THE ANDES OF COLOMBIA AND ECUADOR AS A BARRIER TO FERN AND LYCOPHYTE SPECIES FROM MESOAMERICA[1,2]

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Abstract

We compiled a list of the fern and lycophyte species that occur in Mesoamerica and extend into Colombia and Ecuador, where they are restricted to the western side of the Andes; that is, they occur only west of the crest of the easternmost cordillera and are absent from that cordillera's eastern slope and in adjacent Amazonia. We found 131 species with this Mesoamerican and west-of-the-eastern-cordillera distribution. Those 131 species constitute 7% of the total 1805 fern and lycophyte species that have been recorded west of the crest of the easternmost cordillera in Colombia and Ecuador. All 131 species have elevation ranges with midpoints at low (0–900 m) or middle (900–3000 m) elevations, and none occur above 3000 m. This suggests the cordilleras have acted as elevational barriers. We also investigated the blockage of these 131 species by each of the Andean cordilleras. We found that 75 (57%) of the 131 species were limited eastward by the western cordillera, 15 (11%) by the central cordillera (this cordillera in Colombia only), and 40 (31%) by the eastern cordillera. If estimates of endemics to the western Andean region are considered, then at least 20%–22% of all fern and lycophyte species in the region are restricted west of the crest of the easternmost cordillera. Although usually exhibiting larger geographic distributions compared to angiosperms, fern and lycophyte species may show significant geographic restriction by mountain ranges.

Resumen

Recopilamos una lista de las especies de helechos y licófitas que se encuentran en Mesoamérica y que se extienden hasta Colombia y Ecuador, pero que se encuentran restringidos al occidente de los Andes, es decir, solo se encuentran hasta la vertiente occidental de la cordillera oriental, y están ausentes en la vertiente oriental de la cordillera oriental de Colombia y Ecuador y en la Amazonia. Encontramos 131 especies con distribución mesoamericana y que además se encuentran al occidente de la cordillera oriental, las cuales constituyen el 7% del total de las 1805 especies de helechos y licófitas que han sido registradas al occidente de la cordillera oriental de Colombia y Ecuador. Las 131 especies tienen rangos de elevación con puntos medios ubicados en elevaciones bajas (0–900 m) o medias (900–3000 m), y ninguna por encima de los 3000 m de elevación. Esto sugiere que las cordilleras han actuado como barreras de elevación. También investigamos el bloqueo de estas 131 especies por cada una de las cordilleras andinas. Encontramos que 75 (57%) especies estaban limitadas hacia el oriente por la cordillera occidental, 15 (11%) especies por la cordillera central (esta cordillera sólo en Colombia) y 40 (31%) por la cordillera oriental. Si se tienen en cuenta las estimaciones de endemismos para la región andina occidental, al menos el 20%–22% de todas las especies de helechos y licófitas están restringidas al occidente de la cordillera oriental. Aunque usualmente exhiben distribuciones geográficas mayores comparadas con las angiospermas, las especies de helechos y licófitas pueden mostrar una restricción geográfica significativa debido a las cadenas montañosas.

Key words: Biogeography, Chocó region, long-distance dispersal, Neotropics, pteridophytes, vicariance.

Alwyn H. Gentry was one of the most prolific botanists of all time. Despite his untimely death in 1993 at age 48, he made more than 80,000 gatherings of plants and authored more than 200 publications, including phytogeographic studies, systematic and floristic treatments, and his landmark *Field Guide to the Families and Genera of Woody Plants of Northwest South America* (1993). Gentry wrote extensively on phytogeography, one of his favorite topics, and he was among the first botanists to emphasize the importance of the Andes as

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[1] This article is part of a special collection commemorating the life and work of Alwyn Gentry (1945–1993), a highly respected botanist whose contributions left a lasting impact on the field. August 3, 2023, marked 30 years since his passing. Thomas L.P. Couvreur, Carmen Ulloa Ulloa, and J. Sebastián Tello served as guest editors.

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a barrier to plant dispersal and driver of species diversification (Gentry, 1977, 1986, 1992a; Gentry & Dodson, 1987). Using data from a transect-inventory method he pioneered, he showed that plants west of the Andes, especially in the Chocó region, had a stronger floristic affinity to Central America than to Amazonia (Gentry, 1977, 1978, 1982a, 1982b, 1982c, 1986, 1988). His phytogeographic work on vascular plants in northwestern South America, along with the thousands of ferns he collected, helps provide a foundation for the fern and lycophyte distribution patterns documented here.

The distribution patterns of ferns and lycophytes are influenced by the dispersal of these plants' wind-borne spores (Moran, 2008; Kessler, 2010). The ease with which these spores disperse is evidenced by the wider distributions of the fern and lycophyte species compared to those of angiosperms, and by the overrepresentation of fern and lycophyte species on volcanic islands (Smith, 1972). These observations suggest that spores have few barriers to their dispersal (Tryon, 1972; Barrington, 1993; Moran, 1995a; Moran & Smith, 2001). Yet as pointed out by Moran (1996), the Andes have acted as a barrier to the eastward migration of certain species of ferns and lycophytes that extend from Mesoamerica into western regions of Colombia and Ecuador. These species occur in the Pacific lowlands of Colombia and Ecuador and extend various distances eastward to the crest of the easternmost Andean cordillera, beyond which they are absent eastward (Fig. 1, inset).

The Mesoamerican species that extend into and are confined to the western Andean region of Colombia and Ecuador have been noted by some monographers and floristicians, such as Lellinger (1989) for *Pleopeltis wiesbaurii* (Sodiro) Lellinger, *Pteris navarrensis* Christ, and *Selaginella mollis* A. Braun, and various authors of the fern and lycophyte treatments published in volume 1 of *Flora Mesoamericana* (Davidse et al., 1995). Nevertheless, a large-scale synthesis of species with this distribution pattern has never been attempted. Moran (1996) provided an abstract of the pattern but did not include a list of species. He found that 9% of the fern and lycophyte species in western Colombia and Ecuador extended into Mesoamerica but not east of the Andes. Also, he estimated that 13% of the species in western Colombia and Ecuador were endemic; that is, they did not occur in Mesoamerica or east of the crest of the easternmost cordillera (i.e., on the eastern slopes of the eastern cordillera, or in Amazonia). Together, the two groups of species (i.e., those from Mesoamerica extending into western Colombia and Ecuador, and those endemic to the Andean region west of the crest of the eastern cordillera) represent 22% (9% + 13%) of the total fern and lycophyte flora in the region. For this 22%, the Andes have apparently acted as a barrier to eastward migration.

We provide here, for the first time, a documented list of the fern and lycophyte species in Mesoamerica that extend into western Colombia and/or Ecuador and are restricted by the Andes from occurring farther eastward (Fig. 1). Also, we examine the role of each Andean cordillera (three in Colombia and two in Ecuador) in blocking the eastward migration of fern and lycophyte species.

Methods

study area

The study area consists of the Pacific lowlands of Colombia and Ecuador, the Caribbean region of northern Colombia (including the Sierra Nevada de Santa Marta), and all the Andean cordilleras and intervening valleys except for the eastern slope of the eastern cordilleras of Colombia and Ecuador (Fig. 1). In other words, it includes those regions west of the crest of the eastern cordilleras in Colombia and Ecuador. The southernmost limit of the study area is the Ecuadorian-Peruvian border. In Colombia, the study area includes the geographic regions of the Pacific lowlands, western cordillera, central cordillera, Magdalena River valley, and western slopes of the eastern cordillera. As to political divisions of Colombia, it includes the departments of Antioquia, Atlántico, Bolívar, Boyacá (westernmost region), Caldas, Cauca (western region), Cesar, Chocó, Córdoba, Cundinamarca (western region), Huila (western region), La Guajira, Magdalena, Nariño, North Santander (westernmost region), Quindío, Risaralda, Santander (western region), Sucre, Tolima, and Valle del Cauca. In far northeastern Colombia, the western boundary of the study area is limited by the Serranía de Perijá, a north–south mountain range that separates Colombia from Venezuela (Zulia State). In Ecuador, the study area includes the Pacific lowlands, western cordillera, central valley, and western slopes of the eastern cordillera. This includes the provinces of Azuay (western region), Bolívar, Cañar (western region), Carchi (western region), Chimborazo (western region), Cotopaxi, El Oro, Esmeraldas, Guayas, Imbabura, Loja (western region), Los Ríos, Manabí, Pichincha, Santa Elena, Santo Domingo de los Tsáchilas, and Tungurahua (western region).

To analyze the separate effects of each of the Andean cordilleras as barriers to migration, the study area was subdivided into three regions limited by the cordilleras: Regions A, B, and C (Fig. 1). Region A consists of the Pacific lowlands and the western slopes of the western cordillera up to its crest. Region B consists of the eastern slopes of the western cordillera, the intervening valley (mostly the Valle del Cauca in Colombia), the western slope of the central cordillera in

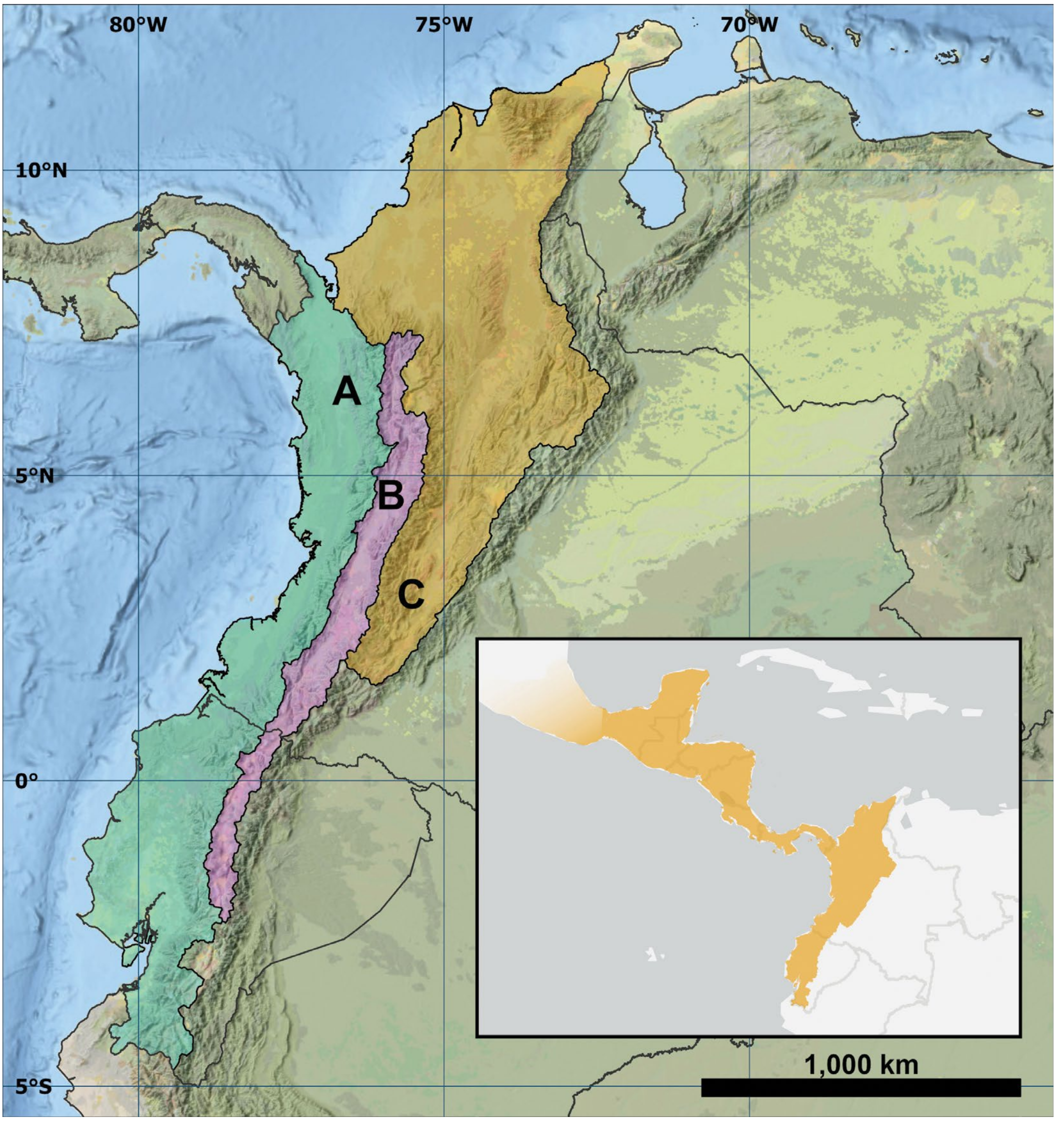

Figure 1. Regions A, B, and C in Colombia and Ecuador. Inset shows the general distribution (including Mesoamerica) of the 131 species studied in this paper (Table 1).

