Journal of Economic Entomology, XX(XX), 2025, 1–8
https://doi.org/10.1093/jee/toaf175
Research

ENTOMOLOGICAL SOCIETY OF AMERICA
SHARING INSECT SCIENCE GLOBALLY

OXFORD

Forest Entomology

Ecological niche modeling and potential dispersal of emerald ash borer in the Pacific Northwest

Gengping Zhu[1,*], Max Ragozzino[2], Mark Cody Holthouse[2], Mattthew Mills[3], Jessica L. Celis[4], Stacy Johnson[4], and David W. Crowder[1]

[1]Department of Entomology, Washington State University, Pullman, WA, USA
[2]Oregon Department of Agriculture, Wilsonville, OR, USA
[3]Oregon Department of Forestry, Salem, OR, USA
[4]Bureau of Land Management, Oregon/Washington State Office, Grants Pass, OR, USA

*Corresponding author. Department of Entomology, Washington State University, Pullman, WA 99163, USA (Email: gengping.zhu@wsu.edu).

Subject Editor: Christopher Fettig

Received on 14 January 2025; revised on 16 June 2025; accepted on 25 June 2025

The emerald ash borer, *Agrilus planipennis* Fairmire (Coleoptera: Buprestidae), is a notorious invasive pest that can devastate ash trees, *Fraxinus* spp. L., and embedded communities. While emerald ash borer is established in eastern North America, it was recently detected in Forest Grove, Oregon and in Vancouver, British Columbia, raising concerns that it may spread across the Pacific Northwest riparian ecosystems dominated by ash. A quarantine zone has been established in Oregon, but future mitigation depends on assessing the spread to new regions. Here, we used habitat suitability models and dispersal simulations to predict the potential spread of emerald ash borer. Specifically, we compared climate spaces occupied by Oregon and British Columbia populations with other native and introduced populations, and then used habitat suitability models and dispersal simulations to predict future distributions. We show that the newly established Oregon and British Columbia populations currently occupy relatively narrow climate niche, and many suitable niche spaces are unoccupied in the Pacific Northwest, indicating potential for range expansion. We also show there are vast areas of suitable habitat that extend south of the present quarantine zone throughout inland western Oregon and north into Washington. In Vancouver, the most suitable habitat was found along the Fraser River, where emerald ash borer could disperse inland. Dispersal models suggest that, without intervention, emerald ash borer could disperse into Washington within 2 yr, throughout western Oregon in 15 yr, and reach California in 20 yr. Our work supports intensive quarantine efforts for emerald ash borer and identifies areas where monitoring and management efforts should focus.

Keywords: dispersal simulation, habitat suitability, invasive species, species distribution model.

Introduction

The temperate climate and ever-increasing human transport of plant materials into ports of entry across the Pacific Northwest make the region vulnerable to biological invasions, and the region has been deemed an invasive species hotspot (Epanchin-Niell et al. 2021, NatureServe 2021). Over the past 5 yr, the Pacific Northwest has been threatened by invasions from northern giant hornet, *Vespa mandarinia* (Zhu et al. 2020), Japanese beetle, *Popillia japonica* (Zhu et al. 2023), European green crab, *Carcinus maenas* (Washington Department of Fish & Wildlife 2024), and emerald ash borer, *Agrilus planipennis* Fairmire (Coleoptera: Buprestidae) (Oregon Department of Agriculture 2024). Early detection and rapid responses are the most cost-effective way to manage invaders, where models are linked with field work to guide strategies to anticipate and eradicate invaders (Valentin et al. 2018).

The emerald ash borer is among the most destructive invasive pests in the United States, where it has killed tens of millions of ash trees, *Fraxinus* spp., in 37 states (Herms and McCullough 2014). Emerald ash borer was initially believed to be host-specific to *Fraxinus* spp. (Anulewicz et al. 2008), but it is capable of attacking other trees in the Oleaceae family, such as white fringetree, *Chionanthus virginicu*

© The Author(s) 2025. Published by Oxford University Press on behalf of Entomological Society of America. All rights reserved. For commercial re-use, please contact reprints@oup.com for reprints and translation rights for reprints. All other permissions can be obtained through our RightsLink service via the Permissions link on the article page on our site—for further information please contact journals.permissions@oup.com.

Downloaded from https://academic.oup.com/jee/advance-article/doi/10.1093/jee/toaf175/8202831 by ESA Member Access user on 11 August 2025

and olive *s* L. (Cipollini 2015, 2025), *Olea europea* L. (Cipollini 2025), indicating risk of host range expansion. Emerald ash borer was not documented west of the Rocky Mountains until 2022 when it was first detected in Forest Grove, Oregon (Oregon Department of Agriculture 2024). In summer 2023, it was also found in Vancouver, British Columbia. Unmitigated, emerald ash borer may destroy Oregon ash, *Fraxinus latifolia* Benth., swales and sensitive riparian zones (Oregon Department of Agriculture 2024). Over the past 2 yr, the Oregon Department of Agriculture has set a quarantine area to slow the spread of emerald ash borer by restricting the movement of host materials. This controlled area includes counties with confirmed detections of emerald ash borer, which include Clackamas, Marion, Washington, and Yamhill counties as of 1 January 2025. To effectively mitigate the spread of emerald ash borer in Oregon and the broader Pacific Northwest, land and pest managers require information regarding the potential future occurrence of emerald ash borer.

Ecological niche models are widely used in invasion risk assessment. Yet, the reliability of models is based on several assumptions, including whether the model accounts for physiological tolerances that affect species distributions (Zhu et al. 2021). Ecological niche models also suffer from uncertainty in habitat suitability predictions, as different models have variations in their predictions (Araújo and New 2007). The integration of physiological and correlative models into ensembles could mitigate these effects, offering more reliable predictions than individual models. Further, combining habitat suitability predictions and dispersal simulations offers more dynamic distributions than static maps (Zhu et al. 2020, 2023). Models can also compare climate niche spaces occupied by native and introduced populations. Integration between models and field observations on the ground can best guide mitigation efforts.

