

Modeling the current habitat suitability of genus *Selaginella* in Java, Indonesia

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Abstract. *Setyawan AD, Sutarno, Sugiyarto, Sunarto, Sulton MN, Nugroho GD, Nursamsi I. 2026. Modeling the current habitat suitability of genus Selaginella in Java, Indonesia. Biodiversitas 27 (3): d270342. <https://doi.org/10.13057/biodiv/d270342>. Species Distribution Models (SDMs) have become essential tools in ecology, biogeography, biodiversity conservation, and natural resource management. Among the available approaches, Maximum Entropy (MaxEnt) is widely used to predict species distributions based on occurrence records and environmental variables. *Selaginella* (Selaginellaceae) is a lycophyte genus that depends on moist environmental conditions because free water is required for fertilization, making its distribution closely associated with climatic factors. This study aimed to model the current habitat suitability of *Selaginella* in Java, Indonesia, and to identify the climatic and topographic variables influencing its distribution. Occurrence records were compiled from field surveys, herbarium collections, and biodiversity databases, yielding 1,962 filtered records representing 21 accepted species and one unidentified accession. After data cleaning and 5-km spatial thinning, 811 occurrence records from 434 localities were retained for modeling. Twenty-two environmental predictors were evaluated, and model performance was assessed using cross-validation and Jackknife analyses. The MaxEnt model achieved good predictive performance (AUC = 0.811), indicating reasonably reliable discrimination between suitable and unsuitable habitats. Habitat suitability was primarily influenced by elevation (28.9%), Solar Radiation in April (19.4%), Precipitation of the Warmest Quarter (17.2%), and Annual Precipitation (17.0%). Response curves indicated optimal suitability at elevations of approximately 1,000–1,500 m above sea level under humid climatic conditions with high annual rainfall. Suitable habitats covered approximately 63,870 km², representing 49.19% of Java's land area, and were concentrated in mountainous regions of West Java, Central Java, East Java, and the Dieng Plateau. These findings demonstrate that climatic and topographic conditions strongly influence the distribution of *Selaginella* in Java and provide a valuable baseline for conservation planning, habitat management, and future climate-change assessments.*

Keywords: Climate variables, habitat suitability, Java, MaxEnt, *Selaginella*

INTRODUCTION

The spike mosses (*Selaginella* P.Beauv.; approximately 750 species) represent not only the most species-rich extant genus of lycophytes but also one of the largest genera of land plants worldwide (Schmidt et al. 2020). Members of the genus are characterized by the presence of ligules, rhizophores, and typically dimorphic leaves arranged in four rows along the stem. The genus exhibits remarkable morphological diversity, including erect, creeping, climbing, prostrate, rosette-forming, and epiphytic growth forms (Zhou and Zhang 2015). Most species occur in warm and humid environments, although *Selaginella* (Selaginellaceae) occupies an exceptionally broad ecological spectrum ranging from tropical rainforests to deserts, alpine habitats, and even arctic environments (Zhou and Zhang 2015; Weststrand and Korall 2016). This ecological versatility has enabled the genus to colonize diverse habitats and persist under a wide range of environmental conditions

(Klaus et al. 2017).

Java Island represents one of the most important centers of *Selaginella* diversity in Indonesia. Recent taxonomic and floristic studies have documented 21 accepted species of *Selaginella* in Java (Setyawan et al. 2026a, 2026b), including several taxa with restricted distributions such as *S. zollingeriana* (Setyawan et al. 2013) and *S. rothertii* (Setyawan et al. 2015c), two introduced species, namely *S. uncinata* (Setyawan 2014) and *S. kraussiana* (Setyawan et al. 2025). The island's complex topography, extensive volcanic mountain systems, and wide climatic gradients provide a variety of ecological conditions suitable for the establishment and persistence of *Selaginella* populations. Several species exhibit narrow ecological amplitudes and occur predominantly in humid montane environments, whereas others occupy a broader range of habitats extending from lowland forests to disturbed landscapes. Such variation suggests that environmental factors play a major role in shaping the distribution patterns of the genus

across Java.

Despite its relatively high diversity, *Selaginella* faces increasing pressures from habitat degradation and environmental change. Agricultural expansion, forest conversion, infrastructure development, mining activities, illegal logging, and human population growth continue to reduce the extent and quality of natural habitats throughout Java. At the same time, climate change is altering temperature and precipitation regimes that influence vegetation patterns, species persistence, and ecosystem structure (Thuiller et al. 2008; Kumar 2012). Because many *Selaginella* species depend on humid microhabitats and adequate moisture availability for successful reproduction, environmental changes may directly affect their distribution and long-term survival. Consequently, understanding the spatial distribution of suitable habitats has become increasingly important for conservation planning and biodiversity management.

Species Distribution Models (SDMs) have become fundamental tools in ecology, biogeography, conservation biology, and natural resource management (Guillera-Arroita et al. 2015). These models relate species occurrence records to environmental variables in order to estimate potential geographic distributions and identify suitable habitats. Among the available approaches, the Maximum Entropy (MaxEnt) algorithm is widely used because of its strong predictive performance and ability to utilize presence-only data (Elith et al. 2011). Its effectiveness has been demonstrated across a wide range of habitat suitability and species distribution studies (Préau et al. 2018). MaxEnt combines environmental predictors and occurrence records using machine-learning techniques to estimate habitat suitability and has been successfully applied in numerous biodiversity and conservation studies (Martinez-Minaya et al. 2018).

Previous studies have employed MaxEnt to investigate the distribution and habitat suitability of *Selaginella* in Southeast Asia and Indonesia. These studies include assessments of xero-epiphytic species (Setyawan et al. 2017), widespread species (Setyawan et al. 2018), mountainous species (Setyawan et al. 2020a), high-altitude species in Java (Setyawan et al. 2020b), and future range expansion of *S. zollingeriana* under climate change (Setyawan et al. 2021). However, although the taxonomy and floristic diversity of *Selaginella* in Java have been relatively well documented, quantitative information regarding habitat suitability, environmental determinants of distribution, and island-wide spatial patterns remains limited. To our knowledge, this study represents the first island-wide habitat suitability assessment of the genus *Selaginella* in Java based on an extensive occurrence dataset compiled from field surveys, herbarium collections, and biodiversity databases.

Despite the ecological importance and broad distribution of *Selaginella* in Java, the environmental factors governing its habitat suitability at an island-wide scale remain insufficiently quantified. Given the strong dependence of *Selaginella* on humid microclimates and montane environments, we hypothesized that topographic and moisture-related variables would be the primary

determinants of habitat suitability across Java. Specifically, we expected habitat suitability to increase under intermediate-to-high elevations and in areas with high precipitation and favorable solar radiation conditions. Therefore, this study aimed to: (i) model the current habitat suitability of *Selaginella* across Java using a MaxEnt approach; (ii) identify the most influential climatic and topographic variables governing its distribution; and (iii) provide a spatial framework to support conservation planning, cultivation efforts, and future ecological research. The resulting habitat suitability maps are expected to improve understanding of the ecological requirements of *Selaginella*, identify areas of high conservation value, and provide baseline information for evaluating potential responses of the genus to future environmental change.

MATERIALS AND METHODS

Study area

This study was conducted in Indonesia, particularly on Java Island and its surrounding small islands, covering six administrative provinces, i.e.: Banten, Jakarta, West Java, Central Java, Yogyakarta, and East Java. Java covers approximately 128,000-139,000 km² depending on the spatial dataset used and the inclusion of surrounding small islands. This area was selected for modeling the potential distribution of *Selaginella* because Java contains numerous mountain ranges and diverse environmental conditions that provide suitable habitats for the genus (Setyawan et al. 2020b). The occurrence and diversity of *Selaginella* in Java have been documented since the taxonomic work of Alston (1935). In the present study, 21 accepted species of *Selaginella* and one unidentified accession (*Selaginella* sp.) were recorded across Java based on field surveys conducted between 2007 and 2021 and supplemented by herbarium and biodiversity database records. Geographic coordinates were recorded using a Garmin GPS receiver during field surveys, while additional occurrence data were obtained from verified herbarium specimens and online biodiversity databases (Figure 1).

