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Predicting the future distribution of *Astraeus* spp. in Thailand under climate change scenarios using MaxEnt modeling

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Abstract. *Khunkrai R, Suksavate W, Ngernsaengsaruay C, Nipitwattanaphon M, Sakolrak B, Phosri C, Nakpong L, Bunlerlerd K, Kaewgrajang T. 2025. Predicting the future distribution of* Astraeus *spp. in Thailand under climate change scenarios using MaxEnt modeling. Biodiversitas 26: 4662-4674.* Climate change poses a significant threat to global biodiversity by altering species distributions, disrupting ecological interactions, and transforming habitat suitability. This study investigates the potential impact of climate change on three ectomycorrhizal fungi species from the genus *Astraeus*—*A. asiaticus*, *A. odoratus*, and *A. sirindhorniae*—which form critical symbiotic relationships with tree species, particularly members of the Dipterocarpaceae family. These fungi contribute to forest ecosystem health by enhancing nutrient and water uptake in host plants and have considerable economic and medicinal value due to their edibility and pharmacological properties. Species Distribution Models (SDMs) were constructed using MaxEnt to predict the current and future potential distribution of the three *Astraeus* species in Thailand under three climate change scenarios: SSP1-2.6 (low emissions), SSP2-4.5 (intermediate), and SSP5-8.5 (high), for two periods, 2021-2040 and 2041-2060. The models incorporated key environmental variables, including tree cover, precipitation during the wettest month, and temperature range. The MaxEnt models demonstrated acceptable predictive performance, with AUC values ranging from 0.686 to 0.799. The most influential predictors were precipitation during the wettest month (Bio13) and tree cover. The results indicated that *A. asiaticus* currently occupies high-suitability habitats predominantly in northern Thailand and would have a relatively stable distribution with localized fluctuations. In contrast, *A. odoratus* and *A. sirindhorniae* are projected to experience pronounced reductions in high-suitability areas. By 2041-2060, under SSP5-8.5, suitable habitats for *A. odoratus* and *A. sirindhorniae* are expected to decline by approximately 69.02% and 87.59%, respectively. These reductions are associated with shifts from high-moisture to low-moisture forest types driven by rising temperatures and reduced precipitation. These findings highlight the importance of adaptive conservation strategies, including protecting suitable habitats, restoring degraded forests, and integrating climate-resilient forest management practices.

Keywords: Climate change, ectomycorrhizal fungi, habitat suitability, MaxEnt, shared socioeconomic pathways

INTRODUCTION

Climate change is a major driver of shifts in species distribution and global biodiversity, forcing many taxa to relocate as their habitats become inhospitable (Yue and Gao 2018; Fawzy et al. 2020). Rising temperatures and intensifying droughts are linked to declines in flowering frequency and reproductive output in certain plants (Deb et al. 2018; Dorji et al. 2020). Species unable to adapt to rapid environmental changes face higher extinction risk (Román-Palacios and Wiens 2020).

Tropical regions are particularly vulnerable, as ecosystems are highly diverse but sensitive to disturbances. Although tropical forests cover only 4% of the Earth's terrestrial surface, they host 15-25% of global biodiversity (Achard et al. 2002; Hansen et al. 2013). Rapid degradation and climate-induced stressors threaten these ecosystems. Southeast Asia, a biodiversity hotspot, faces ecological challenges from habitat loss, land-use change, and climate variability (Tan et al. 2022).

Regional climate models project substantial changes in Southeast Asia's monsoonal system, including greater variability in precipitation and temperature. Annual rainfall is expected to rise, with more frequent extreme events such as floods, droughts, and tropical cyclones (Breshears et al. 2008; Stocker et al. 2013). Average temperatures may increase 2-4°C by the end of the 21st century, with shifts in precipitation patterns (Loo et al. 2015; IPCC 2021). These changes could increase evapotranspiration, reduce soil water retention, and decrease moisture-dependent plant populations (Breshears et al. 2008).

In Thailand, climate change may severely alter phenology, disrupt ecological interactions, and reduce suitable habitats for endemic and climate-sensitive species

(Marks 2011; Trisurat et al. 2015, 2023; World Bank Group and the Asian Development Bank 2021). Impacts vary among species, necessitating adaptive conservation strategies (Trisurat et al. 2019; Pomoim et al. 2022).

Ectomycorrhizal fungi (EMF) are highly sensitive to environmental changes but play key roles in forests by facilitating nutrient uptake, enhancing drought resistance, and improving soil health (Lan et al. 2025). Warming and reduced soil moisture may alter EMF diversity and richness, weaken host–fungi interactions, and reduce tree growth and survival (Mucha et al. 2018; Fernandez et al. 2023; Nieves et al. 2024). Changes in host tree distributions can create mismatches with EMF, affecting forest resilience (Usman et al. 2021).

The genus *Astraeus*, known as barometer earthstars, includes hygroscopic EMF forming symbioses with Pinaceae, Fagaceae, and Dipterocarpaceae (Dewangan and Shahi 2024; Kaewgrajang et al. 2024). Eleven species exist globally; five occur in Asia: *A. hygrometricus, A. koreanus, A. asiaticus, A. odoratus,* and *A. sirindhorniae* (Phosri et al. 2014; Wijayawardene et al. 2020). In Thailand, three species—*A. asiaticus, A. odoratus,* and *A. sirindhorniae*—have been recorded (Phosri et al. 2004, 2007, 2014).

Astraeus species contribute to dipterocarp forest regeneration by supporting seedling establishment (Kaewgrajang et al. 2013, 2019; Suwannasai et al. 2020) and are consumed as edible mushrooms in Thailand and Laos (Mortimer et al. 2012; Vinayaka et al. 2024). They contain bioactive compounds with antimicrobial and therapeutic properties (Biswas et al. 2017; Basu et al. 2023; Pandey and Ghosh 2023), supporting ecosystem functions, food security, and traditional medicine.

Despite their importance, the spatial ecology of *Astraeus* under climate change remains underexplored. Research has focused on taxonomy, phylogeny, and ecological interactions (Phosri et al. 2014; Suwannasai et al. 2020; Pandey and Ghosh 2022), with few predictive modeling studies. No comprehensive SDM exists for *Astraeus* in Thailand or Southeast Asia. This study applies MaxEnt SDM to predict current and future distributions under climate scenarios. By integrating climatic, edaphic, and ecological predictors, it advances fungal SDM methodology and informs biodiversity conservation and sustainable fungal management.

MaxEnt, widely used for presence-only data, has modeled plant distributions in Thailand (Promnikorn et al. 2019; Pomoim et al. 2022; Trisurat et al. 2023) and fungi (Buebos-Esteve et al. 2023). This study uses MaxEnt to predict distributions of three *Astraeus* species under RCP 2.6, 4.5, and 8.5, identify suitable habitats, key environmental variables, and provide guidance for conservation and sustainable cultivation under climate change.

MATERIALS AND METHODS

Occurrence data of *Astraeus* species

Occurrence records for three *Astraeus* species, *Astraeus asiaticus*, *A. odoratus*, and *A. sirindhorniae*, were compiled from both published literature (Phosri et al. 2014; Bodeerat 2018; Saensuk and Suntararak 2018; Suntararak 2019; Kaewgrajang et al. 2024) and field data provided graciously by personnel from national parks, protected forest reserves, forest parks, and heads of research stations across various locations. As such, the field data collection was not conducted directly by the authors. All field records were pre-identified to species level based on morphological characteristics according to taxonomic criteria established by Phosri et al. (2004, 2007, 2014) and Pandey and Ghosh (2023). After removal of duplicate records, a total of 125 unique occurrence points remained, which included 26 locations for *A. asiaticus*, 83 for *A. odoratus*, and 16 for *A. sirindhorniae* (Figure 1). These georeferenced data served as input for the SDM.

