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Revisiting *Selaginella* diversity in Java (Indonesia) through combined ecological and taxonomic reassessment

AHMAD DWI SETYAWAN[1,2,♥], TATIK CHIKMAWATI[3], MIFTAHUDIN[3], SUTARNO[4], SUGIYARTO[4], SUNARTO[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, Institut Pertanian Bogor. Jl. Raya Dramaga, Bogor 16680, West Java, Indonesia
[4]Department of Biology, Faculty of Mathematics and Natural Sciences, Universitas Sebelas Maret. Jl. Ir. Sutami 36A, Surakarta 57126, Central Java, Indonesia

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Abstract. *Setyawan AD, Chikmawati T, Miftahudin, Sutarno, Sugiyarto, Sunarto. 2026. Revisiting* Selaginella *diversity in Java (Indonesia) through combined ecological and taxonomic reassessment. Biodiversitas 27 (1): d270150. https://doi.org/10.13057/biodiv/d270150.* *Selaginella* species have traditionally been distinguished mainly by vegetative traits. Because these traits vary with environmental conditions, the taxonomy of this lycophyte genus has remained complex, especially in tropical Asia. In Java, species diversity estimates remain inconsistent among classical floristic treatments, global databases, and recent field observations. This study reassessed *Selaginella* diversity in Java using field surveys, herbarium examination, taxonomic standardization, and ecological analyses. A total of 1,962 occurrence records were compiled across multiple habitat types and elevational zones. Species identities were verified through comparison of field collections, herbarium specimens, and published taxonomic references. Ecological structuring was analyzed using descriptive habitat analysis, Principal Component Analysis (PCA), and Non-metric Multidimensional Scaling (NMDS). The reassessment recognized 21 confirmed *Selaginella* species in Java, consisting of 17 native non-endemic taxa, two endemic taxa, and two introduced or naturalized species. Species richness was highest in humid submontane forests, whereas disturbed habitats contained simplified assemblages dominated by ecological generalists. NMDS analysis indicated significant habitat differentiation (ANOSIM: $R = 0.684$; $p < 0.05$ after 999 permutations), while several historically recognized taxa, including *S. ascendens*, *S. springiana*, and *S. caudata*, were not retained as independent species because of extensive overlap with broader species complexes. These results suggest that relying solely on vegetative morphology may overestimate *Selaginella* species richness in Java. This assessment updates our knowledge of *Selaginella* diversity in Java by integrating field observations, herbarium evidence, and ecological analyses. Conservation efforts should prioritize humid forest habitats, particularly submontane areas, which support the highest diversity and several habitat-specialist *Selaginella* species.

Keywords: Java, lycophytes, phenotypic plasticity, *Selaginella*, taxonomic reassessment

INTRODUCTION

Selaginella (Selaginellaceae) is one of the most diverse lycophyte genera in tropical and subtropical regions (PPG I 2016; Zhou et al. 2016), occurring in habitats ranging from lowland rainforests to montane ecosystems (Jermy 1990). In humid tropical environments, the genus forms an important component of understory vegetation in shaded forest floors, riparian corridors, rocky cliffs, and moist ravines. Some species enhance moisture retention, promote litter accumulation, and stabilize microhabitats, thus affecting local ecological processes and microclimate (Watkins et al. 2006; Corlett 2014). In Malesia, including Java, *Selaginella* diversity is closely associated with environmental heterogeneity, particularly elevational gradients, canopy structure, and humidity availability (Kessler 2001; Grytnes and Beaman 2006).

The ecological distribution of *Selaginella* is strongly influenced by habitat structure and disturbance intensity. Species such as *S. plana* and *S. ciliaris* commonly occur in disturbed habitats, plantations, agroforestry systems, and secondary forests, whereas other taxa are primarily associated with humid montane forests and stable microclimatic conditions. This ecological differentiation indicates that *Selaginella* assemblages respond sensitively to variation in vegetation structure, substrate characteristics, and land-use change (Kluge et al. 2006). Accurate diversity assessments are needed to document Javan fern and lycophyte diversity and to identify habitats that deserve conservation attention.

Ecologically important as *Selaginella* is, its taxonomy remains complex. Historically, species delimitation has relied heavily on vegetative morphology. Traditional classifications are based mainly on branching architecture, leaf arrangement, anisophylly, and growth form, many of which vary substantially under different environmental conditions (Weststrand and Korall 2016; Zhou et al. 2016). Variation in humidity, light exposure, and substrate condition may strongly influence plant architecture and leaf morphology, often obscuring taxonomic circumscription among morphologically similar taxa. As a result, morphologically overlapping taxa are common, particularly within the *S. plana*, *S. intermedia*, and *S. repanda* complexes. Such conditions increase the risk of taxonomic inflation, where environmentally induced forms are interpreted as distinct species (Tryon and Tryon 1982; Wiens and Graham 2005).

The classical treatment of *Selaginella* in Java, Indonesia, remains Alston (1935), which recognized 23 species primarily from herbarium materials collected across the island. Although this work established the historical basis for subsequent floristic studies, it was constrained by uneven geographic sampling, incomplete ecological information, and limited understanding of intraspecific variation. More recent compilations, particularly Hassler's global checklist (1994-2026), provide updated nomenclatural syntheses and broader geographic coverage, but many records still rely heavily on historical collections that may perpetuate misidentifications or unverified occurrences (Nic Lughadha et al. 2016).

Several regional studies have documented the diversity and ecological distribution of *Selaginella* in specific landscapes of Java, including karst ecosystems, montane forests, and elevational gradients (Setyawan et al. 2013, 2015, 2016). These studies demonstrated strong habitat association and ecological variability within the genus, but most remained geographically localized and focused primarily on descriptive diversity patterns. Consequently, uncertainty persists regarding taxonomic circumscription, synonymy, endemicity, and the actual diversity of *Selaginella* in Java.

Global databases such as Plants of the World Online (POWO 2026) have improved nomenclatural consistency and taxonomic standardization, but they may still include doubtful records, unresolved synonymy, and distributions lacking regional verification, particularly in morphologically complex tropical plant groups (Nic Lughadha et al. 2016). In Java, several taxa listed in global databases remain poorly supported by herbarium evidence or contemporary field observations, whereas introduced ornamental species observed in the field are inconsistently represented in secondary databases. Consequently, species records in Java require verification using local field and herbarium evidence.

Although Java is one of the most intensively explored islands in Malesia, no modern integrative reassessment of *Selaginella* diversity has been conducted. Existing records remain fragmented and continue to rely largely on historical floristic treatments and secondary databases despite increasing global emphasis on comprehensive plant diversity assessment and documentation (Antonelli et al. 2020). Moreover, few studies have evaluated whether morphologically defined taxa correspond to ecologically differentiated assemblages, even though weak ecological separation may reflect environmentally induced variation rather than clearly differentiated taxonomic entities (Wiens and Graham 2005; Weststrand and Korall 2016). Therefore, this study provides an integrative reassessment of *Selaginella* diversity in Java by combining field observations, herbarium verification, taxonomic standardization, and multivariate ecological analyses to: (i) compile an updated and validated checklist of *Selaginella* species in Java, (ii) evaluate discrepancies among historical taxonomy, global databases, and contemporary field evidence, and (iii) assess whether morphologically defined taxa are supported by ecological differentiation. We hypothesized that environmental heterogeneity and phenotypic plasticity cause substantial morphological overlap among several historically recognized *Selaginella* taxa in Java. This overlap may lead to taxonomic inflation and overestimation of species diversity.

MATERIALS AND METHODS

Study area

The study was conducted across Java, Indonesia, one of the major islands in the Malesian region, characterized by high environmental heterogeneity resulting from volcanic topography, elevational gradients, and tropical monsoonal climate. Java extends from coastal lowlands to volcanic mountains exceeding 3,000 m asl and contains a broad range of habitats occupied by *Selaginella*, particularly humid and shaded environments associated with forest understories, riparian corridors, ravines, and rocky substrates.

Sampling locations were distributed across western, central, and eastern Java to represent multiple elevational zones and habitat types. Surveyed habitats included primary and secondary forests, montane forests, riparian vegetation, volcanic slopes, rocky cliffs, agroforestry systems, plantations, roadside embankments, and other disturbed environments. Forested and riparian habitats generally exhibited higher humidity and canopy cover, whereas open habitats were characterized by greater environmental fluctuation and anthropogenic disturbance.

The study integrated field observations and herbarium-based locality records to maximize geographic representation and improve coverage of historically under-sampled regions. Sampling sites covered lowland, submontane, and montane environments to evaluate patterns of species distribution, ecological differentiation, and taxonomic consistency within *Selaginella* across Java. The distribution of sampling locations is presented in Figure 1.

Field surveys and specimen collection

Field surveys were conducted across western, central, and eastern Java using an exploratory sampling approach to document the distribution patterns and habitat associations of *Selaginella* species. Sampling sites were selected to represent diverse environmental conditions, including variation in elevation, habitat type, vegetation structure, and land-use systems. Surveys targeted habitats commonly associated with *Selaginella*, particularly forest understories, riparian corridors, moist rocky slopes, ravines, volcanic substrates, and forest edges. Additional observations were also conducted in agroforestry systems, plantations, roadside embankments, and urban green spaces to document disturbance-tolerant and introduced taxa.