Procedures

Data collection

Occurrence data were compiled from both field surveys and herbarium-based records across Java, Indonesia. Field surveys conducted between 2007 and 2021 yielded 1,362 occurrence records representing 684 localities. Sampling was undertaken across a broad range of environmental and climatic conditions to maximize geographic and ecological representation and to minimize sampling bias. Geographic coordinates were recorded using a Garmin GPS unit with an estimated positional accuracy of less than 5 m, which was considered adequate for species distribution modeling at the spatial resolution used in this study (Merry and Bettinger 2019). Occurrence records were tabulated in Microsoft Excel and subsequently stored in CSV format for further analyses (Gunawan et al. 2021a, 2021b).

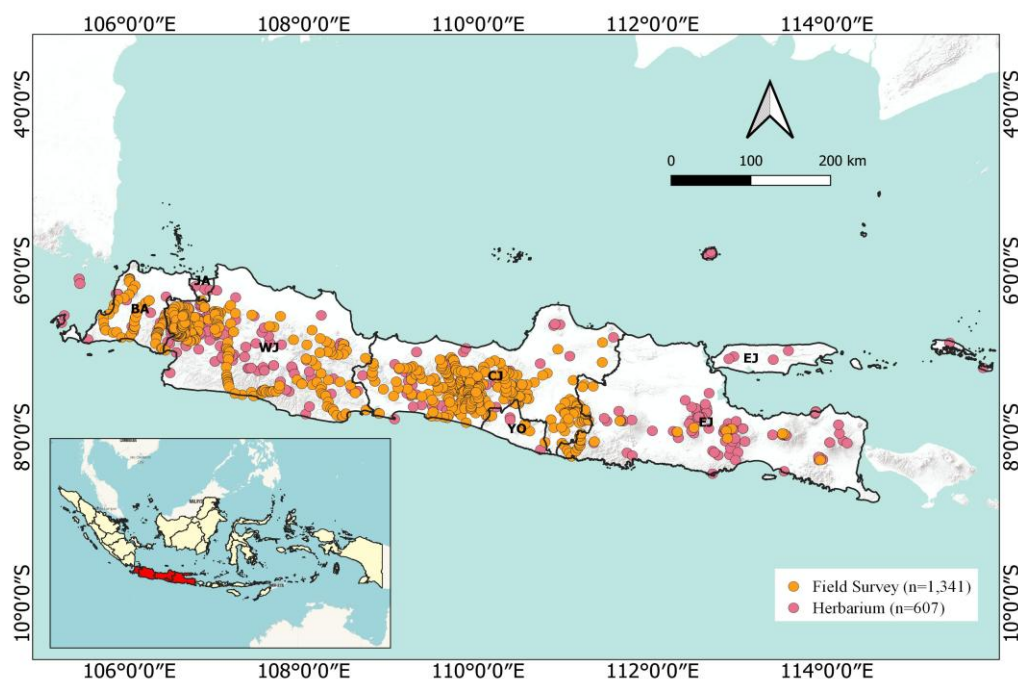


Figure 1. Study area and occurrence records of genus *Selaginella* in Java, Indonesia. Records were obtained from field surveys, herbarium specimens, and biodiversity databases. BA: Banten, JA: Jakarta, WJ: West Java, CJ: Central Java, YO: Yogyakarta, and EJ: East Java

Additional occurrence records were obtained from herbarium specimens and biodiversity databases, contributing an additional 600 occurrence records from 309 localities. Herbarium records were derived primarily from Herbarium Bogoriense (BO; 559 collections), representing more than 90% of all herbarium records), supplemented by specimens from BM, L, CANB, K, P, S, BGBM, and WRSI accessed through virtual herbarium collections, as well as occurrence records retrieved from the Global Biodiversity Information Facility (GBIF). In total, 1,962 georeferenced occurrence records from 993 localities were assembled, representing the known distribution of *Selaginella* across Java. The assembled dataset represented 21 accepted species of *Selaginella* and one unidentified accession retained as *Selaginella* sp. because the available material was insufficient for confident species-level identification. The recorded species were *Selaginella alutacea* Spring, *Selaginella aristata* Spring, *Selaginella bififormis* A.Braun ex Kuhn, *Selaginella ciliaris* (Retz.) Spring, *Selaginella cupressina* (Willd.) Spring, *Selaginella frondosa* Warb., *Selaginella intermedia* (Blume) Spring, *Selaginella involvens* (Sw.) Spring, *Selaginella kraussiana* (Kunze) A.Braun, *Selaginella opaca* Warb., *Selaginella ornata* (Hook. & Grev.) Spring, *Selaginella plana* (Desv.) Hieron., *Selaginella remotifolia* Spring, *Selaginella repanda* (Desv.) Spring, *Selaginella rothertii* Alderw., *Selaginella singalanensis* Hieron., *Selaginella subalpina* Alderw., *Selaginella subspinulosa* Spring, *Selaginella uncinata* (Desv.) Spring, *Selaginella willdenowii* (Desv.) Baker, and *Selaginella zollingeriana* Spring.

Species identification was verified through comparison with authenticated herbarium specimens and major taxonomic

treatments of *Selaginella* from Southeast Asia and adjacent regions, including Alston (1935a, 1935b, 1937, 1940), Wong (1982, 2010), Tagawa and Iwatsuki (1979), Pham-Hoang (1991), Tsai and Shieh (1994), and Zhang et al. (2013). Taxonomic nomenclature and synonymy were standardized following Plants of the World Online (POWO; <https://powo.science.kew.org/>), while supplementary photographic observations and occurrence information were consulted through iNaturalist (<https://www.inaturalist.org/>). Historical records reported by Alston (1935b) were re-evaluated whenever corresponding specimens or metadata were available. To improve data reliability and minimize potential identification errors, occurrence records were verified using herbarium specimens, published taxonomic literature, and biodiversity databases, whereas geographic coordinates were checked against specimen metadata and Google Earth Pro when necessary.

All occurrence records were subsequently subjected to geographic verification, taxonomic standardization, removal of duplicate and geographically inconsistent records, and exclusion of records located outside the terrestrial boundaries of Java. Following these quality-control procedures, a total of 1,962 verified occurrence records were retained. To reduce spatial sampling bias and spatial autocorrelation, occurrence records were evaluated using ArcMap 10.6 and SDM Toolbox v2.5, and spatial thinning was applied using a minimum distance threshold of 5 km between occurrence points (Brown et al. 2017). Because many occurrence records originated from nearby localities sampled in different years or from closely spaced sites, spatial thinning substantially reduced the dataset to 811 occurrence records representing 434 unique localities. This procedure minimized the influence

of spatially clustered records that could overrepresent heavily sampled areas and artificially inflate model performance. The resulting dataset was used in all subsequent MaxEnt analyses. Because the objective of this study was to model the collective climatic niche of the genus *Selaginella* rather than individual species, all occurrence records were pooled into a single dataset prior to analysis.

Environmental variable

Environmental variables are used to model the potential distribution of genus *Selaginella* on Java Island. We used 22 datasets consisting of 19 variables of bioclimates, elevation, precipitation (12 months), and solar radiation (12 months) (Table 1). We got the environment variables via the WorldClim version 2.1 datasets released in January 2020 (<https://www.worldclim.org/>). This environmental dataset represents the WorldClim baseline climate period (1970-2000), which was used as the reference for current habitat suitability modeling (Fick and Hijmans 2017). The variables obtained are in raster form with a spatial resolution of 1 km² (30 arc seconds).

