



Using CLIMEX and MaxEnt models to simulate the influence of climate change on the global distribution of the ghost ant *Tapinoma melanocephalum* (Hymenoptera: Formicidae)

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Key words. Biological invasion, early detection, species distribution modeling, water stress, temperature, ecological niche, biogeography

Abstract. The ghost ant, *Tapinoma melanocephalum* (Fabricius), is a globally distributed invasive species whose potential response to climate change remains poorly quantified. We applied MaxEnt and CLIMEX as complementary modeling approaches to estimate its current and future global climatic suitability. Both models showed acceptable performance and produced projections broadly consistent with the known distribution of *T. melanocephalum*. MaxEnt predicted widespread low climatic suitability, with high-suitability areas concentrated mainly in tropical and subtropical regions of Asia, Africa, and the Americas. CLIMEX identified extensive climatic suitability across South America, sub-Saharan Africa, South and Southeast Asia, and parts of Europe. Moderate climatic suitability also extended into several temperate regions. Future MaxEnt projections under SSP2-4.5, SSP3-7.0, and SSP5-8.5 indicated substantial redistribution of climatic suitability during the 2050s and 2070s. Suitability increased across several temperate and higher-latitude regions but declined in some tropical areas. CLIMEX projections under RCP8.5 for 2040–2059 showed broadly similar shifts, although their magnitude varied among global climate models. These findings provide a global climatic baseline for identifying regions that may become increasingly suitable for establishment of *T. melanocephalum*. The projections can support targeted surveillance, early detection, and climate-informed management of this invasive ant.

1. INTRODUCTION

Invasive alien species increasingly threaten biodiversity, ecosystem functioning, and human well-being worldwide (Bradshaw et al., 2016; Seebens et al., 2025). Climate change can alter climatic suitability, creating opportunities for invasive species to establish and spread into new regions (Kumschick et al., 2025). Invasive ants are particularly concerning because temperature and moisture strongly influence their survival, establishment, and geographic

distributions (Tsang et al., 2025). Consequently, climate change may shift invasion risk by creating suitable conditions beyond invasive species' current geographic ranges (Kumschick et al., 2025). Predicting these shifts is essential in order to identify emerging invasion hotspots and prioritize surveillance, early detection, and management.

The ghost ant, *Tapinoma melanocephalum* (Fabricius, 1793) (Hymenoptera: Formicidae), is a widespread invasive ant and an important urban pest (Klimeš & Okrouhlik,

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2015). The species is frequently associated with human-modified environments (Shen et al., 2023). Its mobile, polygynous, multi-nest colonies can complicate eradication once infestations become established (Klimeš & Okrouhlík, 2015). Although its native range remains uncertain, the species is now widely distributed across tropical and subtropical regions (Klimeš & Okrouhlík, 2015). In temperate regions, populations occur mainly indoors, where heated buildings and greenhouses provide suitable conditions for establishment (Klimeš & Okrouhlík, 2015). *Tapinoma melanocephalum* tends honeydew-producing hemipterans and can protect them from natural enemies, potentially increasing their survival (Feng et al., 2015). It can carry clinically important bacteria, raising concerns about its potential role as a mechanical vector in healthcare environments (Rodríguez et al., 2016; Do Nascimento et al., 2020).

Human-induced climate change is reshaping invasion risk by altering environmental conditions that determine the establishment and spread of alien species. Climate change can therefore shift suitable ranges and expose previously unaffected regions to biological invasions (Kumschick et al., 2025). For invasive ants, future climate change may substantially alter geographic suitability and continue to threaten vulnerable ecosystems (Zhuang et al., 2025). Species distribution models (SDMs) can anticipate these changes by identifying areas where climatic conditions may become suitable for establishment (Franklin, 2023). Such predictions can strengthen biosecurity by prioritizing surveillance, early detection, and rapid management in areas facing emerging invasion risks (Jarnevich et al., 2023).

Species distribution models (SDMs) are widely used to estimate climatic suitability and forecast species range shifts in response to environmental change (Franklin, 2023; Yang et al., 2026). Correlative models such as MaxEnt infer suitability from occurrence-environment relationships, whereas CLIMEX incorporates climatic responses and ecophysiological constraints (Early et al., 2022). MaxEnt remains widely used for invasive-species risk assessment because it accommodates presence-only records, supports projections under future climates, and performs well with limited data (Phillips & Dudík, 2008; Yang et al., 2026). CLIMEX provides a complementary framework by integrating population growth with climatic stresses that constrain species persistence across geographic regions (Early et al., 2022). Comparing these approaches can reveal areas of agreement and uncertainty, thereby strengthening interpretation of invasion-risk projections (Early et al., 2022; Hayat et al., 2024).

This study aims to (i) quantify the current global climatic suitability of *T. melanocephalum* using MaxEnt and CLIMEX; (ii) project future climatic suitability using selected SSP scenarios in MaxEnt and RCP8.5 in CLIMEX; and (iii) identify climatic variables influencing its global distribution. By applying both models as complementary approaches, the study provides information to support surveillance, early detection, and climate-informed management.

2. MATERIAL AND METHODS

2.1. MaxEnt model: Occurrence data collection and processing

Occurrences of *T. melanocephalum* were compiled from multiple sources to ensure coverage across all regions of the world. These sources included the Global Biodiversity Information Facility (GBIF), the Centre for Agriculture and Bioscience International (CABI) Invasive Species Compendium, and an extensive literature review. The search yielded 392 occurrence records. To reduce sampling bias and spatial autocorrelation, which can contribute to model overfitting and biased predictions, we spatially filtered the dataset using a minimum separation distance of 5 km (Kramer-Schadt et al., 2013; Boria et al., 2014). This distance balanced the reduction of geographic clustering against the retention of sufficient data for model calibration. Spatial thinning was implemented using the *spThin* package (Aiello-Lammens et al., 2015), resulting in 335 unique occurrence records for subsequent modeling.

2.2. MaxEnt model: Environmental variables

Climatic data were obtained from WorldClim version 2.1 (Booth et al., 2014; Fick & Hijmans, 2017). The baseline climate data represent average conditions for 1970–2000. Initially, we considered all 19 bioclimatic variables for model development. However, BIO8, BIO9, BIO18, and BIO19 were excluded because these variables contain spatial artifacts arising from their derivation (Booth, 2022). We assessed multicollinearity among the remaining variables using variance inflation factors (VIFs) and pairwise correlation analysis. We progressively removed highly correlated variables ($|r| > 0.7$), prioritizing those with greater biological relevance to *T. melanocephalum*. This procedure retained six predictors: Mean Diurnal Range (BIO2), Isothermality (BIO3), Maximum Temperature of Warmest Month (BIO5), Precipitation of Wettest Month (BIO13), Precipitation of Driest Month (BIO14), and Precipitation Seasonality (BIO15). Future climate projections were obtained from CMIP6 datasets and downscaled and bias-corrected using WorldClim version 2.1. We selected the MIROC6 global climate model (GCM) and considered three Shared Socioeconomic Pathways: SSP2-4.5, SSP3-7.0, and SSP5-8.5. Projections were evaluated for the mid-century (2041–2060) and late-century (2061–2080) periods. All current and future environmental layers were maintained at a spatial resolution of 2.5 arc-minutes to ensure spatial consistency. All data processing and analyses were conducted in R version 4.4.1 (R Core Team, 2024).

