RESEARCH ARTICLE





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Current and future global distribution of the peach twig borer, Anarsia lineatella Zeller (Lepidoptera: Gelechiidae)

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Abstract

- Biological invasions and climate change are key drivers of biodiversity redistribution, leading to severe environmental, economic, and public health consequences.
 This issue is particularly problematic for insect pests, which often expand their distribution via transportation with commodities. The peach twig borer, Anarsia lineatella Zeller, exemplifies an agricultural pest with a primarily restricted distribution that expanded its range to other regions.
- 2. This study used species distribution modelling to predict the distribution of *A. lineatella* under current and future climate conditions. The model was developed using the Maxent algorithm, following best practices and recommendations for species distribution modelling.
- 3. The optimized model exhibited strong statistical performance, effectively identifying suitable areas for the species (TSS = 0.76, AUC = 0.91; CBI = 0.89). It predicted suitable areas beyond the pest's current distribution, encompassing countries in the Neotropical region, northern and sub-Saharan Africa, northeastern Asia, and southeastern and southwestern Australia. Under climate change scenarios, the model projected an expansion of A. lineatella's range, especially under the high greenhouse gas emissions scenario (SSP5-8.5) for 2041 to 2060. In this scenario, the model estimated an increase of up to 14% in areas classified as optimal and 52% in areas with a high probability of occurrence, with the expansion primarily concentrated in eastern Europe.
- 4. The results provide valuable insights into the potential distribution of A. lineatella, aiding in the prioritisation of regions for monitoring and adopting preventive measures against this pest.

KEYWORDS

biological invasion, climate change, ecological niche model, insect pests, Maxent

INTRODUCTION

Climate change and biological invasions are interconnected global concerns (Gentili et al., 2021). Projections indicate a global average temperature increase between 1.8 and 4°C by the end of this century,

alongside significant forecasted changes in precipitation patterns worldwide (Skendžić et al., 2021). Climate change and globalization are causing the global redistribution of species, with severe consequences for human well-being (Pecl et al., 2017). Similarly, biological invasions profoundly affect biodiversity, ecosystem services, human

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health, and the economy (Klem & Zaspel, 2019; Mooney & Cleland, 2001; Pejchar & Mooney, 2009; Vilà et al., 2011). Over the past 50 years, studies have revealed that invasive alien species have caused damages totaling at least US\$1.288 trillion, with costs steadily increasing (Diagne et al., 2021). Moreover, these estimates likely underestimate the true economic impact, as data are available for only about 10 percent of known invasive species (Zenni et al., 2021). Given this context, mapping the current suitable areas for invasive alien species and projecting their future distribution is critical for developing effective management strategies.

Insects are among the taxa that have undergone an increasing number of invasions in recent centuries, often spreading beyond their native continents (Seebens et al., 2017). Likewise, several species have expanded their distribution in response to climate change (Hulme, 2017: Taheri et al., 2021). Agricultural pests, in particular, benefit from this phenomenon, as they can hitch rides with trade commodities and exploit abundant food resources in cultivated areas (Guillemaud et al., 2011). The peach twig borer, Anarsia lineatella Zeller (Lepidoptera: Gelechiidae), is an example of an agricultural pest that has successfully invaded continents beyond its native range. Originating from the Mediterranean region, this species has spread to most parts of Europe, Asia, and the United States (Jones, 1935). Its larvae feed primarily on peaches and other cultivated stone fruits such almonds, apricots, apples, and nectarines (Sorenson & Gunnel, 1955). During the larval stage, the peach twig borer feeds on petals and causes significant damage by penetrating ovaries. When fruits are available, larvae burrow into fruit, create internal galleries that cause premature fruit drop, and render fruit unsuitable for consumption or marketing (Mamay et al., 2014). Losses attributed to A. lineatella can vary from 5% to 29%, depending on population levels and the host plant (Damos & Savopoulou-Soultani, 2008; Mamay et al., 2014). Furthermore, fruits showing signs of pest infestation may encounter trade restrictions and rejections in export markets, adversely impacting the agricultural economies of regions heavily reliant on fresh produce exports.

Species distribution models (SDMs) are important tools for supporting and guiding the development and implementation of environmental and phytosanitary policies and management programmes (Addison et al., 2013; Martin et al., 2020; Mukherjee et al., 2021; Schuwirth et al., 2019). These models are typically classified as either correlative or mechanistic. Correlative models relate data from the geographic coordinates of a species' presence/absence (or pseudoabsence, or background samples) to environmental variables to identify habitats that may be suitable for the species (Elith et al., 2011). When only presence records are available, the maximum entropy algorithm (Maxent) is a widely used approach for identifying suitable areas. This machine-learning algorithm is recognised for its strong statistical performance and its ability to outperform other presence-only modelling methods (Elith et al., 2011, 2006; Venette, 2017). Furthermore, models developed based on current climate conditions can be projected onto future climate conditions using different greenhouse gas emissions scenarios from the Sixth Assessment Report of the Intergovernmental Panel for Climate Change (IPCC).

