SIMILAR TURNOVER RATES BETWEEN PTERIDOPHYTES AND ANGIOSPERMS TREES ALONG THE NORTHERN ECUADOR ANDEAN FOOTHILLS

Gabriel M. Moulatlet[1,2,*] 🆔, *Marina Rodes-Blanco*[3] 🆔 *& Byron Maza*[4] 🆔

[1] Instituto de Ecología, A.C. INECOL, Red de Biología Evolutiva, Xalapa, Veracruz, México.

[2] University of Arizona, Department of Ecology and Evolutionary Biology, Tucson, United States of America.

[3] Universidad de Alcalá, Departamento de Geología, Geografía y Medio Ambiente, Environmental Remote Sensing Research Group (GITA), Calle Colegios 2, 28801, Alcalá de Henares, Spain.

[4] Universidad Regional Amazónica Ikiam, Grupo de Investigación en Recursos Hídricos y Acuáticos, Facultad de Ciencias de la Tierra y Agua, Tena, Ecuador.

E-mail: mandaprogabriel@gmail.com (*corresponding author); marinarb89@gmail.com; byron.maza@ikiam.edu.ec

Abstract: Tropical mountain forests are areas of high plant diversity. While alpha diversity patterns are better documented along altitudinal gradients, how beta diversity varies between elevation ranges is less well known. Specifically, how turnover rates, as measured in a distance-decay models, are comparable between co-occurrent groups is still to be explored. We tested whether two distant related plant clades, pteridophytes (ferns and lycophytes) and angiosperm trees, have similar distance-decay rates along the same altitudinal gradient in the east flank of the tropical Andes of Ecuador. We found that both groups showed a strong decay in higher elevations that stabilised in the lower elevations. When sub-setting the data to have samples from both groups for the same elevation ranges, distance-decay curves were more similar, suggesting that the same environmental filters act in the assembly of communities of both groups. This result contributes to the understanding of the mechanisms of species distribution in high diversity areas.

Keywords: Amazonia; angiosperms; beta diversity; Napo; pteridophytes

Species distribution along elevational gradients is among the most well studied ecological patterns (Lomolino 2001). Mountains are ecosystems where abiotic factors often relate to elevation, creating gradients of environmental conditions, a biogeographic pattern reported since Humboldtian times (Rahbek 1995, Morueta-Holme *et al.* 2015). Tropical mountains, are high in endemism given the degree of isolation that some taxonomic groups experienced as consequence connectivity loss between similar ecosystems during mountain orogeny (Antonelli *et al.* 2009). High endemism in mountains partially explains the greater alpha diversity (*i.e.*, species richness) in comparison with lowlands, due to the presence of several unique species. However, other abiotic factors may explain how diversity varies along elevational gradients. In particular climate, due to the strong variation of temperature and moisture with increments in altitude (McCain & Grytnes 2010), and as isolation and historical occupancy (Brown *et al.* 2013, Steinbauer *et al.* 2016, Moulatlet *et al.* 2023), as the lineages that have colonized and diversified in mountains have been isolated during periods of climatic variability (Jablonski *et al.* 2006) are important factors.

To understand species diversity patterns, in addition to species richness, community turnover information is needed (*i.e.* beta diversity, *sensu* Tuomisto [2010]). Information on species turnover can also aid in conservation efforts (Socolar *et al.* 2016). Conservationists and governmental agencies often make use of ecosystem maps based on alpha diversity or degree of endemism to guide the management plan of protected areas, even though species turnover can give better indications of how species communities are structured and how sensitive they are to environmental changes (Socolar *et al.* 2016, Bergamin *et al.* 2017). Even more informative is when different taxonomic groups are inventoried at the same localities, or in the same elevation belts (Fontana *et al.* 2020, Moulatlet *et al.* 2021). Comparisons of turnover rates across species groups can indicate how diversity change in the geographic space. For instance, at tropical lowlands, turnover rates along environmental gradients as evaluated in various taxa have indicated regional differences among forest types (Ruokolainen *et al.* 2007) or biogeographic regionalization (Zuquim *et al.* 2021), and there is no reason to think that this would not be case in mountain ecosystems.

Diversity patterns along elevation gradients are variable depending on the taxonomic group. For some groups, such as pteridophytes, taxonomic alpha diversity tends to peak at mid-elevations (Krömer *et al.* 2005, Kessler *et al.* 2011, Nervo *et al.* 2018, Salazar *et al.* 2015, Riaño & Moulatlet 2022), where climatic conditions such as temperature and precipitation lead to highly productive ecosystems that consequently allows the coexistence of a higher number of species (Barrington 1993). For angiosperm trees, alpha diversity monotonically decreases from the highlands to the lowlands, a pattern that can be associated to an incremental increase in temperature toward lowlands, which favour species exhibiting optimal thermal tolerances (Givnish 1999, Homeier *et al.* 2010). In addition to climatic conditions, other characteristics, such as slope (Nettesheim *et al.* 2014) may also contribute for alpha diversity patterns. Regarding beta-diversity, both groups have high turnover rates along elevational gradients (Ramírez *et al.* 2019, Riaño & Moulatlet 2022). Nevertheless, few studies have been done along the same elevational transect in the tropical Andes to compare the community turnover of different groups. Here, we compare the community turnover rate of two distant related plant groups (pteridophytes [ferns and lycophytes] and angiosperm trees) along an elevational gradient (Figure 1, Table 1) in the northeastern Andes of Ecuador. We hypothesised that communities of these different species groups are exposed to the same environmental pressures and dynamics, and therefore, similar turnover rates would be expected.

