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Evaluating invasion risk and population dynamics of the brown marmorated stink bug across the contiguous United States

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Abstract

BACKGROUND: Invasive species threaten the productivity and stability of natural and managed ecosystems. Predicting the spread of invaders, which can aid in early mitigation efforts, is a major challenge, especially in the face of climate change. While ecological niche models are effective tools to assess habitat suitability for invaders, such models have rarely been created for invasive pest species with rapidly expanding ranges. Here, we leveraged a national monitoring effort from 543 sites over 3 years to assess factors mediating the occurrence and abundance of brown marmorated stink bug (BMSB, *Halyomorpha halys*), an invasive insect pest that has readily established throughout much of the United States.

RESULTS: We used maximum entropy models to estimate the suitable habitat of BMSB under several climate scenarios, and generalized boosted models to assess environmental factors that regulated BMSB abundance. Our models captured BMSB distribution and abundance with high accuracy, and predicted a 70% increase in suitable habitat under future climate scenarios. However, environmental factors that mediated the geographical distribution of BMSB were different from those driving abundance. While BMSB occurrence was most affected by winter precipitation and proximity to populated areas, BMSB abundance was influenced most strongly by evapotranspiration and solar photoperiod.

CONCLUSION: Our results suggest that linking models of establishment (occurrence) and population dynamics (abundance) offers a more effective way to forecast the spread and impact of BMSB and other invasive species than simply occurrence-based models, allowing for targeted mitigation efforts. Implications of distribution shifts under climate change are discussed.

Supporting information may be found in the online version of this article.

Keywords: climate change; distribution change; ecological niche models; invasive species; species distribution models

1 INTRODUCTION

The spread of invasive pest species is a major threat to global biodiversity and agricultural production.[1,2] Understanding the factors that shape the geographical distributions and population dynamics of invasive species has been a key issue in agroecology in recent decades, particularly in the current context of global change.[3–5] Niche-based species distribution models are one of the most effective tools to assess dynamics of invasive species facing current environmental changes[6–8] and their use has become more popular as new powerful statistical techniques and geographical information system (GIS) tools become available. However, application of species distribution models has primarily focused on endangered species or biodiversity indicators, and seldom on insect pests in agroecosystems, particularly for pests with rapidly expanding distributions.

Many invasive insect species have wide host ranges and broad environmental tolerances, allowing them to rapidly expand their range in invaded regions. Moreover, empirical evidence has shown that climate change has caused many species, including insects, to shift their native distributions or realized niche.[9–12] Climate change also plays a key role in altering the distribution and population dynamics of invaders that are expanding their range, thus potentially exacerbating the damage caused by certain invasive agricultural pests.[13–15] However, few studies have assessed whether the environmental factors that mediate the occurrence of invasive pest species also drive population dynamics of invaders. Understanding these dynamics is critical to better assess factors that determine where invasive species are likely to be distributed, and areas where they are likely to have the greatest ecological impacts (i.e. outbreaks).

Here we assessed facs of the brown marmorated stink bug (BMSB), [*Halyomorpha halys* (Stål), Hemiptera: Pentatomidae], a native Asian species that was introduced to the United States in the mid-20th century and has since spread throughout much of North America and Europe.[16] BMSB is a generalist herbivore that feeds on nearly 170 described hosts, including many important crops that have been severely impacted across its introduced range.[16,17] BMSB is also known for its dispersal capacity, which allows it to move among crops, unmanaged forests and between urban and agricultural settings.[18,19] BMSB has proven challenging to manage, because in addition to its broad host range, it associates with humans by inhabiting dwellings in the winter,[20–22] which in turn makes it more difficult to identify limiting predictors if the species is able to mitigate exposure through behavior. In recent years, scientists have focused on controlling the spread of BMSB and managing damage to crops, but populations have been detected in 46 states, it is considered to be established in 32 states across the United States, and its range continues to expand. Moreover, BMSB is considered to be both an urban nuisance pest and an agricultural pest in at least 15 states.[16,23] Far from representing a problem only in the United States, it has also more recently invaded regions in Europe, where severe damage has been reported, particularly in pear and hazelnut orchards,[24,25] Chile[26] and regions of the Caucasus.[27]

