

Research Paper

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Corresponding author:



Yujia Qin;

Email: qinyujia@cau.edu.cn;

Chen Ma;

Email: macfov@hotmail.com

Considering climate change impact on the global potential geographical distribution of the invasive Argentine ant and little fire ant

Tong Li¹ , Pei Jiang², Jingyuan Liu³, Jingquan Zhu², Shouqi Zhao², Zhihong Li¹, Mina Zhong⁴, Chen Ma² and Yujia Qin¹ 

¹Department of Plant Biosecurity, Key Laboratory of Surveillance and Management for Plant Quarantine Pests of MARA, College of Plant Protection, China Agricultural University, Beijing, P. R. China; ²National Agro-tech Extension and Service Center, Ministry of Agriculture and Rural Affairs, Beijing, 100125, China; ³Center for Animal, Plant and Food Inspection and Quarantine of Shanghai Customs District, Shanghai, 200135, China and ⁴Forest Pest Control and Quarantine Station of Xining City, Qinghai, 810008, China

Abstract

The Argentine ant (*Linepithema humile*) and the little fire ant (*Wasmannia auropunctata*) are among the top 100 invasive alien species globally, causing significant ecological and economic harm. Therefore, it is crucial to study their potential geographic distribution worldwide. This study aimed to predict their global distribution under current and future climate conditions. We used distribution data from various sources, including CABI, GBIF, and PIAKey, and key climate variables selected from 19 environmental factors to model their potential geographic distribution using MaxEnt. The AUC values were 0.925 and 0.937 for *L. humile* and *W. auropunctata*, respectively, indicating good predictive performance. Suitable areas for *L. humile* were mainly in southern North America, northern South America, Europe, central Asia, southern Oceania, and parts of Africa, while *W. auropunctata* suitable areas were mostly in southern North America, most of South America, a small part of Europe, southern Asia, central Africa, and some parts of Oceania. Under climate change scenario, suitable areas for *L. humile* increased, while highly suitable areas for *W. auropunctata* decreased. The top four countries with the largest areas of overlapping suitable habitat under current climate were Brazil, China, Australia, and Argentina, while under future SSP585 climate scenario, the top four countries were Brazil, China, Indonesia, and Argentina. Some countries, such as Estonia and Finland, will see an overlapping adaptation area under climate change. In conclusion, this study provides insight into controlling the spread and harm of *L. humile* and *W. auropunctata*.

Introduction

Invasive alien species (IAS) are species that have been introduced into non-native areas, where they can negatively impact local ecosystems and even pose risks to human health and safety (Pejchar and Mooney, 2009; Zhu *et al.*, 2019). The biological impacts of IAS are serious and can include increased risk of local species extinction, reduced species diversity, and altered ecosystem functions (Pysek *et al.*, 2020). Additionally, IAS can harm the agroecological economy, threatening the food security of farmers (Pratt *et al.*, 2017). Climate is generally accepted as an important factor influencing the spread and distribution of IAS (Shi *et al.*, 2010; Verlinden *et al.*, 2014; Ar *et al.*, 2022). Therefore, studying and mapping potential habitats with the help of climate factors can aid in preventing invasion and spread, managing and monitoring current epidemic areas, and understanding the trend of range expansion and invasion (Kumar *et al.*, 2015; Lee *et al.*, 2021).

The Argentine ant (*Linepithema humile*) and the little fire ant (*Wasmannia auropunctata*) are both considered to be among the 100 most dangerous invasive species in the world by the Invasive Species Specialist Group (ISSG). *L. humile* is a highly aggressive and expansive pest that can thrive under human interference and harm ecosystems such as farmland and green spaces (Ness and Bronstein, 2004; Carpintero *et al.*, 2005; Lopez-Collar and Cabrero-Sanudo, 2021). *L. humile* is native to the Paraná River drainage basin in subtropical South America (between northern Argentina, southern Brazil, Uruguay and Paraguay), and it is already widely distributed in Ecuador, Guatemala, the Dominican Republic, Jamaica, Puerto Rico, South Africa, and the western United States (Wild, 2004; CABI Compendium, 2022a). Native to Central and South America, *W. auropunctata* is also aggressive and can even severely bite animals in addition to attacking other colonies (Holway *et al.*, 2002; Wetterer and Porter, 2003). And it has now spread to Cameroon, Gabon, Israel, Germany, Spain, the United Kingdom, and others (CABI Compendium, 2022b). Furthermore, its strong adaptability and competitiveness enable it to outcompete native ants and impact human health (Foucaud

et al., 2009; Bertelsmeier et al., 2015b). Given the invasive and destructive nature of *L. humile* and *W. auropunctata*, it is crucial to understand their potential geographic distribution.

Ecological niche models (ENMs) use current distribution data of species and related environmental variables to construct a model based on certain algorithms, projecting results into different times (past and future) and spaces to predict potential geographic distributions of species. ENMs have been widely used in recent years to predict suitable habitats for IAS, guiding decision-making for early warning, scientific prevention and control of alien species after invasion (Peterson, 2003; Teles et al., 2022). Among the many models, the maximum entropy model (MaxEnt) is the most popular, widely used, and recognised for its accuracy and reliability (Warren and Seifert, 2011; Huercha et al., 2020; Dai et al., 2022). For example, Zhang et al. (2023) used MaxEnt to predict the potential geographic distributions and overlap of *Prunus salicina* and *Monilinia fructicola* in China, while Sopniewski et al. (2022) used MaxEnt to predict the potential geographic distribution of Australian frogs under climate change and analysed their overlap with *Batrachochytrium dendrobatidis*.

Researches on the invasion and distribution of *L. humile* and *W. auropunctata* have been carried out respectively (Harris and Barker, 2007; Roura-Pascual et al., 2009; Li et al., 2022; Mao et al., 2022; Zhao et al., 2022). The overlap areas where are both suitable habitats for *L. humile* and *W. auropunctata* may be a higher risk of their further invasion (Bertelsmeier et al., 2016). Thus, this study utilises the MaxEnt model to predict the current and future global potential geographic distributions of *L. humile* and *W. auropunctata* and their overlapping distribution regions. The purpose is to provide a basis for developing appropriate prevention and control plans for these two invasive ants.

