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Climatic and elevational drivers of *Selaginella* species richness in Java, Indonesia

AHMAD DWI SETYAWAN[1,2,♥], SUTARNO[3], SUGIYARTO[3], SUNARTO[1], 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

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Abstract. *Setyawan AD, Sutarno, Sugiyarto, Sunarto, Sulton MN. 2026. Climatic and elevational drivers of* Selaginella *species richness in Java, Indonesia. Nusantara Bioscience 18 (1): n180106. https://doi.org/10.13057/nusbiosci/n180106.* Understanding environmental factors that shape species richness patterns, yet the determinants of *Selaginella* diversity in Java, Indonesia, remain poorly understood. *Selaginella*, an ancient lycophyte genus widely distributed in tropical regions, is highly sensitive to environmental conditions, particularly moisture availability and temperature. This study examined the relationships between *Selaginella* species richness and elevational and climatic gradients across Java, Indonesia. A total of 1,962 occurrence records representing 21 identified species and one unidentified taxon were compiled from field surveys, herbarium collections, and verified biodiversity databases. Species richness was estimated using a 0.25° × 0.25° grid system and spatially visualized through Inverse Distance Weighting (IDW) interpolation. The influence of elevation, Annual Mean Temperature, Annual Mean Precipitation, Annual Mean Solar Radiation, and Annual Mean Moisture Index on species richness was evaluated using polynomial regression, Pearson correlation analysis, and Principal Component Analysis (PCA). Species richness showed pronounced spatial heterogeneity, with hotspots concentrated in the humid montane regions of West Java. Richness exhibited nonlinear relationships with all environmental variables and peaked at intermediate elevations. Annual Mean Moisture Index ($R^2 = 0.616$) and Annual Mean Precipitation ($R^2 = 0.527$) were the variables most strongly associated with species richness, whereas Annual Mean Temperature and solar radiation showed negative relationships. Correlation and PCA results further indicated that moisture availability is closely linked to richness patterns, while elevation influences richness indirectly through its effects on local climatic conditions. These findings demonstrate that humid submontane and montane environments are critical for maintaining *Selaginella* diversity in Java and highlight the importance of conserving climatically suitable habitats under future environmental change.

Keywords: Climatic gradients, elevation, Java Island, *Selaginella*, species richness

INTRODUCTION

Species richness patterns along elevational gradients have long attracted ecological and biogeographical interest because they provide insights into how environmental conditions shape biodiversity across heterogeneous landscapes. Elevational gradients integrate multiple environmental changes over short geographic distances, including temperature, precipitation, humidity, and solar radiation, making them useful natural systems for investigating biodiversity responses to environmental drivers (Grytnes and McCain 2007; Hernández-Rojas et al. 2020). Despite extensive research, the relationship between species richness and elevation remains unresolved. Some studies have reported declining richness with increasing elevation, whereas others have documented hump-shaped patterns characterized by peak diversity at intermediate elevations (Rahbek 2005; Umair et al. 2023). These contrasting patterns indicate that species richness is influenced not only by elevation itself but also by interactions among climatic conditions, habitat heterogeneity, evolutionary history, and species-specific ecological requirements.

Climatic conditions are widely recognized as major determinants of biodiversity patterns along elevational gradients. Temperature, precipitation, moisture availability, and solar radiation influence physiological processes, growth, reproduction, and survival, thereby affecting species occurrence and richness across landscapes (Bhattarai and Vetaas 2003; Hernández-Rojas et al. 2020). The water-energy dynamics hypothesis proposes that biodiversity patterns are governed by the combined availability of water and energy, with richness generally increasing under favorable balances of moisture and thermal resources (Hawkins et al. 2003; Bhattarai et al. 2025). In tropical mountains, cool and humid environments often support specialized plant assemblages, whereas environmentally stressful habitats tend to harbor fewer species with broader ecological tolerances (Umair et al. 2023). Understanding the relative importance of climatic variables is therefore essential for explaining biodiversity patterns and predicting responses to future environmental change.

The lycophyte genus *Selaginella* provides an excellent model for investigating climatic and elevational influences on species richness. As one of the oldest extant lineages of vascular plants, *Selaginella* is widely distributed throughout humid tropical and subtropical regions. Most species occur in shaded, moisture-rich habitats such as forest floors, stream banks, ravines, and montane ecosystems. Although many species exhibit ecological adaptability, their growth and distribution remain strongly dependent on environmental moisture and microclimatic stability (Pouteau et al. 2016; Hernández-Rojas et al. 2020). Consequently, *Selaginella* species are frequently regarded as indicators of habitat quality and microclimatic conditions. Previous studies have shown that variation in humidity and light availability strongly influences their occurrence along elevational gradients, particularly in tropical mountain ecosystems (Krömer et al. 2013; Rashidi et al. 2015).

Java Island provides an ideal setting for examining environmental drivers of *Selaginella* richness because it encompasses broad topographic and climatic variation within a relatively compact geographic area. Elevation ranges from coastal lowlands to volcanic mountains exceeding 3,000 m above sea level, while rainfall patterns vary markedly between humid western regions and relatively drier eastern areas (Setyawan et al. 2020a, b). Previous studies on *Selaginella* in Java have documented species diversity, distribution patterns, and altitudinal variation in several mountain systems and regions, including Mount Lawu (Setyawan et al. 2013), Dieng Plateau (Setyawan et al. 2015), and Bromo Tengger Semeru National Park (Setyawan and Sugiyarto 2015). A broader analysis across tropical elevational gradients demonstrated that *Selaginella* diversity often peaks at intermediate elevations (Setyawan et al. 2016). More recently, ecological and taxonomic reassessments substantially improved knowledge of *Selaginella* diversity and distribution in Java (Setyawan et al. 2026a). However, these studies were conducted primarily at local or regional scales and did not evaluate richness patterns across the entire island using a standardized spatial framework. Furthermore, the relative importance of elevation and multiple climatic variables in determining *Selaginella* species richness at the island scale has not been quantitatively assessed. Consequently, it remains unclear whether richness patterns are governed primarily by elevational gradients or by climatic factors associated with moisture and energy availability.

Understanding how climatic and elevational gradients influence *Selaginella* species richness is important for both tropical biogeography and biodiversity conservation. We analyzed relationships between *Selaginella* richness and elevational and climatic gradients across Java by evaluating the influence of elevation, Annual Mean Temperature, Annual Mean Precipitation, Annual Mean Solar Radiation, and Annual Mean Moisture Index. We hypothesized that richness is driven primarily by moisture-related environmental factors rather than elevation alone. Specifically, we expected a hump-shaped elevational pattern with peak richness at intermediate elevations and stronger positive associations with moisture index and precipitation than with temperature or solar radiation. Therefore, this study aimed to identify the principal environmental drivers underlying spatial patterns of *Selaginella* species richness across Java, Indonesia.

