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Article

# Integrated Model-Driven Prediction of Xanthium strumarium Distribution Dynamics and Rhizosphere Microbiome Function: Adaptive Assessment Under Multi-Scenario Climate Change

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**Abstract:** Climate change and human activities are profoundly reshaping species distributions, yet their combined impacts on plants with dual ecological-economic roles remain poorly understood. This study investigates *Xanthium strumarium*, a medicinal-invasive plant, across China using an integrated framework of species distribution modeling (Biomod2), niche dynamics (Ecospat), and rhizosphere microbiome analysis (Tax4Fun). Results reveal that human footprint (66.6% contribution), elevation, and slope dominate its distribution, with suitable habitats projected to expand by 8.9–28.6% under future scenarios (SSP1-2.6 to SSP5-8.5), particularly in Yunnan, Guangdong, and Inner Mongolia. Despite high niche conservatism (Schoener's D = 0.8986–0.9338), ecological adaptability slightly declines under high emissions. Rhizosphere microbial communities, dominated by Proteobacteria and enriched in nitrogen-cycling taxa (Nitrospira, Verrucomicrobia), enhance adaptability through metabolic and environmental response functions, enabling colonization of disturbed soils. These findings highlight the synergistic roles of climate-driven habitat shifts and microbiome-mediated resilience in shaping X. strumarium's invasion success. The study provides critical insights for managing its dual roles, advocating for strategies that address both anthropogenic drivers and microbial ecology in biodiversity conservation under global change.

**Keywords:** *Xanthium strumarium*; climate change; species distribution modeling; Biomod2; rhizosphere microbiome; 16S rRNA sequencing; habitat suitability; microbial communities

# 1. Introduction

Climate change has emerged as one of the most significant environmental challenges facing humanity in the 21st century, affecting ecosystems, biodiversity, and species distribution across the globe [1–4]. This phenomenon is no longer a distant concern but a current reality with profound implications for both natural and human systems. Rising temperatures, altered precipitation patterns, and more frequent extreme weather events are increasingly reshaping ecosystems and altering the habitats of numerous species [5–7]. These changes are especially impactful on species distributions, as many plants and animals are forced to migrate, adapt, or face local extinction. The ability of species to respond to these shifts is not only dependent on the changes in temperature and precipitation, but also on the broader interactions within the ecosystem, such as plant-microbe relationships, and human-driven landscape transformations [8–10].

*Xanthium strumarium,* a plant species native to parts of Asia with concentrations in China and India that has spread globally to North and South America, Africa, and Europe, embodies a paradoxical nature—it is both valued in traditional medicine for its anti-inflammatory and analgesic properties and recognized as an aggressive invasive species threatening ecosystems in many regions [11–16]. As a ruderal species, *X. strumarium* thrives in disturbed environments, outcompeting native

vegetation and altering ecosystem dynamics [17–19]. It is well known for its rapid spread, especially in disturbed habitats such as agricultural fields and urban landscapes, where it competes for resources with native flora [20,21]. In China, the effects of climate change are particularly pronounced due to the country's vast geographical expanse and diverse ecological zones, ranging from arid deserts in the northwest to subtropical forests in the south [22]. Home to over 30,000 plant species and a critical hub of global biodiversity, China faces unique challenges as shifting climates threaten its rich ecosystems and agricultural systems [23,24]. As a result, species distributions in China are undergoing significant transformations, with invasive species like Xanthium strumarium exploiting these changes to expand their range, particularly in disturbed environments such as farmlands and urban fringes. Understanding these dynamics within the Chinese context is essential for predicting ecological shifts and informing conservation and management strategies.

Climate change has far-reaching consequences on species distributions, not only because of direct changes in climate parameters such as temperature and precipitation, but also because of the indirect effects resulting from the interactions between plants and their environments. For example, soil microbial communities, recognized as key drivers of plant growth, nutrient uptake, and stress tolerance, are highly sensitive to climatic changes [25,26]. Recent research has increasingly recognized the role of microbes in shaping plant species' ecological success [27–31]. Climate-induced changes in temperature and precipitation can alter microbial community composition and functions, affecting how plants respond to abiotic stressors and how they interact with other species. In turn, these changes can modify plant competition dynamics, nutrient cycling, and ecosystem processes, all of which are critical to understanding the future distribution of species like *X. strumarium*.

The relationship between plants and their microbial symbionts is a pivotal, yet often overlooked, aspect of understanding plant distribution under climate change. Microbes in the soil and rhizosphere play essential roles in facilitating nutrient uptake, enhancing plant tolerance to stressors such as drought and soil salinity, and even protecting plants from pathogens [32–36]. These microbial communities are not static; they evolve and adapt to changing environmental conditions, and their composition can influence how plants cope with the challenges posed by a warming world. For example, some plant species may benefit from symbiotic relationships with beneficial microbes that help them thrive in conditions of water scarcity or higher temperatures [37,38]. Conversely, other species may struggle as their microbial partners are unable to adapt quickly enough to rapid environmental shifts [39,40]. Understanding these complex interactions is vital for predicting how plant species like *X. strumarium* will fare in future climate scenarios, especially considering its status as both a medicinal plant and an invasive species.

