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Global assessment of invasion risk: *Ardisia elliptica*, one of the most noxious tropical shrubs in the world

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Abstract

Background Global risk assessment of invasive weeds is a proactive strategy for identifying high-risk species and regions, predicting invasion rates and extents, and evaluating harmful impacts on native biodiversity, agriculture, and ecosystems. In this study, species distribution modeling was used to assess the global invasion risk of *Ardisia elliptica*, a highly invasive tropical shrub native to South and Southeast Asia that is harmful in other parts of the world, under the current climate and future climate change scenarios [shared socioeconomic pathways (SSPs) SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5] and other environmental variables, including land use and land cover change, soil moisture, soil carbon, soil pH, and human influence index.

Results Our study revealed that annual precipitation, human influence index, and precipitation in the wettest month contributed significantly to the MaxEnt model, with estimated contributions of 31.35%, 22.76%, and 14.77%, respectively. These findings suggest that the global distribution of *A. elliptica* is limited primarily by climatic variables, whereas anthropogenic factors also play an important role in its habitat expansion. The current invasion risk was highest in South America, Oceania (east), and Africa, affecting up to 24.51% of the total land surface area. A risk assessment of 165 countries revealed a risk of invasion in 41 countries with no records of species occurrence. Under future climate change scenarios, a significant global expansion of the distribution was predicted, with invasion in South America covering up to 48.97% of the land surface area by 2061–2080. Habitat suitability analysis revealed that 21 countries under the current climate and 47 countries under SSP5-8.5 had extremely suitable habitats for *A. elliptica*. Additionally, the species has already invaded at least 115 countries, while 15 countries, including Benin, Burundi, Japan, Uruguay, Swaziland, and South Korea, are predicted to shift categories from having unsuitable or poor invasion risk to having high invasion risk.

Conclusions These findings are crucial for understanding the global invasion risk of *A. elliptica* under substantial climate change and anthropogenic activities and support the development of effective biosecurity measures and sustainable management strategies for this harmful species at the global and national levels.

Keywords *Ardisia elliptica*, Climate change, Global risk assessment, MaxEnt, Shared socioeconomic pathway scenarios

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Background

Invasive species alter the productivity, nutrient cycling, and hydrology of invaded areas (Wang et al. 2013; Van Looy et al. 2024), resulting in biodiversity decline, ecosystem disruption, and global change (Diagne et al. 2021; IPBES 2023). There is evidence that 218 invasive alien species have caused 1,215 local extinctions of native biodiversity across the world (IPBES 2023). Therefore, concern over the biological invasion risk of alien species has increased globally in recent years (El-Barougy et al. 2021). Predicting the invading region and quantifying the invasion risk are critical for developing effective preventive and management plans.

Ardisia elliptica, a highly noxious plant listed among the world's 100 worst invasive species, is native to South and Southeast Asia, including India, Chinese Taipei, Malaysia, and Vietnam (Rojas-Sandoval et al. 2022). *A. elliptica* is a tropical shrub that thrives in humid habitats and grows in moist forests, open areas, and disturbed lands such as roadsides and coastal lines (Adams and Proctor 1972; Koop 2004). Several factors contribute to the invasiveness of *A. elliptica*, such as its prolific seed production, fast growth, and long lifespan, resulting in it being able to survive for 25–40 years (Betsy and Kodela 2024). Moreover, *A. elliptica* is a shade-tolerant species that forms dense, monophytic stands beneath the forest canopy (Rojas-Sandoval et al. 2022; Betsy and Kodela 2024). Therefore, it prevents the establishment of all other native plant species, contributing to its invasion success (Langeland 1998).

A. elliptica, introduced globally in the 1900s for ornamental purposes, has escaped cultivation and become naturalized in various tropical regions (USDA 2019). Climate change exacerbates its spread by increasing its tolerance to heat and heavy rainfall, accelerating its growth and boosting its competitive advantages over native species (Weiskopf et al. 2020). Anthropogenic activities, such as modern agricultural practices, urban sprawl, landscape connectivity, and land cover change, further contribute to its spread (Hulme 2017; Weiskopf et al. 2020; Ni et al. 2021).

Climate change accelerates the spread of invasive species by altering landscapes and removing climatic barriers (IUCN 2021). Rising temperatures, increased CO₂ levels, and extreme weather events create favorable conditions for invasive species and reduce the resilience of native biodiversity and agricultural systems (van Der Loop et al. 2023). As the temperature increases, invasive species expand to higher latitudes and elevations, out-competing native species in previously inhospitable areas (Guo et al. 2021).

Effective management of invasive species (e.g., *A. elliptica*) requires detailed information on current and future

distributions under different climate change scenarios (Adhikari et al. 2023b). In this context, species distribution models (SDMs) have been developed over the last 30 years to simulate the spatial and quantitative distributions of species based on environmental variables (Pearson 2010; Franklin 2013). In addition to invasion ecology, SDMs are widely used to address various questions in biogeography, including those related to species distribution ranges, biomes, conservation assessments, and global change impacts (Franklin 2023). Among SDMs, the maximum entropy (MaxEnt) model is a machine learning technique with high predictive accuracy for limited presence-only data and capable to effectively incorporate complex ecological variables such as bioclimatic factors, soil characteristics, and human influence index (Phillips and Elith 2013). Therefore, MaxEnt is a preferred SDM tool for assessing the ecological risks posed by invasive weeds and for obtaining insights for early prevention and management (Wang et al. 2024).

We have previously modeled the biological invasions of invasive weeds in South Korea using machine learning algorithms (e.g., MaxEnt and random forest) and assessed the invasion risk of intentionally introduced economically important species (e.g., *Amorpha fruticosa* and *Myocastor coypus*) (Adhikari et al. 2021) as well as unintentionally introduced species (e.g., *Ambrosia artemisiifolia* and *Paspalum distichum*) via global trade and natural phenomena (e.g., wind and tides) (Hong et al. 2021; Lee et al. 2022). These studies indicate that South Korea is at high risk of invasion by various alien species. Similarly, global risk assessments of highly invasive species (e.g., *Parthenium hysterophorus*, *Chromolaena odorata*, *Lantana camara*, and *Oxalis latifolia*) have been performed (Adhikari et al. 2023a, 2023b, 2024; Poudel et al. 2023). These studies revealed that global climate change substantially increases the invasion risk for each species, with an estimated >50% increase in habitat in currently invaded countries and new introductions, establishment, and spread expected to occur in at least 15 countries worldwide. Additionally, these studies provided an invasion risk profile for each country, which is expected to support policy formation for international efforts to manage noxious invasive species.

In our earlier modeling of invasive weeds, we used two climate change scenarios, shared socioeconomic pathways (SSPs) SSP2-4.5 and SSP5-8.5, which assume intermediate and high levels of greenhouse gas (GHG) emissions, respectively. In this study, we performed a risk assessment of highly invasive *A. elliptica* using four climate change scenarios, SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5, and quantified the changes in the risk of invasion by 2061–2080 compared with the current status. The main objectives of this study were to (1) assess model

performance by comparing species distribution models (SDMs) with and without environmental variables and with and without rarefying occurrence points as inputs in MaxEnt modeling, (2) project the current and future potential distributions of *A. elliptica* worldwide, and (3) evaluate the invasion risk in different countries, categorizing them into distinct risk levels.

Materials and methods

Global species distribution records

A total of 3,308 occurrence records for *A. elliptica* were downloaded from the open-access database of the Global Biodiversity Information Facility (GBIF, www.gbif.org, accessed on March 05, 2024). The GBIF consolidates species occurrence data from various nonsystematic sources, such as museum collections and administrative records (Moudry and Devillers 2020), and facilitates biodiversity data sharing for research, conservation, and policy development (Chapman 2020). To mitigate overfitting and increase model accuracy due to duplicate coordinates and sampling biases, we applied the spatially rarefy occurrence data tool in the ArcGIS SDM toolbox v.2.4 (Boria et al. 2014; Brown et al. 2017). We removed the species records prior to 1970, unreliable data sources, museum collections, records without reporting dates, and points in irrelevant geographical areas, such as oceans, deserts, and polar regions, similar to earlier research (Marcenò et al. 2021; Adhikari et al. 2024).