Environmental variables were clipped to the study area and converted from raster to ASCII format using ArcGIS 10.6 prior to MaxEnt analysis. Multicollinearity among predictors was evaluated using Pearson correlation analysis, and variables exhibiting strong pairwise correlations ($|r| \geq 0.8$) were screened to reduce redundancy. From each highly correlated pair, only one variable was retained based on ecological relevance and potential importance for species distribution. The results of the Pearson correlation analysis are presented in Table S2. Subsequent variable reduction was performed to identify the most informative predictors for habitat suitability modeling.

Table 1. Environmental variables used for modeling the habitat suitability of genus *Selaginella* in Java, Indonesia

Code	Parameter	Unit
30s_elev	Elevation	m
30s_prec	Precipitation (12 months)	mm
30s_srad	Solar radiation (12 months)	W/m ²
30s_bio_1	Mean annual temperature	C
30s_bio_2	Mean diurnal range (max temp – min temp)	C
30s_bio_3	Isothermality	C
30s_bio_4	Temperature seasonality	C
30s_bio_5	Maximum temperature of warmest month	C
30s_bio_6	Minimum temperature of coldest month	C
30s_bio_7	Temperature annual range	C
30s_bio_8	Mean temperature of wettest quarter	C
30s_bio_9	Mean temperature of driest quarter	C
30s_bio_10	Mean temperature of warmest quarter	C
30s_bio_11	Mean temperature of coldest quarter	C
30s_bio_12	Annual precipitation	mm
30s_bio_13	Precipitation of wettest month	mm
30s_bio_14	Precipitation of driest month	mm
30s_bio_15	Precipitation seasonality (coefficient of variation)	mm
30s_bio_16	Precipitation of wettest quarter	mm
30s_bio_17	Precipitation of driest quarter	mm
30s_bio_18	Precipitation of the warmest quarter	mm
30s_bio_19	Precipitation of coldest quarter	mm

After preprocessing, environmental variable reduction was conducted to minimize redundancy and identify predictors that were most relevant to species occurrence (Zeng et al. 2016). To further evaluate the relative importance of environmental predictors, a Jackknife test implemented in MaxEnt was performed (Phillips et al. 2006). The Jackknife procedure was applied to all retained environmental variables included in the MaxEnt model and was used to assess the contribution of each predictor to model performance and habitat suitability prediction. Based on the combined results of Pearson correlation screening and Jackknife evaluation, four environmental variables were identified as the most influential predictors of habitat suitability, namely elevation (30s_elev), solar radiation in April (30s_srad_04), precipitation of the warmest quarter (30s_bio_18), and annual precipitation (30s_bio_12). These variables showed the highest contributions to model performance and are therefore emphasized in the next sections. For clarity of presentation, only these four predictors are presented and discussed in detail.

Species distribution model

MaxEnt modeling is widely used to predict species distributions and habitat suitability based on occurrence records and environmental variables (Phillips et al. 2006; Guillera-Aroita et al. 2015). In this study, occurrence records from all recorded *Selaginella* taxa were pooled to model the collective climatic niche and potential distribution of the genus in Java. MaxEnt is particularly suitable for presence-only datasets and has been shown to provide robust predictions when combined with environmental predictors (Phillips and Dudík 2008; Elith et al. 2011). We used MaxEnt version 3.4.4 (https://biodiversityinformatics.amnh.org/open_source/MaxEnt/) to develop the habitat suitability model (Phillips et al. 2006). Prior to model calibration, multicollinearity among environmental predictors was evaluated using Pearson correlation analysis. Variables with pairwise correlation coefficients of $|r| \geq 0.80$ were considered highly correlated, and only one variable from each correlated pair was retained based on ecological relevance and preliminary contribution to model performance.

To characterize environmental conditions available within the study area, 10,000 randomly distributed background points were generated across Java, representing the accessible environmental space for the genus. MaxEnt was implemented using the default regularization multiplier ($\beta = 1.0$) and default feature classes, including linear (L), quadratic (Q), product (P), threshold (T), and hinge (H) features. Default settings were retained because the study focused on genus-level habitat characterization using a large occurrence dataset (Phillips and Dudík 2008; Elith et al. 2011); and because these settings have been widely applied in previous *Selaginella* distribution studies (Setyawan et al. 2017, 2018, 2020a, 2020b, 2021). Habitat suitability was generated as a continuous logistic output ranging from 0 to 1. For map visualization, suitability values were classified into four equal-interval classes (ESRI 2024): low (0.00-0.22), moderate (0.22-0.45), high (0.45-0.68), and very high suitability (0.68-0.90). To estimate the total

suitable habitat area, suitability values were further grouped into unsuitable (0.00-0.22) and suitable (0.22-0.90) categories, and the total suitable area was calculated by summing all raster cells classified as suitable.

Model parameters were adjusted to improve model performance and reduce sampling bias. Duplicate occurrence records were removed, while occurrence data were previously subjected to geographic filtering and spatial thinning as described in the Data Collection section. The maximum number of iterations was increased to 5,000 to ensure model convergence, and 10,000 background points were generated to characterize the environmental conditions available within the study area. To evaluate model stability and predictive performance, 10 replicate runs were performed using the cross-validation option. Model performance was assessed using a 10-fold cross-validation approach, whereby approximately 90% of the occurrence records were used for model training and 10% for model testing during each replicate (Phillips and Dudík 2008; Abdelaal et al. 2019). All other MaxEnt settings were retained at their default values.

Model performance was evaluated using the Area Under the Receiver Operating Characteristic Curve (AUC), a threshold-independent measure of model accuracy ranging from 0 to 1 (Padalia et al. 2014). AUC values <0.6 indicate poor predictive performance, values between 0.6 and 0.7 indicate low predictive ability, values between 0.7 and 0.8 indicate acceptable performance, values between 0.8 and 0.9 indicate good performance, and values >0.9 indicate excellent predictive performance.

RESULTS AND DISCUSSION

Model performance

Pearson correlation analysis indicated that the retained environmental variables did not exhibit strong multicollinearity ($|r| < 0.8$; Table S2), supporting their ecological interpretation and contribution to habitat suitability prediction. The MaxEnt model achieved a mean AUC value of 0.811 (Figure 2), indicating good predictive performance and a reliable ability to distinguish suitable from unsuitable habitats for the genus *Selaginella* in Java. This result suggests that the selected environmental variables adequately captured the principal ecological gradients influencing habitat suitability across the study area.

Among the environmental variables included in the MaxEnt model, four predictors showed the highest contributions to habitat suitability prediction (Table 2). Altitude/elevation (30s_elev), solar radiation in April (30s_srad_04), precipitation of the warmest quarter (30s_bio_18), and annual precipitation (30s_bio_12) were identified as the most influential environmental variables affecting habitat suitability of *Selaginella* in Java. Among these variables, elevation showed the highest contribution, with predicted suitability extending from 0 to 3,200 masl

and reaching its maximum between 1,000 and 1,500 masl (Figure 3). The strong influence of elevation likely reflects its role as an integrative environmental gradient associated with temperature, precipitation, humidity, and vegetation structure.

Jackknife analysis indicated that solar radiation in April (30s_srad_04) and annual precipitation (30s_bio_12) provided the greatest amount of unique information to model construction, followed by precipitation of the warmest quarter (30s_bio_18) and elevation (30s_elev) (Figure 4). Although solar radiation and annual precipitation exhibited high Jackknife importance, omission of either variable resulted in only a modest reduction in training gain, suggesting that some environmental information was shared among predictors. In contrast, elevation produced the smallest reduction in training gain when omitted, indicating partial overlap with other predictors despite showing the highest percent contribution (Table 2). This discrepancy reflects the different criteria used by MaxEnt, whereby percent contribution measures the relative influence of variables during model training, whereas the Jackknife test evaluates the unique information content contributed by each predictor.