A regional study conducted in California, USA, suggests that climate change is likely to significantly impact the population dynamics and abundance of the peach twig borer in the future (Jha et al., 2024). However, no research to date has assessed the potential effect of climate change on the global suitable range for A. lineatella. Given the critical role of climate in shaping species distributions, the increasing occurrence of biological invasion events involving agricultural pests, and the economic importance of A. lineatella as a pest of several cash crops, this study aimed to identify climatically suitable areas for the peach twig borer under current and future climate change scenarios. The projections considered different climate change scenarios, ranging from a sustainable pathway to a fossil fuel-dependent development. The information generated by the study provides insights into potential changes in suitable areas for the establishment of A. lineatella under climate change, thereby offering a basis for controlling its spread.

MATERIALS AND METHODS

Occurrence data

The occurrence data for A. *lineatella* was obtained from the Global Biodiversity Information Facility (GBIF, 2024) database using the *rgbif* R package version 3.8.0 (Chamberlain et al., 2023). The following procedures were used to clean the occurrence data (Hijmans & Elith, 2013; Ribeiro et al., 2023; Zizka et al., 2019): (i) only records with a spatial resolution ≤1 km were retained for analysis; (ii) occurrence records within a radius of 10 km around the centres of capital cities and 5 km around the centres of countries, states, provinces, or municipalities were removed; (iii) occurrences with the same absolute longitude and latitude, within a radius of 0.5° around the GBIF headquarters, and duplicate coordinates were also removed; and (iv) occurrence records located in water or not associated with environmental variables were removed (Amaro et al., 2025).

Sampling bias is an important factor affecting the performance of presence-background models such as Maxent (Barber et al., 2022; Schartel & Cao, 2024). To address this issue, an environmental filter (Velazco et al., 2022) was applied to reduce sampling bias. Recognising that environmental filters are typically sensitive to bin size, four bin sizes were tested (4, 6, 8, and 10). The process began with the construction of a regular multidimensional grid in environmental space, defined by the selected environmental variables. The grid's cell size depended on the number of bins, which partitioned the variable range into interval classes (Castellanos et al., 2019; Varela et al., 2014). For each bin size, the approach proposed by Velazco et al. (2021), selecting filtered occurrences based on the number of records and spatial autocorrelation, was applied. Finally, a single occurrence was randomly selected within each grid cell.

Occurrence data were partitioned to assess model performance using a spatial block cross-validation approach, as this method allows control for potential spatial autocorrelation between the model training and test data and is recommended for assessing its transferability across space and time (Roberts et al., 2017; Santini et al., 2021; Valavi et al., 2019). Thirty grids were generated with resolutions ranging

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from 0.5° (\sim 56 km) to 5° (\sim 557 km) to select the best grid size, in four partitions, with at least five occurrence records per partition. Eighty percent of the occurrences were used for the autocorrelation test, selecting the grid size with (i) the lowest spatial autocorrelation according to Moran's I; (ii) the maximum environmental similarity based on the Euclidean distance; and (iii) the minimum difference in the number of records between training and test data, indicated by the standard deviation (Velazco et al., 2019), using the part_sblock function from the *flexsdm* R package (Velazco et al., 2022).

Environmental data

To represent current climate conditions, a set of 19 bioclimatic variables derived from monthly temperature and precipitation data for the years 1970 to 2000 was obtained from the Worldclim database version 2.1 (Fick & Hijmans, 2017), with an average spatial resolution of 2.5 min (~4.6 km at the equator) (Hijmans et al., 2023). This climate dataset was chosen because it captures the annual variability and limiting factors that are known to influence the geographic distribution of species (O'Donnel & Ignizio, 2012). In addition to the bioclimate variables, an elevation variable derived from the Shuttle Radar Topography Mission (SRTM) and supplemented with USGS 30 arc-second Global Elevation Data (GTOPO30) data was used.

The same bioclimate variables were obtained for the periods 2021–2040 and 2041–2060 and for different climate change scenarios representing low (SSP1-2.6), medium (SSP2-4.5), and high (SSP5-8.5) greenhouse gas emissions from Coupled Model Intercomparison Projections (CMIP) 6 in the Worldclim 2.1 database. Three General Circulation Models (GCM) were used: (i) MRI-ESM2-0 (Yukimoto et al., 2019), (ii) MIROC6 (Shiogama et al., 2019), and (iii) MPI-ESM1-2-HR (von Storch et al., 2017). Average projections were calculated for each period and climate change scenario.