Additionally, we consulted specialists to validate the occurrence data for *A. elliptica*. We applied rarefaction at multiple resolutions (1, 5, 10, 20, and 50 km) to remove duplicate occurrences within a grid, resulting in six sets of modeling data, including one without rarefaction. This process reduced the dataset to 1,647 points when rarefied at a distance of 1 km, 1,076 points at 5 km, 788 points at 10 km, 548 points at 20 km, and 336 points at 50 km (Fig. 1). These rarefied points were subsequently used in MaxEnt modeling for *A. elliptica*.

Environmental variables

Nineteen bioclimatic variables derived from temperature and precipitation data (Table S1) were considered important for the global distribution of *A. elliptica*. These variables were sourced from the WorldClim 2.1 database (Fick and Hijmans 2017) and were utilized to develop models for estimating the species distribution on a global scale. The current climatic data (1979–2013) were obtained from PaleoClim V1.2 at a 2.5-min resolution (Brown et al. 2018). The historical climate data for the period from 1979 to 2013 were regarded as the current climatic data.

For future climate change scenarios, we implemented four SSP scenarios, SSP1-2.6, SSP3-7.0, SSP2-4.5 and SSP5-8.5, focusing on 2061–2080. The bioclimatic variables were derived from the global climate model developed by the Max Planck Institute for Meteorology

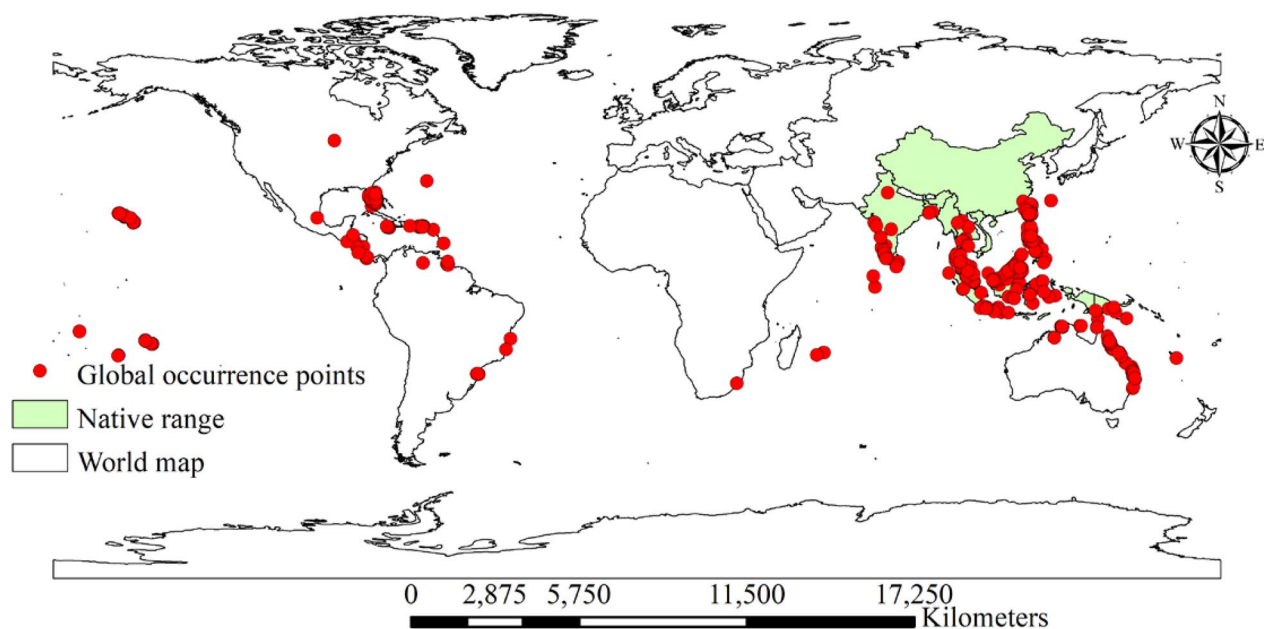


Fig. 1 Global occurrence records of *Ardisia elliptica* ($n = 548$) downloaded from the open-access database of the Global Biodiversity Information Facility (GBIF, www.gbif.org, accessed on March 05, 2024). The red points indicate the global distribution points for *A. elliptica*. Green indicates the native range of *A. elliptica*. The map was generated using ArcGIS Desktop 10.8 (<https://desktop.arcgis.com>)

(MPI-ESM1-2HR) (Gutjahr et al. 2019) under the Coupled Model Intercomparison Project (CMIP6) with a spatial resolution of 2.5 arcmin (approximately 4.5 km at the equator) (Eyring et al. 2016).

SSP scenarios update representative concentration pathways (RCPs), outlining anticipated changes in socio-economic factors such as population dynamics, economic activity, technological advancements, land use, climate impacts, and GHG emissions and other air pollutants (Riahi et al. 2017; Li et al. 2020; Hejazi et al. 2023). These scenarios provide insight into potential future climates and their implications for global ecosystems.

By 2100, temperature increases are projected to reach approximately 1.8 °C in SSP1 (sustainable development), 2.4 °C in SSP2 (middle of the road), 3.0 °C in SSP3 (regional rivalry), and up to 4.0 °C in SSP5 (fossil-fueled development) (O'Neill et al. 2017; Riahi et al. 2017). These temperature changes will significantly impact the dynamics of alien plant species. Proactive management under SSP1 could mitigate the spread of invasive species such as *A. elliptica*, whereas warmer climates and ecosystem disruptions under SSP3 and SSP5 could increase their invasion potential, leading to severe ecological impacts (O'Neill et al. 2017; Riahi et al. 2017).

Soil components, including soil moisture, organic content, soil carbon, and soil pH, directly affect nutrient availability, microbial activity, and overall habitat suitability for invasive species (Nievas et al. 2019). Therefore, we incorporated three soil characteristics—soil moisture, soil carbon, and soil pH—obtained from the Food and Agriculture Organization database (FAO 2025) and used them in the distribution modeling of *A. elliptica*.

The human influence index has emerged as a fundamental factor in modeling invasive species and invasion risk assessment. Here, we used human influence index data obtained from NASA's Socioeconomic Data and Applications Center (<http://sedac.ciesin.columbia.edu>, accessed on 23 February 2025) and land use and land cover changes (Potapov et al. 2022) in the modeling of *A. elliptica*. Similarly, we included biome data to model the distribution of *A. elliptica*. Global biomes, such as tropical rainforests, deserts, and tundras, represent large-scale ecosystems with distinct climatic, vegetative, and ecological traits that influence invasive species distributions (Conradi et al. 2020). Understanding biomes is necessary for predicting the establishment and spread of invasive species. These variables serve as ecological indicators for forecasting species distributions under different climate change scenarios (Zhang et al. 2021).

To improve model accuracy, we eliminated highly correlated environmental variables based on Pearson's correlation coefficients ($r > 0.75$, $P < 0.05$), following previous studies (Shin et al. 2018; Adhikari et al. 2022). Ultimately,

we selected six bioclimatic variables, three related to temperature [annual mean temperature (Bio01), mean diurnal temperature range (Bio02), and isothermality (Bio03)] and three related to precipitation [annual precipitation (Bio12), precipitation in the wettest month (Bio13), and precipitation in the driest month (Bio14)], and six environmental variables (soil carbon, soil moisture, soil pH, the human influence index, land use and land cover change, and biome) for MaxEnt modeling of *A. elliptica* (Table 1).

