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ORIGINAL ARTICLE

Floristic and functional diversity of ferns and lycophytes at three elevational zones in the eastern slopes of the northern Andes, Ecuador

Karolina RIAÑO[1], Gabriel Massaine MOULATLET[2,3]*

[1] Cátedra Conacyt, Universidad de Guadalajara, Centro Universitario de la Costa Sur, Departamento de Ecología y Recursos Naturales, Av. Independencia #151 CP 48900 Autlán, Jalisco, México

[2] Universidad Regional Amazónica Ikiam, Facultad de Ciencias de la Tierra y Agua, CP 150150, Km7 Vía a Muyuna, Tena, Napo, Ecuador

[3] Instituto de Ecología A.C., Red de Biología Evolutiva, CP 91070, Xalapa, Veracruz, Mexico

* Corresponding author: mandaprogabriel@gmail.com; https://orcid.org/0000-0003-2571-1207

ABSTRACT

The northeastern slope of the Andes is an area of high diversity of ferns and lycophytes. In this study we assessed the diversity patterns of ferns and lycophytes in ten 250 m x 2 m plots installed at three elevational zones, from 418 to 3447 m.a.s.l., in the Napo province of Ecuador. Floristic diversity was measured using Hill numbers and by partitioning species diversity. Three functional diversity indices were calculated from a set of five leaf traits and weighted by species abundance: functional richness (FRic), evenness (FEve) and divergence (FDiv). To disentangle functional diversity from species richness, the standardized effect size (SES) of each index was also calculated. We recorded 148 species, Polypodiaceae and Dryopteridaceae being the most representative families. Species richness continuously decreased with elevation. Floristic composition was highly heterogeneous among elevation zones, with total species turnover found between 1500 and 2000 m.a.s.l. SES-FDiv and SES-FEve were higher than the null expectation for plots at mid-elevations, suggesting that deterministic mechanisms, such as biotic or abiotic filters, could explain assemblage composition at these sites. However, SES-FEve, SES-FRic and SES-FDiv did not differ from the null expectations at low and high elevation sites, suggesting the predominance of a stochastic process. By combining floristic and functional diversity, we were able to infer the observed community patterns with the resource-use strategies of fern and lycophytes in a mountain area, an approach that can be used to understand how assemblages might react to changing environmental conditions.

KEYWORDS: elevation gradient, leaf traits, light acquisition, pteridophyte, RAPELD, species richness

Diversidad florística y funcional de helechos y licófitos en tres zonas de elevación en la ladera oriental del noreste de los Andes, Ecuador

RESUMEN

La vertiente noreste de los Andes del Ecuador tiene alta diversidad de helechos y licófitos. En este estudio describimos patrones de diversidad de estos grupos en diez parcelas de 250 m x 2 m instaladas en tres zonas altitudinales, de 418 a 3447 m.s.n.m., en la provincia de Napo, Ecuador. La diversidad se calculó utilizando los números de Hill y particionando la diversidad de especies. Tres índices de diversidad funcional fueron estimados a partir de cinco atributos de las hojas ponderados por la abundancia de las especies: riqueza (FRic), uniformidad (FEve) y divergencia (FDiv). Para separar la diversidad funcional de la riqueza, se calculó el tamaño del efecto estandarizado (SES) de cada índice. Registramos 148 especies, siendo Polypodiaceae y Dryopteridaceae las familias más representativas. La riqueza disminuyó continuamente en el gradiente altitudinal. La composición de la comunidad tuvo un cambio total de especies entre 1500 y 2000 m.s.n.m. En parcelas intermedias, SES-FDiv y SES-FEve registraron valores más altos de lo esperado por el modelo nulo, lo que sugiere que los mecanismos deterministas, como los filtros bióticos y abióticos, podrían explicar el ensamble en estas comunidades. En parcelas de altitudes bajas y altas los tres índices no difirieron del valor nulo, lo que sugiere que predominan procesos estocásticos. Al combinar composición florística y diversidad funcional, pudimos identificar patrones de diversidad y estrategias de uso de recursos de helechos y licófitos. Este enfoque se puede utilizar para comprender cómo el ensamble de las comunidades es afectado por la variación en las condiciones ambientales.

PALABRAS CLAVE: adquisición de luz, gradiente altitudinal, riqueza de especies, pteridófitos, RAPELD, rasgos foliares

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INTRODUCTION

Ferns and lycophytes are abundant groups of vascular plants in the neotropical forests (Ulloa *et al.* 2017). In Ecuador, one of the most species-rich countries, about 1298 fern and lycophyte species have been recorded (Neill 2012; Weigand *et al.* 2020). Although great efforts to map their distribution have been undertaken in the Andes of Ecuador (Salazar *et al.* 2015; Aros-Mualin *et al.* 2021; Hernandez-Rojas *et al.* 2021) and in the adjacent ecosystems (Tuomisto *et al.* 2019), areas such as the north-eastern Andean slope still represent data gaps. The few field inventories in this region are still insufficient to draw general ecological conclusions about the patterns and mechanisms that shape the local community of ferns and lycophytes.

Species distribution patterns along elevational gradients can be determined by diversity indices, such as species richness, alpha and beta diversity, and also by functional diversity (Kessler *et al.* 2009; 2011; Mandl *et al.* 2010; Anderson *et al.* 2011). Species richness, alpha and beta diversity indicate how assemblages are structured and how they are related to environmental heterogeneity. However, diversity metrics are sensitive to sampling effort and, in mountainous areas, where access is often limited, achieving robust sampling is not always feasible (Tuomisto 2018). Thus, other metrics such as species diversity (i.e., the effective number of species) based on Hill numbers, can be useful and complementary to understand other aspects of assemblage structure, such as the proportion of abundant versus rare species along the elevation gradient (Tuomisto 2018; Roswell *et al.* 2021).

