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Article

Assessing geographic dimensions of biological control for *Halyomorpha halys* in United States

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With 5 figures

Abstract: Biological control is often a key component of management strategies for invasive species. Yet, the effectiveness of biological control can be limited by a poor understanding of natural enemy ecology. To overcome this, habitat suitability models can predict distributions of invasive species and identify areas of potential overlap between invaders and natural enemies to guide biological control. Here we used data from a coordinated national monitoring network and a novel modeling method that incorporates physiology into correlative niche models to predict potential distributions of the brown marmorated stink bug, *Halyomorpha halys*, and two natural enemies (a parasitoid, *Trissolcus japonicus*, and a microsporidian, *Nosema maddoxi*) in current and future climates (2070s). We show all three species have broad similarity in habitat suitability, with especially high overlap in the mid-Atlantic and southeastern US where *H. halys* populations were first established. Each species will likely expand their range across the northern US in the future, but the overlap between species may decrease. In much of the central and southeastern US, *H. halys* may decrease its range over time, although natural enemies may be less impacted, and overlap between species may increase. Our study shows that biological control provided by *T. japonicus* and *N. maddoxi* could be key for managing *H. halys* given their overlapping niches, and our models can aid in delineating areas where biocontrol may be most effective. Our method of linking field data with correlative niche models can also be used for other insects.

Keywords: Biological invasion; brown marmorated stink bug; climate change; ecological niche model; natural enemy

1 Introduction

Invasive insects threaten ecosystems worldwide, and their negative impacts are expected to increase over time due to climate change and increased human connectivity (Anton 2021; Bradshaw et al. 2016). Many of the most damaging invasive species establish in areas where they "escape" their native natural enemies, and eradicating these species early is key to limiting invasive spread (Zhao et al. 2023). Classical biological control, where natural enemies from the native range are introduced to control invasive pest populations, is often a promising option for the management of invasive arthropods and weeds (Samways 1988). Generalist predators and pathogens in the invaded range may also provide biological control of invaders (Sun et al. 2017; Zhao et al. 2023). However, it can be difficult to effectively employ biological control for invasive species without knowledge of where natural enemies may best establish.

Habitat suitability models can predict the distributions of invasive species and their natural enemies and identify areas of overlap where biological control may be strongest. Yet, models for invasive species and natural enemies often suffer from low spatial transferability, where models calibrated on native areas fail to capture non-native distributions; this occurs when correlative models fail to incorporate factors that affect populations in new environments, such as propa-

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gule pressure or adaptation (Liu et al. 2020). One way to overcome these hurdles is to create ensemble models that leverage different model techniques, as with correlative as compared to mechanistic models (Feng et al. 2020; Talluto et al. 2016; Zhu et al. 2021a). Models of invasive species and their natural enemies would also typically benefit from greater monitoring and survey data.

The invasive brown marmorated stink bug (*Halyomorpha halys* Stål) has become a major crop pest in North America and Europe (Leskey & Nielsen 2018). After its first detection in the US in the 1990s, the species has spread throughout the country and Canada (Illán et al. 2022). While *H. halys* is challenging to manage, two natural enemies found in the US show promise for biological control. *Trissolcus japonicus* (Ashmead), a parasitoid from Asia, has been detected in North America and populations are being released in certain States (Abram et al. 2020; Conti et al. 2021). *Nosema maddoxi* (Maddox) is an endemic microsporidian across the US that has the potential to impact *H. halys* populations (Hajek et al. 2023; Preston et al. 2020). However, to date we have limited understanding of the geographic overlap among *H. halys*, *T. japonicus* and *N. maddoxi* in the US, both in the present and under future climate change scenarios.

Here, we leveraged monitoring data into models to assess the geographic dimensions of biological control for *H. halys*. First, using data from a coordinated national monitoring study, we built habitat suitability models for each species across the US to predict the current and future habitat suitability. Second, we assessed the potential overlap between each pair of species in habitat suitability across the continental US, and at the scale of States, as State agencies often have oversight over biological control actions. Through these complementary approaches we sought to understand where biological control might help limit the impact of this invader. Our study shows coordinated monitoring studies that consider the distributions of invasive species and natural enemies may aid in efforts to limit the spread and damage of emerging invaders.

2 Materials and methods

2.1 Occurrence records

Occurrence records of *H. halys* from its native range were obtained from Zhu et al. (2012), while North American records were from Illan et al. (Illán et al. 2022); European records were attained using the *spocc* package in R (Owens et al. 2023). The North American data include a 3-yr survey of *H. halys* from nearly 20 US states that involved standardized weekly monitoring (Illán et al. 2022). Records for *T. japonicus* in the US were collected by scientists working on *H. halys* across 10 states, with additional data from recent publications (Avila & Charles 2018; Tortorici et al. 2023; Yonow et al. 2021). In the US, this wasp was actively sampled by placing sentinel eggs on cards and hatching out any parasitized hosts; passive sampling was conducted using yellow sticky traps (Quinn et al. 2019). The hosts of *T. japonicus* include *H. halys* and other Pentatomid species.

