

**UN ACERCAMIENTO FILOGENÉTICO A LA CONSERVACIÓN EN EL BLOQUE
NORTE DE LOS ANDES**

**A PHYLOGENETIC APPROACH FOR CONSERVATION OF THE NORTHERN
ANDEAN BLOCK**

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UNIVERSIDAD INDUSTRIAL DE SANTANDER

FACULTAD DE CIENCIAS

ESCUELA DE BIOLOGÍA

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**Trabajo de grado para optar por el título de
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To my family, especially to my parents by its support over all these years, and to my three furry angels, my cats Tito, Thomas and Patas.

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RESUMEN

TÍTULO: UNA APROXIMACIÓN FILOGENÉTICA A LA CONSERVACIÓN EN EL BLOQUE NORTE DE LOS ANDES*

AUTOR: OMAR DANIEL LEÓN ALVARADO**

PALABRAS CLAVES: DISTINTIVIDAD EVOLUTIVA, CONSERVANDO LA EVOLUCIÓN, DIVERSIDAD FILOGENÉTICA, PRIORIZACIÓN DE ÁREAS, FILOGENIAS

El Bloque Norte de los Andes (BNA) es una de las regiones más biodiversas del Neotrópico, pero posee ecosistemas muy transformados, lo cual la hace un objeto importante para conservación. Muchos tipos de riqueza han sido usados para delimitar áreas protegidas, sin tener en cuenta la historia evolutiva contenida en la filogenia. Por consiguiente nosotros priorizamos áreas para conservación usando tres índices de diversidad phylogenética (TD, PD and AvTD). Se reconstruyeron 93 filogenias moleculares bajo el algoritmo de Máxima Verosimilitud y las distribuciones fueron obtenidas del GBIF. Se calculó el índice de complementariedad y la correlación entre los índices y la riqueza, de igual manera la contribución de las especies endémicas y las áreas protegidas en la diversidad filogenética. Para la priorización se utilizó el índice AvTD ya que fue el menos correlacionado con la riqueza. Las áreas de endemismo más importantes fueron Magdalena, Paramo y Cauca, mientras que para las celdas, los cuantiles más altos se encontraban sobre las Cordilleras Andinas y los valores de complementariedad fueron altos en el BNA. Las especies endémicas y las áreas protegidas no contribuyen notablemente a la diversidad filogenética. Aquí, las celdas que se proponen para propósitos de conservación van a reducir el grado de perturbación en el BNA y van a preservar un cantidad importante de diversidad filogenética reforzando la red actual de áreas protegidas desde distintos aspectos de la biodiversidad.

*TRABAJO DE GRADO

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ABSTRACT

TÍTULO: A PHYLOGENETIC APPROACH TO CONSERVING OF THE NORTHERN ANDEAN BLOCK*

AUTOR: OMAR DANIEL LEÓN ALVARADO**

PALABRAS CLAVES: EVOLUTIONARY DISTINCTIVENESS, CONSERVING EVOLUTION, PHYLOGENETIC DIVERSITY, AREAS PRIORITIZATION, PHYLOGENIES

The Northern Andean Block (NAB) is one of the most biodiversity regions in the Neotropic, but it has very transformed ecosystems, which makes it an important target for conservation. Many types of species richness have been used for delimiting protected areas, without taking into account the evolutionary history contained in a phylogeny. Hence areas for conservation purposes were prioritized using three phylogenetic diversity indices (TD, PD and AvTD). A total of 93 molecular phylogenies were reconstructed under the Maximum Likelihood approach and the distributions were depicted from GBIF. A complementary index and a correlation between indices and richness were calculated, as well as the contribution of phylogenetic diversity by endemic species and protected areas. AvTD was used for the prioritization since it is not correlated to species richness. The most important areas of endemism were Magdalena, Paramo and Cauca, while for grid cells, the highest quantiles were located across the Andean Cordilleras, and the complementarity values in the NAB were high. Endemic species and PAs do not contribute notably to the phylogenetic diversity. Here, the cells proposed for conservation purposes will increase the intactness in the NAB and preserve an important amount of phylogenetic diversity reinforcing the actual PAs network from different biodiversity aspects.

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Introduction

The Northern Andean Block (hereafter NAB) is a tectonic subplate that comprises of the north east of Ecuador, the Pacific, the Caribbean, the Andean regions of Colombia, and the Venezuelan Andes (Kellogg et al 1995; Bird 2003). Due to its biodiversity, it is considered one of the most important areas in the Neotropic, with its Andean portion being a Hotspot (Myers 1988; Myers et al 2000). Its amazingly varied climates and resource availability promoted the settlement of several human populations that grew through time, turning the NAB into one of the most populated regions of South America (Goldewijk 2005), which created a rapid ecosystemic transformation driving the extinction of 16 species and the endangerment of many others. (Extinct in the wild: 6 species. Critically endangered: 479 species. Endangered: 1054 species. IUCN website. Consulted December 9 of 2015).

These perils originated the initiative of Protected Areas (hereafter PAs) for conservation purposes, in which ecological indices have been the main criteria for their delimitation (e.g. PNN Bahia Portete-Kaurrele, Guajira, Colombia. Resolución 2096, 19 of December 2014 follows the works of Diaz-Pulido (2000) and Diaz-Pulido & Díaz-Ruíz (2003)). Nonetheless, these indices do not account for the history and evolutionary information contained in a phylogeny (Vane-Wright et al 1991; Faith 1992).

Phylogenetic diversity indices determine the distinctness between species by quantifying the information contained in a phylogeny (Vane-Wright et al 1991; Faith 1992; Schweiger et al 2008), and between areas given the species distribution (Vane-Wright et al 1991; Posadas et al

2001; Cue-Bar et al 2006). From an evolutionary view, distinctness between areas and taxa is useful when prioritizing areas for conservation. Thus, phylogenetic diversity indices allow us to shelter not only the most distinctive species but to shelter more species in fewer areas (e.g. Vane-Wright et al 1991), when the latter are accompanied by a complementarity index (Colwell & Coddington 1994). Since 1991, publications regarding phylogenetic diversity indices have focused on their applicability and statistical properties (e.g. Vane-Wright et al 1991; Redding & Mooers 2006; Schweiger et al 2008) rather than on proposing actual recommendations aimed for conservation (Rolland et al 2012). Due to this bias there are currently no protected areas delimited using these indices. Therefore, the objectives of this work are: (1) to prioritize geographic and biogeographic areas in the NAB for conservation purposes, (2) to evaluate the relation between phylogenetic diversity indices and richness, and the contribution of endemic species to the NAB's phylogenetic diversity, and (3) to quantify the phylogenetic diversity of the PAs in the NAB and their contribution to its phylogenetic diversity.

1. Methods

1.1 Taxa

We selected taxa according to the gene availability and obtained occurrences from the Global Biodiversity Information Facility (GBIF) for 1255 species of Bryophyta (33 species), Marchantiophyta (7 species), Gimnospermae (89 species), Magnoliopsida (213 species),

Liliopsida (157 species), Insecta (115 species), Testudines (3 species), Squamata (98 species), Amphibia (188 species), Aves (159 species) and Mammalia (193 species) inhabiting the NAB.

1.2 Molecular data

We recollected molecular data available in GenBank for the species listed and we made a phylogenetic reconstruction at different taxonomic levels: 2 orders, 1 superfamily, 19 families, 6 subfamilies, 4 tribes and 61 genera. We selected the terminals in monophyletic clades and excluded the occurrences of the invasive species.

1.3 Phylogenetic reconstruction

For the collected genes at each taxonomic level, we selected the evolutionary nucleotide model under the Akaike Information Criterion (AIC) (Akaike 1974) for each gene. We made a partitioned phylogenetic reconstruction under the Maximum Likelihood algorithm implemented in RAxML v8.2.X (Stamatakis 2014), using the nucleotide model GTR+GAMMA for all genes, we then made a branch length optimization in PhyML v3.0 (20160310) (Guindon et al 2010), using the nucleotide model for each gene. For datasets containing more than 100 terminals we implemented EXaML v3.0 (Kozlov et al 2015) instead of RAxML.

1.4 Area

We used the approach of areas of endemism proposed by Morrone (2014) modified for the NAB (Figure 1E) and the approach of grid cells with varying sizes of 0.25 °, 0.50 ° and 1 °.

1.5 Prioritization

We implemented the most robust index from each kind of phylogenetic diversity index (Krajewski 1994; Schweiger et al 2008). Taxonomic Distinctness (TD), a topological based index (Vane-Wright et al 1991); Phylogenetic Diversity (PD), a minimum spanning tree based index (Faith 1992) and Average Taxonomic Distinctness, a pair-wise distance based index (Clarke & Warwick 1998).

We evaluated the correlation of the phylogenetic diversity indices values against the richness using a Bayesian Simple Linear Regression (hereafter BSLR) (Kruschke 2014). We used two types of richness: Total Richness (TR), considered as all species in a specific taxonomical level that occur within an area, and Phylogenetic Richness (PR), considered as the total number of terminals in a specific phylogeny (e.g. The genus *Maxillaria* has 75 species occurring in the area (TR), but only 32 of them are in the phylogeny (PR)).

The area of endemism with the highest index value was considered as the most important, and from it the second hierarchization was made using the complementarity index (Colwell & Coddington 1994). For the grid cells, the values for the selected index were divided into quantiles. Cells with an index value in the last quantile (hereafter Q5) were considered as the most important and used for the second hierarchization, given the mean of the complementarity values for each cell. Also, we calculated the complementarity index among Q5 cells. We

calculated the distance between each Q5 cell and each complementarity cell, and we correlated these distances with their complementarity values using a BSLR (Kruschke 2014).

We compared the results obtained in the prioritization of areas of endemism and grid cells determining the number of Q5 cells that are within the most important areas of endemism.

1.6 Endemic species

In order to evaluate the influence of endemic species in the prioritization of areas, we recalculated the indices 100 times, randomly removing from the analyses 25%, 50% and 75% of species restricted to one area of endemism (endemic), and once removing all of them.

