

Article

Predicting the Spatiotemporal Distribution Shifts of *Zeugodacus tau* (Diptera: Tephritidae) in China

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Abstract

Zeugodacus (Bactrocera) tau (Walker) (*Z. tau*) is an economically important tephritid pest in Asia. We modelled its climate-associated habitat suitability in China under current and future scenarios using an optimized MaxEnt model, global occurrence records, and WorldClim variables. The most influential predictors were precipitation of the warmest quarter (Bio18), precipitation of the wettest month (Bio13), annual mean temperature (Bio1), mean diurnal temperature range (Bio2), and temperature seasonality (Bio4). Under current climatic conditions, the suitable habitats of *Z. tau* in China were widely distributed across South China, Central China, East China, and Southwest China, with a total area of $272.08 \times 10^4 \text{ km}^2$, accounting for 28.34% of the national land area. Future projections indicated a redistribution of suitability classes rather than a uniform range expansion: moderate-suitability habitat generally increased, whereas high-suitability habitat decreased or fluctuated, and the centroid of suitable habitats generally shifted northwestward and northeastward, with slight fluctuations across different periods. These projections suggest that climate change may alter the spatial pattern of climate-associated habitat suitability for *Z. tau* in China, providing a basis for prioritizing surveillance and quarantine efforts in areas showing increased future suitability.

Keywords: pumpkin fruit fly; optimized MaxEnt; habitat suitability; climatic warming; environmental variables; centroid shifts

1. Introduction

Zeugodacus (Bactrocera) tau (Walker) (Diptera: Tephritidae), commonly known as the pumpkin fruit fly, is one of the most economically destructive tephritid pests in the Asia-Pacific region [1,2]. The species is considered native to South and Southeast Asia, with historical records from southern China and the Indian subcontinent. Its currently reported distribution extends across tropical and subtropical Asia, including China, India, Sri Lanka, Thailand, Myanmar, Vietnam, Malaysia, Singapore, Bangladesh and Indonesia and has also been summarized as ranging from Pakistan to the Philippines and southward to Sumatra and Sulawesi [3,4]. Economic damage caused by this pest is largely associated with oviposition and larval infestation; adult females insert their oviposition tube into the fruit epidermis to lay eggs, and the hatched larvae feed internally, causing fruit decay, tissue damage, and reduced marketability. To date, *Z. tau* has been documented to infest more than 90 fruit and vegetable crops, with cucurbit hosts such as pumpkin, cucumber, and bitter melon being particularly important, as well as solanaceous crops such as tomato [1,5].



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The spread of *Z. tau* is facilitated by both adult movement and human-mediated transport of infested host materials. Adult flight contributes to local dispersal, whereas the movement of infested fruit or soil provides an important pathway for its spread into previously uninfested areas. Once established, outbreaks of this pest can pose serious threats to agricultural production, especially in cucurbit-growing regions [6]. In Asia, *Z. tau* infestation has been estimated to cause approximately 30%–40% annual losses in agricultural products. In northern India, particularly Himachal Pradesh, *Z. tau* and related tephritid fruit flies have been reported to cause severe damage to vegetable crops, with losses reaching up to 80% [1,7]. Beyond direct economic losses, the establishment of invasive tephritid fruit flies may also alter interspecific interactions within local fruit fly communities. Such competition can reduce the abundance of resident fruit fly species or displace less competitive species across host plants, seasons, or habitats, thereby affecting the structure and dynamics of local tephritid assemblages [8]. Together, its dispersal capacity and broad host range may enable *Z. tau* to colonize diverse agricultural ecosystems and facilitate further range expansion.

Current monitoring and identification of *Z. tau* rely primarily on cue-lure-based male trapping and molecular diagnostic tools, including species-specific PCR and COI-based sequence analysis, which together support field surveillance, rapid laboratory diagnosis, and discrimination from closely related taxa [9–11]. Management of *Z. tau* relies largely on area-wide integrated pest management (AW-IPM) frameworks, which combine tactics such as male annihilation, protein bait spraying, sterile insect release, and quarantine-linked surveillance and eradication programs [12]. However, the long-term effectiveness of these measures depends on continuous optimization and adaptive implementation, particularly to reduce the risks of insecticide resistance and minimize non-target environmental impacts [6,12,13]. Although considerable progress has been made in the ecological understanding and control of *Z. tau*, the environmental adaptation mechanisms of this pest remain largely unclear, which severely limits our capacity to foresee its potential establishment in newly introduced regions. To translate ecological information into actionable risk management, identifying broad-scale areas of potential habitat suitability is important. Predicting the potential distribution of suitable habitats can help identify areas where environmental conditions may favor *Z. tau* and support the prioritization of surveillance, monitoring, and further risk assessment [5].

Climate is the primary driver shaping the geographic distribution of invasive pests [14]. Due to their poikilothermic nature, the development, survival, reproduction, and population dynamics of tephritid fruit flies are strongly influenced by temperature and moisture-related climatic conditions. Consequently, climate warming may alter the geographic distribution of suitable habitats, promote poleward or latitudinal range shifts, extend seasonal activity periods, increase population growth potential, and heighten the overall risk of establishment and invasion [15,16]. Over the past century, China has experienced pronounced warming at a rate of 1.3–1.7 °C per century, outpacing the global average and creating highly favorable environments for such warm-adapted and moisture-dependent pests [17–19]. Against this climatic backdrop, *Z. tau* shows strong ecological adaptability. Its development and reproduction are highly temperature-dependent, and it can complete one to several generations annually, with up to eight generations reported in warm regions [5]. In addition to favorable climatic conditions, China's large-scale vegetable production provides an important ecological context for understanding the potential distribution patterns of *Z. tau*. The extensive cultivation of vegetables and large harvested areas in China may contribute to the availability of potential host resources, especially in regions where cucumbers, tomatoes, peppers, and other suitable host crops are widely cultivated [5,20]. Driven by the synergy of climate warming and intensive agriculture, *Z. tau* has successfully estab-

lished widespread populations across South, East, Central, and even parts of North China, posing a persistent threat to horticultural industries. Although the historical occurrence and current distribution of *Z. tau* in China are well-documented [21,22], how future climate change will alter its long-term range shifts and spatial dynamics remains a critical blind spot. Deciphering these potential shifts is imperative for formulating proactive regional risk assessments and early-warning management strategies.

Species Distribution Models (SDMs) are widely used to quantify the potential distribution of invasive species by linking occurrence records with environmental variables [23–26]. Common modeling frameworks include GLM, GAM, BIOCLIM, DOMAIN, ENFA, and MaxEnt [27–32], and comparative studies have consistently demonstrated that MaxEnt 3.4.4 performs effectively with presence-only data, small sample sizes, and complex environmental relationships. MaxEnt has been widely used to predict suitable habitats for many invasive pests, including *Halyomorpha halys*, *Bactrocera dorsalis*, *Drosophila suzukii*, *Tuta absoluta*, and *Diaphorina citri* [33–37], and is particularly suitable for climate-driven, rapid regional risk mapping. In China, *Z. tau* is considered an important agricultural pest, and understanding its potential distribution changes under future climate scenarios is essential for improving risk assessment and management strategies. In this study, we used an optimized MaxEnt model to characterize the current and future climate-associated habitat suitability of *Z. tau* in China under climate change scenarios, identify key environmental variables, and analyze the spatiotemporal dynamics and centroid shifts of suitable habitats. The results provide a scientific basis for identifying areas of relatively high environmental suitability and prioritizing quarantine surveillance, monitoring, and further regional risk assessment.

2. Materials and Methods

2.1. Collection and Screening of Occurrence Data

A total of 4414 global occurrence records of *Z. tau* were collected in this study from multiple sources (Figure S1), including GBIF (GBIF Occurrence Download. Available online: <https://doi.org/10.15468/dl.kxycmv> (accessed on 7 October 2025)) [38], Bold Systems v5 (<https://boldsystems.org/>, accessed on 8 October 2025), iNaturalist (<https://www.inaturalist.org/>, accessed on 8 October 2025), National Center for Biotechnology Information (<https://bcms.ncbi.nlm.nih.gov/loginNcbi>, accessed on 8 October 2025), and relevant literature from CNKI and Web of Science. The collected records were subjected to a standardized screening procedure based on taxonomic identity, temporal coverage, and geographic information before model construction. Taxonomic information was harmonized among different data sources by checking species names against the currently accepted classification of *Zeugodacus tau*. Historical synonyms and alternative taxonomic combinations, particularly the previously used combination *Bactrocera tau*, were examined to ensure consistency among records referring to the same taxon. Occurrence records reported before 2025 were retained, and no additional temporal restriction was applied. Geographic information was subsequently evaluated through a quality-control procedure. Records with missing coordinates, invalid coordinate formats, obvious geographic errors, or inconsistencies between coordinates and locality descriptions were removed. Marine records were excluded because they did not represent terrestrial occurrence environments. Because coordinate uncertainty information was not consistently available across all data sources, no universal uncertainty threshold was applied; instead, coordinate reliability was assessed based on geographic validity and consistency with the associated locality information. The initial occurrence dataset consisted mainly of records from GBIF (88.9%) and iNaturalist (10.6%), whereas BOLD Systems, NCBI, and published literature together contributed the remaining 0.5% of records. To mitigate model overfitting caused by sam-

pling bias and spatial autocorrelation, duplicate records were removed using ENMTools 1.4 at a spatial resolution of 2.5 arc-minutes (approximately 4.5 km), ensuring only one occurrence point was retained per grid cell, which yielded 672 effective occurrence records (Figure 1). Visualization of these distribution points was performed using ArcGIS 10.8.

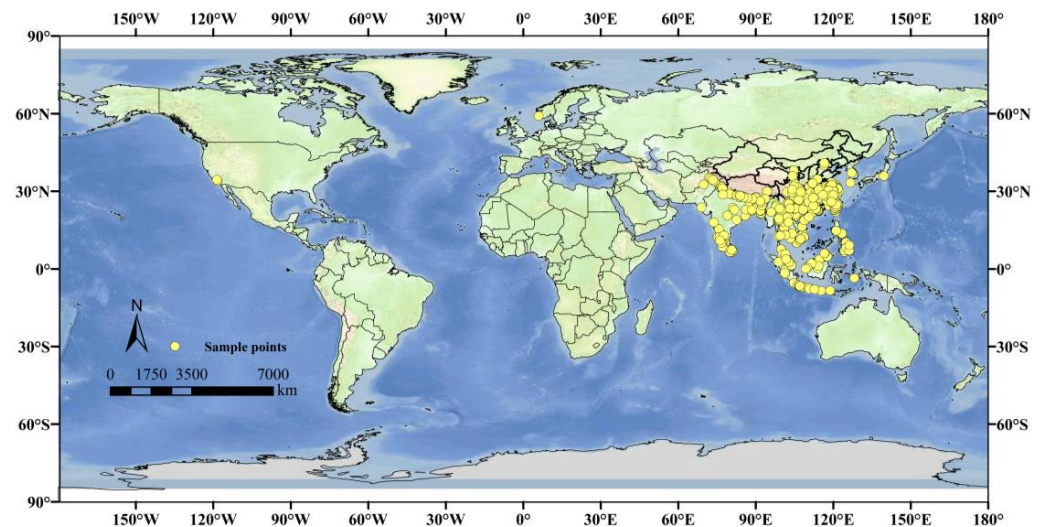


Figure 1. Worldwide distribution map of filtered occurrence records of *Z. tau*.

