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Diversity, distribution, and habitat preferences of *Selaginella* in Java Island, Indonesia

AHMAD DWI SETYAWAN[1,2,♥], **SUTARNO**[3], **SUGIYARTO**[3], **SUNARTO**[1], **GILANG DWI NUGROHO**[4,5], **MUHAMMAD NUR SULTON**[1]
[1]Department of Environmental Science, Faculty of Mathematics and Natural Sciences, Universitas Sebelas Maret. Jl. Ir. Sutami 36A Surakarta 57126, Central Java, Indonesia. Tel./fax.: +62-271-663375, ♥email: volatileoils@gmail.com
[2]Biodiversity Research Group, Universitas Sebelas Maret. Jl. Ir. Sutami 36A Surakarta 57126, Central Java, Indonesia
[3]Department of Biology, Faculty of Mathematics and Natural Sciences, Universitas Sebelas Maret. Jl. Ir. Sutami 36A, Surakarta 57126, Central Java, Indonesia
[4]Biodiversity Study Club, Faculty of Mathematics and Natural Sciences, Universitas Sebelas Maret. Jl. Ir. Sutami 36A Surakarta 57126, Central Java, Indonesia
[5]School of Life Sciences and Technology, Institut Teknologi Bandung. Jl. Ganesa No. 10, Bandung 40132, West Java, Indonesia

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Abstract. *Setyawan AD, Sutarno, Sugiyarto, Sunarto, Nugroho GD, Sulton MN. 2026. Diversity, distribution, and habitat preferences of* Selaginella *in Java Island, Indonesia. Biodiversitas 27 (4): d270442. https://doi.org/10.13057/biodiv/d270442.* *Selaginella* (spike mosses) is an ancient lineage of vascular plants with broad ecological adaptability, yet comprehensive ecological assessments remain limited in many tropical regions. This study investigated the diversity, distribution, and habitat preferences of *Selaginella* across Java Island, Indonesia, along a broad elevational gradient. Field surveys and herbarium records collected between 2007 and 2021 yielded 1,962 occurrence records, comprising 1,362 field collections and 600 herbarium specimens from BO and GBIF. Species occurrences were classified into five elevational zones: colline (0-650 m), submontane (650-1,500 m), montane (1,500-2,400 m), subalpine (2,400-3,000 m), and alpine (>3,000 m). Species diversity indices, Indicator Value Analysis (IndVal), Paired Difference Index (PDI), bipartite networks, and habitat-association analyses were used to evaluate ecological patterns. A total of 21 *Selaginella* species and one unidentified taxon were recorded. Species richness was highest across the colline-montane zones (0-2,400 m asl), with the greatest concentration of species occurring in the submontane zone, where diversity also reached its highest value (H′ = 2.35). Dominant species included *Selaginella plana* (404 individuals), *Selaginella ciliaris* (387), *Selaginella ornata* (214), and *Selaginella willdenowii* (205), whereas several species exhibited restricted distributions and narrow habitat preferences. Community composition differed significantly among elevational zones ($p<0.05$), and indicator-species analyses identified distinct habitat associations, particularly within submontane environments. These findings underscore the influence of elevation on *Selaginella* distribution and highlight the vulnerability of lowland and highland species to threats such as climate warming and habitat fragmentation. Conservation efforts should adopt an elevation-based strategy, emphasizing the protection of humid lowland habitats and maintaining altitudinal corridors in mountainous regions to accommodate climate-driven shifts. Safeguarding *Selaginella* diversity is essential for preserving the ecological integrity of tropical forest ecosystems in Southeast Asia.

Keywords: Elevational gradient, habitat specialization, lycophyte, *Selaginella*, tropical montane forest

INTRODUCTION

The spike mosses (*Selaginella* P. Beauv.) represent an ancient and diverse lineage of vascular plants comprising approximately 700-750 species distributed from tropical and subtropical regions to arctic-alpine environments (Christenhusz and Byng 2016). Around 200 species occur in Southeast Asia, with the highest diversity and endemism concentrated in Papuasia, Borneo, and the Philippines (Camus 1997; Hassler and Swale 2002). In tropical regions, their distribution is strongly influenced by elevation because higher altitudes are generally associated with greater humidity and precipitation (Setyawan et al. 2016, 2017). Although most species thrive in moist habitats, *Selaginella* exhibits remarkable ecological adaptability and can persist under a wide range of environmental conditions. Its long evolutionary history, extending back to the Carboniferous period, and its distinctive morphological and physiological adaptations make the genus an important model for understanding vascular plant evolution (Banks 2009). Moreover, some species have demonstrated a remarkable ability to colonize new and remote habitats rapidly (Klaus et al. 2017).

Indonesia harbors 39 recorded *Selaginella* species, of which 22 occur on Java (Wijayanto 2014). Despite its relatively small size, Java provides an exceptional natural laboratory for studying *Selaginella* ecology because it contains steep environmental gradients within a limited geographic area (Van Steenis 1972; Whitten et al. 1996). Elevation ranges from coastal lowlands to volcanic peaks exceeding 3,600 m asl, creating diverse habitats from humid lowland forests to montane and subalpine ecosystems. Several species, including *S. plana* and *S. ciliaris*, are commonly associated with lowland and foothill environments (Setyawan et al. 2018), whereas *S. opaca*, *S. ornata*, *S. remotifolia*, and *S. zollingeriana* are more characteristic of montane and subalpine habitats (Setyawan et al. 2020a, 2020b, 2021). The occurrence of *Selaginella* across these contrasting environments reflects its ability to tolerate variation in temperature, humidity, and light availability. Many species also exhibit drought-related adaptations, such as leaf curling during dry conditions and rapid recovery after rehydration.

Java's environmental heterogeneity is further enhanced by its geological diversity. Many mountains are active or dormant volcanoes that produce young volcanic soils (andosols), which are porous, mineral-rich, and capable of retaining substantial amounts of moisture (Shoji et al. 1993; Kessler et al. 2011; Supriyadi et al. 2025). These conditions create favorable microhabitats for moisture-dependent understory plants such as *Selaginella*. Species frequently occur on moist slopes, rock crevices, stream banks, and shaded forest floors (Setyawan et al. 2016). While some taxa are restricted to relatively undisturbed forests, others persist in secondary habitats including roadsides, plantations, and scrublands, indicating substantial variation in ecological tolerance among species.

Biogeographically, Java forms part of the Sundaic region, which links the floras of mainland Asia and the Malay Archipelago. This position contributes to high biodiversity and regional endemism. Malesia has long been recognized as a major center of *Selaginella* diversity (Camus 1997), and several Javan species are endemic or restricted to the Greater Sunda region. These distribution patterns are broadly consistent with the phylogenetic and biogeographic framework proposed by Weststrand and Korall (2016b), who identified geographically structured clades within the genus. Recent distribution modeling of montane *Selaginella* species suggested that suitable habitat is concentrated between 1,200 and 2,400 m elevation and may decline substantially under future climate-change scenarios, accompanied by upward elevational shifts (Setyawan et al. 2020a, 2020b, 2021).