To compare turnover rates, ten pteridophyte plots and nine angiosperm tree plots were placed along an elevational gradient ranging from 395 m to 4000 m a.s.l, in the Napo province of Ecuador (Figure 1, Table 1). For both groups, secondary forests were avoided during plot installation, so all plots were established in mature primary forests. Also, plots in middle to high elevations were distributed along or proximate to the main ridges, as the terrain is of difficult access and slopes are very steep, reducing the possibilities of locations for installing sampling plots.

Plots were installed following two methodologies (Table 1, Table 2). Pteridophytes were sampled in RAPELD plots (Magnusson *et al.* 2005), which are 250 m-long and follow terrain topography to minimise environmental variation within plots. The width of the plots is 2 m. Trees were sampled in plots of the Ecuadorian National Forestry Inventory (hereafter NFI) (MAE & FAO 2015). These plots have dimensions of 60 m x 60 m and are organised in conglomerates of three plots, each distributed in a "L" shape, where the minimum distance between each plot is of 250 m. In mountainous landscapes, the plots were established in a straight line instead of in "L" shape due to topographic conditions (Figure 1), with a minimal elevation distance of 100 m between each plot. Each plot from either methodology is considered as an independent sampling unit. The minimum distance between any plots was 250 m and the maximum of 80 km (33.6 km ± 26.5 km). Geographic coordinates were taken at each plot with a GPS.

All terrestrial pteridophyte individuals with a front leaf larger than 5 cm rooted on the right side of the central plot line were counted. Pteridophytes epiphytes and hemiepiphytes were included if they had such leaves < 2 m above ground. For clonal species, including species of the genus *Selaginella*, each rooting stem was considered as an individual, even if connected to other rooting stems. All

species were documented by one or more voucher specimens. A complete set of pteridophytes are stored in the collections at Ikiam University and at Ecuador's National Herbarium (QCNE). A complete description of pteridophyte diversity in the area has been reported by Riaño & Moulatlet (2022).

All trees with a diameter at breast (DBH) higher than 10 cm were measured and identified in the nine NFI plots installed. Tree species were identified by a botanist either in the field or by comparing collected samples to specimens in Ecuador's National Herbarium (QCNE), where they were deposited. At the herbarium, the samples were checked by two specialists and identified at the species level. Unknown species were identified at the genus level. A complete description of tree diversity in the area has been reported by Maza *et al.* (2022).

To calculate community turnover (beta-diversity), numerical analyses were based on dissimilarities or distance measure between sites, according to Anderson *et al.* (2011). Floristic dissimilarities were calculated for proportional abundance data using the Bray-Curtis index separately for each taxonomic group. A subset of pteridophyte data (6 of the 10 plots, Table 1) excluding the higher elevation plots (above 3,000 m a.s.l.) was set to be compared with the tree data set (which has not plots installed above such elevation). Dissimilarities of each group (y axis) were then plotted along the distance gradient (x axis). The distance between plots was calculated as the Euclidian distance between the geographic coordinates of each plot, projected in UTM 18S. To compare turnover rates, we fit exponential nonlinear distance-decay models to compare the slopes (and the pseudo-r^2). Distance-decay models were calculated using the function decay.model from the *betapart* R package (Baselga & Orne 2012) from the models generated for each species set (trees, pteridophytes

