Biol Invasions
DOI 10.1007/s10530-017-1398-0

ORIGINAL PAPER

Mapping of the Asian longhorned beetle's time to maturity and risk to invasion at contiguous United States extent

Alexander P. Kappel · R. Talbot Trotter · Melody A. Keena · John Rogan · Christopher A. Williams

Received: 2 September 2015 / Accepted: 21 February 2017

Abstract *Anoplophora glabripennis*, the Asian Longhorned Beetle (ALB), is an invasive species of high economic and ecological relevance given the potential it has to cause tree damage, and sometimes mortality, in the United States. Because this pest is introduced by transport in wood-packing products from Asia, ongoing trade activities pose continuous risk of transport and opportunities for introduction. Therefore, a geographic understanding of the spatial distribution of risk factors associated with ALB invasions is needed. Chief among the multiple risk factors are (a) the potential for infestation based on host tree species presence/absence, and (b) the temperature regime as a determinant of ALB's growth time to maturity. This study uses an empirical model of ALB's time to maturity as a function of temperature, along with a model of heat transfer in the wood of the host and spatial data describing host species presence/absence data, to produce a map of risk factors across the conterminous United States to define potential for ALB infestation and relative threat of impact. Results show that the region with greatest risk of ALB infestation is the eastern half of the country, with lower risk across most of the western half due to low abundance of host species, less urban area, and prevalence of cold, high elevations. Risk is high in southeastern states primarily because of temperature, while risk is high in northeastern and northern central states because of high abundance of host species.

Keywords Asian Longhorned Beetle · *Anoplophora glabripennis* · Invasion · Colonization · Risk · Maturity · United States · Modeling · Degree days · Temperature · Host species · Distribution · Instar

Introduction

As humans travel and transport goods across the planet, other species become relocated in the process. This results in many introductions of species into novel landscapes (NAS 2002) and an approximated $120 billion in damage each year caused by an estimated 50,000 non-native species in the United States (Pimentel et al. 2005). One such introduction is the current invasion of *Anoplophora glabripennis*, commonly referred to as the Asian Longhorned Beetle (ALB), into North America. ALB is native to China and the Korean Peninsula (Smith et al. 2009; Keena

Electronic supplementary material The online version of this article (doi:10.1007/s10530-017-1398-0) contains supplementary material, which is available to authorized users.

A. P. Kappel (✉) · J. Rogan · C. A. Williams
Graduate School of Geography, Clark University, 950 Main Street, Worcester, MA 01610, USA
e-mail: apkappel@gmail.com

R. T. Trotter · M. A. Keena
U.S. Forest Service, Northern Research Station, 51 Mill Pond Rd, Hamden, CT 06514, USA

Published online: 30 June 2017

and Moore 2010). ALB is of high economic and ecological relevance because of the potential for widespread tree damage and even mortality that it induces in many broadleaf tree species through larval feeding in the cambium and xylem (Smith et al. 2009). With potential to impact property values, tourism, forest products industry, aesthetics, and ecosystem services due to tree mortality following infestation (GAO 2006), ALB and its current, and future, potential spatial distributions are of significant interest to policy makers, and environmental and civil managers.

In a study of urban forests in nine large American cities, it was estimated that ALB could kill up to 30% of trees and destroy up to 35% of canopy cover, resulting in damage collectively valued at $669 billion (Nowak et al. 2001). In the US, between 1998 and 2006, the Animal Plant Health Inspection Service (APHIS) assessed the costs of eradication measures at $249 million (GAO 2006), a figure that includes the costs for survey and detection, tree removal, public-outreach, and prophylactic treatments of landscape trees with pesticides. To date, APHIS has implemented an eradication program comprised of removal and destruction of all trees with signs of beetle infestation, the only method currently deemed effective for containing the spread of infestations (Keena and Moore 2010).

This study aims to provide a US-wide assessment of the threat of ALB by developing a new data product characterizing the rate of ALB population development combined with host species distribution. The method combines knowledge of the temperature-dependent maturation of ALB with climate data across the US to map the number of years required for ALB to reach maturity and emerge from a tree, a proxy for population growth rate. The study also considers host species abundance to focus on areas that are known to be vulnerable. Our approach is distinct from prior efforts to characterize the spatial distribution of ALB risk, which have tended to rely on niche modeling and climate matching as described below.

Infestation biology

The process of invasion by non-native insect species such as ALB can be described as occurring in phases of arrival, establishment, and spread (Liebhold and Tobin 2008). The known pathways for the introduction of ALB to new locations include solid wood packing materials used in international trade (Smith et al. 2009). As such, ALB has generally been found around ports of entry, surrounding areas, and along routes of transportation leaving these areas (Smith et al. 2009). In North America ALB has been found in warehouses in Canada and in 17 states across the United States (Smith et al. 2009). Infestations in North America have been found in the Northeast, including the New York City area, the Chicago area, New Jersey, the Toronto area, Ontario, Canada, Worcester, MA, Boston, MA, and Bethel, Ohio. Adult ALB has also been found in Sacramento, CA, indicating risk for the western United States as well.

Host trees susceptible to ALB can be described broadly (and with safer margins) by genus, or more specifically, based only on the list of species known to support beetle development. Meng et al. (2015) lists these genera and species. While a complete list of known hosts is included in ‘Supporting Information Table 1’, some of the genera demonstrating susceptibility to ALB include *Acer* (Maples), *Aesculus* (Buckeyes and Horse Chestnuts), *Alnus* (Alders), *Betula* (Birches), *Fagus* (Beeches), *Fraximus* (Ashes), *Populus* (Poplars, Aspens, Cottonwoods), *Salix* (Willows), and *Ulmus* (Elms).

The spread of ALB on the landscape following initial establishment, can be described simply as a series of smaller-scale dispersals and establishments. As such, the conditions that drive establishment success (i.e. a suitable physical environment, and suitable hosts) play a major role in determining the ability of a species to expand its geographic range. Studies in natural forests in South Korea, where ALB is native but uncommon, indicate that the beetle’s natural habitat consists of riparian, edge-defined habitats (Williams et al. 2004). Research by Shatz et al. (2013) in Worcester, Massachusetts provides additional support for an edge preference. This pattern in an introduced population is consistent with broader understanding, as ALB is known in its native range to infest areas of man-made-landscapes such as monocultures, urban, industrial, and residential areas, street and yard trees, woodlots, nature preserves, and parks (Smith et al. 2009) which are all areas likely to be defined by fragmentation and edges. In the case of the ALB, as with many poikilothermic organisms, one of the primary determinants of the suitability of the physical environment is temperature. The native climatic range of this species includes cold hardiness zones that span from southern Mexico to southern Canada (Keena and Moore 2010), indicating widespread potential for population establishment and spread throughout the United States (Townsend Peterson and Vieglais 2001; MacLeod et al. 2002; Hu et al. 2009; Townsend Peterson and Scachetti-Pereira 2004).

Effects of temperature on ALB

Insect life history processes such as development, survival, and reproduction are greatly affected by temperature (Keena and Moore 2010). When predicting the potential geographical range of a species or developing phenological models to predict population dynamics and timing of various life-stages (for planning control/survey programs), knowledge regarding the response of insects to temperature is critical (Keena and Moore 2010).