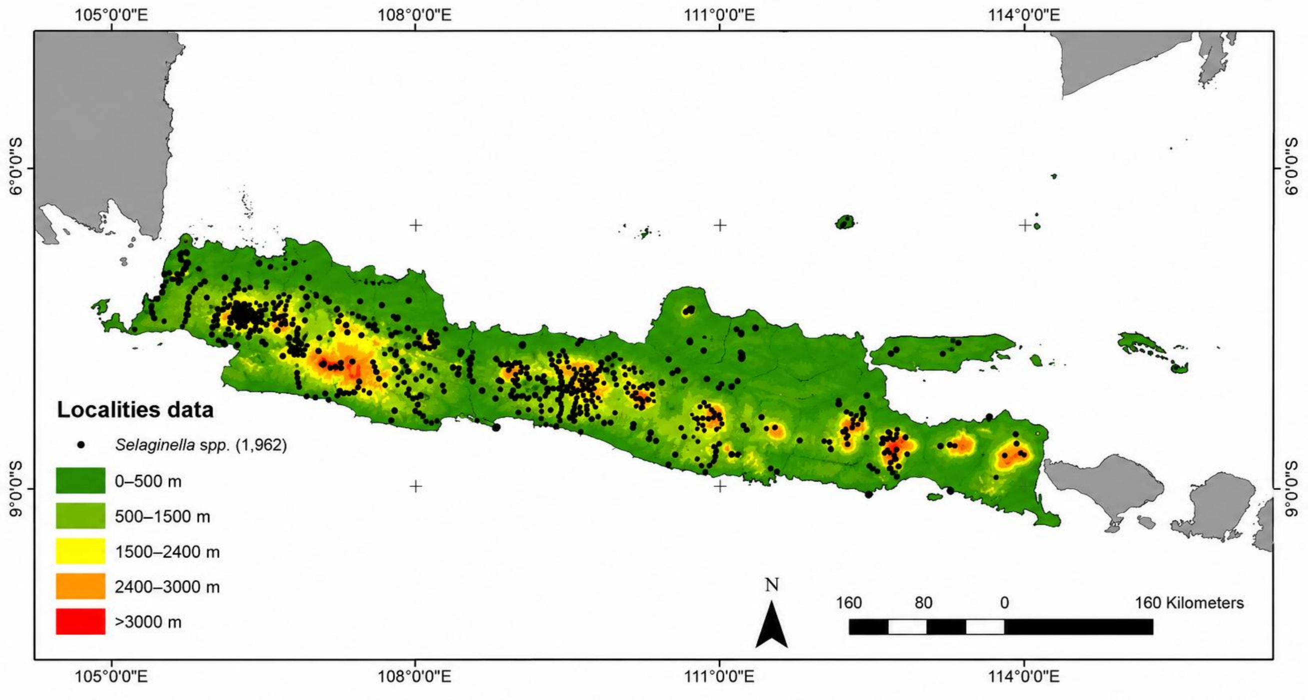

Figure 1. Distribution of *Selaginella* sampling localities across Java, Indonesia

Sampling was performed along accessible trails, riverbanks, volcanic slopes, and other locations where *Selaginella* populations were encountered naturally. At each sampling site, species occurrence was recorded together with ecological information, including habitat type, substrate condition, canopy cover, moisture level, and light exposure. Substrate categories included soil, litter, rock surfaces, moss-covered substrates, and decaying organic material. Geographic coordinates were recorded using handheld Global Positioning System (GPS) devices, while elevation data were obtained directly in the field or extracted from digital elevation sources when necessary. Representative populations were photographed to document variation in growth form, branching pattern, and leaf morphology under natural conditions.

Representative specimens were selectively collected for herbarium verification, particularly from morphologically ambiguous taxa and populations showing unusual phenotypic variation. Specimen collection followed standard herbarium procedures, including pressing, drying, and labeling with locality and habitat information (Bridson and Forman 1998). Field-collected specimens were subsequently compared with herbarium materials and published taxonomic references to confirm species identity and evaluate potential synonymy. The field surveys generated 1,355 occurrence records from 715 unique sampling locations across Java. These records formed the primary dataset for taxonomic reassessment, habitat analysis, elevational distribution analysis, and multivariate ecological analyses conducted in the present study.

Herbarium examination and taxonomic verification

Herbarium examination was conducted to verify species identities, evaluate historical records, and reconcile field observations with published taxonomic treatments. A total of 607 herbarium collections representing 309 localities in Java were examined to assess species identity, nomenclatural consistency, distribution patterns, and morphological variability. The dataset was dominated by specimens deposited in Herbarium Bogoriense (BO; 559 collections, >90%), supplemented by material from the Natural History Museum, London (BM; 22 collections), Naturalis Biodiversity Center, Leiden (L; 18 collections), and a small number of specimens from CANB, K, P, S, BGBM, and WRSL. Historical collections cited in classical taxonomic treatments, particularly Alston (1935), were re-evaluated whenever available.

Morphological examination focused on vegetative characters commonly used in *Selaginella* taxonomy, including branching pattern, growth form, leaf arrangement, degree of anisophylly, leaf margin characteristics, and apex morphology. Observations from herbarium specimens were compared with field-collected material, published descriptions, and taxonomic references to evaluate morphological consistency and species delimitation. Species identification was based on comparative examination of field collections and herbarium materials, supported by reference to authenticated specimens housed at Herbarium Bogoriense (BO).

Taxonomic interpretation followed major floristic accounts, monographic treatments, and regional revisions of *Selaginella* from Malesia and adjacent regions, including Alston (1934a,b, 1935a,b, 1937, 1940), Tagawa (1963, 1973), Tagawa and Iwatsuki (1979), Dahlen (1988), Andrews (1990), Pham-Hoang (1991), Tsai and Shieh (1994), Wong (1982, 2010), Chang et al. (2010), and Zhang et al. (2013). Taxonomic interpretation was further informed by recent regional floristic syntheses and checklists, including Lindsay et al. (2022) and Kalyuzhnyi et al. (2024). Particular attention was given to morphologically complex taxa and historically ambiguous names exhibiting substantial overlap in vegetative morphology.

Field observations and herbarium records were subsequently integrated into a unified dataset comprising 1,962 occurrence records, including 1,355 field observations and 607 herbarium or database records. Duplicate records were removed, and geographic information was standardized prior to analysis. Taxonomic standardization followed Plants of the World Online (POWO 2026) as the primary nomenclatural reference for accepted names and synonymy. Historical names and orthographic variants were harmonized to ensure consistency among field observations, herbarium materials, and published sources.

Species verification followed a conservative evidence-based approach integrating herbarium examination, field observations, taxonomic literature, and biogeographic consistency. Taxa lacking reliable herbarium evidence from Java or exhibiting substantial morphological overlap with broader species complexes were treated cautiously and excluded when necessary. Species were subsequently classified into native, endemic, and introduced or naturalized categories to support subsequent ecological and taxonomic analyses.

Species validation and classification

All *Selaginella* records compiled in this study were evaluated using validation criteria integrating field observations, herbarium evidence, taxonomic literature, and biogeographic consistency to ensure reliable species delimitation and minimize taxonomic inflation associated with morphology-based over-splitting. Species verification emphasized consistency of diagnostic morphology, occurrence records, and agreement among independent taxonomic sources.

Species were classified into four principal categories: confirmed species, taxonomically uncertain species, doubtful or excluded species, and introduced or naturalized species (Table 1). Reliable field observations and herbarium evidence from Java supported the confirmed species. Taxonomically uncertain species included taxa with limited records or incomplete morphological support requiring further verification. Doubtful or excluded taxa consisted of species lacking reliable evidence from Java or exhibiting extensive morphological overlap with broader species complexes. Introduced or naturalized species refer to taxa associated with cultivation or human-mediated dispersal outside their native range. This classification framework provided a standardized basis for checklist compilation, taxonomic reassessment, and subsequent ecological analyses of *Selaginella* diversity in Java.

Ecological and statistical analyses

Comparative taxonomic analysis

Comparative taxonomic analysis was conducted to evaluate differences in species composition among the historical treatment of Alston (1935), Plants of the World Online (POWO 2026), and the present reassessment. Presence-absence data were compiled for all taxa and used to classify species as retained, synonymized, excluded, doubtful, or introduced. Compositional agreement among datasets was evaluated using Sørensen similarity indices based on binary presence-absence matrices.

Table 1. Species validation categories and criteria

Validation category	Definition and validation criteria	Taxonomic implication
Confirmed species	Species supported by reliable field observations, verified herbarium specimens from Java, and relatively consistent morphological characteristics evaluated through comparative assessment using major taxonomic references such as Alston (1935), Hassler (1994-2026), and POWO (2026). Ecological distribution and biogeographic occurrence were also considered consistent with known species ranges.	Accepted as valid components of the contemporary *Selaginella* flora of Java and included in the final checklist and ecological analyses.
Taxonomically uncertain species	Taxa represented by limited occurrence records, incomplete herbarium materials, ambiguous vegetative morphology, or insufficient ecological and geographic evidence. Taxonomic interpretation remained uncertain because available evidence was insufficient for confident comparative reassessment.	Retained provisionally pending additional field surveys, herbarium verification, morphometric evaluation, anatomical investigation, or molecular evidence.
Doubtful or excluded species	Taxa lacking reliable herbarium evidence from Java, represented only by historical or unverifiable reports, or exhibiting extensive morphological overlap with broader species complexes. Several names were interpreted as environmentally associated morphological variants, synonyms, misidentifications, or unsupported records.	Excluded from the final accepted checklist of *Selaginella* species in Java.
Introduced or naturalized species	Non-native taxa associated primarily with ornamental cultivation, horticultural introduction, or human-mediated dispersal. Some species showed localized establishment in disturbed or semi-natural habitats near settlements and cultivation areas.	Recognized separately from native taxa to distinguish anthropogenic introduction from naturally occurring components of the Javan flora.