Figure 1. Study area and each individual plot location of trees (9 plots) and ferns (10 plots) in the Napo province in Ecuador. Plots are located within the Biological Reserve Colonso-Chalupas (RBCC) and the Sumaco Napo-Galeras National Park. The numbers labelling each dot refer to the elevation (a.s.l.) where each plot was established. The background map shows the topographic heterogeneity of the study area, as derived from a digital elevation model.
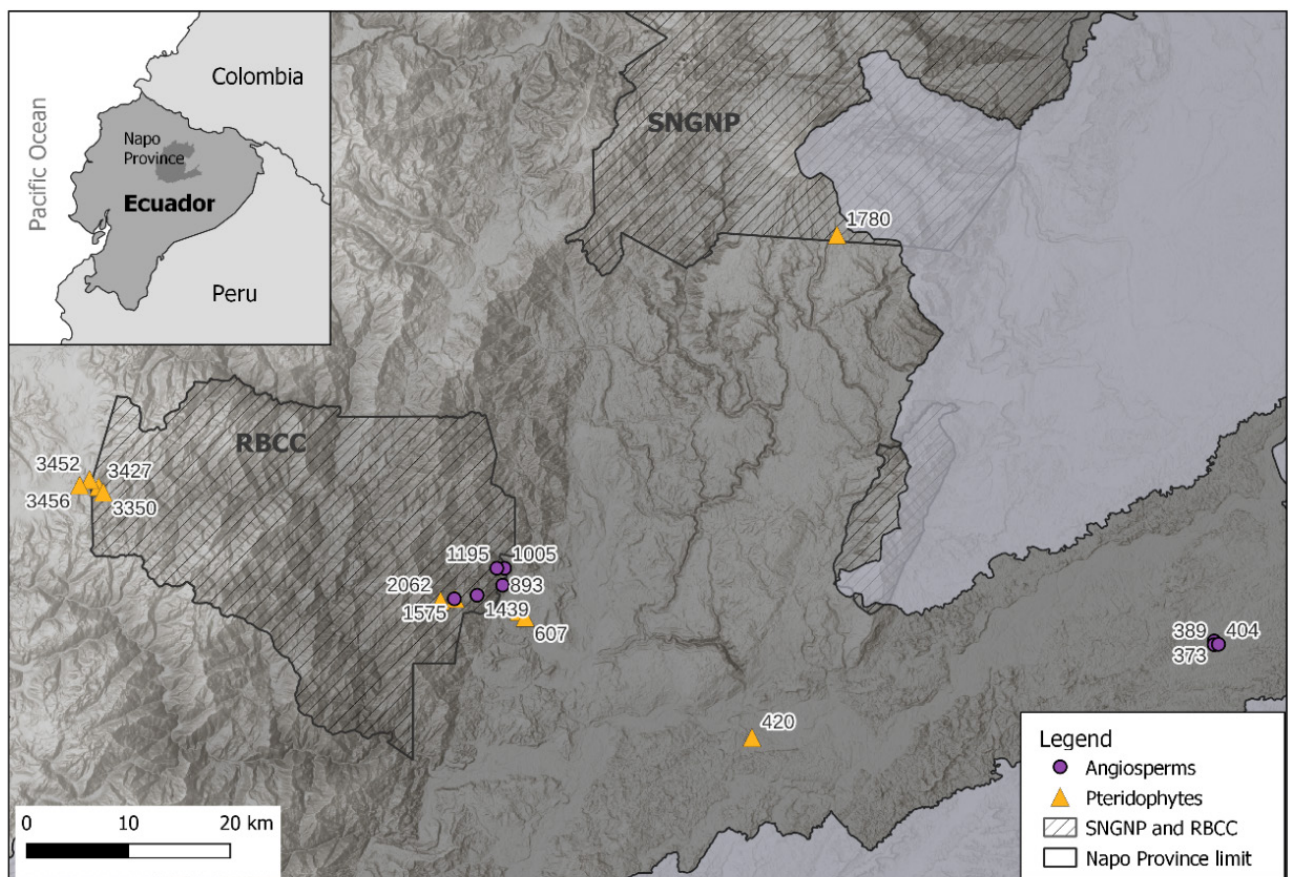
Table 1. Summary of the characteristics of the sampling locations. Data is separate by taxonomic groups as they were not sampled in the same plots. The subset of the fern dataset excludes plots located in higher elevations, to make it comparable with the tree dataset.

Group	Number of Species	Number of individuals	Sampled area (m²)	Density of individuals (ind·m⁻²)	Altitudinal Range (m a.s.l)	Number of plots	Range of species number per plot
Pteridophytes	143	7,235	5,000	1.447	(418 – 3,471)	10	(2 - 36)
Trees	367	2,302	32,400	0.071049	(373 – 1,826)	9	(59 - 100)
Pteridophytes (subset)	122	3,721	3,000	1.240333	(418 – 2,018)	6	(15 - 36)

Table 2. Description of the sampling plots. Ecuadorian ecosystem classification was obtained from Galeas and Guevara (2012).

| Plant group	Elevation (m a.s.l.)	Longitude	Latitude	Ecosystem classification
Angiosperm trees	373	-0.97347	-77.2576	Evergreen lowland forest
Angiosperm trees	389	-0.97657	-77.2575	Evergreen lowland forest
Angiosperm trees	394	-0.9763	-77.2538	Evergreen lowland forest
Angiosperm trees	892	-0.92415	-77.8858	Evergreen lower montane forest
Angiosperm trees	1007	-0.90925	-77.8839	Evergreen montane forest
Angiosperm trees	1195	-0.90921	-77.8909	Evergreen montane forest
Angiosperm trees	1421	-0.933	-77.9083	Evergreen montane forest
Angiosperm trees	1576	-0.93619	-77.9284	Evergreen montane forest
Angiosperm trees	1826	-0.93583	-77.9362	Evergreen montane forest
Pteridophytes	418	-1.0586	-77.6655	Evergreen lower montane forest
Pteridophytes	611	-0.9527	-77.8659	Evergreen lower montane forest
Pteridophytes	643	-0.94734	-77.8713	Evergreen lower montane forest
Pteridophytes	1558	-0.93588	-77.9276	Evergreen montane forest
Pteridophytes	1767	-0.61502	-77.5906	Evergreen montane forest
Pteridophytes	2018	-0.93782	-77.9405	Evergreen montane forest
Pteridophytes	3308	-0.84207	-78.2383	Evergreen upper montane forest
Pteridophytes	3447	-0.83722	-78.2424	Evergreen upper montane forest
Pteridophytes	3465	-0.831	-78.2505	Paramo
Pteridophytes	3471	-0.83584	-78.2592	Paramo

and the subset of pteridophytes). All analyses were done using the R software (R Core Team 2022), using packages *vegan* (Oksanen *et al.* 2022) and *betapart* (Baselga & Orne 2012).

