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Research article

Speciation, dispersal and the build-up of fern diversity in the American tropics

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Understanding how the remarkable biodiversity of the American tropics developed has been a long-standing question, yet knowledge gaps remain. Previous studies examined the roles of bioregions in shaping diversity patterns but often overlooked speciation, a critical driver of species richness, and insufficiently accounted for temporal changes in speciation and dispersal dynamics. To address this, we investigated the temporal mechanisms of speciation and dispersal that have shaped diversity in the American tropics using ferns (Polypodiopsida) as a model group across nine bioregions. We employed biogeographic stochastic mapping (BSM) and a large-scale phylogenetic tree alongside extensive occurrence records to infer historical patterns of speciation and dispersal. We find that the American tropics function as a biogeographical maze composed of interconnected corridors, characterised by high emigration and immigration rates, rather than isolated regions. The Andes emerged prominently as a biodiversity radiator, playing a dual role by generating substantial species richness through speciation and acting as a primary source of dispersal to neighbouring regions. This unique position underscores the Andes' pivotal role in structuring fern diversity across the American tropics, contrasting with the Amazonian-centred patterns typically observed in angiosperms. Our findings highlight the critical importance of considering speciation and historical contexts in relation to changing environments when interpreting patterns of tropical biodiversity.

Keywords: American tropics, biogeographic stochastic modelling, dispersal, evolution, ferns, regional roles, speciation

Introduction

The American tropics are widely celebrated as the world's most species-rich biogeographic realm. However, how this outstanding biodiversity has evolved remains incompletely known. Different regions within the realm are defined by steep climatic gradients and dynamic geomorphological history and have likely contributed to the

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overall species richness in very different ways, with contributions varying over time. The overall accumulation of species richness is determined by speciation, extinction and dispersal between the regions. Speciation increases the continental species pool and can occur either within a region (when a species diverges and both daughter species remain in the same general area) or between regions (through vicariance and jump dispersal accompanied by speciation). Dispersal, on the other hand, increases species richness within regions without increasing continental species richness. Extinction can happen locally (within individual regions) or globally, reducing species richness in one or more regions. The role of different regions in generating the total biodiversity of the American tropics is debated, with biotic assembly often attributed to dispersal sources and sinks, overlooking regional-scale speciation. While previous studies have focused on well-studied lineages such as angiosperms and tetrapods (Antonelli et al. 2018, Pérez-Escobar et al. 2022), recent global-scale studies on ferns (Suissa et al. 2021, Qian et al. 2023, 2024) highlight the value of examining lineages with divergent biology to better understand how dispersal, environmental filtering and evolutionary history shape biogeographic patterns.

The geological history of the American tropics is complicated and has undoubtedly influenced both speciation processes and the emergence of biogeographic patterns. South America was isolated from other continents for a long time (the ‘splendid isolation’ of Simpson (1980)), before the formation of the Isthmus of Panama gradually connected it with Central and North America between 20 and 3.5 million years ago (Ma) (Bacon et al. 2015). The uplift of the Andes and the establishment and subsequent draining of the Pebas and Acre wetland systems created and erased geographical barriers and edaphic environments within the continent (Burnham and Graham 1999, Hoorn et al. 2010). These geological processes have provided a dynamic landscape for species dispersal and speciation, potentially driving adaptive radiation, vicariance, jump dispersal and within-region speciation at various times (Tuomisto 2006, Yoder et al. 2010, Hoorn et al. 2013, Schenk 2021).

Understanding the composition of regional species pools, their connectivity, and the historical and ecological processes that have shaped their development has become a focal point for biogeographical studies of the American tropics. Notably, Amazonia has been proposed to be the primary source of plant diversity in the American tropics (Antonelli et al. 2018), but when normalising by area, the Atlantic Forest of Brazil and the Andes emerge as the main sources of diversity (Pérez-Escobar et al. 2022). Antonelli et al. (2018) found all regions of the American tropics to be highly interconnected, with each region contributing plant lineages to all the others. They observed the largest number of dispersals between Amazonia and Mesoamerica, with nearly three times as many species dispersing from Amazonia to Mesoamerica than the reverse. Their definition of Amazonia was unusual, however, as it included not only Amazonia proper but also areas from the Pacific side of the Andes in coastal Ecuador, Colombia and Panama. Additionally, they did not account for the size of the regional species pools, so it remains to be tested whether these regions are actually the most connected in terms of per-species probability of dispersal. Pérez-Escobar et al. (2022) further highlighted the Northern Andean mid-elevation cloud forests as the most species-rich ecosystems in the Andes and emphasised the Andes’ dual role as both a source and a sink of plant diversity in the American tropics. They also found significant biogeographical links between the Andes, Amazonia and Central America, proposing that within-region speciation has been the dominant evolutionary process in the Andes.

Earlier plant research has focused on angiosperms, and while work has been conducted on seed plants in general, the main signal comes from angiosperms, which constitute the majority of seed plant diversity. The second largest clade of vascular plants, the ferns, could provide interesting complementary insights into speciation and distribution patterns. Fern fertilisation and dispersal are independent of animal vectors, and fern spores are capable of remarkably long dispersal distances (Muñoz et al. 2004). This makes ferns especially well-suited to reflect environmental factors, such as elevation, climate or substrate (Janzen 1967, Qian 2009, Kreft et al. 2010, Suissa and Sundue 2020). Building on Tryon’s (1972) early proposal of fern diversity hotspots, Suissa and Sundue (2020) analysed an expanded dataset and confirmed the existence of six hotspots of fern richness and endemism that were coupled to montane regions. They suggested within-region species proliferation to be a key driver of fern diversity patterns. Recent global studies (Qian et al. 2024) further highlight the role that climatic extremes and environmental heterogeneity play in shaping fern endemism and phylogenetic structure especially in humid, fragmented cloud forests. While Suissa et al. (2021) found environmental heterogeneity to correlate strongly with species richness, they also noted that high dispersal capacity and edaphic specialisation may limit endemism in montane areas. In contrast, Hernández-Rojas et al. (2021) observed endemism to increase with elevation, suggesting spatial isolation as a key driver. Collectively, these findings underscore the importance of climate, topography and physiology in shaping fern biogeography.

Earlier studies have not addressed the relative importance of speciation at different geographic scales, i.e. within-region speciation versus between-region speciation (vicariance and jump dispersal), implicating different drivers of speciation or changes in species pool size through time. We aim to fill this gap and to provide a more complete picture of regional roles in the evolutionary history of the American tropics by focusing specifically on the speciation and dispersal dynamics of ferns through time using ancestral area estimation and biogeographic stochastic mapping (BSM).

Here we use species occurrence data and the most comprehensive phylogenetic tree of the ferns available to address the following questions:

1. How did different regions contribute to the build-up of fern diversity in the American tropics via speciation and dispersal, and how did those contributions change over time?