Model development

The global distribution of *A. elliptica* under the current climate and future climate change scenarios was predicted using MaxEnt Version 3.4.4 (Phillips et al. 2017) based on the species occurrence points of *A. elliptica* and background points. To generate global background points, we used ArcGIS 10.8 (ESRI, Redlands, CA, USA), following guidance from previous research (Barbet-Massin et al. 2012; Adhikari et al. 2023a). For model evaluation, occurrence data were randomly divided at a 3:1 ratio for calibration and validation (Araújo and Guisan 2006). The model was run 100 times to ensure robustness, using default MaxEnt parameters (Hong et al. 2021).

Model evaluation and validation

Model performance was assessed using several metrics, including the area under the receiver operating characteristic (ROC) curve (AUC) (Pearson 2010), true skill statistic (TSS), kappa statistic, sensitivity, and specificity (Allouche et al. 2006). The AUC, ranging from 0 to 1, reflects the model's ability to distinguish between species presence and absence (Thuiller et al.

Table 1 Environmental variables selected for modeling *Ardisia elliptica* distributions

Code	Description	Unit	Model contribution (%)
Bio1	Annual mean temperature	°C	2.72
Bio2	Mean diurnal temperature range	°C	2.22
Bio3	Isothermality (BIO2/BIO7) (× 100)	%	3.13
Bio12	Annual precipitation	mm	31.15
Bio13	Precipitation in the wettest month	mm	14.77
Bio14	Precipitation in the driest month	mm	1.96
Biome	Biome	–	2.76
HII	Human influence index	–	22.76
LULC	Land use and land cover change	–	2.01
SC	Soil carbon	–	2.01
SM	Soil moisture	–	12.97
SpH	Soil pH	–	1.46

2005). AUC values within the ranges of 0.5–0.6, 0.6–0.7, 0.7–0.8, 0.8–0.9, and 0.9–1 correspond to model performances classified as fail, poor, fair, good, and excellent, respectively (Swets 1988).

The performance of SDMs should remain consistent regardless of the data size or prevalence. An ideal model should incorporate both omission and commission errors in the evaluation. The AUC metric is independent of the prevalence, making it a robust measure. However, the AUC is sometimes criticized for two main reasons: it assigns equally to both commission and omission errors, and it avoids real prediction (Lobo et al. 2008). Additionally, the AUC may conceal poor generalization to external datasets and is insensitive to the linear transformation of model outputs, potentially masking important biases in the model (Konowalik and Nosol 2021). The TSS and kappa statistic are threshold-dependent measures that account for both omission and commission errors, offering insights into the model's ability to discriminate between presence and absence (Allouche et al. 2006). TSS and kappa, ranging from -1 to $+1$, account for both commission and omission errors. A value near $+1$ indicates high accuracy, whereas a value zero or lower indicates prediction errors (Allouche et al. 2006; Franklin 2010). The TSS can yield low values for common species when a certain threshold is used, and the kappa statistic is susceptible to prevalence effects and can vary according to the selected threshold (Konowalik and Nosol 2021).

Sensitivity measures the model's ability to correctly identify true presences, whereas specificity assesses its accuracy in predicting true absences. Although sensitivity and specificity are highly influenced by threshold selection methods, leading to inconsistent results across different presence-only datasets, using both metrics offers a more accurate understanding of model performance across various thresholds and prevalence conditions, helping researchers identify potential biases and limitations in their models (Leroy et al. 2018). The sensitivity and specificity ranged from -1 to $+1$, indicating that the agreement level ranged from poor to perfect. Higher scores for these parameters suggest better model performance. Therefore, we applied all these complementary metrics to evaluate model performance. These five evaluation parameters, the AUC, TSS, kappa statistic, sensitivity, and specificity, were used to select the best model from six sets of models with different occurrence points and input variables. The selected model was used to predict the global spatial distribution of *A. elliptica* and assess its invasion risk in different countries.

Global invasion risk assessment of *A. elliptica*

Global binary distribution maps for *A. elliptica* were generated from probability distribution maps produced using the MaxEnt model, utilizing the maximum training sensitivity plus specificity cloglog threshold (Phillips et al. 2006). These maps illustrate the presence and absence of *A. elliptica* habitats for each continent and country worldwide using zonal statistics tools in ArcGIS Desktop 10.8 (Esri Korea, Seoul). Changes in the extent of the spatial invasion risk by 2061–2080 compared with the current potential invasion risk were subsequently evaluated under SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5.

Furthermore, the average habitat suitability of *A. elliptica* in each country was calculated under the current climate and future climate change scenarios and classified into five categories, namely, unsuitable habitat, poorly suitable, moderately suitable, highly suitable, extremely suitable, based on the average habitat suitability, as referenced by Adhikari et al. (2024). Habitat changes were evaluated for *A. elliptica* across 165 countries between the current and future time frames. Subsequently, an invasion risk assessment was conducted for each country and territory worldwide, which were thereby classified into three categories: no invasion risk, current potential invasion risk and future potential invasion risk. All countries within the native range of *A. elliptica* (e.g., in South and Southeast Asia) and those in climatically unsuitable areas predicted by the model were placed in the no invasion risk category. Countries that currently lack occurrence records but were predicted to be climatically suitable for *A. elliptica* invasion under the current climate were classified under the current potential invasion risk category. Countries that do not currently face invasion risk but were predicted by the model to be susceptible to invasion under various climate change scenarios by 2061–2080 were categorized as transitioning from having no or poor invasion risk to having high invasion risk. Finally, we identified and listed countries under high invasion risk under both the current climate and future climate change scenarios based on average habitat suitability ($> 50\%$) to support global invasive species management plans. The overall research methodology is summarized in the flowchart in Fig. 2.

Results

Annual precipitation, human influence index and precipitation in the wettest month were the top contributors to the MaxEnt model of *A. elliptica* distribution

Six bioclimatic variables (Bio01, Bio02, Bio03, Bio12, Bio13, and Bio14) and six environmental variables (biome, human influence index, land use and land cover