We leveraged a widespread monitoring network for BMSB that encompassed 543 sites over 3 years (2017–2019) across the contiguous United States[28] to assess abiotic factors that mediated

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establishment (occurrence) and impact (abundance) of BMSB. We used niche-based ecological models to assess whether the environmental factors that determine BMSB establishment were the same as, or different from, factors that mediated BMSB abundance. Such analyses could aid in mitigating the spread of BMSB into new regions (preventing new occurrences) and regulating BMSB abundance where populations are already established (managing existing populations). We also assessed how the range of BMSB may shift under future climate scenarios, given that studies have shown that BMSB populations in North America are adapting to changing climate conditions.[29,30] Overall, our study shows how widespread monitoring networks can be linked with niche-based models to comprehensively explore factors shaping the dynamics of invasive pest species.

2 MATERIALS AND METHODS

2.1 Study system

Our study assessed occurrence and abundance of BMSB populations across the contiguous United States (Fig. 1). BMSB were sampled from 2017 to 2019 across both recently invaded regions and regions where BMSB is a well-established agricultural pest (Fig. 1). At each site, we deployed three, clear sticky panel traps baited with the commercial BMSB Dual lure (Trécé, Inc., Adair, OK, USA). This lure contains its aggregation pheromone, a combination of the stereoisomers (3*S*,6*S*,7*R*,10*S*)-10,11-epoxy-1-bisabolen-3-ol and (3*R*,6*S*,7*R*,10*S*)-10,11-epoxy-1 bisabolen-3-ol, and the pheromone synergist, methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate,[31] and has been shown to be highly attractive to BMSB adults and nymphs.[32–35] Baited traps were fastened on to wooden stakes spaced at 50 m intervals (after cases in the literature[28,33]). Traps were placed at interfaces between natural habitat patches and crop fields that were suitable hosts for BMSB. Traps were deployed in early spring and collected once every 2 weeks until late autumn at each site to ensure we captured most of the BMSB activity period. Our network included 276 sites in 18 states in 2017, 268 sites in 17 states in 2018, and 280 sites in 17 states in 2019; from these sites we collected 24 476, 28 902, and 38 131 BMSB adult individuals, respectively, per year. We standardized the counts for modeling analyses as average BMSB adults per trap per site per week. To account for misidentification or vagrant individuals not from an established population, we excluded from analyses the sites which only one BMSB in total was recorded.

2.2 Environmental variables

To assess factors affecting BMSB occurrence and abundance, we collected climate data for all sites (Table 1). For most metrics, we acquired gridded variables describing climatic conditions from the Parameter Regression of Independent Slope Model (PRISM)[36] that links meteorological data, digital elevation models, and spatial data to calculate spatially-explicit climate. These variables were calculated per month (averaged over metrics for each day in the month) using terrain variables within a regression framework to interpolate observations from a dense network of weather stations to 800 m resolution grids.[37,38] We included minimum temperature of the coldest month (January), maximum temperature of the warmest month (July), and total precipitation in January and July We used accumulated growing degree days per year (base temperature 10°C) obtained from the US National Phenology Network (www.usanpn.org). Annual evapotranspiration was obtained as a ~1 km cell sized raster from the MOD16 Global Evapotranspiration Product.[39]

We also selected six biologically meaningful landscape variables that may affect BMSB populations (Table 1). We used a digital elevation model at 30 m spatial resolution to estimate the elevation of each site,[40] and the land cover class each year as a categorical predictor obtained from the US Geological Survey (USGS) Cropland Data Layers.[41,42] Based on land cover data, we also calculated (i) distance to water (Euclidean distance to nearest permanent water) and (ii) distance to urban areas (Euclidean distance to nearest population area with more than 2500 residents). We included soil pH (10 km spatial resolution) as a proxy for potentially different plant communities that host BMSB. Our final landscape variable was based on the combination of photoperiod and solar radiation, calculated using the solar radiation analysis tool in