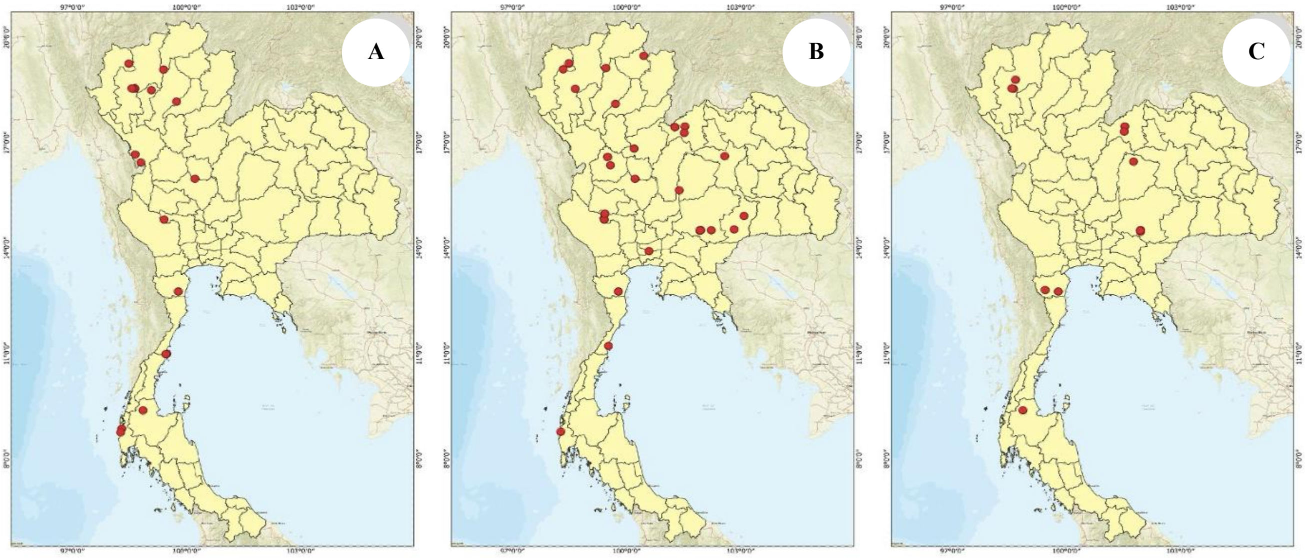

Figure 1. Allocations of 125 *Astraeus* sampling points used in this study. A. *Astraeus asiaticus*, B. *Astraeus odoratus*, C. *Astraeus sirindhorniae*

Table 1. Environmental variables used in the species distribution modeling of *Astraeus* spp. in Thailand

Environmental variables	Code	Data source	Original resolution	Resampled resolution
Climatic variables				
Max temperature of warmest month	bio5	WorldClim	30 arc-seconds	1 km × 1 km
Temperature annual range	bio7	WorldClim	30 arc-seconds	1 km × 1 km
Precipitation of wettest month	bio13	WorldClim	30 arc-seconds	1 km × 1 km
Precipitation of driest month	bio14	WorldClim	30 arc-seconds	1 km × 1 km
Precipitation seasonality	bio15	WorldClim	30 arc-seconds	1 km × 1 km
Land cover variables				
Dry dipterocarp forest	DDF	Forest Land Management Office	30 meters	1 km × 1 km
Dry evergreen forest	DEF	Forest Land Management Office	30 meters	1 km × 1 km
Mixed deciduous forest	MDF	Forest Land Management Office	30 meters	1 km × 1 km
Percent tree cover	tcover	Google Earth Engine	30 arc-seconds	1 km × 1 km
Edaphic variables				
Clay content	clay	OpenGeoHub	30 arc-seconds	1 km × 1 km
Sand content	sand	OpenGeoHub	30 arc-seconds	1 km × 1 km

Environmental variables

The distribution models were developed using 11 environmental predictors (Table 1), which included climatic, edaphic, and vegetation-related variables, as listed in Table 1. Climatic variables were obtained from the WorldClim 2.1 database (https://www.worldclim.org/), based on long-term averages (1970-2000) at 30 arc-second spatial resolution (Fick and Hijmans 2017). Soil-related variables were sourced from OpenLandMap (https://opengeohub.org/), while forest type data were acquired from the Royal Forest Department of Thailand (RFD 2018). Percent tree cover layers were accessed and processed through the Google Earth Engine platform (Sexton et al. 2013; Gorelick et al. 2017).

Preprocessing and variable selection

To reduce multicollinearity among bioclimatic variables, Pearson correlation analysis was conducted. Pairs of variables with high correlation coefficients (r>0.85) were considered collinear and subjected to further evaluation based on ecological relevance (Pradhan 2016; Pradhan and Setyawan 2023). For instance, among precipitation-related variables, bio12 (annual precipitation) and bio13 (precipitation of the wettest month) exhibited a high correlation (r: 0.90); bio12 was excluded in favor of bio13, which better captures the moisture peaks relevant to fungal activity. Similarly, bio13 and bio16 (precipitation of the wettest quarter) were highly correlated (r: 0.99), leading to the exclusion of bio16.

In terms of temperature variables, bio5 (maximum temperature of the warmest month) and bio10 (mean temperature of the warmest quarter) exhibited a strong correlation (r: 0.88); bio10 was excluded as bio5 better represents extreme thermal conditions relevant to physiological stress. Likewise, bio4 (temperature seasonality) and bio7 (temperature annual range) were correlated (r: 0.87); bio7 was retained for its clearer ecological interpretation.

Variance Inflation Factor (VIF) analysis was also conducted to identify and remove variables with VIF values greater than 5, further reducing collinearity and ensuring model stability. Following these steps, five environmental variables were selected for model development: bio5, bio7, bio13, bio14 (precipitation of the driest month), and bio15 (precipitation seasonality) (Pradhan 2016; Pradhan and Setyawan 2023).

Species distribution model evaluation

MaxEnt version 3.4.4 was used to construct species distribution models using the presence records and selected environmental predictors. Modeling was performed in RStudio (version 4.2.1) via the ‘dismo’ package (Hijmans et al. 2017; Davoudi et al. 2023). The models were run with default settings, including 5,000 background points and 10 bootstrap replicates to account for any uncertainty. A random split of the occurrence data was applied, using 75% of the points for model training and 25% for testing (Trisurat et al. 2023). Model performance was evaluated using the Area Under the Curve (AUC), where values closer to 1.0 indicate stronger predictive accuracy (West et al. 2016). Habitat suitability outputs were generated in cloglog format and interpreted using two threshold criteria: (i) minimum training presence and (ii) maximum training sensitivity plus specificity. Suitability was categorized into three classes: Low suitability locations below the minimum cloglog threshold, indicating unsuitable environments; Moderate suitability locations within the threshold range, representing marginal or transitional habitats; and High suitability locations above the maximum threshold, indicating optimal conditions for establishment and growth. Final habitat suitability maps were visualized and produced in QGIS version 3.28 (Figure 2).

Forecasting the future distribution based on specific scenarios

To evaluate potential future changes in species distributions, Shared Socioeconomic Pathway (SSP) scenarios SSP1-2.6, SSP2-4.5, and SSP5-8.5 were selected, corresponding to low-, medium-, and high-emissions trajectories, respectively. Climate projections were sourced from the Coupled Model Intercomparison Project Phase 6 (CMIP6). Distributions were simulated for two future timeframes: near-term (2021-2040) and mid-term (2041-2060). All future models incorporated the same environmental layers viz. climate variables, edaphic data, forest types, and tree cover, to ensure consistency across temporal scales.