2. In what ways do ferns differ from angiosperms in terms of speciation and distribution patterns, and what can these differences reveal about the drivers of biogeographical patterns?

Material and methods

Study area

We focused on the American tropics and subdivided them into nine regions that seemed biologically and biogeographically meaningful: (a) Venezuela, (b) Mesoamerica, (c) Guianas, (d) Amazonia, (e) Antilles, (f) Chaco, (g) Chocó, (h) Paraná and (i) Andes (Fig. 1), with a final category representing (j) the rest of the world. The subdivision was initially inspired by the regions used by Antonelli et al. (2018), but since some of their limits were problematic, we used as a starting point the provinces defined by Morrone et al. (2022). Each of our regions was based on one or more of their provinces (Supporting information); agglomeration was done to increase computational efficiency (Ree and Sanmartín 2009) and to maintain a sufficient number of species in each region. We defined the Andes region to include all the provinces in their 'South American Transition Zone' (Morrone et al. 2022) plus those areas from neighbouring provinces that are above 1000 m a.s.l. to ensure that lowland and montane forests were separated to different regions. Our definition of the Andes is intermediate between definitions used in two previous studies. Antonelli et al. (2018) followed the terrestrial ecoregions proposed by Olson et al. (2001), and their Andes included only areas above the treeline (> 5000 m a.s.l.), with all areas at lower elevations on both sides of the Andes being included in a very broadly defined Amazonia. In contrast, Pérez-Escobar et al. (2022) used a very broad definition of the Andes that included areas down to 100 m a.s.l. Consequently, our analyses classify more lineages as being present in the Andes compared to Antonelli et al. (2018), and fewer compared to Pérez-Escobar et al. (2022).

Data compilation

We downloaded occurrence records, based on preserved specimens and literature from the Global Biodiversity Information Facility (GBIF) using the search word 'Polypodiopsida' (GBIF.org 2024) within the polygon [−125°, −59°; −125°, 35°; −25°, 35°; −25°, −59°], as in Antonelli et al. (2018). These records were cleaned in R ver. 4.4.2 (www.r-project.org) using the 'CoordinateCleaner' package (Zizka et al. 2019), which removed points located in capitals, centroids of countries and biodiversity institutions, as well as records with duplicate, equal or zero coordinates. After cleaning, the coordinates were rounded to two decimals. Species names were standardised using the 'taxastand' package (Nitta 2022, Webb 2022) following the 'pteridocat' reference taxonomy (FTOL Working Group 2022), retaining only records unambiguously matched to an accepted name. Records of hybrids and those not identified to genus level were excluded.

Species were classified as present or absent in each region of the American tropics based on a ≥ 5% occurrence threshold. In other words, a species was considered present in a region if a minimum of 5% of all its occurrences were within that region. This was done to reduce errors from misidentifications, georeferencing inaccuracies and geographic outliers, following Antonelli et al. (2018).

We retrieved the most comprehensive time-calibrated phylogenetic tree of ferns available (Nitta et al. 2022), using the R-package 'ftolr' (FTOL Working Group 2024). The tree includes 5850 species representing ~ 47% of global fern diversity (Hassler 2025). Clades predominantly distributed in the American tropics (≥ 85% of their species occur in the American tropics) and comprising between nine and 100 species extracted using the *CladeByTrait* function in 'SpeciesGeoCoder' (Töpel et al. 2017). Within each clade, we retained only the smallest subclade that included all the species from the American tropics. A summary of the number of species included at different steps is provided in the Supporting information.

After data cleaning and taxonomy resolution, the final dataset consists of 378 115 georeferenced species occurrence records (Supporting information). We identified 56 fern clades largely confined to the American tropics, including 1530 species coded for presence/absence across nine regions of the American tropics and the rest of the world.

Dispersal and speciation through time

We tested several candidate models to estimate ancestral ranges using the R-package 'BioGeoBEARS' ver. 1.1.3 (Matzke 2013). These models included the unconstrained dispersal extinction cladogenesis (DEC) model (Ree and Smith 2008), DIVALIKE (a likelihood version of DIVA; Ronquist 1997) and BAYAREALIKE (a likelihood version of BayArea; Landis et al. 2013), both with and without the J parameter (founder-event speciation through jump dispersal; Matzke 2014). There has been considerable debate about the validity of the J parameter, particularly due to concerns about it artificially inflating the contribution of cladogenetic events to the likelihood (Ree and Sanmartín 2018). However, we chose to test our models also including the J parameter as Matzke (2022) found that +J is statistically valid. Among the models tested, the BAYAREALIKE+J model emerged as the best in most cases based on the AIC criterion (Anderson and Burnham 2004). However, across the 56 clades the BAYAREALIKE+J model was not significantly better than DEC+J, based on Fisher's exact test and a significance level of 0.05. We decided to use the DEC+J model in our main results, as the DEC and DEC+J model was used in previous comparable studies (Antonelli et al. 2018, Pérez-Escobar et al. 2022, Kuhnhäuser et al. 2025), allowing us to compare our results more directly. The maximum number of regions any ancestral species could occupy was set separately for each clade, based on the maximum number of regions occupied by any extant species in the clade.

We estimated the number and type of biogeographical events (Table 1) using BSM in 'BioGeoBEARS' (Matzke

Figure 1. Map of our study area, the American tropics, and focal group, the ferns. (a) Delimitation of biogeographic regions. The map is projected in EPSG:4326. (b–d) Extant fern species native to the American tropics, representing major clades of ferns occurring in the region (photos: Hanna Tuomisto). (b) *Danaea leprieurii*. (c) *Lindsaea tetraptera*. (d) *Pteris pungens*.

2016). Mapping was performed 100 times and event frequencies were estimated by aggregating results from all 56 clades and calculating the average event counts. These results were collected in 1 million year (Myr) time slices to capture the distribution of dispersal events at different points in time.

To reconstruct the historical composition of regional species pools (i.e. the pool of ancestors of the modern species that were present in a region at a given historical time) and assess biogeographic transitions, we applied the approach used by Magalhaes et al. (2021) using the script 'BGB_BSM_multiple_trees' ver. 38. This script uses 'BioGeoBEARS' outputs to infer ancestral ranges and quantify dispersal, extinction and within-region speciation events. It also calculates the number of lineages in each region per time slice and BSM replicate. Following Magalhaes et al. (2021), we generated lineage-through-time (LTT) plots from these lineage counts to visualise temporal patterns of diversification. In addition, we modelled temporal patterns in the numbers of regional endemics, dispersals and dispersals per species.

We calculated the species pool sizes for all regions at four time points (0, 5, 10 and 30 Ma) and quantified the corresponding pairwise similarities between regions using the Jaccard similarity index. To visualise the compositional similarity patterns and their changes through time, we performed principal coordinate analysis (PCoA) for each time slice using the one-complement of the Jaccard similarity as the dissimilarity measure.