Moreover, climate change is intricately intertwined with human activities that are fundamentally altering the landscape and ecosystem dynamics [41,42]. Agricultural expansion, urbanization, deforestation, and the intensification of land-use practices all contribute to habitat destruction, fragmentation, and the creation of novel ecological niches [43–45]. These anthropogenic activities not only alter the physical landscape but also influence the ecological processes that govern species distributions. *X. strumarium* has shown a remarkable ability to colonize disturbed habitats, which are often the result of human activities [46]. The spread of *X. strumarium* has been closely linked to agricultural intensification, where the plant benefits from disturbed soil conditions and the increased availability of resources in disturbed landscapes [47]. Additionally, urbanization has facilitated its expansion by providing fragmented, disturbed environments that allow for its persistence and spread [48,49].

Human-driven habitat fragmentation and alteration can exacerbate the effects of climate change on species [50–52]. Fragmented habitats may reduce the overall fitness of species by isolating populations, thereby limiting gene flow and reducing genetic diversity [53,54]. This can make species more vulnerable to climate-induced stresses, such as changes in temperature, precipitation, or the availability of resources [55]. Furthermore, human activities have introduced new challenges for species like *X. strumarium*, which are already adapting to shifting climates. For instance, land-use changes can disrupt natural plant-microbe interactions, alter nutrient availability, and reduce the

resilience of ecosystems [56]. In this sense, human activities act as both direct and indirect drivers of species distribution shifts, further compounding the challenges posed by climate change.

To better understand how *X. strumarium* will respond to climate change, one of the most powerful tools at our disposal is species distribution modeling (SDM). SDMs are computational tools used to predict the potential distribution of species based on environmental variables, such as temperature, precipitation, and soil characteristics [57–59]. These models can simulate current and future species distributions under different climate scenarios, providing valuable insights into how species may fare under future climate conditions. Among the various modeling approaches, Biomod2 has emerged as a robust and flexible framework for SDM [60–64]. Biomod2 integrates multiple modeling algorithms, including Generalized Linear Models (GLMs), Random Forests (RF), Artificial Neural Networks (ANNs), and Support Vector Machines (SVMs), to create an ensemble model that combines the strengths of each algorithm [65,66]. This ensemble approach reduces the uncertainty inherent in individual models, making Biomod2 particularly valuable for predicting species distributions under complex environmental scenarios [67,68].

To complement the predictive power of SDMs, tools like Ecospat are invaluable for analyzing niche dynamics and species-environment interactions [69]. Ecospat provides a framework for assessing niche overlap and shifts, offering insights into how *X. strumarium* might adapt to future climate scenarios [70]. By evaluating the ecological niche of *X. strumarium* under current and projected climates, Ecospat helps identify potential areas of habitat suitability and the degree of niche conservatism or shift.

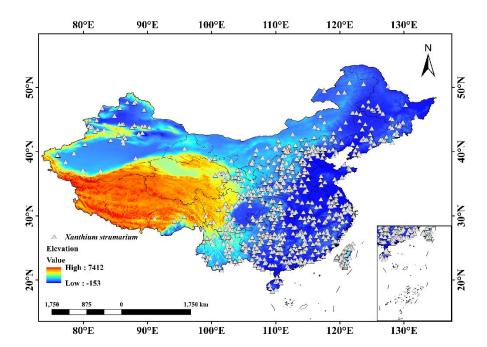
The role of soil microorganisms in influencing plant distribution and adaptation is increasingly acknowledged [71–73]. The rhizosphere, enriched by root exudates and microbial interactions, is crucial for plant health and resilience [74]. To gain a deeper understanding of the microbial community's role, Tax4Fun serves as an invaluable resource [75]. Tax4Fun is a bioinformatics tool that predicts the functional capabilities of microbial communities by translating 16S rRNA gene sequence-based taxonomic data into functional profiles, allowing researchers to infer the communities' metabolic potential [76,77].

This study aims to investigate the potential impacts of climate change on the distribution of Xanthium strumarium across China by utilizing Species Distribution Modeling (SDM) tools, including Biomod2. The research will evaluate how shifts in environmental variables—such as temperature and precipitation—influence the plant's distribution patterns within Chinese ecoregions. To elucidate the species' adaptive capacity under projected climate scenarios, niche dynamics and species-environment interactions will be analyzed using Ecospat. Concurrently, Tax4Fun will be employed to characterize the functional profiles of soil microbial communities and their role in shaping plant-microbe symbiosis critical for the plant's ecological success in China's diverse landscapes. By integrating these multidimensional analyses, this work seeks to deliver a holistic understanding of the plant's future ecological and economic implications, particularly considering its dual role as a medicinal resource and an aggressive invasive species within the Chinese context.

# 2. Materials and Methods

## 2.1. Data Sources and Processing

Distribution data for *X. strumarium* were compiled from the Global Biodiversity Information Facility (GBIF) and complemented by field surveys conducted in Inner Mongolia Autonomous Region, China, between 2022 and 2024 [78]. To mitigate spatial sampling bias and enhance model reliability, we implemented a 5 km² spatial filtering protocol on the initial 2,288 occurrence records using the "Spatially Rarefy Occurrence Data" tool within ArcGIS 10.8 (Environmental Systems Research Institute, Redlands, CA, USA). This preprocessing step effectively reduced spatial autocorrelation while preserving ecological representativeness, yielding 1,689 spatially independent occurrence points suitable for subsequent distribution modeling analyses.



