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Climate-induced habitat contraction and elevational redistribution of *Selaginella willdenowii* and *S. intermedia* in Southeast Asia

AHMAD DWI SETYAWAN[1,♥], SUTARNO[2], SUGIYARTO[2], SUNARTO[1], ILYAS NURSAMSI[3], SUGENG BUDIHARTA[4], JATNA SUPRIATNA[5], PRAKASH PRADHAN[6]

[1]Department of Environmental Science, Faculty of Mathematics and Natural Sciences, Universitas Sebelas Maret. Jl. Ir. Sutami 36A, Surakarta 57126, Central Java, Indonesia. Tel./fax.: +62-271-663375, ♥email: volatileoils@gmail.com
[2]Department of Biology, Faculty of Mathematics and Natural Sciences, Universitas Sebelas Maret. Jl. Ir. Sutami 36A, Surakarta 57126, Central Java, Indonesia
[3]School of Earth and Environmental Science, Faculty of Science, The University of Queensland. St Lucia 4072, Brisbane, Queensland, Australia
[4]Purwodadi Botanic Gardens, Indonesian Institute of Sciences. Jl. Raya Surabaya-Malang Km. 65, Purwodadi, Pasuruan 67163, East Java, Indonesia
[5]Program of Conservation Biology, Department of Biology, Faculty of Mathematics and Natural Sciences, Universitas Indonesia. Kampus UI, Pondok Cina, Depok 16424, West Java, Indonesia
[6]West Bengal Biodiversity Board, Department of Environment, Government of West Bengal. Salt Lake, Sector-III, FD415A, Poura Bhawan, 4th Floor, Kolkata 700106, West Bengal, India

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Abstract. *Setyawan AD, Sutarno, Sugiyarto, Sunarto, Nursamsi I, Budiharta S, Supriatna J, Pradhan P. 2025. Climate-induced habitat contraction and elevational redistribution of* Selaginella willdenowii *and* S. intermedia *in Southeast Asia. Asian J For 9: 440-455.* Climate change is increasingly recognized as a major threat to tropical biodiversity, particularly for moisture-dependent cryptogams with narrow environmental requirements. This study assessed the current and future habitat suitability of *Selaginella willdenowii* and *Selaginella intermedia* across Southeast Asia using Maximum Entropy (MaxEnt) modeling. A total of 726 occurrence records for *S. willdenowii* and 679 records for *S. intermedia* were compiled from field surveys conducted across Java Island, Indonesia and verified records obtained from the Global Biodiversity Information Facility (GBIF). Models were developed using climatic, edaphic, topographic, and UV-B radiation variables and projected under four Representative Concentration Pathway (RCP) scenarios (RCP 2.6, 4.5, 6.0, and 8.5) for 2030, 2050, and 2080. The models showed high predictive performance, with AUC values exceeding 0.93 and TSS values exceeding 0.87. Annual precipitation, temperature, elevation, and UV-B radiation were identified as the most influential predictors of habitat suitability. Current suitable habitats were concentrated in mainland and maritime Southeast Asia, particularly in Indonesia, Peninsular Malaysia, and the Philippines. Java Island emerged as a major regional hotspot, supporting 57.7% and 48.9% suitable habitat coverage for *S. willdenowii* and *S. intermedia*, respectively. Future projections consistently indicated habitat contraction under all climate scenarios, with greater losses occurring under higher emission pathways and later projection periods. By 2080, suitable habitat was projected to decline by 16.9-23.4% for *S. willdenowii* and 27.3-33.2% for *S. intermedia* accompanied by pronounced upslope redistribution toward montane environments. The greater habitat loss predicted for *S. intermedia* reflects its stronger dependence on elevational gradients and narrower climatic niche. These findings identify montane landscapes as critical climate refugia and emphasize the importance of maintaining elevational connectivity to support the long-term persistence of tropical understory cryptogams under climate change.

Keywords: Climate change, elevational shift, MaxEnt, species distribution modeling, tropical lycophytes

INTRODUCTION

Selaginella willdenowii (Desv.) Bak. and *Selaginella intermedia* (Bl.) Spring. are lycophytes belonging to the family Selaginellaceae. Both species have long been used as traditional medicines and edible plants in Indonesia and other parts of Southeast Asia (Setyawan 2009). *Selaginella willdenowii* contains phenolic compounds, flavonoids, and other antioxidant constituents and is traditionally used to treat wounds, fever, gastric disorders, urinary tract infections, menstrual pain, and skin diseases (Setyawan 2009). *Selaginella intermedia* is used for stomach disorders and asthma, and its medicinal properties have been associated with tannins and flavonoids exhibiting antioxidant activity (Winter and Jansen 2003). These uses underscore the ecological, cultural, and ethnobotanical significance of *Selaginella* species throughout Southeast Asia.

Both species commonly occur in forests, agroforests, and shaded gardens, particularly in humid habitats such as forest floors, stream banks, and waterfall surroundings characterized by low light intensity and high humidity (Sartika et al. 2021). Their dependence on moist and thermally stable environments suggests high sensitivity to climatic change. In addition to habitat degradation caused by deforestation, agricultural expansion, logging, and infrastructure development, future changes in temperature and precipitation may substantially affect their habitat suitability and long-term persistence.

Climate change is widely recognized as a major driver of biodiversity loss worldwide (Beckage et al. 2008). Rising temperatures and altered precipitation regimes are expected to modify environmental conditions that determine species distributions, leading to habitat contraction, distributional shifts, population declines, and elevated extinction risk (Thomas et al. 2004; Thuiller et al. 2008; IPCC 2014). These impacts may be particularly severe for species with narrow environmental requirements and limited tolerance to climatic variability.

Southeast Asia is considered one of the regions most vulnerable to climate change because of its exceptional biodiversity, extensive tropical ecosystems, and strong dependence on natural resources (Loo et al. 2015). The region is characterized by monsoonal climatic systems that regulate rainfall seasonality and ecosystem productivity. Projected increases in temperature and changes in precipitation regimes are expected to affect ecological processes throughout the region and may result in habitat contraction, distributional shifts, altered phenology, and reduced reproductive success in many plant species (Thuiller et al. 2008; Brummitt and Bachman 2010).

Understanding species responses to climate change has therefore become a major priority in biodiversity conservation. Ecological Niche Modeling (ENM), also known as Species Distribution Modeling (SDM), is widely used to evaluate potential responses to environmental change by relating species occurrences to environmental predictors (Guisan and Thuiller 2005; Elith and Leathwick 2009). Among available approaches, Maximum Entropy (MaxEnt) is one of the most widely applied methods because of its strong predictive performance with presence-only data and its ability to project species distributions under future climate scenarios (Phillips et al. 2006; Merow et al. 2013).

Despite growing interest in climate-change impacts on biodiversity, cryptogams remain underrepresented in regional-scale vulnerability assessments. This gap is particularly evident in tropical Asia, where studies of *Selaginella* have focused primarily on taxonomy, ecology, distribution, and ethnobotanical uses, whereas assessments of future habitat vulnerability remain scarce. Consequently, little is known about how climate change may affect the distribution and habitat availability of *S. willdenowii* and *S. intermedia* across Southeast Asia.

Given the strong dependence of both species on humid and thermally stable environments, we hypothesized that climate change will reduce the extent of climatically suitable habitats and drive an upward redistribution of suitable areas toward higher elevations. We further hypothesized that *S. intermedia* would experience greater habitat contraction than *S. willdenowii* because of its stronger association with montane environments and narrower elevational niche. Accordingly, this study addressed three questions: (i) Which environmental variables most strongly determine the current distribution of both species? (ii) How will habitat suitability change under alternative climate scenarios through 2080? and (iii) To what extent will climate change alter the elevational distribution and potential refugial habitats of these species across Southeast Asia and Java Island?

This study aimed to model the climatically suitable habitats of *S. willdenowii* and *S. intermedia* across Southeast Asia under future climate scenarios. Using MaxEnt, we evaluated habitat suitability based on species occurrence records and climatic, edaphic, topographic, and UV-B radiation variables. Future projections were generated under four Representative Concentration Pathway (RCP) scenarios for 2030, 2050, and 2080. Particular attention was given to Java Island, an important habitat center for both species and the primary source of field-occurrence data used in model development. By quantifying habitat contraction and elevational redistribution under projected climate conditions, this study provides a regional assessment of climate-related vulnerability in two ecologically and ethnobotanically important *Selaginella* species.

MATERIALS AND METHODS

Study area

Southeast Asia as the regional study area

The study was conducted across Southeast Asia (SEA), extending from approximately 23.5°N to 10°S latitude and 97°E to 141°E longitude, covering about 4,687,481 km² of land area. Southeast Asia comprises eleven countries and is commonly divided into mainland Southeast Asia (Cambodia, Laos, Myanmar, Peninsular Malaysia, Thailand, and Vietnam) and maritime Southeast Asia (Indonesia, the Philippines, Malaysian Borneo, Brunei Darussalam, Singapore, and Timor-Leste) (United Nations Statistics Division 2015). China geographically bounds the region to the north, India to the west, New Guinea to the east, and Australia to the south.