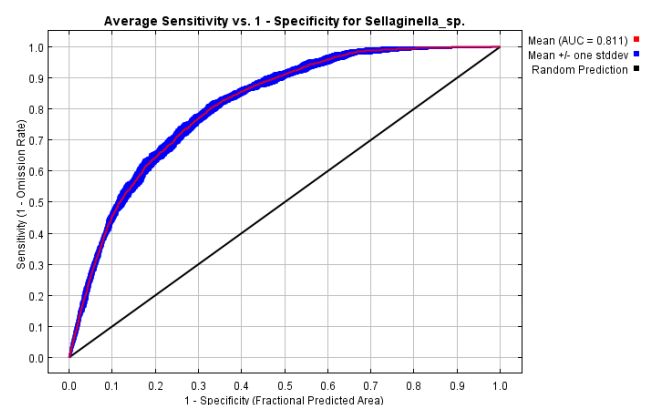


Figure 2. Receiver operating characteristic (ROC) curve and area under the curve (AUC) value for the MaxEnt model predicting habitat suitability of genus *Selaginella* in Java, Indonesia

Table 2. Four environmental predictors with the highest contribution to habitat suitability prediction for the genus *Selaginella* in Java, Indonesia

Code	Environmental variable	Percent contribution (%)
30s_elev	Elevation	28.9
30s_srad_04	Solar radiation in April	19.4
30s_bio_18	Precipitation of the warmest quarter	17.2
30s_bio_12	Annual precipitation	17

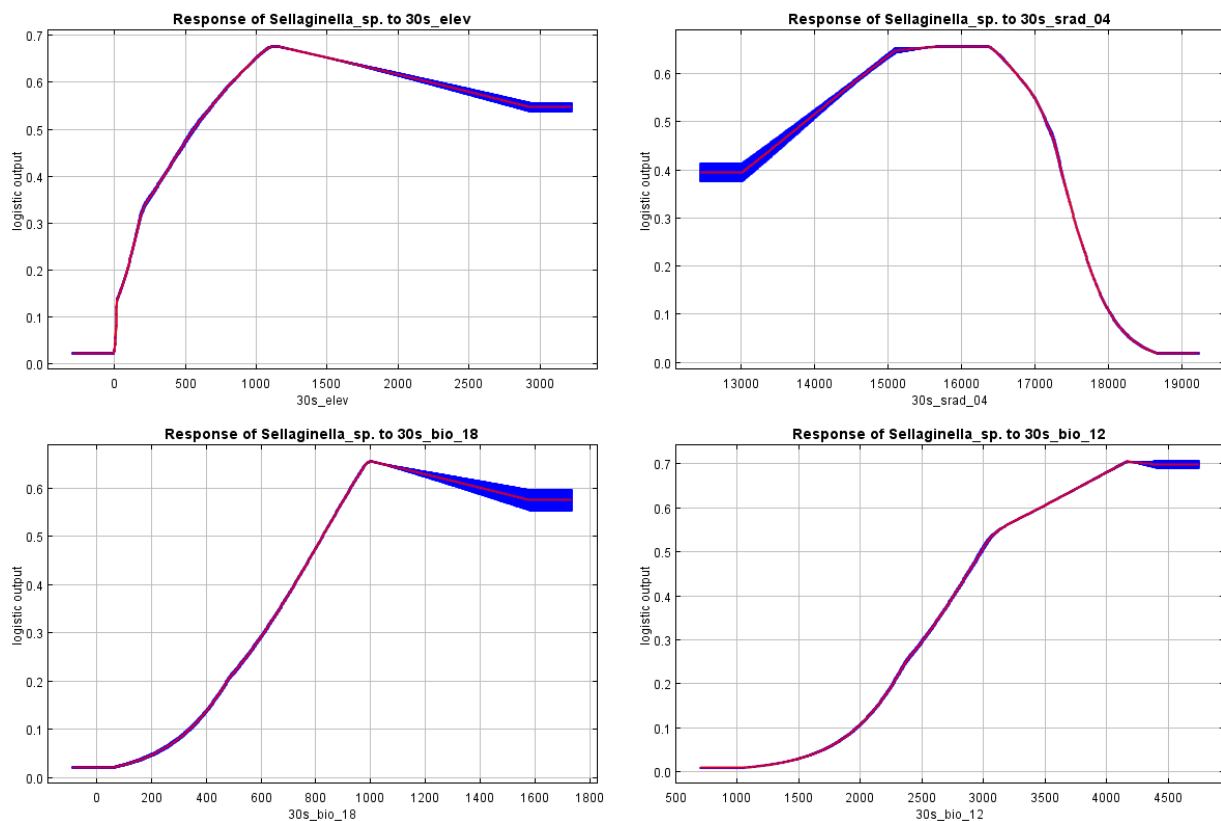


Figure 3. Response curves of the four most influential environmental variables affecting the habitat suitability of the genus *Sellaginella* in Java, Indonesia. Variables include elevation (30s_elev), solar radiation in April (30s_srad_04), precipitation of the warmest quarter (30s_bio_18), and annual precipitation (30s_bio_12). Curves represent the mean response of 10 replicate MaxEnt runs (red), with blue lines indicating ± 1 standard deviation

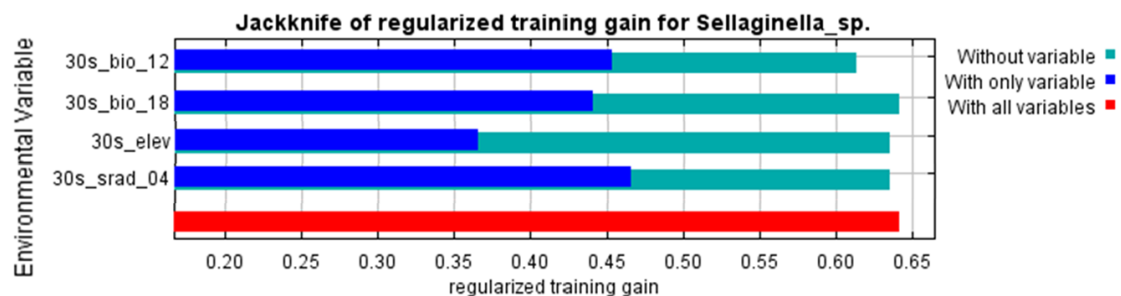


Figure 4. Jackknife test showing the relative importance of the four environmental predictors with the highest contributions to the habitat suitability model of genus *Sellaginella* in Java, Indonesia. Jackknife analysis was conducted using all retained environmental variables included in the final MaxEnt model

Variables' response curves

Response curves were used to illustrate the relationship between environmental variables and the predicted probability of occurrence generated by the MaxEnt model (Phillips and Dudík 2008; Elith et al. 2011). These curves provide a quantitative representation of species responses to environmental gradients and facilitate interpretation of ecological niches, environmental tolerances, and habitat preferences (Yi et al. 2016). The response curves for genus

Sellaginella in relation to the four most influential environmental variables are presented in Figure 3.

The response curves indicate that habitat suitability for genus *Sellaginella* was strongly associated with elevation, solar radiation, and precipitation variables (Figure 3). The suitable elevational range (30s_elev) extended from approximately 0 to 3,200 m asl., with the highest predicted suitability occurring between 1,000 and 1,500 m asl. This pattern suggests that submontane environments provide the most favorable ecological conditions for the genus in Java.