**Figure 1.** The distribution map of *Xanthium strumarium* (Color gradient indicates elevation from -153 m blue to 7412 m red; elevation data sourced from WorldClim v2.1 at 30 arc-second resolution, with a maximum of 7412 m underestimating peaks like Everest at 8848.86 m, though this does not affect the lowland distribution of the species).

For the present research, 23 environmental variables were selected, comprising 19 climatic variables, three topographic variables, and one human activity variable. Climatic and elevation data were obtained from WorldClim at a 5-km resolution [79]. Topographic variables, including slope and aspect, were derived from elevation data using the Surface Analysis tool in ArcGIS 10.8. Human activity data were sourced from the third version of the Global Human Modification dataset at a 1-km resolution [80].

Future climate projections were sourced from the BCC-CSM2-MR model, developed by the Beijing Climate Center and widely recognized for its strong performance in studies exploring vegetation distribution across China [81,82]. This model provided data for three climate scenarios, SSP1-2.6, SSP2-4.5, and SSP5-8.5, which correspond to progressively higher carbon emission levels. For each scenario, data were retrieved for two time periods, spanning 2041 to 2060 and 2061 to 2080, at a spatial resolution of 5 km.

The twenty-three environmental variables obtained above were imported into ArcGIS 10.8. The "Extract by Mask" tool was used to crop the data to the geographical extent of China, and bilinear interpolation was applied to resample the resolution of the environmental variables to a standardized 5 km. This process ensures the necessary data consistency for subsequent spatial analysis and model construction.

Multiple factors may exhibit collinearity, potentially influencing the outcomes of the model [83]. To mitigate the problem of collinearity among variables, a stepwise variable reduction approach was employed. All environmental variables were imported into R, and the Pearson correlation coefficients between them were calculated using the "terra" package. These variables were then loaded into "biomod2" to filter out those with a contribution greater than zero. For pairs of filtered variables with a correlation coefficient exceeding 0.8, the variable with the higher contribution was retained [49,50]. This process culminated in the selection of 13 variables (Figure 2, Table 1).

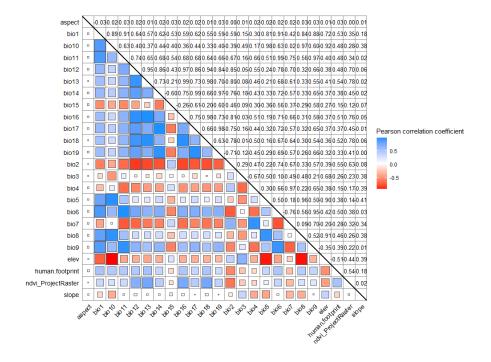


Figure 2. The Pearson correlation coefficients of 23 environmental variables.

Table 1. Environmental variables for the models.

Category	Variable Description		Unit
	Bio2	Mean diurnal range	°C
	Bio3	Isothermality	\
	Bio4	Temperature seasonality	\
Climate	Bio8	Mean temperature of wettest quarter	°C
Cililate	Bio10	Mean temperature of warmest quarter	°C
	Bio11	Mean temperature of coldest quarter	°C
	Bio15	Precipitation seasonality	\
	Bio17	Precipitation of driest quarter	mm
	Elev	Elev	m
Topography	Aspect	Aspect	0
	Slope	Slope	0
Human	Human footprint	Human footprint	\
Vegetation	NDVI	Normalized difference vegetation index	\

## 2.2. Models Construction and Changes in Ecological Niches

The modeling framework incorporated 12 algorithms, such as Random Forest (RF), MaxEnt, and XGBoost, each run 10 times for robustness [64]. Community occurrence data were combined with an equal number of randomly generated pseudo-absences, split into 75% training and 25% test sets via random sampling. Pseudo-absences were generated using the 'BIOMOD\_FormatingData' function, a method proven effective for capturing potential distributions compared to real absence data [84]. Individual model outputs were integrated into an ensemble model (EM) via a weighted average algorithm, enhancing predictive precision [85]. Habitat suitability was classified into four categories:

Unsuitable area (0–0.25), Low suitable area (0.25–0.50), Moderately suitable area (0.50–0.75), and Highly suitable area (0.75–1.0), based on model probability outputs.

Model accuracy was assessed using three metrics: the Area Under the Receiver Operating Characteristic curve (ROC), True Skill Statistic (TSS), and Kappa coefficient, with thresholds of ROC > 0.9, TSS > 0.85, and Kappa > 0.85 indicating high performance [65,86,87].

Under current climate conditions, the distribution points of *X. strumarium* were identified, and a 1-degree buffer zone surrounding these points was established as the background for analysis. For predicted future climate scenarios, background points were determined based on suitable habitat areas projected by an ensemble model. By integrating these distribution points with diverse climate datasets, the "ecospat" R package was employed to evaluate and quantify the niche overlap of Xanthium strumarium under both current and future climate conditions [69]. This package facilitated the visualization of niche dynamics and the computation of the Schoener's D niche overlap parameter (observed value), which ranges from 0 (no overlap) to 1 (complete overlap) [88]. This methodology enables a comprehensive analysis and assessment of the potential effects of climate change on the ecological niche of *X. strumarium*.