The climate of Southeast Asia is predominantly humid tropical and strongly influenced by monsoonal circulation, resulting in distinct wet and dry seasons and considerable spatial variation in precipitation (Aldrian and Susanto 2003). Most areas experience high temperatures and humidity throughout the year, whereas subtropical climatic conditions occur only in limited high-elevation regions of northern Vietnam and the Myanmar Himalayas (NIC 2009). Southeast Asia has experienced substantial climatic changes over the past century, with average annual surface temperatures increasing by approximately 0.5-1.1°C between 1901 and 2005 (NIC 2009). Climate projections further indicate continued warming and increasing climatic variability throughout the twenty-first century (IPCC 2014).

Java Island as a focal assessment region

Although the analysis was conducted at the Southeast Asian scale, Java Island received particular attention because it contributed the majority of primary occurrence records used in model development and represents one of the most environmentally heterogeneous regions within the study area. Java contains strong elevational gradients, diverse forest ecosystems, and a wide range of climatic conditions that support the occurrence of numerous *Selaginella* populations. Furthermore, the island has experienced extensive land-use change and habitat fragmentation, making it an important region for evaluating potential climate-related changes in habitat suitability. Consequently, a separate assessment of current and future habitat suitability was conducted for Java Island to provide a finer-scale interpretation of habitat contraction and elevational redistribution patterns (Figure 1).

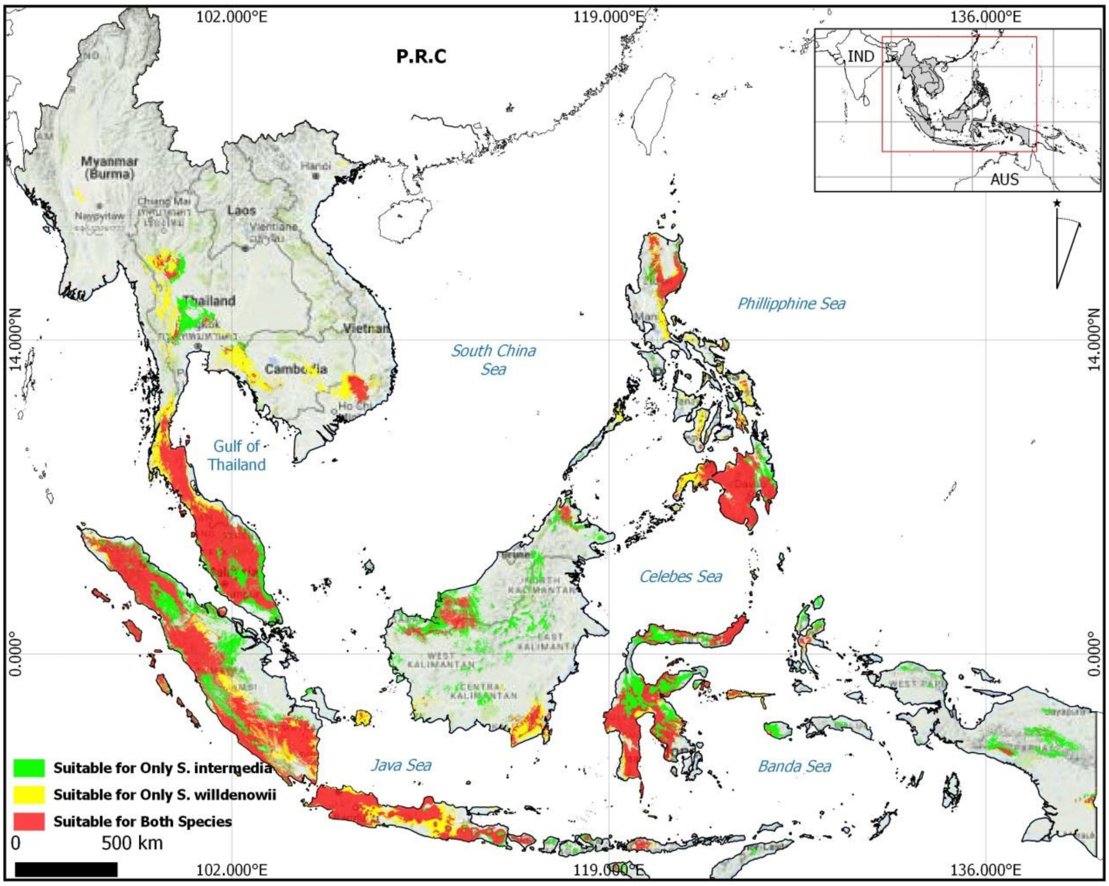


Figure 1. Current predicted distribution of suitable habitats for *Selaginella willdenowii* and *S. intermedia* across Southeast Asia, highlighting Java Island, Indonesia, as a focal assessment region. Basemap source: Google Physical Maps (2014)

Species occurrence data

Field surveys in Java Island

Occurrence records of *Selaginella willdenowii* and *S. intermedia* were obtained from two complementary sources. The primary dataset was derived from field surveys conducted throughout Java Island between 2007 and 2014. During these surveys, species identification was performed using 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). Species identification and distributional information were further supported by previous investigations conducted in Banten (Setyawan 2015a), West Java (Harli 2013), Central Java (Panjaitan 2013), Yogyakarta (Setyawan et al. 2015a), southern West Java (Setyawan 2015b), southern Central Java (Setyawan 2012; Setyawan et al. 2016), Mount Merapi (Setyawan et al. 2012), Mount Lawu (Setyawan et al. 2013), Bromo Tengger Semeru National Park (Setyawan and Sugiyarto 2015), the Dieng Plateau (Setyawan et al. 2015c), and the Sewu Karst region (Setyawan et al. 2015b).

Field sampling was designed to encompass a broad range of environmental conditions across western, central, and eastern Java in order to capture the climatic variability of the island and reduce potential geographic sampling bias. A total of 205 occurrence records of *S. willdenowii* and 161 occurrence records of *S. intermedia* were obtained from field observations. Geographic coordinates were recorded using Global Positioning System (GPS) devices, and no additional coordinate correction was applied because the expected telemetry error was considered negligible relative to the spatial resolution used for modeling (Montgomery et al. 2011).

Occurrence records from GBIF

Additional occurrence records were obtained from the Global Biodiversity Information Facility (GBIF 2024; http://www.gbif.org). All downloaded records were carefully examined to identify potential geographic and taxonomic inconsistencies. Coordinate errors were verified and corrected using Google Earth Pro, whereas records lacking geographic coordinates were georeferenced using Biogeomancer Workbench based on the locality descriptions provided for each specimen. Records with ambiguous or insufficient locality information that could not be reliably georeferenced were excluded from subsequent analyses. The GBIF dataset contributed 521 occurrence records of *S. willdenowii* and 518 occurrence records of *S. intermedia*. These records were subsequently combined with the field-survey dataset, resulting in an initial database of 726 occurrence records for *S.*

willdenowii and 679 occurrence records for *S. intermedia* across Southeast Asia. To reduce spatial sampling bias and spatial autocorrelation, occurrence records were subsequently filtered using a minimum nearest-neighbor distance of 5 km. After spatial filtering, 560 unique occurrence records of *S. willdenowii* and 498 occurrence records of *S. intermedia* were retained for model development and subsequent analyses.

Spatial filtering and sampling bias correction

Occurrence datasets are often affected by spatial sampling bias because records tend to be concentrated in accessible or frequently surveyed locations, potentially influencing model predictions and ecological interpretation (Fourcade et al. 2013). To reduce these effects, two bias-correction procedures were implemented. First, spatial filtering was applied using a 5-km thinning distance, retaining a single occurrence record within each neighborhood to reduce spatial clustering while preserving geographic representation. This procedure was performed in QGIS version 2.18.16 (QGIS Development Team 2017).

Second, a bias file was incorporated into MaxEnt to account for uneven sampling intensity. Because survey-effort data were unavailable, a Gaussian kernel density surface was generated from occurrence locations using SDMToolbox in ArcGIS and rescaled from 1 to 20 following Fourcade et al. (2014). The resulting bias layer was used to guide background-point selection and reduce the influence of spatially uneven sampling effort (Elith et al. 2010; Phillips et al. 2017). Model calibration and projection were restricted to the Southeast Asian region using political boundaries obtained from the Global Administrative Areas (GADM) database (www.gadm.org)

Environmental variables

Environmental variables were selected based on their potential influence on *Selaginella* distribution reported in previous studies (Mod et al. 2016; Setyawan et al. 2016, 2017). Initially, 26 predictors were compiled, including 19 bioclimatic variables, two edaphic variables (soil pH and soil organic carbon), elevation, and four UV-B radiation variables. Bioclimatic variables and elevation data were obtained from WorldClim version 2.0 (Fick and Hijmans 2017), soil variables from the International Center for Tropical Agriculture (CIAT), and UV-B radiation variables (UVB1-UVB4) from the glUV database (Beckmann et al. 2014). All environmental layers were resampled, clipped to the study area, and standardized using QGIS version 2.18.14 (QGIS Development Team 2017).