Nosema maddoxi records were assembled from a survey across 17 US states during 2019 and 2020. At 40 locations, 15 to 30 *H. halys* adults were sampled in spring or fall. The collected specimens were frozen and shipped to a lab at Cornell University. Samples were then assessed using microscopy to determine if each specimen was infected (Preston et al. 2020). A total of 1391 *H. halys* individuals were collected and diagnosed in the 40 locations.

2.2 Physiological trait and climate data

Physiological data for *H. halys* regarding lowest development temperature, growing degree days, and cold and heat tolerant temperatures were obtained from Kriticos et al. (2017); data on these factors for *T. japonicus* were from Avila & Charles (2018). These data were assembled from multiple sources and used to calibrate CLIMEX models that effectively predicted *H. halys* or *T. japonicus* distributions (Avila & Charles 2018; Kriticos et al. 2017). Baseline raster data of global monthly average, minimum, and maximum temperatures, maximum temperature of the warmest month, minimum temperature of the coldest month, monthly precipitation, and annual precipitation at a 2.5 min resolution were obtained from Worldclim2 (Fick & Hijmans 2017).

2.3 Mechanistic models to examine climatic tolerances of *H. halys* and *T. japonicus*

We first developed mechanistic models based on physiological traits of *H. halys* and *T. japonicus* to assess the fundamental niche of each species; these predictions were the basis for predicting pseudo-absence locations (i.e., presumed absence data) for the habitat suitability models. Data on physiological traits of *N. maddoxi* were not available, and a separate approach for predicting pseudo-absences was used (see "*Habitat suitability modeling*" below). Mechanistic models for *H. halys* and *T. japonicus* were fit with physiological data on the low development temperature, growing degree days for development, and cold and heat tolerant temperatures along with raster data of monthly average, minimum, and maximum temperatures. The output of the models was a suitability index (S_i) calculated on a raster basis by multiplying a temperature index (T_i), a growth index (G_i), and a killing index (K_i) (i.e., $S_i = T_i \times G_i \times K_i$) (Grünig et al. 2020) (Fig. 1).

We used independent occurrence records to validate the mechanistic models. We defined a suitable observation as one where the taxa could finish at least one generation (i.e., its monthly mean temperatures were above insects' low threshold development temperature, and the life cycle requirements were met). Accurate global predictions would suggest that thermal tolerances of *H. halys* (Fig. S1) or *T. japonicus* (Fig. S2) were consistent with physiological trait data used. Models generally captured both *H. halys* and *T. japonicus* distributions even if only temperature predictors