Habitat and elevational analysis

Species occurrence records were analyzed to evaluate elevational distribution and habitat association patterns. Elevational ranges were classified into lowland (<500 m asl), submontane (500-1500 m asl), and montane (>1500 m asl) zones following Van Steenis (1972). Habitat categories included forest, agroforestry systems, riparian habitats, rocky or lithophytic habitats, and open or disturbed land. Species richness, occurrence frequency, and habitat association were summarized descriptively based on unique occurrence localities.

Multivariate analyses

Multivariate analyses were conducted to evaluate the ecological structuring of *Selaginella* assemblages and relationships between species distribution and environmental variables. Analyses were based on a site × species presence-absence matrix integrating habitat category, elevation, canopy condition, substrate type, and moisture condition. Environmental variables were standardized prior to analysis.

Principal Component Analysis (PCA) and Non-metric Multidimensional Scaling (NMDS) were performed in PAST version 4.13 (Hammer et al. 2001). NMDS analysis based on Bray-Curtis dissimilarity was used to evaluate ecological similarity among assemblages (Bray and Curtis 1957; Clarke 1993). Analysis of Similarities (ANOSIM) with 999 permutations was additionally performed to assess compositional differentiation among habitat categories and elevational zones. Statistical significance was evaluated using permutation-based probability values generated from the ANOSIM procedure (Clarke 1993).

Statistical analyses

Differences in species richness among elevational zones were evaluated using the Kruskal-Wallis test, while Spearman rank correlation analysis was performed to assess the relationship between elevation and species richness across sampling localities. All statistical analyses were conducted in PAST version 4.13 (Hammer et al. 2001), with significance evaluated at $p<0.05$.

RESULTS AND DISCUSSION

Species diversity and taxonomic reassessment

The integrative reassessment of *Selaginella* diversity in Java resulted in the recognition of 21 confirmed species, consisting of 17 native taxa (81.8%), two endemic taxa (9.1%), and two introduced or naturalized species (9.1%) (Table 2). The revised checklist was developed through integration of field observations, herbarium verification, and taxonomic standardization.

Most confirmed species were widespread native taxa occurring across multiple regions of Malesia, including *S. plana*, *S. intermedia*, *S. ciliaris*, *S. opaca*, and *S. willdenowii*, all of which were repeatedly recorded across multiple habitats and elevational zones. These species occurred in forests, riparian habitats, agroforestry systems, and disturbed environments, indicating relatively broad ecological tolerance and wide geographic distribution across Java.

Several species were recorded only from specific habitats and elevational ranges. Among these, *S. rothertii* is currently regarded as endemic to Java, whereas *S. zollingeriana* appears restricted to Java and the Lesser Sunda Islands and is therefore treated as a regional endemic element. Additional taxa such as *S. subalpina* and *S. subspinulosa* were associated primarily with humid montane habitats and occurred less frequently across the island.

The reassessment also resolved several historical taxonomic ambiguities. Taxa such as *S. ascendens* and *S. springiana* were incorporated into the broader *S. intermedia* complex because their diagnostic characters overlapped extensively with environmentally variable forms. Similarly, *S. caudata* was excluded as a distinct species because the examined specimens fell within the morphological range of *S. plana*. Several names reported in historical compilations or global databases, including *S. grabowskyi*, *S. strobiformis*, *S. stipulata*, and *S. tamariscina*, could not be confirmed through reliable herbarium evidence or contemporary field observations from Java.

Two introduced taxa, *S. uncinata* and *S. kraussiana*, were recorded mainly in cultivated and disturbed habitats associated with human activity. *Selaginella uncinata* showed localized evidence of naturalization in humid, shaded environments near settlements.

Comparative reassessment among Alston (1935), Hassler (1994-2026), POWO (2026), and the present study revealed differences in accepted species composition and nomenclatural interpretation (Table 3). Most historically reported taxa were retained, whereas approximately 13-18% were excluded or synonymized following herbarium re-examination and ecological evaluation. Nomenclatural standardization also resolved several orthographic inconsistencies and outdated combinations.

Pairwise Sørensen similarity analysis demonstrated moderate to high agreement among historical and contemporary taxonomic datasets (Table S1). Similarity values ranged from 0.80 to 0.93, with the highest similarity observed between POWO and the present study ($S = 0.93$), whereas the lowest similarity occurred between Alston (1935) and the present reassessment ($S = 0.80$).

Ecological distribution and habitat association

The distribution of *Selaginella* species in Java showed clear elevational and habitat-related structuring (Table 4; Table 5; Figure 2). Species richness reached its maximum in submontane environments (500-1500 m asl), where 19 of the 21 confirmed species were recorded. Lowland habitats contained 14 species, whereas only four species were restricted to montane environments above 1500 m asl., whereas lowland and upper montane habitats contained comparatively fewer species. Kruskal-Wallis analysis indicated significant differences in richness among elevational zones ($H = 7.84$, $p = 0.020$), while Spearman rank correlation analysis showed a weak but significant unimodal relationship between elevation and species richness ($\rho = 0.41$, $p = 0.031$).

Table 2. Confirmed *Selaginella* species in Java, Indonesia, with accepted names, distribution status, taxonomic status, data sources, and distribution notes

Accepted name	Distribution status	Taxonomic status in the present study	Main data sources	Distribution notes in Java
Selaginella alutacea Spring	Native	Retained	Alston; Hassler; POWO; present study	Confirmed from humid forest habitats in Java
Selaginella aristata Spring	Native	Retained	Alston; Hassler; POWO; present study	Common in disturbed and open humid habitats
Selaginella biformis A.Braun ex Kuhn.	Native	Retained	Alston; Hassler; POWO; present study	Recorded from lowland to montane regions
Selaginella ciliaris (Retz.) Spring	Native	Retained	Alston; Hassler; POWO; present study	Common along moist forest margins and shaded habitats
Selaginella cupressina (Willd.) Spring	Native (uncertain)	Retained but taxonomically uncertain	Alston; Hassler; POWO; present study	Poorly supported from Java and requiring additional taxonomic verification
Selaginella frondosa Warb.	Native	Retained	Alston; Hassler; POWO; present study	Mainly found in humid montane forests
Selaginella intermedia (Blume) Spring	Native	Retained	Alston; Hassler; POWO; present study	Includes historical records formerly treated as *S. ascendens* and *S. springiana*
Selaginella involvens (Sw.) Spring	Native	Absent from Alston (1935) but retained in later taxonomic treatments	Hassler; POWO; present study	Recognized in later floristic revisions and confirmed from Java
Selaginella kraussiana (Kunze) A.Braun	Introduced/ naturalized	Introduced/ naturalized species	POWO; present study	Cultivated ornamental species occasionally naturalize in humid habitats
Selaginella opaca Warb.	Native	Retained	Alston; Hassler; POWO; present study	Common in shaded forest understories in montane forests
Selaginella ornata (Hook. & Grev.) Spring	Native	Retained	Alston; Hassler; POWO; present study	Distributed mainly in submontane and montane forests
Selaginella plana (Desv.) Hieron.	Native	Retained	Alston; Hassler; POWO; present study	One of the most widespread *Selaginella* species in Java
Selaginella remotifolia Spring	Native	Retained	Alston; Hassler; POWO; present study	Frequently found on moist forest floors in montane forests along with *S. opaca*
Selaginella repanda (Desv.) Spring	Native	Retained	Alston; Hassler; POWO; present study	Usually associated with rocky and humid substrates
Selaginella rothertii Alderw.	Endemic	Retained	Alston; Hassler; POWO; present study	Recorded from scattered forest localities ranging from lowland to lower montane habitats in Java
Selaginella singalanensis Hieron.	Native	Retained	Alston; present study	Historical records treated by Alston (1935) as *S. modica* are interpreted here under *S. singalanensis* following current taxonomic usage
Selaginella subalpina Alderw.	Native	Retained	Alston; Hassler; POWO; present study	Mainly restricted to montane habitats
Selaginella subspinulosa Spring.	Native (uncertain)	Retained but taxonomically uncertain	Alston; Hassler; POWO; present study	Rarely collected and poorly understood in Java
Selaginella uncinata (Desv.) Spring	Introduced/ naturalized	Introduced/ naturalized species	POWO; present study	Ornamental species occasionally naturalize in shaded, humid habitats
Selaginella willdenowii (Desv.) Baker	Native	Retained	Alston; Hassler; POWO; present study	Widespread in humid tropical forests
Selaginella zollingeriana Spring	Endemic	Retained	Alston; Hassler; POWO; present study	Recorded from several mountainous regions in Java