To reduce multicollinearity and improve model interpretability, pairwise correlations among predictors were evaluated using Spearman's rank correlation coefficient. Variables with correlation coefficients greater than 0.95 were excluded following Bedia et al. (2013). Correlation analysis and variable selection were performed using SDM Toolbox version 2.0 (Brown 2014) within ArcGIS version 10.3. Following the variable-selection procedure, 13 environmental predictors were retained for model development, comprising six bioclimatic variables (bio_1, bio_2, bio_3, bio_4, bio_12, and bio_19), two edaphic variables (soil_carbon and soil_ph), altitude (Alt), and four UV-B radiation variables (UVB1–UVB4). These variables were subsequently used as predictors in all MaxEnt models (Table 1).

Future climate scenarios

Future climate projections were used to evaluate the potential effects of climate change on the distribution of climatically suitable habitats for *Selaginella willdenowii* and *S. intermedia*. Climate data were obtained from the CGIAR Research Program on Climate Change, Agriculture, and Food Security (CCAFS) database and were based on the HadGEM2-CC Global Climate Model developed by the Hadley Center, United Kingdom (Collins et al. 2011). This model participated in the Coupled Model Intercomparison Project Phase 5 (CMIP5) and was among the most widely used climate datasets available when the analyses were conducted.

Future habitat suitability was projected under four Representative Concentration Pathway (RCP) scenarios (RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5) for three time-horizons: 2030, 2050, and 2080 (Moss et al. 2010; Riahi et al. 2011). Because future projections were unavailable for soil pH, soil organic carbon, UV-B radiation variables (UVB1–UVB4), and elevation, these predictors were assumed to remain constant across all scenarios, while climatic variables were allowed to vary.

Table 1. Environmental variables used in MaxEnt modeling

Code	Name	Unit	Source
Alt	Altitude	m asl	WorldClim v2.0
bio_1	Annual mean temperature	°C×10	WorldClim v2.0
bio_2	Mean diurnal range	°C×10	WorldClim v2.0
bio_3	Isothermality	×100	WorldClim v2.0
bio_4	Temperature seasonality	×100	WorldClim v2.0
bio_12	Annual precipitation	mm	WorldClim v2.0
bio_19	Precipitation of coldest quarter	mm	WorldClim v2.0
soil_carbon	Soil organic carbon	$g\ kg^{-1}$	CIAT
soil_ph	Soil pH	pH	CIAT
UVB1	Annual mean UV-B	$J\ m^{-2}\ day^{-1}$	glUV
UVB2	UV-B seasonality	$J\ m^{-2}\ day^{-1}$	glUV
UVB3	Mean UV-B of highest month	$J\ m^{-2}\ day^{-1}$	glUV
UVB4	Mean UV-B of lowest month	$J\ m^{-2}\ day^{-1}$	glUV

To reduce uncertainties associated with Global Climate Models, bias-corrected climate datasets provided by CGIAR-CCAFS were used. These datasets incorporate Bias Correction, Change Factor, and Quantile Mapping procedures to improve agreement between projected and observed climate conditions (Thrasher et al. 2012). The resulting climate layers were subsequently incorporated into MaxEnt to estimate future habitat suitability, quantify habitat contraction, and evaluate elevational redistribution of *S. willdenowii* and *S. intermedia* across Southeast Asia under alternative climate scenarios.

Species distribution modeling

Species distribution models were developed using MaxEnt version 3.4.1 (Phillips et al. 2017), a machine-learning algorithm widely used for ecological niche modeling based on presence-only occurrence data and environmental predictors (Phillips and Dudík 2008; Merow et al. 2013). MaxEnt was selected because of its strong predictive performance and suitability for assessing climate-driven changes in species distributions (Johnston et al. 2012; Duan et al. 2016).

Model settings were adjusted to improve predictive performance and reduce overfitting. Maximum iterations were set to 5,000, the convergence threshold to 1×10^{-6}, and model performance was evaluated using ten-fold cross-validation, in which 90% of occurrence records were used for model training and 10% for testing in each replicate. Final predictions were generated from the average of ten replicated runs.

Only hinge features were enabled to produce smoother response curves and improve model interpretability, while the regularization multiplier was doubled from the default value to accommodate the broad geographic extent of occurrence records and improve transferability to future climate scenarios (Merow et al. 2013; Radosavljevic and Anderson 2014). Current models were subsequently projected onto future climate scenarios using the MaxEnt projection function to evaluate habitat contraction, persistence, and elevational redistribution of *S. willdenowii* and *S. intermedia* under climate change (Van der Wal et al. 2009).

Model evaluation and data analysis

Model outputs were generated in logistic format, producing habitat suitability values ranging from 0 to 1 for each grid cell. To facilitate quantitative comparisons, continuous suitability maps were converted into binary suitable–unsuitable habitat classes using the "maximum training sensitivity plus specificity" threshold, which provides a balanced compromise between omission and commission errors and is appropriate for widespread species (Liu et al. 2016).

Binary habitat maps were used to quantify current and future habitat extent, habitat contraction, and persistence under different climate scenarios. Spatial analyses, area calculations, and map production were conducted using QGIS version 2.18.16 (QGIS Development Team 2017). The relative contribution of environmental variables was extracted from MaxEnt outputs, and predictor importance was further evaluated using jackknife analysis to identify variables with the greatest independent explanatory power (Phillips et al. 2009) (Table 2; Figure 2). Elevational distributions of suitable habitats were also quantified under current and future climates to assess potential upslope shifts and habitat redistribution (Table 3; Figures 5 and 8).

Model performance was evaluated using the Area Under the Receiver Operating Characteristic Curve (AUC) and the True Skill Statistic (TSS). AUC assesses the discriminatory ability of the model (Araújo et al. 2005), whereas TSS provides a prevalence-independent measure of agreement between observed and predicted distributions (Allouche et al. 2006). Both metrics were used to assess the predictive performance and reliability of the final MaxEnt models.

RESULTS AND DISCUSSION

Environmental drivers and model performance

Following spatial filtering, 560 unique occurrence records of *Selaginella willdenowii* (77.1% of the original dataset) and 498 records of *S. intermedia* (73.3% of the original dataset). These data were retained for model construction and evaluation.

MaxEnt models identified climatic and radiation-related variables as the primary determinants of habitat suitability for both species, although the most influential predictors differed between them (Table 2). For *S. willdenowii*, annual precipitation (22.3%), annual mean UV-B radiation (17.1%), and annual mean temperature (16.8%) collectively explained 56.2% of the model contribution. In contrast, *S. intermedia* was mainly influenced by altitude (32.9%), annual precipitation (15.0%), and UV-B seasonality (11.3%), accounting for 59.2% of total contribution and indicating a stronger dependence on elevational gradients. Jackknife analysis showed that UV-B seasonality (UVB2) contained the greatest independent information for both species, whereas mean diurnal temperature range (bio_2) contributed the most unique information when omitted (Figure 2). Model performance was excellent, with AUC values of 0.948 for *S. willdenowii* and 0.936 for *S. intermedia*, and TSS values of 0.89 and 0.87, respectively, confirming the reliability of the models for predicting current and future habitat suitability.

Environmental response of Selaginella willdenowii

Response curves indicated that annual precipitation, annual mean UV-B radiation, and annual mean temperature were the most influential environmental predictors of habitat suitability for *S. willdenowii* (Figure 3). Habitat suitability was highest in areas receiving approximately 3,100-4,200 mm of annual rainfall, with annual mean UV-B radiation ranging from 4,700 to 4,800 J m^{-2} day^{-1} and annual mean temperatures between 23°C and 27°C (Figures 3.A-C). These results suggest that *S. willdenowii* is strongly associated with humid, moderately warm tropical environments and exhibits a relatively narrow tolerance to variation in both temperature and UV-B radiation.