Given the complex topography, ecological dynamics, and increasing environmental pressures across Java, understanding the diversity and ecological distribution of *Selaginella* has become increasingly important. However, no comprehensive study has yet integrated diversity, distribution, and habitat preference across the entire island. In particular, no island-wide assessment has combined extensive field surveys and herbarium occurrence records to evaluate ecological distribution patterns using quantitative measures of habitat preference, specialization, and species-habitat association. Existing studies have largely focused on taxonomy, floristics, individual species, or restricted geographic areas, leaving broader ecological patterns insufficiently understood. Furthermore, analytical approaches such as Indicator Value Analysis (IndVal), Paired Difference Index (PDI), bipartite network analysis, and habitat-association metrics have rarely been applied to *Selaginella*. This gap is especially important because the genus has been shown to function as a useful biogeographic indicator in Southeast Asian archipelagos, including the Philippines (Tan 2013).

This study aimed to assess the diversity, distribution, and habitat preferences of *Selaginella* throughout Java and to evaluate the role of elevation in shaping species occurrence patterns and ecological specialization. We hypothesized that diversity, community composition, and habitat specialization vary significantly along elevational gradients, with richness and diversity peaking at intermediate elevations where environmental conditions and habitat heterogeneity are most favorable. We further expected individual species to exhibit distinct elevational preferences and habitat associations, resulting in identifiable indicator species and ecological assemblages across the island.

MATERIALS AND METHODS

Study area

This study was conducted on the island of Java and the surrounding small islands. Java Island has an area of approximately 133,900 km². Java is one of the major islands in Indonesia and has the largest population. Geographically, this study covers latitudes from 5° 2' 55" to 8° 46' 49" S and longitudes from 105° 5' 59" to 116° 16' 12" E (Figure 1). Java Island is located in a tropical area with sunshine throughout the year. This island has two seasons that are influenced by the monsoon period (Van Steenis 1972; Whitten et al. 1996). Changes in the monsoon period affect air humidity, temperature, and rainfall in Indonesia. Java Island has many types of habitats that allow the existence of *Selaginella*. Setyawan et al. (2026a, 2026b) reported 21 accepted species of *Selaginella* on Java Island. The island consists of six provinces, i.e., Banten, Jakarta, West Java, Central Java, Yogyakarta, and East Java.

Procedures

The data were obtained from field surveys and herbarium collections throughout all provinces of Java between 2007 and 2021. Field surveys contributed 1,362 occurrence records from 684 localities, whereas herbarium specimens and biodiversity databases contributed an additional 600 occurrence records from 309 localities. Herbarium records were derived primarily from Herbarium Bogoriense (BO), supplemented by specimens from BM, L, CANB, K, P, S, BGBM, and WRSL, as well as occurrence data retrieved from the Global Biodiversity Information Facility (GBIF). *Selaginella* is generally found in moist and shady disturbed habitats, including roadside cliffs, footpaths, tributary banks, moist forest slopes, agroforests, and agricultural lands (Setyawan et al. 2016). All *Selaginella* species were collected as herbarium specimens, and both living plants and herbarium materials were examined. The herbarium collection of *Selaginella* at Herbarium Bogoriense (BO) was also reviewed. Sampling was conducted comprehensively across a wide range of climatic conditions to minimize geographic and environmental bias. In total, 1,962 georeferenced occurrence records were assembled, representing the known distribution of *Selaginella* across Java.

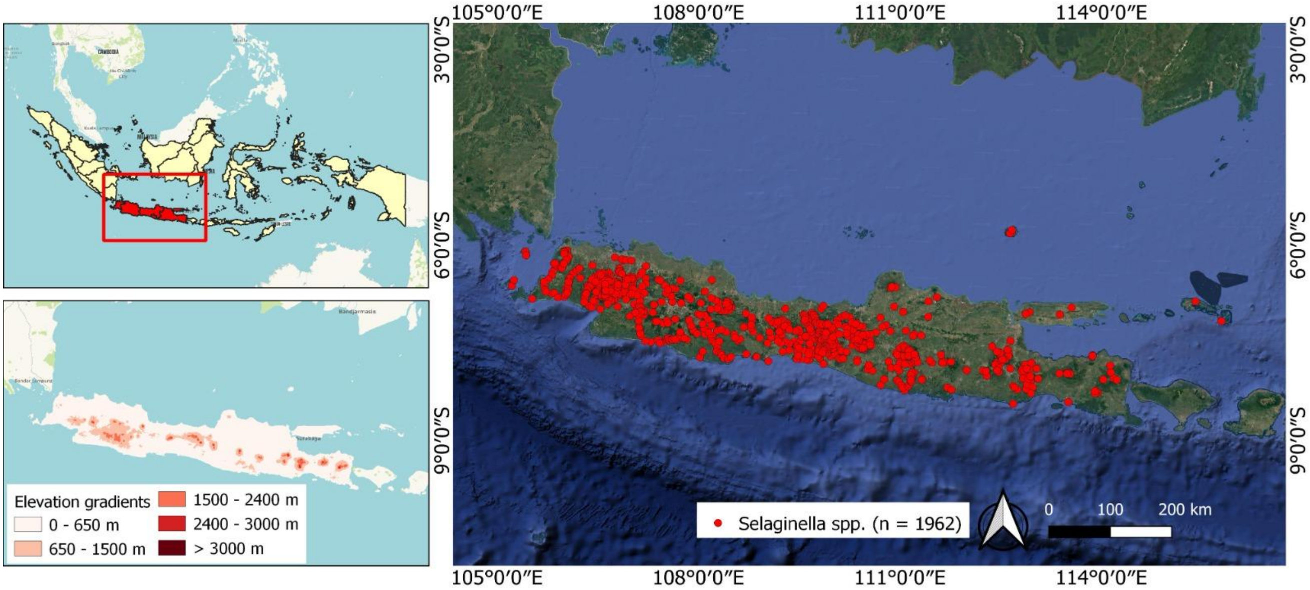


Figure 1. Study area map and the existence of *Selaginella* in Java, Indonesia

Sampling effort was not entirely uniform among provinces and elevational zones because occurrence records were compiled from both field surveys and herbarium collections, which reflect differences in accessibility, collection intensity, and historical sampling effort. Consequently, some regions are represented by more occurrence records than others. Nevertheless, the large number of occurrence records, broad geographic coverage, and inclusion of all major elevational zones provide a robust basis for evaluating island-wide patterns of species diversity, distribution, habitat preference, and habitat association. Because the analyses were based primarily on species occurrences and frequencies rather than abundance estimates, the influence of unequal sampling intensity on the major ecological patterns identified in this study is expected to be limited.

