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EDITED BY

Anouschka R. Hof,
Wageningen University & Research,
Netherlands

REVIEWED BY

Rihui Yan,
Tennessee State University,
United States
Bingxin Wang,
Wageningen University & Research,
Netherlands

*CORRESPONDENCE

Shihao Zhou
zsh88200939@126.com

†These authors have contributed
equally to this work

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Distribution and interaction of the suitable areas of *Beauveria bassiana* and *Bactrocera dorsalis* (Hendel)

Aqiang Wang^{1,2†}, Sihua Peng^{1†}, Yuyang Lian^{1,2†},
Xiaofeng Yang^{1†}, Jingjing Jia^{3†}, Jinlei Li², Shuyan Yang¹,
Rongjiao Zheng² and Shihao Zhou^{1,2*}

¹Sanya Nanfan Research Institute of Hainan University, Sanya, China, ²Key Laboratory of Germplasm Resources Biology of Tropical Special Ornamental Plants of Hainan Province, College of Forestry, Hainan University, Haikou, China, ³Institute of Plant Protection, Hainan Academy of Agricultural Sciences (Research Center of Quality Safety and Standards for Agricultural Products of Hainan Academy of Agricultural Sciences), Haikou, China

Climate is a key factor affecting the potential distribution of insects, and the host is another important constraint for the distribution of pests. To elucidate changes in the potential distribution of *Beauveria bassiana* under climate change scenarios, this paper used the data of two different greenhouse gas (GHG) emission scenarios (RCP2.6, RCP8.5) to predict the potential distribution of *B. bassiana* and its typical host, *Bactrocera dorsalis* (Hendel), based on the MaxEnt model. Then, the potential distribution of *B. bassiana* and *B. dorsalis* (Hendel) was compared, and their suitable growth area's change and expansion trend under two different GHG emission scenarios were mastered. The results of this study show that the potential distribution area of *B. bassiana* will increase by 2,050 under the RCP8.5 climate scenario, mainly in central Europe and southwestern Asia, with an increased area of 3.28×10^5 km². However, under the climate scenario of RCP2.6, the potential distribution area for *B. bassiana* decreased by 2.0×10^5 km², mainly in North America. This study will provide a theoretical basis for the control of *B. dorsalis* (Hendel) with *B. bassiana*.

KEYWORDS

Beauveria bassiana, fungus, *Bactrocera dorsalis* (Hendel), potential distribution areas, MaxEnt model, biological control

Introduction

Due to international trade and travel, the invasion of agricultural pests is frequent and serious in many countries (McCullough et al., 2006; Douma et al., 2016; Lee et al., 2016). Ecological risk assessment of invasive species includes using the historical distribution and infection information of species in the local area to determine risk

and making preventive measures before the invasion and outbreak (Lovett et al., 2016; Martínez-Abraín and Jiménez, 2019). Species distribution models (SDMs), based on data of pest occurrence places and related bioclimatic variables, are a common method used to describe or predict potential distribution areas for risk analysis (Lantschner et al., 2019; Méndez-Vázquez et al., 2019; Early et al., 2022). Among these, the maximum entropy (MaxEnt) model is a widely used and easily available method for predicting species distribution with higher accuracy than other models. When using MaxEnt to predict the potential distribution of species, environmental factors such as temperature and rainfall are considered to be the most important factors (Elith et al., 2011; Silva et al., 2014; Zhang et al., 2016).

Beauveria bassiana is one of the most widely studied and applied entomopathogenic fungi in the field of biological control of pests, with more than 360 species. It has the advantages of high toxicity, wide application, and no environmental pollution (Mascarin and Jaronski, 2016; Liu et al., 2021; Tomson et al., 2021). It has been widely used to control agricultural pests such as *Bactrocera dorsalis* (Hendel), *Tetranychus urticae* (Koch), and *Bemisia tabaci* (Gennadius) (Zibae et al., 2013; Liu et al., 2017; Guo et al., 2021). In a study on the biological control of the *B. dorsalis* (Hendel), it was found that the death rate of *B. dorsalis* (Hendel) in direct contact with the conidia suspension of *B. bassiana* was between 64 and 93%, which confirmed that *B. bassiana* can be transmitted among individual flies (Tora and Azerefeegn, 2021). *B. bassiana* B6 spore suspension has a weak lethal effect on nymphs of *B. dorsalis* (Hendel) in soil, and the mortality rate is below 10%. However, when a certain concentration of *B. bassiana* spore suspension (1×10^8 spores/mL) was sprayed into the cages, 100% of the adults are killed, which indicates that *B. bassiana* spores are effective against adults (Zhang et al., 2010; Pan et al., 2014). Similarly, it is reported that in the soil treated with *B. bassiana*, 83% of the larvae of the *B. dorsalis* (Hendel) died in the process of soil culture (Ugwu and Nwaokolo, 2020). These studies have shown that *B. bassiana* has a good control effect on *B. dorsalis* (Hendel).