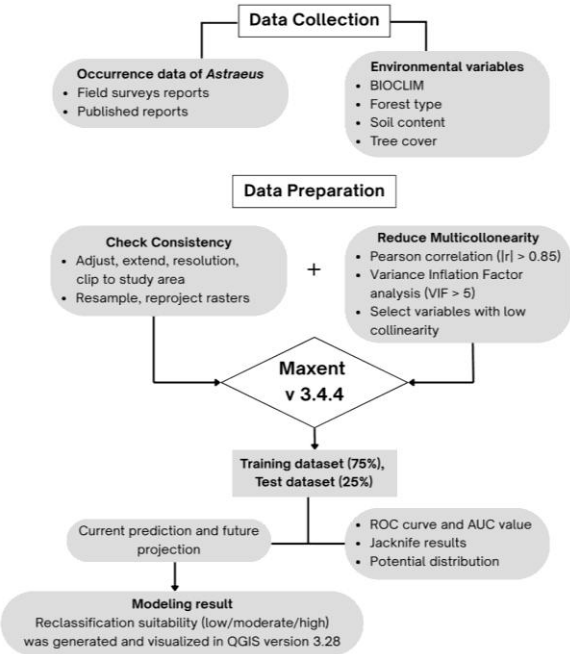

Figure 2. Flowchart of the methodology used for Maxent modeling

RESULTS AND DISCUSSION

Important environmental factors influent on *Astraeus* distribution model

Initially, a Pearson's correlation analysis was conducted to eliminate any multicollinearity among the environmental variables. Variables with a correlation coefficient greater than 0.85 were excluded, resulting in the retention of 11 out of 21 variables that were used to model the distribution of *Astraeus* species (Table 1). The MaxEnt models for *A. asiaticus*, *A. odoratus*, and *A. sirindhorniae* demonstrated reliable predictive performance. The omission rates for test datasets (turquoise lines) closely aligned with the predicted omission rates (black lines) derived from the MaxEnt model, indicating a good model fit and low overfitting (Figures S1.B, S2.B, S3.B). The area under the receiver operating characteristic curve (AUC) values for the training and test datasets were 0.870 (test: 0.699) for *A. asiaticus*, 0.854 (test: 0.686) for *A. odoratus*, and 0.923 (test: 0.799) for *A. sirindhorniae*, confirming a strong discriminatory power. Receiver Operating Characteristic (ROC) plots further supported model robustness, as the curves were consistently above the random prediction line (Figures S1.A, S2.A, S3.A). Omission rate plots using the 10th percentile training presence threshold indicated that predicted omission rates closely matched test data, further indicating a good model generalization.

The Jackknife test was used to evaluate the importance of each environmental predictor (Figure S4). In the resulting plots, turquoise bars represent the model gain when a given variable was excluded, blue bars indicate the gain when the variable was used in isolation, and red bars correspond to the gain when all variables were included. For *A. asiaticus*, tree cover (tcover) emerged as the most informative predictor when considered individually, followed by precipitation of wettest month (bio13). In the case of *A. odoratus*, precipitation of wettest month (bio13) provided the highest gain, with Precipitation seasonality (bio15) as the secondary contributor. For *A. sirindhorniae*, max temperature of warmest month (bio5) was the most influential variable, followed by precipitation of wettest month (bio13). Furthermore, the variable contribution using percent contribution and permutation importance (Table 2) indicated that percent tree cover, precipitation of the wettest month, and temperature variables were the most influential factors in determining the distribution of the three species of *Astraeus*. For *A. asiaticus*, the top three predictors were percent tree cover (48.6% contribution, 59.2% permutation importance), precipitation of the wettest month (bio13; 22.8%, 10.2%), and temperature annual range (bio7; 15.4%, 7.9%), with a combined contribution of 86.8%. This species had a preference for areas with 20-60% tree cover, 100-200 mm of precipitation during the wettest month, and mean annual temperatures between 22-24°C (Figure S5).

The distribution of *A. odoratus* was primarily influenced by precipitation of the wettest month (bio13; 23.6%, 22.2%), dry dipterocarp forest (DDF; 19.0%, 2.5%), and percent tree cover (18.9%, 19.4%), with a cumulative contribution of 61.5% (Table 2). This species predominantly occurred in areas with 200-220 mm of precipitation during the wettest month, while higher levels reduced its likelihood of occurrence (Figure S2.A). Suitable habitats were associated with the occurrence of dry deciduous forest coverage ranging from 20-100%, and tree cover between 10-80% (Figures S6.B and S6.C). For *A. sirindhorniae*, the most influential variables were precipitation of the wettest month (bio13; 43.9%, 49.9%), percent tree cover (30.6%, 8.4%), and the maximum temperature during the warmest month (bio5; 13.9%, 25.9%), contributing a total of 88.4% to the model (Table 2). This species preferred habitats with 100-200 mm of precipitation in the wettest month (Figure S7.A), 70-100% tree cover, and a maximum temperature between 25-32°C during the warmest month (Figures S7.B and S7.C). Similar to *A. odoratus*, occurrence probability declined at higher precipitation levels. Ecologically, these results indicate that tree cover provides essential substrate and microhabitat conditions for growth and reproduction, while precipitation and temperature regulate moisture availability and seasonal activity, together shaping habitat suitability, potential range, and local abundance of the three *Astraeus* species.

Suitable habitats for *Astraeus* spp. in the current climate condition

The species distribution models under current climate conditions revealed distinct habitat suitability patterns for the three *Astraeus* species in Thailand. *Astraeus asiaticus* exhibits a broad distribution range of moderate suitability, with limited extent of high-suitability zones that were primarily concentrated in the northern region of the country.

Table 2. Percent contribution and permutation importance of the various environmental factors on the occurrence of *Astraeus* species in the models

Code	Percent contribution % (Permutation importance)		
	A. asiaticus	*A. odoratus*	*A. sirindhorniae*
tcover	48.6 (59.2)	18.9 (19.4)	30.6 (8.4)
bio13	22.8 (10.2)	23.6 (22.2)	43.9 (48.2)
bio7	15.4 (7.9)	9.9 (8.9)	1.2 (3.7)
DDF	4.0 (0.6)	19.0 (2.5)	0.3 (0.6)
DEF	2.9 (4.6)	7.7 (4.4)	1.5 (1.8)
bio14	2.4 (1.4)	0.3 (0.1)	1.6 (1.9)
MDF	1.8 (6.3)	0.8 (0.7)	6.1 (6.8)
clay	1.8 (4.7)	1.0 (3.2)	0.2 (0.1)
bio15	0.4 (5.1)	13.5 (26.0)	0.5 (2.7)
bio5	-	1.6 (3.9)	13.9 (25.9)
sand	-	3.7 (8.6)	-

These high-suitability areas span approximately 66,038 km², accounting for 10.63% of the study area (Table 3; Figure 3.A), and are predominantly located within the dry dipterocarp forests, dry evergreen forests, and mixed deciduous forests. The species is primarily distributed in the northern provinces, particularly in Chiang Mai, where favorable forest types and environmental conditions support its growth.

Similarly, *A. odoratus* demonstrates a widespread range of moderate suitability across Thailand. However, its high-suitability habitat is relatively more extensive compared to *A. asiaticus*, encompassing approximately 167,280 km² or 26.92% of the study area (Table 3; Figure 4.A). High-suitability regions for *A. odoratus* are distributed across northern, northeastern, and central Thailand. The species frequently inhabits dry dipterocarp and mixed deciduous forests. Prominent areas of occurrence include mountainous forest corridors connecting Mae Hong Son, Chiang Mai, and Tak in the north, as well as border zones between Loei, Chaiyaphum, and Phetchabun provinces, extending into Nakhon Ratchasima in the northeast.