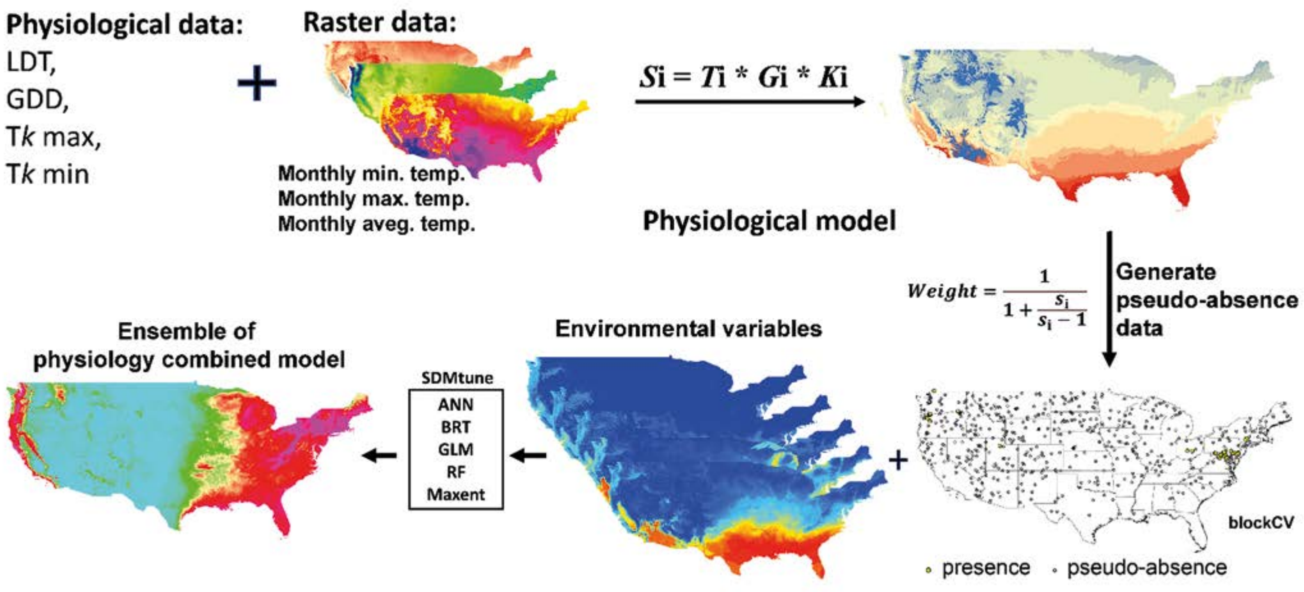

Fig. 1. Schematics of model protocols for incorporating physiology into insect distribution models. The physiological models were fit with physiological data of development temperature (LDT), growing degree days (GDD) and both cold (T*k* min) and heat tolerant (T*k* max) temperatures, and grid data of monthly average, minimum and maximum temperatures, its suitability index (S_i) is calculated on raster pixel basis by multiplying temperature index (T_i), growth index (G_i) and killing index (K_i) (i.e., $S_i = T_i \times G_i \times K_i$), which served as the weight to select pseudo-absence data, that combined with present and environmental data to make model predictions.

were used, with locations where both species have been detected predicted to have suitability values above 0.5 (0 to 1 scale). In *H. halys*, those populations where predictions failed were in high latitude or altitude areas, including northern Japan, southwestern China, central and northern Europe, and northern coastal Pacific West, southern and central US (Fig. S1).

2.4 Habitat suitability modelling

Our primary objective was to build habitat suitability models for *H. halys*, *T. japonicus*, and *N. maddoxi* in the US to assess overlap between these species and identify areas where biological control may be effective. These models were built with occurrence records, generated pseudo-absence records, and climate variables of annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, and annual precipitation (Fig. 1), following the best practices and recent standards (Araújo et al. 2019; Soley-Guardia et al. 2024).

To generate pseudo-absence records for *H. halys* and *T. japonicus*, we used the output from the mechanistic models. As these models were based on temperature, areas that were predicted to have low suitability were areas where the insect should not occur (a pseudo-absence). The outputs of the mechanistic models were thus used as weights to select pseudo-absence data for models (Fig. 1) (Gallien et al. 2012). As physiological data were unavailable for *N. maddoxi*, we obtained pseudo-absence locations using a three-step approach to account for spatial, ecological, and environmental aspects (Iturbide et al. 2015; Senay et al. 2013). First, a geographical area that is accessible and could have realistically been occupied by *N. maddoxi* over relevant ecological and evolutionary time scales was established (Barve et al. 2011), from which we determined locations environmentally dissimilar to presence points, and then K-means clustering was used to refine the pseudo-absence points (Iturbide et al. 2015; Senay et al. 2013).

After occurrence and pseudo-absence records were compiled, we predicted habitat suitability for each species using an ensemble approach (Thuiller et al. 2009). To develop ensemble models, we created five individual models for each species using the *biomod2* platform in R: (i) artificial neural network, (ii) boosted regression tree, (iii) generalized linear, (iv) random forest, and (v) Maxent. Maxent is an efficient modeling algorithm for making predictions from incomplete information, whereas generalized linear models are a statistical approach to ascertain relationships between particular predictor variables and habitat suitability. The other three models (artificial neural networks, boosted regression tree, random forest) are machine learning techniques that fit a parsimonious model from the outputs of individual networks or trees; these techniques can improve predictive performance while minimizing the risks of overfitting, although it can be difficult to ascertain correlations among particular variables (Zhu et al. 2021b; Illan et al. 2022). Each of the models were fine-tuned with the *SDMtune* package in R before consensus processing (Vignali et al. 2020), with the *blockCV* package used to generate environmentally separated folds for crossvalidations (Valavi et al. 2019). Twenty-five individual models were produced for each species (i.e., 5 algorithms × 5 folds cross-validation) and ensemble models were produced by averaging predictions of individual models with AUC > 0.7 (Area Under Receiver Operating Characteristic Curve), a metric used to evaluate model discriminability.

2.5 Projecting distributions in future climates

It is anticipated that global warming of 1.5 ° to 2 °C will be exceeded this century (Calvin et al. 2023). We next projected future habitat suitability for *H. halys*, *T. japonicus*, and *N. maddoxi* to estimate how overlap between the species, and the effectiveness of biological control, may be altered by climate change. A similar approach was used to study potential tri-trophic interactions between *H. halys*, two parasitoids (*T. japonicus* and *Trissolcus mitsukurri*), and a hyperparasitoid (*Acroclisoides sinicus*) in Europe (Gutierrez et al. 2023). Future climate for 2070 was assessed with 9 general circulation models that were averaged from 2061 to 2080: (i) BCC-CSM2-MR, (ii) CNRM-CM6-1, (iii) CNRM-ESM2-1, (iv) CanESM5, (v) GFDL-ESM4, (vi) IPSL-CM6A-LR, (vii) MIROC-ES2L, (viii) MIROC6, and (ix) MRI-ESM2-0 (Fick & Hijmans 2017). We used the intermediate Shared Socio-economic Pathways of 370 scenario because it is considered moderate and more realistic than SSP 126 or 585 scenarios (Fick & Hijmans 2017). We used a "consensus" method to produce an ensemble model for each species, where we sought to identify the most likely potential distribution of each species in future climates (Zhu et al. 2021b).