Geographic coordinates of field-collected specimens were recorded using a Garmin GPS with an accuracy of less than 5 m, which was considered sufficient for analyses of species distribution and habitat preference. Each occurrence record contained geographic coordinates indicating the location where a specimen was collected or observed. To improve data reliability and minimize potential identification errors, occurrence records were verified through examination of herbarium specimens, published taxonomic literature, and biodiversity databases. Because this study aimed to document observed diversity, distribution patterns, habitat preferences, and habitat associations rather than to develop predictive species distribution models, spatial thinning of occurrence records was not applied. Geographically proximate and distant records were treated equally, as each verified record represented a valid observation of species presence within a particular habitat and elevational zone. Retaining all records allowed the full range of ecological variation and habitat occupancy across Java to be represented in subsequent analyses.

Specimen identification was performed using multiple references on *Selaginella*, including early records from the Malay Archipelago, namely Malay Peninsula (Alston 1934), the Philippines (Alston 1935a), Java and the Lesser Sunda Islands (Alston 1935b), Sumatra (Alston 1937), Sulawesi and Moluccas (Alston 1940); and contemporary references for the Malay Archipelago, i.e. Malay Peninsula (Wong 1982, 2010) and Java (Setyawan et al. 2026a,b); and adjacent Asian regions, i.e. China (Zhang et al. 2013), Taiwan (Tsai and Shieh 1994; Chang et al. 2012), Thailand (Tagawa and Iwatsuki 1979), and Vietnam (Pham-Hoang 1991). These were compared with specimens held at BO, particularly those identified by A.G.H. Alston. In addition to direct observations, the literature guided the preparation of species descriptions. Synonyms and global distributions followed Hassler (1994-2026), whereas accepted names and taxonomic status followed Plants of the World Online (POWO 2026). Locality records were assigned to sub-district administrative divisions. A total of 1,962 sample points of *Selaginella* presence were identified throughout Java and its surroundings, comprising 21 identified species and one unidentified sample (Figure 1). The collected data were subsequently analyzed in three parts: species diversity, habitat preference, and habitat association metrics. Elevation zones were used to determine the distribution of each species, following the classification proposed by Van Steenis (1972), as presented in Table 1.

Table 1. Altitudinal ecological zonation of Java, Indonesia (Van Steenis 1972)

Elevation zone	Elevation (m asl)	Characteristics of vegetation	Unique / dominance species
Colline	0-650	Lowland tropical rainforest: high temperature and humidity	*Shorea* spp., Dipterocarpaceae, palms
Submontane	650-1,500	Submontane forest; smaller-leaved trees, decreasing temperature	*Castanopsis*, *Lithocarpus*, *Schima*, large ferns
Montane	1,500-2,400	Cloud forest; frequent mist, rich in epiphytes and mosses	Ericaceae, Lauraceae, various ferns
Subalpine	2,400-3,000	Upper montane shrublands; dwarf forests ("elfin forests")	*Rhododendron*, *Vaccinium*, montane grasse
Alpine	>3,000	Vegetation extremely sparse; cold-tolerant and stress-adapted flora	Mosses, cushion plants, extreme ground covers

Data analysis

Diversity and dominance index analysis

Species diversity was estimated using Shannon's (H') and Simpson's (D) indices. H' reflects species richness and abundance, whereas D quantifies community dominance and evenness. Both indices are widely used in ecological studies because of their ability to characterize community structure with relatively low sensitivity to sample size (Magurran 2004). These indices were estimated using Paleontological Statistics (PAST) version 3.04. Pairwise comparisons of Shannon and Simpson indices between elevation zones were performed using two-sample t-tests (assuming unequal variances) in PAST version 3.04 (Hammer et al. 2001).

Habitat preference

A bipartite network approach was employed to explore the interaction between *Selaginella* species and their habitat types using the Bipartite package (version 2.16). The bipartite graph was constructed using the ggplot2 package to visualize species-habitat interactions. Rectangles at the top and bottom represent *Selaginella* species and habitat types, respectively, whereas connecting lines indicate interactions between them. The width of each rectangle and connecting line is proportional to the number of interactions, providing a visual representation of interaction strength (Dormann et al. 2008).

The Paired Difference Index (PDI) was used to quantify the degree of habitat specificity of each species. PDI accounts for cases in which performance exhibits different statistical distributions and where no universal measure of variability can be uniformly applied to the dataset (Poisot et al. 2011). It has been shown to be highly robust against sampling errors and provides informative results in specialization studies (Poisot et al. 2012). The highest possible value of 1 indicates complete specialization, while lower values suggest decreasing specialization.

Indicator Value analysis (IndVal) was applied to evaluate the uniqueness of each species in a given habitat based on its relative abundance and frequency. IndVal is calculated as the product of specificity (proportion of individuals of a species found in a particular habitat) and fidelity (proportion of sites in that habitat containing the species), ranging from 0 to 1. Statistical significance of IndVal was assessed using 999 permutations, with $p<0.05$ considered significant (Podani and Csányi 2010).

In addition, Pearson's phi coefficient of association was used to estimate the habitat preference of *Selaginella* species. This coefficient ranges from −1 to +1, where positive values indicate positive associations and negative values indicate avoidance of particular habitats. A negative coefficient suggests that a species tends to avoid a specific habitat (Cáceres and Legendre 2009). This analysis was performed using the Indicspecies package (version 1.7.8).

RESULTS AND DISCUSSION

The diversity of *Selaginella* in the Java Islands

A total of 1,962 *Selaginella* individuals, representing 21 species of *Selaginella*, were identified (one sample remained unidentified) and successfully collected from various elevational zones across six provinces in Java Island: Banten, Jakarta, West Java, Central Java, Yogyakarta, and East Java. The species distribution varied across provinces and elevation zones, with different species dominating in each region. The 21 identified species were *Selaginella alutacea* Spring, *Selaginella aristata* Spring, *Selaginella biformis* A.Braun ex Kuhn, *Selaginella ciliaris* (Retz.) Spring, *Selaginella cupressina* (Willd.) Spring, *Selaginella frondosa* Warb., *Selaginella intermedia* (Blume) Spring, *Selaginella involvens* (Sw.) Spring, *Selaginella kraussiana* (Kunze) A.Braun, *Selaginella opaca* Warb., *Selaginella ornata* (Hook. & Grev.) Spring, *Selaginella plana* (Desv.) Hieron., *Selaginella remotifolia* Spring, *Selaginella repanda* (Desv.) Spring, *Selaginella rothertii* Alderw., *Selaginella singalanensis* Hieron., *Selaginella subalpina* Alderw., *Selaginella subspinulosa* Spring, *Selaginella uncinata* (Desv.) Spring, *Selaginella willdenowii* (Desv.) Baker, and *Selaginella zollingeriana* Spring (Table 2).