2.3. MaxEnt model development

The habitat suitability of *T. melanocephalum* was modeled using the Maximum Entropy (MaxEnt) algorithm in R. Following spatial filtering, 335 occurrence records were retained. We defined the calibration region using an 8-degree buffer around the minimum convex polygon encompassing all occurrence records. Within this region, we randomly generated 10,000 background points.

Next, we optimized model complexity using the ENMeval package in R to reduce overfitting and improve model transferability (Muscarella et al., 2014). We evaluated candidate models using combinations of linear (L), quadratic (Q), hinge (H), and product (P) features, with regularization multipliers ranging from 1 to 5. We selected the optimal model based on the lowest corrected Akaike Information Criterion (AICc). The selected model used LQHP features with a regularization multiplier of 1.

We evaluated model performance using 10-fold cross-validation, with approximately 301 occurrence records used for training and 34 for testing in each fold. We used jackknife analyses

to assess the relative importance of individual predictors based on regularized training gain, test gain, and the Area Under the Receiver Operating Characteristic Curve (AUC) (Table S1).

We assessed model performance using AUC, True Skill Statistic (TSS), and Continuous Boyce Index (CBI) (Allouche et al., 2006; Hirzel et al., 2006). AUC values closer to 1 indicate greater discriminatory ability, whereas higher positive TSS and CBI values indicate better predictive performance. We reclassified the continuous MaxEnt suitability output (0–1) using the Maximum Test Sensitivity Plus Specificity threshold (Aidoo et al., 2023). We categorized habitat suitability as unsuitable (<0.3565), low suitability ($0.3565–0.6783$), and high suitability (≥ 0.6783). We calculated the total area within each suitability class for each climatic scenario and expressed the values as km².

2.4. CLIMEX modeling

We estimated the potential climatic suitability of *T. melanocephalum* using CLIMEX, which relates species' climatic tolerances to population growth and climatic stresses (Kriticos et al., 2015). We used the Compare Locations function to estimate climatic suitability across geographic regions based on species-specific biological and climatic parameters. Climatic suitability was expressed using the Ecoclimatic Index (EI), which integrates the Annual Growth Index (GIA), Stress Index (SI), and Stress Interaction Index (SII). EI values range from 0 to 100, with larger values indicating greater climatic suitability (Kriticos et al., 2015). For interpretation, areas with EI = 0 were considered unsuitable, $0 < EI < 30$ moderately suitable, and $EI \geq 30$ highly suitable.

The model was calibrated using the CM30_1995H historical climate dataset available through CliMond at a spatial resolution of 30 arc-minutes (0.5°). Future climatic suitability was projected for 2040–2059 using the ACCESS1.0 and CNRM-CM5 global climate models under the high-emission RCP8.5 scenarios. Both future climate datasets were obtained from CliMond and maintained at 30 arc-minutes to ensure spatial consistency with the historical climate data.

2.5. CLIMEX parameterization

CLIMEX parameters were derived from published information on the development, survival, and environmental tolerances of *T. melanocephalum* and subsequently adjusted against its known geographic distribution (Appel et al., 2004; Klimeš & Okrouhlík, 2015). We defined temperature suitability using four parameters: the lower developmental threshold (DV0), lower optimum temperature (DV1), upper optimum temperature (DV2), and upper developmental threshold (DV3). Available biological evidence indicates that *T. melanocephalum* performs well under warm conditions, and these observations guided temperature parameterization.

Soil-moisture parameters were initially informed by the CLIMEX humid-tropical template and subsequently adjusted to align with the species' known tropical and subtropical distribution. The final moisture parameters were SM0 = 0.01, SM1 = 0.30, SM2 = 0.90, and SM3 = 2.50. Climatic stresses were parameterized to restrict persistence outside biologically plausible conditions. Cold stress was defined by TTCS = 10°C and THCS = −0.00001, while heat stress was defined by TTHS = 38°C and THHS = 0. Dry stress was parameterized using SMDS = 0.10 and HDS = −1, whereas wet stress used SMWS = 2.50 and HWS = 0. Final parameter values used for all simulations are presented in Table S2. A cumulative stress value of zero for the species was used to assess its climatic suitability in Saudi Arabia and Yemen. This indicates that stress caused by higher temperatures and humidity is not a limiting factor for the species' distribution; in other words, the species tolerates these conditions well.

3. RESULTS

The MaxEnt model indicated that the climatic suitability of *T. melanocephalum* was primarily associated with precipitation and temperature variability (Table 1). Mean Diurnal Range (BIO2) and Precipitation of Wettest Month (BIO13) showed the greatest influence on model predictions. BIO2 contributed 32.61% and had a permutation importance of 36.99%, indicating a strong influence on predicted climatic suitability. BIO13 showed a permutation importance of 37.84%, further highlighting the importance of precipitation in shaping the species' potential distribution. Other predictors, including Precipitation Seasonality (BIO15) and Maximum Temperature of Warmest Month (BIO5), contributed comparatively less to model predictions. Response curves further characterized how predicted suitability varied across the observed ranges of these climatic variables (Table 2).

Table 1. Relative contributions of the environmental variables to the MaxEnt model.

Variable	Percent contribution	Permutation importance
bio2	32.61	36.99
bio3	8.86	8.23
bio5	3.10	3.90
bio13	31.36	37.84
bio14	21.44	10.59
bio15	2.63	2.44

Table 2. Descriptive statistics of the variables.

Variable	Minimum	Maximum	Median	Mean	Standard (SD)
bio2	1.00	21.97	12.72	12.44	2.69
bio3	15.99	100.00	55.54	57.30	15.60
bio5	−4.43	48.46	33.41	33.68	6.15
bio13	0.00	2,768.00	157.00	171.85	141.97
bio14	0.00	507.00	4.00	21.01	40.53
bio15	0.00	222.34	76.33	77.22	35.42

3.1. Model performance and current climatic suitability

The MaxEnt model showed acceptable to moderate predictive performance across the evaluation metrics (Table 3). Mean training and test AUC values were 0.8273 and 0.8040, respectively. The small difference (0.0232) suggests limited overfitting and good discrimination between occurrence and background locations. The mean Continuous Boyce Index (CBI) was 0.7970, indicating strong agreement between predicted suitability and observed occurrences. The mean True Skill Statistic (TSS) was 0.4993, indicating moderate predictive performance. The mean correlation coefficient (COR) was relatively low (0.0720), indicating weak correspondence by this metric.

Tapinoma melanocephalum is a predominantly tropical and subtropical species. Native records are concentrated in Southeast Asia, with introduced populations across the Americas, Africa, Europe, and Oceania (Fig. 1A). Under current climatic conditions, predicted suitability broadly corresponded with the observed geographic distribution of *T. melanocephalum* (Fig. 1B). High-suitability areas are predicted in warm, humid regions with mild winters, while

Table 3. Model performance evaluation.

