

Ferns and Lycophytes as new challenges Diversity and composition of ferns and lycophytes in a fragmented landscape in Ecuadorian Amazonia

Gabriel Massaine Moulatlet^{1,2,9}, Karolina Riaño^{3,4}, Flávio R. O. Rodrigues^{5,6}, Pablo Meneses^{2,8}
& Gabriela Zuquim⁷

Abstract

Tropical forests have been subjected to increasing deforestation, leading to severe habitat loss and fragmentation of the landscape. Studies of various plant groups indicate alteration in species diversity and assemblage composition in response to these impacts. How these impacts affect ferns and lycophytes, however, is less well known. In this study we evaluate the effects of habitat loss and fragmentation on ferns and lycophytes in lowland non-inundated forests in Ecuadorian Amazonia. We obtained assemblage information from thirteen plots located in gradients of habitat loss and fragmentation (as measured by the landscape fragmentation index: fragindex) and used community and diversity indices to evaluate species responses. We found 3,824 individuals of 55 species. The plot with the highest fragindex value (more than 20% of habitat loss and fragmentation) had the lowest diversity, but the highest diversity was found in plots with fragindex values from 12% to 21% of habitat loss and fragmentation rather than in the landscapes without deforestation. Although community composition varied along the fragindex gradient, species turnover was not significantly related to this index. These results suggest that changes in the landscape caused by deforestation alter the availability of habitats, consequently affecting the distribution patterns of ferns and lycophytes.

Key words: deforestation, fragindex, landscape configuration, RAPELD, western Amazonia.

Resumo

O incremento do desmatamento em florestas tropicais tem causado uma perda severa de habitats e fragmentação da paisagem. As respostas das espécies a esses impactos antrópicos indicam alteração na diversidade e composição das comunidades de espécies e têm sido estudadas para vários grupos de plantas. Como esses impactos afetam a comunidade de samambaias e licófitas, no entanto, é menos conhecido. Neste estudo, avaliamos os efeitos da perda e fragmentação de habitat em samambaias e licófitas em florestas não inundadas de terras baixas na Amazônia equatoriana (bacia amazônica ocidental). Obtivemos informações da comunidade de treze parcelas localizadas em um gradiente de fragmentação (medido por um índice de fragmentação da paisagem: o fragindex) e usamos índices de comunidade e diversidade para avaliar as respostas das espécies. Encontramos 3.824 indivíduos de 55 espécies de samambaias e licófitas. A parcela com o maior valor de fragindex (mais de 20% de perda e fragmentação de habitat) teve a menor diversidade, mas a maior diversidade foi encontrada em parcelas com valores de fragindex entre 12% e 21% e não nas parcelas em paisagens sem desmatamento. Embora

¹ Instituto de Ecología, Red de Biología Evolutiva, Xalapa, Mexico. ORCID: <<https://orcid.org/0000-0003-2571-1207>>.

² Universidad Regional Amazónica Ikiam, Tena, Napo, Ecuador.

³ Cátedra Conacyt, Mexico. ORCID: <<https://orcid.org/0000-0001-8775-542X>>.

⁴ Universidad de Guadalajara, Centro Universitario de la Costa Sur, Departamento de Ecología y Recursos Naturales, Autlán, Jalisco, Mexico.

⁵ Universidade Federal de Goiás, Prog. Pós-graduação em Ecologia e Evolução, Goiânia, GO, Brazil. ORCID: <<https://orcid.org/0000-0001-8538-0089>>.

⁶ Universidade do Estado de Mato Grosso, Prog. Pós-graduação em Ecologia e Conservação, Nova Xavantina, MT, Brazil.

⁷ University of Turku, Department of Biology, Turku, Finland. ORCID: <<https://orcid.org/0000-0003-0932-2308>>.

⁸ ORCID: <<https://orcid.org/0000-0003-3260-2260>>.

⁹ Author for correspondence: mandaprogabriel@gmail.com

a composição da comunidade tenha variado ao longo do gradiente do fragindex, a renovação de espécies não foi significativamente relacionada a esse índice. Esses resultados sugerem que as mudanças na paisagem causadas pelo desmatamento alteram a disponibilidade de habitats, afetando consequentemente os padrões de distribuição de samambaias e licófitas.

Palavras-chave: desmatamento, fragindex, configuração da paisagem, RAPELD, Amazonia ocidental.

Introduction

Habitat loss and fragmentation are among the main threats to biodiversity (Haddad *et al.* 2015). In Amazonia, these two linked processes caused by deforestation have accelerated in recent decades (Lapola *et al.* 2023). Habitat loss and fragmentation lead to increase in forest edge, decrease in forest area, and isolation of fragments (Fischer & Lindenmayer 2007; Fahrig 2019). How plant species respond to habitat loss and fragmentation depends on the ecological characteristics of the species (Pasion *et al.* 2018). In a fragmented landscape, shade-tolerant plants are more restricted to the core habitats of forest patches, where light availability is lower, and the air and soil moistures are higher than at forest edges. Light-tolerant species, however, tend to occupy newly available habitats, such as open areas, the edge of forest remnants, or the understorey of forest patches where the canopy cover is not as dense due to logging of emergent tree species. For instance, lianas tend to benefit from the forest-edge conditions, while epiphytes tend to be more restricted to areas away from the edges (Laurance *et al.* 2001; Magrach *et al.* 2014). When deforested areas support regeneration of secondary forests after abandonment, the forest is mostly composed of light and drought-tolerant species (Jakovac *et al.* 2022).