2.6 Statistical analysis

We used AUC and the true skill statistic (TSS) to evaluate predictions of ensemble models against validation data. We used Schoener's *D* (Schoener 1968) to evaluate distributional overlaps between *H. halys* and *T. japonicus* and *H. halys* and *N. maddoxi*. Schoener's *D* ranges from 0 (niche models have no overlap) to 1 (niche models identical), permitting comparison of niche overlap (Warren et al. 2008). Schoener's *D* values were calculated at both the national and statewide levels, as States are often the functional unit that implements biological control tactics.

3 Results

3.1 Predicted habitat suitability in the current climate

Ensemble models performed extremely well in predicting the current distribution of each of the three species in the US (AUC and TSS statistics were 0.95 and 0.76 for *H. halys*, 0.94 and 0.74 for *T. japonicus*, and 0.95 and 0.77 for *N. maddoxi*, respectively) (Fig. 2). We also compared our results to a study of *H. halys* in the US (Illan et al. 2022) that used more landscape variables and found a correlation of 92% between predicted habitat suitability, showing our models with only climate factors were effective at capturing the invasive distribution of this species. The predicted suitability for each of the three species while present throughout much of the US did not extend into northern locations across the upper Midwest US and New England, the Great Plains, Rocky Mountains, and desert southwest (Fig. 2).

3.2 Predicted overlap between *H. halys* and natural enemies in current climate

There was variability in the predicted overlap of habitat suitability between *H. halys* and the natural enemies (Fig. 3). Comparing overlap between *H. halys* and *T. japonicus*, every state in the south-central and southeast US had a Schoener's *D* value over 0.90, indicating both species have broadly overlapping distributions in these regions, and the potential for biological control would likely be high. Overlap between *H. halys* and *T. japonicus* was also high throughout the mid-Atlantic and northeast US where *H. halys* initially established, with most states having *D* values between 0.80 and 0.95 (Fig. 3). Western coastal areas in the Pacific Northwest also show high overlap (Fig. 2). However, overlap between *H. halys* and *T. japonicus* was relatively low in states west of the Mississippi River (e.g., most western states had $D < 0.80$) (Fig. 3).

Overlap in predicted habitat suitability between *H. halys* and *N. maddoxi* was considerably more disjointed than for *H. halys* and *T. japonicus* (Fig. 3). While states in the central and eastern US tended to have greater predicted overlap in suitability between *H. halys* and *N. maddoxi* than western states, there was variability among nearby states. As an example, states such as Florida, Georgia, and South Carolina had *D* values > 0.90, while Alabama, Mississippi, and Tennessee had values < 0.85 (Fig. 3). The region where all states were predicted to have high *D* values was the north-central (Michigan, Illinois, Indiana), while the northeastern US was predicted to have relatively low overlap (Fig. 3). The western coastal areas in Oregon and northern California states also have high overlap (Fig. 2). As with *H. halys* and *T. japonicus*, overlap between *H. halys* and *N. maddoxi* was generally low in states west of the Mississippi River (Fig. 3).

3.3 Effects of climate change on habitat suitability

To complement habitat suitability models in current climate conditions, we also generated habitat suitability predictions in future climate scenarios (2070s). For each of the three species, states in the south-central and southeastern US are predicted to generally become less suitable in future compared to current climates (Fig. 4). However, the negative effects of climate change on habitat suitability were predicted to be stronger for *H. halys* compared to both natural enemies in these regions (Fig. 4); negative effects of climate change were also predicted to be stronger for *T. japonicus* compared with *N. maddoxi* (Fig. 4). In contrast, for each of three species, states in the northeast, north-central, and western US were expected to become more suitable in future compared