Colombia, and the western slope of the eastern cordillera in Ecuador.

In Ecuador, which has only two cordilleras, the cordillera directly east is the eastern cordillera. In Colombia, however, three cordilleras are present, and therefore the cordillera directly east is the central one. Region C, located entirely in Colombia, consists of the eastern slopes of the central cordillera, the intervening Magdalena River valley, the adjacent Caribbean region to the north (including the Sierra Nevada de Santa Marta), and the western slopes of the eastern cordillera.

SPECIES STUDIED

For this study, we included only those species that occurred in both Mesoamerica (sensu Davidse et al., 1995) and in western Colombia and western Ecuador, where they were limited to Regions A, B, and C as defined above. Species were excluded if they occurred east of Region C (Fig. 1), such as on the eastern slopes of the easternmost cordillera, or in Amazonia, or in the northern coastal range of Venezuela. Also excluded were species endemic to Regions A, B, and C, because they do not occur in Mesoamerica.

DATA COLLECTION

To determine which species of Mesoamerican ferns and lycophytes were limited to Regions A, B, and C in Colombia and Ecuador, we consulted floras, monographs, and taxonomic papers (see Literature Cited). We also consulted online databases such as the Missouri Botanical Garden's Tropicos® (<https://www.tropicos.org/home>), the Pteridophyte Collections Consortium's Pteridoportal (<https://www.pteridoportal.org/portal/index.php>), the website of the Global Biodiversity Information Facility (GBIF) (<https://www.gbif.org>), the Digital Herbarium of the National University of Colombia, COL (<http://www.biovirtual.unal.edu.co/es/colecciones/search/plants/>), and the Aarhus University Herbarium (AUU) database (<https://www.aubot.dk/search_form.php>). These databases were interpreted with caution because we found that some specimens were misidentified or mapped incorrectly, a problem that has been noted for other plant groups (e.g., Goodwin et al., 2015).

Elevation ranges (Table 1) were obtained from the literature, and from these the midpoint of the elevation ranges was determined. If, for example, a species had an elevation range from sea level to 1200 m, then its midpoint was considered to be 600 m. Following Balslev's (1988) criteria in his phytogeographic analysis of the vascular plants of Ecuador, we defined lowland species as those with an elevation midpoint below 900 m; middle-elevation species at 900–3000 m, and high-elevation species above 3000 m.

DETERMINATION OF THE TOTAL NUMBER OF FERN AND LYCOPHYTE SPECIES IN REGIONS A, B, AND C

To determine the total number of fern and lycophyte species in the three regions, we relied primarily on occurrence records of vouchered specimens downloaded from the Global Biodiversity Information Facility (GBIF, 2024). To avoid duplication of species occurrences resulting from synonyms, species names were standardized in R using two packages: pteridocat (FTOL Working Group, 2022) and taxastand (Nitta, 2024). The names used by the pteridocat taxonomic database (FTOL Working Group, 2022) are based on the World Ferns database (Hassler, 2022), which largely follows the generic names used by the Pteridophyte Phylogeny Group I (PPG I, 2016). Generic names published after PPG I have since been added to pteridocat, and a full list is given in Nitta et al. (2022). Following the removal of synonyms, erroneous data points were removed from occurrence records using the CoordinateCleaner R package (Zizka et al., 2019). After this, a sampling polygon was selected on a map of Regions A, B, and C (Fig. 1) using a series of R packages including rgbif (Chamberlain et al., 2024), sf (Pebesma, 2018), and rnaturalearth (Massicotte & South, 2023). Polygons were delineated using the Watershed tool from the Hydrology Toolset in ArcGIS Pro (ESRI, 2024). This was done through a 1-km-resolution digital elevation model layer derived from WorldClim data (Fick & Hijmans, 2017). A D-8–type direction of water flow was generated using the Flow Direction tool. These tools, in conjunction with specific Point Pour locations positioned at the base of drainage basins, were utilized to model the topographic boundaries of water drainage, which were used to estimate the crests of the mountain ranges. All occurrence records within the polygons selected were analyzed in R version 4.3.2 (R Core Team, 2023). These occurrences were used to calculate the total number of fern and lycophyte species occurring in Regions A, B, and C (Fig. 1). The list of total species occurrences was inspected, and 15 nonnative species were removed. Conversely, we added 30 species not in GBIF but known to occur in Regions A, B, and C based on literature reports (these species are indicated in Table 1 with an asterisk).

MAPS

The distribution map of the study area (Fig. 1) was generated using WorldClim topography (Fick & Hijmans, 2017) and mapping software by ESRI ArcGIS Pro (2024), which was also used to produce the dot-distribution maps (Figs. 2, 3) using specimen data from GBIF (2024).

RESULTS

We found 131 species of Mesoamerican ferns that extend into Colombia and Ecuador and are restricted to Regions A, B, and C; that is, west of the crest of the easternmost cordillera (Table 1). Appendix 1 contains notes about the taxonomy and distribution of some of these species. The second half of Appendix 1 discusses certain species not included in the table. These were previously reported as present in Mesoamerica and, in Colombia and Ecuador, as being restricted to one or more of Regions A, B, and C. Today, however, these species are known to occur outside these regions and were thus excluded from Table 1, as explained in Appendix 1.

The summation of GBIF records within Regions A, B, and C yielded a total of 30,729 occurrences of ferns and 4899 of lycophytes. These represented a total of 1775 species (1569 ferns and 206 lycophytes). Also, we found 30 additional species known to occur in Regions A, B, and C based on literature reports but not present in GBIF. Most of these 30 species not in GBIF were recently described. These additional 30 species

Table 1. The species of Mesoamerican ferns and lycophytes that extend into Colombia and Ecuador and are confined to the western side of the Andes (i.e., Regions A, B, and C as defined in the Methods section). In the first column, an asterisk (*) after a name indicates species not found in the Global Biodiversity Information Facility (GBIF) or, if in GBIF, not recorded for Regions A, B, or C. The abbreviations in the distribution column are Mex = Mexico; G = Guatemala; B = Belize; H = Honduras; ES = El Salvador; N = Nicaragua; CR = Costa Rica; P = Panama; Col = western Colombia, west of the eastern cordillera; Ec = Ecuador, west of the eastern cordillera; Ven = Venezuela.

Species	Distribution	Regions	Elevation (m)	Source(s)
Adiantum acrolobum A. Rojas*	N, CR, P, Col	B	0–500	Rojas-Alvarado, 2008b
Adiantum andicola Liebm.	Mex, G, H, ES, N, CR, P, Col	B, C	1000–3400	Moran, 1995n; Murillo-P. et al., 2016
Adiantum cordatum Maxon	P, Col	A	0–600	Zimmer, 1995
Adiantum isthmicum B. Zimmer	P, Ec	A	0–450	Zimmer, 1989, 1995 (see discussion in Appendix 1)
Adiantum seemannii Hook.	Mex, G, H, N, CR, P, Col	A	0–700	Scamman, 1960; Lellinger, 1989; Zimmer, 1995; Mickel & Smith, 2004
Alsophila firma (Baker) D. S. Conant	Mex, B, G, H, N, CR, P, Col, Ec	A	500–2500	Gastony, 1973; Conant, 1983; Tryon, 1986; Riba, 1995; Mickel & Smith, 2004; L. D. Cárdenas et al., 2019
Amauropelta inaequans (C. Chr.) Salino & T. E. Almeida	N, CR, P, Col, Ec	B	1000–2200	Smith, 1983, 1995c; Murillo-P. et al., 2016
Asplenium holophlebium Baker	N, CR, P, Col, Ec	A, B, C	0–1200	Stolze, 1986; Adams, 1995a
Asplenium oblongatum Mett. ex Kuhn	P, Col	A	600–1500	Forero & Gentry, 1989; Adams, 1995a
Asplenium rosenstockianum Brade	N, CR, P, Col, Ec	A, B	1000–2400	Stolze, 1986; Adams, 1995a
Austroblechnum wardiae (Mickel & Beitel) Gasper & V. A. O. Dittrich	Mex, ES, N, CR, P, Col, Ec	A, B, C	600–2300	Moran, 1995c; Mickel & Smith, 2004; Murillo-P. et al., 2016
Ctenitis equestris (Kunze) Ching*	Mex, G, H, ES, N, CR, P, Col	B	700–2500	Moran, 1995q; Mickel & Smith, 2004; Toro M., 2009
Cyathea acutidens (Christ) Domin	CR, Col	A	1100–1800	Lehnert et al., 2021, fig. 2A (map)
Cyathea chocoensis (Stolze) Lehnert	CR, Col	A	750–1650	Stolze, 1974; Lehnert, 2012
Cyathea choricarpa (Maxon) Domin	CR, P, Col	A, B	30–1700	Stolze, 1974; Moran, 1995i; Lehnert, 2012
Cyathea conformis (R. M. Tryon) Stolze*	P, Col	A, B, C	0–1400	Moran, 1995d; Murillo-P. et al., 2016
Cyathea darienensis R. C. Moran	P, Col, Ec	A	50–1400	Moran, 1995d; Lehnert, 2016
Cyathea falcata (Kuhn) Domin	P, Col	A	200–600	Moran, 1995d; Murillo-P. et al., 2016
Cyathea multiflora Sm.	B?, G, CR, P, Col	A, B, C	400–1750	Lehnert, 2011; Lehnert et al., 2021, fig. 2B (map)
Cyathea nigripes (C. Chr.) Domin	CR, Col, Ec	A, B, C	300–1400(–2000)	Lehnert, 2016
Cyathea nodulifera R. C. Moran	CR, P, Col	A	300–700	Moran, 1995d; L. D. Cárdenas et al., 2019
Cyathea petiolata (C. Chr.) R. M. Tryon	P, Col	A, C	0–430	Moran, 1995d; Lehnert & Weigand, 2017
Cyathea pinnula (Christ) Domin*	CR, P, Col	A	20–2000	Moran, 1995d; Lehner, 2011, 2021, fig. 2B (map) (see discussion in Appendix 1)
Cyathea retanae A. Rojas*	P, Col	A	1100–1500	Lehnert et al., 2021, fig. 2B (map)

Table 1. Continued.