Habitat loss and fragmentation effects on various plant groups in lowland Amazonian forests have been intensively studied (Bruna & Kress 2002; Benchimol & Peres 2015; Ewers *et al.* 2016; Laurance *et al.* 2017), but the ecological effects on ferns and lycophytes (hereafter referred to as ferns) are less known. Ferns are ubiquitous in tropical forests and species have strong affinities to soil conditions, topography and climate (Tuomisto *et al.* 2003, 2014, 2019; Zuquim *et al.* 2014; Figueiredo *et al.* 2018). In forested areas, abrupt turnover of species occurs among Amazonian biogeographic regions, mostly determined by differences in concentration of soil cations (Tuomisto *et al.* 2003, 2016; Higgins *et al.* 2011; Zuquim *et al.* 2012; Moulatlet *et al.* 2019), by topographic conditions (Tuomisto *et al.* 2002; Moulatlet *et al.* 2022) and

by soil texture (Costa *et al.* 2005). Changes in fern community composition and richness are also expected between open (*e.g.*, white-sand areas) and forested areas (Zuquim *et al.* 2012; Rossetti *et al.* 2019). However, how fern diversity and composition are affected by habitat loss and fragmentation have been little studied.

Previous studies of fern responses to habitat loss and fragmentation in tropical forests have shown that smaller forest remnants host different communities than larger remnants in an insular landscape in Amazonia (Zuquim *et al.* 2022), in central Uganda (Bulafu *et al.* 2022) and in Chinese tropical forests (Cicuzza & Mammides 2022). Moreover, forest-patch configurations, such as patch size, isolation, and the distance to edge, have also been related to changes in fern diversity (Murakami *et al.* 2005; Silva *et al.* 2015). Fern richness tends to be lower near forest edges (Silva *et al.* 2014), with some groups, such as the epiphytes, being more vulnerable to the environmental conditions near edges than terrestrial species (Zuleta *et al.* 2016). Due to ferns' sensibility to modifications in their habitat, it has been claimed that they can be used as an indicator group for environmental degradation caused by increasing edge effects in the landscape (Paciencia & Prado 2005b; Silva *et al.* 2015, 2018). The decreased richness in smaller forest remnants and near forest edges occurs at the local scale. Fragmentation can increase habitat diversity and, consequently, increase fern richness in the landscape (Paciencia & Prado 2005a), but in the long term, the distance among populations may restrict movement and gene flow, potentially leading to local extinctions due to reduced recolonization probability (Fischer & Lindenmayer 2007).

In Ecuadorian Amazonia, ferns have mostly been studied in areas that are less susceptible to landscape fragmentation due to steep topography or protected status, *e.g.*, in conservation units (Tuomisto *et al.* 1998, 2002) and along the eastern Andean slopes (Salazar *et al.* 2015; Riaño & Moulatlet 2022). However, forests outside conservation units are subject to increasing

deforestation rates in Ecuadorian Amazonia (Kleemann *et al.* 2022) and those areas constitute gaps in fern collections (André *et al.* 2023). In this study, we describe the patterns of floristic diversity of ferns in thirteen plots distributed in a fragmented landscape in Amazonian Ecuador, in the municipality of Shushufindi, Sucumbíos Province. This area was chosen due to its high deforestation rates and increasing anthropogenic impacts. Oil extraction is the root cause of deforestation and environmental degradation in the province (Lessmann *et al.* 2016). The direct impact of road opening across continuous primary forest to access oil-rich areas is followed by land division and occupation by settlers. Given its high deforestation rates (Kleemann *et al.* 2022), this area has been indicated as a priority for conservation in Ecuador (Cuesta *et al.* 2017). We applied community and diversity indices to assess species co-occurrence mechanisms in assemblages in this area. We expected changes in species composition and abundance patterns of fern and lycophyte assemblages in plots located in areas with different habitat loss and fragmentation levels, as previously shown for other taxa in the same study area (Moulatlet *et al.* 2021).

Material and Methods

Study area

Our study area is located on the north bank of the Napo River, in the municipality of Shushufindi, Sucumbíos Province, Ecuador (Fig. 1). The area has relatively homogeneous soils and climate conditions. Annual precipitation exceeds 2,400 mm and monthly precipitation exceeds 100 mm (INAMHI 2006). Annual gross deforestation in Sucumbios between 2014 and 2016 exceeded 9,000 hectares (MAE 2017). Deforestation in the area occurs primarily on privately owned lands, but also illegally in protected areas and indigenous territories. Deforested areas are converted to cattle pasture and forestry plantations, or they are abandoned after few years, changing the landscape into a mosaic of forest fragments within a matrix of novel habitat conditions.

Sampling design

Plots were installed following the RAPELD methodology (Magnusson *et al.* 2005). The RAPELD plots are 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 m².

Plots were installed in *terra-firme* forest remnants of minimum 1 ha in area, and secondary and logged forests were avoided during plot installation. Geographic coordinates were taken at the initial point of each plot with a hand-held GPS. One-km² grid cells were superimposed on the study area and the RAPELD plots were installed in representative forest remnants, as close as possible of the centroid of the grid cells but depending on the logistic conditions and the authorization of landowners (Fig. 1). The proportion of forest cover in the 1-km² cells containing the plots varied from 15% to 100%. All plots were installed with previous authorization from landowners. The data gathered during this study is stored in the HERBase repository (André *et al.* 2023).

Species survey

Sampling was conducted 10–17 January 2020. In each plot, all terrestrial fern and lycophyte individuals with leaves larger than 10 cm rooted on one side of plot center line were counted. Epiphytes and climbers were included in the inventory if they had 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 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 voucher were also collected. Species were identified using identification keys (Zuquim *et al.* 2017) and by consulting experts on the different taxonomic groups. Specimens that were not identified to species level were sorted into morphotypes and are referred to as “morphospecies” hereafter. Vouchers were deposited in Ecuadorian public institutions: at the Herbario Nacional de Ecuador (QCNE), at the Herbario de Botánica Aplicada of Universidad Técnica de Cotopaxi, Ecuador (UTCEC) and in a private collection at the Universidad Regional Amazónica Ikiam.