## 2.3. 16S rRNA Gene Sequencing of Rhizosphere Microbial Communities

Soil samples were collected from the rhizosphere of *X. strumarium* across five distinct habitat types in Inner Mongolia, China (Table 2).

Table 2. Rhizos	sphere soil	sampling	sites of	Xanthium	strumarium.
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Site	Location	Coordinates	Habitat Type
ZD1	Yematu Village, Xincheng District, Hohhot	111°51′48.194″E, 40°55′52.378″N	Farmland Edge
ZD2	Hadamen National Forest Park	111°35′18.977″E, 41°01′04.115″N	Montane Forest
ZD4	Saihanwula National Nature Reserve	118°39′40.185″E, 44°15′41.225″N	Temperate Steppe
ZD5	East Campus, Inner Mongolia Agricultural University	111°43′00.034″E, 40°49′03.373″N	Urban Green Space
ZD6	Huanghuagou Grassland Cultural Resort	112°32′06.128″E, 41°08′28.420″N	Grassland

Sampling was conducted in July 2024, targeting five replicate *X. strumarium* plants per site. Rhizosphere soil (0–5 cm depth, ~500 g) was collected within 2 mm of roots using a sterile corer, with bulk soil con-trols sampled 1 m away. Samples were stored at 4°C, transported to the laboratory within 24 h, and subsampled for DNA extraction (stored at -80°C) and physicochemical analysis (airdried, sieved <2 mm). Genomic DNA was extracted from 0.5 g soil using the DNeasy PowerSoil Kit (Qiagen, Germany), with quality verified by NanoDrop 2000 and gel electrophoresis [89–91].

The 16S rRNA V3–V4 region was amplified (primers 338F/806R), sequenced on an Illu-mina MiSeq (PE300), and processed in QIIME2 (v2022.8) with DADA2 for ASV identifica-tion. Taxonomy was assigned using SILVA (v138), and datasets were rarefied to 10,000 reads/sample. Microbial diversity (Shannon, Chao1, Bray-Curtis NMDS) was analyzed, and functional profiles were predicted with Tax4Fun (v1.0) against KEGG pathways, val-idated by shotgun metagenomics (Spearman's  $\varrho > 0.85$ ).

Tax4Fun is an R package designed for functional prediction of environmental samples, such as gut microbiota and soil, based on the 16S Silva database [77]. It offers high prediction accuracy and outperforms the PICRUSt functional prediction, particularly for complex environmental samples like soil. The functional prediction in Tax4Fun is achieved through a nearest-neighbor approach based on minimal 16S rRNA sequence similarity. Specifically, it extracts prokaryotic whole-genome 16S rRNA gene sequences from the KEGG database and uses the BLASTN algorithm to align them to the SILVA SSU Ref NR database (with a BLAST bit score >1500), constructing a relevant matrix. The KEGG database's prokaryotic functional annotations, identified by UProC and PAUDA methods, are then mapped to the SILVA database for functional annotation. Sequenced samples are clustered into OTUs using SILVA database sequences as reference, allowing for functional annotation retrieval.

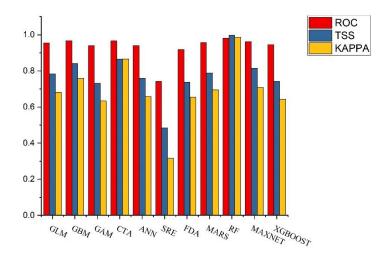
# 3. Results

#### 3.1. Model Precision Assessment

In this study, we conducted a comprehensive evaluation of various machine learning models, focusing on their performance in terms of ROC values and Kappa values (Figure 3).

Regarding the ROC value, which measures the classification ability of a model, a value closer to 1 indicates superior predictive performance. Our analysis reveals that the Random Forest (RF) model stands out with an exceptional ROC value of 0.97, demonstrating its outstanding classification capability with virtually no misclassification. Other models, such as GBM (Gradient Boosting Machine), MARS, MAXNET, FDA, and XGBOOST, also performed well, with ROC values near 0.95, indicating their high predictive accuracy in handling complex datasets. Although ANN (Artificial Neural Network) and GLM (Generalized Linear Model) also yielded favorable results, with ROC values close to 0.95, they were slightly inferior to Random Forest and Gradient Boosting Machine, suggesting that their applicability may be somewhat limited for specific tasks. In contrast, the SRE model exhibited a significantly lower ROC value of 0.74, far below that of other models, indicating poor classification performance and limiting its practical usability in real-world applications.

Next, the Kappa value, which assesses the consistency of the model's predictions, reflects the degree of deviation from random guessing. A value closer to 1 indicates stronger consistency. Among all the models, RF demonstrated the highest Kappa value of 0.981, indicating excellent classification consistency, nearly approaching the ideal state, and reflecting the stability of this model across multiple experiments. Both GBM and MARS showed impressive Kappa values of 0.825 and 0.767, respectively, signifying their strong predictive consistency, making them suitable for tasks that require high classification precision. In contrast, ANN and GLM yielded Kappa values of 0.756 and 0.759, which, although strong in terms of ROC value, were relatively weaker in terms of consistency, suggesting potential biases in specific application scenarios. The SRE model, with a Kappa value of only 0.452, was significantly lower than the other models, indicating poor classification consistency and making it less suitable for high-precision classification tasks.



