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Research article

Spatiotemporal modeling of the potential range distributions of *Usnea* in the Philippines under changing climate scenarios

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Abstract
This study presents the first ecological niche model for the lichen genus *Usnea* in the Philippines, utilizing MaxEnt to project both current and future habitat suitability under two Coupled Model Intercomparison Project Phase 6 climate scenarios (Shared Socioeconomic Pathways: 1-2.6 and 3-7.0) using EC-Earth3-Veg and MIROC6 models. Spatially filtered occurrence records and selected bioclimatic variables were used to build and optimize the model through the ENMeval R package. Results revealed that while *Usnea* currently occupies limited high-suitability areas, projections indicate a slight expansion in suitable habitats, especially in upland regions, driven by probable thermal niche shifts. Mean diurnal range (BIO2) is the dominant predictor under present conditions, whereas mean temperature of the warmest quarter (BIO10) controls future scenarios. Despite this, regional declines were observed in Western Visayas, Zamboanga Peninsula, Northern Mindanao, SoCCSKSarGen, and Bangsamoro Autonomous Region in Muslim Mindanao, which are areas characterized by warming and seasonal drying. These findings highlight both the potential resilience and vulnerability of *Usnea*, offering critical insights for conservation strategies in tropical montane ecosystems.

Keywords
Climate change, fruticose lichen, Philippines, MaxEnt, ecological niche

Introduction

Lichens are complex, composite organisms primarily composed of a fungal host (mycobiont) and photosynthetic partners (photobiont) that are either algal or cyanobacterial. Lichens are highly sensitive biological indicators of environmental change due to their poikilohydric nature (Klamerus-Iwan et al., 2020), lack of a protective cuticle (Asplund and Wardle, 2017), dependence on atmospheric nutrients (Nash and Gries, 1995), and extreme susceptibility to air pollution, climate shifts, and habitat disturbances (Jüriado et al., 2016). Among the diverse morphological forms of lichens are the fruticose lichens, which are characterized by their branched, shrubby appearance.

Fruticose lichens are particularly sensitive to fluctuations in environmental conditions such as humidity, temperature, and air quality (Armstrong, 2017). This sensitivity makes them efficient bioindicators of ecological health and climate change. Despite knowledge of the ecological importance and well-documented sensitivity to environmental changes, lichens remain markedly underrepresented in global conservation frameworks. Compared to vascular plants and vertebrates, lichens are often overlooked in conservation assessments due to taxonomic complexity, limited specialist expertise, and less interest from the public. However, this results to having only a small fraction of lichen species to be formally evaluated. Within this group, the genus *Usnea*, commonly known as beard lichens, stands out because of its occurrence on all continents and widespread presence in montane habitats (Prateeksha et al., 2016) and their potential use in bioprospecting (Prateeksha et al., 2016; Santiago et al., 2022; Jamilano-Llames and dela Cruz, 2025). *Usnea* is especially prone to physiological stress in response to even subtle environmental changes because of their high surface-area-to-volume ratio and epiphytic habit, which enhance exposure to pollutants (Shreshta et al., 2012). With this, *Usnea* species are widely recognized as highly sensitive bioindicators of air quality which exhibit strong responses to sulphur dioxide, nitrogen deposition, and heavy metals (Pradhan et al., 2026). Furthermore, as with lichens in general, there is no comprehensive global IUCN coverage for *Usnea*. Regional and national assessments most especially from Europe show some of the few assessments which express conservation concerns for certain *Usnea* species. *Usnea longissima* Ach. in Sweden is listed as vulnerable (Esseen et al., 2023), *Usnea florida* (L.) F.H. Wigg. and *Usnea articulata* (L.) Hoffm. are listed as near threatened and priority conservation species in the United Kingdom (Wilkins et al., 2025). This makes them an ideal candidate for assessing the impacts of climate variability and guiding conservation strategies for rapidly changing ecosystems (Thakur et al., 2024).

Anthropogenically driven climate change has been recognized as a global threat to biodiversity for decades (Omann et al., 2009; Garcia et al., 2014). Drastic shifts in climatic patterns can profoundly reshape species distribution, forcing organisms either to migrate to more suitable habitats (Peck, 2011) or to adapt to changing conditions (Anderson and Song, 2020; Jiao and Lu, 2020). Failure to migrate or adapt commonly leads to local extinctions of species (Holzmann et al., 2023). These dynamics of climate change are particularly critical for sessile, slow-growing taxa such as lichens, which are unable to relocate in response to environmental stressors or adapt rapidly to the accelerated changes in environmental conditions (Aptroot et al., 2021). Therefore, in biodiversity hotspots such as the Philippine archipelago, understanding potential shifts in lichen distributions under current and future projected climate scenarios serves as a concrete step forward towards conservation and ecological sustainability.