Here, we leveraged field surveys of emerald ash borer with models to achieve 3 goals. First, we compared climate conditions occupied by emerald ash borer populations in Oregon and British Columbia with native populations in Asia and introduced populations in eastern North America and Europe. Second, we used ensemble models to estimate habitat suitability for emerald ash borer in the Pacific Northwest. Third, we used short- and long-distance dispersal simulations to predict the potential for emerald ash borer to expand beyond present observations in Forest Grove and Vancouver. Our models were validated with field observations of emerald ash borer in the Pacific Northwest, providing reliable support for guiding mitigation efforts. Our contribution provides critically needed decision support and can engage scientists and communities in early detection and rapid response efforts for this new invader.

Materials and Methods

Input Data

Emerald ash borer records were attained from Barker et al. (2023) and the Oregon Department of Agriculture, which coordinated field surveys where individual ash trees were checked for signs of emerald ash borer (Knight et al. 2014). Surveyors scored trees as (i) positive: insects or exit holes present, (ii) suspected: signs present (dead branches, epicormic shoots, or woodpecker foraging activity), or (iii) negative: no signs. Occurrence records in Vancouver, British Columbia, were obtained from the Vancouver Board of Parks and Recreation. In total, 2,910 cleaned records with 1 km distance between each other were obtained for analysis. We gathered 4 physiological traits for emerald ash borer (Barker et al. 2023): (i) lower development threshold (12.2 °C), (ii) growing degree days for the life cycle (450 DD), and (iii, iv) cold (−31 °C) or heat (36 °C) tolerant temperatures.

Our models incorporated climate and nonclimate variables affecting emerald ash borer. We gathered raster data on 7 climate variables: (i) annual mean temperature, (ii) mean temperature diurnal range, (iii) max temperature of the warmest month, (iv) min temperature of the coldest month, (v) annual precipitation, (vi) precipitation of the wettest month, and (vii) precipitation of the driest month (Karger et al. 2020). The difference between winter air and under-bark temperature minima can vary considerably (Vermunt et al. 2012). The under-bark winter temperatures experienced by emerald ash borer larvae could differ by more than 4 °C from minimum air temperatures in urban environments. Consequently, we added 4 °C to the minimum temperature of the coldest month (ie bio6, air temperature) for urban areas. Global urban areas were determined based on harmonized nighttime light observations (Zhao et al. 2022). We also considered the prevalence of deciduous broadleaf trees as a nonclimate predictor (Tuanmu and Jetz 2014), as this variable has been measured globally and captures hosts used by emerald ash borer. While emerald ash borer attacks primarily *Fraxinus* spp., and the distribution of ash may be an appropriate variable, other trees in the Oleaceae family also serve as hosts. Moreover, the distribution of ash and other hosts in the Oleaceae family was only available as presence or absence data, and could not be used as continuous predictors that are required in ecological niche models. For these reasons our models did not include the distribution of ash species themselves, although future models could incorporate such datasets if they become available.

Climate Niche Space Comparison

We compared climate niches occupied by emerald ash borer in distinct regions by associating bioclimatic variables with occurrence records in: (i) Oregon, (ii) British Columbia, (iii) Asia, (iv) eastern North America, and (v) Europe. We then used NicheA in R to visualize the realized niche occupied by each geographic population in a 2-dimensional plot, where each axis shows bioclimate variables collapsed into 2 principal components (Qiao et al. 2016); these 2 components summarized aspects of temperature and precipitation and explained 81.8% of the variation in bioclimate variables.

Habitat Suitability Models

We used (i) physiological model and (ii) correlative niche models to assess habitat suitability for emerald ash borer. Our physiological model assessed areas with climate conditions that allow for survival and development by relating emerald ash borer development temperature and growing thresholds to climatic variables in a spatial context. Global habitat suitability was calculated in a spatial raster (grid size 1 km) by multiplying a temperature index (ie temperature conditions above the lower development threshold), a growing index (ie temperature requirements for completing the life cycle), and a killing index (ie temperature conditions below the lethal extremes) of emerald ash borer (Grünig et al. 2020), which is similar to the method in the CLIMEX. Correlative niche models, in contrast, estimate habitat suitability by relating occurrence records to environmental variables (Peterson et al. 2011). We created models with 5 algorithms: (i) generalized additive, (ii) generalized linear, (iii) boosted regression tree (BRT), (iv) Maxent, and (v) random forest (RF). Generalized additive and linear models are statistical models, while BRTs, Maxent, and RF are machine learning approaches.

All correlative habitat suitability models were built with the *sdm* package in R (Naimi and Araújo 2016). Models were built using occurrence data from all accessible areas, delimited by buffering observed points at 400 km. Following best practices for Maxent, we used fine-tuned settings and a "random" method to select

Downloaded from https://academic.oup.com/jee/advance-article/doi/10.1093/jee/toaf175/8202831 by ESA Member Access user on 11 August 2025

10,000 pseudo-absence records from the "accessible" areas (Barve et al. 2011, Araújo et al. 2019). For other models, we selected 2,910 pseudo-absence records from "accessible" areas, which is equal to cleaned occurrence data (Barbet-Massin et al. 2012). After each individual model was created, we built an ensemble model that averaged the predictions of the 6 individual models.

Model Performance

For evaluating model performance, we used the Boyce index and the area under the curve (AUC) ratio of the partial receiver operating characteristic (Peterson et al. 2008). The detection records in Oregon and British Columbia served as testing points. The Boyce index measures how much model predictions differ from a random distribution of observed records across the prediction gradients; this index ranges from −1 to 1, with positive values closer to 1indicating stronger performance (Hirzel et al. 2006). AUC ratios take the quality of occurrence points into account and weight more on omission error, and ratios >1 indicate good performance. We also used bivariate maps and scatterplots to assess the uncertainty in predictions across the 6 models.

Dispersal Simulation

We used the MigClim package (Engler et al. 2012) to simulate emerald ash borer dispersal in the Pacific Northwest. MigClim simulates dispersal away from an incursion zone using a time step, which we set as 1 yr as emerald ash borer completes one generation per year (Engler et al. 2012). We used detection records in Oregon and British Columbia as the "incursion population." MigClim requires grid cells that indicate sites for potential establishment, which were identified using the lowest presence threshold to convert ensemble suitability predictions into binary values (suitable or unsuitable) (Pearson et al. 2007). This model's prediction of emerald ash borer represents areas of habitat that are at least as suitable as those where emerald ash borer has been observed in Oregon or British Columbia. We chose this threshold to maintain zero omission error in Oregon and British Columbia detections.

