UNIVERSIDAD REGIONAL AMAZÓNICA IKIAM

Facultad de Ciencias de la Vida

Ingeniería en Ecosistemas

SPATIAL PATTERNS OF INSECT DIVERSITY IN CONTINENTAL ECUADOR

Proyecto de investigación previo a la obtención de Título de:

INGENIERO EN ECOSISTEMAS

AUTOR: DANING FERNANDO MONTAÑO OCAMPO

TUTOR: HUGO MAURICIO ORTEGA ANDRADE

CO-TUTOR: GABRIEL MASSAINE MOULATLET

Napo – Ecuador

2022

DECLARACIÓN DE DERECHO DE AUTOR, AUTENTICIDAD Y RESPONSABILIDAD

Tena, 6 de junio de 2022

Yo, Daning Fernando Montaño Ocampo con documento de identidad N°1950004109, declaro que los resultados obtenidos en la investigación que presento en este documento final, previo a la obtención del título de Ingeniero en Ecosistemas, son absolutamente inéditos, originales, auténticos y personales.

En virtud de lo cual, el contenido, criterios, opiniones, resultados, análisis, interpretaciones, conclusiones, recomendaciones y todos los demás aspectos vertidos en la presente investigación son de mi autoría y de mi absoluta responsabilidad.

Por la favorable atención a la presente, suscribo de usted,

Atentamente,

Firma:

Daning Fernando Montaño Ocampo

CERTIFICADO DE DIRECCIÓN DE TRABAJO DE INTEGRACIÓN CURRICULAR

Certifico que el trabajo de integración curricular titulado: "**Spatial patterns of insect diversity in continental Ecuador**", en la modalidad de: artículo de revisión, fue **Realizado por**: Daning Fernando Montaño Ocampo, bajo mi dirección.

El mismo ha sido revisado en su totalidad y analizado por la herramienta de verificación de similitud de contenido; por lo tanto, cumple con los requisitos teóricos, científicos, técnicos, metodológicos y legales establecidos por la Universidad Regional Amazónica Ikiam, para su entrega y defensa.

Tena, 6 de junio de 2022

Firmas:

Firmado electrónicamente por:
HUGO MAURICIO ORTEGA ANDRADE

…… ……..……

Hugo Mauricio Ortega
C.I: 1717270811

Gabriel M. Moulatlet
C.I:1758617607

AGRADECIMIENTOS

Gracias a mis padres por darme la fuerza, amor y apoyo incondicional para cumplir todas las metas que me proponga, por siempre creer en mí. A mis hermanos por ser la inspiración para superarme día a día. Sin mi familia no lograría lo que he logrado hasta ahora, gracias por estar para mí.

A mis tutores Mauricio Ortega y Gabriel Moulatlet, excelentes docentes y amigos, han sido guía e inspiración para seguir mi camino en la ciencia, y también en la vida. Mi agradecimiento a Jennifer Guevara por sus consejos, apoyo y ayudarme a incursionar en esta carrera que ahora es mi pasión. A todos mis docentes que han dejado u poco de sus experiencias y conocimiento en mi en todo este trayecto.

Gracias a la maravillosa familia que me permitió formar la universidad, amigos que conocí de todas partes del Ecuador y que siempre los recordaré: Dennys Chalco, Jefferson García, Valeria Valencia, Carolina Cornejo, Ashley Micolta y muchas personas que conocí en el camino.

Al grupo de investigación de Biogeografía y Ecología Espacial por proporcionar las herramientas necesarias con las cuales se logró analizar los datos de este trabajo de investigación.

TABLA DE CONTENIDO

DECLARACIÓN DE DERECHO DE AUTOR, AUTENTICIDAD Y RESPONSABILIDAD ii

CERTIFICADO DE DIRECCIÓN DE TRABAJO DE INTEGRACIÓN CURRICULAR ... iii

AGRADECIMIENTOS iv

ÍNDICES DE TABLAS vi

ÍNDICES DE FIGURAS viii

ABSTRACT viii

1. INTRODUCTION 1

2. MATERIALS AND METHODS 4

2.1. Data Collection 4

2.2. Species records distribution 4

2.3. α-Diversity 4

2.4. β-Diversity 5

2.5. Areas of endemism 5

2.6. Diversity Predictors 6

2.7. Statistical Analysis 6

3. RESULTS 7

3.1. Species records 7

3.2. Density of records 7

3.3. α-Diversity 8

3.4. β-Diversity 9

3.5. Areas of endemism 10

3.6. Spatial predictors of diversity 10

4.DISCUSSION 11

4.1. Species records 11

4.2. α-Diversity 12

4.3. β -Diversity 14

4.4. Areas of endemism 15

CONCLUSIONS 16

ACKNOWLEDGEMENTS 16

CONFLICT OF INTEREST 16

REFERENCES 177

ANEXOS 27

MATERIAL SUPLEMENTARIO 33

ÍNDICES DE TABLAS

Table 1: Results of Generalized Additive Models (GAMs) of Species richness (Log scaled) and the two first axes of Non-metric Dimensional Scaling (NMDS) evaluating the effect of altitude and longitude. P. value significance codes = 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 '-' Variable was not used. Best models are highlighted in gray ….. 32

Table S2-1: Proportion (%) of distribution of records of species insects in SNAPs areas …….……. 33

Table S2-2: Statistical results of α-Diversity and β-Diversity. "- "means that this field do not apply to the variable ……..…… 37

Table S2-3: Comparation of the Biogeographic provinces from Ecuador and the third k-means classification obtained in this investigation. See Figure 4f and 4g ……. 39

ÍNDICES DE FIGURAS

Figure 1: Study area. Records of insect species (pink dots) in buffer area. Names of principal mountain systems are represented in pink and principal rivers in white. Elevation data is presented as background Information …….…….. 27

Figure 2: a) Proportion (%) of distribution of records by Orders. b) Proportion (%) of insects by databases. c) Proportion (%) of insects by Natural Regions. d) Proportion (%) of insects records inside SNAPs in continental Ecuador ……..……..…….. 28

Figure 3: a) Spatial interpolation of species richness (log). b) Areas of endemism delimited by isolines. c) Sampling effort. d) Result of the subtraction between maps a and c; e) Result of the subtraction between maps b and c ……..... 29

Figure 4: a) Spatial interpolation of the 1° axis of NMDS. b) Result of spatial interpolation of the 2° axis of NMDS. c-f) K-means clusters g) Biogeographic provinces in Ecuador proposed by Morrone (2014) …. 30

Figure 5: GAM's plots. a) Richness and altitude. b) Richness and longitude. c) 1° NMDS and Altitude; d) 1°NMDS and longitude. e) 2°NMDS and longitude…….. 31

Figure S2-1: Biogeographical Regions ……. 36

Figure S2-2: a) Cross-Validation of Species richness. b) Cross- Validation of the 1° axis of the NMDS. c) Cross-Validation of the 1° axis of the NMDS…….. 33

Figure S2-3: Stress plot of the Non-metric dimensional scaling of the matrix of multiple comparation with Jaccard index …….……. 36

Figure S2-4: Best groups obtained through the Average silhouette index by K-means classification ……..... 38

ABSTRACT

Insects are one of the most diverse multicellular organisms on the planet, representing an important part of the global biomass, ecological functions. This group present gaps of knowledge, especially in Ecuador, which is considered megadiverse worldwide and the most biodiverse in species per unit area. The main causes are the wide heterogeneity of ecosystems that occurs in small geographic ranges, complex climatic history and several geological events, originated by the Andes uplift. However, there is knowledge gaps, making it difficult the study of their spatial patterns. For these reasons, our objective is to contribute to the knowledge of regional spatial distribution of biodiversity, including altitudinal, in the way to understand the relation of the Andes uplift and the patterns of insects diversity. Through the use of databases generating from different projects in the country and spatial analysis techniques. Results suggest that information was taxonomical and spatial skewed, and Andes uplift seems to be the main biogeographical barrier that generates the actual patterns of regional diversity of insects. This is the first work that map the regional patterns of insects diversity in continental Ecuador

Keywords: Insects, Spatial Patterns, Alfa diversity, Beta diversity, Endemism, Andes, Ecuador

Spatial patterns of insect diversity in continental Ecuador

Daning Montaño-Ocampo [1]

Gabriel M. Moulatlet [2], H. Mauricio Ortega-Andrade [1,3,4]

[1]Grupo de Biogeografía y Ecología Especial, Universidad Regional Amazónica Ikiam, Tena, Ecuador.

[2]Red de Biología Evolutiva, Instituto de Ecología, A.C., Xalapa, Veracruz, Mexico

[3]Instituto Nacional de Biodiversidad, calle Rumipamba 341 y Av. de los Shyris, Quito, Ecuador.

[4]Ingeniería en Ecosistemas, Facultad de Ciencias de la Vida, Universidad Regional Amazónica Ikiam, km 7 road to Muyuna, Tena, Ecuador

1. INTRODUCTION

Insects are one of the most diverse multicellular organisms on the planet, with more than a million described species, representing an important part of the global biomass, ecological functions and terrestrial and aquatic biodiversity (Diniz-Filho et al., 2010; Lewinsohn et al., 2005; Oliveira, Soares-Filho, et al., 2017). In addition, insects maintain ecosystem services such as pollination (Cardinale et al., 2012), secondary seed dispersal, nutrient flow and parasite control (Nichols et al., 2008), being one of the most important functional groups. Despite its importance in ecosystems, insects are systematics neglected in several taxonomic groups with knowledge gaps in spatial diversity patterns on macroecological or biogeography applied to conservation (Brehm et al., 2005; Cardoso et al., 2011; Diniz-Filho et al., 2010; Gaston & May, 1992; Lewinsohn et al., 2005; Oliveira et al., 2016; Thomas et al., 2008; Wilson et al., 2008). These knowledge gaps have been produced by the limitation of the study on taxonomy and the time required to treat large samples of collections of insects (Diniz-Filho et al., 2010; Spector, 2009). This issue is more note in the tropics, where a greater diversity of species from different groups had been recorded on a global scale (Cardoso et al., 2011; Mittermeier et al., 1998; Myers et al., 2000; Samways, 2005), such as the case of Ecuador.

This country is considered megadiverse worldwide and the most biodiverse in species per unit area in insects (Mittermeier et al., 1998; Sierra et al., 2002). The main causes to determinate the distribution and high diversity of insects in the country is the wide heterogeneity of ecosystems that occurs in small geographic ranges, complex climatic history and several geological events (Michaud et al., 2009), being the Andes mountain

range the principal factor that originate these environmental heterogeneity Andes mountain range(Fontana et al., 2020; Henry et al., 2009; Hodkinson, 2005; Jankowski et al., 2009; Pérez-Toledo et al., 2021). This scenario is ideal to study the interaction between altitudinal gradients originated by mountain ranges and their effect in the regional patterns of diversity. For example, there is a lot of evidence of the influences of mountainous ranges to regional α-diversity on several taxa, suggesting an increment in species richness at intermediate elevations (Bass et al., 2010; Cabrera et al., 2019; Cuesta et al., 2017; Leimbeck et al., 2004; Lessmann et al., 2014; Quintana et al., 2017; Richter et al., 2009; Vargas et al., 2004). On the other hand, the attention in understanding the relationships between elevational changes and β-diversity has increased in recent years, principal findings suggest that mountains increase the shift in the communities influenced by topographic changes (Kraft et al., 2011), and the level of habitat specialization of taxa, (Lenoir et al., 2010; Leprieur et al., 2011; Qian, 2009).

Regarding endemism, which we refer as the occurrence of a species in a specific geographic area and dependent of the spatial scale (Fattorini, 2017), Ecuador has been recognized to harbor several taxonomic groups restricted to specific ecosystems and altitudinal ranges (e.g.: Bass et al., 2010; Morales et al., 2006; Seena et al., 2019; Tobar-Suárez et al., 2022; Voss, 2003). For example, plants increase in endemic species groups above 1000 m., with the highest concentration towards the “Páramos”, due to their unique environmental conditions (Valencia et al., 2000; Young et al., 2002). But, most of the regional patterns mentioned are tied to the study of birds, amphibians, mammals, and plants, generating gaps of knowledge in the understanding of the regional spatial patterns of insects diversity (Cardoso et al., 2011; Diniz-Filho et al., 2010; Oliveira et al., 2016; Oliveira, Soares-Filho, et al., 2017).

Despite the lack of regional studies for understanding the spatial patterns of insects diversity, there are studies focused on more “local” patterns. For example, a high diversity of dung beetles (Coleoptera) at the Cutucú mountain range, a southeastern isolated Amazonian range whit high environmental variability (Celi et al., 2004), the same was found in another study at the Napo province (Espinoza & Noriega, 2018). A high endemism and turnover of beetles has also been recorded in the “páramos” (Moret, 2009). Most of the diversity of ants known in at intermediate (Donoso & Ramón, 2009), and low altitude in a the tropical region (Ryder Wilkie et al., 2010). Geometridae (Lepidoptera) family, are mostly located in the southern montane forest (Brehm et al., 2005). All of these studies emphasize the importance of mountain ranges. Extrapolating these findings to a regional context, is expected that Andes mountain range is the main

biogeographical barrier that explain regional patterns of insects diversity in Ecuador. The high topographic complexity on mountain ranges hypothesis propose that mountain ranges promotes habitat diversity and rapidly change of abiotic conditions in relative short distances, consequently generating insects speciation (Bell & Donoghue, 2005; Distler et al., 2009; Hughes & Eastwood, 2006; Pirie et al., 2006; von Hagen & Kadereit, 2003). These rapid change in habitat and abiotic conditions also make the Andes mountain range recognized as an important hot spot, being considered a promoter of evolutive diversification in several taxonomic groups (Antonelli & Sanmartín, 2011; Santos et al., 2009). But not only the topographic and habitat heterogeneity explains the diversity patterns in mountains ranges, the high environmental energy produced by the interaction of temperature and productivity especially in the transition of montane forest and lowlands regions could explain high diversity present here, by increasing physiological activation, regulating foraging time as well as intervening in development and reproduction (Azcárate & Peco, 2007; Colinet et al., 2015; Khaliq et al., 2014), promoting speciation and decreasing the rate of extinction (Kaspari et al., 2004; Seoane et al., 2017; Storch et al., 2018; Wu, Colwell, et al., 2013).Because of this, Andes mountain range, is an important reservoir, being a refugia for species through different historical rapid climate changes, because species change their range distribution in mountains gradients in order to find optimal conditions, especially when temperature increases at lowlands (Chen et al., 2011; Colwell et al., 2008; Sandel et al., 2011), that is more accentuated in tropical regions where species had narrowed their thermal tolerances (Janzen, 1967).