Despite knowledge of the ecological importance of species under the genus *Usnea* globally, studies exploring their biogeographical distribution relative to a changing climate remain scarce in the Philippines. This points to the urgent need to conduct research on the impact of future climate change scenarios on the distribution of sensitive species such as those in the lichen genus *Usnea*. In this study, we utilized the Maximum Entropy (MaxEnt) ecological niche model (ENM) framework (Phillips et al., 2004). MaxEnt is a robust algorithm for predicting suitable habitat ranges using presence-background data and environmental covariates. MaxEnt has become a gold standard in ecological niche modeling due to its predictive accuracy (Dagamac et al., 2021) and ability to accommodate incomplete or biased occurrence records (Comia-Geneta et al., 2024). MaxEnt provides a robust platform for forecasting spatial dynamics of vulnerable taxa such as *Usnea* through the coupling with environmental layers from sources such as WorldClim and future climate projections based on IPCC scenarios. Although MaxEnt is conventionally used for modeling species-level distributions, the current study pursues a genus-level modeling approach due to the limited species-level georeferenced records of species under the genus *Usnea* in the Philippines. Ecological niche estimation can be used above species level especially for exploratory purposes such as for groups exhibiting niche conservatism. The fruticose lichen *Usnea* is one this, as its species share environmental tolerances and niche conservatism such as sensitivity to narrow ranges of temperatures and humidity. Furthermore, the taxonomic complexity of *Usnea* hinders efforts for analyses at the species-level. Based on Smith et al. (2019), in cases such as that of *Usnea*, MaxEnt can be used as an exploratory genus-level tool for macroclimatic suitability which will serve as baseline for further refinement towards species-level resolution towards the future. Furthermore, genus-level MaxEnt modeling has been demonstrated to be feasible in prior studies involving other genus-level taxa such as *Cedrela* (Cotrina Sánchez et al., 2021) and *Avena* (Khwarahm, 2025), albeit these are plants. These studies confirm the utility of using genus-level modeling of taxa that share ecological niches, microclimatic requirements, and respond similarly to environmental drivers. In the case of *Usnea*, species under the genus are assumed to exhibit similar sensitivity to moisture, temperature, and air quality, which allows the construction of a valid and ecologically meaningful genus-level niche model. Consequently, this study aims to model the current and future potential distribution of *Usnea* in the Philippines under various Representative Concentration Pathway (RCP) climate scenarios. Furthermore, by optimizing model performance using R-based algorithms, such as the ENMeval package (Muscarella et al., 2014), the projections are validated as ecologically meaningful and methodologically robust. Beyond mapping suitable habitat shifts, this work also aims to contribute to the emerging framework of lichens as model organisms for climate change monitoring in tropical ecosystems. In the end, the result of the study is projected to offer critical insights for conservation planning by identifying climate refugia and prioritizing areas for long-term lichen habitat protection.

Materials and Methods

Study area

The model covered the whole Philippine archipelago in Southeast Asia, with coordinates extending from latitudes 4°24′53.84″ N to 21°7′18.41″ N and longitudes 116°53′16.64″ E to 126°36′18.16″ E. The geographic coordinates of the Philippines were obtained using the LIPAD Shapefile Generator developed by the University of the Philippines DREAM and NOAH program (University of the Philippines DREAM and NOAH, n.d.). The archipelago consists of three major island groups, Luzon, Visayas, and Mindanao, with a total of around 7640 islands. Its total land area is approximately 300,000 km^2 with elevation extending up to 2954 m asl. The Philippines experiences a tropical and maritime climate characterized by relatively high temperatures, high humidity, and abundant rainfall. The country's climate is strongly influenced by the Northeast and Southwest monsoons as well as the Intertropical Convergence Zone (ITCZ), tropical cyclones, and topographic variations. The Philippine Atmospheric, Geophysical, and Astronomical Services Administration (PAGASA) classifies the Philippine climate into four types primarily based on rainfall distribution: (i) Type 1 has two pronounced seasons – dry from November to April and wet for the rest of the year, with maximum rains occurring from June to September, commonly found in the western part of Luzon and Visayas,

(ii) Type II has no dry season and experiences a very pronounced maximum rainfall from December to February, and minimum monthly rainfall occurring from December to February or from March to May, affecting the eastern parts of the country, (iii) Type III has no pronounced maximum rain period with a dry season lasting only from one to three months either from December to February or March to May, and (iv) Type IV has more or less evenly distributed rainfall throughout the year. These climatic patterns are compiled from long-term records by PAGASA and peer-reviewed climate analyses. The climate variability and habitat diversity of the Philippine archipelago represent an interesting area for research on the impact of climate change on biodiversity.

Occurrence records

The study utilized occurrence records of *Usnea* in the Philippines extracted from the Global Biodiversity Index Facility (GBIF) and published studies, i.e., Galinato et al. (2017), Timbreza et al. (2017), Santiago et al. (2021), dela Cruz et al. (2023) and Gerlach et al. (2023). Past studies without explicit coordinates of their collection sites were not included. A total of 1,241 occurrence records of the lichen genus *Usnea* were established. Records of *Usnea* were present in all the major islands of the Philippine archipelago (see Supplementary Figure S1). An initial filter was done through the removal of ecologically nonsensical occurrence points, such as those in bodies of water. There are more occurrence records in some areas due to the frequency of field sampling done, particularly in Mindanao, due to recent field expeditions of Gerlach et al. (2023). To reduce or eliminate bias brought by repeated occurrence points in proximity with each other, a data-thinning approach was used. The spThin package (Aiello-Lammens et al., 2015) in R was utilized to thin the occurrence data to reduce spatial clustering and ensure a more representative distribution across the study area in 1 km settings. This thinning algorithm reduced the occurrence points to 36 records and was similarly conducted in other papers that yielded a small number of occurrence points (Comia-Geneta et al., 2024; Almadrones-Reyes and Dagamac, 2018). The resulting thinned dataset was then transformed into a comma-delimited (CSV) file format.