MATERIALS AND METHODS

Study area

The study was conducted across Java Island, Indonesia, to examine the relationships between *Selaginella* species richness and elevational and climatic gradients (Figure 1). Java consists of six provinces: Banten, Jakarta, West Java, Central Java, Yogyakarta Special Region, and East Java. The island exhibits substantial environmental heterogeneity, with elevation ranging from sea level to 3,676 m asl at Mount Semeru, creating diverse ecological conditions across relatively short geographic distances (Setyawan et al. 2020b). Java is located within the Pacific Ring of Fire and contains numerous volcanic mountain systems that contribute to its complex topography and ecosystem diversity.

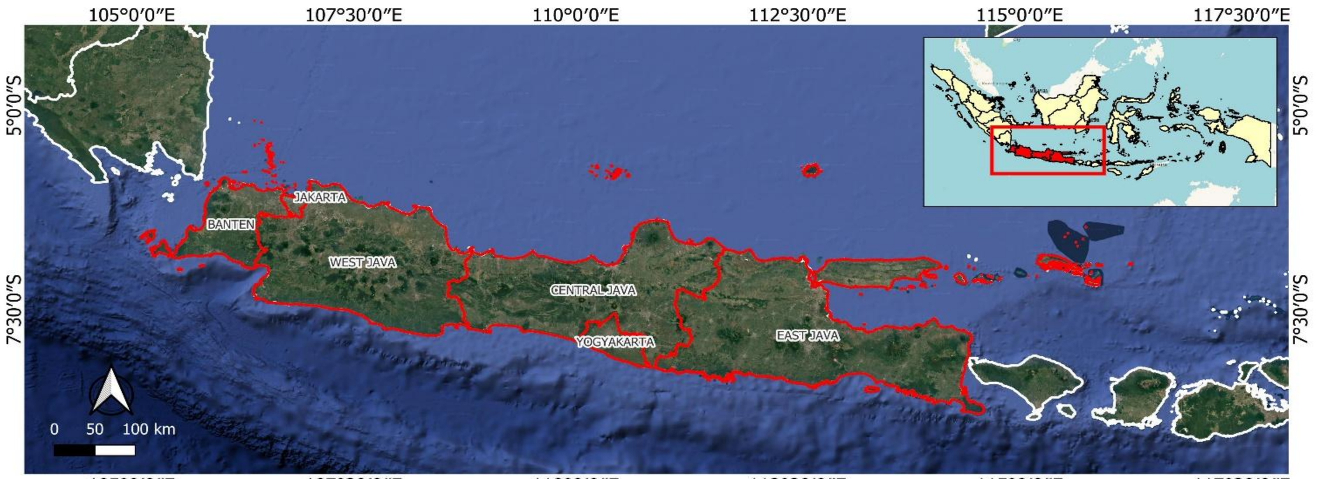

Figure 1. Study area and distribution of *Selaginella* occurrence records across Java, Indonesia

Java experiences a tropical monsoonal climate characterized by distinct wet and dry seasons. However, precipitation patterns vary considerably across the island due to topographic and atmospheric influences. Western and central Java generally receive higher annual rainfall and maintain more humid conditions, whereas eastern Java is relatively drier and experiences longer dry periods (Setyawan et al. 2020b). These climatic gradients influence vegetation composition, habitat suitability, and species distributions throughout the island. The combination of broad elevational variation, contrasting climatic conditions, and diverse habitat types makes Java an ideal region for evaluating the environmental drivers of *Selaginella* species richness and distribution patterns in tropical Southeast Asia.

Species occurrence data

Species occurrence records were compiled from field surveys and herbarium collections conducted throughout Java between 2007 and 2021. A total of 1,962 georeferenced occurrence records were assembled, representing the known distribution of *Selaginella* across the island. Field surveys contributed 1,362 occurrence records from 684 localities, whereas herbarium specimens and biodiversity databases contributed an additional 600 records from 309 localities. Each 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 using herbarium specimens, published literature, and online biodiversity databases.

Taxonomic validation followed recent taxonomic treatments and distributional records for *Selaginella* in Java and Southeast Asia (Setyawan et al. 2026a, b; Weststrand and Korall 2016), nomenclatural information from Plants of the World Online (POWO 2026), and major regional floristic treatments used for species identification (Alston 1935, 1937; Wong 1982, 2010; Zhang et al. 2013). Additional verification was conducted through herbarium examination, digitized specimen records, GBIF data, and published studies on the diversity and distribution of *Selaginella* in Java (Setyawan et al. 2016, 2018, 2020a, b, 2021). Duplicate records, incomplete locality information, and records with uncertain geographic coordinates were excluded from the analysis.

The final dataset comprised 21 identified *Selaginella* species and one unidentified taxon distributed across the six provinces of Java. The identified species were *S. alutacea, S. aristata, S. biformis, S. ciliaris, S. cupressina, S. frondosa, S. intermedia, S. involvens, S. kraussiana, S. opaca, S. ornata, S. plana, S. remotifolia, S. repanda, S. rothertii, S. singalanensis, S. subalpina, S. subspinulosa, S. uncinata, S. willdenowii*, and *S. zollingeriana*. The unidentified taxon was retained as *Selaginella* sp. because available material was insufficient for confident species-level identification. These occurrence records served as the basis for estimating species richness patterns and evaluating their relationships with elevational and climatic variables across the island.

Species richness estimation and spatial interpolation

Species richness was estimated using a grid-based approach to quantify the spatial distribution of *Selaginella* across Java. The study area was divided into equal grid cells measuring 0.25° × 0.25°, and all occurrence records were assigned to their corresponding cells based on geographic coordinates. After clipping the grid to the extent of Java Island and excluding cells without occurrence records, a total of 250 grid cells were included in the analysis. Species richness for each grid cell was calculated as the total number of *Selaginella* species recorded within that cell. This approach enabled standardized comparisons of richness patterns across regions with varying environmental conditions and geographic characteristics and has been widely applied in large-scale biodiversity studies (Rahbek 2005; Kumar et al. 2024).

To visualize spatial variation in species richness, an Inverse Distance Weighting (IDW) interpolation was performed using ArcGIS 10.8. IDW was selected because the objective was to visualize broad spatial patterns of *Selaginella* species richness from grid-based occurrence data rather than to develop a geostatistical prediction model. Unlike Kriging, IDW does not require assumptions regarding spatial stationarity or semivariogram structure. IDW estimates values at unsampled locations based on the principle that nearby observations exert a stronger influence on predicted values than more distant observations (Chen et al. 2016). This method has been widely applied in ecological and biogeographical studies to represent spatial patterns derived from occurrence data and environmental observations (Cavalcante et al. 2022; Kumar et al. 2024). The interpolated surface was generated from species richness values calculated for each grid cell and subsequently clipped using the administrative boundary of Java.

All spatial analyses were conducted using the World Geodetic System 1984 (WGS 1984) coordinate reference system. To evaluate interpolation performance, prediction accuracy was assessed by comparing observed richness values with interpolated estimates using Mean Squared Error (MSE), Root Mean Squared Error (RMSE), and Mean Absolute Error (MAE) (Chen et al. 2016). Lower values of these metrics indicate closer agreement between observed and predicted richness values and higher interpolation accuracy.