Landscape metric

We calculate a fragmentation index (hereafter fragindex), according to Moulatlet *et al.* (2021). For that, we generated a forest/non-forest raster layer based on the classification of land-use maps and land-cover layers with accumulated information from 2000–2017. Over that raster we calculated the fragindex, which is the average value of three

metrics: percentage of non-forest cover in each cell; percentage of edge, *i.e.*, the relative amount of forest with borders adjacent to anthropogenic matrices; and interspersion, a metric that measures isolation or clumping of forested areas in each cell. This combination of metrics allows the estimation and analysis of fragmentation values at the regional scale (Butler *et al.* 2004). The index ranges from 0 to 100, where 0 corresponds to cells with continuous forest and 100 correspond to cells without forest. It is also highly correlated to other landscape configuration metrics commonly applied in landscape fragmentation studies, such as those calculated by the FRAGSTAT software (McGarigal *et al.* 2012). We applied the fragindex to 1-km² cells, considering each cell a local landscape. The fragindex was associated with each sampling plot through the 1-km² cells in which the plots were

embedded. Landscape patterns can be measured at patch, class, or landscape level. We used the class level, which is a unit between patch and mosaic in landscape ecology (Wang *et al.* 2014). We selected landscape units of 1 km × 1 km as adequate for the interpretation of class-level landscape metrics (Long *et al.* 2010). The fragindex calculation and forest-cover maps were generated using the software Qgis v 2.18.14 (QGIS Development Team 2021). The codes can be found at <<https://github.com/gamamo/FragEcuador>>.

Data analysis

To analyse community diversity, we used Hill numbers as indices of species diversity (Jost 2006), and multiplicative alpha, beta, and gamma diversity (gamma = alpha*beta) (*sensu* Tuomisto 2010). We first calculated total species diversity,

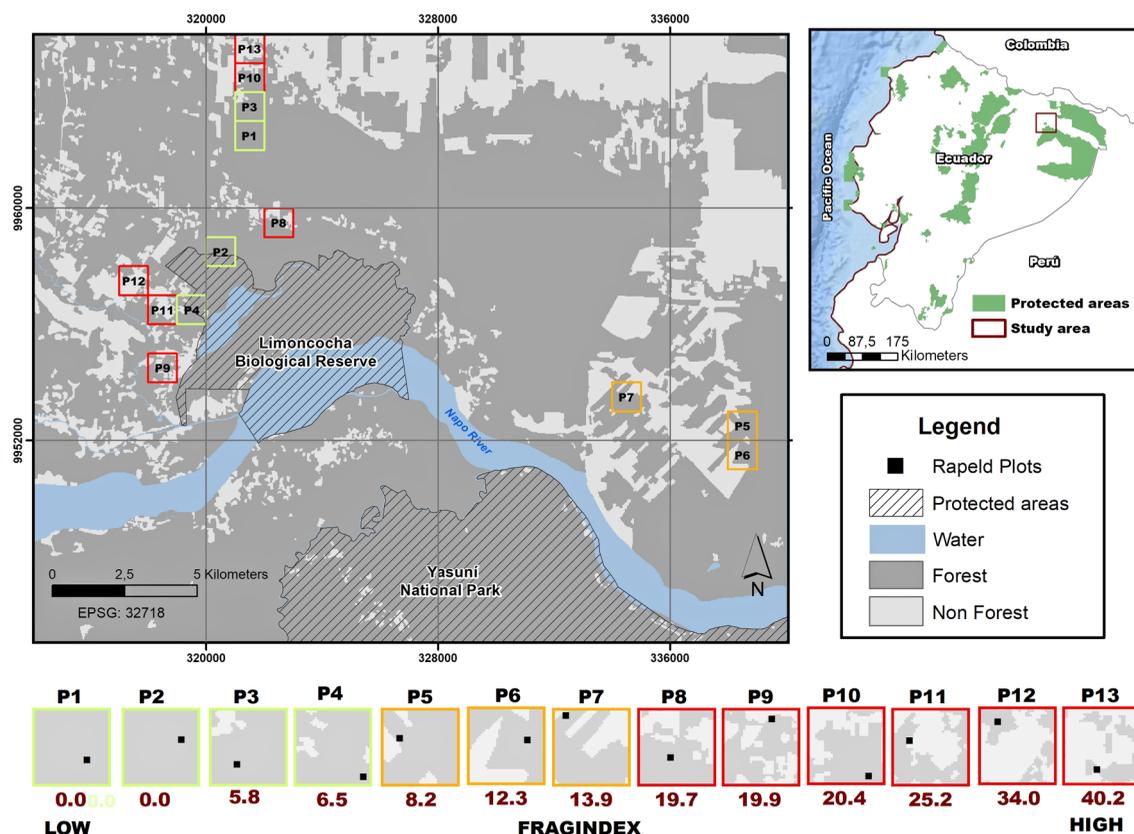


Figure 1 – Location of the study area in the lowland Amazon forests of Ecuador (westerns Amazon basin) – 1 km x 1 km grid were superimposed to the study area, so each plot (P1 to P13) was embedded in on landscape, as indicated by the coloured square cells in the map and in the bottom of the panel. Plots were ordered according to their fragindex values, from low fragindex (no deforestation in the landscape) to high fragindex and classified in three classes, represented by different colours, using geometric intervals. Forest/Non-Forest raster maps classification used to calculate landscape metrics is shown in the background.

which is the effective number of species, *i.e.*, the number of species in a data set if all species were equally abundant, as indicated in equation 3 of Tuomisto (2010). For that, species abundances were first converted to proportions by dividing them by the total abundance of all species in each plot, as 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. The larger the value of q , more weight is given to the abundant species. Based on previous studies on fern diversity (Tuomisto *et al.* 2014; Riaño & Moulatlet 2022), we selected q values ranging from 0 to 5.