Models	auc.train	auc.test	auc.diff	COR	TSS	CBI
0	0.8247	0.8142	0.0105	0.077496168	0.482664706	0.785273519
1	0.8299	0.7473	0.0826	0.056470154	0.406405882	0.739290705
2	0.8264	0.8134	0.013	0.070590481	0.545264706	0.841700766
3	0.8232	0.8328	−0.0096	0.08201746	0.540905882	0.891204197
4	0.8352	0.7306	0.1046	0.051941822	0.402252941	0.710270587
5	0.824	0.8358	−0.0118	0.081743411	0.518193939	0.780442143
6	0.8245	0.8391	−0.0146	0.084533014	0.521987879	0.848694841
7	0.8286	0.8103	0.0183	0.070432217	0.514193939	0.776876028
8	0.8318	0.7688	0.063	0.061335314	0.437875758	0.724535192
9	0.8243	0.8479	−0.0236	0.083503935	0.62369697	0.871219196
Averages	0.82726	0.80402	0.02324	0.072006398	0.49934426	0.796950717

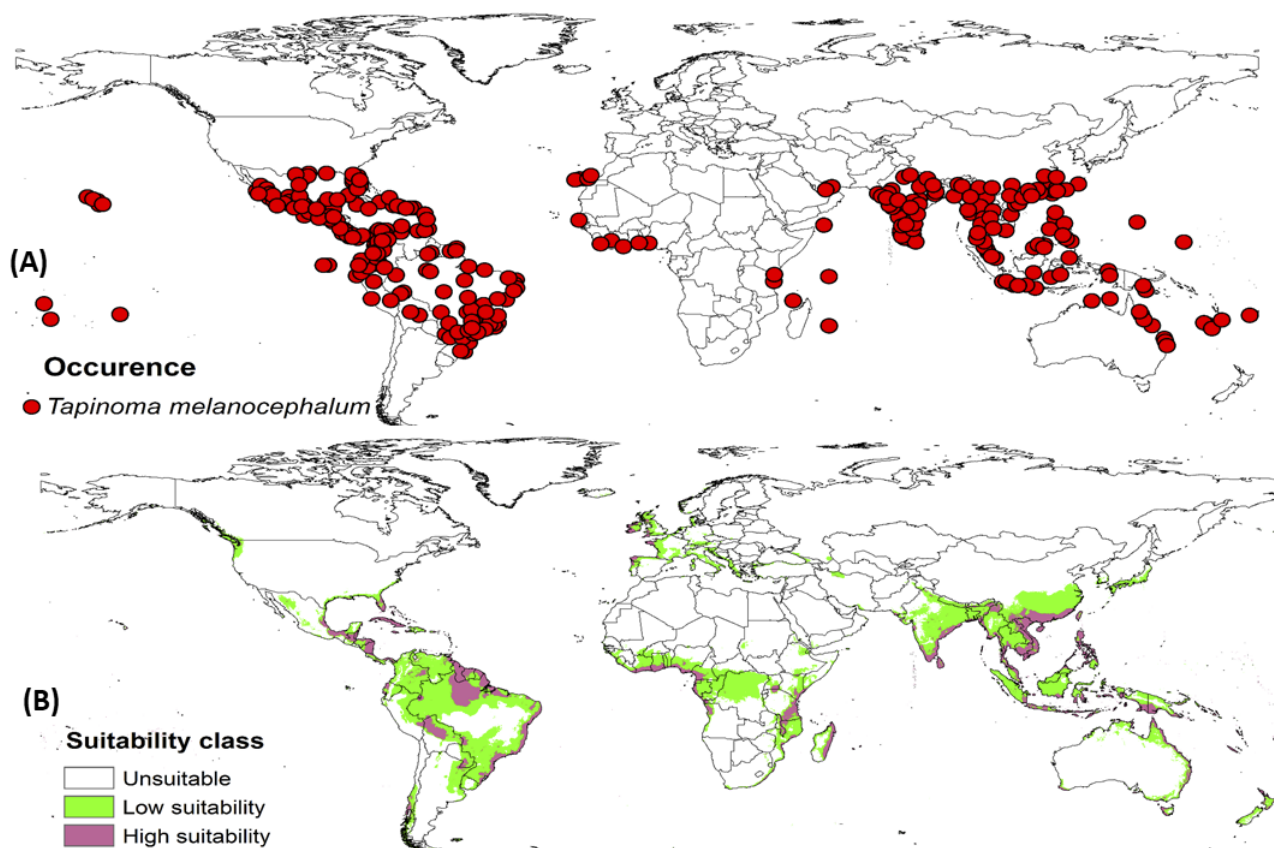
suitability decreases in temperate, arid, and high-latitude regions, consistent with the species' climatic constraints. Occurrence records were concentrated across tropical and subtropical regions, including Brazil, Indonesia, southern China, Florida, and eastern Australia. High climatic suitability was similarly predicted across several of these regions, supporting consistency between observed occurrences and model predictions. We also identified areas of low suitability along the coasts of Japan and the Mediterranean Basin, and in parts of South Africa.

Jackknife analyses and model evaluation curves further characterized the relative importance of environmental variables. (Fig. 2A–E). Precipitation variables contributed substantially to model predictions, highlighting the importance of moisture availability in determining climatic suitability. Precipitation of Driest Month (BIO14), Precipitation

of Wettest Month (BIO13), and Precipitation Seasonality (BIO15) were among the influential predictors. Temperature variables, including Isothermality (BIO3), Maximum Temperature of Warmest Month (BIO5), and Mean Diurnal Range (BIO2), also influenced predicted suitability. These results indicate that both precipitation and temperature regimes influence the potential climatic distribution of *T. melanocephalum*. The omission curves showed reasonable agreement between predicted and observed omission rates across cumulative thresholds (Fig. 2D).

3.2. Projected climatic suitability for the 2050s (2041–2060)

Future projections indicated changes in the magnitude and geographic distribution of climatic suitability by the 2050s (Fig. 3A–C). Under SSP2-4.5, suitable areas were projected to expand into some temperate regions, includ-

**Fig. 1.** Occurrence (A) and potential global distribution (B) of *T. melanocephalum* using the MaxEnt model in the current scenario.