The second most influential variable was solar radiation in April (30s_srad_04), which showed a suitable range of approximately 13,000-19,000 W m⁻², with peak suitability around 15,000 W m⁻². This response indicates that moderate levels of solar radiation are associated with optimal habitat conditions, likely reflecting the balance between energy availability and moisture retention in forested environments.

Precipitation of the warmest quarter (30s_bio_18) exhibited a suitable range of approximately 200-1,700 mm, with maximum suitability occurring at around 1,000 mm. This result highlights the importance of moisture availability during the warmest period of the year, when water stress may otherwise limit plant growth and reproduction. Annual precipitation (30s_bio_12) showed a suitable range of approximately 1,500-4,600 mm, with peak suitability at around 4,500 mm. The strong response to annual precipitation further supports the ecological dependence of *Selaginella* on humid environments, consistent with its requirement for moist habitats and free water during reproductive processes.

Prediction of the current potential distribution

Selaginella is a genus of lycophytes that are traditionally used as medicinal plants. Little is known about the existence and distribution of genus *Selaginella* in Java. The model prediction of the potential distribution of genus *Selaginella* in Java was created based on the observed occurrences and current climate conditions. The maps of the species distribution model produced by MaxEnt and categorized into four suitability classes between 0 and 1 are presented in Figure 5. Meanwhile, we also generated potential distribution maps for selected species, following van Proosdij et al. (2016), using only species represented by more than 12 occurrence records to reduce potential prediction bias (Table S1; Figure S1).

The MaxEnt model was developed using a spatially thinned dataset of 811 occurrence records from 434 localities across Java. These records were retained from 1,962 verified occurrence records after applying a 5-km

minimum distance filter to reduce spatial sampling bias and autocorrelation (see Methods). The potential present-day distribution of suitable habitat for the genus, as derived from MaxEnt (Phillips and Dudík 2008; Elith et al. 2011; Phillips et al. 2017), indicated that approximately 49.19% (63,870.41 km²) of Java provides suitable habitat for genus *Selaginella*, based on the aggregation of moderate, high, and very high suitability classes. Of this total suitable habitat area, 27,901.04 km² (43.68%) occurs in West Java, 17,731.42 km² (27.76%) in Central Java, 10,128.17 km² (15.86%) in East Java, 7,184.34 km² (11.25%) in Banten, 848.32 km² (1.33%) in Yogyakarta, and 77.12 km² (0.12%) in Jakarta (Figure 5; Figure S1).

In Figure 5, the predicted suitable habitat is distributed patchily across the central and southern parts of Banten, Jakarta, West Java, Central Java, and Yogyakarta. In northern Central Java, Karimunjawa Islands, the Mount Muria region, and the Kendeng Mountains were also predicted as suitable habitats for genus *Selaginella*. In East Java, suitable habitat is widely distributed across the southern region of Pacitan and extends through several mountainous landscapes, including Mount Lawu, Mount Kelud, Mount Kawi, Mount Liman, Mount Arjuna, Mount Semeru, Mount Argopuro, and Mount Raung. Additionally, predicted suitable habitats were identified on Bawean Island, Madura Island, and several smaller islands surrounding Madura, including Kangean and Sapudi (Figure 5; Figure S1).

The greatest concentration of highly suitable habitat for genus *Selaginella* in Java [Habitat Suitability Index (HSI) = 0.68-0.90] was predicted mainly in Banten (BA), West Java (WJ), Central Java (CJ), and East Java (EJ). Areas with moderate to high suitability (HSI = 0.22-0.68) were also widely distributed across portions of Banten, West Java, Central Java, and East Java. In contrast, low suitability habitats (HSI = 0.00-0.22) were more commonly predicted in Jakarta (JA), parts of Central Java (CJ), Yogyakarta (YO), and East Java (EJ) (Figure 5; Figure S1).

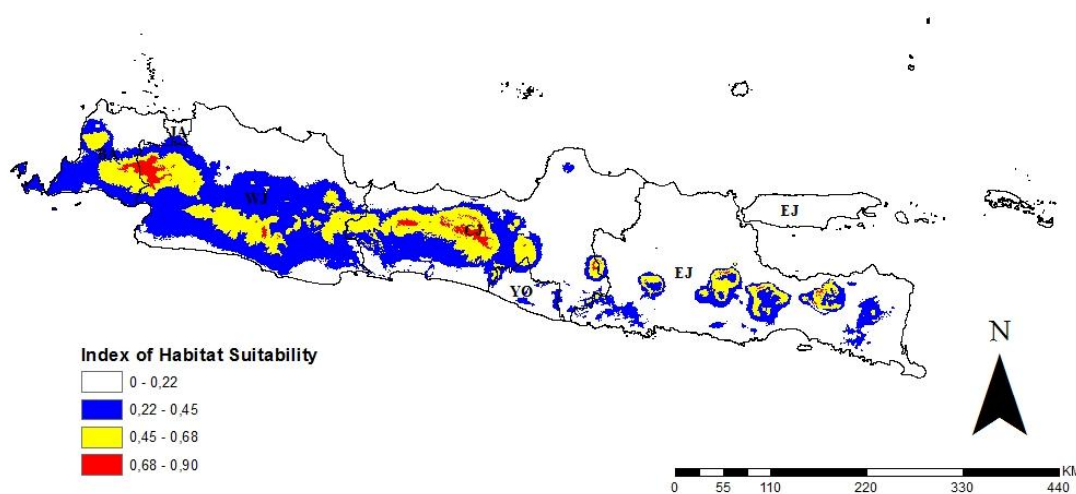


Figure 5. Predicted current habitat suitability of genus *Selaginella* in Java, Indonesia, based on the MaxEnt model. BA: Banten, JA: Jakarta, WJ: West Java, CJ: Central Java, YO: Yogyakarta, and EJ: East Java

Discussion

MaxEnt estimates the relative contribution of environmental variables through iterative optimization and coefficient adjustment during model construction (Table 2). The model achieved a mean AUC value of 0.811, indicating good predictive performance according to commonly accepted AUC classification criteria (Padalia et al. 2014). The ROC curve shown in Figure 2 illustrates the model's predictive performance. The AUC statistic represents the probability that a known occurrence point will be ranked higher than a randomly selected background location (Phillips et al. 2006). Therefore, the obtained AUC value suggests that the selected environmental variables adequately captured the principal ecological gradients influencing habitat suitability and the current distribution of *Selaginella* across Java.

An important limitation of the present study is the uncertainty associated with species distribution modeling and the decision to pool occurrence records from multiple *Selaginella* species into a single genus-level dataset. Although the resulting MaxEnt model demonstrated good predictive performance (AUC = 0.811), model outputs remain sensitive to uncertainties arising from occurrence-data quality, sampling bias, environmental variable selection, and the assumption that current distributions adequately represent the ecological niche of the genus (Fourcade et al. 2014; Guillera-Aroita et al. 2015). Furthermore, habitat suitability predictions are based primarily on climatic and topographic variables and do not incorporate potentially important factors such as land-use change, vegetation structure, microhabitat availability, dispersal limitations, biotic interactions, or anthropogenic disturbance (Guillera-Aroita et al. 2015; Martinez-Minaya et al. 2018).

The pooling of 21 *Selaginella* species into a single modeling framework provides a useful representation of the collective environmental niche of the genus across Java; however, this approach may mask important interspecific ecological differences. Several *Selaginella* species occupy narrow elevational ranges, specialized microhabitats, or restricted geographic distributions, whereas others occur across broader environmental gradients. Such ecological variation has been documented in southern Central Java (Setyawan 2012; Setyawan et al. 2016), Mount Lawu (Setyawan et al. 2013), southern West Java (Setyawan 2015b), Mount Merapi (Setyawan et al. 2012), the Dieng Plateau (Setyawan et al. 2015c), Bromo Tengger Semeru National Park (Setyawan and Sugiyarto 2015), Banten (Setyawan 2015a), West Java (Harli 2013), Central Java (Panjaitan 2013), Yogyakarta (Setyawan et al. 2015a), and the Sewu karst region (Setyawan et al. 2015b). Consequently, the pooled model likely emphasizes environmental conditions shared among species and may underrepresent habitat requirements of ecological specialists or rare taxa. Areas predicted as suitable for the genus, therefore, should not be interpreted as equally suitable for all constituent species.