It is necessary to add that Andes mountain range is not the only explanation by which species diversify, but this biogeographical barrier prepare the scenario to evolutive and environmental process that promote the increase in regional biodiversity (Perrigo et al., 2020), including the Insecta class. For these reasons, is necessary to study the regional spatial distribution of biodiversity, including altitudinal, in the way to understand the relation of the Andes mountain range and the patterns of insects diversity, which could reveal new regional biogeographical and macroecological insights compared to emblematic and widely study groups (Cardoso et al., 2011; Diniz-Filho et al., 2010; Oliveira et al., 2016; Oliveira, Soares-Filho, et al., 2017). Therefore, this work seeks to contribute to the understanding of regional spatial patterns of insects diversity, a taxonomic group catalogued as poorly-known in the country (Diniz-Filho et al., 2010; Inclán Luna et al., 2017). Our objectives are to determinate the influence of Andes mountain range in α-Diversity; β-Diversity and the delimitation of areas of endemism in

continental Ecuador. Following the proposed effect of the Andes, we expected that 1) species richness will change with the presence of Andes mountain; 2) Andes mountain range will be the principal barrier in the shift of species composition and 3) The principal areas of endemism will be delimitated by highlands of Andes. Andes mountain range

2. MATERIALS AND METHODS

2.1. Data Collection

We collected data from five databases: GBIF (https://www.gbif.org/) (Gbif.Org, 2021), iNaturalist (https://www.inaturalist.org/) , IDigBio (https://www.idigbio.org/), Bioweb (https://bioweb.bio/), Base Nacional de Biodiversidad (BNDB); https://bndb.sisbioecuador.bio/bndb/) and Smithsonian collections (https://naturalhistory.si.edu/research/entomology), until September 2021 (Figure 1). Species records only included those found within a 100 km buffer from the political limits of continental Ecuador, and were filtered by selecting the class “Insecta" and the scientific name corresponding to the category “accepted”. We deleted invasive species, repeated records or taxa tagged as *confer* (cf.), *affinis* (aff), or species (sp.). The density of records was estimated with the Kernel interpolation technique in the software QGIS 3.16 (QGIS Development Team, 2021).

2.2. Species records distribution

We calculated the percentage of distribution of the records by Order, the percentage of records coming from the databases, records within different natural regions[as determined by the Ecuador Ecosystems map (Regiones Naturales Ecuador, n.d.)]. Percentages of records within the national system of protected areas (SNAP for the acronym in Spanish) and the records outside these.

2.3. α-Diversity

The species richness (α-Diversity) was estimated using the methodology proposed by Oliveira et al. (2019), which consist in the creation of hexagonal grid, where cells represent a sampling unit with a diameter of 10 km, this measure has been used to previous works of mapping diversity patterns at regional scale (Jenkins et al., 2013). The records were spatially merged with the grid and those cells with less than 30 records (without considering species identifications) were the occurrences eliminated. Then, the number of species was assigned to each cell and the grid was transformed to points taking as reference their centroids. Finally, we interpolate and mapped α-Diversity using

the logarithm of species richness with the Empirical Bayesian Kriging (E.B. Kriging) technique (Pilz & Spöck, 2008), using ArcGIS 10.5 (Redlands, 2016). To evaluate the performance of the models, we conducted a cross-validation test and a simple linear regression model was fitted on the predicted values and the observed values.

Moran's I autocorrelation index was calculated to test spatial autocorrelation, if records are randomly distributed or presented clustered patterns (Goodchild, 1986; Griffith, 1987; Legendre, 1993). To explore spatial autocorrelation on the performance of E.B. Kriging technique, we used the "ape" package (Paradis & Schliep, 2019) in the R project software (R Core Team, 2021).

2.4. β-Diversity

We calculated the regional β-diversity following Oliveira et al.(2017), using a hexagonal grid merged with the records detailed in the section 2.3. The grid was transformed in a presence-absence matrix to calculate a dissimilarity matrix with the Jaccard Index using the "betapart" package (Baselga et al., 2021). The reduction of dimensions was analyzed through Non-metric multidimensional scaling (NMDS) with nine hundred iterations, this is used to find the highest coefficient of determination and the minimum number of axes which represent better the dissimilarity matrix. We use "steapacross" function on the matrix of dissimilarities. This function is useful to estimate dissimilarities between sites which does not share species in common, to subsequently perform a better ordination analysis, to avoid the "horseshoe" effect in the transformation (Williamson, 1978).

NMDS scores obtained from the chosen axes were georeferenced with the centroid of the respective cell and then featured in a shapefile, Moran's I index was calculated to test spatial autocorrelation on these values. Then, NMDS scores were interpolated using the same methodology detailed section 2.3. We conducted a cross-validation test to evaluate the interpolation performance. The results of the interpolation were classified using the K-means technique and visualized in a Red-Green map. The best natural clusters were selected based in average silhouette technique, using the "clusterCrit" package (Desgraupes, 2018). We used the "vegan" package (Oksanen et al., 2020), in the R project software (R Core Team, 2021) for those analyses.

2.5. Areas of endemism

We calculated the regional β-diversity following Oliveira et al.(2017), using a hexagonal grid merged with the records detailed in the section 2.3. The grid was transformed in a

presence-absence matrix to calculate a dissimilarity matrix with the Jaccard Index using the “betapart” package (Baselga et al., 2021). The reduction of dimensions was analyzed through Non-metric multidimensional scaling (NMDS) with nine hundred iterations, this is used to find the highest coefficient of determination and the minimum number of axes which represent better the dissimilarity matrix. We use "steapacross" function on the matrix of dissimilarities. This function is useful to estimate dissimilarities between sites which does not share species in common, to subsequently perform a better ordination analysis, to avoid the “horseshoe” effect in the transformation (Williamson, 1978).

NMDS scores obtained from the chosen axes were georeferenced with the centroid of the respective cell and then featured in a shapefile, Moran’s I index was calculated to test spatial autocorrelation on these values. Then, NMDS scores were interpolated using the same methodology detailed section 2.3. We conducted a cross-validation test to evaluate the interpolation performance. The results of the interpolation were classified using the K-means technique and visualized in a Red-Green map. The best natural clusters were selected based in average silhouette technique, using the “clusterCrit” package (Desgraupes, 2018). We used the “vegan” package (Oksanen et al., 2020), in the R project software (R Core Team, 2021) for those analyses.

2.6. Diversity Predictors

To evaluate the effect of Andes Mountain range, we extracted altitudinal values obtained from: https://srtm.csi.cgiar.org/ and longitudinal values extracted from each centroid in the grid, that contains the logarithm of species richness and the NMDS scores.

2.7. Statistical Analysis

We used Spearman’s rank correlation to evaluate the relationship between the result from Kernel interpolation (density records) and those obtained from the diversity analysis in the previous sections (except β-Diversity). To determinate the correlation of density records and diversity results, we first re-scaled the values from 0 to 1.

To determine “the important areas of biodiversity”, we subtract each raster which resulted from the interpolation of the logarithm of species richness and the areas of endemism, with the raster of density of records, respectively; then the results were classified

according to the following categories: >0.4 = High, 0.4-1 = Medium and <0 = Low. We conducted these analysis in the R project software (R Core Team, 2021).

The relationships between altitude, longitude, α and β diversities were assessed using Generalized Additive Models (GAMs) using the "mgcv" package (Wood, 2011). GAM was chosen because it is a non-parametric regression, which allows data to determine the shape of the response curve and is not limited by the shapes of parametric regression(Crawley, 2002). Model selection was based on the lowest Akaike's information criterion (AIC) value, Adj-R^2, the highest percentage of deviance explained (D2) and the concurvity, being this last one estimated to determine relationships between independent variables and avoid the probability of Type I error with a threshold of ± 0.8. For the analyzes we used the R project software (R Core Team, 2021).

3. RESULTS

3.1. Species records

A total of 82,469 records of insects were found in the databases that fulfill the parameters of filtering, belonging to 8,014 species, 3,107 genus and 357 families (Table S1). The orders with highest number of records were Lepidoptera (34%), Coleoptera (19%), and Hymenoptera (19%) (Figure 2a). The databases with the highest number of records were the citizen science project - iNaturalist (35%), followed by Ecuadorian national databases - Bioweb (31%) and BNDB (18%), and by GBIF (15%) (Figure 2b).

From the total number of records, the Amazon region represented 35% of the records of the insect's species in Ecuador, followed by western montane region (13%) and eastern foothill region (9%). The regions with lowest records were the Dry Shrub with 3% and Paramos with 1% (Figure 2c; Figure S2.1). 18% of the records of insects identified to species level in Ecuador were found within the polygons of the SNAPs (Figure 2d), of with 12% corresponded to the Yasuní National Park, 1.8% to Limoncocha Biological Reserve and the rest were distributed to other protected areas with least of 1% (Table S2.1).

3.2. Density of records

We found a high density (0.7-1) of records in the transition between the northern Andes and Chocó region, especially in the foothills of the north-west of Andes mountain range, near the Esmeraldas River, along the transition between montane forest of the Andes, especially near to the upper Napo, and Amazon lowlands, , in the intersection between

Napo and Aguarico rivers, being located the last one in the surroundings of the Limoncocha Biological station and at the north-western part of the Yasuní National Park (Figure 3c).

The lowest (0-0.4) density of records were found, in the south-eastern part of the Ecuadorian Amazon basin, as well towards the central Andes region, and in the middle of the coastal region, indicating information gaps for insects (Figure 3c).

3.3. α-Diversity

In the coastal region of Ecuador, the highest values (0.7-1) of species richness were found in the Choco Tropical forest, the montane and the foothill forests of the north-western Andes, along the Esmeraldas river basin. The Amazon region, in the Napo rivers basin, have highest values (0.7-1) along the transition of three biogeographical regions: Amazon lowlands, foothill and montane forest of the north-eastern Andes, and areas located between Napo and Aguarico rivers. We also found highest values (0.7-1) in the south-eastern Ecuador, specifically in the Cóndor mountain ranges and the highlands of Andes mountain range, which comprise three different regions: part of the Andean shrub, the eastern montane and the foothill forests. The lowest values (0-0.4) were presented in the south-western part continental Ecuador, mostly associated to dry shrub and deciduous forest regions (Figure 3a).

We detected areas of importance, defined by highest values of α-diversity compares to the record densities, located along the Amazon region, especially in the middle and the south of this region, in areas in central Andes and the coastal region, especially in the middle of these regions. Areas of medium and low importance concerns of knowledge were found mainly from north-western (towards the upper part of the Esmeraldas basin), north-eastern (towards the upper part of the Napo basin) and south-eastern (in the deciduous forest and dry shrub regions) of Andean slopes (Figure 3d).

A total of 319 of 8595 (3.71%) cells fulfill the parameters of filtering and were transformed to points feature shapefile to be used for spatial interpolation. The result of the Moran's I index was 0.09 (p. value < 0.05), meaning spatial autocorrelation, because the index value is close to 0, the positive spatial autocorrelation exists but is weak. The cross-validation results of the E.B. Kriging interpolation indicated a good performance of the technique and that the model capture the variability of the data, the results are detailed

in Figure S2.2a and Table S2.2. The Spearman's rank correlation between the sampling effort and the logarithm of the species richness was rs =0.451 (p. value <0.05).

3.4. β-Diversity

The community composition obtained through the interpolation of NMDS first axis, showed changes from the lowlands to the highlands (Figure 4a) with principal breaks between the limits of western and eastern Andean basins, in the Andean shrub and páramo natural regions A shift of communities is observed in Chongo-Colonche and Mache-Chindul mountains. There were no community changes in the Amazon region. Rivers does not represent barriers for community composition in any region (Figure 4a).

The interpolation of the NMDS second axis showed a longitudinal pattern in the shift of the communities, showing a pattern in the limits between western and eastern part of the basins from the Andes (Figure 4b).

The red-green composition map showed a pattern of difference in species composition between western and eastern basins, where Andes seems to be the principal barrier that breaks the community composition of insects (Figure 4c). The classification of NMDS scores through K-means technique, generated three main domains classifications, with the best average silhouette (Figure S2.4). The first domain divides Ecuador in two regions, the first one in the surrounding Andes region, over the eastern and western montane forest, the union with the deciduous forest and the dry shrub below, towards the Guayas basin, and a second region located towards the union of Amazon a Chocó tropical forest (Figure 4d). The second domain classification divided Ecuador in three biogeographic regions: Coast, Andean and Amazon (Figure 4e). Finally, the third domain classification matched roughly with the biogeographic provinces proposed by Morrone (2014) (Figure 4f, 4g and Table S2.3).

NMDS analysis performed a high correlation between the observed distance and the distance of ordination (Non-metric fit R2 = 0.91 and Linear fit R2 = 0.589) (Figure S2.3), representing the regional variation of the communities, the detailed results of NMDS analysis are showed in Table S2.2. The result of the Moran's I index for NMDS axis-1 was 0.186 (p. value < 0.05) and for NMDS axis-2 was 0.061 (p. value < 0.05), therefore, spatial autocorrelation exists, showing a weak positive spatial autocorrelation. The cross-validation results of the E.B. Kriging interpolation of the NMDS axis 1 and NMDS axis-2 indicated a good performance of the interpolation, showing that the model captures the

variability of both axes. The results of cross-validation for both axes of NMDS analysis are detailed in table S2.2

3.5. Areas of endemism

We identified 7 areas of endemism of insects in Ecuador (Figure 2b). The consensus GIE showed a correlation with the areas of endemism obtained from six categories of distribution ($rs > 0.720$, $p. < 0.05$) and a weaker correlation with the density of records ($rs = 0.555$, $p. < 0.05$). All areas were geographically separated, except the transition between the upper parts of the Napo and Esmeraldas basins (Figure 3b). Rivers and highlands of Andes represent barriers that isolate endemic areas in Ecuador, mostly towards the páaramo and Andean shrubs biogeographic regions.

The areas of endemism were: 1) Upper of Santiago basin, in the transition between páramo, western and eastern montane forest (congruence in the distribution of 344 sp.), 2) In páramo region in the limit of Chimbo and Pastaza rivers basins (congruence in the distribution of 733 sp.), 3) The upper of Napo and Esmeraldas basins, delimitated by Napo and Esmeraldas rivers, included the Paramo and Andean shrub regions (congruence in the distribution of 1411 sp.) (Figure 2b).The Guayas basin presented two areas of endemism: 1) between Daule river and Chongo-Colonche Mountain range, in Choco tropical rainforest (distribution of 393 sp.), 2) Deciduous forest in the Guayas basin (distribution of 263 sp.). Three distinguished endemic areas were located in the Amazon region: 1) The conflux between Coca and Napo rivers (distribution of 1219 sp.), 2) Along the Napo river approximately 50 km downstream (distribution of 930 sp.). 3) The conflux of Palora and Pastaza rivers (distribution of 1552 sp.). (Figure 2b). The areas of importance, defined in this section by high Kernel values of endemism but low record densities, were principally located along the highland of Andes mountain range, and near Daule, Guayas and Napo rivers.

