- 1 Article
- 2 Geomorphology and Altitude effects on diversity and
- 3 structure of vanishing montane forest of Southern
- 4 Ecuador.
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- 20 Abstract:

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- 21 Keywords: Alpha diversity, beta diversity, floristic arrangement, geological landscapes,
- geomorphology, Ecuador, mountain forests.
- 23 1) Background: Neotropical montane forests represent one of the most diverse ecosystems;
- however, they are also the most threatened for deforestation. Our main goal is to evaluate the
- 25 change in Basal Area (BA), Density and Species Composition of montane forests in the southern
- 26 Ecuador and to determine the influence on some critical ecological and geomorphological factors.
- 2) Methods: One hundred thirty-two temporary plots of 400 m<sup>2</sup> each were installed; we identified
- and measured all trees> 10 cm DBH. We modeled species diversity (Fisher's alpha) change in
- 29 relation to climatic, elevational and geomorphological gradients with GLM and Kruskall-Wallis
- 30 analyses. The change in composition was determined using Cluster Analyses (BIOENV analysis
- 31 followed by a LINKTREE procedure). Non-metric multidimensional scaling (NMDS) was used to
- 32 analyze changes across climatic and geomorphological gradients. Finally, we used SIMPER analysis
- to identify the species that contributed most to the dissimilarity among the different elevations.
- 3) **Results:** Formation of floristic groups was influenced by altitude, temperature and Isothermality;
- 35 physiographic province, great landscape, geological landscape and lithology. Plots located in low
- 36 hills have higher alpha diversity with respect to the high hills and dissected mountains.

**4) Conclusions**: The elevation is first hierarchical factor responsible of the division of structural and floristic groups. Plots located on the whitish tuff have a higher alpha value diversity compared with plots in andesitic tuffs. Wettest quarter (> 839 mm) and Isothermality (> 90.5) are the climatic factors that driven de floristic divisions.

#### 1. Introduction

Neotropical montane forests represent one of the most diverse ecosystems in the world and an outstanding biodiversity hotspot [1]. Unfortunately, they are also included among the most threatened ones and those in which deforestation is reaching the highest rates [2]. As a consequence, those located in the northern Andes are considered as a conservation priority worldwide [3].

In Ecuador, montane tropical forests are enlisted among the most endangered ecosystems [4] with only a tiny fraction of their historical range remaining (< 7%) [5]. Surprisingly and in spite of the valuable ecosystem services they provide; information on their critical ecological determinants is still limited [6]. Ecuadorian montane forests remnants are confined to zones where agricultural practices are limited and, logically, of very difficult access on very steep slopes [7, 8]. Some basic questions related to their response to environmental gradients such as to altitude a well-known surrogate of foreseeable climate variation remains open to discussion.

We have observed to some attempts to describe the altitudinal variation of these forests in the Andes but a consensus is far to be achieved. For instance, [9] synthetizing the work done by geobotanists in Ecuador [10-14] 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, [15] considered that the 2300 to 3500 m elevation which constitutes the natural distribution limit for an important group of tree families, genera and species is too ample and consequently they proposed two additional categories: sub-Andean and Andean forests respectively. Although sub-Andean forests have its own floristic composition; some of the genera thriving there such as Acnistus, Pavonia, Vismia, Markea, others subandine genera are able to reach higher altitudes entering in their 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, 3400-3800 m, Andean forest gives way to the High-Andean forest and paramo. The intention to classify altitudinally the forest implies to leave aside several other attributes that influence its composition and structure that is why the intention to support its classification is more priority when Ecuador suffers high rates of deforestation [16].

In parallel [17] suggested a complete different classification which has become to be the most used and probably the current reference classification in the country. In what they called the subregion south of Ecuador, the presence of eight types of forest vegetation was proposed; four present in the western mountains influenced by the dry climate influence 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), 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 montane forests of southern Ecuador. This is critical due to their outstanding diversity probably linked to a very complex geology and patent influence of the Tumbesian region which actively comes from northern Peru [18] and especially for their critical conservation status consequence of severe fragmentation and degradation. As a consequence, to determine the patterns of diversity variation of montane forests of southern Ecuador and their main ecological drivers [19,20] is a priority challenge to guarantee their management, restoration and conservation.

A syntaxonomical classification of these southern Ecuadorian forests have recently been proposed by [18,20-22], but their work is confined to the eastern most cordillera forests in the region. As a consequence, absent of information of these types of forests at a broad regional scale is lacking.

Our main goal is to evaluate the variability in the structure and Species Composition of montane forests in the southernmost Ecuador and to determine the influence on some critical ecological and geomorphological factors.

#### 2. Materials and Methods

#### 2.1 Study Area

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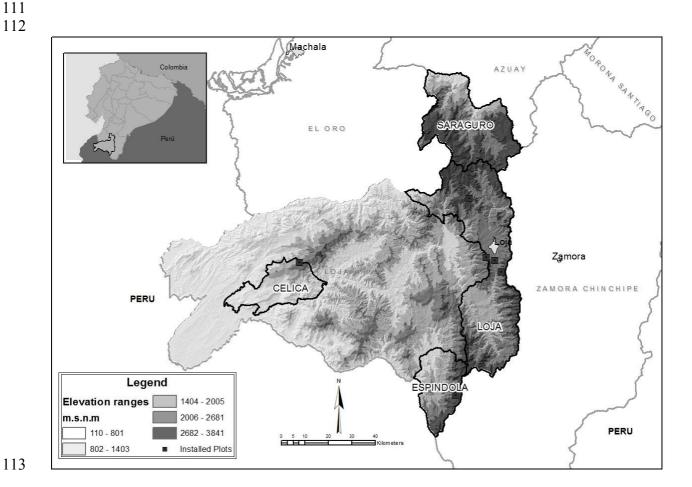
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The study was conducted in Loja province, located in southern Ecuador and covering an area of more than 11,000 km<sup>2</sup>. Except in the case of the plots taken in Cajanuma (Loja county) which is part of a protected area and belongs to a continuum extensive forest > 500 ha (Podocarpus National Park) the remaining sites are a mosaic of forest remnants of different size imbibed in territories devoted to livestock and agriculture. The distances between plots at each sampling site range from 100 m (Cajanuma) to 1km (Espíndola). Plots are distributed between 2300-2900 m. (Fig. 1, Appendix S1).