Elevational and climatic variables

To evaluate the environmental drivers of *Selaginella* species richness, elevational and climatic variables were extracted and analyzed for each grid cell across Java. Elevation data were obtained from the WorldClim version 2 database at a spatial resolution of 30 arc-seconds (approximately 1 km²), which provides globally standardized climatic and topographic datasets suitable for ecological analyses (Fick and Hijmans 2017). Elevation was included because it integrates multiple environmental gradients and has been widely recognized as an important predictor of plant diversity patterns along mountain systems (Bhattarai and Vetaas 2003; Umair et al. 2023).

Four climatic variables representing major components of water and energy availability were selected: Annual Mean Temperature (AMT), Annual Mean Precipitation (AMP), Annual Mean Solar Radiation (AMR), and Annual Mean Moisture Index (AMMO). Climatic data were obtained from the CliMond database, which provides high-resolution historical climate surfaces commonly used in ecological and biogeographical studies (Kriticos et al. 2012, 2014). These variables were selected because previous studies have demonstrated their strong influence on the distribution and diversity of ferns and lycophytes, particularly moisture-dependent taxa (Hernández-Rojas et al. 2020; Kumar et al. 2024).

All raster layers were clipped to the extent of Java Island and resampled to a common spatial resolution to ensure consistency among datasets. Climatic and elevational values were subsequently extracted for each analysis grid and used as predictor variables in statistical analyses. The selected variables represent key environmental gradients associated with thermal conditions, water availability, and energy input, which are considered major factors influencing the occurrence and richness of *Selaginella* species in tropical ecosystems.

Statistical analyses

Statistical analyses were performed to evaluate the relationships between *Selaginella* species richness and environmental variables across Java. Species richness was treated as the response variable, whereas elevation, Annual Mean Temperature (AMT), Annual Mean Precipitation (AMP), Annual Mean Solar Radiation (AMR), and Annual Mean Moisture Index (AMMO) were used as predictor variables. Prior to analysis, all environmental variables were examined for consistency and suitability for subsequent statistical modeling (Zuur et al. 2010).

Pearson correlation analysis was also used to evaluate potential collinearity among environmental variables. Variables with absolute correlation coefficients ($|r|$) greater than 0.70 were considered highly correlated and were interpreted cautiously during subsequent analyses (Dormann et al. 2013). Because the objective of this study was to examine individual relationships between species richness and environmental variables rather than to construct a multivariable predictive model, highly correlated variables were retained to facilitate ecological interpretation.

The relationships between species richness and environmental variables were assessed using second-order polynomial regression analyses. Polynomial models were selected because preliminary exploration indicated nonlinear relationships between species richness and environmental variables. Model performance was evaluated using the coefficient of determination (R^2), F-statistics, and significance levels (p-values). Polynomial regression curves were used to visualize species richness responses along elevational and climatic gradients.

Pearson correlation analysis was conducted to examine the strength and direction of associations among species richness and environmental variables. Correlation coefficients (r) were interpreted to identify positive or negative relationships and to assess potential collinearity among predictor variables. This analysis also provided a preliminary understanding of how environmental gradients covary across the island (Zuur et al. 2010; Dormann et al. 2013).

To identify the principal environmental gradients associated with species richness patterns, Principal Component Analysis (PCA) was performed using standardized variables. PCA reduces multidimensional datasets into a smaller number of orthogonal components, facilitating the interpretation of relationships among environmental variables and species richness (Jolliffe and Cadima 2016). Variables with high loadings on the principal components were interpreted as major contributors to the observed environmental gradients.

All statistical analyses were conducted using PAST version 5.2.1 (Hammer et al. 2001). Then, graphical visualizations were prepared using RAWGraphs (Mauri et al. 2017).

RESULTS AND DISCUSSION

Species richness and spatial distribution patterns of *Selaginella* in Java

The distribution of *Selaginella* species varied among provinces across Java (Figure 2). A total of 21 identified species and one unidentified taxon were recorded from 1,962 occurrence records compiled throughout the island. West Java exhibited the highest species richness, containing all recorded species except the unidentified taxon, whereas Jakarta supported only three species. Central Java contained 14 species, while Banten and East Java each supported 10 species. Yogyakarta showed intermediate richness with fewer species than the western part of the island. Several species, including *S. ciliaris* and *S. plana*, were recorded in all provinces, indicating broad geographic occurrence across Java. In contrast, species such as *S. frondosa*, *S. kraussiana*, *S. cupressina*, *S. rothertii*, and *S. uncinata* were recorded in fewer provinces and showed more limited geographic occurrence.

Spatial interpolation revealed distinct hotspots and low-richness regions across the island (Figure 3). Areas with the highest predicted species richness were concentrated primarily in the montane regions of West Java, particularly around major volcanic mountain systems characterized by high rainfall and humid environmental conditions. Additional richness hotspots occurred in several mountainous areas of Central Java and East Java, although their spatial extent was considerably smaller. While extensive lowland areas, especially in northern and eastern Java, were characterized by low predicted richness values. These regions generally experience lower precipitation and higher temperatures than the montane areas, conditions that may be less favorable for moisture-dependent *Selaginella* species.