We ran simulations for 20 yr with both short- and long-distance dispersal. To estimate short-distance dispersal, we used data showing emerald ash borer spread at a rate of 20 km/yr in the eastern United States from 1998 to 2006 (Prasad et al. 2010). To estimate long-distance dispersal, we used data showing emerald ash borer spread in North America and Europe at around 47 km/yr from 2002 to 2018 (Webb et al. 2021). A dispersal kernel that assumed an exponential decline in movement at greater distances was adopted. Settings included as dispersal probability within any suitable cell as 1, which means all occupied patches can be sources of dispersal, and there were no barriers to dispersal.

Results

Climate Niche Space Comparison

The extracted bioclimatic variables from occurrence records show that Oregon and British Columbia emerald ash borer populations occupy a narrow range of annual mean temperature (Oregon: 10.9 to 11.6 °C; British Columbia: 10.46 to 10.66 °C) and precipitation (Oregon: 1,038 to 1,439 mm; British Columbia: 1,692 to 1,787 mm) (Fig. 1A). Comparing climate niches, the Oregon population overlapped with the eastern North American population but differed from the Asian and European populations (Fig. 1A). The Oregon population differed from all others in temperature extremes (Fig. 1B). Considering precipitation, the Oregon population overlapped with the Asian population but differed from eastern North American and European populations (Fig. 1C). The British Columbia population does not overlap with other populations in either temperature and precipitation dimensions (Fig. 1). Principal component 1 was associated with temperature and explained 57% of the variance, and principal component 2 was related to precipitation and explained 25% of variance. In these reduced dimensions, the Oregon population largely overlaps with the North American and Asian populations but differs from the European population (Fig. 1D).

Distributional Predictions

The RF attained the highest AUC ratio (1.95), followed by BRT (1.79), Maxent (1.78), and generalized additive model (GAM) (1.68). The generalized linear model (GLM) was the worst (AUC = 1.36). Ranked by Boyce index, the highest performing model was RF (0.88), followed by boost regression tree (0.82), Maxent (0.76), and generalized additive (0.28). The GLM had a value below 0 (-0.24). All detection testing points attained a suitability prediction of 0.42 in physiological models.

Individual models had variable habitat suitability predictions (Fig. 2). The Maxent, BRT, and RF models were the most conservative, with the fewest highly suitable areas (Fig. 2). In contrast, the physiological model and poor-performing GLM identified vast suitable habitat around the Cascade and Olympic mountains. Several models, particularly physiological model, generalized linear and additive models, identified large swaths of suitable habitats that extend directly to the south and north of the present quarantine zone and into the low elevations of the Cascade Mountain (Fig. 2). The suitable habitats were also predicted in northern Idaho by correlative models but not by physiological model (Fig. 2).

Our ensemble model showed good performance (AUC = 1.81; Boyce Index = 0.80), and identified areas where Oregon populations have already been detected as having high suitability and low uncertainty; this showed all habitat suitability models correctly identified the introduced sites as highly suitable (Fig. 3A). Using this model, emerald ash borer has considerable area of highly suitable habitat that extends to the south and north of present Oregon detections and into the low elevation areas around the Cascade Mountains (Fig. 3B). Most suitable habitat along the coast were overlapped with Oregon ash distribution (Fig. 3A). However, prediction uncertainty varied across regions. The suitable habitats identified in the east of present Oregon detections and in northern Idaho had great uncertainty in predictions (Fig. 3A), together with suitable habitats found along the Fraser River in Vancouver, British Columbia (Fig. 3C).

Dispersal Simulation

Simulations of short- and long-distance dispersal show that, without intervention, emerald ash borer populations could disperse from their current location into Washington in 2 yr (Fig. 4B) and reach California in 20 yr (Fig. 4A). All simulations suggest the beetle could spread across all of inland western Oregon within 15 yr and that most suitable areas in western Washington and northern California could be occupied in 20 yr (Fig. 4A). However, the unsuitable Pacific Coastal Ranges could be a geographic barrier against further westward expansion (Fig. 3A). In British Columbia, the emerald ash borer could disperse inland along the Fraser River (Fig. 4C).

Discussion

The establishment of emerald ash borer in Pacific Northwest is of great concern, as it could devastate ash swales, sensitive riparian

Downloaded from https://academic.oup.com/jee/advance-article/doi/10.1093/jee/toaf175/8202831 by ESA Member Access user on 11 August 2025