# **Figure 1**. Map location of sampling plots.

# 2.2 Sampling design

One hundred thirty-two plots of 400 m² were installed (three for each of 44 sites). According to [23] this plot size is adequate to sample the vegetation in this type of ecosystems. In each plot it was measured the DBH of trees ≥10 cm and each of the individuals identified. The identification of species was made in the field, if not it was collected for identification in Herbaria. Vouchers were included in HUTPL, LOJA, QCA, QCNE. We followed the Catalogue of the vascular plants of Ecuador for the nomenclature of the species [24].

Nineteen climate variables available in Worldclim (http://www.worldclim.org) [25] were used. We also included some additional variables such as the physiographic province, the orogenic geological-landscape and lithology of each sector where the plots settle (Appendix S2). The sets of variables were analyzed independently to isolate its effect on diversity and composition i.e. climate versus diversity and geomorphological variables. Some plots share these geomorphological attributes. Other plots have different geomorphological characteristics, the physiographic province, the great landscape and the lithology are attributes that cover wide territories for which they are the most shared. Principal component methods are also used for selecting subsets of variables for a regression equation [26]. Its main goal is retaining a subset of the original variables associated with each of the first few components (Appendix S3), which are the used as predictors in the regression [27, 28].

We tested the significance of the correlation among (19 variables) for 44 plots. Principal components analysis (PCA) of the correlation matrix (Appendix S4) was performed using "prcomp" function of R (R Core Team). As an evaluation, we examined the bivariate plot of PCA scores along the first two principal components for the original variable matrix (Appendix S5).

## 2.3 Statistical Analysis

# 2.3 1 Taxonomic Diversity

In this study, we combine the PCA and the generalized linear models (GLM) to obtain prediction models for Fisher's alpha diversity with other climate variable (rainfall, Isothermality, etc.) as predictor variables. PCA analysis was used for selecting the data so that only the significant independent variables responsible for the diversity observed could be determined. The new variables from PCA are suitable to use as predictor 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) was used. With respect to linear models, an advantage of GLM is that they can deal with a range of distributions in the error component [29].

The Kruskal-Wallis one-way analysis-of-variance by rank test (H test) was used to determine whether alpha diversity is affected by Great Landscape levels.

The basal area was calculated for each of the trees. To determine differences between the values of the dasometric and floristic variables of each community (plots grouped in the NMDS) were performed an ANOVA analysis using the aov function, to adjust the model of each of the tests we used the Tukey's test using the tukey test function both in the software R [30], when the resulting value of p < 0.05 the difference is significant.

# 2.3.2 Composition

Whether to determine the floristic composition and structure of montane forest in southern Ecuador are homogeneous or heterogeneous first step was made an arrangement of Cluster (complete linkage), to classify species groups or species assemblages using a measure of similarity Bray Curtis distance and the transformed data density (square root). This cluster was tested by means of a profile similarity permutation test (SIMPROF procedure) and a similarity percentage analysis. To know species which are responsible for the similarity / dissimilarity between floristic groups, SIMPER similarity percentage analysis was tested. To identify the environmental and geological variables that underlied 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 software PRIMER v6 [31].

Non-metric multidimensional scaling (NMDS) was performed to detect the main environmental and geomorphological factors that influence the grouping of plant communities. To calculate the resemblance matrix between plots, the Bray–Curtis dissimilarity distance was used. The results were plotted in a NMDS ordination diagram. Values of species abundance, Basal Area, density and environmental and geomorphological variables were then fitted onto the first two axes of the NMDS ordination. Squared correlation coefficients (r2) and empirical p-values (p) were calculated for these linear fittings. Ordination was performed with package 'vegan' [32] in the R [30].

#### 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 Cunnoniaceae nine species each (5.5%). There were 22 families who own a single species (0.6%). Lauraceae with 502 individuals (11.6%; Table 1), followed by Melastomataceae with 368 (8.5%) and Clusiaceae with 367 (8.49%). There were 10 families that have 100- 200 individuals (2.5 – 5.5%; Table 2); and 24 families were between 10 and 100 individuals (0.3 – 2.4%). 14 rare families with 2-9 individuals (0.09 to 0.2%).

**Table 1.** Families more diverse s in four floristic groups of montane forest in southern Ecuador.

Groups	Families	# species	Relative Diversity
	MELASTOMATACEAE	10	9,01
	LAURACEAE	8	7,21
I	ASTERACEAE	6	5,41
	CUNNONIACEAE	6	5,41
	RUBIACEAE	6	5,41
	AQUIFOLIACEAE	6	9,38
II	MELASTOMATACEAE	6	9,38
	CUNNONIACEAE	5	7,81

	LAURACEAE	5	7,81
	SYMPLOCACEAE	5	7,81
	AQUIFOLIACEAE	6	9,38
	MELASTOMATACEAE	6	9,38
III	CUNNONIACEAE	5	7,81
	LAURACEAE	5	7,81
	SYMPLOCACEAE	5	7,81
	LAURACEAE	6	11,11
	EUPHORBIACEAE	5	9,26
IV	MYRTACEAE	4	7,41
	ASTERACEAE	3	5,56
	MELASTOMATACEAE	3	5,56

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%). 24 families with basal area between 1-10 m2 (0.6 – 5.6%) and other 24 families with 0.1 -1m2 (0.2 to 0.6%). In each floristic group there are species with the highest value of basal area, some are characteristic and others exclusive to each group (Table 2).

