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Mesoamerican roots: the biogeographic history of the fern genus *Pleopeltis*

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Abstract

The genus *Pleopeltis* stands out for its high species richness in tropical montane regions and its disjunct neotropical-afrotropical distribution, with most species occurring in the Neotropics. This distribution provides a unique opportunity to explore dispersal patterns, a key mechanism in fern biogeography. In this study, we aimed to identify the biogeographic processes shaping the distribution of *Pleopeltis* and the directionality of its dispersal events throughout evolutionary history. We analyzed a combined dataset of three plastid regions from 70 species to infer divergence times. Ancestral area reconstruction and stochastic biogeographic mapping were employed to elucidate biogeographic patterns and processes. Our findings showed that dispersal was the main process driving the genus's distribution, accounting for nearly half of the inferred biogeographic events. Notably, we identified a recent west-to-east dispersal pattern connecting the Neotropics with the Paleotropics, highlighting the significance of long-distance dispersal in ferns. Mexico and Central America were identified as the center of origin and diversity for the genus and the main source of dispersal. The Andes were the second most important center, functioning as a source and sink for dispersal events. These findings emphasize the critical roles of these dynamic centers in the diversification and distribution of global biodiversity.

Keywords: dispersal directionality, long-distance dispersal, phylogenetic inferences, source-sink

Introduction

The distribution of a population is influenced by several dynamic factors, including dispersal, adaptation, environmental characteristics, and natural selection (Morris 2011, Huang *et al.* 2021, Wu *et al.* 2023). Interaction between populations and these factors can create opportunities for changes in the size and extent of the distribution area of a species over time (Sheth *et al.* 2020). An isolated distribution often suggests restricted adaptation, whereas a generalized distribution may indicate broader adaptive capabilities (Eckhart 2011). In contrast, disjunct distributions typically point to long-distance dispersal or vicariant events (Tryon 1972, Lewis *et al.* 2014, Almeida *et al.* 2021).

As with seed plants, the primary evolutionary biogeographic processes in ferns include vicariance, dispersal, and extinction, which can act simultaneously to shape the distribution of groups (Barrington 1993). The distribution of fern richness mirrors that of angiosperms, with both groups being predominantly concentrated in tropical regions (Suissa *et al.* 2021). While three diversity hotspots exist for ferns in the Paleotropics, the Neotropical region is home to five (Suissa *et al.* 2021). These hotspots are all associated with montane environments, which support a remarkable diversity of habitats and high levels of biodiversity (Körner 2000, Antonelli *et al.* 2018, Marder *et al*. 2025). Much of the fern diversity in tropical regions at medium to high elevations is represented by epiphytic ferns (Cardelús *et al.* 2006, Suissa and Sundue 2020). Families such as Hymenophyllaceae and Polypodiaceae are especially diverse in these environments, including terrestrial, lithophytic, and, in particular, epiphytic lineages (Schuettpelz and Pryer 2009, Testo and Sundue 2016).

Long-distance dispersal (LDD) is an important process in shaping fern distributions (Suissa *et al.* 2021). Unlike seed plants, which often rely on pollinators or animal dispersers, ferns depend on abiotic vectors such as wind, ocean currents, and extreme climatic events like hurricanes and cyclones to disperse (Munoz *et al.* 2004, Wu *et al.* 2023). Their tiny, lightweight spores are well-suited for travel across large distances (Haufler *et al.* 2016) and have even been detected in high atmospheric concentrations (Gradstein and van Zanten 1999). Studies on islands have demonstrated that spore rain can traverse great distances to colonize new habitats, further emphasizing the dispersal potential of ferns, primarily by wind (Tryon 1970, Perrie *et al.* 2010, Groot *et al.* 2012).

For LDD to succeed, several complex steps are required, including the production and transport of numerous spores, their arrival in suitable environments where establishment is possible, and their reproductive viability (Wolf *et al.* 2001, Wu *et al.* 2023). Following arrival, one of the main limiting factors for fern establishment is their dependency on water for fertilization, which is essential for their reproduction (Haufler *et al.* 2016). In their life cycle, most homosporous ferns produce bisexual gametophytes, a trait that facilitates self-fertilization (Haufler *et al.* 2016). While self-fertilization may reduce genetic variability, it can also be advantageous for establishing populations in isolated areas after long-distance dispersals (Haufler *et al.* 2016).

Moran and Smith (2001) recorded several fern groups occurring in a neotropical–afrotropical disjunction, among which is *Pleopeltis*. This genus belongs to Polypodiaceae, one of the diverse fern families with abundant epiphytic species in tropical and subtropical regions (Benzing 2008). *Pleopeltis* is a monophyletic genus comprising approximately 90 species with terrestrial, lithophytic, and epiphytic habits (Otto *et al.* 2009, Smith and Tejero-Díez 2021). While most species are distributed throughout the Neotropics, three species and one hybrid are found in Africa and Asia (Smith and Tejero-Díez, 2021). The major center of diversity for the genus is located between southern Mexico and Panama (Otto *et al.* 2009).

The predominantly neotropical distribution of *Pleopeltis* suggests that its evolutionary history has significantly shaped the genus' richness and endemism in this region (Otto *et al.* 2009, Suissa *et al.* 2021). Studying the flora of Neotropics and Afrotropics helps us understand dispersal and vicariance processes that have shaped the history of the genus and ferns' biogeography. In this study, we tested the hypothesis that dispersal has been one of the key drivers of the current distribution of *Pleopeltis*, supported by previous studies indicating the importance of this process in fern biogeography (Barrington 1993). Additionally, based on previous studies (Bauret *et al.* 2017a, 2017b, Testo *et al.* 2018, Moura 2021, Almeida *et al.* 2021, Wan *et al.* 2023, Medeiros & Almeida 2025), we expect *Pleopeltis* to present a West–East dispersal directionality pattern, as observed in other groups exhibiting a neotropical–afrotropical disjunction (Moran and Smith, 2001).

Materials and Methods

Our sample comprised 70 species (Table 1), including 61 *Pleopeltis* species (64 specimens) and nine outgroups. The outgroups are: *Adenophorus oahuensis*, *Adetogramma chrysolepis*, *Campyloneurum phyllitidis*, *Microgramma percussa*, *Pecluma ptilodon*, *Phlebodium pseudoaureum*, *Polypodium eatonii*, *P. echinolepis* and *P. puberulum*. The sample included 68 newly generated sequences for 26 species and 139 accessions obtained from GenBank (Table 1) for *Pleopeltis* sensu PPG I (2016) and Smith and Tejero-Díez (2014).

Total DNA was extracted from fresh tissue collected in the field or stored in silica gel using the Qiagen DNeasy Plant Mini Kit (Qiagen Inc. Valencia, CA, USA). For species without fresh collections, samples were obtained from recent herbarium specimens, and DNA extraction was performed using either the CTAB protocol adapted from Doyle and Doyle (1987) or the Qiagen DNeasy Plant Mini Kit (Qiagen Inc., Valencia, CA, USA). Polymerase chain reaction (PCR) amplifications were performed for plastid regions: *rbcL* (coding region; approximately 1,300 bp), *rps4* (gene *rps4* and intergenic spacer *rps4-trnSR*; approximately 1,100 bp), and *trnL – trnF* (intron, parts of the *trnL* and *trnF* exons, and *trnL – trnF* intergenic spacer; approximately 1,200 bp). Amplifications used primers 1F and 1365R for *rbcL* (Haufler and Ranker 1995), primers rps5F (Nadot *et al.* 1995) and trnSR (Smith and Cranfill, 2002) for the *rps4* gene and the *rps4-trnSR* intergenic spacer, and Fern1 (Trewick *et al.* 2002) and TRNTFF (Taberlet *et al.* 1991) for the fragment spanning the *trnL* intron, *trnL-trnF* intergenic spacer, and parts of the *trnL* and *trnF* genes. These regions are commonly used for inferring phylogenetic relationships within Polypodiaceae, as demonstrated in various studies, for example, Schneider *et al.* (2004), Otto *et al.* (2009), and Almeida *et al.* (2017, 2021).