Environmental variables

The study incorporated various environmental variables to assess their influence on the ecological niche of *Usnea* in the Philippines. The 19 bioclimatic variables for the current climate period (1970-2000) were obtained from the WorldClim website (https://www.worldclim.org/) at a resolution of 30 seconds. Further information regarding the 19 bioclimatic variables can be found in USGS data series 691 (O'Donnell and Ignizio, 2012). Furthermore, the study considered two shared socioeconomic pathways (SSP) scenarios, SSP1-2.6 (optimistic) and SSP3-7.0 (pessimistic), for the period of 2081–2100. These scenarios were developed by the Intergovernmental Panel on Climate Change to outline possible future socioeconomic and environmental conditions based on different assumptions on population growth, economic development, energy use, land use, and many other variables (Burgess et al., 2021). SSP1-2.6 models a pathway distinguished by sustainable development and low greenhouse gas emissions. It presumes strong international cooperation, accelerated technological advancements, and effective implementation of climate change mitigation strategies. In this scenario, global greenhouse gas emissions are significantly reduced, which stabilizes radiative forcing levels. The SSP1-2.6 pathway envisions a future focused on sustainability, social equity, and environmental protection. On the other hand, SSP3-7.0 represents a pathway characterized by high population growth, slow economic development, and ineffective efforts to address climate change. It assumes limited global cooperation, regional conflicts, and challenges in the implementation of climate change mitigation measures. Subsequently, this scenario leads to high greenhouse gas emissions and a continuation of business-as-usual practices of most populations. The SSP3-7.0 pathway envisions a future with increased inequality, limited environmental policies, and higher vulnerability to climate change impacts. The projected bioclimatic variables data were downloaded from EC-Earth3-Veg and the Model for Interdisciplinary Research on Climate version 6 (MIROC6) Global Circulation Models from the WorldClim database (https://worldclim.org/). EC-Earth3-Veg integrates dynamic vegetation processes into the standard EC-Earth configuration by coupling the LPJ-GUESS dynamic global vegetation model with the ECNMWF IFS atmosphere model, HTESSEL land surface module, NEMO ocean model, and LIM3 sea ice model (Döscher et al., 2022). EC-Earth3-Veg enables interactive feedback between climate and vegetation through the dynamic simulation of vegetation distribution, biomass, and associated biogeophysical properties such as albedo and evapotranspiration. Using EC-Earth3-Veg is suited for studies on biosphere-climate feedback, carbon cycle dynamics, and the role of vegetation in modulating surface energy and hydrological exchanges under future climate scenarios (Döscher et al., 2022). On the other hand, MIROC6 features improved atmospheric and oceanic vertical resolution, shallow convective parameterization, and upgraded representation of internal variability and large-scale circulation patterns compared to its older predecessor, MIROC5 (Tatebe et al., 2019). The improvement in the model allows better reliability projections of temperature and precipitation patterns critical to habitat suitability modeling. The 2.6 K equilibrium climate sensitivity of MIROC6 ensures consistency with global climate response benchmarks supporting its application in biodiversity impact assessments.

Filtering of bioclimatic variables for autocorrelations

Considerations in choosing which among the 19 bioclimatic variables to include for optimal MaxEnt building in the current study included statistical, model performance, and ecological criteria. The statistical criteria utilized a Pearson correlation matrix with a $p < 0.8$ threshold. Model performance was evaluated by initially running all 19 bioclimatic variables in MaxEnt with the optimized parameters from the ENMeval results. The jackknife, omission, and contribution parameters of each variable relative to the model building were assessed. Lastly, the potential parameters to be considered for the MaxEnt-optimized model building were further characterized in terms of their known ecological significance to lichen biology, based on the literature.

An initial MaxEnt run was done using the optimized parameters generated from ENMeval package. The results of percent contribution and permutation importance were considered to guide variable selection, reduce overfitting and improve model robustness. Percent contribution provides insight into the MaxEnt's algorithm's use of variables during model training, while Permutation Importance offers an objective measure of each variable's influence on model performance (Phillips et al., 2004). Variables with low importance or high collinearity were excluded to ensure a parsimonious and ecologically relevant model (Li et al., 2020).

Pearson correlation matrix for threshold-based filtering was used to address multicollinearity among the bioclimatic variables. Collinearity can obscure the contribution of individual environmental predictors and affect model interpretability (De Marco and Nóbrega, 2018). Therefore, this filtering is critical for the optimization of input variables in ecological niche modeling.

The bioclimatic variables used in the study were provided as raster layers in ASCII format. The raster layers were loaded into R using the "terra" package. The correlation analysis was done with randomly sampled 10,000 points across the raster stack. This sample size was chosen to balance computational efficiency with the statistical robustness of the correlational matrix. The "spatSample" function from the "terra" package was used to extract values from the raster stack. The Pearson correlation matrix among the 19 bioclimatic variables was then calculated using the "cor()" function in R. A threshold of $p > 0.8$ was applied to identify highly correlated pairs of variables, which is a commonly accepted threshold in ecological modelling. Pairs of variables with a correlation coefficient of more than 0.8 were flagged for potential removal. The "which()" function was used to extract the indices of these highly correlated pairs, and the "apply()" function was then used to reorganize them into a list of variable pairs.

Model optimization

The ecological niche model for *Usnea* in the study was optimized using ENMeval R package (v.2.0) (Muscarella et al., 2014). This package allows automated tuning of the MaxEnt model parameters through a robust model evaluation framework. Specifically, we aimed to identify the most parsimonious combination of feature classes (fc) and regularization multipliers (rm) that balances model complexity with predictive performance while minimizing overfitting.