Materials and methods

Materials

The map data was downloaded from the world map of Natural Earth (<https://www.naturalearthdata.com/>). The distribution data

of *L. humile* and *W. auropunctata* were obtained from CABI (<https://www.cabi.org/isc>; Gómez and Abril, 2022; Gunawardana and Wetterer, 2022), Global Biodiversity Information Facility (<https://www.gbif.org/>, <https://doi.org/10.15468/dl.v8ap26> and <https://doi.org/10.15468/dl.y56zsq>, respectively) and PIAK (<http://idtools.org/id/ants/pia/index.html>; Sarnat, 2008). Both historical and future climatic data including 19 bioclimatic variables were downloaded from the World Climate WorldClim2.1 Database (<https://www.worldclim.org/>). The historical climatic data covers minimum, average, and maximum temperature and precipitation from 1970 to 2000 with a spatial resolution of 5arc-min. Future climate data was in 2050 (2041–2060) come from CMIP6 BCC-CSM2-MR model, which is an atmospheric-oceanic coupled climate model developed by the Beijing Climate Center for simulating future climate change (Wu et al., 2019). There are four future climate scenarios: SSP126, SSP245, SSP370, and SSP585. These scenarios represent different levels of radiative forcing and greenhouse gas emissions. From SSP126 to SSP585, greenhouse gas emissions increase progressively (O'Neill et al., 2017). MaxEnt 3.4.4 was downloaded from https://biodiversityinformatics.amnh.org/open_source/maxent/. R4.1.2 was downloaded from <https://cran.r-project.org/> and rstudio is downloaded from <https://www.rstudio.com/>. ArcGIS 10.2 purchased by Plant Quarantine and Invasion Biology Laboratory, College of Plant Protection, China Agricultural University.

Distributional data and environmental variables

The distribution data for *L. humile* and *W. auropunctata* were obtained from CABI, GBIF, and PIAKey, as shown in fig. 1. After combining the three datasets, we checked for bias in the distribution points. To reduce sampling bias, we standardised the geographical distribution data and environmental variables to the same accuracy (5 minutes) and removed duplicate data, resulting in 1309 distribution data points for *L. humile* and 717 distribution data points for *W. auropunctata*. We imported the distribution data and 19 climate variables into ArcGIS 10.2 and used the Spatial Analyst tool in the ArcToolbox to perform

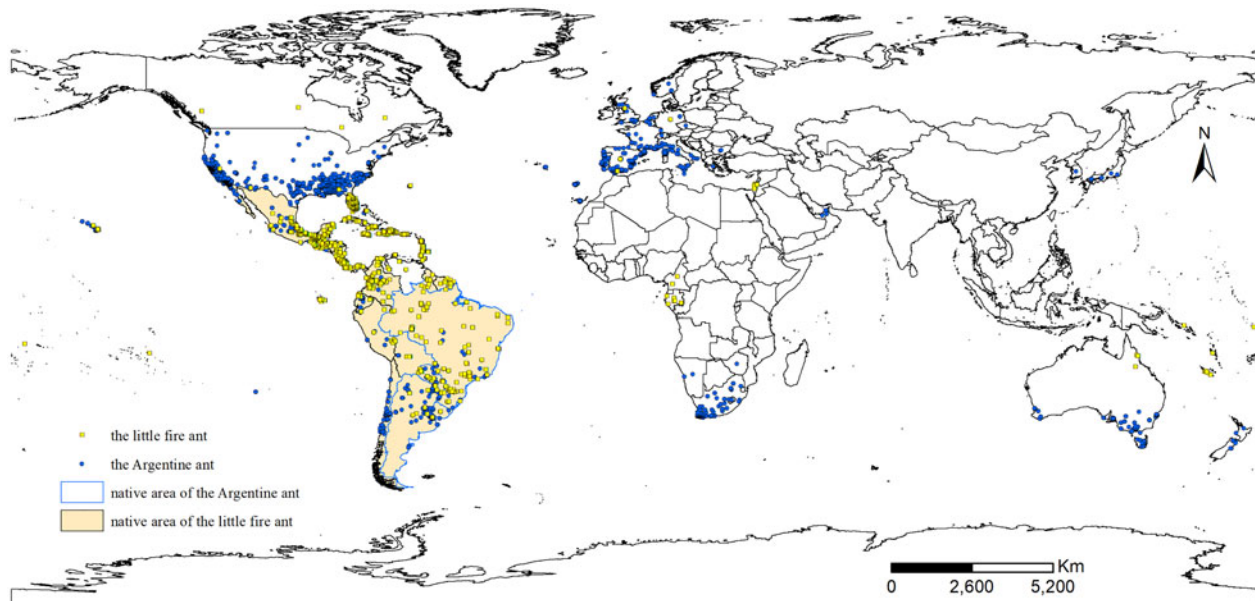


Figure 1. The distribution data of *L. humile* and *W. auropunctata*.

sampling analysis. We then imported the sampling results into IBM SPSS Statistics version 26 for factor analysis and correlation analysis. If the correlation between two climate variables was greater than 0.8, we retained the factor with the higher contribution rate in principal component analysis.

Maxent model parameter setting

To avoid overfitting, we adjusted the regularisation multiplier (RM) and Feature Combination (FC) parameters of the MaxEnt model for different species using the ENMeval package in R. The FC comprises five items: 'Linear features', 'Quadratic features', 'Product features', 'Threshold features' and 'Hinge features'. Based on the FC, we set six combination forms of L, H, LQ, LQH, LQHP, and LQHPT in RStudio. For RC, we set eight levels: 0.5, 1, 1.5, 2, 2.5, 3, 3.5, and 4. We used the 'delta.AIcc' value to determine the desired RM and FC, which resulted in RM = 0.5 and FCs = LQHPT for *L. humile* and RM = 1 and FCs = LQHPT for *W. auropunctata*.

Additionally, we set the following parameters: 25% of the distributed data was used as the test set, and the remaining 75% was used as the training set. We conducted 10 repeat runs using the 'Subsample' method. The maximum number of iterations was set to 5000, a 10 percentile training presence threshold was added, and we used 'Jackknife' to evaluate the importance of climate variables. Finally, we saved the MaxEnt model running results in *avg.asc format and imported them into ArcGIS 10.2. We divided the suitable area into four levels (negligible risk, low risk, medium risk, and high risk), and used the natural break classification method to determine the threshold of classification.

Maxent model accuracy test

To assess the effectiveness of our models in incorporating environmental variables, we utilised receiver operating characteristic (ROC) curves and area under the curve (AUC) values as accuracy measures (Liu et al., 2022). AUC values range from 0 to 1, with higher values indicating greater precision. A score of 0.5–0.7 indicates poor predictive performance, while a value of 0.7–0.9 represents good performance (Zhang et al., 2022). A value of 0.9–1.0 indicates very good performance of the model in predicting outcomes (da Silva Galdino et al., 2016).

Calculation of suitable areas for *L. humile* and *W. auropunctata*

The suitable areas of *L. humile* and *W. auropunctata* were calculated by Arcmap10.2. The MaxEnt result files were imported into the Spatial Analyst tool in ArcToolbox and reclassified. The unsuitable area is assigned 0 and the suitable area is assigned 1. The region with a value of 1 is extracted through the 'extract by attribute' function of the analysis tool, namely, the suitability region. Finally, the raster data of suitable areas were imported and assigned through the 'Display partition statistics in tables' of regional analysis in the Spatial Analyst tool. The suitable area in each administrative region was obtained.