2.2. Acquisition and Screening of Environmental Variables

Nineteen bioclimatic variables and elevation data were obtained from the WorldClim database (<https://www.worldclim.org/>, accessed on 23 November 2023), and all environmental layers were converted to raster format and resampled to a spatial resolution of 2.5 arc-minutes in ArcGIS. The Slope and Aspect variables were derived from the elevation data using the surface analysis tools in ArcGIS. Current climatic conditions were represented by the average values from 1970 to 2000, and future climatic scenarios were derived from the BCC-CSM2-MR model under CMIP6, covering four shared socioeconomic pathways (SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5) across four time periods including the 2030s, 2050s, 2070s, and 2090s. To reduce variable redundancy and multicollinearity, a stepwise screening procedure was implemented: first, all occurrence points and 22 environmental variables were imported into MaxEnt to construct a preliminary model, and the contribution rate and permutation importance of each variable were assessed via the Jackknife test; second, raster values of each variable were extracted in ArcGIS, and Pearson correlation analysis was conducted in SPSS Statistics v32 to identify highly correlated variables ($|r| \geq 0.8$). For pairs of variables showing high correlation, the variable with the lower contribution rate was removed, whereas the variable with higher contribution rate was retained. Variables that were not strongly correlated with other predictors ($|r| < 0.8$) were retained directly. Based on this procedure, ten variables (Bio1, Bio2, Bio4, Bio10, Bio13, Bio14, Bio18, Bio19, Slope, and Aspect) were selected for subsequent modeling (Figure 2).

2.3. Optimization of MaxEnt Model Parameters

The regularization multiplier (RM) and feature class (FC) combinations were systematically optimized using the ENMeval package in R 4.5.0. Occurrence records were divided into four spatial blocks, with three blocks used for model training and one block for independent testing. Eight RM levels ranging from 0.5 to 4 at 0.5 intervals and eight feature combinations (L, LQ, LQP, QHP, LQH, LQHP, QHPT, and LQHPT), where L, Q, H, P, and T represent linear, quadratic, hinge, product, and threshold features, respectively, were set, producing 64 parameter combinations in total. The optimal parameter combination

was selected based on the lowest corrected Akaike information criterion (AICc) to balance model goodness of fit and complexity and avoid overfitting.

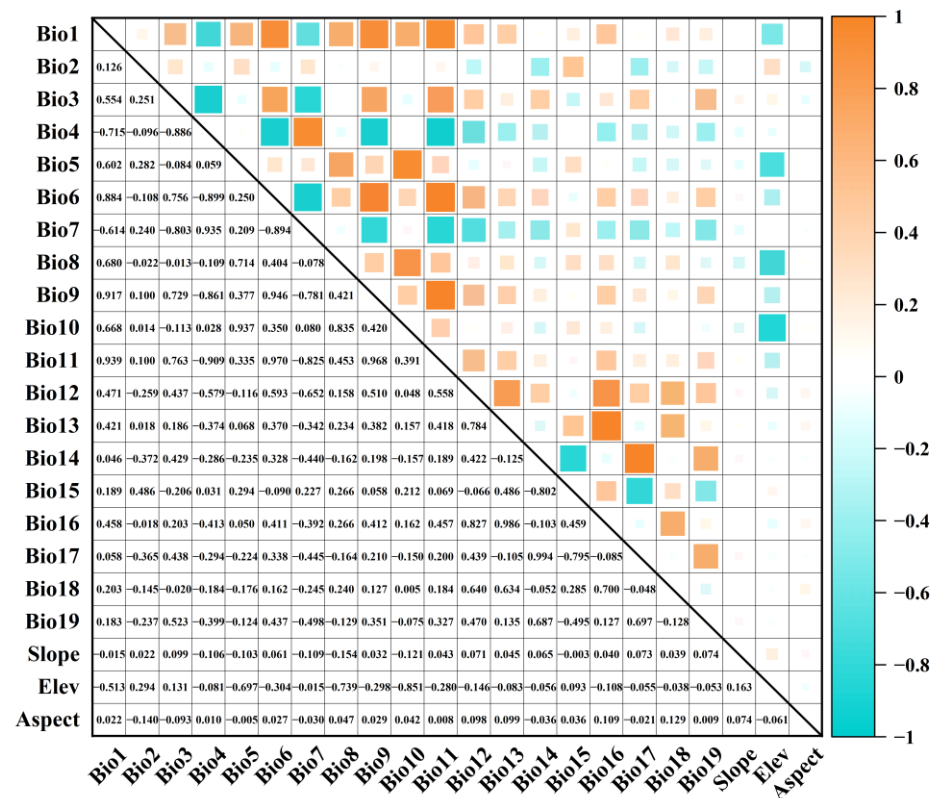


Figure 2. Pearson correlation matrix of the 22 environmental variables (orange indicates positive correlations, whereas blue indicates negative correlations).

2.4. Model Execution and Accuracy Evaluation

The 672 effective occurrence records and ten screened environmental variables were imported into MaxEnt using the optimized parameters for final model execution. The optimized parameter combination was selected using the ENMeval package in R, in which spatial block partitioning was applied to evaluate candidate models under spatially structured conditions and minimize the potential influence of spatial autocorrelation during model selection. After parameter optimization, the final MaxEnt model was constructed using the selected settings. For final model execution, 75% of the occurrence records were randomly assigned for training and 25% for testing, the maximum number of iterations was set to 5000, 10,000 background points were used, and the model was run for 10 replicates. Background points were randomly sampled from the global extent of the environmental layers. In the present modelling framework, this broad calibration extent was used to characterize the climatic associations represented by the assembled occurrence dataset against a broad environmental background before projecting climate-associated habitat suitability to China. Figure S1 illustrates the global distribution of occurrence records before spatial filtering together with the calibration/background extent used for background sampling. Model outputs were generated in logistic format. The resulting suitability maps were interpreted as relative climate-associated suitability values. Response curves were constructed to evaluate the relationships between environmental variables and habitat suitability, and the Jackknife test was performed to assess the relative contribution of each environmental variable.

Model performance was primarily evaluated using the mean test AUC obtained from the 10 replicate runs of the final MaxEnt model. AUC values were classified as excellent

($AUC > 0.9$), good ($0.8 \leq AUC \leq 0.9$), moderate ($0.7 \leq AUC < 0.8$), poor ($0.6 \leq AUC < 0.7$), and invalid ($AUC \leq 0.5$). In addition, the mean validation AUC, continuous Boyce Index (CBI), and 10% omission rate obtained from ENMeval spatial block evaluation were used as complementary metrics to further assess model performance under spatially structured validation.

2.5. Habitat Classification and Centroid Shift Analysis

Habitat suitability indices generated by MaxEnt were classified into four suitability classes using the natural breaks (Jenks) method in ArcGIS: unsuitable habitat (0–0.13), low-suitability habitat (0.13–0.38), moderate-suitability habitat (0.38–0.56), and high-suitability habitat (0.56–1.00), and the area and proportion of each suitability level were calculated. The Jenks method determines class boundaries by minimizing within-class variance and maximizing between-class variance. This classification was used only for visualization and area statistics. Raster data representing different suitability classes were converted into vector data, and centroid coordinates of the suitable habitat classes under current and future climatic scenarios were calculated using spatial statistical tools to analyze their directional shifts and migration distances.

3. Results

3.1. Model Optimization and Accuracy Assessment

The initial MaxEnt model was constructed using the default settings ($RM = 1$ and $FC = LQHP$). After parameter optimization, the optimal model configuration was identified as $RM = 1$ and $FC = LQHPT$, which exhibited the lowest AICc value among all evaluated combinations ($\Delta AICc = 0$) (Figure 3). The selected model showed an AICc weight of 0.9456, indicating strong support for this parameter combination relative to other candidate models. Therefore, the optimized parameter setting ($RM = 1$ and $FC = LQHPT$) was used for subsequent habitat suitability projections.

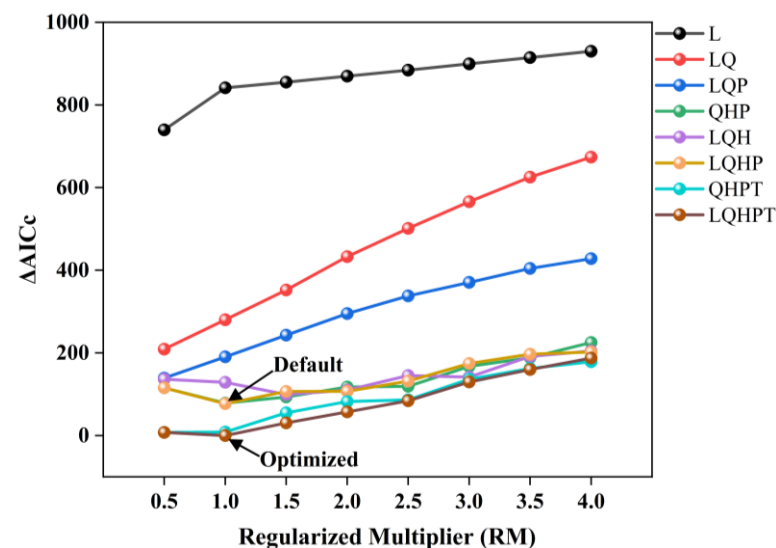


Figure 3. $\Delta AICc$ values of MaxEnt models under different regularization multiplier (RM) and feature class (FC) combinations. Feature classes: L = linear, Q = quadratic, H = hinge, P = product, T = threshold.

The final optimized MaxEnt model achieved a mean test AUC of 0.957 ± 0.003 (Figure S2) across 10 replicate runs, indicating stable model performance. Additional evaluation metrics obtained during ENMeval optimization with spatial block partitioning included a mean validation AUC of 0.969 ± 0.009 , a continuous Boyce Index of 0.976 ± 0.013 ,

and a 10% omission rate of $14.1\% \pm 1.5\%$. These results provided support for the reliability of the optimized model under spatially structured evaluation.