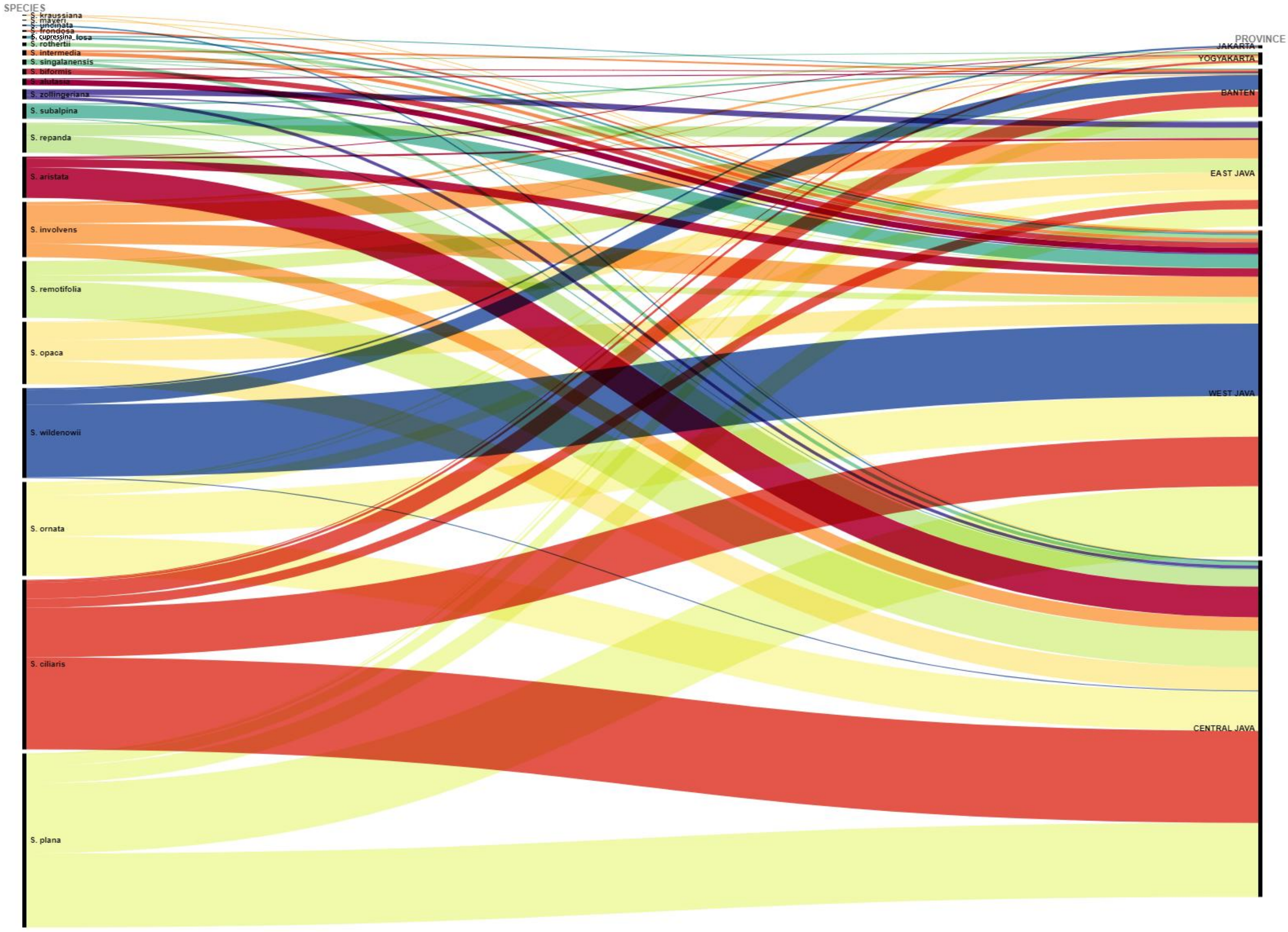

Figure 2. Provincial richness and occurrence patterns of *Selaginella* species across Java, Indonesia

Table 1. Spatial extent of *Selaginella* species richness classes across provinces of Java, Indonesia

Species richness class	Area (km^2)							
	Banten	Jakarta	West Java	Central Java	Yogyakarta	East Java	Total area (km²)	Percentage of Java (%)
0.00-2.79	4,770	372	18,492	18,423	1,845	39,766	83,667	63.36
2.79-5.59	3,475	271	13,331	9,977	1,074	7,166	35,295	26.73
5.59-8.38	1,050	0	3,813	5,574	222	548	11,207	8.49
8.38-11.17	1	0	1,122	354	21	71	1,569	1.19
11.17-13.97	0	0	311	0	0	0	311	0.24
Total	9,296	643	37,069	34,327	3,162	47,551	132,047	100.00

The spatial extent of each richness class differed considerably among provinces (Table 1). Low-richness areas (0.00-2.79 species) dominated the island, covering approximately 83,667 km² or 63.36% of Java's total land area. Intermediate richness classes (2.79-8.38 species) occupied 46,502 km² (35.22%), whereas areas with high richness values (>8.38 species) were restricted to only 1.43% of the island. The highest richness class (11.17-13.97 species) occupied merely 311 km² (0.24% of Java) and occurred exclusively in West Java. These findings indicate that centers of *Selaginella* diversity are spatially limited and largely associated with mountainous landscapes.

The interpolation model showed low prediction errors and high agreement between observed and predicted richness values (Table 2). The model produced an MSE value below 0.001, an RMSE value of 0.008, and an MAE value of 0.004, indicating that interpolated richness estimates closely reflected observed richness patterns across the study area. The low error values suggest that the IDW approach provided a reliable representation of the spatial variation in *Selaginella* species richness throughout Java.

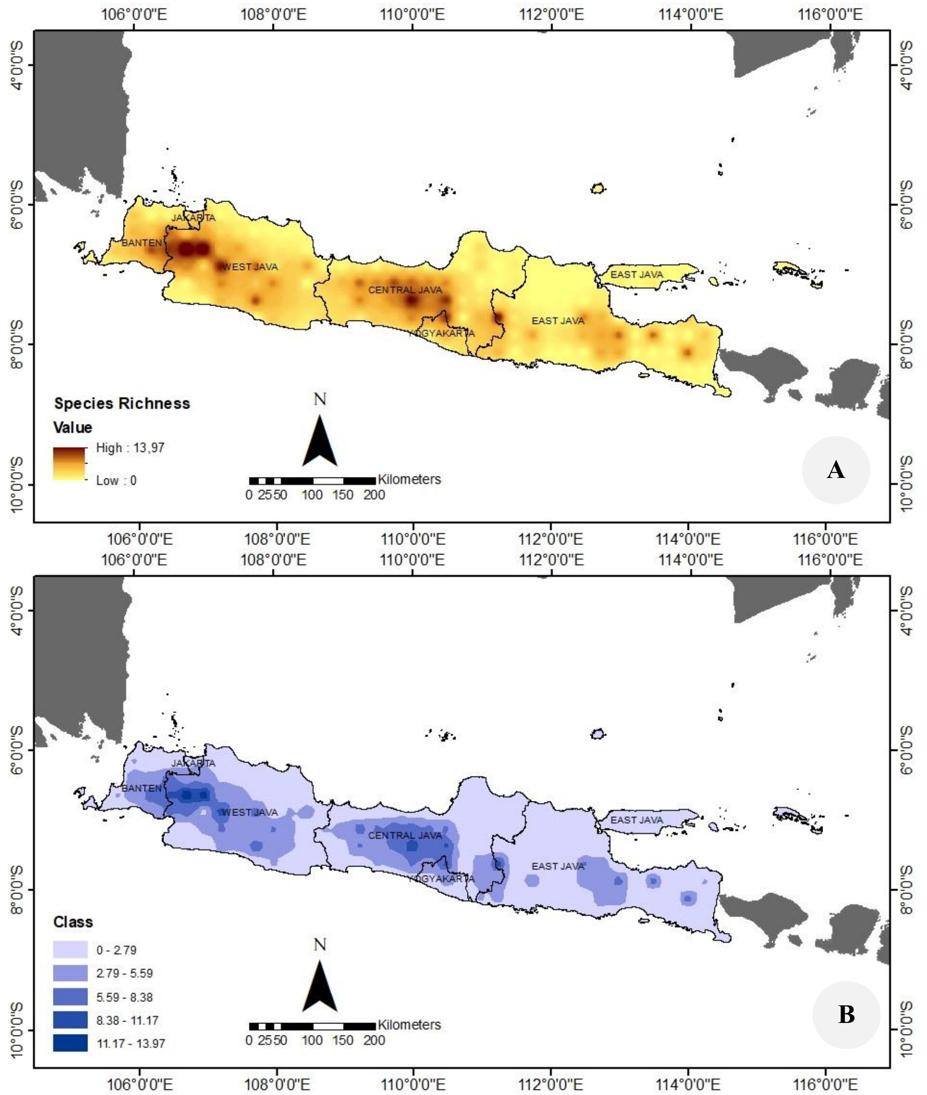

Figure 3. Spatial patterns of *Selaginella* species richness across Java, Indonesia. A. IDW-interpolated richness surface derived from 250 analysis grids. B. Classification of richness values into five categories highlighting richness hotspots concentrated in montane regions of Western and Central Java. Interpolation performance is summarized in Table 2 (RMSE = 0.008; MAE = 0.004)