3.6. Spatial predictors of diversity

According to Generalized Additive Models, the altitude and longitude were the best supported variables (lowest AIC), with a concurvity under the established threshold (concurvity = 0.749) and explain a high proportion of species richness) variation (Adj-R^2= 0.242, D2 = 26.40%; Table 1). The altitude showed a hump-shaped pattern along the gradient, with a peak between 500 – 1000 m, followed by a linear decrease of the values (Figure 5a). The longitudinal variation of species richness showed an toward the Andes mountain range, with a peak of Log Species Richness located in the beginning of

western montane and foothill forest, in an east-west direction but did not show a notable decrease toward the eastern region. The lowest values (approximately 1.2-1.3) were found near the Ecuadorian coastal region (Figure 5b).

NMDS axis-1 was better explained by longitude and altitude with the lowest AIC, with concurvity under the established threshold (concurvity = 0.749) and a high proportion of variation explained (Adj-R^2= 0.732, D2 = 74.00%; Table 1). The altitude explained the shift in the communities, that begins from 500 m in the Andes slopes, maintaining a linear relation of species composition change with (Figure 5c). Longitude showed a linear shift in the composition of communities until the end of the Andes (east-west direction), but did not present significant changes (Figure 5d).

NMDS axis-2 was better explained by longitude, altitude was not significant in any model (Concurvity = 0.815). The best model explained the highest proportion of variation (Adj-R^2= 0.090, D2 = 10.49%; Table 1) when the concurvity was minimized. The longitudinal shift in the communities seems to be influenced by the Andes mountain range, and the change began passing the boundaries between western and eastern basins, a different pattern was explained in the Amazon region in contrast with the NMDS axis-1, showing longitudinal change in species composition across Amazonian region (Figure 5e).

4. DISCUSSION

4.1. Species records

The areas with high density of records clustered in our study is consistent with the findings of previous studies, concentrating in the northern part of the country, with the Amazon region having the largest number of records, and gaps of information in the SNAPs across Ecuador (Donoso et al., 2009; Salazar et al., 2015). The bias may be explained by accessibility towards the main cities (e.g. Quito, Guayaquil), roads towards the north of Amazon region by the ways opened by oil companies, the presence of biological stations, the proximity to major museums of the country and highly accessible areas near highways and towns (Donoso et al., 2009; Moerman & Estabrook, 2006; Monsarrat et al., 2019; Oliveira et al., 2016; Salazar et al., 2015). This bias is more pronounced in tropical regions with high diversity, such as Ecuador(Collen et al., 2008; Kier et al., 2005). Regarding the distribution of the records in different databases, Bioweb contains the information from the Museum of Zoology QCAZ at the Pontifical Catholic University of Ecuador, considered the major collection of native taxa of the country (including insects) (Donoso et al., 2009). iNaturalist records were well

represented, this could be explained by the local support given to this platform, as well as the different events and programs of citizen science that increase the number of records, also there is evidence that users are usually specialized on record insects on the platform, but potentially could be skewing the information to urban areas (Di Cecco et al., 2021; Nugent, 2019).

Bias was not only spatial, we found that the information was skewed towards few taxonomic groups, at the order level. For example, Lepidoptera, Coleoptera and Hymenoptera, were the most represented groups in Ecuador, and matches with previous entomological studies in the country (Dangles et al., 2009; Donoso et al., 2009). The high percentage of Lepidoptera records in Ecuador may be explained by research efforts lead by the Florida Museum of Natural History and J. Hall from the National Museum of Natural History (online access: http://www.butterfliesofecuador.com), and the interest of the public to record this taxa in iNaturalist (Drapeau Picard et al., 2021; Mesaglio & Callaghan, 2021). In the case of Coleoptera and Hymenoptera, the information was biased to both groups since the creation of the Invertebrate Section of the Museum of Zoology QCAZ of the Pontificia Universidad Católica in 1981 (Barragán et al., 2009; Dangles et al., 2009).

In this study, areas of importance represent high values of species richness and endemism, but low density of records. Those results are both biases, which suggest spatial and taxonomical autocorrelation, these results encouraging scientist to make public data about insects distribution and change how data are spatial collected in the country. For example: priority areas for collect new information and records might be pristine areas located in Protected Areas, and regions with very characteristic environments would provide valuable data to scientific collections and promote actions of conservation from a biogeographical and macroecological perspective (Beck et al., 2012; Dangles et al., 2009; Diniz-Filho et al., 2010; Hortal et al., 2015; Meier & Dikow, 2004; Oliveira et al., 2016; Salazar et al., 2015).

4.2. α-Diversity

Areas of high species richness obtained was congruent with previous studies of emblematic groups such as birds, plants, mammals and amphibians, especially in the eastern Andes, Amazon and Choco tropical forest regions (e.g.: Antonelli et al., 2018;

Bass et al., 2010; Maestri & Patterson, 2016; Mateo et al., 2013; Schulman et al., 2007; Vargas et al., 2004).

Regional spatial patterns of α-Diversity could be explained by the uplift of the Andes that generated a relationship between topographic heterogeneity, habitat diversity and species richness (Distler et al., 2009; Esquerré et al., 2019; Kreft & Jetz, 2007; Svenning et al., 2010). This pattern was observed by GAMs, which showed an altitudinal and longitudinal pattern of alpha diversity influenced by Andes region. In this altitudinal gradient high topographic heterogeneity exist and promotes habitat diversity and rapidly change of abiotic conditions in relative short distances, consequently generating insects speciation (Bell & Donoghue, 2005; Distler et al., 2009; Hughes & Eastwood, 2006; Pirie et al., 2006; von Hagen & Kadereit, 2003) and acted as "species pump" on other biomes due to environmental changes (Esquerré et al., 2019). In addition, the interaction of high productivity with temperature generates high-energy environments, especially in the transition between montane forest and lowlands, included Amazon a Chocó regions (Letnic & Ripple, 2017; Raich et al., 1991), where the highest species richness is predicted. High-energy environments benefits ectotherms such as insects because temperature intervening in development, reproduction a, physiological activation and regulating foraging time in high productivity environments (Azcárate & Peco, 2007; Colinet et al., 2015; Khaliq et al., 2014), decreasing the rate of extinction too (Kaspari et al., 2004; Seoane et al., 2017; Storch et al., 2018; Wu, Colwell, et al., 2013).

When we focused only in the altitudinal gradient, we find that the change in alpha diversity is not a simple linear relation, contrary GAMs results showed "hump-shape" pattern, with the peak at a range from 500 to 1000 meters, this pattern had been widely documented in different taxa and insects (e.g.: Alvarado et al., 2020; Andrade & Monjeau, 2014; Bharti et al., 2013; Celi et al., 2004; Fontana et al., 2020; Pérez-Toledo et al., 2021; Wu, Yang, et al., 2013). A possible explication for this spatial pattern in mountain ranges had been proposed, this correspond to the "lowland biotic attrition" (Colwell et al., 2008; Huang et al., 2010). This suggest that historical interglacial climatic changes could promote the displacement of species from lowlands to middle-high elevations, where favorable environmental conditions could appear. Loss diversity in lowlands communities is produced by thermal intolerance, especially affecting ectotherms in tropical areas where the ranges of thermal tolerance are narrow (Anderson et al., 2012; Bush et al., 2007; Corlett, 2011; Janzen, 1967; McCain, 2009). Increasing

the importance of Andes mountain range as species reservoir to face historical climate changes.

4.3. β -Diversity

Based on the results of the composition of E.B. Kriging interpolation of the NMDS axes, the Andes mountain range seems to be the principal biogeographical barrier that shifts species composition. At the altitudinal dimension, the results of GAMs and E.B. Kriging interpolation of NMDS axis 1, showed a vertical change in the communities from lowlands to highlands, this shift begins above the 500 m in both sides of the Andes. By the other hand, the almost null change in lowlands communities could be explained by low environmental heterogeneity and the absence of mountain ranges which generates that break the species composition by different habitats, as it happens in the Andes region (Chazot et al., 2016; Dambros et al., 2020; Engemann et al., 2015; Jorgensen & Leon-Yanez, 1999).

Over this threshold, the increase in the differentiation of communities it tends to be linear and positive correlated with altitude, similar pattern found in other tropical regions in birds (Longino & Colwell, 2011), mammals (Maestri & Patterson, 2016; Melo et al., 2009), plants (Engemann et al., 2015), ants (Pérez-Toledo et al., 2021), moths (Brehm et al., 2003) and dung beetles (Nunes et al., 2016).. The evidence suggest that tropical species have the narrower altitudinal distributions, denoting in more rapid shits in the communities in different taxa (e.g.: Brehm et al., 2003; Fontana et al., 2020; Herzog et al., 2005; Melo et al., 2009). In the case of insects, this effect increases due mountains are stronger physiological barriers too, especially in tropical regions where rapid altitudinal chance in temperature occurs and the shorter range of thermal tolerance of ectothermic species is present (Colinet et al., 2015; Janzen, 1967). These factors explain the great influence of the Andes in the spatial pattern of beta diversity of insects.

On the other hand, a regional longitudinal distance pattern is explained by the results of GAMs and E.B. Kriging interpolation of the NMDS axis 2. This pattern of longitudinal distance seems to be affected by the presence of Andes mountain range, especially in the limit between west and east Andes basins. Longitudinal patterns in the shift of species composition, has been less documented, but our results are similar to the findings of other studies, that found a continuous replacement in a west-east sense (Brown Jr & Freitas, 2000; Galindo-Leal et al., 2003; Hanisch et al., 2015). We suggest that this could be explained by the low dispersal ability and the habitat affinity of most of the insects groups, the effect of dispersal limitation in the change of species composition

among sites is expected to increase with spatial scale (Cottenie, 2005; Heino & Heino, 2011), but more information is necessary to understand this pattern.

In Addition, the percentage of similitude of the third k-means classification of the NMDS scores suggest a match of endemic areas by species composition with the biogeographic provinces for the Neotropics proposed by Morrone (2014). These biogeographical regions acts like limits in species composition, similar patterns had been found to other groups (e.g.: birds, ants, palms, bats) in the neotropics (Dambros et al., 2020). But in the case of Ecuador the biogeographic provinces for the Neotropics proposed by Morrone (2014), are strongly bounded by Andes mountain range, suggesting again the importance of this mountain range in species composition.

4.4. Areas of endemism

The areas of endemism in this study were found in Andes region. This mountain range is characterized by specialization of species associated with specific environments across altitudinal gradients (Jankowski et al., 2009; Pyrcz & Wojtusiak, 2002). This is more noticeable in upper parts of the Andes, where areas of endemism are present, more specify in the limits between the west-east basins. The areas match with páramos and Andean shrub biogeographical regions denominated “sky islands” due the evidence of high number of endemic species registered in these areas that evolve through spatio-temporal isolation in these biogeographical regions characterized by different topography, climate and vegetation (Flantua et al., 2019, 2020; Quintana et al., 2017; Simpson, 1974). The historical events that conduced to delimitate areas of endemism in highlands were warm climate conditions changed that fragmented and isolated regions that were connected during glacial periods, these events drove the formation of endemic communities composed by “recent” immigrants in interglacial periods (Hazzi et al., 2018; Morrone, 2018). Endemic species that evolved in highlands present special behaviors and adaptations which contributed to the limited dispersal inside the areas of endemism (Cook, 2002; Moret, 2009; Sites et al., 2003; Smithers & Atkins, 2001). Therefore, in future climate change scenarios, those species may be susceptible to have limitations on restricted areas with suitable environmental conditions (Jankowski et al., 2009).

In this study we suggest that rivers did not represent a barrier in areas of endemism, despite some areas of endemism were delimitated near principal rivers in the country. The “river-barrier hypothesis” had been debated, showing that main rivers proposed as barriers did not affect the distribution of many taxa, including insects (Santorelli et al., 2018). Because principal rivers present in Ecuador are generally straits or the

hydrological conditions change across time, it which does not represent a barrier, compared with larger rivers, i.e. the Amazon river (Dambros et al., 2020; Hoorn et al., 2017; Rossetti et al., 2014; Ruokolainen et al., 2019). Therefore, rivers are determine as barrier of areas of endemism due the bias in the records by the accessibility that bring some rivers (Salazar et al., 2015), that was discussed above. Napo and Esmeraldas basins are interesting areas of endemism because the interaction of Andes slopes and the páramo region. However, is necessary to take into account the higher density of records in those areas.

5. CONCLUSIONS

Andes mountain range seems to be the main biogeographical barrier that generates the actual patterns of regional diversity of insects in Ecuador. Topographic and environmental heterogeneity by habitats could explain those patterns which coincides with the patterns found in the principal surrogate groups by speciation (Distler et al., 2009; Esquerré et al., 2019; Kreft & Jetz, 2007; Svenning et al., 2010). Our findings, suggest importance of the mountain ranges in the maintenance of diversity and the processes that originated it, in spite of Andes is not the only explanation by which species diversify (Perrigo et al., 2020) this study helps to understand the actual regional spatial patterns especially in a group with low regional knowledge, as insects. This is the first work that maps the regional patterns of the insects diversity in continental Ecuador. New information generated herein could support conservation actions for this group, from biogeographical and macroecological perspective.

6. ACKNOWLEDGEMENTS

Daning Montaño thanks the Biogeography and Spatial Ecology Group for the support given to perform the analyses.

7. CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

8. REFERENCES

Alvarado, F., Salomão, R. P., Hernandez-Rivera, Á., & de Araujo Lira, A. F. (2020). Different responses of dung beetle diversity and feeding guilds from natural and disturbed habitats across a subtropical elevational gradient. *Acta Oecologica*, *104*, 103533. https://doi.org/https://doi.org/10.1016/j.actao.2020.103533

Anderson, A. S., Reside, A. E., VanDerWal, J. J., Shoo, L. P., Pearson, R. G., & Williams, S. E. (2012). Immigrants and refugees: the importance of dispersal in mediating biotic attrition under climate change. *Global Change Biology*, *18*(7), 2126–2134. https://doi.org/https://doi.org/10.1111/j.1365-2486.2012.02683.x

Andrade, A., & Monjeau, A. (2014). Patterns in community assemblage and species richness of small mammals across an altitudinal gradient in semi-arid Patagonia, Argentina. *Journal of Arid Environments*, *106*, 18–26. https://doi.org/https://doi.org/10.1016/j.jaridenv.2014.02.004

Antonelli, A., Kissling, W. D., Flantua, S. G. A., Bermúdez, M. A., Mulch, A., Muellner-Riehl, A. N., Kreft, H., Linder, H. P., Badgley, C., Fjeldså, J., Fritz, S. A., Rahbek, C., Herman, F., Hooghiemstra, H., & Hoorn, C. (2018). Geological and climatic influences on mountain biodiversity. *Nature Geoscience 2018 11:10*, *11*(10), 718–725. https://doi.org/10.1038/s41561-018-0236-z

Antonelli, A., & Sanmartín, I. (2011). Why are there so many plant species in the Neotropics? *TAXON*, *60*(2), 403–414. https://doi.org/https://doi.org/10.1002/tax.602010

Azcárate, F. M., & Peco, B. (2007). Harvester ants (Messor barbarus) as disturbance agents in Mediterranean grasslands. *Journal of Vegetation Science*, *18*(1), 103–110. https://doi.org/10.1111/J.1654-1103.2007.TB02520.X

Barragán, A. R., Dangles, O., Cardenas, R. E., & Onore, G. (2009). The History of Entomology in Ecuador. *Annales de La Société Entomologique de France (N.S.)*, *45*(4), 410–423. https://doi.org/10.1080/00379271.2009.10697626

Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieur, F., & Logez, M. (2021). *betapart: Partitioning Beta Diversity into Turnover and Nestedness Components*. https://cran.r-project.org/package=betapart

Bass, M. S., Finer, M., Jenkins, C. N., Kreft, H., Cisneros-Heredia, D. F., McCracken, S. F., Pitman, N. C. A., English, P. H., Swing, K., Villa, G., Di Fiore, A., Voigt, C. C., & Kunz, T. H. (2010). Global Conservation Significance of Ecuador's Yasuní National Park. *PLoS ONE*, *5*(1), e8767. https://doi.org/10.1371/journal.pone.0008767

Beck, J., Ballesteros-Mejia, L., Buchmann, C. M., Dengler, J., Fritz, S. A., Gruber, B., Hof, C., Jansen, F., Knapp, S., Kreft, H., Schneider, A.-K., Winter, M., & Dormann, C. F. (2012). What's on the horizon for macroecology? *Ecography*, *35*(8), 673–683. https://doi.org/https://doi.org/10.1111/j.1600-0587.2012.07364.x

Bell, C. D., & Donoghue, M. J. (2005). Phylogeny and biogeography of Valerianaceae (Dipsacales) with special reference to the South American valerians. *Organisms Diversity & Evolution*, *2*(5), 147–159. https://doi.org/10.1016/J.ODE.2004.10.014

Bharti, H., Sharma, Y. P., Bharti, M., & Pfeiffer, M. (2013). Ant species richness, endemicity and functional groups, along an elevational gradient in the Himalayas. *Asian Myrmecology*, *5*(1), 79–101.

Brehm, G., Homeier, J., & Fiedler, K. (2003). Beta diversity of geometrid moths (Lepidoptera: Geometridae) in an Andean montane rainforest. *Diversity and Distributions*, *9*(5), 351–366. https://doi.org/10.1046/J.1472-4642.2003.00023.X

Brehm, G., Pitkin, L. M., Hilt, N., & Fiedler, K. (2005). Montane Andean rain forests are a global diversity hotspot of geometrid moths. *Journal of Biogeography*, *32*(9), 1621–1627. https://doi.org/10.1111/j.1365-2699.2005.01304.x

Brown Jr, K. S., & Freitas, A. V. L. (2000). Atlantic forest butterflies: indicators for landscape conservation 1. *Biotropica*, *32*(4b), 934–956.

Bush, M. B., Gosling, W. D., & Colinvaux, P. A. (2007). Climate change in the lowlands of the Amazon Basin. In *Tropical Rainforest Responses to Climatic Change* (pp. 55–76). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-540-48842-2_3

Cabrera, O., Benítez, Á., Cumbicus, N., Naranjo, C., Ramón, P., Tinitana, F., & Escudero, A. (2019). Geomorphology and Altitude Effects on the Diversity and Structure of the Vanishing Montane Forest of Southern Ecuador. *Diversity*, *11*(3). https://doi.org/10.3390/d11030032

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., MacE, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*(7401), 59–67. https://doi.org/10.1038/nature11148

Cardoso, P., Erwin, T. L., Borges, P. A. V., & New, T. R. (2011). The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation*, *144*(11), 2647–2655. https://doi.org/10.1016/j.biocon.2011.07.024

Celi, J., Terneus, E., J, T., & Ortega-Andrade, H. M. (2004). Dung beetles (Coleoptera: Scarabaeinae) diversity in an altitudinal gradient in the Cutucú range, Morona Santiago, Ecuadorian Amazon. *Lyonia*, 37–52.

Chazot, N., Willmott, K. R., Condamine, F. L., De-Silva, D. L., Freitas, A. V. L., Lamas, G., Morlon, H., Giraldo, C. E., Jiggins, C. D., Joron, M., Mallet, J., Uribe, S., & Elias, M. (2016). Into the Andes: multiple independent colonizations drive montane diversity in the Neotropical clearwing butterflies Godyridina. *Molecular Ecology*, *25*(22), 5765–5784. https://doi.org/10.1111/MEC.13773

Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*(6045), 1024–1026. https://doi.org/10.1126/SCIENCE.1206432/SUPPL_FILE/CHEN.SOM.PDF

Colinet, H., Sinclair, B. J., Vernon, P., & Renault, D. (2015). Insects in Fluctuating Thermal Environments. *Annual Review of Entomology*, *60*(1), 123–140. https://doi.org/10.1146/annurev-ento-010814-021017

Collen, B., Ram, M., Zamin, T., & McRae, L. (2008). The Tropical Biodiversity Data Gap: Addressing Disparity in Global Monitoring. *Tropical Conservation Science*, *1*(2), 75–88. https://doi.org/10.1177/194008290800100202

Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., & Longino, J. T. (2008). Global Warming, Elevational Range Shifts, and Lowland Biotic Attrition in the Wet Tropics. *Science*. https://doi.org/10.1126/SCIENCE.1162547

Cook, J. (2002). A revision of the neotropical genus Cryptocanthon Balthasar (Coleoptera: Scarabaeidae: Scarabaeinae). *The Coleopterists Bulletin*, *56*(mo1), 3–96.

Corlett, R. T. (2011). Impacts of warming on tropical lowland rainforests. *Trends in Ecology \& Evolution*, *26*(11), 606–613.

Cottenie, K. (2005). Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters*, *8*(11), 1175–1182. https://doi.org/10.1111/J.1461-0248.2005.00820.X

Crawley, M. J. (2002). *Statistical computing: an introduction to data analysis using S-plus*. John Wiley & Sons Ltd.

Cuesta, F., Peralvo, M., Merino-Viteri, A., Bustamante, M., Baquero, F., Freile, J. F., Muriel, P., & Torres-Carvajal, O. (2017). Priority areas for biodiversity conservation in mainland Ecuador. *Neotropical Biodiversity*, *3*(1), 93–106. https://doi.org/10.1080/23766808.2017.1295705

Dambros, C., Zuquim, G., Moulatlet, G. M., Costa, F. R. C., Tuomisto, H., Ribas, C. C., Azevedo, R., Baccaro, F., Bobrowiec, P. E. D., Dias, M. S., Emilio, T., Espirito-Santo, H. M. V, Figueiredo, F. O. G., Franklin, E., Freitas, C., Graça, M. B., d'Horta, F., Leitão, R. P., Maximiano, M., … Magnusson, W. E. (2020). The role of environmental filtering, geographic distance and dispersal barriers in shaping the turnover of plant and animal species in Amazonia. *Biodiversity and Conservation*, *29*(13), 3609–3634. https://doi.org/10.1007/s10531-020-02040-3

Dangles, O., Barragán, A., Cárdenas, R. E., Onore, G., & Keil, C. (2009). Entomology in Ecuador: Recent developments and future challenges. *Https://Doi.Org/10.1080/00379271.2009.10697627*, *45*(4), 424–436. https://doi.org/10.1080/00379271.2009.10697627

Desgraupes, B. (2018). *clusterCrit: Clustering Indices*. https://cran.r-project.org/package=clusterCrit

Di Cecco, G. J., Barve, V., Belitz, M. W., Stucky, B. J., Guralnick, R. P., & Hurlbert, A. H. (2021). Observing the Observers: How Participants Contribute Data to iNaturalist and Implications for Biodiversity Science. *BioScience*, *71*(11), 1179–1188. https://doi.org/10.1093/biosci/biab093

Diniz-Filho, J. A. F., de Marco, P., & Hawkins, B. A. (2010). Defying the curse of ignorance: Perspectives in insect macroecology and conservation biogeography. *Insect Conservation and Diversity*, *3*(3), 172–179. https://doi.org/10.1111/j.1752-4598.2010.00091.x

Distler, T., Jørgensen, P. M., Graham, A., Davidse, G., & Jimenez, I. (2009). Determinants and prediction of broad-scale plant richness across the western neotropics1. *Annals of the Missouri Botanical Garden*, *96*(3), 470–491.

Donoso, D. A., & Ramón, G. (2009). Composition of a high diversity leaf litter ant community (Hymenoptera: Formicidae) from an Ecuadorian pre-montane rainforest. *Annales de La Société Entomologique de France*, *45*(4), 487–499.

Donoso, D. A., Salazar, F., Maza, F., Cárdenas, R. E., & Dangles, O. (2009). Diversity and distribution of type specimens deposited in the Invertebrate section of the Museum of Zoology QCAZ, Quito, Ecuador. *Https://Doi.Org/10.1080/00379271.2009.10697628*, *45*(4), 437–454. https://doi.org/10.1080/00379271.2009.10697628

Drapeau Picard, A.-P., Giroux, M., Saint-Germain, M., & Larrivée, M. (2021). "What's This Bug?" Questions from the Public Provide Relevant Information on Species Distribution and Human-Insect Interactions. *Insects*, *12*(10). https://doi.org/10.3390/insects12100921

Engemann, K., Enquist, B. J., Sandel, B., Boyle, B., Jørgensen, P. M., Morueta-Holme, N., Peet, R. K., Violle, C., & Svenning, J. C. (2015). Limited sampling hampers "big data" estimation of species richness in a tropical biodiversity hotspot. *Ecology and Evolution*, *5*(3), 807–820. https://doi.org/10.1002/ECE3.1405

Espinoza, V. R., & Noriega, J. A. (2018). Diversity of the dung beetles (Coleoptera: Scarabaeinae) in an altitudinal gradient in the east slope of los Andes, Napo province, Ecuador. *Neotropical Biodiversity*, *4*(1),

145–151. https://doi.org/10.1080/23766808.2018.1512199

Esquerré, D., Brennan, I. G., Catullo, R. A., Torres-Pérez, F., & Keogh, J. S. (2019). How mountains shape biodiversity: The role of the Andes in biogeography, diversification, and reproductive biology in South America's most species-rich lizard radiation (Squamata: Liolaemidae). *Evolution*, *73*(2), 214–230. https://doi.org/10.1111/EVO.13657

Fattorini, S. (2017). Endemism in historical biogeography and conservation biology: concepts and implications. *Biogeographia--The Journal of Integrative Biogeography*, *32*(1), 47–75.

Flantua, S. G. A., O'Dea, A., Onstein, R. E., Giraldo, C., & Hooghiemstra, H. (2019). The flickering connectivity system of the north Andean páramos. *Journal of Biogeography*, *46*(8), 1808–1825. https://doi.org/10.1111/JBI.13607

Flantua, S. G. A., Payne, D., Borregaard, M. K., Beierkuhnlein, C., Steinbauer, M. J., Dullinger, S., Essl, F., Irl, S. D. H., Kienle, D., Kreft, H., Lenzner, B., Norder, S. J., Rijsdijk, K. F., Rumpf, S. B., Weigelt, P., & Field, R. (2020). Snapshot isolation and isolation history challenge the analogy between mountains and islands used to understand endemism. *Global Ecology and Biogeography*, *29*(10), 1651–1673. https://doi.org/10.1111/GEB.13155

Fontana, V., Guariento, E., Hilpold, A., Niedrist, G., Steinwandter, M., Spitale, D., Nascimbene, J., Tappeiner, U., & Seeber, J. (2020). Species richness and beta diversity patterns of multiple taxa along an elevational gradient in pastured grasslands in the European Alps. *Scientific Reports*, *10*(1), 12516. https://doi.org/10.1038/s41598-020-69569-9

Galindo-Leal, C., Câmara, I. G., & others. (2003). *The Atlantic Forest of South America: biodiversity status, threats and outlook*.

Gaston, K. J., & May, R. M. (1992). Taxonomy of taxonomists. In *Nature* (Vol. 356, Issue 6367, pp. 281–282). Nature Publishing Group. https://doi.org/10.1038/356281a0

Gbif.Org. (2021). *Occurrence Download*. The Global Biodiversity Information Facility. https://doi.org/10.15468/DL.HQGQRR

Goodchild, M. F. (1986). *Spatial autocorrelation* (Vol. 47). Geo Books.

Griffith, D. A. (1987). Spatial autocorrelation: A primer resource publications in geography. *Association of American Geographers, Washington, DC*.

Hanisch, P. E., Calcaterra, L. A., Leponce, M., Achury, R., Suarez, A. V, Silva, R. R., & Paris, C. I. (2015). *Check list of ground-dwelling ant diversity (Hymenoptera: Formicidae) of the Iguazú National Park with a comparison at regional scale*.