1.7 Protected areas

To determine the contribution of the Protected Areas (hereafter PAs) to the phylogenetic diversity in the NAB, we quantified the number of Q5 cells that are within the PAs. Also, the three indices were recalculated considering only PAs and the NAB without PAs. The differences between the total phylogenetic diversity of the PAs and the NAB without PAs was used to determine the contribution of PAs to the total phylogenetic diversity. We obtained the used polygons from the World Database of Protected Areas project (IUCN 2014).

2. Results

2.1 Correlations

For both types of richness, TD presented the highest relation values (posterior slope mean > 0.98) followed by PD (posterior slope mean > 0.75), while AvTD presented the lowest values (posterior slope mean > 0.38) (Fig 2), supporting the findings of previous works where PD presented high correlation values (Morlon et al 2011; Howard et al 2016), and studies that claim AvTD has low sampling bias (Clarke & Warwick 1998; Schweiger et al 2008). However, the Q5 cell for PD and AvTD are not correlated with richness, while the remaining cells were correlated with richness only for PD (Fig 2). Furthermore, TD was more correlated with PD (posterior slope mean 0.74), than AvTD with PD and TD (posterior slope means 0.35 and 0.38 respectively).

2.2 Prioritization

We used the AvTD index for the prioritization of both, grid cells and areas of endemism because it was not correlated with richness or any of the other indices; due to the sampling bias, an index that is not related to richness is more suitable (see Discussion below). For the grid cells, the results obtained with AvTD were very similar to the other indices, sharing the 80% and 90% of the Q5 cells with TD and PD respectively, but the amount of Q5 cells varied, being 215 for

AvTD, and 219 for PD and TD. In contrast, for areas of endemism this pattern is not true (see below). So, at least for grid cells the choice of AvTD is not biased.

2.3 Areas of endemism prioritization

The three areas of endemism with the highest index values in decreasing order were Cauca, Paramo and Magdalena for TD, Cauca, Magdalena and Choco-Darien for PD and Magdalena, Paramo and Cauca for AvTD (Table 1). We considered Cauca and Magdalena as the most important areas, because they were constant in all indices, and about 64% of the Q5 cells were within these areas (Fig 1F). For the complementarity index, we followed the results of the AvTD index considering Magdalena as the most important area of endemism. The most complementary areas to Magdalena were Imeri, Venezuela and Napo (complementarity values > 0.80). Moreover, the other areas presented high values (> 0.60), including Cauca and Paramo, the nearest to Magdalena.

2.4 Grid cells prioritization

The Q5 cells obtained in the three grid cells sizes for AvTD were very similar, specially with the size 0.50° against 1° , and the 0.25° against 0.50° where the Q5 cells overlapped 83% and 78% respectively; likewise, the 0.25° against 1° overlapped by 63% (Appendices). We used the 0.25° size because this allows a more detailed analysis.

The 76% of Q5 cells were located in three main places, two of them in Colombia and one in Ecuador. In Colombia they are in the East and in the West, with the latter divided in two subsets: The north of the western and central Cordillera, Magdalena and Cauca valleys, and Pacific lowlands; and the middle of the western Cordillera, Cauca valley, western flank of the central Cordillera and Pacific lowlands close to the western Cordillera (Fig 1A). The east place is in the north and the middle of the eastern Cordillera, including some cells in the Magdalena valley and the Piedemonte. In Ecuador, the Q5 cells are mainly located across the western and eastern Cordilleras, and the west Amazonian lowlands, and some cells in the Pacific lowlands (Fig 1A).

The remaining Q5 cells are located in several places across the NAB, in locations like the "Nudo de los Pastos", the south of the central, western and eastern Cordilleras, and the Cauca valley. In the north of the NAB there are some Q5 cells distributed across the Venezuelan Andes, the west of the Caribbean region of Colombia and the lowlands close to the Sierra Nevada (Fig 1A).

The complementarity values across the NAB is high with an average range of 0.86-1 (Fig 1C). This pattern was also found in the complementarity among Q5 cells with an average range of 0.85-0.99 (Fig 1B). Furthermore, the mean of all 215 posterior slopes obtained from the relation between distance and complementarity was low (0.25) (Appendices).

2.5 Endemic species

For all three indices the ranking of areas of endemism never changed for any removal percentage. The removal percentage in each area is inversely proportional to TD and PD. This

was specially evident for the areas with high index values (Appendices). However, the pattern showed by TD and PD differs for some areas with AvTD like Choco-Darien, Guajira, Venezuela and Napo whereas the removal percentage is directly proportional to the index value (Appendices). Notoriously, Cauca and Paramo increased their index values in the absence of endemic species, compared with their initial values (Appendices).

2.6 Protected areas

Of the 115 PAs, 15% lack occurrences, having a value of zero for all the three indices. For TD and PD there are more phylogenetic diversity within the PAs, representing 59% and 64% of the total phylogenetic diversity respectively. But, having less phylogenetic diversity within PAs and only representing 0.8% of the total phylogenetic diversity AvTD behaved inversely. This pattern is also evident in PR (Table 2). However, when we evaluated the dependence of the indices against richness, we confirmed that TD and PD are more correlated with richness than AvTD (posterior slope mean: 0.97, 0.76 and 0.32 respectively) (Appendices). When we calculated the number of Q5 cells that match PAs, just 9.9% (TD), 18% (PD) and 18% (AvTD) of Q5 cells did (Fig 1D).

3. Discussion

With the available information hitherto, adding phylogenies to our analyses will not drastically modify our results because the ranking of the three most important areas of endemism remains the same regardless the number of phylogenies used in different iterations. In fact, from 63 out of phylogenies randomly selected the three most important areas of endemism kept their positions (Appendices). To use information from different taxa is more important than the number of phylogenies, because each taxon went through different evolutionary processes and will not tell the same stories (Richardson & Pennington 2016). Sechrest et al (2002) used two Mammalian orders finding that there is more evolutionary information within the Andean Hotspot than outside. Herein, we found that there are important amounts of evolutionary information in the Andean valleys, Amazonian and Pacific lowlands outside the Andean Hotspot (Fig 1A). Also, plants had more phylogenetic diversity than animals, but given their dissimilar evolutionary processes, the prioritized cells by each group differ (Appendices).

The use of a single taxon and other approaches such as endemic, small ranged or threatened species will probably generate different results. Generally, endemic species diversified recently and could be associated with short branch lengths (Hubbell 2001; Richardson et al 2001; Davies et al 2011). Accordingly, we found that the identified endemic species presented shorter branch lengths (mean: 0.03, SD: 0.06) than widespread species (mean: 0.11, SD: 1.8) (Appendices), and only represent 0.4% of the accumulated branch lengths, so their contribution to the phylogenetic diversity of the areas is low, specially for PD and AvTD. For Cauca and Paramo, their AvTD

values increased when we removed all endemic species. This pattern was found in another study (Schweiger et al 2008) when the less distinctive species were removed, showing that the endemic species are the less distinctive species. Nonetheless, the low contribution for TD will only happen if the endemic species present a recent divergence so should be located farther from the root (specially for large phylogenies), giving them a low weight (Vane-Wright et al 1991). *Ceroxylon amazonicum* and *Ceroxylon saisamae* who were identified as endemic species and present a recent diversification of 0.46 and 2.5 Ma (sensu Sanín et al 2016) are an example. Both have short branch lengths (0.0002 and 0.0008 respectively) compared with the mean branch lengths of endemic species (0.039) and are farther from the root (6 nodes) compared with *C. vogelianum* (3 nodes). Endemic species are more sensitive to environmental disruption and are strong predictors of extinction risk (Manne et al 1999; Jenkins et al 2013), so the use of these species to identify conservation priorities has been common (e.g. Silva 1997; Stattersfield et al 1998; Nori et al 2016). However, these species incorrectly predict evolutionary history, so the conservation priorities derived from them will underestimate phylogenetic diversity. Therefore, endemic species should not be used as a single estimator. The EDGE index (Isaac et al 2007) measures the species distinctness and weighs it by the IUCN categories index (Butchart et al 2004), prioritizing distinctive species in relevant IUCN categories like Critically Endangered (CR). Notwithstanding, if we apply this index to our data, the 53% of the 1255 species become useless for being catalogued as No Evaluated (NE), as a consequence, from the remaining species just those catalogued as Critically Endangered (CR) and Endangered (EN) will weigh more. However, 55% of these heavier species are endemic (Appendices), with a low amount of evolutionary history.

Generally the PAs around the world have more biodiversity within them (Gray et al 2016). In the NAB, this is true just for the PR (Table 2) meanwhile, the TR is very homogeneous within and outside the PAs (Table 2), from phylogenetic diversity, regarding TD and PD there is more phylogenetic diversity within PAs, while AvTD shows the opposite. However, as for the grid cells, TD and PD are more correlated with richness than AvTD, therefore, we consider that it is necessary to pay more attention to what AvTD shows, which is clearly reflected in the low percentage of Q5 cells that matched with PAs (< 18%) (Fig 1D); even with the richness bias, we found this pattern with TD and PD. Over the years PAs had been a useful tool for preserving the richness, but failed to preserve the evolutionary history of the NAB. The collectors usually remain close to areas with research facilities (Nelson et al 1990), so there is a sampling and richness bias from main roads, easy access places and places near to cities or human populations (Balmford et al 2001; Reddy 268 & Dávalos 2003). This pattern is observed in our data with higher richness near to main cities, and the effect of that has affected the results obtained, not only in grid cells and PAs, but also in the areas of endemism. The three most important areas of endemism prioritized by TD were the richest areas (Table 1), but for PD which is less biased by richness and takes into account the branch lengths (Faith 1992; Schweiger et al 2008) the three most important areas prioritized were those with more accumulated branch lengths (Table 1), showing another parameter that could influence the analyses. Moreover, AvTD, although being the less biased by richness, prioritized the richest areas, but the ranking did not correspond with richness or even the accumulated branch lengths (Table 1). The richness bias has already been evaluated for some indices (Schweiger et al 2008; Morlon et al 2011; Howard et al 2016), but the possible bias for branch lengths is an open question.