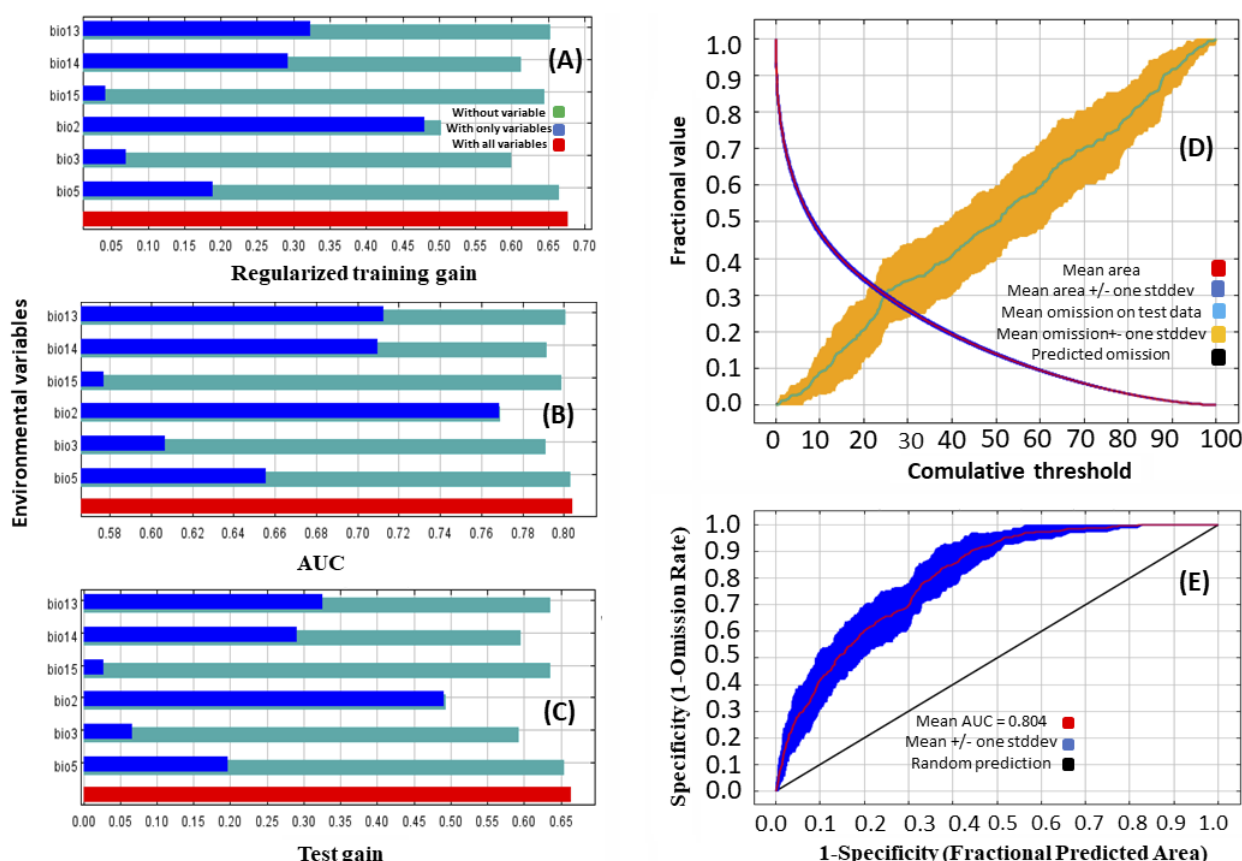


Fig. 2. Relative importance of environmental variables derived from jackknife tests. Variable contributions are evaluated for (A) regularized training gain, (B) area under the curve (AUC), and (C) test gain. Model performance metrics include (D) the average omission rate and predicted area, and (E) the receiver operating characteristic (ROC) curve, expressed as averaged sensitivity versus 1-specificity.

ing southern Japan, Mediterranean Europe, southeastern China, and the southeastern United States. Low-suitability areas were also projected to extend into regions that were comparatively marginal under current climatic conditions (Fig. 3A).

The projected expansion became more pronounced under SSP3-7.0 and SSP5-8.5. High climatic suitability emerged or increased across parts of Europe, the Korean Peninsula, New Zealand, and the highlands of Central and South America. Conversely, suitability declined in some tropical regions, particularly parts of northern South America and equatorial Africa (Fig. 3B–C). Overall, climatically suitable areas expanded across scenarios, in reference to the current prediction.

3.3. Projected climatic suitability for the 2070s (2061–2080)

Projections for the 2070s showed further geographic shifts in climatic suitability relative to current conditions and the 2050s (Fig. 3D–F). Under SSP2-4.5, high suitability increased across parts of the Iberian Peninsula, the Balkans, and southeastern Australia. Low climatic suitability also extended into southern Canada, northern China, and central Chile (Fig. 3D).

Under SSP3-7.0, suitable areas expanded further across Western Europe, the Korean Peninsula, and New Zealand's North Island. Low suitability also emerged across some

higher-latitude regions, including parts of southern Scandinavia and Patagonia (Fig. 3E).

The strongest geographic changes were projected under SSP5-8.5. High climatic suitability expanded substantially across Western and Central Europe, the eastern United States, and temperate coastal regions of South America and southern Africa. Low suitability also extended into parts of southern Scandinavia and coastal southern Alaska (Fig. 3F). In contrast, suitability declined across portions of the Amazon Basin and Central Africa.

Across scenarios, the projections indicate an overall expansion and redistribution of climatically suitable areas for *T. melanocephalum*, particularly toward temperate and higher-latitude regions. However, some tropical regions were projected to experience a decline in suitability under future climatic conditions. Table 4 summarizes changes in

Table 4. Changes in suitable habitat area (km²) for *T. melanocephalum* under current and future climate scenarios (SSP245, SSP370, SSP585) for the 2050s and 2070s, as predicted by MaxEnt modeling.

Period	Scenario	Unsuitable	Low suitability	High suitability	Total suitability
Current	Current	117135108.5	23402258.63	8958653.87	32360912.5
2050s	SSP245	116040274.1	23949290.51	9502798.37	33452088.87
	SSP370	116180374.5	23338227.27	9973761.18	33311988.45
	SSP585	116627167.8	23138353.33	9726841.87	32865195.19
2070s	SSP245	116092696.7	23829715.55	9569950.74	33399666.29
	SSP370	116352818.4	23101030.18	10038514.38	33139544.56
	SSP585	116635090.6	22714174.34	10143098.01	32857272.35