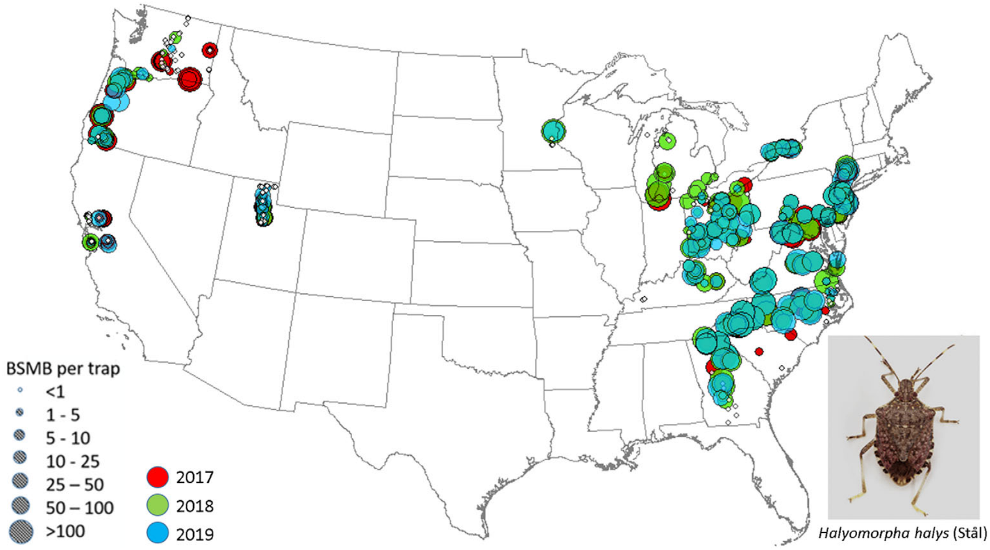

Figure 1. Map showing the geographical extent of the study. Sites monitored in each of three study years (2017–2019) are shown in different colors (points overlap across years). The diameter of the circles in each year represents the average weekly captures of adult *Halyomorpha halys* per three pheromone-baited traps throughout each season at each site.

ArcGIS 10.5 (ESRI, Redlands, CA, USA) and the SRTM digital elevation model.

Before analyses, all environmental layers were re-sampled to 30 arc-seconds grid cell size[43] and variance inflation factors (VIFs) were calculated[44] (Supporting Information, Table S1). VIFs showed no significant multicollinearity between our selected variables except maximum temperature in summer, where the VIF was slightly above a recommended threshold of 5 (5.14). However, we retained this variable in the analyses as it has been deemed ecologically important for BMSB distributions.[45–47]

2.3 Model development

Factors affecting BMSB occurrence were assessed using maximum entropy (MAXENT) models and factors affecting abundance with generalized boosted models (GBMs). MAXENT models were used as they often outperform other algorithms (i.e. GARP, CART) with presence-only data[48,49] and are far less sensitive to sample size.[50] MAXENT models compare presence locations with randomly selected points within a potential habitat to find the largest spread (maximum entropy) of current conditions relative to a 'background' of environmental variables. These analyses create maps of habitat suitability and determine contributions of specific variables on patterns of occurrence.

GBMs were created using the 'gbm' package[51] in R.[52] GBMs employ machine-learnicbine the strengths of regression trees and boosting to fit a parsimonious model from the outputs of individual trees.[53] By combining many simple models, GBMs can include different types of predictor variables and can accommodate missing data, both of which improve predictive performance while minimizing the risks of overfitting.[48] In addition, GBMs are sufficiently flexible to include non-linear relationships and interactions between predictors and responses.[54,55] One of the reasons we chose GBM is that, although training generally takes longer, GBM performs generally better than other similar algorithms, such as Random Forests, if parameters are tuned correctly.[56,57] This is mainly because GBMs try to add new trees that complement the already built ones, thereby providing better accuracy with fewer trees.[55]

Table 1. Climate and landscape variables included in the models, with associated means and ranges (in parentheses), original data resolution, data sources, and units