Table 2. Accuracy assessment of the IDW interpolation model used to estimate *Selaginella* species richness in Java, Indonesia

Metric	Value	Interpretation
Mean Squared Error (MSE)	<0.001	Very low average squared prediction error
Root Mean Squared Error (RMSE)	0.008	High agreement between observed and predicted richness values
Mean Absolute Error (MAE)	0.004	Very small average prediction deviation

Relationships between species richness and elevational and climatic variables

Species richness exhibited nonlinear relationships with elevation and climatic variables (Figure 4). Across Java, *Selaginella* richness generally increased along elevational gradients before reaching a maximum at intermediate elevations and subsequently declining at higher elevations. The relationship between species richness and elevation displayed a hump-shaped pattern, with peak richness occurring at approximately 900 m above sea level. This pattern suggests that intermediate elevations provide favorable environmental conditions that combine moderate temperatures, high humidity, and sufficient habitat heterogeneity to support a greater number of species.

A similar nonlinear pattern was observed for Annual Mean Temperature. Species richness was highest at approximately 22.5°C and declined toward both lower and higher temperature ranges. In contrast, Annual Mean Precipitation exhibited a generally positive relationship with species richness, with wetter areas supporting a greater number of *Selaginella* species. Areas receiving high annual rainfall were typically associated with montane environments characterized by persistent moisture availability. Annual Mean Solar Radiation showed an inverse relationship with species richness, indicating that richness tended to decrease as solar radiation increased. Conversely, Annual Mean Moisture Index displayed the strongest positive relationship with species richness, with richness increasing substantially under more humid environmental conditions. These results collectively suggest that moisture availability plays a critical role in shaping *Selaginella* richness patterns across Java.

Polynomial regression analysis indicated significant associations between species richness and all environmental predictors (Table 3). Among the evaluated variables, Annual Mean Moisture Index produced the strongest model performance (R^2 = 0.616), explaining approximately 61.6% of the observed variation in species richness. Annual Mean Precipitation also showed a strong relationship (R^2 = 0.527), followed by Annual Mean Solar Radiation (R^2 = 0.334), Annual Mean Temperature (R^2 = 0.289), and elevation (R^2 = 0.240). All regression models were highly significant ($p < 0.001$), indicating that both climatic and elevational variables contributed substantially to observed richness patterns. The comparatively higher explanatory power of moisture-related variables suggests that water availability may exert a stronger influence on *Selaginella* richness than elevation alone.

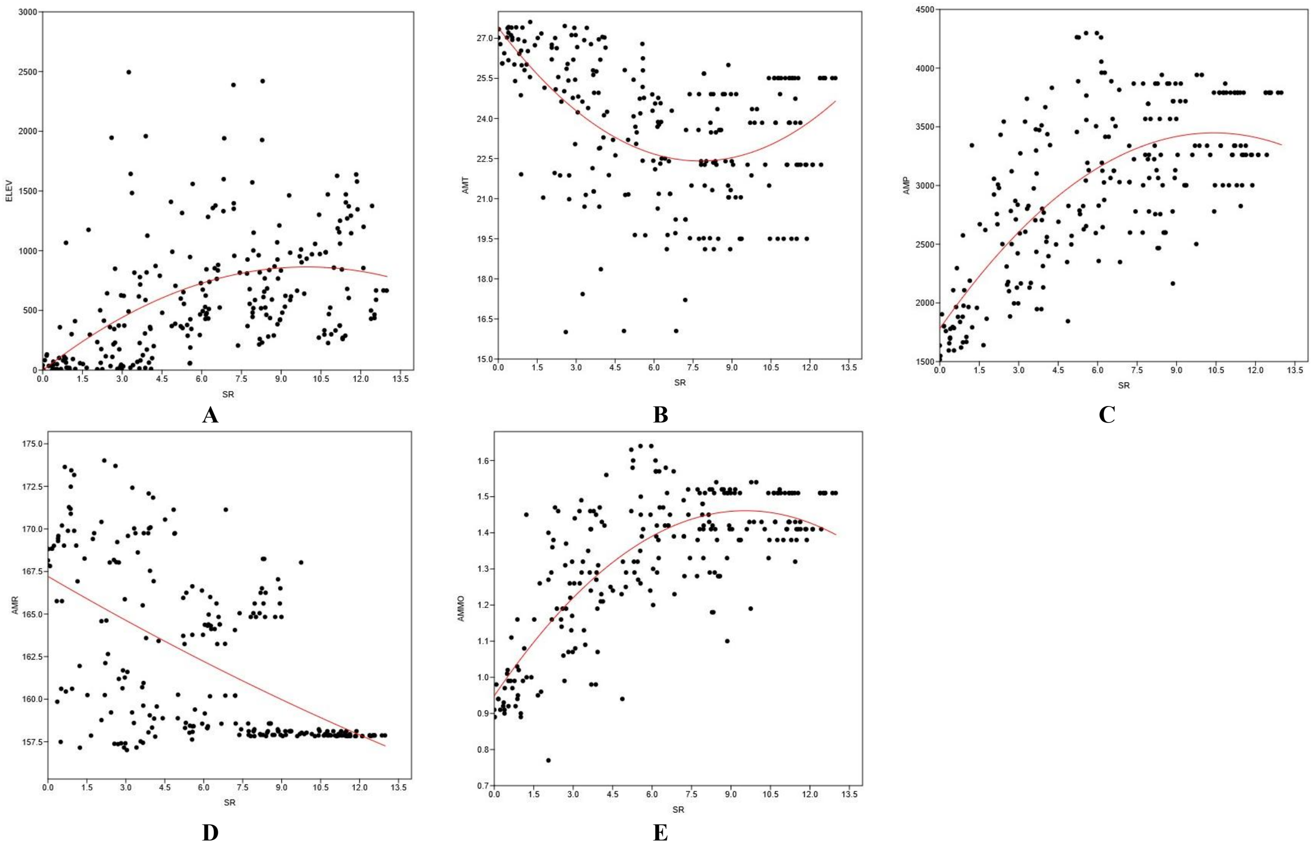

Figure 4. Relationships between *Selaginella* species richness (SR) and elevational and climatic variables in Java, Indonesia. A. Elevation, B. Annual Mean Temperature (AMT), C. Annual Mean Precipitation (AMP), D. Annual Mean Solar Radiation (AMR), E. Annual Mean Moisture Index (AMMO)

Table 3. Polynomial regression models describing relationships between *Selaginella* species richness and environmental variables.