PCR reactions were conducted in a 21 µL solution containing 1.0 µL of undiluted genomic DNA, 2.0 µL of PCR buffer (Qiagen 10× PCR Buffer), 1.0 µL of BSA (5 mg/mL), 0.4 µL of dNTPs (10 mM), 0.3 µL of each forward and reverse primer (10 µM), 0.12 µL (0.6 units) of Taq DNA polymerase (Qiagen, 5 units/µL), and 15.88 µL of ultrapure water. Thermal cycling conditions consisted of an initial denaturation step at 94°C for 3 minutes, followed by 35 cycles of denaturation at 94°C for 45 seconds, annealing at 53°C for 60 seconds, and extension at 72°C for 90 seconds, with a final extension step at 72°C for 5 minutes. Amplification products were purified using the EDTA 125 mM and absolute ethanol and resuspended in ultrapure deionized water. The samples were sequenced in both directions by Macrogen (Seoul, South Korea).

The sequences were edited, and consensus sequences were assembled using Geneious software (Geneious R11 - https://www.geneious.com). After this, the edited sequences were aligned automatically with the MUSCLE package (Edgar 2004), and the alignment was manually inspected using MEGA 7 software (Kumar *et al.* 2018).

Divergence times were estimated using BEAST 2.7.6 software (Bouckaert *et al.* 2019), with all parameters set using BEAUti (Drummond *et al.* 2012). Each DNA region (*rbcL*, *rps4* gene, *rps4* IGS, *trnL* intron, and *trnL-trnF* IGS) was treated as a separate partition. Evolutionary models for each DNA region were determined using jModelTest2 (Table S1) (Darriba *et al.* 2012, Guindon and Gascuel 2003). An optimized log-normal relaxed clock model and a Birth-Death Model tree were employed. Calibration was based on a 15.97 mya fossil record from the Dominican Republic of *Pleopeltis dominicensis* H.Schneid., Heinrichs, A.R.Schmidt, the only known fossil of the genus (Schneider *et al.* 2015). Two Markov Chain Monte Carlo (MCMC) chains were run with 70 million generations, recording trees every 70,000 generations. The runs were analyzed using Tracer 1.7.2 (Rambaut *et al.* 2018) to ensure sufficient ESS values for all parameters. The maximum clade credibility tree was generated from 1,000 trees, discarding 10% as burn-in, using TreeAnnotator (Bouckaert *et al.* 2019).

A total of 45,555 occurrence records with geographic coordinates were obtained from the Global Biodiversity Information Facility (GBIF – doi: 10.15468/dl.5rew99) and SpeciesLink. Although these platforms are integrated, data transfer from SpeciesLink to GBIF may be delayed, thus, records were retrieved from both sources. Data were verified and filtered using the *openxlsx* package in R (Schauberger & Walker, 2024). Duplicate records, such as identical coordinates for the same species, collector, and collection number, were removed. Records without precise locality descriptions were excluded. For specimens lacking coordinates but with detailed locality data, geographic coordinates were assigned. To do this, we used QGIS v3.34.4 (QGIS Development Team 2024) and Google Earth (https://earth.google.com) to visualize occurrence records, exclude records with coordinates located in the ocean, and manually verify species distributions against bibliographic data (Tejero-Díez and Smith 2014; Souza and Salino 2021). The resulting dataset consisted of 18,277 occurrence records.

After verification, the records and topology recovered from the phylogenetic analyses were input into Infomap Bioregions v2.0.0 (Edler *et al.* 2017). This software clusters species in geographic space based on their occurrences and phylogenetic relationships. We conducted ten trials with a minimum cell size of 1/2° and a maximum of 4°, with a record capacity of 10 to 700 per cell. Based on the results from Infomap Bioregions (Fig. S1), we made adjustments to the bioregions according to the distribution patterns of the genus described in previous studies (Otto *et al.* 2009, Tejero-Díez and Smith 2014). The defined bioregions were: A – Africa, B – eastern South America, C – Amazon, D – Andes, E – Mexico+Central America, F – Antilles, and G – Hawaii.

The biogeographic history was reconstructed using the BioGeoBEARS package (Matzke 2013) in R 4.3.0 (R Core Team 2023). All models implemented in BioGeoBEARS were tested, including DEC (Dispersal–Extinction–Cladogenesis) (Ree and Smith, 2008), DIVALIKE (Dispersal–Vicariance) (Ronquist 1997), and BAYAREALIKE (Bayesian inference for discrete areas) (Landis *et al.* 2013). Models were evaluated with and without the "j" parameter, which accounts for founder-event speciation (Matzke, 2014). The best-fit model was selected based on AICc values (Matzke, 2016). Using this model, estimates of the biogeographic events shaping the genus’s history were conducted through Stochastic Biogeographic Mapping (BSM) (Dupin *et al.* 2016, Matzke 2016). Event frequencies were estimated using 100 iterations in BSM.

Results

Divergence Time

Our results indicate that *Pleopeltis* likely originated from an ancestor that diverged, on average, 16.82 mya (7.69–26.31 mya 95% HPD) (Fig. S2) from the clade formed by *Pecluma* and *Phlebodium*. Subsequent divergence is marked by the diversification of the genus, averaging 15.43 mya (8.44–21.88 mya, 95% HPD) (Fig. S2), which led to the formation of the Squamata clade and the group comprising the Angusta and Macrocarpa clades (Fig. S2). In the Squamata clade, estimates show that lineage divergence occurred approximately 10.97 mya (4.78–17.06 mya, 95% HPD) (Fig. S2). The divergence between the Angusta and Macrocarpa clades is marked by a node with an average age of 12.8 mya (6.46–18.06 mya, 95% HPD) (Fig. S2). The Macrocarpa clade diverged around 10.78 mya (5.19–15.96 mya, 95% HPD) (Fig. S2), followed by divergence within the Angusta clade, averaging 10.37 mya (5.11–14.99 mya, 95% HPD) (Fig. S2).

Biogeographic Analysis

According to AICc (Corrected Akaike Information Criterion) and log-likelihood values, the best-fit model was DEC+J (AIC = 418.98; LnL = -206.49) (Table 2), followed by DEC (AIC = 419.73; LnL = -207.86) and DIVALIKE (AIC = 439.04; LnL = -217.52) (Table 2). Based on the best-fit model, we present the ancestral area reconstruction results from BioGeoBEARS using the DEC+J model (Dispersal Extinction Cladogenesis with jump dispersal) (Fig. 1).

The ancestral area reconstruction indicates that *Pleopeltis* originated from an ancestral lineage likely occurring in Mexico+Central America (Fig. 1). The three major clades (Macrocarpa, Angusta, and Squamata) have Mexico+Central America as their putative area of origin (Fig. 1). In the Squamata clade, the species *P. bombycina* appears polyphyletic. One terminal from Bolivia appears as sister to the remaining species, with a likely origin in Mexico+Central America (Fig. 1), with possible subsequent dispersals to the Andes and the Amazon, forming the current distribution of the species. The area of origin for the other specimen of *P. bombycina* could not be established. This specimen appears in a clade with *P. trindadensis*, *P. alborufula*, and *P. lepidopteris*, whose origin was recovered as eastern South America (Fig. 1).

Subsequently, the clade formed by *P. tridens* and *P. insularum*, endemic to the Galápagos archipelago, likely has an Andean ancestor that dispersed via long-distance dispersal. The sister clade, comprising *P. collinsii*, *P. hirsutissima*, *P. lepidotricha*, *P. macrolepis*, *P. minarum*, *P. myriolepis*, *P. pyrrholepis*, *P. rosei*, and *P. sanctae-rosae*, originated in Mexico+Central America with a dispersal to eastern South America that gave origin to a clade with *P. minarum* and *P. hirsutissima* (Fig. 1).

Within the Macrocarpa clade, *P. muenchii*, the sister lineage to the remaining clades, originated in Mexico+Central America (Fig. 1). The clade that includes *P. rzedowskianum*, *P. plebeia*, *P. montigena*, *P. madrense*, *P. guttata*, *P. platylepis*, and *P. thysanolepis* likely also originated in Mexico+Central America (Fig. 1), with *P. platylepis* and *P. thysanolepis* expanding to other bioregions. In a separate clade, *P. crassinervata*, *P. mexicana*, *P. polylepis*, and *P. conzattii* also trace their origins to Mexico+Central America. The ancestral area reconstruction for *P. macrocarpa*, was inconclusive (Fig. 1). *Pleopeltis macrocarpa* has the widest distribution within the genus, occurring throughout the Neotropics and Afrotropics, and extending as far as Sri Lanka (Smith and Tejero-Díez, 2014). Our sampling did not cover all localities for a more accurate reconstruction of the biogeographic history of this lineage at a population level. Our analysis recovered the most recent common ancestor of *P. macrocarpa* and its sister species, *P. crassinervata*, as likely occurring in Mexico+Central America.