While species diversity reveals ecological patterns within and between assemblages, functional diversity reveals how assemblages make use of the available resources (Villéger *et al.* 2008), through the quantification of morphological, anatomical, or physiological species traits. Functional diversity is composed by a set of metrics of the assemblage response to environmental stressors based on species morphological traits (Mason *et al.* 2013), and considers the functional complementarity and redundancy of co-occurring species (Aros-Mualin *et al.* 2021). Assemblages with higher functional diversity are formed by species with diverse resource-use strategies, which increase niche complementarity in unlimited resource environments (Mason *et al.* 2005; Mason *et al.* 2013; Sanaphre-Villanueva *et al.* 2016). Assemblages with low functional diversity tend to be found where abiotic stress favours a low range of resource-use strategies, which diminishes niche complementarity (Mason *et al.* 2005). Studies on ferns and lycophytes along elevation gradients in tropical mountainous areas indicated that mid-elevation areas have higher functional diversity compared to low elevations, which could be associated to the diversity of resource-use strategies in local assemblages (Carvajal-Hernández *et al.* 2018).

The local distribution of ferns and lycophytes can be affected by light availability (Zuquim *et al.* 2009; Riaño and Briones 2015) and CO_2 concentrations (Kluge and Kessler 2007), as these environmental conditions are related to rates of photosynthesis and transpiration. For instance, mountain species tend to present higher stomatal density than low elevation species to compensate the low CO_2 concentrations in high altitudes (Kluge and Kessler 2007). Moreover, in contrast to dry and sun-exposed sites, leaves of shady and wet habitats are expected to possess larger laminas, longer petioles, lower stomatal density and stomata of greater length (Valladares and Niinemets 2008). Thus, resource-use related functional traits can be used for comparing species assemblages and to infer species co-existence mechanisms in heterogeneous environments (Zhang *et al.* 2017). In a context of accelerated environmental changes, understanding the relative contribution of community assemblage mechanisms through functional diversity may help to improve conservation and forest management strategies.

In this study, our aim was to describe the patterns of floristic and functional diversity of ferns and lycophytes in ten plots distributed at three elevation zones in the Napo province of Ecuador. To achieve this goal, we made use of community and functional diversity indices to assess species co-occurrence mechanisms in each assemblage. Given the high environmental heterogeneity that characterizes mountainous areas, we expected that fern and lycophyte assemblages at different elevations have different resource-use strategies, and that within-site heterogeneity would determine local species composition and abundance patterns.

MATERIAL AND METHODS

Study area and sampling

This study was conducted in the Napo province of Ecuador (Figure 1). Ten plots were placed at three elevational zones (low, middle, and high) in elevations ranging from 418 to 3471 m.a.s.l. (Supplementary Material, Table S1). Eight plots were located in the Biological Reserve Colonso-Chalupas (hereafter RBCC) and its buffer zone. RBCC is a biological reserve created in 2015 to establish a corridor of protected areas between the Antisana Reserve and the Llanganates National Park, all with headwaters draining to the Amazon basin. RBCC covers about 94,000 ha of the eastern Andean slopes, where several ecosystems, from paramo (~4000 m.a.s.l) to foothill forests (~600 m.a.s.l) can be found.

One plot was installed on the ascent route to the Sumaco Volcano, at the Sumaco Napo - Galeras National Park (SNGNP), in the north of the Napo province. Another single plot was installed within a flat wetland dominated by *Mauritia flexuosa* and *Euterpe precatoria* palms in the southern terrains of the Napo River, near the municipality of Misahuallí, in an