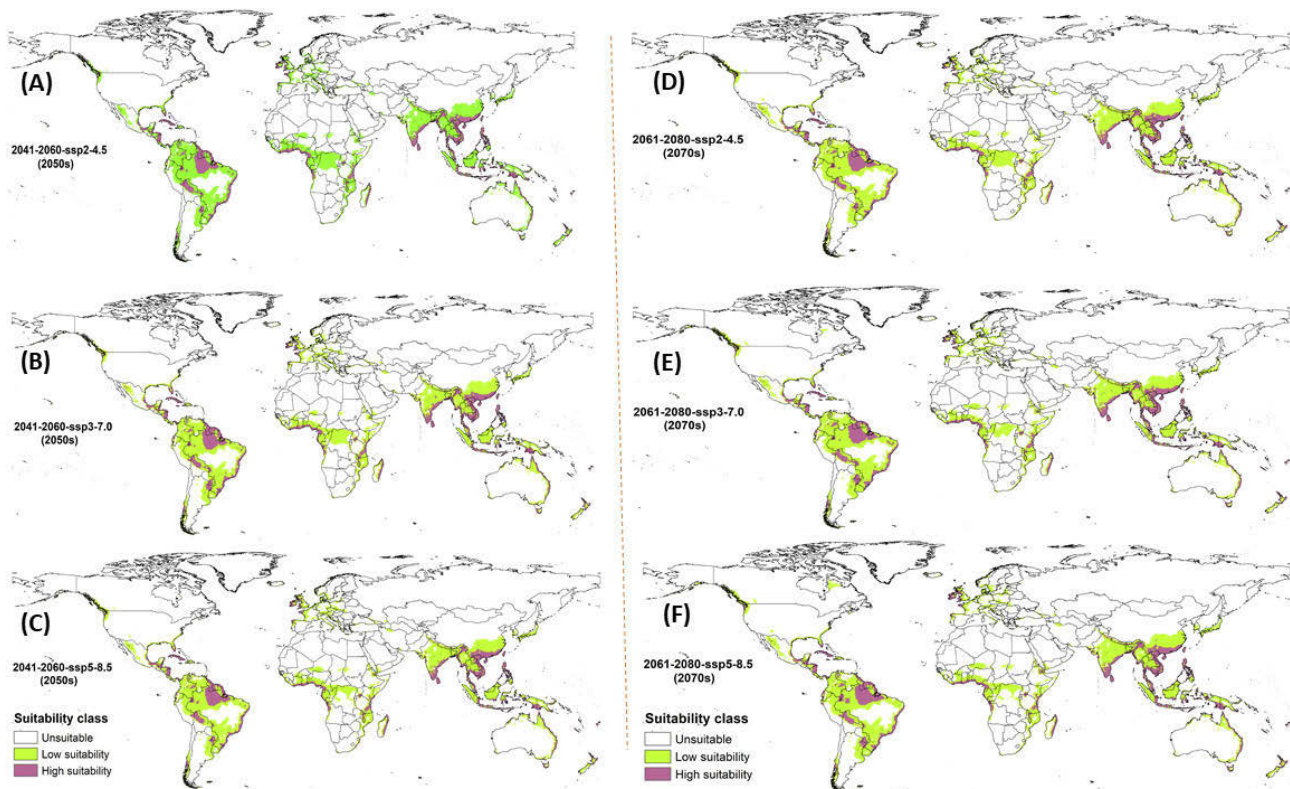


Fig. 3. Global projections of climatically suitable habitat for the ghost ant, *T. melanocephalum*, under future climate scenarios for the mid- and late-21st century. Projections are based on a Maximum Entropy (MaxEnt) model and show three Shared Socioeconomic Pathways (SSPs): (A) ssp2-4.5 (2050s), (B) ssp3-7.0 (2050s), (C) ssp5-8.5 (2050s), (D) ssp2-4.5 (2070s), (E) ssp3-7.0 (2070s), and (F) ssp5-8.5 (2070s). Suitability classes are defined as Unsuitable (white), Low suitability (yellow), and High suitability (purple). The models project a poleward and altitudinal expansion of suitable areas under all scenarios, with the magnitude of expansion increasing with higher greenhouse gas concentrations and later time periods. Notable contractions in high-suitability areas were projected across parts of the Amazon Basin and Central Africa.

the extent of unsuitable, low-suitability, and high-suitability areas across scenarios.

3.4. CLIMEX model: current climatic suitability and model performance

The CLIMEX model showed strong agreement between observed occurrences and predicted climatic suitability for *T. melanocephalum* (Fig. 4A). Approximately 95% of occurrence records fell within areas predicted as climatically suitable (EI > 0). Under current climatic conditions, high suitability was concentrated predominantly across tropical and subtropical regions (Fig. 4B). These areas included northern South America and the Amazon Basin, Central Africa, Southeast Asia, and northern Australia. Moderate suitability extended into several warm-temperate regions, including southern Europe, the southern United States, northern Africa, and parts of eastern Asia.

3.5. CLIMEX model: future climatic suitability under the high-emission scenario

Future projections for 2040–2059 indicated substantial geographic redistribution of climatic suitability for *T. melanocephalum* under the high-emission scenario (Fig. 4C–D). Both ACCESS1.0 and CNRM-CM5 projected an expansion of suitable climatic conditions into several temperate regions. Moderate suitability extended across southern Brazil, Uruguay, northern Argentina, the south-

ern United States, northern China, the Korean Peninsula, Japan, and southern Europe.

Conversely, both projections indicated declining suitability across some equatorial regions. This reduction was particularly pronounced under CNRM-CM5, including portions of the Amazon Basin and Central Africa (Fig. 4C).

Although both GCMs showed a broadly similar redistribution toward higher latitudes, the magnitude and spatial configuration of these changes differed. ACCESS1.0 projected greater persistence and southward extension of high suitability across South America. In contrast, CNRM-CM5 projected greater reductions in suitability across some equatorial regions.

3.6. Climatic stresses

CLIMEX identified cold and dry stresses as important constraints on the potential climatic distribution of *T. melanocephalum* (Fig. 5). Under current climatic conditions, cold stress was greatest across high-latitude regions, particularly Canada, northern Europe, and Russia. These patterns corresponded with low or absent climatic suitability across much of these regions. Cold stress was substantially lower across tropical and subtropical regions, where climatic suitability was generally greater.

Future projections under ACCESS1.0 and CNRM-CM5 indicated reductions in cold stress across parts of the Northern Hemisphere by 2040–2059. This reduction coin-