Species	Distribution	Regions	Elevation (m)	Source(s)
Cyathea stolzei A. R. Sm. ex Lellinger	CR, P, Ec	A	100–1000	Moran, 1995d; Lehnert, 2012
Cyathea suprastrigosa (Christ) Maxon	CR, P, Col	A, B	(1400–)2400–2800(–3100)	Moran, 1995d; Giraldo G. et al., 2003; Murillo-P. et al., 2016
Cyathea williamsii (Maxon) Domin	P, Col	A	300–1300(–1500)	Moran, 1995d; Lehnert, 2012 (see discussion in Appendix 1)
Cyclodium chocoense (A. R. Sm.) Bohn & Labiak	P, Col, Ec	A, C	100–400	Smith, 1986; Bohn et al., 2019, 2021
Danaea cuspidopsis Keskiniva & Tuomisto*	CR, P, Col, Ec	A	550–2300	Keskiniva & Tuomisto, 2024
Danaea gracilis Tuomisto & Keskiniva*	P, Col, Ec	A, B	0–600(–1000)	Keskiniva & Tuomisto, 2022
Danaea megaphylla A. Rojas*	P, Col	A	0–550	Rojas-Alvarado, 2013
Danaea pumila Keskiniva & Tuomisto*	P, Col	A	250–600	Keskiniva & Tuomisto, 2024
Danaea stricta Tuomisto & Keskiniva*	P, Col	A, B	0–1000	Keskiniva & Tuomisto, 2022
Dennstaedtia dissecta (Sw.) T. Moore	(Greater Antilles), CR, P, Col, Ec	A, B, C	100–800	Navarrete & Øllgaard, 2000
Dennstaedtia werckleana (Christ) Navarrete & B. Øllg.*	CR, P, Ec	A	600–1800	Navarrete & Øllgaard, 2000
Dicksonia navarrensis Christ	Mex, G, H, ES, N, CR, P, Col, Ec	A	940–2450(–2800)	Noben et al., 2018
Didymochlaena mesoamericana Li Bing Zhang & H. Shang*	Mex, B, G, H, N, CR, P, Col, Ec	A	200–2200	Shang & Zhang, 2023, fig. 3 (map) (see discussion in Appendix 1)
Didymoglossum godmanii (Hook.) Ebihara & Dubuisson	(Cuba), Mex, B, G, H, N, CR, P, Col	C	100–800	Wessels Boer, 1962; Mickel & Smith, 2004; Idárraga-Piedrahíta et al., 2011
Didymoglossum gourlianum (Grev. ex J. Sm.) Pic. Serm.	N, CR, P, Col, Ec	A	0–500	Wessels Boer, 1962; Pacheco, 1995; Murillo-A., 2004
Diplazium ceratolepis (Christ) Christ	CR, P, Ec	A	500–2000	Stolze et al., 1994; Adams, 1995b; Pacheco & Moran, 1999
Diplazium croatianum C. D. Adams*	CR, P, Col	B	750–900	Rojas-Alvarado, 1996; Idárraga-Piedrahíta, 2011
Diplazium moccennianum (Sodiro) C. Chr.	B, CR, P, Col, Ec	A, B	30–1500	Forero & Gentry, 1989; Stolze et al., 1994; Rojas-Alvarado, 2012 (see discussion in Appendix 1)
Diplazium pactile Lellinger	G, N, CR, P, Ec	A	600–3200	Lellinger, 1977a; Stolze et al., 1994; Pacheco & Moran, 1999
Diplazium palmense Rosenst.	CR, P, Col, Ec	A, B, C	100–1800	Stolze et al., 1994; Adams, 1995b
Diplazium panamense C. D. Adams	P, Col, Ec	A	450–2200	Adams, 1992, 1995b (see discussion in Appendix 1)
Diplazium pseudocarnosum A. Rojas	CR, P, Col	A	380–1450	Rojas-Alvarado, 2012 (see discussion in Appendix 1)
Diplazium sanctae-rosae Christ	CR, P, Col, Ec	A	1000–2500	Adams, 1995b (see discussion in Appendix 1)
Diplazium sanderi (C. Chr.) Pacheco	CR, P, Col, Ec	A	100–1500	Stolze et al., 1994; Pacheco & Moran, 1999
Diplazium seemannii T. Moore	CR, P, Col, Ec	A	400–1600	Forero & Gentry, 1989; Stolze et al., 1994; Adams, 1995b

Table 1. Continued.

Species	Distribution	Regions	Elevation (m)	Source(s)
Diplazium striatastrum Lellinger	Mex, B, H, N, CR, P, Col, Ec	A, B, C	100–1400(–2200)	Lellinger, 1977b; Adams, 1995b (see discussion in Appendix 1)
Diplazium turubalense Rosenst.	CR, P, Col	A	100–800	Adams, 1995b; Rojas-Alvarado, 2008a (see discussion in Appendix 1)
Elaphoglossum adrianae A. Rojas*	CR, P, Col	A	0–1900	Rojas-Alvarado, 2002; Rojas-Alvarado & Rodríguez-Duque, 2012; Murillo-P. et al., 2016
Elaphoglossum amygdalifolium (Mett. ex Kuhn) Christ	(Cuba), G, H, N, CR, P, Col, Ec	A	0–1500	Mickel, 1995; Lagomarsino et al., 2012
Elaphoglossum atrobarbatum Mickel	P, Col	C	100–1250	Rojas-Alvarado, 2002
Elaphoglossum backhouseanum T. Moore	CR, P, Col	A	(35–)80–850	Matos et al., 2021, fig. 2E (map)
Elaphoglossum decursivum Mickel	(Dominican Republic, Haiti), Mex, G, H, ES, N, CR, P, Col	A, B	450–2200	Matos et al., 2019, fig. 8B (map)
Elaphoglossum delgadilloanum A. Rojas*	CR, P, Col	A	950–1450	Rojas-Alvarado & Rodríguez-Duque, 2012; Murillo-P. et al., 2016
Elaphoglossum doanense L. D. Gómez	CR, P, Col, Ec	A, C	10–1800	Matos et al., 2018, fig. 5 (map) (see discussion in Appendix 1)
Elaphoglossum furfuraceum (Mett. ex Kuhn) Christ*	N, CR, P, Col	A	(600–)900–4000	Mickel, 1995; Rojas-Alvarado & Rodríguez-Duque, 2012
Elaphoglossum gomezianum A. Rojas*	CR, P, Col	A	1550–1650	Rojas-Alvarado, 2002
Elaphoglossum latum (Mickel) Atehortúa ex Mickel*	(Dominican Republic, Haiti), Mex, B, G, H, CR, P, Col, Ec	A	0–1000	Matos et al., 2021, fig. 2A (map)
Elaphoglossum longicrure Christ	N, CR, P, Col	A	0–2700	Mickel, 1995; Rojas-Alvarado, 2002
Elaphoglossum maculatum Mickel	P, Col	A, B, C	300–1400	Mickel, 1992, 1995; Idárraga-Piedrahíta et al., 2011; Murillo-P. et al., 2016
Elaphoglossum micropogon Mickel	CR, P, Col	A, B	1000–1400	Mickel, 1995; Idárraga-Piedrahíta et al., 2011
Elaphoglossum mitorrhizum Mickel	CR, P, Ec, Col	A	400–1500	Mickel, 1995 (see discussion in Appendix 1)
Elaphoglossum neeanum A. Rojas	P, Col	A, C	800–1850	Rojas-Alvarado, 2003
Elaphoglossum oblanceolatum C. Chr.	CR, P, Col, Ec	A, B	100–1300	Mickel, 1995; Murillo-P. et al., 2016 (see discussion in Appendix 1)
Elaphoglossum omissum Mickel	CR, P, Col	A	100–1700	Mickel, 1995; Murillo-A., 2004
Elaphoglossum orosiense A. Rojas*	CR, Col	A	1600–1800	Rojas-Alvarado, 2002
Elaphoglossum phoras Mickel	N, CR, P, Col, Ec	A, B, C	800–1800	Mickel, 1995 (see discussion in Appendix 1)
Elaphoglossum proliferans Maxon & C. V. Morton	CR, P, Col	B, C	800–1600	Mickel, 1995; Murillo-P. et al., 2016
Elaphoglossum pseudoboryanum Mickel	P, Col, Ec	A, B, C	950–2000	Mickel, 1995; Murillo-P. et al., 2016

Table 1. Continued.

Species	Distribution	Regions	Elevation (m)	Source(s)
Elaphoglossum siliquoides (Jenman) C. Chr.	(Jamaica, Dominican Republic), G, N, CR, P, Ec	A	400–2000	Mickel, 1995 (see discussion in Appendix 1)
Elaphoglossum stenoglossum Mickel	CR, P, Col	A, B	2200–2900	Mickel, 1995 (see discussion in Appendix 1)
Goniopteris francoana (E. Fourn.) Á. Löve & D. Löve	N, P, CR, Col, Ec	A	0–650	Smith, 1983, 1995c
Goniopteris fraseri (Mett. ex Kuhn) Salino & A. R. Sm.	P, Col, Ec	A	0–2200	Smith, 1983, 1995c
Goniopteris urbanii (Sodiro) Salino & T. E. Almeida*	N, CR, P, Col, Ec	A, B	0–1400	Smith, 1983, 1995c
Grammitis bufonis L. D. Gómez	P, Col, Ec	A	900–2000	Moran & Smith, 1995; Idárraga-Piedrahíta et al., 2011
Hymenasplenium volubile (N. Murak. & R. C. Moran) L. Regalado & Prada	CR, P, Col, Ec	A, B, C	300–2200	Murakami & Moran, 1993
Hymenophyllum crassipetiolatum Stolze	CR, P, Col	B, C	1500–3000	Mickel & Smith, 2004; Idárraga-Piedrahíta et al., 2011 (see discussion in Appendix 1)
Hymenophyllum horizontale C. V. Morton	CR, P, Col	A, B, C	400–1400	Pacheco, 1995; Idárraga-Piedrahíta et al., 2011 (see discussion in Appendix 1)
Hymenophyllum paucicarpum Jenman	(Greater Antilles), Mex, H, CR, P, Col	C	800–3200	Mickel & Smith, 2004; Murillo-P. et al., 2016
Hymenophyllum saenzianum L. D. Gómez	CR, P, Col	C	500–2800	Pacheco, 1995; Idárraga-Piedrahíta et al., 2011
Hymenophyllum semiglabrum Rosenst.	CR, P, Col	B	1000–2500	Pacheco, 1995; Idárraga-Piedrahíta et al., 2011
Jamesonia glaberrima (Maxon) Christenh.	N, CR, P, Col, Ec	A, B, C	1200–2950	Tryon, 1970; Toro M., 2009; Murillo-P. et al., 2016
Leucotrichum mitchelliae (Baker) Labiak*	(Cuba, Dominican Republic, Haiti), Mex, B, G, H, CR, P	A	100–1000	Forero-M. & Murillo, 2010, Labiak et al., 2010;
Lindsaea seemannii J. Sm.*	P, Col	A	0–500	Moran, 1995p; Murillo-P. et al., 2016
Lomariopsis vestita E. Fourn.	Mex, B, G, H, N, CR, P, Col, Ec	A, C	0–1100	Moran, 2000
Maxonia apiifolia (Sw.) C. Chr. var. *dualis* (Donn. Sm.) C. Chr.	G, H, N, CR, P, Ec	A	0–1200	Christensen, 1916; Moran, 1995e; Moran & Labiak, 2015, fig. 6 (map)
Megalastrum ctenitoides A. Rojas	CR, Col	A	1300–1400	Rojas-Alvarado, 2001a; Moran & Prado, 2010; Moran et al., 2014[a]
Megalastrum reductum A. Rojas	P, Col, Ec	A	100–1300	Moran et al., 2014b
Meniscium turrialbae (Rosenst.) Pic. Serm.	N, CR, P, Col, Ec	A	0–700	Fernandes & Salino, 2020
Microgramma brunei (Wercklé ex Christ) Lellinger	CR, P, Col, Ec	A	200–1400	Moran, 1995f
Oleandra costaricensis Maxon*	CR, P, Col	A	600–1900	Scamman, 1961; Palacios-Rios, 1995a
Phlegmariurus dichaeoides (Maxon) B. Øllg.	G, H, N, CR, P, Col, Ec	A, B, C	100–1350	Øllgaard, 1988, 1995, 2019; Øllgaard & Testo, 2021

Table 1. Continued.