A comprehensive set of model configurations with varying regularization multipliers from 1 to 5 was tested. Different combinations of feature classes, including linear (L), quadratic (Q), hinge (H), and their combinations (e.g., LQ, LQH), were applied. Selection of the optimal model was based on multiple criteria incorporating the following metrics: (1) the average area under the curve for validation data, indicating the model's discriminatory ability, (2) the average different between training and validation AUC, to penalize overfitting, (3) the omission rate at the 10% training presence threshold which assesses predictive sensitivity, and (4) the Akaike Information Criterion that is corrected for small sample sizes (AICc) which accounts for model complexity and penalizes over-parameterization. Furthermore, the Boyce Index was also determined. This measures how well predicted suitability values correspond to actual species occurrences, with a value nearing to 1 indicates good habitat suitability scores (Hirzel et al., 2006). These optimization metrics pinpoint that the selected model configuration effectively captures the optimal ecological niche model for *Usnea* in the Philippine ecoregion while maintaining generalizability. Afterwards, the optimized model configuration was used for projecting the current and future distributions of *Usnea* under various climate scenarios.

Modeling process

MaxEnt version 3.4.4 (http://biodiversityinformatics.amnh.org/open_source/maxent/) was used to build the ecological niche model (ENM) in this study. MaxEnt is an open-source software for ENM utilizing a machine-learning approach known as Maximum Entropy. MaxEnt employs machine-learning techniques to predict ecological niche based on the most influential environmental conditions. The generated spatially thinned occurrence points in CSV file format and environmental variables in ASCII format were used as input files in the MaxEnt software. The option "create a response curve" was toggled to generate a curve that illustrates the relationship between the species occurrence and environmental variables. Furthermore, a "jackknife test" was performed to measure the importance of each environmental variable in the modeling process, identifying the variables that significantly influence the ecological niche. For training the model, the study used 70% of the occurrence points and the remaining 30% to test the model's performance. "crossvalidate" option for replication run type was set. For the MaxEnt settings, an RM value of 3 and an FT of linear and quadratic (LQ) were followed as suggested by the ENMeval package model tuning. The background points were set as the default value of 10,000 points for all three models with ten replicates. Lastly, the output format was set as "cloglog".

Data analysis
The generated output suitability maps from MaxEnt were raster analyzed in QGIS 3.34.1 and R 4.4.3 using the terra package. Map pixel values transformed to 0 to 1. Afterwards, these habitat suitability values were categorized into division classes as follows: very low = 0–0.2, low = 0.2–0.4, moderate = 0.4–0.6, high = 0.6–0.8, very high = 0.8–1.0. In generating the habitat suitability maps, a red to green linear band pseudocolor gradient was used to visualize the habitat suitability of the different areas in the Philippines as showed in Figure 2.

Results

Model optimization and assessment
Model optimization through the ENMeval package indicated the best-performing model on the lowest (ΔAICc = 0) which used linear quadratic (LQ) feature classes with a regularization multiplier of 3. This model achieved a mean validation AUC of 0.902, a Boyce index of 0.805, and a 10^{th} percentile omission rate of 0.125, which indicates high predictive performance with moderate model complexity. Among all evaluated models, the configuration with linear and quadratic (LQ) feature classes and a regularization multiplier of 3 was suggested as the optimal configuration of parameters (AICc = 718.74; delta AICc = 0). These results indicate that this configuration is the most parsimonious model with the highest empirical support. Furthermore, the configuration also demonstrated strong discriminatory performance with a validation Area Under the Curve (AUC) value of 0.929, a low AUC difference of 0.0586, and an acceptable 10% omission rate of 0.149.

The results of the analysis of the variable contribution and permutation importance were analyzed. Variables BIO3-BIO9, BIO12-BIO13, BIO17, and BIO19 all had 0% contribution and 0 permutation importance. The highest percent contribution is for BIO2 – Mean Diurnal Range at 60.4%, while the highest permutation importance is for BIO14 - Precipitation of Driest Month at 54.7%. Afterwards, the generated models were primarily assessed in terms of AUC values (Fig. 1). AUC values of the generated models ranged from 0.870 to 0.882. In the current scenario, Mean Diurnal Range (BIO2) had the highest percent contribution and permutation importance, with values of 93.3% and 82.3%, respectively. However, for all future scenarios, the Mean Temperature of the Warmest Quarter had the highest percent contribution and permutation importance, ranging from 99.4% to 99.6% and 97.9% to 99.1%, respectively. Furthermore, other bioclimatic variables showed minimal influence in the model with precipitation of driest month (BIO10) and mean temperature of the coldest quarter (BIO11) contributing 3.5% and 2.6%, respectively. Despite its low percent contribution, mean temperature of warmest quarter (BIO14) had a permutation importance of 4.0% which suggests certain levels of interaction or redundancy with other variables. A summary of the selected predictors, their statistical relationships, model performance, and ecological relevance is provided in Supplementary Tables S1 and S3.