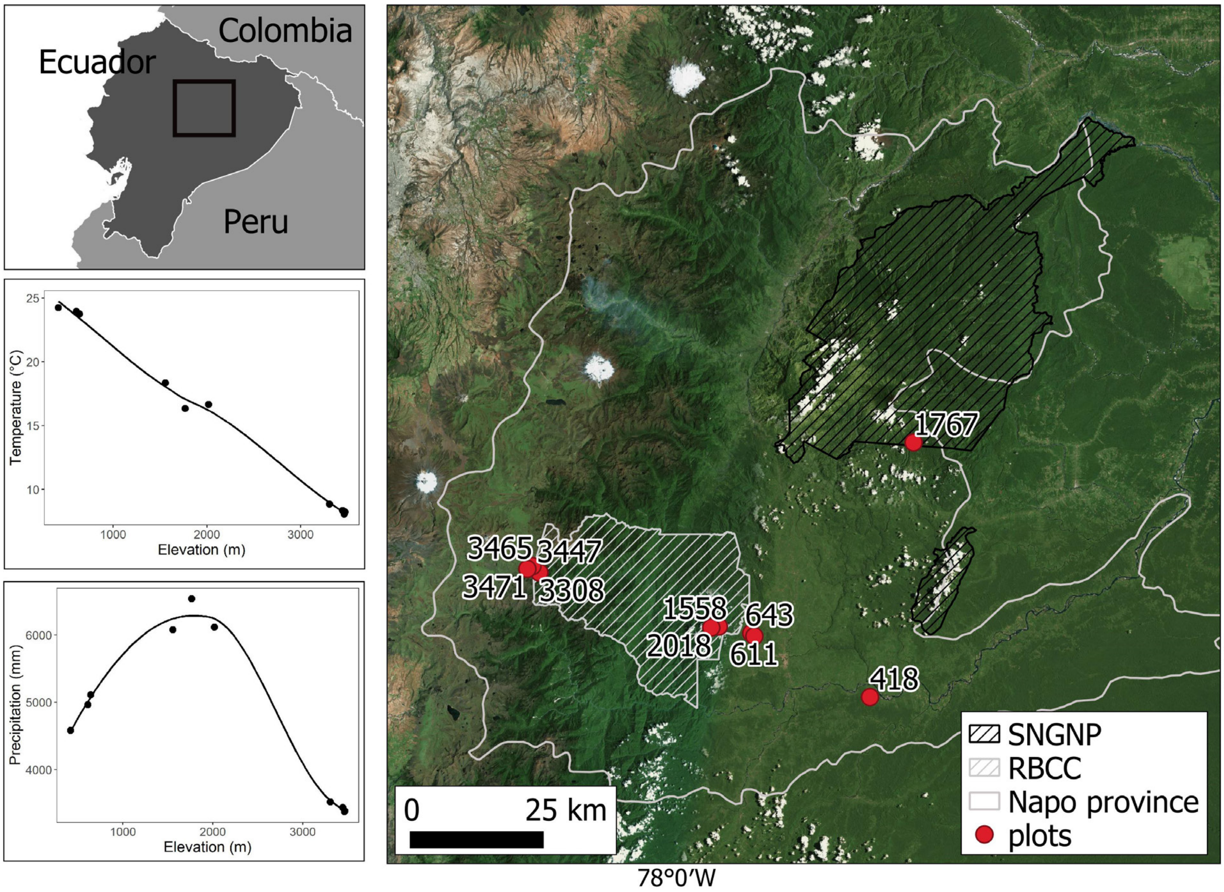

Figure 1. Distribution of ten sampling plots in the Napo province of Ecuador. Plots are located within the Biological Reserve Colonso-Chalupas (RBCC) and the Sumaco Napo-Galeras National Park. A single plot is located outside protected areas (418 m.a.s.l plot). Inset graphics show trends in annual mean temperature and mean annual precipitation in relation to the elevation, as derived for each sampling plot from the CHELSA climate project for the year interval of 1981 and 2010 (Karger *et al.* 2017). The trend lines were adjusted with LOESS regressions. This figure is in color in the electronic version.

area affected by deforestation and road construction (Figure 1; Supplementary Material, Table S1).

All plots were installed following the RAPELD methodology (Magnusson *et al.* 2005). The RAPELD plots were 250 m long and followed terrain topography to minimize environmental variation within plots. Plot width was 2 m (Zuquim *et al.* 2012), resulting in a total sampling area of 500 m^2. Because of the terrain complexity in the mountainous areas, plots were placed on or adjacent to mountain ridges at a minimum distance of 800 m between each other. Geographic coordinates were taken at the initial point of each plot with a hand-held GPS (Supplementary Material, Table S1).

At each plot, all terrestrial individuals with leaves larger than 10 cm rooted in one of the sides of the central plot line were counted. Epiphytes and climbers were included in the inventory if they had their leaves < 2 m above ground, therefore excluding canopy specialist species, except when they were found growing on falling trees or tree branches. For clonal species, 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, but additional specimens of individuals that could not be assigned to a species with a recent voucher were also collected. Species were identified using specialized identification keys (Zuquim *et al.* 2017) and by consulting experts on the different taxonomic groups. Specimens not identified to species level were sorted into morphotypes and are referred to as "species" hereafter. Vouchers were deposited at the Herbario Nacional de Ecuador (QCNE) and at the Herbario de Botánica Aplicada of Universidad Técnica de Cotopaxi, Ecuador (UTCEC).

Functional traits

The light acquisition traits leaf area (cm^2) and petiole longitude (cm) were measured for all dried specimens using the ImageJ software (Rasband 1997). The gas exchange traits stomatal density (number of stomata per mm^2), stomatal length and width (µm) were measured by taking leaf impressions of fresh material from at least two individuals of the same species in each plot and then averaged, following Zhu *et al.* (2018). Stomatal characteristics were obtained by applying a small layer of transparent nail polish on a small area (ca. 1 mm^2) in the abaxial side of the species' pinnae. The selected area was close to the central part of the pinnae, whenever possible, and from tissues that had no clear signs of superficial contamination or physical damage. After drying, the nail polish layer was carefully removed with the aid of tweezers, placed in a glass holder, and immediately covered with a slide. Leaf impressions were observed under a microscope (Nikon, Eclipse NI-U) and stomata characteristics were measured in three different sectors per slide sample, applying the differential-interference-contrast technique (40xDIC). It was not possible to apply nail polish in some species from the genera *Selaginella*, *Blechnum*, *Elaphoglossum*, and *Microgramma* due to reduced pinnae area. Species from these genera were dominant in the plots located at the high elevation zone (between 3308 and 3447 m.a.s.l), thus the functional diversity for these elevations could not be quantified. Our final trait data set had information for 84 species distributed from 418 to 3447 m.a.s.l.

Data analysis

To analyze community diversity, we made use of species diversity at Hill numbers, evenness and alpha, beta, and gamma diversity, as detailed by Tuomisto (2010). We first calculated total species diversity, which is the effective number of species, i.e., the number of species in a data set if all species were equally abundant. For that, species abundances were first converted to proportions by dividing them by the total abundance of all species in each RAPELD plot. Then, total species diversity was calculated as indicated in equation 3 of Tuomisto (2010). Species diversity is the inverse of the weighted mean of proportional species abundances. Total species diversity depends on the exponent q, which defines the weight that is given to abundant or rare species. When q = 0, species diversity equals species richness (i.e., the number of species in the dataset), meaning that abundant and rare species have the same weight. Evenness was also calculated by dividing species diversity by species richness, for each value of the parameter q. The larger the value of q, more weight is given to the abundant species. Based on previous studies on pteridophytes diversity (Tuomisto *et al.* 2014), we selected q values ranging from 0 to 5 (Chao *et al.* 2014).