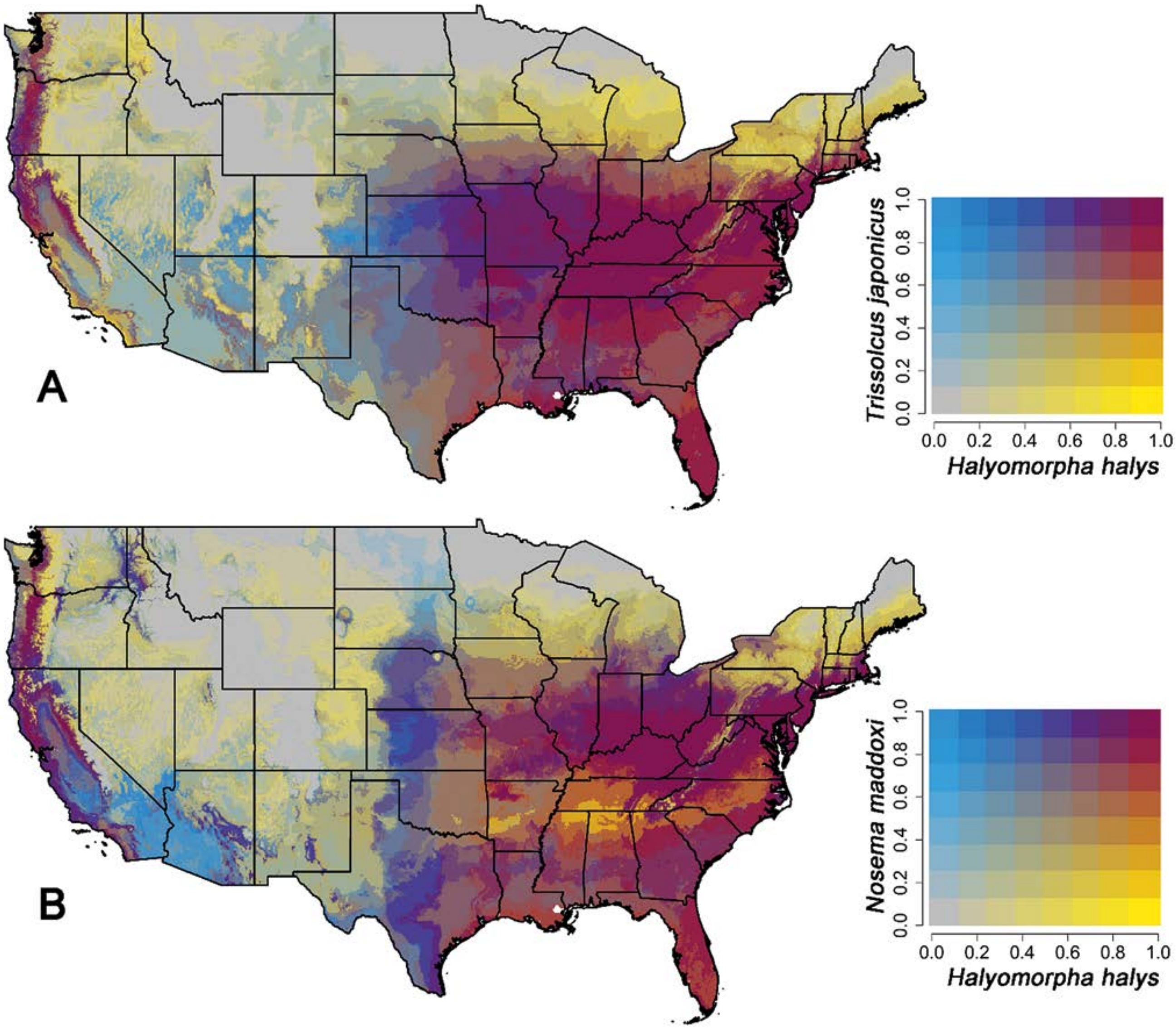

Fig. 2. Present-day suitability predictions for *H. halys, T. japonicus* and *N. maddoxi* by ensemble models in contiguous United States. Yellow – high suitability *H. halys*; blue – low suitability *H. halys* but high suitability *T. japonicus* (A) or *N. maddoxi* (B); red – high suitability *H. halys*, with *T. japonicus* (A) or *N. maddoxi* (B). The bivariate color ramp based on 10 equal quantiles in suitability predictions was used for graphing purposes only.