Previous publications have indicated ALB is primarily univoltine, with sub-portions of the population requiring two years to complete development, citing Hua et al. (1992) as summarized by Lingafelter and Hoebeke (2002), and Li and Wu (1993) as described by Hu et al. (2009). The development time is determined by both the cumulative heat load, defined by local heating degree days (*HDD*), and the timing of oviposition, as eggs laid in the fall may not develop until the following spring (Keena and Moore 2010). In the United States, female ALB lay eggs from July to November (Keena and Moore 2010). Initially, the first through third instar larvae will feed in the cambial region, late third and later instars will feed on the xylem (Keena and Moore 2010), and the final instar will create a cavity in the outer xylem in which it pupates (Keena and Moore 2010) before becoming an adult and emerging from the tree, a process which requires time to scleritize and chew through the remaining xylem, phloem, and bark. This process is also temperature dependent as described in Sánchez and Keena (2013).

Modeling spatial potential for infestations

Despite regulations to prevent transport and spread of disease and insects through treatment of wood materials used in international shipping (ISPM 15 2009), wood boring insects continue to be intercepted in U.S. ports (Haack et al. 2014), though rates of arrival may be decreasing. Therefore, management efforts are often reactive (as with the APHIS response) in nature (Townsend Peterson 2003), though efforts are under way to expand the ability to proactively identify areas of vulnerability (e.g., Shatz et al. 2013; Townsend Peterson and Vieglais 2001; MacLeod et al. 2002; Hu et al. 2009; Townsend Peterson and Scachetti-Pereira 2004).

One of the major approaches available to predict the population behavior of an invading species is based on the concept of "climate-matching" (NAS 2002). This approach is derived from Grinnell's (1917, 1924) concept of ecological niches as a limiting factor on the potential distribution of a species. It is assumed that species are able to establish populations in locations only if the conditions in that location fit within the ecological limitations of the invading species. This approach has been applied to a broad diversity of species' invasions (Townsend Peterson 2003), including numerous studies regarding the invasive potential of ALB at large (sometimes continental) extents (Townsend Peterson and Vieglais 2001; MacLeod et al. 2002; Hu et al. 2009; Townsend Peterson and Scachetti-Pereira 2004).

In a study by Townsend Peterson and Vieglais (2001), ecological niche modeling for ALB, based on temperature and precipitation, indicated suitable habitat across a large portion of the eastern United States with high suitability in the region south of the Great Lakes. The Pacific coast, where much of the cargo from Asia arrives in North America, was predicted to be largely inhospitable to ALB. Another study (MacLeod et al. 2002), used the climate-matching computer program CLIMEX to identify the distribution of ALB suitable habitat for Asia, North America, and Europe using temperatures, precipitation regimes, and cold, hot, dry, and wet stress indices. Data from this study, composed of points and associated risk assessment values, were then mapped by Hu et al. (2009), indicating much of the United States was suitable for ALB, with suitability decreasing towards northern latitudes, high elevations in western mountain ranges, and around coastal Mississippi and Louisiana. A third study (Townsend Peterson and Scachetti-Pereira 2004) used the Genetic Algorithm for Rule-set Prediction (GARP) to model ecological niches and potential geographic distributions in North America. This model combined outbreak simulation with the suitability of habitat and determined that ALB could potentially invade a large portion of eastern North America but only limited areas of western North America.

The purpose of this study was to incorporate the factors of host species abundance and temperature-dependent development to spatially predict the number of years required for ALB to reach maturity and emerge from a tree, i.e. the generation time (a proxy for population growth rate), as well as areas that may be vulnerable to infestation due to the presence of suitable host-tree species. These data, in combination, provide a form of threat assessment for the landscape following introduction of the beetles.

Here, we expand on these assessments of landscape suitability for ALB in the continental United States by linking a newly developed phenology model for ALB with high spatial and temporal resolution climate data derived from the Parameter-elevation Relationships on Independent Slopes Model (PRISM www.prism.oregonstate.edu) and the distribution and abundance of host trees described by the U.S. Forest Service Forest Inventory and Analysis program (FIA www.fia.fs.fed.us).

Methodology

This study develops and analyzes a map of ALB time to maturity and risk of invasion for the contiguous United States. The core of this approach relies on the temperature-dependent nature of ALB development. The general approach consisted of using continental scale surface air temperatures to estimate temperatures under the bark of host trees (the environment to which the beetles are exposed), and using these under-bark temperatures to drive an empirically-derived relationship between temperature-controlled accumulated degree days and the speed of beetle maturation, here described by 'years to maturity'. The speed of beetle maturation was used as a metric of the relative risk of ALB population growth, as time to maturity is a dominant factor in determining population growth rates. The resulting output map was then filtered with two variants of a spatial filter of host tree species to estimate susceptibility to invasion by the beetle. Implementation involved the following three key steps, each described further below: (1) estimating daily climate-normal minimum and maximum under-bark temperatures; (2) estimating ALB years to maturity; and (3) masking with host presence and summary statistics.

Estimating daily minimum and maximum under-bark temperatures

Daily minimum (*TMIN*) and maximum temperature (*TMAX*) data covering the period from 1983 to 2012 (inclusive) was obtained from the PRISM Climate Group website, http://www.prism.oregonstate.edu/recent/. These data, which are provided at a 4 km resolution, were then averaged to produce daily minimum and maximum temperature normals for each 4 km location.

Daily normals were interpolated to a time step of 15-minutes using the 'wave' method described by Reicosky et al. (1989). The wave method employs three modified sine functions, each describing a different portion of the day. The shape and position of the functions is determined using three variables, maximum temperature (*TMAX*), minimum temperature (*TMIN*), and time of sunrise (*TOS*). The first sine function, which describes the cooling period between midnight and the current days' *TOS*, is defined by the previous days' *TMAX*, the current days' *TMIN*, and the temporal distance between them defined by the current days' *TOS*. The second sine function, which describes the warming period between the current days *TOS* and an assumed constant daily temperature peak of 2 pm, is defined by the current days' *TMIN*, the current days' *TMAX*, and the temporal distance between them, again defined by the current days' *TOS*. The third sine function defines cooling similarly to the first, but in this case from 2 pm to midnight in such a way that allows for a smooth transition into the next days' *TMIN*. The corresponding equations

for $0 \le \boldsymbol{H} < \boldsymbol{TOS}$:

$$\boldsymbol{T}(\boldsymbol{H}) = \boldsymbol{TAVE} + \boldsymbol{AMP} \times \cos\left(\frac{\pi \times (\boldsymbol{H} + 10)}{10.0 + \boldsymbol{TOS}}\right) \tag{1}$$

for $\boldsymbol{TOS} \le \boldsymbol{H} \le 14$:

$$\boldsymbol{T}(\boldsymbol{H}) = \boldsymbol{TAVE} - \boldsymbol{AMP} \times \cos\left(\frac{\pi \times (\boldsymbol{H} - \boldsymbol{TOS})}{14.0 - \boldsymbol{TOS}}\right) \tag{2}$$

for $14 < \boldsymbol{H} \leq 24$:

$$\boldsymbol{T}(\boldsymbol{H}) = \boldsymbol{TAVE} + \boldsymbol{AMP} \times \cos\left(\frac{\pi \times (\boldsymbol{H} - 14)}{10.0 + \boldsymbol{TOS}}\right) \tag{3}$$

where $\boldsymbol{TOS}$ is the time of sunrise in hours, $\boldsymbol{T}(\boldsymbol{H})$ is the temperature at any hour, $\boldsymbol{H}$ is time in hours, and $\boldsymbol{TAVE}$ and $\boldsymbol{AMP}$ are defined as $\boldsymbol{TAVE} = (\boldsymbol{TMIN} + \boldsymbol{TMAX})/2$ and $\boldsymbol{AMP} = (\boldsymbol{TMAX} - \boldsymbol{TMIN})/2$, respectfully.