Table 2. Dominant species in each floristic groups

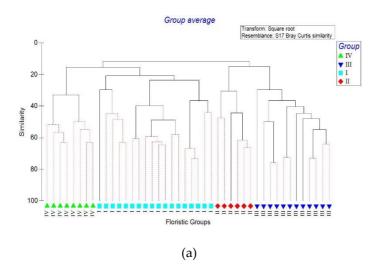
Groups	Species	Basal Area (m²)	Relative Dominance
	Schefflera ferruginea (Kunth) Harms	4	8,1
I	Critoniopsis pycnantha (Benth.) H. Rob.	2,5	5,1
	Oreopanax eriocephalus Harms	2,2	4,5
	Nectandra reticulata (Ruiz & Pav.) Mez	2,2	4,5
	Clusia alata Triana & Planch.	1,6	3,3
	Prumnopitys montana (Humb. & Bonpl.) Laub.	1,8	8,6
II	Persea ferruginea Kunth	1,4	6,4
	Clusia alata Triana & Planch.	1,3	6,2
	Gordonia fruticosa (Schrad.) H. Keng.	1,3	6
	Weinmannia ovata Cav.	1,3	5,9
	Podocarpus oleifolius D. Don ex Lamb.	10,1	17,4
TTT	Clusia alata Triana & Planch.	4,1	7,1
III	Persea ferruginea Kunth	3,7	6,3
	Citronella sp.	3,5	6

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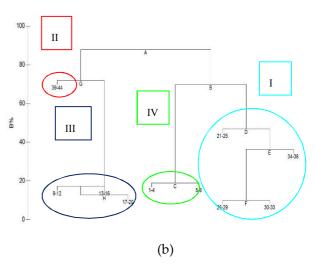
	Podocarpus sprucei Parlatore	3,4	5,9
	Guarea kunthiana A. Juss.	2,6	8,8
	Miconia jahnii Pittier	2,3	7,9
IV	Endlicheria sp.	2,1	7
	Nectandra laurel Ness	1,8	6,1
	Myrcianthes discolor (Kunth) McVaugh.	1,8	6

## 3.2 Beta diversity

The cluster based on the SIMPROF test (with permutations) classifies the plots into four groups obeying a taxonomic affinity (Fig. 2). In each cluster node the percentage of each species contributes to the differentiation with other nodes identified. The species that contribute to the dissimilarity between the groups (SIMPER) are *Podocarpus oleifolius*, *Podocarpus sprucei* characteristics species of humid montane forests and the absence of the species in the floristic group located further west (Group IV) where in the absence of the species is notorious for low humidity of the forest. *Guarea kuntiana* A. Juss characterizes the floristic group IV, the abundance of this species in this group is significant to separate from the rest of 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 5). Floristic groups are also strongly influenced by environmental variables and altitude. Groups I and IV are separated from the other groups influenced by altitude (> 2700 m) these groups in turn are separated by the influence of the wettest quarter (> 839 mm). On the other node floristic groups II and III are separated influenced by isotermality (> 90.5) representing a high oscillation between the average temperature during the day (Table 3).







B: R=0.77; B%=70; Wett. Quarter >839(<444)
G: R=0.97; B%=72; Isothermality>90,5 (<87)
C: R=1,00; B%=19; altitud<2,1E3(>2,1E3)
D: R=0,65; B%=47; Driest.Quarter<88(>137)
E: R=0,99; B%=36; Isothermality<86,8(>88,7)
F: R=0,35; B%=10; altitud<2,5E3(>2,5E3)
H: R=-0,01; B%=13; altitud<2,7E3(>2,7E3)
I: R=0,26; B%=17; altitud<2,7E3(>2,7E3)

A: R=0,64; B%=88; altitud >2,7E3 (<2,6E3)

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**Figure 2.** (a) Cluster (SIMPROF) and (b) Dendrogram (LINKTREE) grouping plots of montane forest in southern Ecuador, same color represents the same floristic group.

