

Effects of climate on emerald ash borer mortality and the potential for ash survival in North America



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ABSTRACT

Non-native invasive insects such as the emerald ash borer (*Agrilus planipennis* Fairmaire; EAB) cause billions of dollars' worth of economic damage and unquantifiable but substantial ecological damage in North America each year. There are methods to mitigate, contain, control, or even eradicate some non-native invasive insects, but so far the spread of EAB across eastern North America appears to be unimpeded. Similar to the effect of chestnut blight (*Cryphonectria parasitica* (Murrill) Barr) on American chestnut (*Castanea dentata* (Marsh.) Borkh.) nearly 100 years ago, it is estimated that EAB will eventually decimate nearly all ash (*Fraxinus* spp.) in North America. Although previous literature suggests no impediment to the spread of EAB, we propose the possibility that obstacles to EAB population expansion into the northern ranges of ash could be formidable. We combined USDA Forest Service Forest Inventory and Analysis (FIA) 2010 ash data, historical climate data, beneath-snow and beneath-tree bark temperature modeling, and our current understanding of EAB physiology. We found that between 1945 and 2012, while some Canadian locations experienced temperatures potentially cold enough to kill all EAB, very few locations in the United States experienced such temperatures. However, more than 7% and 42% of weather stations located in the ranges of ash in the United States and Canada, respectively, experienced temperatures potentially cold enough to kill the majority of the EAB population. By killing the majority of the EAB population, EAB spread may be slower and EAB population may be held to densities to which ash trees can tolerate infestation. As in its native range in Asia, lower EAB densities may not cause ash mortality. This information should be helpful for the future sustainable management of ash.

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1. Introduction

1.1. EAB in North America

The emerald ash borer (*Agrilus planipennis* Fairmaire; EAB) was first discovered in North America in southeastern Michigan and nearby Windsor, Ontario in 2002, but may have become established there during the early- to mid-1990s (Haack et al., 2002; Siegert et al., 2007). Since being introduced to a novel environment, EAB has done extensive damage to the ash (*Fraxinus* spp.) resource

in eastern North America. EAB does not normally cause extensive damage to ash trees throughout its native range in Asia because host trees have defensive mechanisms that confer some level of resistance (Eyles et al., 2007; Rebek et al., 2008). Related species of ash in North America are suitable hosts for the non-native invasive EAB and their lack of resistance makes them prone to EAB infestation, decline, and mortality.

During infestations, EAB larval phloem galleries and outer sapwood cavities girdle trees; this disrupts water and nutrient transport and eventually kills trees (Cappaert et al., 2005). However, at low population densities EAB feeding can be difficult to detect due to the low probability of finding external signs including characteristic D-shaped exit holes, chlorosis, crown thinning and dieback, epicormic shoots, and bark splits (McCullough and Roberts, 2002; Siegert et al., 2010). For this reason, it is estimated that it can take up to 10 years from EAB site establishment until it is detected (Poland and McCullough, 2006). This discrepancy between establishment and detection is common with other invasive insect

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pests, which remain at low densities until some other predisposing factor leads to tree stress, an exponential increase in insect density, or both (Shigesada and Kawasaki, 1997). In addition, detecting EAB by assessing ash tree health status is difficult because many North American ash species are susceptible to numerous diseases which cause chlorosis, witches' brooms, and abundant epicormic branching (PSU CAS, 1987). Recent research suggests the EAB spread rate from the core infested area centered in southeastern Michigan is influenced by short-range insect dispersal and long-range human-facilitated dispersal. Non-assisted EAB spread from the core infested area appears to be approximately 20 km per year (Prasad et al., 2010). However when factoring in the inadvertent human-assisted transport of overwintering EAB in firewood, satellite infestations can appear, grow, and coalesce with the core infested area, thereby increasing the spread rate of EAB to more than 20 km/year.