Table 2. Relative contribution (%) of environmental variables to the MaxEnt models for *Selaginella willdenowii* and *S. intermedia*

Variables	Description	Contribution (%)	
		S. *willdenowii*	**S. *intermedia***
Alt	Altitude	1.5	32.9
bio_1	Annual mean temperature	16.8	7.3
bio_2	Mean diurnal range	12.2	5.1
bio_3	Isothermality	4.1	5.6
bio_4	Temperature seasonality	2.9	4.7
bio_12	Annual precipitation	22.3	15
bio_19	Precipitation of coldest quarter	7.5	1.0
soil_carbon	Soil organic carbon	1.4	0.4
soil_ph	Soil pH	3.9	5.4
UVB1	Annual mean UV-B	17.1	0.8
UVB2	UV-B Seasonality	9.6	11.3
UVB3	Mean UV-B of lightest month	0.6	3.5
UVB4	Mean UV-B of lowest month	0.1	7.0

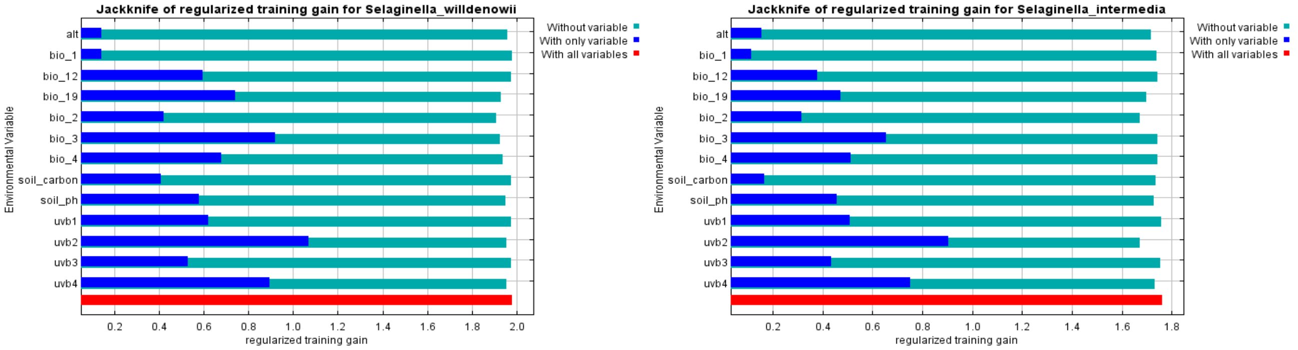


Figure 2. Jackknife test of environmental variable importance for *Selaginella willdenowii* and *S. intermedia*

Environmental response of Selaginella intermedia

The response curves indicated that altitude, annual precipitation, and UV-B seasonality were the most influential predictors of habitat suitability for *S. intermedia* (Figure 4). Habitat suitability was highest at elevations of approximately 700-1,500 m asl, in areas receiving 3,000-4,000 mm of annual rainfall, and under UV-B seasonality values ranging from 0.45×10^5 to 0.65×10^5 J m^{-2} day^{-1} (Figures 4.A-C). These results indicate that *S. intermedia* is primarily associated with humid submontane and lower montane environments and may be sensitive to variations in both hydroclimatic conditions and seasonal UV-B radiation.

Current habitat suitability across Southeast Asia

Regional distribution of suitable habitat

Using 560 occurrence records of *Selaginella willdenowii* and 498 records of *S. intermedia*, the MaxEnt models predicted extensive suitable habitats across Southeast Asia (Figure 1). Suitable habitat for *S. willdenowii* covered approximately 982,246 km² (21% of the regional land area) and was distributed from 100 to 3,233 m asl, with major concentrations in southern Thailand, Peninsular Malaysia, Sumatra, Java, Sulawesi, and the southern Philippines. For *S. intermedia*, suitable habitat covered approximately 1,068,808 km² (22% of the regional land area) and occurred between 700 and 2,994 m asl. Its distribution was broadly similar but extended more widely across southern Peninsular Malaysia and included additional suitable areas in Borneo and Papua.

Altitudinal distribution of suitable habitat

A separate analysis revealed distinct elevational preferences between the two species (Figure 5). Suitable habitats of *S. willdenowii* were concentrated between 400 and 2,200 m asl, accounting for 87.9% of the total suitable area, indicating a strong association with low- to mid-elevation humid environments. In contrast, *S. intermedia* exhibited a narrower and higher elevational distribution, with 85.9% of suitable habitat occurring between 800 and 1,600 m asl and a greater proportion extending above 1,600 m asl. These results indicate that *S. intermedia* is more strongly associated with submontane and montane environments, providing an important baseline for evaluating future climate-driven elevational shifts.

Current habitat suitability in Java Island

Distribution of suitable habitat in Java Island

Java Island emerged as a major center of habitat suitability for both *Selaginella* species in Southeast Asia due to its high environmental heterogeneity and extensive occurrence records. Suitable habitat for *S. willdenowii* was widely distributed across the island, particularly in mountainous and upland areas from western to eastern Java (Figure 1). A similar pattern was observed for *S. intermedia*, although its distribution was more strongly associated with upland and montane environments, reflecting the greater influence of elevation on habitat suitability. Despite these differences, both species exhibited substantial overlap in suitable habitats, especially within the major mountain systems of western, central, and eastern Java.

Relative habitat availability in Java Island

The model predicted that 57.7% of Java Island (77,370.1 km²) provides suitable habitat for *S. willdenowii*, while 48.9% (65,508.6 km²) is suitable for *S. intermedia*. These proportions are substantially higher than those predicted across Southeast Asia as a whole, highlighting Java as a major regional stronghold for both species. The extensive habitat availability, high environmental heterogeneity, and importance of Java as a source of occurrence records further emphasize its value as a focal region for assessing future climate-induced habitat contraction and elevational redistribution.

Future habitat contraction across Southeast Asia

Changes in suitable habitat under future climate scenarios

Future climate projections consistently predicted habitat contraction for both *Selaginella willdenowii* and *S. intermedia* across Southeast Asia (Figure 6), with losses increasing through time and under higher emission scenarios. By 2030, habitat reductions ranged from 2.2-7.5% for *S. willdenowii* and 6.2-12.3% for *S. intermedia*. Habitat loss became more pronounced by 2050, particularly under RCP 8.5, with declines of approximately 14% and 24%, respectively. The greatest reductions were projected for 2080, reaching 16.9-23.4% for *S. willdenowii* and 27.3-33.2% for *S. intermedia*. Major habitat losses were concentrated in southern Cambodia, Thailand, Java, Sulawesi, and Papua. Across all scenarios, *S. intermedia* consistently experienced greater habitat contraction than *S. willdenowii*, indicating higher vulnerability to future climate change. The results suggest a progressive reduction in climatically suitable habitats throughout Southeast Asia under continued warming.

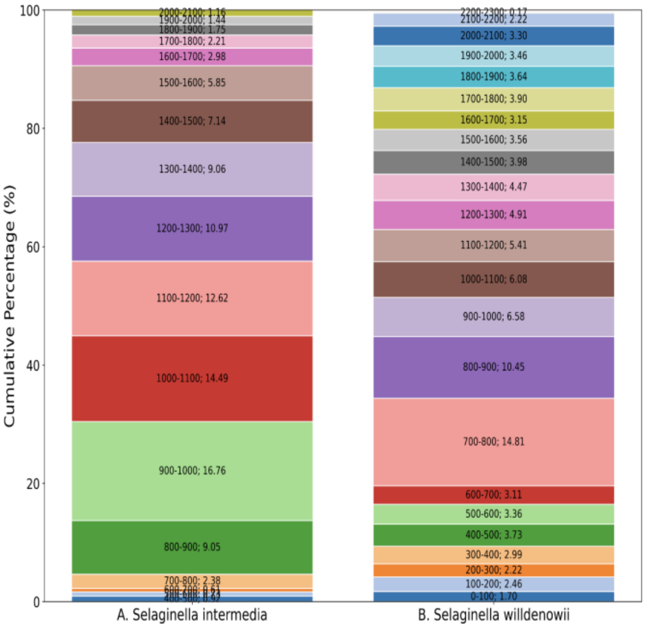


Figure 5. Current elevational distribution of suitable habitat for *Selaginella willdenowii* and *S. intermedia* across Southeast Asia. Values indicate the proportion of suitable habitat occurring within each elevational band

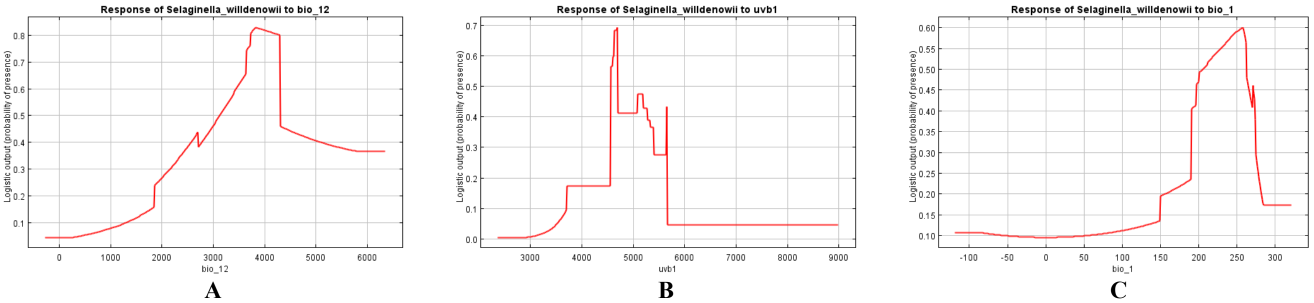


Figure 3. Response curves of the three most influential environmental variables affecting habitat suitability of *Selaginella willdenowii*: A. Annual precipitation (bio_12), B. Annual mean UV-B radiation (UVB1), and C. Annual mean temperature (bio_1)