In another study (Warwick & Clarke 1995) found by using AvTD, that the negative effect of environmental contamination in phylogenetic diversity, is not reflected in number of species. Results show, that AvTD had found different patterns not detected by richness and the other indices implemented, such as the negative effect of endemic species found in some areas of endemism and the low amount of phylogenetic diversity within PAs. This was less influenced by richness and possibly presents low branch lengths bias, however, with PD, this parameter remains unevaluated. The answer to the question of which is the best phylogenetic diversity index always relies on the data. Herein, AvTD had the best performance, so the phylogenetic diversity indices based on pair-wise distance (Krajewski 1994; Schweiger et al 2008) like AvTD, TTD (Clarke & Warwick 2001) or J (Izsák & Papp 2000) should be taken into account in further studies with empirical data. Likewise, we recommend in these type of studies not to use just one index, but several and contrast the results obtained with each index used to guarantee the best conclusions.

Several of the few published works that use phylogenetic diversity for conservation purposes were made using areas of endemism (e.g. Posadas et al 2001; López-Osorio & Miranda-Esquivel 2010), but using grid cells is uncommon. Preservation of large places such as areas of endemism is economically and politically unrealistic, for this reason smaller areas has been proposed as a better approach (López-Osorio & Miranda-Esquivel 2010). The majority of Q5 cells matched with Magdalena and Cauca (Fig 1D), suggesting that indices are not biased by the shape and size of the areas implemented. Implying, if the previous works which used areas of endemism are reproduced implementing grid cells, possibly the priority cells would match the same area. Which means that the use of areas of endemism is useful just for quick primary approaches but,

within an area of endemism just specific places are truly important and the grid cells allow the identification of those important places.

The prioritized areas for conservation by the local government in Colombia (CONPES et al 2010), are those ecosystems poorly represented in the actual PAs, such as the Tropical Dry Forest and the Caribbean Coast. In our results, some Q5 cells matched with areas of Tropical Dry Forest (sensu Olson et al 2001) in the Magdalena and Cauca valleys, and Ecuadorian eastern lands. Moreover, other Q5 cells matched with areas of Montane and Moist Tropical Forest whose areas are very diverse and threatened (Bubb et al 2004; Hassan et al 2005; Bush et al 2007; Pennington et al 2010). Echeverría-Londoño et al (2016) found that for Colombia, the Caribbean, the Pacific and the Andean regions (fully included in the NAB) were less intact. Many Q5 cells correspond with those cells less intact, specially in the Andean region, and if these Q5 cells are selected for preservation, the intactness within will increase from an average of 77% to 86 % by 2095 (see Echeverría-Londoño et al 2016). Therefore, these Q5 cells that correspond with threatened ecoregions and less intact cells should be main targets for conservation actions. Although it is still debated (Aarssen 1997; Venail et al 2015; Davies et al 2016), communities with high phylogenetic diversity (sensu Faith 1992) present more traits of diversity (Davies et al 2016) and the variation in plant biomass is better explained (Yuan et al 2016). Also, it is known that species 327 perform better when grow with more distant or distinct relatives (Burns & Strauss 2011; Cadotte 2013), so the Q5 cells will not only contribute to increase the intactness in the NAB and shelter a high amount of evolutionary history but, at local level the forest remnants within Q5 cells will possibly present a better restoration process and will be more productive, especially those remnants which are close to mature forests (Hermy & Verheyen 2007). Such an unexpected

and interesting result was the high complementarity values. For the Neotropic, the similarity declines when increases the distance between two forests (Condit et al 2002), but here the distance does not influence the complementarity values (Appendices), notorious in some complementary cells that are next to Q5 cells and in the complementarity values among Q5 cells or even the high values of the nearest areas of endemism to Magdalena. So, the low similarity presented could be associated with other factors such the variation of climes (Nekola & White 1999), gradients in the rainfall seasons (Davidar et al 2007) or the complex topography and dispersal limitation (Condit et al 2002; Leigh Jr et al 2004) in the NAB, yet this hypothesis remains unevaluated for the study area. Due to the high complementarity values among Q5 cells, it is preferable to first prioritize the Q5 cells rather than complementarity cells, because these Q5 cells will have more species and a high amount of evolutionary history, thereby, the protected areas network will be reinforce from several biodiversity aspects. It is important to clarify that NAB's zones did not correspond with Q5 cells or even with complementarity cells are not useless. In fact, those places should be the focus on future explorations and checklist works in order to improve our knowledge about their biodiversity and get more homogeneous sampling effort across the NAB, so in fact, in the future we could make better decisions for conservation.

From a evolutionary perspective, the use of specific taxa, endemic species or even richness for conservation purposes would be an incorrect estimator, and the decisions taken from them would leave protected areas with low phylogenetic diversity, what has been happening within NAB. Here, with the less biased index, we propose a set of cells for future conservation actions that not only will preserve a high number of species, threatened ecoregions and will improve the intactness, but, it will also preserve an important amount of evolutionary history.

References

- Aarssen LW. 1997. High productivity in grassland ecosystems: effected by species diversity or productive species. *Oikos* 80:183–184.
- Akaike H. 1974. A new look at the statistical model identification. *IEEE transactions on automatic control* 19(6):716–723.
- Balmford A, Moore JL, Brooks T, Burgess N, Hansen LA, Williams P, Rahbek C. 2001. Conservation conflicts across africa. *Science* 291(5513):2616–2619.
- Bird P. 2003. An updated digital model of plate boundaries. *Geochemistry, Geo- physics, Geosystems* 4(3). DOI:10.1029/2001GC000252.
- Bubb P, May IA, Miles L, Sayer J. 2004. *Cloud forest agenda*. 1st edition. UNEP World Conservation Monitoring Centre, Cambridge, United Kingdom.
- Burns JH, Strauss SY. 2011. More closely related species are more ecologically similar in an experimental test. *Proceedings of the National Academy of Sciences* 108(13):5302–5307.
- Bush MB, Hanselman J, Hooghiemstra H. 2007. Andean montane forests and climate change. Chapter 2, Pages 33–54. In *Tropical rainforest responses to climatic change*. Springer Berlin Heidelberg, New York, United States.
- Butchart SH, Stattersfield AJ, Bennun LA, Shutes SM, Akçakaya HR, Baillie JE, Stuart SN, Hilton-Taylor C, Mace GM. 2004. Measuring global trends in the status of biodiversity: Red list indices for birds. *PLoS Biol* 2(12). DOI: 10.1371/journal.pbio.0020383.
- Cadotte MW. 2013. Experimental evidence that evolutionarily diverse assemblages result in higher productivity. *Proceedings of the National Academy of Sciences* 110(22):8996–9000.

- Clarke K, Warwick R. 1998. A taxonomic distinctness index and its statistical properties. *Journal of applied ecology* 35(4):523–531.
- Clarke K, Warwick R. 2001. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. 2nd edition. Plymouth: PRIMER E Ltd, Plymouth, United Kingdom.
- Colwell RK, Coddington JA. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 345(1311):101–118.
- Condit R, Pitman N, Leigh EG, Chave J, Terborgh J, Foster RB, Núñez P, Aguilar S, Valencia R, Villa G, et al. 2002. Beta-diversity in tropical forest trees. *Science* 295(5555):666–669.
- CONPES, MAVDT, UAESPNN, DNP-SDAS. 2010. Documento Conpes 3680 de 2010: Lineamientos para la Consolidación del Sistema Nacional de Áreas Protegidas. Departamento Nacional de Planeación, Bogota, Colombia.
- Cue-Bar EM, Villaseñor JL, Morrone JJ, Ibarra-Manriquez G. 2006. Identifying priority areas for conservation in mexican tropical deciduous forest based on tree species. *Interciencia* 31(10):712–719.
- Davidar P, Rajagopal B, Mohandass D, Puyravaud JP, Condit R, Wright S, Leigh E. 2007. The effect of climatic gradients, topographic variation and species traits on the beta diversity of rain forest trees. *Global Ecology and Biogeography* 16(4):510–518.
- Davies TJ, Smith GF, Bellstedt DU, Boatwright JS, Bytebier B, Cowling RM, Forest F, Harmon LJ, Muasya AM, Schrire BD, et al. 2011. Extinction risk and diversification are linked in a plant biodiversity hotspot. *PLoS Biol* 9(5). DOI: 10.1371/journal.pbio.1000620.

Davies TJ, Urban MC, Rayfield B, Cadotte MW, Peres-Neto PR. 2016. Deconstructing the relationships between phylogenetic diversity and ecology: a case study on ecosystem functioning. *Ecology* 97(9):2212–2222.

Diaz-Pulido G. 2000. Vegetación marina de un sector de la plataforma continental de la guajira (caribe colombiano). *Boletín de Investigaciones Marinas y Costeras-INVEMAR* 29(1):27–34.

Diaz-Pulido G, Díaz-Ruíz M. 2003. Diversity of benthic marine algae of the colombian atlantic. *Biota Colombiana* 4(2):203–246.

Echeverría-Londoño S, Newbold T, Hudson LN, Contu S, Hill SL, Lysenko I, Arbeláez-Cortés E, Armbrrecht I, Boekhout T, Cabra-García J, et al. 2016. Modelling and projecting the response of local assemblage composition to land use change across colombia. *Diversity and Distributions* 22(11):1099–1111.

Faith DP. 1992. Conservation evaluation and phylogenetic diversity. *Biological conservation* 61(1):1–10.

Goldewijk KK. 2005. Three centuries of global population growth: a spatial referenced population (density) database for 1700–2000. *Population and Environment* 26(4):343–367.

Gray CL, Hill SL, Newbold T, Hudson LN, Börger L, Contu S, Hoskins AJ, Ferrier S, Purvis A, Scharlemann JP. 2016. Local biodiversity is higher inside than outside terrestrial protected areas worldwide. *Nature Communications* 7. DOI:10.1038/ncomms12306.

Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of phylml 3.0. *Systematic biology* 59(3):307–321.

Hassan R, Scholes R, Ash N, et al. 2005. Ecosystems and human well-being: current state and trends, findings of the condition and trends working group of the Millennium Ecosystem Assessment. Volume 1. Island Press, Washington, United States.

Hermly M, Verheyen K. 2007. Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. *Ecological research* 22(3):361–371.

Howard MG, McDonald WJ, Forster PI, Kress WJ, Erickson D, Faith DP, Shapcott A. 2016. Patterns of phylogenetic diversity of subtropical rainforest of the great sandy region, australia indicate long term climatic refugia. *PloS one* 11(4). DOI:10.1371/journal.pone.0153565.

Hubbell SP. 2001. The unified neutral theory of biodiversity and biogeography. Volume 32. Chapter 8, Pages 231–280. Princeton University Press, New Jersey, United States.

Isaac NJ, Turvey ST, Collen B, Waterman C, Baillie JE. 2007. Mammals on the edge: conservation priorities based on threat and phylogeny. *PloS one* 2(3). DOI:10.1371/journal.pone.0000296.

IUCN UW. 2014. The world database on protected areas (wdpa). Available from. <https://www.protectedplanet.net>. (accessed: October 2016).

Izsák J, Papp L. 2000. A link between ecological diversity indices and measures of biodiversity. *Ecological Modelling* 130(1):151–156.

Jenkins CN, Pimm SL, Joppa LN. 2013. Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences* 110(28):E2602–E2610.

- Kellogg JN, Vega V, Stailings T, Aiken CL. 1995. Tectonic development of panama, costa rica, and the colombian andes: constraints from global positioning system geodetic studies and gravity. *Geological Society of America Special Papers* 295:75–90.
- Kozlov AM, Aberer AJ, Stamatakis A. 2015. Examl version 3: a tool for phylogenomic analyses on supercomputers. *Bioinformatics* 31(15):2577–2579.
- Krajewski C. 1994. Phylogenetic measures of biodiversity: a comparison and critique. *Biological Conservation* 69(1):33–39.
- Kruschke J. 2014. *Doing Bayesian data analysis: A tutorial with R, JAGS, and Stan*. 2nd edition. Academic Press / Elsevier.
- Leigh Jr EG, Davidar P, Dick CW, Puyravaud JP, Terborgh J, ter Steege H, Wright SJ. 2004. Why do some tropical forests have so many species of trees? *Biotropica* 36(4):447–473.
- López-Osorio F, Miranda-Esquivel DR. 2010. A phylogenetic approach to conserving amazonian biodiversity. *Conservation Biology* 24(5):1359–1366.
- Manne LL, Brooks TM, Pimm SL. 1999. Relative risk of extinction of passerine birds on continents and islands. *Nature* 399(6733):258–261.
- Miranda-Esquivel DR. 2016. Support in area prioritization using phylogenetic information. Pages 219–235. Roseli P, Philippe G, editors, In *Biodiversity Conservation and Phylogenetic Systematics*. Springer, Gewerbestrasse, Switzerland.
- Morlon H, Schwilk DW, Bryant JA, Marquet PA, Rebelo AG, Tausch C, Bohannan BJ, Green JL. 2011. Spatial patterns of phylogenetic diversity. *Ecology letters* 14(2):141–149.
- Morrone JJ. 2014. Biogeographical regionalisation of the neotropical region. *Zootaxa* 3782(1):1–110.

- Myers N. 1988. Threatened biotas: "hot spots" in tropical forests. *Environmentalist* 8(3):187–208.
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403(6772):853–858.
- Nekola JC, White PS. 1999. The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* 26(4):867–878.
- Nelson BW, Ferreira CA, da Silva MF, Kawasaki ML. 1990. Endemism centres, refugia and botanical collection density in brazilian amazonia. *Nature* 345(6277):714–716.
- Nori J, Torres R, Lescano JN, Cordier JM, Periago ME, Baldo D. 2016. Protected areas and spatial conservation priorities for endemic vertebrates of the gran chaco, one of the most threatened ecoregions of the world. *Diversity and Distributions* 22(12):1212–1219.
- Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GV, Underwood EC, D'amico JA, Itoua I, Strand HE, Morrison JC, et al. 2001. Terrestrial ecoregions of the world: A new map of life on earth a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience* 51(11):933–938.
- Pennington RT, Lavin M, Särkinen T, Lewis GP, Klitgaard BB, Hughes CE. 2010. Contrasting plant diversification histories within the andean biodiversity hotspot. *Proceedings of the National Academy of Sciences* 107(31):13783–13787.
- Posadas P, Esquivel DRM, Crisci JV. 2001. Using phylogenetic diversity measures to set priorities in conservation: an example from southern south america. *Conservation Biology* 15(5):1325–1334.

Redding DW, Mooers AØ. 2006. Incorporating evolutionary measures into conservation prioritization. *Conservation Biology* 20(6):1670–1678.

Reddy S, Dávalos LM. 2003. Geographical sampling bias and its implications for conservation priorities in africa. *Journal of Biogeography* 30(11):1719–1727.

Richardson JE, Pennington RT. 2016. Editorial: from clades to communities. Origin of tropical diversity: *Frontiers in Genetics* 7. DOI:10.3389/fgene.2016.00186.

Richardson JE, Weitz FM, Fay MF, Cronk QC, Linder HP, Reeves G, Chase MW. 2001. Rapid and recent origin of species richness in the cape flora of southafrica. *Nature* 412(6843):181–183.

Rolland J, Cadotte MW, Davies J, Devictor V, Lavergne S, Mouquet N, Pavoine S, Rodrigues A, Thuiller W, Turcati L, et al. 2012. Using phylogenies in conservation: new perspectives. *Biology Letters* 8(5):692–694.

Sanín MJ, Kissling WD, Bacon CD, Borchsenius F, Galeano G, Svenning JC, Olivera J, Ramírez R, Trénel P, Pintaud JC. 2016. The neogene rise of the tropical andes facilitated diversification of wax palms (ceroxylon: Arecaceae) through geographical colonization and climatic niche separation. *Botanical Journal of the Linnean Society* 182(2):303–317.

Schweiger O, Klotz S, Durka W, Kühn I. 2008. A comparative test of phylogenetic diversity indices. *Oecologia* 157(3):485–495.

Sechrest W, Brooks TM, da Fonseca GA, Konstant WR, Mittermeier RA, Purvis A, Rylands AB, Gittleman JL. 2002. Hotspots and the conservation of evolutionary history. *Proceedings of the National Academy of Sciences* 99(4):2067–2071.

Silva JMCD. 1997. Endemic bird species and conservation in the cerrado region, south america. *Biodiversity and Conservation* 6:435–450.

Stamatakis A. 2014. Raxml version 8: a tool for phylogenetic analysis and postanalysis of large phylogenies. *Bioinformatics* 30(9):1312–1313.

Stattersfield AJ, Crosby MJ, Long AJ, Wege DC. 1998. Endemic bird areas of the world: priorities for biodiversity conservation. Volume 7. Birdlife International, Cambridge, United Kingdom.

Vane-Wright RI, Humphries CJ, Williams PH. 1991. What to protect? Systematics and the agony of choice. *Biological conservation* 55(3):235–254.

Venail P, Gross K, Oakley TH, Narwani A, Allan E, Flombaum P, Isbell F, Joshi J, Reich PB, Tilman D, et al. 2015. Species richness, but not phylogenetic diversity, influences community biomass production and temporal stability in a re-examination of 16 grassland biodiversity studies. *Functional Ecology* 29(5):615–626.

Warwick R, Clarke K. 1995. New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. *Marine Ecology Progress Series* 129:301–305.

Yuan Z, Wang S, Gazol A, Mellard J, Lin F, Ye J, Hao Z, Wang X, Loreau M. 2016. Multiple metrics of diversity have different effects on temperate forest functioning over succession. *Oecologia* 182(4):1175–1185.

Table 1.

Different measures for the areas of endemism.

Area	TR	PR	BL	EndBL	TD	PD	AvTD
Cauca	1754	727	109.28	5.05	1489.26	182.70	461.13
Paramo	1452	662	48.30	1.37	1279.63	118.35	461.59
Magdalena	1298	547	101.15	1.42	1175.55	171.27	537.39
Guajira	701	314	13.91	0.47	718.36	76.68	14.22
Choco-Darien	695	284	95.73	1.19	750.36	159.27	16.44
Napo	658	272	16.62	1.44	711.82	80.78	12.70
WEcuador	505	215	90.85	0.26	577.907	150.56	86.44
Sabana	417	176	13.61	0.43	544.96	38.97	12.35
Venezuela	222	100	6.80	0.18	295.31	22.91	13.10
Imeri	132	52	3.90	0.05	114.93	16.37	11.97

Total Richness (TR), Phylogenetic Richness (PR), the accumulate branch length for all (BL) and endemic species (EndBL), and finally the three phylogenetic diversity indices

Table 2.

Indices values and richness within and outside Protected Areas.