The ancestral area of the subsequent clade, including *P. fallax*, *P. fructuosa*, *P. intermedia*, and *P. wiesbauri*, could have been either Mexico+Central America or the

Andes, with the same ambiguity found for the ancestor of *P. wiesbaurii*+*P. fructuosa*. Meanwhile, *P. fallax* likely originated in Mexico+Central America, whereas the sister lineage, *P. astrolepis*, had an inconclusive origin (Fig. 1).

In the Angusta clade, two major clades were identified. The first lineage possibly originated from a dispersal from Mexico+Central America to the Andes. This Andean ancestor gave rise to *P. apressa*, *P. balliviani*, *P. buchtienii*, *P. fraserii*, *P. monosora*, *P. murora*, *P. pycnocarpa*, *P. remota*, and *P. tweediana* (Fig. 1). However, for *P. pleopeltifolia* and *P. pleopeltidis*, the analysis recovered a more recent origin from an ancestor in eastern South America, suggesting two possible dispersal events to this region from an Andean origin (Fig. 1). The recent origins of *P. remota* and *P. murora*, species with broader distributions, were inconclusive.

In the second major lineage within the Angusta clade, the ancestor of the clade including *P. christensenii*, *P. furcata*, and *P. desvauxii* was inconclusive. In contrast, its sister clade—composed of *P. angusta var. angusta*, *P. angusta var. stenoloma*, *P. complanata*, and *P. marginata*—was inferred to have originated in Mexico+Central America. Additionally, an LDD event to the Antilles was observed for *P. marginata*.

The last clade within the Angusta clade likely originated in Mexico, with *Pleopeltis bradeorum*, sister to the remaining taxa, also originating in this Bioregion. The ancestor of most species (*P. disjuncta*, *P. friedrichsthaliana*, *P. furfuracea*, *P. polypodioides* var. *acicularis*, *P. polypodioides* var. *polypodioides*, and *P. vilagranii*) was inferred to have originated in Mexico+Central America, with the following exceptions. An LDD event to the Andes gave rise to *P. minima* and *P. burchellii*, which subsequently expanded to eastern South America and the Amazon. Additionally, *P. disjuncta* from the Andes appears to have originated from another LDD event (Fig. 1).

Stochastic biogeographic mapping indicated that the main biogeographic process in the history of *Pleopeltis* was dispersal, accounting for 49.2% (64.45) of events, with 45.7% (59.87) (Table 3) attributed to range expansion and 3.4% (4.58) to founder events. Speciation by area accounts for 50.7% (66.42) of all modes, with 44.2% (57.85) (Table 3) attributed to sympatry and 6.5% (8.57) to vicariance.

In the total count of dispersal events (Table 4a), which includes both founder (Table 4b) and range expansion events (Table 4c), Mexico+Central America stood out as the main source, accounting for 37.3% (24.05) of total dispersal events (Table 4a). The Andes followed, contributing 29.5% (19.36) of total dispersal events (Table 4a). Together, these two bioregions represent the origin of 66.8% (43.41) of the total (64.45) dispersal events mapped (Table 4a). Eastern South America, the Amazon, the Antilles, Hawaii, and Africa collectively accounted for 33.2% (21.04) (Table 4a) of dispersal events. The main destinations for these dispersal events were the Andes with 25.3% (16.28), the Amazon with 24.8% (15.97), and eastern South America with 18.2% (11.74) (Table 4a), collectively accounting for approximately 68.3% (43.99) of destination areas.

For range expansion events (Table 4c), the results for major dispersal origins were similar to those of the total dispersal events, as range expansion represents the majority of these occurrences, accounting for 92.9% (59.9) of the total dispersal events (100% = 64.45) (Table 4c). The primary destination (sink) areas for range expansion events were the Amazon with 26.1% (15.56), the Andes with 24.3% (14.45), the Antilles with 17.5% (10.44), eastern South America with 17.2% (10.26), Mexico+Central America with 13% (7.77), Africa with 1.7% (1), and Hawaii with 0.7% (0.39) (Table 4c).

Founder events, which represent long-distance dispersal (LDD), accounted for 7.1% (4.58) (Table 4b) of the total estimated dispersals. The primary sources were Mexico+Central America with 57.6% (2.64) and the Andes with 31.9% (1.46) of the total events (Table 4b). Subsequently, bioregions such as eastern South America, Hawaii, the Amazon, and the Antilles collectively account for only 10.5% (0.48) of founder event origins (Table 4b). The Andes, one of the main areas of origin, was also recovered as the primary sink, receiving 40% (1.83) of the total LDD events (Table 4b). Eastern South America is another significant sink, accounting for 32.3% (1.48) of these events (Table 4b). Mexico+Central America, the Amazon, Hawaii, and the Antilles together represent 28% (1.27) of the LDD destinations (Table 4b).

Discussion

Dispersal was one of the most important processes shaping the distribution of *Pleopeltis*, accounting for nearly half of the estimated biogeographic events (Table 3). These results support our initial hypothesis that dispersal is an important process responsible for the current distribution of this genus, aligning with the widely recognized role of dispersal in ferns (e.g. Barrington 1993, Moran and Smith 2001, Groot *et al.* 2012, Xiang *et al.* 2015). Dispersal efficiency in ferns is a reflection of the tiny, lightweight spores that facilitate both short- and long-distance dispersal (Haufler *et al.* 2000, Page 2002).

Our analyses revealed a predominant dispersal pattern originating dispersal from Mexico+Central America toward South America, especially the Andes (Figs 3, 4). Dispersal flows were bidirectional but asymmetrical, with a stronger signal from Mexico+Central America to the Andes than the reverse (Fig. 2). The Andes appear to act as a secondary dispersal source, facilitating subsequent colonization of adjacent regions, including Amazonia and eastern South America. This suggests a stepwise colonization pattern, in which lineages first establish in the Andes before expanding into other tropical South America regions. These findings highlight the importance of the Andes and

Mesoamerica as key biogeographic sources for diversification within the neotropical region, with occasional dispersal to other continents.

This pathway, connecting Mexico and Central America to the Andes and subsequently to eastern South America, fits into a broader West-to-East dispersal pattern. Our data support this pattern not only within the neotropical region but also at an intercontinental scale, through long-distance dispersal (LDD) events connecting the Neotropics and Paleotropics (Fig. 3). These events primarily follow a West-to-East route, aligning with patterns widely observed in other fern groups (Bauret *et al.* 2017a, 2017b, Testo *et al.* 2018, Moura 2021, Almeida *et al.* 2021, Wan *et al.* 2023, Medeiros and Almeida 2025), especially in cases of neotropical–afrotropical disjunctions (Moran and Smith 2001).

Most of the dispersal events analyzed occurred via range expansion, which is expected since spores will have a higher probability of dispersing to areas close to the parent plant (Wolf *et al.* 1991). This process allows populations to gradually extend their geographic ranges by occupying adjacent areas (Shigesada and Kawasaki 2002). During these expansions, populations may encounter favorable environmental variations, allowing them to explore new habitats (Suarez and Tsutsui 2008). These environmental gradients act as selective filters, determining occupiable areas based on the species' adaptations (Suarez and Tsutsui 2008). In both range expansion and long-distance dispersal, when a species reaches and establishes in a new area, gene flow can decrease due to increased geographic distance and different adaptations to local selective pressures (Slatkin 1987, Edelaar and Bolnick 2012). As a result, these processes can generate genetic divergence within populations, potentially leading to speciation (Liu *et al.* 2023).

Long-distance dispersal events are rare, but several potential cases have been identified in *Pleopeltis* (Fig. 2). For example, *P. marginata* likely reached the Antilles through an LDD event of Mesoamerican origin, crossing the Caribbean Sea between 11.6 - 3 mya (Fig. 3). In other fern genera found in the Antilles, the origins of potential dispersal remain uncertain, as seen with *Amauropelta firma* and *A. basisceletica* (Moura 2021).

In South America, LDD events in *Pleopeltis* can be observed in the colonization of oceanic volcanic islands, such as the Galápagos Archipelago in the Pacific and Trindade Island in the Atlantic. Another example is *Pleopeltis macrocarpa*, which has populations not only in the Neotropics but also in Africa, Madagascar, and Sri Lanka (Smith and Tejero-Díez 2014). This species has a recent neotropical origin, dated between 2.6–0.2 mya (Fig. 3), suggesting recent LDD across the Atlantic. Similar dispersals from the Neotropics to Africa and Asia have also been observed in other fern genera, such as *Rumohra* (Bauret *et al.* 2017a), *Cochlidium*, *Melpomene* (Bauret *et al.* 2017b), *Amauropelta* (Moura 2021), *Microgramma* (Almeida *et al.* 2021), *Lomaridium*, *Parablechnum* (Testo *et al.* 2022), *Tectaria* (Wan *et al.* 2023), as well as in lycophytes such as *Phlegmariurus* (Bauret *et al.* 2018, Testo *et al.* 2018). The role of long-distance dispersal in the disjunction pattern of neotropical-afrotropical ferns and lycophytes (Moran and Smith 2001) is further supported by our findings, underscoring its strong influence on the distribution of spore-bearing vascular plants (Barrington 1993).