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

Species  Podocarpus oleifolius D. Don ex Lamb Miconia jahnii Pittier Guarea kunthiana A. Juss. Clusia latipes Triana & Planch. Aniba muca (Ruiz&Pav) Mez Groups IV & I  Guarea kunthiana A. Juss. Miconia jahnii Pittier Aniba muca (Ruiz&Pav) Mez Cupania cinerea Poepp. Nectandra laurel Ness		Group III  Av.Abund  3,06  0,14  0  2,19  0,22  Average  Group I  0,21  1,15  0,57	3,65 3,41 3,1 2,61 2,59	Diss/SD  2,98  2,66  2,51  1,71  1,4  clarity = 84  1,96  1,35	3,83 3,58 3,24 2,74 2,72	3,83 7,41 10,65 13,39 16,11
Podocarpus oleifolius D. Don ex Lamb Miconia jahnii Pittier Guarea kunthiana A. Juss. Clusia latipes Triana & Planch. Aniba muca (Ruiz&Pav) Mez Groups IV & I  Guarea kunthiana A. Juss. Miconia jahnii Pittier Aniba muca (Ruiz&Pav) Mez Cupania cinerea Poepp.	0 2,98 2,62 0 2,25  Group IV 2,62 2,98 2,25	3,06 0,14 0 2,19 0,22 <b>Averag</b> <b>Group I</b> 0,21 1,15	3,65 3,41 3,1 2,61 2,59 ge dissimi 2,85 2,43	2,98 2,66 2,51 1,71 1,4 larity = 84	3,83 3,58 3,24 2,74 2,72 4,56	7,41 10,65 13,39 16,11
Miconia jahnii Pittier Guarea kunthiana A. Juss. Clusia latipes Triana & Planch. Aniba muca (Ruiz&Pav) Mez Groups IV & I  Guarea kunthiana A. Juss. Miconia jahnii Pittier Aniba muca (Ruiz&Pav) Mez Cupania cinerea Poepp.	2,98 2,62 0 2,25 Group IV 2,62 2,98 2,25	0,14 0 2,19 0,22 Average Group I 0,21 1,15	3,41 3,1 2,61 2,59 ge dissimi 2,85 2,43	2,66 2,51 1,71 1,4 !larity = 84	3,58 3,24 2,74 2,72 4,56	7,41 10,65 13,39 16,11
Guarea kunthiana A. Juss.  Clusia latipes Triana & Planch.  Aniba muca (Ruiz&Pav) Mez  Groups IV & I  Guarea kunthiana A. Juss.  Miconia jahnii Pittier  Aniba muca (Ruiz&Pav) Mez  Cupania cinerea Poepp.	2,62 0 2,25 Group IV 2,62 2,98 2,25	0 2,19 0,22 <b>Averag</b> <b>Group I</b> 0,21 1,15	3,1 2,61 2,59 ge dissimi 2,85 2,43	2,51 1,71 1,4 !larity = 84	3,24 2,74 2,72 4,56	10,65 13,39 16,11 3,37
Clusia latipes Triana & Planch.  Aniba muca (Ruiz&Pav) Mez  Groups IV & I  Guarea kunthiana A. Juss.  Miconia jahnii Pittier  Aniba muca (Ruiz&Pav) Mez  Cupania cinerea Poepp.	0 2,25 Group IV 2,62 2,98 2,25	2,19 0,22 <b>Averag</b> <b>Group I</b> 0,21 1,15	2,61 2,59 ge dissimi 2,85 2,43	1,71 1,4 larity = 84 1,96	2,74 2,72 4,56 3,37	13,39 16,11 3,37
Aniba muca (Ruiz&Pav) Mez  Groups IV & I  Guarea kunthiana A. Juss.  Miconia jahnii Pittier  Aniba muca (Ruiz&Pav) Mez  Cupania cinerea Poepp.	2,25  Group IV 2,62 2,98 2,25	0,22  Average Group I  0,21 1,15	2,59 ge dissimi 2,85 2,43	1,4 larity = 84 1,96	2,72 4,56 3,37	3,37
Groups IV & I  Guarea kunthiana A. Juss.  Miconia jahnii Pittier  Aniba muca (Ruiz&Pav) Mez  Cupania cinerea Poepp.	Group IV 2,62 2,98 2,25	Average Group I 0,21 1,15	2,85 2,43	larity = 84 1,96	3,37	3,37
Guarea kunthiana A. Juss. Miconia jahnii Pittier Aniba muca (Ruiz&Pav) Mez Cupania cinerea Poepp.	2,62 2,98 2,25	Group I 0,21 1,15	2,85 2,43	1,96	3,37	
Miconia jahnii Pittier Aniba muca (Ruiz&Pav) Mez Cupania cinerea Poepp.	2,62 2,98 2,25	0,21 1,15	2,43			
Miconia jahnii Pittier Aniba muca (Ruiz&Pav) Mez Cupania cinerea Poepp.	2,98 2,25	1,15	2,43			
Aniba muca (Ruiz&Pav) Mez Cupania cinerea Poepp.	2,25			1,35	2,87	<i>(</i> 25
Cupania cinerea Poepp.		0,57	2 30		•	6,25
, 11	1.72		2,39	1,27	2,82	9,07
Nectandra laurel Ness	,	0	2,13	0,88	2,52	11,6
	1,65	0,9	1,87	1,09	2,21	13,8
Groups III & I	Average dissimilarity = 86,22					
	Group III	Group I				
Podocarpus oleifolius D. Don ex Lamb	. 3,06	0,22	3,35	2,25	3,88	3,88
Clusia latipes Triana & Planch.	2,19	0,23	2,36	1,48	2,74	6,62
Ilex andicola Loes	2,09	0,11	2,35	1,61	2,72	9,34
Podocarpus sprucei Parlatore	1,98	0	2,28	2,15	2,64	11,99
Citronella sp.	1,93	0	2,18	1,18	2,53	14,51
Groups IV & II		Averaş	ge dissimi	larity = 91	,53	
	Group IV	Group II				
Weinmannia ovata Cav.	0	2,75	2,83	1,59	3,09	3,09
Guarea kunthiana A. Juss.	2,62	0	2,76	2,39	3,01	6,1
Aniba muca (Ruiz&Pav) Mez	2,25	0	2,39	1,4	2,61	8,72
Persea ferruginea Kunth	0	2,2	2,31	1,22	2,53	11,24
Gordonia fruticosa	0	2,19	2,24	2,25	2,45	13,69
Groups III & II		Averag	ge dissimi	larity = 85	,12	
	Group III	Group II				

Weinmannia elliptica Kunth

Miconia jahnii Pittier

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Weinmannia ovata Cav.	0	2,75	2,79	1,59	3,28	3,28
Miconia jahnii Pittier	0,14	2,61	2,55	1,9	2,99	6,27
Gordonia fruticosa	0	2,19	2,21	2,25	2,6	8,87
Clusia alata Triana & Planch.	1,64	2,07	2,18	1,31	2,57	11,43
Ilex andicola Loes	2,09	0	2,18	1,7	2,56	13,99
Groups I & II		Averag	e dissimi	larity = 85,	.28	
	Group I	Group II				
Weinmannia ovata Cav.	0	2,75	2,76	1,54	3,23	3,23
Gordonia fruticosa (Schrad.)H.Keng	0	2,19	2,18	2,15	2,56	5,79
Clusia alata Triana & Planch.	1,11	2,07	2,1	1,15	2,46	8,25

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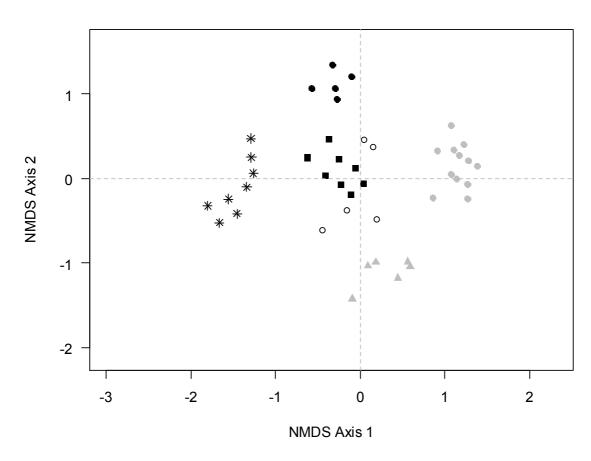
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The arrangement of the plots studied clearly indicates that there is influence of environmental and geomorphologic factors for ordination (Fig. 3). Samples of montane forest in southern Ecuador form four groups: Group I (North – Center) consists of the plots on Santiago, Madrigal-Punzara-; Group II comprise it Cajanuma plots (South Central), the Group III Cofradia plots (South) and Group IV Achiral plots (West).

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**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) are conforming the group I, Cajanuma forest (gray triangle) group II, Cofradia forest (gray circle) group III and Achiral forest (star) conforming group IV.