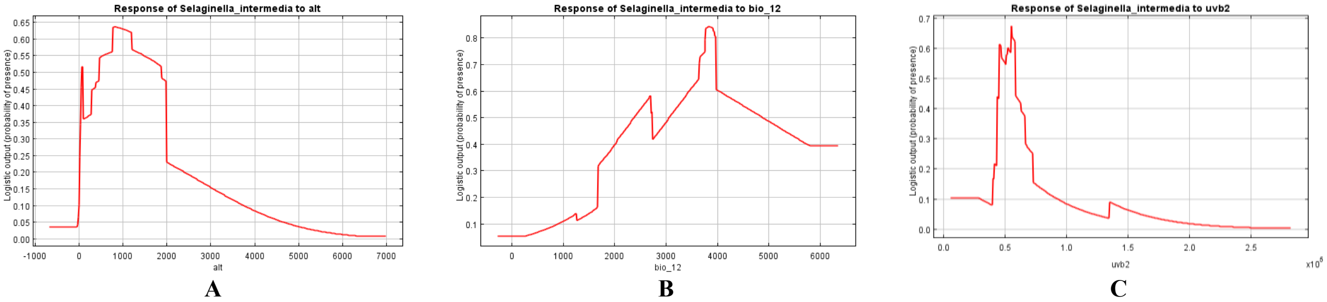


Figure 4. Response curves of the three most influential environmental variables affecting habitat suitability of *Selaginella intermedia*: A. Altitude, B. Annual precipitation (bio_12), and C. UV-B seasonality (UVB2)

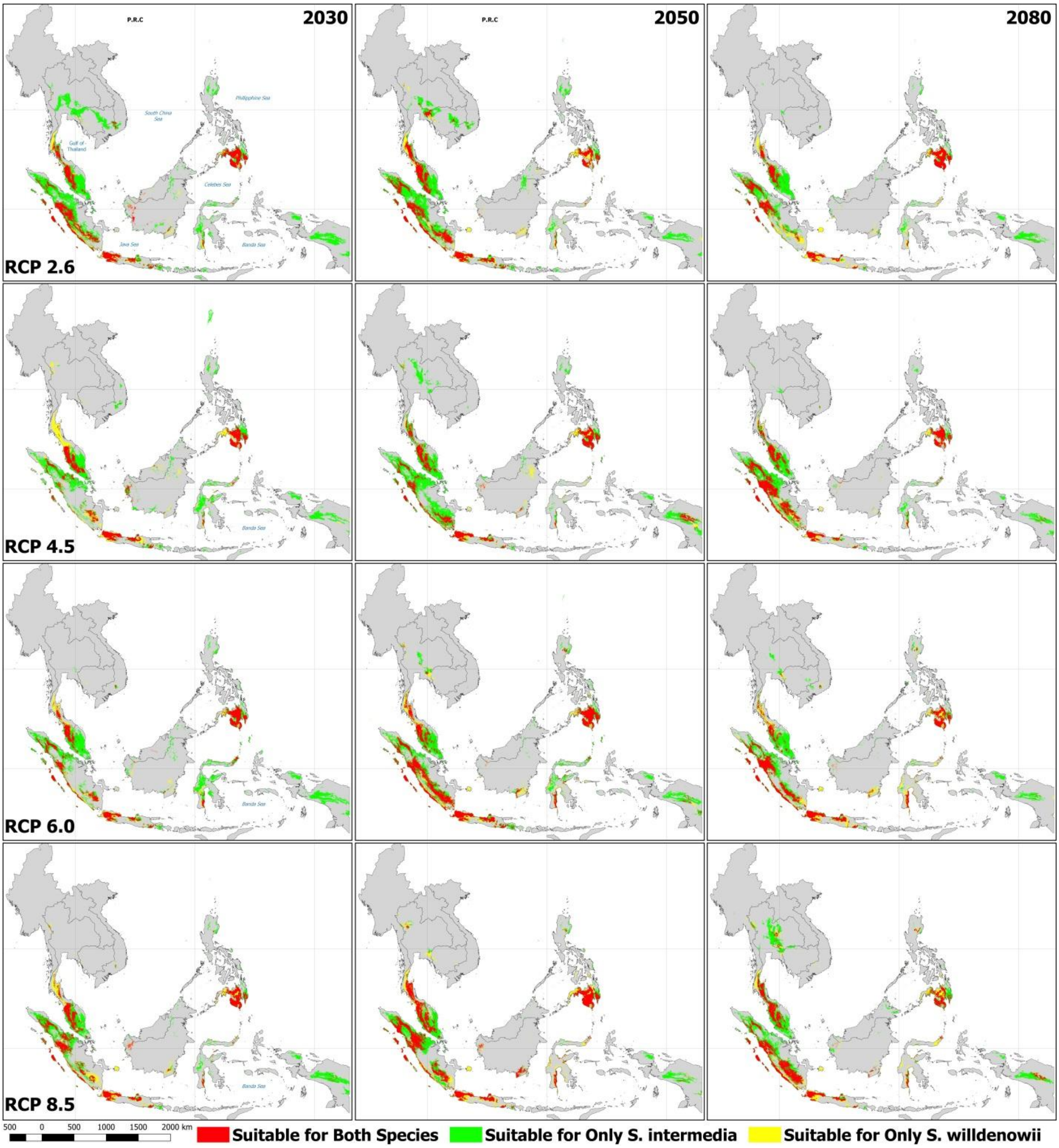


Figure 6. Projected distribution of suitable habitats for *Selaginella willdenowii* and *S. intermedia* across Southeast Asia under four Representative Concentration Pathway (RCP) scenarios (2.6, 4.5, 6.0, and 8.5) for 2030, 2050, and 2080. Colors indicate areas suitable for both species, only *S. willdenowii*, or only *S. intermedia*

Future habitat contraction in Java Island

Habitat loss under RCP 2.6-8.5 scenarios

Future climate projections indicated progressive habitat loss for both *S. willdenowii* and *S. intermedia* in Java Island under all emission scenarios, with reductions increasing through time and under higher greenhouse-gas trajectories. By 2080, suitable habitat for *S. willdenowii* was projected to decline by 15.6%, 16.3%, 17.9%, and 21.6% under RCP 2.6, 4.5, 6.0, and 8.5, respectively. Corresponding habitat losses for *S. intermedia* were greater, reaching 20.0%, 22.9%, 25.4%, and 27.2%. These results indicate that climate change is likely to substantially reduce habitat availability across Java Island, with *S. intermedia* consistently exhibiting higher vulnerability than *S. willdenowii*.

Comparison between Selaginella willdenowii and S. intermedia

Across all climate scenarios, *S. intermedia* consistently exhibited greater habitat losses than *S. willdenowii*, indicating higher vulnerability to future climate change (Figure 7). This difference likely reflects the broader environmental tolerance of *S. willdenowii* and the more restricted elevational niche of *S. intermedia*. Despite these differences, both species showed a similar pattern of progressive habitat contraction under future warming. These findings highlight Java Island as an important region for monitoring climate-driven habitat changes and developing conservation strategies for climate-sensitive forest understory cryptogams.

Elevational redistribution under climate change

Elevational shifts in Southeast Asia

Future climate projections indicated that both *S. willdenowii* and *S. intermedia* will experience upslope redistribution of suitable habitats across Southeast Asia (Table 3; Figure 8). Suitable habitats at lower elevations progressively declined, whereas those at higher elevations increased under all climate scenarios. For *S. willdenowii*, habitat suitability shifted from low- and mid-elevation zones toward higher elevations, while *S. intermedia* exhibited a more pronounced upward shift from its current core distribution of 800-1,600 m asl. This trend became stronger over time and under higher-emission scenarios, resulting in suitable habitats becoming increasingly concentrated within mountain systems and upland regions throughout Southeast Asia.

Elevational shifts in Java Island

Java Island exhibited a clear pattern of climate-driven elevational redistribution, with suitable habitats for both species shifting toward higher elevations under future climate scenarios (Figure 8). For *S. willdenowii*, habitat losses occurred mainly at low and mid elevations, while montane areas remained relatively suitable, suggesting a potential refugial role of mountain ecosystems. The shift was more pronounced in *S. intermedia*, which experienced greater habitat losses at lower elevations and increasing restriction to higher-altitude environments. Under the RCP 8.5 scenario, suitable habitats for both species became concentrated in the highest mountain systems of Java, indicating that future persistence may depend heavily on the availability and connectivity of montane habitats. Despite this upslope redistribution, the overall extent of suitable habitat is projected to decline substantially.

