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Predicting the effects of future climate change on the distribution of the genus *Selaginella* in Java, Indonesia

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Abstract. *Setyawan AD, Sutarno, Sugiyarto, Sunarto, Nugroho GD, Supriatna J, Sulton MN. 2026. Predicting the effects of future climate change on the distribution of the genus* Selaginella *in Java, Indonesia. Asian J For 10 (1): r100134. https://doi.org/10.13057/asianjfor/r100134.* Ongoing climate change poses significant threats to ecosystems and species by altering environmental conditions beyond historical norms. Climatic factors strongly influence the distribution of plant species. *Selaginella* is a fern ally that relies on water for fertilization, making it potentially sensitive to climatic changes. This study assessed the current and future climatic suitability of *Selaginella* using the Maximum Entropy (MaxEnt) model based on 1,962 occurrence records in Java, Indonesia, and selected bioclimatic, topographic, edaphic, and ultraviolet radiation variables. Model performance was excellent, with a training AUC of 0.934 ± 0.006 and a test AUC of 0.921 ± 0.011. The most influential predictors were precipitation of the driest month (31.6%), elevation (27.6%), and mean temperature of the warmest quarter (12.7%), together accounting for 71.9% of total model contribution. Current climatically suitable habitat covered approximately 63,865 km^2, concentrated primarily in humid montane regions of West, Central, and East Java. Future projections were generated for three time periods (2030, 2050, and 2080) under four climate scenarios (RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5). Stable habitats remained dominant across all scenarios, while centroid analyses revealed a general eastward and northeastern shift of suitable habitat. These results suggest that climate change is likely to drive geographic redistribution rather than widespread collapse of the collective climatic niche of *Selaginella* in Java. The study highlights the importance of precipitation and elevation in determining habitat suitability and provides a basis for anticipating future conservation challenges associated with climate-driven shifts in species distributions.

Keywords: Gain, genus, habitat, loss, *Selaginella,* species

INTRODUCTION

Climate change is a major driver of ecological change, affecting biodiversity, ecosystem processes, and species distributions across multiple spatial scales. Future climatic shifts are expected to occur at an unprecedented rate and interact with other environmental pressures, including habitat modification, pollution, and land-use change, thereby increasing extinction risks and altering species distributions (Oliver and Morecroft 2014). Because temperature and precipitation strongly influence species performance, survival, and geographic ranges, terrestrial ecosystems are particularly sensitive to climatic change (Chen et al. 2014). Consequently, predicting species responses to future climate conditions has become a central objective of ecological and biogeographical research.

The IPCC projects continued global warming throughout the twenty-first century, accompanied by changes in precipitation regimes and climatic extremes (Masson-Delmotte et al. 2018). In Southeast Asia, temperatures are expected to increase by approximately 1.5-2°C by mid-century and 2-4°C by the end of the century, depending on emission trajectories (Avia 2019). Such changes may substantially alter habitat suitability, ecological interactions, and species persistence, particularly in tropical mountain ecosystems where environmental gradients are pronounced and many species occupy relatively narrow climatic niches.

Java, Indonesia, is one of the most biologically diverse islands in Southeast Asia and contains ecosystems ranging from coastal lowlands to volcanic mountains exceeding 3,000 m above sea level. This environmental heterogeneity creates strong gradients in temperature, precipitation, and humidity that influence species distributions and may shape biological responses to future climate change. Understanding how climatic suitability may change across these gradients is therefore important for anticipating future biodiversity patterns on the island.

Among plant groups potentially affected by climate change, lycophytes are of particular interest because many species are closely associated with humid environments. The genus *Selaginella* P. Beauv. (Selaginellaceae), one of the most diverse lycophyte genera, is widely distributed throughout tropical and subtropical regions and occupies habitats ranging from forest understories and riparian zones to rocky slopes, disturbed habitats, and montane ecosystems. Successful fertilization in *Selaginella* requires the presence of free water, making many species sensitive to changes in moisture availability. Consequently, shifts in temperature and precipitation may influence reproduction, population persistence, dispersal opportunities, and geographic distributions.

Selaginella occupies a wide range of habitats in Java, from lowland forests to montane environments (Setyawan and Darusman 2008). Previous species distribution modeling studies have consistently identified precipitation, temperature, and elevation as major determinants of habitat suitability. Climate change has been projected to cause habitat loss, habitat gain, elevational shifts, and geographic redistribution in *S. involvens* and *S. repanda* (Setyawan et al. 2017), *S. ciliaris* and *S. plana* (Setyawan et al. 2018), *S. ornata*, *S. opaca*, and *S. remotifolia* (Setyawan et al. 2020a), *S. zollingeriana* (Setyawan et al. 2020b), and *S. willdenowii* and *S. intermedia* (Setyawan et al. 2025). These studies provide valuable insights into species-specific responses but do not address broader patterns governing the distribution of the genus as a whole.

Species Distribution Modeling (SDM) provides an effective framework for relating species occurrences to environmental conditions and projecting potential distributions under future climate scenarios. Among available approaches, Maximum Entropy (MaxEnt) is widely used because of its strong predictive performance and ability to utilize presence-only data (Phillips and Dudík 2008). By integrating occurrence records with environmental variables, MaxEnt can identify climatically suitable habitats and estimate potential distributional changes under future climatic conditions.

Most previous climate-based studies of *Selaginella* in Southeast Asia have focused on individual species. While such studies are important for understanding the ecology and vulnerability of particular taxa, they provide limited information on the collective climatic niche occupied by the genus. A genus-level approach can reveal the principal environmental factors associated with the overall distribution of *Selaginella* in Java and complement previous species-specific studies. This perspective may help identify broad conservation priorities and improve understanding of how environmental change affects the distribution of genus diversity across Java.