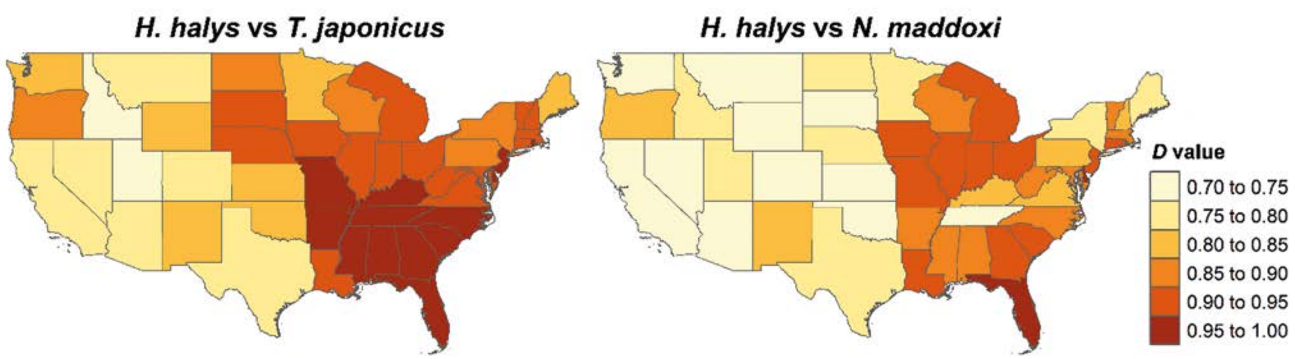

Fig. 3. Overlap in predicted habitat suitability for current climate scenarios for *H. halys* and *T. japonicus* (left) and *H. halys* and *N. maddoxi* (right), measured as Schoener's *D* (range from 0 to 1); higher *D* values indicate greater niche overlap and high potential for biological control.

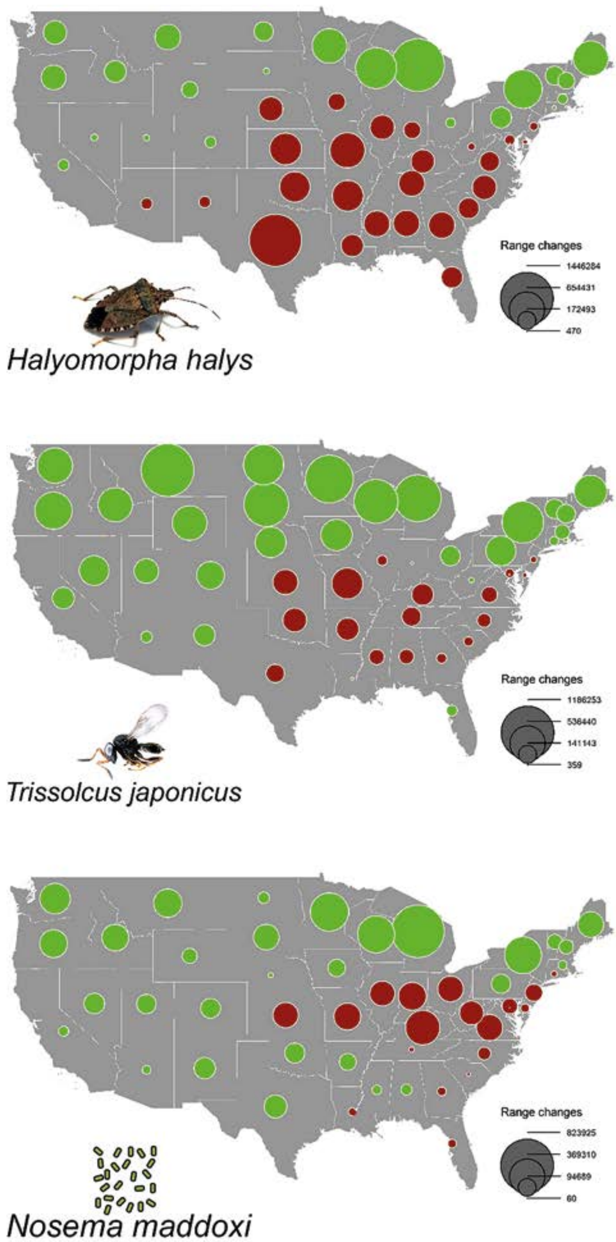

Fig. 4. Estimated distributional changes for *H. halys* (top panel), *T. japonicus* (middle panel) and *N. maddoxi* (lower panel) between the present and 2070s climate conditions in contiguous United States. Maps have circle sizes that represent distributional changes in each state, where red indicates distributional decrease and green indicates increase.

to current climates (Fig. 4). The impacts of climate change were expected to be particularly strong for the two natural enemy species in each of these regions (Fig. 4).

Lastly, we compared how overlap in habitat suitability may change between *H. halys* and the two natural enemies in future compared to current climates. For comparisons of *H. halys* and *T. japonicus*, most states (36 of 48) were not predicted to have major changes in habitat suitability in future compared to current climates (delta D values between −0.05 and 0.05) (Fig. 5). Only seven states were predicted to have a considerable increase in overlap between *H. halys* and *T. japonicus* (delta D values > 0.05), with five in the north-central or northeastern US and two in the southwest US (Fig. 5). Only five states were predicted to have a considerable decrease in overlap between *H. halys* and *T. japonicus* (delta D values < −0.05), and all of these were in the north-central US (Fig. 5). For comparisons of *H. halys* and *N. maddoxi*, 26 states were not predicted to have major changes in habitat suitability in future compared to current climates (Fig. 5). Unlike comparisons of *H. halys* and *T. japonicus*, predicted overlap between *H. halys* and *N. maddoxi* was expected to increase in 17 out of 48 states, although these states were distributed throughout the US (Fig. 5). Only 5 out of 48 states were predicted to have a decrease in future niche overlap between *H. halys* and *N. maddoxi*, and all of these were in the central US (Fig. 5).