Future studies should develop species-specific distribution models for taxa with sufficient occurrence records and compare their environmental responses with the genus-

level model. Ensemble modeling approaches, spatial bias correction procedures, independent validation datasets, and incorporation of additional environmental layers such as land cover, forest structure, and microclimatic variables would further reduce prediction uncertainty (Fourcade et al. 2014; Kaky et al. 2020). Such analyses would improve understanding of niche differentiation among *Selaginella* species and provide more precise guidance for conservation planning, habitat management, and climate-change vulnerability assessments.

The model identified elevation, solar radiation in April, precipitation of the warmest quarter, and annual precipitation as the most influential variables affecting habitat suitability (Table 2; Figure 3). These findings are ecologically reasonable because *Selaginella* species are strongly associated with environmental conditions that regulate moisture availability and microclimate stability. Java supports approximately 21 accepted species of *Selaginella* (Setyawan et al. 2026a, 2026b), including several endemic taxa (Setyawan et al. 2015b, 2021); and introduced taxa (Setyawan 2014, 2025), making the island one of the most important centers of *Selaginella* diversity in Indonesia. Although species occupy a broad elevational range, their distributions are not uniform across environmental gradients. Instead, individual species exhibit distinct ecological preferences that reflect differences in physiological tolerance and habitat requirements.

Among the environmental variables identified by MaxEnt, elevation showed the strongest contribution to habitat suitability. Elevation is not merely a topographic parameter but also represents a complex environmental gradient that integrates temperature, humidity, cloud formation, precipitation patterns, and vegetation structure (Austin 2002). Field observations and model outputs consistently indicated that *Selaginella* is most frequently encountered between 1,000 and 1,500 m asl (Figure 3). This elevational range corresponds to the submontane zone, which appears to provide optimal ecological conditions for many species. Submontane environments generally combine moderate temperatures, high atmospheric humidity, and relatively stable microclimatic conditions that reduce desiccation stress while maintaining sufficient light availability beneath forest canopies.

The strong contribution of elevation in the present genus-level model is consistent with previous MaxEnt studies of *Selaginella*. In a Southeast Asian species-level analysis, elevation was identified as the most important predictor for the montane species *S. involvens*, whereas precipitation variables were more influential for the lowland species *S. repanda* (Setyawan et al. 2017). Similarly, elevation was the dominant predictor in habitat suitability models of montane *Selaginella* species in Java (Setyawan et al. 2020a) and in projections of the endemic species *S. zollingeriana*, where elevation contributed 35.5% of total model performance (Setyawan et al. 2021). These findings collectively indicate that elevational gradients act as integrative environmental surrogates reflecting multiple climatic factors, including humidity, moisture availability,

and temperature, that shape the distribution of *Selaginella* across diverse ecological settings.

The concentration of suitable habitat within the submontane belt may also reflect the importance of cloud-affected forest ecosystems. Submontane and lower montane forests often experience persistent fog, high humidity, and reduced evapotranspiration relative to lowland environments (Hemp 2006; Fyllas et al. 2017). These conditions are particularly favorable for *Selaginella* because successful fertilization requires free water for sperm movement, a characteristic shared by most lycophytes and ferns (Klaus et al. 2017). Consequently, humid mountain forests provide both suitable microhabitats and favorable reproductive conditions. The response curve generated by MaxEnt therefore reflects not only elevational preferences but also the dependence of *Selaginella* on moist and environmentally stable habitats.

Solar radiation and precipitation were also identified as important predictors of habitat suitability. Solar radiation regulates photosynthesis, growth, and physiological performance, while precipitation directly influences water availability and ecosystem productivity (Hemp 2006; Fyllas et al. 2017). The importance of precipitation is especially relevant for *Selaginella* because water availability influences both vegetative growth and reproductive success. Similar patterns have been reported in previous MaxEnt studies of *Selaginella* in Java and Southeast Asia. For example, precipitation-related variables and elevation were among the principal predictors influencing the distributions of *S. involvens* and *S. repanda* (Setyawan et al. 2017), mountainous *Selaginella* species in Java (Setyawan et al. 2020a), and high-altitude species under future climate scenarios (Setyawan et al. 2020b). The present genus-level model therefore supports earlier findings that moisture availability and elevational gradients are the primary environmental factors shaping *Selaginella* distributions. However, compared with species-specific models, the pooled dataset used here likely emphasizes environmental conditions shared across multiple taxa, resulting in a broader representation of the collective climatic niche of the genus.

The predicted distribution pattern highlights the importance of Java's montane landscapes, with the largest and most continuous areas of suitable habitat concentrated in the western and central parts of the island. Highly suitable habitats were primarily associated with volcanic mountain systems and adjacent uplands extending from Banten through West Java to the central Javan highlands, including the Dieng region. Additional suitable habitats occurred as more fragmented patches around major volcanic complexes in eastern Central Java and East Java, including Mount Lawu, Mount Kelud, Mount Arjuna, Mount Semeru, Mount Argopuro, and Mount Raung. These mountain landscapes are characterized by high rainfall, rugged topography, abundant moisture, and diverse microhabitats, including humid forest floors, ravines, stream corridors, and shaded slopes. Long-term volcanic activity has generated pronounced elevational gradients and environmentally heterogeneous habitats that provide favorable conditions for moisture-dependent taxa such as

Selaginella. Consequently, the predicted suitability pattern reflects the strong association of the genus with humid montane environments and underscores the ecological importance of Java's volcanic mountain ecosystems for its persistence.

Although many *Selaginella* species remain underutilized, several possess recognized medicinal potential (Setyawan 2009, 2011; Chikmawati et al. 2012). Habitat suitability maps can therefore support future exploration, cultivation, and conservation efforts by identifying areas where populations are most likely to occur. These findings are particularly relevant in Java, where agricultural expansion, infrastructure development, plantation establishment, and forest degradation continue to reduce the extent and quality of suitable habitats. Consequently, areas predicted to have high habitat suitability should be prioritized for conservation and habitat management.

Based on the habitat suitability map, the largest contiguous areas with very high habitat suitability are concentrated in the montane regions of western and central Java, particularly around the Halimun-Salak, Gede-Pangrango, Papandayan-Ciremai, Dieng, Merapi-Merbabu, Lawu, Semeru, and Argopuro mountain systems. These landscapes may serve as practical priorities for future field validation, long-term monitoring, and conservation planning because they encompass extensive areas predicted to provide highly suitable habitat for *Selaginella*.

Climate change represents an additional challenge for the long-term persistence of *Selaginella* in Java. Because climate is a major determinant of plant distribution (Forman 1964), projected changes in temperature and precipitation may alter the extent and spatial distribution of suitable habitats. Species responses to climate warming commonly include upward elevational shifts (Setyawan et al. 2016; Setyawan et al. 2020b) as well as changes in growth, phenology, and reproductive performance (Thuiller et al. 2008; Hill and Preston 2015). Given the strong dependence of *Selaginella* on moisture availability, future increases in temperature and potential reductions in precipitation may reduce the suitability of humid mountain habitats that currently support many populations. These ecosystems are already vulnerable to anthropogenic disturbance and may become less effective as refugia for moisture-dependent taxa under future climatic conditions.