Daily time of sunrise was defined based on each grid cell's latitude and longitude and equations obtained from NOAA, at http://www.esrl.noaa.gov/gmd/grad/solcalc/calcdetails.html. This approach provides time in UTC format and was converted to a local time with an offset defined by 24 (hours) times the fraction of longitudinal distance from the prime meridian out of a total possible 360°.

Quarter-hourly air temperatures were used in conjunction with a modified version of the Newtonian Cooling Model from Vermunt et al. (2012) to generate quarter-hourly estimates of under-bark temperature. Conceptually, the Newtonian Cooling Model dampens and lags air temperature fluctuations with the following equation:

$$\boldsymbol{Tu}_{\mathbf{t}+\Delta\mathbf{t}} = \boldsymbol{Tu}_{t} + \boldsymbol{K}(\boldsymbol{Ta}_{\mathbf{t}+\Delta\mathbf{t}} - \boldsymbol{T}_{t}) \tag{4}$$

where $\boldsymbol{Tu}$ is under-bark temperature, $\boldsymbol{Ta}$ is air temperature, $\boldsymbol{K}$ is an empirical constant determined to be 0.11 for an hourly time step but adjusted here to 0.0275 (=0.11/4) for quarter-hourly application, and the subscripts **t** and **t + Δt** refer to the previous and current time steps, respectively.

A one-day spin up to the model was used for day 1 of year 1, cycling through that day's air temperature series and stabilizing under-bark temperature within this 96-interval time period. The process then cycled throughout the year, with each quarter-hourly interval stored for use with the ALB phenology model.

The above approach allowed us to incorporate a couple of key phenomena deemed important for assessing climatological controls on temperature and thus ALB development. First, daily temperature is sensitive to latitudinal and seasonal variations in day length, determined in this methodology by *TOS*. Second, it considers lags and dampening in under-bark temperatures relative to ambient air temperatures, thus providing a more realistic representation of the temperatures experienced by the beetles.

Estimating rates of ALB maturation

The 'years to maturity' factor defining ALB maturation speed was modeled with a modified version of the phenology model described in Trotter and Keena (2016). Briefly summarized, the phenology model estimates years to maturity by determining the instar and life-stage specific accumulation of heating degree days based on instar and life-stage specific heating degree day requirements, using daily minimum and maximum temperatures. Life-stage specific *HDD* sums and upper and lower critical temperatures were derived from published empirical laboratory studies (Sánchez and Keena 2013; Keena and Moore 2010; Keena 2006). Upper critical temperatures of ~40 °C were generalized by Keena and Moore (2010), though we recognize that these temperatures would rarely be observed in wood in a forested setting, particularly in the environments where hosts genera (such as *Acer*) are likely to be common. Based on this and the analysis of the phenology model (Trotter and Keena 2016) this parameter was superfluous, and functionally removed by setting the upper critical temperature arbitrarily at 50 °C. The model was further modified in two ways for use in estimating patterns of voltanism on the landscape. First, the original model used daily minimum and maximum temperatures to estimate the accumulation of heating degree days, however, to allow for heat transfer through host wood, temperature increments were changed to 15 min increments to yield 96 daily time steps. Daily *HDD* was then calculated as:

$$HDD_{daily} = \frac{\sum_{n=1}^{96} \max(Tu_n - T_{crit}, 0)}{96} \tag{5}$$

where Tu_n is under-bark temperature at each time-step and T_{crit} is the stage-specific low temperature threshold. This process was used to produce *HDD* values for each life-stage, for each day. The phenology model was then run for each grid cell's annual *HDD* series in the contiguous United States domain to estimate years to maturity.

The increase in temporal resolution resulted in increased computation requirements. To compensate for part of the increased processing time, the phenology model was also modified by simplified beetle instars. Rather than beetles progressing though variable numbers of instars as described in Trotter and

Keena (2016), the variable instars were pooled into a synthetic "ultimate instar" category based on Keena and Moore (2010).

Masking with host presence and summary statistics

The years to maturity map was filtered with two variants of a spatial mask of host tree species presence/absence data. This step removed areas from the map where the beetle cannot survive due to an absence of suitable hosts. Host species masks were constructed by combining presence/absence data, provided by the USDA Forest Service's Forest Inventory and Analysis program (http://www.fia.fs.fed.us), with spatial extents of urban areas, provided by the United States Census Bureau (https://www.census.gov/geo/maps-data/data/cbf/cbf_ua.html). Urban areas were included because they may contain planted, non-native tree species that may be vulnerable. This masking was conducted in two variants in a best and worst case scenario. The best case scenario included all species known to be vulnerable to infestation which were present in the Forest Inventory and Analysis dataset. These species are listed in 'Supporting Information Table 1'. This scenario is considered best case because it includes only species that have so far been observed as infested by ALB, and assumes that no additional species will be found vulnerable. In this study, this best case scenario is referred to as the 'species scenario.' In contrast, the worst case scenario included all genera known to be vulnerable to infestation and their associated species, which were present in the FIA dataset, even if not all of these species are known to be vulnerable to ALB. These species are listed in 'Supporting Information Table 2' and this worst case scenario is referred to as the 'genus scenario.'

State boundaries and boundaries for the top 100 largest urban municipalities (by population) were then used to generate summary statistics describing ALB 'years to maturity.' Summary statistics included mean and standard deviation, and minimum and maximum. Also, a percent vulnerable area statistic was developed based on the grid cell percentage of the state's area that could potentially host ALB, and a percent vulnerable timber statistic was calculated based on a state's vulnerable mean basal area of timber divided by that state's total mean basal area of timber. Mean basal area is representative of tree cross-sectional stem area in square feet per acre.

Results

Simulated under-bark temperatures and heating degree-days

The conversion from ambient to under-bark temperatures results in both a temporal lag and a dampening of the temperature signal. As can be seen in the example locations shown in Fig. 1, the maximum and minimum under-bark temperatures are less extreme when compared to that day's ambient temperatures. Also, the occurrence of the under-bark minima and maxima occur later in the day than their ambient temperature counterparts. When looking at annual temperatures and (egg specific) *HDD* accumulation in the Fig. 2 test case, *HDD* accumulation begins as soon as temperatures begin to exceed an egg's lower critical threshold of 10.2 °C. It is apparent that in Georgia, where temperatures are almost always above the lower critical threshold, *HDD* are generally consistently accumulating. This is in contrast to Maine, where temperatures are only seasonally above the lower critical threshold, a factor restricting the annual accumulation of *HDD*. In one year, the Maine case study has accumulated just under 1000 *HDD* while the Georgia case study has accumulated over 3000 *HDD*.