The ability of the fungus to parasitize is affected by several factors, of which temperature and humidity are especially important for the germination of *B. bassiana* spores (Zimmermann, 2007; Labbé et al., 2009; Jackson et al., 2010; Li et al., 2011; Gonzalez et al., 2016). *B. bassiana* spores can't survive above 50°C, but completely inactivate after several months at 21°C, and they can be stored at 8°C for at least 1 year (Meyling and Eilenberg, 2007). In addition, temperature and humidity are not the only key factors of *B. bassiana* spore germination, but also play a key role in the growth and development of this pest. Some scholars have found that at a certain relative humidity (from 25 to 70%), the emergence success rate of egg and adult black soldier flies, *Hermetia illucens* (L.) increases with the increase of relative humidity, while

the development time shortens with the increase of relative humidity (Holmes et al., 2012). In a study on the influence of temperature on the development of *B. dorsalis* (Hendel), it was found that *B. dorsalis* (Hendel) successfully developed from the egg stage to the adult stage at all tested temperatures except the lowest (13.0 and 14.4°C) (Samayoa et al., 2018). The optimum temperatures for the egg, larval, pupal, and egg-to-pupal stages were 20.7, 21.8, 21.1, and 22.4°C, respectively (Motswagole et al., 2019). In an external environment above 47 or below 7°C, adults and larvae of *B. dorsalis* (Hendel) can't survive, and the survival rate of *B. dorsalis* (Hendel) at all developmental stages decreased with the increase of these two extremes of temperature and the prolongation of their duration (Wei et al., 2015). After a short period of high temperature (45°C) treatment, *Zeugodacus cucurbitae* (Coquillett) can adapt to extreme conditions by changing their protein expression, as evidenced by an acceleration of ovarian development, leading to earlier egg-laying. But when the number of high-temperature treatments increases, egg-laying behavior is inhibited (Walstad et al., 1970; Pham et al., 2010; Dara et al., 2015; Zhou, 2016; Lee et al., 2017; Zeng et al., 2018).

In this study, we used environmental data from two different GHG emission scenarios (RCP2.6 and RCP8.5) based on the MaxEnt ecological model and selected *B. dorsalis* (Hendel) as the host of *B. bassiana* to investigate the distribution and trends in the suitable areas of *B. bassiana* and *B. dorsalis* (Hendel). This study provides a theoretical basis for pest control by pathogenic fungi.

Materials and methods

Sources of geographic distribution data

By collecting and reading a large number of published academic papers and visiting GBIF¹ to obtain the geographic coordinate data of *B. bassiana* and *B. dorsalis* (Hendel). To avoid overfitting, we first delete the coordinate data falling on the sea surface, and then we create a 2 km × 2 km grid, and the data in the same grid only retains one. Finally, we screened out the geographic distribution data of 310 *B. dorsalis* (Hendel) and 525 *B. bassiana*. The geographic coordinate data of historical places are saved in “.CSV” format.

Climate data acquisition and screening

The current 19 bioclimatic variables data used in this study were obtained from WorldClim² (Table 1), which was

¹ <https://www.gbif.org/>

² <https://www.worldclim.org/>

TABLE 1 Climate and bioclimatic variables.