The overall heterogeneity among sampling units (the ten RAPELD plots) was assessed by partitioning the total species diversity in the entire data set (i.e., the gamma diversity) into two independent components: alpha diversity (mean species density per site) and beta diversity (the effective number of sampling units), as indicated by Tuomisto (2010). Gamma diversity equals the alpha diversity multiplied by beta diversity (gamma = alpha*beta). The exponent q was applied in the calculation of alpha diversity, leading to different values of gamma and beta diversities for given values of q ranging from 0 to 5.

Principal coordinates analysis (PCoA) was used to visualize ordination of floristic similarities among plots, specifying a determined number of dimensions (hereafter PCoA Axis). Extended similarities were used to avoid the arch effect when dissimilarities between plots are closer to 1 (De'Ath, 2002) and then floristic similarities were calculated for proportional abundance data and occurrence (presence-absence) data using the Bray-Curtis index. Community patterns were evaluated by direct gradient analysis, where species and families were ordinated along the mean value of the gradient in the plots where they occurred.

Functional diversity was measured by the use of three indices that consider the position of the species of an assemblage and their abundances in the functional multi-trait space: functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv), according to Mason *et al.* (2005) and Villéger *et al.* (2008). Analogous to species richness, functional richness (FRic) indicates the number of functional responses in the community. The functional divergence (FDiv) shows the degree of separation in the functional response of the species weighted by their abundance in each community. The functional evenness (FEve) reveals the degree of functional similarity between the species that make up a community and is also weighted by abundance. To calculate these indices, two matrices were used, one with mean species functional traits values and another with species abundances. Before analysis, trait values were standardized to mean of 0 and unit variance. The functional space was first defined by PCoA and then the PCoA axis were used to calculate the functional diversity indices.

Functional diversity indices have been reported to be highly correlated with species richness (Carvajal-Hernández *et al.* 2018; Aros-Mualin *et al.* 2021). Thus, the effect of species richness can be eliminated by testing whether the observed ecological patterns differ from null expectations (Sanaphre-Villanueva *et al.* 2016). Community null models were used to estimate the standardized effect size (SES) of each index, randomizing 999 times the species identities in the functional trait matrix. SES values between 1.96 and -1.96 indicate that the community assembly is explained by stochastic processes; values outside that range indicate that the community assembly is explained by deterministic mechanisms, such as biotic factors (i.e., the functional index is higher than expected, due to functional over-dispersion) and abiotic factors (i.e., the functional index is lower than expected, due to low niche complementarity) (Ortega-Martínez *et al.* 2020).

All analyses were done using the R software (R Core Team 2020), using the packages vegan (Oksanen *et al.* 2018), vegetarian (Charney and Record 2012), and FD-package (Laliberté *et al.* 2014). R codes and the complete species list can be found at the GitHub repository of the corresponding author (https://github.com/gamamo/FernsEasternAndes).

RESULTS

A total of 7235 individuals from 148 species belonging to 51 genera and 22 families were recorded. The density of individuals was 1.447 ind m^{-2}, and the number of species per plot ranged between 2 (plot 3471 m) and 36 (plot 611 m). *Parablechnum sp.5* and *Amauropelta caucaensis* (Hieron.) A.R. Sm. were the most abundant species of the dataset, both growing above 3000 m.a.s.l. *Polybotrya caudata* Kunze was the third most abundant species, being reported in two plots below 600 m.a.s.l. The most species-rich genera were *Elaphoglossum* (15 species), *Serpocaulon* (10 species) and *Selaginella* (10 species). An abrupt change in species composition was detected between 1700 and 2000 m.a.s.l, as no species was shared between plots located at these elevations (Supplementary Material, Figure S1). Polypodiaceae was the most species-rich family (29 species), followed by Dryopteridaceae (23 species) and Blechnaceae (12 species) (Figure 2). Blechnaceae was the family with the highest number of individuals (1519), followed by Dryopteridaceae (1313) and Thelypteridaceae (974).

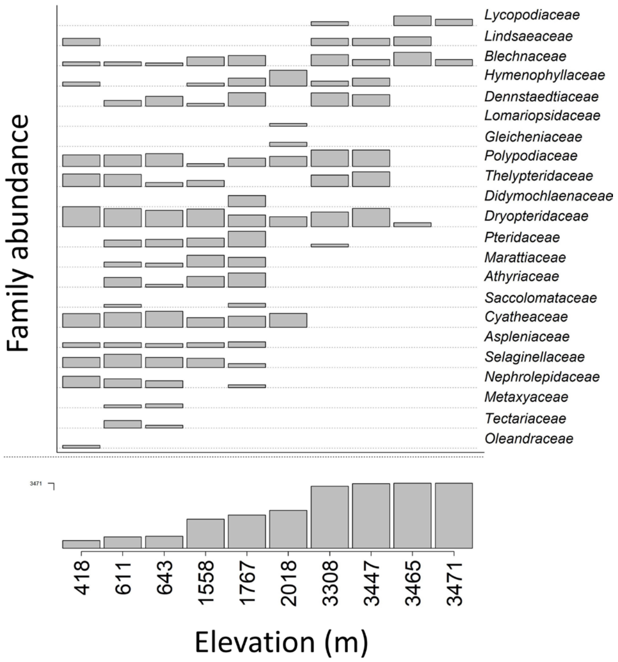

Figure 2. Abundance of fern and lycophyte families along the elevational gradient in the Napo province of Ecuador. The plots are listed in order of increasing elevation, and the families in order of decreasing mean elevation in the plots where the family was observed.