Simulated years to ALB maturation

It is important to note that the egg-specific annual accumulation of *HDD* in Fig. 2 serves as only a test case and does not accurately reflect the variety of ALB development stages. In the phenology model there are a variety of ALB life stages including (in order) an initial egg, successive instars (1–8), the ultimate instar, the pupa, a scleritizing adult, an emerging adult, and an emergence from tree adult. Figure 3 displays these successive life stages as they relate to individual, stage-specific, accumulation of *HDD*, as well as how many years it takes for a beetle to develop from an egg to the final 'emergence from tree' adult. As can be seen in this figure, every time a beetle graduates from one stage to the next, the *HDD* sum resets to zero. This is because each instar has its own *HDD* definitions (based in unique temperature thresholds required for

Fig. 1 A 7 day test case showing the relationship between ambient air temperature, under-bark air temperature, and daily heating degree-days (*HDD*) from May 1st through May 7th

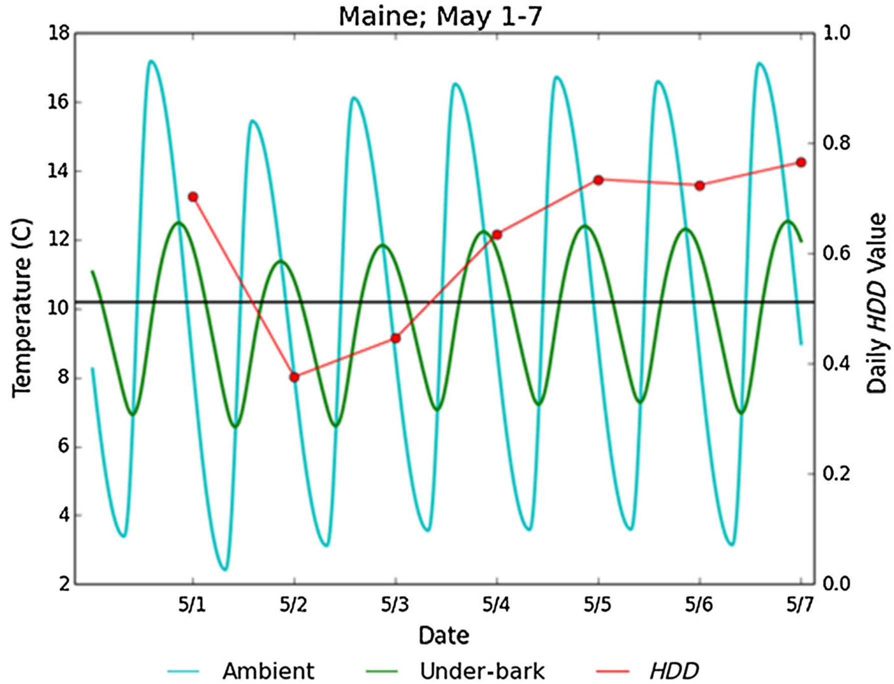
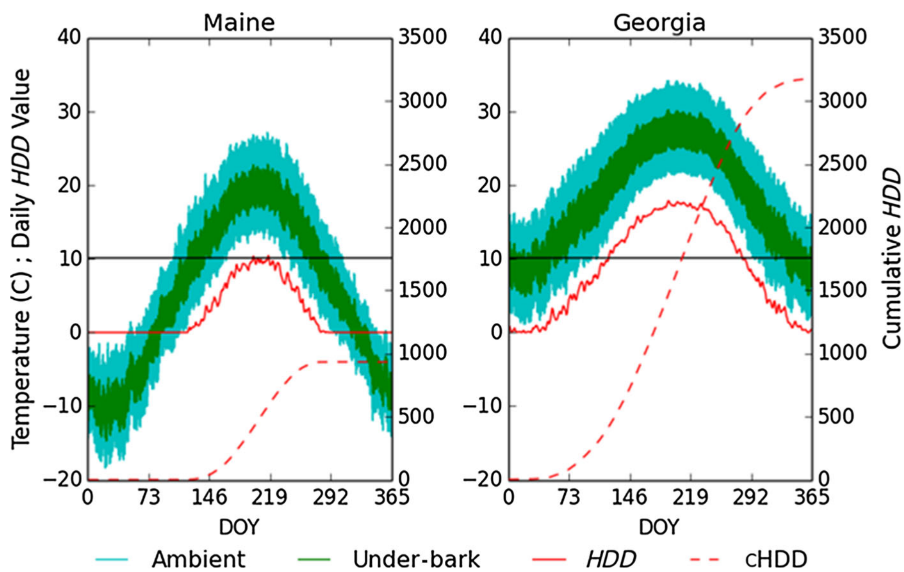


Fig. 2 Annual test cases showing the relationship between ambient air temperature, under-bark air temperature, daily *HDD*, and cumulative *HDD* (cHDD) for a full year in both Maine and Georgia. The *black horizontal line* is the lower critical temperature of 10.2 °C for an ALB egg



HDD accumulation and unique numbers of *HDD* required for graduation). Also, curved accumulation profiles occurring around the coldest parts of the year (this is most apparent in the Maine graph, characterized by flat sections of zero *HDD* accumulation, during winter temperatures below the lower critical threshold) are a result of the increasing availability of heat above the threshold in the spring, therefore steepening the curve, and decreasing availability of heat above the threshold in the fall, therefore diminishing the curve. In contrast, straight lines represent *HDD* accumulation during parts of the year that are warm enough to allow for maximum *HDD* accumulation. Years to maturity is defined by the moment at which the beetle reaches its final life stage. As shown in Fig. 3, the Georgia example yields maturity in

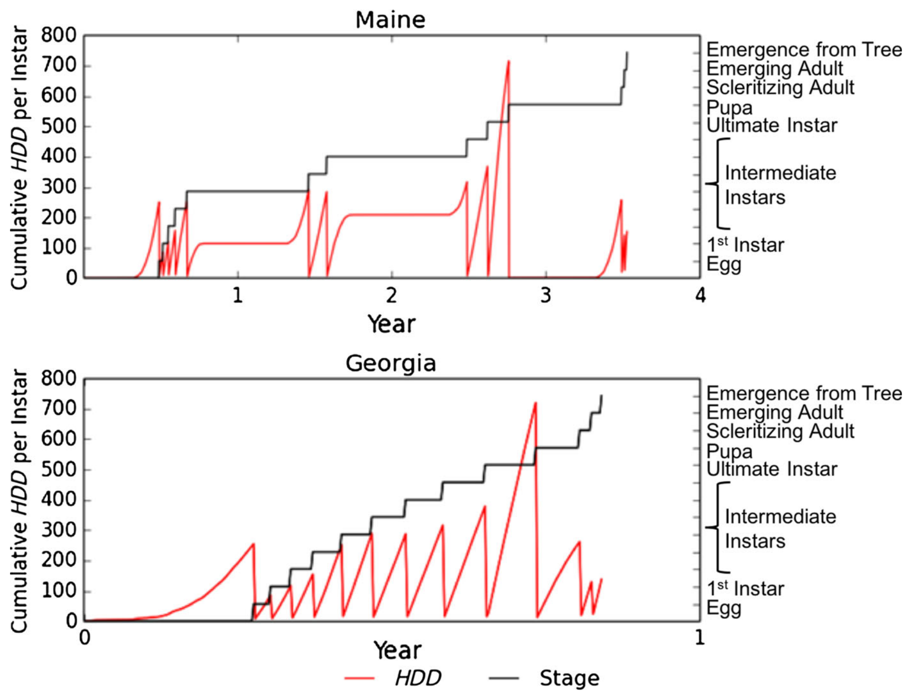


Fig. 3 Annual test cases showing the relationship between cumulative *HDD* per instar and ALB life stage development from initial 'egg' to 'emergence from tree' adult in both Maine and Georgia

under 1 year, while the Maine example yields maturity in over three years.