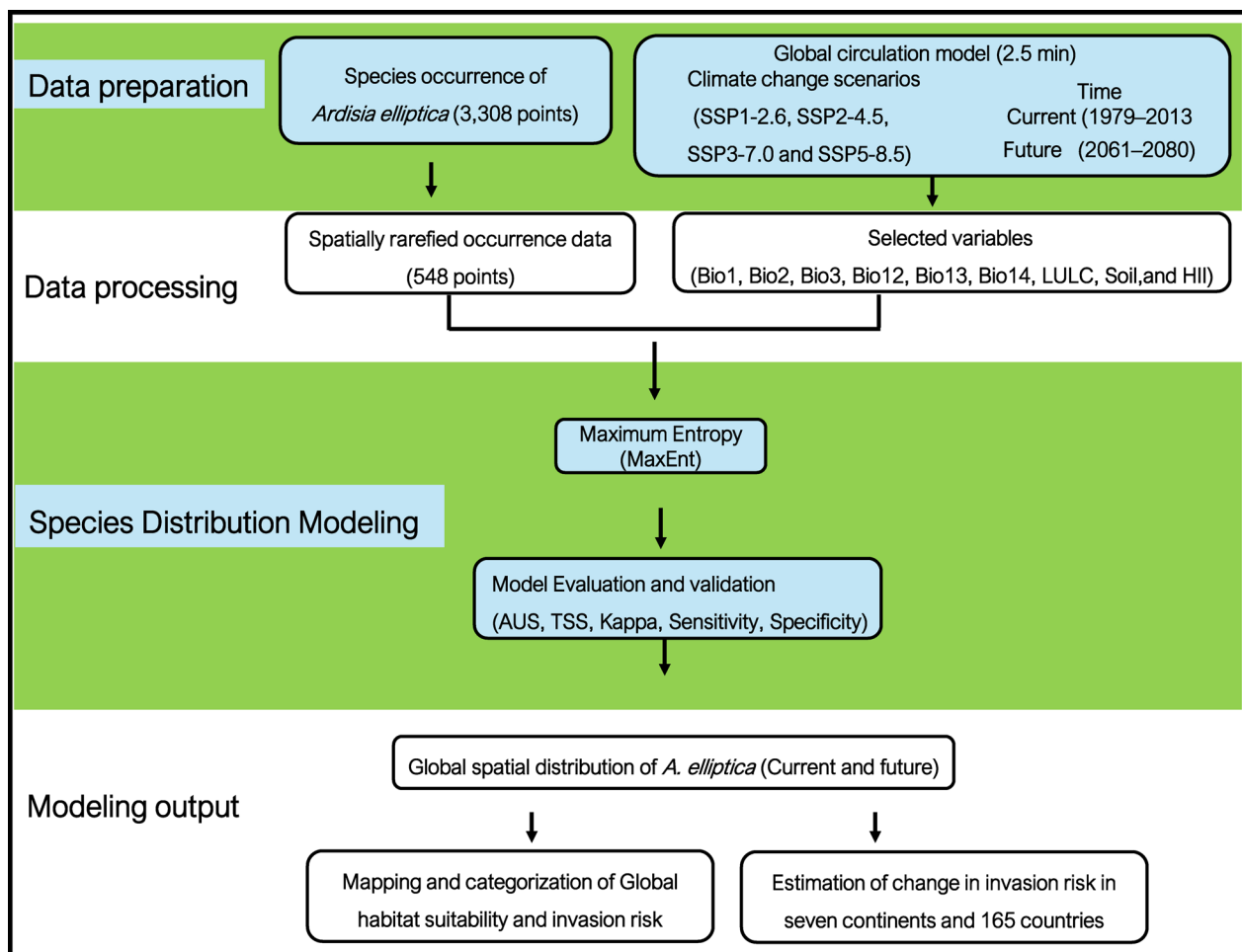


Fig. 2 Flow chart showing the database and modeling methods for estimating the global invasion risk of *Ardisia elliptica*

change, soil carbon, soil moisture, and soil pH) were selected based on Pearson's correlation coefficients of $r \leq 0.75$ (Table S1). Among the 12 variables, Bio12, human influence index, Bio13, and soil moisture had relatively high estimated contributions to the model, of 31.35%, 26.96%, 14.77%, and 12.97%, respectively (Table 1). Other variables, including soil characteristics, temperature, and biome, play minor roles in the model.

Rarefying species occurrence records at a resolution of 20 km provided the highest predictive performance for *A. elliptica*

The predictive accuracies of six MaxEnt model sets, which were developed using different rarefied species occurrence data and input variables for *A. elliptica*, were assessed using the AUC, TSS, kappa statistic, sensitivity, specificity, and TAI. The model built with species occurrence data rarefied at a resolution of 20 km with bioclimatic variables and five environmental variables (land use and land cover change, human influence index, soil

carbon, soil moisture, and soil pH) as inputs presented the highest scores across various metrics. The AUC, TSS, kappa statistic, sensitivity, and specificity were 0.96, 0.84, 0.78, 0.88, and 0.89, respectively, when the test datasets were used (Table 2).

The current potential invasion risk of *A. elliptica* is highest in South America and Oceania

Setting the period from 1979 to 2013 as the current climate period, we evaluated the potential invasion risk of *A. elliptica* using species distribution modeling, as presented in Fig. 3. The current invasion risk was concentrated primarily in the tropical climate zone, between the Tropic of Cancer and the Tropic of Capricorn, roughly between 23.5° North and South latitudes. The current invasion risk of *A. elliptica* covered 737,982 cells, representing 9.13% of the global land surface area (Table 3). The invasion risk was highest in South America (24.52%) and Oceania (14.59%), with moderate risk in Asia (11.48%), Africa (7.99%), North America (3.78%), and

Table 2 Predictive performance of MaxEnt models of *A. elliptica* with and without environmental variables at different resolutions to rarefy global occurrence points

Resolution to rarefy (km)	Presence points	Without environmental variables ^a					With environmental variables ^b				
		AUC	TSS	Kappa	Sensitivity	Specificity	AUC	TSS	Kappa	Sensitivity	Specificity
No rarefying	3,308	0.61	0.51	0.40	0.49	0.52	0.63	0.52	0.41	0.47	0.53
1 km	1,647	0.71	0.64	0.61	0.69	0.68	0.72	0.65	0.62	0.61	0.63
5 km	1,076	0.76	0.67	0.59	0.71	0.72	0.78	0.71	0.63	0.74	0.71
10 km	788	0.75	0.69	0.64	0.73	0.71	0.76	0.70	0.64	0.74	0.76
20 km	548	0.95	0.83	0.76	0.88	0.87	0.96	0.84	0.78	0.88	0.89
50 km	336	0.70	0.65	0.56	0.61	0.68	0.73	0.68	0.64	0.58	0.64

AUC area under the receiver operating curve, TSS true skill statistic, TAI total accuracy index

^a Predictive performance of the MaxEnt model using only bioclimatic variables

^b Predictive performance of the MaxEnt model using both bioclimatic and environmental variables, including land use and land cover change, the human influence index, soil carbon, soil moisture, and soil pH. The bold letters in the row of 20 km resolution indicate the highest values of each evaluation parameter in the table

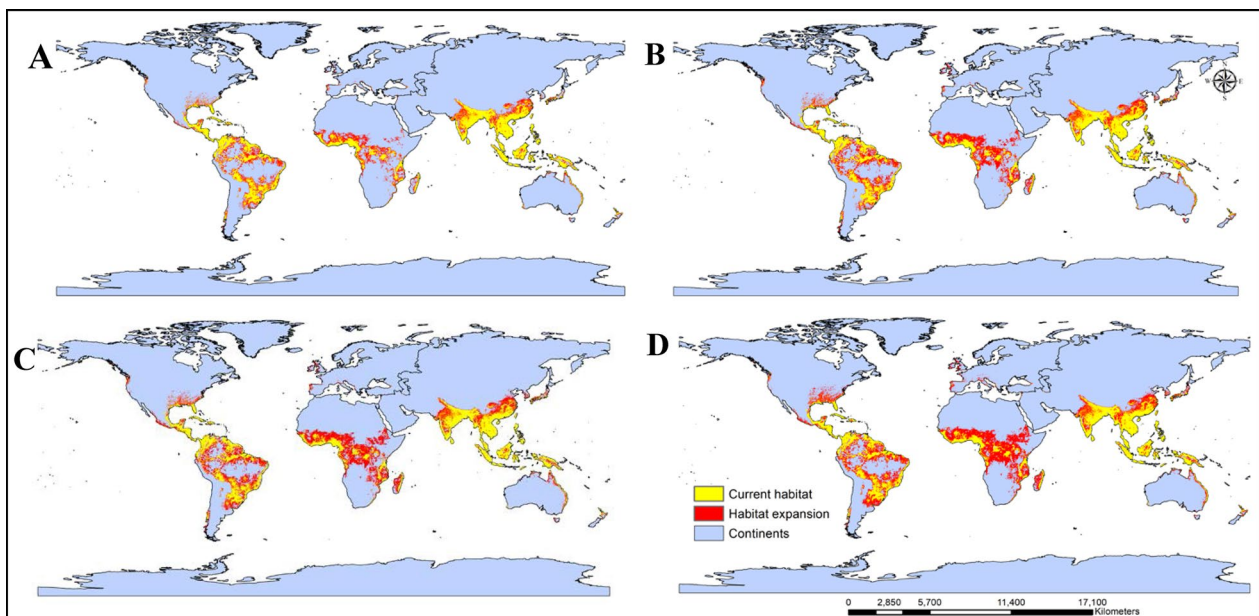


Fig. 3 Global potential distribution of *Ardisia elliptica* under the current climate and future climate change scenarios SSP1-2.6 (A), SSP2-4.5 (B), SSP3-7.0 (C), and SSP5-8.5 (D) by 2061–2080. Red and yellow indicate the current potential habitat and habitat expansion by 2061–2080, respectively. Blue indicates habitats unsuitable for *A. elliptica*. The map was generated using ArcGIS Desktop 10.8 (<https://desktop.arcgis.com>)

Australia (2.08%) and minor risk in Europe (0.21%). There is currently no significant threat in Antarctica (Table 3).