Background selection

The accessible area approach was used to define the calibration area (CA) for A. lineatella. This is an important step in the modelling process because the size of the calibration area affects the performance metrics of the models (Amaro et al., 2023; Anderson & Raza, 2010; Barbet-Massin et al., 2012). In this study, the Köppen-Geiger climate zones with at least one occurrence record were used to delimit the CA (Brunel et al., 2010; Datta et al., 2019; Hill et al., 2017; Hill & Terblanche, 2014; Marchioro, 2016; Webber et al., 2011). Both native and invasive occurrence records were used to delimit the CA (Beaumont et al., 2009; Broennimann & Guisan, 2008; Zhang et al., 2020), considering that the species may undergo a climatic niche shift during the invasion process.

Presence-background-based distribution models, such as Maxent, estimate the relative probability of presence by comparing occurrence sites to a background (an environmental context) consisting of all the

sites in the calibration area (Halvorsen et al., 2015; Phillips & Elith, 2013). Ideally, the background samples should reflect the environmental conditions that contrast with the species occurrences (Saupe et al., 2012). Therefore, 10,000 points were randomly selected throughout the calibration area (Barbet-Massin et al., 2012; Phillips & Dudík, 2008), equally stratified to the presence points in each partition (Hirzel & Guisan, 2002).

Model development

All procedures relating to data processing, model development, and creation of maps and graphs were carried out using the R environment, version 4.4.0 (R Core Team, 2023), in a fully automated framework, developed based on best practices and recommendations relating to species distribution modelling with Maxent (Araújo et al., 2019; Jarnevich et al., 2015; Low et al., 2021; Merow et al., 2013; Rojas-Soto et al., 2024; Santini et al., 2021; Sillero, 2011; Sillero & Barbosa, 2021; Srivastava et al., 2021). The maximum entropy model (Maxent) was used through an inhomogeneous Poisson point process (Phillips, 2008, 2017; Phillips et al., 2006, 2017; Renner et al., 2015; Renner & Warton, 2013) because this method is one of the most widely used to model species distributions and has shown good performance compared to other algorithms (Elith et al., 2006, 2011; Heikkinen et al., 2012; Helmstetter et al., 2021; Hijmans, 2012; Valavi et al., 2022; Venette, 2017).

Two main parameters adjusted in Maxent significantly affect model complexity and performance: (i) the regularization multiplier (RM), and (ii) the feature classes (FC) (Elith et al., 2011; Merow et al., 2013). The RM determines penalties for including variables or their transformations (features) in the model. Higher RM values impose a stronger penalty on model complexity, resulting in simpler (flatter) forecasts. FCs are transformations of the original predictor variables and shape the potential marginal response curves. A model that includes only linear features is likely to be simpler than one that incorporates all possible features (Elith et al., 2010). In Maxent, FCs used to build the model can be linear (L), quadratic (Q), threshold (T), hinge (H), product (P), and categorical (Merow et al., 2013). Hinge features often make linear and threshold features redundant. To obtain a relatively smoother fitted model, similar to a GAM (generalized additive model), using only hinge features is recommended (Elith et al., 2010, 2011). Excluding product features results in an additive model that is easier to interpret, although less capable of representing complex interactions (Elith et al., 2011).

In this study, the Maxent model was implemented using a 4-fold cross-validation approach with RM set to 1 and FC set to LQHP, which are the default settings in Maxent. The selection of the most important uncorrelated variables for A. lineatella was conducted using a data-driven approach. Initially, a model was constructed using the species occurrence records along with all the predictor variables. From this base model, an iterative process was carried out, starting with the variable with the highest permutation importance. If a variable was found to be correlated with others (Sperman rank coefficient > |0.7|),

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a jackknife test was performed. The variable that caused the least decrease in model performance, measured by the True Skill Statistics metric (TSS) (Allouche et al., 2006), when removed, was excluded from the analysis. This process was repeated until only uncorrelated variables remained (Vignali et al., 2020). To optimise the model's parsimony, the largest number of variables was removed without affecting model performance using the jackknife test and the TSS metric. Only variables with permutation importance greater than 3% were kept in the analysis.

Previous research suggests that different combinations of FC and RM should be tested to determine the best settings for the species under study (Merow et al., 2013; Moreno-Amat et al., 2015; Radosavljevic & Anderson, 2014; Syfert et al., 2013). Therefore, the final model was defined by fine-tuning 171 models consisting of nine FCs ('L', 'Q', 'H', 'LQ', 'QH', 'LQH', 'LQP', 'QHP', 'LQHP') and 19 RM values ranging from 0.5 to 5, with increments of 0.25 using the *flexsdm* package (Velazco et al., 2022). The TSS was used to select the best combination of FCs and RMs. The permutation importance of the variables for the final model was estimated using the varImportance function from the *fitMaxnet* package (Wilson, 2024).