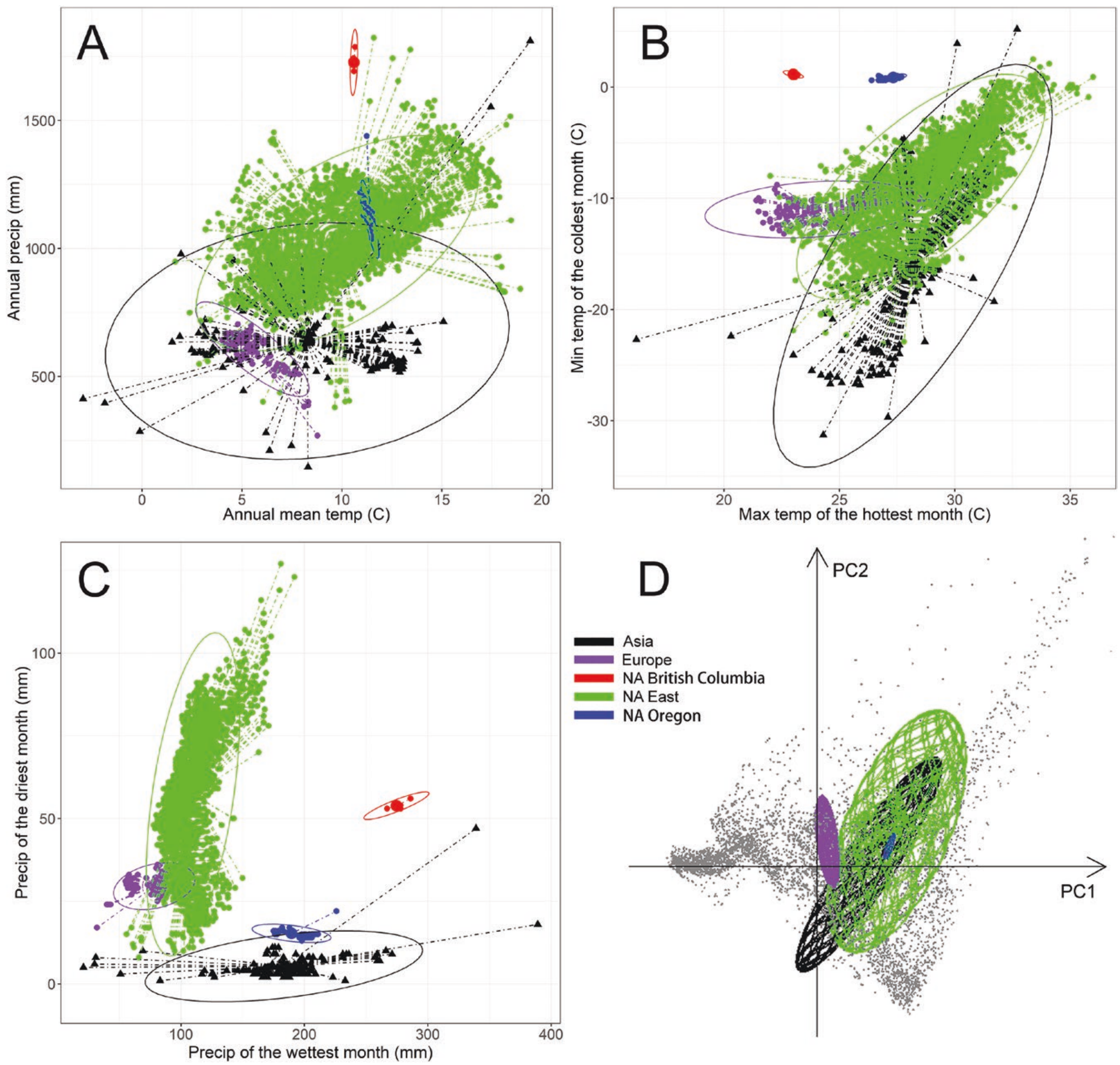

Fig. 1. Comparing climate niche spaces occupied by the introduced Oregon and British Columbia populations with populations in Asia, Europe, and eastern North America. Scatterplots show A) annual trends, B) extreme temperature, or C) extreme precipitation conditions associated with the above populations. Panel D) shows the realized climate niche occupied by emerald ash borer populations in reduced dimensions (principal components PC1 and PC2). The British Columbia population was not shown in Panel D) due to there being insufficient data to generate an ellipsoid volume.

zones, and urban forests, as well as species that depend on these habitats (Herms and McCullough 2014, Maze et al. 2024, Sun et al. 2024). As with other invasive species, predicting potential distributions and dispersal of early established populations is a key step in monitoring and pest management (Keller et al. 2008, Valentin et al. 2018).

Our climate niche space comparisons suggest the Oregon and British Columbia emerald ash borer populations currently occupy relatively narrow temperature and precipitation window. Oregon populations fell within the broader climate niche of eastern North American and native Asian populations. The British Columbia population did not overlap with other populations (Fig. 1). There could be several reasons for this observation. First, the newly established populations may have the potential to access a broader climate niche space, but have only occupied a small niche space. If so, the established populations could continue to expand into other suitable areas and fill these niche spaces in the Pacific Northwest (Fig. 3). Climate niche filling in introduced areas has been observed in many invasive species (Strubbe et al. 2013). If, however, the newly established populations have undergone a bottleneck or adapted to novel conditions (Wiens et al. 2019), then the realized climate niche space may truly be smaller in Oregon and British Columbia than other regions, which may restrict the established population from further spreading. Whether or not the realized niche of the Oregon and British Columbia populations has evolved to Pacific Northwest climate conditions remains unclear. Future laboratory tests of physiological tolerances could reveal whether niche evolution has occurred during the Pacific Northwest establishment.

Downloaded from https://academic.oup.com/jee/advance-article/doi/10.1093/jee/toaf175/8202831 by ESA Member Access user on 11 August 2025