Environmental variable	Unit	R²	F-value	p-value	Relationship pattern
Annual Mean Moisture Index (AMMO)	Dimensionless	0.616	198.310	<0.001***	Positive, nonlinear
Annual Mean Precipitation (AMP)	mm year^{-1}	0.527	137.630	<0.001***	Positive, nonlinear
Annual Mean Solar Radiation (AMR)	MJ m^{-2} day^{-1}	0.334	62.000	<0.001***	Negative, nonlinear
Annual Mean Temperature (AMT)	°C	0.289	50.187	<0.001***	Hump-shaped
Elevation	m asl	0.240	39.011	<0.001***	Hump-shaped

Note: R^2 = Coefficient of determination; F = F-statistic; p = Significance level; *** $p < 0.001$. Polynomial regression models were used to evaluate nonlinear relationships between species richness and each environmental variable. Regression curves are shown in Figure 4

Correlation structure among environmental variables

Correlation analysis revealed strong associations among several climatic variables (Figure 5). Species richness showed positive correlations with Annual Mean Moisture Index (r = 0.61), elevation (r = 0.60), and Annual Mean Precipitation (r = 0.59), indicating that *Selaginella* richness generally increased in cooler and wetter environments. Among these variables, Annual Mean Moisture Index exhibited the strongest correlation with species richness, highlighting the importance of environmental moisture availability for the distribution of *Selaginella* across Java.

Species richness was negatively correlated with Annual Mean Temperature (r = −0.49) and Annual Mean Solar Radiation (r = −0.29). These relationships suggest that warmer and more exposed environments tend to support fewer *Selaginella* species, whereas humid habitats with lower thermal and radiation stress provide more suitable conditions for species persistence. Although the negative correlation with solar radiation was relatively weak, its direction was consistent with the ecological preference of most *Selaginella* species for shaded and moisture-rich habitats.

Several environmental variables also exhibited strong intercorrelations. Annual Mean Precipitation and Annual Mean Moisture Index showed an exceptionally strong positive correlation (r = 0.98), reflecting their shared association with water availability. Although this correlation exceeded the threshold used to identify potential collinearity (|r| > 0.70), both variables were retained because they represent closely related but ecologically meaningful aspects of environmental moisture availability and were analyzed separately. Elevation was strongly negatively correlated with Annual Mean Temperature (r = −0.85), indicating that higher elevations generally experience cooler climatic conditions. Elevation also showed positive associations with Annual Mean Precipitation and moisture index, further emphasizing the role of mountainous regions as favorable environments for *Selaginella* diversity.

The correlation matrix indicates that species richness is most closely associated with moisture-related variables, while elevation influences richness indirectly through its effects on temperature and water availability. These relationships provide an initial indication of the environmental gradients underlying the spatial distribution of *Selaginella* species richness across Java.

Climatic and elevational drivers of species richness

Principal Component Analysis identified the major environmental gradients associated with species richness patterns (Figure 6). The first two principal components together accounted for 100% of the variance explained in the ordination (PC1 = 68.55%, PC2 = 31.45%). The ordination revealed a clear separation between moisture-related variables and temperature-related gradients, indicating that multiple environmental factors contribute to the spatial distribution of *Selaginella* richness across Java.

The PCA biplot showed that species richness was closely associated with Annual Mean Moisture Index, Annual Mean Precipitation, and elevation. These variables were positioned in the same direction as the species richness vector, indicating positive relationships among them. Annual Mean Moisture Index and Annual Mean Precipitation contributed strongly to PC1 and formed the dominant environmental gradient in the ordination space. Their proximity reflects the strong correlation between the two variables and suggests that moisture availability represents a major environmental condition associated with areas of high *Selaginella* richness.

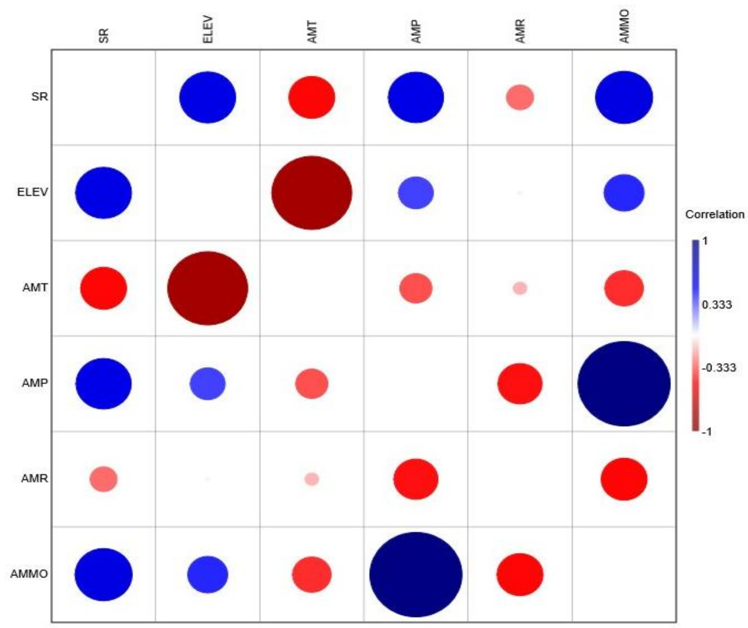

Figure 5. Pearson correlation matrix among species richness, elevation, and climatic variables. Note: SR: *Selaginella* species richness, ELEV: Elevation, AMT: Annual Mean Temperature, AMP: Annual Mean Precipitation, AMR: Annual Mean Solar Radiation, AMMO: Annual Mean Moisture Index

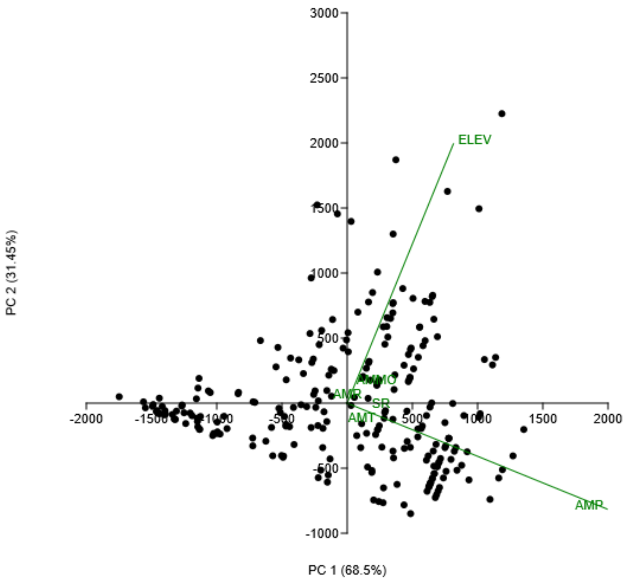

Figure 6. Principal environmental gradients associated with *Selaginella* species richness in Java, Indonesia. Note: SR: *Selaginella* species richness, ELEV: Elevation, AMT: Annual Mean Temperature, AMP: Annual Mean Precipitation, AMR: Annual Mean Solar Radiation, AMMO: Annual Mean Moisture Index

Elevation was positively associated with species richness and moisture-related variables but contributed primarily to PC2. This pattern indicates that elevational gradients influence richness indirectly through their effects on local climatic conditions, particularly temperature and moisture availability. By contrast, Annual Mean Temperature and Annual Mean Solar Radiation were positioned opposite to species richness, indicating negative associations with *Selaginella* richness. Areas characterized by higher temperatures and greater solar radiation generally supported fewer species than cooler and more humid environments.