The heterogeneity among sampling units (the RAPELD plots) was assessed by partitioning the total species diversity within plots (*i.e.*, gamma diversity) into the components alpha (the mean species density per site) and beta (the effective number of sampling units). 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, so ${}^q\text{gamma} = {}^q\text{alpha} * {}^q\text{beta}$ (Tuomisto 2010, 2013).

To analyse community composition, dissimilarity matrices were calculated on the sites *per* species matrix using the Bray-Curtis index. Both presence-absence data and relative-abundance data (number of individuals of a species divided by the total number of individuals in the plot) were used in parallel. The main floristic patterns were illustrated with ordination diagrams based on non-metric multidimensional scaling (NMDS) in two dimensions. Extended dissimilarities were used to allow recovery of long gradients and avoid an arch effect (De'ath 1999).

We modelled the relationship between the first NMDS axis and species diversity at $q = 0$ and at $q = 1$ and the fragindex using linear regression models. We tested both the simple and the quadratic form of the independent variable.

All data analyses were carried out using the R statistical program (R Core Team 2022). The package *vegan* (Oksanen *et al.* 2018) was used to construct the distance matrices (function *vegdist*) and to run NMDS (function *monoMDS*). The calculation of the Hill numbers was done with a code written by the first author and available at <<https://github.com/gamamo/FernsEasternAndes>>.

Results

We found 3,824 individuals of 55 fern species in thirteen plots (Tab. 1). *Mickelia lindigii* and *Didymochlaena truncatula* were the most common species, with 32% and 10% of the total individuals, respectively. *Tectaria microsora* and *Lomariopsis japurensis* were found in all plots; *Mickelia lindigii* and *Didymochlaena truncatula* were found in 12 plots and *Diplazium tungurahuae* was found in 9 plots. Twenty-three species (41%) were detected in only one plot.

At $q = 0$, the mean diversity was 16.28 species. Site P10 (fragindex = 20.4) had the higher diversity (26), and sites P13 (fragindex = 40.2) and P2 (fragindex = 19.9) had the lowest diversity (9 species each) (Fig. 2a). The sites with fragindex values between 12 and 21, with the exception of site P9 had 31–62% more diversity than the mean diversity. Overall, diversity curves declined with the increment of q , indicating the dominance of few species. This trend was not as strong in sites P9, P12 and P13, those with the lowest diversity at $q = 0$, indicating the presence of few rare species and more species with higher abundances in these assemblages.

The total number of species in the area (gamma diversity) at $q = 0$ was 55. Gamma diversity quickly declined with the increment value of q . Alpha diversity decreased from 16.38 (at $q = 0$) to 4.7 (at $q = 2$) and then stabilized in values below 3. Beta diversity valued ranged from 1.47 to 3.41, suggesting a high turnover between plots in the area (Fig. 2b).

The direct-gradient analysis showed that the community composition was structured along the habitat loss and fragmentation gradient as measured by the fragindex gradient. The composition of species was markedly different between plots in the extremes of the gradient, but plots at the intermediate fragmentation values shared more species (Fig. 3).

The visual inspection of the NMDS ordination revealed a clear floristic separation (*i.e.*, strong floristic dissimilarity) among plots at different fragmentation zones for both abundance (Fig. 4a) and presence-absence data (Fig. 4b).

The linear relationship between the variable fragindex and the first ordination axis of NMDS ordination was not significant for presence-absence and abundance data with linear or polynomial adjustments (linear: PA [$p = 0.42$, Adj. $r^2 < 0.1$], ABU [$p = 0.49$, Adj. $r^2 < 0.1$]; polynomial: PA [$p = 0.72$, Adj. $r^2 < 0.1$], ABU [$p = 0.58$, Adj. $r^2 < 0.1$]) (Fig. 5a,b). The best adjustment between the

Table 1 – Full list of ferns and lycophytes species and their abundances as inventoried in thirteen plots located in the north shore of the Napo River, in the municipality of Shushufindi, Sucumbíos province, Ecuador. Taxonomic classification follows the PPG I proposal (PPG I 2016).