**Figure 3.** Evaluation indices of individual predictive models (AUC: area under the receiver operating characteristic, ANN: artificial neural network, CTA: classification tree analysis, FDA: flexible discriminant analysis, GAM: generalised additive model, GBM: generalised boosting model, GLM: generalised linear model, MARS: multivariate adaptive regression spline, MAXENT: maximum entropy, MAXNET: Maxent's network equivalent, RF: random forest, XGBOOST: eXtreme gradient boosting, SRE: surface range envelope).

In conclusion, RF (Random Forest) and GBM (Gradient Boosting Machine) emerged as the most outstanding models, exhibiting the highest ROC and Kappa values, making them well-suited for tasks requiring high classification accuracy, stability, and consistency. While all models

demonstrated ROC values greater than 0.7, the SRE model was excluded from further consideration due to its low Kappa value.

For the ensemble modeling approach, we employed the EMmean method, which yielded an ROC value of 0.971 and a Kappa value of 0.888. This method demonstrated high accuracy and is well-suited for predictive modeling tasks.

#### 3.2. Bioclimatic Variable Contribution

The modeling results demonstrate the relative contributions of different environmental variables to *X. strumarium* (Figure 4), with human activity having the most significant impact, accounting for 66.6% of the contribution. This indicates that in areas with intensive human activity, its influence on the ecosystem or species distribution far exceeds other Variables such as topography and climatic variables. Elevation and slope contribute 4.7% and 3.7%, respectively, indicating that topographic Variables have a certain degree of influence on ecological processes. Additionally, vegetation cover (NDVI) and a series of bioclimatic variables have relatively smaller contributions but still provide necessary insights into environmental complexity. Overall, these results emphasize the importance of prioritizing the impact of human activity in ecological conservation and management strategies to effectively address its potential threats to ecosystems.

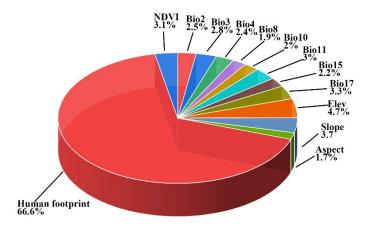


Figure 4. Contribution rates of bioclimatic variables to the habitat distribution.

# 3.3. Present Potential Geographic Spread

The integrated modeling results indicate that the current primary potential suitable habitats for *X. strumarium* are predominantly distributed across southern, central, eastern, northeastern, and southeastern China, encompassing a total suitable area of 329.816×10<sup>4</sup> km<sup>2</sup> (Figure 5). Specifically, high-suitability areas (36.871528×10<sup>4</sup> km<sup>2</sup>) are principally concentrated in the following administrative regions: Inner Mongolia, Hebei, Tianjin, Beijing, Shandong, Henan, Shanxi, Hainan, Hunan, Hubei, Guangdong, and Taiwan, while scattered occurrences are observed in Xinjiang, Tibet, and Yunnan provinces.

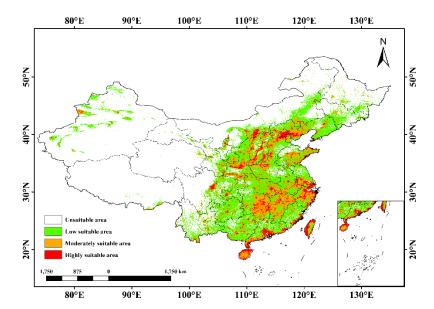
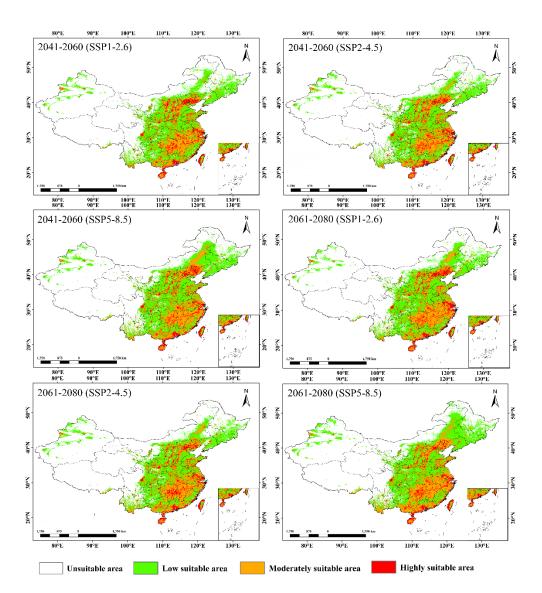


Figure 5. Potential geographical distribution under current climate conditions.

This Table 3 and Figure 6 shows the changes in the suitable growth areas of *X. strumarium* under different climate scenarios over the next few decades. In the coming decades, regardless of whether it is a low, medium, or high emission scenario (SSP1-2.6, SSP2-4.5, SSP5-8.5), the areas of low and moderately suitable zones for *X. strumarium* are showing an increasing trend, especially under high emission scenarios, where the growth is more significant. However, the area of highly suitable zones changes little and even decreases in some scenarios, indicating that the optimal growing conditions for *X. strumarium* remain limited. Overall, climate change has a positive impact on the growth environment of *X. strumarium*, particularly under high emission scenarios, where its suitable growth area has significantly expanded.