Continental pattern of risk of invasion and time to maturity

The spatial distribution of potential risk of invasion, regardless of scenario, indicates a larger distribution of host-species in the eastern contiguous United States when compared to the western contiguous United States. Regions devoid of known host-species include an area surrounding the Mississippi River, the mid-western plains, the arid west, parts of the mid-west south of the Great Lakes, and interior California and Florida. Areas deemed unsuitable because of years to maturity greater than 10 years included swaths of high elevation in the mountainous west and high elevations in the north-east. The only major differences between the genus and species scenarios are the additional presence of host species along the west coast and in Texas for the genus scenario. The full extent of each species inclusion scenario is displayed in 'Supporting Information Fig. 1'.

The spatial distribution of years to maturity shows correspondence with latitude and elevation (Fig. 4 species scenario, 'Supporting Information Fig. 2' genus scenario). The longest times to maturity occur in the mountainous west, the mountainous north-east, and the north-west. Times defining these regions include values greater than 4 years, with the highest times of 7–10 years occurring only at high elevations. The shortest times occur in the most southern latitudes. Times defining these regions include values of approximately 0.5–1 years in the Deep South and along the Gulf of Mexico, and 2 years in a large swath throughout the middle third of the eastern contiguous United States. State specific statistics describing this variable are found in Table 1 for the species scenario and 'Supporting Information Table 3' for the genus scenario.

Areas of high risk to ALB

For either scenario, states with a mean time to maturity of less than one year include Florida, Louisiana, and Texas. The states Mississippi, Georgia, Alabama, South Carolina, Oklahoma, Arkansas, North Carolina, Tennessee, the District of Columbia, Kansas, Missouri, Kentucky, Delaware, Maryland, Illinois, Virginia, Indiana and New Jersey each had mean times to maturity of less than 2 years (Table 1, 'Supporting Information Table 3'). Among these, the District of Columbia, Alabama, Georgia, South Carolina, and

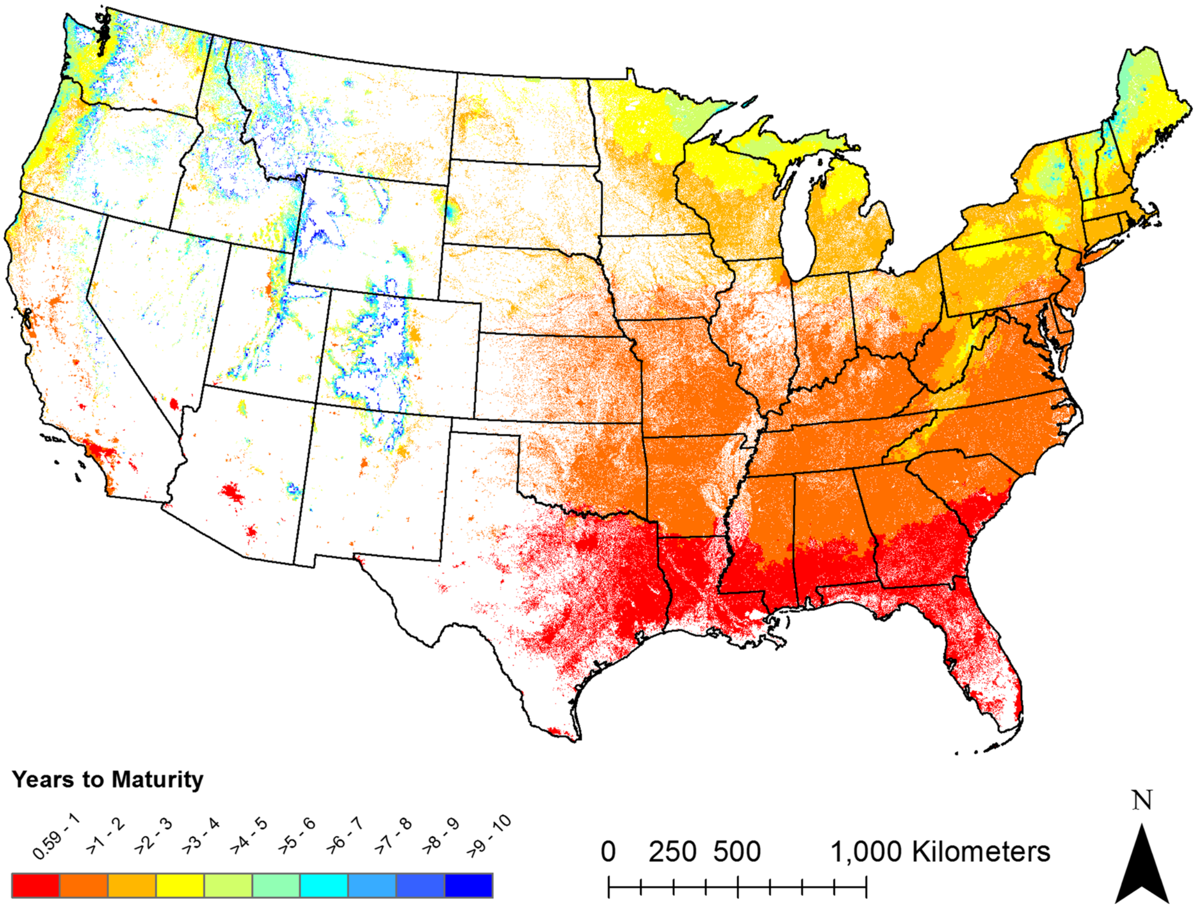


Fig. 4 ALB years to maturity for viable host area defined by urban areas and species scenario risk extent

Tennessee all had greater than 90% of their state areas at risk, and all states (excluding Illinois, Texas, and Kansas) had greater than 50% of state areas at risk.

Regardless of scenario, states that were concluded to have over 50% of their area at potential risk to ALB (defined as urban area, area containing host species, and area where ALB can complete growth in ≤10 years) include the District of Columbia, West Virginia, Connecticut, New Hampshire, Massachusetts, Maine, Vermont, Pennsylvania, Alabama, New York, Rhode Island, South Carolina, North Carolina, Virginia, Georgia, Tennessee, Mississippi, New Jersey, Kentucky, Michigan, Maryland, Delaware, Wisconsin, Arkansas, Missouri, Ohio, Louisiana, Indiana, Minnesota, Florida, and Oklahoma (Table 1, 'Supporting Information Table 3').

Under the species scenario condition ('Supporting Information Table 1'), states with greater than 50% of their timber's basal area vulnerable to ALB include North Dakota, Indiana, Ohio, Iowa, Wisconsin, New York, Kansas, Vermont, Michigan and Minnesota. Under the genus scenario condition ('Supporting Information Table 2'), states with greater than 50% of their timber's basal area vulnerable to ALB includes all of the aforementioned as well as the additional Pennsylvania, Indiana, Connecticut, West Virginia, and New Hampshire. Associated spatial patterns of the percent of timber that is vulnerable are displayed in Fig. 5 and 'Supporting Information Fig. 3' for species and genus scenarios, respectively. Figure 6 and 'Supporting Information Fig. 4', displaying the total basal area that is vulnerable to attack for species and genus scenarios, respectively, are included as reference by which to relate the percentages.