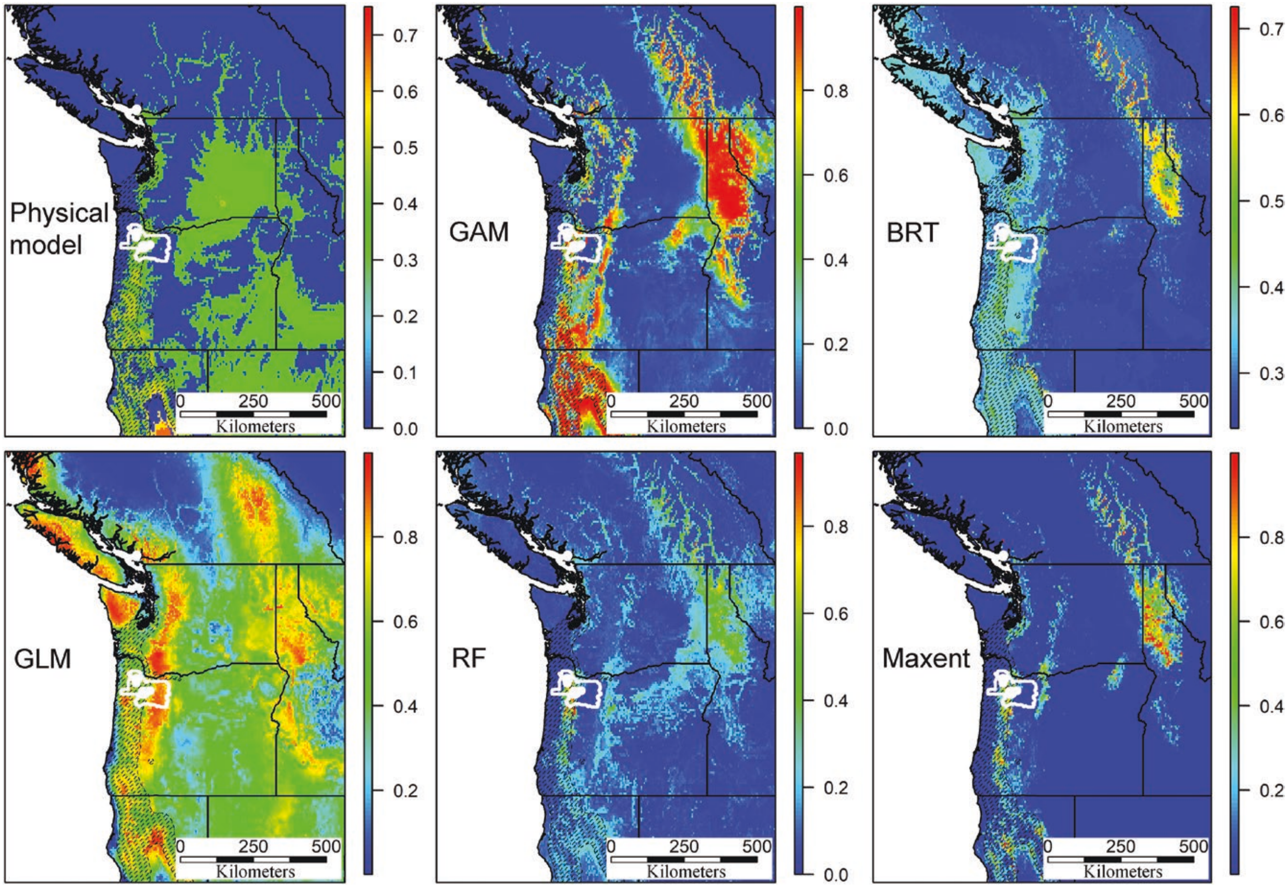

Fig. 2. Individual model habitat suitability predictions in the Pacific Northwest. The habitat suitability was estimated by a physiological model (physical model) and 5 correlative niche models, ie GAM, BRT, GLM, RF, and Maxent. Warm red colors indicate high suitability, white dots denote emerald ash border detections in Oregon and British Columbia, white solid line denotes the quarantine areas established by the Oregon Department of Agriculture, and the slash area denotes Oregon ash distribution.

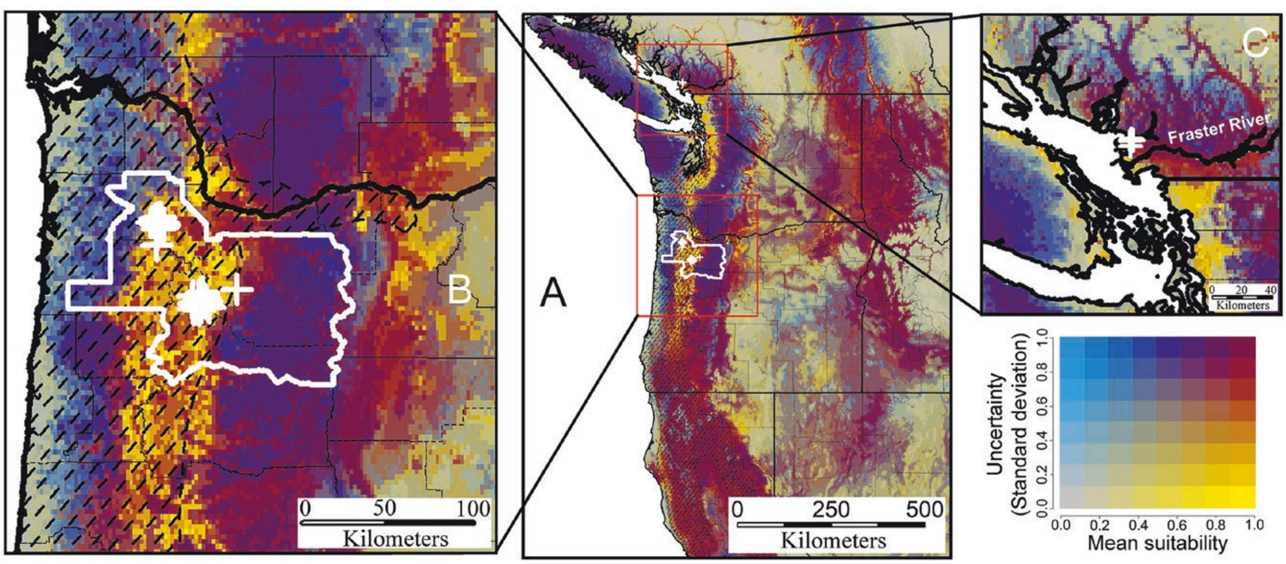

Fig. 3. Ensemble habitat suitability model prediction for emerald ash borer in the Pacific Northwest. Bivariate maps denote ensemble predictions and their uncertainty; the increasing intensities of yellow represent increasing habitat suitability, and increasing blue represent increasing uncertainty. Insert panels on central map A) denote ensemble prediction around recent detections (white plus) in Oregon B) and British Columbia C). The white solid line denotes the quarantine areas established by the Oregon Department of Agriculture, and the slash area denotes Oregon ash distribution.

Downloaded from https://academic.oup.com/jee/advance-article/doi/10.1093/jee/toaf175/8202831 by ESA Member Access user on 11 August 2025