	TD	PD	AvTD	TR	PR
PAin ^a	1293.84	172.33	14.06	1509	731
PAout ^b	896.96	95.62	1578.38	1510	524
Δ	396.88	76.71	1564.32	1	207

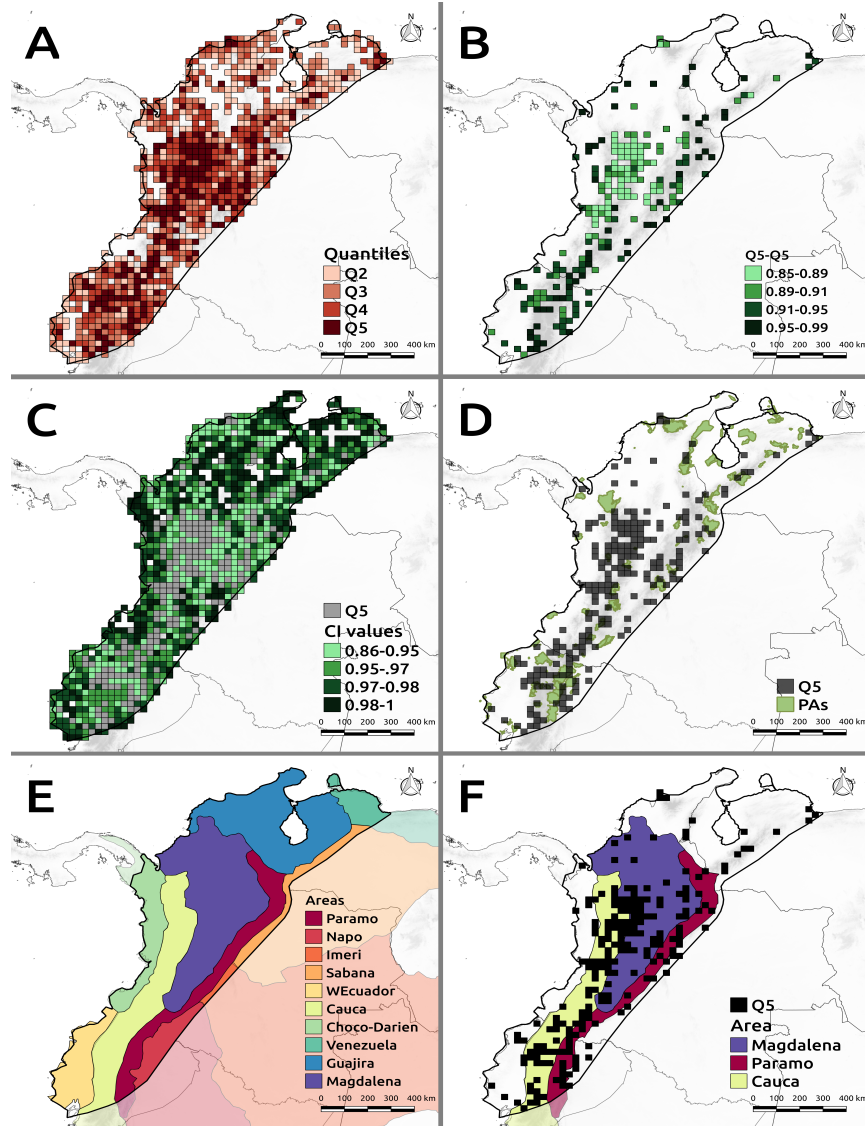
^a Values within Protected Areas.

^b Values outside Protected Areas.

The delta is defined as the difference within and outside Protected Areas for both measures:

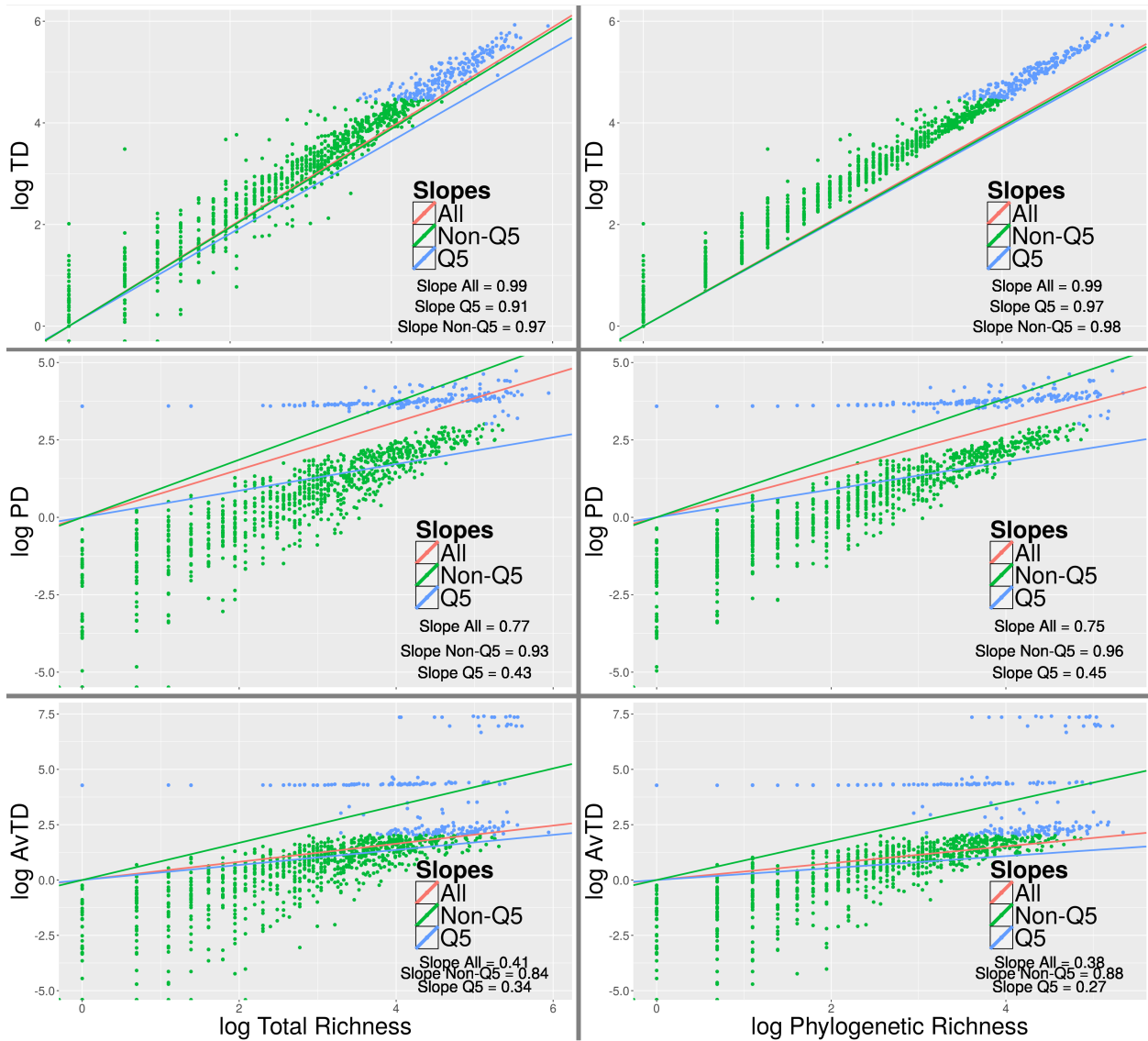
Phylogenetic diversity and specific richness

Figure 1.



Last four quantiles of the grid cells prioritization with AvTD index (A). The complementarity values among Q5 cells (B) and the complementarity index (CI) values for the Q5 cells (C). The Q5 cells overlapped with the NAB's protected areas (D). The areas of endemism modified for the NAB (E) and the Q5 cells overlapped with the three most important areas of endemism prioritized by AvTD (F)

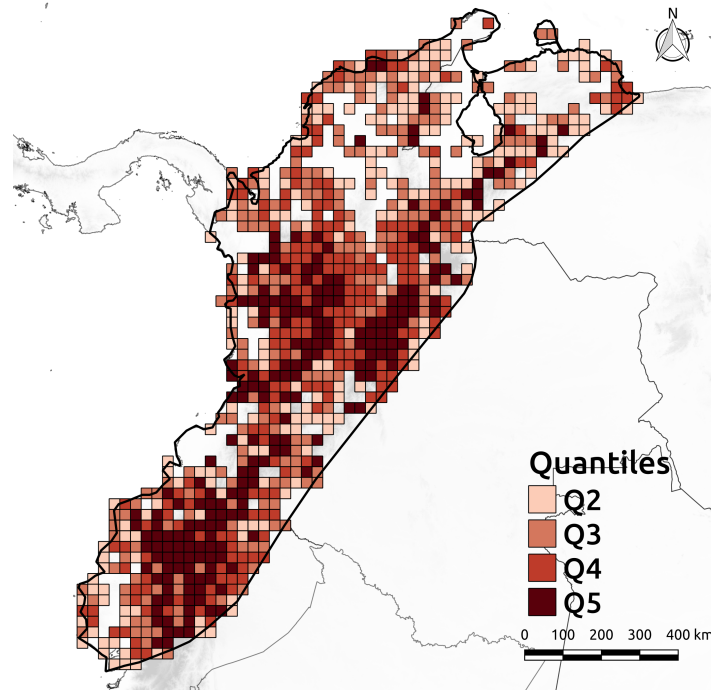
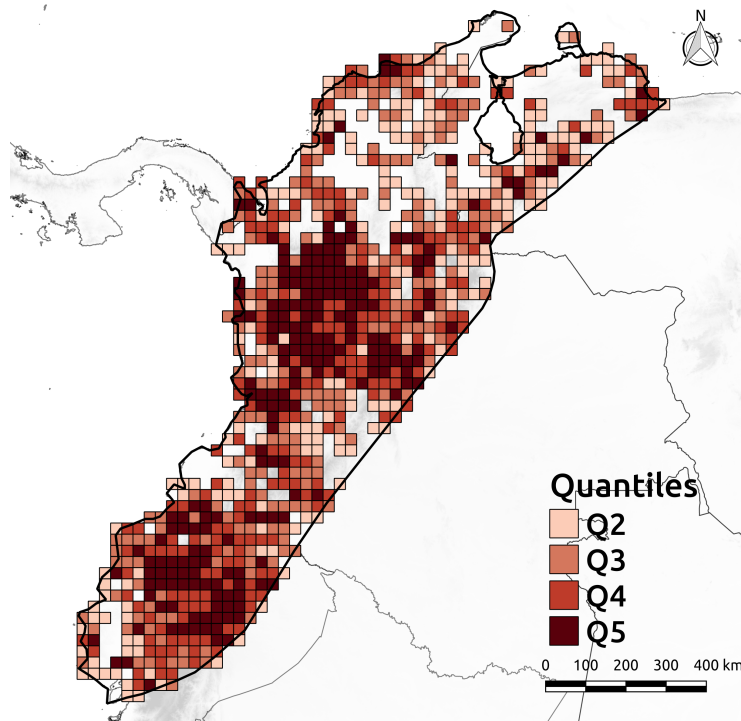
Figure 2.