Note: Excluded taxa include *S. caudata, S. caulescens, S. grabowskyi, S. springiana, S. strobiformis, and S. tamariscina.* These are either unconfirmed from Java or treated as synonyms or species complexes. *Selaginella ascendens* is treated within the *S. intermedia* complex. *S. stipulata* was not retained because diagnostic characters overlapped extensively with *S. plana*

Table 3. Comparison of *Selaginella* species recorded by Alston (1935), Hassler (1994-2026), POWO (2026), and the present study, and taxonomic interpretation in the present study

Species	Alston (1935)	Hassler (1994-2026)	POWO (2026)	Present study	Taxonomic status/remarks
Selaginella alutacea	Yes	Yes	Yes	Yes	Retained
Selaginella aristata	Yes	Yes	Yes	Yes	Retained
Selaginella ascendens	Yes	No	No	No	Interpreted within the *S. intermedia* complex based on overlapping morphology and ecological distribution
Selaginella biformis	Yes	Yes	Yes	Yes	Retained
Selaginella caudata	No	No	Yes	No	Accepted in POWO, but interpreted within the *S. plana* complex in the present study
Selaginella caulescens	Yes	No	No	No	Interpreted within the *S. involvens* complex
Selaginella ciliaris	Yes	Yes	Yes	Yes	Retained
Selaginella cupressina	Yes	Yes	Yes	Yes	Retained provisionally because available evidence from Java remains limited
Selaginella frondosa	Yes	Yes	Yes	Yes	Retained
Selaginella grabowskyi	No	Yes	Yes	**No**	Reported in later databases, but poorly supported for Java
Selaginella intermedia	Yes	Yes	Yes	Yes	Retained
Selaginella involvens	No	Yes	Yes	Yes	Added in later treatments
Selaginella singalanensis	Yes	No	No	Yes	Historical record treated by Alston (1935) as *Selaginella modica*; accepted here as *S. singalanensis* following current nomenclatural interpretation
Selaginella opaca	Yes	Yes	Yes	Yes	Retained
Selaginella ornata	Yes	Yes	Yes	Yes	Retained
Selaginella plana	Yes	Yes	Yes	Yes	Retained
Selaginella remotifolia	Yes	Yes	Yes	Yes	Retained
Selaginella repanda	Yes	Yes	Yes	Yes	Retained
Selaginella rothertii	Yes	Yes	Yes	Yes	Retained
Selaginella springiana	Yes	No	No	No	Interpreted within the *S. intermedia* complex in the present study
Selaginella stipulata	Yes	Yes	Yes	No	Poorly supported for Java and interpreted within the *S. plana* complex
Selaginella strobiformis	No	No	Yes	No	POWO-accepted species; not confirmed from Java
Selaginella subalpina	Yes	Yes	Yes	Yes	Retained
Selaginella subspinulosa	Yes	Yes	Yes	Yes	Retained provisionally because available records from Java remain limited
Selaginella tamariscina	Yes	No	Yes	No	Reported from the Lesser Sunda Islands; not confirmed from Java
Selaginella willdenowii / willdenovii	Yes	Yes	Yes	Yes	Orthographic standardization to *willdenowii*
Selaginella zollingeriana	Yes	Yes	Yes	Yes	Retained

Note: The table includes both accepted species and historically reported taxa evaluated during taxonomic reassessment. Several names were not retained in the final checklist because they were interpreted as synonyms, doubtful records, or species complexes

Lowland habitats (<500 m asl) were dominated primarily by widespread taxa such as *S. plana*, *S. ciliaris*, and *S. willdenowii*, particularly in riparian corridors, shaded ravines, and secondary vegetation. Submontane habitats supported the highest richness and contained taxa including *S. intermedia*, *S. opaca*, *S. ornata*, *S. involvens*, and *S. repanda*. Montane environments above 1500 m asl supported fewer but more habitat-restricted taxa, including *S. subalpina*, *S. subspinulosa*, *S. frondosa*, and *S. remotifolia*, which were recorded mainly from humid montane forests and volcanic slopes.

Forest ecosystems contained the highest richness, supporting 18 of the 21 confirmed species (85.7%). Riparian habitats and humid rocky substrates also supported relatively high richness, with 14 (66.7%) and 13 species (61.9%), respectively. Agroforestry systems contained 11 species (52.4%), whereas open and disturbed habitats supported only seven species (33.3%).

Agroforestry systems supported moderate richness and were dominated mainly by widespread taxa such as *S. plana*, *S. aristata*, *S. repanda*, and *S. involvens*. Open and disturbed habitats contained the lowest richness and were characterized primarily by disturbance-tolerant taxa, including *S. aristata*, *S. ciliaris*, and the introduced *S. uncinata*.

Clustered heatmap analysis showed several major assemblage groups corresponding to forest-associated taxa, montane and riparian taxa, lithophytic assemblages, and disturbance-associated species. Forest-associated taxa such as *S. intermedia*, *S. opaca*, *S. ornata*, *S. willdenowii*, and *S. plana* were grouped primarily within humid and shaded habitats, whereas *S. aristata*, *S. ciliaris*, and *S. uncinata* were associated mainly with disturbed and semi-open environments. Montane and riparian taxa, including *S. remotifolia*, *S. subalpina*, and *S. frondosa,* formed relatively distinct assemblages associated with permanently humid microhabitats, while lithophytic taxa such as *S. repanda* and *S. alutacea* were linked mainly to rocky and volcanic substrates.

Multivariate ecological analyses

PCA ordination

Principal Component Analysis (PCA) was used to examine relationships between species occurrence and environmental variables (Figure 3). The first two principal components explained 66.1% of the total ecological variation, with PC1 accounting for 41.8% and PC2 accounting for 24.3% of the variance. Variation along the ordination axes was associated primarily with humidity, canopy condition, substrate type, and elevational gradient.

Positive values along PC1 were associated mainly with humid forest environments and stable canopy cover, where taxa such as *S. remotifolia*, *S. frondosa*, *S. subalpina*, and *S. opaca* were more frequently recorded in riparian habitats and humid montane forests. Negative values were associated primarily with disturbed and semi-open habitats occupied by *S. aristata*, *S. ciliaris*, and *S. uncinata*. PC2 reflected substrate differentiation and elevational variation, particularly separating lithophytic taxa such as *S. repanda* and *S. alutacea* from soil-associated forest species.

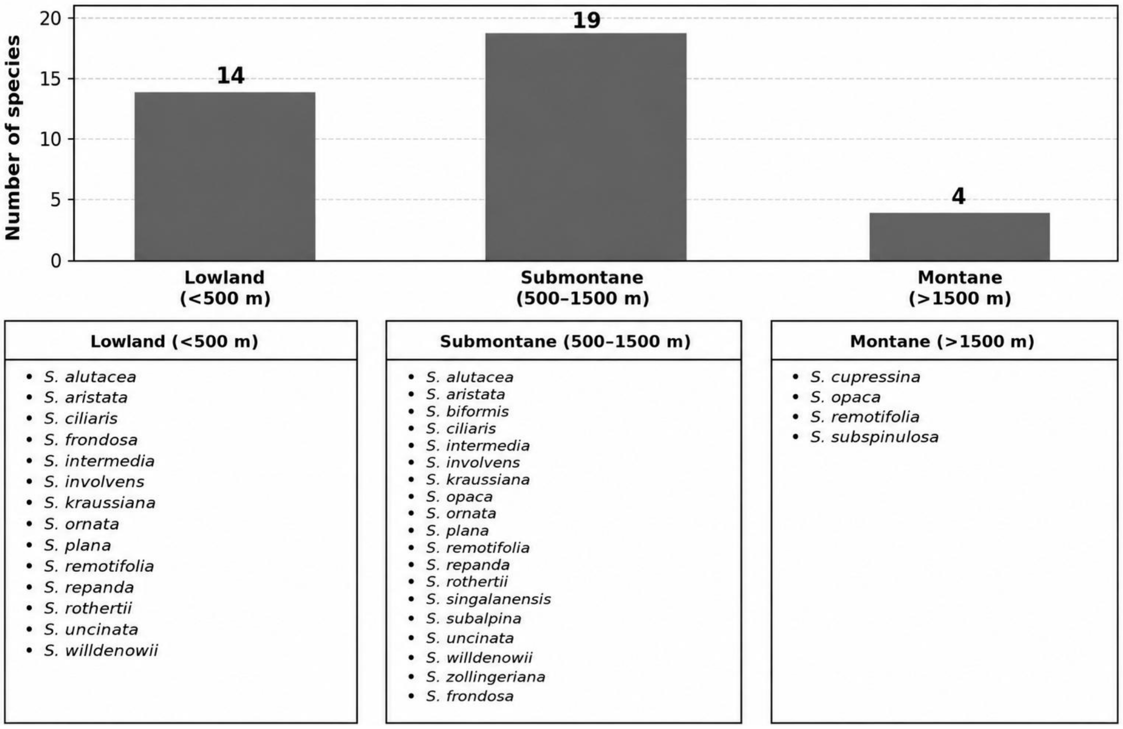

Figure 2. Species richness across elevational zones in Java, Indonesia

Table 4. Distribution of *Selaginella* species across elevation zones in Java, Indonesia

Elevation zone	Elevation range (m asl)	Species richness (S)	Relative richness (%)	Occurrence pattern	Representative species	Dominant species characteristics	Associated habitat characteristics
Lowland	<500	14	66.7	Sparse, fragmented, and locally patchy	*S. aristata*, *S. ciliaris*, *S. plana*, *S. willdenowii*, *S. uncinata*	Dominated by disturbance-tolerant generalists in warm habitats.	Frequently associated with fragmented habitats, warmer conditions, and anthropogenic disturbance
Submontane	500-1500	19	90.5	Widespread and relatively continuous	*S. intermedia*, *S. opaca*, *S. ornata*, *S. involvens*, *S. repanda*, *S. singalanensis*, *S. subalpina*	Mixture of ecological generalists and moisture-dependent forest taxa	Associated with relatively humid habitats, dense canopy cover, and heterogeneous vegetation structure
Montane	>1500	4	19.0	Localized and environmentally restricted	*S. cupressina*, *S. opaca*, *S. remotifolia*, *S. subspinulosa*	Dominated by humidity-dependent and habitat-specialist taxa	Restricted to humid montane habitats, especially volcanic slopes and shaded ravines.