Altitude showed a significant and strong correlation with the NMDS ordination axes, while seasonal temperature and isothermally showed a correlation weak (Table 4). Consistently altitude, landscape and lithology factors were the most relevant predictors of plant communities of tropical montane forests (Table 4). The values indicate high variability of the composition although there are species that grow indifferently in all groups as *Miconia jhanii*, *Meliosma arenosa*, *Ilex rupícola*, *Meriania tomentosa* representing 2.2% of certain species. There were 14 families that occur either in the four groups, in each floristic group, values of relative density of families changes, indicating the dominance of certain families along the altitudinal gradient.

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

Vectors				
	NMDS1	NMDS2	$r^2$	<i>P</i> -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		
East Cordillera	0.324	0.023		
Physiographic province			0.3924	<0.0001
Denudative	0.5856	0.128		
Fluvial Erosional	-0.488	-0.106		
Great landscape			0.2474	<0.0001
Low Hills	-0.2503	0.093		
High Hills	0.7127	0.436		
High Mountain	0.2963	-1.111		
Low Mountain	-0.0453	-0.131		
Dissected Mountain	-1.458	-0.105		
Landscape			0.7057	<0.0001
Andesitic collade	1.142	0.151		
Intrusive	-0.045	-0.131		
Metamorphic	0.016	-0.096		
Andesitic Tuffs	-1.458	-0.105		
Whitish Tuffs	-0.250	0.093		
Litology			0.6351	< 0.0001

# 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 includes in each component are shown in Appendix S3 and the cumulative values of each component are shown in Appendix S5.

**Table 5**. Generalized linear models of total tree diversity (Shannon Index) and evenness 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 '\*' 0.05 '.' 0.1 ' ' 1

AIC: 244.85

There was a highly significant relationship between "Great Landscape" variable and Alpha-diversity (Kruskal-Wallis, degrees of freedom [df] = 4,  $\chi 2$  = 20.14, p < 0.001). Additionally, to this analysis of variance, we compared Fisher's alpha-diversity index between pairs of geomorphologic levels of "Landscape" "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 relationship with "Lithology" (Kruskal-Wallis, degrees of freedom [df] = 4,  $\chi^2$  = 23.42, p < 0.001). Then, were compared alpha-diversity with each level of "Lithology". "Whitish Tuffs" exhibited significantly larger alpha-diversity respect to "Andesitic Washings" (Wilcoxon rank-sum test W=96, p < 0.001) and "Andesitic Tuffs" (Wilcoxon rank-sum test, W= 64, p < 0.01).

 At altitudinal level dominated individuals of smaller diameter classes. Structurally montane forest is heterogeneous, the number of trees in each floristic group showed significant differences (Table 6), especially in the number of individuals in the floristic group II (Cajanuma, position south center) number of trees is higher than in the other groups confirming what determined compared the mountain forests of southern Ecuador to the north forest, despite this all groups have the same tendency in structure.

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

Parameters	G1	G2	G3	G4
Tree Diversity (total species /400m)	28.9 ±8.6a	30±4.51b	21.1 ±4.3a	22.8 ±2.3a
Species Tree Richness/400 m	2.6±0.4a	2.58±0.22a	2.44±0,34a	2.88±0.12b
Trees/400m (> 10 cm DAP)	86.1±28.9 a	127.3±40.9 b	112±15.3 a	96.7±17.9 a
Basal Area (> 10 cm DAP)	2.7±0.9 a	3.6±1.2 a	4.9±1.8 b	3.7±0.6 a

#### 4. Discussion

Our results showed significant changes in floristic diversity, structure and species composition related to ecological (altitude) and geomorphological (lithology and landscape) gradients in montane tropical forests. Major shifts in species diversity were caused by changes in elevation, landscape and lithology. Historically it recognized that lifting the Andes produced the appearance of particular environments, becoming a unique region with an enormous environmental heterogeneity and complex distribution patterns of diversity and ecosystems [33], this is one of the reasons behind the processes of adaptation and speciation in tropical mountain forests, especially those sitting in the Tropical Andes considered the world center of diversity [34 - 36].

Geomorphological factor related with landscape and 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 richness driven to certain environmental and topographic gradients [37, 38]. Worldwide mountainous regions show abrupt climate gradients over short distances, in fact, the world centers of diversity most renowned vascular plants found in the mountainous regions of the tropics and sub-humid tropics, these areas with high geodiversity characterized by heterogeneous geology and a high diversity of soil condition. According to [39] diversity of the physical environment promotes ecological specialization and complex ecological landscapes offer greater potential for allopatric speciation. [38] determined high correlation between soil nutrients and tree diversity, being the availability of these elements (Ca, Mg and pH) which determines or affects species richness.

In addition, the seasonality of precipitation appears to be an important factor when defining patterns of diversity and distribution of some species in the tropics are particularly sensitive to the duration of period, particularly species with shallow roots as shrubs and small trees dry season [40], the alpha diversity decreases as the seasonal increases along a latitudinal gradient in tropical areas of India [41]. A large-scale theory of latitudinal diversity gradient (LDG) which explains the trend that diversity accumulates in tropical regions is probably the most studied pattern and best known event. This approach was noted by Foster in 1778 and later by Humboldt in 1807 [42- 44] although [45] believe that the latitude itself is not an ecological gradient, if the numerous factors that vary with latitude may be responsible for creating such patterns.

Theories of distribution patterns of diversity have tried to be explained for centuries however concerns about the causes that determine the distribution patterns the richness of animals and plants [46] persist. According to [47] for a better understanding, these phenomena can be studied at different scales, regional diversity and gamma diversity including the number of species over wide geographical areas and alpha diversity and number of species or local wealth in small geographic areas normally  $\leq 1$  ha. According to [46, 48] there are about 100 different hypotheses that attempt to explain the phenomenon and can be grouped in six interrelated areas in part these are: availability of area, climatic variables, energy availability and productivity, historical and evolutionary processes, and stochasticity neutral theories and population processes as "mass effect" and "source-sink", all of these theories or groups of theories, have a global approach on a large scale, many of which have led to theories and local models that have been developed based on more specific studies.