3.2. Dominant Environmental Variables and Response Curves

Figure 4 illustrates the relative percent contribution and permutation importance of the ten environmental variables governing habitat suitability for *Z. tau*, alongside their corresponding individual response curves. Precipitation of Warmest Quarter (Bio18) emerged as the most dominant driving factor, exhibiting a percent contribution of 35.6% and a permutation importance of 10.3%. The remaining nine variables, in descending order of their contribution, were Precipitation of Wettest Month (Bio13), Annual Mean Temperature (Bio1), Mean Diurnal Temperature Range (Bio2), Temperature Seasonality (Bio4; expressed as standard deviation $\times 100$), Precipitation of Driest Month (Bio14), Mean Temperature of Warmest Quarter (Bio10), Slope, Precipitation of Coldest Quarter (Bio19), and Aspect, which collectively defined the pest's ecological profile.

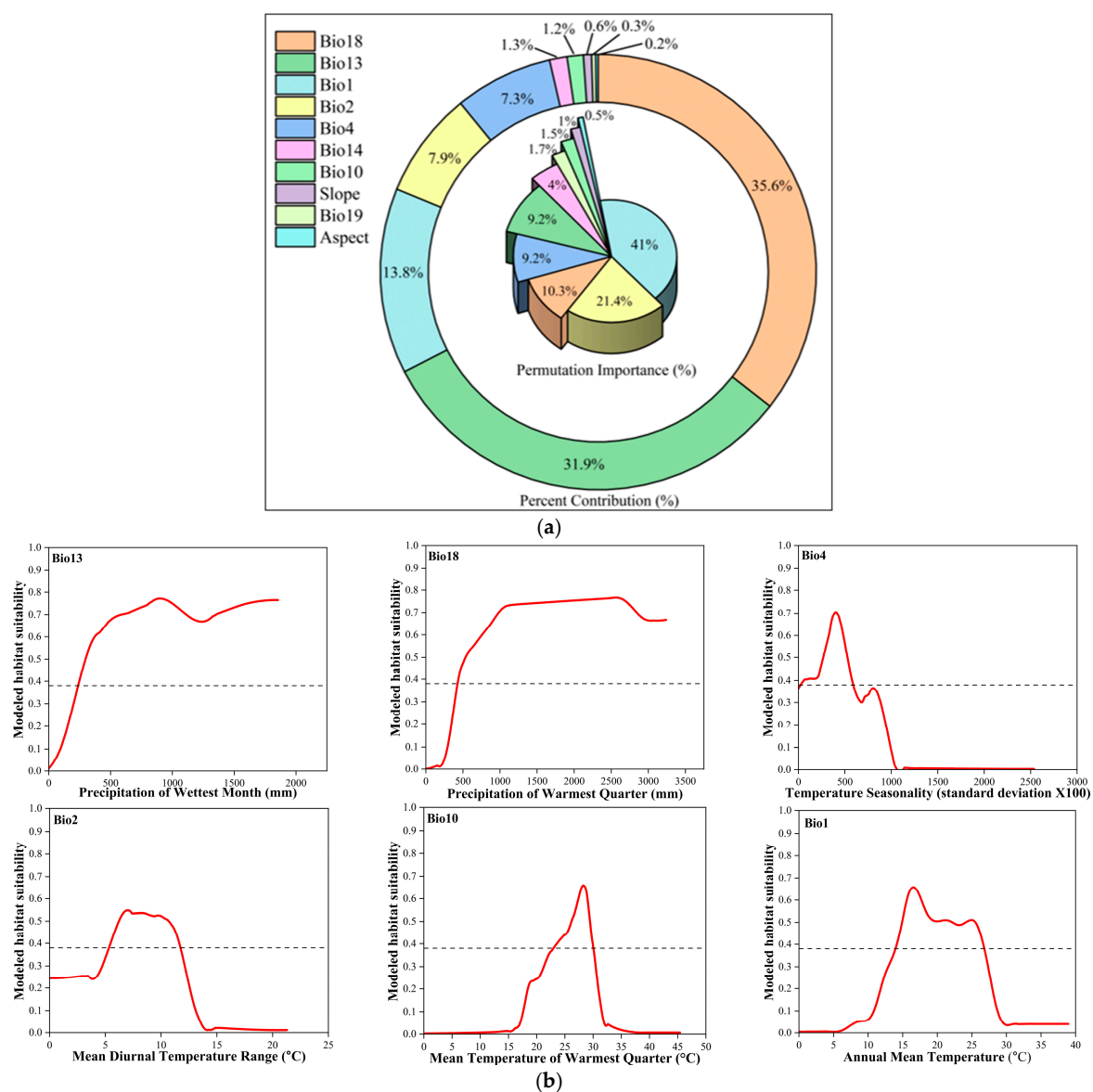


Figure 4. Relative importance and response curves of environmental variables determining the habitat suitability of *Zeugodacus tau*. (a) Percent contribution and permutation importance of the ten key environmental variables; (b) response curves illustrating modeled habitat suitability of *Z. tau* under the six primary bioclimatic variables.

Analysis of the response curves revealed clear suitability patterns for six primary bioclimatic variables. Based on the Jenks natural breaks classification of MaxEnt suitability outputs in ArcGIS, habitat suitability values were categorized into four classes, and areas with suitability values ≥ 0.38 were grouped as moderate-to-high suitability habitats. This threshold represents the boundary between suitability classes derived from the natural breaks classification and was used only for habitat suitability categorization rather than as a biological threshold for species occurrence. The critical environmental ranges and their corresponding optimal values were identified as follows: 14.35–26.39 °C for Bio1 (optimum: 16.09 °C); 5.44–11.57 °C for Bio2 (optimum: 7.26 °C); 21.21–530.13 for Bio4 (optimum: 372.48); 23.07–29.85 °C for Bio10 (optimum: 28.40 °C); 183.44–1854.60 mm for Bio13 (optimum: 1057.46 mm); and 429.82–3238.40 mm for Bio18 (optimum: 2602.50 mm). These six variables exhibited typical unimodal response patterns, with habitat suitability declining sharply beyond the peak thresholds. Conversely, the remaining four variables displayed unclosed curves, suggesting that their response patterns may be less stable at the edges of the observed environmental range and could introduce additional uncertainty when projecting model outputs into novel environmental spaces.

3.3. Current Distribution of Suitable Habitats

The current climate-associated suitable habitats of *Z. tau* were mapped according to the model simulation results (Figure 5). Under current climatic conditions, the total suitable habitat area for *Z. tau* in China was $272.08 \times 10^4 \text{ km}^2$, accounting for 28.34% of the country's terrestrial area. This comprised $128.19 \times 10^4 \text{ km}^2$ of high-suitability habitat, accounting for 13.35% of China's total area and 47.11% of the total suitable habitat; $76.38 \times 10^4 \text{ km}^2$ of moderate-suitability habitat, accounting for 7.96% of the national area and 28.07% of the total suitable habitat; and $67.52 \times 10^4 \text{ km}^2$ of low-suitability habitat, accounting for 7.03% of the national area and 24.82% of the total suitable habitat.

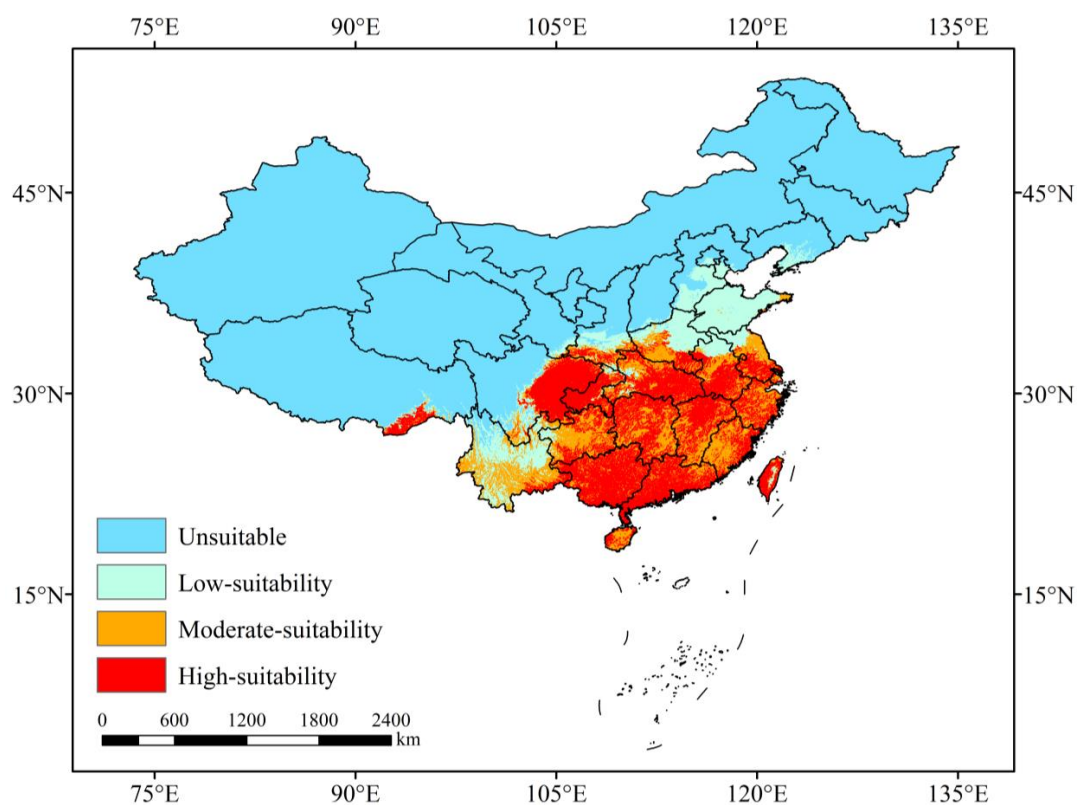


Figure 5. Climate-associated potential suitable habitats of *Z. tau* under current climatic conditions in China.

Spatially, suitable habitats of *Z. tau* were mainly concentrated in South China, southern Central China, the southeastern coastal zone, and eastern Southwest China, showing a gradual transitional pattern toward northern and western regions. High-suitability regions were concentrated in Guangdong, Guangxi, Hainan, Fujian, Jiangxi, Taiwan, Hunan, southern Hubei, southern Zhejiang, Chongqing, the eastern edge of the Sichuan Basin, Guizhou, and eastern Yunnan. Moderate- and low-suitability zones extended into northern Guangxi, northern Guangdong, northern Jiangxi, central Zhejiang, southern Anhui, southern Jiangsu, northern Hunan, central Hubei, and transitional zones among Sichuan, Yunnan, and Guizhou. Most northern regions, the Qinghai–Tibet Plateau, and the north-west inland regions were unsuitable, with only scattered low-suitability patches in southern Henan, southern Shaanxi, and southern Shandong.