Analysis of overlap of suitable areas for *L. humile* and *W. auropunctata*

The maxent result files of *L. humile* and *W. auropunctata* were imported into the Spatial Analyst tool in ArcToolbox for reclassification. The two reclassification results were calculated using Raster Calculator.

Result

Contribution rate of environmental variables and model evaluation

To predict the distribution range, all 19 environment variables obtained from WorldClim were tested. From these variables, the five variables that best predicted the range of species were identified. For *L. humile* the contribution rates of variables from high to low were 'Mean Temperature of Coldest Quarter' (BIO11), 'Precipitation of Coldest Quarter' (BIO19), 'Max Temperature of Warmest Month' (BIO5), 'Precipitation of Wettest Quarter' (BIO16), and 'Precipitation Seasonality' (BIO15). The contribution rates were 65.5%, 25.7%, 4.1%, 4.1%, and 0.5%, respectively. According to the Jackknife test, BIO11 and BIO19 showed higher scores under 'with only variable', indicating that these variables had good predictive ability; The BIO11 score was the lowest under 'without variable', indicating that species distribution was more affected by precipitation (fig. 2A).

For *W. auropunctata*, the contribution rates of variables from high to low were "Temperature Annual Range" (BIO7), "Precipitation of Wettest Month" (BIO13), "Mean Temperature of Warmest Quarter" (BIO10), "Precipitation of Driest Month" (BIO14), and "Precipitation Seasonality" (BIO15). The contribution rates were 49.1%, 22.6, 14.2%, 12.8%, 1.2%, respectively. Jackknife test showed BIO7 and BIO13 had higher scores under "with only variable", BIO7 score was the lowest under 'without variable' (fig. 2B).

The average AUC of 10 replicate runs was calculated separately for *L. humile* and *W. auropunctata*, resulting in an average AUC of 0.925 and 0.937, respectively. These values indicated that the prediction effect of the model is good (fig. 2C-D).

Global potential geographic distribution of *L. humile* and *W. auropunctata* under current climate conditions

Fig. 3A depicted the suitable area of *L. humile* under the current climate conditions (total $3498.3125 \times 10^4 \text{ km}^2$). Under current climate conditions, suitable areas for *L. humile* were identified in various regions around the world. In Asia, suitable areas were found in multiple countries, including Turkey, Egypt, Iran, India, China, and Japan. In Europe, suitable areas were found in countries such as Norway, France, Germany, and Italy. North America had suitable areas in countries such as the United States and Canada, while South America had suitable areas in countries such as Brazil and Argentina. Suitable areas were also identified in many African countries, including Morocco, Tanzania, and South Africa, as well as in parts of Oceania, such as Indonesia and Australia. Under the current climate conditions, the top ten countries with the largest suitable areas of *L. humile* were shown in Table 1.

Fig. 3B depicted the suitable area of *W. auropunctata* in the current climate conditions (total $3310.1389 \times 10^4 \text{ km}^2$). Under current climate conditions, suitable areas for *W. auropunctata* are primarily located between the Tropic of Cancer and the

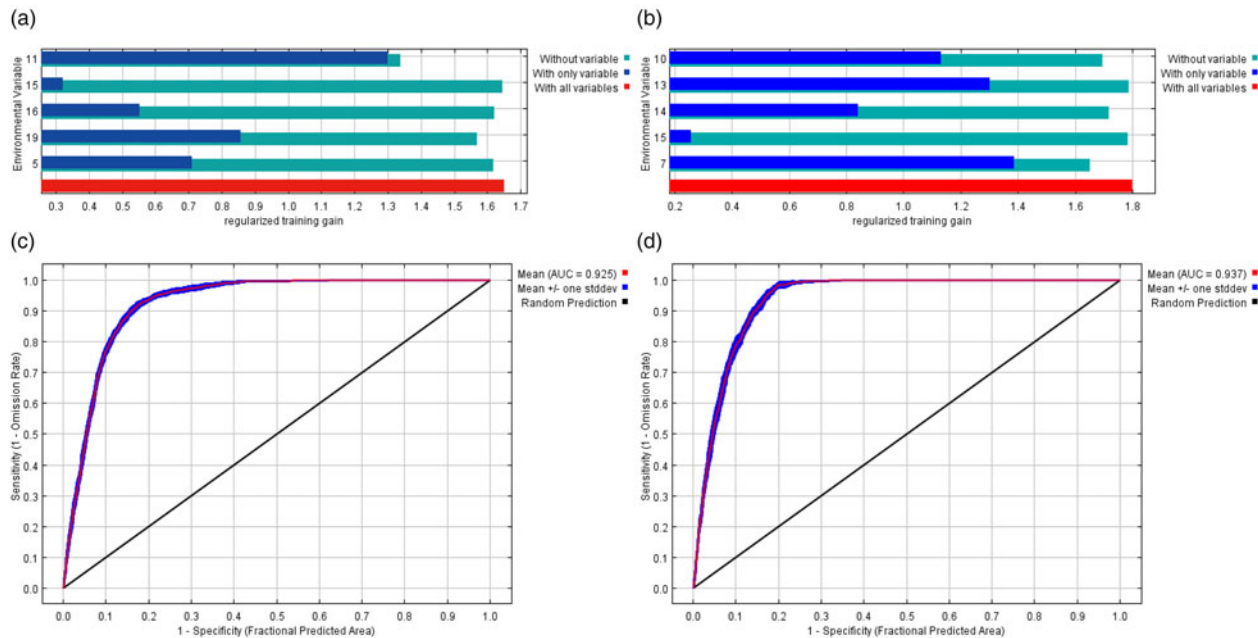


Figure 2. Contribution rate of the five selected environmental variables (A, B) and model evaluation (C, D). Panel A shows the contribution rate of the environmental variables for *L. humile*, while panel B shows the contribution rate for *W. auropunctata*. Panel C and D show the model evaluation for *L. humile* and *W. auropunctata* in terms of AUC.

Tropic of Capricorn. Suitable areas in Asia include regions such as the Indian subcontinent, Southeast Asia, and Japan. Suitable areas in Europe include parts of Portugal, Spain, France, the UK, Italy, Turkey, and other countries. In North America, suitable areas include countries such as the United States, Canada, and Mexico. In South America, suitable areas are found in countries such as Brazil, Argentina, and Uruguay. In Africa, suitable areas include parts of Ghana, Nigeria, Ethiopia, and other countries. Suitable areas are also identified in Oceania, including parts of Indonesia, Australia, and Papua New Guinea. Under the current climate conditions, the top ten countries with the largest suitable areas of *W. auropunctata* were shown in Table 1.