Variables	Bioclimatic variables
Bio1	Annual average temperature
Bio2	Monthly mean temperature difference between day and night
Bio3	Ratio of diurnal temperature difference to annual temperature difference
Bio4	Seasonal variance of temperature
Bio5	Maximum temperature in the warmest month
Bio6	Lowest temperature in the coldest month
Bio7	Annual variation range of temperature
Bio8	Average temperature in the wettest quarter
Bio9	Average temperature in the driest quarter
Bio10	Average temperature of the warmest quarter
Bio11	Average temperature in the coldest quarter
Bio12	Average annual precipitation
Bio13	Precipitation in the wettest month
Bio14	Precipitation in the driest month
Bio15	Seasonal variation coefficient of precipitation
Bio16	Precipitation in the wettest quarter
Bio17	Precipitation in the driest quarter
Bio18	Precipitation in the warmest quarter
Bio19	Precipitation in the coldest quarter

released in January 2020, spanning the period from 1,970 to 2,000, and its accuracy was 2.5 arc-minutes. MaxEnt 3.4.4 was used to analyze the correlation between environmental factors, and the contribution of environmental factors was ranked, and then SPSS 26.0 was used to analyze the correlation between environmental factors. When the absolute value of the correlation between two ecological factors was greater than or equal to 0.8, only one representative environmental factor will be kept (Lobo, 2016). At last, eight environmental factors (Bio2 Bio10, Bio11, Bio13, Bio14, Bio15, Bio18, Bio19) and nine environmental factors (Bio2, Bio4, Bio5, Bio6, Bio12, Bio14, Bio15, Bio18, Bio19) of *B. dorsalis* (Hendel) and *B. bassiana* bioclimatic variables were selected (Li et al., 2022; Table 1). In this study, environmental data from two GHG emission scenarios, RCP2.6, and RCP8.5, were selected to project the future climate suitability areas for the *B. bassiana* and *B. dorsalis* (Hendel) under future climate conditions. These bioclimatic variables ran in the model were selected from Coupled Model Intercomparison Project Phase 6 (CMIP6), and their accuracy was 2.5 arc-minutes.

Model construction and evaluation

Construction of the model

At first, we imputed the filtered current environmental data (1,970–2,000) into MaxEnt. We then input the geographical

distribution data of the *B. bassiana* and *B. dorsalis* (Hendel) into the model separately, and randomly selected 75% of the data as the training set for the experiments. The remaining 25% coordinate data were used as the test set, which is repeated 10 times, and the remaining parameters are used as the default values of the software. The simulation data obtained above were input into ArcMap 10.6 to visualize the simulation results. By using the Spatial Analyst option of the Arc toolbox in the software, the raster files were reclassified using the reclassification tool, and the distribution area was set to four gradients (Welch and Harwood, 2014): unsuitable areas (0–0.2), low suitable areas (0.2–0.4), moderately suitable areas (0.4–0.6), and high suitable areas (0.6–0.1).

Evaluation of the model

In this study, the area under the receiver operating characteristic curve (AUC) was used as a measure of the accuracy of the model prediction. The interval range is 0.5–0.1, 0.5 corresponds to a completely random prediction, 0.5–0.7 indicates that the accuracy of the prediction result is poor, and 0.7–0.9 indicates that the accuracy of the prediction result is moderate. When the prediction result is > 0.9, it shows that the prediction result has higher accuracy (Barry and Elith, 2006).

Result and analysis

The precision of the model prediction results was assessed

The AUC values of each prediction result were above 0.90 at the end of the model operation (Table 2), indicating a high degree of accuracy of the prediction result.

Distribution of suitable areas of *Beauveria bassiana* and *Bactrocera dorsalis* (Hendel) under different climatic conditions