The performance of the final model was assessed using multiple evaluation metrics, including both threshold-dependent and -independent metrics, as recommended in the literature (Konowalik & Nosol, 2021; Sofaer et al., 2019). Threshold-dependent metrics include the True Positive Rate (TPR) (Elith et al., 2006; Fielding & Bell, 1997; Liu et al., 2013), True Negative Rate (TNR) (Fawcett, 2006; Hanley & McNeil, 1982), and TSS (Fawcett, 2006; Hanley & McNeil, 1982). Threshold-independent metrics include the area under the curve of the receiver operating characteristic (AUC) and the Continuous Boyce Index (CBI) (Boyce et al., 2002). TPR and TNR assess the model's ability to accurately identify true positives and true negatives, respectively, while TSS combines both metrics to evaluate the model's overall discriminatory capacity. In contrast, AUC and CBI assess the model's ability to discriminate between observed presences and background locations.

The final model was projected on a global scale and across different time periods and climate change scenarios evaluated. Maxent generates a probability of occurrence map with values ranging from 0 to 1. This map was divided into five fixed probability classes representing (i) inadequate conditions (0-0.1); (ii) marginal conditions (0.1-0.2); (iii) moderate conditions (0.2-0.5); (iv) optimal conditions (0.5-0.8); and (v) high probability of occurrence (0.8-1). The area of each class was estimated and used as a reference to assess the effect of climate change on the distribution of A. lineatella. For environmental management and phytosanitary policy applications, suitability was also represented as presence/absence (Liu et al., 2013). A binary map was generated by applying a threshold that maximises the sum of sensitivity (true positive rate) and specificity (true negative rate) (Liu et al., 2005, 2016). In addition, binary maps were created with the Minimum Training Presence (MTP) and 10th Percentile Training Presence (10TP) thresholds. MTP represents the minimum environmental suitability considered sufficient for the species to occur (marginal conditions), while 10TP considers only the top 90% of the presence

points as suitable, thereby reducing the inclusion of marginal conditions.

RESULTS

Model performance and variable importance

A total of 389 occurrences were collected from the GBIF database. After the data-cleaning and filtering processes, 150 occurrences remained: nine in the native range and 141 in the invaded range (Figure 1). The data-driven variable selection process resulted in six variables used in the model development (Appendix S1). The optimal model for A. *lineatella* incorporated quadratic, hinge, and product feature classes with a regularization multiplier of 0.5 (QHP0.5) and demonstrated strong performance across commonly used metrics (Appendix S1). The selected model showed good discriminatory ability, as demonstrated by both threshold-dependent (TSS = 0.812) and threshold-independent metrics (AUC = 0.915; CBI = 0.893). This result was confirmed when considering the partial AUC (Jiang et al., 1996; McClish, 1989) (Appendix S1).

According to the permutation importance, four out of the six variables were important for the optimal model: mean temperature of warmest quarter (Bio10–54.0%), precipitation of coldest quarter (Bio19–21.3%), precipitation seasonality (Bio15–11.7%), and mean diurnal range (Bio02–6.9%), respectively (Figure 2). Individual marginal response curves for the most important variables show that the probability of occurrence of A. *lineatella* follows a sine curve for Bio10 and Bio19. The curves indicate a high probability of occurrence in regions with an average temperature of the warmest quarter around 22°C and precipitation of the coldest quarter around 268 mm (Figure 3). In contrast, the probability of occurrence decreases as the precipitation seasonality and mean diurnal range increase (Figure 3).

Distribution of A. lineatella under current climate conditions

The optimal model predicted high-probability areas for the occurrence of *A. lineatella* in southern and western Europe, the entire southern coast of the Black Sea, the Himalayas, southern China near the border with Vietnam, parts of South Korea and Japan, as well as isolated areas in the United States (Figure 4a). The map depicting the specified probability classes and the estimate of the corresponding areas indicates that environments with a high probability of *A. lineatella* occurrence cover 1,952,031 km², while those with an optimal probability cover 4,181,620 km² (Figure 4b).

When considering marginal climatic conditions (Figure 4c), much of the world was predicted to be suitable for *A. lineatella*, except for extremely dry and cold regions. Conversely, the binary map generated by excluding marginal environments restricted the predictions of suitable areas to Europe, some regions in sub-Saharan Africa, the northeastern and western United States, and isolated areas in eastern

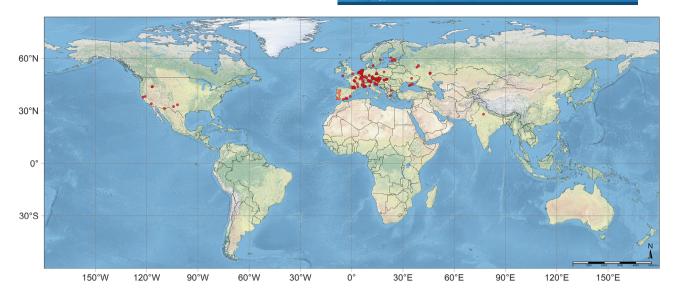


FIGURE 1 Global distribution of *Anarsia lineatella* based on occurrence records collected from the Global Biodiversity Information Facility (GBIF, 2024). *Anarsia lineatella* is native to Portugal; all other records represent invaded regions.