Discussion

Climatic determinants of Selaginella *distribution*

The results indicate that climatic variables are the primary determinants of habitat suitability for *S. willdenowii* and *S. intermedia* across Southeast Asia. Precipitation, temperature, altitude, and UV-B radiation accounted for most of the variation in habitat suitability (Table 2; Figures 2-4), reflecting the strong association of *Selaginella* species with humid environments, shaded understory habitats, and stable microclimatic conditions. Similar patterns have been reported for many lycophytes and ferns, whose distributions are strongly regulated by hydrothermal conditions because adequate moisture is essential for growth, reproduction, and physiological functioning (Kessler et al. 2011; Testo and Sundue 2016). Consequently, even modest changes in temperature and precipitation can alter habitat suitability and distribution patterns (Setyawan et al. 2017). The high predictive performance of the MaxEnt models (AUC > 0.93; TSS > 0.87) indicates that these environmental variables effectively captured the major ecological gradients influencing both species. The projected habitat contractions under all future climate scenarios further suggest that both species occupy relatively narrow climatic niches and may be particularly vulnerable to future environmental change across Southeast Asia.

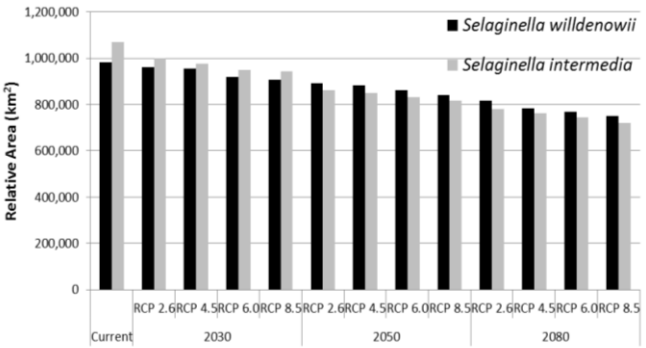
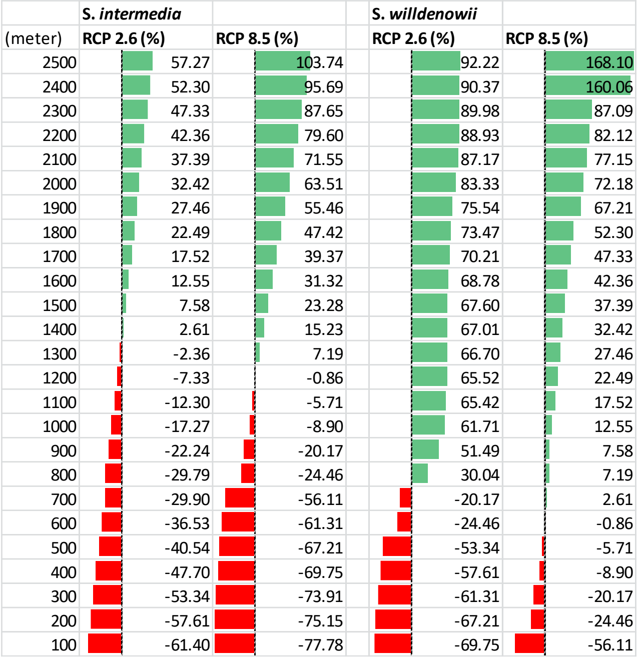


Figure 7. Projected suitable habitat area (km²) of *Selaginella willdenowii* and *S. intermedia* under current and future climate scenarios (RCP 2.6-8.5) for 2030, 2050, and 2080. Bars represent absolute habitat area rather than percentage change.

Table 3. Projected elevational changes (%) in suitable habitat of *Selaginella intermedia* and *S. willdenowii* under RCP 2.6 and RCP 8.5 scenarios in 2080

Elevation (m)	*S. intermedia*		*S. willdenowii*	
	RCP 2.6 (%)	**RCP 8.5 (%)**	**RCP 2.6 (%)**	**RCP 8.5 (%)**
2500	57.27	103.74	92.22	168.10
2400	52.30	95.69	90.37	160.06
2300	47.33	87.65	89.98	87.09
2200	42.36	79.60	88.93	82.12
2100	37.39	71.55	87.17	77.15
2000	32.42	63.51	83.33	72.18
1900	27.46	55.46	75.54	67.21
1800	22.49	47.42	73.47	52.30
1700	17.52	39.37	70.21	47.33
1600	12.55	31.32	68.78	42.36
1500	7.58	23.28	67.60	37.39
1400	2.61	15.23	67.01	32.42
1300	-2.36	7.19	66.70	27.46
1200	-7.33	-0.86	65.52	22.49
1100	-12.30	-5.71	65.42	17.52
1000	-17.27	-8.90	61.71	12.55
900	-22.24	-20.17	51.49	7.58
800	-29.79	-24.46	30.04	7.19
700	-29.90	-56.11	-20.17	2.61
600	-36.53	-61.31	-24.46	-0.86
500	-40.54	-67.21	-53.34	-5.71
400	-47.70	-69.75	-57.61	-8.90
300	-53.34	-73.91	-61.31	-20.17
200	-57.61	-75.15	-67.21	-24.46
100	-61.40	-77.78	-69.75	-56.11



	S. intermedia		*S. willdenowii*	
(meter)	RCP 2.6 (%)	RCP 8.5 (%)	RCP 2.6 (%)	RCP 8.5 (%)
2500	57.27	103.74	92.22	168.10
2400	52.30	95.69	90.37	160.06
2300	47.33	87.65	89.98	87.09
2200	42.36	79.60	88.93	82.12
2100	37.39	71.55	87.17	77.15
2000	32.42	63.51	83.33	72.18
1900	27.46	55.46	75.54	67.21
1800	22.49	47.42	73.47	52.30
1700	17.52	39.37	70.21	47.33
1600	12.55	31.32	68.78	42.36
1500	7.58	23.28	67.60	37.39
1400	2.61	15.23	67.01	32.42
1300	-2.36	7.19	66.70	27.46
1200	-7.33	-0.86	65.52	22.49
1100	-12.30	-5.71	65.42	17.52
1000	-17.27	-8.90	61.71	12.55
900	-22.24	-20.17	51.49	7.58
800	-29.79	-24.46	30.04	7.19
700	-29.90	-56.11	-20.17	2.61
600	-36.53	-61.31	-24.46	-0.86
500	-40.54	-67.21	-53.34	-5.71
400	-47.70	-69.75	-57.61	-8.90
300	-53.34	-73.91	-61.31	-20.17
200	-57.61	-75.15	-67.21	-24.46
100	-61.40	-77.78	-69.75	-56.11

Figure 8. Projected elevational redistribution of suitable habitat for *Selaginella willdenowii* and *S. intermedia* under RCP 2.6 and RCP 8.5 climate scenarios in 2080. Positive values indicate gains and negative values indicate losses of suitable habitat relative to current conditions within each 100-m elevational interval.

Effects of precipitation and temperature

Precipitation was one of the most influential predictors for both species and the most important climatic variable for *S. willdenowii*, with optimal habitat suitability occurring in areas receiving more than 3,000 mm of annual rainfall (Figure 3; Table 2). This pattern reflects the strong dependence of *Selaginella* on moist environments, as water availability regulates photosynthesis, nutrient transport, growth, and reproduction (Thuiller et al. 2008). Experimental studies have also shown that dehydration can substantially reduce physiological performance in *Selaginella* (Deeba et al. 2009), explaining the close relationship between habitat suitability and precipitation observed in this study.

Temperature was likewise a major determinant of habitat suitability. *Selaginella willdenowii* responded strongly to annual mean temperature, whereas *S. intermedia* was more influenced by elevation-associated temperature gradients (Table 2; Figures 3-4). Both species exhibited relatively narrow thermal niches, suggesting sensitivity to climatic warming. Because increasing temperatures can elevate evapotranspiration and reduce environmental humidity, future habitat losses are likely driven by the combined effects of warming and altered precipitation regimes rather than by either factor alone. This interpretation is consistent with studies identifying hydrothermal balance as a key driver of plant distribution shifts under climate change (Parmesan and Yohe 2003; Thuiller et al. 2008).