We found that the turnover rate was similar for pteridophytes (b = -0.04) and trees (b = -0.04) (Figure 2). The curves for both groups showed a strong decay and then stabilised. When trees and pteridophytes occurring at similar elevation range were compared,

the subset of pteridophytes showed stronger turnover rates than the trees (b = -0.02 and b= -0.04, respectively).

Overall, our results showed similar turnover rates of ferns and trees along the elevational gradient of the northeastern Andes of Ecuador, in agreement with our initial hypothesis. It is particularly interesting that pteridophytes and trees have similar turnover rates, even though both groups have different
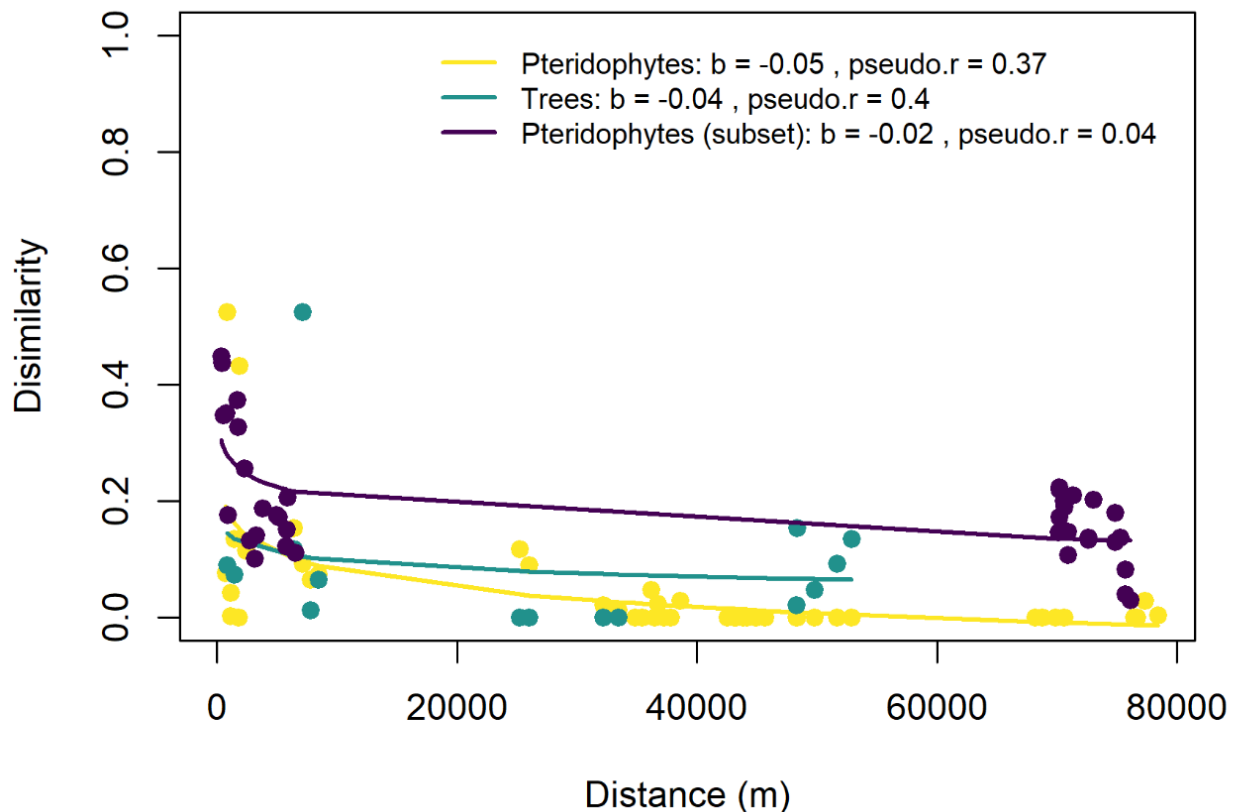
Figure 2. Rates of turnover of species groups along the elevational gradient, as measured by the pairwise distance between plots. The rate of turnover is given by the slope (b) and the pseudo-r² of the distance-decay models. The distance is in meters.

dispersal syndromes. While trees have a multitude of dispersal strategies that could constrain their occurrences (Correa *et al.* 2023), pteridophytes are less dispersal limited, as their spores are wind-dispersed (Barrington 1993). Pteridophytes and trees are distant related plant clades, but the similar turnover patterns suggest that environmental filters may have actuated in the assembly of both communities. Both groups responded in a similar manner to differences in elevation, with their dissimilarity increasing as the distance between plots increases, a pattern that follows the decrease in species richness from mid- to low- elevations in the study area (Riaño & Moulatlet 2022, Maza *et al.* 2022). Indeed, the regional species richness can largely influence turnover patterns along elevational gradients in the Andes (Olivares & Kessler 2020), but dissimilarity changes with increasing distance could also be related to the changes in the environmental conditions (such as local climate and soils) in such heterogenous landscape (Tuomisto *et al.* 2003, Moulatlet *et al.* 2019). Further studies are needed to disentangle the role of

regional richness and environmental conditions in explaining turnover patterns. However, the fact that angiosperm trees and pteridophytes have similar turnover rates suggests that the same mechanisms are influencing the diversity patterns of both groups in this area.