Species diversity in the plots located at the highest elevations quickly declined and then stabilized with the increment of q (Figure 3a). When several species were abundant in a plot, diversity decline was less abrupt. For example, in the 611-m plot, which was dominated by a single species (*Cyathea cf. tortuosa*), the diversity decline was more abrupt than at the 1767-m plot, where at least eight locally abundant species, represented by more than 20 individuals, were found. In plots at the highest elevations (3465 m and 3471 m) we recorded the lowest species number (2 and 4,

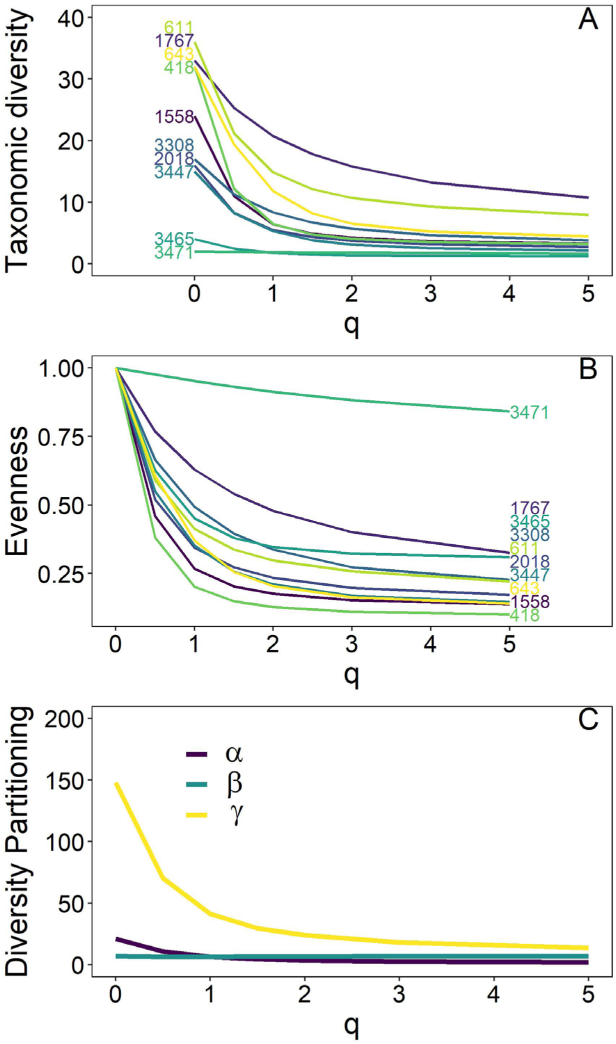

Figure 3. Trends in true species diversity (effective number of species) within and across sites as a function of q. Total species diversity depends on the exponent q, which defines the weight that is given to abundant or rare species. When q = 0, species diversity equals species richness (i.e., the number of species in the dataset), meaning that abundant and rare species have the same weight. Increasing q gives increased weight to the most abundant species when calculating species diversity, which leads to a smaller effective number of species. A – Within-site species diversity shown separately for each of the 10 sites; B – Species evenness; C – Gamma diversity (total species diversity in the data set), alpha diversity (mean species diversity per site) and beta diversity (gamma/alpha). Alpha, beta and gamma diversity are represented by the Greek letters α, β, and γ, respectively. This figure is in color in the electronic version.

respectively), but a high number of individuals (>20) of each species, indicating high assemblage evenness (Figure 3b).

The overall heterogeneity among sites indicated that, when q = 0, gamma diversity was 148 and alpha diversity was 21.1. At the opposite extreme of q values, when q = 5, gamma diversity was 13.7 and alpha diversity was 1.99. Beta diversity remained between 7.01 and 6.88, indicating a strong turnover in species composition among plots (Figure 3c). This last result was confirmed by the visual inspection of the PCoA ordination, which revealed a clear floristic separation (i.e., strong floristic dissimilarity) among plots at different elevation zones (Supplementary Material, Figure S2). Regular dissimilarities for occurrence (presence-absence) data ranged from 0.4 and 1 and extended similarities ranged from 0.47 to 2.87. For abundance data, regular dissimilarities ranged from 0.52 to 1 and extended dissimilarities ranged from 0.52 to 2.91.

Functional divergence (FDiv) values were higher in plots located at low elevations, the 1558-m plot showing the lowest value of FDiv. SES-FDiv was higher than expected by chance for the same plot (SES-FDiv = 2.23), suggesting that deterministic mechanisms explain this assemblage structure (Figure 4a,b). The highest values of functional evenness (FEve) were found in the 1767-m and 2018-m plots, located at mid elevations. The SES-FEve value for the 1767-m plot was lower than expected by chance (-2.06), which also suggests that deterministic mechanisms explain this assemblage structure (Figure 4c,d). Finally, functional richness (FRiv) was higher for plots at low elevations than for plots at mid or high elevations. SES-FRic values of all fern assemblages ranged between -1.96 and 1.96 and could not be distinguished from random expectations (Figure 4e,f).