4 Discussion

Invasive species are often difficult to manage, because they establish within areas where their coevolved natural enemies are absent (Thomas & Reid 2007). While both classical and conservation biological control can be implemented to manage invasive species (Samways 1988), effective biological control for invasive species is often limited by a lack of available data on the distributions of invaders and natural enemies during the course of invasions. For example, classical biological control involves importation of natural enemies, and this may fail if releases occur in areas that are not suitable for natural enemies' survival and development (Tortorici et al. 2023). The likelihood of establishment can also vary considerably across regions. Our study showed that coordinated national monitoring efforts can rapidly gather data on an invasive species and natural enemies to aid in the geographical assessment of biological control.

We harnessed monitoring data from coordinated surveys across 10 to 20 states for *H. halys*, *T. japonicus*, and *N. maddoxi*. This allowed us to overcome barriers associated with only using data from the native range of *H. halys* and the natural enemies, while assessing how populations in the US may have adapted to bottlenecks during invasions. Combining niche suitability maps for each of these species provides insights into locations where each species may be introduced, or conserved, to maximize biological control (Avila & Charles 2018). Similar approaches have been used to rank biological control agents for their potential impacts on weedy plants, where species with greater niche overlap are prioritized (Sun et al. 2017). Our study complements prior work that assessed overlap between native stink bug species and *T. japonicus* in New Zealand (Avila & Charles 2018) and Europe (Tortorici et al. 2023), together with a

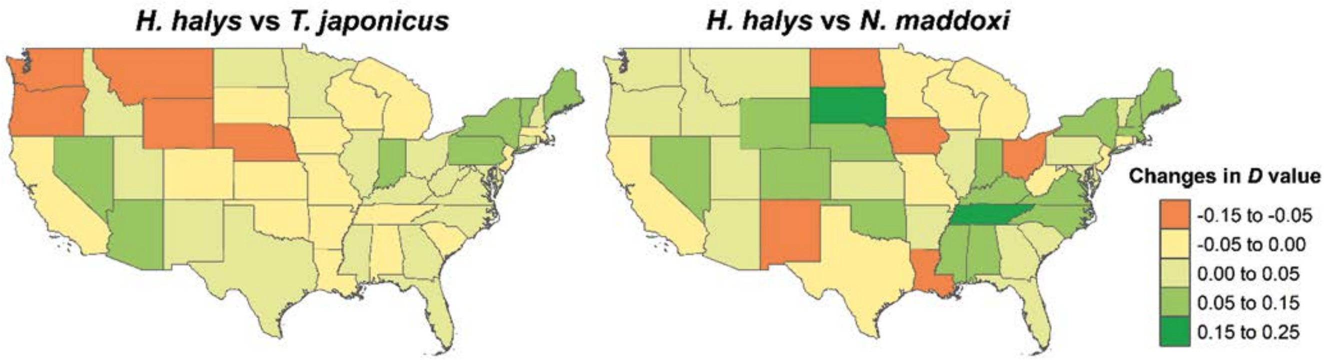

Fig. 5. Overlap changes in predicted habitat suitability for future climate scenarios for *H. halys* and *T. japonicus* (left) and *H. halys* and *N. maddoxi* (right). Overlap changes in Schoener's *D* values were predicted between current and future (2070s) climate scenarios; values greater than 0 indicate niche overlap is predicted to increase while values less than 0 indicate niche overlap is likely to decrease.

physiologically based demographic model used to assess *T. japonicus* (Gutierrez et al. 2023). Our study also builds on work that uses population dynamics modelling to estimate the potential impacts of biological control of *H. halys* in current and future climates (Illán et al. 2022).

Most *H. halys* populations were well predicted by its mechanistic model (Fig. S1); those populations where we failed to predict occurrence were distributed in high latitude or altitude areas, the failure of models to predict occurrence in these regions might be due to poor climate data in these regions (Kriticos & Leriche 2010), or because these specific populations have evolved and adapted to high latitude or altitude climates (Fig. S1). Similar results were observed in prior CLIMEX model predictions for East Asia (Kriticos et al. 2017), which failed to capture *H. halys* populations that occurred in western mountainous areas in China. Our results call for laboratory testing of thermal tolerance for these poorly-predicted populations, and novel methods that combine mechanistic and correlative models to predict *H. halys* distribution. The using of more meaningful and high resolutionary climate data could also improve *H. halys* distributional predictions (Gutierrez et al. 2023; Kriticos & Leriche 2010; Stoeckli et al. 2020).