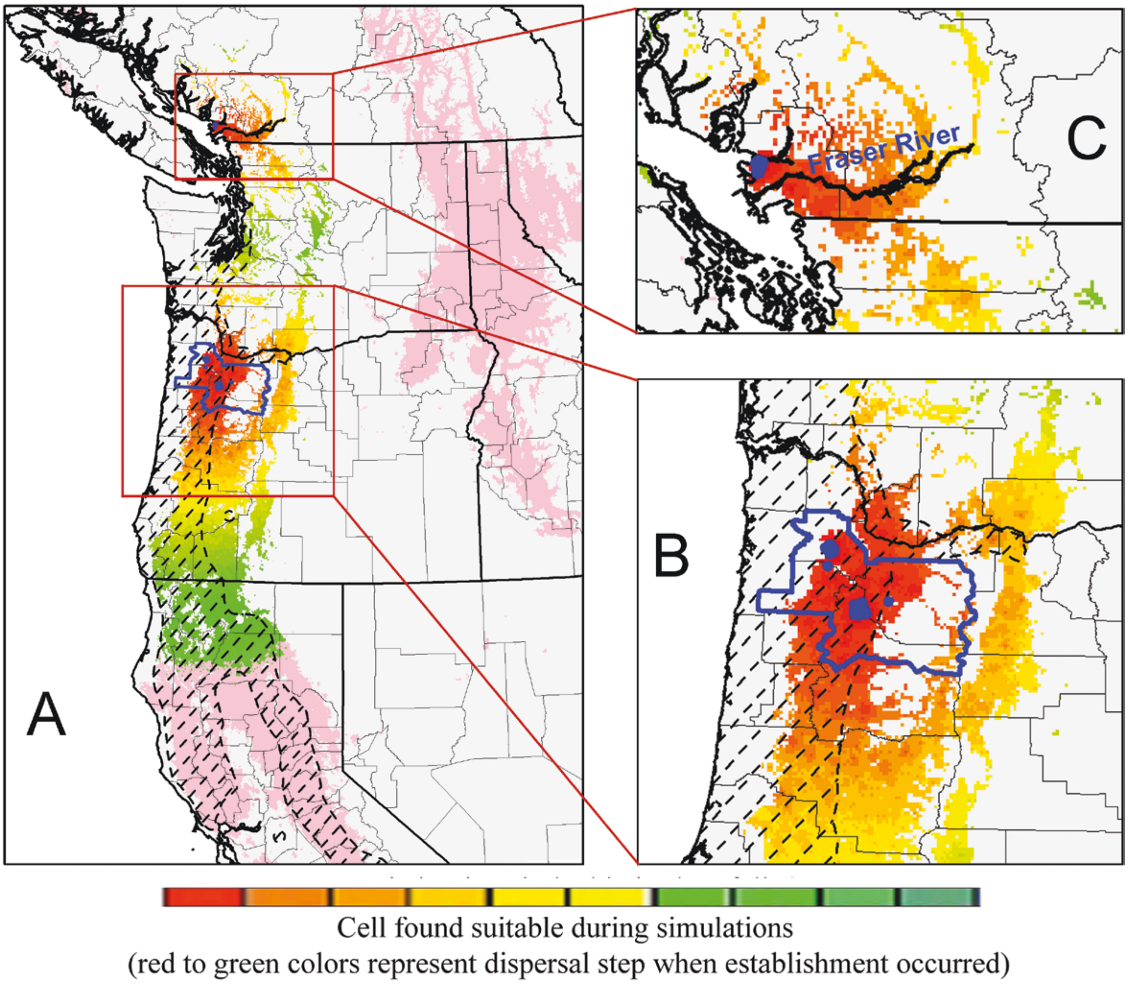

Fig. 4. Dispersal simulation of emerald ash borer in the Pacific Northwest. Each distinct color represents 2 dispersal steps (total 20) (red = current; yellow = 10-yr prediction; green = 20-yr prediction). Insert panels on the left map A) denote enlargement around recent detections (blue dots) in Oregon B) and British Columbia C). Blue line denotes the quarantine area established by the Oregon Department of Agriculture, slash area denotes Oregon ash distribution.

Our models all effectively predicted that areas where emerald ash borer could be found in Oregon had high suitability and low uncertainty. Areas to the south and north of present detections were also predicted to have high suitability and low uncertainty (Fig. 3B), and they overlapped with Oregon ash distributions (Fig. 3A). However, we found uncertainty in predictions across models in other areas, especially areas with high suitability, a common limitation in habitat suitability modeling (Zhu et al. 2023). For example, the suitable habitat found on the east of Oregon detections, northern Idaho (Fig. 3B) and around the Fraser River in British Columbia (Fig. 3C) had great uncertainty in predictions. It is unlikely that emerald ash borer will establish outside of its known niche, and areas predicted to have low suitability also have low uncertainty. However, areas with predicted high habitat suitability will not necessarily be invaded (Araújo and Peterson 2012). Host plants, geographic barriers to dispersal, natural enemies or other competitors, or even microclimatic variation are factors that might deter establishment of an invader in suitable areas. For example, there are suitable habitats identified in northern Idaho (Fig. 3); however, the lack of ash trees in northern Idaho might prevent emerald ash borer establishment there. Our models also included the prevalence of deciduous broadleaf trees as a nonclimate predictor, given that the distribution of ash was not available as a continuous predictor variable. However, this might have caused our models to overpredict the amount of suitable habitat, for instance, in areas where broadleaf trees are prevalent but these do not include ash. Thus, while vast suitable habitats were identified to the south, east, and north of the present quarantine zone in Oregon and northern Idaho, emerald ash borer may not spread to these regions even without interventions to mitigate the expansion.

The emerald ash borer quarantine boundaries in Oregon are defined largely on established administrative (ie county lines) rather than natural boundaries due to feasibility and policy implications. This means the quarantine area is also limited by focusing detection within the quarantine zone, risking undetected infestations outside of the zone. Furthermore, due to county-level granularity, uninfested areas may be encompassed within the quarantine boundaries, and it is important to continue to prevent and minimize the movement of untreated ash wood materials, such as firewood, nursery stock, and wood waste. Without aggressive intervention to mitigate the expansion, our models suggest emerald ash borer will spread beyond the current quarantine boundary zone through natural or anthropogenic means.

Our dispersal model suggests that without mitigation, emerald ash borer will disperse into Washington in 2 yr, California in 20 yr, and across all of inland western Oregon within 15 yr. These may be conservative estimates as they are based on gradual historical

Downloaded from https://academic.oup.com/jee/advance-article/doi/10.1093/jee/toaf175/8202831 by ESA Member Access user on 11 August 2025

expansion rates (ie in eastern United States, and Europe) (Prasad et al. 2010) and largely discount that human transportation to any (disjunct) suitable area at any time is possible (Fig. 3). As an example, emerald ash borer was detected for the first time in British Columbia, Canada in summer 2023, but it is not yet clear whether this long range movement was from Oregon, eastern Canada, or elsewhere (Invasive Species Council of British Columbia 2024). Conversely, preliminary data (Ragozzino unpublished) suggest that the Oregon emerald ash borer population may exhibit a 2-yr life cycle and have a slower-than-anticipated natural dispersal. The natural spread of emerald ash borer may also be mitigated by biological control agents (Duan et al. 2018, Quinn et al. 2022). We also assumed no geographic barriers in dispersal simulations; however, the unsuitable Pacific Coastal Ranges or the absence of ash trees in northern Idaho could be barriers against expansion (Fig. 3A).