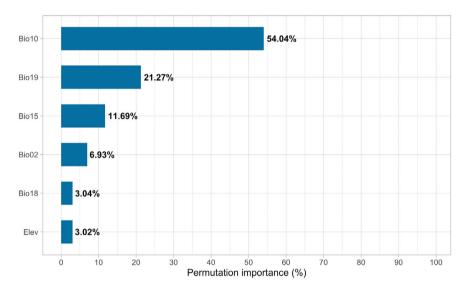


FIGURE 2 Percentage of permutation importance for variables in the highest performing Maxent model developed for Anarsia lineatella. Variables are Bio2, mean diurnal range (°C); Bio10, mean temperature of warmest quarter (°C); Bio15, precipitation seasonality (mm); Bio18, precipitation of warmest quarter (mm); Bio19, precipitation of coldest quarter (mm); Elev, elevation (m).

South America (Figure 4c). This result was quite similar to that obtained using a threshold that maximises the sum of sensitivity and specificity (estimated at 0.3312) (Figure 4d).

Predicted distribution under climate change

A comparison between the predicted current and future distributions of *A. lineatella* shows an increase in suitability as a result of climate change (Figure 5, Appendix S1). This increase was more pronounced in the 2021 to 2040 (Appendix S1) and 2041 to 2060 periods under the SSP5-8.5 scenario, representing high increases in greenhouse gas

emissions. The projected expansion in suitable areas primarily encompasses Europe and North America. In Europe, most of the areas with increased suitability are in the northern and eastern regions. In North America, these areas mainly include an expansion to the northern regions, including Canada.

The general increase in suitability is confirmed when the probability classes are considered in defining the distribution shifts due to climate change (Table 1). The model predictions indicate a decrease in areas unsuitable for A. *lineatella* and an increase in the percentage of areas classified as optimal and moderate for the species. Supporting the results observed in the maps, the largest increase relates to an estimated average rise of 52% in areas with a high probability of

FIGURE 3 Individual response curves (left) with residuals (light green dots) and frequency histograms (in light blue), and density curves (left, in orange) with average values (dashed lines), from the optimal Maxent model for *Anarsia lineatella*.

occurrence under the SSP5-8.5 for the period 2041 to 2060. The second largest average for the same probability class (43%) was predicted under the SSP2-4.5 scenario for the same period. Interestingly, for

0.00

most of the time periods and climate change scenarios studied, a decrease in areas classified as moderately suitable for the species was also observed. The exception is the period 2041 to 2060 under the

10 Mean Diurnal Range

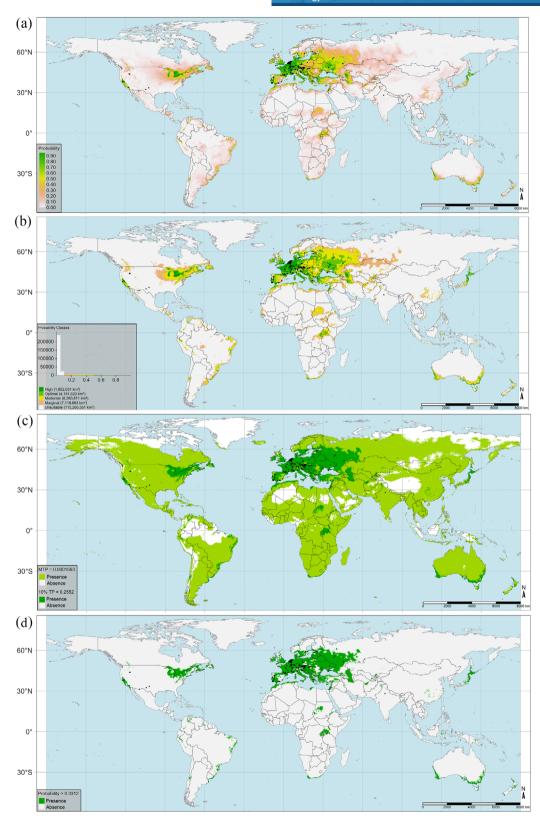


FIGURE 4 Predicted global distribution under current climate conditions and observed occurrences for *Anarsia lineatella*: (a) shows the continuous probability of occurrence generated by Maxent, (b) shows the probability classes for unsuitable conditions, marginal, moderate, optimal, and high probability of occurrence, (c) show the map created with the thresholds Minimum Training Presence (MTP) (dark green), and 10th Percentile Training Presence (10TP) (light green), and (d) depicts a binary map created using a threshold that maximizes the sum of sensitivity and specificity.