The future potential invasion risk of *A. elliptica* increased on all continents except Antarctica and was highest under the SSP5-8.5 scenario

Under future climate change scenarios, the invasion risk is expected to increase substantially. As a result, new invasions and the expansion of existing habitats of *A. elliptica* were projected to occur on all continents except Antarctica. The modeling outputs for the global potential distributions under the future climate change

scenarios SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5 by 2061–2080 are presented in Fig. 3. South America and Africa were projected to experience the most significant increases, with suitable habitats potentially covering up to 48.97% and 30.86% of the total cells, respectively (Table 3). Asia and Oceania also showed notable predicted increases, with future risks reaching 15.97% and 29.29%, respectively.

In contrast, the risk in Antarctica remained unchanged across all scenarios. Even in regions with negligible risk under the current climate, such as Europe and North America, the potential for suitable habitats for *A. elliptica*

Table 3 Estimation of suitable habitats for *Ardisia elliptica* on different continents

Continents	Total cell number ^a	Current climate ^b	Future climate change scenarios ^c			
			SSP1-2.6	SSP2-4.5	SSP3-7.0	SSP5-8.5
Africa	1,448,243	7.99	17.99	23.81	27.27	30.86
Antarctica	3,444,160	0.00	0.00	0.00	0.00	0.00
Asia	2,941,792	11.48	14.83	15.49	15.89	15.97
Australia	390,902	2.08	4.11	4.84	5.47	5.49
Europe	815,123	0.21	0.97	1.21	1.32	2.17
North America	1,600,333	3.78	5.47	6.00	6.39	7.25
Oceania (East)	14,204	14.59	24.97	28.45	26.89	29.29
South America	865,871	24.52	41.26	45.28	47.65	48.97

^a Estimation of the total cell number of each continent. The size of each cell is 2.5 min resolution. ^b and ^c, The proportions of suitable habitat estimated to be covered under the current climate and future climate change scenarios, respectively

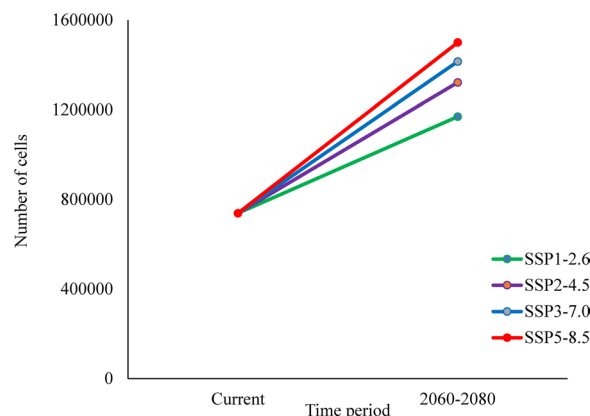


Fig. 4 Estimating the total number of cells invaded by *Ardisia elliptica* around the world under the current climate and future climate change scenarios. The X-axis and Y-axis represent the number of invaded cells and the time period, respectively. The resolution of one cell is 2.5 min (approximately 4.5 km at the equator)

was projected to increase, particularly under more severe climate change scenarios. Figure 4 illustrates the increase in invasion risk under each climate change scenario, showing that SSP5-8.5 has the highest number of invaded cells worldwide, followed by SSP3-7.0, SSP2-4.5, and SSP1-2.6. The rate of change in the invasion risk area was projected to be highest in Europe by 2061–2080, with the current invasion area expected to increase by 914.52% under the most extreme future climate change scenario (SSP5-8.5). These findings suggest that the range of *A. elliptica* is likely to expand significantly in response to climate change and human activities, with a higher risk in tropical and subtropical regions.

Habitat suitability analysis revealed that 21 countries under the current climate and 47 countries under SSP5-8.5 had extremely suitable habitats for *A. elliptica*

Habitat suitability analysis was performed across 165 countries worldwide, which were classified based on average habitat suitability into five habitat suitability categories: unsuitable, poorly suitable, moderately suitable, highly suitable, extremely suitable. These categories were assigned under both the current climate and future climate change scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5), as shown in Fig. 5.

Under the current climate, 50 countries were classified as climatically unsuitable for *A. elliptica*. However, 12 countries, including Guatemala, Ghana, and Papua New Guinea, had high suitability, whereas 21 countries, including Cuba, El Salvador, Cambodia, the Dominican Republic, and the Philippines, had extremely suitable habitat (Table 4 and Fig. 5). The number of unsuitable countries was projected to decrease under different climate change scenarios, specifically SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5, with an estimated reduction to 32 countries under SSP5-8.5 by 2061–2080. However, the number of countries classified as having extremely suitable habitats (e.g., Colombia, Liberia, Sierra Leone, Costa Rica, Honduras, Ghana, and Madagascar) was projected to increase to 47 under SSP5-8.5 (Table 4).

This trend remained consistent across other suitability categories, with both poor and extremely suitable categories expanding, particularly under SSP3-7.0 and SSP5-8.5. These findings indicate that climate change could significantly expand the potential range of *A. elliptica*, increasing the risk of invasion in many countries.