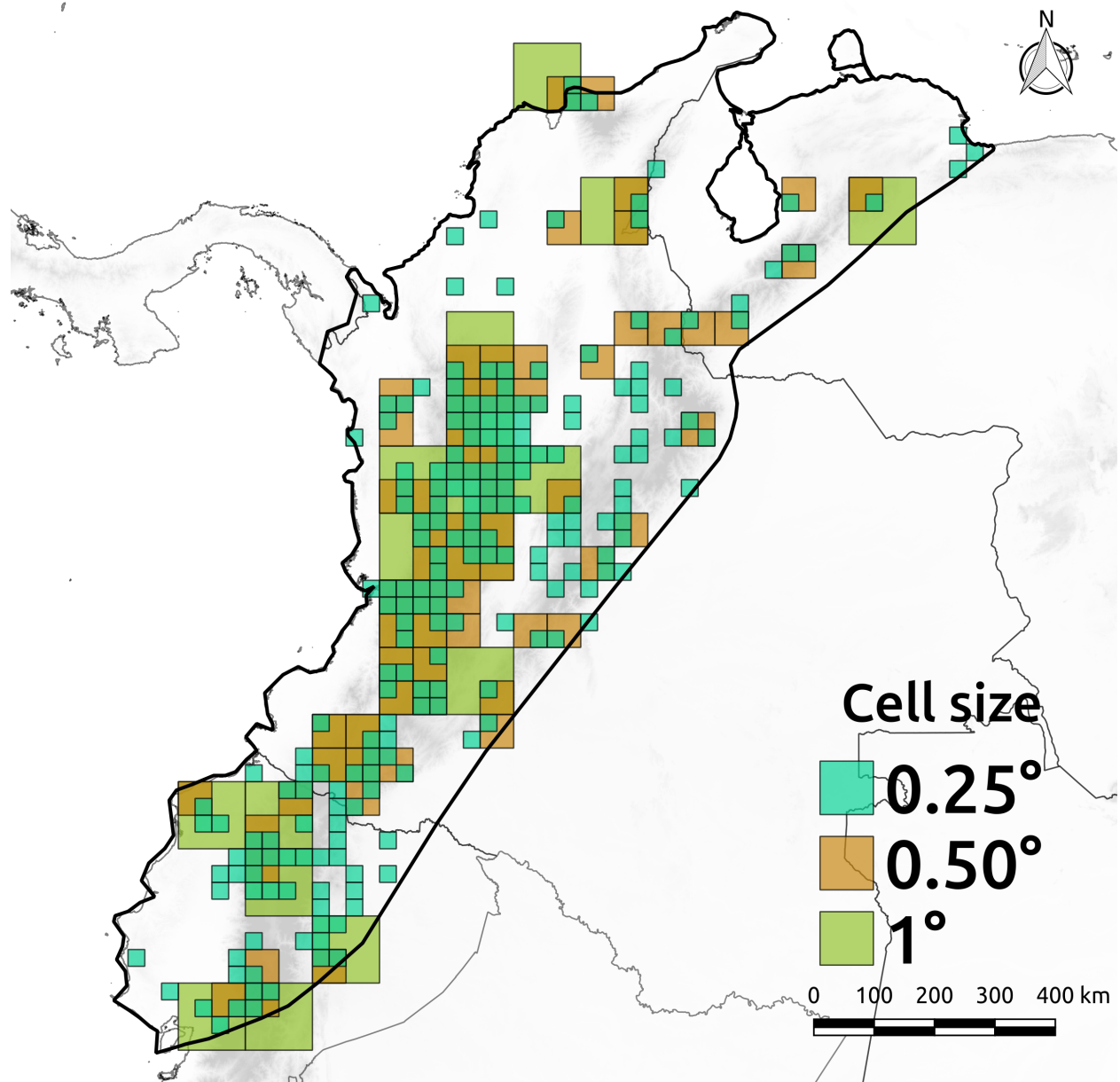
Posterior slope means for the Bayesian Simple Linear Regression between indices values and the both type of richness. Three slopes were calculated: using all cells (red slope), using only the Q5 cells (blue slope) and using only the non-Q5 cells (green slope)

Appendices

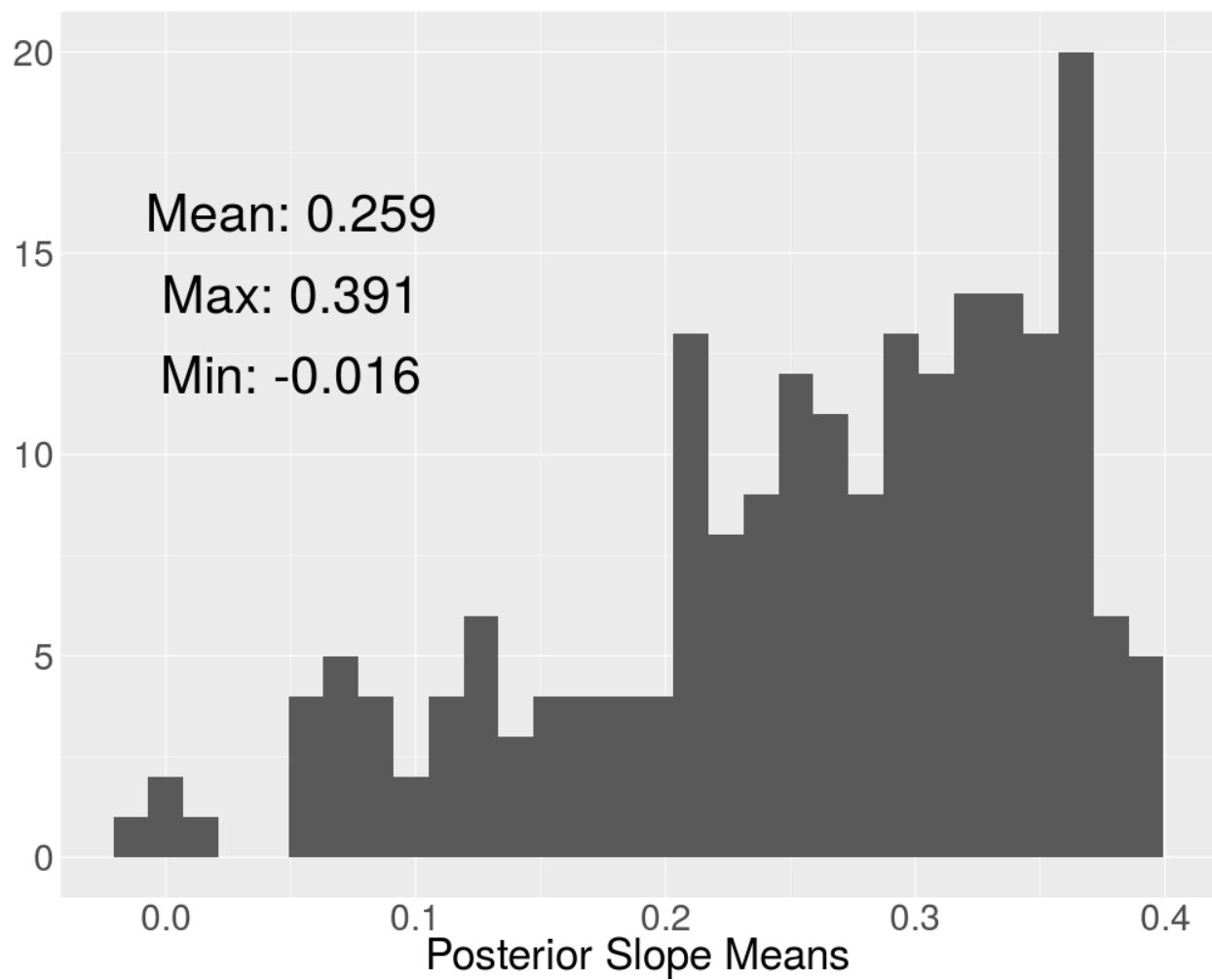
Appendix A



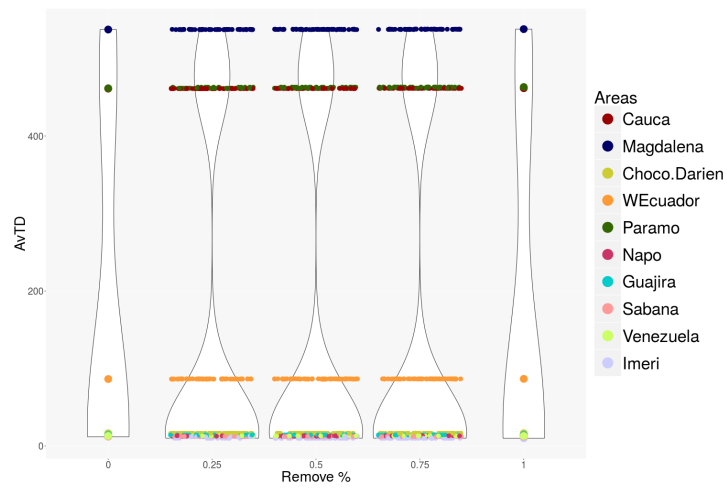
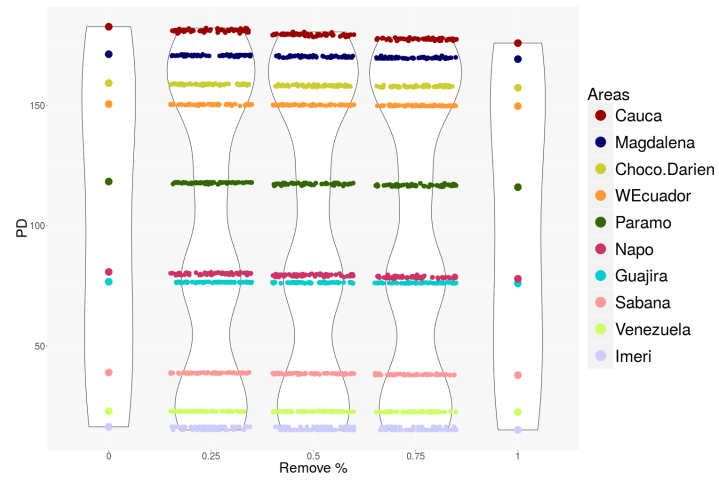
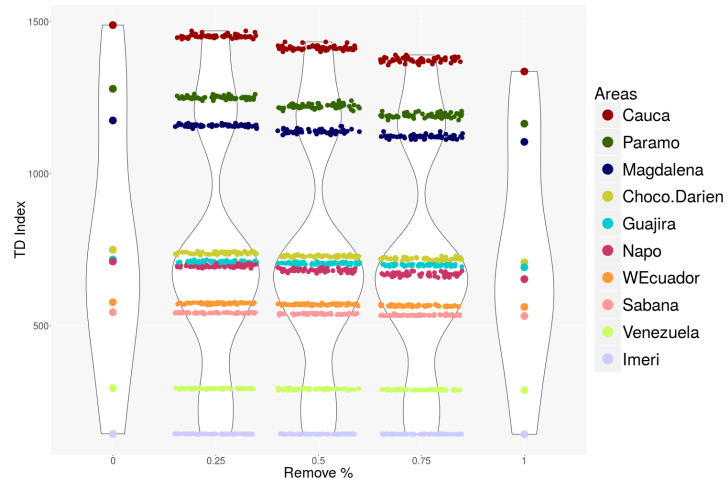
Appendix B