The construction of an optimal species distribution model requires the integration of multiple environmental variables that directly or indirectly influence species occurrence. The model represents a genus-level assessment based on pooled occurrence records from 21 species and one unidentified accession, potentially masking species-specific ecological differences. Although the climatic and topographic variables used in this study provided a reliable baseline for predicting habitat suitability, additional ecological information could further improve model performance. Future studies should incorporate factors such as land-use change, species interactions, dispersal constraints, and higher-resolution occurrence data to better represent the ecological niche of *Selaginella*. Nevertheless, the present model provides valuable baseline information on habitat suitability patterns and offers a useful framework for future

conservation planning and climate-change assessments in Java.

In conclusion, the MaxEnt model successfully predicted the current habitat suitability of the genus *Selaginella* in Java, Indonesia, with good predictive performance (AUC = 0.811), providing a useful approximation of habitat suitability patterns across Java. From 22 initial environmental variables, four key predictors were identified as the primary determinants of habitat suitability: elevation (28.9% contribution), solar radiation in April (19.4%), precipitation of the warmest quarter (17.2%), and annual precipitation (17.0%). Response-curve analyses indicated that habitat suitability was highest at elevations of approximately 1,000-1,500 m asl., highlighting the ecological importance of submontane environments. The model predicted that 63,870.41 km², equivalent to 49.19% of Java, provides suitable habitat for *Selaginella*, with the highest suitability concentrated in the mountainous regions of West Java, Central Java, and East Java. These findings emphasize the importance of mountain forests as refugia for moisture-dependent lycophytes. Although the model was developed at the genus level using pooled occurrence records and primarily climatic and topographic predictors, it provides a useful baseline for understanding habitat suitability patterns across Java. Protection of highly suitable habitats, particularly in submontane and montane regions, should be prioritized to support the long-term conservation of *Selaginella* diversity under ongoing land-use and climate change pressures.

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Table S1. Number of occurrence records of *Selaginella* species used for species distribution modeling in Java, Indonesia

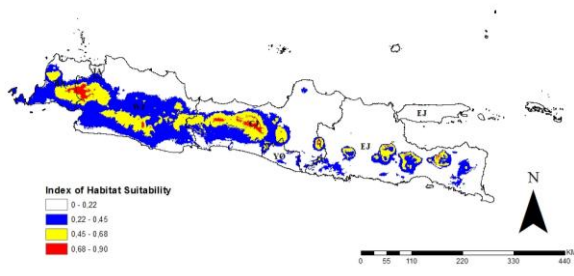
Species name	Number of records
<i>Selaginella alutacea</i>	15
<i>Selaginella aristata</i>	94
<i>Selaginella biformis</i>	13
<i>Selaginella ciliaris</i>	387
<i>Selaginella frondosa</i>	4
<i>Selaginella intermedia</i>	66
<i>Selaginella involvens</i>	126
<i>Selaginella kraussiana</i>	2
<i>Selaginella cupressina</i>	2
<i>Selaginella opaca</i>	142
<i>Selaginella ornata</i>	214
<i>Selaginella plana</i>	404
<i>Selaginella remotifolia</i>	129
<i>Selaginella repanda</i>	68
<i>Selaginella rothertii</i>	8
<i>Selaginella singalanensis</i>	12
<i>Selaginella subalpina</i>	35
<i>Selaginella subspinulosa</i>	7
<i>Selaginella uncinata</i>	5
<i>Selaginella willdenowii</i>	205
<i>Selaginella zollingeriana</i>	23
<i>Selaginella</i> sp.	1
Total	1,962

Note: Total 21 accepted species. Of 1,962 compiled occurrence records, 811 records from 434 localities were retained after data verification and 5-km spatial thinning

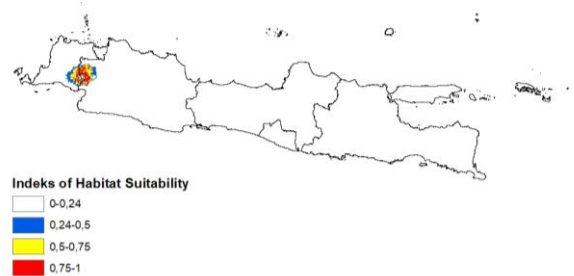
Table S2. Pearson correlation coefficients among the four most influential environmental variables identified by the MaxEnt model

Variable	Elevation (30s_elev)	Solar radiation in April (30s_srad_04)	Precipitation of the warmest quarter (30s_bio_18)	Annual precipitation (30s_bio_12)
Elevation (30s_elev)	1.000	0.43	0.58	0.64
Solar radiation in April (30s_srad_04)	0.43	1.000	-0.36	-0.48
Precipitation of the warmest quarter (30s_bio_18)	0.58	-0.36	1.000	0.71
Annual precipitation (30s_bio_12)	0.64	-0.48	0.71	1.000

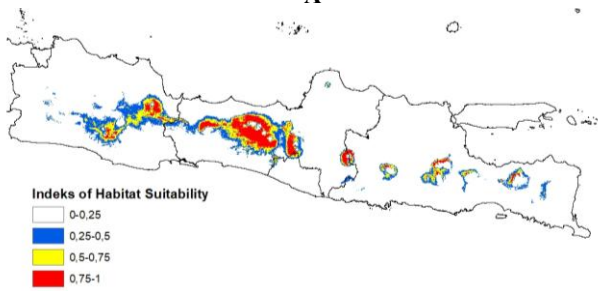
Note: The four most influential variables identified by MaxEnt exhibited acceptable correlation levels and were therefore considered suitable for interpretation in habitat suitability analyses