Dispersals were quantified both as absolute counts and as dispersal rate (number of dispersals divided by number of species in a given 1-million-year time slice). In the analyses of 'all dispersal' ('BioGeoBEARS' dispersal and jump dispersal; Table 1), we used both dispersal counts and the average dispersal rate through time (0–135 Ma). For specific time slices (0–1, 1–5, 5–15 and 15–30 Ma), we averaged the dispersal rates within each time slice to enable comparison of time slices of different lengths.

We calculated proportions of specific biogeographic speciation events, between-region speciation (dispersal), between-region speciation (vicariance), within-region speciation (single region) and within-region speciation (widespread ancestor), relative to the total number of speciation events to understand the relative importance of different speciation modes over time. This was done separately for each region and for all regions combined.

Regional roles

We were interested in the relative roles of dispersal and speciation, and to visualise these relationships, we applied the framework of Kuhnhäuser et al. (2025). They introduced the concept of regional roles, a more nuanced extension of the traditional source-sink framework in archipelagos. Regional roles were defined based on the values of two variables, S = (extant regional species pool – immigration)/ extant regional species pool) and E = (emigration/ extant regional species pool). *Radiators* ($S \geq 0.5$, $E \geq 0.5$) play a key role in generating new species and distributing species across the archipelago, *incubators* ($S \geq 0.5$, $E < 0.5$) generate high diversity in isolation, *corridors* ($S < 0.5$, $E \geq 0.5$) produce few new species but are important in linking other regions and *accumulators* ($S < 0.5$, $E < 0.5$) are mostly composed of immigrant species.

Our data contained several cases of extirpation. Not taking this into account when estimating the contribution of immigration to the regional species pool would hugely underestimate the importance of speciation. To expand the application of the Kuhnhäuser et al. (2025) framework to continental settings with potentially high extirpation levels, we therefore modified the calculation of S by adding extirpations to the extant regional species pool before subtracting immigrations: S = (extant regional species pool + extirpations – immigration)/ extant regional species pool).

Results

Species richness and endemism

A lineages-through-time plot shows that both extant and historical species pool size has been largest in the Andes. The next largest species pool was in Mesoamerica until about 3 Ma, when it was surpassed by Chocó and Amazonia (Fig. 2a). The regions with clearly smallest species pools 10 Ma were Guianas, Venezuela and Chaco (Supporting information), but since then the net species accumulation rate in Antilles has been so slow that Chaco has reached almost the same current species pool size.

In our data, 39% of fern species in the American tropics are endemic to a single region (Fig. 2a–b). Mesoamerica has the most endemics, followed by the Andes. However, the highest percentage of endemics in relation to species pool

Table 1. Biogeographic event names used in the present paper with explanation and 'BioGeoBEARS' equivalent.

Present paper	Description	BioGeoBEARS
Range expansion	Colonisation of a new region without speciation	Dispersal
Extirpation	Species range loses a previously inhabited region	Extinction
Between-region speciation through dispersal	Colonisation of a new region followed by instantaneous speciation	Jump dispersal
Between-region speciation through vicariance	Speciation via fragmentation of a large geographic range	Vicariance
Within-region speciation of single region ancestor	Speciation in a single-region endemic lineage without range expansion	Sympatry
Within-region speciation of widespread ancestor	Speciation within one region of a species with a range including two or more regions	'Subset sympatry'

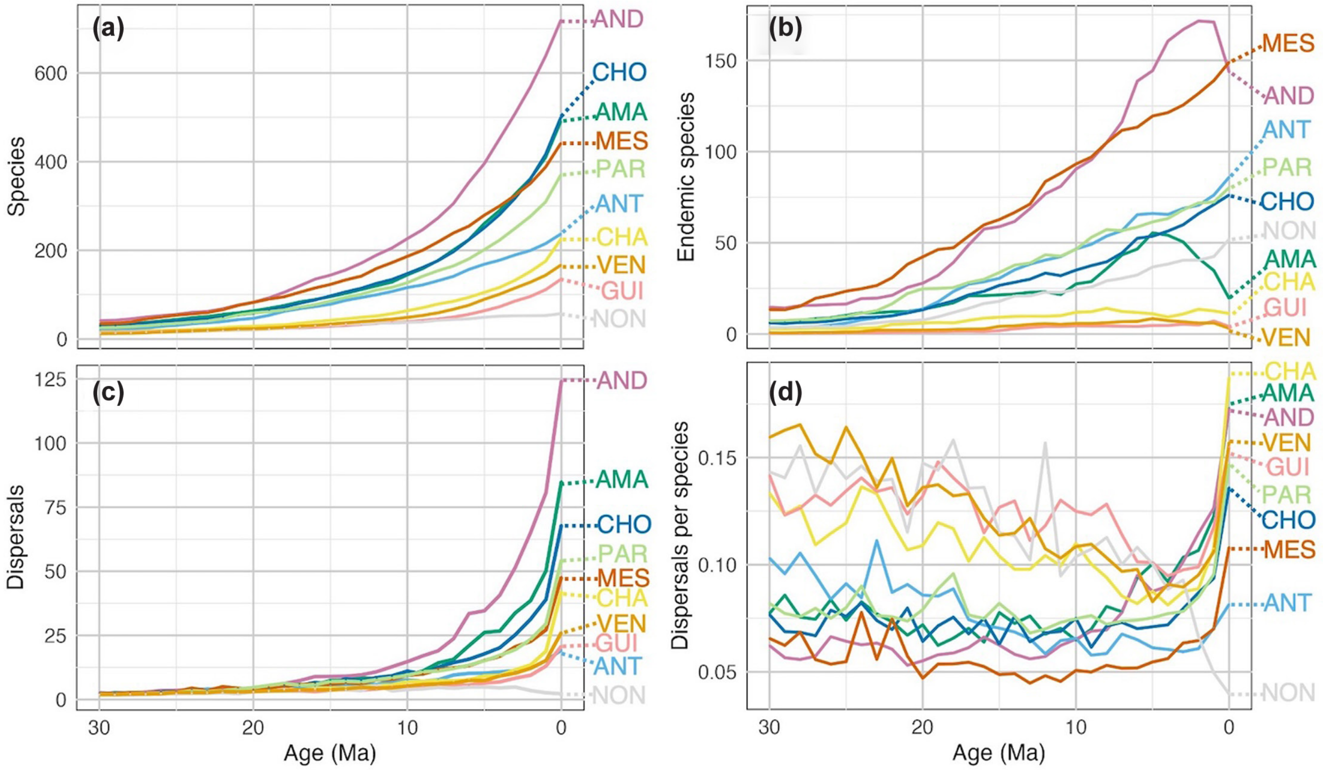

Figure 2. Development of regional fern species richness (disregarding extinct lineages) and dispersal patterns in the American tropics during the last 30 million years as inferred from ancestral range estimates using biogeographic stochastic mapping (BSM) with 100 iterations and the DEC+J model. (a) Lineages-through-time plots. (b) Endemic lineages through time. (c) Dispersal (emigration) events through time. (d) Per-species dispersal (emigration) rates (number of dispersal events in 1 Myr divided by the size of the source species pool as shown in (a). Regions: AMA = Amazonia, AND = Andes, ANT = Antilles, CHA = Chaco, CHO = Chocó, GUI = Guianas, MES = Mesoamerica, PAR = Paraná, VEN = Venezuela and NON = non-American tropics, i.e. outside of the American tropics as defined in Fig. 1(a).