The ordination further suggests that moisture availability, precipitation, and elevation collectively define the principal environmental gradients underlying species richness patterns in Java. While elevation provides an important topographic framework, the close association between richness and moisture-related variables indicates that climatic conditions play a dominant role in determining habitat suitability for *Selaginella*. These results are consistent with the regression and correlation analyses, which identified Annual Mean Moisture Index and Annual Mean Precipitation as the variables most strongly associated with richness variation across the island.

Discussion

Spatial patterns of Selaginella species richness in Java

The distribution of *Selaginella* species richness across Java exhibited pronounced spatial heterogeneity, with richness concentrated primarily in mountainous regions and declining toward extensive lowland areas (Figure 3). The highest richness values were observed in West Java, particularly in montane landscapes characterized by high rainfall, persistent humidity, and relatively stable environmental conditions. In contrast, northern coastal plains and many lowland areas of eastern Java supported substantially lower richness. This pattern suggests that the distribution of *Selaginella* is strongly influenced by environmental gradients associated with mountain ecosystems.

The concentration of richness in montane regions is consistent with previous studies showing that ferns and lycophytes frequently attain their highest diversity under cool and humid conditions (Bhattarai et al. 2004; Krömer et al. 2013). Mountain environments provide favorable microclimatic conditions, including reduced temperature fluctuations, high atmospheric moisture, and shaded habitats that promote the establishment and persistence of moisture-dependent species. These conditions are particularly important for *Selaginella*, whose growth and reproduction are closely associated with water availability and humid microhabitats (Rashidi et al. 2015; Pouteau et al. 2016).

The spatial extent analysis further demonstrated that areas with high richness occupied only a small proportion of the island (Table 1). More than 63% of Java was classified within the lowest richness category, whereas the highest richness class covered only 0.24% of the total land area. This uneven distribution indicates that biodiversity hotspots for *Selaginella* are geographically restricted and concentrated within relatively limited mountainous areas. Similar patterns have been reported for other fern and lycophyte assemblages, where suitable habitats are often fragmented and confined to environmentally favorable locations (Rahbek 2005; Umair et al. 2023).

The observed spatial pattern highlights the importance of montane ecosystems as centers of *Selaginella* diversity in Java. This suggests conservation efforts should prioritize humid mountainous regions where species richness is concentrated.

Influence of elevation on Selaginella *species richness*

Elevation was positively associated with *Selaginella* species richness across Java, although the relationship was distinctly nonlinear (Figure 4.A). Species richness increased from lowland areas to intermediate elevations, reaching its highest values at approximately 900 m above sea level before declining toward higher elevations. This hump-shaped pattern is consistent with studies reporting peak fern and lycophyte diversity at intermediate elevations, where environmental conditions are often most favorable for growth and survival (Bhattarai et al. 2004; Umair et al. 2023).

Similar hump-shaped richness patterns have been reported in other tropical mountain regions. In the Himalayas, fern and lycophyte richness typically peaks at intermediate elevations where temperature and moisture conditions are most favorable, before declining toward both lower and higher elevations (Bhattarai et al. 2004). A comparable pattern was observed in the montane forests of Veracruz, Mexico, where species richness reached maximum values at mid-elevations and decreased toward environmental extremes (Acebey et al. 2017). The richness peak observed at approximately 900 m asl in Java therefore falls within the range commonly reported for tropical mountain systems, although the exact elevation of maximum richness varies according to regional climatic conditions and mountain configuration.

The observed pattern suggests that elevation influences species richness primarily through its effects on local environmental conditions rather than acting as a direct ecological driver. Intermediate elevations in Java generally experience moderate temperatures, high humidity, and abundant precipitation, creating suitable habitats for many *Selaginella* species. In contrast, lowland environments are frequently characterized by higher temperatures, greater evaporative demand, and more intensive anthropogenic disturbance, whereas high-elevation habitats may impose physiological limitations associated with lower temperatures and reduced habitat availability.

Despite its ecological importance, elevation alone explained a relatively modest proportion of richness variation compared with climatic variables. The polynomial regression model indicated that elevation accounted for approximately 24% of the observed variation in species richness (R^2 = 0.240; Table 3). This result suggests that elevational gradients provide a broad environmental framework within which climatic conditions ultimately determine habitat suitability. Similar findings have been reported in tropical mountain systems, where elevation serves as a surrogate for changes in temperature, moisture, and energy availability rather than functioning as an independent determinant of biodiversity patterns (Körner 2004; Krömer et al. 2013).

The influence of elevation on *Selaginella* richness in Java appears to be largely indirect, operating through the environmental gradients associated with increasing altitude. The concentration of richness at intermediate elevations further emphasizes the importance of montane environments as key habitats supporting *Selaginella* diversity across the island.

Influence of climatic factors on species richness

Climatic variables exhibited stronger relationships with *Selaginella* species richness than with elevation, highlighting the importance of environmental conditions in determining habitat suitability across Java. The regression analyses revealed significant nonlinear relationships between species richness and all climatic variables examined, including Annual Mean Temperature, Annual Mean Precipitation, Annual Mean Solar Radiation, and Annual Mean Moisture Index (Figures 4.B-E; Table 3). Among these variables, Annual Mean Moisture Index showed the highest explanatory power (R^2 = 0.616), followed by Annual Mean Precipitation (R^2 = 0.527), indicating that water availability is a major factor associated with richness patterns.

The positive relationships between species richness, precipitation, and moisture index suggest that humid environments support a greater number of *Selaginella* species. Similar relationships have been reported for other plant groups, where precipitation and water availability strongly influence distribution patterns and habitat suitability (Li et al. 2022). Most members of this genus are strongly dependent on moist microhabitats because successful growth, reproduction, and spore establishment require adequate water availability (Rashidi et al. 2015; Pouteau et al. 2016). Areas with high rainfall and favorable moisture conditions provide suitable habitats for species persistence and coexistence. Similar patterns have been reported for ferns and lycophytes in tropical mountain ecosystems, where moisture availability is frequently identified as a primary determinant of species richness (Bhattarai et al. 2004; Acebey et al. 2017).