Therefore, this study evaluated the collective climatic niche of *Selaginella* in Java using pooled occurrence records from 21 species and projected future habitat suitability under alternative climate scenarios. We hypothesized that climate change would promote habitat turnover and geographic redistribution of suitable areas, with precipitation, temperature, and elevation acting as the primary determinants of habitat suitability.

MATERIALS AND METHODS

Study area

This study was conducted on Java and its adjacent islands, Indonesia, which served as the focal region for modeling the current and future climatically suitable habitat of the genus *Selaginella*. Java and its adjacent islands constitute one of the largest and most densely populated regions in Indonesia and comprise six administrative provinces: Banten, Jakarta, West Java, Central Java, Special Region of Yogyakarta, and East Java. The study area covers approximately 129.8 × 10^3 km² and extends from 5°02′55″ to 8°46′49″ S and from 105°05′59″ to 116°16′12″ E (Figure 1).

Java exhibits considerable environmental heterogeneity, ranging from coastal lowlands to volcanic mountain systems exceeding 3,000 m above sea level. These environmental gradients generate substantial variation in temperature, precipitation, and humidity, which influence the distribution of plant species across the island. Indonesia lies within the tropical climatic zone and experiences distinct wet and dry seasons driven by the Asian–Australian monsoon system (Whitten et al. 1996; Aldrian and Susanto 2003). Variations in monsoon intensity and timing affect rainfall patterns, air humidity, and temperature regimes across Java (Sekaranom 2023), making the island an appropriate region for evaluating potential climate-driven changes in the distribution of *Selaginella*.

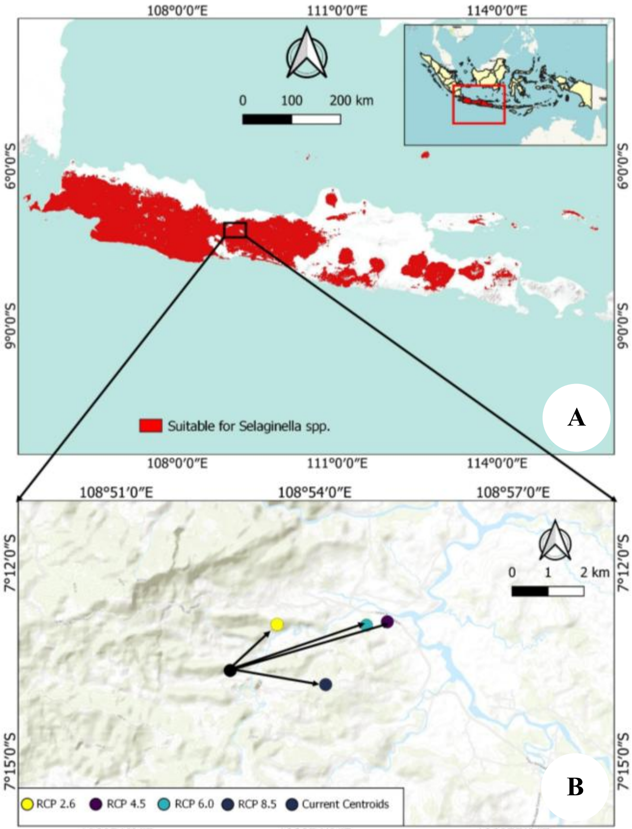

Figure 1. A. Predicted climatically suitable habitat for the genus *Selaginella* under current climatic conditions in Java, Indonesia. B. Projected shifts in the centroid of climatically suitable habitat under four climate scenarios (RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5) for the year 2080.

Procedures

Occurrence data collection

The data used in this study were derived from both primary and secondary sources. Field surveys conducted throughout Java between 2007 and 2021 yielded 1,362 occurrence records from 684 localities. Sampling was undertaken across a wide range of environmental and climatic conditions to maximize geographic and ecological representation while minimizing sampling bias. Collected specimens were identified through comparison with authenticated specimens deposited at Herbarium Bogoriense (BO) and major taxonomic treatments of *Selaginella* from Java and the Lesser Sunda Islands (Alston 1935b), Sumatra (Alston 1937), Celebes and the Moluccas (Alston 1940), Peninsular Malaysia (Wong 1982, 2010), the Philippines (Alston 1935a), Thailand (Tagawa and Iwatsuki 1979), Vietnam (Pham-Hoang 1991), Taiwan (Tsai and Shieh 1994), and China (Zhang et al. 2013b).

Taxonomic nomenclature and synonymy were verified using Plants of the World Online (POWO 2026; https://powo.science.kew.org/), while supplementary occurrence information was consulted through iNaturalist (2026). 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 employed in this study.

Additional occurrence records were obtained from herbarium specimens and biodiversity databases. A total of 600 records representing 309 localities were examined to verify species identity, assess nomenclatural consistency, and complement field observations. Most herbarium records originated from Herbarium Bogoriense (BO; 559 specimens, >90%), while additional specimens from BM, L, CANB, K, P, S, BGBM, and WRSL were accessed through virtual herbarium collections and the Global Biodiversity Information Facility (GBIF). Geographic coordinates were compiled from specimen labels and supplemented, where available, with georeferenced records retrieved from GBIF (GBIF Secretariat 2026). Historical records reported by Alston (1935b) were re-examined whenever supporting specimens or metadata were available, and all coordinates were validated before analysis.

Field and herbarium data collectively documented 21 recognized 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 *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*.

All records were integrated into a unified occurrence database. Taxonomic names were harmonized following POWO, and historical synonyms and orthographic variants were standardized to ensure consistency among data sources. Quality-control procedures included taxonomic verification, nomenclatural standardization, geographic validation, removal of duplicate and geographically inconsistent records, and exclusion of records located outside the terrestrial boundaries of Java. Following these procedures, 1,962 georeferenced occurrence records representing 993 localities were retained as the final verified occurrence dataset.