size is in the Antilles (36%) and the lowest in Guianas and Venezuela (less than 3%). Historically, Mesoamerica has had the most endemics in absolute terms, but Mesoamerica and Andes have alternated in having the highest percentage of endemics. The percentages of endemics have mostly been relatively stable or declined through time, except in Guianas and Venezuela where they have increased in the last 5 Myr. Andes and Amazonia have seen a rapid decline in endemics in the last 5 Myr, and Chaco in the last 10 Myr. Despite a general decline from 30 Ma to now, some regions (Venezuela, Mesoamerica, Chocó and Paraná) experienced a burst of endemism between 5 and 10 Ma.

The inferred patterns of species pool similarity have changed during the last 30 Myr (Fig. 3; Supporting information). Chocó and Mesoamerica have grown gradually more similar to each other (Jaccard index increased from 0.26 to 0.34) but more different from Amazonia (Jaccard index with Chocó decreased from 0.3 to 0.21 and with Mesoamerica from 0.22 to 0.1). At the same time, Chaco and Paraná have become floristically closer to each other (Jaccard index increased from 0.21 to 0.4) but more isolated from all the other regions (e.g. Jaccard index between Paraná and Chocó decreased from 0.25 to 0.12).

Connectivity and dispersal

Our analyses indicate that all regions in the American tropics have acted as both sources and sinks of fern diversity, with 3039 dispersal events identified in total across regions (Fig. 2c, 4; Supporting information). Andes has been the most connected region, having received 434 species from the other regions and been the source of 676 emigrant species (Fig. 4a–b; Supporting information). The next most connected regions in absolute terms (number of dispersal events) were Amazonia and Chocó, both of which received from the Andes almost twice as many species as they contributed to the Andes. Other strong connections were Chocó–Mesoamerica (both ways), Paraná to Chaco and Amazonia to Guianas (Supporting information). Per-species dispersal probabilities (which consider source species pool size) varied much less than the absolute numbers did (1.8-fold versus 9-fold, respectively), with the highest average per-species emigration rates seen from Chaco to Paraná and from Guianas to Amazonia (Fig. 4c–d; Supporting information).

The number of dispersal events detected per time slice has increased over time (Supporting information), which is partly because the resolution of ancestral area reconstruction is higher in the more recent times. Nevertheless, there are

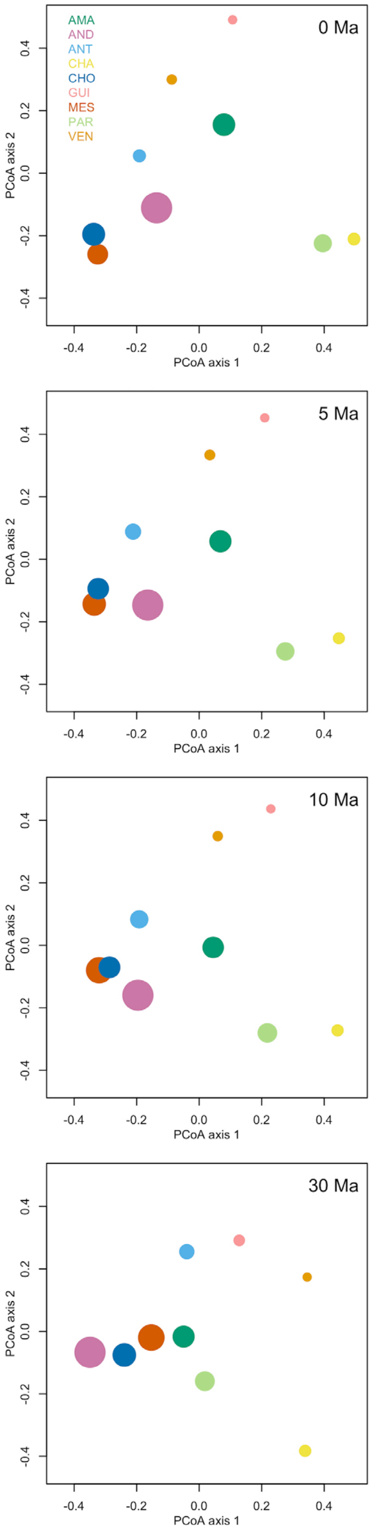

Figure 3. Development of compositional similarity patterns between the regional fern species pools over time (principal coordinates analysis based on the Jaccard index). AMA = Amazonia, AND = Andes, ANT = Antilles, CHA = Chaco, CHO = Chocó, GUI = Guianas, MES = Mesoamerica, PAR = Paraná, VEN = Venezuela and NON = non-American tropics, i.e. outside of the American tropics as defined in Fig. 1(a). Age in millions of years ago (Ma).

some differences among regions. Andes has been the most connected region in terms of absolute number of dispersals for more than 10 Myr, but its per-species dispersal rate was relatively low until it started to increase about 8 Ma. At the same time, the per-species dispersal rate of Amazonia started to increase as well. In contrast, the less species-rich regions Guianas, Venezuela and Chaco experienced decreasing dispersal rates in the interval 8–4 Ma. After that period, the dispersal rate in Chaco in particular has increased considerably, mainly due to increasing migration between Chaco and Paraná. Antilles has had a relatively low dispersal rate throughout both in absolute and relative terms (Fig. 2c; Supporting information).

Biogeographical overview

Within-region speciation was the primary mode of speciation among ferns in the American tropics, accounting for 77% of all speciation events (Fig. 5a). The regions were quite different in this respect, with the values ranging from 49% in Venezuela to 85% in Andes. Speciation that took place within a single region was most common in the Andes, Mesoamerica, Paraná and Amazonia, and least common in Venezuela and Guianas (Fig. 5a). The latter two had instead high percentages of speciation that involved widespread ancestor species within larger regions. The most common region combinations in this kind of speciation were Andes+Chocó and Andes+Amazonia, followed by Mesoamerica+Andes and Mesoamerica+Chocó (Fig. 5b). This was a result of Andes and Mesoamerica having given rise to large numbers of species (437 and 235 species, respectively), much larger than Venezuela and Guianas (27 and 25 species, respectively).

Venezuela and Guianas also differed from the other regions in having very high percentages of between-region vicariance (38–39%), which in most other regions was in the range 10–20% and in Andes as little as 5%. Nevertheless, due to the large species pool of Andes, the region combination involved in the largest number of vicariance events was Andes+Chocó, followed by Andes+Mesoamerica, Andes+Antilles and Andes+Paraná (Fig. 5c).