Variable	Code	Mean (minimum–maximum)	Original resolution	Source	Units/classes
Climatic					
Maximum temperature summer	tmax_jul	30.5 (23.2–36.7)	30 arc-seconds	PRISM	°C
Minimum temperature January	tmin_jan	−3.3 (−16.3–7.4)	30 arc-seconds	PRISM	°C
Precipitation summer	ppt_jul	88.7 (0.1–316.4)	30 arc-seconds	PRISM	mm
Precipitation January	ppt_jan	511.6 (11.4–2614.9)	30 arc-seconds	PRISM	mm
Evapotranspiration	evapot	48.6 (16.6–72.0)	927 m	MODIS	mm/yr
Growing degree days	gdd	996 (547–1415)	2500 m	USA-NPN	NA
Landscape					
Distance to water bodies	hidro	19.8 (0.2–191.7)	30 arc-seconds	GLWD	m
Distance to urban areas	urban	400.5 (0–4110.6)	30 m	USGS	m
Land cover class	cdl	categorical	30 m	Cropscape	82-classes
Soil pH	soilph	5.9 (5.0–8.1)	1000 m	FAO	NA
Photoperiod/solar radiation	sol_pho	12 515 (1.6–255 618)	30 arc-seconds	PRISM	kJ h m^{-2}
Elevation	dem	350.1 (1.1–1702)	3 arc-seconds	USGS	m

Note: NA, not available.

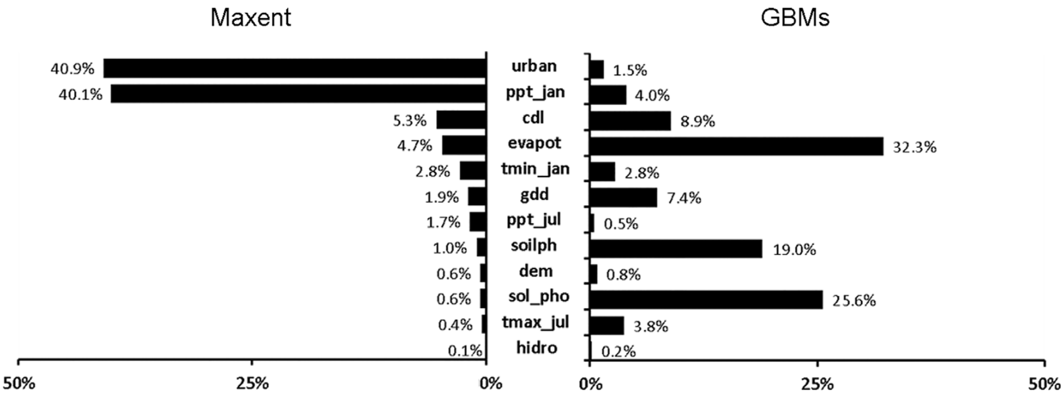

Figure 2. The relative contribution of each climate and landscape metric in MAXENT (occurrence) models and GBMs (abundance). Values shown are the result of the ten-fold model averaging. Scale bars show the proportion of variance explained by each factor in the combined models with both climate and landscape factors. (i) cdl: landcover class; (ii) dem: elevation; (iii) evapot: evapotranspiration; (iv) gdd: growing degree days; (v) hidro: distance to water bodies; (vi) ppt_jan: precipitation in January; (vii) ppt_jul: precipitation in July; (viii) tmax_jul: maximum temperature in July; (ix) tmin_jan: minimum temperature in January; (x) soilph: soil pH; (xi): sol_pho: interaction solar radiation and photoperiod; (xii): urban: distance to urban areas.

We generated MAXENT models (with default settings) and GBMs with six climate and six landscape variables as predictors and observed BMSB occurrence and abundance at each site as responses (Fig. 2). Both occurrence and abundance models can suffer from imperfect detection,[58,59] but we did not account for detection in models for three reasons. First, data were collected by trained personnel accustomed to identifying BMSB. Second, no machine learning methods currently exist to account for imperfect detection, and machine learning methods such as GBMs enable fitting of complex structures (non-linearities, interactions) that would be computationally challenging in an occupancy framework. Third, 'occupancy', after accounting for imperfect detection, is a latent variable that cannot be validated on independent data because the true state of independent data is unknown.[60] As our primary objectives were model validation and prediction, we considered our approach to be the most appropriate. Finally, we acknowledge that the introduced models would potentially estimate a truncated niche, as they do not account for native Asian populations, and therefore might underestimate BMSB potential distribution in the United States.[61,62] To control for this effect, we calculated the realized niche occupied by native and introduced populations, as well as the predicted habitat suitability based on these two models (Supporting Information, Fig. S1). Nevertheless, because the purpose of this study was to explore and compare factors driving BMSB distribution and abundance in the contiguous United States, we argue that the introduced US BMSB populations represent the best source of information to calculate their realized niche in the United States.