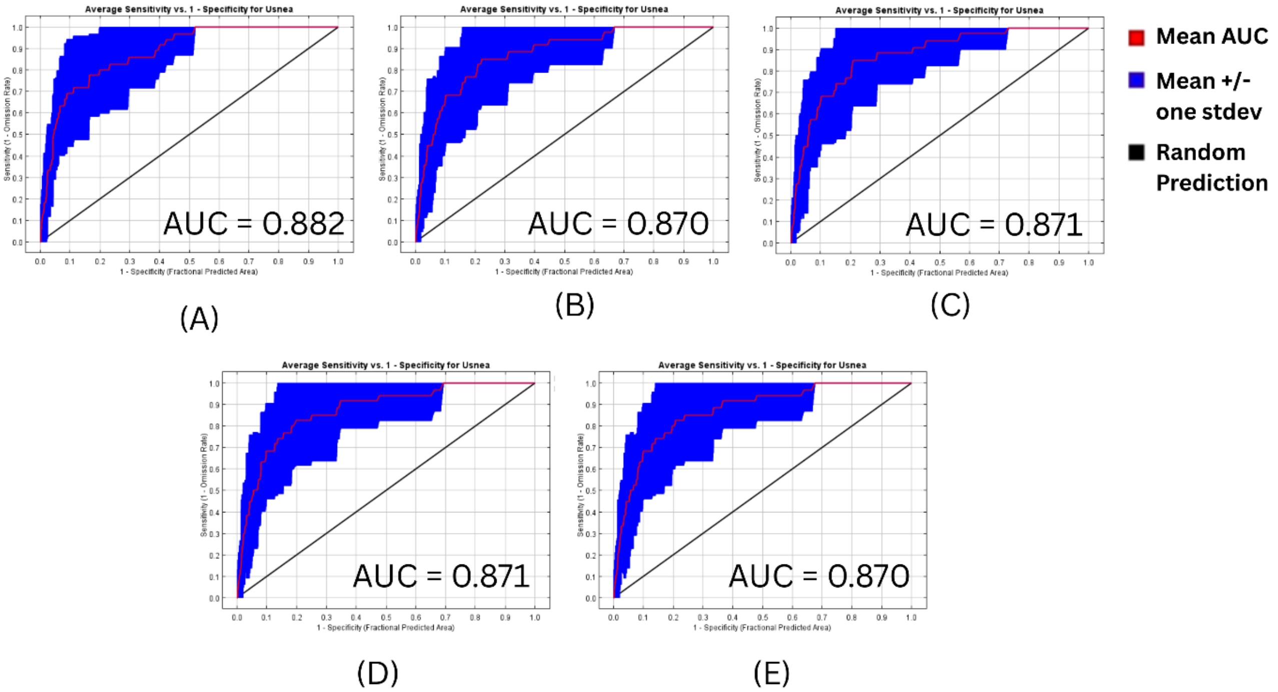

Fig. 1 - ROC curves showing the sensitivity of all 5 models in this study. EC-Earth3-Veg and the Model for Interdisciplinary Research on Climate version 6 (MIROC6) were the Global Circulation Models used in the study. (A) Current, (B) EC-Earth3-Veg SSP1-2.6, (C) EC-Earth3-Veg SSP3-7.0, (D) MIROC6 SSP1-2.6, and (E) MIROC6 SSP3-7.0.

Habitat suitability of Usnea in the Philippines in future climate scenarios using MaxEnt

The total land area of suitable habitats for *Usnea* in the Philippines under the current and future climate scenarios is presented in Table 1. In the current scenario, the largest area is characterized by very low habitat suitability, covering 210,814 km². For the future scenarios, all habitat suitability categories—low, moderate, high, and very high — had increased areas, ranging from 2.71% to 11.95% while very low habitat suitability decreased in area under all future climate scenarios, with changes ranging from -2.28% to -3.90. Under both EC-Earth-3-Veg and MIROC6 Shared Socioeconomic Pathway (SSP) 126, which projects an optimistic scenario of reduced carbon emissions and global collaborations for sustainable development, very low suitability areas were reduced to 67.9% and 68.7%, respectively. Interestingly, in both models for SSP 3-7.0, a relatively pessimistic, high-emissions scenario, very low suitability still decreased for both to 67.6% and 68.1%, respectively. The minimal changes in areas classified as very low suitability reflect negligible changes in the suitability of *Usnea* in lowland areas, with variations inferred to be due to changes in temperature and precipitation in upland ecosystems.

Furthermore, all the other classifications of low, moderate, high, and very high habitat suitability increased in all model projections, with EC-Earth-3-Veg and MIROC increasing in area (Fig. 2). This is interesting as, instead of the expected reduction in habitat suitability, *Usnea* increased in its potential suitable habitat in the archipelago.

Table 1 - Total land area (km^2) of suitable habitats for *Usnea* under the current, EC- Earth3-Veg (SSP126 & SSP370), and MIROC6 (SSP126 &370). Percentage values indicate the change of area relative to the current.

Habitat Suitability[a]		**EC-Earth3-Veg**		**MIROC6**	
	Current	**SSP 126**	**SSP 370**	**SSP 126**	**SSP 370**
Very Low	210,814	203,662 (-3.39%)	202,588 (-3.90%)	206,002 (-2.28%)	204,268 (-3.11%)
Low	47,904	52,635 (+9.88%)	53,627 (+11.95%)	51,241 (+6.97%)	52,280 (+9.14%)
Moderate	18,630	19,968 (+7.18%)	20,352 (+9.25%)	19,330 (+3.76%)	19,855 (+6.57%)
High	11,122	11,754 (+5.68%)	11,572 (+4.04%)	11,590 (+4.21%)	11,708 (+5.27%)
Very High	11,294	11,745 (+4.00%)	11,624 (+2.92%)	11,600 (+2.71%)	11,653 (+3.18%)

[a]Habitat suitability values: very low = 0-0.2, low = 0.2-0.4, moderate = 0.4-0.6, high = 0.6-0.8, very high = 0.8-1.0

Region-specific analysis

Region-specific habitat suitability was also analyzed and presented in the Supplementary Table S2. The greatest decrease in mean habitat suitability occurred in region VI (Western Visayas), ranging from -13.3% to -20.3%. Other regions with a significant decrease in mean habitat suitability under all future climate scenarios were Region IX (Zamboanga Peninsula), Region X (Northern Mindanao), Region XII (SOuth Cotabato, Cotabato, Sultan Kudarat, SARangani, and GENeral Santos City - SoCCSKSarGen), Region IVB (MIndoro occidental and oriental, MArinduque, ROmblon, PAlawan - MiMaRoPa), and Bangsamoro Autonomous Region in Muslim Mindanao.