In contrast, *A. sirindhorniae* has the largest area categorized as low suitability among the three species. Nonetheless, its suitable habitats are concentrated in the northern, northeastern, and central regions, with additional patches identified in the south. High- and moderate-suitability areas for *A. sirindhorniae* cover approximately 133,412 km², representing 21.47% of the study area (Table 3; Figure 5.A). These habitats are typically associated with dry evergreen forests, montane forests, and dry dipterocarp forests, particularly in fragmented or minimally disturbed patches that provide relatively stable microclimatic conditions. The species is most commonly found in Chiang Mai in the north, Phetchaburi and Prachuap Khiri Khan in the central region, and Nakhon Ratchasima in the northeast. Southern distributions include scattered sites in Surat Thani, Nakhon Si Thammarat, Satun, and Songkhla provinces.

Comparative analysis of the three species reveals that *A. odoratus* occupies the largest high-suitability area, more than twice that of *A. asiaticus*, indicating a broader ecological amplitude and greater adaptability to varied environmental conditions. In contrast, *A. asiaticus* is confined to the smallest high-suitability zone, suggesting a narrower ecological niche and more specific habitat requirements. *Astraeus sirindhorniae* exhibits an intermediate extent of high-suitability area; however, a substantial portion of its predicted distribution falls within low-suitability zones, highlighting a more restricted and patchy occurrence.

Distribution of suitable habitat under global warming scenarios

Species distribution models incorporating projected bioclimatic, edaphic, and land cover variables were used to evaluate the future habitat suitability of *Astraeus* species under three climate change scenarios viz. SSP1-2.6, SSP2-4.5, and SSP5-8.5, across two future timeframes: 2021-2040 and 2041-2060. The results indicate that climate change will markedly influence the spatial extent and distribution patterns of suitable habitats for all three species, with both contractions and expansions observed across suitability classes (Tables 3-4, Figures 3-5).

For *A. asiaticus*, a consistent reduction in high-suitability habitat is projected under most scenarios. During 2021-2040, high-suitability areas are predicted to decline by 30.31% under SSP1-2.6 and by 6.70% under SSP5-8.5, whereas a modest increase of 23.75% is observed under SSP2-4.5. By 2041-2060, the high-suitability zones would continue to decline by 23.88% under SSP1-2.6, while showing gains of 14.98% and 56.55% under SSP2-4.5 and SSP5-8.5, respectively. Despite these fluctuations, suitable habitats remain largely fragmented and confined to the northern parts of Thailand. While *A. asiaticus* currently occurs in both mixed deciduous and dry evergreen forests, projections as per SSP5-8.5 (2041-2060) suggest an expansion of mixed deciduous forest and a reduction in dry evergreen forest. This implies that future persistence of the species may increasingly rely on the stability of mixed deciduous forest ecosystems.

Astraeus odoratus is projected to experience the most extensive habitat contraction among the three species, particularly in high-suitability areas. Between 2021-2040, these areas would decrease by 55.39% under SSP1-2.6 and 61.09% under SSP5-8.5. In 2041-2060, further reductions of 72.55% and 69.02% are projected under SSP1-2.6 and SSP5-8.5, respectively. Although a slight increase in high-suitability area is observed under SSP2-4.5 in the later period, it does not compensate for the losses recorded in other scenarios. Concurrently, low-suitability zones would expand significantly, particularly under SSP5-8.5, with a projected increase of 91.42% by 2041-2060. This shift reflects a potential ecological transition for *A. odoratus*, which is presently associated with both dry dipterocarp and mixed deciduous forests. The predicted decline in mixed deciduous forest suggests a possible shift toward drier habitats, favoring the drought-resilient dry dipterocarp forest type. This adaptation trend indicates the species' potential response to aridification and increasing climate stress.

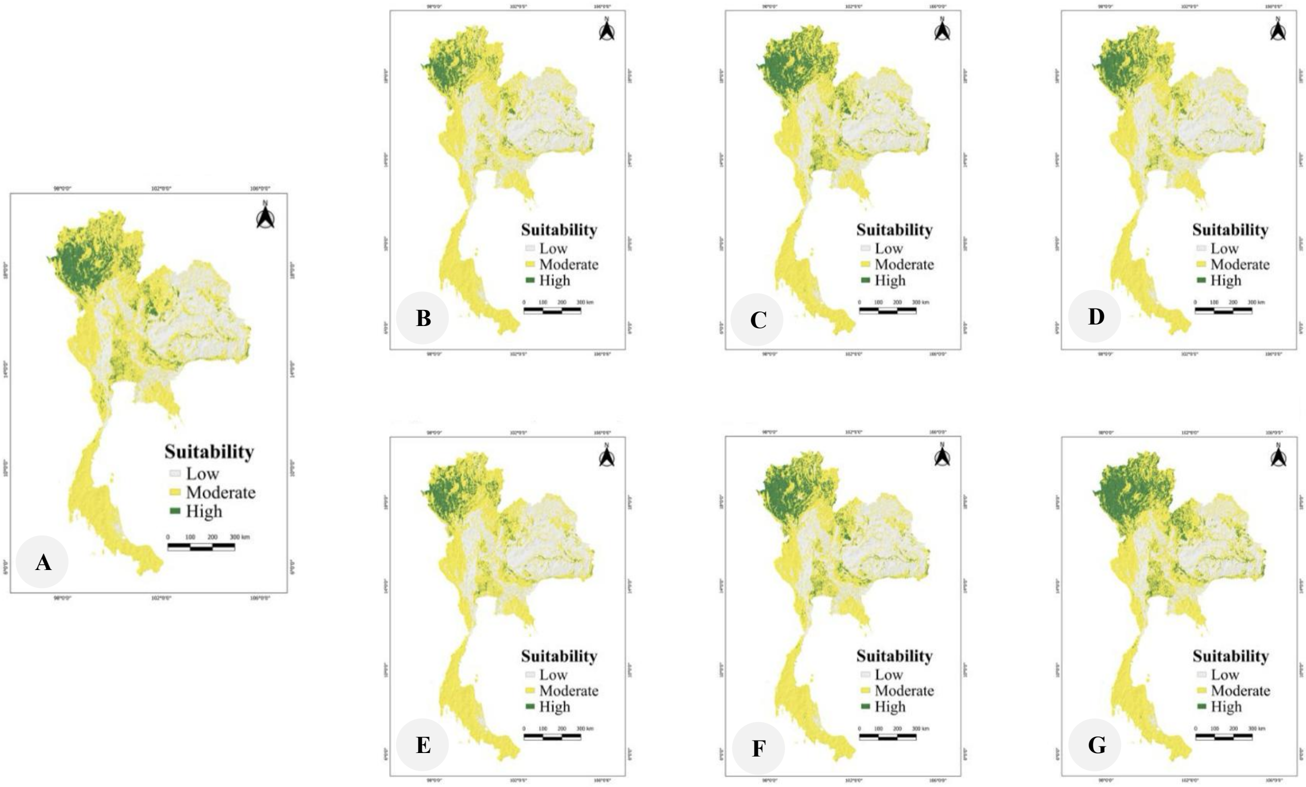

Figure 3. Projected habitat suitability for *Astraeus asiaticus* under current and future climate scenarios. A: Current climatic suitability, B, E: Future suitability under SSP1-2.6, C, F: Under SSP2-4.5, D, G: Under SSP5-8.5 scenarios