3.4. Dynamics of Future Suitable Habitats

Under all four SSP scenarios (Figure 6), suitable habitats remained predominantly in southern and eastern China, with high- and moderate-suitability zones continuously distributed across South China, East China, and eastern Southwest China. Over time, the spatial pattern of suitable habitats generally shifted northward and westward under most scenarios, with some peripheral regions in central China and south of the Huang-Huai Basin (southern Henan, southern Shaanxi, and southeastern Gansu) showing transitions from low to moderate or high suitability. Unsuitable areas were mainly confined to northern and northwestern regions, with the Qinghai–Tibet Plateau remaining largely unsuitable.

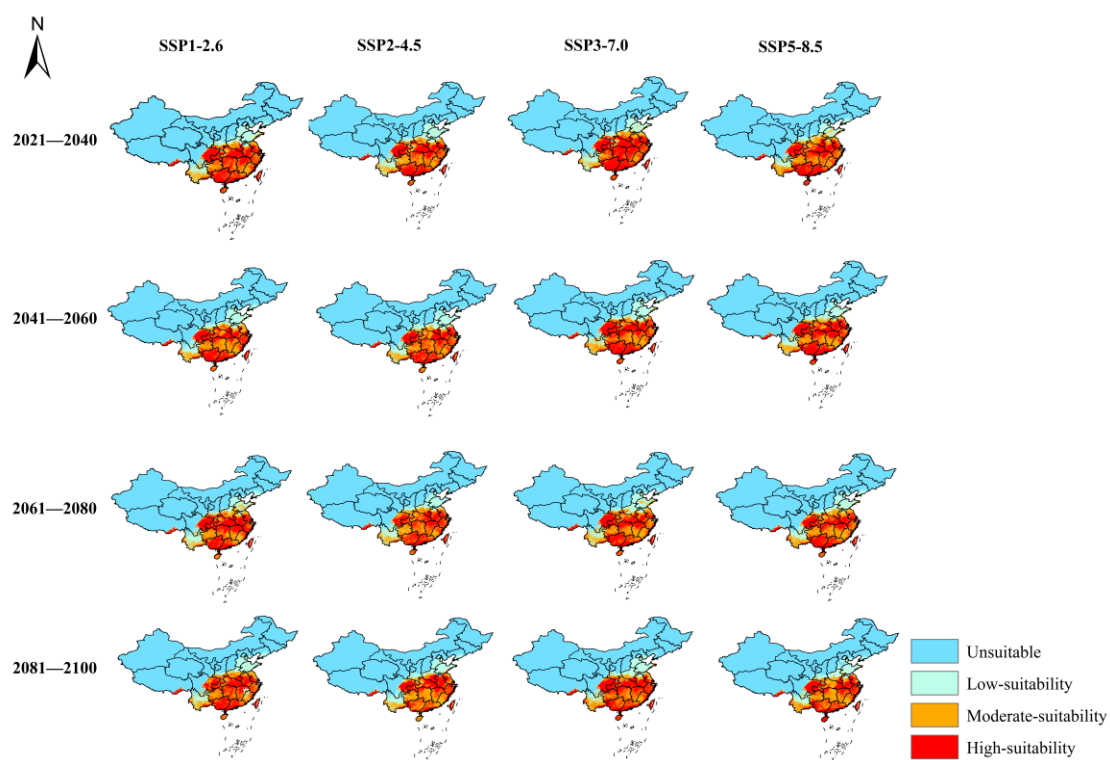


Figure 6. Climate-associated suitable habitats of *Z. tau* in China under different climate scenarios.

In terms of areal dynamics, the projected future changes in area are illustrated in Figure 7, with detailed information provided in Table 1. Across all future SSP scenarios and time periods, the total suitable habitat area showed only minor fluctuations, generally ranging between approximately $268.40 \times 10^4 \text{ km}^2$ and $278.95 \times 10^4 \text{ km}^2$, indicating relative stability. Compared with the current period, the total suitable area in the 2090s changed by only -0.40% to 1.55% among different SSP scenarios, suggesting limited variation in overall

habitat extent. For all scenarios, high-suitability habitat generally decreased over time, with the most pronounced reduction under SSP2-4.5 in the 2090s ($95.34 \times 10^4 \text{ km}^2$), representing a 25.62% decline compared with the current period. Similar reductions were observed under SSP5-8.5 and SSP1-2.6, with decreases of 21.79% and 13.37%, respectively, whereas SSP3-7.0 showed a relatively smaller decline (5.18%). In contrast, moderate-suitability habitat consistently increased across future scenarios, with expansions of 29.59%, 42.97%, 19.55%, and 38.02% by the 2090s under SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5, respectively. The increase in moderate-suitability habitat was particularly evident under SSP2-4.5 and SSP5-8.5, reaching $109.20 \times 10^4 \text{ km}^2$ and $105.42 \times 10^4 \text{ km}^2$ in the 2090s, respectively. Low-suitability habitat fluctuated slightly, with the largest contraction observed under SSP5-8.5 in the 2030s ($56.16 \times 10^4 \text{ km}^2$). Overall, despite the limited changes in total suitable habitat area, considerable redistribution and turnover among habitat suitability classes occurred across future climate scenarios.

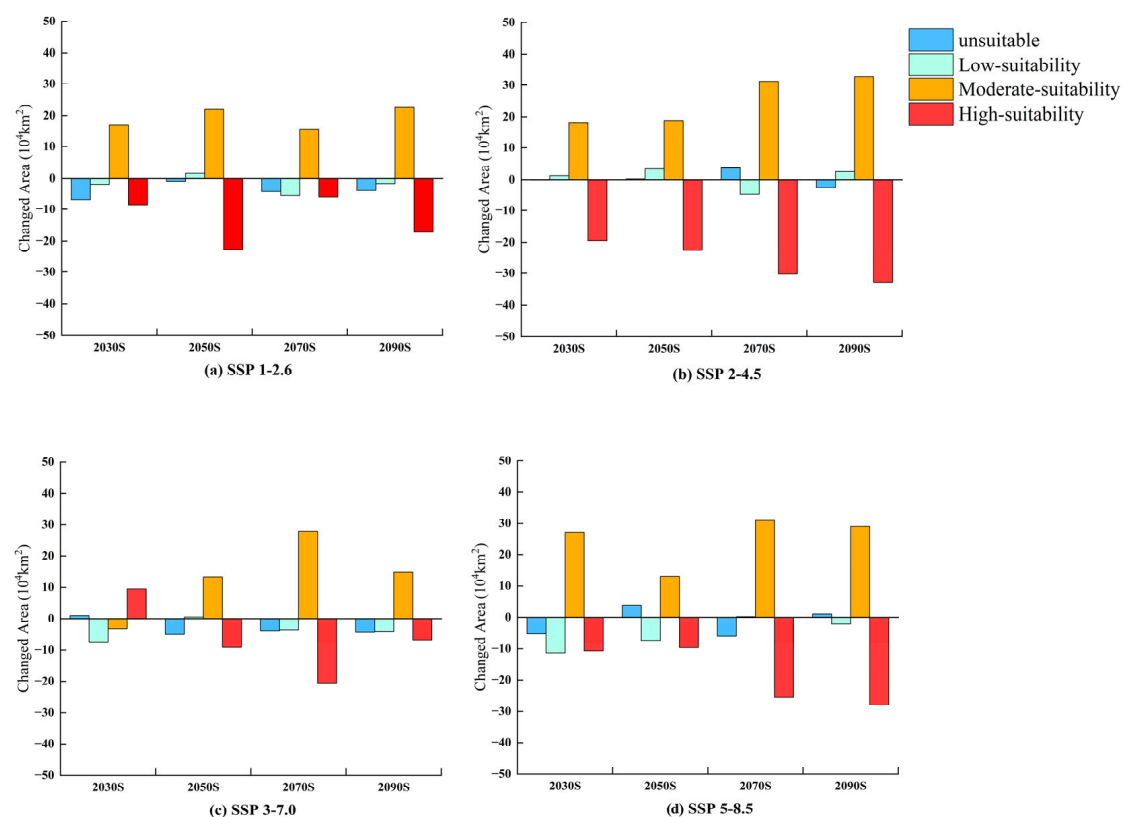


Figure 7. Differences between current and future suitable habitat areas in China under different climate change scenarios.

Table 1. Detailed data on changes in the suitable habitat area of *Z. tau* under different future climate scenarios.

Scenario	Decade	Total Suitable Area		Low Suitability		Moderate Suitability		High Suitability	
		Area ($\times 10^4 \text{ km}^2$)	Area Change (%)	Area ($\times 10^4 \text{ km}^2$)	Area Change (%)	Area ($\times 10^4 \text{ km}^2$)	Area Change (%)	Area ($\times 10^4 \text{ km}^2$)	Area Change (%)
— —	Current	272.08	— —	67.52	— —	76.38	— —	128.19	— —
SSP1-2.6	2030s	278.95	2.52	65.68	−2.72	93.62	22.57	119.65	−6.66
	2050s	272.98	0.33	69.14	2.40	98.35	28.77	105.49	−17.71
	2070s	276.26	1.53	62.05	−8.10	92.00	20.45	122.21	−4.66
	2090s	275.91	1.41	65.89	−2.41	98.98	29.59	111.04	−13.37

Table 1. Cont.

Scenario	Decade	Total Suitable Area		Low Suitability		Moderate Suitability		High Suitability	
		Area ($\times 10^4$ km ²)	Area Change (%)	Area ($\times 10^4$ km ²)	Area Change (%)	Area ($\times 10^4$ km ²)	Area Change (%)	Area ($\times 10^4$ km ²)	Area Change (%)
SSP2-4.5	2030s	272.17	0.03	68.76	1.84	94.67	23.95	108.75	−15.17
	2050s	271.83	−0.09	70.91	5.02	95.29	24.76	105.63	−17.59
	2070s	268.40	−1.35	62.83	−6.95	107.63	40.91	97.95	−23.59
	2090s	274.59	0.92	70.05	3.75	109.20	42.97	95.34	−25.62
SSP3-7.0	2030s	271.09	−0.37	60.25	−10.76	73.15	−4.23	137.69	7.41
	2050s	276.95	1.79	68.03	0.76	89.85	17.63	119.07	−7.11
	2070s	275.95	1.42	63.96	−5.26	104.28	36.53	107.70	−15.98
	2090s	276.31	1.55	63.44	−6.03	91.32	19.55	121.55	−5.18
SSP5-8.5	2030s	277.21	1.88	56.16	−16.83	103.56	35.58	117.49	−8.34
	2050s	268.41	−1.35	60.26	−10.76	89.55	17.25	118.60	−7.47
	2070s	277.96	2.16	67.75	0.34	107.42	40.63	102.79	−19.81
	2090s	271.01	−0.40	65.34	−3.23	105.42	38.02	100.25	−21.79

“— —”: Not applicable.