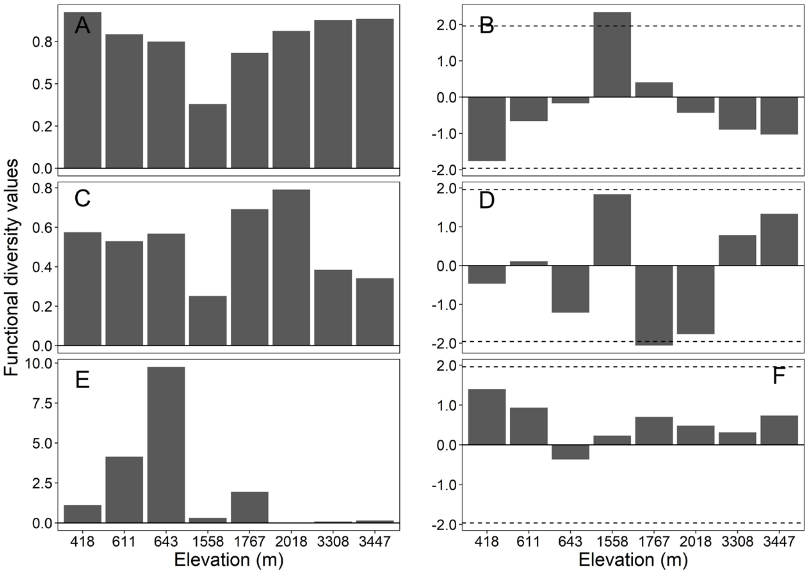

Figure 4. Variation in functional diversity indices along elevation. A – Fdiv = functional divergence; B – SES-Fdiv = standardized effect size of functional divergence; C – FEve = functional evenness; D – SES-FEve = standardized effect size of functional evenness; E – FRic = functional richness; F – SES-FRic = standardized effect size of functional richness. Dashed lines mark the values of SES 1.96 and -1.96, which are the SES limits to indicate whether community assemblage is explained by stochastic processes (whenever values are within the interval); or by deterministic mechanisms (whenever values are outside the interval).

DISCUSSION

In this study we report the community and functional diversity of ferns and lycophytes in 10 plots located at three elevational ranges in the Napo province of Ecuador. Our results of species richness (i.e., the number of species in the dataset) reinforce the high number of species in the area, as across 5000 m^2 we found an equivalent of about 14% of the total number of pteridophyte species registered in Ecuador (Neill 2012). In a previous assessment along an elevational gradient in the Napo province, Salazar *et al.* (2015) reported a similar number of species of ferns and lycophytes, with highest species richness at mid-elevations.

In our study, the highest species richness was found at the low elevation sites, differing from Salazar *et al.* (2015), who reported that species richness peaked at 2000 m.a.s.l. and declined towards higher and lower elevations. We believe that the differences between both studies could be related to: 1) the low number of epiphytes in our inventory, as we only included epiphytes found up to 2 m in height, and did not systematically include canopy epiphytes, and strictly epiphytic species can represent up to half of the total fern species in elevational gradients (Hernández-Rojas *et al.* 2018); 2) a sampling bias towards the ridge versus mountain slopes, as our plots were located only on ridges, which are dryer environments, more exposed to light than mountain slopes (Kessler and Lehnert 2009); and 3) particularly harsh environmental conditions of our study site above 2000 m, where the terrain was much more exposed to the extreme weather of a mountain ridge, than, for instance, the valley terrain at similar elevations sampled by Salazar *et al.*, (2015).

Dryopteridaceae and Polypodiaceae, two of the largest fern families, were the most species-rich families in the area. Previous inventories of ferns and lycophytes in Ecuador reported the same pattern (Krömer *et al.* 2005; Kluge and Kessler 2007; Salazar *et al.* 2015). The high number of species of these families in the tropical eastern Andes might be owed to that several of their species are epiphytes, that directly benefit from the moist conditions and moderate temperatures of mid and low-elevations in the tropical Andean slopes (Krömer *et al.*, 2005). When compared with the relatively dry sites of the Amazon basin, species of Polypodiaceae and the epiphyte species of Dryopteridaceae are less abundant (Tuomisto *et al*. 2014). Under the conditions of seasonal precipitation of lowland Amazonia, composition of fern and lycophyte assemblages are dominated by species with terrestrial habit, as epiphytic plants may be more sensitive to desiccation than their terrestrial counterparts (Zuleta *et al.* 2016), who are able to avoid desiccation by having roots in the soil.

The change in species composition in our data was detected at mid elevations, between 1558 and 2000 m.a.s.l. The complete species turnover occurred within the same vegetation type (evergreen montane forest), as classified in the ecosystem map of Ecuador (Galeas and Guevara 2012). Vegetation classification usually separates floristic units based on species composition and endemism (Borchsenius 1997) and species turnover is more expected between vegetation types (Dambros *et al.* 2020) than within vegetation types (Zuquim *et al.* 2021). Although we did not provide a formal test for a possible mechanistic explanation for the dissimilar fern and lycophyte composition, we cannot discard the hypothesis that specific site conditions were determinant (Kessler and Lehnert 2009), as the 1558-m plot was located in a less exposed area with higher canopy and tree density, while the 2018-m plot was located on a mountain ridge with lower-canopy vegetation, more exposed to weather conditions.

The analysis of species diversity under various Hill numbers showed that at mid and low elevations assemblages were more species-diverse and had few very abundant species. The abundance of few species over rare species in fern and lycophyte assemblages was previously reported in lowland Amazonia (Tuomisto and Poulsen 2000) and could be related to the fact that resources are not limiting in these sites. The diversity of fern and lycophyte assemblages generally increases with resource availability, such as soil nutrients and climate moisture (Tuomisto *et al.* 2014). In fact, previous studies suggest that the combination of high climate moisture with intermediate temperatures is a key factor for the diversity of these groups in mountains (Kessler *et al.* 2011). The study area has moderate climatic conditions (Salazar *et al.* 2015) and nutrient-rich soils at mid and low elevations, where the sediments that erode from ancient terrains of non-volcanic bedrocks tend to be deposited (Unger *et al.* 2010). Therefore, based on previous assessments in the Andes of Ecuador, at mid and low elevations species diversity could be related to resource availability. At high elevations, few highly abundant species were found, a similar pattern to that detected in fern and lycophyte communities in other sites in the tropical Andes (Krömer *et al.* 2005). This pattern is likely due to that few species of these plant groups seem to be able to cope with the harsh environmental conditions such as low temperatures of the high elevations. In this case, despite resource availability, within-site environmental selection might prevail.