Potential geographic distribution of *L. humile* and *W. auropunctata* under future climate scenarios

Under the future climate scenarios, the predicted geographical distribution of *L. humile* in 2050 were shown in fig. 4. Under the SSP126 scenario in 2050, the suitable areas of *L. humile* were projected to change globally. In Asia, the suitable area of *L. humile* was expected to expand, with new suitable areas appearing in places like Hokkaido in Japan, Qingdao in China, New Delhi in India, and Armenia. However, suitable areas were predicted to disappear in Riyadh in Saudi Arabia, Oman, and parts of India. In Europe, the suitable areas of *L. humile* were projected to expand to cover almost all of central and southern Europe. In North America, the suitable areas of *L. humile* were expected to expand, with new suitable areas appearing in places such as Seward in the United States and Halifax in Canada. In South America, the suitable area of *L. humile* was also projected to expand, with new suitable areas appearing in Suriname, Fontiboa in Brazil, Arica in Colombia, and eastern Guyana. In Africa, the suitable area of *L. humile* was expected to change little, with contractions in both northern and southern Africa in suitable areas, such as Algeria, Libya, and Egypt. However, suitable

areas appeared in some parts of central Africa, such as the border of Cameroon, Gabon, and Congo. In Oceania, the suitable areas of *L. humile* were projected to slightly expand.

Under the SSP245 scenario in 2050, in Asia, the suitable areas of *L. humile* were expected to expand, with new suitable areas emerging in central Uzbekistan, New Delhi in India, Yantai in China, Hokkaido in Japan, and Palembang in Indonesia. Highly suitable areas in countries such as China, Japan, Nepal, and Pakistan were also predicted to expand. In Europe, the suitable area of *L. humile* was projected to expand to cover most of Europe, with highly suitable areas expanding from west to east. In North America, the suitable areas of *L. humile* were predicted to expand from south to north, with the suitable areas in the United States spreading to the middle, but highly suitable areas shrinking slightly. In South America, the suitable areas of *L. humile* were expected to expand, with new suitable areas appearing in Suriname and French Guiana. However, highly suitable areas in Argentina, Brazil, and Paraguay were projected to contract southward. In Africa, the suitable areas of *L. humile* were projected to change little, with suitable areas in South Sudan expanding, while those near Uganda and Rwanda shrinking. In Oceania, the suitable areas of *L. humile* changed little, with the suitable areas in eastern Australia expanding towards the central part.

Compared with the current climate in the SSP370 scenario in 2050, the changes in the suitable areas of *L. humile* were as follows: In Asia, the suitable area of *L. humile* expanded. Suitable areas in Uzbekistan moved northward, and suitable areas in Iran, Afghanistan, Indonesia and Pakistan expanded slightly around them. Highly suitable areas in China expanded significantly, while suitable areas in central India disappeared. In Europe, the suitable areas of *L. humile* expanded northward from Poland, Romania, Bulgaria and Ukraine to Moscow in Russia, southern Finland and southern Sweden. The highly suitable areas in Spain and France moved north. In North America,

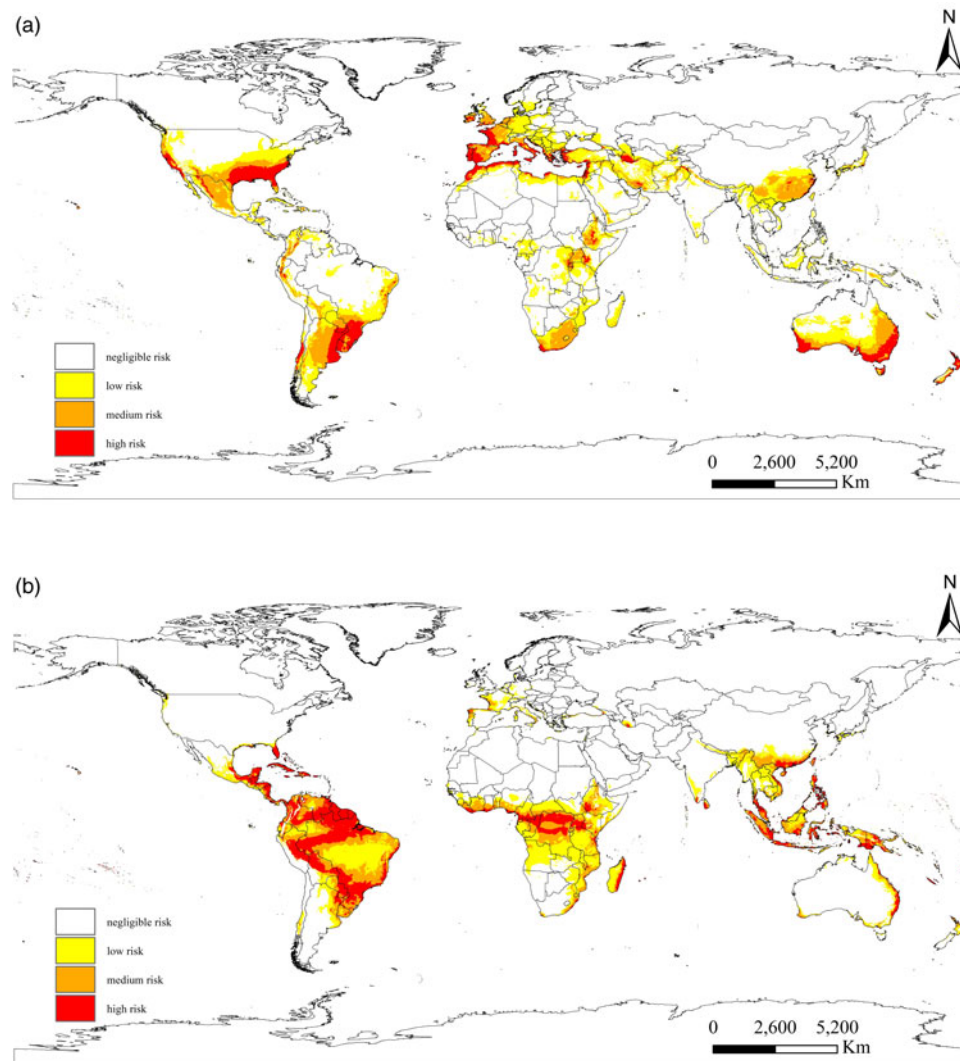


Figure 3. Potential geographic distribution of *L. humile* and *W. auropunctata* under current climate conditions. Panel A shows the suitable area for *L. humile*, panel B shows the suitable area for *W. auropunctata*.

the suitable areas of *L. humile* expanded. The suitable areas in the United States expanded from the edge to the centre, and the suitable areas near Boston expanded to the northeast. The suitable areas appeared near Merida, Mexico. In South America, the suitable areas of *L. humile* expanded. Suitable areas appeared in northern parts of South America, such as Brazil, Peru and Colombia, Suriname and French Guiana. In Africa, the suitable areas of *L. humile* varied little. Suitable areas in northern Africa shrunk northward. In central Africa, suitable areas expanded around Ghana, Togo and Benin, while suitable areas shrunk in South Sudan and Ethiopia. In Oceania, the suitable areas of *L. humile* increased slightly. The suitable areas in northern Oceania expanded to the periphery.