Species	Distribution	Regions	Elevation (m)	Source(s)
Pityrogramma dealbata (C. Presl) R. M. Tryon*	Mex, G, H, ES, N, CR, P, Col	A	200–1300	Mickel & Smith, 2004; Murillo-P. et al., 2016
Pleopeltis christensenii A. R. Sm.	H, N, CR, P, Col, Ec	A, B, C	0–500(–1400)	Christensen, 1929; Moran, 1995m; Murillo-A., 2004 (see discussion in Appendix 1)
Pleopeltis wiesbaurii (Sodiro) Lellinger	CR, P, Col, Ec	A, B, C	200–1300	Lorea-Hernández, 1995
Polytaenium chlorosporum (Mickel & Beitel) E. H. Crane	Mex, N, CR, P, Col	A	900–1800	Moran, 1995o; Mickel & Smith, 2004; Murillo-P. et al., 2016
Pteris navarrensis Christ	CR, P, Col, Ec	A	450–2100	Moran, 1995g; Arbeláez, 1996 (see discussion in Appendix 1)
Radiovittaria minima (Baker) E. H. Crane	CR, P, Col	C	800–1900	Moran, 1995l; Idárraga-Piedrahíta et al., 2011
Saccoloma quadripinnatum A. Rojas	CR, P, Col	A, B, C	400–800(–1200)	Rojas-Alvarado, 2010
Salpichlaena volubilis (Kaulf.) J. Sm. subsp. *thalassica* (Grayum & R. C. Moran) G. G. Cárdenas & Tuomisto	N, CR, P, Col, Ec	A, B, C	25–2400	G. G. Cárdenas et al., 2019, map 1 (see discussion in Appendix 1)
Selaginella arthritica Alston	CR, P, Col, Ec	A, B, C	0–1700	Alston et al., 1981; Forero & Gentry, 1989; Somers & Moran, 1995; Vega-Betancur et al., 2003
Selaginella euclimax Alston ex Crabbe & Jermy	P, Col	A, B, C	1100–1300	Alston et al., 1981; Fraile, 1995; Vega-Betancur et al., 2003
Selaginella mollis A. Braun	B, H, N, CR, P, Col	A, C	0–1800	Alston et al., 1981; Lellinger, 1989; Mickel & Valdespino, 1992; Fraile, 1995; Vega-Betancur et al., 2003
Selaginella tanyclada Alston ex Crabbe & Jermy	P, Col	A	0–1000	Alston et al., 1981; Lellinger, 1989
Serpocaulon maritimum (Hieron.) A. R. Sm.	N, CR, P, Col, Ec	A	50–1600	Sanín et al., 2023, map 65F (see discussion in Appendix 1)
Serpocaulon ptilorhizon (Christ) A. R. Sm.	N, CR, P, Col	A, C	650–2680	Sanín et al., 2023 (see discussion in Appendix 1)
Sphaeropteris brunei (Christ) R. M. Tryon	CR, P, Col	C	500–2000	Tryon, 1971; Palacios-Rios, 1995b; Giraldo G. et al., 2003; Murillo-P. et al., 2016
Steiropteris seemannii (J. Sm.) Salino & T. E. Almeida	CR, Col, Ec	A	0–1900	Smith, 1980, 1983, 1995c
Steiropteris valdepilosa (Baker) Pic. Serm.	CR, P, Col, Ec	A	150–1200	Smith, 1980, 1983, 1995c (see discussion in Appendix 1)
Sticherus gnidioides (Mett.) Nakai	P, Col, Ec	A	0–600	Moran, 1995j; Andersen & Øllgaard, 2001
Stigmatopteris killipiana Lellinger	CR, P, Col, Ec	A	70–1450	Moran, 1991, map 4
Stigmatopteris michaelis (Baker) C. Chr.	P, Col, Ec	A	300–1000	Moran, 1991, map 7
Stigmatopteris sordida (Maxon) C. Chr.	Mex, G, H, N, CR, P, Col, Ec	A, C	70–1450	Moran, 1991, map 11
Tectaria acutiloba (Hieron.) Maxon*	B, H, N, CR, P, Col, Ec	A	40–60	Rojas-Alvarado, 2004 (see discussion in Appendix 1)
Tectaria athyrioides (Baker) C. Chr.	CR, P, Col	A	100–1200(–2000)	Moran, 1995k; Ramírez P. & Macias P., 2007; Murillo-P. et al., 2016

Table 1. Continued.

Species	Distribution	Regions	Elevation (m)	Source(s)
Tectaria darienensis A. Rojas	P, Col	A, C	0–900	Rojas-Alvarado, 2001a, 2006
Tectaria faberiana A. Rojas*	B, CR, P, Col	A	50–700	Rojas-Alvarado, 2001a, 2006 (see discussion in Appendix 1)
Tectaria longipinnata A. Rojas*	P, Col	A	0–500	Rojas-Alvarado, 2001a (see discussion in Appendix 1)
Tectaria moranii Li Bing Zhang & G. D. Tang*	B, CR, P, Col	C	0–300	Tang & Zhang, 2018 (see discussion in Appendix 1)
Tectaria panamensis (Hook.) R. M. Tryon & A. F. Tryon	Mex, G, B, H, N, CR, P, Col, Ec	A, C	0–400(–700)	Moran, 1995k; Mickel & Smith, 2004; Gómez & Arbaláez, 2009
Tectaria rivalis (Mett. ex Kuhn) C. Chr.	B, G, H, ES, N, CR, P, Col, Ec	A	0–1200	Grayum, 1987; Moran, 1995h
Tectaria rivalis var. *gemmipara* A. Rojas	G, H, B, ES, N, CR, Col, Ec	A	0–1200	Rojas-Alvarado, 2006 (see discussion in Appendix 1)
Terpsichore alsophilicola (Christ) A. R. Sm.	CR, P, Col, Ec	A	200–900(–1300)	Smith & Moran, 1995; Murillo-P. et al., 2016
Terpsichore lehmanniana (Hieron.) A. R. Sm.	B, G, H, ES, N, CR, P, Col	A, B, C	400–1000(–1400)	Smith & Moran, 1995
Trichomanes anceps Hook.*	H, N, CR, P, Col, Ec	A, B, C	0–1700	Pacheco, 1995 (see discussion in Appendix 1)
Trichomanes kalbreyeri Baker	CR, P, Col, Ec	A	1100–1500	Pacheco, 1995 (see discussion in Appendix 1)
Trichomanes micayense Hieron.	CR, Col, Ec	A	500–1600	Jørgensen & León-Yánez, 1999; Rojas-Alvarado, 2001b; Ramírez P. & Macias P., 2007
Triplophyllum chocoense J. Prado & R. C. Moran*	P, Col	A	70–900	Prado & Moran, 2008

are indicated in Table 1 by an asterisk. Adding these 30 species to the 1775 in GBIF brings the total number of fern and lycophyte species recorded from Regions A, B, and C to 1805.

Of these 1805 fern and lycophyte species occurring in Regions A, B, and C, a total of 131 (7%) species were confined to Regions A, B, and C in Colombia and Ecuador and also occurred in Mesoamerica (Fig. 1, Table 2). Of these 131 species, 75 (57%) were limited to Region A, 15 (11%) to Region B, and 40 (31%) to Region C (Table 2, Fig. 3). We found that of the 1805 fern and lycophyte species occurring in Regions A, B, and C, about 1000 also occurred east of the crest of the easternmost cordillera.

As to elevation, all 131 species (Table 1) had elevation midpoints at either low (0–900 m) or middle elevations (901–3000 m) (Table 3). No species had an elevation midpoint above 3000 m (Fig. 4).

Discussion

The Mesoamerican and western Andean distribution is a significant floristic pattern among ferns and lycophytes. Exhibiting the pattern are 131 species (Table 1), which constitute 9% of the 1358 species of ferns and lycophytes treated in *Flora Mesoamericana* (Davidse et al., 1995) and 7% of the 1805 species of ferns and lycophytes that we found in Regions A, B, and C of Colombia and Ecuador (Fig. 1).

All 131 species (Table 1) have had their ranges limited eastward by the Andean cordilleras (Table 2). In this respect, the most important cordillera has been the western one, whose crest forms the boundary between Regions A and B (Fig. 1). This cordillera limits the eastward extent of 75 (57%) of the 131 species. In terms of restriction, the second most important cordillera was the eastern one, whose crest defines the eastern boundary of Region C (Fig. 1). A total of 40 (31%) of the 131 species were limited in their eastward extent to Region C. In contrast, Region B played a relatively minor role, confining the eastward distribution of only 15 (11%) of the 131 species (Table 2). This lesser role likely reflects the region's smaller areal extent and thus fewer species (Fig. 1), and the fact that much of the region consists of dry valleys that tend to support fewer species of ferns and lycophytes (Salazar R. et al., 2002; Cardona et al., 2012; Galeano, 2016).