Regionally, environmental heterogeneity is one of the theories linked to the high diversity of plants and other taxa [49]. Another theory refers to the elevational patterns that basically fall into four patterns linked to particular taxonomic groups: the first indicates that diversity decreases with increasing elevation (decreasing) small not winged mammals [50] and bats [51]. Another pattern called low plateau indicates that in birds, a maximum of species is achieved at lower elevations, decreasing with increasing altitude [52]. In reptiles the pattern low plateau called intermediate peak (low plateau mid peak) proposed by [53] is observed. Finally, the pattern called intermediate peak (mid Peak) plant proposed by [54] shows that the highest expression of diversity occurs in middle

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elevations, starting the pattern with a low number of species at lower elevations, reaching the peak of diversity middle elevations and decreasing as the altitude increases. In Ecuador Andes range mountain crosses the country from north to south, an area in which the ridge at its lowest point initiating what is known as the "Huancabamba depression" [20]. Under this premise mountain forests of southern Ecuador are considered highly diverse and structurally different from other montane forests in other Ecuadorian latitudes [55].

Locally, the montane forest has been extensively studied in the eastern slope of the Andes, where it is shown that the influence of environmental factors results in a high diversity of species, although the types of vegetation that are repeated in different areas are similar. There are two spaces occupied by the same communities as the vegetation changes continuously [56]. [21] systematized information 221 plots (1030 species) implanted covering an area about 10,000 km² in Loja and Zamora south of Ecuador and found matches with the results obtained in this study as it relates to zoning altitudinal and certain types of vegetation. It has not been reported information about montane forest in the western mountains and this work the first analysis in a southwestern montane forest considering regional floristic-structural information. [57] reported the use of useful plants in mountain areas low (less than 2000 m) without any specific reference to its composition or structure.

Our results indicate that the first hierarchical factor in the division of structural and floristic groups is elevation, following by lithology and landscape and this same factor that determines the order by [21] and [18], giving as a result altitudinal strips in the branches of the ranges studied. The results obtained in terms of different families in our study confirm this pattern being the two families mentioned above the most diverse in the four specific floristic groups, although this event is very common in Andean forests located at a certain height, that is, they are similar in floristic composition to family and genus level, while at the species composition varies 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 seasonally dry tropical forests [58] that are geographically 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 forests the eastern precipitation is distributed proportionally throughout the year, climate process according to [45] is linked to distribution patterns of diversity in mountainous areas.

The elevation is one of the main factors 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 influence is one of the major factors for the group, undoubtedly influenced by the seasonally dry forests located below, influence the composition of montane forest Group IV (Achiral), differentiating it structurally and floristically. The elevation in this area influences the presence of haze in certain months [59] and seasonality of precipitation are also important factors, as demonstrated by the above analysis.

This first attempt to classify and search for a pattern of distribution of diversity of montane forests in southern Ecuador confirms the great diversity of it. Not only at the species level since the weather conditions, physiographic and altitudinal, result a fairly wide montane forest types, including mosaic floristic groups with a deep taxonomic study can result in reaching easily identifiable plant communities and determine the presence of indicator species.

**Supplementary Materials:** The following are available online at www.mdpi.com/xxx/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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393 **Author Contributions:** Conceptualization, O.C., A.B. and A.E.; methodology, O.C., A.B., A.E.; formal analysis, 394 O.C., A.B., and P.R.; investigation, O.C, N.C, C.N. and F.T.; data curation, P.R.; writing—original draft 395 preparation, O.C., A.B., A.E.; writing—review and editing, A.E.