2.4 Model performance and evaluation

We assessed MAXENT models using area under the receiver operating characteristic curve (AUC) of plots and binary omission rates,[63,64] which are widely recognized as reliable performance metrics for species distribution models,[65–67] although we also acknowledge potential limitations that have been identified (see Lobo *et al.*[68]). AUC is a threshold-independent metric that weights omission error (predicted absence in areas of observed presence) and commission error (predicted presence in areas of observed absence) equally. AUC juxtaposes correct and incorrect predictions over a range of thresholds, and values of model fit range from 0.5 (no better than random association) to 1 (perfect fit). Useful models produce AUC values of 0.7 to 0.9 and 'good discriminating models' have values above 0.8.[66] Final results of MAXENT models were the average of ten model runs. We assessed GBMs using Spearman's non-parametric rank correlation coefficients (rho, ρ) between predicted and observed abundance values. We used rank correlation coefficients because observed BMSB counts were low at many sites (leading to deviations from normality) and due to potential non-linear relationships between predicted and observed abundance. To account for data independence, we randomly selected 70% (573) of sites to train the models and 30% (245) for validation.[69]

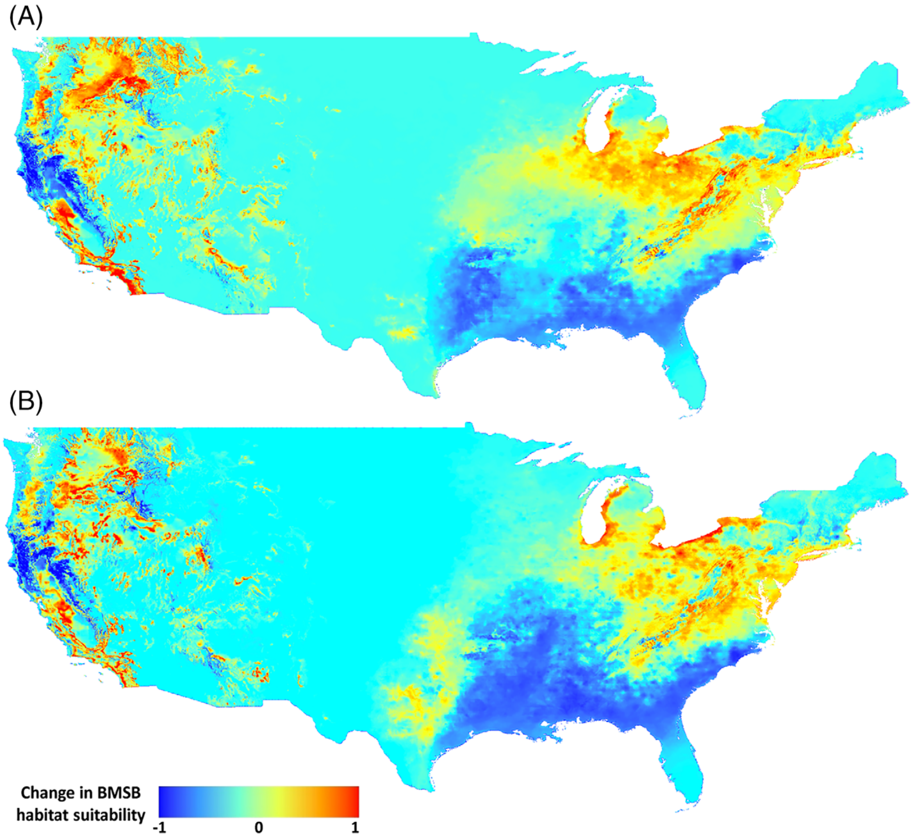

Figure 3. Predicted change in habitat suitability for *Halyomorpha halys* in the 2080s compared to current conditions under the climate scenarios (A) B1 (emphasis on global solutions to economic, social, and environmental sustainability, but without additional climate initiatives) and (B) A1B (a future world of very rapid economic growth, low population growth and rapid introduction of new and more efficient technology) (both rated as moderate). Both panels show changes in climatic habitat suitability from cold (decrease in suitability) to warm colors (increase in suitability). Green tonalities denote no change in habitat suitability for BMSB.