The distribution of the two habitats under current climatic conditions

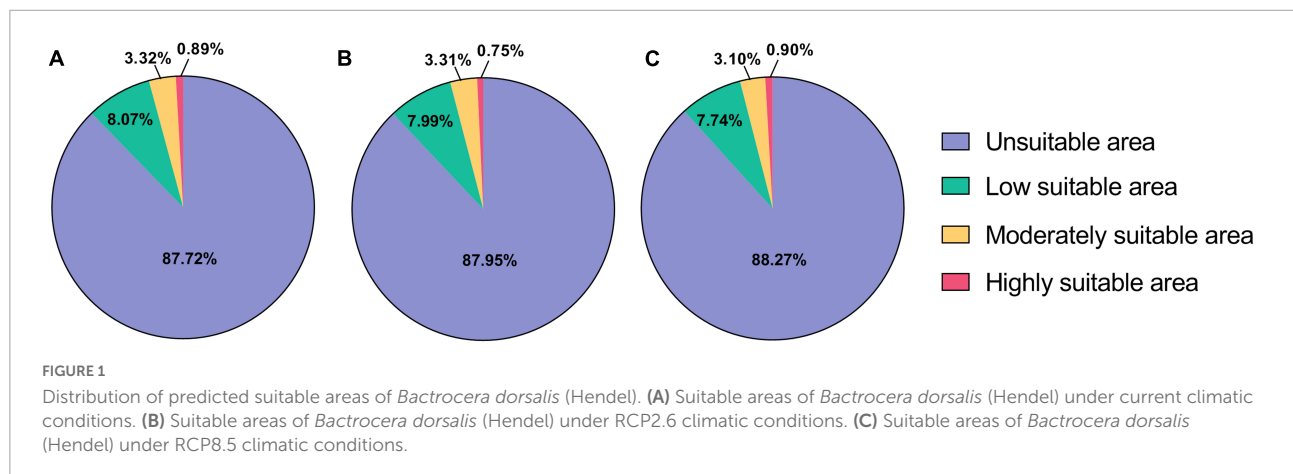
Under current climatic conditions (1,970–2,000), the highly suitable areas of *B. dorsalis* (Hendel) are mainly distributed in Asian regions, such as Africa and southern coastal areas of China, and sporadically in African regions, with a total area of 1.30×10^6 km² (Table 3), accounting for 0.89% of the global land area (Figure 1). The moderately and low suitable areas are mainly distributed in central Africa and South America, with a total area of 1.65×10^7 km². The potential global

TABLE 2 Area under the receiver operating characteristic curve.

Species	Area under curve	Current	2,050 s	
			RCP2.6	RCP8.5
<i>Bactrocera dorsalis</i> (Hendel)	Testing data	0.945	0.939	0.943
<i>Citrus reticulata</i> (Blanco)	Testing data	0.939	0.939	0.941
<i>Beauveria bassiana</i>	Testing data	0.943	0.939	0.955

TABLE 3 Suitable area of *Bactrocera dorsalis* (Hendel).

Categories	Current	RCP2.6	RCP8.5
Unsuitable area (km ²)	127245502.9	127576237.9	128037906.9
Low suitable area (km ²)	11702011.84	11590891.29	11221882.78
Moderate suitable area (km ²)	4810382.718	4803206.683	4492904.464
High suitable area (km ²)	1296221.814	1083790.086	1301418.507

TABLE 4 Suitable area of *Beauveria bassiana*.

Categories	Current	RCP2.6	RCP8.5
Unsuitable area (km ²)	125056558.6	124916091.2	123721818.6
Low suitable area (km ²)	11618371.42	12319588.26	12400642
Moderately suitable area (km ²)	5999543.998	5638743.527	6224163.121
Highly suitable area (km ²)	2379606.565	2179686.898	2707513.538

distribution of *B. bassiana* is concentrated between 30°N–60°N and 0°–60°S, with a total area of 2.0×10^7 km². The highly suitable areas of *B. bassiana* are mainly distributed in the European region and sporadically in the American region, with a total area of 2.38×10^6 km² (Table 4). The moderately suitable areas include the southeastern part of South America and North America, the central to the eastern part of Europe, and the coastal areas of Asia, with a total area of 6.0×10^6 km². The low suitability areas of *B. bassiana* are mainly distributed in three regions, Africa, Oceania, and Asia. The prediction results showed that the contribution rate of Bio13 (Precipitation in the wettest month) to the

model prediction of *B. dorsalis* (Hendel) accounted for 66.6%, indicating that Bio13 played a key role in the distribution of *B. dorsalis* (Hendel).