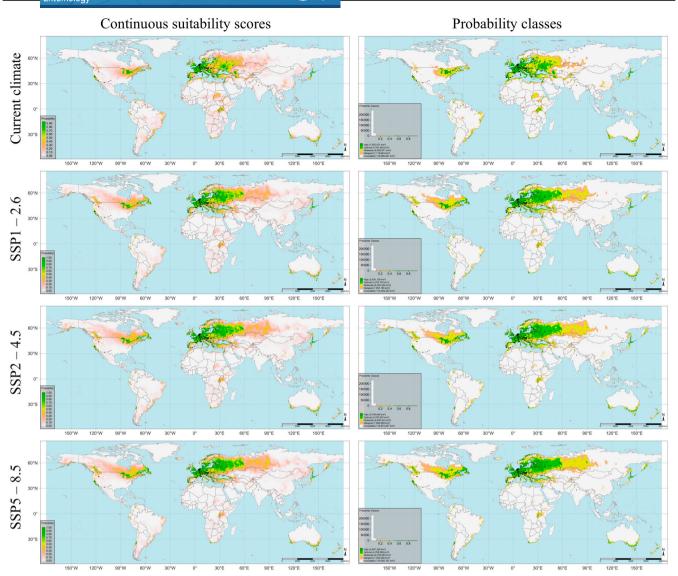


FIGURE 5 Predicted distribution for Anarsia lineatella under current and future climate conditions for different climate change scenarios by 2060 (2041–2060), expressed by continuous probability and probability classes.

SSP5-8.5 scenario, where an increase in the areas classified as suitable was predicted for all classes.

DISCUSSION

In this study, we developed a Maxent model to predict globally suitable areas for A. *lineatella*, an important pest of stone fruits in Europe and the United States. Using a fully automated framework based on best practices and recommendations for species distribution modelling with Maxent (Araújo et al., 2019; Jarnevich et al., 2015; Low et al., 2021; Merow et al., 2013; Rojas-Soto et al., 2024; Santini et al., 2021; Sillero, 2011; Sillero & Barbosa, 2021; Srivastava et al., 2021), we generated an optimised model. This model demonstrated strong discrimination of suitable areas for A. *lineatella*, as confirmed by all threshold-dependent and -independent performance metrics.

In addition to statistical performance, the reliability of model predictions depends on their ability to describe the species' ecology. In this study, four of the six variables used in the modelling process contributed most to the model, as assessed by the permutation importance: mean temperature of the warmest quarter, precipitation of the coldest quarter, precipitation seasonality, and mean diurnal range. The response curves for each of these variables indicate a species adapted to temperate continental and subtropical climates. For example, a high probability of presence was observed in regions where the mean temperature of the warmest quarter is around 22°C, a characteristic of humid continental climates with hot summers, such as those found in parts of Europe and the northeastern United States (Peel et al., 2007). In most of these regions, precipitation is well distributed throughout the year (Ahrens & Henson, 2015), which may explain the decrease in the probability of occurrence with increasing precipitation seasonality. Further evidence of the model's accuracy in capturing the

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TABLE 1 Estimated areas (km²) and percentage change for the probability classes and climate scenarios studied, according to the optimal Maxent model developed for *Anarsia lineatella*.