The neotropical region underwent major climatic and geological events during the Cenozoic, such as the uplift cycles of the Andes, the formation of the Isthmus of Panama, and the rise of new mountain chains in the Antilles. These changes contributed to the emergence of new habitats (Gregory-Wodzicki 2000, Garzione *et al.* 2006, 2008). Thus, the various types of dispersal may not only have expanded the geographic range of *Pleopeltis* over time but also increased biodiversity in response to different environmental conditions along the neotropical gradient.

When analyzing the main sources of dispersal, southern Mexico, Central America, and the Andes stand out (Fig. 2). These areas have the highest number of endemic lineages of the genus (Smith and Tejero-Díez 2014) and are recognized hotspots of fern diversity (Suissa *et al.* 2021). The region including Mexico and Central America was not only recovered as the ancestral area of *Pleopeltis* but also emerged as the primary source of dispersal events (Figs. 2, 3), both through range expansion (Table 4c) and long-distance dispersal (Table 4b). Our results also showed that most sympatric speciation events also occurred within these regions (Table S2).

The Andes, a region known for hosting multiple radiations of vascular plants (Lagomarsino *et al.* 2016, Pérez-Escobar *et al.* 2017, Testo *et al.* 2019), stood out for its preponderant role as both source and sink (Table 4a). In contrast, the Amazon and eastern South America mainly stand out as sink regions. The Amazon's central location relative to the other bioregions favors its connectivity with migratory flows, although it predominantly hosts broadly distributed lineages, with only two known endemic species (Smith and Tejero-Díez 2014). Eastern South America, another sink region for *Pleopeltis* lineages, is part of the tropical montane biodiversity hotspots (Suissa *et al.* 2021) and is home to several relictual fern endemics (Suissa and Sundue 2020). The dynamic between sources and sinks directly influences distribution patterns over time (Novaes *et al.* 2024). Here, the main source bioregions for dispersal are recognized as sources of tropical fern diversity (Suissa *et al.* 2021). These patterns reinforce the central role of Mexico+Central America and the Andes as primary sources for generating diversity and dispersal of *Pleopeltis*, playing a fundamental role in the origin and maintenance of lineages over time.

Our findings revealed that the probable area of origin of *Pleopeltis* between the late Oligocene and late Miocene (Fig. S2) coincides with the genus's current diversity center (Fig. 1; Otto *et al.* 2009). During the Miocene, Central America experienced the initial uplift of the Isthmus of Panama (Leigh *et al.* 2014), altering ocean current directions and causing climate changes that influenced rainfall and wind patterns in Neotropical ecosystems (Leigh *et al.* 2014). These changes may have generated new environmental gradients that favored the isolation and initial diversification of the ancestral group of *Pleopeltis*, which diverged from the clade formed by *Pecluma* and *Phlebodium*.

Furthermore, the divergence of the genus, which resulted in the major clades Angusta, Squamata, and Macrocarpa, may have occurred between the Miocene and Pliocene (Fig. 1). During the Pliocene, the closure of the Isthmus of Panama (Leigh *et al.* 2014) coincided with the ongoing uplift of the central to northern Andean cordilleras (Pennington and Dick 2010). The uplift of the Andes created a barrier that disrupted Pacific winds, shifting precipitation regimes eastward (Garzione *et al.* 2008) and altering the course of several South American rivers, giving rise to basins like the Amazon (Hoorn 2006, Hoorn *et al.* 2010). The late Pliocene marked the beginning of glacial cycles (Berger 1988), which extended into the Pleistocene and led to repeated habitat expansions and contractions (Hooghiemstra and Van der Hammen 2004). Studies show a strong correlation between the uplift of the Andes, the closure of the Isthmus of Panama, and high diversification rates in several vascular plant groups (Antonelli *et al.* 2009, Bacon *et al.* 2012, Testo *et al.* 2018). These geological and climatic events, by fragmenting habitats and contracting montane forest habitats during glacial cycles (Hooghiemstra and Van der Hammen 2004), may have driven the diversification of *Pleopeltis*, resulting in the formation of major groups coinciding with significant events in Neotropical history.

Conclusion

This study demonstrates that dispersal was the primary process shaping the distribution of the genus *Pleopeltis*, accounting for nearly half of the inferred biogeographic events and reinforcing its crucial role in the diversification of the genus. Furthermore, a distinct West–East dispersal pattern was observed, connecting the Neotropics to the Paleotropics and corroborating the role of long-distance dispersal (LDD) in ferns, a pattern consistent with findings in other groups (Bauret *et al.* 2017a, 2017b, Testo *et al.* 2018, Moura 2021, Almeida *et al.* 2021, Wan *et al.* 2023) and often associated with neotropical-afrotropical disjunctions (Moran and Smith 2001). Additionally, the Mexico+Central America bioregion was identified as the center of origin, diversity, and primary source of dispersal for *Pleopeltis*, while the Andes served as both a secondary source and a sink for dispersal events. These findings underscore the importance of these dynamic regions in generating and redistributing diversity.

CRediT authorship contribution statement

Carolina do Valle: Writing – original draft, Writing – review & editing, Data curation, Formal analysis, Investigation, Methodology, Visualization, Conceptualization. **Alexandre Salino:** Writing – review & editing, Funding acquisition. **Lucas Vieira Lima:** Writing – review & editing, Conceptualization, Supervision. **Ingridy Oliveira Moura:** Writing – review & editing, Methodology, Investigation. **Thaís Elias Almeida:** Writing – original draft, Writing – review & editing, Supervision, Methodology, Investigation, Validation, Conceptualization.