Among the top 100 most populous urban areas that were sampled for years to maturity and the

Table 1 Summary statistics for states and District of Columbia, sorted by percent area at risk, given the species scenario

	Name	Mean	STD	Min	Max	% Area	% Timber
State summary statistics: species vulnerability scenario							
1	District of Columbia	1.568	0.019	1.540	1.616	100.000	35.293
2	West Virginia	2.235	0.561	1.594	4.553	98.527	37.887
3	Connecticut	2.504	0.149	1.751	3.441	98.428	36.644
4	New Hampshire	3.665	1.212	2.488	9.630	97.708	33.381
5	Massachusetts	2.697	0.353	2.395	3.773	95.988	31.684
6	Maine	4.114	0.876	2.600	9.633	95.096	28.384
7	Vermont	3.835	0.826	2.480	6.595	95.089	43.460
8	Pennsylvania	2.607	0.476	1.589	3.726	94.890	39.135
9	Alabama	1.144	0.243	0.751	1.660	94.773	19.605
10	New York	3.124	0.757	1.644	7.606	94.666	45.235
11	Rhode Island	2.488	0.035	2.405	2.633	93.895	29.292
12	South Carolina	1.209	0.210	0.808	2.416	93.546	21.345
13	North Carolina	1.561	0.384	1.282	3.778	93.499	29.788
14	Virginia	1.774	0.370	1.386	4.518	93.414	30.097
15	Georgia	1.093	0.289	0.764	2.468	92.160	17.774
16	Tennessee	1.562	0.212	1.321	4.389	91.177	30.127
17	Mississippi	1.087	0.227	0.770	1.482	88.745	21.114
18	New Jersey	1.912	0.347	1.589	2.677	88.248	26.982
19	Kentucky	1.613	0.094	1.389	2.474	86.674	36.512
20	Michigan	3.221	0.721	1.770	7.649	86.270	43.221
21	Maryland	1.753	0.360	1.518	3.488	84.491	38.600
22	Delaware	1.631	0.018	1.592	1.726	84.374	39.663
23	Wisconsin	3.006	0.513	2.384	4.595	80.236	46.059
24	Arkansas	1.363	0.126	0.858	1.652	79.294	14.412
25	Missouri	1.603	0.054	1.370	1.797	73.048	15.622
26	Ohio	2.146	0.341	1.627	2.658	71.375	47.502
27	Louisiana	0.822	0.060	0.712	1.252	68.518	19.331
28	Indiana	1.849	0.306	1.512	2.480	59.942	47.529
29	Minnesota	3.417	0.721	2.438	6.622	58.502	42.030
30	Florida	0.738	0.053	0.592	0.847	53.890	7.457
31	Oklahoma	1.351	0.088	0.866	1.704	50.302	11.235
32	Illinois	1.766	0.293	1.471	2.504	43.441	40.393
33	Washington	4.894	1.584	1.723	9.674	39.043	4.643
34	Iowa	2.098	0.348	1.649	2.627	31.252	46.123
35	Kansas	1.575	0.055	1.400	2.373	28.749	45.186
36	Texas	0.829	0.126	0.619	1.693	25.835	6.414
37	Oregon	4.406	1.465	1.778	9.800	23.966	3.061
38	Idaho	5.408	1.774	1.751	9.677	20.243	2.202
39	Nebraska	2.057	0.368	1.633	2.767	16.685	39.276
40	Colorado	5.838	2.184	1.586	9.677	15.983	12.420
41	Utah	5.281	2.000	0.803	9.666	12.138	6.559
42	Montana	5.676	2.205	2.493	9.668	11.624	2.553
43	California	2.537	1.781	0.619	9.986	11.004	0.679
44	North Dakota	3.065	0.491	2.490	4.562	10.954	57.246

Table 1 continued

	Name	Mean	STD	Min	Max	% Area	% Timber
45	Wyoming	6.255	2.081	2.485	9.677	10.013	5.663
46	South Dakota	3.024	1.222	1.740	8.594	9.464	12.828
47	New Mexico	4.501	2.346	0.847	9.644	4.412	1.694
48	Nevada	4.651	2.155	0.627	9.663	3.625	1.315
49	Arizona	2.740	2.466	0.619	9.636	3.479	1.164

'% Area' refers to the vulnerable grid cell percent of a state's area and '% Timber' refers to the vulnerable percent of a state's timber basal area. Mean, standard deviation, min, and max, refer to time to maturity

associated zonal statistics ('Supporting Information Table 4'), there were 23 with a mean time to maturity of less than 1 year, and there were 67 with a mean time to maturity of less than 2 years. In these urban areas, time to maturity ranged from a mean of 0.628 years in McAllen, TX to a mean of 3.568 years in Seattle, WA.

Discussion and conclusions

The results of this study can be used to approximate an ALB risk profile for the conterminous US. These results characterize aspects of the potential impact of invasive ALB populations as this factor depends on their rates of maturation (in time to maturity, a variable

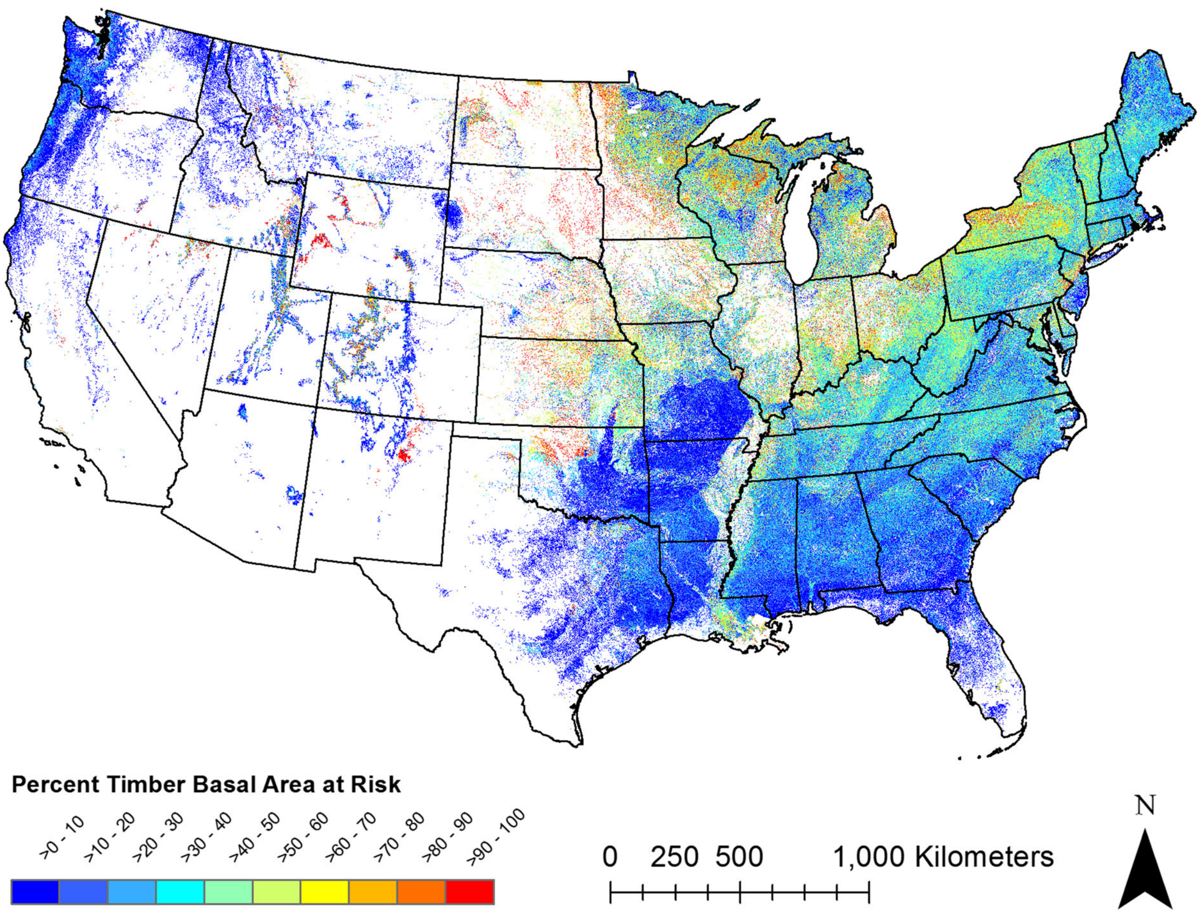


Fig. 5 The percent timber basal area at risk to ALB given a species scenario risk extent