2.5 Predicting BMSB distribution under future climate scenarios

Our final analysis involved predicting changes in habitat suitability for BMSB under future climate change scenarios. We assessed these scenarios to project how BMSB populations might expand in the near and long-term future. We developed climate-only distribution MAXENT models and calculated the environmental niche suitability under two climate change scenarios for 2080.[70] Climate data for the IPCC (Intergovernmental Panel on Climate Change) scenarios considered were generated with ClimateNA version 5.10 software.[71] We chose the A1B and B1 scenarios, which are moderate scenarios often used in recent global change studies to project future climatic conditions.[72–75] Scenario A1B assumed a balanced global energy portfolio, generating moderate emission levels and describes a future world of very rapid economic growth. Scenario B1 described a world with similar global population than A1B but transitioning to sustainable energy, generating lower greenhouse gas emissions.[76,77]

3 RESULTS

3.1 Model performance and validation

Model validation showed both MAXENT (occurrence) models and GBMs (abundance) accurately captured the current distribution of BMSB in the United States. The three MAXENT models with climate variables only, landscape variables only, or climate and landscape variables combined had an AUC of 0.93, 0.89, and 0.95, respectively. We also built a MAXENT model with the top three climate and top three landscape variables, which had an AUC of 0.94. The climate-only, landscape-only, and combined GBMs had a ρ of 0.44, 0.48, and 0.44, respectively. The reduced combined model had a ρ of 0.52 (Table S2).

3.2 Relative contribution of variables

Although both MAXENT models and GBMs effectively predicted BMSB occurrence and abundance, the relative contribution of factors across these models differed considerably (Figs 2, S2 and S3). This held whether we considered the single top variable in each model, or whether a variable was one of the three top predictors. In the MAXENT models, the distance to urban areas and January precipitation were by far the most important factors mediating BMSB occurrence, accounting for more than 80% of the variance, followed by land cover and evapotranspiration (Figs 2 and S4). In the GBMs, in contrast, BMSB abundance was primarily mediated by evapotranspiration and the interaction between photoperiod and solar radiation, followed by soil pH and land cover (Fig. 2).

3.3 Predicted effects of climate change on the distribution of BMSB

Our models showed that habitat suitability for BMSB will likely change considerably under future climate scenarios. Under both moderate scenarios considered, areas of high suitability habitat are expected to increase in future decades (Fig. 3). In general, we found that habitat suitability will increase moving northward over time, especially under the A1B scenario (Fig. 3(B)). On the west coast, we also showed that habitat would become more suitable moving inland in future years, particularly in the northwest. However, there were some areas that are expected to decline in suitability by the 2080s, such as some parts of the Sacramento Valley of California (Fig. 3). Overall, our models suggest that currently 2.3% of the contiguous United States has a BMSB habitat suitability above 0.5, and less than 0.01% has suitability above 0.7. Those values are predicted to increase to 13% and 7%, respectively, under the A1B and B1 scenarios (Table S3).

4 DISCUSSION

We show that ecological niche models, created with data from a nationwide monitoring effort, accurately predicted the occurrence and abundance of BMSB populations throughout the United States. These results conform with those from studies showing high predictive ability of ecological niche models that are trained and tested over short time periods.[78–80] While both types of models were accurate, the most important factors mediating BMSB occurrence differed from those regulating BMSB abundance (Fig. 2), possibly reflecting different processes involved in the establishment of an invasive species, as opposed to those driving regional population dynamics.[81,82] For example, the most important predictor for BMSB occurrence was proximity to populated areas, which may reflect human-assisted transport of BMSB to urban locations, the availability of human structures that can serve as overwintering sites for BMSB, and the diversity of ornamental plants (e.g. *Ailanthus altissima*) acting as additional resources to BMSB in the spring. However, it is important to note that the different nature of the two model approaches and the interaction of the presence and abundance data with the predictors can also influence the ranking of the variables. Urban areas might thus provide better availability of hosts for BMSB feeding and oviposition in spring, which may in turn increase its abundance and contribute to its subsequent spread in nearby areas. However, for populations that are already established, climate factors had the greatest impacts on abundance.[83] Overall, these results suggest that predicting the distribution and population dynamics of an invasive species requires complementary modeling approaches to assess both establishment and population regulation.