A comparison of the distribution of the suitable areas under the same climatic reveals some differences between the two species in distribution, most notably in Europe, where large areas are suitable for *B. bassiana*, but not for *B. dorsalis* (Hendel). However, in other areas, there was a large area overlap between the two suitable areas, and the total area of *B. bassiana* suitable areas is much larger than that of *B. dorsalis* (Hendel), which indicates that *B. bassiana* is more adaptable to the environment than

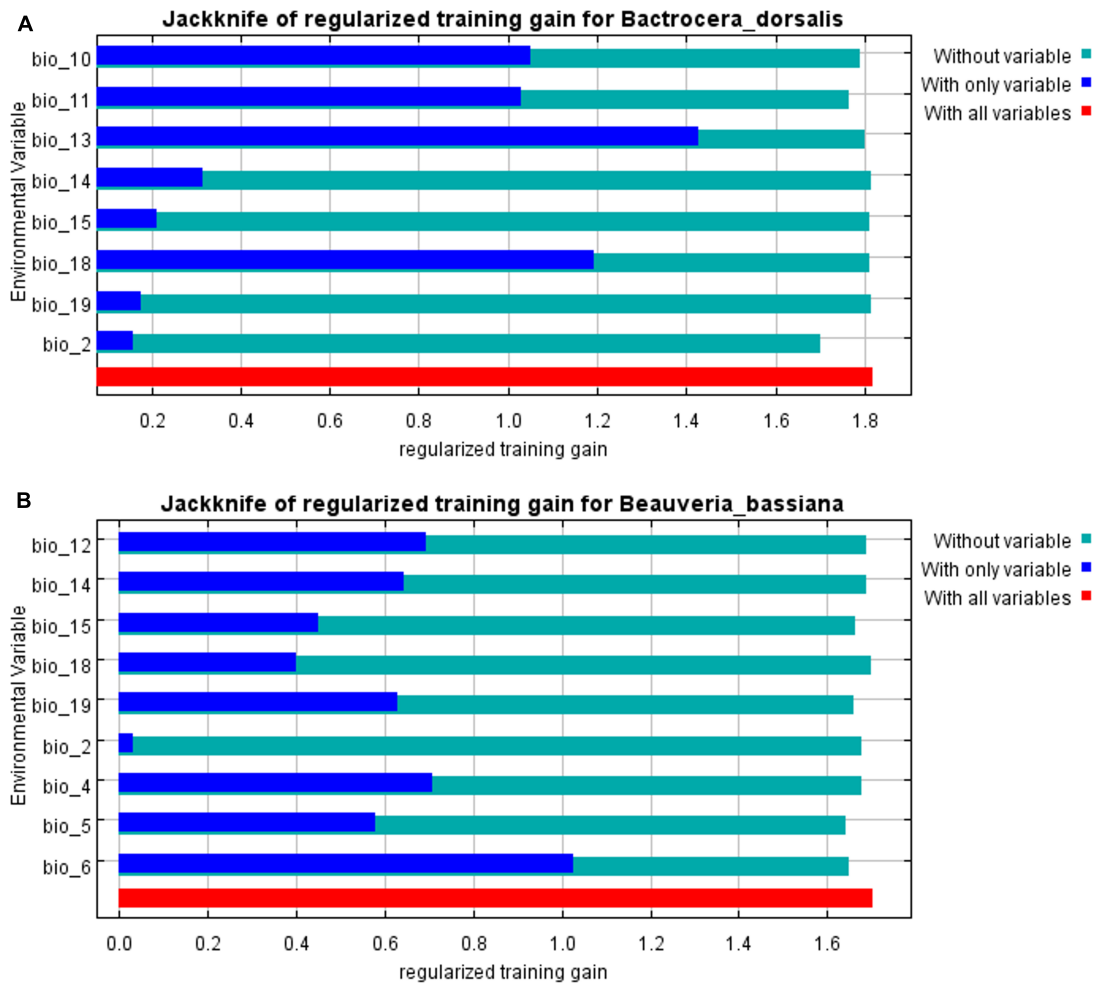


FIGURE 2 The results of the Jackknife test of *Beauveria bassiana* and its host. (A) Jackknife test of *Bactrocera dorsalis* (Hendel). (B) Jackknife test of *Beauveria bassiana*.