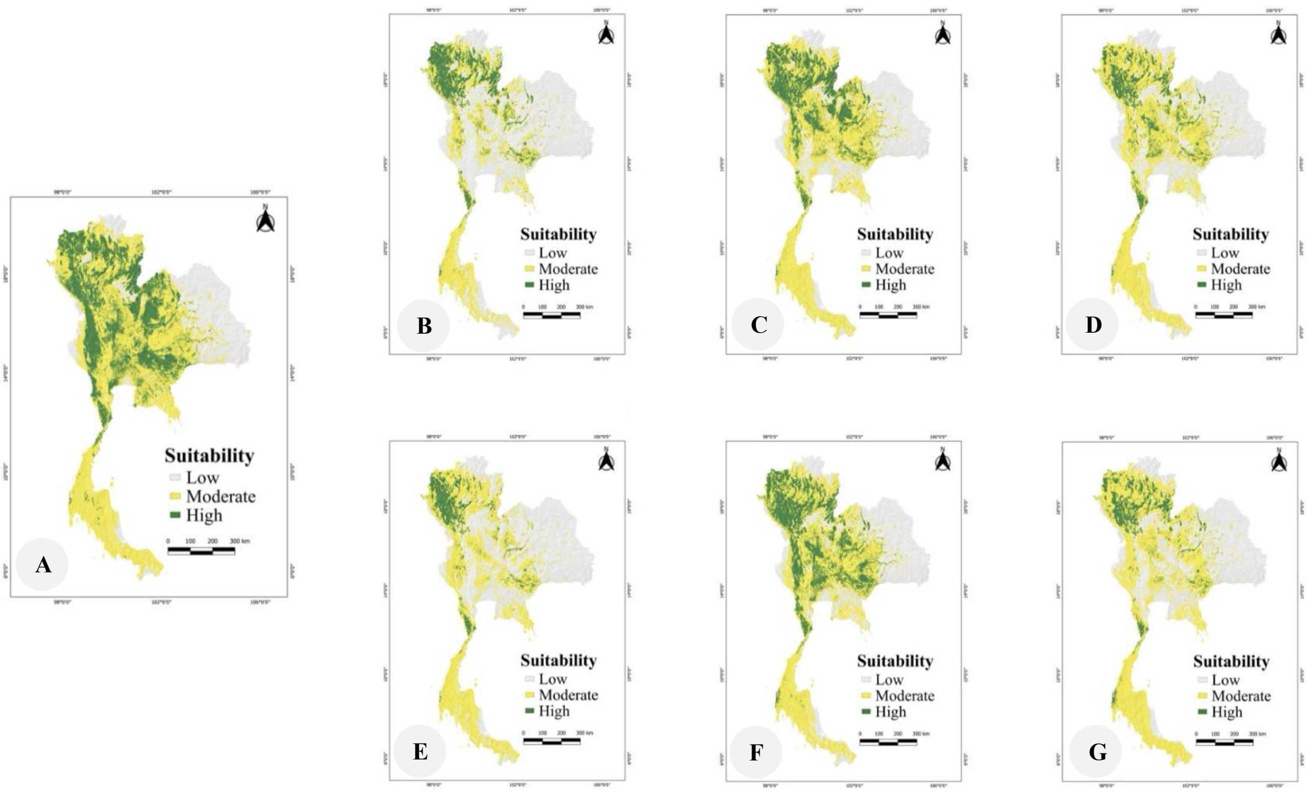

Figure 4. Potential habitat suitability of *Astraeus odoratus* under current and future climate scenarios. A: Current climatic suitability, B, E: Future projections under SSP1-2.6, C, F: Under SSP2-4.5, D, G: Under SSP5-8.5 scenarios

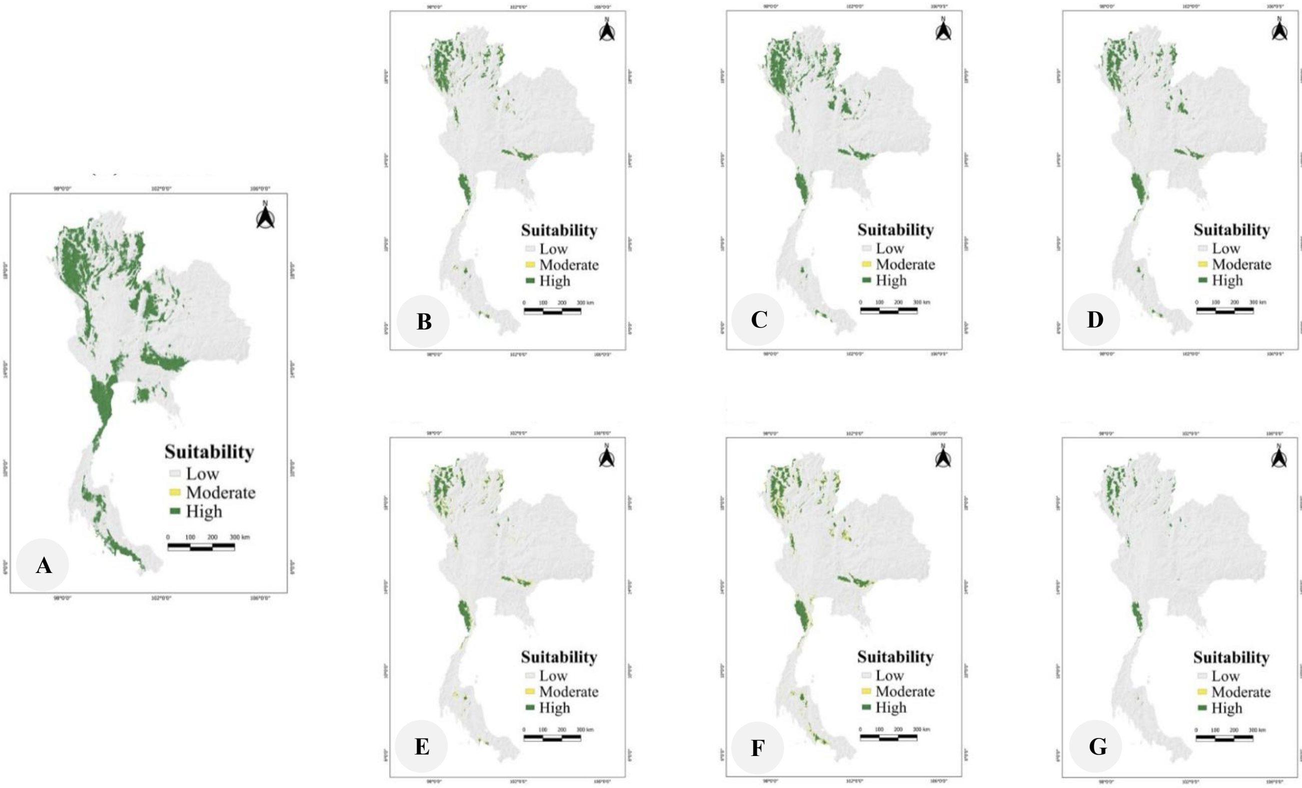

Figure 5. Potential habitat suitability of *Astraeus sirindhorniae* under current and future climate scenarios. A: Current climatic suitability, B, E: Future projections under SSP1-2.6, C, F: Under SSP2-4.5, D, G: Under SSP5-8.5 scenarios

Table 3. The habitat suitability of different *Astraeus* species under current and future climate conditions (SSP1-2.6, SSP2-4.5, and SSP5-8.5) for the period 2021-2040. The predicted increase/decrease in suitable habitat for each classification is indicated in brackets