The elevation midpoints of all 131 species in Table 1 were at low (0–900 m) to middle (901–3000 m) elevations (Fig. 4, Table 3). In both, the percentage of species

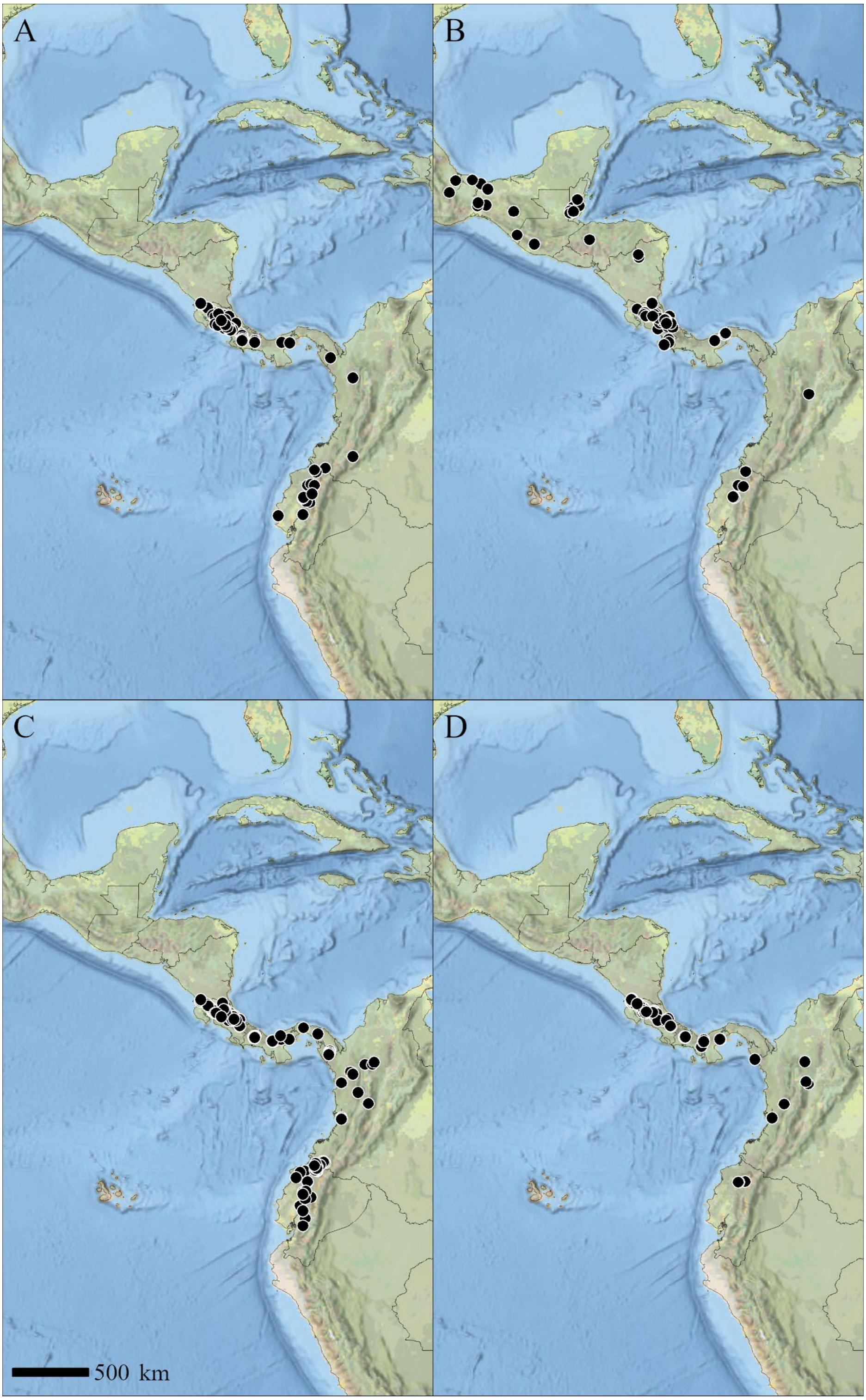

Figure 2. Distribution of four fern species that occur in Mesoamerica and are restricted west of the crest of the easternmost cordillera in Ecuador and Colombia. —A. *Pleopeltis wiesbaurii* (Sodiro) Lellinger. —B. *Stigmatopteris sordida* (Maxon) C. Chr. —C. *Asplenium holophlebium* Baker. —D. *Elaphoglossum doanense* L. D. Gómez.

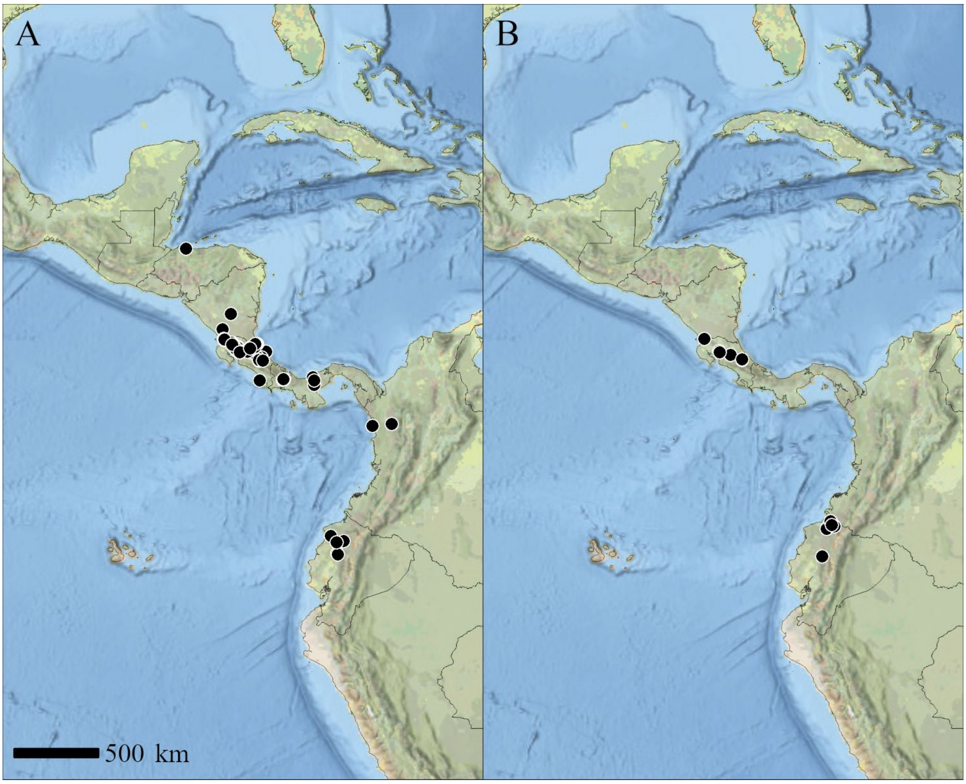

Figure 3. Distribution of two fern species that occur in Mesoamerica and are restricted west of the crest of the western cordillera in Ecuador and Colombia. —A. *Elaphoglossum amygdalifolium* (Mett. ex Kuhn) Christ. —B. *Steiropteris seemannii* (J. Sm.) Salino & T. E. Almeida.

was nearly equal, with roughly 52% falling in the low-elevation range and 47% at middle elevations. None of the 131 species had a midpoint above 3000 m. These data indicate that the cordilleras have been an elevational barrier to species distributions. This finding is exceptionally notable for lowland species, which are expected to have the broadest distributions (Tryon, 1972; Suissa & Sundue, 2020).

Possible habitat differences to the east of the crest of the eastern cordillera are unlikely to have played a role in preventing the 131 species (Table 1) from migrating to that side. We found from GBIF occurrences that nearly 1000 species of ferns and lycophytes that occur in Regions A, B, and C also occur east of the crest of the eastern cordillera, suggesting that suitable habitat is present on both sides of the Andes. Importantly, nearly all the species in Table 1 grow in wet forests (pers. obs.), a habitat that occurs abundantly on both sides (Balslev, 1988; Galeano, 2016). Among the many species occurring on both sides are *Ascogrammitis an-*

Table 2. Analysis of the number of fern and lycophyte species in Regions A, B, and C for the Colombian and Ecuadorian Andes. The third column shows the number of species in the Global Biodiversity Information Facility (GBIF) that are restricted to Region A, B, or C in Colombia and Ecuador. The right-hand column shows the number of species restricted eastward by region. For each species, the region(s) of occurrence is given in Table 1.

Region	No. spp. in GBIF (no. spp. in Table 1 not in GBIF)	No. spp. in GBIF unique to region (no. spp. in Table 1 not in GBIF)	No. spp. in Table 1	No. spp. in Table 1 at their eastern limit (% of the 131 spp. in Table 1)
A	1475 (26)	503 (20)	116	75 (57%)
B	921 (7)	78 (3)	41	15 (11%)
C	1040 (3)	195 (1)	40	40 (31%)

Table 3. Number of species limited eastward by each region (A, B, C) according to their elevational midpoints.

Region	No. spp. with midpoint ≤ 900 m	No. spp. with midpoint 901–3000 m	No. spp. with midpoint > 3000 m
A	34	38	0
B	10	5	0
C	25	19	0
Totals	69	62	0

fractuosa (Kunze ex Klotzsch) Sundue (Sundue, 2010), *Elaphoglossum ciliatum* (C. Presl) T. Moore (Vasco et al., 2009), and *Megalastrum pulverulentum* (Poir.) A. R. Sm. & R. C. Moran (Moran et al., 2014a, 2014b).

Although the Andean cordilleras have acted as a barrier to the 131 species of ferns and lycophytes in Table 1, these species do not tell the whole story. Also restricted by the Andes are species endemic to Regions A, B, and C. Two estimates of fern and lycophyte endemism have been made for the Chocó region, a phytogeographic zone lying entirely within Region A. For the Chocó region, Lellinger (1975) and Moran (1996) estimated 15% and 13% (respectively) endemism of fern and lycophyte species. If these percentages (15% and 13%) are added to the 7% of Mesoamerican species extending into and confined by Regions A, B, and C (Table 1), the total is 20%–22%. This is a minimum percentage restriction because it considers only species endemic to part of Region A (the Chocó phytogeographic region); it does not consider endemics in Regions B and C, whose ranges could also be considered restricted by the cordilleras. Compiling a list of all the endemic fern and lycophyte species in these three regions would require a careful review of specimen records and specimens themselves, consultation with other taxonomic experts, and a review of the literature. While beyond the scope of this study, documenting these endemics would be a worthwhile endeavor for future research.

Aside from the endemics and the 131 species in Table 1, another group of species restricted by the Andes occurs only on the eastern, or Amazonian, side; that is, the area east of Region C (Fig. 1). These species occur on the eastern slope of the eastern cordillera and/or in Amazonia. For these species, the eastern cordillera has been a barrier to westward migration. Among the hundreds of such species are *Metaxya contamanensis* Tuomisto & G. G. Cárdenas (Cárdenas et al., 2016), *Polybotrya crassirhizoma* Lellinger (Moran, 1987), and *Serpocaulon latipes* (Langsd. & L. Fisch.) A. R. Sm. (Sanín et al., 2023). The documentation of these and other eastern-side species would provide yet another worthy project for study.

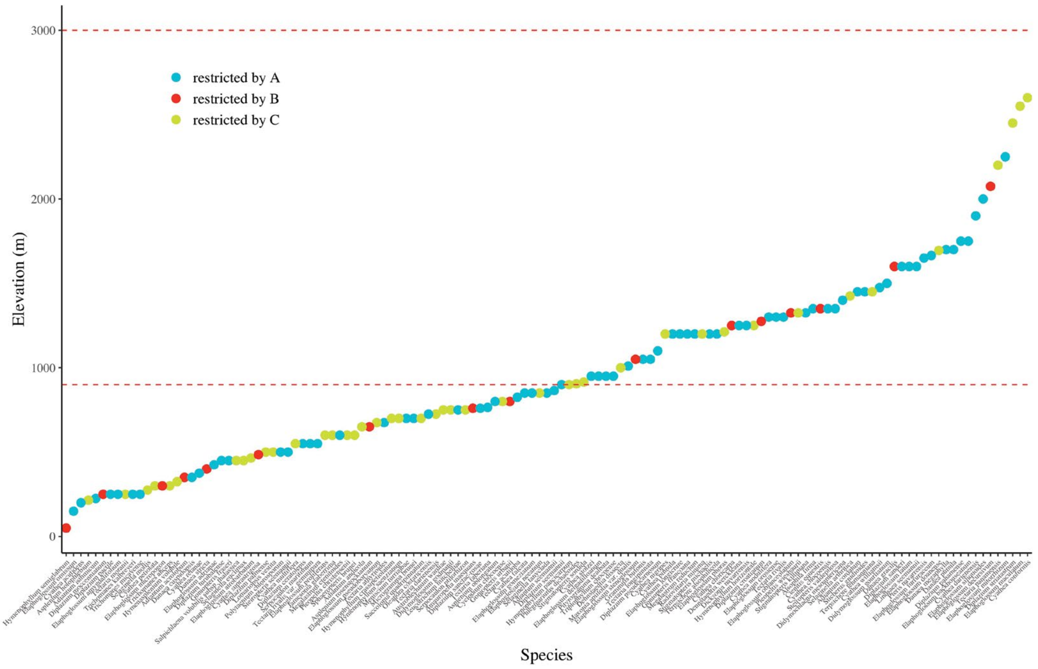

Figure 4. Elevation midpoints of the 131 species of ferns and lycophytes that occur in Mesoamerica and are restricted west of the crest of the easternmost Andean cordillera in Ecuador and Colombia (i.e., to Regions A, B, and C of this study). Complete elevation ranges for each species are given in Table 1.