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# 401 References

- 402 1. Myers, N.; Mittermeier, R.A.; Mittermeier, C.G.; Da-Fonseca, G.A. & Kent, J. Biodiversity hotspots for conservation priorities *Nature*, **2000**, *403*, 853–858. DOI: 10.1038/35002501.
- Brown, A.D. & Kappelle, M. Introducción a los bosques nublados del neotrópico: una síntesis regional. In
   Bosques nublados del neotrópico, Kappelle, M.; Brown, A.D. Eds.; Instituto Nacional de Biodiversidad (INBio):
   Santo Domingo de Heredia, Costa Rica, 2001, pp. 27–40, ISBN 9968-702-50-1.
- 407 3. Olson, D.M. & Dinerstein, E. The Global 200: Priority ecoregions for global conservation, (2002) *Ann Mo Bot* 408 *Gard*, **2002**, *89*, 199–224. DOI: 10.2307/3298564.
- 412 5. Valencia, R. Composition and structure of an Andean forest fragment in Eastern Ecuador. In *Biodiversity*413 and conservation of neotropical Montane forests, Churchill, P.; Balslev, H.; Forero, E.; Luteyn, J.L. Eds.; The
  414 New York Botanical Garden: New York, USA, 1995, pp. 239–249, ISBN 10: 0893273902.
- 415 6. Uday, V.; Bussman, R. Floristic distribution of the montane cloud forest at the Tapichalaca Reserve, Canton Palanda, Zamora province *Lyonia*, **2004**,7, 92–98.
- 417 7. Madsen, J.E. & Øllgaard, B. Floristic composition, structure, and dynamics of an upper montane rain forest in Southern Ecuador *Nord J Bot*, **1994**, *14*, 403–423. DOI 10.1111/j.1756-1051.1994.tb00626.x.
- 8. Bussmann, R.W. The montane forests of Reserva Biologica San Francisco (Zamora-Chinchipe, Ecuador)-vegetation zonation and natural regeneration *Erde*, **2001**, *1*32, 9–25.
- 421 9. Van der Hammen, T. History of the montane forests of the northern Andes *Plant Syst Evol*, **1989**, *162*, 109–422 114.
- 423 10. Sodiro, L. Ojeada general sobre la vegetación ecuatoriana. Universidad de Quito, Ecuador, 1874.
- 424 11. Diels, L. *Contribuciones al conocimiento de la flora y vegetación de Ecuador*. Espinosa, R. Ed. Anales de la Universidad Central: Quito, Ecuador. 1937.
- 426 12. Acosta-Solís, M. *Divisiones fitogeográficas y formaciones geobotánicas del Ecuador*. Casa de la Cultura ecuatoriana: Quito, Ecuador. 1968.
- 428 13. Harling, G. The vegetation types of Ecuador: a brief survey. In *Tropical Botany*, Larsen, K. & Holm-Nielsen, L.B. Eds.; Academic Press: London, England, 1979, pp. 164–174. ISBN-10:012437350X.
- 430 14. Cañadas-Cruz, L.; Cogez, X.; Lyannaz, J.P.; Ammerman, C. B.; Henry, P. R.; Muñoz, K.A. & Wilson, P.N. 431 El mapa bioclimático y ecológico del Ecuador. Ministerio de Agricultura y Ganadería: Quito, Ecuador. 1983.
- 432 15. Ulloa-Ulloa, C. & Jorgensen, P.M. *Árboles y arbustos de los Andes del Ecuador*. Department of Systematic Botany: Aarhus, Denmark.1993.
- 434 16. Mosandl, R.; Günter, S.; Stimm, B. & Weber, M. Ecuador suffers the highest deforestation rate in South
  435 America. In *Gradients in a tropical mountain ecosystem of Ecuador*; Beck, E.; Bendix, J.; Kottke, I.; Makeschin,
  436 F.; Mosandl, R. Eds. Springer: Berlin; Germany, 2008. pp. 37-40. ISBN 9783540735267.
- 437 17. Sierra, R. Propuesta preliminar de un sistema de clasificación de vegetación para el Ecuador continental. 438 EcoCiencia: Quito, Ecuador. 1999. ISBN 9789978409435.
- 439 18. Bussmann, R.W. Bosques andinos del sur de Ecuador, clasificación, regeneración y uso. *Rev Per Biol*, **2005**, 12, 203–216. DOI:10.15381/rpb.v12i2.2394.
- Lozano, P. Los tipos de bosque en el sur de Ecuador. In Botánica Austroecuatoriana–Estudios sobre los recursos vegetales en las provincias de El Oro, Loja y Zamora Chinchipe; Aguirre, Z.; Madsen, J.E.; Cotton, E. & Balslev,
   H. Eds. Abya Yala: Quito; Ecuador, 2002. pp. 29–50. ISBN 9789978222515.
- 444 20. Lozano, P.; Bussmann, R.W. & Küppers, M. Diversidad florística del bosque montano en el Occidente del Parque Nacional Podocarpus, Sur del Ecuador y su influencia en la flora pionera en deslizamientos naturales. *Revista Científica UDO Agrícola*, 2007, 7,142–159.
- 447 21. Becking, M. Sistema Microregional de Conservación Podocarpus. Tejiendo (micro) corredores de conservación hacia la cogestión de una Reserva de la Biosfera Podocarpus-El Cóndor. Programa Podocarpus: Loja, Ecuador. 2004.
- 450 22. Lozano, P.; Busmann, R.W.; Küppers, M. & Lozano, D. Natural landslides and pioneer communities in the Mountain Ecosystems of Eastern Podocarpus National Park. *Caldasia* **2008**, *30*; 1–19. DOI: 10.15446/caldasia.
- 452 23. Homeier, J. & Breckle, S. Gap-dynamics in a tropical lower montane forest in South Ecuador. In *Gradients*453 *in a tropical mountain ecosystem of Ecuador*; Beck, E.; Bendix, J.; Kottke, I.; Makeschin, F.; Mosandl, R. Eds.
  454 Springer: Berlin; Germany, 2008. pp. 311-317. ISBN 9783540735267.