3.5. Centroid Shifts

Figure 8 and Table 2 show the centroid shift trajectory of suitable habitats for *Z. tau* during future periods. The centroid of current suitable habitats was located in Xiangxi Tujia and Miao Autonomous Prefecture, Hunan Province (110°04' E, 28°06' N). Under all future scenarios, the centroid of suitable habitats generally shifted northwestward and northeastward relative to the current centroid. Across the four SSP scenarios, the centroid remained mainly within Xiangxi Tujia and Miao Autonomous Prefecture and Huaihua City, Hunan Province, showing modest fluctuations between these areas over time. Specifically, the future centroid locations were distributed within a relatively narrow geographic range, approximately between 109°27' E–110°27' E and 28°09' N–28°54' N across different SSP scenarios and periods, with corresponding displacement distances relative to the current centroid ranging from 39.62 km to 98.52 km. These results indicate that although the centroid of suitable habitats exhibited directional shifts under future climate scenarios, the magnitude of centroid migration remained relatively small.

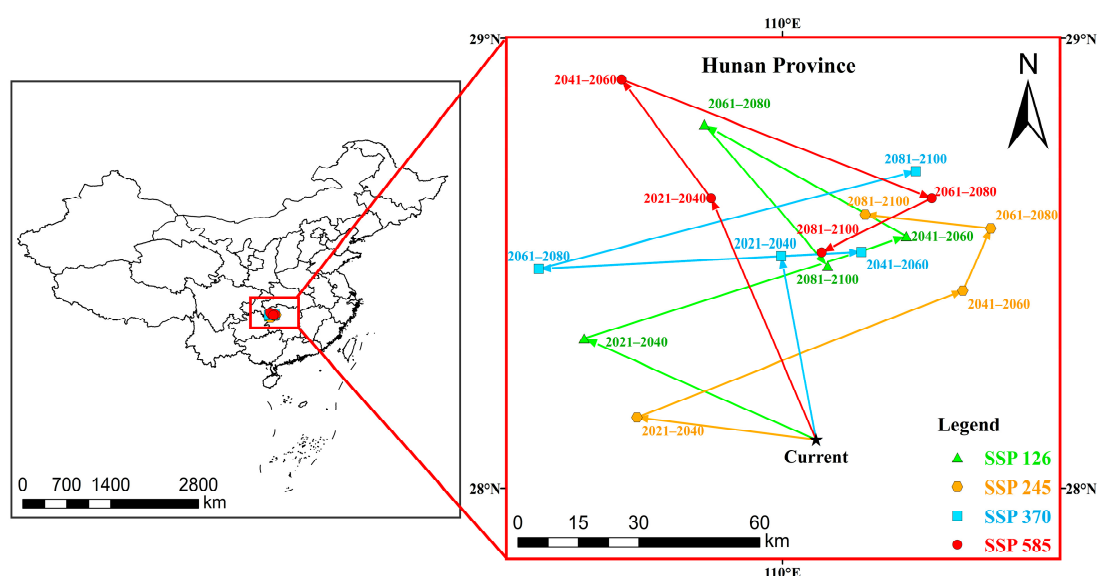


Figure 8. Centroid shifts of the potential suitable habitat of *Z. tau* under current and future climate scenarios.

Table 2. Detailed data on centroid shifts of suitable habitats for *Z. tau* under different future climate scenarios.

Climate Scenario	Period	Future Centroid Location	Longitude (°E)	Latitude (°N)	Shift Distance (km)	Azimuth (°)	Direction
— —	Current	Xiangxi Tujia and Miao Autonomous Prefecture, Hunan Province	110°04′	28°06′	— —	— —	— —
SSP1-2.6	2030s	Xiangxi Tujia and Miao Autonomous Prefecture, Hunan Province	109°33′	28°19′	56.07	295.57	NW
	2050s	Huaihua City	110°16′	28°33′	53.73	21.32	N
	2070s	Xiangxi Tujia and Miao Autonomous Prefecture, Hunan Province	109°49′	28°48′	81.58	342.63	N
	2090s	Xiangxi Tujia and Miao Autonomous Prefecture, Hunan Province	110°6′E	28°29′	42.75	4.37	N
SSP2-4.5	2030s	Xiangxi Tujia and Miao Autonomous Prefecture, Hunan Province	109°40′	28°9′	39.62	278.16	W
	2050s	Huaihua City	110°24′	28°26′	49.39	41.29	NE
	2070s	Huaihua City	110°27′	28°34′	64.03	35.78	NE
	2090s	Xiangxi Tujia and Miao Autonomous Prefecture, Hunan Province	110°11′	28°36′	56.76	11.58	N
SSP3-7.0	2030s	Xiangxi Tujia and Miao Autonomous Prefecture, Hunan Province	109°59′	28°30′	45.22	349.63	N
	2050s	Huaihua City	110°10′	28°31′	47.35	11.91°	N
	2070s	Xiangxi Tujia and Miao Autonomous Prefecture, Hunan Province	109°27′	28°29′	73.91	305.37°	NW
	2090s	Huaihua City	110°17′	28°42′	70.00	17.57	N
SSP5-8.5	2030s	Xiangxi Tujia and Miao Autonomous Prefecture, Hunan Province	109°50′	28°38′	63.55	339.00	N
	2050s	Xiangxi Tujia and Miao Autonomous Prefecture, Hunan Province	109°38′	28°54′	98.52	334.65	NW
	2070s	Huaihua City	110°19′	28°38′	64.15	22.36°	N
	2090s	Xiangxi Tujia and Miao Autonomous Prefecture, Hunan Province	110°5′	28°31′	46.36	2.01	N

“— —”: Not applicable.

4. Discussion

4.1. Model Optimization and Predictive Reliability

The MaxEnt model has been widely applied to predict the potential suitable habitats of tephritid pests; however, its default parameter settings frequently lead to overfitting and reduced reliability in spatial extrapolation [39]. To improve predictive accuracy, the present study optimized the regularization multiplier (RM) and feature class (FC) combinations using the ENMeval package, with the optimal parameter combination selected based on the lowest corrected Akaike information criterion (AICc). The optimized model substantially reduced complexity and overfitting risk, thereby improving the representation of relationships between *Z. tau* occurrence and the selected environmental predictors, consistent with contemporary modeling protocols for invasive tephritid fruit flies [40–42].

The mean test AUC of 0.957 ± 0.003 in this study far exceeds the threshold of 0.9 for excellent model performance, while the continuous Boyce Index (CBI) reached 0.976 ± 0.013 ; together, these two metrics indicate a strong correlation between climatic variables and the occurrence records of *Z. tau* and high model stability. Under current climatic conditions, the predicted suitable regions are mainly concentrated in South China, southeastern Central China, and eastern Southwest China, broadly corresponding to the documented occurrence and distribution records of *Z. tau* in China and further supporting the reliability of our predictions [5]. While these findings reinforce the value of ecological niche modeling in identifying climatically suitable areas for destructive tephritid pests, as seen in previous studies on *Bactrocera dorsalis*, *Bactrocera tsuneonis*, *Neoceratitis asiatica*, and *Bactrocera minax*, they can also provide practical support for risk-based pest management. Specifically, the predicted suitability patterns can help prioritize area-wide integrated pest management (AW-IPM) planning, quarantine resource allocation, and long-term regional surveillance efforts [34,40,43,44].

4.2. Key Climatic Predictors Associated with Habitat Suitability of *Z. tau*

Climate represents the dominant factor shaping the geographic range of tephritid insects, with temperature and precipitation jointly governing species distribution by regulating development, survival, reproduction, and the availability of host resources [45,46]. Our results revealed that Precipitation of Warmest Quarter (Bio18) exhibited the highest percent contribution (35.6%) and was the most influential environmental predictor associated with the distribution of *Z. tau*, followed by Precipitation of Wettest Month (Bio13, 31.9%). This suggests that precipitation-related conditions may play an important role in shaping habitat suitability for this species. Unlike many temperate pests whose northern expansion is strongly restricted by low winter temperatures, *Z. tau* is mainly distributed in tropical and subtropical regions where thermal conditions are generally favorable. Therefore, moisture availability may represent an important environmental constraint associated with its potential distribution, although further physiological and ecological studies are needed to clarify the direct mechanisms underlying these relationships.

The importance of precipitation in our model closely parallels studies on *B. tsuneonis*, for which Precipitation of Warmest Quarter was also identified as a key limiting factor [40]. Previous biological studies provide a possible mechanistic context for this modeled association. Sufficient precipitation during the warm season may enhance soil moisture and thereby favor pupal survival and adult emergence, while increased environmental humidity may also benefit embryonic and larval development [5,47]. Adequate rainfall may indirectly contribute to the persistence of *Z. tau* populations by supporting host plant growth and maintaining suitable environmental conditions. In our model, the response of habitat suitability to precipitation exhibited a broad suitable range rather than a sharp threshold effect. Suitability increased with Bio13 and reached an optimum at approximately

1057.46 mm, while Bio18 remained favorable across a wider range, with an optimum at approximately 2602.50 mm. Overall, these response patterns indicate that moderate to high precipitation conditions are associated with higher modeled habitat suitability for *Z. tau*, whereas extremely low precipitation is associated with lower predicted suitability. This pattern suggests a stronger modeled association between reduced suitability and dry conditions than between reduced suitability and high precipitation within the environmental range represented by the calibration data. The broad precipitation response may partly reflect the ecological importance of moisture availability for immature development, as previous studies have shown that soil moisture influences pupal survival and developmental processes in tephritid flies [47,48].

Although specific studies linking precipitation conditions with the population dynamics of *Z. tau* remain limited, humid subtropical regions such as Hunan, Hubei, and Guizhou experience persistently high seasonal rainfall that overlaps with the suitable precipitation range identified in this study [49–51]. This spatial agreement between observed climatic conditions and modeled precipitation suitability provides additional ecological support for the precipitation-related patterns predicted by the model.

While precipitation-related variables showed strong predictive associations with habitat suitability at the macro-scale, temperature-related variables further contributed to explaining spatial variation in the model. Among the retained thermal predictors, temperature seasonality (Bio4) and mean diurnal temperature range (Bio2) played important roles in the model, with Bio2 exhibiting the highest permutation importance (21.4%). The high contribution of Bio2 suggests that diel thermal variability is an important environmental factor associated with the potential distribution of *Z. tau*. Previous studies have shown that diurnal temperature fluctuations can influence the developmental rate, growth, and reproductive performance of arthropods by affecting physiological processes and degree-day accumulation under fluctuating thermal conditions. Similarly, strong temperature seasonality (Bio4) may impose additional physiological constraints by increasing thermal stress and metabolic costs associated with seasonal temperature fluctuations [14,52,53]. Climate-based distribution modelling studies of tropical fruit flies have further demonstrated that climatic conditions can strongly influence potential range shifts and invasion risks under future environmental scenarios, highlighting the importance of thermal factors in assessing fruit fly distribution dynamics [54]. Accordingly, the relatively stable thermal regimes characterized by lower diurnal and seasonal temperature variations in South China and the lower Yangtze region are consistent with the higher modeled habitat suitability of *Z. tau* in these regions, as reflected by the response curves obtained in this study.