The resemblance in turnover rates may indicate similar underlying mechanisms of community assembly. Knowing taxa distribution is important when establishing conservation strategies. While alpha diversity infers the local species richness, beta diversity is a more consistent method for identifying diversity patterns (Kessler *et al.* 2011) and can be a tool to quantify the impacts derived from human intervention on ecosystem functions and services and in the planning of protected areas (Mori *et al.* 2018). In the context of climate change, scarcity of resources for conservation, and land-use changes as a result of anthropogenic activities, beta-diversity is a tool that generates information on how diversity changes along the geographic space, which can be useful to identifying areas that may serve as refuges in the face

of climate change (Sylvester *et al.* 2014). For instance, beta-diversity has been used as management tool to assess the number and distance between each protected area for mammal and insect conservation and management (Wiersma & Urban 2005), so the quantification of the distance decay rates along elevational gradients can help to map important areas where diversity is changing. Particularly for the study area, the high turnover rate at the transition between mid- and low elevations indicates the importance of the transitional areas between the Andes-Amazonia for the regional diversity.

The eastern flank of the Andes is one of the most species-rich zones of the Neotropics (Gentry 1988, Antonelli *et al.* 2009), and also one of the most data-deficient (Cornwell *et al.* 2019). High deforestation rates have threatened Andean ecosystems (Tapia-Armijos *et al.* 2015). For instance, about 60 % of Andean natural vegetation remains in Ecuador (Cuesta *et al.* 2017), most of it is located in the steep mountains within protected areas. Additionally, climate change has led to detectable species migration and extinctions in the past decades (Feeley *et al.* 2011, de Meyer *et al.* 2022) as a consequence of temperature rising and land-use changes. In face of those multiple threats, conservation strategies in the Andes-Amazonia ecotone need to be supported by the understanding of multi-taxa diversity along the elevational gradient formed by these mountains, such as those for pteridophytes and angiosperm trees.

ACKNOWLEDGMENTS

REFERENCES

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F., Harrison, S. P., Kraft, N. J. B., Stegen, J. C., & Swenson, N. G. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecology Letters, 14(1), 19–28. DOI: 10.1111/j.1461-0248.2010.01552.x

Antonelli, A., Nylander, J. A., Persson, C., & Sanmartín, I. 2009. Tracing the impact of the Andean uplift on Neotropical plant evolution. Proceedings of the National Academy of Sciences, 106(24), 9749–9754.

Baselga, A., & Orme, C. D. L. 2012. betapart: an R package for the study of beta diversity. Methods in ecology and evolution, 3(5), 808-812. DOI: 10.1111/j.2041-210X.2012.00224.x

Barrington, D. S. 1993. Ecological and Historical Factors in Fern Biogeography. Journal of Biogeography, 20(3), 275. DOI: 10.2307/2845635

Bergamin, R. S., Bastazini, V. A. G., Vélez-Martin, E., Debastiani, V., Zanini, K. J., Loyola, R., & Müller, S. C. 2017. Linking beta diversity patterns to protected areas: lessons from the Brazilian Atlantic Rainforest. Biodiversity and Conservation, 26(7), 1557–1568. DOI: 10.1007/s10531-017-1315-y

Brown, C., Burslem, D. F. R. P., Illian, J. B., Bao, L., Brockelman, W., Cao, M., Chang, L. W., Dattaraja, H. S., Davies, S., Gunatilleke, C. V. S., Gunatilleke, I. A. U. N., Huang, J., Kassim, A. R., LaFrankie, J. V., Lian, J., Lin, L., Ma, K., Mi, X., Nathalang, A., Noor, S., Ong, P., Sukumar, R., Su, S. H., Sun, I. F., Suresh, H. S., Tan, S., Thompson, J., Uriarte, M., Valencia, R., Yap, S. L., Ye, W., & Law, R. 2013. Multispecies coexistence of trees in tropical forests: spatial signals of topographic niche differentiation increase with environmental heterogeneity. Proceedings of the Royal Society B: Biological Sciences, 280(1764), 20130502–20130502. DOI: 10.1098/rspb.2013.0502

Cornwell, W. K., Pearse, W. D., Dalrymple, R. L., & Zanne, A. E. 2019. What we (don't) know about global plant diversity. Ecography, 42(11), 1819–1831. DOI: 10.1111/ecog.04481