**Figure 6.** Potential distributions of *X. strumarium* in different future periods.

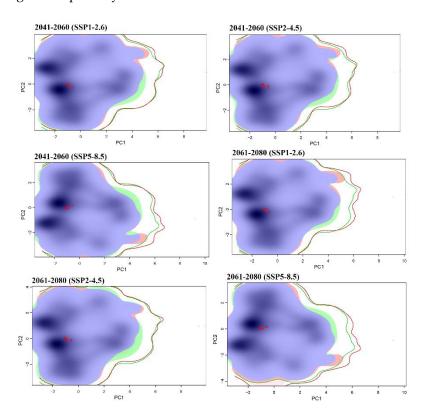
**Table 3.** Changes in the distribution area of X. strumarium during different periods under different scenarios ( $10^4$  km<sup>2</sup>).

Period	Climate Scenario	Low suitable area	Moderately suitable area	High suitable area
current		198.70486	94.239585	36.871528
2041	SSP1-2.6	214.12327	121.80209	47.453126
2041- 2060	SSP2-4.5	214.8698	122.04167	46.569445
2060	SSP5-8.5	225.38889	134.07813	46.918404
2071	SSP1-2.6	210.57292	127.92188	46.440973
2061-	SSP2-4.5	209.90973	127.00695	46.953126
2080	SSP5-8.5	228.59375	141.42361	46.119792

# 3.4. Niche Dynamics

The niche comparison analysis for *X. strumarium* across current and projected future climate scenarios reveals a substantial degree of ecological niche overlap, as quantified by Schoener's D

metric (Figure 7). Specifically, the overlap ranges from a minimum of 89.86% (Schoener's D = 0.8986) between the current climate and the 2061–2080 period under the SSP5-8.5 scenario, characterized by high levels of greenhouse gas emissions, to a maximum of 93.38% (Schoener's D = 0.9338) for the same timeframe under the more sustainable SSP1-2.6 pathway. Intermediate values include 93.20% (Schoener's D = 0.9320) for the 2041–2060 period under SSP1-2.6, 93.17% (Schoener's D = 0.9317) under SSP2-4.5, and 91.20% (Schoener's D = 0.9120) under SSP5-8.5, while the overlap for 2061–2080 under SSP2-4.5 stands at 90.38% (Schoener's D = 0.9038). These results suggest a high degree of niche conservatism across diverse climate trajectories, with variations reflecting the influence of differing emission scenarios on X. strumarium's ecological adaptability. Notably, the overlap is slightly higher under the SSP1-2.6 and SSP2-4.5 scenarios, which represent more sustainable emissions pathways, while the SSP5-8.5 scenario, associated with high emissions, shows slightly lower overlap, indicating a reduced ecological adaptability under more extreme climate conditions.

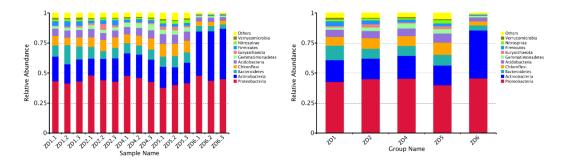


## 3.5. Rhizosphere Microbial Abundance in Xanthium strumarium Habitats

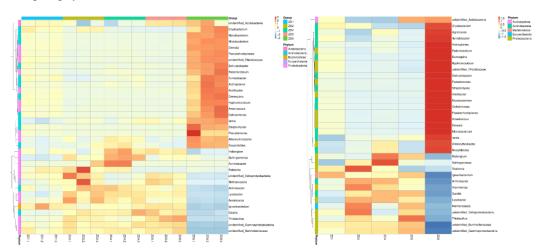
The structure of the rhizosphere microbial community exhibits significant differences across various samples and groups, which are effectively illustrated by the species relative abundance bar chart and species abundance clustering chart at the phylum level (Figure 8 and Figure 9). Proteobacteria dominates in several samples, particularly in ZD1 and ZD2, where its abundance often exceeds 50%, indicating its strong metabolic and adaptive capacity in the soil, potentially promoting organic matter decomposition and nutrient cycling. Firmicutes and Bacteroidetes are more evenly distributed in other samples, suggesting these phyla have a good adaptability to soil environments, while Acidobacteria shows higher abundance in ZD2 and ZD4, possibly related to the adaptation to acidic or nutrient-poor soil environments. The composition of these microbes may assist *X. strumarium* in surviving in variable soil conditions, especially in acidic or nutrient-deficient environments.

Among different groups, ZD5 and ZD6 samples show higher microbial diversity, particularly with an increased proportion of Others categories, reflecting the complexity of rhizosphere microbial interactions, which may enhance the plant's adaptability to environmental stresses. Additionally, the increase of Nitrospira and Verrucomicrobia in ZD6 suggests active nitrogen cycling in these samples, potentially improving nitrogen availability and supporting *X. strumarium*'s growth in nitrogen-limited areas. Furthermore, the higher

abundance of Pseudomonas and Streptomyces in ZD5 may aid in organic matter degradation and pathogen suppression, further promoting the plant's survival in polluted or highly competitive environments. Overall, these characteristics of the rhizosphere microbial community suggest that *X. strumarium* can expand its distribution across different soil conditions through its microbiome, particularly in disturbed or marginal soils.