Dispersed by wind-borne spores, ferns and lycophytes generally exhibit larger geographic ranges compared to angiosperms, which typically disperse by heavier propagules (Smith, 1972; Moran, 1996; Kessler, 2010). Accordingly, ferns and lycophytes would be expected to show less restriction than seed plants to Regions A, B, and C. This appears to be the case, although comparison is hindered by the lack of large-scale documentation for angiosperm species restricted to Regions A, B, and C. Instances of species restricted to one side of the Andes or the other can usually be found in taxonomic monographs of seed-plant clades. For example, Grayum's (1996) partial revision of the aroid clade *Philodendron* Schott subg. *Pteromischum* (Schott) Mayo found that all but one of the Colombian and Ecuadorian species of the clade occurred on only one side. In other words, the species of *Philodendron* subg. *Pteromischum* show nearly complete restriction to either the east or west side of the crest of the eastern cordillera. In contrast, ferns and lycophytes show less restriction, with only 21%–23% of the species confined to the western side (see above paragraph); the other 77%–79% occur on both sides. These percentages agree with ferns and lycophytes generally exhibiting wider ranges compared to those of seed plants (Smith, 1972).

An intriguing extension of the research presented here would be molecular phylogenetic studies of the species in Table 1 and their most closely related species. Such studies, especially if accompanied by divergence-time estimates, should provide insight as to whether the species and their sister taxa evolved autochthonously on the western side of the Andes or in Mesoamerica, or whether they evolved by vicariance resulting from the final uplift of the northern Andes about 4.5 million years ago (Ma) (Hoorn et al., 2010), an event that might have severed formerly continuous ancestral populations.

Future fieldwork and taxonomic studies will undoubtedly reveal species to be added or deleted from Table 1. Two instances of this that occurred while the present study was underway came from *Didymochlaena* Desv. and *Danaea* Sm. In the former genus, all American plants had long been considered to belong to a single species called *Didymochlaena truncatula* (Sw.) J. Sm. (e.g., Shimek, 1897; Tryon & Tryon, 1982; Stolze, 1983; Mickel & Smith, 2004). Today, that name is applied to an Asian species, and in the American tropics, *Didymochlaena* is construed as having six species (Shang & Zhang, 2023). We found that one of these six species, *D. mesoamericana* Li Bing Zhang & H. Shang, exhibits the Mesoamerican and western Andean distribution pattern, thus providing an additional species for Table 1 (see discussion in Appendix 1).

In contrast, an instance of a species excluded from Table 1 while this study was underway comes from the American tropical genus *Danaea*. In their study of this genus, Keskiniva and Tuomisto (2024) found that *D. wendlandii* Richb. f., a species previously thought (e.g., by Camus & Pérez-García, 1995; Tuomisto & Moran, 2001) to occur in Costa Rica, Panama, western Colombia, and western Ecuador, was endemic to Costa Rica and Panama, and the plants previously called this in Colombia and Ecuador represented an undescribed species. Accordingly, *D. wendlandii* was excluded from Table 1 (see further discussion in Appendix 1).

These examples from *Didymochlaena* and *Danaea* highlight how biogeographic analysis is ultimately based on taxonomic studies that determine what the species are and where they occur. Such studies are, in turn, based on specimens collected in the field and preserved in the world's herbaria. This is exactly the kind of research carried out by Alwyn H. Gentry throughout his productive career in many parts of the American tropics (Gentry, 1977, 1978, 1982a, 1982b, 1982c, 1986, 1988). His numerous published papers and extensive collections have provided us with not only raw materials for biogeographic studies, but also inspiration for further research.

DATA AVAILABILITY STATEMENT

The data for the total number of ferns and lycophytes in the study area are available in the Dryad Digital Repository at <https://doi.org/10.5061/dryad.79cnp5j3v>. The specific files in the repository are:

- Shapefile for Regions A, B, and C of Colombia and Ecuador
- R script used to calculate the total number of fern and lycophyte species in Regions A, B, and C
- Cleaned list of species present in Regions A, B, and C of Colombia and Ecuador

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Appendix 1. Notes about Table 1.

CERTAIN SPECIES INCLUDED IN THE TABLE

Adiantum isthmicum B. Zimmer was reported by Zimmer (1989, 1995) as endemic to Panama; however, a specimen of this species (*Barfod et al. 48261*, AAU!) was later identified by Zimmer from the western side of the Andes at 200 m in Esmeraldas Province, Ecuador. Accordingly, this species is listed in Table 1.

Cyathea pinnula (Christ) Domin in western Colombia (i.e., Chocó Department) differs slightly from plants in Costa Rica (type) and Panama. The pinnules of the Colombian plants (e.g., *Killip 35279*, *39084*, both MO!, and *Gentry & Brand M. 36866*, MO!) are more acute (vs. obtuse in Costa Rica and Panama), the costule scales flatter or only slightly arched (vs. bullate), and the veins adaxially glabrous or nearly so (vs. moderately pubescent). Until these differences can be assessed, it seems best to include the species in Table 1, in agreement with its presence in Colombia as reported by previous workers (e.g., Moran, 1995d; Lehnert, 2021).

Cyathea williamsii (Maxon) Domin has sometimes been cited as occurring in southern Venezuela (e.g., Barrington, 1978; Moran, 1995d; Smith, 1995b), which would make it ineligible for inclusion in Table 1. The southern Venezuelan plants, however, are now referred to as *C. maguirei* (R. M. Tryon) Lehnert (Lehnert, 2012). Thus, *C. williamsii* is listed in Table 1.

Didymochlaena mesoamericana Li Bing Zhang & H. Shang was cited by Shang and Zhang (2023) as occurring from Mexico to Panama and Colombia (Antioquia), but they did not specify which side of the Andes the species occurred on in Colombia. All Colombian specimens we have seen of this species were collected on the western side of the Andes. Shang and Zhang (2023) did not cite Ecuador in the distribution of this species, but we have seen several specimens from the western side of the Ecuadorian Andes (e.g., Cañar Province, *Vargas & Defas 5583*, MO!; Esmeraldas, *Clark & Troya 630*, MO!). We have not seen any specimens of this species from the eastern side of the Andes in Ecuador. Accordingly, *D. mesoamericana* is included in Table 1.

Diplazium moccennianum (Sodiro) C. Chr. is newly reported here from Panama based on *Correa et al. 3980* (MO!) and *Santamaria et al. 7341* (MO!). The species (type from western Ecuador) has also been reported by Arana et al. (2017) and Mynssen and Sylvestre (2019) from Bolivia, southeastern coastal Brazil, and northern Argentina. They noted that *D. moccennianum* formed a complex with seven other morphologically similar species. The taxonomy of this complex needs to be clarified; until then, we maintain *D. moccennianum* in the strict sense (i.e., as not occurring in southern South America) and include it in Table 1.

Diplazium panamense C. D. Adams was described by Adams (1992, 1995b), who listed it as endemic to Panama. We find, however, that *D. oellgaardii* Stolze, known from Carchi and Esmeraldas Provinces in western Ecuador (Stolze et al., 1994), agrees well with the type of *D. panamense*, which is the earlier name. Thus, the species occurs both in Mesoamerica and on the western side of the Andes in South America. Accordingly, the species is included in Table 1.

Diplazium pseudocarnosum A. Rojas was stated in the protologue (Rojas-Alvarado, 2012) as occurring in the state of Aragua, Venezuela, based on *Croat 21432* (MO!), as well as in Panama and western Colombia. In our opinion, this specimen does not represent *D. pseudocarnosum*, although we are unsure which species it is. Because we have confirmed specimens of *D. pseudocarnosum* from Costa Rica, Panama, and western Colombia only, we include this species in Table 1.

Diplazium sanctae-rosae Christ was cited by Adams (1995b) as occurring in Costa Rica, Panama, and Ecuador, but there was no indication of which side(s) of the Andes the Ecuadorian specimen was collected on. All Ecuadorian specimens of this species that we have seen come from west of the eastern cordillera; that is, in either Region A or B. Also, we report this species as new to Colombia (Region A) based on *Alston 9717* (MO!) from the department of El Valle del Cauca, and *Gerardo 9286* (UC [3 sheets] images!) from the department of Nariño. Because of these reports from western Colombia and Ecuador, this species is included in Table 1.

Diplazium striatastrum Lellinger was described by Lellinger (1977b) based on specimens collected mostly from Mesoamerica, western Colombia, and western Ecuador. He cited three specimens from northern Venezuela that, according to A. R. Smith (pers. comm.), appear to be *D. striatum* (L.) C. Presl. Also, Lellinger (1977b) cited a specimen (*King 6090*, US) from the eastern side of the Colombian Andes in the department of Putumayo. Similarly, this specimen appears to us to be *D. striatum.* With the exclusion of these misidentified specimens from northern Venezuela and eastern Colombia, *D. striastastrum* is known only from the Mesoamerican and western Andean region. Accordingly, we include it in Table 1.

Diplazium turubalense Rosenst. was cited for Nicaragua by Gómez and Arbeláez (2009), but the specimens cited represent *D. wilsonii* (Baker) Diels. Accordingly, Nicaragua has not been included in the distribution of this species in Table 1.

Elaphoglossum doanense L. D. Gómez has been erroneously cited for several regions. Mickel (1995) reported it for Venezuela but did not cite a specimen. We have not seen a specimen from that country, and neither did Matos et al. (2019) in their monographic treatment of the clade that contains *E. doanense*. Gómez and Arbeláez (2009) cited *E. doanense* from Nicaragua based on three specimens (*Grijalva 297*, CR, MO!; *Pipoly 5922*, CR, MO!; *Rueda et al. 14680*, MO!); however, Rojas-Alvarado (2002) regarded these as *E. decursivum* Mickel, with which Matos et al. (2019) agreed. Finally, Rojas-Alvarado (2002) cited the species from the province of Zamora-Chinchipe, Ecuador, on the eastern side of the Andes, but the voucher specimen (*Øllgaard 74977*, NY!) represents *E. nidiforme* Mickel (Matos et al., 2018). In short, and as concluded by Matos et al. (2019), *E. doanense* occurs only in the Mesoamerican and western Andean region. Accordingly, it is included in Table 1.

Elaphoglossum mitorrhizum Mickel was cited by Mickel (1995) as endemic to Costa Rica and Panama. We have found specimens of this species from the department of Antioquia, Colombia (*Sanín et al. 5108*, MO!, NY!) and the province of Esmeraldas, Ecuador (*Bass et al. 146*, MO!, NY!). Thus, this species is included in Table 1.