Conflict of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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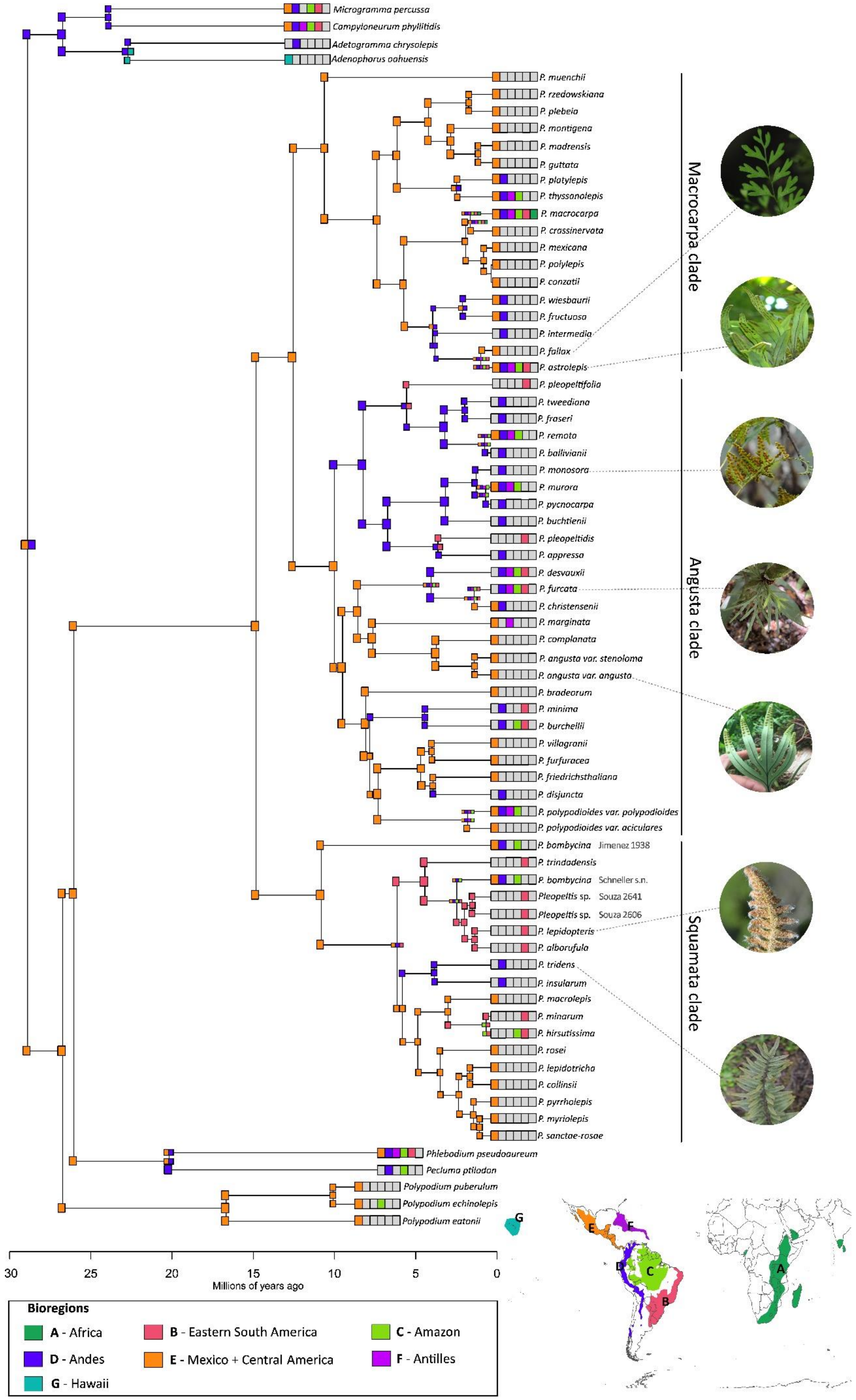
Microgramma percussa
Campyloneurum phyllitidis
Adetogramma chrysolepis
Adenophorus oahuensis
P. muenchii
P. rzedowskiana
P. plebeia
P. montigena
P. madrensis
P. guttata
P. platylepis
P. thyssanolepis
P. macrocarpa
P. crassinervata
P. mexicana
P. polylepis
P. conzatii
P. wiesbaurii
P. fructuosa
P. intermedia
P. fallax
P. astrolepis
Macrocarpa clade
P. pleopeltifolia
P. tweediana
P. fraseri
P. remota
P. ballivianii
P. monosora
P. murora
P. pycnocarpa
P. buchtienii
P. pleopeltidis
P. appressa
P. desvauxii
P. furcata
P. christensenii
P. marginata
P. complanata
P. angusta var. stenoloma
P. angusta var. angusta
P. bradeorum
P. minima
P. burchellii
P. villagranii
P. furfuracea
P. friedrichsthaliana
P. disjuncta
P. polypodioides var. polypodioides
P. polypodioides var. aciculares
Angusta clade
P. bombycina Jimenez 1938
P. trindadensis
P. bombycina Schneller s.n.
Pleopeltis sp. Souza 2641
Pleopeltis sp. Souza 2606
P. lepidopteris
P. alborufula
P. tridens
P. insularum
P. macrolepis
P. minarum
P. hirsutissima
P. rosei
P. lepidotricha
P. collinsii
P. pyrrholepis
P. myriolepis
P. sanctae-rosae
Squamata clade
Phlebodium pseudoaureum
Pecluma ptilodon
Polypodium puberulum
Polypodium echinolepis
Polypodium eatonii
30
25
20
15
10
5
0
Millions of years ago
Bioregions
A - Africa
B - Eastern South America
C - Amazon
D - Andes
E - Mexico + Central America
F - Antilles
G - Hawaii
G
E
F
D
C
B
A

Figure 1 - Ancestral areas estimated by BioGeoBEARS based on the divergence time estimation tree resulting from the BEAST analysis for the genus *Pleopeltis*. Colors represent the different bioregions: dark green = Africa (A), pink = Eastern South America (B), light green = Amazonia (C), blue = Andes (D), orange = Mexico (E), magenta = Antilles (F), cyan = Hawaii (G). Image credits: *Pleopeltis fallax* and *P. monosora* by M. Sundue (https://www.fernsoftheworld.com); *P. angusta* by A. Santiago; *P. furcata* by D.V.S. Silva; *P. angusta* var. *angusta* by A. San José Elizundia.

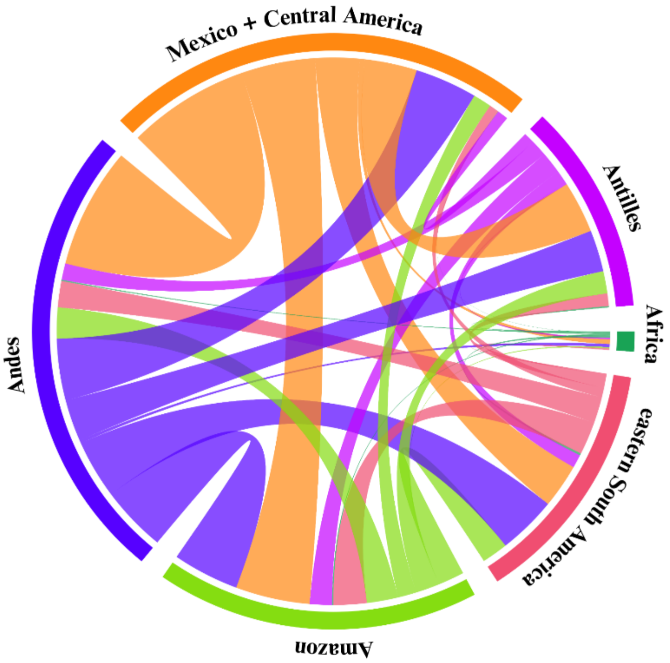

Figure 2 – Dispersal events estimated using stochastic biogeographic mapping. The lines indicate the direction and frequency of all events, with thicker lines representing higher event frequency. The colors of the bioregions correspond to those in Fig. 1.

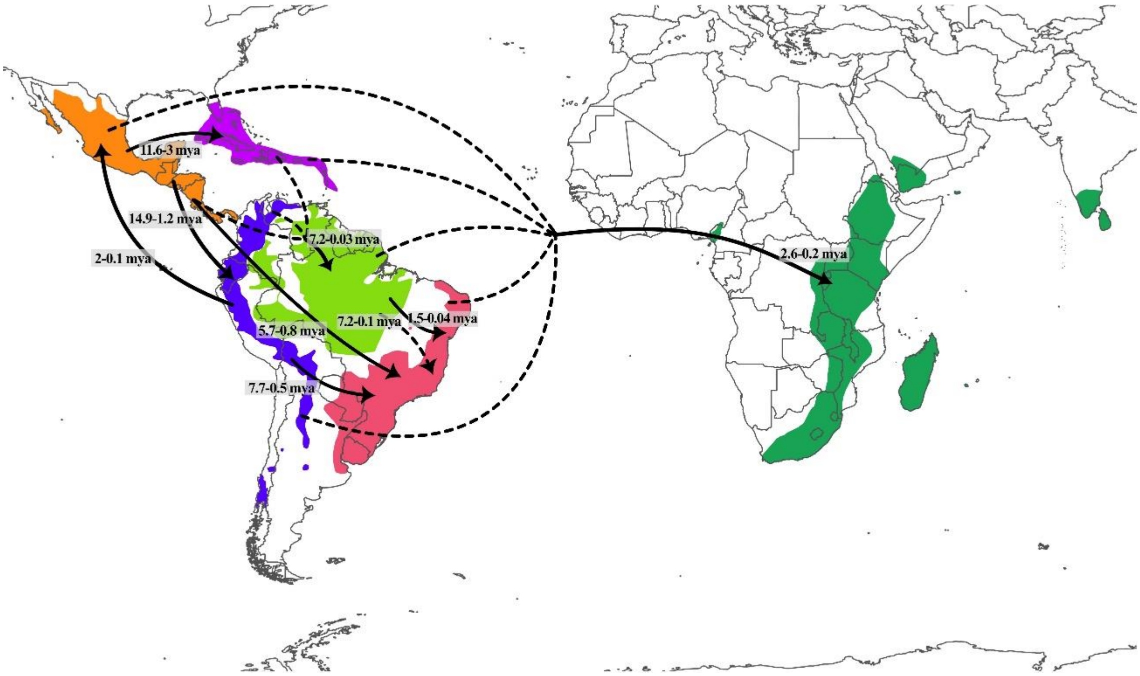

Figure 3 - Long-distance dispersal events inferred in the biogeographic history of *Pleopeltis*. Dashed lines indicate origins with low credibility, while solid lines indicate high confidence in origin and/or destination. The colors of the bioregions correspond to those in Fig. 1. Figure drawn based on data from Fig. 1 and Table 4.