1.2. Effects of EAB on ash

It is estimated that given enough time nearly 100% of all green (*Fraxinus pennsylvanica* Marsh.), white (*Fraxinus americana* L.), and black ash (*Fraxinus nigra* Marsh.; the three most important and abundant North American ash species) will be killed by EAB throughout their ranges in North America (Herms et al., 2010). EAB infestation of ash will have negative economic consequences for a variety of stakeholders; the ecological impacts will likely include altered forest composition and structure and negative effects on associated wildlife and ecosystem function, especially in hydric and mesic systems where ash is common. The long-term and broad-scale impacts of EAB appear to pose the greatest threat to sustaining ash forests in North America. EAB has the potential to cause substantial changes in forest composition and structure. Excluding industrial and specialty market losses, the economic value of ash timber loss due to EAB infestation could be hundreds of millions of dollars for forest landowners in the United States over the next decade (Robert Haight, pers. comm., USDA Forest Service, February 8, 2011).

1.3. A scenario of ash resistance to EAB in North America

EAB overwinters as larvae or pre-pupae in the xylem-phloem interface of ash. Research suggests EAB often requires two years to complete development and overwinters as larvae rather than pre-pupae in satellite locations away from the main infestation area in southeastern Michigan (Tluczek et al., 2011). EAB larvae overwinter in situ in their feeding galleries whereas pre-pupae overwinter in pupal cells constructed in the sapwood of thin-barked trees or the outer bark of thick-barked trees. Unpublished research suggested overwintering EAB pupal cell depth was consistently 1.5 cm beneath the bark surface (Therese Poland, pers. comm., USDA Forest Service, February 17, 2011). There may be differences in larval overwintering depth (i.e., how far into host trees EAB overwinters), which may have implications in satellite infestations such as the ones most likely to spread to the northern United States and Canada. However, differences in overwintering depth are so small that it would be unlikely to affect the overwintering EAB microclimate (Kim Cuddington, pers. comm., University of Waterloo, November 4, 2011).

Although there are established, thriving EAB satellite populations in the northern United States and Canada (e.g., in northwestern Michigan and central Minnesota, USA), there is a substantial difference in extreme low temperature minima between the locations of these satellite populations and the northern ranges of ash (Cathey, 1990; Vogel et al., 2005). This is relevant considering the coldest EAB supercooling point reported to date is -35.3°C (Crosthwaite et al., 2011). The supercooling point is the coldest temperature at which EAB can no longer resist hard-freezing and

subsequent temperature-related mortality. Therefore, northern satellite infestations may not experience temperatures low enough to have a substantial effect on overwintering EAB survival, but it is possible that the lowest temperatures in the northern United States and Canada would be lower than the lowest EAB supercooling point (Venette and Abrahamson, 2010).

Previous research suggested EAB will eventually kill nearly all native ash (*Fraxinus* spp.) in North America (Poland and McCullough, 2006; Herms et al., 2010) but EAB host tree mortality rates could be lower with trees that are located in colder areas. By including other factors, such as the timing of EAB life stages and their intolerance to cold temperatures, we sought to identify limitations to EAB spread throughout its potential future range. To determine potential locations unsuitable for future EAB establishment we used the current knowledge of EAB physiology (Venette and Abrahamson, 2010; Crosthwaite et al., 2011; Tluczek et al., 2011), 2010 USDA Forest Service Forest Inventory and Analysis (FIA) data, beneath-snow and beneath-tree bark temperature modeling (Bartlett et al., 2004, 2005; Vermunt, 2011; Vermunt et al., 2012a,b), and Canadian and United States historical climate data (Environment Canada, 2012; National Oceanic and Atmospheric Administration, 2012). We accomplished this by examining more than 20,000 FIA plots in the United States, interpolated maps of ash presence, and historical climate data from 494 weather stations throughout the ranges of ash in North America.

2. Materials and methods

2.1. U.S. Forest Service Forest Inventory and Analysis

FIA estimates United States forest inventory attributes using a nationwide randomly-located systematic sampling system. The base sampling intensity is one plot per 2400 ha, but it is sometimes augmented by intensification for an entire state or for a particular public owner, such as a National Forest. Nationally, the plots are measured on a 5- to 10-year interval, with approximately 20% of the FIA plots in each north-central and northeast state measured each year. The FIA program defines forest land as land that is at least 0.4 ha in size, 36.6 m in width at the smallest dimension, and possessing at least 10% cover by live trees of any size, unless the land has been recently harvested or otherwise disturbed and is anticipated to remain forested. Each FIA plot is approximately 0.067 ha and is comprised of four 7.32 m-radius subplots where all trees at least 12.7 cm dbh are measured. In addition, each subplot contains a 13.5 m²-microplot where trees from 2.5 cm to 12.7 cm dbh are measured. The plot design is arranged with one central subplot and three subplots located in a spoke-like fashion at azimuths of 0, 120 and 240° and 36.6 m from the plot center of the central subplot. More information on FIA plot design, estimation procedures, and techniques can be found in Bechtold and Patterson (2005) and Woudenberg et al. (2010).