Ecological significance of UV-B radiation

A notable finding of this study is the importance of UV-B radiation in shaping habitat suitability for both species. Annual mean UV-B radiation (UVB1) was among the most influential predictors for *S. willdenowii*, while UV-B seasonality (UVB2) contributed strongly to the *S. intermedia* model and provided the greatest independent information in the jackknife analysis (Table 2; Figure 2). UV-B radiation affects numerous physiological processes, including photosynthesis, growth, secondary metabolism, and stress responses (Caldwell et al. 1998). The relatively narrow optimum UV-B ranges identified in the response curves suggest that both species are adapted to specific radiation environments associated with humid and shaded forest habitats. Previous studies have also shown that light conditions strongly influence the physiology and distribution of *Selaginella* species (Eickmeier 1986). Because UV-B radiation is closely linked to canopy cover, temperature, and humidity, it may serve as an integrated indicator of habitat quality rather than acting as an isolated environmental factor. Nevertheless, the mechanisms underlying UV-B responses in tropical lycophytes remain poorly understood and warrant further investigation.

Current habitat suitability patterns in Southeast Asia

Mainland Southeast Asia. Mainland Southeast Asia provides extensive suitable habitat for both *S. willdenowii* and *S. intermedia*, particularly in southern Thailand, southern Cambodia, southern Vietnam, and parts of Myanmar (Figure 1). These regions are characterized by high rainfall, relatively stable temperatures, and extensive forest cover, corresponding closely with the environmental conditions identified as important by the MaxEnt models (Table 2; Figures 3-4). The predicted distributions are consistent with documented occurrence records of both species in Thailand (Tagawa and Iwatsuki 1979) and Vietnam (Pham-Hoang 1991; Kalyuzhnyi et al. 2024), indicating that the models successfully captured their broad ecological requirements and regional distribution patterns. The fragmented distribution of suitable habitats across the mainland likely reflects the region's pronounced climatic and topographic heterogeneity, where mountain systems, complex geological history (Woodruff 2010), monsoonal climatic dynamics that shape biodiversity patterns (Sodhi et al. 2004), and extensive land-use change (Corlett 2014) have produced a mosaic of favorable and unfavorable environments.

Maritime Southeast Asia (Malesia region). Maritime Southeast Asia represents the principal center of suitable habitat for both species, with extensive climatically suitable areas predicted across Peninsular Malaysia, Singapore, Sumatra, Java, Sulawesi, parts of Borneo, the southern Philippines, and Papua for *S. intermedia* (Figure 1). These regions contain some of the wettest tropical environments in the world and support extensive rainforest ecosystems characterized by high rainfall and relatively stable climatic conditions. The predicted distributions correspond closely with documented occurrence records of both *S. willdenowii* and *S. intermedia* from Java (Alston 1935b), Sumatra (Alston 1937), Peninsular Malaysia (Alston 1934; Wong

1982, 2010), Singapore (Tan et al. 2014; Lindsay et al. 2022), and the Philippines (Alston 1935a). In addition, *S. intermedia* has also been reported from Sulawesi (Alston 1940), further supporting the predicted suitability of this island within the species' potential distribution range.

Among these areas, Java emerged as a particularly important habitat center, supporting suitable habitat across 57.7% and 48.9% of its land area for *S. willdenowii* and *S. intermedia*, respectively. This high suitability likely reflects the island's exceptional environmental heterogeneity, including strong gradients in elevation (Setyawan et al. 2015c), rainfall and humidity (Setyawan 2012), geology (Setyawan and Sugiyarto 2015), and vegetation structure across different regions of the island (Setyawan 2009; Setyawan et al. 2015a, b). The concentration of suitable habitats in maritime Southeast Asia highlights the importance of humid tropical islands and mountain systems as regional refugia for climate-sensitive cryptogams.

Java Island as a regional hotspot for Selaginella

Environmental heterogeneity and habitat availability. Java Island emerged as a major habitat center for *S. willdenowii* and *S. intermedia*, supporting 57.7% and 48.9% of its land area as suitable habitat, respectively, compared with only 21-22% across Southeast Asia as a whole (Figure 1). This high habitat availability likely reflects the island's exceptional environmental heterogeneity, including steep elevational gradients, volcanic mountain systems, diverse soils, variable rainfall regimes, and a mosaic of forests, agroforests, and shaded anthropogenic habitats. Such conditions create numerous humid microhabitats favorable for forest-floor cryptogams and are consistent with previous records of *Selaginella* diversity across Java, including island-wide surveys (Setyawan 2009), studies in southern Central Java (Setyawan 2012), Bromo Tengger Semeru National Park (Setyawan and Sugiyarto 2015), Yogyakarta and the Sewu Karst region (Setyawan et al. 2015a, b), and the Dieng Plateau (Setyawan et al. 2015c). Despite extensive human modification, montane forests, riparian corridors, forest fragments, and traditional agroforestry systems continue to provide suitable microclimatic conditions, where canopy cover helps maintain humidity (Testo and Sundue 2016), topographic complexity generates diverse microhabitats (Kessler et al. 2011), and remnant habitats may persist within modified tropical landscapes (Corlett 2014).

Importance of Java-derived occurrence records. Java Island was also methodologically important because it contributed the primary field-occurrence dataset used for model development, comprising 205 records of *S. willdenowii* and 161 records of *S. intermedia*. These field-verified records strengthened model calibration and provided high-confidence occurrence data based on direct observations and taxonomic verification. Beyond sampling intensity, Java offers a broad range of climatic and elevational conditions within a relatively small area, allowing occurrence records to capture substantial ecological niche variation from lowland to montane environments. This environmental breadth makes Java an effective focal region for assessing climate-related habitat changes. Nevertheless, because sampling effort was greater in Java than in other parts of Southeast Asia, model predictions may partly reflect the environmental conditions represented on the island. The use of spatial filtering and bias-correction procedures helped minimize this effect, although additional surveys in Borneo, Sulawesi, the Philippines, Papua, and mainland mountain systems would further improve model robustness.

Conservation significance of montane landscapes in Java. The conservation importance of Java becomes more evident when current habitat availability is considered alongside future climate projections. Although the island currently supports extensive suitable habitats, climate change is projected to reduce habitat availability by 15.6-21.6% for *S. willdenowii* and 20.0-27.2% for *S. intermedia* by 2080. Despite these declines, Java is likely to remain an important habitat center for both species. The projected upslope redistribution of suitable habitats suggests that montane landscapes may function as climate refugia, where cooler and moister conditions persist under future warming (Lenoir et al. 2008; Chen et al. 2011). However, the effectiveness of these refugia depends on habitat integrity and elevational connectivity, which are increasingly threatened by forest fragmentation, agriculture, settlements, and tourism development. Protecting montane forests, riparian corridors, and other humid habitats is therefore essential to facilitate species persistence and dispersal. Given their sensitivity to changes in canopy cover and microclimatic conditions, *S. willdenowii* and *S. intermedia* may also serve as useful indicators of forest understory health, reinforcing the importance of Java as a priority landscape for *Selaginella* conservation and climate-change monitoring.

Climate-induced habitat contraction

Regional patterns of habitat loss. The results consistently indicate that climate change will reduce suitable habitats for *Selaginella willdenowii* and *S. intermedia* across Southeast Asia, with habitat losses increasing through time and under higher emission scenarios. By 2080, suitable habitat is projected to decline by 16.9-23.4% for *S. willdenowii* and 27.3-33.2% for *S. intermedia*, indicating substantial reductions even under relatively optimistic climate pathways. These projections are consistent with expectations of continued warming, altered precipitation regimes, and increasing climatic variability in Southeast Asia (IPCC 2014). Habitat losses were particularly pronounced in southern Cambodia, Thailand, Java, Sulawesi, and Papua, suggesting that several current habitat strongholds may become increasingly vulnerable. Similar climate-driven range contractions have been documented for many plant species worldwide, with studies reporting projected habitat losses (Thuiller et al. 2008), biodiversity declines under future climate change (Bellard et al. 2012), and broad-scale redistribution of species ranges across ecosystems (Pecl et al. 2017). Beyond reducing geographic range size, habitat contraction may also decrease population connectivity and dispersal opportunities, potentially lowering the long-term resilience of *Selaginella* populations to ongoing environmental change.

Species-specific vulnerability. Although both species are projected to lose suitable habitat under future climate scenarios, *S. intermedia* consistently exhibited greater habitat losses than *S. willdenowii*, indicating higher climate vulnerability. This difference is likely related to the stronger dependence of *S. intermedia* on elevation, which contributed 32.9% to its model compared with only 1.5% for *S. willdenowii* (Table 2). In addition, *S. intermedia* occupies a narrower elevational range (approximately 700-1,500 m asl), whereas *S. willdenowii* occurs across a much broader gradient. Species with restricted climatic niches are generally more sensitive to environmental change and often experience greater range contractions under future climate scenarios, as demonstrated by projections of habitat loss under climate change (Thuiller et al. 2008), theoretical and empirical analyses of species vulnerability (Araújo and Peterson 2012), global assessments of climate-change sensitivity (Pacifici et al. 2015), and documented patterns of climate-driven range redistribution across taxa (Pecl et al. 2017). The narrower environmental tolerance of *S. intermedia* may therefore limit its ability to persist under changing climatic conditions. Furthermore, habitat fragmentation may hinder dispersal toward newly suitable areas, causing realized future distributions to be more restricted than model projections suggest (Chen et al. 2011; Corlett and Westcott 2013). These findings suggest that *S. intermedia* warrants particular conservation attention, although both species are likely to be adversely affected by future climate change.