The framework of Kuhnhäuser et al. (2025) classified regions by the relative importance of emigration and speciation, which in our data produced negative estimates of speciation (S) in several cases (Fig. 6a). These calculations did not consider regional extirpations, which were common in our continental system. After modifying the framework to include extirpations (Fig. 6b), the Andes fell in the category of *radiators* (high speciation and high emigration) and the other regions in the category *corridors*, with Venezuela and Guianas having especially high emigration but low speciation (the latter implying high immigration).

Discussion

Biogeography

Our results suggest that the American tropics differ clearly from the Asian tropics (Kuhnhäuser et al. 2025) in terms of

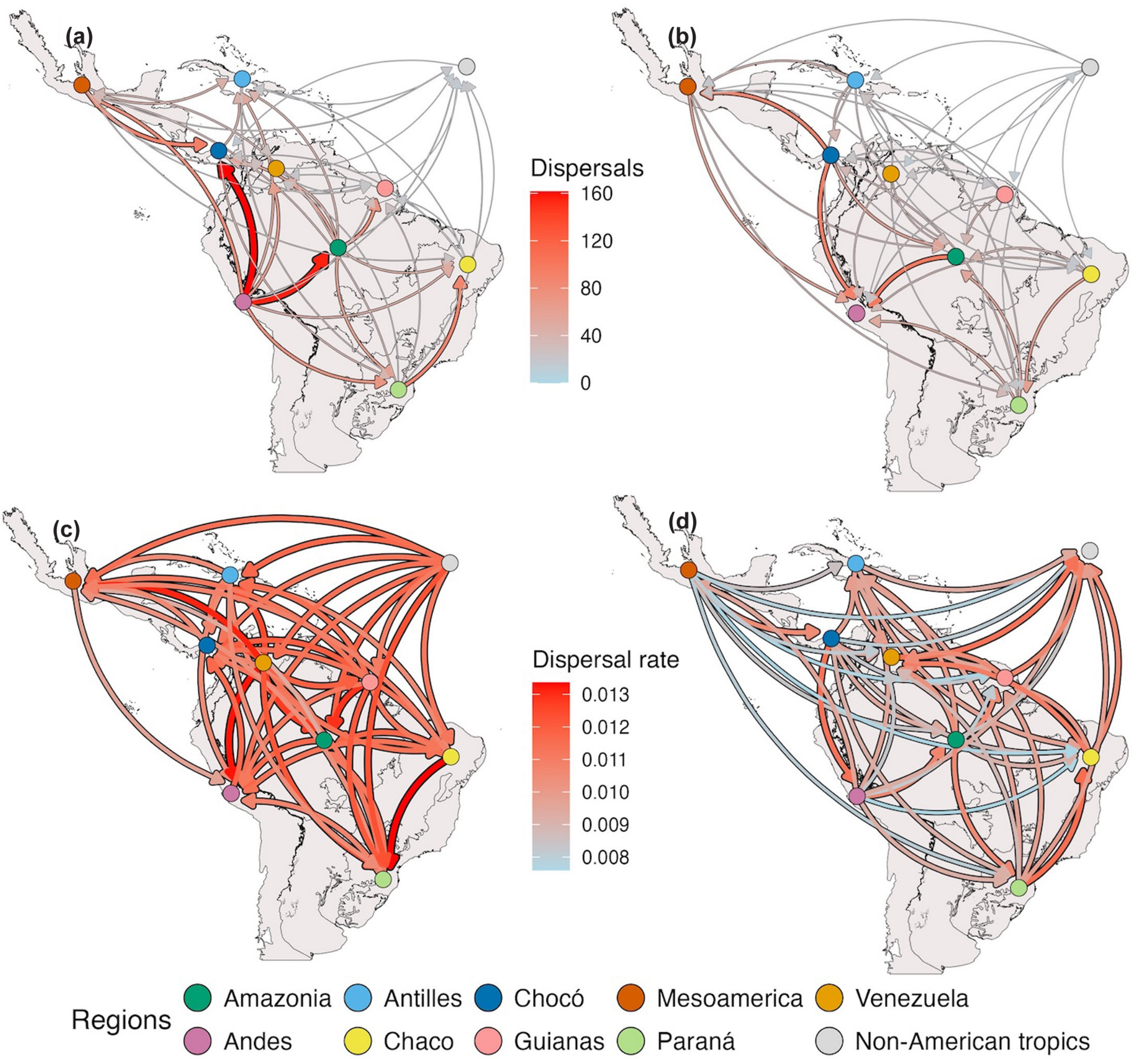

Figure 4. All dispersals (range expansions and dispersal-driven between-region speciation events) in ferns of the American tropics throughout the entire time span (0–135 Ma). Average dispersal was inferred from ancestral range estimates using biogeographic stochastic mapping (BSM) with 100 iterations and the DEC+J model. Line thickness and colour indicate counts of dispersal events in (a) and (b), and dispersal rates in (c) and (d). These rates are expressed in dispersal events per average rate of per species dispersal over time (all years averaged), based on the source region for a dispersal connection. For each pair of regions, (a) and (c) show the dispersals from the overall source region to the overall sink region (predominant direction of dispersal), while (b) and (d) show dispersals in the reverse direction. Age in millions of years ago (Ma).

the role of regions in the build-up of species richness over time. In our continental setting, most regions emerged as interwoven *corridors*, with the Andes being the only region classified as a *radiator*. All regions of the American tropics exhibited relatively high emigration rates, so their classification was mostly based on the amount of speciation, which can be considered the inverse of immigration. In other words, regions with smaller proportions of speciation are predominantly characterised by immigration and emigration, thereby functioning as *corridors* for species movement at the continental extent. The *radiator* role implies both high speciation and high emigration, and positions the Andes as the most influential region shaping fern diversity in the American tropics.