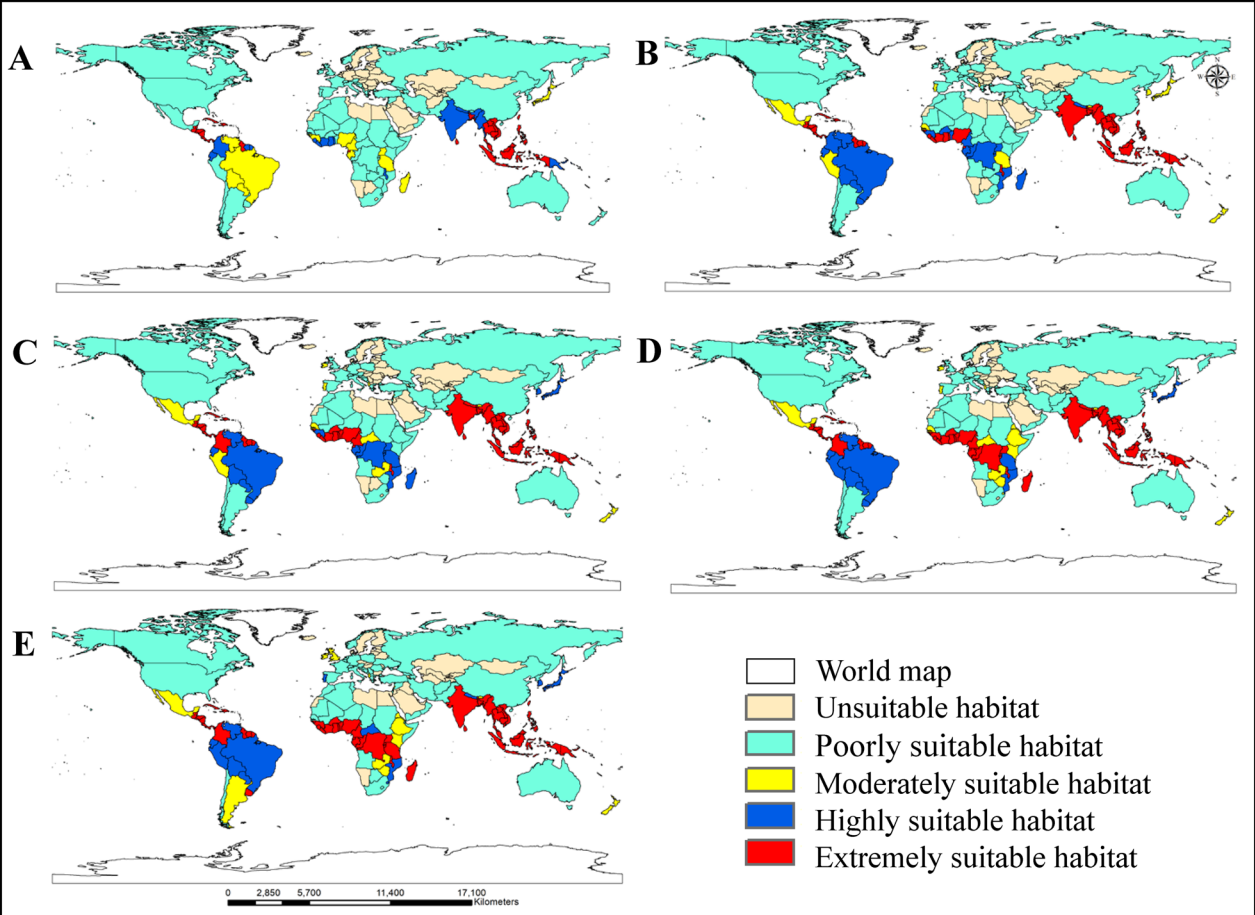


Fig. 5 Habitat suitability of *A. elliptica* in different countries and territories under the current climate (A) and future climate change scenarios, specifically SSP1-2.6 (B), SSP2-4.5 (C), SP3-7.0 (D), and SSP5-8.5 (E), by 2061–2080. The habitat suitability has been categorized into unsuitable habitat, poorly suitable, moderately suitable, highly suitable, extremely suitable based on the average habitat suitability 0, < 0.25, 0.25–0.50, 0.50–0.75, and > 0.75, respectively. The map was generated using ArcGIS Desktop 10.8 (<https://desktop.arcgis.com>)

Table 4 Estimating the number of countries in different habitat categories of *Ardisia elliptica*

Habitat suitability	Current climate (1979–2013)	Future climate change scenarios			
		SSP1-2.6	SSP2-4.5	SSP3-7.0	SSP5-8.5
Unsuitable	50	44	46	43	32
Low	67	56	52	51	58
Moderate	15	18	11	13	13
High	12	12	17	15	15
Extremely high	21	35	39	43	47

Invasion risk assessment revealed that 15 countries under the current climate and SSP5-8.5 were at high risk of invasion
An invasion risk assessment of *A. elliptica* was conducted to identify countries at high risk of invasion under the current climate and future climate change scenarios. Currently, numerous countries in South America, including

Costa Rica, Cuba, Guatemala, Honduras, Nicaragua, and Panama, are at high risk (Table 5). Although these countries have no occurrence records of the species, the model predicted an invasion risk of over 50%. However, future climate change by 2061–2080 is expected to create climatically suitable habitats to transition several countries, particularly in Africa, that currently have no or

Table 5 List of countries with a high invasion risk of *A. elliptica* under the current climate

S. No	Countries ^a	Invading area (%) ^b
1	Belize	99.55
2	Costa Rica	92.63
3	Cuba	100.00
4	Columbia	50.80
5	Dominican Republic	74.20
6	El Salvador	79.89
7	French Guiana	50.80
8	Guatemala	73.46
9	Guyana	83.18
10	Haiti	85.97
11	Honduras	92.81
12	Ivory Coast	50.00
13	Nicaragua	99.03
14	Panama	97.35
15	Suriname	54.30

^a Countries currently with no species occurrence records but a high invasion risk predicted using the model (> 50%)

^b Proportion of invasion to the total area of each country

poor invasion risk to having high invasion risk. For example, under SSP1-2.6, countries such as Benin and Burundi emerged as high-risk areas, whereas SSP3-7.0 and SSP5-8.5 predicted a broader and more intense spread into countries such as Burundi, Portugal, Japan, South Korea, and Uruguay (Table 6).

Discussion

This study presents several significant findings regarding the global invasion risk of *A. elliptica*. First, in addition to bioclimatic variables, the human influence index plays an important role in the distribution of *A. elliptica* (Table 1). Second, the current spatial invasion risk of *A. elliptica* is high in South America and Oceania, affecting approximately 14.59–24.52% of the total land surface of each continent. Global climate change is likely to exacerbate invasion risk across all continents, potentially impacting up to 48.97% of the land surface area (Table 3). Third, a habitat suitability analysis of 165 countries revealed that 33 countries under the current climate and 47 countries under SSP5-8.5 had extremely suitable habitat for *A. elliptica* (Table 4). Fourth, a global spatial invasion risk assessment revealed that 15 countries are currently at high risk of invasion, whereas under SSP5-8.5, an additional 15 countries were projected to transition from having no or poor invasion risk to having high risk, with over 50% of their land surface area affected (Table 5). Countries with notable shifts in risk level include Benin, Japan, Mozambique,

Table 6 Estimating countries with a high invasion risk of *A. elliptica* under global climate change

S. No	Future climate change scenarios ^a			
	SSP1-2.6	SSP2-4.5	SSP3-7.0	SSP5-8.5
1	Benin	Benin	Benin	Benin
2	Burkina Faso	Burkina Faso	Burkina Faso	Burkina Faso
3	Burundi	Burundi	Burundi	Burundi
4	Congo	Congo	Gambia, The	Central African Republic
5	Gambia, The	Gambia, The	Mozambique	Congo
6	Rwanda	Mozambique	Rwanda	Japan
7		Rwanda	South Korea	Mozambique
8		Zaire	Tanzania	Portugal
9			Uruguay	Rwanda
10			Zaire	San Marino
11				South Korea
12				Swaziland
13				Tanzania
14				Uruguay
15				Zaire

^a Transition from having no or poor invasion risk (< 25%) under the current climate to having high invasion risk (> 50%) by 2061–2080

Rwanda, and Portugal. Our findings suggest that *A. elliptica* could potentially expand into suitable habitats under future global climate change and anthropogenic activities. However, these results are based on predictive modeling, and real-world establishment may differ due to various factors such as dispersal, competition, and local management practices. Therefore, field-based validation is required for applying these findings into real-world scenarios.

Over the past few decades, more than six dozen techniques have been developed for this purpose, with the weed risk assessment (WRA) technique pioneered by the Australian government being one of the earliest and most widely applied methods in countries such as Australia, Canada, USA, and New Zealand (Roy et al. 2023). The United States Department of Agriculture (USDA) has created guidelines for risk analyses based on the Australian risk assessment model (USDA 2019) aimed at safeguarding plant resources in the United States from pests, including noxious weeds. Although the USDA uses three types of variables, namely, plant hardiness zones, Köppen-Geiger climate classification, and mean annual precipitation, to examine the distribution of invasive plants (USDA 2019, 2024), it is limited in its ability to incorporate future climatic and environmental variables, including land use and land cover changes, as well as anthropogenic disturbances, for predicting future potential distributions (Adhikari et al. 2024).

The selection and validation of species occurrence records are critical steps in species distribution modeling, as they greatly influence model performance and reliability. Occurrence data must be recent, accurate, and spatially representative of the current range of the species (Liu et al. 2016; Zarzo-Arias et al. 2022). Public databases such as the GBIF require careful scrutiny to ensure data quality (Moudrý and Devillers 2020). A key question in the modeling process is whether to use all available data regardless of potential errors and ecological relevance or to filter the data to reduce bias (Kramer-Schadt et al. 2013; Guillera-Aroita et al. 2015). In this study, we performed rarefaction of species occurrence points, which involves reducing the spatial clustering of occurrence records to mitigate sampling bias and address issues of spatial autocorrelation and overrepresentation of certain areas due to uneven sampling effort, ultimately leading to improved model performance (Boria et al. 2014; Moudrý et al. 2024). In this study, we found higher model performance after rarefying the occurrence points (Table 2) and achieved the best model performance with occurrence data rarefied at a resolution of 20 km, indicating excellent model accuracy and a strong match between the observed and predicted outcomes.