Note: Relative richness (%) represents proportional estimates derived from compiled occurrence records from field observations and herbarium collections in Java (n = 1,962 records). Elevational patterns were interpreted from recurrent locality data associated with lowland forests, submontane forests, montane forests, volcanic slopes, ravines, and humid upland habitats. Species richness categories and occurrence patterns are based on descriptive and exploratory analyses rather than formal statistical testing

Table 5. Distribution of *Selaginella* species across habitat types in Java, Indonesia

Habitat type	Species richness (S)	Relative richness (%)	Occurrence pattern	Representative species	Habitat complexity	Dominant species characteristics	Associated habitat characteristics
Forest (primary and secondary)	18	85.7	Widespread and relatively continuous	*S. plana, S. willdenowii, S. ornata, S. intermedia, S. opaca*	High	Shade-tolerant and humidity-dependent species	Associated with humid understories, dense canopy cover, and heterogeneous substrates
Agroforestry systems	11	52.4	Patchy but locally frequent	*S. plana, S. aristata, S. repanda, S. involvens*	Moderate	Generalist and semi-shade-tolerant taxa	Associated with semi-natural vegetation structure and relatively humid microhabitats
Riparian zones and spring areas	14	66.7	Localized clusters along humid corridors	*S. remotifolia, S. frondosa, S. subalpina, S. ciliaris*	High	Moisture-dependent and riparian-associated species	Characterized by permanently humid substrates and relatively stable environmental conditions
Rocky substrates and cliffs	13	61.9	Scattered but recurrent	*S. repanda, S. aristata, S. involvens, S. alutacea*	Moderate-high	Lithophytic and substrate-adapted taxa	Associated mainly with moist cliffs, ravines, and volcanic rock surfaces
Open and disturbed land	7	33.3	Sparse and discontinuous	*S. aristata, S. ciliaris, S. plana, S. uncinata*	Low	Disturbance-tolerant and habitat-flexible species	Associated with higher temperature fluctuation, reduced humidity, and simplified vegetation structure

Note: Species richness (S) represents the number of confirmed *Selaginella* species recorded within each habitat category based on the combined occurrence dataset (1,962 records). Relative richness (%) was calculated as the proportion of the 21 confirmed *Selaginella* species recorded in each habitat type. Because many species occur across multiple habitat categories, percentages are not additive and may exceed 100% when summed.

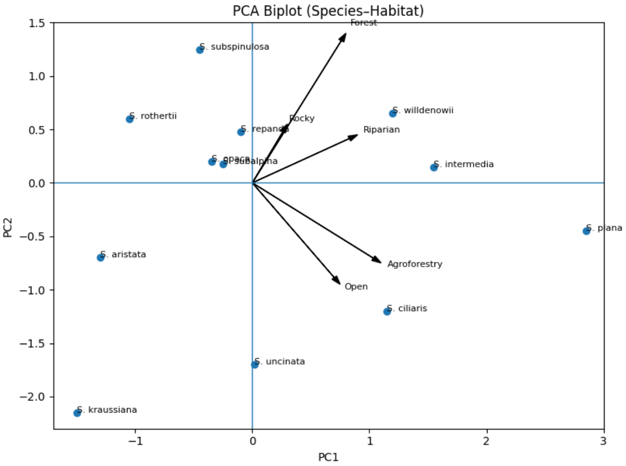

Figure 3. PCA ordination of *Selaginella* assemblages across habitat types in Java, Indonesia

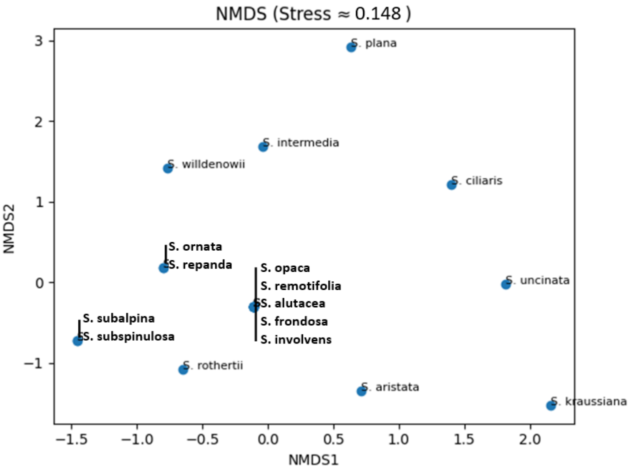

Figure 4. NMDS ordination showing ecological overlap among *Selaginella* species complexes in Java, Indonesia

Several widespread taxa, including *S. intermedia*, *S. plana,* and *S. involvens*, occupied intermediate ordination positions and occurred across multiple habitat categories.

NMDS ordination

The NMDS analysis demonstrated ecological similarity patterns among *Selaginella* assemblages across habitat categories in Java (Figure 4). The ordination produced a stress value of 0.148, indicating an acceptable representation of ecological relationships within the dataset. ANOSIM analysis additionally indicated significant compositional differentiation among habitat categories (R = 0.684, permutation p = 0.001 based on 999 permutations).

Several species occupied overlapping positions in the ordination space, indicating shared ecological affinities across habitat types. The closest associations were observed among *S. opaca*, *S. frondosa*, *S. remotifolia*, *S. alutacea*, and *S. involvens*, which formed a central cluster characterized by substantial ecological overlap. In contrast, *S. plana*, *S. ciliaris*, *S. uncinata*, and *S. kraussiana* occupied more isolated positions, suggesting broader ecological amplitudes or distinctive habitat preferences. Species such as *S. repanda*, *S. ornata*, and *S. willdenowii* showed intermediate positions, reflecting partial overlap with multiple ecological groups. Overall, the NMDS ordination supported the existence of both shared and differentiated ecological niches among *Selaginella* species in Java.

Morphological overlap and identification challenges

Substantial morphological variation was observed among *Selaginella* populations across different habitats and elevational zones in Java, particularly in characters traditionally used for species identification such as branching architecture, stem orientation, leaf arrangement, leaf size, and degree of anisophylly (Figure 5). Much of this variation was associated with environmental conditions, especially humidity, canopy cover, and substrate exposure.

Figure 5 summarizes several ecological and morphological adaptations observed among Javan *Selaginella*. Species differed in their responses to light availability, humidity, and substrate conditions, ranging from shade-adapted forms associated with humid forest understories to taxa capable of persisting in more exposed environments with periodic moisture stress. Some species, such as *S. involvens*, exhibited desiccation-tolerant characteristics typical of resurrection plants, whereas others remained strongly associated with persistently humid habitats. Variation in substrate preference was also evident, with terrestrial, lithophytic, and epiphytic growth strategies occurring across different ecological settings. Five principal growth forms were recognized: erect, ascending, compact lithophytic, creeping, and climbing habits.

Species occurring in humid forest interiors generally exhibited elongated stems, broader branching patterns, and loosely arranged foliage, whereas populations from exposed rocky substrates and disturbed habitats developed more compact growth forms with denser branching and smaller leaves. These environmentally associated differences were especially evident in widespread taxa such as *S. plana*, *S. intermedia*, and *S. repanda*, which showed broad morphological variability across ecological gradients.

The greatest identification difficulties occurred within morphologically overlapping species complexes, particularly the *S. plana* and *S. intermedia* groups (Table S2). Characters such as branch width, stem flattening, leaf symmetry, and growth habit varied continuously among populations and frequently overlapped among taxa. Within the *S. plana* complex, variation in branching architecture and leaf arrangement overlapped with characters previously used to distinguish *S. caudata* and *S. stipulata*. Likewise, forms historically recognized as *S. ascendens* and *S. springiana* showed no consistent morphological separation from the broader *S. intermedia* complex.

Environmental plasticity was also evident among lithophytic and montane taxa. Populations of *S. alutacea*, *S. repanda*, and *S. subspinulosa* growing on exposed volcanic rocks frequently developed smaller leaves and more compact architecture compared with individuals from shaded and humid habitats. Preservation quality in herbarium specimens additionally complicates identification because flattened vegetative structures often obscure subtle morphological characters.