Under the SSP585 scenario in 2050, in Asia, the suitable areas of *L. humile* increased, but highly suitable areas decreased. Suitable areas disappeared in northern India but appeared near Sri Lanka. Suitable areas in China expanded northward but highly suitable areas shrunk. Suitable areas around Indonesia and Malaysia expanded slightly. In Europe, the suitable areas of *L. humile* expanded, with central suitable areas extending further northeast and suitable areas around France and Spain moving

further north. In North America, the suitable areas of *L. humile* expanded, but highly suitable areas decreased, with suitable areas spreading to the middle and suitable areas in Boston expanding northeast to St. Johns, Canada. In South America, the suitable areas of *L. humile* expanded, but highly suitable areas shrunk, with new suitable areas emerging in places such as Suriname, French Guiana, and western Brazil, and highly suitable areas in southeastern South America shrinking. In Africa, the suitable areas of *L. humile* decreased, with suitable areas in northern and southern Africa shrinking, and suitable areas around Ghana, Benin, and Togo expanding slightly. In Oceania, the suitable areas of *L. humile* varied greatly, with suitable areas in northern Oceania expanding, while the suitable areas in Australia shrunk to the south.

Under the future climate scenarios, the predicted geographical distribution of *W. auropunctata* in 2050 were shown in [fig. 5](#). Under the SSP126 scenario in 2050, in Asia, the suitable areas of *W. auropunctata* tended to move toward south, with suitable areas in China, Myanmar, Thailand, and India decreasing, while highly suitable areas around Malaysia and Indonesia expanded. In Europe, the suitable areas of *W. auropunctata* increased

Table 1. The top 10 countries with the largest suitable areas for *Linepithema humile* and *Wasmannia auropunctata*

| <i>Linepithema humile</i> | | | <i>Wasmannia auropunctata</i> | | |
|---------------------------|--------------------------|---|-------------------------------|----------------------------------|---|
| Number | Country | Area (10 ⁴ km ²) | Number | Country | Area (10 ⁴ km ²) |
| 1 | United States of America | 402.9027 | 1 | Brazil | 707.0208 |
| 2 | Australia | 398.8472 | 2 | Democratic Republic of the Congo | 189.4444 |
| 3 | Argentina | 228.6250 | 3 | Indonesia | 151.3125 |
| 4 | China | 227.0694 | 4 | China | 126.9583 |
| 5 | Brazil | 215.1666 | 5 | Australia | 111.1875 |
| 6 | Mexico | 137.2152 | 6 | Argentina | 87.5000 |
| 7 | South Africa | 108.5486 | 7 | Colombia | 85.6527 |
| 8 | Iran | 106.7986 | 8 | Angola | 84.8402 |
| 9 | Turkey | 65.9097 | 9 | United Republic of Tanzania | 76.7430 |
| 10 | France | 63.3125 | 10 | Ethiopia | 75.6527 |

slightly, spreading eastward from Western Europe, while highly suitable areas in Portugal, Spain, and France expanded to the periphery. In North America, the suitable areas of *W. auropunctata* varied little. In South America, the suitable areas of *W. auropunctata* decreased slightly, mainly due to the contraction of highly suitable areas and the appearance of hollow zones in some suitable areas, such as the border between Colombia and Venezuela and northeastern Brazil. In Africa, the suitable areas of *W. auropunctata* changed little, with suitable areas around Togo and Ghana shrinking. In Oceania, the suitable areas of *W. auropunctata* expanded, with highly suitable areas in Indonesia, Papua New Guinea, and New Zealand expanding to the periphery.

Under the SSP245 scenario in 2050, in Asia, suitable areas in China, Myanmar, Thailand, and India shrunk but moved

northward, while highly suitable areas near Malaysia and Indonesia expanded to the periphery. In Europe, the suitable areas of *W. auropunctata* moved north. In North America, the suitable areas of *W. auropunctata* decreased slightly, with highly suitable areas shrinking in southern Mexico and the southeastern United States, while suitable areas in the northwestern United States expanded slightly. In South America, the suitable areas of *W. auropunctata* decreased slightly, mainly due to the shrinkage of highly suitable areas and the appearance of hollow zones, with highly suitable areas in northern Brazil disappearing. In Africa, the suitable areas of *W. auropunctata* changed little. In Oceania, the suitable areas of *W. auropunctata* increased slightly, with areas such as northern Australia and southern New Zealand appearing.