Correa, D. F., Stevenson, P. R., Umaña, M. N., Coelho, L. de S., Lima Filho, D. de A., Salomão, R. P., Amaral, I. L. do, Wittmann, F., Matos, F. D. de A., Castilho, C. V., Phillips, O. L., Guevara, J. E., Carim, M. de J. V., Magnusson, W. E., Sabatier, D., Molino, J.-F., Irume, M. V., Martins, M. P., Guimarães, J. R. da S., Bánki, O. S., Piedade, M. T. F., Pitman, N. C. A., Monteagudo Mendoza,

A., Ramos, J. F., Luize, B. G., Novo, E. M. M. de L., Núñez Vargas, P., Silva, T. S. F., Venticinque, E. M., Manzatto, A. G., Reis, N. F. C., Terborgh, J. W., Casula, K. R., Honorio Coronado, E. N., Montero, J. C., Schöngart, J., Cárdenas López, D., Costa, F. R. C., Quaresma, A. C., Zartman, C. E., Killeen, T. J., Marimon, B. S., Marimon-Junior, B. H., Vasquez, R., Mostacedo, B., Demarchi, L. O., Feldpausch, T. R., Assis, R. L., Baraloto, C., Engel, J., Petronelli, P., Castellanos, H., Medeiros, M. B. de, Simon, M. F., Andrade, A., Camargo, J. L., Laurance, S. G. W., Laurance, W. F., Maniguaje Rincón, L., Schietti, J., Sousa, T. R., Farias, E. de S., Lopes, M. A., Magalhães, J. L. L., Nascimento, H. E. M., Queiroz, H. L. de, Aymard C., G. A., Brienen, R., Cardenas Revilla, J. D., Vieira, I. C. G., Cintra, B. B. L., Feitosa, Y. O., Duivenvoorden, J. F., Mogollón, H. F., Araujo-Murakami, A., Ferreira, L. V., Lozada, J. R., Comiskey, J. A., de Toledo, J. J., Damasco, G., Dávila, N., García-Villacorta, R., Lopes, A., Vicentini, A., Draper, F. C., Castaño Arboleda, N., Cornejo Valverde, F., Alonso, A., Dallmeier, F., Gomes, V. H. F., Neill, D., de Aguiar, D. P. P., Arroyo, L., Carvalho, F. A., de Souza, F. C., Amaral, D. D. do, Feeley, K. J., Gribel, R., Pansonato, M. P., Barlow, J., Berenguer, E., Ferreira, J., Fine, P. V. A., Guedes, M. C., Jimenez, E. M., Licona, J. C., Peñuela Mora, M. C., Villa Zegarra, B. E., Cerón, C., Fonty, É., Henkel, T. W., Householder, J. E., Maas, P., Silveira, M., Stropp, J., Thomas, R., Durgante, F. M., Baker, T. R., Daly, D., Huamantupa-Chuquimaco, I., Milliken, W., Pennington, T., Ríos Paredes, M., Molina, P., Fuentes, A., Klitgaard, B., Marcelo Peña, J. L., Peres, C. A., Silman, M. R., Tello, J. S., Campelo, W., Chave, J., Di Fiore, A., Hilário, R. R., Phillips, J. F., Rivas-Torres, G., van Andel, T. R., von Hildebrand, P., Pereira, L. de O., Barbosa, E. M., Barbosa, F. R., Bonates, L. C. de M., Carpanedo, R. de S., Dávila Doza, H. P., Zárate Gómez, R., Gonzales, T., Gallardo Gonzales, G. P., Hoffman, B., Junqueira, A. B., Malhi, Y., Miranda, I. P. de A., Mozombite Pinto, L. F., Prieto, A., Rodrigues, D. de J., Rudas, A., Ruschel, A. R., Silva, N., Vela, C. I. A., Vos, V. A., Zent, S., Zent, E. L., Noronha, J. C., Albuquerque, B. W., Cano, A., Carrero Márquez, Y. A., Costa, J. B. P., Flores, B. M., Galbraith, D., Holmgren, M., Kalamandeen, M., Nascimento, M. T., Oliveira, A. A., Ramirez-Angulo, H., Rocha, M., Scudeller, V. V., Sierra, R., Tirado, M., van der Heijden, G., Vilanova Torre, E., Vriesendorp, C., Pombo, M. M., Ahuite Reategui, M. A., Baider, C., Balslev, H., Cárdenas, S., Casas, L. F., Farfan-Rios, W., Ferreira, C., Linares-Palomino, R., Mendoza, C., Mesones, I., Torres-Lezama, A., Urrego Giraldo, L. E., Villarroel, D., Zagt, R., Parada, G. A., Alexiades, M. N., de Oliveira, E. A., Garcia-Cabrera, K., Hernandez, L., Palacios Cuenca, W., Pansini, S., Pauletto, D., Ramirez Arevalo, F., Sampaio, A. F., Valderrama Sandoval, E. H., Valenzuela Gamarra, L., & ter Steege, H. 2023. Geographic patterns of tree dispersal modes in Amazonia and their ecological correlates. Global Ecology and Biogeography, 32(1), 49–69. DOI: 10.1111/geb.13596

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. DOI: 10.1080/23766808.2017.1295705

de Meyer, A. P. R. R., Ortega-Andrade, H. M., & Moulatlet, G. M. 2022. Assessing the conservation of eastern Ecuadorian cloud forests in climate change scenarios. Perspectives in Ecology and Conservation, 20(2), 159–167. DOI: 10.1016/j.pecon.2022.01.001

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2024). _vegan: Community Ecology Package_. R package version 2.6-6.1, <https://CRAN.R-project.org/package=vegan>.