Beyond these macro-climatic drivers, topographic features such as slope and aspect may further influence the habitat suitability of *Z. tau* by modifying local environmental conditions. Variations in slope and aspect can affect localized solar radiation exposure, near-surface temperature patterns, and soil drainage characteristics, which may subsequently influence insect development, adult activity, and microhabitat suitability [55,56]. Therefore, incorporating slope and aspect into the MaxEnt model helped represent fine-scale environmental heterogeneity and captured additional topographic variation that may contribute to explaining the spatial distribution patterns of *Z. tau* beyond broad-scale climatic gradients.

4.3. Spatiotemporal Dynamics of Suitable Habitats for *Z. tau*

Under current climatic conditions, the total suitable habitat area for *Z. tau* in China was $272.08 \times 10^4 \text{ km}^2$, accounting for 28.34% of the national terrestrial area, and was mainly distributed in South China, southern Central China, the southeastern coastal zone, and eastern Southwest China. These regions also include several major agricultural production areas where important host crops of *Z. tau* are widely cultivated. As a highly polyphagous

pest, *Z. tau* can utilize a broad range of fruit and vegetable crops, including Cucurbitaceae crops such as cucumber, pumpkin, and bitter melon, as well as Solanaceae crops such as tomato and pepper. The overlap between climatically suitable regions and areas with abundant host resources suggests that host availability may provide additional ecological context for interpreting the predicted suitability pattern. However, host distribution was not explicitly incorporated into the present model, and the realized occurrence and spread of *Z. tau* are likely influenced by multiple ecological and management factors beyond climatic suitability [5,20,57].

As a key driver of global biodiversity change, climate warming can have species-specific effects on the geographic distributions of insect pests by inducing range expansion, contraction, and latitudinal or altitudinal shifts [58–60]. Previous studies have shown that rising temperatures may alleviate thermal limitations in higher-latitude or high-altitude regions, thereby facilitating northward or upward range shifts in some pest species [61]. Meanwhile, changes in precipitation regimes may further modify habitat suitability by influencing resource availability and environmental conditions. High-altitude regions often experience more pronounced temperature increases than low-altitude areas [62], making them particularly sensitive to climate-driven changes in insect distributions. Therefore, the future responses of insect pests to climate change are likely influenced by their ecological adaptability to changing temperature and precipitation conditions, which may affect their potential establishment in newly suitable areas and persistence in existing habitats [63,64].

Under the four future SSP climate scenarios, the suitable habitats of *Z. tau* generally exhibited a northward and westward shift tendency, with southern Henan, southern Shaanxi, and southeastern Gansu showing transitions from low-suitability to moderate- or high-suitability areas. These projected changes may be associated with climate warming, which could reduce thermal constraints in some currently less suitable regions and increase modeled climatic suitability at higher latitudes [17,65]. In addition, the ongoing spatial expansion and regional reorganization of fruit and vegetable cultivation in China may increase the availability of potential host resources, which could interact with favorable climatic conditions and influence the future establishment risk and population dynamics of *Z. tau* [66,67]. Similar climate-associated redistribution patterns have also been reported for other tephritid pests, such as *B. tsuneonis* and *B. dorsalis* [34,40].

In terms of areal dynamics, the total suitable habitat area of *Z. tau* showed only limited changes under future scenarios, while a clear redistribution among suitability classes occurred. Moderate-suitability habitats generally increased, whereas high-suitability habitats tended to decrease or fluctuate, and low-suitability habitats showed comparatively smaller variations. This pattern suggests that future climate change may redistribute habitat suitability through simultaneous increases in suitability in some regions and decreases in others, rather than uniformly increasing the overall suitable area of *Z. tau*. Specifically, under the SSP2-4.5 scenario, moderate-suitability areas increased by 40.91% and 42.97% in the 2070s and 2090s, respectively, suggesting a shift from lower suitability classes toward higher suitability classes under future climates. Centroid analysis further revealed that the current centroid of suitable habitats was located in Xiangxi Tujia and Miao Autonomous Prefecture, Hunan Province, and shifted slightly northwestward and northeastward under all future scenarios, fluctuating near the Chongqing–Hunan border with limited migration. It should be noted that the centroid shift is a statistical summary of the net spatial balance between gains and losses of suitable habitat, rather than the actual dispersal or migration of the species itself. The relatively small displacement (39.62–98.52 km) therefore indicates that the core suitable region of *Z. tau* remains relatively stable, with future changes occurring mainly through the redistribution among suitability classes and increased suitability in peripheral areas, rather than through large-scale displacement of the distribution center.

Such peripheral changes can inform the adjustment of regional surveillance and quarantine priorities. The centroid shifts were consistent with the overall westward and northward transition of suitable habitats, which may be partly related to reduced thermal constraints at the northern edge under future warming scenarios.

4.4. Limitations of This Study

As a climate-based ecological niche model, this study has several limitations. First, the model incorporates mainly climatic and topographic variables and does not include several important non-climatic factors that may influence the establishment and spread of *Z. tau*, such as host plant distribution, land use patterns, agricultural intensity, irrigation practices, soil properties (including soil type, soil moisture, drainage conditions, and soil organic matter content), natural enemies, and human-mediated transportation networks. These factors may affect resource availability, habitat connectivity, local population persistence, and dispersal processes [14,47]. In addition, the occurrence records were obtained from multiple sources with heterogeneous sampling efforts, and residual sampling bias may still exist despite spatial filtering. Future studies incorporating sampling-effort information or bias-correction approaches may further improve the robustness of species distribution modelling.

Second, uncertainty is also associated with the projection of habitat suitability under future climatic conditions. The future projections were based on a single global climate model (BCC-CSM2-MR), which may not fully represent uncertainties arising from differences among climate models. Different GCMs may generate divergent regional projections of temperature and precipitation, particularly over longer future time horizons, and these differences could consequently influence the magnitude and spatial pattern of projected habitat suitability changes. Therefore, the projected changes reported in this study should be interpreted as scenario-dependent estimates obtained under a consistent single-GCM framework, rather than as forecasts that fully account for inter-model climate uncertainty. Future studies incorporating multi-GCM ensemble approaches could further improve the robustness of climate-driven distribution projections [68]. In addition, the use of a global calibration and background extent represents a modelling choice rather than a uniquely defined ecological accessible area (M); alternative biologically informed definitions of the calibration area could influence background environmental conditions, fitted response relationships, variable importance, and projected suitability patterns. Moreover, although the same predictor variables were used for model calibration and future projection, this does not necessarily ensure that future environmental conditions remain within the ranges or multivariate combinations represented by the calibration data. Novel environmental values or combinations may occur under future climate scenarios, and predictions under such conditions may involve extrapolation beyond the environmental space represented during model calibration [69]. Because formal environmental-novelty analyses such as MESS, MOP, or ExDet were not performed in this study, the precise geographic locations where future projections may involve extrapolation beyond the calibration space remain uncertain, and the magnitude of this risk cannot be explicitly quantified. Accordingly, projections for later future periods, particularly the 2090s, should be interpreted with additional caution as scenario-dependent estimates of relative habitat suitability rather than as precise forecasts of future species occurrence.

Third, the use of long-term average climatic data cannot fully capture the short-term impacts of extreme weather events, including heatwaves, droughts, and persistent rainfall [70]. Biological traits such as thermal adaptation, insecticide resistance, and behavioral plasticity were also not considered [53,71]. Furthermore, human management interventions were excluded from the model, which may introduce additional uncertainty into the esti-

mation of suitable areas. Future research integrating dynamic climate variables, host plant phenology and distribution, land use types, agricultural practices, irrigation conditions, transportation networks, trade intensity, and explicit assessments of environmental novelty may help develop more comprehensive models and improve the ecological realism and practical applicability of future projections.

5. Conclusions

This study used an optimized MaxEnt model to characterize habitat suitability patterns and identify key environmental predictors associated with the potential distribution of *Z. tau* in China under current and future climate scenarios. Precipitation of the Warmest Quarter (Bio18), Precipitation of Wettest Month (Bio13), Annual Mean Temperature (Bio1), Mean Diurnal Temperature Range (Bio2), and Temperature seasonality (standard deviation $\times 100$) (Bio4) were identified as the main environmental variables associated with its potential distribution. Under current climatic conditions, suitable habitats for *Z. tau* are widely distributed across South China, Central China, East China, and Southwest China, covering approximately 28.34% of China's terrestrial area. Future climate scenarios indicate a redistribution of habitat suitability patterns rather than a simple expansion of the overall suitable range. Although the total suitable habitat area remains relatively stable, moderate-suitability habitats generally increase, while high-suitability habitats show a decreasing or fluctuating trend, accompanied by slight northwestward and northeastward shifts of the distribution centroid. These results suggest that climate change may reshape the spatial configuration of suitable habitats for *Z. tau* through redistribution and spatial turnover among different suitability classes. These projected patterns represent climate-associated suitability under the current model framework and should not be interpreted as the actual current or future occurrence range of *Z. tau*. The predicted suitability patterns can inform risk-based prioritization of quarantine monitoring, early warning, and regional surveillance. To reduce uncertainties associated with omitted ecological drivers, future studies should incorporate additional factors, including host distribution, human activities, and biological interactions, to further improve the ecological realism and applicability of species distribution predictions.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/d18100615/s1>: Figure S1: Global distribution of occurrence records of *Zeugodacus tau* before spatial filtering and the calibration extent used for MaxEnt background sampling; Figure S2: AUC values from 10 replicate runs of the final optimized MaxEnt model.