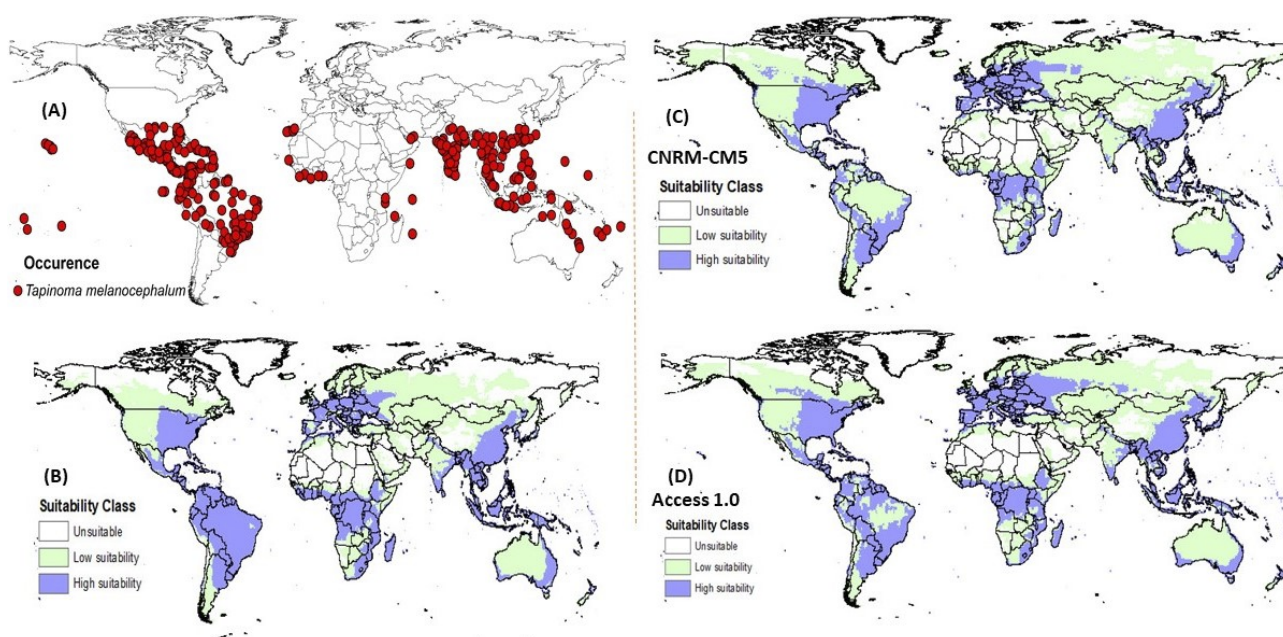


Fig. 4. Modeled global climatic suitability for the ghost ant, *T. melanocephalum*, under current and future (2040–2059) climate conditions. (A) Current potential distribution predicted by the CLIMEX model, showing strong concordance with known occurrence records (red dots). (B) Overall potential distribution under current climate, depicting areas of High (amethyst), Low (mint), and Unsuitable (white) climatic suitability. Future projections for the period 2040–2059 under the high-emission scenario (RCP8.5) from two global climate models: (C) CNRM-CM5 and (D) ACCESS1.0. Suitability classes are consistent across all panels. The future projections indicate a poleward expansion of suitable areas, particularly in temperate regions of the Americas, Europe, and East Asia, alongside a contraction of high-suitability zones in some equatorial regions. Inter-model variability (C vs. D) highlights uncertainty in the magnitude, but not the direction, of these distributional shifts.

cided with increased climatic suitability across portions of North America, Europe, and Asia.

Dry stress remained pronounced across arid and semi-arid regions, particularly the Sahara, Arabian Peninsula, southern Africa, and interior Australia. High dry stress was also predicted across arid portions of South America, including the Atacama region. Future projections showed comparatively smaller changes in the geographic extent of dry stress than in cold stress. Some subtropical regions showed increased dry stress under future climates, although the magnitude varied between GCMs.

The stress projections indicate contrasting responses of the major climatic constraints affecting *T. melanocephalum*. Cold stress is projected to decline across several higher-latitude regions, potentially increasing their climatic suitability. In contrast, persistent dry stress may continue to constrain suitability across strongly arid regions.

4. DISCUSSION

We compared the correlative MaxEnt and mechanistic CLIMEX approaches to establish a global climatic baseline for *T. melanocephalum*. The models highlight regions that may provide climatically suitable conditions for establishment. Comparing both approaches provides complementary perspectives on climatic suitability and model uncertainty (Pietrek et al., 2021; Early et al., 2022; Hayat et al., 2024). Such baseline predictions can support proactive surveillance and management of *T. melanocephalum* (Wet-terer, 2009; CABI, 2016).

Temperature and moisture emerged as key components of *T. melanocephalum*'s climatic suitability. Appel et al. (2004) reported low ghost ant mortality at 15–35°C but complete mortality at 45°C under 75% relative humidity. These findings indicate that thermal responses may vary with moisture conditions. At approximately 45°C, *T. melanocephalum* survival declines sharply (Appel et al., 2004). This suggests that extreme heat may constrain activity and habitat suitability near the species' upper thermal tolerance. In contrast, populations in temperate Korea and Europe are predominantly found in heated buildings (Choe et al., 2009; Klimeš & Okrouhlík, 2015). These observations support the temperature-precipitation relationships identified by MaxEnt and the cold- and dry-stress conditions detected by CLIMEX. Similar temperature-moisture interactions influence ant thermal ecology more broadly (Phillips et al., 2006; Roeder et al., 2021; Parr & Bishop, 2022). Overall, these results suggest that temperature variability and precipitation patterns are important determinants of the potential climatic suitability of *T. melanocephalum*.

Future projections indicate a redistribution of climatic suitability rather than a uniform global expansion of *T. melanocephalum*. Both models projected increased suitability across several temperate regions. This pattern may reflect warming that reduces climatic constraints currently limiting outdoor establishment. This interpretation aligns with the present distribution of ghost ants, as *T. melanocephalum* occurs both indoors and outdoors throughout much of the tropics and subtropics. However, populations at latitudes above approximately 30° are largely restrict-

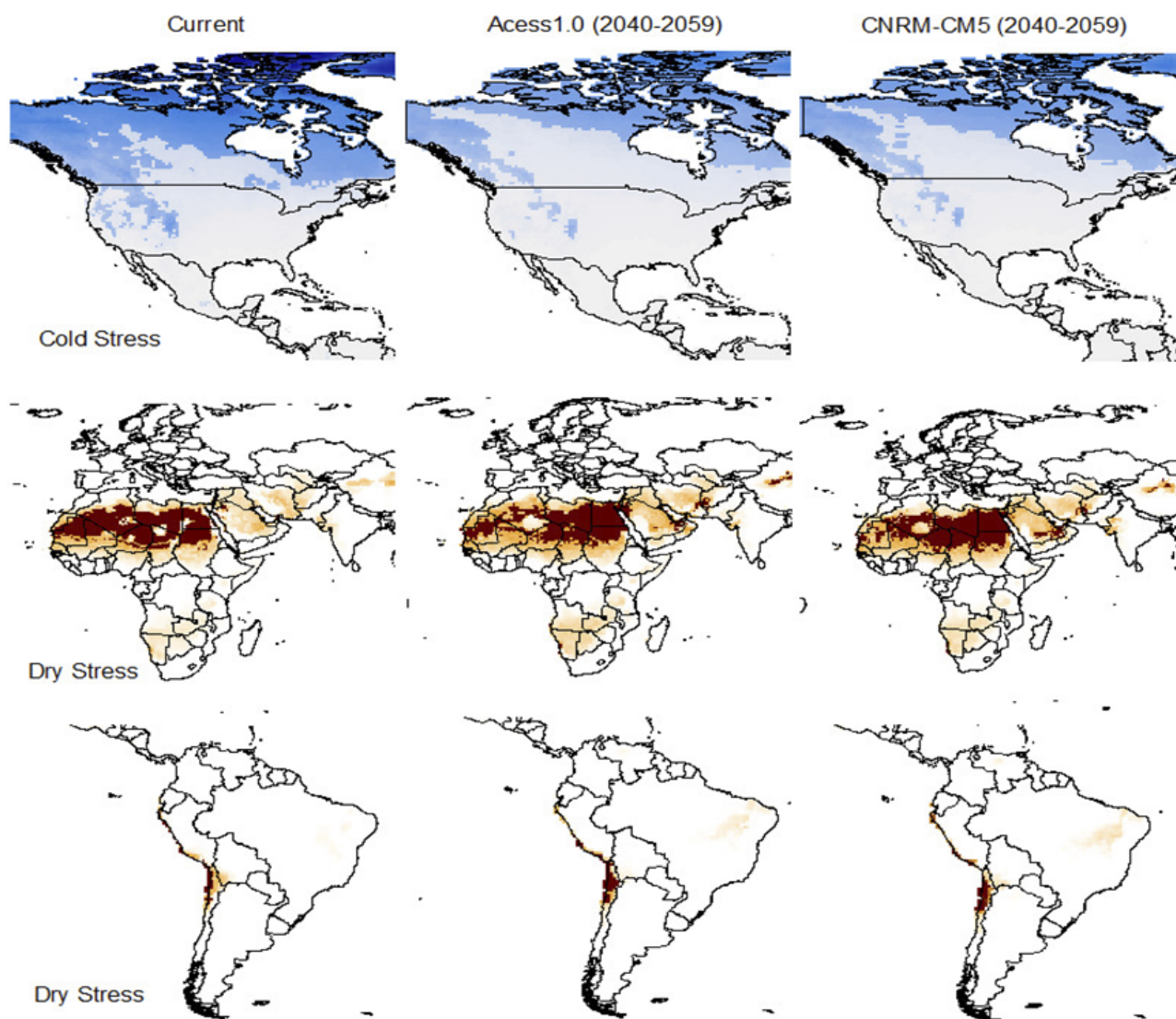


Fig. 5. Current and future predictions of cold and dry stress affecting the climatic suitability of *T. melanocephalum* under ACCESS 1.0 and CNRM-CM5 scenarios (2040–2059), based on the CLIMEX model.