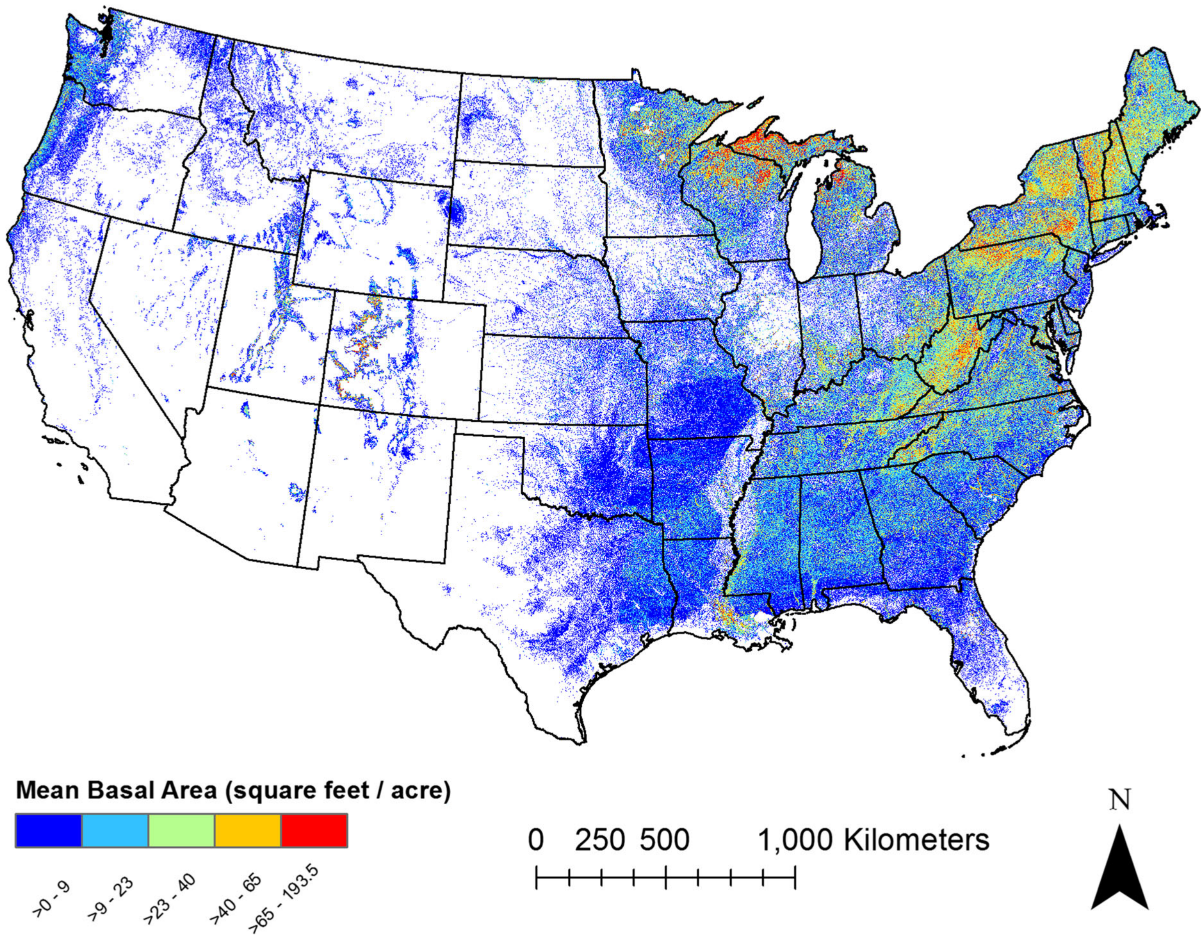


Fig. 6 The mean basal area of vulnerable timber, given a species scenario risk extent

indicative of how fast a population might grow and spread) and helps to identify areas that are most susceptible to infestation (in percent area and percent basal area of timber at risk).

We find that the greatest risk of ALB infestation occurs in the eastern half of the country. Risk is lower across the western half because of the low abundance of host species, relatively low urban area, as well as cold, high elevation locations where time to maturity is deemed unsuitable (≥10 years). We also find that time to maturity increases with both latitude and elevation, a function of temperature decreasing the rate at which individuals develop. Within the beetle's native range in China, populations have been inferred to be primarily univoltine, with subsets of the population expressing semivoltine development (Hua et al. 1992; Li and Wu 1993), as summarized by Lingafelter and Hoebeke (2002) and Hu et al. (2009), which agrees with the projected development for much of the eastern United States as shown in Fig. 4.

Correspondingly, southern and eastern contiguous US states and municipalities are expected to be at highest risk of ALB impact given extensive host presence (especially in the northeast) as well as warmer conditions more conducive to rapid beetle maturation and thus faster population growth (especially in the southeast). States and municipalities with high shipping activity (ALB's vector of introduction), low time to maturity, and extensive host species presence should recognize higher risk of significant impact by ALB. It may be important for these states and municipalities to discuss the possibility of an ALB introduction and its likely impacts and to evaluate relative risk and local factors which define that risk.

These findings could help guide municipal and state managers in efforts to plan and conduct more well-prepared responses to the threat of ALB invasion. For example, areas with faster ALB maturation may merit more frequent and intensive monitoring, as populations in these regions may grow quickly, making eradication both more difficult and more expensive. Areas of the landscape where generation times are longer may merit less frequent or intense monitoring based on the potential for slow population growth. Similarly, areas of potentially rapid beetle population growth might benefit from preemptive, rather than reactionary, ALB response measures such as community outreach and education, training in eradication procedures, and a general emergency action plan tailored based on a state's spatial distribution of areas at risk and where years to maturity values are highest.

Comparison of results to other ALB risk assessments

Similar to the study by Townsend Peterson and Vieglais (2001) this study found suitable habitat across a large portion of the eastern Contiguous United States as a result of the inclusion of host species presence as a limiting factor. Also, similar to the data and map by MacLeod et al. (2002) and Hu et al. (2009) where risk was found to decrease at more northern latitudes, around western mountain ranges, and around coastal Louisiana and Mississippi, this study found the risk of greater impact to decrease in these same areas, with the exclusion of Louisiana and Mississippi (which may be attributed to limitations in this study only using temperature and susceptible tree species extent in its modeling effort) as years to maturity values increased with elevation and latitude.

While this research agrees with prior work regarding the general spatial delineation of vulnerable areas in the United States, it adds value to ALB spatial modeling attempts by providing empirically derived years to maturity values. This metric might aide in efforts to model ALB population growth dynamics, as well as support an economic metric of percent timber basal area at risk, which may prove useful when justifying investment in ALB combative efforts.

In recent work, Shatz et al. (2013) demonstrated methods that can be used for more local definition of the likelihood of ALB infestation, with an example from Worcester, MA. The approach presented here lacks such city-level specificity, which could be beneficial for locally tailored and more detailed planning of ALB response measures. Instead, this study provides standardized coverage for the entire contiguous United States.