Several *Selaginella* species exhibited distinct distribution patterns, ranging from low-elevation coastal zones to high-elevation mountain summits. *S. plana* was recorded as the most abundant species with 404 individuals, widely distributed across various sites, especially in the colline (0-650 m asl), submontane (650-1,500 m asl), and montane zones (1,500-2,400 m asl). Other dominant species included *S. willdenowii* (205 individuals), *S. ornata* (214 individuals), and *S. ciliaris* (387 individuals), which were mostly found in colline and submontane zones (Table 2 and Figures 2-3). Their occurrence in humid habitats with dense vegetation cover suggests a generalist ecological behavior.

Table 2. Distribution of *Selaginella* and species diversity analyses in contrasting habitats elevation from Java Islands, Indonesia

***Selaginella* species**	**Number of individuals at location**																														**Total**
	Banten					**Jakarta**					**West Java**					**Central Java**					**Yogyakarta**					**East Java**					
	A	**B**	**C**	**D**	**E**	**A**	**B**	**C**	**D**	**E**	**A**	**B**	**C**	**D**	**E**	**A**	**B**	**C**	**D**	**E**	**A**	**B**	**C**	**D**	**E**	**A**	**B**	**C**	**D**	**E**	
S. alutacea	-	2	-	-	-	-	-	-	-	-	10	3	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	15
S. aristata	-	-	-	-	-	-	-	-	-	-	7	12	-	-	-	18	52	-	-	-	-	1	-	-	-	1	2	1	-	-	94
S. biformis	-	1	-	-	-	-	-	-	-	-	3	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13
S. ciliaris	33	3	-	-	-	2	-	-	-	-	89	24	-	-	-	121	89	-	-	-	3	2	-	-	-	12	8	1	-	-	387
S. frondosa	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
S. intermedia	-	3	-	-	-	-	-	-	-	-	22	37	-	-	-	1	2	-	-	-	-	-	-	-	-	1	-	-	-	-	66
S. involvens	2	-	-	-	-	-	-	-	-	-	5	37	4	-	-	4	26	1	-	-	1	4	-	-	-	6	30	6	-	-	126
S. kraussiana	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
S. cupressina	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
S. opaca	-	-	-	-	-	-	-	-	-	-	4	34	9	-	-	-	31	22	-	-	-	2	-	-	-	-	16	24	-	-	142
S. ornata	-	3	-	-	-	-	-	-	-	-	20	66	7	-	-	18	70	2	-	-	-	4	-	-	-	8	14	2	-	-	214
S. plana	25	5	-	-	-	1	-	-	-	-	124	34	2	-	-	126	43	-	-	-	3	2	-	-	-	33	6	-	-	-	404
S. remotifolia	-	-	-	-	-	-	-	-	-	-	-	8	6	-	-	-	57	26	-	-	-	1	-	-	-	-	6	23	2	-	129
S. repanda	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	35	4	-	-	-	4	-	-	-	-	22	2	-	-	-	68
S. rothertii	-	-	-	-	-	-	-	-	-	-	6	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	8
S. singalanensis	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	7	1	-	-	-	1	-	-	-	-	1	1	-	-	12
S. subalpina	-	3	-	-	-	-	-	-	-	-	3	27	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	35
S. subspinulosa	-	2	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7
S. uncinata	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	5
S. willdenowii	27	7	-	-	-	4	-	-	-	-	111	53	1	-	-	1	1	-	-	-	-	-	-	-	-	-		-	-	-	205
S. zollingeriana	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-	7	-	-	-	-	-	-	-	-	3	9	1	-	-	23
Selaginella sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Total individuals (N)	87	29	-	-	-	7	-	-	-	-	414	353	30	-	-	325	395	53	-	-	11	17	-	-	-	86	94	59	2	-	1,962
Shannon's Index (*H'*)	1.16	2.04				0.96					1.82	2.35	1.70			1.39	2.09	0.99			1.30	1.94				1.62	1.96	1.35	0.00		
Simpson's Index (D)	0.33	0.15				0.43					0.22	0.11	0.21			0.31	0.14	0.43			0.29	0.16				0.25	0.17	0.33	1.00		
p value	0.08	0.004				0.13					0.027	0.0006	0.023			0.069	0.004	0.13			0.06	0.008				0.039	0.011	0.08	0.3		

Note: A: Habitat zone altitude 0-650 m asl (Colline), B: Habitat zone altitude 650-1,500 m asl (submontane), C: Habitat zone altitude 1,500-2,400 m asl (montane), D: Habitat zone altitude 2,400-3,000 m asl (subalpine), E: Habitat zone altitude above 3,000 m asl (alpine), -: No individuals found