Feeley, K. J., Silman, M. R., Bush, M. B., Farfan, W., Cabrera, K. G., Malhi, Y., Meir, P., Revilla, N. S., Quisiyupanqui, M. N. R., & Saatchi, S. 2011. Upslope migration of Andean trees: Andean trees migrate upslope. Journal of Biogeography, 38(4), 783–791. DOI: 10.1111/j.1365-2699.2010.02444.x

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. Version 1. Scientific Reports, 10(1), 12516. DOI: 10.1038/s41598-020-69569-9

Galeas, R., & Guevara, J.E. 2012. Sistema de Clasificación de Ecosistemas del Ecuador Continental. Ministerio del Ambiente del Ecuador. Subsecretaría de Patrimonio Natural. Quito, 136p.

Gentry, A. H. 1988. Changes in Plant Community Diversity and Floristic Composition on Environmental and Geographical Gradients. Annals of the Missouri Botanical Garden, 75(1), 1–34. DOI: 10.2307/2399464

Givnish, T. J. 1999. On the causes of gradients in tropical tree diversity. Journal of Ecology, 87(2), 193–210. DOI: 10.1046/j.1365-2745.1999.00333.x

Goslee, S., & Urban, D. 2017, July 13. ecodist: Dissimilarity-Based Functions for Ecological Analysis.2.0.1 (Version 2.0.1).

Homeier, J., Breckle, S.-W., Günter, S., Rollenbeck, R. T., & Leuschner, C. 2010. Tree Diversity, Forest Structure and Productivity along Altitudinal and Topographical Gradients in a Species-Rich Ecuadorian Montane Rain Forest. Biotropica, 42(2), 140–148. DOI: 10.1111/j.1744-7429.2009.00547.x

Jablonski, D., Roy, K., & Valentine, J. W. 2006. Out of the Tropics: Evolutionary Dynamics of the Latitudinal Diversity Gradient. Science, 314(5796), 102–106. DOI: 10.1126/science.1130880

Kessler, M., Kluge, J., Hemp, A., & Ohlemüller, R. 2011. A global comparative analysis of elevational species richness patterns of ferns. Global Ecology and Biogeography, 20(6), 868–880. DOI: 10.1111/j.1466-8238.2011.00653.x

Krömer, T., Kessler, M., Robbert Gradstein, S., & Acebey, A. 2005. Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. Journal of Biogeography, 32(10), 1799–1809. DOI: 10.1111/j.1365-2699.2005.01318.x

Lomolino, M. V. 2001. Elevation gradients of species-density: historical and prospective views. Global Ecology and Biogeography, 10(1), 3–13. DOI: 10.1046/j.1466-822x.2001.00229.x

MAE, & FAO. 2015. Metodología para la Generación de Modelos Alométricos para la Estimación de Biomasa de árboles y bosques. p. ed. Ministerio del Ambiente del Ecuador y Organización de las Naciones Unidas para la Alimentación y la Agricultura., Quito, Ecuador.

Magnusson, W. E., Lima, A. P., Luizão, R., Luizão, F., Costa, F. R. C., Castilho, C. V. de, & Kinupp, V. F. 2005. RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. Biota Neotropica, 5, 19–24.

Maza, B., Rodes-Blanco, M., & Rojas, E. 2022. Aboveground Biomass Along an Elevation Gradient in an Evergreen Andean–Amazonian Forest in Ecuador. Frontiers in Forests and Global Change, 5.

McCain, C. M., & Grytnes, J.-A. 2010. Elevational Gradients in Species Richness. In: John Wiley & Sons, Ltd (Ed.), Encyclopedia of Life Sciences. Chichester, UK: John Wiley & Sons, Ltd.

Mori, A. S., Isbell, F., & Seidl, R. 2018. β-Diversity, Community Assembly, and Ecosystem Functioning. Trends in Ecology & Evolution, 33(7), 549–564. DOI: 10.1016/j.tree.2018.04.012

Morueta-Holme, N., Engemann, K., Sandoval-Acuña, P., Jonas, J. D., Segnitz, R. M., & Svenning, J.-C. 2015. Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. Proceedings of the National Academy of Sciences, 112(41), 12741–12745. DOI: 10.1073/pnas.1509938112

Moulatlet, G., Zuquim, G., & Tuomisto, H. 2019. The role of soils for pteridophyte distribution in tropical American forests. Fern Gazette, 21(1), 1-20.