Limitations and suggested additions to research

A few potential limitations to this approach are worth noting. First, climate change may adjust time to maturity compared to that estimated here based on climate normals from 1983 to 2012. Second, conversion of air temperatures to under-bark temperatures relied here on a generic parameterization that is likely to require adjustment for improved realism in diverse tree species. In addition, ideally it would be best to validate these results with field observations, however field data has been extremely limited due to the focus on eradication, as discussed in Trotter and Keena (2016).

This flexibility in cold tolerance, as well as the importance of high host species concentration to the success of an infestation, may be demonstrated by examining sites of known infestations within the context of this study's data products (Table 2). Ontario, Canada, while not defined within the context of this study, is most likely outside of the native, 1–2 year time to maturity window of the ALB, based on latitude. Massachusetts, with an infestation in Worcester, is characterized by a time to maturity value of almost 2.7 years. Ohio, Illinois, New Jersey, and New York City all also have time to maturity values varying around 2 years. Each of these states has

Table 2 Summary statistics for states with known infestations

State	Mean years to maturity	% Area	% Timber
States with known infestations (genus vulnerability)			
Illinois	1.769	44.11	46.924
New Jersey	1.909	89.763	32.681
New York (City)	3.123 (1.910)	94.968	65.703
Massachusetts	2.697	96.138	44.903
Ohio	2.147	72.66	62.073

New York entry includes New York City statistics in parentheses as time to maturity at the state scale differs from that for local infestation sites such as the New York City metropolitan area relatively high % area at risk, and % vulnerable timber, given the presence of vulnerable host species, with few exceptions. The relatively high time to maturity but also high presence of host species in regions with ALB infestations suggests that (a) ALB populations may be capable of developing flexibly in response to local temperature regimes even where time to maturity is expected to be long, and (b) that the presence of host tree species is a more strict requirement for population development. Future research could consider how these factors might be combined, for example, possibly by excluding areas with a low basal area of vulnerable species with a threshold such as 30–40%. This would exclude land that does not contain a viable concentration of host tree species by discerning between host dominant and non-host dominant areas.

Nonetheless, the broad geographic patterns displayed in this work are likely to remain in spite of these sources of uncertainty, yielding a robust depiction of the relative risk of ALB population development if introduced.

Acknowledgements The authors thank Peter Meng for access to pre-publication host lists. Support for this research was provided by the Graduate School of Geography at Clark University, and the US Forest Service, Northern Research Station. We also thank the editor and 2 anonymous reviewers for comments on previous versions of the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

GAO (2006) Invasive forest pests: lessons learned from three recent infestations may aid in managing future efforts: report to the Chairman, Committee on Resources, House of Representatives. http://www.gao.gov/assets/250/249776.pdf

Grinnell J (1917) Field tests of theories concerning distributional control. Am Nat 51(602):115–128

Grinnell J (1924) Geography and evolution. Ecology 5(3):225–229

Haack RA, Britton KO, Brockerhoff EG, Cavey JF, Garrett LJ, Kimberley M, Lowenstein F, Nuding A, Olson LJ, Turner J, Vasilaky KN (2014) Effectiveness of the International Phytosanitary Standard ISPM No. 15 on reducing wood borer infestation rates in wood packaging material entering the United States. PLoS ONE 9(5):e96611

Hu J, Angeli S, Schuetz S, Luo Y, Hajek AE (2009) Ecology and management of exotic and endemic Asian Longhorned Beetle. Agric For Entomol 11(4):359–375

Hua L, Li S, Zhang X (1992) Coleoptera: Cerambycidae. In: Peng J, Liu Y (eds) Iconography of forest insects in Hunan, China. China Hunan Sci. Technol. Press, Changsha, pp 467–534

ISPM 15 (2009) Regulation of wood packaging material in international trade. https://www.ippc.int/static/media/files/publications/en/2014/06/30/ispm_15_2009_en_2014-06-16.pdf

Keena MA (2006) Effects of temperature on (Coleoptera: Cerambycidae) adult survival, reproduction, and egg hatch. Environ Entomol 35(4):912–921

Keena MA, Moore PM (2010) Effects of temperature on (Coleoptera: Cerambycidae) larvae and pupae. Environ Entomol 39(4):1323–1335

Li W, Wu C (1993) Integrated management of longhorn beetles damaging poplar trees. China Forest Press, Beijing (in Standard Chinese)

Liebhold AM, Tobin PC (2008) Population ecology of insect invasions and their management. Annu Rev Entomol 53(1):387–408

Lingafelter SW, Hoebeke ER (2002) Revision of *Anoplophora* (Coleoptera: Cerambycidae). Entomological Society of Washington, Washington, DC, p 236

Macleod A, Evans HF, Baker RHA (2002) An analysis of pest risk from an Asian longhorn beetle (*Anoplophora glabripennis*) to hardwood trees in the European community. Crop Prot 21(8):635–645

Meng PS, Hoover K, Keena MA (2015) Asian longhorned beetle (Coleoptera: Cerambycidae), an introduced pest of maple and other hardwood trees in North America and Europe. J Integr Pest Manag 6:1–13

NAS (2002) Predicting invasions of nonindigenous plants and plant pests. National Academy Press, Washington, DC

Nowak DJ, Pasek JE, Sequeira RA, Crane DE, Mastro VC (2001) Potential effect of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) on urban trees in the United States. J Econ Entomol 94(1):116–122

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol Econ 52(3):273–288

Reicosky DC, Winkelman LJ, Baker JM, Baker DG (1989) Accuracy of hourly air temperatures calculated from daily minima and maxima. Agric For Meteorol 46(3):193–209

Sánchez V, Keena MA (2013) Development of the teneral adult *Anoplophora glabripennis* (Coleopteran: Cerambycidae): time to initiate and completely bore out of maple wood. Environ Entomol 42(1):1–6

Shatz AJ, Rogan J, Sangermano F, Ogneva-Himmelberger Y, Chen H (2013) Characterizing the potential distribution of the invasive Asian longhorned beetle (*Anoplophora glabripennis*) in Worcester County, Massachusetts. Appl Geogr 45(1):259–268

Smith MT, Turgeon JJ, De Groot P, Gasman B (2009) Asian longhorned beetle *Anoplophora glabripennis* (Motschulsky): lessons learned and opportunities to improve the process of eradication and management. Am Entomol 55(1):21–25

Townsend Peterson A (2003) Predicting the geography of species invasions via ecological niche modeling. Q Rev Biol 78(4):419–433

Townsend Peterson A, Scachetti-Pereira R (2004) Potential geographic distribution of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in North America. Am Midl Nat 151(1):170–178

Townsend Peterson A, Vieglais DA (2001) Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. Bioscience 51(5):363–371

Trotter RT, Keena MA (2016) A variable-instar climate-driven individual beetle-based phenology model for the invasive Asian longhorned beetle (*Anoplophora blabripennis,* Coleoptera: Cerambycidae). Environ Entomol 45(6): 1360–1370

Vermunt B, Cuddington K, Sobek-Swant S, Crosthwaite J (2012) Cold temperature and emerald ash borer: modelling the minimum under-bark temperature of ash trees in Canada. Ecol Model 235–236:19–25

Williams D, Lee HP, Kim IK (2004) Distribution and abundance of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in natural Acer stands in South Korea. Popul Ecol 33(3):540–545