ed to heated buildings and other protected environments (Wetterer, 2009; Klimeš & Okrouhlík, 2015). Consequently, warmer conditions could increase opportunities for outdoor persistence in some currently cool regions.

In contrast, our models projected declining suitability across parts of the Amazon Basin and equatorial Africa. This contraction may reflect increasing exposure to temperatures approaching the species' upper thermal tolerance. Laboratory experiments show that *T. melanocephalum* mortality increases substantially at high temperatures, reaching 100% at 45°C in some humidity treatments (Appel et al., 2004). More generally, ant thermal tolerances are closely associated with environmental temperatures. Populations inhabiting warm environments can have relatively small thermal safety margins under further warming (Diamond et al., 2012). Thus, continued warming may simultaneously facilitate expansion toward cooler regions while reducing climatic suitability in some already-hot tropical areas.

Climate warming may also modify the ecological impacts of ghost ants after establishment (Hulme, 2021; Hovorková et al., 2025; Ramzan et al., 2025). Experimental

warming strengthened the mutualistic interaction between *T. melanocephalum* and the invasive mealybug *Phenacoccus solenopsis*, including increased ant activity, aggression, mealybug tending, and honeydew consumption (Zhou et al., 2017). Therefore, climate change could affect not only the potential geographic distribution of *T. melanocephalum* but also its ecological interactions and pest impacts in newly suitable agricultural environments.

Nevertheless, several limitations should be considered when interpreting these projections. Occurrence records compiled from GBIF, CABI, and the published literature are unlikely to represent a uniform global sampling effort for MaxEnt modeling. Spatial thinning reduces geographic clustering but cannot fully eliminate sampling bias. Both models describe climatic suitability rather than actual invasion probability. Neither model directly incorporates propagule pressure, international trade, competition, habitat disturbance, or management interventions. Macroclimatic layers may also underestimate persistence in heated buildings and other thermally buffered urban habitats. MaxEnt predictions remain sensitive to occurrence quality, back-

ground selection, predictor choice, and assumptions about future climate relationships. CLIMEX projections depend on biological parameterization, climate datasets, and assumptions about climatic stress responses. Differences among GCMs further underscore uncertainty in the magnitude and spatial configuration of future suitability. Consequently, projected suitable areas should be interpreted as potential climatic opportunities for establishment rather than as deterministic forecasts of future invasion.

5. CONCLUSION

Our study indicates that climate change may redistribute the global climatic suitability of *T. melanocephalum*. MaxEnt and CLIMEX projected increasing suitability across several temperate regions, while some tropical areas projected declining suitability. These projections represent potential climatic opportunities for establishment rather than deterministic forecasts of future invasion. Their interpretation should therefore consider dispersal, propagule pressure, habitat conditions, biotic interactions, and management interventions. Nevertheless, the projected changes provide a useful climatic baseline for prioritizing surveillance and early detection in regions where suitability may increase. Proactive biosecurity should particularly target ports and other pathways associated with human-mediated transport. Public awareness and climate-informed monitoring may also help reduce the potential impacts of future range expansion.

ACKNOWLEDGEMENTS. We thank the Deanship of Scientific Research, Vice Presidency for Graduate Studies and Scientific Research, King Faisal University, Saudi Arabia (grant number KFU261579) and Guangdong Academy of Sciences Project of Science and Technology Development, China (2024GDA-SZH-2024010101) for financial support of this research.

AUTHOR CONTRIBUTIONS. Conceptualization: M.R. and J.L.; methodology: M.R., G.L. and J.L.; software: M.R., G.L., O.F.A. and J.L.; validation: M.R., G.L., R.M., O.F.A. and J.L.; formal analysis: M.R. and J.L.; investigation: M.R. and J.L.; resources: M.R., G.L. and J.L.; data curation: M.R., G.L., R.M., O.F.A. and J.L.; visualization: M.R., L.J., G.L., R.M. and J.L.; writing-original draft preparation: M.R., L.J., G.L., R.M. and J.L.; writing-review and editing: M.R., G.L., R.M., O.F.A., A.M.I., M.J.H., N.M.E., S.N.A.K., H.S.E.B. and J.L.; supervision, J.L.; project administration: J.L.; funding acquisition: A.M.I. and J.L. All authors have read and agreed to the published version of the manuscript.

CONFLICT OF INTEREST. The authors have no conflict of interest to declare.

FUNDING. This work was funded by the Deanship of Scientific Research, Vice Presidency for Graduate Studies and Scientific Research, King Faisal University, Saudi Arabia, through grant number KFU261579. This research was also funded by Guangdong Academy of Sciences Project of Science and Technology Development, China (2024GDASZH-2024010101).

DATA AVAILABILITY STATEMENT. All data generated or analyzed during this study are available within the published article and the supplementary data.

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Received June 1, 2026; revised and accepted September 10, 2026

Published online October 16, 2026

Supplementary Tables S1 and S2 follow on next pages.

Table S1. Evaluation and selection of MaxEnt model configurations using different feature combinations and regularization multipliers.