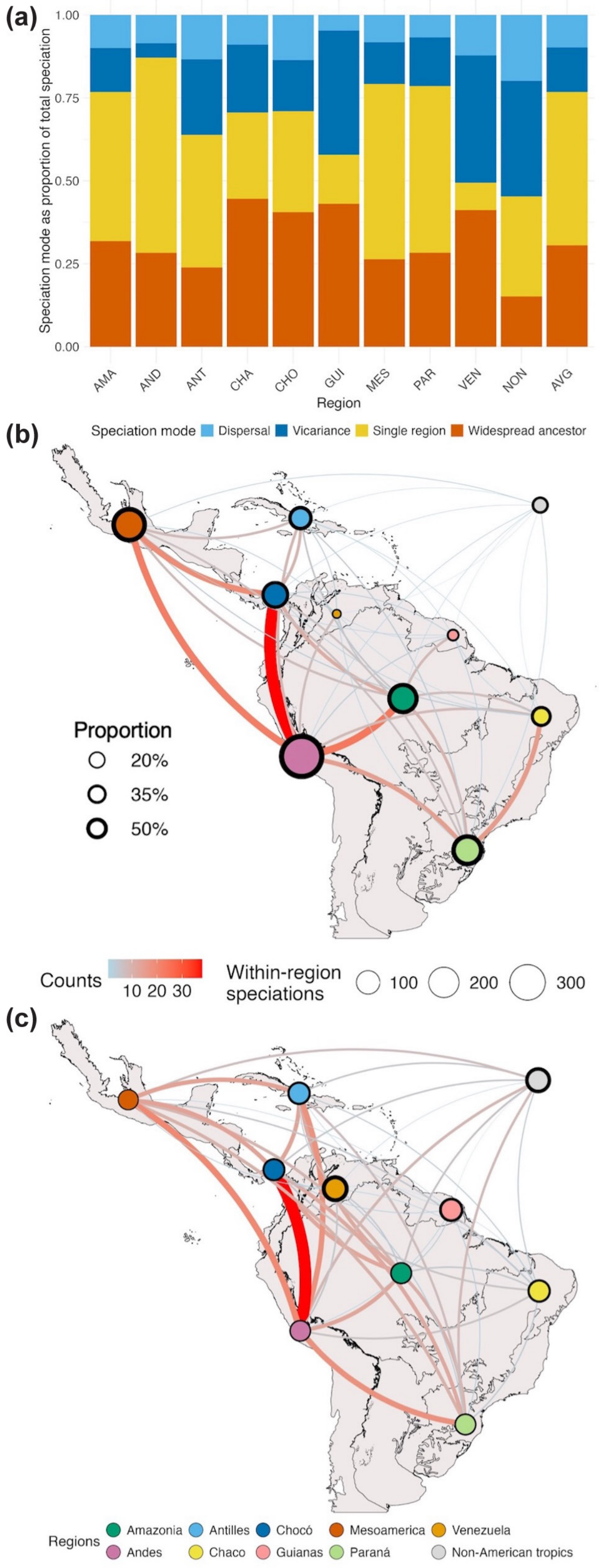

Figure 5. Speciation modes in ferns of the American tropics as inferred from ancestral range estimates using biogeographic stochastic mapping (BSM) with 100 iterations and the DEC+J model. (a) Proportions of fern species that originated by different speciation modes out of all speciation events for each region. Warm colours indicate within-region speciation, cold colours between-region speciation. (b) Number of within-region speciation events (either within a single named region or within a group of regions occupied by the ancestor species) is indicated by size of the coloured circle. The percentage of within-region speciation out of all speciation events in the region is shown by thickness of the black ring. Regions involved in the same within-region speciation event are connected by lines, with line thickness and colour indicating number of events. (c) Between-region speciation (vicariance and dispersal). Regions involved in the same between-region speciation event are connected by lines, with line thickness and colour indicating number of events. The percentage of between-region speciation out of all speciation events in the region is shown by thickness of the black ring. Region names are written in full in (c) and abbreviated to the first three letters in (a). mean = mean for all regions within the American tropics.

In the island-rich Asian tropics, regional isolation is much more restrictive of emigration and promotes speciation (MacArthur and Wilson 1967, Whittaker et al. 2017). Consequently, most regions qualified as *accumulators* or *incubators* in the study of Kuhnhäuser et al. (2025). In our data the per species dispersal rate of extant American tropics ferns is 0.1464 compared to ∼ 0.0658 in angiosperms (Antonelli et al. 2018). Thus, the observed difference between the studies may be accentuated because ferns (our focal group) likely have higher dispersal capacity (Muñoz et al. 2004, Ranker and Haufler 2008, Lagomarsino 2019, Suissa and Sundue 2020) than rattan palms (the focal group of Kuhnhäuser et al. (2025)).

When we applied the framework of Kuhnhäuser et al. (2025) to our system, we initially followed their method of estimating speciation (extant species pool minus immigrations). This led to negative speciation values for several regions, because in well-connected continental systems such as ours, the total historical species pool may be considerably larger than the extant one due to extirpations (species disappearing from a region where they occurred in the past but continuing to exist in other regions). In isolated island systems, the number of extirpations may be negligible (as in the case of Kuhnhäuser et al. (2025)), but the more extirpations there are, the more the calculation tends to underestimate the role of speciation and overestimate the role of immigration. Therefore, we modified the estimation of speciation such that it takes into account all species inferred to have occurred in a region, even if they are no longer present. This generalisation allows quantifying regional contributions to overall diversity in systems with any level of connectivity.

By integrating speciation, immigration and emigration relative to species pool sizes and temporal shifts, our study provides a more nuanced understanding of regional contributions to fern diversity in the American tropics than prior studies (Antonelli et al. 2018, Pérez-Escobar et al. 2022), which have largely categorised biogeographical regions as either dispersal sources or sinks. These studies, in contrast to our findings, ranked Amazonia as the primary source of diversity for angiosperms. Differences in regional delineation