Hazzi, N. A., Moreno, J. S., Ortiz-Movliav, C., & Palacio, R. D. (2018). Biogeographic regions and events of isolation and diversification of the endemic biota of the tropical Andes. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(31), 7985–7990. https://doi.org/10.1073/PNAS.1803908115/-/DCSUPPLEMENTAL

Heino, J. I., & Heino, J. (2011). A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biology*, *56*(9), 1703–1722. https://doi.org/10.1111/J.1365-2427.2011.02610.X

Henry, H., Wijninga, V., & Cleef, A. M. (2009). The paleobotanical record of Colombia: Implications for biogeography and biodiversity. *Annals of the Missouri Botanical Garden*, *93*, 297–325. https://doi.org/10.3417/0026-6493(2006)93[297:TPROCI]2.0.CO;2

Herzog, S. K., Kessler, M., & Bach, K. (2005). The elevational gradient in Andean bird species richness at the local scale: a foothill peak and a high-elevation plateau. *Ecography*, *28*(2), 209–222. https://doi.org/https://doi.org/10.1111/j.0906-7590.2005.03935.x

Hodkinson, I. D. (2005). Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews*, *80*(03), 489. https://doi.org/10.1017/S1464793105006767

Hoorn, C., Bogotá-A, G. R., Romero-Baez, M., Lammertsma, E. I., Flantua, S. G. A., Dantas, E. L., Dino, R., do Carmo, D. A., & Chemale Jr, F. (2017). The Amazon at sea: Onset and stages of the Amazon River from a marine record, with special reference to Neogene plant turnover in the drainage basin. *Global and Planetary Change*, *153*, 51–65.

Hortal, J., de Bello, F., Diniz-Filho, J. A. F., Lewinsohn, T. M., Lobo, J. M., & Ladle, R. J. (2015). Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *46*(1), 523–549. https://doi.org/10.1146/annurev-ecolsys-112414-054400

Huang, X. L., Qiao, G. X., & Lei, F. M. (2010). Use of parsimony analysis to identify areas of endemism of chinese birds: Implications for conservation and biogeography. *International Journal of Molecular Sciences*, *11*(5), 2097–2108. https://doi.org/10.3390/IJMS11052097

Hughes, C., & Eastwood, R. (2006). Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences*, *103*(27), 10334–10339.

Inclán Luna, D., Mora, A., & Prieto, F. (2017). *Agenda Nacional de Investigación sobre la Biodiversidad*.

Jankowski, J. E., Ciecka, A. L., Meyer, N. Y., & Rabenold, K. N. (2009). Beta diversity along environmental gradients: implications of habitat specialization in tropical montane landscapes. *Journal of Animal Ecology*, *78*(2), 315–327. https://doi.org/https://doi.org/10.1111/j.1365-2656.2008.01487.x

Janzen, D. H. (1967). Why Mountain Passes are Higher in the Tropics. *The American Naturalist*, *101*(919), 233–249. http://www.jstor.org/stable/2458977

Jenkins, C. N., Pimm, S. L., & Joppa, L. N. (2013). Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences*, *110*(28), E2602–E2610. https://doi.org/10.1073/pnas.1302251110

Jorgensen, P. M., & Leon-Yanez, S. (1999). Catalogue of the vascular plants of Ecuador. *Monographs of Systematic Botany of the Missouri Botanical Garden*, *75*, 1–1182.

Kaspari, M., Ward, P. S., & Yuan, M. (2004). Energy gradients and the geographic distribution of local ant diversity. *Oecologia*, *140*(3), 407–413. https://doi.org/10.1007/s00442-004-1607-2

Khaliq, A. M., Javed, M., Sohail, M., & Sagheer, M. (2014). Environmental effects on insects and their population dynamics. *Journal of Entomology and Zoology Studies*, *2*(2), 1–7.

Kier, G., Mutke, J., Dinerstein, E., Ricketts, T. H., Küper, W., Kreft, H., & Barthlott, W. (2005). Global patterns of plant diversity and floristic knowledge. *Journal of Biogeography*, *32*(7), 1107–1116. https://doi.org/10.1111/j.1365-2699.2005.01272.x

Kraft, N. J. B., Comita, L. S., Chase, J. M., Sanders, N. J., Swenson, N. G., Crist, T. O., Stegen, J. C., Vellend, M., Boyle, B., Anderson, M. J., Cornell, H. V, Davies, K. F., Freestone, A. L., Inouye, B. D., Harrison, S. P., & Myers, J. A. (2011). Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science (New York, N.Y.)*, *333*(6050), 1755–1758. https://doi.org/10.1126/science.1208584

Kreft, H., & Jetz, W. (2007). Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(14), 5925–5930. https://doi.org/10.1073/pnas.0608361104

Legendre, P. (1993). Spatial Autocorrelation: Trouble or New Paradigm? *Ecology*, *74*(6), 1659–1673. http://www.jstor.org/stable/1939924

Leimbeck, R. M., Valencia, R., & Balslev, H. (2004). Landscape diversity patterns and endemism of Araceae in Ecuador. *Biodiversity and Conservation*, *13*(9), 1755–1779. https://doi.org/10.1023/B:BIOC.0000029332.91351.7a

Lenoir, J., Gégout, J.-C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N. E., Dullinger, S., Pauli, H., Willner, W., Grytnes, J.-A., Virtanen, R., & Svenning, J.-C. (2010). Cross-Scale Analysis of the Region Effect on Vascular Plant Species Diversity in Southern and Northern European Mountain Ranges. *PLOS ONE*, *5*(12), 1–13. https://doi.org/10.1371/journal.pone.0015734

Leprieur, F., Tedesco, P. A., Hugueny, B., Beauchard, O., Dürr, H. H., Brosse, S., & Oberdorff, T. (2011). Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecology Letters*, *14*(4), 325–334. https://doi.org/10.1111/j.1461-0248.2011.01589.x

Lessmann, J., Muñoz, J., & Bonaccorso, E. (2014). Maximizing species conservation in continental Ecuador: A case of systematic conservation planning for biodiverse regions. *Ecology and Evolution*, *4*. https://doi.org/10.1002/ece3.1102

Letnic, M., & Ripple, W. J. (2017). Large-scale responses of herbivore prey to canid predators and primary productivity. *Global Ecology and Biogeography*, *26*(8), 860–866.

Lewinsohn, T. M., Freitas, A. V. L., & Prado, P. I. (2005). Conservation of terrestrial invertebrates and their habitats in Brazil. *Conservation Biology*, *19*(3), 640–645. https://doi.org/10.1111/j.1523-1739.2005.00682.x

Longino, J. T., & Colwell, R. K. (2011). Density compensation, species composition, and richness of ants on a neotropical elevational gradient. *Ecosphere*, *2*(3), art29. https://doi.org/https://doi.org/10.1890/ES10-00200.1

Maestri, R., & Patterson, B. D. (2016). Patterns of Species Richness and Turnover for the South American Rodent Fauna. *PLOS ONE*, *11*(3), e0151895. https://doi.org/10.1371/journal.pone.0151895

Mateo, R. G., de la Estrella, M., Felicísimo, Á. M., Muñoz, J., & Guisan, A. (2013). A new spin on a compositionalist predictive modelling framework for conservation planning: A tropical case study in Ecuador. *Biological Conservation*, *160*, 150–161. https://doi.org/https://doi.org/10.1016/j.biocon.2013.01.014

McCain, C. M. (2009). Vertebrate range sizes indicate that mountains may be 'higher' in the tropics. *Ecology Letters*, *12*(6), 550–560. https://doi.org/https://doi.org/10.1111/j.1461-0248.2009.01308.x

Meier, R., & Dikow, T. (2004). Significance of Specimen Databases from Taxonomic Revisions for Estimating and Mapping the Global Species Diversity of Invertebrates and Repatriating Reliable Specimen Data. *Conservation Biology*, *18*(2), 478–488. http://www.jstor.org/stable/3589226

Melo, A. S., Rangel, T. F. L. V. B., & Diniz-Filho, J. A. F. (2009). Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography*, *32*(2), 226–236. https://doi.org/https://doi.org/10.1111/j.1600-0587.2008.05502.x

Mesaglio, T., & Callaghan, C. T. (2021). An overview of the history, current contributions and future outlook of iNaturalist in Australia. *Wildlife Research*, *48*(4), 289–303.

Michaud, F., Witt, C., & Royer, J.-Y. (2009). Influence of the subduction of the Carnegie volcanic ridge on Ecuadorian geology: Reality and fiction. *Geological Society of America Memoirs*, *204*, 217–228. https://doi.org/10.1130/2009.1204(10)

Mittermeier, R. A., Myers, N., Thomsen, J. B., da Fonseca, G. A. B., & Olivieri, S. (1998). Biodiversity Hotspots and Major Tropical Wilderness Areas: Approaches to Setting Conservation Priorities. *Conservation Biology*, *12*(3), 516–520. https://doi.org/10.1046/j.1523-1739.1998.012003516.x

Moerman, D. E., & Estabrook, G. F. (2006). The botanist effect: counties with maximal species richness tend to be home to universities and botanists. *Journal of Biogeography*, *33*(11), 1969–1974. https://doi.org/https://doi.org/10.1111/j.1365-2699.2006.01549.x

Monsarrat, S., Boshoff, A. F., & Kerley, G. I. H. (2019). Accessibility maps as a tool to predict sampling bias in historical biodiversity occurrence records. *Ecography*, *42*(1), 125–136. https://doi.org/10.1111/ECOG.03944

Morales, M., Øllgaard, B., Lars, K., Borchsenius, F., & Balsev, H. (2006). Botánica Económica de los Andes Centrales. In *Ecología en Bolivia* (Vol. 42, Issue 1). UNIVERSIDAD MAYOR DE SAN ANDRÉS.

Moret, P. (2009). Altitudinal distribution, diversity and endemicity of Carabidae (Coleoptera) in the páramos of Ecuadorian Andes. *Annales de La Société Entomologique de France*, *45*(4), 500–510.

Morrone, J. J. (2014). Biogeographical regionalisation of the Neotropical region. *Zootaxa*, *3782*(1), 1–110.

Morrone, J. J. (2018). *Evolutionary biogeography of the Andean region*. CRC Press.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature 2000 403:6772*, *403*(6772), 853–858. https://doi.org/10.1038/35002501

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., & Favila, M. E. (2008). Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation*, *141*(6), 1461–1474. https://doi.org/10.1016/j.biocon.2008.04.011

Nugent, J. (2019). Summer squash citizen science. *Science Scope*, *42*(9), 22–25. https://www.jstor.org/stable/26899026

Nunes, C. A., Braga, R. F., Figueira, J. E. C., De Siqueira Neves, F., & Fernandes, G. W. (2016). Dung Beetles along a Tropical Altitudinal Gradient: Environmental Filtering on Taxonomic and Functional Diversity. *PLOS ONE*, *11*(6), e0157442. https://doi.org/10.1371/JOURNAL.PONE.0157442

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2020). *vegan: Community Ecology Package*. https://cran.r-project.org/package=vegan

Oliveira, U., Pereira Paglia, A., Brescovit, A. D., B de Carvalho, C. J., Paiva Silva, D., Rezende, D. T., Fortes Leite, F. S., Aguiar Nogueira Batista, ao, Paulo Peixoto Pena Barbosa, ao, Renato Stehmann, ao, Ascher, J. S., Ferreira de Vasconcelos, M., De Marco Jr, P., Guimar, P., Dias, aes, Gianluppi Ferro, V., & Santos, A. J. (2016). The strong influence of collection bias on biodiversity knowledge shortfalls of Brazilian terrestrial biodiversity. *Diversity and Distributions*, *22*, 1232–1244. https://doi.org/10.1111/ddi.12489

Oliveira, U., Soares-Filho, B., Leitão, R. F. M. H., & Rodrigues, H. O. (2019). BioDinamica: A toolkit for analyses of biodiversity and biogeography on the Dinamica-EGO modelling platform. *PeerJ*, *2019*(7), e7213. https://doi.org/10.7717/peerj.7213

Oliveira, U., Soares-Filho, B. S., Paglia, A. P., Brescovit, A. D., De Carvalho, C. J. B., Silva, D. P., Rezende, D. T., Leite, F. S. F., Batista, J. A. N., Barbosa, J. P. P. P., Stehmann, J. R., Ascher, J. S., De Vasconcelos, M. F., De Marco, P., Löwenberg-Neto, P., Ferro, V. G., & Santos, A. J. (2017). Biodiversity conservation gaps in the Brazilian protected areas. *Scientific Reports*, *7*(1), 1–9. https://doi.org/10.1038/s41598-017-08707-2

Oliveira, U., Vasconcelos, M. F., & Santos, A. J. (2017). Biogeography of Amazon birds: rivers limit species composition, but not areas of endemism. *Scientific Reports 2017 7:1*, *7*(1), 1–11. https://doi.org/10.1038/s41598-017-03098-w

Paradis, E., & Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in {R}. *Bioinformatics*, *35*, 526–528.

Pérez-Toledo, G. R., Valenzuela-González, J. E., Moreno, C. E., Villalobos, F., & Silva, R. R. (2021). Patterns and drivers of leaf-litter ant diversity along a tropical elevational gradient in Mexico. *Journal of Biogeography*, *48*(10), 2512–2523. https://doi.org/https://doi.org/10.1111/jbi.14217

Perrigo, A., Hoorn, C., & Antonelli, A. (2020). Why mountains matter for biodiversity. *Journal of Biogeography*, *47*(2), 315–325. https://doi.org/https://doi.org/10.1111/jbi.13731

Pilz, J., & Spöck, G. (2008). Why do we need and how should we implement Bayesian kriging methods. *Stochastic Environmental Research and Risk Assessment*, *22*(5), 621–632. https://doi.org/10.1007/s00477-007-0165-7

Pirie, M. D., Chatrou, L. W., Mols, J. B., Erkens, R. H. J., & Oosterhof, J. (2006). 'Andean-centred'genera in the short-branch clade of Annonaceae: testing biogeographical hypotheses using phylogeny reconstruction and molecular dating. *Journal of Biogeography*, *33*(1), 31–46.

Pyrcz, T. W., & Wojtusiak, J. (2002). The vertical distribution of pronophiline butterflies (Nymphalidae, Satyrinae) along an elevational transect in Monte Zerpa (Cordillera de Mérida, Venezuela) with remarks on their diversity and parapatric distribution. *Global Ecology and Biogeography*, *11*(3), 211–221. https://doi.org/https://doi.org/10.1046/j.1466-822X.2002.00285.x

Qian, H. (2009). Beta diversity in relation to dispersal ability for vascular plants in North America. *Global Ecology and Biogeography*, *18*, 327–332. https://doi.org/10.1111/j.1466-8238.2009.00450.x

Quintana, C., Girardello, M., Barfod, A. S., & Balslev, H. (2017). Diversity patterns, environmental drivers and changes in vegetation composition in dry inter-Andean valleys. *JOURNAL OF PLANT ECOLOGY*, *10*(3), 461–475. https://doi.org/10.1093/jpe/rtw036

R Core Team. (2021). *R: A Language and Environment for Statistical Computing*. https://www.r-project.org/

Raich, J. W., Rastetter, E. B., Melillo, J. M., Kicklighter, D. W., Steudler, P. A., Peterson, B. J., Grace, A. L., Moore, B. 3rd, & Vorosmarty, C. J. (1991). Potential Net Primary Productivity in South America: Application of a Global Model. *Ecological Applications : A Publication of the Ecological Society of America*, *1*(4), 399–429. https://doi.org/10.2307/1941899

Redlands, C. E. S. R. I. (2016). *ArcGIS Desktop: Release 10.5*.