Discussion

The current study presented the first genus-level MaxEnt ecological niche model (ENM) for the fruticose lichen *Usnea* in the Philippines. It offered novel insights into its current and potential future biogeographic distribution in response to a changing climate, considering both optimistic and pessimistic scenarios. The performance of the models in terms of predictive accuracy was evaluated using Receiver Operating Characteristic (ROC) curves. All the generated MaxEnt models have high mean AUC scores ranging from 0.870 to 0.882, which is indicative of consistent high model performance across all scenarios. In ecological niche models, AUC values approaching 0.9 suggest excellent model reliability in terms of distinguishing suitable from unsuitable habitats (Phillips et al., 2006). These findings indicate that the models effectively captured the environmental correlates shaping the distribution of *Usnea* in the Philippine archipelago under current and select future projected climate scenarios. These values are consistent with previous MaxEnt-based studies on sensitive taxa under climatic stress (Li et al., 2020).

To determine the influence of the selected bioclimatic variables in shaping the predicted ecological niche of *Usnea* in the Philippines, the percent contribution and permutation importance of each were assessed (Table 2). Both are key metrics in MaxEnt modeling for evaluating the relative influence of environmental variables on ecological niche. Percent contribution quantifies the influence of each variable during model training, while permutation importance measures the sensitivity of the model to each variable by assessing the performance reduction that occurs when the variable values are randomized. These metrics provide complementary insights in assessing the quality and robustness of the generated MaxEnt models. A significant finding in the fine-tuning of the models is the shift in key environmental predictors. Under the current scenario, *Usnea* distributions are primarily driven by mean diurnal range (BIO2), or daily temperature variability, which highlights their sensitivity to microclimatic variations involving temperature and moisture. This highlights that daily temperature variability is the primary driver of *Usnea* habitat suitability under present-day climatic conditions. This cryptogamic trait is well-known for fruticose lichens such as *Usnea* (Jonsson et al., 2008).

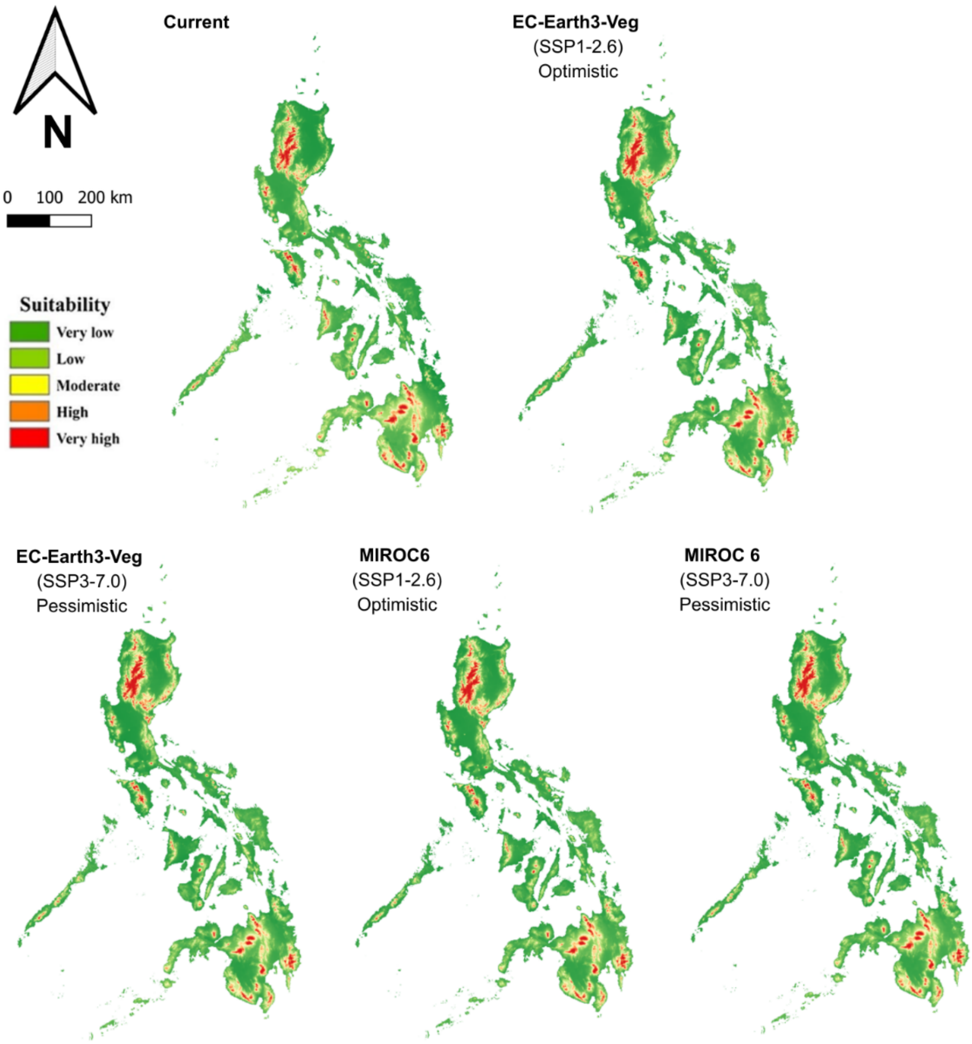

Fig. 2 - MaxEnt models for *Usnea* predicting its potential distribution under different climate scenarios. EC-Earth3-Veg and the Model for Interdisciplinary Research on Climate version 6 (MIROC6) were the Global Circulation Models used in the study.