Our study identified vast overlapping areas in habitat suitability between *H. halys* and two of its natural enemies and suggested areas where biological control may be most effective. Similar work involving *H. halys* and *T. japonicus* showed high overlap in Europe as well (Gutierrez et al. 2023). Perhaps not surprisingly, predicted niche overlap between *T. japonicus* and *H. halys* was generally higher than between *N. maddoxi* and *H. halys*. This could result from the fact that *T. japonicus* and *H. halys* have co-evolved in Asia (Avila & Charles 2018), whereas *N. maddoxi* is native to the US (Preston et al. 2020). Yet, all three species had generally high overlap across the US, suggesting both classical and conservation biological control may be key for management of invasive *H. halys*. However, some areas where niche overlap was predicted to be high, such as Florida, are areas where *T. japonicus* has not been found and where *H. halys* populations are not well established (Illán et al. 2022); a prior agent-based model also predicted difficulty for *H. halys* to experience population growth in Florida due to the shorter duration of time in which the 13 h photoperiod for termination and induction of diapause is met (McDougall et al. 2021; Nielsen et al. 2016). This shows that predictions of potential habitat suitability do not necessarily equate to species distributions or whether they will thrive in these suitable areas, and ongoing monitoring of all three species is needed across the US (Jiménez-Valverde et al. 2011).

Our study is novel in that we provide a simple way to incorporate physiology into correlative niche models for insect distribution modelling and assess potential overlap between two natural enemies and a key invasive species both in current and projected future climates. Through this analysis, we show that habitat overlap between the three species is likely to remain largely stable over the next 50 years. In some areas where *H. halys* populations are likely to become more restricted as temperatures warm, such as the southeast US, populations of *T. japonicus* and *N. maddoxi* are also likely to decline (Fig. 5). Yet, for states where climate change was predicted to negatively impact *H. halys*, impacts were weaker for the natural enemies, and niche overlap was predicted to increase with climate change. A similar result was found in Europe, where biological control impacts are predicted to increase due to climate change and greater expansion of suitable habitat for natural enemies (Gutierrez et al. 2023). In other areas of the US where all three species were predicted to have increased habitat suitability from climate change (northwest US), the habitat suitability for natural enemies was predicted to be greater than for *H. halys*, similarly resulting in a prediction of increased niche overlap in future climates. Our work shows that considering how multiple species distributions and habitat requirements may change in future climates is indispensable in implementing sustainable biological control (Lu et al. 2015).

As with all models of habitat suitability, our predictions must be interpreted cautiously, as they were subject to common limitations (Peterson et al. 2011). First, the future forecasts assumed that present climate niches of each of the three species will be conserved in 2070s. However, adaptation of invasive populations of *H. halys* or populations of the two natural enemies could alter these predictions, and natural enemies may not evolve similarly to pests (Sun et al. 2022). Second, although we combined mechanistic and correlative modeling approaches to enhance estimation of niche suitability, we were unable to obtain some trait data for *N. maddoxi* that might affect its performance, as has been produced for other microsporidia species (Méténier & Vivarès 2001). Third, our models assumed that all three species can eventually disperse into areas with suitable climates (Conti et al. 2021), but while *H. halys* is a broad generalist that can survive across many plant hosts, *T. japonicus* and *N. maddoxi* require stink bugs as hosts and are limited to areas occupied by these species. Other factors (e.g., insect behavior, local host availability, and overwintering sites) might also impact our model predictions.

Our study harnessed the most recent occurrence and physiological data that were available to calibrate habitat suitability models. Yet, as with all models, the quality of these input data can impact model predictions (Zhu & Peterson 2017). In turn, we used ensemble models, which is an effective method to reduce uncertainty (Araújo & New 2007), especially for species with few records (Breiner et al. 2018). We also used cross-validation, which is the best strategy to assess future models when independent testing data were not available (Valavi et al. 2019). We adopted these approaches to mitigate data- or model- based uncertainties in habitat suitability predictions. Given the inevitable uncertainty, continued field validations of biological control across regions of the US are needed to refine our model predictions.

In conclusion, our study linked a network of scientists across the US to conduct nationwide monitoring of an invasive species (*H. halys*) and two of its natural enemies to assess geographic dimensions of biological control. Our models predicted large areas of suitable climate for *T. japonicus* and *N. maddoxi* throughout the contiguous US are expected to overlap broadly with *H. halys*. We show that this overlap is likely to be largely stable in future climates, as all species are expected to respond similarly to climate change. Our work supports the notion that biological control can be a key component of *H. halys* management, as both natural enemies are expected to thrive in areas that *H. halys* occupies. More broadly, our study shows how linking large numbers of monitoring sites with models can allow for a relatively rapid assessment of biological control for invasive species. The method that we provided for incorporating physiological traits into correlative niche model could also be used for other insect's distribution prediction.

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