Moulatlet, G. M., Ambriz, E., Guevara, J., López, K. G., Rodes-Blanco, M., Guerra-Arévalo, N., Ortega-Andrade, H. M., & Meneses, P. 2021. Multi-taxa ecological responses to habitat loss and fragmentation in western Amazonia as revealed by RAPELD biodiversity surveys. Acta Amazonica, 51(3), 234–243. DOI: 10.1590/1809-4392202004532

Moulatlet, G. M., Kusumoto, B., Pinto-Ledezma, J., Shiono, T., Kubota, Y., & Villalobos, F. 2023. Global patterns of phylogenetic beta-diversity components in angiosperms. Journal of Vegetation Science, 34(4), e13203. DOI: 10.1111/jvs.13203

Nettesheim, F. C., Damasceno, E. R., & Sylvestre, L. S. 2014. Different slopes of a mountain can determine the structure of ferns and lycophytes communities in a tropical forest of Brazil. Anais da Academia Brasileira de Ciências, 86, 199–210. DOI: 10.1590/0001-3765201495912

Nervo, M. H., Andrade, B. O., Tornquist, C. G., Mazurana, M., Windisch, P. G., & Overbeck, G. E. 2019. Distinct responses of terrestrial and epiphytic ferns and lycophytes along an elevational gradient in Southern Brazil. Journal of Vegetation Science, 30(1), 55–64. DOI: 10.1111/jvs.12709

Olivares, I., & Kessler, M. 2020. Regional species richness determines local species turnover in ferns. Frontiers of Biogeography, 12(4). DOI: 10.21425/F5FBG46818

R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (Retrieved on February 28th, 2019, from https://www.r-project.org/).

Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? Ecography, 18(2), 200–205. DOI: 10.1111/j.1600-0587.1995.tb00341.x

Ramírez, S., González-Caro, S., Phillips, J., Cabrera, E., Feeley, K. J., & Duque, Á. 2019. The influence of historical dispersal on the phylogenetic structure of tree communities in the tropical Andes. Biotropica, 51(4), 500–508. DOI: 10.1111/btp.12661

Riaño, K., & Moulatlet, G. M. 2022. Floristic and functional diversity of ferns and lycophytes at three elevational zones in the eastern slopes of the northern Andes, Ecuador. Acta Amazonica, 52, 149–157. DOI: 10.1590/1809-4392202102232

Ribeiro, D. B., Prado, P. I., Brown Jr, K. S., & Freitas, A. V. L. 2008. Additive partitioning of butterfly diversity in a fragmented landscape: importance of scale and implications for conservation. Diversity and Distributions, 14(6), 961–968. DOI: 10.1111/j.1472-4642.2008.00505.x

Ruokolainen, K., Tuomisto, H., Macía, M. J., Higgins, M. A., & Yli-Halla, M. 2007. Are floristic and edaphic patterns in Amazonian rain forests congruent for trees, pteridophytes and Melastomataceae? Journal of Tropical Ecology, 23(01), 13–25. DOI: 10.1017/S0266467406003889

Salazar, L., Homeier, J., Kessler, M., Abrahamczyk, S., Lehnert, M., Krömer, T., & Kluge, J. 2015. Diversity patterns of ferns along elevational gradients in Andean tropical forests. Plant Ecology & Diversity, 8(1), 13–24. DOI: 10.1080/17550874.2013.843036

Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. 2016. How Should Beta-Diversity Inform Biodiversity Conservation? Trends in Ecology & Evolution, 31(1), 67–80. DOI: 10.1016/j.tree.2015.11.005

Steinbauer, M. J., Field, R., Fernández-Palacios, J. M., Irl, S. D. H., Otto, R., Schaefer, H., & Beierkuhnlein, C. 2016. Biogeographic ranges do not support niche theory in radiating Canary Island plant clades. Global Ecology and Biogeography, 25(7), 792–804. DOI: 10.1111/geb.12425

Sylvester, S. P., Sylvester, M. D., & Kessler, M. 2014. Inaccessible ledges as refuges for the natural vegetation of the high Andes. Journal of vegetation Science, 25(5), 1225-1234. DOI: 10.1111/jvs.12176

Tapia-Armijos, M. F., Homeier, J., Espinosa, C. I., Leuschner, C., & Cruz, M. de la. 2015. Deforestation and Forest Fragmentation in South Ecuador since the 1970s – Losing a Hotspot of Biodiversity. PLOS ONE, 10(9), e0133701. DOI: 10.1371/journal.pone.0133701

Tuomisto, H. 2010. A consistent terminology for quantifying species diversity? Yes, it does exist. Oecologia, 164(4), 853–860. DOI: 10.1007/s00442-010-1812-0

Tuomisto, H., Ruokolainen, K., & Yli-Halla, M. 2003. Dispersal, Environment, and Floristic Variation of Western Amazonian Forests. Science, 299(5604), 241–244. DOI: 10.1126/science.1078037

Wiersma, Y. F., & Urban, D. L. 2005. Beta Diversity and Nature Reserve System Design in the Yukon, Canada: Beta Diversity and Nature Reserves. Conservation Biology, 19(4), 1262–1272. DOI: 10.1111/j.1523-1739.2005.00099.x

Zuquim, G., Tuomisto, H., Chaves, P. P., Emilio, T., Moulatlet, G. M., Ruokolainen, K., Van doninck, J., & Balslev, H. 2021. Revealing floristic variation and map uncertainties for different plant groups in western Amazonia. Journal of Vegetation Science, 32(5), e13081. DOI: 10.1111/jvs.13081