Our functional diversity indices suggested similar patterns as those found for floristic diversity. The influence of species richness on the functional indices cannot be disregarded because the standardized effect size (SES) had no relationship with floristics. We only found that, at mid elevations (1558-m and 1776-m plots) the functional diversity indices differed from the null expectation, suggesting that deterministic mechanisms prevail there. Positive SES-FDiv values for the 1558-m plot suggest that the high within-site environmental heterogeneity supports diverse resource-use strategies (i.e., a more complementarity niche), while negative SES-FEve values for the 1767-m plot support the idea of more similar resource-use strategies (i.e., environmental filters promote the functional redundancy). Deterministic processes can be associated with within-site environmental trait selection appropriate to a given site (Zhang *et al.* 2017). In our study area, higher ecosystem productivity at mid-elevation sites (Unger *et al.* 2012) may affect trait selection. Interestingly, the negative values of our functional divergence index at low and high elevations indicate that the functional traits of the most abundant species are probably result from the selection of dissimilar phenotypes (Adler *et al.* 2013; Kergunteuil *et al.* 2018). At low elevations, our results suggests that stochastic processes are modulating the structure of the assemblages, as sites at low elevations are located in forests in advanced ecological successional stage, which could lead to the absence of functional diversity different from null expectations. It is likely that these assemblages are subject to long-term stochastic demographic processes, such as spore dispersion, that could lead to further stabilization (Adler *et al.* 2007), as reported for fern and lycophyte assemblages in other successional sites (Zhang *et al.* 2017).

CONCLUSIONS

The integration of taxonomic and functional information of ferns and lycophytes demonstrated to be a useful tool for the detection of diversity patterns and to infer co-existence mechanisms along a tropical Andean elevational gradient. Overall, species diversity was the highest at low elevations, although mid elevation sites were more species diverse and high elevation sites more even. These patterns could be due to resource-use strategies at low and mid elevations and to within-site selection at high elevations. Our results also suggest that assemblages are likely structured by either deterministic or stochastic mechanisms at different elevation zones. We reinforce the need of further studies for the understanding of the magnitude of co-existence mechanisms in regions of high diversity of fern and lycophyte.

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SUPPLEMENTARY MATERIAL (only available in the electronic version)

Riaño & Moulatlet. Floristic and functional diversity of ferns and lycophytes at three elevational zones in the eastern slopes of the northern Andes, Ecuador