Species	Family	Abundance	Habit
<i>Adiantum humile</i> Kunze	Pteridaceae	41	Terrestrial
<i>Adiantum pulverulentum</i> L.	Pteridaceae	34	Terrestrial
<i>Adiantum tuomistoanum</i> J. Prado	Pteridaceae	4	Terrestrial
<i>Alsophila cuspidate</i> (Kunze) D.S.Conant	Cyatheaceae	20	Terrestrial
<i>Asplenium juglandifolium</i> Lam.	Aspleniaceae	3	Epiphyte
<i>Asplenium pearcei</i> Baker	Aspleniaceae	8	Epiphyte
<i>Asplenium serratum</i> L.	Aspleniaceae	7	Epiphyte
<i>Campyloneurum brevifolium</i> Link	Polypodiaceae	1	Epiphyte
<i>Campyloneurum fuscusquamatum</i> Lellinger	Polypodiaceae	30	Epiphyte
<i>Cyathea</i> sp. 1	Cyatheaceae	13	Terrestrial
<i>Cyclodium guianense</i> (Klotzsch) van der Werff ex L.D.Gómez	Dryopteridaceae	1	Hemiepiphyte
<i>Cyclopeltis semicordata</i> (Sw.) J.Sm.	Lomariopsidaceae	22	Terrestrial
<i>Danaea nodosa</i> (L.) Sm.	Marattiaceae	56	Terrestrial
<i>Didymochlaena truncatula</i> (Sw.) J.Sm.	Didymochlaenaceae	368	Terrestrial
<i>Diplazium cuneifolium</i> Rosenst.	Athyriaceae	10	Terrestrial
<i>Diplazium roemerianum</i> (Kunze) C.Pres	Athyriaceae	1	Terrestrial
<i>Diplazium tungurahuae</i> (Sodiro) C.Chr.	Athyriaceae	179	Terrestrial
<i>Diplazium</i> sp.1	Athyriaceae	7	Terrestrial
<i>Elaphoglossum amygdalifolium</i> (Mett. ex Kuhn) Christ	Dryopteridaceae	1	Epiphyte
<i>Indet</i> sp.1		1	Terrestrial
<i>Indet</i> sp.2		7	Terrestrial
<i>Lastreopsis effusa</i> (Sw.) Tindale	Dryopteridaceae	4	Terrestrial
<i>Lomariopsis fendleri</i> D.C.Eaton	Lomariopsidaceae	17	Epiphyte
<i>Lomariopsis japurensis</i> J.Sm.	Lomariopsidaceae	196	Epiphyte
<i>Mickelia guianensis</i> (Aubl.) R.C.Moran, Labiak & Sundue	Dryopteridaceae	2	Hemiepiphyte
<i>Mickelia lindigii</i> (Mett.) R.C.Moran, Labiak & Sundue	Dryopteridaceae	1248	Hemiepiphyte
<i>Mickelia nicotianifolia</i> (Sw.) R.C.Moran, Labiak & Sundue	Dryopteridaceae	13	Terrestrial
<i>Microgramma dictyophylla</i> (Kunze ex Mett.) de la Sota	Polypodiaceae	22	Epiphyte
<i>Microgramma</i> sp.1	Polypodiaceae	1	Epiphyte
<i>Pechuma hygrometrica</i> (Splitg.) M.G.Price	Polypodiaceae	1	Epiphyte
<i>Pechuma pectinata</i> (L.) M.G.Price	Polypodiaceae	1	Epiphyte
<i>Polybotrya caudata</i> Kunze	Dryopteridaceae	173	Hemiepiphyte
<i>Polybotrya crassirhizoma</i> Lellinger	Dryopteridaceae	177	Hemiepiphyte
<i>Polytaenium citrifolium</i> (L.) Splitg.	Pteridaceae	3	Epiphyte
<i>Polytaenium guayanense</i> (Hieron.) Alston	Pteridaceae	1	Epiphyte
<i>Pteris altissima</i> Poir.	Pteridaceae	14	Terrestrial
<i>Saccoloma inaequale</i> (Kunze) Mett.	Saccolomataceae	2	Terrestrial

Species	Family	Abundance	Habit
<i>Selaginella exaltata</i> (Kunze) Spring	Selaginellaceae	13	Terrestrial
<i>Selaginella haematodes</i> (Kunze) Spring	Selaginellaceae	63	Terrestrial
<i>Selaginella pedata</i> Klotzsch	Selaginellaceae	1	Terrestrial
<i>Selaginella</i> sp.1	Selaginellaceae	16	Terrestrial
<i>Selaginella</i> sp.2	Selaginellaceae	19	Terrestrial
<i>Serpocaulon articulatum</i> (C.Presl) Schwartsb. & A.R.Sm.	Polypodiaceae	1	Hemiepiphyte
<i>Serpocaulon caceresii</i> (Sodi-ro) A.R.Sm.	Polypodiaceae	1	Hemiepiphyte
<i>Stigmatopteris opaca</i> C.Chr.	Dryopteridaceae	2	Terrestrial
<i>Tectaria andina</i> Cav.	Tectariaceae	5	Terrestrial
<i>Tectaria microsora</i> A.R.Sm.	Tectariaceae	339	Terrestrial
<i>Tectaria pilosa</i> (Fée) R.C.Moran	Tectariaceae	15	Terrestrial
<i>Tectaria</i> sp.1	Tectariaceae	218	Terrestrial
<i>Thelypteris abrupta</i> (Desv.) Proctor	Thelypteridaceae	107	Terrestrial
<i>Thelypteris ancyriothrix</i> (Rosenst.) A.R.Sm.	Thelypteridaceae	6	Terrestrial
<i>Thelypteris glandulosa</i> (Desv.) Proctor	Thelypteridaceae	173	Terrestrial
<i>Thelypteris opulenta</i> (Kaulf.) Fosb.in Fosb. & Sachet	Thelypteridaceae	2	Terrestrial
<i>Thelypteris pennata</i> (Poir.) C.V.Morton	Thelypteridaceae	124	Terrestrial
<i>Trichomanes</i> sp.1	Hymenophyllaceae	30	Epiphyte