Introduced ornamental taxa also exhibited substantial variability. *S. uncinata* varied in pigmentation intensity and iridescent coloration depending on humidity and light exposure, whereas *S. kraussiana* showed variation in stem elongation and mat density between cultivated and semi-naturalized populations.

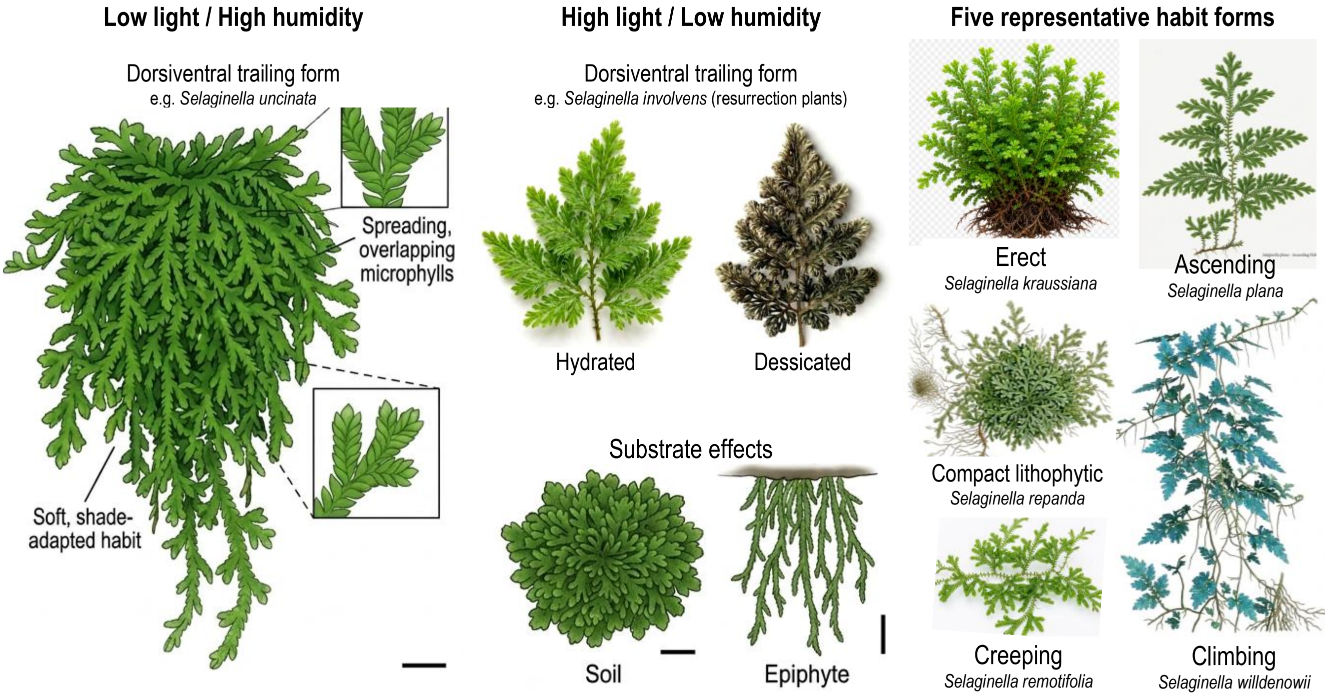

Figure 5. Ecological and morphological diversity of *Selaginella* species in Java, Indonesia.

Discussion

Taxonomic reassessment and morphological complexity of Javan Selaginella

By combining field records, herbarium specimens, and ecological analyses, this study re-evaluated *Selaginella* diversity in Java. The reassessment indicates that species diversity in Java is lower than suggested by several historical and database-based compilations, largely because earlier classifications relied heavily on environmentally variable vegetative morphology. Similar problems occur in other tropical lycophytes and ferns. Morphology-based classification often overestimates diversity when vegetative characters overlap and phenotypic plasticity is strong (Korall and Kenrick 2002; Arrigo et al. 2013; Weststrand and Korall 2016).

Historical taxonomy, particularly Alston's (1935) work, established the main floristic baseline for *Selaginella* in Java, despite its limitations. Historical classifications suffered from uneven sampling, poor ecological data, and few comparative specimens. Many early collections originated primarily from accessible montane regions and botanical exploration routes, whereas disturbed lowland habitats and anthropogenic landscapes remained poorly represented. In addition, habitat condition, canopy structure, substrate type, and microclimatic information were often absent from herbarium labels, making ecological interpretation difficult.

Several historically recognized taxa showed extensive morphological overlap, particularly within the *S. plana* and *S. intermedia* complexes. Characters traditionally used for species recognition included branching architecture, stem orientation, leaf symmetry, anisophylly, and growth habit. These characters varied continuously across field populations and herbarium materials, making morphological interpretation more difficult in several species complexes. Variations in these characters were frequently associated with humidity, canopy openness, and substrate stability, suggesting that vegetative morphology responds dynamically to local environmental conditions. Similar complexity has also been observed in molecular studies of Indonesian *Selaginella* (Jafron et al. 2025; Setyawan et al. 2025).

The greatest taxonomic complexity was observed within the *S. plana* complex. Populations assigned to *S. plana* showed broad variation in branch structure and leaf morphology across contrasting habitats and elevational zones. Characters previously used to distinguish *S. caudata* and *S. stipulata* overlapped extensively with environmentally variable forms of *S. plana*, preventing consistent separation based solely on vegetative morphology. Comparable overlap was also observed within the *S. intermedia* complex, where forms historically recognized as *S. ascendens* and *S. springiana* showed no stable morphological separation from broader *S. intermedia* populations. Detailed taxonomic justification for excluded, provisionally retained, and morphologically overlapping taxa is provided in Figure 6 and Table S3.

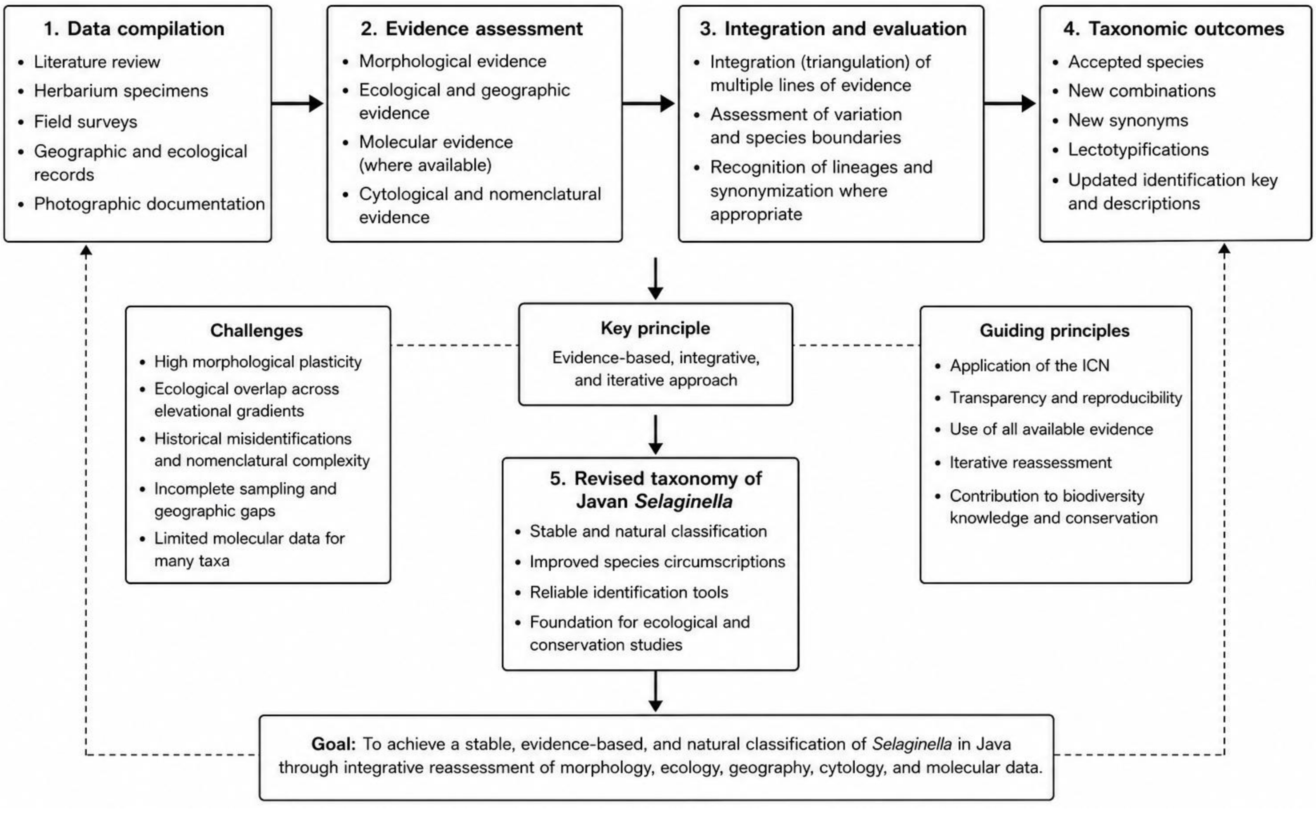

Figure 6. Conceptual framework of taxonomic reassessment in Javan *Selaginella*

Ecological analyses additionally showed that several morphologically similar taxa occupied overlapping habitat categories and elevational ranges. Widespread taxa such as *S. plana*, *S. intermedia*, and *S. involvens* occurred across multiple habitat types and occupied broad ordination space in PCA and NMDS analyses. In contrast, montane and riparian taxa such as *S. subalpina*, *S. remotifolia*, and *S. frondosa* formed more restricted ecological assemblages associated with humid forest environments.