Table 1 – Generated sequences and GenBank accessions. The codes represent accession numbers for sequences previously published and available in GenBank. "-" indicates unavailable sequences. "x" indicates new sequences generated in this study to be deposited in GenBank.

Taxa	**Voucher**	**Country**	***rbc*L**	***rps*4**	***trn*L-*trn*F**
Adenophorus oahuensis (Copel.) L.E.Bishop	Ranker 969	USA	AY057382	AY096236	AY096236
Adetogramma chrysolepis (Hook.) T.E.Almeida	Almeida 3083	Brazil	KY847865	KY847858	-
Campyloneurum phyllitidis C.Presl	Almeida 2329	Brazil	KT780752	KT794132	-
Microgramma percussa (Cav.) de la Sota	Almeida 2235	Brazil	MT583762	MT806130	MT568823
Pecluma ptilodon (Kunze) M.G.Price	Lefebre 3085	Mexico	AY362588	AY362588	AY362588
Phlebodium pseudoaureum (Cav.) Lellinger	Souza 2648	Brazil	x	x	x
Pleopeltis alborufula (Brade) Salino	Salino 16252	Brazil	x	x	x

Pleopeltis alborufula (Brade) Salino	Souza 2606	Brazil	x	x	x
Pleopeltis angusta Humb. & Bonpl. ex Willd.	Salino 15851	Mexico	x	x	x
Pleopeltis angusta var. stenoloma Farw.	Krömer 2122	Mexico	x	x	x
Pleopeltis appressa M.Kessler & A.R.Sm.	Jimenez 2356	Bolivia	DQ642172	DQ642211	DQ642259
Pleopeltis astrolepis (Liebm.) E.Fourn.	Krömer 2775	Mexico	EU650106	EU650145	EU650067
Pleopeltis ballivianii (Rosenst.) A.R.Sm.	Jimenez 2462	Bolivia	DQ642173	DQ642212	DQ642260
Pleopeltis bombycina (Maxon) A.R.Sm.	Jimenez 1938	Bolivia cult.	DQ642174	DQ642213	DQ642261
Pleopeltis bombycina (Maxon) A.R.Sm.	Schneller s.n.	BGZ	EU650136	EU650175	EU650097
Pleopeltis bradeorum (Rosenst.) A.R.Sm. & Tejero	cult. source (NYBG 336/89)	Costa Rica	AY362614	AY362686	-
Pleopeltis buchtienii (Christ & Rosenst.) A.R.Sm.	Jimenez 1113	Bolivia	DQ642175	DQ642214	DQ642262

Pleopeltis burchellii (Baker) Hickey & Sprunt ex A.R.Sm.	Almeida 4763	Brazil	x	x	x
Pleopeltis christensenii A.R.Sm.	Schuettpelz s.n.	cult. BGBD	EU650099	EU650138	-
Pleopeltis collinsii (Maxon) A.R.Sm. & Tejero	Krömer 2705	Mexico	EU650130	EU650169	EU650091
Pleopeltis complanata (Weath.) E.A.Hooper	Nitta 823	Costa Rica	MW138186	-	-
Pleopeltis conzattii (Weath.) R.M.Tryon & A.F.Tryon	Tejero-Diez 4937	Mexico	EU650103	EU650142	EU650064
Pleopeltis crassinervata T.Moore	Salino 15731	Mexico	x	x	x
Pleopeltis desvauxii (Klotzsch) Salino	Lehnert 086	Bolivia	AY362584	AY362657	-
Pleopeltis disjuncta M.Kessler & A.R.Sm.	Jimenez 664	Bolivia	EU650127	EU650166	EU650088
Pleopeltis fallax (Schltdl. & Cham.) Mickel & Beitel	Salino 15714	Mexico	x	x	x
Pleopeltis fraseri (Kuhn) A.R.Sm.	Jimenez 817	Bolivia	DQ642176	DQ642215	DQ642263

Pleopeltis friedrichsthaliana (Kunze) A.R.Sm. & Tejero	Krieger 2332	Costa Rica	EU650128	EU650167	EU650089
Pleopeltis fructuosa (Maxon & Weath.) Lellinger	Krieger 2328	Costa Rica	EU650101	EU650140	EU650062
Pleopeltis furcata (L.) A.R.Sm.	Salino 16213	Mexico	x	x	x
Pleopeltis furfuracea (Schltdl. & Cham.) A.R.Sm. & Tejero	Salino 15759	Mexico	x	x	x
Pleopeltis guttata (Maxon) E.G.Andrews & Windham	Tejero-Diez 4951	Mexico	EU650111	EU650150	EU650072
Pleopeltis hirsutissima (Raddi) de la Sota	Almeida 4431	Brazil	x	x	x
Pleopeltis insularum (C.V.Morton) A.R.Sm.	van der Werff 901	Ecuador	-	x	x
Pleopeltis intermedia M.Kessler & A.R.Sm.	Jimenez 2508	Bolivia	EU650107	EU650146	EU650068
Pleopeltis lepidopteris (Langsd. & Fisch.) de la Sota	Almeida 4785	Brazil	x	-	x

Pleopeltis lepidotricha (Fée) A.R.Sm. & Tejero	Tejero-Diez 4905	Mexico	EU650129	EU650168	EU650090
Pleopeltis macrocarpa (Bory ex Willd.) Kaulf.	Souza 2611	Brazil	x	x	x
Pleopeltis macrocarpa (Bory ex Willd.) Kaulf.	Hemp 3538	Tanzania	DQ642177	DQ642216	DQ642264
Pleopeltis macrolepis (Maxon) A.R.Sm. & Tejero	Sundue 960	Costa Rica	EU650134	EU650173	EU650095
Pleopeltis madrensis (J.Sm.) A.R.Sm. & Tejero	Tejero-Diez 4940	Mexico	EU650110	EU650149	EU650071
Pleopeltis marginata A.R.Sm. & Tejero	Monro 3217	Costa Rica	EU650100	EU650139	EU650061
Pleopeltis Mexicana (Fée) Mickel & Beitel	Tejero-Diez 4929	Mexico	EU650102	EU650141	EU650063
Pleopeltis minarum (Weath.) Salino	Moura 174	Brazil	x	x	x
Pleopeltis minima (Bory) J.Prado & R.Y.Hirai	Gissi 317	Brazil	x	x	x

Pleopeltis monosora (Desv.) A.R.Sm.	Moran 6768	Ecuador	EU650118	EU650157	EU650079
Pleopeltis montigena (Maxon) A.R.Sm. & Tejero	Sundue 961	Costa Rica	EU650114	EU650153	EU650075
Pleopeltis muenchii (Christ) A.R.Sm.	Tejero-Diez 4933	Mexico	EU650113	EU650152	EU650074
Pleopeltis murorum (Hook.) A.R.Sm. & Tejero	Sundue 920	Costa Rica	EU650119	EU650158	EU650080
Pleopeltis myriolepis (Christ) A.R.Sm. & Tejero	Krieger 2327	Costa Rica	EU650131	EU650170	EU650092
Pleopeltis platylepis (Mett. ex Kuhn) A.R.Sm. & Tejero	Tejero-Diez 4943	Mexico	EU650115	EU650154	EU650076
Pleopeltis plebeia (Schltdl. & Cham.) A.R.Sm. & Tejero	Tejero-Diez 4930	Mexico	EU650116	EU650155	EU650077
Pleopeltis pleopeltidis (Fée) de la Sota	Souza 2610	Brazil	x	x	x
Pleopeltis pleopeltifolia (Raddi) Alston	Bohs 3185	Paraguay	EU650121	EU650160	EU650082

Pleopeltis polylepis T.Moore	Tejero-Diez 4947	Mexico	EU650104	EU650143	EU650065
Pleopeltis polypodioides var. acicularis (Weath.) E.G.Andrews & Windham	Tejero-Diez 4942	Mexico	EU650125	EU650164	EU650086
Pleopeltis polypodioides var. polypodioides (L.) E.G.Andrews & Windham	Salino 15853	Mexico	x	x	x
Pleopeltis pycnocarpa (C.Chr.) A.R.Sm.	Sundue 815	Bolivia	EU650120	EU650159	EU650081
Pleopeltis pyrrholepis (Fée) A.R.Sm. & Tejero	Lautner 02- 44	Mexico	EU650133	EU650172	EU650094
Pleopeltis remota (Desv.) A.R.Sm.	Jimenez 1450	Bolivia	DQ642180	DQ642220	DQ642268
Pleopeltis rosei (Maxon) A.R.Sm. & Tejero	Kimnach 107	Mexico	AY362608	AY362680	AF159197
Pleopeltis rzedowskiana (Mickel) A.R.Sm. & Tejero	Krömer 2646	Mexico	EU650117	EU650156	EU650078
Pleopeltis sanctae-rosae (Maxon) A.R.Sm. & Tejero	Tejero-Diez 4946	Mexico	EU650132	EU650171	EU650093