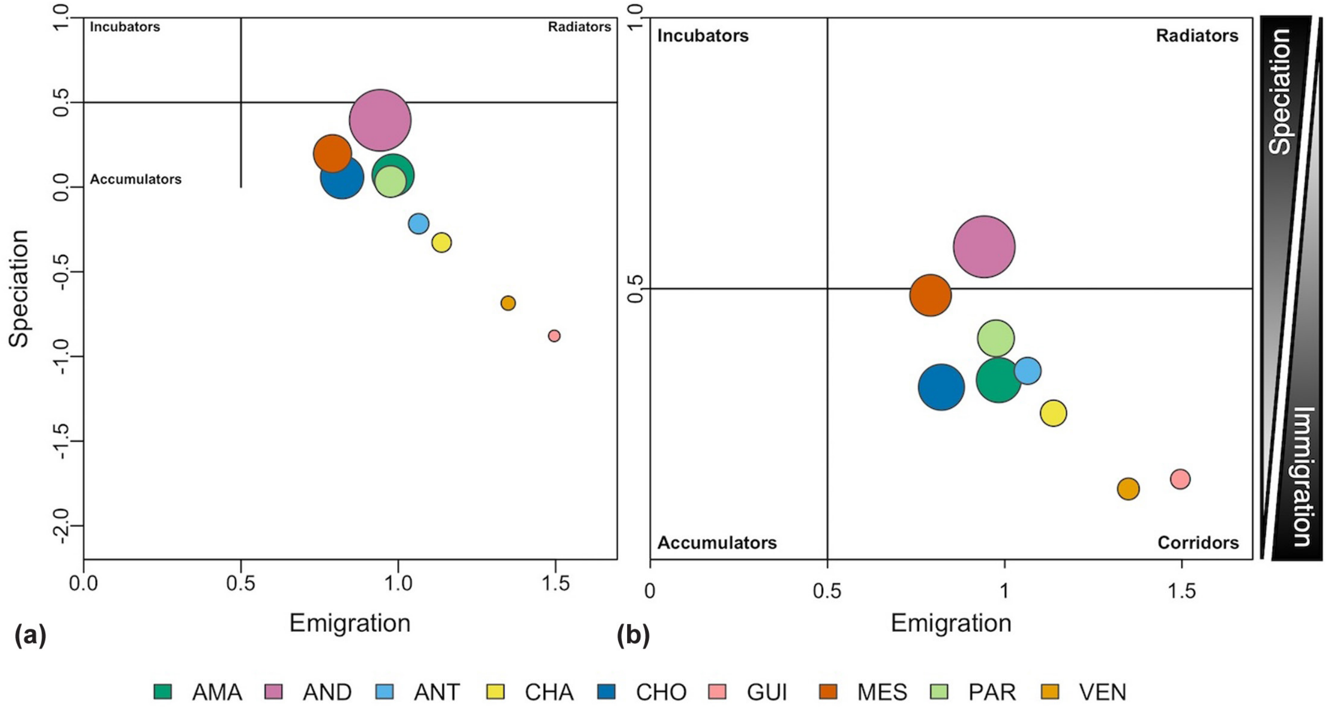

Figure 6. Roles of the regions in shaping the overall diversity of ferns in the American tropics. Results are inferred from ancestral range estimates using biogeographic stochastic mapping (BSM) with 100 iterations and the DEC+J model. Roles were defined based on the proportions of speciation and emigration relative to the extant regional species pool (a) speciation not including extirpated number of species (calculated according to Kuhnhäuser et al. (2025)). (b) Speciation calculated relative to the regional extant and extirpated number of species (see Methods section). Note that the total number of species to the proportion of immigration and speciation sum to 1 (the total species present). Circle area is proportional to regional species pool size.

no doubt contribute to these contrasting conclusions, especially in relation to Amazonia, which Antonelli et al. (2018) defined so broadly that it contained not only our Amazonia but also our Chocó and most of our Andes. Partly the differences may reflect differences in life forms, dispersal mechanisms and environmental preferences. Gentry (1982) proposed that Amazonian-centred taxa are predominantly trees and lianas, whereas Andean-centred taxa are primarily shrubs and epiphytes. Our results agree with this notion, as ferns are relatively small plants, and their diversity was clearly Andean-centred.

Like any biogeographical study, ours has limitations related to biases and shortfalls in the data. Our analyses are based on a phylogenetic tree that, although well-sampled, is still far from complete (Nitta et al. 2022). Many species, especially from the poorly explored regions, were not represented in the tree, and systematic revisions continue to describe new species. This often reduces the distribution areas of known species, as species complexes with broad distribution get split into new species with narrower distributions (Keskiniva and Tuomisto 2024).

Speciation

Speciation plays a fundamental role in shaping both historical and present-day species pools. Our analyses indicated that most speciation in the American tropics happened within regions. This was especially the case in the Andes, which had both the highest number of within-region speciation events and the highest proportion of speciation events where the ancestor species was a single-region endemic. Similar patterns are observed in other montane regions, including Mesoamerica and Paraná, but also Amazonia, where the proportion of speciation events with single-region ancestors was slightly lower, and the proportion of between-region speciation events (vicariance and dispersal-related speciation) correspondingly higher. These results are consistent with the idea that local speciation is promoted in montane ecosystems (Tryon 1986, Rahbek et al. 2019, Suissa and Sundue 2020, Pérez-Escobar et al. 2022).

In the northern Andes, local climates have gradually changed as the mountain chain has uplifted in the past ~ 80 Myr (Horton 2018), driving gradual adaptation in the local species. At the same time, the within-region differences in local climates have increased, as higher elevations both make cooler habitats available and increase the contrast in the amount of precipitation between windward and leeward slopes (Hoorn et al. 1995, Armijo et al. 2015).

In Amazonia, within-region speciation has emerged from widespread rather than endemic ancestor species slightly more commonly than in Mesoamerica and Paraná. This is consistent with the fact that Amazonia shares long borders with other moist forest areas, whereas Mesoamerica is geographically relatively isolated and has been so even more in the past, and Paraná shares a border with a clearly drier region. Although within-region speciation is less prevalent in Amazonia than in Andes, it is still common and potentially driven by edaphic heterogeneity associated with geological history, such as the Pebas drainage system and fluvial sediment input from the Andes (Brumfield and Edwards 2007, Tuomisto 2007, Antonelli et al. 2009, Hoorn et al. 2010).

Dispersal

The analysis of per-species dispersal rates between region pairs revealed patterns of historical connectivity that are related to altitude and climate variations over time (Supporting information). Dispersal rates after the Andean orogeny (5–0 Ma) have been clearly higher from Andes to Chocó and Amazonia than in the reverse direction, i.e. species have been more likely to migrate from high elevations with cool climates to low elevations with warmer climates. Prior to the Andean orogeny (30–5 Ma), dispersal rates were more balanced in both directions. This is consistent with the idea that speciation triggered by the uplift of the Andes has also triggered emigration from the Andes to the neighbouring areas and may also be related to regional cooling (Testo et al. 2018). For seed plants, Pérez-Escobar et al. (2022) reported high dispersal between the Andes and Amazonia both ways, but they focused on absolute dispersal counts, so the results cannot be interpreted in terms of dispersal probability from the individual species' point of view.

Another notable trend is that, in the last 5 Myr, the species-wise probability of dispersal has been higher in the direction of drier to wetter regions than in reverse. For example, the probability that a species disperses from Chaco to Paraná has been larger than the probability of dispersal in the reverse direction, especially in the last 1 Myr. These patterns are not evident when considering counts alone, because the species pools in the wetter areas are so much larger that the wet-to-dry direction dominates (Supporting information). This directional asymmetry is consistent with the findings of Della et al. (2025) whose biogeographical reconstructions suggest that dispersal events, particularly in the last 2 Myr, have played a key role in shaping the distribution of taxa across the Brazilian Atlantic Forest (our Paraná), the Amazon Forest and the dry diagonal (our Chaco). Many of these species are relatively young and occur in moist microhabitats such as riparian forests within otherwise dry regions. This supports our conclusion that recent dispersal from drier to wetter regions has been both feasible and frequent.

The Andes emerge as the principal source of dispersal, connecting all other regions and acting as a highway for range expansion, particularly toward Amazonia and Chocó (Fig. 4; Supporting information; Luebert and Weigend 2014). This connectivity is consistent with Gentry's (1982) concept of Andean-centred distributions extending into adjacent lowlands. However, our results indicate a stronger dispersal bias towards the Pacific (Chocó) side compared to Amazonia, except during the 0–1 Ma interval. The delayed colonisation of Amazonia may reflect the extensive marine-influenced Pebas mega-wetland, which persisted into the Late Miocene, hindering terrestrial dispersal from the Andes. Although geological evidence points to an initial drainage during the late Miocene (~ 10–7 Ma, Figueiredo et al. 2009, Hoorn et al. 2010, 2017), the exact timing of the establishment of today's Amazon River system is still debated. Recent geological and biogeographical studies increasingly support a younger formation of the modern Amazon basin (~ 2.5 Ma; Campbell et al. 2006, Latrubesse et al. 2010, Ribas et al. 2012, Rossetti et al. 2015), potentially explaining why Andean dispersal into Amazonia significantly increased only within the last million years.