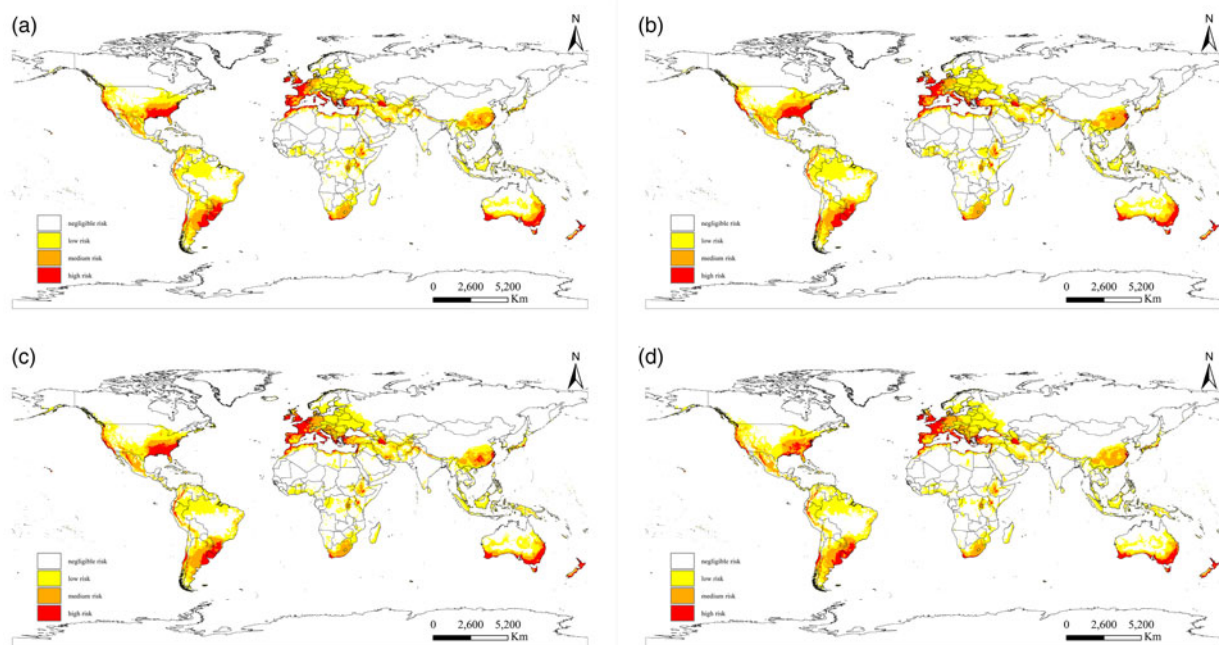


Figure 4. Potential geographical distribution of *L. humile* under four future climate scenarios. A-D showed the potential geographical distribution of *L. humile* in 2050 under the scenarios SSP126, SSP245, SSP370, and SSP585, respectively.

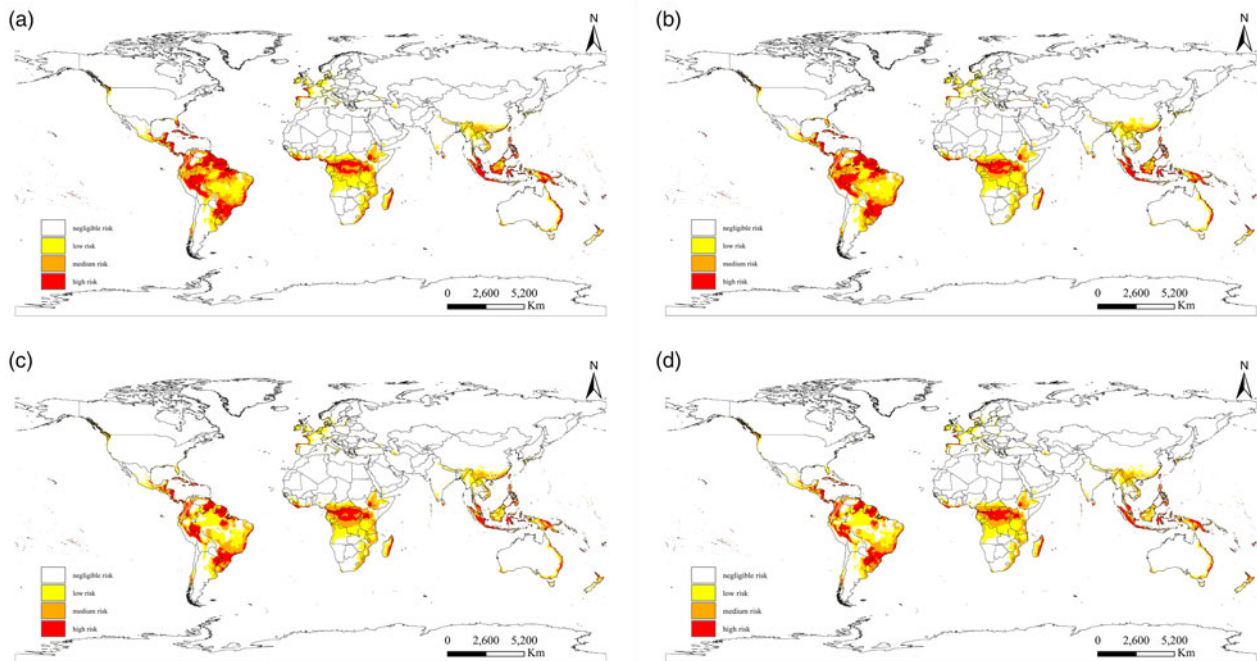


Figure 5. Potential geographical distribution of *W. auropunctata* under four future climate scenarios: SSP126, SSP245, SSP370, and SSP585 (A–D).

Under the SSP370 scenario in 2050. In Asia, the suitable areas of *W. auropunctata* decreased, with suitable areas declining in southern Vietnam, India, Myanmar, Thailand, and southern China, while suitable areas around Malaysia and Indonesia expanded. In Europe, the suitable areas of *W. auropunctata* moved northward, with suitable areas appearing in places such as Lithuania, northern Ukraine, and Sweden. In North America, the suitable areas of *W. auropunctata* decreased, with the suitable areas in the southeastern United States and southern Mexico shrinking to the south, and highly suitable areas decreasing. In South America, a large number of suitable areas of *W. auropunctata* disappeared or shrunk, such as central Brazil, Venezuela, Colombia, and northern Paraguay. In Africa, the suitable areas of *W. auropunctata* decreased slightly, but the highly suitable areas expanded around it. In Oceania, the suitable areas of *W. auropunctata* changed little, with the suitable areas in Australia shrinking slightly, such as the disappearance of the suitable area in the north, while the suitable areas in New Zealand expanded slightly.

Under the SSP585 scenario in 2050, in Asia, the suitable areas of *W. auropunctata* decreased, with highly suitable areas in southern China almost disappearing. In Europe, the suitable areas of *W. auropunctata* moved northwest, with Ireland and the UK mostly covered by suitable areas, while suitable areas in eastern France disappeared, but appeared in Sweden and southern Norway. In North America, the suitable areas of *W. auropunctata* decreased, with suitable areas in the southeastern United States and southern Mexico shrinking, but suitable areas in the northwestern United States expanding northward. In South America, the suitable areas of *W. auropunctata* reduced, with a large number of gaps, such as Venezuela, central Brazil, Bolivia, and Paraguay. In Africa, the suitable areas of *W. auropunctata* decreased, but the highly suitable areas were more concentrated, with suitable areas shrinking in places such as South Sudan,

Ghana, Togo, and Zambia, but highly suitable areas more concentrated near the Democratic Republic of Congo. In Oceania, the suitable areas of *W. auropunctata* changed little, with the suitable area of northwest Australia disappearing, but the suitable areas of southern New Zealand appearing.

Changes in the overlap of potential geographical distribution of *L. humile* and *W. auropunctata* under climate change

Fig. 6A showed the overlap of suitable areas of *L. humile* and *W. auropunctata* under the current climate conditions (total $1539.0625 \times 10^4 \text{ km}^2$). The overlap of suitable areas for both *L. humile* and *W. auropunctata* under current climate conditions was identified in various regions around the world. In Asia, suitable areas were found in countries such as Nepal, India, and Indonesia. In Europe, suitable areas were identified in parts of Portugal, Spain, France, and other countries. North America had suitable areas in countries such as the United States and Mexico, while South America had suitable areas in countries such as Brazil and Argentina. Suitable areas were also identified in many African countries, such as Ethiopia and Madagascar, as well as in parts of Oceania, including Australia and New Zealand.

