of diversity have tried to be explained for centuries. However, concerns about the causes that determine the distribution patterns and the richness of animals and plants persist [44]. According to Kessler et al. [45], for a better understanding of the diversity distribution patterns, these can be studied at different scales. The first is at the regional scale, where the distribution of gamma diversity is determined, including the number of species in broad geographic areas. The second approach includes the determination of alpha diversity and the number of species or local richness in small geographic areas, usually ≤ 1 ha, as reflected by the approach used in our study. According to Kessler [44] and Willig et al. [46], there are around 100 different hypotheses that try to explain the distribution patterns of diversity which can be grouped into six interrelated areas. In part, these are area availability, climatic variables, energy availability and productivity, historical and evolutionary processes, and neutral theories of stochasticity and population processes such as the “mass effect” and “sink–source” theories.

Regionally, environmental heterogeneity is one of the theories used to explain the high diversity of plants and other taxa [47]. Another critical factor in the distribution of diversity is related to altitude which recognizes four different patterns linked to particular taxonomic groups: The first indicates that diversity decreases with increasing altitude and decreasing particular groups of species, in this particular case small non-winged mammals [48] and bats [49]. Another pattern, called low plateau, indicates that in birds, a maximum of species is achieved at lower elevations, decreasing with increasing altitude [50]. In reptiles, a pattern the low plateau called the intermediate peak (low plateau mid-peak) proposed by McCain [51] is observed. Finally, the pattern called the intermediate peak (mid-peak) proposed by Rahbek [52] shows that the highest expression of diversity occurs in middle elevations, whose pattern starts with a low number of species at lower elevations, reaching the peak of diversity on middle elevations and decreasing when the altitude increases. In Ecuador, the range mountain range crosses the country from North to South, an area in which the ridge is at its lowest point initiating what is known as the “Huancabamba depression” [21]. Under this premise, mountain forests of Southern Ecuador are considered highly diverse, and they are structurally different (supported by a high geomorphological diversity) from other montane forests found at other Ecuadorian latitudes [53].

Locally, montane forestry has been extensively studied in the Eastern slope of the Andes, where the influence of environmental factors results in a high diversity of species, although there are the same types of vegetation in different areas along the mountain range slope [54]. Becking [21] systematized and analyzed the floristic information of 221 sample plots (1030 species) that cover a territory of

approximately 10,000 km² in Loja and Zamora in Southern Ecuador, and their results coincide with the results obtained in our study in relation to altitudinal zoning and montane forest types. However, they did not include montane forests of the western mountain range, which is part of our study. Jørgensen et al. [53] reported the occurrence of plants in low mountain areas (less than 2000 m) without any specific reference to composition or structure.

Our results indicate that the first hierarchical factor in the division of structural and floristic groups is altitude, following by lithology and geologic landscapes; this same factor determines the ordenación made by Becking [22] and Bussman [19], giving results of altitudinal strips and similar groups in the geographic ranges studied. The results confirm that Lauraceae and Melastomataceae are the most diverse in the four specific floristic groups, although this pattern is very common in Andean forests, which means they are similar in floristic composition to family and genus level, while at the species composition levels they vary considerably. For instance, the floristic group IV (Achiral) located in the Western mountains, unlike the rest of floristic groups, is influenced by the seasonality of dry tropical forests [55] that are nearby. Despite having similar precipitation values with other mountainous areas of the Eastern mountain range, this is concentrated in a relatively short term (three to four months), and the rest of the year is characterized by the lack of rain, while in forests the Eastern precipitation is distributed proportionally throughout the year. The climate process, according to Kessler et al. [45], is linked to distribution patterns of diversity in mountainous areas.

The elevation is the main factor for grouping montane forest plots in four floristic groups, and non-symmetrical shape diversity in these groups is distributed under the concept of diversity mean peak [50]. The climatic factors influence the separation of group IV. The seasonally dry forests that are located in the lower altitude contribute to the composition of the montane forest of group IV (Achiral) structurally and floristically are different from the rest of the forests that appear in the study. Elevation in this area influences the presence of important factors such as fog in certain months [56] and seasonal precipitation, as demonstrated by the previous analysis.

This research confirms the high diversity in the composition and structure of the montane forest in Southern Ecuador. The determined floristic groups are the product of the interaction of climatic, physiographic, and altitudinal conditions, factors that must be present in future forest classifications in the South of Ecuador. The inclusion of other factors apart from the altitude in the ordering of the montane forest shows the variability in the composition and structure and suggests the presence of several communities that can be identified with a deep taxonomic and functional study of the species that compose it. Finally, with respect to the floristic composition of the groups, there are six species that are present in a large part of the transects of all the groups, and they can be considered generalist species, although *Podocarpus oleifolius* is not present in the transects of Santiago. Contrarily, there are at least 60 species presents in very few transects. In Achiral (Group IV), there are 4 species that do not occur anywhere else. In Group III (Cofradía), there are 10 species that do not occur in any other group. In Group II (Cajanuma), there are 23 exclusive species. In Group I (Santiago-Madrigal-Punzara), there are 23 exclusive species that do not occur in the rest of the groups. According to Becking [21], this specific richness reflects the so-called “ecosystemic singularity” that has also been confirmed in the works of Bussman [9] and Homeier et al. [24].

Supplementary Materials: The following are available online at <http://www.mdpi.com/1424-2818/11/3/32/s1>, Table S1: Geographical location, altitude and number of plots installed in different study sites; Table S2: Variables used for analysis of the composition and structure of montane forest Southern Ecuador; Table S3: Rotated principal component loadings; Table S4: Pearson correlation matrix of different environmental variables; Table S5: Values of Principal Components Analyses.

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