	Estimated area (km²)					Percent change				
Climate	Unsuitable	Marginal	Moderated	Optimal	High	Unsuitable	Marginal	Moderated	Optimal	High
Currently (1991-2020)	115,266,561	7,119,663	8,260,871	4,181,620	1,952,031	0.00%	0.00%	0.00%	0.00%	0.00%
CMIP6 MIROC6 SSP126 (2021-2040)	114,408,374	7,774,619	7,559,599	4,732,227	2,305,926	-0.74%	9.20%	-8.49%	13.17%	18.13%
CMIP6 MRI-ESM2-0 SSP126 (2021-2040)	113,798,778	7,818,076	7,886,090	4,914,195	2,363,606	-1.27%	9.81%	-4.54%	17.52%	21.08%
CMIP6 CMCC-ESM2 SSP126 (2021-2040)	114,503,552	8,067,591	7,306,153	4,627,147	2,276,302	-0.66%	13.31%	-11.56%	10.65%	16.61%
CMIP6 Mean SSP126 (2021- 2040)	114,165,430	7,908,052	7,679,262	4,774,135	2,253,867	-0.96%	11.07%	-7.04%	14.17%	15.46%
CMIP6 MIROC6 SSP126 (2041-2060)	114,293,587	7,585,651	7,869,876	4,666,296	2,365,336	-0.84%	6.55%	-4.73%	11.59%	21.17%
CMIP6 MRI-ESM2-0 SSP126 (2041-2060)	113,839,539	7,683,374	8,000,220	4,908,761	2,348,852	-1.24%	7.92%	-3.16%	17.39%	20.33%
CMIP6 CMCC-ESM2 SSP126 (2041-2060)	112,516,303	8,073,530	8,689,436	4,762,958	2,738,520	-2.39%	13.40%	5.19%	13.90%	40.29%
CMIP6 Mean SSP126 (2041- 2060)	113,439,253	7,891,185	8,262,426	4,767,742	2,420,139	-1.59%	10.84%	0.02%	14.02%	23.98%
CMIP6 MIROC6 SSP245 (2021-2040)	114,402,363	7,669,127	7,528,285	4,770,507	2,410,464	-0.75%	7.72%	-8.87%	14.08%	23.48%
CMIP6 MRI-ESM2-0 SSP245 (2021-2040)	113,911,988	7,686,501	7,765,112	4,970,247	2,446,898	-1.18%	7.96%	-6.00%	18.86%	25.35%
CMIP6 CMCC-ESM2 SSP245 (2021-2040)	114,379,022	7,691,945	7,585,122	4,804,061	2,320,596	-0.77%	8.04%	-8.18%	14.89%	18.88%
CMIP6 Mean SSP245 (2021- 2040)	114,107,594	7,765,311	7,697,258	4,885,353	2,325,229	-1.01%	9.07%	-6.82%	16.83%	19.12%
CMIP6 MIROC6 SSP245 (2041-2060)	114,192,992	7,308,042	7,935,268	4,727,571	2,616,872	-0.93%	2.65%	-3.94%	13.06%	34.06%
CMIP6 MRI-ESM2-0 SSP245 (2041-2060)	113,455,625	7,279,836	8,497,173	4,893,541	2,654,571	-1.57%	2.25%	2.86%	17.03%	35.99%
CMIP6 CMCC-ESM2 SSP245 (2041-2060)	111,459,093	7,877,737	9,303,878	4,855,483	3,284,556	-3.30%	10.65%	12.63%	16.11%	68.26%
CMIP6 Mean SSP245 (2041- 2060)	112,875,297	7,666,689	8,655,432	4,787,637	2,795,690	-2.07%	7.68%	4.78%	14.49%	43.22%
CMIP6 MIROC6 SSP585 (2021-2040)	114,513,913	7,615,210	7,477,437	4,716,105	2,458,081	-0.65%	6.96%	-9.48%	12.78%	25.92%
CMIP6 MRI-ESM2-0 SSP585 (2021-2040)	113,865,709	7,615,459	7,913,261	4,811,263	2,575,054	-1.22%	6.96%	-4.21%	15.06%	31.92%
CMIP6 CMCC-ESM2 SSP585 (2021-2040)	114,232,834	7,931,130	7,627,445	4,764,806	2,224,531	-0.90%	11.40%	-7.67%	13.95%	13.96%
CMIP6 Mean SSP585 (2021- 2040)	114,037,019	7,818,126	7,773,666	4,817,996	2,333,939	-1.07%	9.81%	-5.90%	15.22%	19.56%
CMIP6 MIROC6 SSP585 (2041-2060)	113,898,931	7,039,288	8,351,595	4,555,022	2,935,910	-1.19%	-1.13%	1.10%	8.93%	50.40%
CMIP6 MRI-ESM2-0 SSP585 (2041-2060)	113,047,469	6,923,291	8,598,044	5,063,002	3,148,939	-1.93%	-2.76%	4.08%	21.08%	61.32%
CMIP6 CMCC-ESM2 SSP585 (2041-2060)	112,486,103	7,489,383	9,060,924	4,684,408	3,059,928	-2.41%	5.19%	9.68%	12.02%	56.76%
CMIP6 Mean SSP585 (2041-2060)	113,005,131	7,250,008	8,789,989	4,768,289	2,967,328	-1.96%	1.83%	6.41%	14.03%	52.01%

species' ecology is its ability to predict the currently known distribution of the species in both its native and invaded range, as demonstrated in this study.

Although several regions of the world have favourable conditions for the occurrence of A. *lineatella*, its distribution remains largely restricted to Europe and North America (Figure 1). Factors that may explain this limited distribution include effective border protection systems and the absence of host plants, preventing the establishment of A. *lineatella* in new areas. Interestingly, A. *lineatella* possesses several traits commonly associated with invasiveness. For example, an analysis of 113,185 interception records from 52 Lepidoptera families revealed that micromoths, including those of the family Gelechiidae, were underrepresented in interceptions but had a higher rate of establishment as non-native species than their interceptions would suggest (Mally et al., 2023). Additionally, borers and leaf-rollers, which disperse faster than external feeders (Paynter & Bellgard, 2011), are more likely to establish than external feeders (Kimberling, 2004).