The relatively strong influence of moisture-related variables observed in this study is consistent with findings from other tropical and subtropical regions. For example, annual precipitation and water availability were identified as major determinants of plant species distributions in southwestern China (Li et al. 2022), while recent analyses from the Tibetan Plateau demonstrated that water-energy dynamics explained a substantial proportion of plant richness variation across environmental gradients (Bhattarai et al. 2025). The explanatory power of Annual Mean Moisture Index (R^2 = 0.616) and Annual Mean Precipitation (R^2 = 0.527) in Java suggests that moisture availability exerts a comparable influence on *Selaginella* richness, reinforcing the importance of hydrological conditions in shaping biodiversity patterns across tropical landscapes.

Conversely, species richness was negatively associated with Annual Mean Temperature and solar radiation (Figures 4.B-E and 5). Higher temperatures can increase evapotranspiration rates and reduce environmental moisture, whereas elevated solar radiation may intensify water stress and limit the availability of shaded microhabitats preferred by many *Selaginella* species. The correlation analysis further demonstrated strong relationships among climatic variables, particularly between precipitation and moisture index (r = 0.98), reflecting their shared influence on environmental humidity (Figure 5).

The strong correlation between precipitation and moisture index reflects their shared association with environmental water availability. Therefore, interpretations focused on their ecological significance rather than on independent statistical effects.

The results support the water-energy dynamics hypothesis, which predicts that biodiversity patterns are shaped by the interaction between water availability and energy conditions (Hawkins et al. 2003; Bhattarai et al. 2025). The strong influence of moisture index and precipitation observed in this study is consistent with evidence showing that water availability is a major determinant of plant species richness across environmentally heterogeneous landscapes.

Climatic and elevational drivers of Selaginella *distribution*

The combined analyses indicate that the distribution of *Selaginella* species in Java is governed by the interaction between climatic conditions and elevational gradients rather than by elevation alone. The PCA ordination revealed that species richness was closely associated with Annual Mean Moisture Index, Annual Mean Precipitation, and elevation, whereas Annual Mean Temperature and solar radiation were negatively associated with richness (Figure 6). These patterns suggest that environmental moisture is a key component of habitat suitability for *Selaginella*, while temperature and radiation may act as limiting factors in less favorable environments.

The correlation structure among variables further supports this interpretation (Figure 5). Elevation was strongly negatively correlated with Annual Mean Temperature and positively associated with moisture-related variables, indicating that elevational gradients influence local climatic conditions across Java. As elevation increases, temperatures generally decrease, and moisture availability tends to increase, creating environmental conditions that favor the establishment and persistence of many *Selaginella* species. Thus, elevation acts primarily as an indirect environmental gradient that modifies the climatic factors controlling species distributions.

The close association between species richness and moisture-related variables observed in this study is consistent with previous findings demonstrating the importance of precipitation and water balance in shaping plant distributions (Li et al. 2022). Similar relationships have been reported in other mountain ecosystems, where water-energy interactions strongly influence plant richness patterns across broad environmental gradients (Bhattarai et al. 2025). Most *Selaginella* species possess physiological characteristics that make them highly dependent on humid microhabitats, particularly during growth and reproduction. Areas characterized by high rainfall, persistent humidity, and reduced exposure to solar radiation provide optimal conditions for species occurrence. Conversely, warmer and drier environments may restrict distribution by increasing evapotranspiration and reducing habitat moisture.

These findings are consistent with studies from other tropical mountain regions, where moisture-related variables have been identified as major predictors of fern and lycophyte diversity (Krömer et al. 2013; Umair et al. 2023). In Java, the interaction between topographic gradients and climatic conditions appears to generate a mosaic of suitable and unsuitable habitats, resulting in the observed spatial variation of *Selaginella* richness. Both climatic and elevational gradients should be considered when assessing the current distribution and future conservation of *Selaginella* under changing environmental conditions.

Conservation implications under environmental change

The spatial distribution patterns identified in this study have important implications for the conservation of *Selaginella* in Java under ongoing environmental change. Areas with the highest species richness were concentrated within relatively small montane regions, particularly in western Java, whereas extensive lowland areas supported comparatively low richness (Figure 3). The restricted spatial extent of richness hotspots suggests that a substantial proportion of *Selaginella* diversity is concentrated within limited geographic areas that may be vulnerable to habitat degradation and climatic disturbances.

The strong association between species richness and moisture-related variables further indicates that future changes in precipitation regimes and environmental humidity could significantly affect the distribution of *Selaginella* (Figure 6). Previous distribution modeling studies have predicted substantial changes in suitable habitat availability for several *Selaginella* species under future climatic conditions, indicating potential range shifts and redistribution of climatically suitable environments (Setyawan et al. 2020b, 2021). Such changes may reduce habitat suitability for moisture-dependent species by increasing evapotranspiration rates and decreasing the availability of humid microhabitats. Species restricted to montane environments may be particularly vulnerable because suitable climatic conditions are often confined to narrow elevational zones.

In addition to climate change, land-use conversion, forest fragmentation, and infrastructure development continue to threaten many natural habitats in Java. The loss of forest cover can alter local microclimatic conditions by increasing temperature and solar radiation while reducing humidity, thereby decreasing habitat suitability for *Selaginella*. These impacts may be especially severe in regions where richness hotspots coincide with areas experiencing increasing human pressure.

Effective conservation strategies should prioritize the protection of humid montane ecosystems that support high *Selaginella* richness. Maintaining forest cover, conserving elevational habitat connectivity, and reducing habitat fragmentation are important measures for preserving suitable environmental conditions. Furthermore, long-term monitoring of climatically sensitive populations may provide valuable information for detecting distributional shifts associated with environmental change. Such efforts will contribute to the conservation of *Selaginella* diversity and enhance the resilience of montane ecosystems in Java under future climatic scenarios.

In conclusion, this study documented 21 Selaginella species and one unidentified taxon from 1,962 occurrence records across Java, Indonesia, and demonstrated that species richness is strongly structured by elevational and climatic gradients. Richness exhibited a hump-shaped elevational pattern, reaching its maximum at approximately 900 m asl, while moisture-related variables showed the strongest relationships with richness. Among all predictors, the Annual Mean Moisture Index (AMMO) was the most influential variable ($R^2 = 0.616$), explaining 61.6% of the observed variation in species richness, followed by Annual Mean Precipitation (AMP) ($R^2 = 0.527$), whereas Annual Mean Temperature and solar radiation showed negative relationships with richness. PCA analysis further indicated that the first two principal components explained 100% of the total environmental variation, with PC1 accounting for 68.55% and PC2 accounting for 31.45%, confirming that moisture availability is the primary environmental gradient governing *Selaginella* diversity across Java. Richness hotspots were concentrated in humid submontane and montane regions, emphasizing the ecological importance of these environments for species persistence. Several limitations should be acknowledged. The study was based on occurrence records and broad-scale environmental variables and did not incorporate local habitat characteristics such as canopy cover, soil properties, or microclimatic variation. Future research should incorporate standardized field sampling, fine-scale environmental measurements, species distribution modeling under climate-change scenarios, and molecular approaches to assess cryptic diversity and population connectivity across elevational gradients.

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