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). This procedure was intended solely to reduce spatial clustering and did not constitute an additional data-cleaning step. Consequently, the verified dataset of 1,962 records was reduced to 811 occurrence records representing 434 unique localities for MaxEnt modelling. Because the objective of this study was to characterize the collective climatic niche of the genus *Selaginella* rather than individual species, all occurrence records were pooled into a single dataset for subsequent analyses.

Current environmental and bioclimatic variables

Bioclimatic, edaphic, and environmental variables were used to model the potential distribution of the genus *Selaginella* in Java. An initial set of 26 predictor variables, comprising 19 bioclimatic variables, two edaphic variables, and five environmental variables, was screened for multicollinearity. Following correlation analysis, five bioclimatic variables, two edaphic variables, and five environmental variables (12 variables in total) were retained for model development (Table 1).

The bioclimatic dataset was obtained from WorldClim version 2.1 (https://www.worldclim.org/) at a spatial resolution of 30 arc-seconds (approximately 1 km) (Fick and Hijmans 2017). Historical climate layers were used to represent current climatic conditions across Java. Ultraviolet-B radiation variables (UV-B variables; UVB1–UVB4) were obtained from the global UVB dataset (gIUV; https://www.ufz.de/gluv/) (Beckmann et al. 2014), which provides spatially explicit information on biologically relevant UV-B radiation. Edaphic variables consisted of soil organic carbon and soil pH and were obtained from ISRIC World Soil Information (https://data.isric.org/) (Hengl et al. 2017).

Table 1. Environmental variables used to build the model

Code	Name	Unit
30s_elev	Elevation	m a.s.l.
30s_bio_1	Annual Mean Temperature	°C × 10
30s_bio_10	Mean Temperature of Warmest Quarter	°C × 10
30s_bio_14	Precipitation of Driest Month	mm
30s_bio_18	Precipitation of Warmest Quarter	mm
30s_bio_19	Precipitation of Coldest Quarter	mm
soc	Soil Organic Carbon	g kg^{-1}
ph	Soil pH	pH
uvb1	Annual Mean UV-B	J m^{-2} day^{-1}
uvb2	UV-B Seasonality	J m^{-2} day^{-1}
uvb3	Mean UV-B of the Highest Month	J m^{-2} day^{-1}
uvb4	Mean UV-B of Lowest Month	J m^{-2} day^{-1}

All environmental layers were clipped to the extent of Java using ArcMap 10.6. Subsequently, the layers were resampled to a common spatial resolution and converted into ASCII (*.asc*) format prior to model development. To avoid multicollinearity, which can distort model interpretability and overestimate variable importance, we removed correlated predictors before analysis (Yoon and Lee 2021). Variable selection was performed using SDM Toolbox v2.5 in ArcMap 10.6 (Brown 2014). Highly correlated variables were identified using Pearson correlation analysis, and variables with $|r| > 0.90$ were excluded. Following this procedure, five bioclimatic variables (bio1, bio10, bio14, bio18, and bio19), two edaphic variables (soil organic carbon and soil pH), and five environmental variables (elevation and UVB1-UVB4) were retained for subsequent MaxEnt modeling (Table 1).

Future climate scenario

Future climate scenarios were developed using Representative Concentration Pathways (RCPs) to evaluate potential changes in the distribution of the genus *Selaginella* under projected climatic conditions. Future climate data were obtained from the International Center for Tropical Agriculture (CIAT) and the CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS) (https://www.ccafs-climate.org/data_spatial_downscaling/) (Navarro-Racines et al. 2020). The HadGEM2-ES (Hadley Center Global Environment Model 2-Earth System) was selected because it provides complete projections for all four RCP scenarios used in this study (RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5) within the CMIP5 (Coupled Model Intercomparison Project Phase 5) framework (Mohan and Bhaskaran 2019). Although CMIP6-based Shared Socioeconomic Pathway (SSP) scenarios are now available, CMIP5-RCP projections remain widely used in ecological niche modeling and biodiversity assessments. The use of RCP scenarios in the present study facilitates direct comparison with previous climate-change studies on individual *Selaginella* species in Southeast Asia and Indonesia, all of which were developed using the CMIP5 framework. Consequently, the present analysis provides continuity with earlier studies while allowing evaluation of the collective climatic niche of the genus under comparable climatic assumptions.

Future habitat suitability was projected for three time periods representing near-, mid-, and late-century conditions (2030, 2050, and 2080). These projections were used to assess potential changes in the collective climatic niche of the genus *Selaginella* under alternative greenhouse-gas emission trajectories. Only climatic variables were allowed to vary among future scenarios. Elevation, soil organic carbon, soil pH, and UV-B variables (UVB1–UVB4) were held constant because reliable future projections for these variables were unavailable at a spatial resolution comparable to the climate datasets used in this study.

Future climate projections are subject to uncertainties arising from differences in model structure, spatial resolution, parameterization, and numerical schemes (Teutschbein and Seibert 2013). To reduce discrepancies between observed and modeled climatic conditions, bias-correction procedures were applied following Setyawan et al. (2018). The objective of this study was not to generate precise forecasts of future distributions but to evaluate general patterns of habitat redistribution under alternative climate scenarios. Therefore, HadGEM2-ES was used as a representative climate projection framework, and the results should be interpreted as scenario-based estimates rather than absolute predictions.