Pleopeltis sp.	Souza 2641	Brazil	x	-	x
Pleopeltis thyssanolepis (A.Braun ex Klotzsch) E.G.Andrews & Windham	Tejero-Diez 4938	Mexico	EU650112	EU650151	EU650073
Pleopeltis tridens J.Sm.	Hagen 1051B	Ecuador	-	x	x
Pleopeltis trindadensis (Brade) Salino	Alkmin-Faria 1081	Brazil	x		x
Pleopeltis tweediana (Hook.) A.R.Sm.	Jimenez 1318	Bolivia	DQ642182	DQ642222	DQ642270
Pleopeltis villagranii (Copel.) A.R.Sm. & Tejero	Salino 15730	Mexico	-	x	x
Pleopeltis wiesbaurii (Sodiro) Lellinger	Sundue 913	Costa Rica	EU650109	EU650148	EU650070
Polypodium eatonii Baker	Salino 15783	Mexico	x	x	x
Polypodium echinolepis Fée	Salino 15722	Mexico	x	x	x
Polypodium puberulum Schltdl. & Cham.	Salino 15801	Mexico	x	x	-

Table 2 - Comparative statistics among tested biogeographic models. LnL = log-likelihood; d = dispersal rate; e = extinction rate; j = founder-event speciation; AIC = Akaike Information Criterion; DEC = Dispersal-Extinction-Cladogenesis model; DIVALIKE = BioGeoBEARS implementation of the DIVA model; BAYAREALIKE = BioGeoBEARS implementation of the BayArea model.

Model	N° Free Parameters	LnL	d	e	j	AIC	AICc
DEC+J	3	-206.49	0.02	4.19e-09	0.00902	418.98	419.3
DEC	2	-207.86	0.0209	2.20e-08	0	419.73	419.9
DIVALIKE	2	-217.52	0.0247	1.00e-12	0	439.04	439.2
DIVALIKE+J	3	-217.19	0.0241	1.00e-13	0.00319	440.38	440.7
BAYAREALIKE+J	3	-226.43	0.0148	0.059	0.00748	458.87	459.2
BAYAREALIKE	2	-228.39	0.0178	0.085	0	460.79	461

Table 3 – Stochastic biogeographic mapping counts for *Pleopeltis* using the DEC+j model. Average numbers and percentages for the different types of estimated events are presented here.

Mode	Type	Means	%
Within-area speciation	Vicariance	8.57	6.54
	Sympatry	57.85	44.2
Dispersal	Founder events	4.58	3.49
	Range expansions	59.87	45.74
Total		130.87	100

Table 4 - Events estimated in the evolutionary history of *Pleopeltis* through Stochastic Biogeographic Mapping (BSM). a– Counts of all dispersal events; b – Founder counts; c – Range expansion counts. Rows represent the origin, and columns represent the destination areas. Standard deviations are shown in parentheses. The warmer the color, the more common the event. The values on the right and below the table represent the sum and percentage of events for each area. Letters correspond to different bioregions represented in parentheses.

a) Range expansions+ Founder events (Standard deviations)

	A (Africa)	**B (eastern of South America)**	**C (Amazon)**	**D (Andes)**	**E (Mexico and Central America)**	**F (Antilles)**	**G (Hawaii)**	
A (Africa)	**-**	**0.17** **(0.38)**	**0.1** **(0.3)**	**0.1** **(0.3)**	**0.02** **(0.14)**	**0.12** **(0.33)**	**0** **(0)**	**0.51** **(0.8%)**
B (eastern of South America)	**0.13** **(0.34)**	**-**	**2.68** **(1.34)**	**2.14** **(1.5)**	**0.78** **(0.85)**	**1.02** **(1.05)**	**0.02** **(0.14)**	**6.77** **(10.5%)**
C (Amazon)	**0.1** **(0.3)**	**2.12** **(1.47)**	**-**	**2.53** **(1.64)**	**1.49** **(1.42)**	**1.82** **(1.31)**	**0.01** **(0.1)**	**8.07** **(12.5%)**
D (Andes)	**0.25** **(0.44)**	**4.76** **(1.7)**	**5.36** **(2.04)**	**-**	**5.03** **(2.52)**	**3.38** **(1.55)**	**0.58** **(0.5)**	**19.36** **(29.5%)**
	0.39	**3.59**	**6**	**9.83**	**-**	**4.22**	**0.02**	

E **(Mexico and Central America)**	**(0.49)**	**(1.58)**	**(2.12)**	**(2.52)**		**(1.53)**	**(0.14)**	**24.05** **(37.3%)**
F **(Antilles)**	**0.13** **(0.34)**	**1.08** **(1.09)**	**1.79** **(1.17)**	**1.34** **(1.12)**	**0.88** **(0.81)**	**-**	**0.05** **(0.22)**	**5.27** **(8.1%)**
G **(Hawaii)**	**0** **(0)**	**0.02** **(0.14)**	**0.04** **(0.2)**	**0.34** **(0.5)**	**0.02** **(0.14)**	**0** **(0)**	**-**	**0.42** **(0.6%)**
	1 **(1.5%)**	**11.74** **(18.2%)**	**15.97** **(24.7%)**	**16.28** **(25.2%)**	**8.22** **(12.7%)**	**10.56** **(16.3%)**	**0.68** **(1.0%)**	**64.45** **(100%)**

b) Founder events (Standard deviations)

	A **(Africa)**	**B** **(eastern of South America)**	**C** **(Amazon)**	**D** **(Andes)**	**E** **(Mexico and Central America)**	**F** **(Antilles)**	**G** **(Hawaii)**	
A **(Africa)**	**-**	**0** **(0)**	**0** **(0)**	**0** **(0)**	**0** **(0)**	**0** **(0)**	**0** **(0)**	**0** **(0%)**
B **(eastern of South America)**	**0** **(0)**	**-**	**0.06** **(0.24)**	**0.09** **(0.29)**	**0.07** **(0.26)**	**0** **(0)**	**0.01** **(0.1)**	**0.23** **(5%)**
C **(Amazon)**	**0** **(0)**	**0.01** **(0.1)**	**-**	**0.04** **(0.2)**	**0.02** **(0.14)**	**0** **(0)**	**0** **(0)**	**0.07** **(1.5%)**
D **(Andes)**	**0** **(0)**	**0.73** **(0.71)**	**0.05** **(0.22)**	**-**	**0.36** **(0.61)**	**0.04** **(0.2)**	**0.28** **(0.45)**	**1.46** **(31.8%)**
E **(Mexico and Central America)**	**0** **(0)**	**0.73** **(0.72)**	**0.29** **(0.56)**	**1.54** **(1.14)**	**-**	**0.08** **(0.27)**	**0** **(0)**	**2.64** **(57.6%)**
F (Antilles)	**0**	**0.01**	**0**	**0.01**	**0**	**-**	**0**	

	(0)	(0.1)	(0)	(0.1)	(0)		(0)	0.02 (0.4%)
G (Hawaii)	0 (0)	0 (0)	0.01 (0.1)	0.15 (0.36)	0 (0)	0 (0)	-	0.16 (3.4%)
	0 (0%)	1.48 (32.3%)	0.41 (8.9%)	1.83 (39.9%)	0.45 (9.8%)	0.12 (2.6%)	0.29 (6.6%)	4.58 (100%)

c) Range expansions (Standard deviations)

	A (Africa)	B (eastern of South America)	C (Amazon)	D (Andes)	E (Mexico and Central America)	F (Antilles)	G (Hawaii)	
A (Africa)	-	0.17 (0.38)	0.1 (0.3)	0.1 (0.3)	0.02 (0.14)	0.12 (0.33)	0 (0)	0.51 (0.5%)
B (eastern of South America)	0.13 (0.34)	-	2.62 (1.35)	2.05 (1.43)	0.71 (0.82)	1.02 (1.05)	0.01 (0.1)	6.54 (11%)
C (Amazon)	0.1 (0.3)	2.11 (1.47)	-	2.49 (1.62)	1.47 (1.39)	1.82 (1.31)	0.01 (0.1)	8 (13.4%)
D (Andes)	0.25 (0.44)	4.03 (1.79)	5.31 (2.03)	-	4.67 (2.31)	3.34 (1.55)	0.3 (0.46)	17.9 (30%)
E (Mexico and Central America)	0.39 (0.49)	2.86 (1.48)	5.71 (1.98)	8.29 (2.46)	-	4.14 (1.49)	0.02 (0.14)	21.41 (35.9%)
F (Antilles)	0.13 (0.34)	1.07 (1.09)	1.79 (1.17)	1.33 (1.11)	0.88 (0.81)	-	0.05 (0.22)	5.25 (8.3%)
G (Hawaii)	0 (0)	0.02 (0.14)	0.03 (0.17)	0.19 (0.42)	0.02 (0.14)	0 (0)	-	0.26 (0.4%)

	1 **(1.6%)**	**10.26** **(17.2%)**	**15.56** **(26.1%)**	**14.45** **(24.2%)**	**7.77** **(13%)**	**10.44** **(17.5%)**	**0.39** **(0.6%)**	**59.87** **(100%)**

Appendix A - Supplementary data

Table S1 – Selected nucleotide substitution models for each partition obtained through JModelTest. The first column represents the partition, the second column indicates the sequence length and the third column specifies the models.