Given the potential for emerald ash borer to rapidly expand its distribution, it is probable that the quarantine zone in Oregon will extend eastward and southward, encompassing highly suitable habitats in these regions. Coordination between Washington and Oregon agencies will be essential to restrict movement across state borders. However, logistical and technological constraints impede comprehensive monitoring in all suitable locations. Currently, there are very few early detection tools for emerald ash borer, with trapping strategies showing inconsistent results (Francese et al. 2011), prompting researchers to adopt rigorous visual inspection and tree-girdling approaches (Mercader et al. 2013). The habitat suitability models developed in this study may be used to inform monitoring strategies and optimize resource allocation for surveillance and eradication initiatives (Zhu et al. 2024). For example, the suitable habitat identified around the Fraser River (Fig. 4C) could be prioritized for surveillance initiatives in British Columbia.

Acknowledgements

We thank E. Perkins, A. Vogelgesang, J. Bartosz, H. Brewer, R. Fredlund, M. Morris, and O. Forester for contributing to the survey data. We also thank the many cooperating staff from Oregon Department of Forestry, Clean Water Services, Oregon Metro, Clackamas Soil and Water Conservation District, Marion Soil and Water Conservation District, Tualatin Soil and Water Conservation District, Multnomah Soil and Water Conservation District, Yamhill Soil and Water Conservation District, USDA APHIS PPQ, USFS, and countless others for their continuing support with several emerald ash borer management and data collection efforts.

Author contributions

Gengping Zhu (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Validation, Visualization, Writing—original draft [equal]), Max Ragozzino (Data curation, Investigation, Validation, Writing—review & editing [equal]), Mark Holthouse (Data curation, Funding acquisition, Investigation, Project administration, Supervision, Validation, Writing—review & editing [equal]), Mattthew Mills (Data curation, Investigation, Validation, Writing—review & editing [equal]), Jessica L. Celis (Funding acquisition, Validation, Writing—review & editing [equal]), Stacy Johnson (Funding acquisition, Project administration, Validation, Writing—review & editing [equal]), and David W. Crowder (Funding acquisition, Project administration, Supervision, Validation, Writing—review & editing [equal])

Funding

Funding for this publication was provided by the Oregon Department of Agriculture, Oregon Department of Forestry, and the Oregon/Washington Bureau of Land Management.

Conflicts of interest. None declared.

References

Anulewicz AC, McCullough DG, Cappaert DL, et al. 2008. Host range of the emerald ash borer (Agrilus planipennis Fairmaire) (Coleoptera: Buprestidae) in North America: results of multiple-choice field experiments. Environ. Entomol. 37:230–241. https://doi.org/10.1603/0046-225x(2008)37[230:hrotea]2.0.co;2

Araújo MB, New M. 2007. Ensemble forecasting of species distributions. Trends Ecol. Evol. 22:42–47. https://doi.org/10.1016/j.tree.2006.09.010

Araújo MB, Peterson AT. 2012. Uses and misuses of bioclimatic envelope modeling. Ecology 93:1527–1539. https://doi.org/10.1890/11-1930.1

Araújo MB, Anderson RP, Barbosa AM, et al. 2019. Standards for distribution models in biodiversity assessments. Sci. Adv. 5:4858–4874. https://doi.org/10.1126/sciadv.aat4858

Barbet-Massin M, Jiguet F, Albert CH, et al. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol. Evol. 3:327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x

Barker BS, Coop L, Duan JJ, et al. 2023. An integrative phenology and climatic suitability model for emerald ash borer. Front. Insect Sci. 3:1239173. https://doi.org/10.3389/finsc.2023.1239173

Barve N, Barve V, Jiménez-Valverde A, et al. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecol. Model. 222:1810–1819. https://doi.org/10.1016/j.ecolmodel.2011.02.011

Cipollini D. 2015. White fringetree as a novel larval host for emerald ash borer. J. Econ. Entomol. 108:370–375. https://doi.org/10.1093/jee/tou026

Cipollini D. 2025. The potential risk posed by emerald ash borer to cultivated and wild olive trees. Forests 16:357. https://doi.org/10.3390/f16020357

Duan JJ, Bauer LS, Van Driesche RG, et al. 2018. Progress and challenges of protecting North American ash trees from the emerald ash borer using biological control. Forests 9:142. https://doi.org/10.3390/f9030142

Engler R, Hordijk W, Guisan A. 2012. The MIGCLIM R package – seamless integration of dispersal constraints into projections of species distribution models. Ecography 35:872–878. https://doi.org/10.1111/j.1600-0587.2012.07608.x

Epanchin-Niell R, McAusland C, Liebhold A, et al. 2021. Biological invasions and international trade: managing a moving target. Rev. Environ. Econ. Policy 15:180–190. https://doi.org/10.1086/713025

Francese JA, Fraser I, Lance DR, et al. 2011. Efficacy of multifunnel traps for capturing emerald ash borer (Coleoptera: Buprestidae): effect of color, glue, and other trap coatings. J. Econ. Entomol. 104:901–908. https://doi.org/10.1603/ec11038

Grünig M, Calanca P, Mazzi D, et al. 2020. Inflection point in climatic suitability of insect pest species in Europe suggests non-linear responses to climate change. Global Change Biol. 26:6338–6349. https://doi.org/10.1111/gcb.15313

Herms DA, McCullough DG. 2014. Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Annu. Rev. Entomol. 59:13–30. https://doi.org/10.1146/annurev-ento-011613-162051

Hirzel AH, Lay GL, Helfer V, et al. 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecol. Model. 199:142–152. https://doi.org/10.1016/J.ECOLMODEL.2006.05.017

Invasive Species Council of British Columbia. 2024. Emerald ash borer. Invasive Species Council of British Columbia. https://bcinvasives.ca/invasives/emerald-ash-borer/. Accessed 26 Nov 2024.