Model development

MaxEnt version 3.4.4 (Phillips et al. 2006) was used to predict the current distribution of climatically suitable habitat for the genus *Selaginella* and to project future habitat suitability under alternative climate scenarios. MaxEnt is widely used in species distribution modeling because it effectively utilizes presence-only occurrence data and performs well with complex environmental datasets (Phillips and Dudík 2008). The maximum number of iterations was set to 5,000 and the convergence threshold to 1×10^{-6}. Model performance was evaluated using 10-fold cross-validation, in which occurrence records were randomly partitioned into ten subsets; nine subsets were used for model training and one for testing during each iteration. Average values from the ten replicates were used in subsequent analyses.

Habitat redistribution and centroid shifts

To further evaluate changes in the spatial configuration of climatically suitable habitat, we quantified shifts in the geographic centroid of suitable areas under current and future climate conditions. Centroid analysis was used to summarize the overall direction and magnitude of geographic redistribution of suitable habitat for the genus *Selaginella* across Java.

The analysis was conducted using SDM Toolbox, a Python-based GIS extension for ArcGIS (Brown 2014). Binary habitat suitability maps generated from the current and future MaxEnt models were used as inputs. The centroid of each suitable habitat map was calculated by averaging the latitude and longitude coordinates of all suitable pixels, thereby identifying the geographic center of climatically suitable habitat. Comparisons between current and future centroids were subsequently used to quantify the direction and distance of projected habitat redistribution under different climate scenarios.

To facilitate comparison among climate scenarios, centroid shifts were calculated using habitat suitability maps projected for the year 2080, representing the late-century climate period. This approach was adopted because 2080 projections are expected to capture the cumulative effects of long-term climatic change and therefore provide the clearest representation of potential future redistribution patterns of climatically suitable habitat for the genus *Selaginella*.

Data analysis

The primary output of MaxEnt is a habitat suitability map that predicts the potential distribution of climatically suitable habitat across the study area. Suitability values are expressed on a continuous scale ranging from 0 to 1, where higher values indicate greater environmental suitability (Phillips and Dudík 2008). In the present study, these maps represent the collective climatic suitability of the genus *Selaginella* in Java rather than the distribution of individual species.

MaxEnt also provides estimates of the relative contribution of environmental variables to model performance. To further evaluate predictor importance, a jackknife analysis was performed. According to Phillips et al. (2006), the jackknife test identifies variables that contain the greatest amount of unique information and assesses their individual contribution to model performance. Variables producing high training gain when used independently are considered highly informative, whereas variables whose omission substantially reduces model gain contain information that other predictors do not adequately represent.

To quantify changes in habitat distribution under future climate scenarios, continuous habitat suitability maps were converted into binary maps representing suitable and unsuitable habitat. This conversion was performed using the maximum training sensitivity plus specificity threshold criterion. Threshold selection is an important step in species distribution modeling because different threshold values may influence estimates of habitat extent and model interpretation (Phillips and Dudík 2008). The selected threshold was chosen to balance omission and commission errors while minimizing overprediction of suitable habitat.

Model performance was evaluated using the Area Under the Receiver Operating Characteristic Curve (AUC), which is widely used to assess the discriminatory ability of species distribution models. AUC values range from 0 to 1, where values close to 1 indicate strong predictive performance and values near 0.5 indicate predictions no better than random expectation. Following commonly accepted criteria, AUC values below 0.7 were considered to indicate low model performance, values between 0.7 and 0.9 indicated good discrimination, and values greater than 0.9 indicated excellent model performance (Padalia et al. 2014).

RESULTS AND DISCUSSION

Contribution of the variables and model evaluation

Based on pooled occurrence records representing 21 *Selaginella* species in Java and a set of climatic, topographic, edaphic, and UV-B variables (UVB1–UVB4), we developed habitat suitability models to predict the potential distribution of the genus *Selaginella* across Java. The resulting model represents the collective climatic niche of the genus rather than species-specific ecological responses. Model performance was excellent, with a mean training AUC of 0.934 ± 0.006 and a mean test AUC of 0.921 ± 0.011, indicating strong discriminatory ability between suitable and unsuitable environmental conditions. The relatively small standard deviations of training and test AUC values among cross-validation replicates indicate consistent model performance and limited variability in predictive accuracy across model runs.

The relative contributions of environmental variables are presented in Table 2. Precipitation of the Driest Month (30s_bio_14) was the most influential predictor (31.6%), followed by Altitude (30s_elev; 27.6%) and Mean Temperature of the Warmest Quarter (30s_bio_10; 12.7%). Together, these variables accounted for 71.9% of total model contribution, indicating that habitat suitability was primarily associated with moisture availability, temperature, and elevation. In contrast, UV-B variables (UVB1–UVB4) contributed relatively little to model performance (<6% each), suggesting that broad-scale habitat suitability is governed more strongly by moisture and temperature than by variation in solar radiation.

To further evaluate predictor importance, a jackknife analysis was performed (Figure 2). Mean Temperature of the Warmest Quarter (30s_bio_10) produced the highest training gain when used alone, indicating that it contained the greatest amount of unique information for predicting habitat suitability (Phillips et al. 2006). Conversely, omission of Mean Temperature of the Warmest Quarter (30s_bio_10), Precipitation of the Warmest Quarter (30s_bio_18), Annual Mean Temperature (30s_bio_1), and Precipitation of the Driest Month (30s_bio_14) resulted in the largest reductions in model gain. These results highlight the dominant role of temperature and precipitation variables in shaping the distribution of climatically suitable habitat for the genus *Selaginella* in Java.