Species	Suitability level	Suitable habitat (km²)			
		Current	SSP1-2.6 (2021-2040)	SSP2-4.5 (2021-2040)	SSP5-8.5 (2021-2040)
Astraeus asiaticus	Low	191,207	234,856 (+22.83%)	214,770 (+12.32%)	239,507 (+25.26%)
	Moderate	364,184	340,554 (-6.49%)	324,937 (-10.78%)	320,306 (-12.05%)
	High	66,038	46,019 (-30.31%)	81,722 (+23.75%)	61,616 (-6.70%)
Astraeus odoratus	Low	144,662	363,087 (+150.99%)	212,959 (+47.21%)	271,239 (+87.50%)
	Moderate	309,487	183,722 (-40.64%)	290,904 (-6.00%)	285,099 (-7.88%)
	High	167,280	74,620 (-55.39%)	117,566 (-29.72%)	65,091 (-61.09%)
Astraeus sirindhorniae	Low	488,017	578,689 (+18.58%)	558,661 (+14.48%)	580,132 (+18.88%)
	Moderate	0	4,204 (+)	2,740 (+)	2,227 (+)
	High	133,412	38,536 (-71.12%)	60,028 (-55.01%)	39,070 (-70.71%)

Table 4. The habitat suitability of different *Astraeus* species under current and future climate conditions (SSP1-2.6, SSP2-4.5, and SSP5-8.5) for the period 2041-2060. The predicted increase/decrease in suitable habitat for each classification is indicated in brackets

Species	Suitability level	Suitable habitat (km²)			
		Current	SSP1-2.6 (2041-2060)	SSP2-4.5 (2041-2060)	SSP5-8.5 (2041-2060)
Astraeus asiaticus	Low	191,207	220,709 (+15.43%)	215,091 (+12.49%)	180,934 (-5.37%)
	Moderate	364,184	350,454 (-3.77%)	330,410 (-9.27%)	337,115 (-7.43%)
	High	66,038	50,266 (-23.88%)	75,928 (+14.98%)	103,380 (+56.55%)
Astraeus odoratus	Low	144,662	320,747 (+121.72%)	206,863 (+43.00%)	276,911 (+91.42%)
	Moderate	309,487	254,758 (-17.68%)	281,696 (-8.98%)	292,693 (-5.43%)
	High	167,280	45,924 (-72.55%)	132,870 (-20.57%)	51,825 (-69.02%)
Astraeus sirindhorniae	Low	488,017	588,445 (+20.58%)	575,222 (+17.87%)	603,973 (+23.76%)
	Moderate	0	7,730 (+)	12,228 (+)	905 (+)
	High	133,412	25,254 (-81.07%)	33,979 (-74.53%)	16,551 (-87.59%)

Astraeus sirindhorniae is expected to experience the highest reductions in high-suitability habitats under future climate conditions. By 2021-2040, these areas would decline by 70.71% under SSP5-8.5, and the trend worsening by 2041-2060, with projected declines of 81.07% under SSP1-2.6 and 87.59% under SSP5-8.5. Although moderate-suitability areas are projected to emerge in all scenarios, they remain spatially limited. In contrast, low-suitability habitats are expected to expand by 14.48% to 23.76%, resulting in a more restricted and fragmented distribution range. By the end of the mid-century projection (2041-2060), high-suitability habitats for all three *Astraeus* species would still be concentrated in the northern parts of Thailand, but their spatial extent will greatly diminish, particularly under the high-emissions SSP5-8.5 scenario. This pattern highlights the significant vulnerability of ectomycorrhizal fungi to warming in tropical regions. For *A. sirindhorniae*, suitable habitats are projected to increasingly consolidate within the dry evergreen forests under SSP2-4.5 by 2041-2060, relative to the previously favorable environments such as montane rainforests and dry dipterocarp forests. This suggests a contraction into climatically more stable forest types, potentially reflecting an ecological refugia effect.

Discussion

Astraeus mushrooms serve important ecological and economic functions in Southeast Asia, where they form ectomycorrhizal associations with trees, contributing to forest health and soil nutrient cycling (Phosri et al. 2014; Punsung et al. 2024). In addition to ecological significance, *Astraeus* species are highly valued as edible fungi and possess pharmacologically active compounds with potential medicinal applications (Biswas et al. 2017; Ung and Chen 2024). The present study is the first of its kind to explore the environmental determinants governing the distribution of three *Astraeus* species found in Thailand, *A. asiaticus*, *A. odoratus*, and *A. sirindhorniae*, and to predict their suitable habitat under future climate scenarios using species distribution modeling.

The results demonstrate that percent tree cover, precipitation during the wettest month, and temperature-related variables are the most influential factors in determining the distributions. Among these, tree cover emerged as a key driver, aligning with the ecological dependence of ectomycorrhizal fungi on host tree species for carbon exchange and microhabitat stability (Khullar and Reddy 2019). Host tree identity and forest composition can strongly influence the EMF communities, as different tree species support distinct fungal assemblages (Otsing et al. 2021). In Thailand, *Astraeus* species are predominantly associated with dipterocarp forests (Phosri et al. 2004, 2007, 2014), which dominate the country's lowland forest landscape. However, climate-induced stress, particularly increased drought frequency and reduced seedling survival, may cause a reduction in the dipterocarp tree populations, especially those that have a lower tolerance to drought, potentially disrupting host-fungus associations. Consequently, these shifts may affect the symbiotic nutrient exchange and overall forest productivity, highlighting the ecological consequences of changes in host-fungus interactions (Ichie et al. 2023; Trisurat et al. 2023).

Interestingly, the species exhibited differential sensitivities to tree cover. *Astraeus asiaticus* was found to tolerate lower tree cover densities, suggesting a broader tolerance for forest structure, while *A. sirindhorniae* preferred areas with high canopy cover. This indicates that deforestation and canopy loss may disproportionately affect the latter species. In terms of climatic variables, rainfall and temperature significantly influenced species-specific distributions. These findings are consistent with previous researches showing that fungal phenology, diversity, and productivity are highly sensitive to rainfall and temperature regimes (Karavani et al. 2018; Procházka et al. 2023). For instance, annual precipitation has been reported as a strong determinant of *Tricholoma matsutake* distribution (Guo et al. 2017), and factors such as temperature and soil pH shape the spatial patterns of European truffles (*Tuber* spp.) (Čejka et al. 2020). Similar patterns have been observed in other fungal and plant distributions in Southeast Asia, indicating that rainfall and temperature are usually the key determinants of habitat suitability across taxa. In our study, *A. odoratus* was shown to require the highest levels of precipitation among the three species, while *A. sirindhorniae* had the broadest thermal tolerance, with optimum temperatures that were higher than those preferred by *A. asiaticus* and *A. odoratus*. Comparable patterns have been observed in other fungal and plant distributions across Southeast Asia. For instance, Buebos-Esteve et al. (2023) modeled *Ganoderma lucidum* and *Gynostemma pentaphyllum* in the Philippines using MaxEnt and GARP (Genetic Algorithm for Rule-set Production), two widely applied species distribution modeling approaches, and found that precipitation and temperature were the main determinants of habitat suitability under future climate scenarios. Pradhan (2024) also reported precipitation of warmest quarter and mean temperature of wettest quarter to contribute majorly in the potential distribution of *Ophiocordyceps sinensis*. These findings are in agreement with our results for the *Astraeus* species, suggesting that climate-driven environmental variables consistently shape species distributions in the region. These interspecific differences highlight the importance of accounting for species-specific climatic requirements and adaptive responses when predicting distributional changes under climate change.