**Figure 8.** The species relative abundance bar chart at the phylum level (the x-axis represents the sample name; the y-axis represents relative abundance; "Others" represents the sum of the relative abundance of all phyla other than the top 10 phyla in the chart).



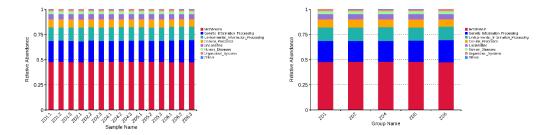
**Figure 9.** The species abundance clustering chart (the vertical axis represents sample information, and the horizontal axis represents species annotation information. The clustering tree on the left side of the chart is the species clustering tree. The values in the heatmap correspond to the Z-scores of the relative abundance of each species in each row after standardization. That is, the Z-score for a sample in a specific classification is the difference between the relative abundance of the sample in that classification and the average relative abundance of all samples in that classification, divided by the standard deviation of the relative abundance of all samples in that classification).

## 3.6. Functional Prediction of Soil Microorganisms

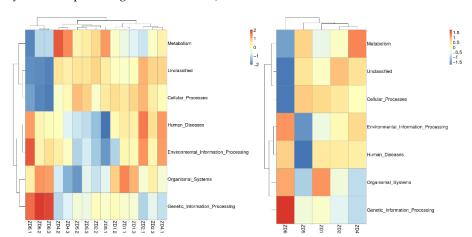
The functional diversity of the rhizosphere microbial community of *X. strumarium* is revealed through the Tax4Fun relative abundance bar chart and clustering analysis, highlighting differences in microbial genome functions across different samples and groups (Figure 10, Figure 11 and Figure 12). At the sample level, Metabolism consistently dominates the microbial genomes, with most samples showing relative abundances exceeding 0.5, indicating the central role of metabolic processes, possibly linked to environments rich in organic matter. Genetic Information Processing also maintains a high relative abundance, highlighting the importance of processes such as DNA replication and transcription in microbial survival and reproduction across different habitats. While Environmental Information Processing is generally lower, it exhibits some increase in specific groups like ZD6, reflecting the microbial community's ability to sense and respond to environmental fluctuations. In contrast, categories such as Human Diseases and Organismal Systems show minimal presence, reinforcing

that these microbial communities are primarily from natural ecosystems rather than environments closely linked to human health or diseases.

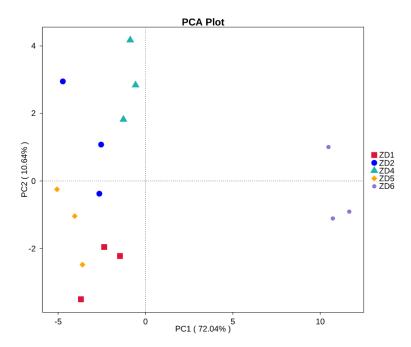
At the group level, differences in functional distributions are observed. The ZD1, ZD2, ZD4, ZD5, and ZD6 groups all show Metabolism as the dominant functional category, yet subtle variations in other functions emerge. For example, ZD4 and ZD5 exhibit a slight increase in Environmental Information Processing, suggesting a heightened need for environmental adaptation. Notably, the ZD6 group stands out, exhibiting a significantly higher relative abundance of Metabolism and lower abundance in Genetic Information Processing and Environmental Information Processing. This could indicate a microbial community highly active in metabolic processes, possibly due to environmental conditions that favor energy and nutrient conversion over genetic adaptation or environmental sensing. Overall, the microbial functional composition reflects the ecological conditions of each group, with implications for how Xanthium strumarium adapts to various soil environments, particularly in terms of resource utilization and environmental adaptability.



**Figure 10.** The Tax4Fun functional annotation relative abundance bar chart (the x-axis represents the sample name; the y-axis represents relative abundance; "Others" represents the sum of the relative abundance of all categories beyond the top 10 categories in the chart).



**Figure 11.** The Tax4Fun functional annotation clustering heatmap (the vertical axis represents sample information, and the horizontal axis represents species annotation information. The clustering tree on the left side of the chart is the species clustering tree. The values in the heatmap correspond to the Z-scores of the relative abundance of each species in each row after standardization. That is, the Z-score for a sample in a specific classification is the difference between the relative abundance of the sample in that classification and the average relative abundance of all samples in that classification, divided by the standard deviation of the relative abundance of all samples in that classification).



**Figure 12.** Display of Tax4Fun functional annotation PCA results (samples with more similar functional compositions are closer to each other in the dimensionality reduction plot).

# 4. Discussion

## 4.1. Impact of Climate Change on Habitat Distribution of Xanthium strumarium

This study applied the widely used Biomod2 model to explore the impact of global climate change on the suitable habitats of *X. strumarium* in China. Our results indicate that climate change is expected to significantly alter the distribution of suitable habitats for this species, with varying impacts depending on emission scenarios. Under current climate conditions, the primary suitable habitats for *X. strumarium* are concentrated in southern, central, eastern, northeastern, and southeastern China, representing regions with optimal climatic conditions for plant growth.