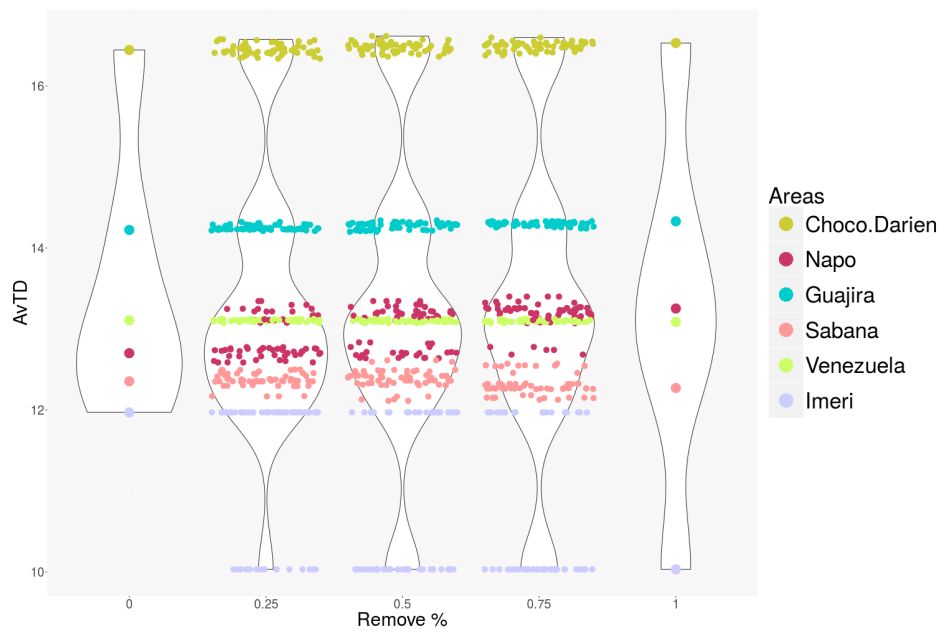
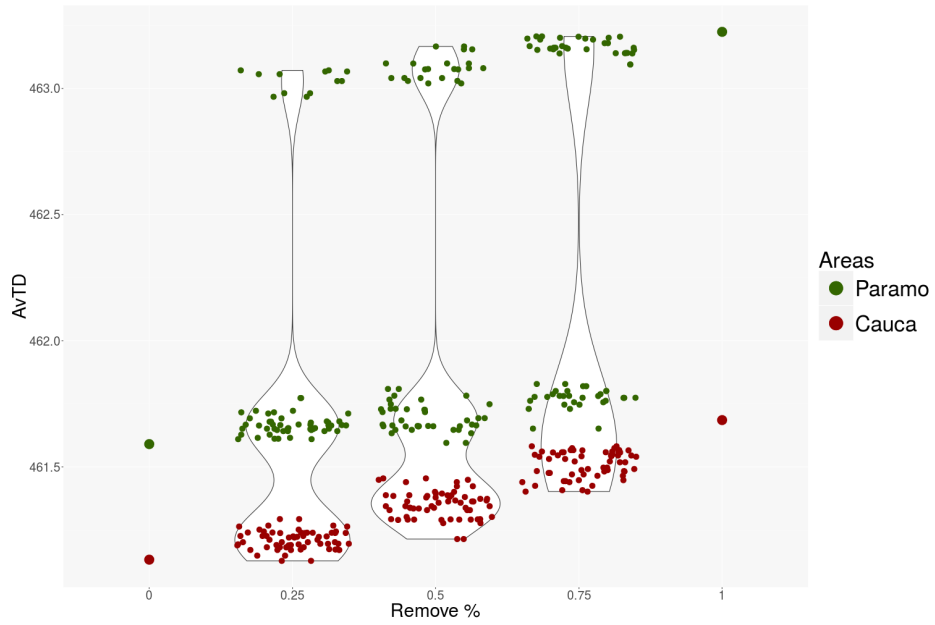
Appendix C



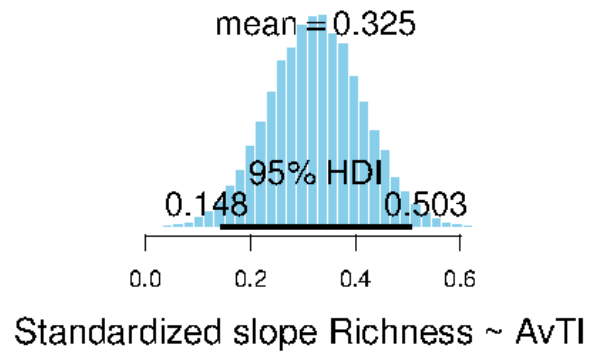
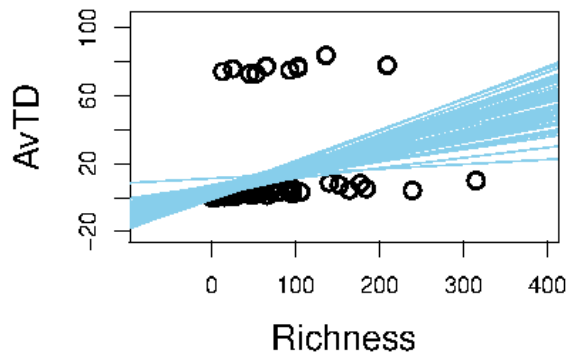
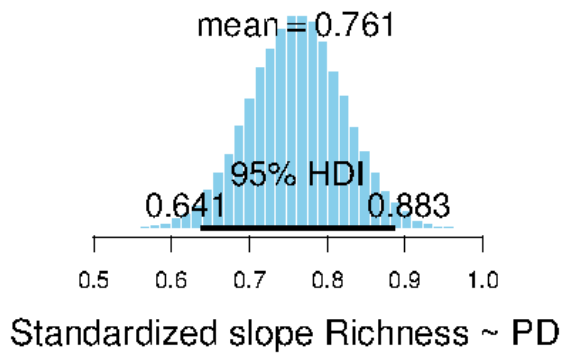
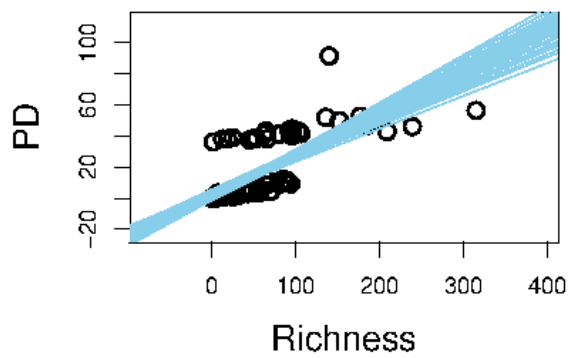
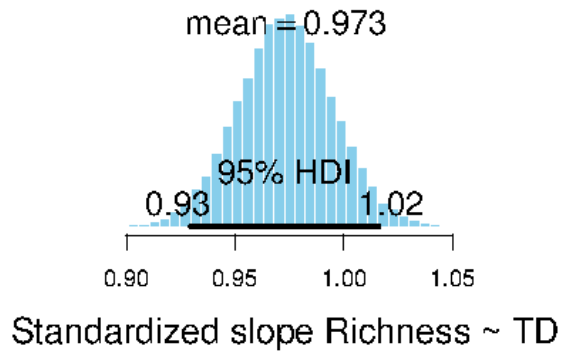
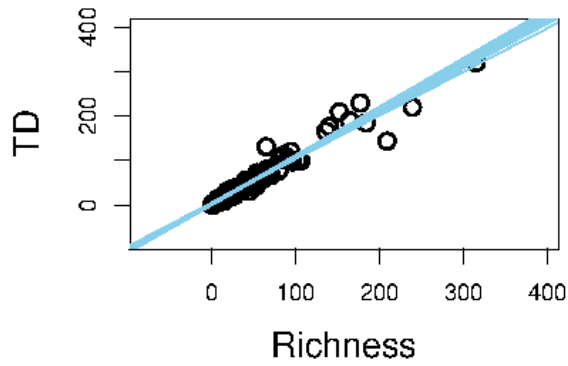
Appendix D