Predicted distribution of current potential habitat

We compiled 1,962 occurrence records of *Selaginella* from field surveys and herbarium data across Java. Following taxonomic verification, data cleaning, and spatial filtering, 811 occurrence records representing 434 unique localities were retained and used to characterize the collective climatic niche of the genus. The predicted present-day distribution of suitable habitat derived from MaxEnt (Phillips and Dudík 2008) indicated that approximately 49.19% of Java (63,865.17 km^2) provides suitable habitat for the genus *Selaginella* (Figure 1A). Under current climatic conditions, suitable habitat was distributed across all provinces of Java, including Banten, Jakarta, West Java, Central Java, Yogyakarta, and East Java. Of the total predicted suitable habitat area, approximately 11.25% (7,184.34 km^2) occurred in Banten Province, 0.12% (77.12 km^2) in Jakarta, 43.68% (27,901.04 km^2) in West Java, 27.76% (17,731.42 km^2) in Central Java, 1.33% (848.32 km^2) in Yogyakarta, and 15.86% (10,128.17 km^2) in East Java.

Suitable habitat was distributed patchily across much of Java. Large areas of suitable habitat were predicted in the central and southern parts of Banten, West Java, Central Java, and Yogyakarta. In northern Central Java, suitable habitat was concentrated around Karimunjawa, Mount Muria, and the Kendeng Mountains. In East Java, suitable habitat was widely distributed in the southern region of Pacitan and throughout several mountainous landscapes, including Mount Lawu, Mount Kelud, Mount Kawi, Mount Liman, Mount Arjuna, Mount Semeru, Mount Argopura, and Mount Raung. Additional suitable habitat was predicted on Madura Island and several surrounding islands, including Kangean and Sapudi, indicating that climatically favorable conditions for the genus extend beyond the main island of Java.

Potential future changes in the distribution of suitable habitat

Projected habitat suitability maps revealed substantial redistribution of climatically suitable areas for the genus *Selaginella* under future climate scenarios (Table 3; Figure 3). Although the balance between habitat loss and habitat gain varied among RCP scenarios and projection periods, gross habitat turnover was generally high while net changes in total suitable habitat area remained small. Across most scenarios, habitat losses were largely compensated by gains in newly suitable areas, indicating spatial reorganization of suitable habitat rather than major changes in overall habitat extent.

Under the RCP 2.6 scenario, suitable habitat area increased by approximately 3.95% in 2030, representing the largest habitat gain among all future projections. Habitat expansion was concentrated in northern Banten and West Java, the border region between West and Central Java, southern Central Java and Yogyakarta, central and eastern East Java, and the eastern half of Madura Island. During subsequent periods, habitat losses slightly exceeded gains, resulting in modest net reductions in suitable habitat area. Habitat losses were concentrated in the border region between West and Central Java in 2050 and in mountainous areas of East Java in 2080.

Under RCP 4.5, the largest gross habitat losses were projected, ranging from 1.75% to 5.39% of the current suitable habitat area. However, these losses were largely offset by habitat gains (1.21-4.97%), resulting in relatively small net reductions in total suitable habitat area. Habitat loss was projected in several regions of Banten Province, the Menoreh Mountains of Central Java, the Sewu Mountains and slopes of Mount Merapi in Yogyakarta, and the slopes of Mount Semeru, Mount Kawi, and Mount Arjuna in East Java.

Under RCP 6.0, habitat losses ranged from 1.38% to 1.96% of the current suitable habitat area and were accompanied by habitat gains of 0.82-1.43%, resulting in only minor net changes in total suitable habitat area. Habitat losses were consistently concentrated in Banten Province, the Menoreh Mountains of Central Java, and the Sewu Mountains of Yogyakarta throughout all projection periods.

Under RCP 8.5, habitat losses reached 2.89%, 4.42%, and 2.09% of the current suitable habitat area in 2030, 2050, and 2080, respectively, while habitat gains ranged from 1.56% to 3.97%. Consequently, net reductions in suitable habitat area remained limited despite substantial habitat turnover. Newly suitable habitats emerged in several regions across Java, whereas habitat losses were concentrated in localized areas. The projections indicate that future climate change will primarily redistribute suitable habitat across Java while maintaining a relatively stable total extent of climatically suitable habitat.

Habitat redistribution and centroid shifts

Habitat redistribution and centroid shifts were evaluated across Java and its adjacent islands under current and future climate scenarios. Under current climatic conditions, approximately 49.19% (63,865.17 km²) of the study area was predicted to provide climatically suitable habitat for the genus *Selaginella*. Future climate scenarios suggest that suitable habitat will undergo spatial redistribution across the region, although changes in total suitable habitat area are generally projected to be modest (Table 3). This redistribution is expected to alter the geographic center of habitat suitability while maintaining a broadly similar overall extent of suitable habitat.

The centroid of the currently suitable habitat for the genus *Selaginella* was located at 108.878722°E and 7.226917°S in Brebes District, Central Java (Figure 1B). Under future climate scenarios, the centroid was projected to shift to 108.890597°E and 7.215392°S under RCP 2.6, 108.918436°E and 7.214652°S under RCP 4.5, 108.913024°E and 7.215509°S under RCP 6.0, and 108.902823°E and 7.230537°S under RCP 8.5, indicating continued redistribution of climatically suitable habitat across Java.