Given the substantial influence of global warming on the projected changes in precipitation and climate patterns, the expansion and contraction of plant species are expected to have strong ecological impacts across China. Under future climate scenarios, particularly those associated with high emissions (SSP5-8.5), the distribution of suitable habitats is predicted to expand, driven by rising temperatures and changing precipitation patterns. These changes are expected to create favorable conditions for the species in areas where competition was previously less intense. The predicted expansion primarily includes regions such as Yunnan, Guizhou, Guangdong, Hainan, and parts of Inner Mongolia, with coastal areas also becoming increasingly susceptible to invasion.

Climate change can promote plant invasions by increasing disturbances through extreme climatic events and changing environmental conditions. Previous studies have identified different key environmental variables for *X. strumarium* in various regions. For example, Kekeç and Kadıoğlu [92] identified Bio4, Bio10, Bio11, and Bio12 as the dominant environmental variables in Turkey; Waheed *et al.* [14] highlighted Bio4, Bio8, and nitrogen content (soil nitrogen) as influential in Pakistan; and Chikuruwo *et al.* [93] found NDVI to be the most significant factor in southeastern Zimbabwe. The variation in these influential environmental variables across studies may be due to differences in study areas, selected variables, and distribution points [94]. In this study, we identified human activity (human footprint) as the dominant environmental variable affecting *X. strumarium* distribution, followed by topography, and then NDVI along with a series of bioclimatic variables. These findings suggest that human activity and topography are key drivers of *X. strumarium*'s spread. Human activity exacerbates the spread of invasive species, while factors such as elevation, slope, and aspect are among the limiting factors for plant distribution. Therefore, it is not surprising to find that

human activity and topographic changes significantly influence the species' spread. Meanwhile, the changes in the dynamic ecological niche reflect a decrease in the ecological adaptability of *X. strumarium* with the increase in fossil fuel emissions.

In conclusion, the predicted expansion of suitable habitats under climate change, particularly in regions with increased human activity and altered topography, highlights the ongoing shifts in the potential distribution of *X. strumarium* across China.

## 4.2. Role of Rhizosphere Microbial Communities in Adaptation

The rhizosphere microbial communities play a pivotal role in the adaptation of *X. strumarium* to diverse environmental conditions. The microbial community structure varies significantly across different samples and groups, with Proteobacteria being the dominant phylum in most samples, suggesting its strong role in soil metabolism and nutrient cycling [95,96]. Other microbial phyla like Firmicutes and Bacteroidetes contribute to the adaptability of *X. strumarium* in various soil conditions, including nutrient-deficient and acidic environments [97,98]. Additionally, the higher microbial diversity observed in samples such as ZD5 and ZD6, coupled with the increased proportion of Nitrospira and Verrucomicrobia, points to active nitrogen cycling in these habitats, which could help improve nutrient availability for the plant. The interactions between the plant and its rhizosphere microbiome support its growth in disturbed or marginal soils, allowing *X. strumarium* to thrive in diverse and challenging environments.

## 4.3. Uncertainties of the Present Study

In this study, we first employed an integrated modeling approach to simulate the potential distribution of *X. strumarium* in China under current and future climate scenarios, thereby reducing uncertainties arising from differences in model algorithms. Although the distribution points were carefully selected, the spatial dispersion of these points and the lack of field surveys in some regions may have influenced the prediction of the species' potential suitable areas. The selection of environmental variables plays a crucial role in species distribution prediction and model accuracy. This study did not account for various factors such as soil characteristics and land use, which could significantly impact the species' distribution. Future research should consider incorporating additional environmental variables and conduct field surveys in other provinces to supplement the data. Furthermore, dispersal dynamics can notably influence a species' response to global changes, potentially affecting the study's outcomes [99,100]. Future investigations could integrate different dispersal scenarios to further explore the potential changes in hotspots under climate and land use variations.

## 5. Conclusions

This study analyzes the potential suitable distribution changes of *X. strumarium* in China under climate change, dynamic ecological niche shifts, and the composition, abundance, and functional validation of its rhizosphere microbiota. The results indicate that human footprint, slope, and elevation are the dominant environmental variables influencing the distribution of *X. strumarium*. With the intensification of climate change, the potential suitable distribution of *X. strumarium* gradually expands. Moreover, the dynamic ecological niche analysis reveals a reduction in the ecological adaptability of *X. strumarium* with the increasing fossil fuel emissions. The validation of rhizosphere microbiota abundance and function confirms its role in the distribution and environmental adaptation of *X. strumarium*. This study provides insights into the potential distribution changes, dynamic ecological niche shifts, and the composition and function of soil rhizosphere microbiota of *X. strumarium* under climate change, offering theoretical support for the future utilization and management of *X. strumarium*.

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resources, J.D. and H.J.; data curation, Y.Z. and M.Z.; writing—original draft preparation, J.D. and L.Z.; writing—review and editing, Y.Z., X.W., M.Z., and H.J.; visualization, M.Z. and X.W.; supervision, H.J.; project administration, J.D.; funding acquisition, H.J. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: We encourage all authors of articles published in MDPI journals to share their research data. In this section, please provide details regarding where data supporting reported results can be found, including links to publicly archived datasets analyzed or generated during the study. Where no new data were created, or where data is unavailable due to privacy or ethical restrictions, a statement is still required. Suggested Data Availability Statements are available in section "MDPI Research Data Policies" at https://www.mdpi.com/ethics.

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