row	fc	rm	tune.args	auc.train	cbi.train	auc.diff.avg	auc.diff.sd	auc.val.avg	auc.val.sd	cbi.val.avg	cbi.val.sd	or.10p.avg	or.10p.sd	or.mtp.avg	or.mtp.sd	AICc	delta.AICc	w.AIC	ncoef
1	L	1	fc.L_rm.1	0.778802836	0.939	0.037451981	0.034874684	0.776119135	0.047444892	0.7844	0.088351822	0.104723708	0.074170162	0.009300817	10817.0508	905.8598173	1.91E-197	6	
2	LQ	1	fc.LQ_rm.1	0.803059254	0.981	0.035319161	0.032032569	0.796853556	0.044698551	0.8336	0.095780072	0.119518717	0.04722764	0.002941176	10211.83044	300.6394582	5.05E-66	11	
3	H	1	fc.H_rm.1	0.828596567	0.979	0.027956082	0.019435165	0.811586453	0.027428054	0.7423	0.145337194	0.140909091	0.066975445	0.006060606	10205.45811	294.2671281	1.22E-64	134	
4	LQH	1	fc.LQH_rm.1	0.829351791	0.984	0.028899991	0.01922029	0.811491123	0.027728439	0.7578	0.11979241	0.131907308	0.059694838	0.006060606	0.012776879	9925.835038	14.64405703	0.00064039	73
5	LQHP	1	fc.LQHP_rm.1	0.837358358	0.989	0.027099811	0.019007438	0.816717299	0.025844871	0.7794	0.106990342	0.146702317	0.044903042	0.006060606	0.012776879	9911.190981	0	0.969083636	71
6	L	2	fc.L_rm.2	0.778451791	0.94	0.037077132	0.034854957	0.775905223	0.047127069	0.7944	0.091494019	0.104723708	0.074170162	0.009300817	10862.56529	951.3743121	2.50E-207	5	
7	LQ	2	fc.LQ_rm.2	0.79481806	0.982	0.036602527	0.034471934	0.790562536	0.046621574	0.8131	0.120166043	0.110695187	0.056902808	0.002941176	10446.90161	535.7106338	4.55E-117	10	
8	H	2	fc.H_rm.2	0.820225522	0.964	0.024316398	0.024108146	0.807141693	0.029825553	0.779	0.104564706	0.122994652	0.058342923	0.00597148	10074.90633	163.7153448	2.73E-36	82	
9	LQH	2	fc.LQH_rm.2	0.822839552	0.971	0.026874114	0.023091834	0.80961943	0.031332019	0.8054	0.090527098	0.114081996	0.05885653	0.00597148	0.012590737	9932.259595	21.06861452	2.58E-05	41
10	LQHP	2	fc.LQHP_rm.2	0.82467209	0.988	0.025987042	0.021771349	0.811138039	0.029906744	0.8166	0.10487474	0.117023173	0.049198525	0.009001783	0.014496277	9918.124678	6.933697012	0.030250188	38
11	L	3	fc.L_rm.3	0.77800791	0.943	0.036760824	0.034805531	0.775497166	0.04686568	0.7903	0.088059387	0.107664884	0.070023206	0.002941176	0.009300817	10909.19003	997.9990534	1.88E-217	5
12	LQ	3	fc.LQ_rm.3	0.785593284	0.971	0.036784152	0.035568269	0.782540169	0.047218054	0.823	0.08327598	0.104812834	0.052193306	0.002941176	0.009300817	10658.26201	747.0710317	5.78E-163	9
13	H	3	fc.H_rm.3	0.81350791	0.974	0.024734686	0.024191671	0.802521225	0.030755997	0.7939	0.141107091	0.114171123	0.066929306	0.006060606	0.012776879	10166.19317	255.0021937	4.11E-56	84
14	LQH	3	fc.LQH_rm.3	0.817567164	0.973	0.027965368	0.025458152	0.805640873	0.034460996	0.7862	0.137192322	0.117112299	0.060032764	0.00597148	0.012590737	10003.74006	92.54907584	7.76E-21	30
15	LQHP	3	fc.LQHP_rm.3	0.819621642	0.989	0.026757742	0.024364033	0.807064439	0.03283146	0.836	0.098897253	0.117112299	0.055020283	0.00597148	0.012590737	9977.306441	66.11546041	4.26E-15	24
16	L	4	fc.L_rm.4	0.777495075	0.944	0.036514414	0.034779883	0.77496738	0.046660211	0.7928	0.094698117	0.11372549	0.069576079	0.002941176	0.009300817	10955.33291	1044.141932	1.79E-227	5
17	LQ	4	fc.LQ_rm.4	0.781623134	0.962	0.036732913	0.035495072	0.778617308	0.04715232	0.8024	0.093710192	0.101782531	0.053830934	0.002941176	0.009300817	10811.38543	900.1944509	3.25E-196	7
18	H	4	fc.H_rm.4	0.807919701	0.991	0.02421405	0.024711049	0.798309987	0.030938629	0.8127	0.160618285	0.11426025	0.075491827	0.003030303	0.00958266	10177.81202	266.6210359	1.23E-58	62
19	LQH	4	fc.LQH_rm.4	0.811566119	0.972	0.028905449	0.02654953	0.802469795	0.035956185	0.8052	0.13725548	0.110962567	0.0518081	0.002941176	0.009300817	10097.14161	185.9506256	4.05E-41	24
20	LQHP	4	fc.LQHP_rm.4	0.81372403	0.989	0.02775662	0.025710804	0.803857852	0.034511488	0.8239	0.162623936	0.113903743	0.051205861	0.00597148	0.012590737	10097.67759	186.486607	3.10E-41	25
21	L	5	fc.L_rm.5	0.776838955	0.949	0.03617416	0.034756492	0.774308895	0.046409147	0.7846	0.101393842	0.110695187	0.055187823	0.002941176	0.009300817	11000.94307	1089.752087	2.24E-237	5
22	LQ	5	fc.LQ_rm.5	0.777740448	0.949	0.036576563	0.034840362	0.775203422	0.046562337	0.7919	0.094992924	0.107664884	0.055377812	0.002941176	0.009300817	10272.75617	1061.565189	2.95E-231	6
23	H	5	fc.H_rm.5	0.803074627	0.99	0.024344838	0.026035159	0.793422839	0.032178756	0.8248	0.135816707	0.10828877	0.06913838	0.003030303	0.00958266	10261.36332	350.1723367	8.86E-77	60
24	LQH	5	fc.LQH_rm.5	0.806917761	0.984	0.029191182	0.028042703	0.797543712	0.037207587	0.8079	0.124566007	0.116934046	0.050703535	0.00597148	0.012590737	10194.91322	283.7222398	2.38E-62	19
25	LQHP	5	fc.LQHP_rm.5	0.809635075	0.986	0.028451378	0.026669734	0.799518142	0.035890608	0.8139	0.14292535	0.11684492	0.048461779	0.00597148	0.012590737	10202.16087	290.9698885	6.35E-64	26

Table S2. Environmental variables used as predictors in the model.

Parameters	Parameter description	Unit	Value
DV0	Lower temperature threshold for growth	°C	10
DV1	Lower limit of optimal temperature for growth	°C	15
DV2	Upper limit of optimal temperature for growth	°C	30
DV3	Upper temperature threshold for growth	°C	38
SM0	Lower limit of soil moisture necessary for growth	–	0.01
SM1	Lower limit of optimal soil moisture for growth	–	0.3
SM2	Upper limit of optimal soil moisture for growth	–	0.9
SM3	Upper limit of soil moisture necessary for growth	–	2.5
TTCS	Cold stress temperature threshold	°C	10
THCS	Weekly rate of cold stress accumulation	week ⁻¹	–0.00001
TTHS	Heat stress temperature threshold	°C	38
THHS	Weekly rate of heat stress accumulation	week ⁻¹	0
SMDS	Dry stress threshold	–	0.1
HDS	Weekly rate of dry stress accumulation	week ⁻¹	–1
SMWS	Wet stress threshold	–	2.5
HWS	Weekly rate of accumulation of wet stress	week ⁻¹	0
TDD	Thermal degree-days for the development	–	0