A. elliptica is one of the most destructive invasive plants worldwide (Rojas-Sandoval et al. 2022); it grows in single-species stands in forest understories, crowding out native plants and displacing native ground cover, particularly in areas with wet soils. It thrives in low areas, intermittent stream bottoms, hammocks, disturbed wetlands, and tree islands in marshes (Adams and Proctor 1972; Koop 2004). To our knowledge, this study provides the first risk assessment for *A. elliptica* and evaluations of the current and future potential invasion risks of the species at the global scale, yielding a list of countries with a high invasion risk.

MaxEnt is a widely used and reliable tool for predicting species distributions. It relies on presence-only data and can manage both continuous and categorical variables (Phillips et al. 2006). It also allows for variable interactions and uses regularization techniques to minimize overfitting (Phillips and Dudík 2008). However, it can be influenced by sampling bias and limitations in spatial transferability (Václavík and Meentemeyer 2012). Previous studies have demonstrated that the model performance and predictions can vary significantly when the training and testing regions differ geographically (Václavík and Meentemeyer 2012; Goedecke et al. 2020). Consequently, the invasion patterns predicted by our models should be approached with caution. Instead of serving as definitive forecasts, these results are better considered as preliminary hypotheses that can guide subsequent field validation and experimental investigations.

In this study, we developed two sets of MaxEnt models for *A. elliptica*: one using only bioclimatic variables and another incorporating both bioclimatic variables and additional environmental factors, including land use and land cover change, human influence index, and key soil characteristics such as soil carbon, soil moisture, and soil pH. The results indicated that incorporating both bioclimatic and other environmental variables led to higher predictive accuracy (Table 2). Invasive distribution is influenced by multiple ecological and anthropogenic factors in addition to climate alone. By integrating these diverse predictors, MaxEnt can better capture complex ecological relationships, leading to improved model accuracy and more reliable species distribution predictions. Our results are in line with those of earlier climate change studies carried out on a global scale (Hong et al. 2021; Adhikari et al. 2023b, 2024; Zheng et al. 2024), highlighting the important contributions of environmental variables such as annual precipitation, human influence index, precipitation in the wettest month, and soil moisture to the distribution of *A. elliptica* (Table 1). The greater contribution of the precipitation-related variables to the model indicates that adequate moisture for seeds, particularly during dry seasons, is a critical factor in the establishment and spread of this species (Rojas-Sandoval et al. 2022).

A. elliptica prefers consistently moist soils, and its intolerance to drought further emphasizes the importance of precipitation in determining its distribution. Soil moisture influences invasion success by regulating the water supply and affecting plant physiology, including seed germination, plant growth, resource allocation, and competitive interactions with native species (Herod and Martina 2024). *A. elliptica* is found predominantly in regions with tropical rainforest or tropical monsoon climates, with an average annual precipitation of 1200–1500 mm and an average annual temperature range of 15.5–32 °C (Rojas-Sandoval et al. 2022). Notably, research conducted in Everglades National Park suggests that variations in water availability across different habitats may contribute to the patchy distribution of *A. elliptica*, as seed mortality is greater and germination occurs more slowly in closed-canopy forests than in more exposed environments (Koop 2004).

Soil components, including organic content, soil carbon, and soil pH, directly affect nutrient availability, microbial activity, and overall habitat suitability for invasive species (Nievas et al. 2019). Invasive plants exhibit unique physiological characteristics that allow them to thrive in and modify soil conditions both directly, through the deposition of leaf litter and increasing carbon and nitrogen contents, and indirectly, by influencing microbial communities such as mycorrhizal fungi

and their activity (Szumańska et al. 2021; Vujanović et al. 2022). These soil alterations can create favorable conditions for the establishment and spread of invasive species while simultaneously reducing native plant diversity (Kuebbing and Nuñez 2016). Integrating these key soil parameters into SDMs is essential for better understanding invasive species distributions and the overall health and resilience of ecosystems. Therefore, we incorporated three soil characteristics—soil moisture, soil carbon, and soil pH—in the species distribution modeling of *A. elliptica*. Although soil variables have a moderate influence in our model, their ecological impact—especially the role of soil characteristics in the spread of this species—remains largely unclear, emphasizing a significant research gap. Moreover, the model predictions could not be sufficient for understanding the complex soil–plant interactions. It is assumed that tropical soil could be a limiting factor for the habitat expansion of *A. elliptica* in temperate regions. However, climate plays a major role in its distribution, and it is expected to invade temperate regions in the future.

The human influence index incorporates various anthropogenic activities, including global trade and tourism, transportation networks, infrastructure development, urban and industrial expansion, and agricultural practices, facilitating the breakdown of natural biogeographical barriers and the spread of invasive species (Gallardo et al. 2015). Studies have shown that integrating anthropogenic factors into SDMs can significantly improve the prediction accuracy of models (Gallardo and Aldridge 2013). The human influence index has emerged as an important factor in modeling *A. elliptica*, contributing the second highest percentage to the model (22.76%). Accurate prediction of invasive species distributions is not possible without considering socioeconomic factors; however, very few studies have incorporated human disturbance into species distribution models (SDMs) for invasive species (Gallardo 2014; Gallardo et al. 2015; Wang and Xu 2016). Moreover, land use and land cover change promotes disturbances, facilitates seed dispersal, and creates new favorable habitats for invasive species (Wang et al. 2016; Adhikari et al. 2022). Therefore, we incorporated the human influence index and land use and land cover change as key socioeconomic factors in modeling *A. elliptica*.

Our model predicted that current suitable habitats for *A. elliptica* generally occur in tropical to temperate regions between 23.5° North and South latitudes, particularly in the northern and central parts of South America, Central America, Central Africa, South and Southeast Asia (native regions), and Oceania (Fig. 3). The model also predicted current suitable habitats in southeastern parts of the United States, including

Hawaii, Florida, Alabama, and Mississippi, at approximately 30° North latitude. Although *A. elliptica* is native to South and Southeast Asia, it has been intentionally or inadvertently introduced to other regions, where it has established itself in the wild (USDA 2009; Van Wilgen 2021). In several countries in Central and South America, Africa, and Europe, including Anguilla, Dominica, Guatemala, Honduras, Nicaragua, Congo, Ghana, Portugal, Spain, and the United Kingdom, there are no records of *A. elliptica* occurrence. However, the model predicted a poor to extreme invasion risk (Fig. 5). These countries may possess suitable environmental conditions for *A. elliptica* to thrive if introduced. This underscores the importance of proactive monitoring and preventive measures, as the absence of current records may simply reflect a lag in detection or introduction rather than immunity to invasion. Interestingly, large areas of North America and Europe, particularly northern regions, have no or poor risk of invasion in future. This indicates that *A. elliptica* invasion may be limited by cold climates and a warming climate in the future may not be sufficient to create suitable conditions for its growth. Moreover, in temperate and boreal regions, the growing season is short, and other essential factors, such as soil conditions and humidity, may be insufficient for *A. elliptica*.

The SSP scenarios describe alternative futures for global society, biodiversity, and natural ecosystems through the end of the twenty-first century based on different narratives of socioeconomic development ranging from sustainable development (SSP1) to fossil-fueled development (SSP5) (Riahi et al. 2017; Li et al. 2020; Hejazi et al. 2023). In this study, we assessed the future potential invasion risk of *A. elliptica* across eight continents and 165 countries worldwide. Under SSP1-2.6 and SSP2-4.5, which represent more sustainable development trajectories with lower greenhouse gas emissions, the invasion risk was relatively low, estimated to affect 1.21–45.28% of the land mass on each continent (Table 3). However, SSP3-7.0 and SSP5-8.5 both face significant challenges in mitigating climate change, including slow technological development, high fossil fuel usage, and indiscriminate development focused on rapid industrial and technological advancements (O'Neill et al. 2017; Riahi et al. 2017), resulting in a higher invasion risk under these scenarios than under SSP1-2.6 or SSP2-4.5.