Karger DN, Schmatz DR, Dettling G, et al. 2020. High-resolution monthly precipitation and temperature time series from 2006 to 2100. Sci. Data 7:248. https://doi.org/10.1038/s41597-020-00587-y

Downloaded from https://academic.oup.com/jee/advance-article/doi/10.1093/jee/toaf175/8202831 by ESA Member Access user on 11 August 2025

Keller RP, Frang K, Lodge DM. 2008. Preventing the spread of invasive species: economic benefits of intervention guided by ecological predictions. Conserv. Biol. 22:80–88. https://doi.org/10.1111/j.1523-1739.2007.00811.x

Knight KS, Flash BP, Kappler RH, et al. (2014) Monitoring ash (*Fraxinus* spp.) decline and emerald ash borer (*Agrilus planipennis*) symptoms in infested areas. U.S. Department of Agriculture, Forest Service, Northern Research Station.

Maze D, Bond J, Mattsson M. 2024. Modelling impacts to water quality in salmonid-bearing waterways following the introduction of emerald ash borer in the Pacific Northwest, USA. Biol. Invasions 26:2691–2705. https://doi.org/10.1007/s10530-024-03340-3

Mercader RJ, McCullough DG, Bedford JM. 2013. A comparison of girdled ash detection trees and baited artificial traps for *Agrilus planipennis* (Coleoptera: Buprestidae) detection. Environ. Entomol. 42:1027–1039. https://doi.org/10.1603/EN12334

Naimi B, Araújo MB. 2016. sdm: a reproducible and extensible R platform for species distribution modelling. Ecography 39:368–375. https://doi.org/10.1111/ecog.01881

NatureServe. 2021. iMapInvasives. ArcGIS StoryMaps. https://storymaps.arcgis.com/stories/4ea4876c3a2d4a16b9cbdf3ff8ffe4d3. Accessed 29 May 2024.

Oregon Department of Agriculture. 2024. Survey and treatment projects for emerald ash borer in Oregon. https://www.oregon.gov/oda/programs/IPPM/SurveyTreatment/Pages/EmeraldAshBorer.aspx. Accessed 26 Nov 2024.

Pearson RG, Raxworthy CJ, Nakamura M, et al. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J. Biogeogr. 34:102–117. https://doi.org/10.1111/j.1365-2699.2006.01594.x

Peterson AT, Papeş M, Soberón J. 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecol. Model. 213:63–72. https://doi.org/10.1016/j.ecolmodel.2007.11.008

Peterson AT, Soberón J, Pearson RG, et al. 2011. Ecological niches and geographic distributions. Princeton University Press.

Prasad AM, Iverson LR, Peters MP, et al. 2010. Modeling the invasive emerald ash borer risk of spread using a spatially explicit cellular model. Landsc. Ecol. 25:353–369. https://doi.org/10.1007/s10980-009-9434-9

Qiao H, Peterson AT, Campbell LP, et al. 2016. NicheA: creating virtual species and ecological niches in multivariate environmental scenarios. Ecography 39:805–813. https://doi.org/10.1111/ecog.01961

Quinn NF, Gould JS, Rutledge CE, et al. 2022. Spread and phenology of *Spathius galinae* and *Tetrastichus planipennisi*, recently introduced for biocontrol of emerald ash borer (Coleoptera: Buprestidae) in the northeastern United States. Biol. Control 165:104794. https://doi.org/10.1016/j.biocontrol.2021.104794

Strubbe D, Broennimann O, Chiron F, et al. 2013. Niche conservatism in non-native birds in Europe: niche unfilling rather than niche expansion. Glob. Ecol. Biogeogr. 22:962–970. https://doi.org/10.1111/geb.12050

Sun J, Koski T-M, Wickham JD, et al. 2024. Emerald ash borer management and research: decades of damage and still expanding. Annu. Rev. Entomol. 69:239–258. https://doi.org/10.1146/annurev-ento-012323-032231

Tuanmu M-N, Jetz W. 2014. A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. Glob. Ecol. Biogeogr. 23:1031–1045. https://doi.org/10.1111/geb.12182

Valentin RE, Fonseca DM, Nielsen AL, et al. 2018. Early detection of invasive exotic insect infestations using eDNA from crop surfaces. Front. Ecol. Environ. 16:265–270. https://doi.org/10.1002/fee.1811

Vermunt B, Cuddington K, Sobek-Swant S, et al. 2012. Temperatures experienced by wood-boring beetles in the under-bark microclimate. Forest Ecol. Manag. 269:149–157. https://doi.org/10.1016/j.foreco.2011.12.019

Washington Department of Fish & Wildlife. 2024. Species facet of European green crab. https://wdfw.wa.gov/species-habitats/invasive/carcinus-maenas. Accessed 26 Nov 2024.

Webb CR, Mona T, Gilligan CA. 2021. Predicting the potential for spread of emerald ash borer (*Agrilus planipennis*) in Great Britain: what can we learn from other affected areas? Plants People Planet 3:402–413. https://doi.org/10.1002/ppp3.10195

Wiens JJ, Litvinenko Y, Harris L, et al. 2019. Rapid niche shifts in introduced species can be a million times faster than changes among native species and ten times faster than climate change. J. Biogeogr. 46:2115–2125. https://doi.org/10.1111/jbi.13649

Zhao M, Cheng C, Zhou Y, et al. 2022. A global dataset of annual urban extents (1992–2020) from harmonized nighttime lights. Earth Syst. Sci. Data 14:517–534. https://doi.org/10.5194/essd-14-517-2022

Zhu G, Illan JG, Looney C, et al. 2020. Assessing the ecological niche and invasion potential of the Asian giant hornet. Proc. Natl. Acad. Sci. USA 117:24646–24648. https://doi.org/10.1073/pnas.2011441117

Zhu G, Illan JG, Crowder DW. 2021. The use of insect life tables in optimizing invasive pest distributional models. Ecography 44:1501–1510. https://doi.org/10.1111/ecog.05710

Zhu G, Oeller LC, Wojahn R, et al. 2023. Potential distribution and spread of Japanese beetle in Washington State. J. Econ. Entomol. 116:1458–1463. https://doi.org/10.1093/jee/toad116

Zhu G, Osorio-Olvera L, Pfeiffer V, et al. 2024. Enhancing monitoring to promote early detection and eradication of invasive species. Ecography 2025:e07105. https://doi.org/10.1111/ecog.07105

Downloaded from https://academic.oup.com/jee/advance-article/doi/10.1093/jee/toaf175/8202831 by ESA Member Access user on 11 August 2025