Table 2. Percentage of variable contribution to the final model

Variables	Description	Contribution (%)
30s_elev	Altitude	27.6
30s_bio_1	Annual Mean Temperature	1.7
30s_bio_10	Mean Temperature of Warmest Quarter	12.7
30s_bio_14	Precipitation of Driest Month	31.6
30s_bio_18	Precipitation of Warmest Quarter	7.5
30s_bio_19	Precipitation of Coldest Quarter	1.8
soc	Soil Organic Carbon	1.5
ph	Soil pH	2.8
uvb1	Annual Mean UVB	2.3
uvb2	UVB Seasonality	4.6
uvb3	Mean UVB of Lightest Month	0.4
uvb4	Mean UVB of Lowest Month	5.5

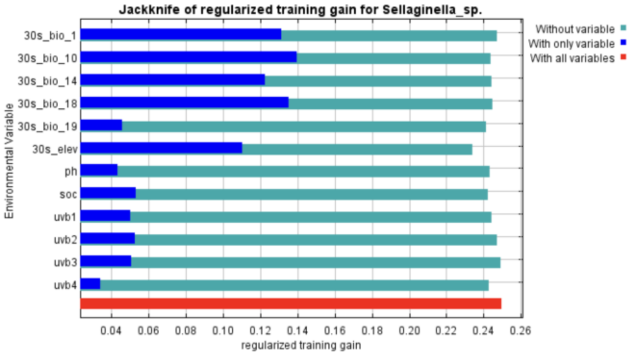

Figure 2. Results of the jackknife test of relative importance of predictor variables for genus *Selaginella*

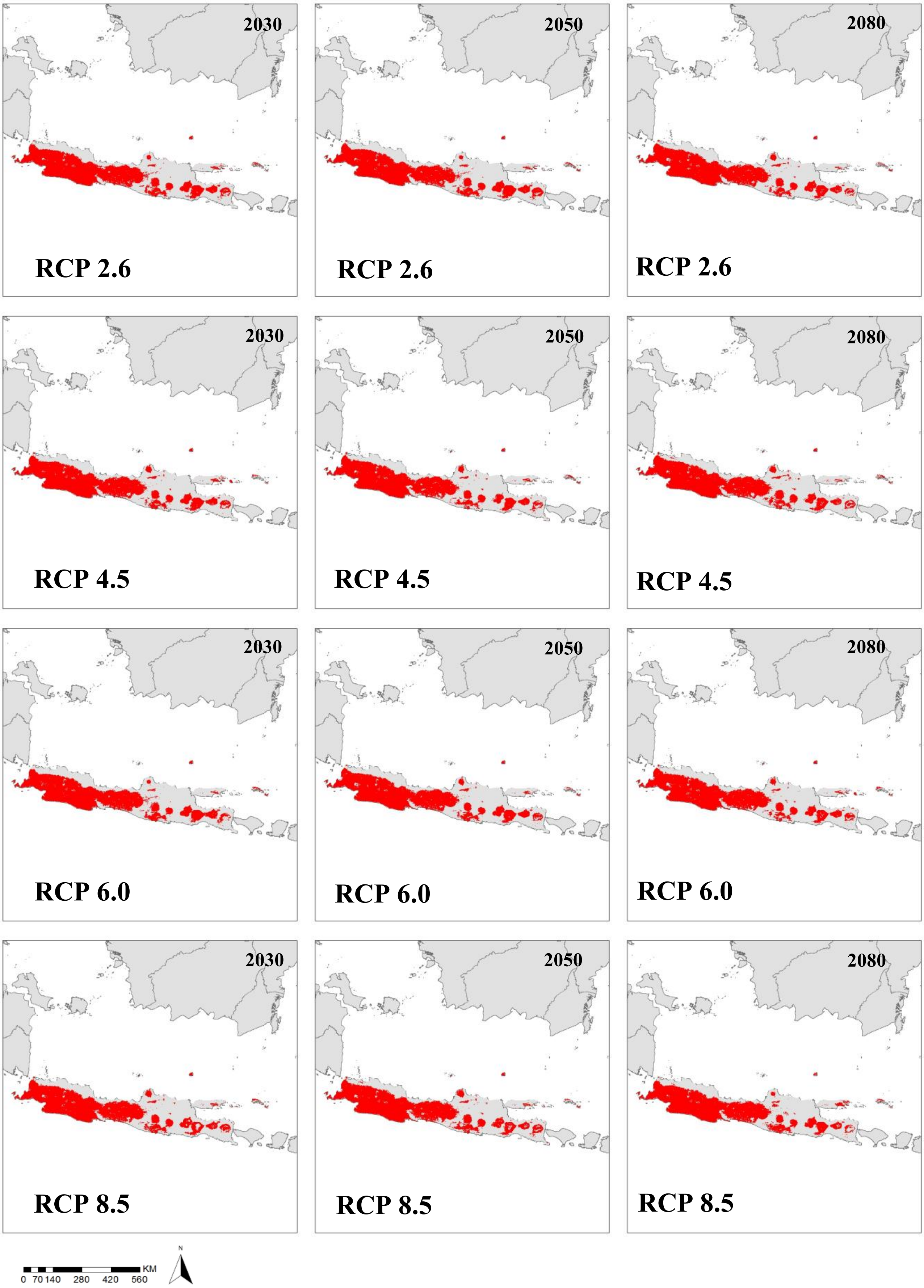

Figure 3. Predicted distribution of climatically suitable habitat for the genus *Selaginella* in Java, Indonesia, under current and future climate scenarios. Red indicates suitable habitat and gray indicates unsuitable habitat

Table 3. Dynamics of suitable habitat area changes for genus *Selaginella* in Java and its adjacent islands, Indonesia, under four future climate scenarios and three projection periods

Year	RCP projection	Genus *Selaginella* (Area × 10^3 km^2)			
		Loss	Gain	Net change	Future suitable area
2030	2.6	0.850 (-1.33%)	2.520 (3.95%)	+1.670	65.535
	4.5	2.260 (-3.54%)	1.880 (2.94%)	-0.380	63.485
	6.0	0.910 (-1.43%)	0.530 (0.83%)	-0.380	63.485
	8.5	1.900 (-2.98%)	1.530 (2.40%)	-0.370	63.495
2050	2.6	1.970 (-3.08%)	1.590 (2.49%)	-0.380	63.485
	4.5	1.150 (-1.80%)	0.770 (1.21%)	-0.380	63.485
	6.0	1.300 (-2.04%)	0.910 (1.43%)	-0.390	63.475
	8.5	2.910 (-4.56%)	2.530 (3.96%)	-0.380	63.485
2080	2.6	1.040 (-1.63%)	0.660 (1.03%)	-0.380	63.485
	4.5	3.550 (-5.56%)	3.170 (4.96%)	-0.380	63.485
	6.0	0.900 (-1.41%)	0.530 (0.83%)	-0.370	63.495
	8.5	1.380 (-2.16%)	1.000 (1.57%)	-0.380	63.485

Note: Current suitable habitat area = 63.865 × 10^3 km^2 (49.19% of the study area). Loss and gain represent gross habitat turnover relative to the current suitable habitat area. Net change was calculated as gain minus loss. The future suitable area was calculated as the current suitable habitat area plus the net change. Negative values indicate net contraction of suitable habitat, whereas positive values indicate net expansion.