Elaphoglossum oblanceolatum C. Chr. was cited by Mickel (1995) for Costa Rica, Panama, and western Ecuador. We have also seen Colombian specimens from the departments of Antioquia (*Pipoly et al. 16571*, MO!) and Nariño (*Croat 69608*, MO!). Thus, Colombia has been added to the distribution of this species in Table 1.

Elaphoglossum phoras Mickel was cited by Mickel (1995) for Nicaragua, Costa Rica, Panama, and western Colombia. Here we report this species from Pichincha Province in northwestern Ecuador (*Croat 72085*, MO!; *Moran & Rohrbach 5231*, MO!). Therefore, Ecuador has been added to the distribution of this species in Table 1.

Elaphoglossum siliquoides (Jenman) C. Chr. was cited by Mickel (1995) for Mesoamerica but not Colombia or Ecuador. We have not seen specimens from Colombia but know of two from Esmeraldas Province in northwestern Ecuador (*Clark & Troya 663*, MO!; *Bass et al. 99*, MO!). Based on these two specimens, the species is included in Table 1.

Elaphoglossum stenoglossum Mickel, which belongs to section *Setosa* (Christ) Mickel & Atehortúa, was cited by Mickel (1995) as occurring only in Costa Rica, Panama, and Colombia. Subsequently, the species was cited by Rojas-Alvarado

(2002) for Bolivia (*Kessler et al. 7145*, UC) and Venezuela (*Steyermark 55235*, F, MO!, US). The Bolivian reports represent misidentifications (Kessler et al., 2018), and the Venezuelan gathering represents a mixed collection of two unidentified species (R. Moran, pers. obs.), both of which belong to section *Elaphoglossum*, not section *Setosa*. With the exclusion of Venezuela and Bolivia, *E. stenoglossum* occurs only in the Mesoamerican and western Andean region. Accordingly, it is included in Table 1.

Hymenophyllum crassipetiolatum Stolze was the name used by Stolze (although qualified with a "cf.") in 1991 when he annotated a specimen (*Marín 109*, F image!) from the state of Mérida, Venezuela. The specimen appears to represent *H. lindenii* Hook., a similar species that is common in the Mérida region (A. R. Smith, pers. comm.). Because *H. crassipetiolatum* is known only from Mesoamerica and west of the Andes in Colombia and Ecuador, it is included here in Table 1.

Hymenophyllum horizontale C. V. Morton was reported to occur in Napo Province on the eastern side of the Ecuadorian Andes (Jørgensen & León-Yánez, 1999), which would disqualify it from inclusion in Table 1. The specimen upon which the report is based (*Cerón et al. 5816*, MO!) was misidentified, however; it represents the similar *H. sieberi* (Bosch) C. Presl.

Pleopeltis christensenii A. R. Sm. was cited by Moran (1995m, as "*Dicranoglossum panamense* (Hook.) Lellinger") from western Colombia but not western Ecuador. In Table 1, we list this species from Ecuador based on *Moran & Rohrbach 5282* (MO!, QCA!, QCNE!).

Pteris navarrensis Christ was attributed by Moran (1995g) to Peru, but the specimen upon which this record was based is unknown. It might represent a misidentification of *P. livida* Mett. or *P. podophylla* Sw., both of which are similar, large, pedate-leaved species occurring in Peru (Tryon & Stolze, 1989). In their treatment of *Pteris* for Peru, Tryon and Stolze (1989) did not mention *P. navarrensis*. Arbeláez (1996) treated this species in Colombia but did not list Peru in its distribution. For these reasons, we consider *P. navarrensis* as occurring only in the Mesoamerican and western Andean region of Colombia and Ecuador. Accordingly, it is included in Table 1.

Salpichlaena volubilis (Kaulf.) J. Sm. subsp. *thalassica* (Grayum & R. C. Moran) G. G. Cárdenas & Tuomisto is tentatively included in Table 1. All specimens cited in the monograph and phylogenetic analysis by G. Cárdenas et al. (2019) were from the western side of the Andes, but in the protologue by Moran (1990), a single specimen was cited from the eastern side of the Andes in the department of Meta (*Philipson & Idrobo 1838*, BM!). Until this specimen can be further investigated, we include this species in Table 1 to bring attention to the matter.

Serpocaulon maritimum A. R. Sm. was mapped by Sanín et al. (2023, fig. 65F) as occurring on the western side of the Andes except for one specimen on the eastern side in central Ecuador. This specimen (*Bell 290*, RB; D. Sanín, pers. comm.) was mapped in error. It was collected in "Pichincha Province, at confluence of Río Toachi and Pilatón," a locality on the western side of the Andes, thus agreeing with the inclusion of this species in Table 1. *Serpocaulon maritimum* was also cited for Peru by Smith et al. (2006), but in their monograph of *Serpocaulon*, Sanín et al. (2023) did not cite a specimen from that country. Accordingly, Peru is not listed in the distribution of this species (Table 1). In short, *S. maritimum* is known in South America only from the western side of the Andes in Colombia and Ecuador.

Serpocaulon ptilorhizon (Christ) A. R. Sm. has long been considered to occur only in Nicaragua, Costa Rica, Panama, and Colombia (e.g., by Lellinger, 1989; Moran, 1995b). Smith et al. (2018), however, tentatively applied this name to a Bolivian species of *Serpocaulon* with similar rhizome scales and laminar cutting, noting that these Bolivian plants might not be conspecific with *S. ptilorhizon* (type from Costa Rica). The Bolivian plants are now treated as *S. subandinum* (Sodiro) A. R. Sm. (D. Sanín, pers. comm.).

Tectaria acutiloba (Hieron.) Maxon, as recognized for this paper, was included by Moran (1995h) as part of *T. mexicana* (Fée) C. V. Morton, a highly variable species. The two are similar in leaf size and cutting, but *T. acutiloba* differs in having less pubescence along the leaf axes abaxially, and ascending pinnae and pinnules. Also, *T. acutiloba* is typically rheophytic, whereas *T. mexicana* grows in upland soils away from streams (R. C. Moran, pers. obs.).

Tectaria faberiana A. Rojas is cited here for the first time from Belize based on *Brewer & Dourson 5821* (MO!) and *Brewer et al. 5660* (MO!).

Tectaria longipinnata A. Rojas has been considered endemic to Panama (Rojas-Alvarado, 2001a), but we have seen a specimen from the department of Chocó, Colombia (*Forero et al. 1972*, COL image!, MO!). Thus, this species is included in Table 1.

Tectaria moranii Li Bing Zhang & G. D. Tang was described by Tang and Zhang (2018) based on a single specimen from Costa Rica. We found additional specimens of this species from Belize (*Davidse 36477*, MO!), Panama (*Ibáñez et al. 2400*, MO!), and the department of Antioquia, Colombia (*Fonnegra et al. 7079*, MO!). Accordingly, this species is included in Table 1.

Tectaria rivalis (Mett. ex Kuhn) C. Chr. var. *gemmipara* A. Rojas is tentatively included in Table 1. It is said to differ from variety *rivalis* by the presence of buds at the pinna bases (Rojas-Alvarado, 2006). Given that this is the only difference, variety *gemmipara* might represent part of the variation in *T. rivalis* var. *rivalis* and thus not merit taxonomic distinction. We have been unable to find specimens or online images of this variety. Further study is needed.

Trichomanes anceps Hook. is a name used here for the plants previously called *T. elegans* Rich. in Mesoamerica, western Colombia, and western Ecuador (e.g., by Lellinger, 1989; Pacheco, 1995). Our use of the name should be considered tentative until it can be lectotypified. The syntypes also include specimens from Asia, and the matter is being studied by J. Dubuisson (pers. comm.). *Trichomanes anceps* has strikingly blue-green iridescent laminae with tissue three cells thick at the segment tips, and thus these tips appear opaque and without individual cells discernible under a dissecting microscope. In contrast, *T. elegans* (type from French Guiana) represents a different species occurring primarily in the Guianas and Amazonia (J. Dubuisson, pers. comm.). Its laminae are noniridescent adaxially, and the lamina tissue is only one cell thick at the tips of the ultimate segments, so that the tips appear translucent with individual cells discernible under a dissecting microscope.

Trichomanes kalbreyeri Baker has been previously cited as occurring in Costa Rica, Panama, and Colombia (Pacheco, 1995). We found specimens from northwestern Ecuador (e.g., *Øllgaard et al. 57587*, AAU!) and therefore have included that country in the distribution of this species in Table 1.

Certain Species Not Included in the Table

The following species are excluded from Table 1, even though they have been cited in the taxonomic literature as occurring in Mesoamerica and only on the western side of the Andes in Colombia and Ecuador. Reasons why they are excluded from Table 1 are provided.

Alansmia longa (C. Chr.) Moguel & M. Kessler was cited (as *Terpsichore longa* (C. Chr.) A. R. Sm.) by Smith and Moran (1995) for Mesoamerica, western Colombia, and western Ecuador. All South American specimens were collected on the western side of the Andes except for *Holm-Nielsen & Jeppesen 653* (AAU image!; cited by Moguel & Kessler, 2013), from the eastern side of the Andes in Napo Province, Ecuador. Accordingly, *A. longa* is excluded from Table 1.

Asplenium excelsum Lellinger was listed by Adams (1995a) as occurring in Nicaragua, Costa Rica, Panama, and Ecuador, but for the latter country, he did not specify which side(s) of the Andes the species occurred on. The species was not included by Stolze (1986) in his treatment of *Asplenium* for Ecuador, and we have been unable to find any specimen of this species from Ecuador or Colombia. Accordingly, we have not included this species in Table 1.

Asplenium minimum M. Martens & Galeotti was cited by Adams (1995a) as occurring in Mexico, Guatemala, Panama, and Colombia. It was not specified which side of the Colombian Andes this species was collected on. Mickel and Smith (2004) did not find specimens of this species from Colombia, and neither did we. The species was not cited in the checklist of ferns and lycophytes of Colombia by Murillo-P. et al. (2016). Because its presence cannot be confirmed for Colombia, the species is excluded from Table 1.

Asplenium rosenstockianum Brade was cited by Adams (1995a) as occurring in Nicaragua, Costa Rica, Panama, western Colombia, and western Ecuador. Although most specimens of this species come from these areas, we have found specimens from the eastern side of the Andes of Ecuador (e.g., from Napo, *Palacios 5385*, MO!; Loja, *Croat 92012*, MO!; and Zamora-Chinchipe, *Moran & Rohrbach 5398*, MO!). These eastern occurrences exclude the species from Table 1.

Bolbitis simplex R. C. Moran, which grows in wet forests from 600 to 1000 m, is known from Costa Rica and Panama (Rojas-Alvarado, 1996). When reporting the first record of this species in Costa Rica, Rojas-Alvarado (1996) suggested that the species might also occur in western Colombia. We agree that this is likely but have not seen specimens from the region. Accordingly, the species is not included in Table 1.

Ceradenia knightii (Copel.) L. E. Bishop was cited by Smith (1995a) and León-Parra (2012) as occurring in Costa Rica and western Colombia (as well as in Haiti and the Dominican Republic), thus making it eligible for inclusion in Table 1. Recently, however, the species has been collected on the eastern side of the Andes in southern Ecuador (*Olivares et al. 80*, VT image on GBIF!). Accordingly, this species is not included in Table 1.