Regiones naturales Ecuador. (n.d.). Retrieved January 12, 2022, from https://bioweb.bio/faunaweb/reptiliaweb/RegionesNaturales

Richter, M., Diertl, K.-H., Emck, P., Peters, T., & Beck, E. (2009). Reasons for an outstanding plant diversity in the tropical Andes of Southern Ecuador. *Landscape Online*, *12*(0 SE-Research Article), 1–35.

https://doi.org/10.3097/LO.200912

Rossetti, D. F., Cohen, M. C. L., Bertani, T. C., Hayakawa, E. H., Paz, J. D. S., Castro, D. F., & Friaes, Y. (2014). Late Quaternary fluvial terrace evolution in the main southern Amazonian tributary. *Catena*, *116*, 19–37.

Ruokolainen, K., Moulatlet, G. M., Zuquim, G., Hoorn, C., & Tuomisto, H. (2019). Geologically recent rearrangements in central Amazonian river network and their importance for the riverine barrier hypothesis. *Frontiers of Biogeography*, *11*(3).

Ryder Wilkie, K. T., Mertl, A. L., & Traniello, J. F. A. (2010). Species Diversity and Distribution Patterns of the Ants of Amazonian Ecuador. *PLoS ONE*, *5*(10), e13146. https://doi.org/10.1371/journal.pone.0013146

Salazar, F., Reyes-Bueno, F., Sanmartin, D., & Donoso, D. A. (2015). Mapping continental Ecuadorian ant species. *Sociobiology*, *62*(2), 132–162. https://doi.org/10.13102/sociobiology.v62i2.132-162

Samways, M. J. (2005). *Insect diversity conservation*. Cambridge University Press.

Sandel, B., Arge, L., Dalsgaard, B., Davies, R. G., Gaston, K. J., Sutherland, W. J., & Svenning, J. C. (2011). The influence of late quaternary climate-change velocity on species endemism. *Science*, *334*(6056), 660–664. https://doi.org/10.1126/SCIENCE.1210173/SUPPL_FILE/SANDEL-SOM.PDF

Santorelli, S., Magnusson, W. E., & Deus, C. P. (2018). Most species are not limited by an Amazonian river postulated to be a border between endemism areas. *Scientific Reports 2018 8:1*, *8*(1), 1–8. https://doi.org/10.1038/s41598-018-20596-7

Santos, J. C., Coloma, L. A., Summers, K., Caldwell, J. P., Ree, R., & Cannatella, D. C. (2009). Amazonian Amphibian Diversity Is Primarily Derived from Late Miocene Andean Lineages. *PLOS Biology*, *7*(3), e1000056. https://doi.org/10.1371/JOURNAL.PBIO.1000056

Schulman, L., Toivonen, T., & Ruokolainen, K. (2007). Analysing botanical collecting effort in Amazonia and correcting for it in species range estimation. *Journal of Biogeography*, *34*, 1388–1399.

Seena, S., Bärlocher, F., Sobral, O., Gessner, M. O., Dudgeon, D., McKie, B. G., Chauvet, E., Boyero, L., Ferreira, V., Frainer, A., Bruder, A., Matthaei, C. D., Fenoglio, S., Sridhar, K. R., Albariño, R. J., Douglas, M. M., Encalada, A. C., Garcia, E., Ghate, S. D., … Graça, M. A. S. (2019). Biodiversity of leaf litter fungi in streams along a latitudinal gradient. *Science of The Total Environment*, *661*, 306–315. https://doi.org/https://doi.org/10.1016/j.scitotenv.2019.01.122

Seoane, J., Laiolo, P., & Obeso, J. R. (2017). Abundance leads to more species, particularly in complex habitats: a test of the increased population size hypotheses in bird communities. *Journal of Biogeography*, *44*(3), 556–566. https://doi.org/10.1111/JBI.12877

Sierra, R., Campos, F., & Chamberlin, J. (2002). Assessing biodiversity conservation priorities: Ecosystem risk and representativeness in continental Ecuador. *Landscape and Urban Planning*, *59*, 95–110. https://doi.org/10.1016/S0169-2046(02)00006-3

Simpson, B. B. (1974). Glacial Migrations of Plants: Island Biogeographical Evidence. *Science*, *185*(4152), 698–700. https://doi.org/10.1126/SCIENCE.185.4152.698

Sites, R. W., Willig, M. R., & Linit, M. J. (2003). Macroecology of aquatic insects: a quantitative analysis of taxonomic richness and composition in the Andes mountains of northern Ecuador. *Biotropica*, *35*(2), 226–239.

Smithers, P., & Atkins, N. (2001). Altitudinal variation in páramo invertebrate communities on Volcán Chiles,

with particular reference to Carabidae (Coleoptera). *The Ecology of Volcán Chiles: High-Altitude Ecosystems on the Ecuador-Colombia Border. Pebble \& Shell. Plymouth*, 145–151.

Spector, S. (2009). Scarabaeine Dung Beetles (coleoptera: Scarabaeidae: Scarabaeinae): An Invertebrate Focal Taxon for Biodiversity Research and Conservation. *The Coleopterists Bulletin*, *60*, 71–83. https://doi.org/10.1649/0010-065X(2006)60[71:SDBCSS]2.0.CO;2

Storch, D., Bohdalková, E., & Okie, J. (2018). The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity–diversity relationship. *Ecology Letters*, *21*(6), 920–937. https://doi.org/10.1111/ELE.12941

Svenning, J.-C., Fitzpatrick, M. C., Normand, S., Graham, C. H., Pearman, P. B., Iverson, L. R., & Skov, F. (2010). Geography, topography, and history affect realized-to-potential tree species richness patterns in Europe. *Ecography*, *33*(6), 1070–1080.

Thomas, C. D., Bulman, C. R., & Wilson, R. J. (2008). Where within a geographical range do species survive best? A matter of scale. *Insect Conservation and Diversity*, *1*(1), 2–8. https://doi.org/10.1111/j.1752-4598.2007.00001.x

Tobar-Suárez, C., Urbina-Cardona, N., Villalobos, F., & Pineda, E. (2022). Amphibian species richness and endemism in tropical montane cloud forests across the Neotropics. *Biodiversity and Conservation*, *31*(1), 295–313. https://doi.org/10.1007/s10531-021-02335-z

Valencia, R., Leon-Yanez, S., & Jørgensen, P. M. (2000). *Libro rojo de las plantas endémicas del Ecuador*. Herbario QCA, Universidad Católica del Ecuador.

Vargas, J. H., Consiglio, T., Jorgensen, P. M., & Croat, T. B. (2004). Modelling distribution patterns in a species-rich plant genus, Anthurium (Araceae), in Ecuador. *DIVERSITY AND DISTRIBUTIONS*, *10*(3), 211–216. https://doi.org/10.1111/j.1366-9516.2004.00081.x

von Hagen, K. B., & Kadereit, J. W. (2003). The diversification of Halenia (Gentianaceae): ecological opportunity versus key innovation. *Evolution; International Journal of Organic Evolution*, *57*(11), 2507–2518.

Voss, R. S. (2003). A new species of Thomasomys (Rodentia: Muridae) from eastern Ecuador, with remarks on mammalian diversity and biogeography in the Cordillera Oriental. *American Museum Novitates*, *2003*(3421), 1–47.

Williamson, M. H. (1978). The Ordination of Incidence Data. *Journal of Ecology*, *66*(3), 911–920. http://www.jstor.org/stable/2259303

Wilson, R. F., Goosem, M. W., & Wilson, G. W. (2008). Resilience of arboreal folivores to habitat damage by a severe tropical cyclone. *Austral Ecology*, *33*, 573–579. https://doi.org/10.1111/j.1442-9993.2008.01913.x

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, *73*(1), 3–36. https://doi.org/https://doi.org/10.1111/j.1467-9868.2010.00749.x

Wu, Y., Colwell, R. K., Rahbek, C., Zhang, C., Quan, Q., Wang, C., & Lei, F. (2013). Explaining the species richness of birds along a subtropical elevational gradient in the Hengduan Mountains. *Journal of Biogeography*, *40*(12), 2310–2323. https://doi.org/https://doi.org/10.1111/jbi.12177

Wu, Y., Yang, Q., Wen, Z., Xia, L., Zhang, Q., & Zhou, H. (2013). What drives the species richness patterns of non-volant small mammals along a subtropical elevational gradient? *Ecography*, *36*(2), 185–196.

https://doi.org/https://doi.org/10.1111/j.1600-0587.2011.07132.x

Young, K. R., Ulloa, C. U., Luteyn, J. L., & Knapp, S. (2002). Plant evolution and endemism in Andean South America: An introduction. *The Botanical Review*, *68*(1), 4–21. https://doi.org/10.1663/0006-8101(2002)068[0004:PEAEIA]2.0.CO;2

ANEXOS

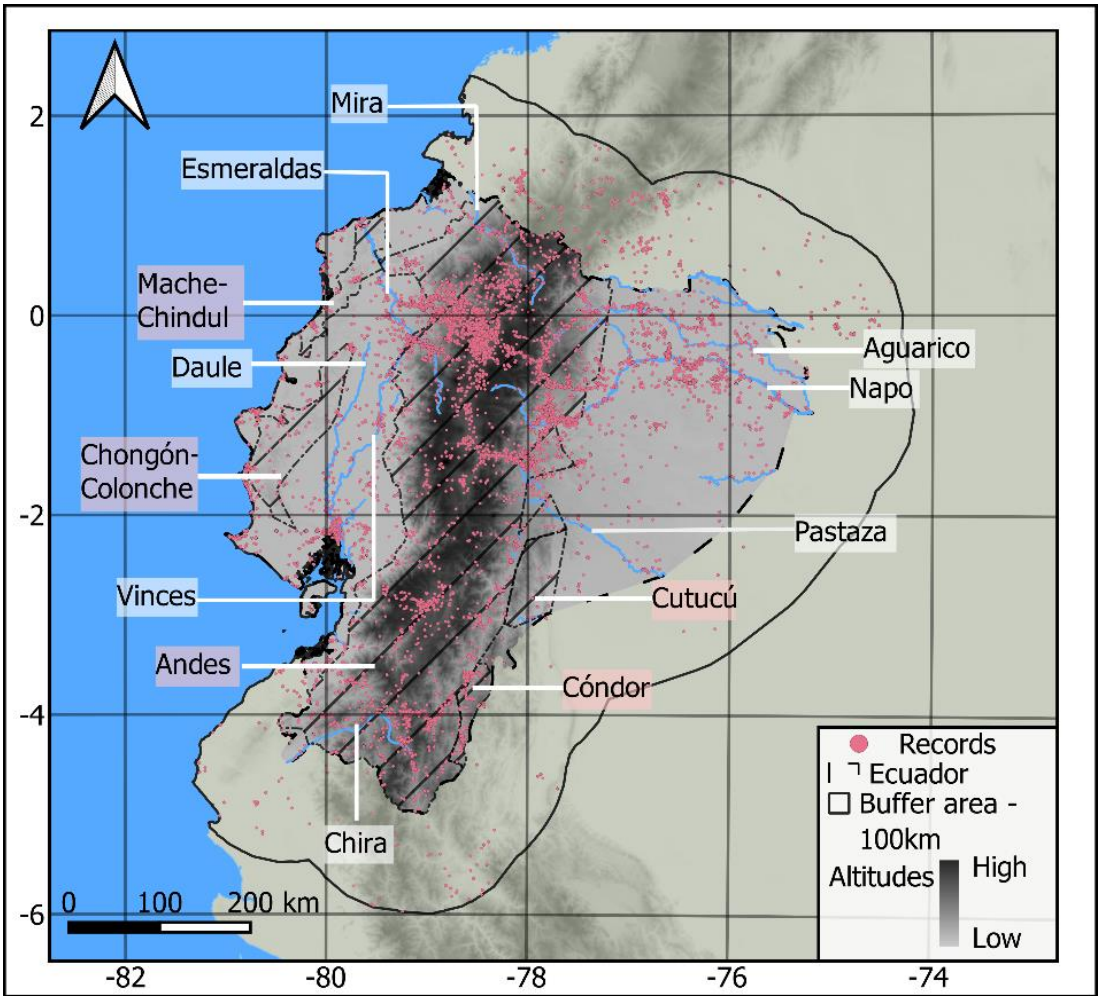

Figure 1: Study area. Records of insect species (pink dots) in buffer area. Names of principal mountain systems are represented in pink and principal rivers in white. Elevation data is presented as background information. **Realizado por**: Montaño, 2022.

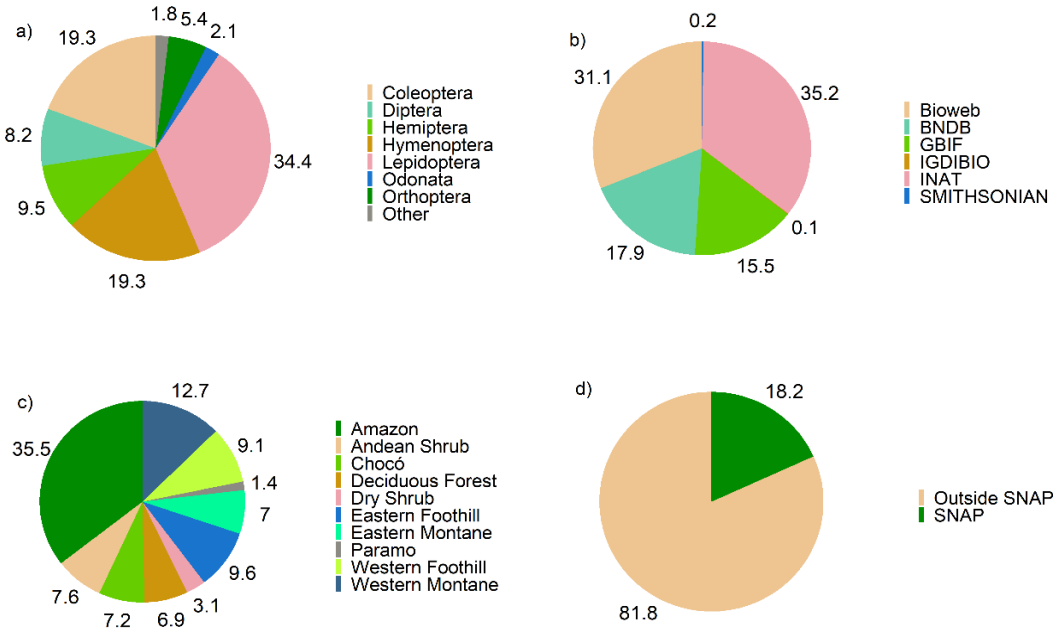

Figure 2: a) Proportion (%) of distribution of records by Orders. b) Proportion (%) of records by databases. c) Proportion (%) of records by Natural Regions. d) Proportion (%) of records inside SNAPs in continental Ecuador. **Realizado por**: Montaño, 2022.