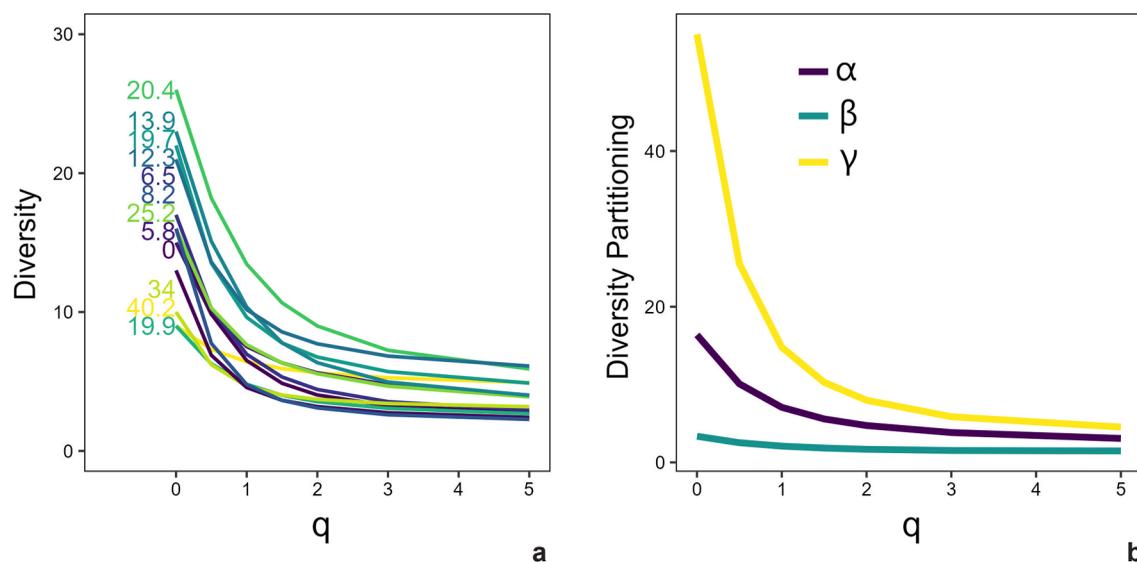


Figure 2 – a-b. Trends in true species diversity (effective number of species) within and across sites as a function of q . Total species diversity depends on the exponent q , which defines the weight that is given to abundant or rare species. When $q = 0$, species diversity equals species richness (*i.e.*, 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 13 sites. The numbers in front of each line refers to the fragindex value; b. 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.

relationship between fern diversity at $q = 0$ (equals species richness) and at $q = 1$ was also polynomial (Fig. 5c-d), being significant only when species diversity $q = 0$ (Adj. $r^2 = 0.31$, $p = 0.036$), and not when $q = 1$ (Adj. $r^2 = 0.14$, $p = 0.19$).

Discussion

Our results revealed that fern communities are influenced by the landscape configuration,

so that habitat loss and fragmentation affect fern community composition and diversity. We expected and abrupt negative effect on species diversity and composition due to the increase of habitat loss and fragmentation, as measured with the fragindex, so that diversity would be the lowest in the areas with high fragindex and composition would abruptly change (turnover) along the fragindex gradient. Although diversity was the lowest in the plot with

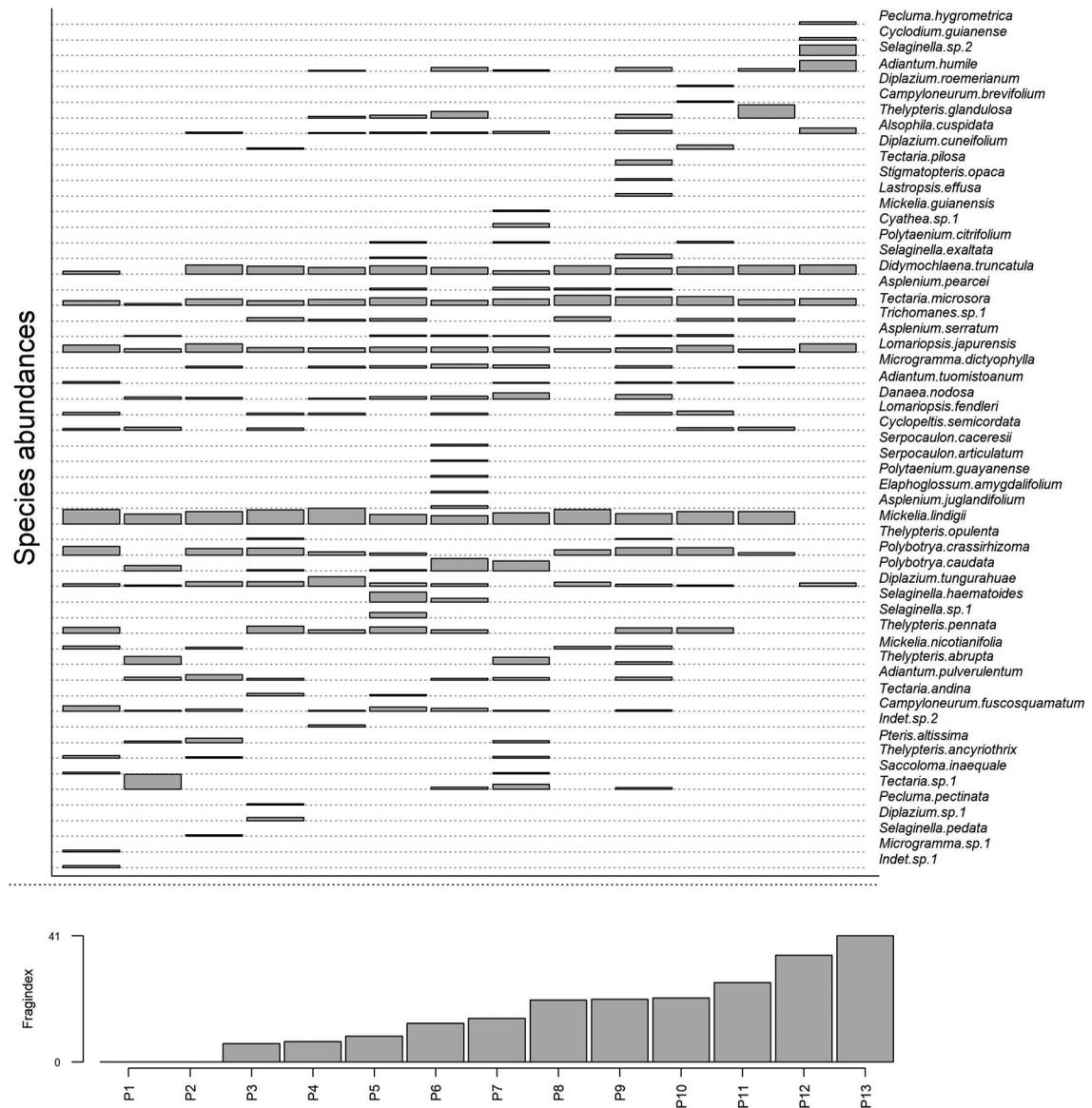


Figure 3 – Relative abundance of fern species along the habitat loss and fragmentation gradient in the Ecuadorian Amazonia. The plots are listed in order of increasing fragindex, and the species in order of mean fragindex in the plots where the species was observed. Relative abundances have been square rooted transformed to improve data visualization.

the highest fragindex, and composition has changed in plots with different fragindex values, our results did not return the expected patterns. Instead, plots with intermediate fragindex values (from 12 to 20) held the highest diversity and species turnover had a hump-shaped pattern for abundance data. This suggests that during the modifications in the landscape produced by deforestation has, so far, led to the creation of new environmental conditions for light and drought-tolerant species (common in early succession environments) and for shade-tolerant species (restricted to more preserved areas).