The projected centroid displacement was approximately 1.80 km under RCP 2.6, 4.58 km under RCP 4.5, 4.00 km under RCP 6.0, and 2.68 km under RCP 8.5. Overall, centroid displacement ranged from 1.80 to 4.58 km and was predominantly eastward. RCP 2.6, RCP 4.5, and RCP 6.0 exhibited slight northeastward shifts, whereas RCP 8.5 showed a weak southeastward component (Figure 1B). The largest displacement was projected under RCP 4.5, whereas the smallest occurred under RCP 2.6. Despite these shifts, the magnitude of centroid movement remained relatively small, indicating spatial redistribution of suitable habitat rather than major displacement of the collective climatic niche of the genus in Java.

The relatively small magnitude of centroid displacement despite measurable habitat turnover likely reflects the spatially distributed nature of habitat gain and loss across Java. Newly suitable areas emerged in multiple regions, while habitat losses occurred elsewhere, producing compensatory spatial changes that largely balanced one another. Consequently, substantial gross habitat turnover can occur without causing major shifts in the overall geographic center of climatically suitable habitat. These results suggest that future climate change is more likely to reorganize the spatial configuration of suitable habitats within Java than to drive large-scale directional migration of the collective climatic niche of Selaginella.

Discussion

Climate change and the collective climatic niche of Selaginella

The present study was designed to evaluate climate-related changes in the collective distribution of the genus *Selaginella* rather than species-specific responses. Consequently, the resulting projections should be interpreted as changes in the overall climatic suitability of Java for the genus as a whole. Individual species may respond differently because of differences in ecological preferences, geographic distributions, and climatic tolerances.

Recent climate change has been shown to influence the distribution of numerous plant species worldwide (Agnihotri et al. 2017; Evans and Brown 2017). Although substantial progress has been made in understanding climate-driven distributional changes in vascular plants, comparatively fewer studies have focused on lycophytes and other cryptogamic plant groups (Cornelissen et al. 2007). Because successful growth and reproduction in *Selaginella* are closely associated with environmental moisture availability, changes in precipitation and temperature regimes are expected to influence habitat suitability across its distribution range. Evaluating future habitat suitability of Selaginella may help identify moisture-sensitive plant groups that are vulnerable to climatic change in tropical ecosystems.

Pooling occurrence records from all 21 species enabled characterization of the climatic envelope occupied by *Selaginella* in Java. Rather than predicting the response of individual taxa, the model identifies areas that are climatically suitable for maintaining the overall diversity of *Selaginella* under current and future environmental conditions.

Current distribution patterns of Selaginella *in Java*

The genus *Selaginella* is the most species-rich extant lycophyte, comprising more than 750 species worldwide (Schmidt et al. 2020). Members of the genus occupy a wide range of habitats, including tropical rainforests, montane ecosystems, open habitats, and occasionally seasonally dry environments (Wong 2010; Weststrand and Korall 2016). This ecological breadth enables the genus to occupy diverse environmental conditions and contributes to its broad distribution across Java.

A total of 21 *Selaginella* species have been recorded from Java (Setyawan 2014; Setyawan et al. 2013, 2015a, b, c, 2016). Most species are native to the island, whereas *S. uncinata* and *S. kraussiana* are introduced species originating from East Asia and Africa, respectively. Several species, including *S. zollingeriana*, *S. rothertii*, *S.*

subalpina, and *S. subspinulosa*, have relatively restricted distributions and may therefore be more vulnerable to environmental change.

The model predicted climatically suitable habitats throughout Banten, Jakarta, West Java, Central Java, Yogyakarta, and East Java. Suitable areas were concentrated mainly in humid regions associated with mountain systems, including Mount Muria, the Kendeng Mountains, Mount Lawu, Mount Kelud, Mount Arjuna, Mount Semeru, Mount Argopura, and Mount Raung. This distribution pattern is consistent with the strong influence of moisture-related environmental variables identified in the MaxEnt model and reflects the ecological dependence of many *Selaginella* species on humid microclimatic conditions. The concentration of suitable habitat in these regions further supports the importance of precipitation and temperature as major determinants of the genus distribution in Java.

Environmental determinants of habitat suitability

The modeling results indicate that precipitation, temperature, and elevation are the primary determinants of habitat suitability for the genus *Selaginella* in Java. Precipitation of the Driest Month (bio14), elevation, Mean Temperature of the Warmest Quarter (bio10), and Precipitation of the Warmest Quarter (bio18) were the most influential predictors. Water availability is particularly important because successful fertilization in *Selaginella* depends on the presence of free water, making precipitation a key factor influencing growth, reproduction, and habitat persistence. The high contribution of precipitation-related variables highlights the importance of moisture availability in determining the collective climatic niche of the genus. Similar relationships have been reported for *Selaginella* and other lycophytes in humid environments, including China and Southeast Asia, where precipitation-related variables consistently rank among the most important predictors of habitat suitability and future distributional change (Ruszala et al. 2011; Zhang et al. 2013a; Setyawan et al. 2017, 2018, 2020a, b, 2021).