Cheilanthes skinneri (Hook.) T. Moore, which grows in seasonally dry forests (Moran, pers. obs.), occurs primarily from Mexico to Panama (Mickel & Smith, 2004) and is known in Colombia from a collection in the north made in the Sierra Nevada de Santa Marta in Region C (*H. H. Smith 1087*, MO!). With this distribution, the species qualifies for inclusion in Table 1; however, given its rare and isolated occurrence only in the Sierra Nevada de Santa Marta, it seems unlikely the species has been blocked by the Andes from occurring farther eastward. Accordingly, we have excluded this species in Table 1. This should be reevaluated if future fieldwork finds the species to be more widespread in Region A, B, or C.

Cnemidaria spectabilis (Kunze) R. M. Tryon var. *colombiensis* Stolze (= *Cyathea spectabilis* (Kunze) Domin var. *colombiensis* (Stolze) comb. ined.) was cited by Moran (1995i) from Panama and by Stolze (1974) and Moran (1995i) from the western side of the Colombian Andes. A single specimen, however, is now known from the eastern side of the Andes in Pastaza Province, Ecuador (*Jaramillo 3682*, AAU image!). It was identified as this variety by Tryon (1986), and we agree with the determination. Because of this single eastern Andean occurrence, the species is excluded from Table 1.

Cyathea brunnescens (Barrington) R. C. Moran is endemic to western Colombia and western Ecuador (Moran, 1995d). Lehnert (2016) erroneously cited Costa Rica and Panama for this species (M. Lehnert, pers. comm.). Accordingly, the species is not listed in Table 1.

Cyathea trichiata (Maxon) Domin was cited by Lehnert (2016) as occurring in Costa Rica and Panama and on the western Andean slopes of Colombia and Ecuador. Several gatherings, however, are now known from east of the Andes from Cerro de la Neblina in southern Venezuela (M. Lehnert, pers. comm.). Accordingly, this species is excluded from Table 1.

Danaea wendlandii Rchb. f. was cited by Camus and Pérez-García (1995) and Tuomisto and Moran (2001) as occurring in Nicaragua, Costa Rica, Panama, western Colombia, and western Ecuador. Keskiniva and Tuomisto (2024), however, concluded that plants previously called *D. wendlandii* comprise three closely related species, each with narrow ranges. None of the three species occur in both Mesoamerica and western Colombia or Ecuador. Accordingly, *D. wendlandii* is excluded from Table 1.

Didymoglossum rhipidophyllum (Sloss.) Pic. Serm., a montane species, occurs in Costa Rica and the Sierra Nevada de Santa Marta in northern Colombia (Wessels Boer, 1962). It is excluded from Table 1 because its distribution in Colombia does not appear to be limited eastward by the Andes.

Diplazium werckleanum Christ was cited for Colombia by Adams (1995b), who did not indicate which side of the Andes the species occurred on. We have been unable to find specimens of this species from Colombia. For these two reasons, *D. werckleanum* is excluded from Table 1.

Elaphoglossum biolleyi Christ was cited by Mickel (1995) for Colombia without specifying which side of the Andes the species occurred on, nor was a voucher cited (Murillo-P. et al., 2016). For these reasons, the species is not included in Table 1.

Elaphoglossum boragineum (Sodiro) Christ occurs only in Mesoamerica and the western Andean region (Mickel, 1995) except for one collection from southern Venezuela (*Liesner 18255* p.p., MO!). Because this one occurrence is east of the Andes, the species is excluded from Table 1.

Elaphoglossum curtii Rosenst. was cited by Mickel (1995) as occurring in Costa Rica, Panama, and Colombia, without specifying which side of the Andes in Colombia. This report is based on *Lellinger & de la Sota 906*, US image!), which was subsequently identified by Alexander Rojas-Alvarado as *E. adrianae* A. Rojas, an identification followed here. This leaves *E. curtii* endemic to the mountains of Costa Rica and Panama; therefore, it is not included in Table 1.

Ephemeropteris skinneri (Baker) R. C. Moran & Sundue was found by Moran et al. (2019, fig. 7) to have a Mesoamerican and western Andean distribution in Colombia and Ecuador. Throughout most of its range, it occurs primarily on the Pacific side of Mesoamerica, from Mexico to Costa Rica, where it grows in seasonally dry forests. South of Costa Rica, it occurs rarely in Panama, Colombia, and Ecuador, being known in the latter two countries only from the western side of the Andes. In Venezuela, the species is known from a single collection (*Fendler 163*, YU) from the northern coastal range in the state of Carabobo. Based on this Venezuelan occurrence, we exclude the species from Table 1.

Goniopteris eggersii (Hieron.) Alston (type from the Pacific coast of Ecuador, Manabí Province) was cited by Smith (1983) as occurring in Mesoamerica and on the western side of the

Andes in Colombia and Ecuador. Later, Smith (1992, 1995c) found this species in Amazonian Peru. Because this species is now known from east of the Andes, it is excluded from Table 1.

Goniopteris nicaraguensis (E. Fourn.) Salino & T. E. Almeida, a widespread species in Mesoamerica (Smith, 1995c; Mickel & Smith, 2004), was cited by Murillo-A. (2004) for the department of Chocó, Colombia. We have examined two of the vouchers cited for this report and find that they represent *G. tristis* (Kunze) Brade, a species widespread in Amazonia (Smith, 1995c). Accordingly, *G. nicaraguensis* is not included in Table 1.

Hypoderris nicotianifolia (Baker) R. C. Moran, Labiak & J. Prado was cited by Moran (1995h) as occurring in Mesoamerica, western Colombia, and western Ecuador; however, the species is now known from Amazonian Ecuador and northwestern Venezuela (Moran et al., 2014c).

Metaxya elongata Tuomisto & G. G. Cárdenas has an entirely Mesoamerican and western Andean distribution except for a single specimen collected near the border of the study area in Venezuela (Zulia State) (Cárdenas et al., 2016). Accordingly, this species is excluded from Table 1.

Mickelia bernoullii (Kuhn ex Christ) R. C. Moran, Labiak & Sundue has a mostly Mesoamerican and western Andean distribution (Moran et al., 2010), but a specimen (*Betancur et al. 1865*, HUA!, MO!) is now known from the eastern side of the Andes in the department of Caquetá, Colombia. Accordingly, this species is excluded from Table 1. Also, the species was listed by Moran et al. (2010) for Venezuela, but it is not known to occur in that country (A. R. Smith, pers. comm.).

Parablechnum chiriquanum (Broadh.) Gasper & Salino, which has long been considered endemic to Costa Rica and Panama (e.g., Moran, 1995c), was cited by Murillo-P. et al. (2016) for western Colombia (Chocó Department), based on *Silverstone-Sopkin 4689* (MO!). In our opinion, this specimen represents *P. stipitellatum* (Sodiro) Gasper & Salino, a widely occurring species in the Andes of Colombia and Ecuador (Jørgensen & León-Yánez, 1999; Murillo-P. et al., 2016). Accordingly, *P. chiriquanum* is excluded from Table 1.

Pleopeltis fructuosa (Maxon & Weath.) Lellinger was cited by Lorea-Hernández (1995) from Costa Rica, Panama, and Colombia. It is unknown, however, which side of the Colombian Andes the specimen was collected on, and we have been unable to find specimens of this species from Colombia. For that reason, *P. fructuosa* is excluded from Table 1.

Pleopeltis hookeri A. R. Sm. was cited by Murillo-P. et al. (2016) as occurring from Costa Rica to Peru. The species was not cited in Mesoamerica by Lorea-Hernández (1995), nor have we seen specimens from Costa Rica or Panama. Accordingly, *P. hookeri* is not included in Table 1. All South American specimens of this species that we have seen occur on the western side of the Andes.

Polytaenium intramarginale (Baker ex Jenman) Alston was cited by Moran (1995o) from the Greater Antilles, Costa Rica, Panama, and western Colombia. Subsequently, we have seen specimens from the western side of the Andes in Esmeraldas Province, Ecuador (*Kvist 40842*, AAU!), and from the eastern side of the Andes in Cuzco Department, Peru (*Clark 11428*, US!). Because the latter specimen is from the eastern side of the Andes, *P. intramarginale* is excluded from Table 1. We suspect that further taxonomic studies might find this species to be only a small, narrow-leaved form of *P. lineatum* (Sw.) J. Sm.

Saccoloma sunduei A. Rojas was cited by Rojas-Alvarado (2010) as occurring in Costa Rica, Panama, and the western Andean region of Colombia and Ecuador. A single gathering (*Beitel 85091*, NY!, UC!), however, is now known from east of the Andes from Cerro de la Neblina in southern Venezuela. Accordingly, this species is excluded from Table 1.

Selaginella arthritica Alston was cited by Somers and Moran (1995) as being distributed in Mesoamerica and western Colombia and western Ecuador; however, we have seen specimens from the eastern side of the Andes in southern Ecuador around the region of Podocarpus National Park (e.g., *Madsen & Ellemann 75117*, AAU image!; *Øllgaard et al. 99931*, *105805*, both AAU images!). Accordingly, this species is not included in Table 1.

Selaginella hoffmannii Hieron. occurs throughout Mesoamerica from Mexico to Panama (Fraile, 1995; Mickel & Smith, 2004). It was reported by Jørgensen and León-Yánez (1999) from Pichincha Province, Ecuador, on the western side of the Andes, based on *Barclay & Juajibioy 7893* (MO!). This specimen was subsequently reidentified by Iván Valdespino (PMA) as *S. novae-hollandiae* (Sw.) Spring, and we agree with this identification. Therefore, *S. hoffmannii* is known only from Mesoamerica, not from South America, and is excluded from Table 1.

Sphaeropteris brunei (Christ) R. M. Tryon occurs in Costa Rica, Panama, and northern Colombia (Tryon, 1971). In the latter, it is isolated in the Sierra Nevada de Santa Marta. This species is excluded from Table 1 for the same reasons as *Cheilanthes skinneri* (see above).

Steiropteris polyphlebia (C. Chr.) Salino & T. E. Almeida was reported by Smith (1980, 1983, 1995c) from Mesoamerica and the western side of the Andes in Ecuador and Colombia. We have found two specimens from the eastern side of the Ecuadorian Andes in Pastaza Province (*Fay & Fay 3703*, *3783*, MO!). Therefore, this species is excluded from Table 1.

Steiropteris setulosa (A. R. Sm.) A. R. Sm. & S. E. Fawc. is known with certainty only from the department of Chocó, Colombia (*Lellinger & de la Sota 768*, US image!), but the type (*Seemann s.n.*, K image!, US image!) was labeled "Isthmus of Darien," which might be in Panama or Colombia. Because of the uncertainty, this species is not included in Table 1.

Trichomanes galeottii E. Fourn. occurs only in Mesoamerica and the western Andes (Windisch, 1992; Pacheco, 1995; Mickel & Smith, 2004) except for one collection (*van der Werff 13052*, MO!) from the eastern side of the Andes in southern Ecuador. Accordingly, the species is excluded from Table 1.

Trichomanes ludovicinum Rosenst., long considered endemic to Costa Rica and Panama (Lellinger, 1989; Pacheco, 1995), was cited by Toro M. (2009) for Antioquia, Colombia, based on *Denslow 2620* (HUA not seen, MO not found, WIS image!). This gathering was identified tentatively by Lellinger (1989), who noted on his annotation label that the specimen lacked sori and therefore could not be identified with certainty. Accordingly, we have not included this species in Table 1.

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