The existence of suitable areas outside the current distribution of A. lineatella indicates a potential risk of this species spreading throughout fruit production areas worldwide. In particular, China, Brazil, Republic of Korea, and Russia (FAOSTAT, 2024) are among the main producers of major hosts (peaches, nectarines, and apricots) predicted to be suitable for A. lineatella. Other countries with significant production of almonds (Australia), apples (Russia), and pears (Argentina and Chile) also have suitable conditions for A. lineatella. The suitability map presented here provides initial information for developing phytosanitary measures to prevent the spread of this species. However, further analysis should consider not only habitat suitability but also local or regional production areas of plants used as hosts by A. lineatella, as well as their proximity to ports of entry, to fully understand the invasion risk posed by this pest. The primary routes of introduction for A. lineatella are likely through international trade or travellers carrying infested fruits (Champan et al., 2017). For instance, this species was recently intercepted at the international airport of São Paulo, Brazil, in peaches imported from the United States. This underscores the importance of prioritising phytosanitary measures, especially the surveillance of airports and seaports associated with international trade in countries where A. lineatella is categorised as an absent quarantine pest, such as in Argentina, Brazil, and Chile in South America (IPPC, 2024).

Apart from the accidental introduction of species, climate change is another factor contributing to the observed shifts in species distribution. Empirical evidence of distribution shifts due to climate change is increasing, with significant movement to higher elevations and latitudes for several taxa (Pecl et al., 2017; Rubenstein et al., 2023). In this context, ecological niche models are widely used to anticipate range shifts, especially for economically important species such as insect pests. Several studies projected that many insect pests are expected to increase their distribution (e.g., Chen et al., 2023; Gilioli et al., 2014; Qin et al., 2019), which may have significant implications for risk assessment. Here, our findings suggest a range expansion of A. *lineatella* under climate change, especially in the northern hemisphere. A pronounced increase in the areas classified as optimal and of high probability of occurrence was predicted, particularly in the climate change scenario representing high greenhouse gas emissions.

Most of the expansion in the suitable areas was predicted towards the northern and eastern distribution of *A. lineatella* in Europe and the northern and western direction in the United States. This result suggests that this species may become even more problematic in these regions.

Although a state-of-the-art methodology was used in this study, it is recognised that the model projections may have limitations due to uncertainties related to the nature of invasive species, particularly niche shifts and their ability to adapt to climate changes. A growing body of evidence supports the occurrence of niche shifts during biological invasions of insect pests (e.g., Hill et al., 2017; Marchioro & Krechemer, 2023; Zhou et al., 2023), which may lead to an underestimation of the species ranges if only native occurrences are considered. In this study, this issue was addressed by using occurrence records for both native and invasive ranges. Furthermore, only elevation and climate variables were included in the model. Future studies should consider incorporating non-climatic factors such as biotic interactions, dispersal capacity, likelihood of introduction, and the presence of host plants.

In conclusion, this study developed a Maxent model for A. *lineatella* considering the best recommendations from the literature. The optimized model demonstrated good statistical performance and effectively identified suitable sites for A. *lineatella*. Suitable areas were predicted for this species in continents beyond its current distribution, including host fruit-producing countries such as Argentina, Australia, Brazil, Chile, China, and the Republic of Korea. An increase in the distribution of A. *lineatella* was projected under climate change, with a more pronounced expansion in the high greenhouse gas emission scenario (SSP5-8.5) for 2041 to 2060. These findings provide initial information on the potential distribution of A. *lineatella* and can support the prioritization of areas for the development of phytosanitary measures against this pest, particularly in fruit-producing regions.

AUTHOR CONTRIBUTIONS

George Amaro: Conceptualization; data curation; formal analysis; methodology; writing – review and editing. Cesar Augusto Marchioro: Methodology; writing – original draft; writing – review and editing. Ricardo Siqueira da Silva: Conceptualization; methodology; writing – review and editing. Elisangela Gomes Fidelis: Conceptualization; methodology; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data used in this manuscript are available from the Mendeley Data Digital Repository at https://doi.org/10.17632/5snp7kzdrb.1 (Amaro et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Correlation between bioclimatic variables estimated using the *corrplot* R package version 0.92^{98} : (a) lilac with a slope to the right indicates a positive correlation, while orange with a slope to the left indicates a negative correlation. The intensity of the correlation coefficient increases as the shape changes from circle ($|\rho|=0$) to ellipse ($|\rho|=$ intermediate) to line ($|\rho|=1$). Correlated variables were grouped by Ward's method (internally homogeneous groups, most heterogeneous among themselves) through hierarchical cluster analysis; (b) estimated values of the correlation coefficients between the variables, following the same color pattern.

Table S1. Descriptive statistics of the covariates used in the models considering their values associated with occurrence records of *Anarsia lineatella*. Bold lines indicate the variables included in the model based on the data-driven selection process.

Figure S2. Area under the Curve ROC (AUC) (a), and partial AUC at a 10% threshold (b) of the optimal model for *Anarsia lineatella*.

Table S2. Evaluation metrics used to assess the performance of the selected Maxent model for *Anarsia lineatella*.

Figure S3. Predicted distribution for *Anarsia lineatella* under current and future climate conditions for different climate change scenarios by 2040 (2021–2040), expressed by continuous probability and probability classes.

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