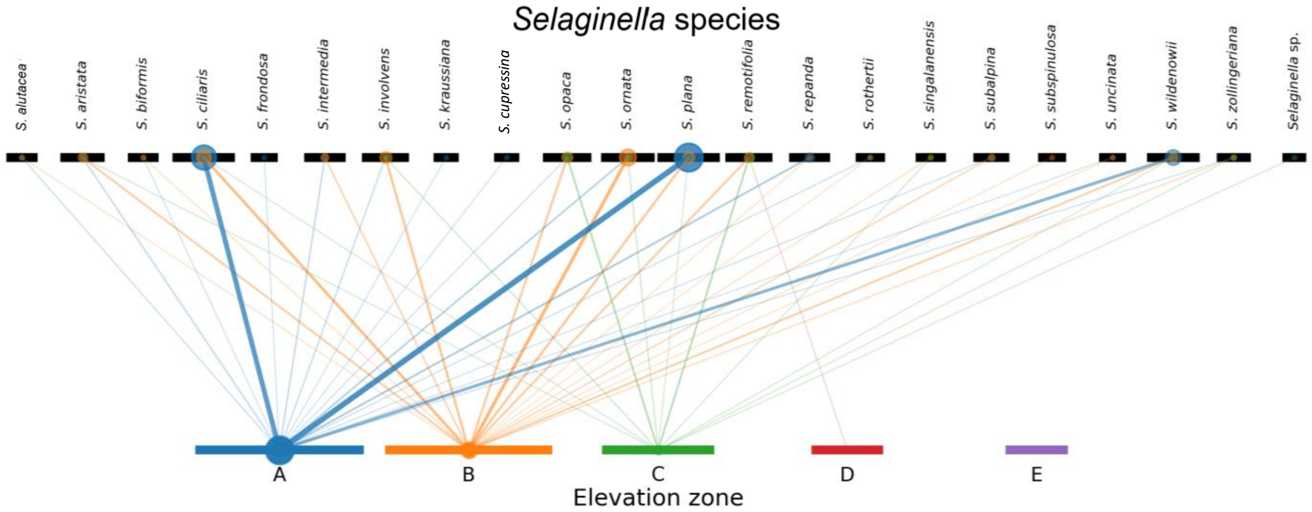
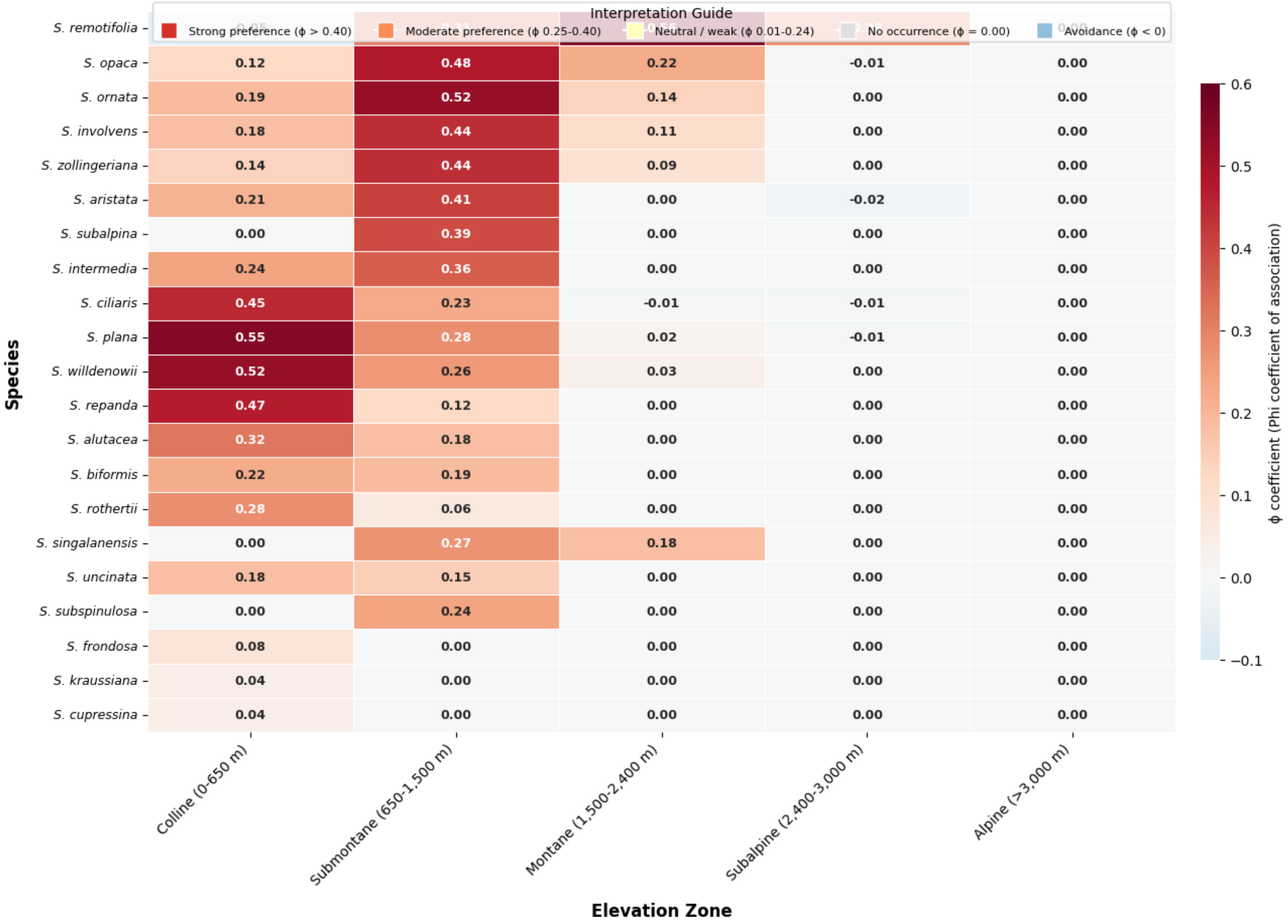


Figure 2. The bipartite network of the *Selaginella* spp. and habitat types in Java Island, Indonesia. The upper bar represents *Selaginella* species, and the lower bar represents habitat elevation. The width of the bar indicates abundance, while the width of the link indicates the frequency of interaction. The wider the bar and link, the higher the abundance and frequency of interaction. A. Habitat zone altitude 0-650 m asl (Colline), B. Habitat zone altitude 650-1,500 m asl (submontane), C. Habitat zone altitude 1,500-2,400 m asl (montane), D. Habitat zone altitude 2,400-3,000 m asl (subalpine), E. Habitat zone altitude above 3,000 m asl (alpine)



Species	Colline (0-650 m)	Submontane (650-1,500 m)	Montane (1,500-2,400 m)	Subalpine (2,400-3,000 m)	Alpine (>3,000 m)
S. remotifolia	-0.05	0.31	0.56	0.28	0.00
S. opaca	0.12	0.48	0.22	-0.01	0.00
S. ornata	0.19	0.52	0.14	0.00	0.00
S. involvens	0.18	0.44	0.11	0.00	0.00
S. zollingeriana	0.14	0.44	0.09	0.00	0.00
S. aristata	0.21	0.41	0.00	-0.02	0.00
S. subalpina	0.00	0.39	0.00	0.00	0.00
S. intermedia	0.24	0.36	0.00	0.00	0.00
S. ciliaris	0.45	0.23	-0.01	-0.01	0.00
S. plana	0.55	0.28	0.02	-0.01	0.00
S. willdenowii	0.52	0.26	0.03	0.00	0.00
S. repanda	0.47	0.12	0.00	0.00	0.00
S. alutacea	0.32	0.18	0.00	0.00	0.00
S. biformis	0.22	0.19	0.00	0.00	0.00
S. rothertii	0.28	0.06	0.00	0.00	0.00
S. singalanensis	0.00	0.27	0.18	0.00	0.00
S. uncinata	0.18	0.15	0.00	0.00	0.00
S. subspinulosa	0.00	0.24	0.00	0.00	0.00
S. frondosa	0.08	0.00	0.00	0.00	0.00
S. kraussiana	0.04	0.00	0.00	0.00	0.00
S. cupressina	0.04	0.00	0.00	0.00	0.00