Diversity, as measured by the Hill numbers (q values) gives more weight to the abundant species when q values increase. In our study, when $q=0$, diversity was the highest for the plots with intermediate fragindex values. When $q = 5$, all plots had similar diversity. Indeed, the species *Tectaria microsora*, *Lomariopsis japurensis*, *Mickelia lindigii*, *Diplazium tungurahuae* and *Didymochlaena truncatula* were present in almost all plots and were dominant (*i.e.*, had higher relative abundance) in the plots they occur. As such, these species largely influence on the diversity patterns found in this study. High diversity in intermediate-fragmentation areas could be due to the capacity of fern species of tolerate environmental conditions of the new habitats or because the degree of degradation has not significantly decreased the microclimatic conditions within the forests in those landscapes. In this case, some species that

are more light-tolerant may occupy recently opened habitats taking advantage of the increasing light availability in the understory. Because ferns have few dispersal limitations, in a new landscape configuration, the diversity of habitats can increase initially (Fahrig 2020), so new species could be able to colonize them, and species diversity increases (Paciencia & Prado 2005a). This would explain why forest remnants in areas of intermediate fragmentation levels in our study area have higher diversity and a different community composition than forest remnants in areas with high or low fragindex values. If deforestation continues, the new habitats can be lost, and forest remnants may become too small to sustain diversity (Fahrig 2019). Fern diversity is often lower in forest remnants of small areas than in those of larger areas (Bulafu *et al.* 2022; Zuquim *et al.* 2022). In our study area, it appears that fragmentation has not reach the levels where forests remnants are no longer able to sustain diversity.

Of the 55 species found in the study area, about 12 species (20%) were rare, being recorded in a single plot (Tab. 1). Of those, seven are epiphytes or hemiepiphytes and occurred in plots with fragindex values below 15. These co-occurrence patterns could suggest that epiphytes with high specificity to tree species that have been removed in the deforestation process may disappear too, but this process need to be tested with appropriate data. Alternatively, terrestrial species are more tolerant to

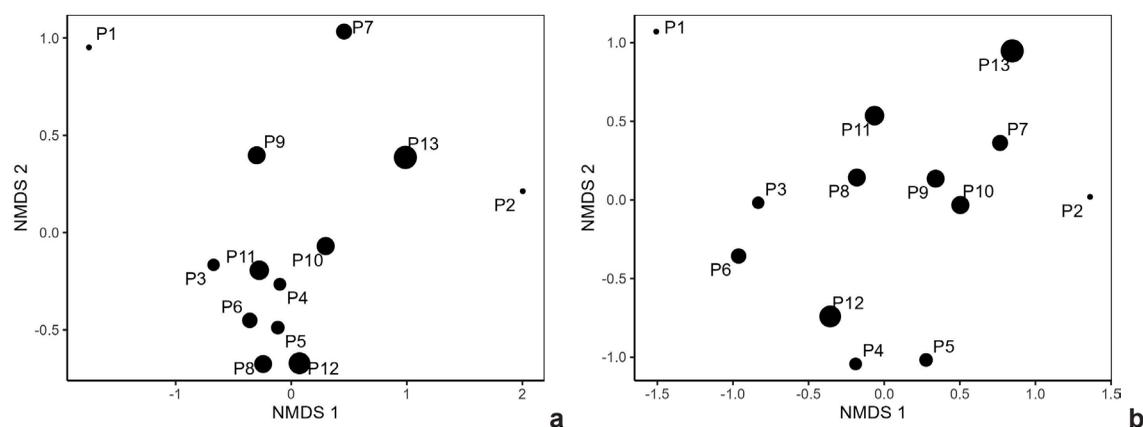


Figure 4 – a-b. Patterns of floristic dissimilarity among thirteen RAPELD sampling plots along a habitat loss and fragmentation gradient in the Sucumbíos province (Ecuador), as visualized with NMDS ordination optimized for two dimensions – a. for abundance; b. for occurrence (presence/absence) data. Each symbol represents one plot and numbers indicate the fragindex. Symbol size increases with the associated fragindex to each plot. The closer the plots, the larger is the proportion of shared species between two plots, calculated by Bray-Curtis extended distances. Explained variance was 71.5% for occurrence (presence/absence) and 42% for abundance.

the environmental conditions in more fragmented landscapes than epiphytes and hemiepiphytes. It has been suggested that the gametophytes of ferns are more drought tolerant than the sporophytes (Watkins *et al.* 2007), so a likely mechanism to explain the absence of epiphytes in areas of high fragindex values is that species are able to disperse through the landscape, but the establishment of sporophytes of epiphytes may not be successful in forest remnants in fragmented landscapes due to the harsher environmental conditions or to the absence of trees that allow the climbing and establishment of epiphytes and hemiepiphytes. Forest remnants in more fragmented landscapes tend to become more susceptible to drought and to light entrance (Laurance *et al.* 2002). Previous studies have

shown that few fern species from a community in central Amazonia were able to tolerate increasing light conditions, and most of them were restricted to low-light plots (Zuquim *et al.* 2009) and to moister plots (Tuomisto *et al.* 2014). Although we did not measure species traits, in our plots, the most common species *Tectaria microsora*, *Lomariopsis japurensis*, *Mickelia lindigii*, *Diplazium tungurahuae* and *Didymochlaena truncatula* were all species that occurred in most plots and are of intermediate height, suggesting that terrestrial and hemiepiphyte species could be more resistant to the environmental conditions of forest remnants in fragmented landscapes. Larger terrestrial species may have more access to water due to their longer root systems than smaller