SSP3-7.0 reflects a fragmented world characterized by regional rivalries, weak international cooperation, and slow technological advancement, leading to high emissions, severe environmental degradation, and uneven climate resilience (Riahi et al. 2017). In contrast, SSP5-8.5 depicts a fossil-fueled, high-growth world with rapid economic and technological expansion but minimal climate policies, resulting in extreme emissions and severe

climate impacts (Riahi et al. 2017). SSP3-7.0 and SSP5-8.5 had similar but higher invasion risk than did SSP1-2.6 and SSP2-4.5, with estimates of up to 48.97% land mass invasion per continent. Moreover, 10 new countries under SSP3-7.0 and 15 under SSP5-8.5 were predicted to transition from having no or poor invasion risk to having high invasion risk (Table 6). The higher rates of invasion projected under SSP3-7.0 and SSP5-8.5 than under SSP1-2.6 and SSP2-4.5 can be attributed to the higher greenhouse gas emissions resulting in more severe climate change. These scenarios projecting intense climate change may increase stress on native plant communities, increasing their vulnerability to invasion and potentially allowing invasive species to outcompete native species and to establish and spread into new habitats (Diez et al. 2012). However, the accuracy of future predictions depends heavily on the assumptions of the SSP scenarios and the ecological niche stability of *A. elliptica*, which remains uncertain. Our study shows that climate change may not only expand the current range of *A. elliptica* but also result in its introduction to entirely new regions, highlighting the dynamic and escalating nature of invasion risks in response to global climate change.

Consistent results have been obtained in many earlier studies of invasion risks within individual countries, such as China, India, and South Korea, or in broader, large-scale studies around the world (Adhikari et al. 2022; Wang et al. 2023; Kishore et al. 2024). Under SSP5-8.5, 15 new countries without species occurrence records and lacking suitable habitats were expected to transition to having a high invasion risk by 2061–2080. These results indicate that SSP3-7.0 and SSP5-8.5, which are considered high-challenge scenarios due to their relatively high rates of greenhouse gas emissions, will lead to more significant changes in precipitation patterns. This, in turn, will increase the likelihood of *A. elliptica* establishing and spreading, thereby increasing the vulnerability of natural ecosystems.

Increasing temperatures and changes in precipitation patterns can impact specific traits, such as the phenology, reproduction, and physiology, of tropical invasive plants, including *A. elliptica* (Kharivha et al. 2022). Higher temperatures during seed development may shorten seed dormancy of *A. elliptica*, favoring its establishment in new environments (Rojas-Sandoval et al. 2022). Similarly, high temperature accelerates growth and extend growing seasons, allowing *A. elliptica* to produce more biomass and seeds (Koop and Horvitz 2005; Funk 2013). Hou et al. (2014) suggested that temperature between 10 and 25 °C supports *A. elliptica* in maintaining pollen viability, floral development, and germination. Similarly, increased precipitation can provide more favorable moisture conditions

for germination and seedling establishment, potentially enhancing invasion success (Kharivha et al. 2022). This increased reproductive output can lead to faster population growth and the spread of invasive species.

In addition to environmental factors, biotic factors may facilitate the spread of *A. elliptica*. The eco-physiological traits of a species, particularly its shade tolerance and rapid growth, may enhance its competitive advantage, particularly in forest understories (Rojas-Sandoval et al. 2022). The reproductive biology of this species supports its invasive success, with self-compatibility and autogamy enabling reproduction without the presence of specialized pollinators (Pascarella 1997). However, the fruits of *A. elliptica* are consumed by frugivorous birds and small mammals, methods of seed dispersal that are likely to favor long-distance dispersal and invasion into geographical regions (Rojas-Sandoval et al. 2022). Plants interact with soil microorganisms, e.g., mycorrhizal fungi, which can change their morphology and physiology and affect seedling growth (Bray et al. 2003). These biological interactions collectively influence the complex dynamics of the invasion potential and spread of *A. elliptica*. To improve the accuracy of predictive models, incorporating all these biotic factors as inputs to the model is essential. This represents a limitation of our study, as current models cannot incorporate such biotic interactions. Future studies should integrate ecological networks, dispersal dynamics, and empirical field surveys to refine predictions.

Ardisia elliptica has already been declared one of the world's worst invasive plants despite its ornamental and economic value. Our study highlights the immediate need for a comprehensive approach to managing its invasion risk. We recommend a combination of international coordination among countries within 23.5° North and South latitudes, policy enforcement, and regional management strategies, including early detection, eradication, and biosecurity measures. Nonetheless, caution is suggested when applying model outputs into policy actions, especially in such countries where field-based evidence is lacking. It is essential to promote noninvasive and native species with similar aesthetic value. Horticulturists, land managers, and the public should be made aware of the ecological and economic risks associated with nonnative ornamental plants. Additionally, research should focus on the biological control and sustainable management of *A. elliptica*. Collaboration among policy-makers, horticulturists, and conservationists is crucial to enforcing strict regulations against the trade of *A. elliptica*. These integrated strategies are essential for mitigating the ecological and economic consequences of *A. elliptica* invasion in a changing global climate.

Conclusions

We conducted an invasion risk assessment of *Ardisia elliptica* using MaxEnt modeling under current and future climate scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5), incorporating six environmental variables, including soil characteristics, human influence index, and land use and land cover change. Our model-based projections suggest that, in addition to climate, anthropogenic factors such as human influence index may significantly contribute to the invasion potential of alien species like *A. elliptica*. The results highlight that current suitable habitats are primarily located between 23.5° North and South latitudes, encompassing parts of Asia, Africa, Australia, and the Americas. Future projections indicate a potential expansion of invasion risk across all continents except Antarctica, with the highest increase under the SSP5-8.5 scenario. Notably, countries in Africa and South America may become increasingly vulnerable, with at least 15 nations predicted to shift from unsuitable to high-risk status by 2061–2080.

However, these projections should be interpreted with caution. The modeling approach is limited by its reliance on abiotic variables and can not account for biotic interactions, dispersal mechanisms, or potential barriers to establishment. Moreover, recent studies have highlighted regional sensitivity in MaxEnt outputs when different training and testing regions are used, which may affect transferability and generalizability. As such, field-based validation and further regional assessments are needed to verify model predictions and improve risk estimation.

Despite these limitations, our findings offer a preliminary global perspective on the potential spread of *A. elliptica*, providing useful guidance for prioritizing surveillance and early intervention strategies. We encourage the use of these results as a beginning point for more detailed region-specific investigations. Future research should aim to integrate empirical data, biotic factors, and socio-ecological dimensions to strengthen predictive accuracy. Coordinated international efforts, data sharing, and adaptive management frameworks will be essential to effectively address the growing risk posed by this noxious invasive shrub.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-025-00622-z>.

Additional file 1

Author contributions

Pradeep Adhikari: Conceptualization, methodology, validation, formal analysis, investigation, data curation, writing (original draft preparation, writing) review and editing. Yong Ho Lee: Conceptualization, investigation, validation, Prabhath Adhikari: formal analysis, data curation. Anil Poudel: formal analysis, data curation. Changwan Seo: Conceptualization, investigation and funding acquisition.

Do-Hun Lee: data curation, Yong-Soon Park: writing (review and editing) and Supervision. Sun Hee Hong: Conceptualization, project administration, supervision, funding acquisition.

Funding

This work was supported by Korea Institute of Planning and Evaluation for Technology in Food, Agriculture and Forestry (PET) through Agriculture and Food Convergence Technologies Program for Research Manpower Development, funded by Ministry of Agriculture, Food and Rural Affairs (MAFRA) (RS-2024-00400922) and Korea Environment Industry & Technology Institute (KEITI) through Climate Change R&D Project for New Climate Regime, funded by Korea Ministry of Environment (MOE) (RS-2022-KE002369).

Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Received: 15 November 2024 Accepted: 20 May 2025

Published online: 05 June 2025

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