The habitat suitability modeling revealed distinct ecological strategies among the three species. *Astraeus odoratus*, which occupies the largest area of high-suitability habitat, appears to be the most ecologically flexible, capable of inhabiting a wide range of environmental conditions and forest types across the northern, northeastern, and central parts of Thailand. Conversely, *A. asiaticus* exhibits a narrower distribution, with a preference for cooler montane environments, reflecting its higher sensitivity to environmental changes. *Astraeus sirindhorniae* demonstrates an intermediate distribution, with large areas of low suitability but substantial high-suitability zones in fragmented forests with relatively stable microclimates. These ecological patterns have implications for sustainable harvesting, as species with restricted or fragmented habitats may be more vulnerable to overcollection. Furthermore, these important implications for species-specific conservation and cultivation efforts, particularly for supporting sustainable harvests of wild mushrooms and preserving forest symbioses.

Projections under future climate scenarios (SSP1-2.6, SSP2-4.5, and SSP5-8.5) resulted in divergent responses among the species, reflecting differences in ecological plasticity and climate resilience. *Astraeus odoratus* exhibited a moderate ability to persist across scenarios, although high-suitability habitats declined considerably, especially under the high-emissions (SSP5-8.5) scenario. The species appears to be shifting toward more drought-tolerant dry dipterocarp forests, suggesting an adaptation to increasingly arid conditions. In contrast, *A. asiaticus* displayed a significant reduction in suitable habitat under low and intermediate emission scenarios, although some recovery was projected under SSP5-8.5, indicating possible range expansion into newly emerging forest types, such as mixed deciduous forests. Nonetheless, its overall fragmentation suggests vulnerability. *Astraeus sirindhorniae* was the most sensitive among the three, and is predicted to undergo extensive habitat contraction under all future scenarios, with high-suitability zones becoming increasingly restricted to dry evergreen forests. The decline of montane and dipterocarp habitats further reinforces concerns over the species' long-term persistence. These projections highlight the potential impacts of climate change on forest symbioses, as altered host tree distributions may cascade to affect the EMF communities.

Overall, these findings highlight the pressing threat that climate change poses to ectomycorrhizal fungi in the tropical forest ecosystems. The projected shifts in habitat suitability for the three *Astraeus* species, driven primarily by temperature, precipitation, and vegetation structure, point to significant alterations in ecological niches and species-habitat relationships. The anticipated expansion of drought-tolerant dry dipterocarp forests and concurrent contraction of mixed deciduous and montane forests may exacerbate these trends.

In conclusion, this study emphasizes the critical influence of environmental variables, particularly percent tree cover, precipitation during the wettest month, and annual temperature range, in shaping the present and future distribution of *Astraeus* species in Thailand. Among these, precipitation species the wettest month (Bio13) and annual temperature range (Bio7) consistently emerged as the most influential predictors in the models, as shown by the variable contribution and jackknife tests. The modeling results predict a substantial contraction in high-suitability habitats, particularly for *A. sirindhorniae* and *A. odoratus*, under future climate scenarios, whereas *A. asiaticus* shows relatively greater stability with suitable areas projected to persist in northern and northeastern Thailand. These findings highlight the urgent need for adaptive conservation planning, including the protection and restoration of key forest habitats, especially in northern and northeastern Thailand, where suitable habitats are projected to persist. Our projections also suggest that the species will experience notable declines in central and southern regions with regards to habitat suitability, highlighting the importance of regional prioritization in land-use planning. These observations underline the importance of adaptive conservation planning, including sustainable harvesting strategies, protection and restoration of key forest habitats, and monitoring of symbiotic interactions, to maintain both ecological functionality and economic benefits. Furthermore, expanding our understanding of the symbiotic relationships, ecological thresholds, and adaptive potential of *Astraeus* species will be essential for developing sustainable forest management practices and informed cultivation strategies. Such efforts are critical to ensure the continued ecological functionality and food security role of ectomycorrhizal fungi in the face of accelerating climate change.

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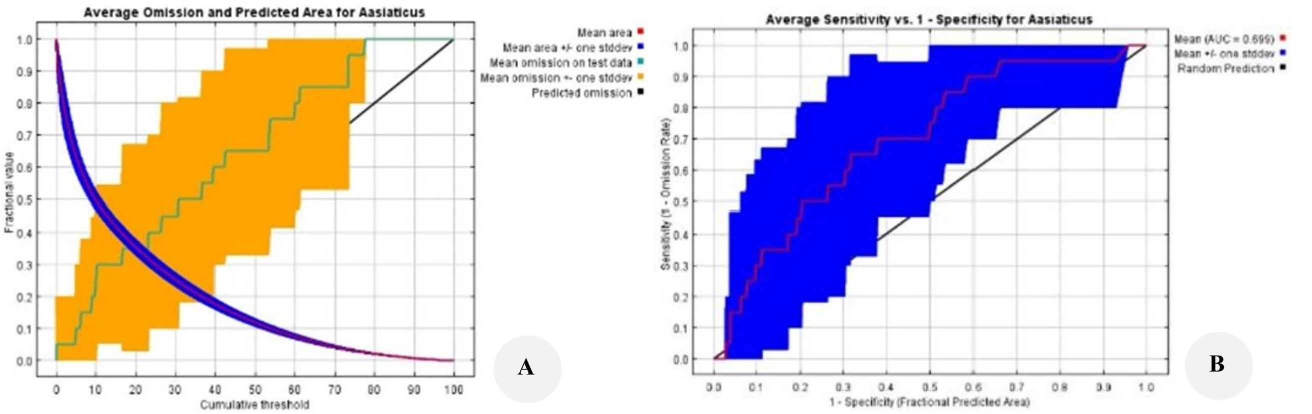


Figure S1. A. Omission analysis of MaxEnt training and test datasets and predicted suitable areas for *Astraeus asiaticus*, B. Receiver Operating Characteristic (ROC) curves and Area Under the Curve (AUC) values for training and test datasets

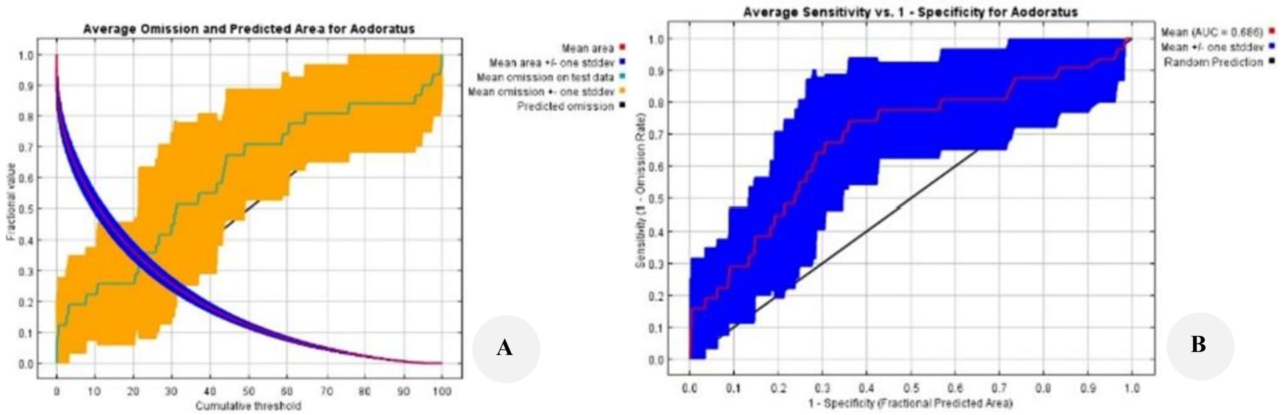


Figure S2. A. Omission analysis of MaxEnt training and test datasets and predicted suitable areas for *Astraeus odoratus*, B. Receiver Operating Characteristic (ROC) curves and Area Under the Curve (AUC) values for training and test datasets