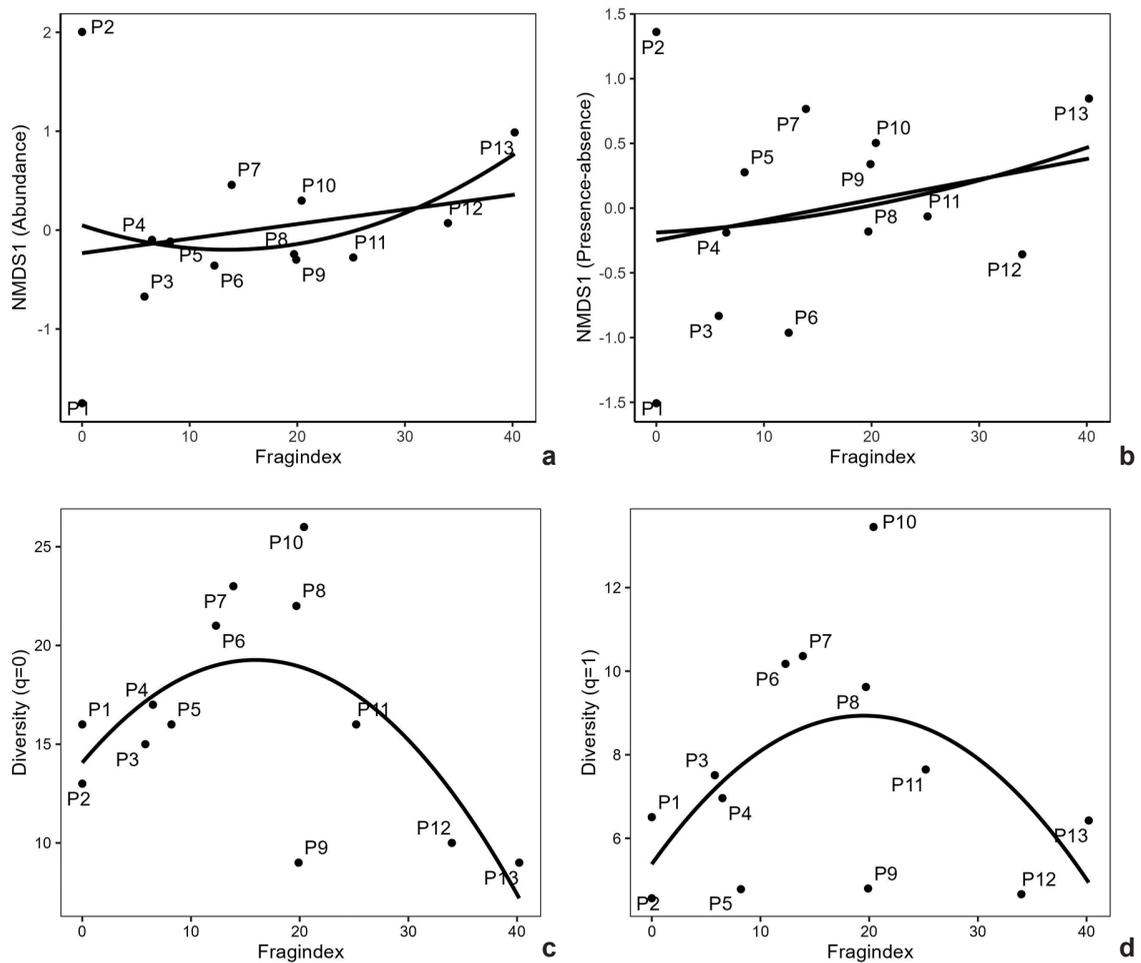


Figure 5 – a-d. Relationship between the first NMDS axis (NMDS1) and the fragindex for both abundance (a) and occurrence data (presence-absence) (b), and between diversity at (c) $q = 0$ (equals richness) and (d) $q = 1$. The best adjustment, either linear or polynomial is shown, while the statistics of the adjustments can be found in the main text.

species, which tend to dry out due to the increase in the air temperature in forest remnants (Arroyo-Rodríguez *et al.* 2017).

We evaluated the effects of habitat loss and fragmentation in one of the areas with largest deforestation pressure in Ecuador. Due to the low topographic variation and low degree of protection in comparison with the nearby area of Yasuní, our study area constitutes an important model to test the effects of deforestation. The study areas have low soil heterogeneity, an environmental condition that could be determinant to explain differences fern species composition in fragmented landscapes (Cicuzza & Mammides 2022). Because ferns are indicators of soil conditions (Tuomisto & Poulsen 1996; Zuquim *et al.* 2014; Tuomisto *et al.* 2016), the presence of species in one or another plot could indicate important edaphic differences between plots. However, our results show that many species were abundant and present in most plots. For instance, *Didymochlaena truncatula* is a species with distribution restricted to soils with high cation concentration and it was only present in 85% of the plots. As such, our results suggest that the landscape configuration rather than another unmeasured environmental condition was the main determinant of fern community composition and diversity.

We showed that species individual responses are affected by habitat loss and fragmentation and how species composition differs along fragmentation gradients. We reinforce the need of further studies for the understanding of the magnitude of co-existence mechanisms in regions of high diversity of ferns and lycophytes and how they are affected by deforestation. It is also important to evaluate of the functional ecology of this community, so the resource-use strategies could be informative of individual species responses to habitat loss and fragmentation. Changes in landscape configuration in Ecuadorian Amazonia should be minimized to diminish the effects of habitat loss and fragmentation on species occurrences and community composition.

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Data availability statement

In accordance with Open Science communication practices, the authors inform that additional data is available in the data repository Github, that provides free access and guaranteed preservation: <<https://github.com/gamamo/FragEcuador>>.

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