However, under the future climate scenarios, the mean temperature of the warmest quarter (BIO10) emerged as the dominant predictive factor. This shift is suggestive of a growing ecological pressure brought by seasonal heat extremes, which can potentially be linked to increased desiccation stress and photobiont breakdown in lichens during warmer periods (Gasulla et al., 2021). These results thoroughly align with climate-driven vulnerability trends observed in other poikilohydric organisms, most especially for tropical montane ecosystems (Aptroot et al., 2021).

Contrastingly, there was a marked shift in variable influence in the future climate scenarios for both EC-Earth-3-Veg and MIROC6 General Circulation Models (GCMs) in the selected Representative Concentration Pathways (RCPs) of SSP1-2.6 and SSP3-7.0. For both EC-Earth-3-Veg and MIROC6 of RCP SSP1-2.6 and SSP3-7.0 scenarios, BIO10 became the dominant influencing variable, which contributed up to 99.7% in the training model and permutation importance of above 97%. This consistent dominance of BIO10 across models and scenarios pinpoint to the potential future shift in the sensitivity of *Usnea* to warm season temperatures. The previously dominant BIO2 in current climatic conditions dramatically decreased in both percent contribution and permutation importance, with below 1.0% and 1.2% values, respectively. Furthermore, BIO11 and BIO14 remained negligible across future models and projections for both percent contribution and permutation importance metrics, which indicates limited relevance under projected future climatic conditions. These findings demonstrate a climate-driven shift in the primary ecological factors affecting *Usnea* distribution, with a likely transition from daily temperature variability (BIO2) under current climatic conditions to a strong dependence on seasonal thermal maxima (BIO10) in future climates. These findings are key considerations for conservation planning with the warming and increasingly variable future climate scenarios. One of the consequences of increasing BIO10 on future climate scenarios is the climatically driven atmospheric vapour pressure deficit (VPD).

The generated MaxEnt ENM projections challenge conservative expectations of climate-driven biogeographic range contractions for sensitive lichens. While lichens in Arctic regions have faced indirect impacts due to climate change, it is hypothesized that their severe effects, which may lead to extinctions, are expected in high tropical mountain regions (Devkota et al., 2019). However, such extinctions have not yet been observed due to the absence of intensive surveys and/or limited research efforts in such areas (Aptroot et al., 2021). To date, limited studies show a correlation between global change and alterations in lichen habitats (Ellis, 2019). These pinpoint that lichens on tropical mountains are of high conservation concern (Allen and Lendemer, 2016). Despite these extrapolations from the literature, the MaxEnt ENM projections in the current study showed slight expansion in suitable habitats under all models, most pronounced in regions with high elevations. We propose that these findings may be explained primarily through microclimatic variations, which lead to thermal niche buffering. However, studies regarding the modelling and determination of the influence of microclimatic variation on the diversity of lichens in tropical montane ecosystems are virtually non-existent. Investigations into the impact of microclimate on lichen diversity are focused on alpine meadows and temperate forest ecosystems (Dent et al., 2013; Haesen et al., 2021). Dense forest cover, especially in upland ecosystems, can buffer temperature and humidity, thereby extending the thermal niches of organisms.

Usnea in the Philippines is mostly corticulous with various trees such as *Cocos nucifera* L., *Pinus* sp., and various dipterocarp species as commonly observed hosts. Thus, the increase in the habitat suitability of tree species that can harbor *Usnea* may also lead to the expansion in the habitat suitability of *Usnea*. Though the literature regarding this is still scarce for tropical montane ecosystems, the occurrence of this ecological phenomenon is well established in other biomes. In the Western Himalayan region, the upslope expansion of tree species such as *Abies spectabilis* (D. Don) Mirb. indicates climate-driven shifts in habitat suitability (Suwal et al., 2016). In South Korea, climate change is also projected to expand the suitable range of several coastal evergreen tree species, which supports the thermally driven forest area increase (Koo et al., 2017). Furthermore, species modeling in the boreal and alpine zones of Slovakia demonstrated that thermophilic tree species like oaks are projected to gain suitable habitat, which further implies potential altitudinal or polar expansion (Oravec et al., 2023). All these supports the hypothesis that the increase in the corticolous *Usnea* habitat suitability may also be driven by the potential increase in the suitability of their host trees.

While the MaxEnt Ecological niche models generated in the study provide foresight on the potential shifts in the range of *Usnea* in the Philippines, it is important to take note that *Usnea* is highly sensitive to microclimatic factors (Dent et al., 2013; Gauslaa, 2014), which ENM usually don't thoroughly consider because of free-air assumptions and coarse resolution (Lembrechts et al., 2019). Furthermore, the lack of a species-level distribution model for *Usnea* limits the niche specificity of the projected models; thus, species characterization in terms of ecological, physiological, and molecular parameters should be pursued to allow for the construction of more optimized and informative models.