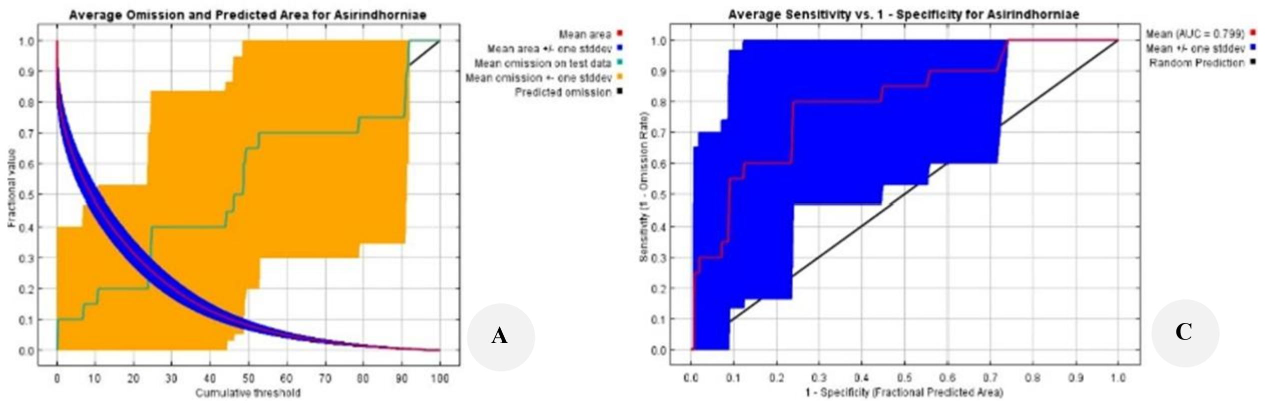
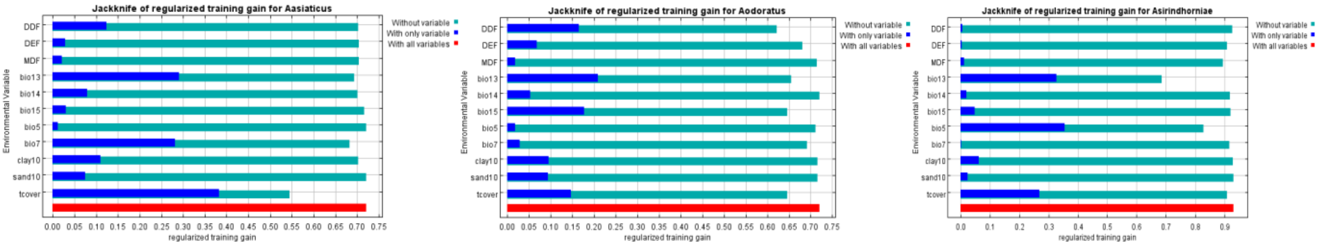
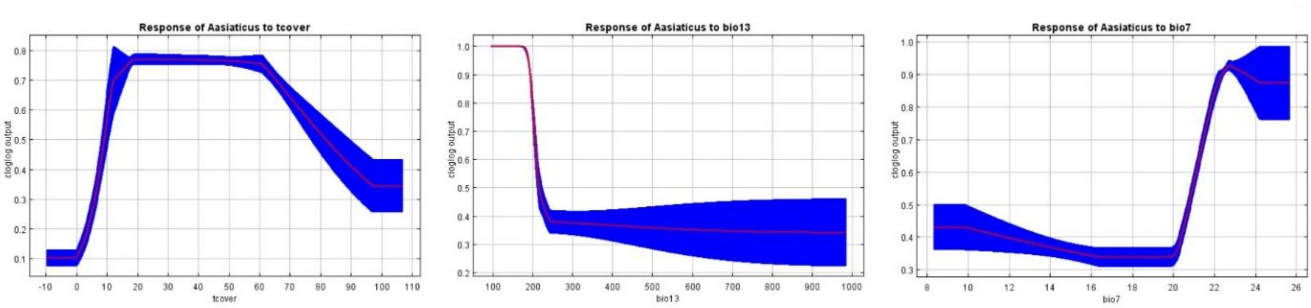


Figure S3. A. Omission analysis of MaxEnt training and test datasets and predicted suitable areas for *Astraeus sirindhorniae*, B. Receiver Operating Characteristic (ROC) curves and Area Under the Curve (AUC) values for training and test datasets



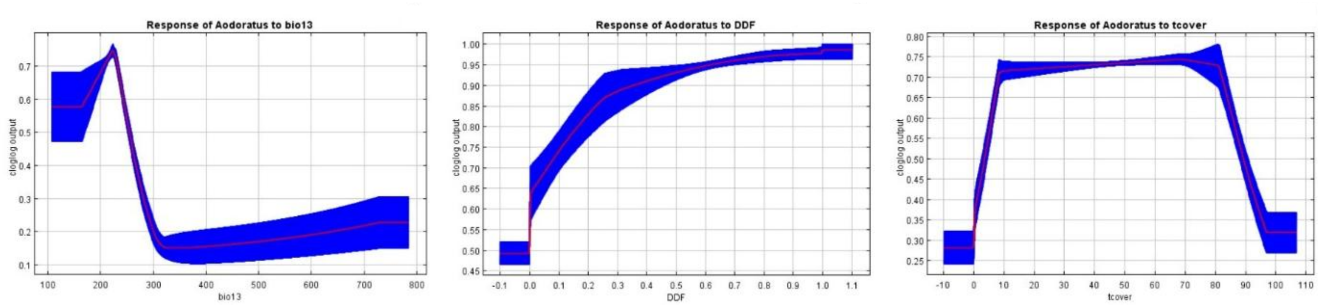
A B C

Figure S4. Jackknife test of variable importance for modeling the spatial distribution of: A. *Astraeus asiaticus*, B. *Astraeus odoratus*, C. *Astraeus sirindhorniae*



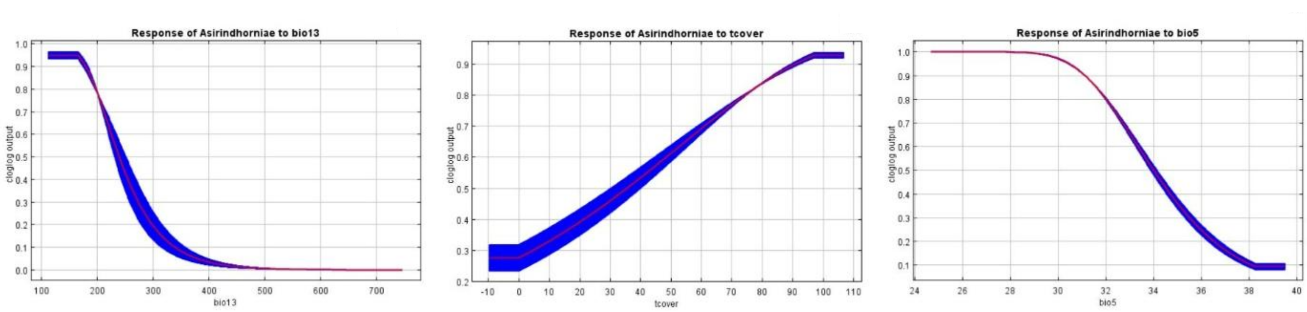
A B C

Figure S5. Environmental factors influencing the occurrence of *Astraeus asiaticus*: A. Percent tree cover, B. Precipitation of wettest month; C. Temperature annual range



A B C

Figure S6. Environmental factors influencing the occurrence of *Astraeus odoratus*: A. Precipitation of wettest month, B. Dry Dipterocarp Forest, C. Percent tree cover



A B C

Figure S7. Environmental factors influencing the occurrence of *Astraeus sirindhorniae*: A. Precipitation of wettest month, B. Percent tree cover, C. Max temperature of warmest month