- 455 24. Jørgensen, P.M. & León-Yánez, S. Catálogo de las plantas vasculares del Ecuador. *Monogr Syst Bot Missouri* 456 *Bot Gard*, **1999**, 75, 1–1181.
- 457 25. 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.
- 459 26. Sabah, A.A.W.; Charles, S.B. & Salem, M.A.A. Principal component and multiple regression analysis in modeling of ground-level ozone and factors affecting its concentrations. *Environ Model Softw*, **2005**, 20, 1263–1271. DOI: 10.1016/j.envsoft.2004.09.001.
- 462 27. Malinowski, R.M. Factor Analysis in Chemistry. Wiley: New York, USA. 1991. ISBN: 978-0-471-53009-1.
- 463 28. Statheropoulos, M.; Vassiliadis, N. & Pappa, A. Principal component and canonical correlation analysis for examining air pollution and meteorological data. *Atmos Environ*, **1998**, 32, 1087–1095. DOI: 10.1016/S1352-2310(97)00377-4.
- 466 29. Cayuela, L.; Benayas, J.M.R.; Justel, A. & Salas-Rey, J. Modelling tree diversity in a highly fragmented tropical montane landscape. *Glob Ecol Biogeogr*, **2006**, *15*, 602–613. DOI: 10.1111/j.1466-822x.2006.00255.x
- 468 30. R Development Core Team. R. *A language and environment for statistical computing*. R Foundation for Statistical Computing: Vienna, Austria. 2013. ISBN 3-900051-07-0, URL.
- 470 31. Clarke, K. R. & Gorley, R. N. PRIMER v6: user manual/tutorial (Plymouth routines in multivariate ecological research): Plymouth, USA. Primer-E Ltd. 2006.
- 472 32. 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.
- 474 33. Josse, C.; Navarro, G.; Comer, P.; Evans, R.; Faber-Langendoen, D.; Fellows, M.; Kittel, G.; Menard, S.; Pyne, M.; (....) & Teague, J. Ecological Systems of Latin America and the Caribbean: A Working Classification of Terrestrial Systems. NatureServe, Arlington, VA. 2003.
- 477 34. Churchill, S. P.; Balslev, H.; Forero, E. & Luteyn, J. L. Biodiversity and Conservation of Neotropical Montane Forests. New York Botanical Garden: New York, USA. 1995. DOI: 10.1016/0169-5347(96)81144-X.
- 479 35. Bush, M. B.; Hanselman, J. A. & Hooghiemstra, H. Andean montane forests and climate change. In: Bush, 480 M. B. & Flenley, J. Eds. *Tropical rainforest response to climatic change*. Springer: Berlin, Heidelberg, Germany. 481 2007. pp. 59–79. ISBN 978-3-642-05383-2.
- 482 36. Antonelli, A. & Sanmartín, I. Why are there so many plant species in the Neotropics?. *Taxon* **2011**, *60*, 403–483 414.
- 484 37. Givnish, T. J. Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlán. *J Ecol* **1998**, *86*, 999–1020.
- 486 38. Homeier, J.; Breckle, S. W.; Günter, S.; Rollenbeck, R. T. & 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.
- 489 39. Rafiqpoor, D.; Kier, G. & Kreft, H. Global centers of vascular plant diversity. *Nova Act Lc* 2005, 92, 61–83.
- 490 40. Condit, R.; Hubbell, S. P. & Foster, R. B. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecol Monogr* **1995**, *65*, 419–439. DOI: 10.2307/2963497.
- 492 41. Davidar, P.; Rajagopal, B.; Mohandass, D.; Puyravaud, J. P.; Condit, R.; Wright, S. J. & Leigh, E. G. The effect of climatic gradients, topographic variation and species traits on the beta diversity of rain forest trees. *Glob Ecol Biogeogr* **2007**, *16*, 510–518. DOI: 10.1111/j.1466-8238.2007.00307.x.
- 495 42. Gaston, K. J.; Williams, P. H.; Eggleton, P. & Humphries, C. J. Large scale patterns of biodiversity: spatial variation in family richness. *P Roy Soc Lond B Bio* **2005**, 260: 149–154. DOI: 10.1098/rspb.1995.0072.
- 497 43. Lomolino, M. A. R. K. Elevation gradients of species-density: historical and prospective views. *Global Ecol Biogeogr*, **2001**, *10*, 3–13. DOI: 10.1046/j.1466-822x.2001.00229.x.
- 499 44. Morales-Castilla, I. & García-Valdés, R. Gradientes latitudinales de diversidad inversos, ¿excepciones que prueban la regla?. *Ecosistemas* 2014, 23: 4–12. DOI: 10.7818/ECOS.2014.23-1.02.
- 45. Kessler, M.; Grytnes, J. A.; Halloy, S. R.P.; Kluge, J.; Krömer, T.; León, B.; Macía, M. J. & Young, K. R.
   502 Gradientes de diversidad vegetal: Patrones y procesos locales. In *Cambio Climático y la Biodiversidad en los* 503 Andes Tropicales, Herzog, S. K.; Martínez, R.; Jørgensen, P. M. & Tiessen, H. Eds. Instituto Interamericano
   504 para la Investigación del Cambio Global: (IAI), São José dos Campos, Brasil; Comité Científico sobre
   505 Problemas del Medio Ambiente (SCOPE): Paris, France. 2012. pp. 235-253. *ISBN*: 978-85-99875-06-3.
- 506 46. Kessler, M. The impact of population processes on patterns of species richness: lessons from elevational gradients. *Basic appl Ecol* **2009**, *10*, 295–299. DOI: 10.1016/j.baae.2008.10.006.
- 508 47. Kessler, M.; Kluge, J.; Hemp, A. & Ohlemüller, R. A global comparative analysis of elevational species richness patterns of ferns. *Glob Ecol Biogeogr*, **2011**, 20, 868-880. DOI: 10.1111/j.1466-8238.2011.00653.x.

- Willig, M. R.; Kaufman, D. M. & Stevens, R. D. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annu Rev Ecol, Evol S* **2003**, *34*, 273–309. DOI: 10.1146/annurev.ecolsys.34.012103.144032.
- 512 49. Kreft, H. & Jetz, W. Global patterns and determinants of vascular plant diversity. *P Natl Acad Sci Biol* **2007**, 104, 5925–5930. DOI:10.1073/pnas.0608361104.
- 514 50. McCain, C. M. Elevational gradients in diversity of small mammals. *Ecology* **2005**, *86*, 366–372. DOI:10.1890/03-3147.
- 51. McCain, C. M. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Glob Ecol Biogeogr* **2007**, *16*, 1–13. DOI: 10.1111/j.1466-8238.2006.00263.x.
- 518 52. McCain, C. M. Global analysis of bird elevational diversity. *Glob Ecol Biogeogr* **2009**, *18*: 346–360. DOI: 10.1111/j.1466-8238.2008.00443.x.
- 520 53. McCain, C. M. Global analysis of reptile elevational diversity. *Glob Ecol Biogeogr* **2010**, *4*: 541-553. DOI: 10.1111/j.1466-8238.2010.00528.x.
- 522 54. Rahbek C. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecol Lett* 2005, *8*: 224–239. DOI: 10.1111/j.1461-0248.2004.00701.x
- 55. Jørgensen PM, Ulloa-Ulloa C, Madsen JE & Valencia R. A floristic analysis of the high Andes of Ecuador.

  In *Biodiversity and conservation of neotropical montane forests*, Churchill, S. P.; Balslev, H.; Forero, E. & Luteyn,

  J. L. Eds. New York Bot. Gard: New York, USA, 1995, pp. 221–238. DOI: 10.1016/0169-5347(96)81144-X.
- 527
   56. Matteucci SD & Colma A. Metodología para el estudio de la vegetación. 1982. Secretaría General de la
   528 Organización de los Estados Americanos, Programa Regional de Desarrollo Científico y Tecnológico,
   529 Washington.
- 57. Kvist, L. P.; Aguirre, Z. & Sánchez, O. Bosques montanos bajos occidentales en Ecuador y sus plantas
  531 medicinales. In *Botánica Económica de los Andes Centrales*, Moraes, M.; Øllgaard, B.; Kvist, L. P.;
  532 Borchsenius, F. & Balslev, H. Eds. Universidad Mayor de San Andrés, La Paz, Bolivia, 2006, pp. 205-223.
  533 ISBN 9995401215.
- 534 58. Espinosa, C. I.; De la Cruz, M.; Luzuriaga, A. L. & Escudero, A. Bosques tropicales secos de la región Pacífico Ecuatorial: diversidad, estructura, funcionamiento e implicaciones para la conservación. *Ecosistemas* **2012**, 21:1–2.
- 537 59. Richter, M. & Moreira-Muñoz, A. Heterogeneidad climática y diversidad de la vegetación en el sur de Ecuador: un método de fitoindicación. *Rev Per Biol*, **2005**, 12: 217–238.