Figure 3. Phi coefficient of association between *Selaginella* species and elevation zones in Java, Indonesia. Positive values (red to dark red) indicate affinity for a particular zone, while negative values (light blue to dark blue) indicate avoidance. Subalpine zone (2,400-3,000 m asl) contains only *S. remotifolia* (2 individuals); Alpine zone (>3,000 m asl) contains no *Selaginella*; data based on 1,962 specimens collected across six provinces in Java (2007-2021). Elevation classification follows Van Steenis (1972)

In contrast, species such as *S. frondosa*, *S. kraussiana*, *S. cupressina*, *S. singalanensis*, *S. subspinulosa*, *S. rothertii*, and *S. uncinata* were recorded in very limited numbers and restricted locations, indicating narrow habitat preferences and potential specialization to specific elevational bands. *S. remotifolia*, for example, was found predominantly in the submontane (650-1,500 m asl) and montane zones (1,500-2,400 m asl) across West Java, Yogyakarta, Central Java, and East Java, with the highest number of individuals recorded in Central Java. Only two individuals were recorded in the subalpine zone (2,400-3,000 m asl). It was absent from both the colline and alpine zones (>3,000 m asl), indicating a relatively narrow elevational preference for mid- to high-altitude environments. Its consistent presence in submontane and montane regions supports the interpretation that *S. remotifolia* is a mid-elevation specialist adapted to cool and humid conditions, with the strongest association with submontane environments (φ = 0.31; Figure 3).

Diversity index analysis revealed that species diversity was highest in the submontane zone, particularly in West Java and Central Java, where Shannon's Index (H′) reached 2.35 and 2.09, respectively. In contrast, the lowest diversity values were recorded in the colline zone (H′ = 0.96) and the subalpine zone (H′ = 0), indicating reduced species richness and greater dominance by a few taxa. Pairwise diversity t-tests revealed significant differences among elevational zones (t = 2.14–4.87, df = 8–42, p<0.05). Specifically, diversity in the submontane zone was significantly higher than in the colline zone (t = 3.45, df = 12, p = 0.005) and the subalpine zone (t = 4.87, df = 8, p = 0.001). These differences were not only statistically significant but also ecologically meaningful, reflecting the concentration of species richness and more balanced community structure in mid-elevation habitats. Collectively, these findings demonstrate that elevation is a major factor shaping *Selaginella* diversity in Java, with submontane environments supporting the most diverse and stable assemblages.

Simpson's Dominance Index (D), calculated for each elevational zone across the six provinces, revealed variation in community structure among locations. D values ranged from 0.11 to 1.00, where higher values indicate stronger dominance by one or a few species. The subalpine zone in East Java exhibited the highest dominance value (D = 1.00), suggesting that the community was dominated by one or two species, consistent with its low species diversity. Conversely, the lowest dominance was observed in the submontane zone of West Java (D = 0.11), reflecting a more balanced community structure without significant dominance by a single species. These results suggest that mid-elevation mountain zones tend to support more stable species assemblages, with more equitable distribution of individuals among *Selaginella* species. Overall, the elevational gradient not only influences species richness but also shapes the patterns of dominance and distribution within these lycophyte communities.

The habitat preference of *Selaginella* in the Java Islands

The bipartite network (Figure 2) shows that most *Selaginella* species are strongly associated with the colline (A) and submontane (B) elevation zones, where both abundance and interaction intensity are highest. These zones are characterized by numerous and thicker links, indicating that they serve as the main habitats for the genus in Java. In contrast, higher elevation zones (D and E) display very limited connections, reflecting low species occurrence and reduced ecological suitability. This graphical structure reveals distinct patterns of ecological specialization and indicator potential across elevation gradients. Several species show strong and significant associations with specific elevation zones, as corroborated by their high Indicator Values (IndVal). Their PDI scores further indicate moderate to high ecological specialization (Table 3). For instance, *S. ciliaris*, *S. willdenowii*, and *S. rothertii* exhibit clear affinity to the colline zone (0-650 m asl), supported by their relatively high specificity (0.78-0.88) and fidelity scores. Both *S. ciliaris* and *S. willdenowii* also showed statistically significant IndVal scores (p<0.05), suggesting their reliable presence in lowland habitats, likely due to adaptation to warmer and more humid microclimates.

Similarly, the submontane zone (650-1,500 m asl) harbored the majority of *Selaginella* species in this study, indicating a possible elevational hotspot. Notable indicator species in this zone include *S. singalanensis* (IndVal = 0.818; p = 0.033), *S. subalpina* (IndVal = 0.914; p = 0.028), and *S. remotifolia* (IndVal = 0.558; p = 0.004). Their PDI values ranged from 0.76 to 0.96, indicating a gradient from moderate to high ecological specialization. However, following Poisot et al. (2012), values below 0.95 suggest that most of these species retain some habitat flexibility, while values above 0.95 indicate narrower niche breadth. *S. zollingeriana* also emerged as a distinct submontane indicator species (p = 0.046) and exhibited the highest PDI score (0.96) among all species, which suggests strong elevation-constrained habitat preferences that are possibly linked to climatic thresholds and vegetation type.

Generalist patterns were also detected. *Selaginella plana* and *S. alutacea*, although more abundant in lowland zones, displayed broader elevational distributions and lower IndVal scores (≤0.25). Their PDI values (0.77 and 0.85, respectively) suggest moderate specialization, indicating they are not strict generalists but rather habitat-flexible species with preferences for lowland conditions (Poisot et al. 2012). In contrast, species like *S. intermedia*, *S. aristata*, and *S. opaca* exhibited intermediate specialization within submontane belts, with modest IndVal scores and PDI values between 0.79 and 0.83, reflecting moderate indicator potential. Interestingly, no species showed high fidelity to the highest zones (subalpine and alpine), indicating limited colonization or sampling in these extreme environments. This absence may reflect physiological constraints of *Selaginella* in colder, less vegetated habitats, or could signify conservation-relevant rarity in high-elevation ecosystems.

Altogether, this integrated analysis of bipartite species-zone associations and indicator values underscores the ecological heterogeneity across Java's elevation gradients. Species with high IndVal and PDI scores in distinct zones represent promising bioindicators for elevational habitat types and can aid in future biodiversity monitoring and conservation planning, particularly under scenarios of climate change-induced upslope shifts.