- Region	Size (bp)	Model
*rbc*L	1250	GTR+I+G
*rps*4 gene	592	GTR+I+G
*rps*4 IGS	433	GTR+I+G
trnL-trnF	846	TIM1+I+G
TOTAL	3120	

Table S2 – Sympatry by bioregion. These results are based on all 100 BSM models. The columns represent the bioregions, and the rows indicate the average sympatry for each bioregion.

Mean/ Bioregions	Africa (A)	Eastern South America (B)	Amazon (C)	Andes (D)	Mexico+Central America (E)	Antilles (F)

Sympatry	0	3.96	0.15	7.35	27.78	0.01

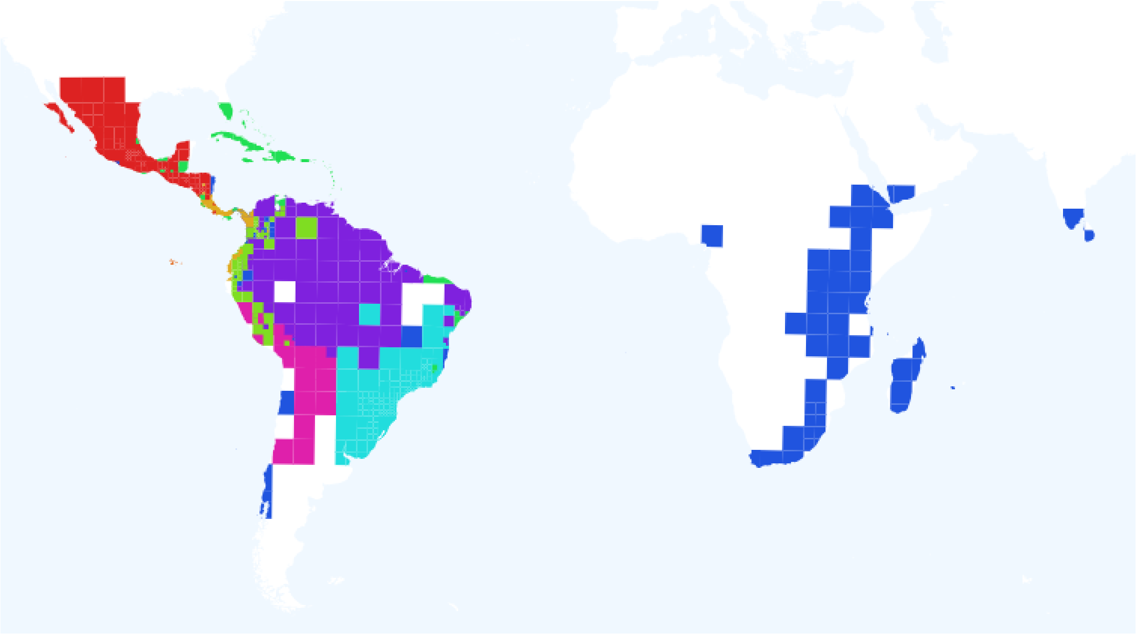

Figure S1 – Bioregion definitions by Infomap. Dark blue = Africa (A); light blue = Eastern South America (B); purple = Amazon (C); pink and light green = Andes (D); red and yellow = Mexico+Central America (E); dark green = Antilles (F).

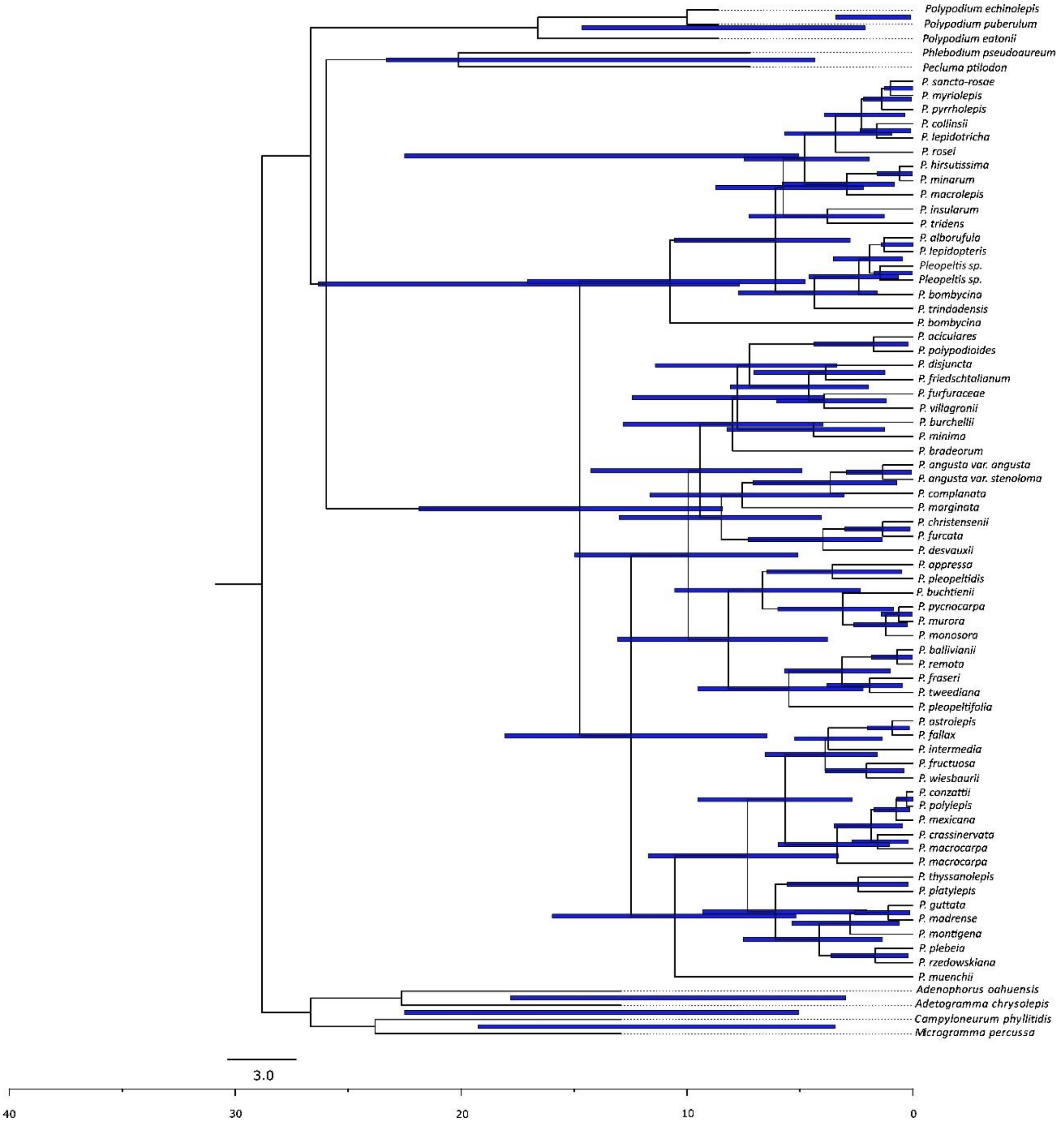

Figure S2 – Maximum credibility tree based on the combined dataset using *rbcL*, *rps4*, and *trnL-trnF* sequences of *Pleopeltis*. Horizontal blue bars correspond to 95% HPD intervals for median ages. Dates are provided millions of years ago (Mya).

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