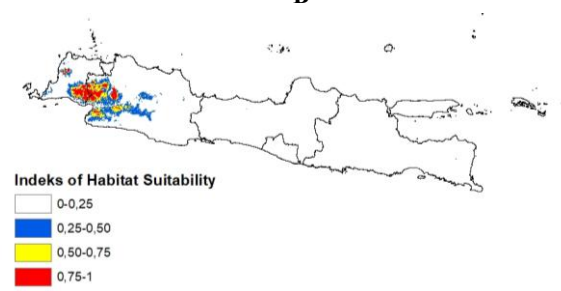
A



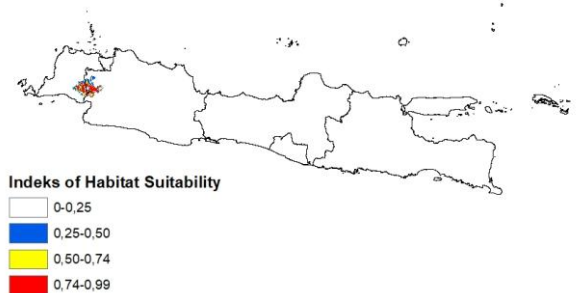
B



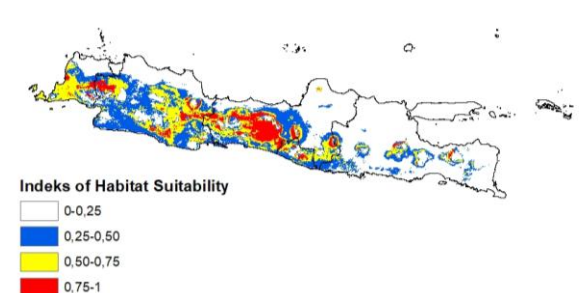
C



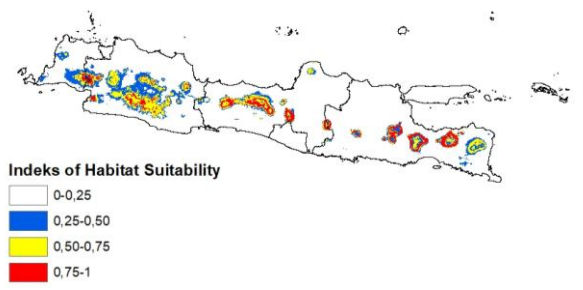
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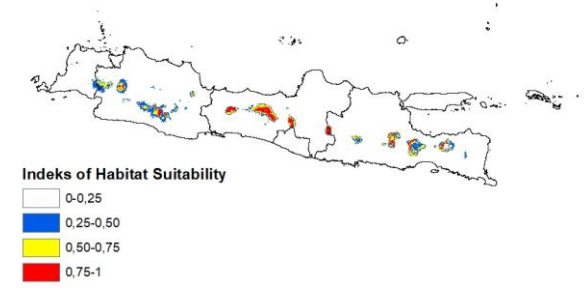
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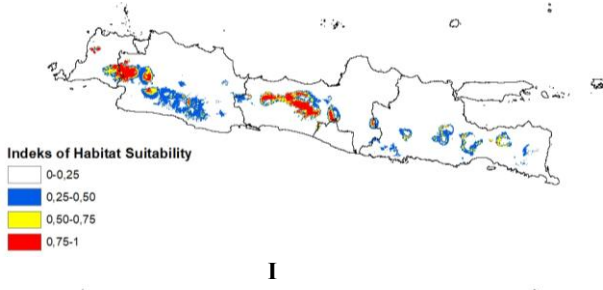
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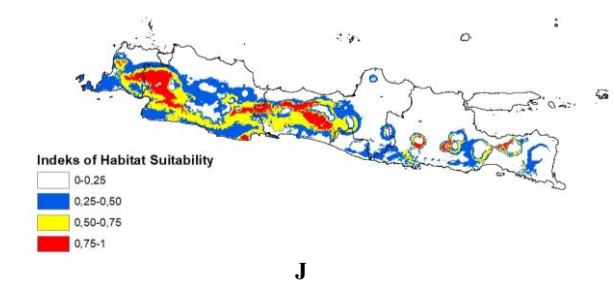
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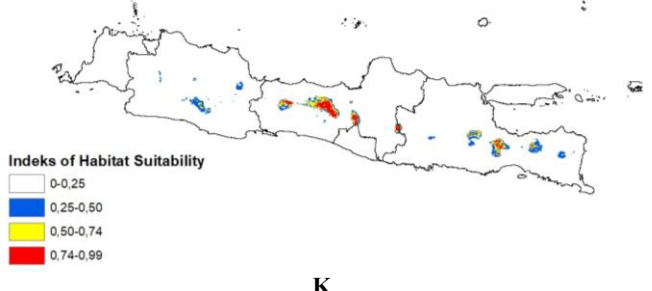
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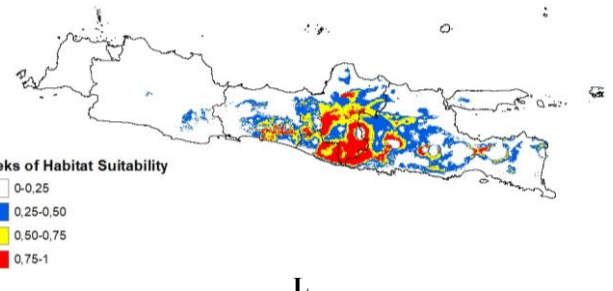
I



J



K



L

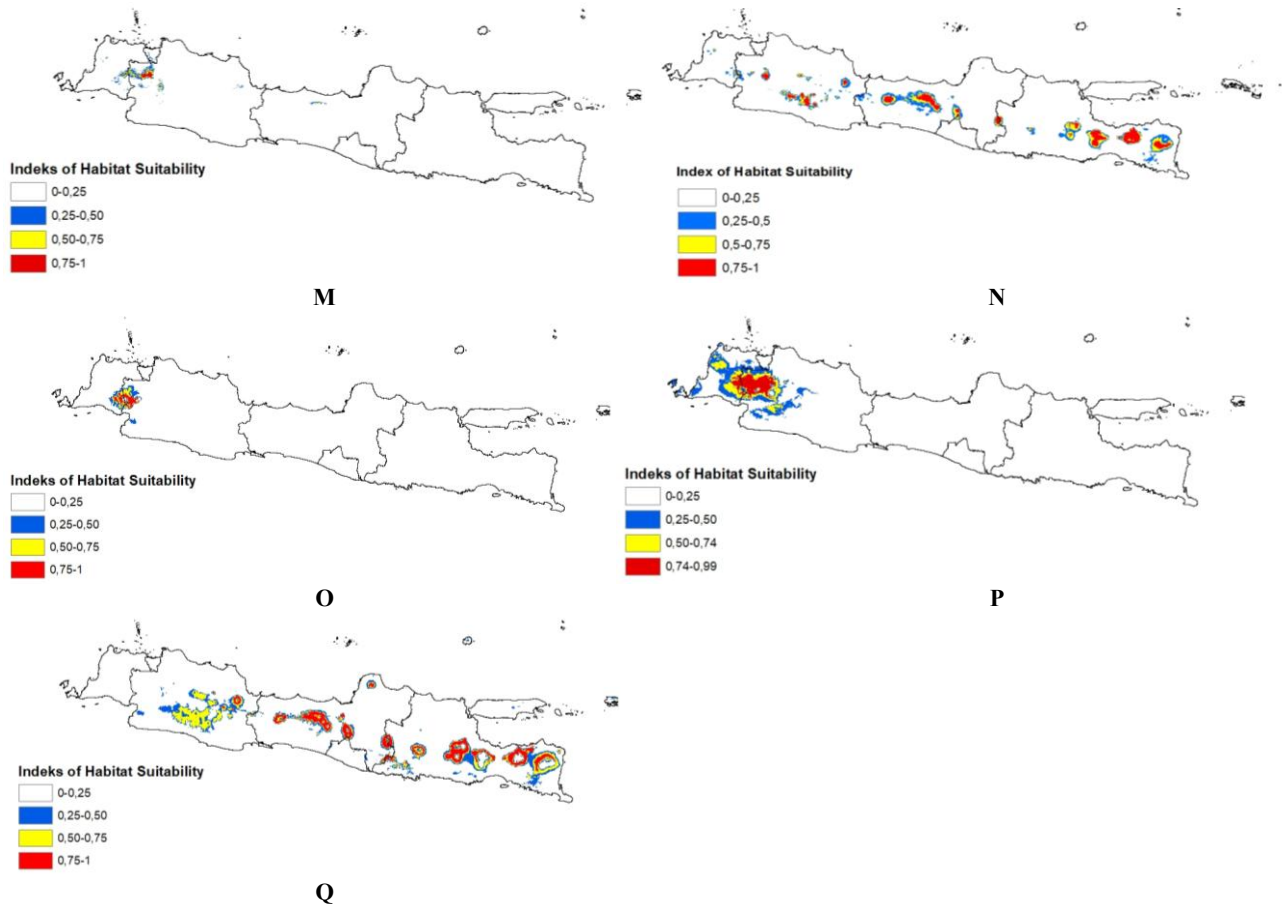


Figure S1. Predicted current habitat suitability maps of genus *Selaginella* and selected *Selaginella* species in Java, Indonesia, generated using the MaxEnt model. A. Genus *Selaginella*, B. *S. alutacea*, C. *S. aristata*, D. *S. biformis*, E. *S. ciliaris*, F. *S. intermedia*, G. *S. involvens*, H. *S. opaca*, I. *S. ornata*, J. *S. plana*, K. *S. remotifolia*, L. *S. repanda*, M. *S. rothertii*, N. *S. singalanensis*, O. *S. subalpina*, P. *S. willdenowii*, Q. *S. zollingeriana*. Only species represented by at least 12 occurrence records were modeled individually. BA: Banten, JA: Jakarta, WJ: West Java, CJ: Central Java, YO: Yogyakarta, EJ: East Java