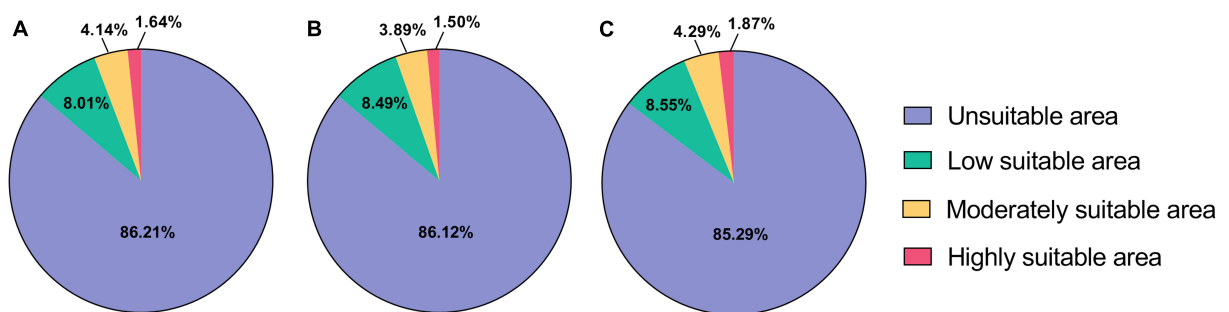


FIGURE 3 Distribution of predicted suitable areas of *Beauveria bassiana*. (A) Suitable areas of *Beauveria bassiana* under current climatic conditions. (B) Suitable areas of *Beauveria bassiana* under RCP2.6 climatic conditions. (C) Suitable areas of *Beauveria bassiana* under RCP8.5 climatic conditions.

B. dorsalis (Hendel), which provides the conditions for the use of *B. bassiana* to control of *B. dorsalis* (Hendel) in all areas. The prediction results showed that Bio6 (Lowest temperature in the coldest month) and Bio12 (Average annual precipitation) have a total contribution rate of 65.3%, which indicates that low temperature and annual precipitation have decisive effects on the survival of *B. bassiana* (Figure 2).

Changes in the suitable areas of both under future climate conditions

Based on environmental data from two future GHG emission scenarios, the results of this study predicted the suitable areas of *B. bassiana*, and the results are shown in the following figure (Figure 3). The results show that the total area of the habitat of *B. bassiana* increases under the two scenarios, RCP2.6 and RCP8.5. However, under RCP2.6, the moderate and high suitable areas of *B. bassiana* decreased, and the decrease of suitable areas of *B. bassiana* was less than the change of suitable areas of *B. dorsalis* (Hendel), indicating that *B. bassiana* is more adaptable to its environment than *B. dorsalis* (Hendel). In the RCP8.5 scenario, there is a more significant increase in the size of the *B. bassiana* suitable areas, with an additional area of 1.33×10^6 km², when compared with the predicted *B. bassiana* suitable areas map for the current climate scenario, shows an expansion of the *B. bassiana* suitable areas from near the equator to higher latitudes, suggesting that climate change is causing the higher latitude environment to reach a level of suitable for the fungus. This indicates that climate change is causing the environment at higher latitudes to meet the conditions suitable for the fungus to live, and *B. bassiana* spores can germinate and grow in these areas. Under the RCP8.5 climate scenario, there is a trend toward a reduction in the size of the habitat for the *B. dorsalis* (Hendel), which will help to control the damage and spread of the *B. dorsalis* (Hendel).

Discussion

In recent years, a large amount of GHG emissions into the atmosphere have led to the rise of the global average temperatures, which creates conditions for the invasion and expansion of pests (Boggs, 2016; Marshall et al., 2020; Colares et al., 2021). Due to global climate change, these threats may increase in many countries located in tropical areas (Ou et al., 2021). This finding is consistent with our prediction of the distribution of the suitable areas of the *B. dorsalis* (Hendel) under the current climate conditions. MaxEnt is a correlation model, which generates predictions according to the statistical

relationships between occurrence patterns and environmental data (Soares et al., 2021).