The results indicate that morphology-based taxonomy alone is often insufficient for consistent interpretation of species diversity in tropical *Selaginella*. Ecological overlap and morphological similarity alone do not prove taxonomic synonymy. Other patterns of differentiation remain possible. Molecular phylogenetic studies in lycophytes have repeatedly demonstrated incongruence between vegetative morphology and phylogenetic relationship (Korall and Kenrick 2002; Weststrand and Korall 2016; Setyawan et al. 2025).

This reassessment provides a conservative, morphology-based taxonomic framework for Javan *Selaginella*, integrating field observations, herbarium reassessment, ecological evidence, and nomenclatural standardization. Future studies incorporating morphometric, anatomical, reproductive, and molecular evidence will be important for further refinement of taxonomic interpretation within morphologically complex groups.

Ecological structuring of Selaginella *assemblages*

The present study demonstrates that *Selaginella* assemblages in Java are structured primarily by environmental gradients and habitat characteristics, particularly humidity stability, canopy cover, substrate condition, and elevational variation. Multivariate analyses consistently showed that species composition varied across forest, riparian, lithophytic, agroforestry, and disturbed habitats. PCA and NMDS ordinations additionally revealed clear ecological clustering among habitat-associated assemblages, with forest and montane taxa generally separated from disturbance-tolerant species occupying semi-open environments.

Forest ecosystems represented the principal ecological center of *Selaginella* diversity in Java. Species richness and occurrence frequency were highest in humid primary and secondary forests characterized by stable canopy cover and moist understory conditions. Taxa such as *S. opaca*, *S. ornata*, *S. intermedia*, and *S. willdenowii* were consistently associated with shaded forest habitats and formed relatively cohesive ecological clusters in ordination analyses. Other studies have found similar forest-linked patterns in tropical ferns and lycophytes where humidity and vegetation complexity strongly influence community structure (Kessler 2001; Watkins et al. 2006).

Submontane forests represented the most important diversity zone because they supported the highest concentration of taxa across the island. These environments combined relatively stable humidity, moderate temperature, and heterogeneous microhabitats. Species richness declined toward both lowland and upper montane zones, producing a broadly unimodal elevational pattern similar to that reported for other tropical pteridophyte assemblages (Kluge et al. 2006; Suissa et al. 2021).

Riparian habitats and humid ravines also functioned as important ecological refugia. Species such as *S. remotifolia*, *S. subalpina*, and *S. frondosa* were closely associated with permanently moist stream margins, shaded ravines, and spring systems characterized by stable humidity throughout the year. Lithophytic taxa, including *S. repanda* and *S. alutacea,* were associated primarily with volcanic rocks, humid cliffs, and rocky substrates, forming partially distinct ecological assemblages in ordination analyses.

In contrast, open and disturbed habitats supported relatively simplified assemblages dominated mainly by widespread taxa and disturbance-tolerant species. *S. plana*, *S. aristata*, *S. ciliaris*, and *S. uncinata* occurred frequently in habitats characterized by greater light exposure, reduced canopy cover, and stronger anthropogenic disturbance. These taxa occupied broader ecological space in PCA and NMDS ordinations compared with habitat-restricted montane and riparian species.

The ecological analyses also showed broad habitat overlap among several morphologically similar taxa, particularly within the *S. plana*, *S. intermedia*, and *S. involvens* complexes. Several taxa occupied overlapping ordination space and occurred across similar elevational and habitat ranges. Similar ecological overlap has been reported in other morphologically variable tropical plant groups influenced strongly by environmental heterogeneity and habitat plasticity (Wiens and Graham 2005; Sundue et al. 2016).

Selaginella diversity in Java is closely tied to humid, structurally complex habitats. Forested environments, riparian corridors, and lithophytic microhabitats supported the highest richness and the most distinct assemblage structure, whereas disturbed habitats contained comparatively simplified communities dominated by ecologically tolerant taxa.

Biogeography and conservation implications

The revised checklist clarifies the distribution of *Selaginella* species in Java and identifies habitats that support the highest diversity. The flora was dominated primarily by widespread native taxa, whereas endemic and habitat-restricted species represented only a small proportion of the total diversity. Species such as *S. plana*, *S. intermedia*, *S. ciliaris*, and *S. willdenowii* occurred broadly across multiple habitat types and elevational zones, indicating relatively broad ecological tolerance and effective regional dispersal capacity. Similar distribution patterns have been reported widely in tropical fern and lycophyte assemblages where efficient spore-mediated dispersal contributes to broad geographic ranges (Tryon 1970; Barrington 1993).

Despite relatively low endemism, montane and riparian habitats supported several localized taxa, including *S. rothertii*, *S. zollingeriana*, *S. subalpina*, and *S. remotifolia*. These taxa were associated mainly with humid forests, shaded ravines, volcanic slopes, and permanently moist habitats characterized by stable understory conditions. Submontane forests appeared particularly important because they combined high environmental heterogeneity with favorable humidity and canopy conditions, resulting in the highest species richness across the island. Similar elevational richness patterns have been documented widely in tropical pteridophyte assemblages and mountain ecosystems (Kessler 2001; Grytnes and Beaman 2006).

The close ecological association between *Selaginella* diversity and humid forest environments indicates that habitat degradation and forest fragmentation may disproportionately affect habitat-restricted taxa. Riparian corridors, humid ravines, and volcanic montane forests appeared especially important for maintaining populations of moisture-dependent species. Canopy opening, hydrological alteration, and microclimatic instability may therefore reduce habitat suitability for taxa requiring stable humidity and shaded understory conditions.

The study also documented the occurrence of two introduced taxa, *S. uncinata* and *S. kraussiana*, primarily in cultivated landscapes, agroforestry margins, roadside embankments, urban green spaces, and other disturbed habitats. *S. uncinata* showed localized evidence of naturalization in humid shaded habitats near settlements and disturbed forest margins, whereas *S. kraussiana* remained more strongly associated with cultivation. Similar ornamental introduction pathways have been reported widely in tropical and subtropical regions where horticultural activities facilitate species dispersal and establishment in disturbed habitats (Reichard and White 2001; van Kleunen et al. 2015).

The predominance of introduced taxa in disturbed and semi-open environments further suggests that anthropogenic landscape modification facilitates colonization by non-native *Selaginella*. In contrast, relatively intact humid forests and structurally complex riparian systems appeared less affected by introduced taxa. Although non-native species currently represent only a minor component of the flora, continued ornamental introduction and habitat disturbance may facilitate future expansion into semi-natural habitats.

The present reassessment indicates that conservation of *Selaginella* diversity in Java depends strongly on the persistence of humid and structurally complex habitats, particularly submontane forests, riparian corridors, and volcanic montane ecosystems. Protection of these environments remains important for maintaining both species richness and habitat-specialist assemblages within tropical lycophyte communities.

Limitations and future research directions

Several limitations should be considered when interpreting these results, but it has several limitations. Sampling intensity remained influenced by accessibility and historical collection bias, with remote montane systems, volcanic slopes, karst habitats, and fragmented lowland forests sampled less intensively than accessible areas (Daru et al. 2018). In addition, the reassessment relied primarily on vegetative morphology, whereas characters such as branching architecture, leaf arrangement, anisophylly, and growth habit are strongly influenced by environmental conditions, including humidity, canopy openness, and substrate stability (Weststrand and Korall 2016). Although herbarium verification and ecological analyses reduced interpretative uncertainty, several species complexes, particularly *S. plana*, *S. intermedia*, *S. repanda*, and *S. involvens*, remained difficult to interpret consistently.

The study also did not incorporate morphometric, anatomical, or molecular phylogenetic analyses, despite recent molecular studies demonstrating substantial genetic variation and differentiation in Indonesian *Selaginella* (Jafron et al. 2025; Setyawan et al. 2025). Molecular approaches are increasingly important for evaluating taxonomic complexity and comparative relationships in tropical lycophytes (Korall and Kenrick 2002; Pryer et al. 2004). Consequently, some morphotypes interpreted here as environmentally associated variants may require further reassessment following future integrative evaluation. Ecological interpretation was additionally constrained by limited quantitative microclimatic measurements such as canopy openness, soil moisture, humidity, and substrate chemistry. Future research should therefore prioritize integrative approaches combining molecular phylogenetics, morphometrics, anatomy, ecology, herbarium reassessment, and biogeographic analysis. Species complexes such as *S. plana* and *S. intermedia* represent particularly important targets for future investigation because of their extensive morphological and ecological overlap. Long-term monitoring of introduced taxa such as *S. uncinata* and *S. kraussiana* is also needed to evaluate their ecological dynamics and potential expansion in disturbed tropical habitats.