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Abbreviations

The following abbreviations are used in this manuscript:

GBIF	Global Biodiversity Information Facility
CNKI	China National Knowledge Infrastructure
AICc	Akaike information criterion
RM	regularization multiplier
FC	feature class
AUC	area under the receiver operating characteristic curve

References

1. Jaleel, W.; Lu, L.; He, Y. Biology, Taxonomy, and IPM Strategies of *Bactrocera tau* Walker and Complex Species (Diptera; Tephritidae) in Asia: A Comprehensive Review. *Environ. Sci. Pollut. Res.* **2018**, *25*, 19346–19361. [CrossRef] [PubMed]
2. Jia, P.; Zhang, X.; Ji, Q. Analysis of the Attractant Effect and Main Attractant Compounds of *Broussonetia papyrifera* on Females of *Zeugodacus tau*. *J. Biosaf.* **2025**, *33*, 222–228.
3. Yesmin, F.; Haymer, D.; Uddin, M.N.; Hasanuzzaman, M. Cytological Characterisation of Autosomes and Sex Chromosomes in Tephritid Fruit Flies *Bactrocera zonata* and *Zeugodacus tau* (Diptera, Tephritidae). *Zoodiversity* **2025**, *59*, 21–34. [CrossRef]
4. Ohno, S.; Tamura, Y.; Haraguchi, D.; Kohama, T. First Detection of the Pest Fruit Fly, *Bactrocera tau* (Diptera: Tephritidae), in the Field in Japan: Evidence of Multiple Invasions of Ishigaki Island and Failure of Colonization. *Appl. Entomol. Zool.* **2008**, *43*, 541–545. [CrossRef]
5. Liu, X.; Ji, Q. Review of *Zeugodacus tau* (Walker) (Diptera: Tephritidae): Biological Characteristics and Control Strategy. *CABI Agric. Biosci.* **2024**, *5*, 90. [CrossRef]
6. Johnson, D.R.N. Tau Fruit Fly Cooperative Eradication Program Los Angeles County, California Environmental Assessment, July 2023. Available online: <https://www.aphis.usda.gov/sites/default/files/tau-los-angeles-california-ea.pdf> (accessed on 16 June 2026).
7. Sharma, I.D.; Kumar, S.; Chandel, R.S.; Patyal, S.K. Evaluation of Drek, Melia Azadirach for the Management of Fruitflies, *Bactrocera tau* in Tomato. *J. Biopestic.* **2011**, *4*, 1. [CrossRef]
8. Clarke, A.R.; Measham, P.F. Competition: A Missing Component of Fruit Fly (Diptera: Tephritidae) Risk Assessment and Planning. *Insects* **2022**, *13*, 1065. [CrossRef] [PubMed]
9. Asokan, R.; Rebijith, K.B.; Singh, S.K.; Sidhu, A.S.; Siddharthan, S.; Karanth, P.K.; Ellango, R.; Ramamurthy, V.V. Molecular Identification and Phylogeny of *Bactrocera* Species (Diptera: Tephritidae). *Fla. Entomol.* **2011**, *94*, 1026–1035. [CrossRef]
10. Liu, X.; Zhang, Q.; Xu, W.; Yang, Y.; Fan, Q.; Ji, Q. The Effect of Cuelure on Attracting and Feeding Behavior in *Zeugodacus tau* (Walker) (Diptera: Tephritidae). *Insects* **2023**, *14*, 836. [CrossRef] [PubMed]
11. Afroz, S.; Noman, M.S.; Zhang, Y.; Ali, M.Y.; Mahmud, M.R.; Li, Z. Species Identification of Economic Important Adult Fruit Flies Based on Dna Barcoding (Mt DNA COI) and Larvae Based on Species Specific Primers from Central and South Parts of Bangladesh. *Malays. J. Sustain. Agric.* **2022**, *6*, 110–116. [CrossRef]
12. Vargas, R.; Piñero, J.; Leblanc, L. An Overview of Pest Species of *Bactrocera* Fruit Flies (Diptera: Tephritidae) and the Integration of Biopesticides with Other Biological Approaches for Their Management with a Focus on the Pacific Region. *Insects* **2015**, *6*, 297–318. [CrossRef] [PubMed]
13. Dias, N.P.; Zotti, M.J.; Montoya, P.; Carvalho, I.R.; Nava, D.E. Fruit Fly Management Research: A Systematic Review of Monitoring and Control Tactics in the World. *Crop Prot.* **2018**, *112*, 187–200. [CrossRef]
14. Skendžić, S.; Zovko, M.; Živković, I.P.; Lešić, V.; Lemić, D. The Impact of Climate Change on Agricultural Insect Pests. *Insects* **2021**, *12*, 440. [CrossRef] [PubMed]
15. Michel A., D.K.; Fiaboe, K.K.M.; Kekeunou, S.; Nanga, S.N.; Kuate, A.F.; Tonnang, H.E.Z.; Gnanvossou, D.; Hanna, R. Temperature-Based Phenology Model to Predict the Development, Survival, and Reproduction of the Oriental Fruit Fly *Bactrocera dorsalis*. *J. Therm. Biol.* **2021**, *97*, 102877. [CrossRef] [PubMed]
16. Sultana, S.; Baumgartner, J.B.; Dominiak, B.C.; Royer, J.E.; Beaumont, L.J. Impacts of Climate Change on High Priority Fruit Fly Species in Australia. *PLoS ONE* **2020**, *15*, e0213820. [CrossRef] [PubMed]
17. Yan, Z.; Ding, Y.; Zhai, P.; Song, L.; Cao, L.; Li, Z. Re-Assessing Climatic Warming in China since 1900. *J. Meteorol. Res.* **2020**, *34*, 243–251. [CrossRef]
18. Intergovernmental Panel on Climate Change (IPCC). *Climate Change 2021—The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, 1st ed.; Cambridge University Press: Cambridge, UK, 2023; ISBN 978-1-009-15789-6.

19. Tang, C.; Yang, R.; Xie, K.; Feng, S.; Wang, Z.; Song, Y.; Cai, P. Regional- and Generation-Specific Phenological Shifts of *Scirpophaga incertulas* (Lepidoptera: Crambidae) in China under Climate Warming. *J. Econ. Entomol.* **2026**, *119*, 937–948. [CrossRef] [PubMed]
20. Tang, Y.; Dong, J.; Gruda, N.; Jiang, H. China Requires a Sustainable Transition of Vegetable Supply from Area-Dependent to Yield-Dependent and Decreased Vegetable Loss and Waste. *Int. J. Environ. Res. Public Health* **2023**, *20*, 1223. [CrossRef] [PubMed]
21. Shi, W.; Kerdelhué, C.; Ye, H. Genetic Structure and Colonization History of the Fruit Fly *Bactrocera tau* (Diptera: Tephritidae) in China and Southeast Asia. *J. Econ. Entomol.* **2014**, *107*, 1256–1265. [CrossRef] [PubMed]
22. He, Y.; Xu, Y.; Chen, X. Biology, Ecology and Management of Tephritid Fruit Flies in China: A Review. *Insects* **2023**, *14*, 196. Correction in *Insects* **2024**, *15*, 93. [CrossRef] [PubMed]
23. Guisan, A.; Thuiller, W. Predicting Species Distribution: Offering More than Simple Habitat Models. *Ecol. Lett.* **2005**, *8*, 993–1009. Correction in *Ecol. Lett.* **2007**, *10*, 435. [CrossRef] [PubMed]
24. Elith, J.; Leathwick, J.R. Species Distribution Models: Ecological Explanation and Prediction across Space and Time. *Annu. Rev. Ecol. Evol. Syst.* **2009**, *40*, 677–697. [CrossRef]
25. Soberón, J.; Nakamura, M. Niches and Distributional Areas: Concepts, Methods, and Assumptions. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 19644–19650. [CrossRef] [PubMed]
26. Peterson, A.T. Predicting the Geography of Species' Invasions via Ecological Niche Modeling. *Q. Rev. Biol.* **2003**, *78*, 419–433. [CrossRef] [PubMed]
27. Guisan, A.; Edwards, T.C.; Hastie, T. Generalized Linear and Generalized Additive Models in Studies of Species Distributions: Setting the Scene. *Ecol. Model.* **2002**, *157*, 89–100. [CrossRef]
28. Leathwick, J.R.; Elith, J.; Hastie, T. Comparative Performance of Generalized Additive Models and Multivariate Adaptive Regression Splines for Statistical Modelling of Species Distributions. *Ecol. Model.* **2006**, *199*, 188–196. [CrossRef]
29. Booth, T.H.; Nix, H.A.; Busby, J.R.; Hutchinson, M.F. BIOCLIM: The First Species Distribution Modelling Package, Its Early Applications and Relevance to Most Current MAXENT Studies. *Divers. Distrib.* **2014**, *20*, 1–9. [CrossRef]
30. Carpenter, G.; Gillison, A.N.; Winter, J. DOMAIN: A Flexible Modelling Procedure for Mapping Potential Distributions of Plants and Animals. *Biodivers. Conserv.* **1993**, *2*, 667–680. [CrossRef]
31. Hirzel, A.H.; Hausser, J.; Chessel, D.; Perrin, N. Ecological-Niche Factor Analysis: How to Compute Habitat-Suitability Maps without Absence Data? *Ecology* **2002**, *83*, 2027–2036. [CrossRef]
32. Phillips, S.J.; Anderson, R.P.; Schapire, R.E. Maximum Entropy Modeling of Species Geographic Distributions. *Ecol. Model.* **2006**, *190*, 231–259. [CrossRef]
33. Zhu, G.; Illan, J.G.; Hajek, A.E.; Nielsen, A.L.; Leskey, T.C.; Walgenbach, J.F.; Beers, E.H.; Crowder, D.W. Assessing Geographic Dimensions of Biological Control for *Halyomorpha halys* in United States. *Entomol. Gen.* **2024**, *44*, 895–904. [CrossRef]
34. Qin, Y.; Wang, C.; Zhao, Z.; Pan, X.; Li, Z. Climate Change Impacts on the Global Potential Geographical Distribution of the Agricultural Invasive Pest, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae). *Clim. Change* **2019**, *155*, 145–156. [CrossRef]
35. Dos Santos, L.A.; Mendes, M.F.; Krüger, A.P.; Blauth, M.L.; Gottschalk, M.S.; Garcia, F.R.M. Global Potential Distribution of *Drosophila suzukii* (Diptera, Drosophilidae). *PLoS ONE* **2017**, *12*, e0174318. [CrossRef] [PubMed]
36. Gao, T.; Feng, R.; Liu, Z.; Zhu, Z. Modeling the Potential Climatic Suitability and Expansion Risk of *Tuta absoluta* (Meyrick, 1917) (Lepidoptera: Gelechiidae) under Future Climate Scenarios. *Insects* **2025**, *16*, 185. [CrossRef] [PubMed]
37. Wang, R.; Yang, H.; Luo, W.; Wang, M.; Lu, X.; Huang, T.; Zhao, J.; Li, Q. Predicting the Potential Distribution of the Asian Citrus Psyllid, *Diaphorina citri* (Kuwayama), in China Using the MaxEnt Model. *PeerJ* **2019**, *7*, e7323. [CrossRef] [PubMed]
38. GBIF Occurrence Download. Available online: <https://doi.org/10.15468/dl.kxycmv> (accessed on 7 October 2025).
39. Merow, C.; Smith, M.J.; Silander, J.A. A Practical Guide to MaxEnt for Modeling Species' Distributions: What It Does, and Why Inputs and Settings Matter. *Ecography* **2013**, *36*, 1058–1069. [CrossRef]
40. Mao, J.; Meng, F.; Song, Y.; Li, D.; Ji, Q.; Hong, Y.; Lin, J.; Cai, P. Forecasting the Expansion of *Bactrocera tsuneonis* (Miyake) (Diptera: Tephritidae) in China Using the MaxEnt Model. *Insects* **2024**, *15*, 417. [CrossRef] [PubMed]
41. Zhang, Y.; Hughes, A.C.; Zhao, Z.; Li, Z.; Qin, Y. Including Climate Change to Predict the Global Suitable Area of an Invasive Pest: *Bactrocera correcta* (Diptera: Tephritidae). *Glob. Ecol. Conserv.* **2022**, *34*, e02021. [CrossRef]
42. Fu, C.; Wang, X.; Huang, T.; Wang, R. Future Habitat Changes of *Bactrocera minax* Enderlein along the Yangtze River Basin Using the Optimal MaxEnt Model. *PeerJ* **2023**, *11*, e16459. [CrossRef] [PubMed]
43. Song, Z.; Fan, G.; Deng, C.; Duan, G.; Li, J. Predicting the Distribution of *Neoceratitis asiatica* (Diptera: Tephritidae), a Primary Pest of Goji Berry in China, under Climate Change. *Insects* **2024**, *15*, 558. [CrossRef] [PubMed]
44. Wan, Y.; Li, C.; Yin, Z.; Wang, Z. The Potential Geographic Distribution of *Bactrocera minax* and *Bactrocera tsuneonis* (Diptera: Tephritidae) in China. *Insects* **2025**, *16*, 1277. [CrossRef] [PubMed]
45. Bale, J.S.; Masters, G.J.; Hodkinson, I.D.; Awmack, C.; Bezemer, T.M.; Brown, V.K.; Butterfield, J.; Buse, A.; Coulson, J.C.; Farrar, J.; et al. Herbivory in Global Climate Change Research: Direct Effects of Rising Temperature on Insect Herbivores. *Glob. Change Biol.* **2002**, *8*, 1–16. [CrossRef]