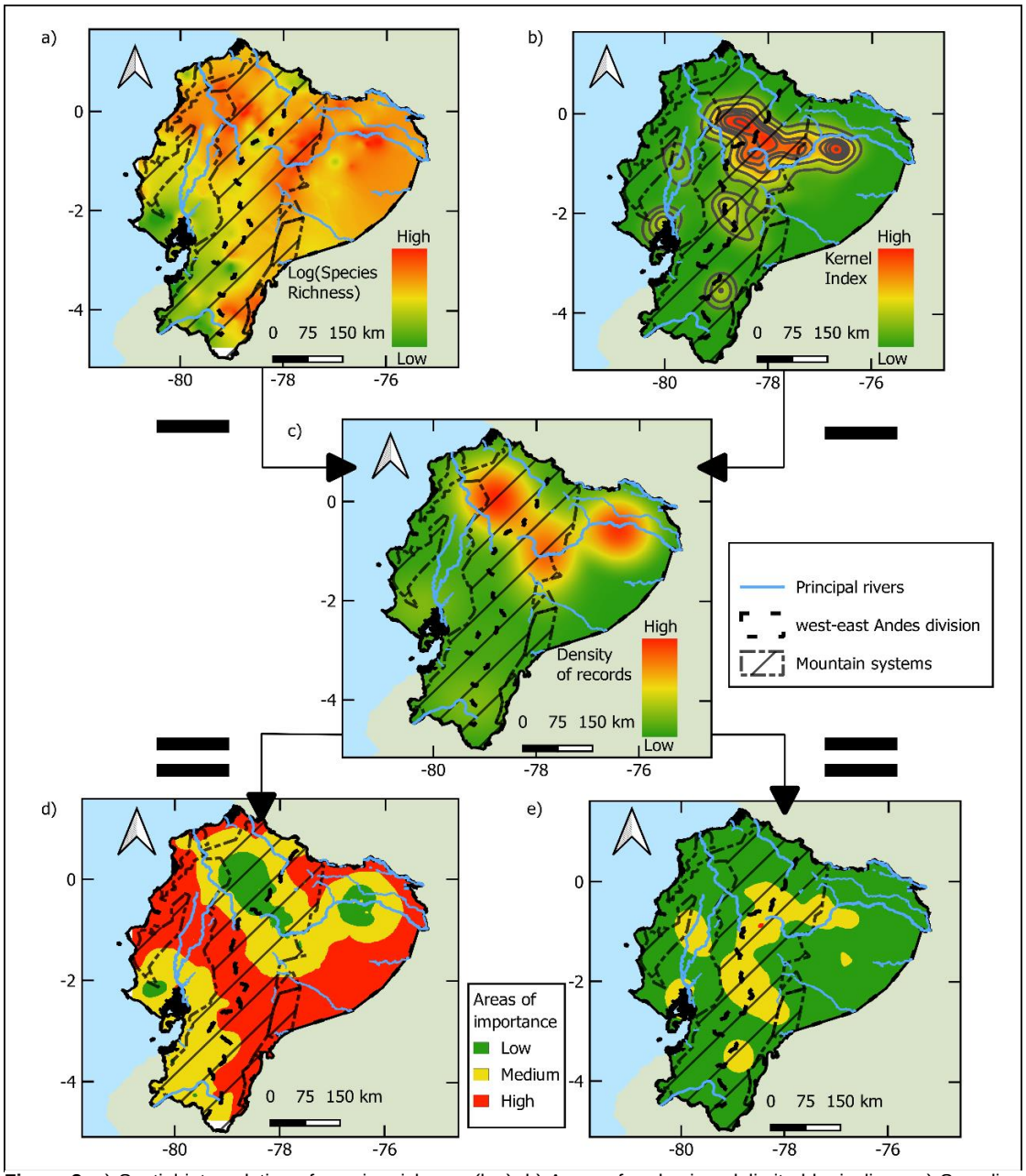

Figure 3: a) Spatial interpolation of species richness (log). b) Areas of endemism delimited by isolines. c) Sampling effort. d) Result of the subtraction between maps a and c; e) Result of the subtraction between maps b and c. **Realizado por**: Montaño, 2022.

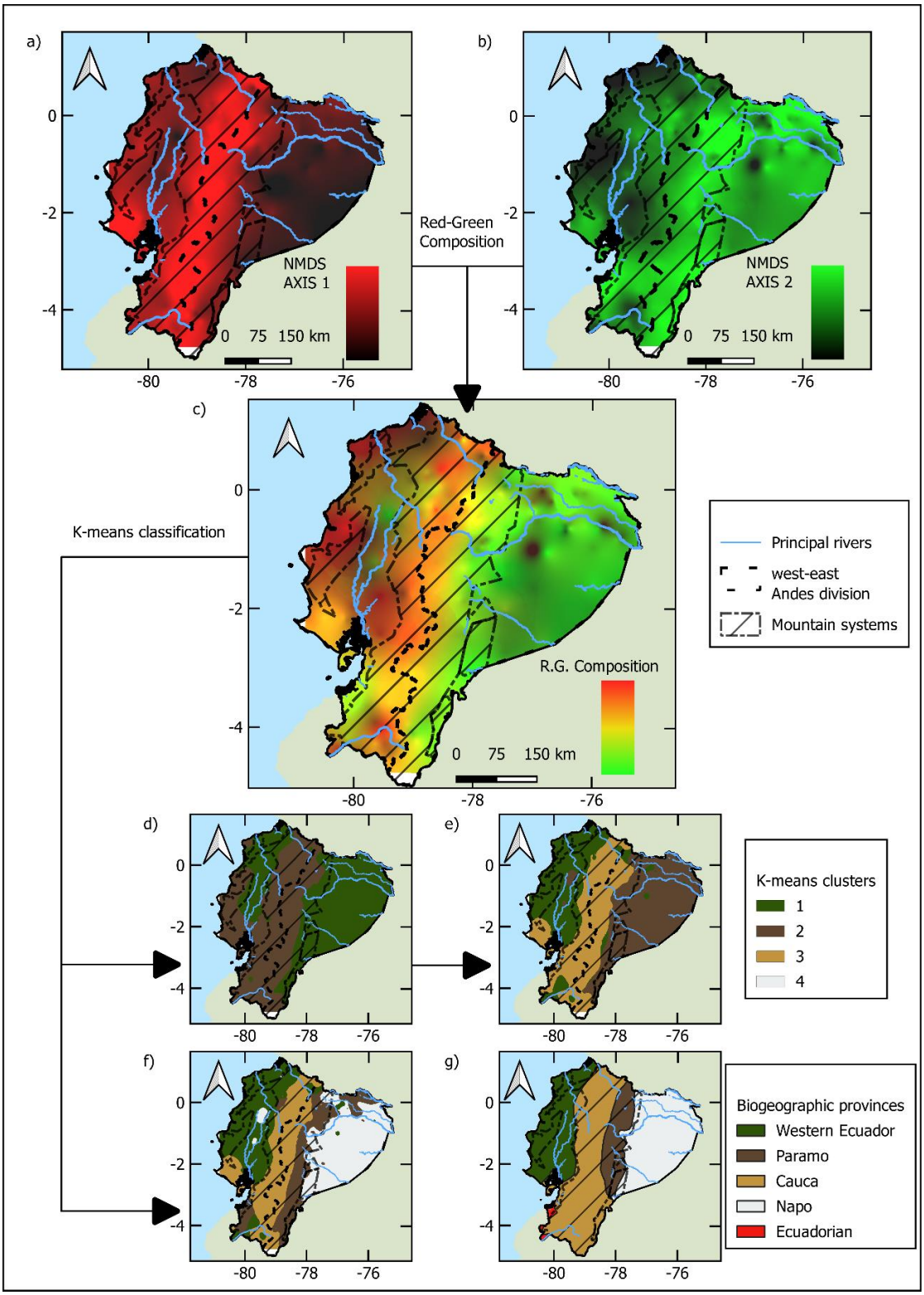

Figure 4: a) Spatial interpolation of the 1° axis of the NMDS. b) Result of spatial interpolation of the 2° axis of the NMDS. c) Red-Green composition. c-f) K-means clusters. g) Biogeographical provinces proposed by Morrone (2014). **Realizado por**: Montaño, 2022.

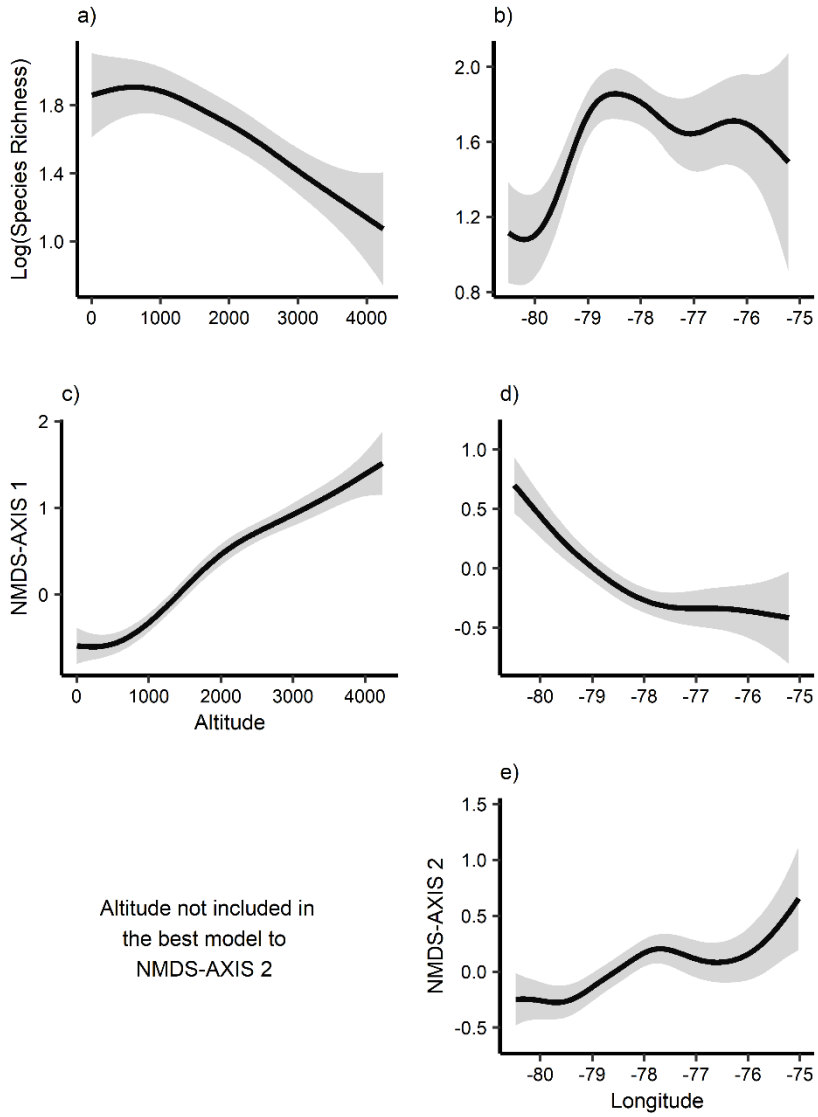

Figura 5: GAM's plots. a) Richness and altitude; b) Richness and longitude; c) 1° NMDS and Altitude; d) 1° NMDS axis and longitude e) 2° NMDS and longitude.
Realizado por: Montaño, 2022.

Tablas

Table 1: Results of Generalized Additive Models (GAMs) of Species richness (Log scaled) and the two first axes of Non-metric Dimensional Scaling (NMDS) evaluating the effect of altitude and longitude. P. value significance codes = 0 '***' 0.001 '**' 0.01 '*' 0.

Response Variables	Predictors		AIC	Adj-R^2	D^2	Concurvity (worst)
	s(Altitude)	s(Longitude)				
	P value					
Log (Species richness)	***	-	404	0.184	20.10%	-
Log (Species richness)	-	***	449	0.104	11.30%	-
Log (Species richness)	***	***	386	0.242	26.40%	0.749
NMDS axis-1	***	-	370	0.643	65.20%	-
NMDS axis-1	-	***	581	0.371	38.40%	-
NMDS axis-1	***	***	287	0.732	74.00%	0.749
NMDS axis-2	.	-	573	0.020	2.75%	-
NMDS axis-2	-	***	623	0.090	10.40%	-
NMDS axis-2		***	559	0.081	9.83%	0.815

Realizado por: Montaño, 2022.