Elevation and temperature also contributed strongly to model performance. Elevation integrates multiple environmental factors, including temperature, humidity, cloud formation, and precipitation, thereby creating gradients that influence habitat suitability across mountain landscapes. Temperature directly affects physiological processes such as photosynthesis, respiration, and water balance in *Selaginella* (Jagels 1970; Eickmeier 1986). Previous studies have similarly identified elevation, rainfall, and temperature as major determinants of *Selaginella* distributions and future habitat shifts in Southeast Asia and Indonesia (Setyawan et al. 2017, 2018, 2020a, b, 2021). Comparable climate-driven responses have also been documented in the Himalayas and Neotropical forests, where moisture and temperature strongly influence the distribution of mountain plants and lycophytes (Agnihotri et al. 2017; Campany et al. 2019). Collectively, the results suggest that moisture, temperature, and elevation are the main factors influencing the distribution of *Selaginella* in Java.

Projected redistribution of suitable habitat under future climate change

The projections indicate that future climate change will alter the spatial distribution of climatically suitable habitat for the genus *Selaginella* across Java. Rather than causing extensive habitat loss, future climatic conditions are projected to promote habitat turnover and geographic redistribution of suitable areas. Under RCP 2.6, suitable habitat expanded during the early projection period, particularly in 2030, whereas most subsequent scenarios showed habitat losses slightly exceeding gains. Nevertheless, gross habitat losses were largely compensated by newly suitable areas, resulting in relatively small net changes in total suitable habitat extent. The largest gross habitat loss was projected under RCP 4.5 in 2080. The results suggest that future climate change is more likely to reorganize the spatial distribution of suitable habitats than to substantially reduce their overall extent. Similar patterns have been reported for several *Selaginella* species, including *S. ciliaris*, *S. plana* (Setyawan et al. 2018), *S. involvens*, *S. repanda* (Setyawan et al. 2017), and *S. zollingeriana* (Setyawan et al. 2021), as well as montane species in Java (Setyawan et al. 2020a, b).

Projected centroid shifts further support the occurrence of habitat redistribution. Centroid displacement ranged from 1.80 to 4.58 km and was predominantly eastward, indicating modest geographic reorganization of suitable environments. Similar redistribution patterns have been reported for *S. zollingeriana* and several montane *Selaginella* species, where future climate change altered the spatial configuration of suitable habitats without causing complete habitat loss (Setyawan et al. 2020a, b, 2021).

Future climate projections for Java indicate increasing temperatures and spatially heterogeneous changes in precipitation (IPCC 2014). Because *Selaginella* depends strongly on moisture availability, projected warming and altered rainfall regimes may reduce suitability in some areas while creating favorable conditions elsewhere. Consequently, future distributional changes are likely to reflect habitat redistribution rather than widespread contraction of the collective climatic niche. Similar climate-driven redistribution patterns have been documented in many terrestrial plant groups worldwide (Parmesan 2006).

The projected redistribution of suitable habitat should be considered in future conservation planning. Areas that remain suitable under both current and future climate scenarios may function as climatic refugia, particularly in humid montane and submontane environments. Conversely, areas showing repeated habitat loss across multiple scenarios may become increasingly vulnerable to climatic change. Because future changes are driven primarily by habitat redistribution, conservation efforts should emphasize habitat connectivity and the protection of environmentally heterogeneous landscapes across elevational gradients, thereby facilitating species persistence and range adjustment under changing climatic conditions (Corlett and Westcott 2013).

Limitations and implications for future research

Several factors may contribute to discrepancies between predicted and realized distributions, including microclimatic variation not captured by available datasets, limitations in environmental data resolution, and anthropogenic habitat modification such as deforestation and land conversion. In addition, the pooled occurrence dataset used to characterize the collective climatic niche of *Selaginella* may not fully represent ecological differences among individual species, particularly those with restricted distributions or specialized habitat requirements. Additional uncertainty arises from the use of a single Global Climate Model (HadGEM2-ES) and CMIP5-based climate projections. Although newer CMIP6-based Shared Socioeconomic Pathway (SSP) scenarios are now available, CMIP5-RCP projections remain widely used in ecological niche modeling and facilitate direct comparison with previous studies of individual *Selaginella* species in Southeast Asia and Indonesia. Consequently, the projected distributions should be interpreted as scenario-based estimates rather than precise forecasts.

Future studies could improve projection robustness by incorporating higher-resolution environmental and microclimatic data, species interactions, dispersal constraints, land-use change, multiple Global Climate Models, and CMIP6-based climate scenarios. Species-specific models may also provide additional insights into variation among taxa in their responses to climate change. Despite these limitations, the study establishes a reference point for future assessments of climate-related distributional change in *Selaginella* across Java and offers a framework for future conservation planning.

In conclusion, future climate change is projected to alter the spatial distribution of climatically suitable habitat for the genus *Selaginella* across Java. The MaxEnt model showed high predictive performance (training AUC = 0.934 ± 0.006; test AUC = 0.921 ± 0.011), with habitat suitability primarily influenced by precipitation of the driest month, elevation, and mean temperature of the warmest quarter. Although habitat losses were projected under most future climate scenarios, these were largely compensated by gains in newly suitable areas, resulting in relatively small net changes in total suitable habitat extent. The results suggest that future climate change will mainly alter the spatial arrangement of suitable habitats rather than substantially reduce their overall extent. Conservation efforts should therefore prioritize habitat connectivity and the protection of environmentally heterogeneous humid landscapes across elevational gradients. Future studies incorporating multiple climate models, species-specific analyses, and land-use dynamics may further improve predictions of climate-driven distributional change.

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