Under the SSP585 scenario, the overlapping potential geographical distribution of *L. humile* and *W. auropunctata* in 2050 was shown in fig. 6B. Compared to the overlap areas of potential distribution under current climate conditions, the results showed that with the climate change, the global suitable overlap areas of *L. humile* and *W. auropunctata* increased from $1539.0625 \times 10^4 \text{ km}^2$ to $1579.9028 \times 10^4 \text{ km}^2$, representing a 2.65% increase or a difference of $40.8403 \times 10^4 \text{ km}^2$. The top ten countries with the largest increase overlap suitable areas were shown in Table 2.

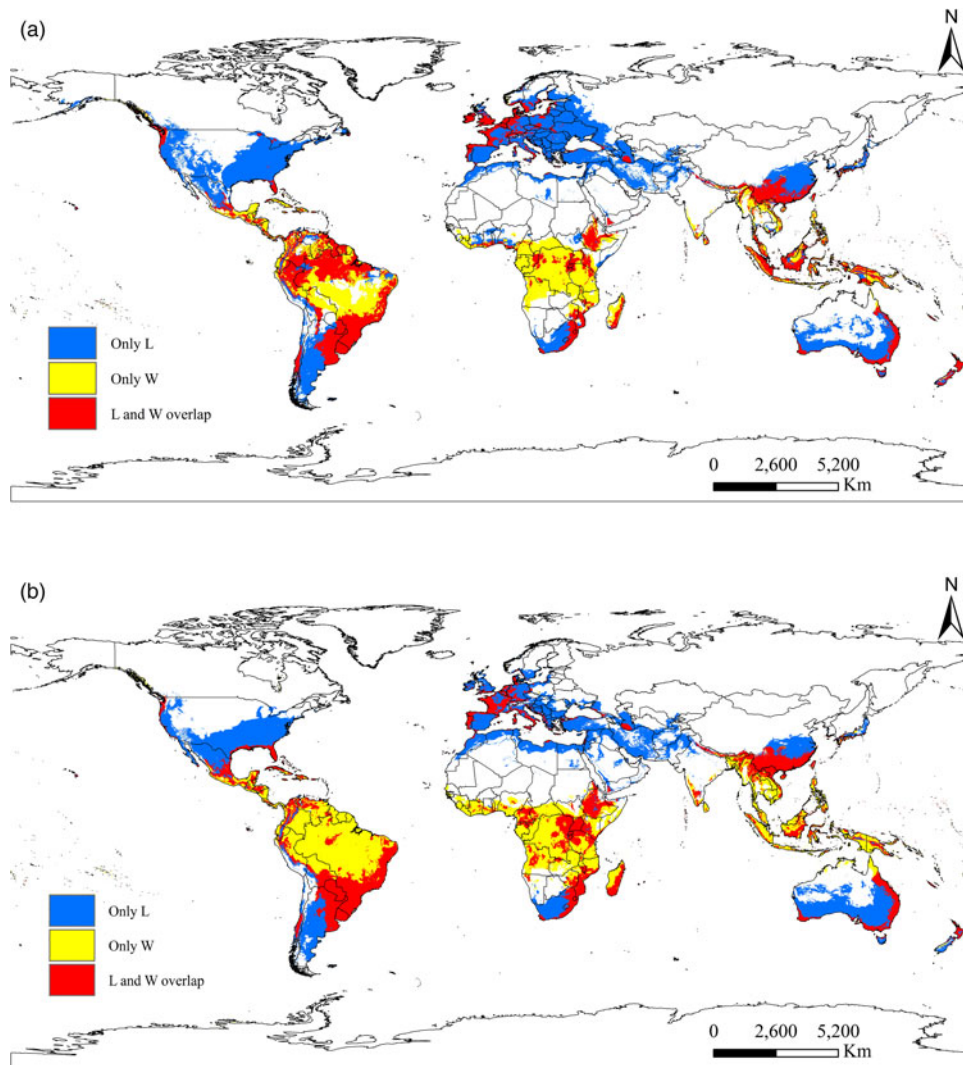


Figure 6. The overlap areas of potential geographic distributions of *L. humile* and *W. auropunctata* under current (A) and future SSP585 climate scenario (B).

Table 2. Top ten countries with the largest expansion of suitable overlap areas of *L. humile* and *W. auropunctata* under the SSP585 climate change scenario, including percentage increase

| Number | Country | Current suitable area (10 ⁴ km ²) | Future suitable area (10 ⁴ km ²) | Increased suitable area (10 ⁴ km ²) | Percentage increase in area, % |
|--------|----------------|--|---|--|--------------------------------|
| 1 | Brazil | 215.1458 | 333.4792 | 118.3333 | 55.0014 |
| 2 | Indonesia | 47.9097 | 98.1597 | 50.2500 | 104.8848 |
| 3 | Peru | 19.2014 | 48.4028 | 29.2014 | 152.0795 |
| 4 | Colombia | 22.8889 | 48.2431 | 25.3542 | 110.7707 |
| 5 | United Kingdom | 5.0417 | 23.0069 | 17.9653 | 356.3341 |
| 6 | Canada | 1.5000 | 15.2917 | 13.7917 | 919.4466 |
| 7 | Guyana | 1.9653 | 14.6944 | 12.7292 | 647.6975 |
| 8 | Sweden | 0.7083 | 11.4722 | 10.7639 | 1519.6809 |
| 9 | Suriname | 0.0139 | 10.4097 | 10.3958 | 74,789.9280 |
| 10 | Malaysia | 5.6458 | 15.7083 | 10.0625 | 178.2298 |

With climate change, overlap suitable areas emerged in some countries such as Latvia, Estonia, Finland, Aland, Afghanistan, Barbados, Saint Pierre, and Miquelon, Singapore and Grenada. There were also some countries that used to have overlapping suitable areas disappeared with climate change, such as Aruba, Bulgaria, Jordan, Guinea, Burkina Faso, and Zambia.

Discussion

This study presented a unique contribution by concurrently examining the potential geographical distribution and overlap suitable areas for both *L. humile* and *W. auropunctata* utilising the MaxEnt model. While previous studies have individually explored these two species using the MaxEnt or other SDM models, this is the first investigation to compare them side by side and assess their overlapping areas (Jung *et al.*, 2022; Li *et al.*, 2022; Mao *et al.*, 2022).