Elevational redistribution and climate refugia

Upslope migration trends. A consistent finding of this study is the projected upslope redistribution of suitable habitats for *Selaginella willdenowii* and *S. intermedia* under future climate scenarios. Although total habitat area is expected to decline, the remaining suitable habitats become increasingly concentrated at higher elevations, particularly under RCP 6.0 and RCP 8.5. This pattern is consistent with one of the most widely documented biological responses to climate warming, whereby species track suitable climatic conditions through climate-driven range shifts (Parmesan and Yohe 2003), particularly by moving toward higher elevations (Lenoir et al. 2008), as part of broader species redistributions observed across ecosystems worldwide (Pecl et al. 2017). The trend is especially pronounced in *S. intermedia*, which occupies a narrower elevational range and exhibits stronger dependence on altitude than *S. willdenowii*. Increasing temperatures and evapotranspiration may reduce habitat suitability at lower elevations, forcing moisture-dependent species toward cooler and wetter montane environments, as documented by studies of climate-driven range shifts (Walther et al. 2002), habitat contraction (Thuiller et al. 2008), and biodiversity vulnerability (Bellard et al. 2012). However, because land area generally decreases with elevation, upslope migration may alleviate climatic stress while simultaneously reducing available habitat, a phenomenon known as the "escalator to extinction" (Colwell et al. 2008; Freeman et al. 2018).

Potential refugia in montane environments. The concentration of future suitable habitats in mountain regions suggests that montane environments may function as important climate refugia for both *Selaginella* species (Keppel et al. 2012; Morelli et al. 2016). Across Southeast Asia, suitable habitats persisted mainly in the mountainous landscapes of Peninsular Malaysia, Sumatra, Java, Sulawesi, Borneo, and Papua, where strong elevational gradients, high rainfall, and relatively stable microclimates may buffer the effects of future warming. Java appears particularly important, as the remaining suitable habitats increasingly became concentrated within its volcanic mountain systems. Previous studies have shown that montane environments often provide microclimatic refugia through topographic complexity (Dobrowski 2011), microclimatic buffering (Maclean et al. 2015), and the persistence of cool, moist habitats in cloud forests and shaded ravines (Greiser et al. 2020). For moisture-dependent understory species such as *Selaginella*, these habitats may facilitate persistence despite regional climatic change. However, the effectiveness of such refugia depends on habitat integrity and landscape connectivity, both of which are increasingly threatened by habitat loss (Sodhi et al. 2004), land-use change (Corlett 2014), and deforestation (Hughes 2017) in Southeast Asia. Consequently, protecting montane forests and maintaining elevational connectivity should be prioritized to support long-term species persistence under climate change.

Implications for forest biodiversity conservation

Vulnerability of forest understory cryptogams. The projected habitat contraction and upslope redistribution of *Selaginella willdenowii* and *S. intermedia* have broader implications for tropical forest biodiversity because these species represent moisture-dependent understory cryptogams that contribute to nutrient cycling (Cornelissen et al. 2007), microhabitat formation (Patiño and Vanderpoorten 2018), and ecosystem functioning and biodiversity maintenance (Sabovljević et al. 2022). Cryptogams are particularly sensitive to environmental change because their growth and survival depend strongly on moisture availability (Proctor 2000), climate (Kessler et al. 2011), and canopy-regulated forest microclimates (Testo and Sundue 2016). Consequently, even moderate climatic shifts may alter their distribution and population dynamics. These risks may be intensified by forest degradation and fragmentation, which reduce humidity and increase temperature fluctuations within forest understories (Laurance et al. 2011; Haddad et al. 2015). Because the present models do not explicitly incorporate future land-use change or habitat degradation, actual population declines may exceed those predicted from climate scenarios alone, owing to interactions between climate change and habitat loss (Brook et al. 2008), ongoing land-use impacts on biodiversity (Newbold et al. 2015), and multiple anthropogenic pressures identified in global assessments (IPBES 2019).

Protected areas and elevational connectivity. The projected upslope redistribution of suitable habitats highlights the importance of protected mountain landscapes for the long-term persistence of *Selaginella* populations. As lower-elevation habitats become less suitable, montane protected areas may serve as critical refugia by maintaining cooler and wetter environmental conditions. Many protected areas in Southeast Asia already encompass extensive elevational gradients that can facilitate local climate-driven range shifts. However, the effectiveness of these areas depends not only on protection status but also on elevational connectivity. Species responding to climate change often require continuous habitat corridors to facilitate range shifts (Heller and Zavaleta 2009), enhance landscape connectivity (Krosby et al. 2010), and enable movement across elevational gradients (Nuñez et al. 2013). This issue is particularly relevant in densely populated regions such as Java, where many mountain forests are increasingly isolated by agriculture and urban development. Maintaining connectivity among montane forests, riparian corridors, and other humid habitats may enhance dispersal opportunities (Hannah et al. 2007), promote climate adaptation through landscape connectivity (Corlett and Westcott 2013), and facilitate species tracking of shifting environmental conditions (Costanza and Terando 2019).

Conservation priorities under climate change. The results highlight several priorities for biodiversity conservation under future climate change. First, montane forests should be prioritized because they are projected to retain the largest proportion of suitable habitat for both *S. willdenowii* and *S. intermedia*. Second, conservation planning should incorporate future habitat projections (Araújo et al. 2005), climate refugia (Morelli et al. 2016), and anticipated distributional shifts under climate change (Hannah et al. 2014), as suitable habitats may not coincide with current distribution centers. Third, maintaining habitat connectivity across elevational gradients is essential to facilitate natural range shifts and dispersal. Long-term ecological monitoring should also be strengthened because *Selaginella* species are sensitive to changes in temperature, moisture, and canopy conditions and may serve as useful indicators of climate-driven changes in forest understory environments (Chen et al. 2011; Steinbauer et al. 2018). Overall, protecting montane refugia, maintaining elevational connectivity, and integrating climate projections into conservation planning will be critical for safeguarding *Selaginella* populations and associated understory biodiversity in Southeast Asia.

Study limitations and future directions

Several limitations should be considered when interpreting the results of this study. First, the models were developed using CMIP5 climate projections and Representative Concentration Pathway (RCP) scenarios because these datasets were the most comprehensive and widely available at the time the analyses were conducted. In addition, future projections were based on a single Global Climate Model (HadGEM2-CC); therefore, uncertainty associated with alternative climate models was not evaluated and may influence the magnitude of projected habitat changes. Second, future projections assumed that soil properties, UV-B radiation variables, and elevation remained unchanged due to the limited availability of reliable future datasets. Third, the models primarily incorporated climatic and environmental predictors and did not explicitly account for future land-use change, habitat fragmentation, biotic interactions, or dispersal constraints. Consequently, realized future distributions may differ from the projected climatically suitable habitats. Future research should utilize updated CMIP6 and Shared Socioeconomic Pathway (SSP) scenarios, incorporate multiple GCMs to better characterize projection uncertainty, incorporate land-use and forest-cover dynamics, and evaluate dispersal limitations and population connectivity. Long-term monitoring and ecophysiological studies are also needed to better understand the mechanisms underlying climate sensitivity and adaptive responses of tropical *Selaginella* species.

In conclusion, climate change is projected to substantially alter the distribution of climatically suitable habitats for *Selaginella willdenowii* and *S. intermedia* across Southeast Asia. Habitat suitability was primarily determined by precipitation, temperature, elevation, and UV-B radiation, reflecting the strong dependence of both species on humid and environmentally stable conditions. The MaxEnt models showed high predictive performance (AUC = 0.948 and 0.936; TSS = 0.89 and 0.87 for *S. willdenowii* and *S. intermedia*, respectively), providing robust estimates of current and future habitat suitability. Suitable habitats currently cover approximately 982,246 km² for *S. willdenowii* and 1,068,808 km² for *S. intermedia*, with Java Island representing a major regional habitat center. Future projections consistently indicated habitat contraction under all climate scenarios, reaching 16.9-23.4% for *S. willdenowii* and 27.3-33.2% for *S. intermedia* by 2080. Both species are also expected to undergo upslope redistribution, resulting in an increasing concentration of suitable habitats within montane environments. These findings identify mountain ecosystems as important climate refugia and highlight the need to conserve montane forests and maintain elevational connectivity to support the long-term persistence of climate-sensitive tropical cryptogams under future environmental change.

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