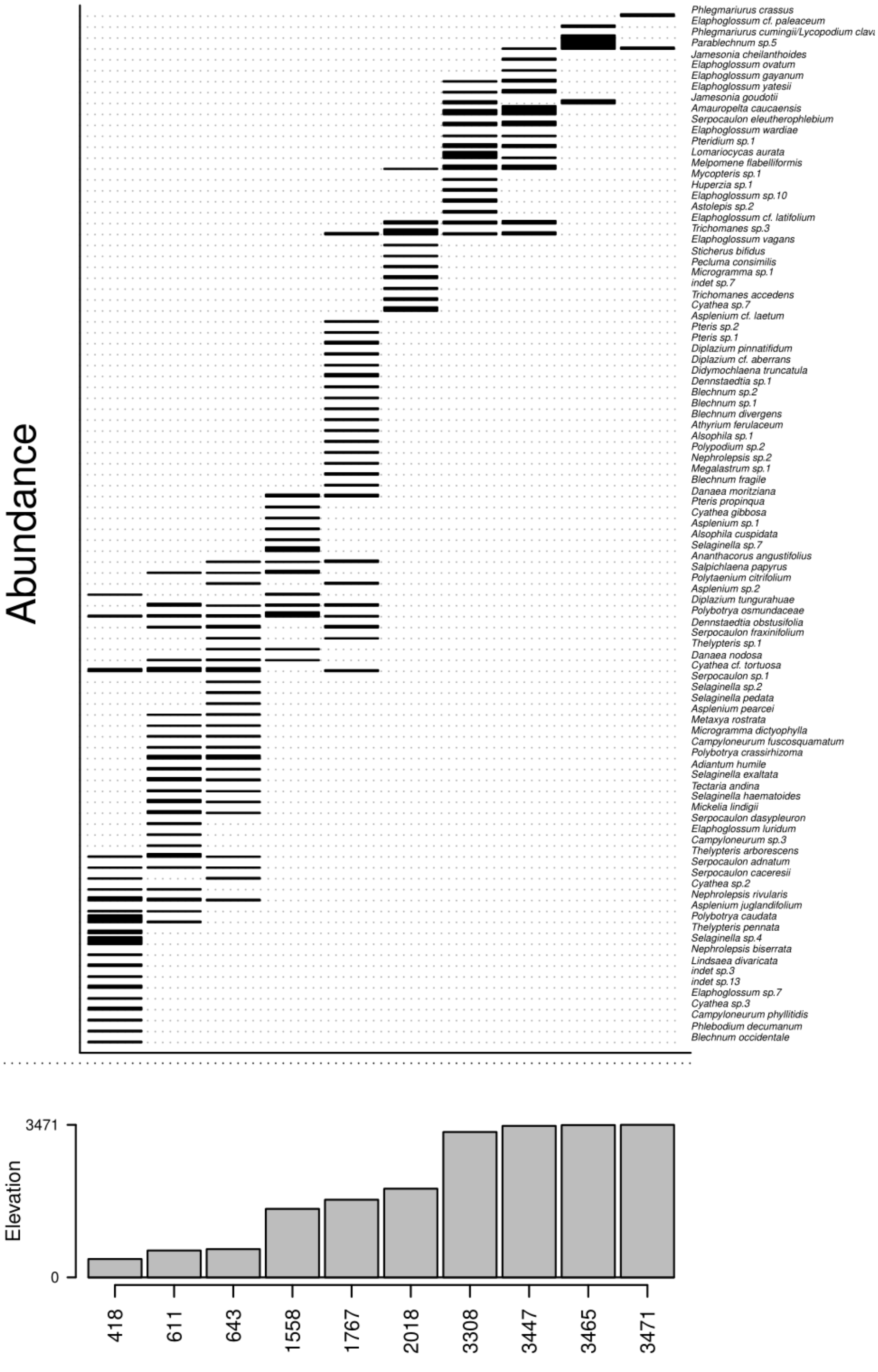

Figure S1. Relative abundance of fern and lycophyte species in ten RAPELD plots ordinated along an elevation gradient in Napo province, Ecuador.

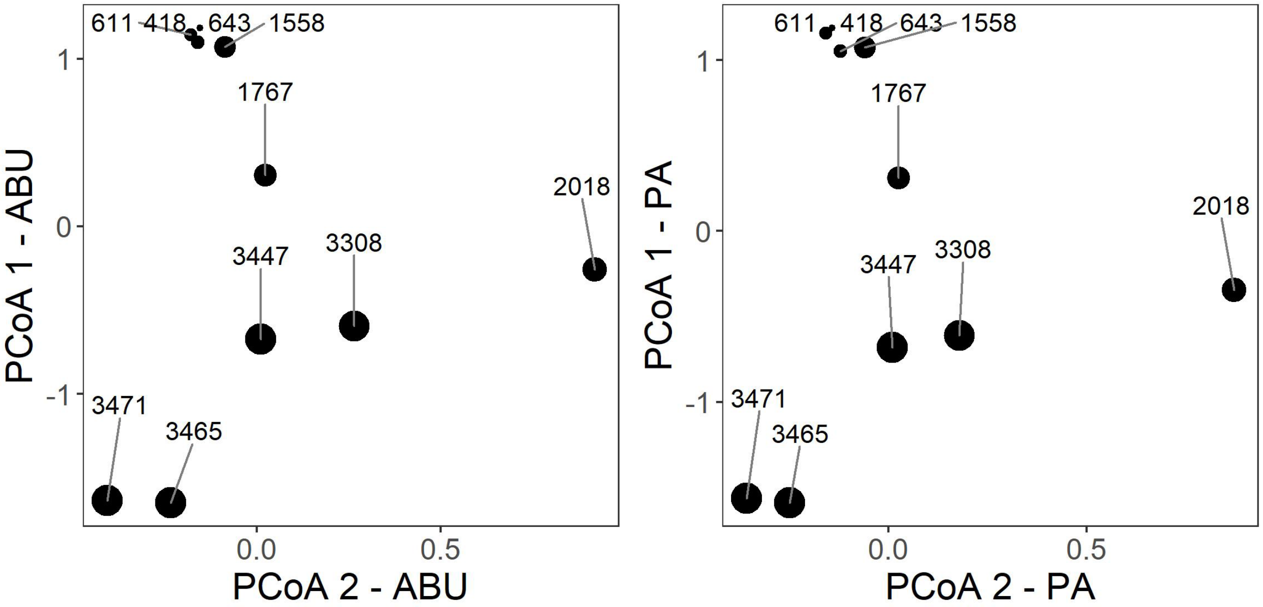

Figure S2. Patterns of floristic dissimilarity among ten RAPELD sampling plots along an elevation gradient in Napo province (Ecuador), as visualized with PCoA ordination optimized for two dimensions. Each symbol represents one plot and numbers indicate the elevation. Symbol size increases with plot altitude. The closer the plots, the larger is the proportion of shared species between two plots, calculated by Bray-Curtis extended distances. Explained variance was 82.1% for abundance (ABU) and 84.1% for occurrence (presence/absence) (PA).

Table S1. Location coordinates and environmental characteristics of ten sampling plots along an altitudinal gradient in Napo province, Ecuador. Annual mean temperature and mean annual precipitation data were obtained from the CHELSA project (Karger *et al*. 2017). Ecuadorian ecosystem classification was obtained from Galeas and Guevara (2012).

Elevation (m)	Temperature (°C)	Precipitation (mm)	Latitude	Longitude	Ecuadorian Ecosystem classification	Elevation zone
418	24.25	4582	1.0586°S	77.6655°W	Evergreen lower montane forest	Low
611	23.95	4965	0.9527°S	77.8659°W	Evergreen lower montane forest	Low
643	23.75	5111	0.9473°S	77.8713°W	Evergreen lower montane forest	Low
1558	18.35	6078	0.9359°S	77.9276°W	Evergreen montane forest	Mid
1767	16.35	6538	0.615°S	77.5906°W	Evergreen montane forest	Mid
2018	16.65	6116	0.9378°S	77.9405°W	Evergreen montane forest	Mid
3308	8.85	3522	0.8421°S	78.2383°W	Evergreen upper montane forest	High
3447	8.35	3437	0.8372°S	78.2424°W	Evergreen upper montane forest	High
3465	8.05	3377	0.831°S	78.2505°W	Páramo	High
3471	8.25	3384	0.8358°S	78.2592°W	Páramo	High