In conclusion, this study provides an integrative reassessment of *Selaginella* diversity in Java through field surveys, herbarium examination, ecological analysis, and taxonomic standardization. Analysis of 1,962 occurrence records resulted in the recognition of 21 confirmed species comprising 17 native non-endemic taxa (81.0%), two endemic taxa (9.5%), and two introduced or naturalized taxa (9.5%). Comparative evaluation among historical and contemporary taxonomic datasets revealed substantial differences in species interpretation, synonymy, and occurrence records, while several historically recognized taxa were incorporated into broader species complexes because of extensive morphological and ecological overlap. Ecological analyses showed that *Selaginella* assemblages in Java are structured primarily by habitat characteristics, humidity, canopy cover, substrate condition, and elevational gradients, with the highest species richness occurring in submontane habitats (500-1,500 m asl). Multivariate analyses additionally revealed broad ecological overlap among several morphologically defined taxa (ANOSIM: $R = 0.684$, permutation $p = 0.001$ based on 999 permutations), with PCA explaining 66.1% of the total ecological variation, indicating that morphology-based classification alone may contribute to inconsistent taxonomic interpretation in tropical *Selaginella*. The results show that taxonomic interpretation is more reliable when field observations, herbarium evidence, and ecological information are evaluated together. The checklist presented here should be regarded as a working taxonomic framework that can be refined through future molecular and population-level studies, while acknowledging that future molecular and population-level studies may further refine taxonomic interpretation within several morphologically complex groups.

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Table S1. Sørensen similarity among historical and contemporary taxonomic datasets of *Selaginella* in Java, Indonesia

Dataset comparison	Shared species (C)	Total species A	Total species B	Sørensen similarity (S)	Interpretation
Alston (1935) vs Present study	18	23	22	0.80	Moderate-high agreement; several historical taxa interpreted within broader species complexes
Hassler (1994-2026) vs Present study	21	25	22	0.89	High agreement with minor discrepancies
POWO (2026) vs Present study	21	23	22	0.93	Very high agreement in species composition and taxonomic interpretation
Alston (1935) vs POWO (2026)	20	23	23	0.87	High agreement despite nomenclatural revision
Alston (1935) vs Hassler (1994-2026)	21	23	25	0.88	High overlap with later checklist compilations
Hassler (1994-2026) vs POWO (2026)	22	25	23	0.92	Strong agreement between later taxonomic datasets

Note: Sørensen similarity values were calculated using binary presence–absence matrices based on accepted species records from each dataset. Differences among datasets primarily reflect alternative taxonomic interpretation, exclusion of doubtful taxa, nomenclatural standardization, and inclusion of introduced or naturalized species.

Table S2. Comparative morphological characteristics commonly associated with morphologically overlapping *Selaginella* taxa in Java, Indonesia.

Character	***Selaginella plana* complex**			***Selaginella intermedia* complex**		
	S. plana	***S. caudata***	***S. stipulata***	***S. intermedia***	***S. ascendens***	***S. springiana***
Taxonomic status in the present study	Retained	Not retained; interpreted within the *S. plana* complex	Excluded/doubtful	Retained	Interpreted within the *S. intermedia* complex	Interpreted within the *S. intermedia* complex
General growth form	Creeping to ascending	Generally creeping	Commonly creeping to ascending	Creeping to suberect	Commonly ascending	Creeping to ascending
Stem architecture	Flattened and flexible	Generally similar to *S. plana*	Broadly similar to *S. plana*	More irregularly branched	Generally similar to *S. intermedia*	Typically intermediate among *S. intermedia* forms
Branching pattern	Broadly spreading	Often with slightly narrower branches	Variable, frequently overlapping with *S. plana*	Loosely branched	Commonly with slightly ascending branches	Intermediate branching tendency
Leaf symmetry	Variable, often anisophyllous	Strongly overlapping with *S. plana*	Strongly overlapping with *S. plana*	Moderately anisophyllous	Generally similar to *S. intermedia*	Generally similar to *S. intermedia*
Leaf apex	Acute to acuminate	Usually acute	Usually acute	Acute to shortly acuminate	Comparable to *S. intermedia*	Comparable to *S. intermedia*
Character historically emphasized in species delimitation	General vegetative morphology	Caudate branch appearance	Tristelic stipe	Branch arrangement and leaf proportions	Ascending growth habit	Slightly modified branch architecture
Stability of historically emphasized character	Moderate to low	Low	Low to moderate	Moderate	Low	Low
Degree of morphological overlap	High overlap with related taxa	Extensive overlap with *S. plana*	Extensive overlap with *S. plana*	High overlap with allied forms	Extensive overlap with *S. intermedia*	Extensive overlap with *S. intermedia*
Habitat association	Forests, riparian habitats, agroforestry, and disturbed habitats	Commonly associated with humid shaded habitats	Typically associated with humid forest habitats	Humid forests and ravines	Frequently associated with humid forest habitats	Frequently associated with humid forest habitats
Elevational distribution	Broad (lowland–montane)	Mostly submontane	Submontane-montane	Mainly submontane	Primarily submontane	Primarily submontane
Environmental plasticity	High	High	High	Moderate-high	High	High
Main reason for taxonomic revision	Retained as a widespread species complex	Lack of consistently stable morphological separation	Historically emphasized character considered insufficiently stable	Retained as a morphologically variable species complex	Morphological variation broadly continuous with *S. intermedia*	Morphological variation broadly continuous with *S. intermedia*

Note: Morphological traits listed here are comparative tendencies, not absolute diagnostic characters. Several traits vary with environment and overlap among taxa. Interpretations are based on combined field observations, herbarium examination, ecological distribution patterns, and comparative morphological assessment. Several characters historically used for species delimitation showed considerable overlap and environmental variability, particularly within the *S. plana* and *S. intermedia* complexes

Table S3. Taxonomic justification for excluded, provisionally interpreted, or morphologically overlapping *Selaginella* taxa in Java, Indonesia

Historical name	Current interpretation in the present study	Reason for exclusion/interpreted status	Supporting evidence
Selaginella ascendens	Interpreted within the *S. intermedia* complex	Diagnostic vegetative characters overlapped extensively with environmentally variable forms of *S. intermedia*	Overlapping ecological positions in PCA/NMDS analyses, branching architecture, anisophylly, habitat association, and absence of consistently stable morphological separation across field and herbarium specimens
Selaginella springiana	Interpreted within the *S. intermedia* complex	Morphological separation inconsistent and environmentally unstable	Continuous variation in stem architecture and leaf arrangement; similar ecological distribution and humid forest association as *S. intermedia*
Selaginella caudata	Interpreted within the *S. plana* complex	Characters historically used for delimitation fall within the morphological variation of *S. plana*	Broad overlap in branch flattening, leaf arrangement, growth habit, habitat distribution, and ecological amplitude
Selaginella stipulata	Excluded from the confirmed checklist	Most examined specimens are morphologically closer to the *S. plana* complex	Lack of stable diagnostic characters; inconsistent herbarium interpretation; ecological overlap with widespread *S. plana* populations
Selaginella grabowskyi	Excluded	Lack of reliable occurrence evidence from Java	No verified herbarium specimens or contemporary field records from Java; probable regional misidentification or database carry-over
Selaginella strobiformis	Excluded	Distribution inconsistent with confirmed Javan flora	Absence of verifiable specimens and uncertain historical records; biogeographic inconsistency
Selaginella tamariscina	Excluded	No convincing evidence of natural occurrence in Java	Lack of authenticated herbarium material from Java and absence during contemporary field surveys
Selaginella singalanensis	Provisionally retained under current nomenclatural interpretation	Historical nomenclatural interpretation remains inconsistent among available records	Limited records and inconsistent morphological interpretation among herbarium specimens
Selaginella cupressina	Retained provisionally	Species delimitation remains uncertain	Restricted occurrence records and overlapping morphology with related taxa; requires molecular and anatomical evaluation
Selaginella subspinulosa	Retained provisionally as a distinct taxon	Morphological interpretation is still partly ambiguous	Montane ecological restriction supports provisional recognition, but quantitative morphometric and molecular evidence remains unavailable
Selaginella involvens complex	Retained as a broad species complex	Considerable ecological and morphological variation was observed across populations	Overlapping habitat association, branching variability, and broad ecological overlap in PCA/NMDS analyses among populations from different elevational zones
Selaginella plana complex	Retained as a broad species complex	High phenotypic plasticity complicates the delimitation of associated morphotaxa	Extensive overlap in vegetative morphology across environmental gradients and broad ecological distribution
Selaginella intermedia complex	Retained as a broad species complex	Historical taxa likely represent environmentally associated morphological variants	Weak ecological segregation in PCA/NMDS ordination and absence of consistently stable morphological separation
Selaginella repanda complex	Provisionally retained	Environmentally induced variation complicates interpretation	Lithophytic and forest populations exhibit continuous variation in branching pattern and leaf morphology

Note: Taxonomic interpretations presented in this appendix are based on a combined evaluation of field observations, herbarium examination, ecological distribution patterns, multivariate ordination analyses, comparative morphology, and nomenclatural standardization. Several taxa remain provisionally interpreted because molecular phylogenetic, morphometric, and anatomical evidence are not yet available. This appendix is intended to improve the transparency and reproducibility of taxonomic decisions adopted in the present study