Environmental variables

In this study, five key environmental variables were screened for *L. humile*, and it was found that the two factors that most affect *L. humile* were ‘Mean Temperature of Coldest Quarter’ and ‘Precipitation of Coldest Quarter’. This result indicated that *L. humile* is highly sensitive to cold temperature and humidity which is consistent with previous research findings. For example, Krushelnycky *et al.*, 2005 found that the invasion of *L. humile* in low-altitude regions is limited by rainfall and temperature, while in high-altitude regions, it is influenced by elevation and temperature. (Krushelnycky *et al.*, 2005) Schilman *et al.*, 2007 also highlighted that in the invaded region of southern California, *L. humile* is influenced by water-loss rates and critical water content, resulting in shorter survival time compared to native ants. This further confirms that humidity is one of the key climatic variables affecting the survival of *L. humile* (Schilman *et al.*, 2007). There have also been studies indicating that temperature has a significant impact on *L. humile* (Jumbam *et al.*, 2008; Brightwell *et al.*, 2010). Jung *et al.*, 2022 discovered that the factors limiting the occurrence frequency of *L. humile* are the monthly average maximum temperature, monthly average minimum temperature, and monthly precipitation. Additionally, the occurrence of *L. humile* is associated with the lowest temperatures. (Jung *et al.*, 2022).

For *W. auropunctata*, five important variables were screened, and the variable with the highest influence on its distribution was ‘Temperature Annual Range’, which contributed to 49.1% of the variation. This finding is consistent with previous studies that have shown temperature as a key factor affecting the distribution of *W. auropunctata* (Vonshak *et al.*, 2010; Calcaterra *et al.*, 2016). Moreover, according to the findings of Chifflet *et al.*, 2016, temperature is likely an important factor contributing to the differentiation of the two clades within the native distribution range of *W. auropunctata*. Additionally, temperature may impose limitations on the distribution range of *W. auropunctata*, allowing only the subtype adapted to colder climates to expand further south (Chifflet *et al.*, 2016). Similarly, Coulin *et al.*, 2019 correlated the thermal tolerance of *W. auropunctata* with the minimum temperature of the coldest month, explaining the southernmost limit of its native distribution and its physiological capacity to expand in the Mediterranean region (Coulin *et al.*, 2019). However, the variables considered in this study were not sufficient, soil status, geomorphology and topography, water

resources, impact of human activities, interspecific competition and other limited factors were not included (Zhao *et al.*, 2020; Geng *et al.*, 2022). Considering these variables in future studies could improve the accuracy and effectiveness of the research, as ‘overcomplicating’ the model may be better than ‘not complicating enough’ (Warren and Seifert, 2011; Li and Ding, 2016; Bradie and Leung, 2017).

Potential geographic distribution under climate change

By comparing our results with previous predictions (Li *et al.*, 2022; Mao *et al.*, 2022), we have predicted a wider range of potential distribution due to the differences from the selected environmental factors (Li and Ding, 2016). It was found that the potential distribution area of *L. humile* is larger than that of *W. auropunctata*. Given the strong colonisation ability of both *L. humile* and *W. auropunctata*, these two species will invade new habitats whenever they have the opportunity (Vogel *et al.*, 2010; Calcaterra *et al.*, 2016).

Under climate change, the suitable areas for *L. humile* were expected to increase, but the highly suitable areas will decrease. Global warming may allow *L. humile* to invade areas that were once unsuitable due to cold weather (Nelson *et al.*, 2023). Conversely, with the changing climate, the suitable areas for *W. auropunctata* in the world will decline. This could be good news for urban ecosystems where *W. auropunctata* invasion leads to reduced species richness (Mbenoun Masse *et al.*, 2019).

In terms of land area, the suitable region for *L. humile* was expected to increase with climate change, while the suitable region for *W. auropunctata* is expected to decrease, leading to a slight reduction in the overlapping suitable areas for the two species. However, under specific climate scenarios, the suitable area for *L. humile* reaches its maximum under the SSP245 scenario ($4119.1111 \times 104 \text{ km}^2$), while the suitable area for *W. auropunctata* reaches its minimum under the SSP370 scenario ($2778.5347 \times 104 \text{ km}^2$). In terms of regional distribution, the temperate suitable area for *L. humile* will expand with climate change, while the changes in tropical suitable areas are relatively small. However, there is no clear similar trend for *W. auropunctata*.

Control measure suggestions for *L. humile* and *W. auropunctata*

This study identified areas where *L. humile* and *W. auropunctata* may overlap in their suitable habitats under current and future climate conditions. This information provided a basis for prevention, control, and monitoring of these two invasive ant species. Both species have negative impacts on local ant species during invasions, and they can also form mutualistic relationships with some honeydew-producing insects (Krushelnycky and Gillespie, 2008; Helms, 2013). Furthermore, when facing common enemies, they may exhibit a degree of inter-specific collaboration, which could increase their invasion success rate (Bertelsmeier *et al.*, 2016). Therefore, in areas where their suitable habitats overlap, there will be a high probability for both ant species to successfully invade.

Argentine ants exhibit a high level of sociability and cooperation, and can form super colonies through recruitment and trail-marking behaviours (Sanders and Suarez, 2011; Silverman and Buczkowski, 2016). Little fire ants, on the other hand, demonstrate strong aggression and predation behaviours, which enables them to compete for resources and establish new nests through

attacking and raiding (Montgomery *et al.*, 2022). In the wild, there may not be a single invasive species, but rather different species occupying different areas (Bertelsmeier *et al.*, 2015a, 2015b). Therefore, ecological and biological perspectives should be considered to prevent the invasion of these ants (Walters and Mackay, 2005). Strategies for their prevention should be carefully considered to prevent excessive administrative costs or economic losses caused by invasive species (Lee *et al.*, 2015; Cuthbert *et al.*, 2022).

Chemical methods were often used to prevent them (Ellis *et al.*, 2008; Souza *et al.*, 2008; Hara *et al.*, 2011). However, in some cases, pesticides can be counterproductive to managing and eliminating invasive ants (Lester and Gruber, 2016). Old pest management is costly, and chemical control can be harmful to the land (Cuthbert *et al.*, 2022; Kumari *et al.*, 2022). From a biological perspective, intensifying interspecific resource competition and using pheromones to interfere with ant foraging and nesting may have unexpected effects (Mothapo and Wossler, 2014; Suiter *et al.*, 2021). Strengthening the research on the biological behaviour of pests will also help to reveal the secrets of their invasion (Sanmartin-Villar *et al.*, 2021).

In actual production, both chemical and biological control methods have their own advantages, and plans should be made based on practical considerations (Huang *et al.*, 2022). Quarantine is the best way to control *L. humile* and *W. auropunctata*, as it involves stopping them in the path of transmission (Suhr *et al.*, 2019; Si-qi *et al.*, 2022) and finding effective quarantine treatment measures (Follett *et al.*, 2016). Monitoring in the potential distribution areas of these two species will help with early warning and prevention of their invasion.

Data availability statement. The data that support the findings of this study are available in Zenodo at <https://doi.org/10.5281/zenodo.7678538>.

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