It has been found that these two models may produce different results due to different spatial resolutions and bioclimatic variables (Stephens et al., 2007; De Villiers et al., 2015). SDMs can predict the changes in the potential habitat of a known geographical distribution species over time through climate changes, thus guiding pest control. The three most commonly used SDMs are CLIMEX, DIVA-GIS, and MaxEnt. They operate according to different principles and require different data (Gonzalez et al., 2016; Rana et al., 2017; Wang et al., 2019). In this study, we tried to use only a small part of geographical data about the historical position of the *B. dorsalis* (Hendel) to predict the potential range of *B. dorsalis* (Hendel), and obtained results highly similar to the original result, indicating a situation with only a small amount of data, the MaxEnt model can also accurately predict insect range (Sultana et al., 2017). The predicted results were compared with the suitable areas for *B. dorsalis* (Hendel) under the same climate scenario, and it was found that the suitable areas for *B. bassiana* and *B. dorsalis* (Hendel) overlap greatly, and the suitable areas for *B. dorsalis* (Hendel) *B. bassiana* is much larger than *B. dorsalis* (Hendel), suggesting that *B. bassiana* can adapt to more environmental types than *B. dorsalis* (Hendel). In this study, it was found that in Asia, where *B. dorsalis* (Hendel) is highly suitable for living, is not the high suitable area for *B. bassiana*. It may be because the high temperatures in these areas hinder the normal germination of *B. bassiana* spores, and thus preventing them from surviving in this area. There is a large area of high suitable areas for *B. bassiana* with high adaptability in high latitudes of in Europe, which indicates that the temperatures in these areas are more suitable for growth and spore germination of *B. bassiana*. In conclusion, the current and future climate conditions are suitable for the normal survival of *B. dorsalis* (Hendel), and also for the survival of *B. bassiana*, which indicates that *B. bassiana* can adapt to the environment better than *B. dorsalis* (Hendel).

In the ecosystems, the degree to which pest populations is controlled or regulated by natural enemies depends on their ability to adapt to the local environment. An important step to successfully introduce natural enemy is to evaluate their suitable areas (Fargues et al., 1997; Uma Devi et al., 2008; Amobonye et al., 2020). In addition to climatic variables, factors that limit the potential geographical distribution of pathogenic fungi include host, species competition, natural enemies, soil type, geographical features, natural, and geographical obstacles and human activities (Kannan and Rao, 2006; Cheng et al., 2017; Zhang et al., 2018; Clarke et al., 2019). Relevant research shows that *B. bassiana* is the most widespread pathogenic fungus in agricultural land, and it can easily colonize in different plant

hosts, such as corn, wheat, tobacco, and melon (Greenfield et al., 2016; Mckinnon et al., 2018; Mahmood et al., 2019). The above studies show that *B. bassiana* can colonize on the leaves of many plants. Combined with the purpose of this research, it is possible to control *B. dorsalis* (Hendel) by inoculating *B. bassiana* on plant leaves.

In this paper, *B. dorsalis* (Hendel) was used as the host of *B. bassiana* to study the suitable areas of *B. bassiana*. The results show that the area of the habitat of *B. dorsalis* (Hendel) increases by 3.31×10^5 km² by 2,050 under the RCP2.6 scenario, and increases by 7.92×10^5 km² under the RCP8.5 scenario. When studying the impact of climate change on the potential global geographical distribution of the *B. dorsalis* (Hendel), it was found that under future climate conditions, the suitable area of *B. dorsalis* (Hendel) in the northern hemisphere is expected to expand northward, and the suitable area in the southern hemisphere is expected to expand southward (Qin et al., 2019). Under the RCP8.5 scenario, both the suitable area and habitat suitability of *B. dorsalis* (Hendel) are projected to increase, with the climatically suitable area in North America projected to increase by 1.52×10^5 km² in 2,050. The above conclusions are consistent with the findings of this paper, and the differences of suitable regional changes may be caused by the selection of bioclimatic variables and data processing methods. We also found that in the prediction results, the distribution probability of *B. dorsalis* (Hendel) reached a peak when Bio13 (Precipitation in the wettest month) was around 1,200 mm, and that of *B. bassiana* reached a peak when Bio12 (Average annual precipitation) was at 7,000–8,000 mm. This shows that *B. bassiana* has a great demand for precipitation, which will increase the difficulty of using *B. bassiana* to control *B. dorsalis* (Hendel) in arid areas.

In this study, the potential distribution areas of *B. bassiana* and *B. dorsalis* (Hendel) were predicted by using the MaxEnt model, and the expected results were achieved. However, the model can't combine the data of the two species' bioclimatic variable for statistical analysis, and the final result is slightly different from the actual result, which is also the place where the model needs to be optimized.

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Data availability statement

The original contributions presented in this study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

AW, SP, YL, XY, and SZ participated in the study design and analysis of the manuscript. JJ, JL, SY, and RZ participated in the study design and helped to draft the manuscript. Supervision and financial support by SZ, revised and processed. All authors have read and approved the final manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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