BMSB has been spreading rapidly throughout the United States, and its population status still has not reached complete equilibrium, as it has in the native Asian range.[84] Our models showed that the most suitable areas for BMSB establishment are in the Mid-Atlantic region and surrounding the Great Lakes, with additional favorable regions in south-eastern states and valleys of the West Coast (Fig. S4). These regions include highly productive croplands that are vulnerable to significant economic losses due to BMSB each year. Importantly, our models predicted regions of high suitability where BMSB has not yet been detected, suggesting that its further spread and greater impacts on agriculture may be anticipated (e.g. southern California, Treasure Valley, Idaho). However, our models also suggest that BMSB is unlikely to establish a continuous distribution throughout the contiguous United States, given the lack of suitable habitat throughout much of the central and southern United States (Figs 3 and S4). It is worth noting that a previous model by Kriticos *et al.*[6] had identified certain regions of Florida and the Gulf coast as favorable for BMSB colonization whereas our models do not show those areas at high risk of invasion. Our predictions seem to be at least partially supported by observations from collaborators in Florida, who have detected adults of BMSB but very rarely found nymphs or eggs, suggesting BMSB have not established their population in Florida and might not be a climatically suitable region.[85]

When analyzing factors affecting BMSB occurrence, we showed that January precipitation was the most important climatic factor, followed by evapotranspiration and minimum temperature. Interestingly, BMSB are chill-intolerant, with rapidly increasing mortality at temperatures below 10 °C.[29,86] The greater role of precipitation, compared with temperature, however, has been reported for multiple other insect taxa in North America[4,87] and for some non-insect taxa.[9] The role of higher winter precipitation and humidity potentially leading to a lower mortality of BMSB has been reported to be important factors for other insect species.[88,89] Indeed, cold, dry air is known to exacerbate desiccation stress for insect species,[90] and as BMSB overwinters in aggregations, a mechanism considered to help reduce desiccation stress,[91] winter precipitation is likely another factor that is important to survivorship. Increased precipitation during January likely increases the relative humidity and reduces evapotranspiration from overwintering bugs. However, BMSB have only been found overwintering in dry, tight locations in nature in location such as beneath the bark and deep within the wood of dead, standing trees, but never in moist locations such as leaf litter or damp, downed trees lying on the ground based on extensive surveys by detector canine and human surveyors.[84,91] Overwintering BMSB also choose to shelter in dry locations over moist sites in significantly greater numbers.[92] Studies of aggregating insect species, specific abiotic conditions found within overwintering sites and their impact on subsequent insect survivorship are rare as articulated by Susset *et al.*[93]; their study of the ladybird beetle *Hippodamia undecimnotata* (Schneider) revealed abiotic conditions within aggregation sites did not provide optimal conditions to combat unfavorable temperatures or the potential for fungal pathogen infection. Finally, higher humidity during this time of the year might make natural hosts more abundant and more suitable, increasing BMSB abundance and their potential to establish in crops the following season. It is clear that more detailed studies of factors influencing overwintering survivorship success of BMSB are warranted.

Distance to urban areas was the most important landscape variable affecting BMSB occurrence, accounting for almost 41% of the variance, making it the most important variable overall. Factors associated with human-dominated landscapes, including roads and urban areas, similarly affect other invasive pests[94,95] and non-pest insects.[96] Our results suggest that BMSB is most likely to establish in agricultural regions where it already represents a nuisance pest,[97] because individuals that overwinter in human structures may disperse into crop fields each spring, and also because higher diversity of crops provide more options for optimal BMSB development.[98] However, the proximity to populated areas was not an important variable predicting BMSB abundance. This suggests that once populations establish, they may not need to rely on humans for overwintering or transport, and population dynamics are primarily driven by climate. In other words, if a BMSB population has already established, the proximity of human structures is no longer a critical factor for BMSB abundance, which become more influenced by the regional climate.