Table 3. Summary of IndVal and Bipartite analysis

Elevation zone habitat	Specificity	Fidelity	IndVal analysis		Bipartite analysis
			IndVal	p	PDI
Colline					
S. alutacea	0.582	0.143	0.083	0.057	0.85
S. rothertii	0.875	0.008	0.007	0.125	0.73
S. ciliaris	0.785	0.152	0.119	0.024	0.75
S. repanda	0.912	0.068	0.062	0.146	0.87
S. plana	0.768	0.332	0.254	0.107	0.77
S. willdenowii	0.698	0.156	0.109	0.028	0.74
Submontane					
S. subalpina	0.914	0.036	0.033	0.028	0.76
S. singalanensis	0.818	0.01	0.008	0.033	0.87
S. remotifolia	0.558	0.082	0.046	0.004	0.85
S. ornata	0.734	0.179	0.131	0.091	0.92
S. involvens	0.768	0.109	0.084	0.01	0.81
S. intermedia	0.607	0.042	0.026	0.024	0.79
S. biformis	0.769	0.011	0.009	0.09	0.87
S. aristata	0.713	0.076	0.054	0.143	0.83
S. opaca	0.585	0.094	0.055	0.13	0.83
S. zollingeriana	0.783	0.02	0.016	0.046	0.96

Note: Colline (0-650 m asl), Submontane (650-1,500 m asl). IndVal (Indicator value) = Specificity × Fidelity (0-1). PDI: Paired Difference Index (Poisot et al. 2012). $p<0.05$

The Pearson's phi coefficient of association between *Selaginella* species and elevational zones (Figure 3) offers insight into the degree of preference or avoidance by each species across the altitudinal gradient in Java. The phi coefficient (φ) ranges from −1 to +1, with positive values indicating species affinity for particular zones and negative values suggesting avoidance. This analysis is based on species presence-absence data across five elevational habitat zones: colline (A), submontane (B), montane (C), subalpine (D), and alpine (E).

Most species display relatively low φ values ($|\varphi| < 0.2$) across all elevation zones, suggesting that many taxa are not strictly confined to a single habitat type but occur across a range of elevations. Nevertheless, several consistent patterns can be observed. Species associated with the colline zone (A) tend to show higher φ values at low elevations. In particular, *S. plana*, *S. ciliaris*, and *S. willdenowii* exhibit stronger associations with this zone, indicating their preference for lowland habitats. This pattern is in line with their higher abundance and frequency in warmer environments, as also reflected in the IndVal results. The submontane zone (B) emerges as the most important habitat for several species. *Selaginella remotifolia*, *S. singalanensis*, *S. subalpina*, and *S. involvens* consistently show the highest φ values in this zone, indicating a clear affinity for mid-elevation habitats. Among these, *S. remotifolia* demonstrates the strongest association, suggesting that this species is particularly characteristic of submontane environments. Other species such as *S. ornata*, *S. opaca*, *S. aristata*, and *S. zollingeriana* also show moderate associations with this zone, although their distributions appear to be more flexible.

In contrast, associations with higher elevation zones (C and D) are generally weak. Only *S. remotifolia* shows preference for the subalpine zone, and the values in these zones remain close to zero or slightly negative. Similarly, the alpine zone (E) shows no meaningful association for any species, indicating that *Selaginella* is largely absent or extremely rare above 3,000 m asl. The results suggest that most *Selaginella* species in Java have relatively broad ecological tolerances, with a tendency to occur more frequently in lowland and especially submontane habitats. Only a few species exhibit clearer habitat preferences, and even these are not strictly restricted to a single elevation zone.

Discussion

The results support the study hypothesis that *Selaginella* diversity, community composition, and habitat specialization vary along elevational gradients in Java. Higher diversity in submontane habitats, significant differences among elevational zones, and the presence of indicator species with distinct habitat associations collectively demonstrate the importance of elevation in shaping species occurrence patterns and ecological specialization. These findings are consistent with previous studies showing that elevational gradients strongly influence the diversity, distribution, and habitat occupancy of *Selaginella* and other pteridophytes in tropical mountain ecosystems (Kessler et al. 2001; Setyawan et al. 2016; Karger et al. 2021).

Taxonomic and biogeographic context

The taxonomic identification of *Selaginella* species in this study followed the phylogenetic framework established by Weststrand and Korall (2016a), who demonstrated that morphological characters previously considered homoplastic can be phylogenetically informative when evaluated within a broader evolutionary context. Their revised classification (Weststrand and Korall 2016b), recognizing seven subgenera within *Selaginella*, provides a robust framework for interpreting ecological and biogeographic patterns.

The elevational distribution of *Selaginella* in Java shows strong biogeographic parallels with other regions of Malesia. The Malesian region harbors more than 200 *Selaginella* species, with elevational specialization playing an important role in structuring local assemblages (Camus 1997). In Borneo, species richness peaks in montane rainforests between 1,000 and 2,200 m asl, where persistent cloud cover and high humidity favor lycophyte-rich understories (Kessler et al. 2001). This elevational pattern is consistent with the broader distribution of Malesian pteridophytes, in which species richness typically reaches a maximum in the submontane to lower montane belt (Karger et al. 2011). Such patterns are generally associated with humid, relatively undisturbed forests that provide stable microclimatic conditions and sustained moisture availability, which favor the establishment and persistence of diverse *Selaginella* assemblages (Kessler et al. 2001; Setyawan et al. 2016).

Biogeographically, Java forms part of Sundaland and shares a long geological history with Sumatra and Borneo through repeated land connections during periods of lowered sea level. The occurrence of widespread species such as *S. plana*, *S. ciliaris*, and *S. willdenowii* across these regions suggests strong historical connectivity and dispersal opportunities within the Sunda Shelf. The concentration of species richness in submontane habitats observed in this study therefore reflects not only contemporary environmental conditions but also broader biogeographic processes that have shaped the distribution of *Selaginella* throughout Malesia.

Ecological specialization and elevational restriction

The PDI values obtained in this study (0.73-0.96) indicate varying degrees of ecological specialization among *Selaginella* species in Java. Following the interpretation proposed by Poisot et al. (2012), higher PDI values indicate stronger ecological specialization, whereas lower values reflect broader habitat use. Overall, most species exhibited moderate to high levels of habitat specialization, indicating that they occupy preferred elevational habitats while retaining some ecological flexibility. Only *S. zollingeriana* (PDI = 0.96) approached complete specialization, suggesting a particularly narrow ecological niche. By contrast, species with comparatively lower PDI values, such as *S. rothertii*, *S. willdenowii*, and *S. ciliaris*, appear to tolerate a wider range of environmental conditions despite maintaining identifiable habitat preferences. These findings suggest that ecological specialization within Javan *Selaginella* forms a continuum rather than discrete specialist-generalist categories, reflecting varying degrees of adaptation to local environmental conditions.

Biogeographically, Java represents a transitional island between the continental flora of Sundaland and the Wallacean elements to the east. Similar to the pattern observed in the Philippines by Tan (2013), Java's *Selaginella* assemblages show stronger affinity with Sumatra and Borneo (Sundaland core) than with Wallacean islands, consistent with its geological history as part of the Sunda Shelf. The presence of widespread species like *S. ciliaris*, *S. plana*, and *S. willdenowii* across these regions suggests high dispersal capability. In contrast, narrow-range species such as *S. frondosa*, *S. kraussiana*, *S. cupressina*, *S. singalanensis*, *S. subspinulosa*, *S. rothertii*, and *S. uncinata* were recorded in very limited numbers and restricted locations.