A region-specific analysis of the habitat suitability of *Usnea* in the Philippines was also done to determine if the expansion of *Usnea* in all ENM is true when partitioned into the different regions. Changes in the habitat suitability of *Usnea* per region are expressed in Table 4 using mean habitat suitability as values. The generated maps reveal that the overall increase in habitat suitability is not true for all regions of the Philippine Archipelago. For example, the Panay and Negros islands have reduced suitability areas for *Usnea* (Supplementary Figure S2). The mountain ranges of western Panay Island, spanning the borders of Aklan, Antique, and Iloilo, and the volcanic mountains in the northern and southern portions of Negros Island, both have decreased habitat suitability for *Usnea*. These findings highlight the differential impact of a globally changing climate on specific regions of the Philippines.

Although the overall habitat suitability of *Usnea* in the Philippines was expected to increase, this general trend masks notable regional variations. Across both climate GCPs – EC-Earth-3-Veg and MIROC6, and the SSPs 1-2.6 and 3-7.0, several key regions experienced significant localized declines. Notably, Western Visayas (Region VI), Zamboanga Peninsula (Region IX), Northern Mindanao (Region X) SoCCSKSarGen (Region XII), and Bangsamoro Autonomous Region in Muslim Mindanao (BARMM) consistently show declining mean habitat suitability across all future projected climate models. The MiMaRoPa region (Region IVB) had varying changes in mean habitat suitability, with all GCPs and SSPs decreasing except EC-Earth-3-Veg for SSP 3-7.0 Largest mean habitat suitability decline occurred in Western Visayas under GCP EC-Earth-3-Veg under SSP 1-2.6. These regions are known to have characteristic warmer climates and have seasonally drier climates (Sander et al., 2017). This may cause exceeding upper thermal or desiccation thresholds that can be tolerated by *Usnea* species. This is supported by the finding that BIO10 (Mean Temperature of Warmest Month) is the predominant bioclimatic variable that influences the future ecological niche models. As epiphytic, fruticose lichens such as *Usnea* are highly sensitive to ambient humidity, air temperature, and pollution, even minor variations in the microclimatic characteristics of their environment can lead to reduced viability (Gauslaa, 2014). Furthermore, these regions have experienced significant deforestation, forest fragmentation, and land-use change. These will likely further compromise the availability of suitable microhabitats for *Usnea*. Reduced forest cover in these regions may also decrease the buffering capacity of forest microclimates, which then exposes *Usnea* thalli to harsher environmental fluctuations. Thus, the exploration of the microclimatic factors driving this potential decline of *Usnea* in these specific regions is also warranted.

The current study is the first to model current and future distributions of a lichen in the Philippine archipelago, and its findings provided strong support for the conservation of montane forest ecosystems. Therefore, as demonstrated in the study, the varying impact of the GCPs and SSPs using the fruticose lichen *Usnea* as a model organism can be used to explore the heavy impact of climate change on tropical montane ecosystems and their biodiversity. Most intact forest cover in the country with high biodiversity and species richness occurs in upland ecosystems (Dechimo and Buot, 2023; Llait, 2024). Despite the limitations of ecological niche models, these remain an important tool in forecasting the future projected impact of climate change on biodiversity. Cross-validation of ENM with ground-truthing surveys is then necessary. ENM coupled with ground-truthing can serve as powerful tools in calibrating species conservation strategies (Fois et al., 2018; Smith et al., 2021).

The current study is mainly exploratory due to the broader research gap surrounding lichens in the Philippines and the broader Southeast Asian Region. Lichen research in the Philippines and the wider Southeast Asian Region remains largely confined to taxonomic inventories, species checklists, and metabolite profiling, while ecological and spatial modelling remains scarce (Weerakoon et al., 2015; Galinato et al., 2018; Ellis, 2019). This is of particular concern as most of the Southeast Asian region is a biodiversity hotspot, which ideally requires extensive analysis of the regional distribution data for species. Furthermore, scarcity in regional distribution and occurrence datasets limits our understanding of how sensitive organisms such as lichens respond to climate gradients in these biodiverse yet understudied regions. Future frameworks should therefore integrate modelling techniques such as MaxEnt ENM to complement the existing literature and ongoing taxonomic and ecological research on lichens in the region. These will enable the development of frameworks for regional conservation prioritization in a changing climate. Furthermore, coupling ENM with more recent microclimatic data sets and models, as well as molecular phylogeographic techniques, can elucidate the mechanistic understanding of lichen resilience and adaptive capacity in tropical montane ecosystems. Lastly, the increase in understanding of lichen biogeography in Southeast Asia represents a crucial step toward integrating cryptogamic diversity into mainstream biodiversity conservation and climate adaptation strategies.

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Author Contributions

Conceptualization, J.R.M.M. and T.E.E.D.C.; methodology, J.R.M.M.; software, J.R.M.M. and N.H.A.D.; validation, J.R.M.M., N.H.A.D. and T.E.E.D.C.; formal analysis, J.R.M.M.; investigation, J.R.M.M.; resources, T.E.E.D.C.; data curation, J.R.M.M.; writing—original draft preparation, J.R.M.M.; writing—review and editing, J.R.M.M., N.H.A.D. and T.E.E.D.C.; visualization, J.R.M.M.; supervision, N.H.A.D. and T.E.E.D.C.; project administration, T.E.E.D.C.; funding acquisition, T.E.E.D.C. All authors have read and agreed to the published version of the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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