In contrast to MAXENT models, GBMs revealed that evapotranspiration had the strongest impacts on BMSB abundance, followed by the interaction of solar radiation and photoperiod. Together, these two predictors accounted for more than 50% of the variance in abundance. This suggests water availability, and sunlight exposure, are limiting factors regulating BMSB populations. Other studies have similarly shown that moisture can strongly affect sap-feeding insects, both in their adult stage and especially during nymphal development.[4,99–101] Reduced evapotranspiration and the associated temperature increase can impact survival of insect herbivores that are unable to move to more suitable sites,[102] and could prove to be a factor in BMSB nymphal survival in hotter and drier locations. Moisture is also a factor determining the availability and suitability of host plants, increasing BMSB success after they break diapause and start feeding. This in turn enhances the potential for population increase and ultimately to establish in crop hosts the following season. Policymakers and growers might be able to use potential evapotranspiration to better predict the risk of BMSB impact in the following year, allowing them to make more proactive management decisions.

By analyzing future climate scenarios, we showed that BMSB populations have a large potential to continue to expand within the United States, and particularly northward. Similar expected shifts have been reported for other insect species in the Northern Hemisphere.[103–105] The change in future habitat suitability was similar under both climate scenarios, and both reflected steady increases in the proportion of highly suitable habitat for BMSB by 2080 compared with 2020 (Fig. 3). According to our models, BMSB may expand its range considerably in future decades, threatening crops in regions where it has not yet been detected. Nevertheless, our models can be used to estimate areas at highest risk of potential spread so that mitigation and eradication efforts might be implemented in new regions. As reported by Stoeckli *et al.*,[14] BMSB is also expected to expand its current distribution in Europe, where extensive range expansion into higher altitudes and an increased number of generations per year is predicted under several climate change scenarios.

While our models accurately described BMSB occurrence and abundance, we note that substantial variance remained unexplained. We suggest that biotic factors, such as the presence and abundance of competitors and natural enemies, also likely affect BMSB distributions.[80,106] For example, recent studies show that parasitoid wasps can help suppress BMSB populations.[107–109] Similarly, other native stink bug species may compete with BMSB for resources and limit their spread.[110,111] Another source of variance arises from the scale of the predictors, as most variables included in ecological niche models do not reflect microclimates that can provide refugia for insects[112]; however, such datasets are not yet available. However, the capacity of BMSB to adapt physiologically to new environmental conditions may affect the interpretation of predictions. Finally, variation in management strategies for BMSB, such as the intensity of pesticide use, might affect regional distributions.[113] Despite these confounding sources of variance, we showed that our models could accurately capture variability in BMSB occurrence and abundance at the national scale of the BMSB invasion. Finally, while it is common to consider climate and landscape factors independently, they may interact in some contexts. For example, over longer timescales, insect populations that are invading new areas due to anthropogenic land-use change may be more likely to behaviorally adapt to climate change. However, the connectivity of landscapes may be reduced due to landscape fragmentation, decreasing the potential for population establishment and range shifts due to climate change. Of course, a major step forward will be to efficiently assess the interactive effects of climate and landscape factors, but this has proven too challenging to date, at least for most observational studies.

Our study highlights the applicability of ecological niche models for assessing the potential spread and impacts of an invasive pest species in agroecosystems. Such models can in turn be used to guide mitigation and eradication strategies before invaders establish in new regions, while maximizing the effectiveness of limited resources available for tracking invasive spread. Moreover, we addressed the complementarity of two modeling approaches, occurrence and abundance models, that offer different information related to managing an invasive pest insect. While the distance to populated areas seems to be key for BMSB occurrence, climatic factors, particularly those related to water availability, were the most important drivers of BMSB abundance. This study leveraged a rare, large-scale monitoring effort across most of the contiguous United States that included sampling sites across a wide range of environmental conditions. Thus, results presented here are robust, and predictions made at such a continental level are likely more reliable than could be achieved with a smaller scale study. Our models thus represent a powerful tool for ecologists and policymakers to better understand expansion of an invasive insect pest across diverse agroecosystems.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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