The restriction of *S. remotifolia* to montane and subalpine zones (1,500-3,000 m asl) may be associated with several interacting factors suggested by previous studies: (i) lower mean annual temperatures (<18°C) that reduce evapotranspiration stress, (ii) persistent cloud cover maintaining leaf wetness, and (iii) differences in habitat suitability, potentially combined with biotic interactions that were not evaluated in the present study. Previous experimental studies on *Selaginella* physiology have shown that montane species exhibit reduced photosynthetic efficiency at temperatures >25°C (Soni et al. 2012; Campany et al. 2019). These restricted distributions may reflect relictual or recently evolved lineages adapted to specialized microhabitats, consistent with the phylogenetic framework of Weststrand and Korall (2016a) and Lu et al. (2025). Islands with pronounced altitudinal variation, such as Java, Sumatra, and Mindanao, tend to harbor both higher richness and more elevational zonation in *Selaginella* communities, likely due to the availability of diverse thermal niches and microclimatic buffering in montane environments (Kessler et al. 2001; Bautista et al. 2018).

Elevational pressures and climate change threats

Each elevational zone presents distinct environmental pressures that may influence the persistence of *Selaginella* populations. Lowland habitats (0-650 m asl) are increasingly affected by urbanization, agricultural expansion, and degradation of riparian ecosystems, potentially reducing suitable habitats for widespread lowland species such as *S. plana* and *S. ciliaris*. In addition, continued habitat conversion may alter local humidity regimes that are important for the growth and reproduction of many *Selaginella* species.

The submontane and montane zones (650-2,400 m asl), which support the highest species richness and diversity, may be particularly vulnerable to climate-driven changes in moisture availability. Water availability has been identified as a major driver of elevational diversity patterns in tropical pteridophytes (Karger et al. 2021), suggesting that shifts in hydrological conditions could substantially affect *Selaginella* communities. Previous modeling studies further predict an upward shift of suitable habitats under future climate scenarios, potentially reducing available habitat and altering species distributions across Java (Setyawan et al. 2020a, 2020b).

High-elevation habitats (>2,400 m asl) contain few species and depend strongly on stable microclimatic conditions. Although species such as *S. remotifolia* may be locally abundant within suitable environments, previous studies have projected substantial reductions in habitat suitability under future climate-change scenarios. Geographic isolation may further limit altitudinal range shifts, while anthropogenic disturbances such as mining and habitat fragmentation continue to threaten the integrity of montane ecosystems (Utteridge and Edwards 2009). Collectively, these pressures highlight the vulnerability of *Selaginella* communities across the entire elevational gradient and emphasize the importance of climate-adaptive conservation strategies.

Conservation implications

From a conservation perspective, these findings highlight the importance of adopting an elevation-based strategy (Hu et al. 2026). In lowland areas (0-650 m asl), which face threats from urban expansion and agricultural conversion, efforts should focus on preserving riparian habitats that provide critical refugia for generalist species such as *S. plana* and *S. ciliaris* because these species were among the most abundant and were predominantly associated with lowland and submontane habitats in the present study (Majumdar and Avishek 2025). In the submontane and montane zones (650-2,400 m asl), which supported the highest species diversity and contained several elevational specialists identified in this study, conservation priorities should include maintaining canopy connectivity and cloud forest integrity to accommodate upslope migration and provide stable microclimates for sensitive taxa (Psistaki et al. 2024). In highland areas (>2,400 m asl), conservation must prioritize the protection of climate refugia for narrow-endemic species such as *S. remotifolia*, which exhibited a restricted elevational distribution in the present dataset, while preventing infrastructure development and implementing long-term climate monitoring (Hoveka et al. 2016; Abdelaal et al. 2019). Through these elevation-specific strategies, a more integrated and adaptive approach can be achieved to safeguard *Selaginella* biodiversity in the face of rapid environmental change, ensuring the long-term survival of both generalist and specialist species across Java's diverse elevational gradients.

Study limitations

This study provides a broad-scale assessment of *Selaginella* diversity, distribution, and habitat preferences across Java Island using a large occurrence dataset compiled from field surveys and herbarium records collected between 2007 and 2021. However, several limitations should be acknowledged. First, the integration of field and herbarium data may introduce spatial and temporal sampling heterogeneity because collection intensity was not uniform across provinces and elevational zones. Second, some species and habitats were represented by relatively few records, particularly in subalpine and alpine environments, which may affect the precision of habitat-association analyses. Third, environmental conditions were inferred primarily from elevational zonation and occurrence patterns, as direct measurements of microclimatic variables such as temperature, humidity, canopy cover, and soil moisture were not consistently available for all records. Consequently, the observed habitat associations should be interpreted as broad ecological patterns rather than direct evidence of causal environmental mechanisms. Future studies incorporating standardized sampling designs, long-term monitoring, and detailed microclimatic measurements would provide a more comprehensive understanding of the ecological requirements and climate-change vulnerability of *Selaginella* species in Java.

In conclusion, this study documented 21 identified *Selaginella* species and one unidentified taxon from 1,962 occurrence records collected across Java Island, spanning five elevational zones from 0 to >3,000 m asl. Species richness was concentrated in the colline to montane zones (0-2,400 m asl), while diversity peaked in the submontane zone, reaching H′ = 2.35 in West Java and H′ = 2.09 in Central Java. In contrast, the subalpine zone exhibited the lowest diversity (H′ = 0) and the highest dominance (D = 1.00). Dominant species included *S. plana*, *S. ciliaris*, *S. ornata*, and *S. willdenowii*, whereas several species were recorded only rarely and displayed restricted distributions. Indicator-species and habitat-specialization analyses demonstrated that several taxa were strongly associated with particular elevational zones, especially the submontane belt, confirming the importance of elevation in shaping *Selaginella* diversity, distribution, and community composition in Java. The concentration of both species richness and habitat specialists in mid-elevation environments highlights the ecological significance of elevational gradients for maintaining *Selaginella* assemblages. Given the sensitivity of these species to elevation-related environmental conditions, including humidity, temperature, and forest structure, conservation efforts should prioritize maintaining elevational habitat continuity and suitable microclimatic conditions across Java's forest landscapes. Furthermore, the comprehensive island-wide dataset presented here provides an important ecological baseline for long-term monitoring of changes in *Selaginella* distribution and habitat occupancy under future climate change and ongoing landscape modification.

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