Venezuela emerged as a key dispersal *corridor*, linking the Andes, Mesoamerica and the Antilles, a pattern especially apparent when analysed on a per-species dispersal rate basis. Similarly, the Guianas facilitated dispersal toward Paraná. The Chaco-Paraná dispersal corridor appears to have intensified over the last 15 Myr, potentially in response to increasing aridity along the South American dry diagonal (Masa-Iranzo et al. 2021).

The aridification of Mesoamerica (Graham 2010, De-Nova et al. 2012) was also related to shift in dispersal rates in our data. Our results suggest that moisture-dependent ferns show a tendency of migrating to suitable wet conditions rather than adapting to drier environments and thus may be constrained by ancestral climatic tolerances (Hernandez-Rojas et al. 2021). This contrasts with the results of Antonelli et al. (2018), who found that angiosperms were more likely to transition from wet to dry habitats rather than vice versa. However, their results were based on absolute dispersal counts, so they also reflected the larger species pools of the wet regions when compared to the dry ones.

Despite similar climatic conditions, species exchange between Chocó and Amazonia remains limited, supporting the hypothesis that the Andes act as a dispersal barrier even for the relatively well-dispersed ferns (Janzen 1967). Our analyses suggest that Chocó-Andes connectivity declined with time (~ 10–30 Ma) and increasing elevation, whereas Andes-Amazonia connectivity remained strong despite the elevational gradient.

Species distributions and similarity

Fern diversity peaks in the Andes, aligning with observed speciation and dispersal patterns, and supporting the findings of Suissa and Sundue (2020). This contrasts with the general pattern observed in angiosperms, where diversity is highest in Amazonia (Antonelli et al. 2018, Pérez-Escobar et al. 2022). This likely reflects ferns' reproductive constraints, which favour humid montane forests and wet lowlands (Barrington 1993, Page 2002). Additionally, the greater prevalence of epiphytism in ferns compared to angiosperms (Dubuisson et al. 2008, Taylor et al. 2022) further supports their more Andean-centred distribution, as epiphytes, especially, are prevalent in cloud forests (Suissa et al. 2021). Although fewer angiosperms are epiphytic overall, predominantly epiphytic lineages like orchids (Pérez-Escobar et al. 2017) and bromeliads (Givnish et al. 2011) similarly exhibit Andean diversity peaks.

The Andes showed high species richness and endemism following the Andean orogeny (Fig. 2a–b; Supporting information). The uplift of the Andes likely provided a mosaic of ecological niches across spatial and temporal scales, facilitating adaptive radiations (Hughes and Eastwood 2006, Pérez-Escobar et al. 2017, Testo et al. 2019, Dellinger et al. 2024). Another pattern consistent with the Andean orogeny is the increasing dissimilarity between Amazonia and Chocó and Mesoamerica over the past 30 Myr (Fig. 3). Here, the Andes 'wedge' themselves between Amazonia and Chocó + Mesoamerica, both geographically, as a minimum acting as a semi-permeable physical and ecological barrier to gene flow and dispersals (Ranker and Haufler 2008, Hoorn et al. 2010, Smith et al. 2014, Morris and Moran 2025), and compositionally, by increasing the compositional distance, coinciding with the declining dispersals between the regions.

At 30 Ma, Paraná was compositionally more similar to Amazonia and distinct from the Chaco. However, from ~ 10 Ma onwards, this pattern shifted as Paraná became increasingly similar to Chaco, while its similarity to Amazonia progressively declined. This temporal shift suggests a historical dispersal pathway from Amazonia to the Atlantic Forest via the Chaco region, likely facilitated by mid-Miocene tropical forest corridors in what is today the semi-arid Chaco, a result of the formation of the South American dry diagonal (Costa 2003, Sobral-Souza et al. 2015, Thode et al. 2019, Della et al. 2025). Thus, by the present (0 Ma), the Atlantic Forest stands out as compositionally isolated from the other regions.

The relatively high endemism of Mesoamerica and the Antilles may in part be explained by the montane characteristics of these regions, corresponding to the patterns seen in the Andes, but could also reflect their historical geographic isolation (Nieto-Blázquez et al. 2017, Roncal et al. 2020) with the Antilles functioning as an island system and Mesoamerica remaining isolated from South America until the final closure of the Isthmus of Panama (~ 5 Ma; Burnham and Graham 1999). Nonetheless, the inclusion of North American taxa would likely reduce perceived endemism in Mesoamerica.

Despite Amazonia's high absolute diversity, much of it owing to the region's large area (Raven et al. 2020), our results indicate that immigration, rather than speciation, primarily explains its fern diversity, contrasting with patterns in angiosperms (Antonelli et al. 2018). Our findings suggest that Amazonian fern diversity largely comprises widespread species shared with surrounding upland regions, as Amazonia – when averaging species pool similarity to other regions – has the highest similarity, reinforcing the interpretation that immigration rather than within-region speciation primarily explains Amazonian fern diversity (Fig. 3, 6; Supporting information). This could partly be because Amazonian species are relatively poorly known taxonomically, so their species concepts may be broader than in surrounding areas, which are better sampled. Finer resolution of these biogeographical patterns awaits more taxonomical work to sort out the species complexes and improve the coverage of data on Amazonian species occurrences.

Conclusion

The American tropics emerge as a biogeographical maze characterised by interconnected corridors rather than distinct source or sink regions. Fern diversity clearly shows an Andean-centred pattern, differing from the Amazonian-centred pattern typical for angiosperms. This distribution is probably largely due to fern habitat preferences, favouring humid montane forests and cloud-forest epiphytism, along with their superior dispersal ability, enabling exploitation of niches shaped by Andean uplift and climatic changes.

Compared to angiosperms, the enhanced dispersibility of ferns increases complexity in regional connectivity and diversification, influenced strongly by historical climatic and geological events. Recent dispersal patterns notably show bias from drier to wetter and colder to warmer regions, underscoring the importance of climatic tolerances in fern distributions.

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Author contributions

Laura Kragh Frederiksen: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Methodology (lead); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Wolf L. Eiserhardt**: Methodology (supporting); Supervision (supporting); Writing – review and editing (supporting). **Hanna Tuomisto**: Conceptualization (supporting); Funding acquisition (lead); Methodology (supporting); Supervision (lead); Visualization (supporting); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.n02v6wx88 (Frederiksen et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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