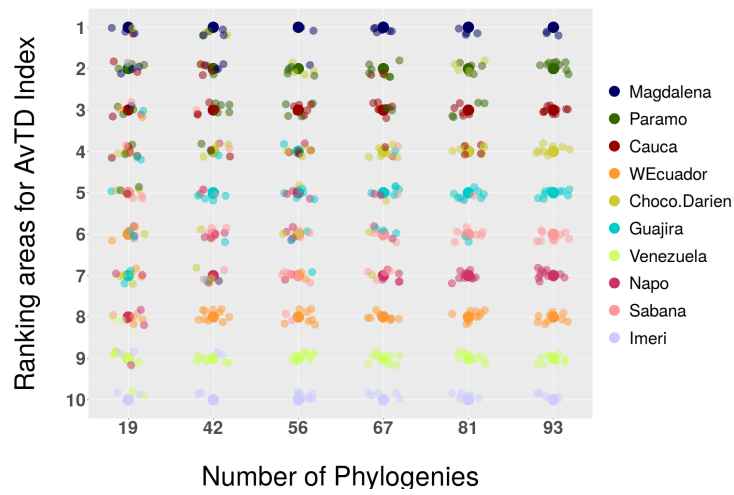
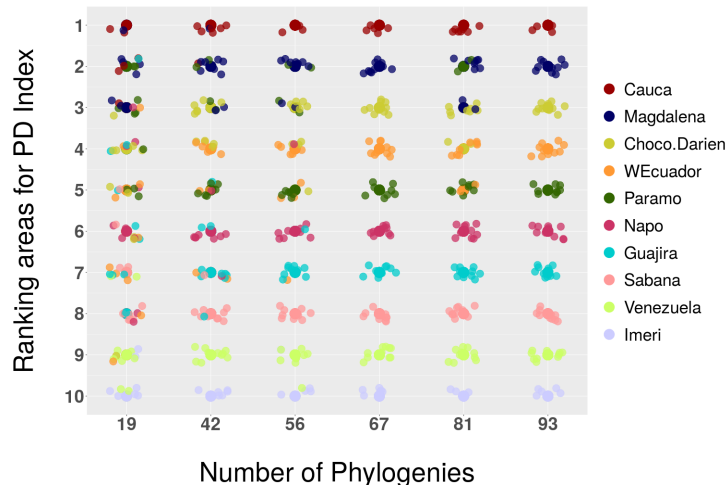
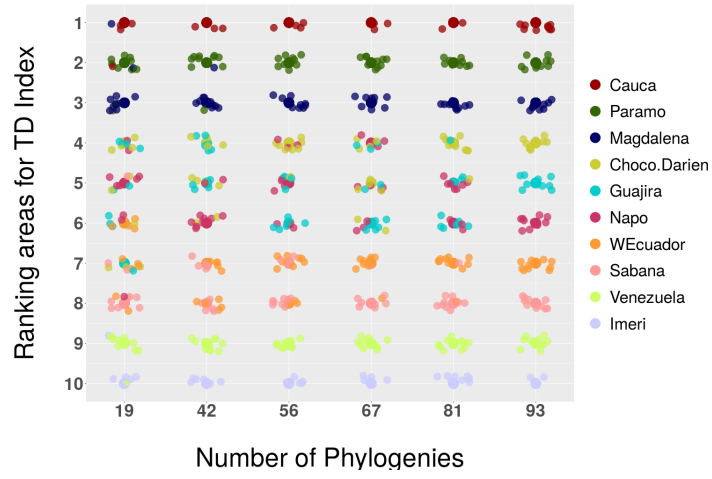
Appendix E



Appendix F



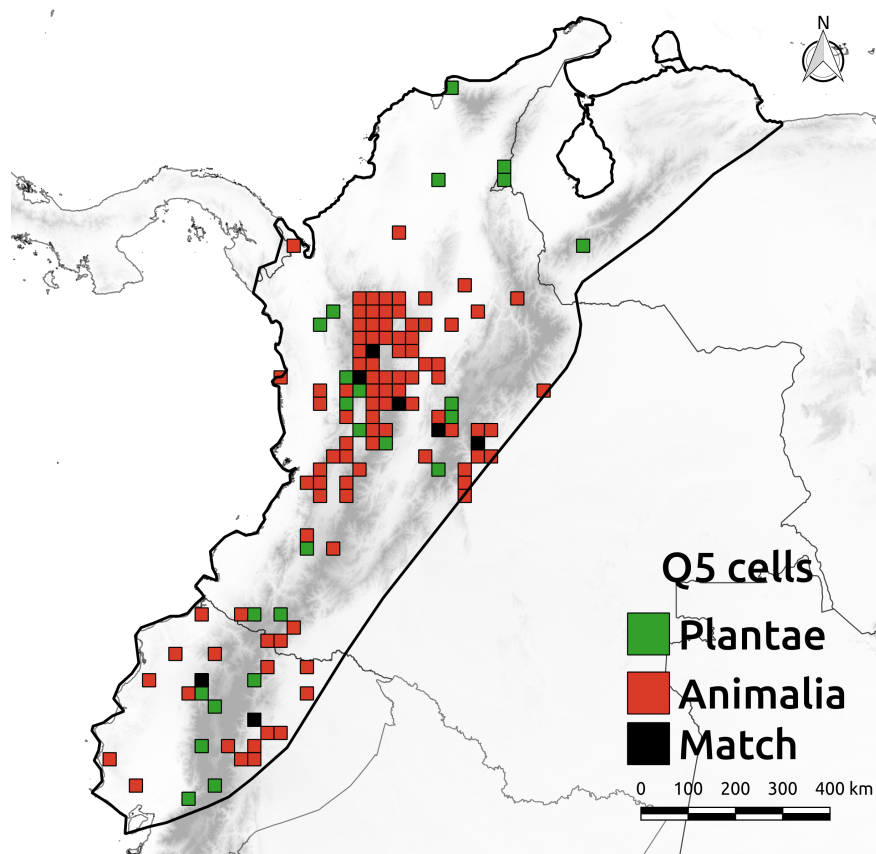
Appendix G



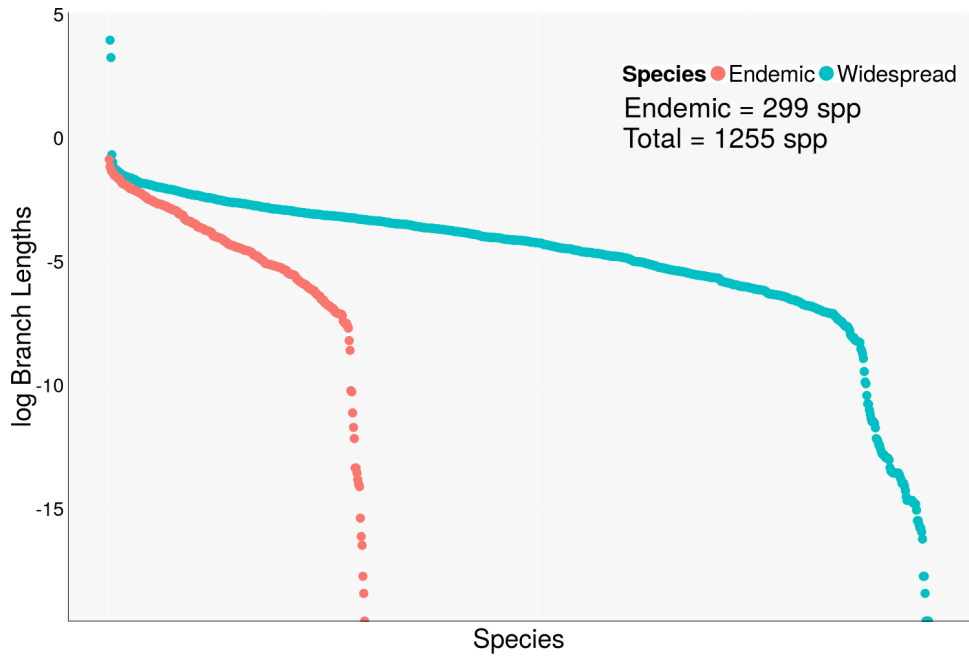
Appendix H

Index	Plantae	Animalia	Animalia Rarefied
TD	305.73	355139.40	141201.12
PD	52806.94	81545.37	33616.91
AvTD	31016.33	110920.10	52646.02

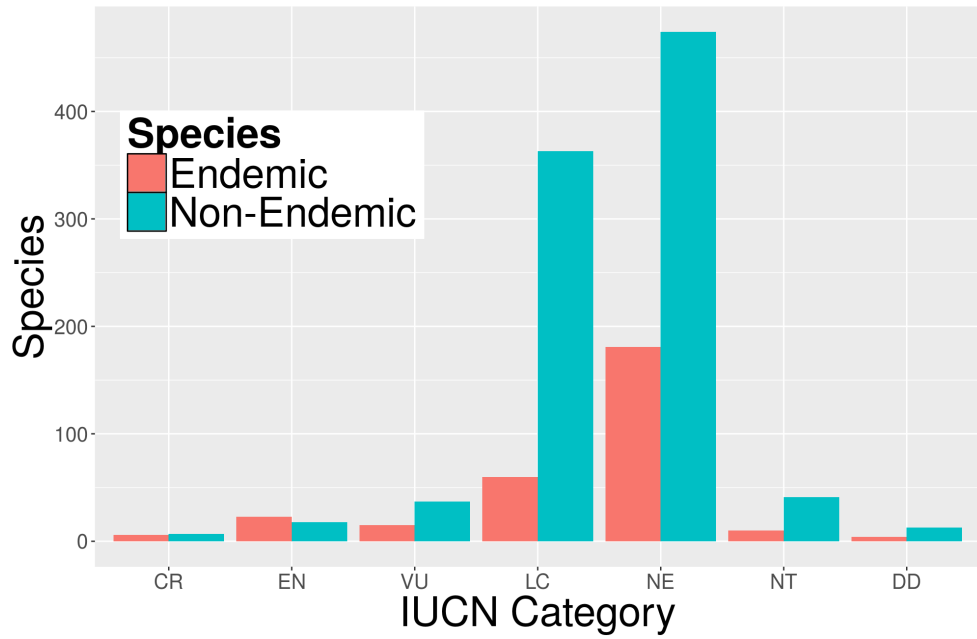
Appendix I



Appendix J



Appendix K



Appendix L