46. Deutsch, C.A.; Tewksbury, J.J.; Huey, R.B.; Sheldon, K.S.; Ghalambor, C.K.; Haak, D.C.; Martin, P.R. Impacts of Climate Warming on Terrestrial Ectotherms across Latitude. *Proc. Natl. Acad. Sci. USA* **2008**, *105*, 6668–6672. [[CrossRef](#)] [[PubMed](#)]
47. Quesada-Moraga, E.; Valverde-García, P.; Garrido-Jurado, I. The Effect of Temperature and Soil Moisture on the Development of the Preimaginal Mediterranean Fruit Fly (Diptera: Tephritidae). *Environ. Entomol.* **2012**, *41*, 966–970. [[CrossRef](#)]
48. Li, X.Z.; Liu, Y.H.; Wang, J.J.; Li, S.B. Growth, Development and Water-Loss Dynamics in *Bactrocera tau* (Walker) (Diptera: Tephritidae) Pupae Exposed to Determined Humidity. *Pan-Pac. Entomol.* **2009**, *85*, 150–158. [[CrossRef](#)]
49. Huang, L.; Zeng, G.; Liang, J.; Hua, S.; Yuan, Y.; Li, X.; Dong, H.; Liu, J.; Nie, S.; Liu, J. Combined Impacts of Land Use and Climate Change in the Modeling of Future Groundwater Vulnerability. *J. Hydrol. Eng.* **2017**, *22*, 05017007. [[CrossRef](#)]
50. Wang, W.; Tang, H.; Li, J.; Hou, Y. Spatial-Temporal Variations of Extreme Precipitation Characteristics and Its Correlation with El Niño-Southern Oscillation during 1960–2019 in Hubei Province, China. *Atmosphere* **2022**, *13*, 1922. [[CrossRef](#)]
51. Qin, N.X.; Wang, J.N.; Hong, Y.; Lu, Q.Q.; Huang, J.L.; Liu, M.H.; Gao, L. The Drought Variability Based on Continuous Days without Available Precipitation in Guizhou Province, Southwest China. *Water* **2021**, *13*, 660. [[CrossRef](#)]
52. Vangansbeke, D.; Audenaert, J.; Nguyen, D.T.; Verhoeven, R.; Gobin, B.; Tirry, L.; De Clercq, P. Diurnal Temperature Variations Affect Development of a Herbivorous Arthropod Pest and Its Predators. *PLoS ONE* **2015**, *10*, e0124898. [[CrossRef](#)] [[PubMed](#)]
53. Hance, T.; Van Baaren, J.; Vernon, P.; Boivin, G. Impact of Extreme Temperatures on Parasitoids in a Climate Change Perspective. *Annu. Rev. Entomol.* **2007**, *52*, 107–126. [[CrossRef](#)] [[PubMed](#)]
54. Chen, J.; Xie, J.; Michaud, J.P.; Zhou, X.; Liu, X.; Li, Z. Predicting Range Expansion of Three Tropical Fruit Flies and Risks to Pome and Stone Fruit Production in Temperate Regions. *J. Econ. Entomol.* **2026**, *in press*. [[CrossRef](#)] [[PubMed](#)]
55. Bennie, J.; Huntley, B.; Wiltshire, A.; Hill, M.O.; Baxter, R. Slope, Aspect and Climate: Spatially Explicit and Implicit Models of Topographic Microclimate in Chalk Grassland. *Ecol. Model.* **2008**, *216*, 47–59. [[CrossRef](#)]
56. Wang, L.; Zhang, F.-X.; Li, L.-P.; Wang, C.-J.; Wan, J.-Z. Effects of Habitat Heterogeneity and Topographic Variation on Insect Pest Risks in Alpine Regions. *Land* **2023**, *12*, 1314. [[CrossRef](#)]
57. Li, X.; Yang, H.; Hu, K.; Wang, J. Temporal Dynamics of *Bactrocera* (*Zeugodacus*) *tau* (Diptera: Tephritidae) Adults in North Jiangxi, a Subtropical Area of China Revealed by Eight Years of Trapping with Cuelure. *J. Asia-Pac. Entomol.* **2020**, *23*, 1–6. [[CrossRef](#)]
58. Kumar, S.; Graham, J.; West, A.M.; Evangelista, P.H. Using District-Level Occurrences in MaxEnt for Predicting the Invasion Potential of an Exotic Insect Pest in India. *Comput. Electron. Agric.* **2014**, *103*, 55–62. [[CrossRef](#)]
59. Shimwela, M.M.; Blackburn, J.K.; Jones, J.B.; Nkuba, J.; Narouei-Khandan, H.A.; Ploetz, R.C.; Beed, F.; Van Bruggen, A.H.C. Local and Regional Spread of Banana Xanthomonas Wilt (BXW) in Space and Time in Kagera, Tanzania. *Plant Pathol.* **2017**, *66*, 1003–1014. [[CrossRef](#)]
60. Santana, P.A.; Kumar, L.; Da Silva, R.S.; Pereira, J.L.; Picanço, M.C. Assessing the Impact of Climate Change on the Worldwide Distribution of *Dalbulus maidis* (DeLong) Using MaxEnt. *Pest Manag. Sci.* **2019**, *75*, 2706–2715. [[CrossRef](#)] [[PubMed](#)]
61. Ji, W.; Han, K.; Lu, Y.; Wei, J. Predicting the Potential Distribution of the Vine Mealybug, *Planococcus ficus* under Climate Change by MaxEnt. *Crop Prot.* **2020**, *137*, 105268. [[CrossRef](#)]
62. Root, T.L.; Price, J.T.; Hall, K.R.; Schneider, S.H.; Rosenzweig, C.; Pounds, J.A. Fingerprints of Global Warming on Wild Animals and Plants. *Nature* **2003**, *421*, 57–60. [[CrossRef](#)] [[PubMed](#)]
63. Ramasamy, M.; Das, B.; Ramesh, R. Predicting Climate Change Impacts on Potential Worldwide Distribution of Fall Armyworm Based on CMIP6 Projections. *J. Pest Sci.* **2022**, *95*, 841–854. [[CrossRef](#)]
64. Bertrand, R.; Lenoir, J.; Piedallu, C.; Riofrío-Dillon, G.; De Ruffray, P.; Vidal, C.; Pierrat, J.-C.; Gégout, J.-C. Changes in Plant Community Composition Lag behind Climate Warming in Lowland Forests. *Nature* **2011**, *479*, 517–520. [[CrossRef](#)] [[PubMed](#)]
65. Cai, P.; Song, Y.; Meng, L.; Liu, R.; Lin, J.; Zhao, M.; Nie, C.; Li, Y.; Ji, Q. Climate Warming Affects Phenology of *Bactrocera dorsalis*: A Case Study of Fujian and Guangxi, China. *Bull. Insectology* **2023**, *76*, 73–81.
66. Qiu, L.; Ouyang, Q.; Eastham, J.; Wang, J.; Wu, L. Production Agglomeration and Spatiotemporal Evolution of China's Fruit Industry over the Last 40 Years. *Agriculture* **2025**, *15*, 634. [[CrossRef](#)]
67. Ji, L.; You, L.; See, L.; Fritz, S.; Li, C.; Zhang, S.; Li, G. Spatial and Temporal Changes of Vegetable Production in China. *J. Land Use Sci.* **2018**, *13*, 494–507. [[CrossRef](#)]
68. Gould, S.F.; Beeton, N.J.; Harris, R.M.B.; Hutchinson, M.F.; Lechner, A.M.; Porfirio, L.L.; Mackey, B.G. A Tool for Simulating and Communicating Uncertainty When Modelling Species Distributions under Future Climates. *Ecol. Evol.* **2014**, *4*, 4798–4811. [[CrossRef](#)] [[PubMed](#)]
69. Owens, H.L.; Campbell, L.P.; Dornak, L.L.; Saupe, E.E.; Barve, N.; Soberón, J.; Ingenloff, K.; Lira-Noriega, A.; Hensz, C.M.; Myers, C.E.; et al. Constraints on Interpretation of Ecological Niche Models by Limited Environmental Ranges on Calibration Areas. *Ecol. Model.* **2013**, *263*, 10–18. [[CrossRef](#)]

70. González-Trujillo, J.D.; Román-Cuesta, R.M.; Muñoz-Castillo, A.I.; Amaral, C.H.; Araújo, M.B. Multiple Dimensions of Extreme Weather Events and Their Impacts on Biodiversity. *Clim. Change* **2023**, *176*, 155. [[CrossRef](#)]
71. Li, M.; Wei, X.-M.; Li, J.; Wei, S.-M.; Zhang, J.-L.; Chen, G.-H.; Zhang, X.-M. Effect of Short-Term Exposure to High Temperatures on the Reproductive Behavior and Physiological Enzyme Activities in the Fruit Fly *Zeugodacus tau* (Walker). *Front. Physiol.* **2023**, *14*, 1036397. [[CrossRef](#)] [[PubMed](#)]

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