

Turnover rates of two plant groups in Ecuador

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

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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 angiosperms 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, for example, are high in endemism given the degree of isolation that some taxonomic groups experienced as consequence of the loss of connectivity 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).

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 in the same localities, or in the same elevation belts (Fontana *et al.* 2020, Moulatlet *et al.* 2021), such that comparisons of turnover rates across species groups can indicate how diversity is distributed and changing 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 angiosperms 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). However, 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.

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 (m ²)	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)

Group	Number of Species	Number of individuals	Sampled area (m ²)	Density of individuals (ind·m ⁻²)	Altitudinal Range (m a.s.l)	Number of plots	Range of species number per plot
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)

To compare the 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 the 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.

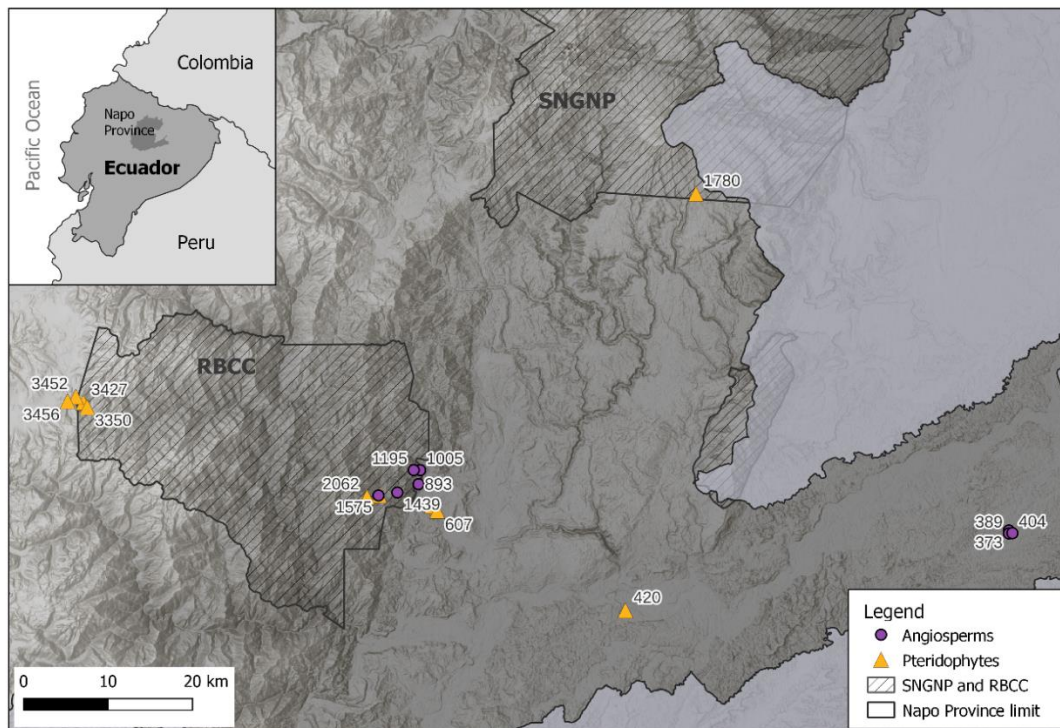


Figure 1. Study area and each individual plot location of trees (9 plots) and ferns (10 plots) in the Napo province in Ecuador. Plots are located within the Biological Reserve Colonso-Chalupas (RBCC) and the Sumaco Napo-Galeras National Park. The numbers labelling each dot refer to the elevation (a.s.l.) where

each plot was established. The background map shows the topographic heterogeneity of the study area, as derived from a digital elevation model.

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 \pm 26.5 km). Geographic coordinates were taken at each plot with a GPS.

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

Plant group	Elevation (m a.s.l.)	Longitude	Latitude	Ecosystem classification
Pteridophytes	3471	-0.83584	-78.2592	Paramo

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 and the subset of pteridophytes). All analyses were done using the R software (R Core Team 2022), using packages *vegan* (Oksanen 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).

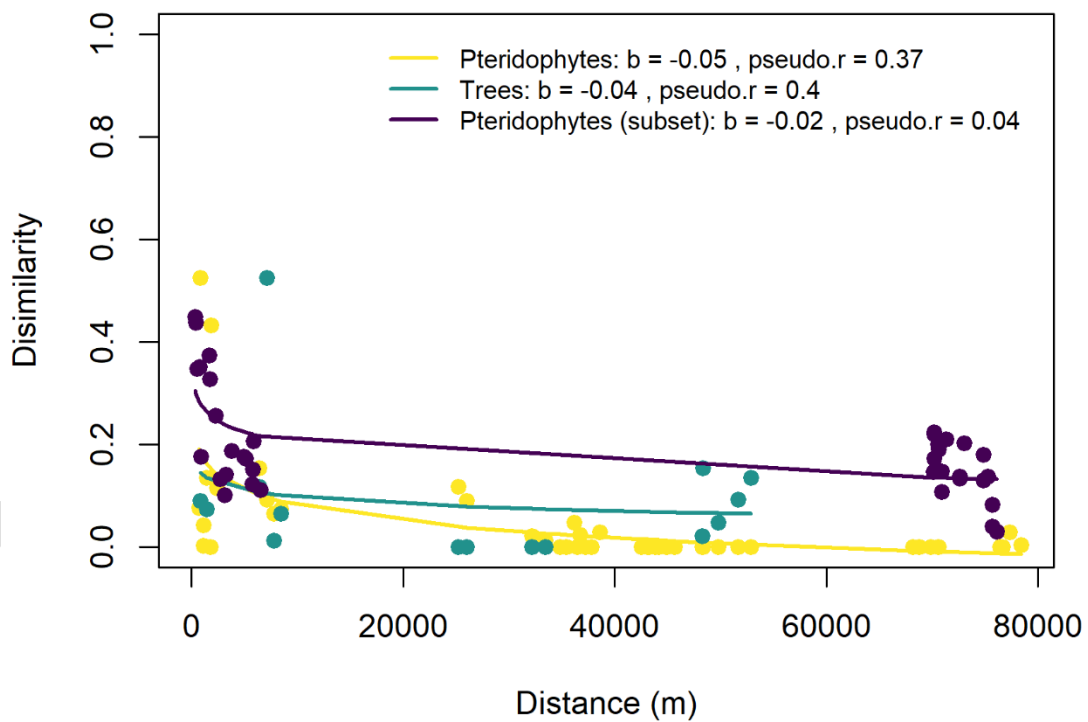


Figure 2. Rates of turnover of species groups along the elevational gradient, as measured by the pairwise distance between plots. The rate of turnover is given by the slope (b) and the pseudo- r^2 of the distance-decay models. The distance is in meters.

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 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 acted 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 angiosperms 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 trees.

ACKNOWLEDGMENTS

The project received a grant from SENESCYT – ENSAMBLE financing program (Number: PIC-17-BENS-002) for the development of the project “Carbon Storage for Three Types of Forest in the Ecuadorian Amazon Region”. The project has a research permit 008-018-IC-FAU/FLO-DPAN/MA for tree inventory. Research permits for the ferns inventory were granted by Ministerio del Ambiente de Ecuador (MAE-DNB-CM-2017-0062-IKIAM). GMM was funded by the Rufford Foundation (#28285-1).

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DOI: 10.1111/jvs.13081

Submitted: 4 September 2023

Accepted: 6 November 2023

Published online: 27 December 2023

Associate Editor: Bianca Ott Andrade