MATERIA SUPLEMENTARIO

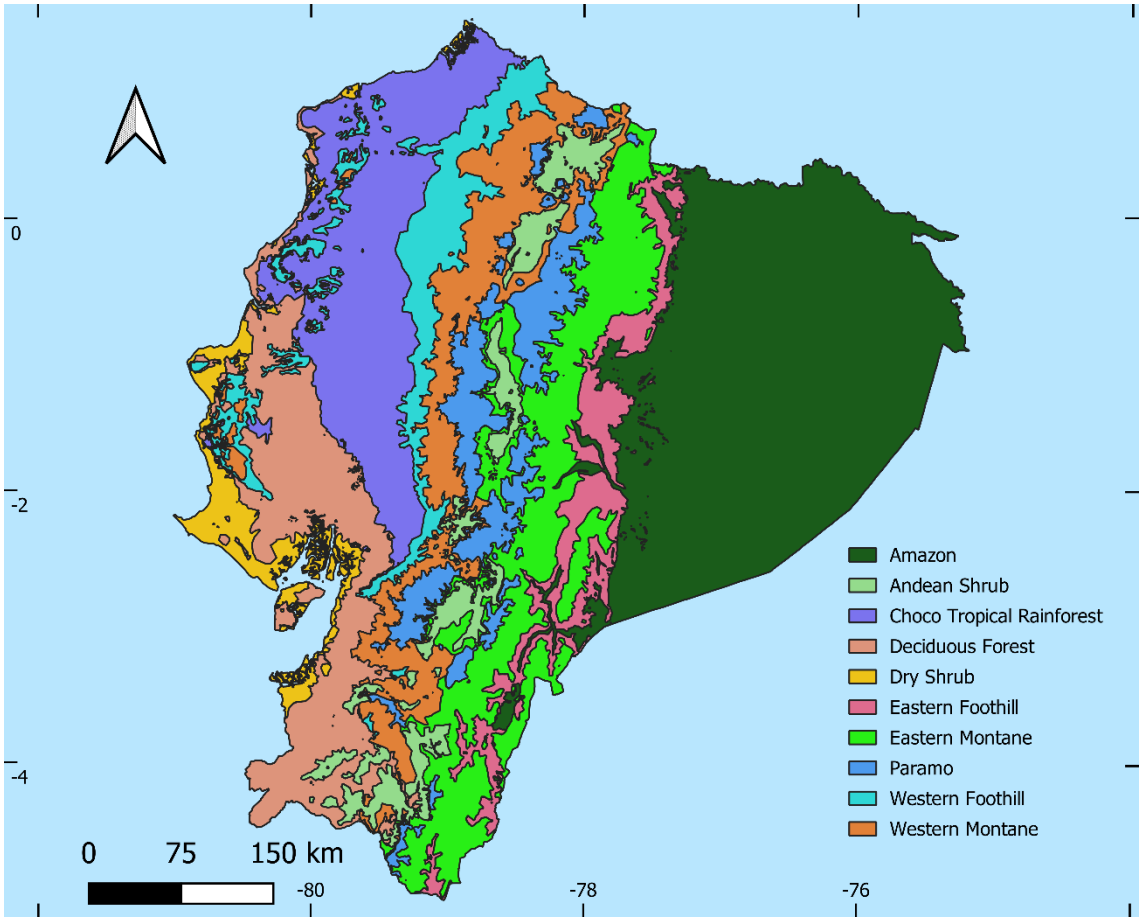

Figure S2.1: Biogeographical Regions. **Realizado por**: Montaño, 2022.

Table S2-1: Proportion (%) of distribution of records of species insects in SNAPs areas.

SNAPs	Percentage (%)
Outside SNAPs	81.76584947
PARQUE NACIONAL YASUNI	12.03448885
RESERVA BIOLOGICA LIMONCOCHA	1.801449239
PARQUE NACIONAL CAYAMBE COCA	0.954376752
PARQUE NACIONAL PODOCARPUS	0.53147171
RESERVA DE PRODUCCION DE FAUNA CUYABENO	0.436791476
AREA PROTEGIDA PRIVADA BELLAVISTA	0.337061631

PARQUE NACIONAL ANTISANA	0.258792638
RESERVA DE PRODUCCION DE FAUNA CHIMBORAZO	0.258792638
REFUGIO DE VIDA SILVESTRE PASOCHOA	0.256267831
PARQUE NACIONAL SANGAY	0.223445351
RESERVA ECOLOGICA MACHE CHINDUL	0.18683566
PARQUE NACIONAL COTOPAXI	0.142651551
PARQUE NACIONAL MACHALILLA	0.128765117
PARQUE NACIONAL LLANGANATES	0.127502714
PARQUE NACIONAL SUMACO NAPO-GALERAS	0.108566668
PARQUE NACIONAL COTACACHI CAYAPAS	0.055545737
PARQUE NACIONAL CAJAS	0.049233721
RESERVA BIOLOGICA EL CONDOR	0.046708915
RESERVA ECOLOGICA LOS ILINIZAS	0.041659303
RESERVA GEOBOTANICA PULULAHUA	0.039134496
AREA NACIONAL DE RECREACION ISLA SANTAY	0.026510465
AREA NACIONAL DE RECREACION LOS SAMANES	0.022723256
REFUGIO DE VIDA SILVESTRE EL ZARZA	0.022723256
RESERVA BIOLOGICA COLONSO CHALUPAS	0.017673644
RESERVA ECOLOGICA EL ANGEL	0.017673644
RESERVA ECOLOGICA ARENILLAS	0.015148837
AREA ECOLOGICA DE CONSERVACION MUNICIPAL SIETE IGLESIAS	0.013886434
AREA PROTEGIDA AUTONOMA DESCENTRALIZADA CORDILLERA ORIENTAL DEL CARCHI	0.010099225
RESERVA BIOLOGICA EL QUIMI	0.008836822
PARQUE NACIONAL YACURI	0.007574419
REFUGIO DE VIDA SILVESTRE PACOCHE	0.007574419
RESERVA ECOLOGICA MANGLARES CAYAPAS MATAJE	0.007574419

RESERVA ECOLOGICA MANGLARES CHURUTE	0.007574419
RESERVA ECOLOGICA COFAN BERMEJO	0.006312016
AREA ECOLOGICA DE CONSERVACION MUNICIPAL LA BONITA	0.003787209
AREA NACIONAL DE RECREACION PARQUE LAGO	0.003787209
RESERVA BIOLOGICA CERRO PLATEADO	0.003787209
AREA ECOLOGICA DE CONSERVACION MUNICIPAL TAITA IMBABURA	0.002524806
REFUGIO DE VIDA SILVESTRE MANGLARES ESTUARIO DEL RIO MUISNE	0.002524806
RESERVA DE PRODUCCION DE FAUNA MANGLARES EL SALADO	0.002524806
AREA NACIONAL DE RECREACION EL BOLICHE	0.001262403
AREA NACIONAL DE RECREACION QUIMSACOCHA	0.001262403
AREA PROTEGIDA COMUNITARIA MARCOS PEREZ DE CASTILLA	0.001262403

Realizado por: Montaño, 2022.

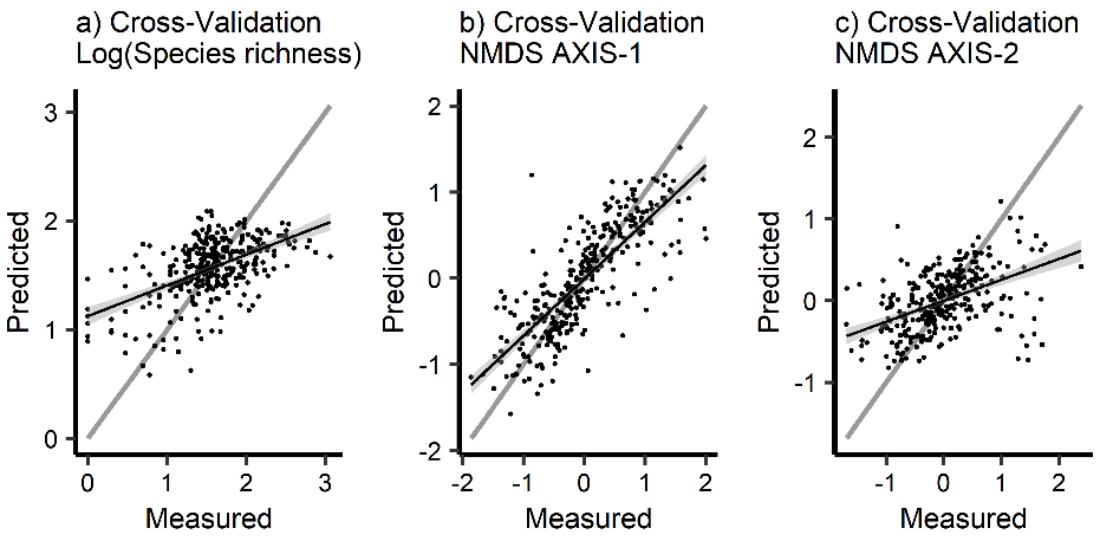

Figure S2-2: Cross-Validation with the "leave one out" technique. a) Cross-Validation of Species richness (in the log-scale) - α-Diversity. b) Cross-Validation of the axis 1 of the Non-metric Dimensional Scaling (NMDS AXIS-1) - β -Diversity. c) Cross- Validation of the axis 1 of the Non-metric Dimensional Scaling (NMDS AXIS-2) - β - Diversity. **Realizado por**: Montaño, 2022.

Table S2-2: Statistical results of α-Diversity and β-Diversity. "- "means that this field do not apply to the variable.

Variable	Non-metric fit R^2	Linear fit R^2	Correlation between axes	Moran's I	P. value of Moran´s I	Slope of cross-validation linear relationship	Cross-validation prediction errors		
							The Root Mean Square Standardized Error (R.M.S.S.E.)	Average Standard Error (A.S.E)	Root Mean Square Error (R.M.S.E.)
Log Species richness	-	-	-	0.09	< 0.05	0.251	0.996	0.437	0.434
NMDS- axis 1	0.79	0.42	-	0.186	< 0.05	0.772	1.06	0.401	0.445
NMDS- axis 2	0.12	0.17	-	0.061	< 0.05	0.38	1.09	0.544	0.59
Both NMDS Axes	0.91	0.59	r ≈ 0	-	-	-	-	-	-

Realizado por: Montaño, 2022.

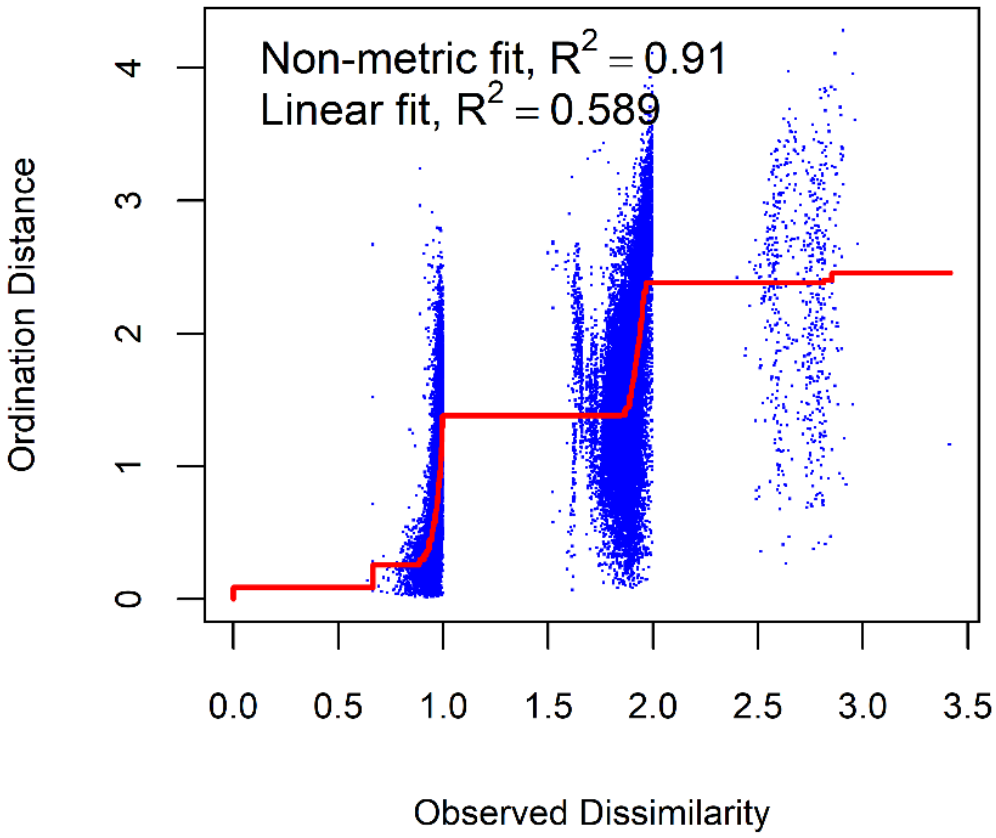

Figure S2-3: Stress plot of the Non-metric dimensional scaling of the matrix of multiple comparation with Jaccard index. **Realizado por**: Montaño, 2022.

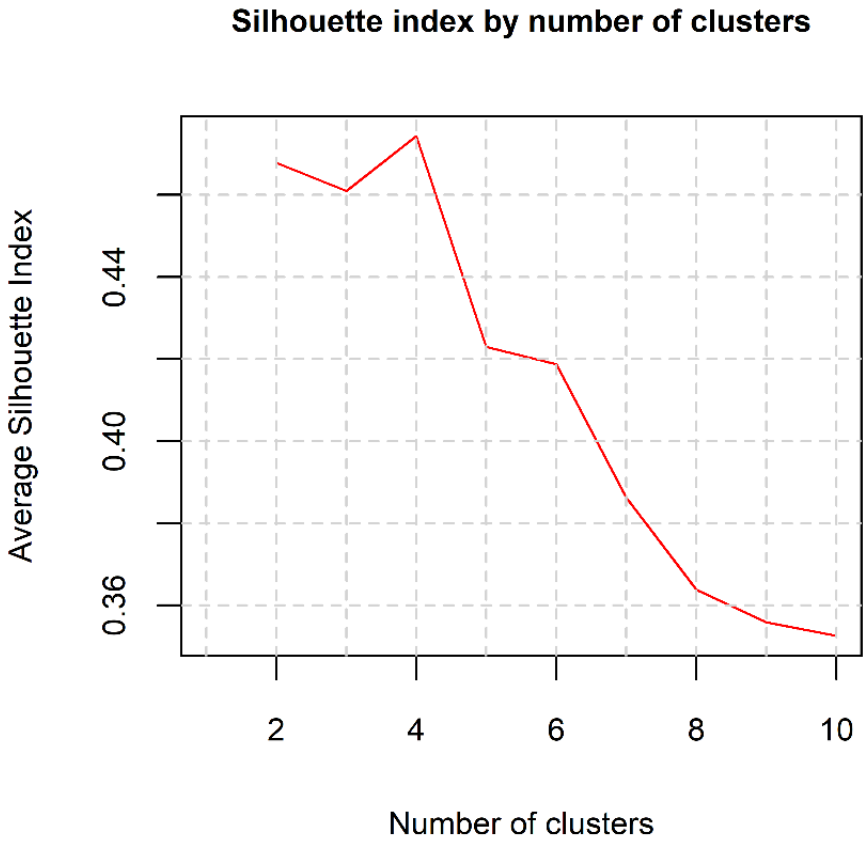

Figure S2-4: Best groups obtained through the Average silhouette index by K-means classification. **Realizado por**: Montaño, 2022.

Table S2-3: Comparation of the Biogeographic provinces from Ecuador and the third k-means classification obtained in this investigation. See Figure 4f and 4g.

Biogeographic provinces	Similitude percentage of third k-means classification of the NMDS scores (%)
Western Ecuador	69.41
Napo	87.87
Cauca	81.64
Paramo	35.76

Realizado por: Montaño, 2022.