2.2. Study area

We used Little's range maps (United States Geological Survey, 1999; digitized from Little, 1971) to delineate the necessary areal extent of our weather station coverage which would correspond with the ranges of green, white, and black ash. We utilized United States first-order weather stations and FIA plots located in a 32-state area from Montana to Maine to Virginia and Tennessee to Oklahoma, and back to Montana (Fig. 1). Because we were interested in estimating the coldest temperatures EAB would experience, we did not use data from weather stations or FIA plots in southern states containing ash, such as North Carolina, South Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana, and Texas.

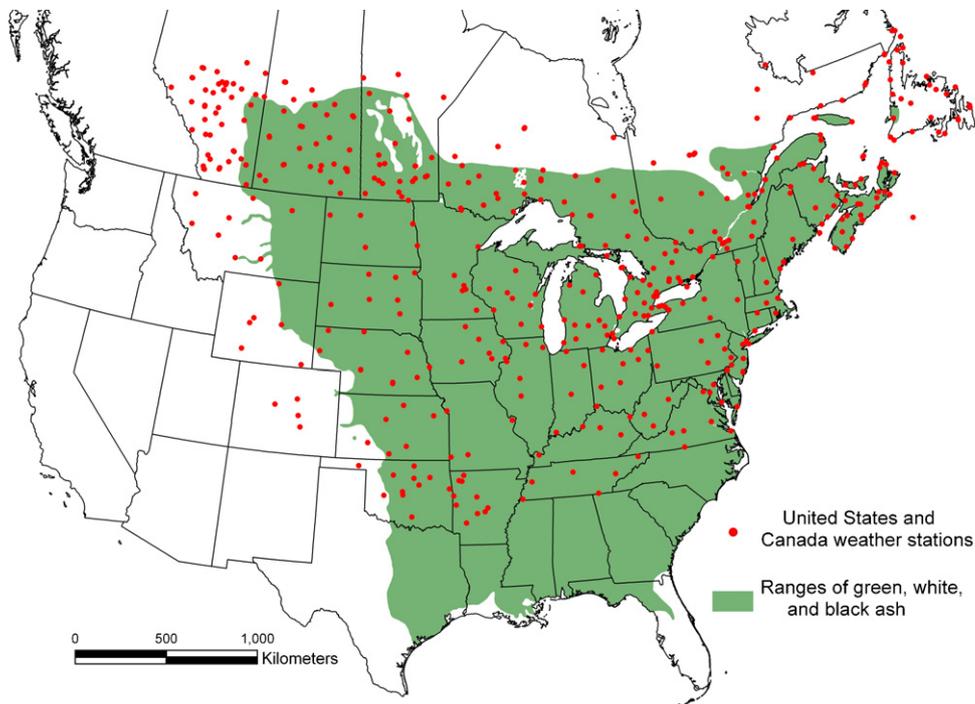


Fig. 1. Location of United States and Canada weather stations used in this study, and ranges of green, white, and black ash in North America according to Little (1971). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Because there is currently no Canadian equivalent to United States FIA data we were unable to obtain detailed data on Canadian ash. We used data from Canadian weather stations in Alberta, Saskatchewan, and Manitoba that were South of 55° N Latitude, in Ontario that were South of 53° N Latitude, and in Newfoundland and Labrador, Prince Edward Island, Nova Scotia, New Brunswick, and Québec South of 52° N Latitude. Weather stations North and West of these areas were well outside the known ranges of ash. Weather stations slightly outside the ranges of ash were included because we did not want weather stations inside the ranges of ash to unrealistically extrapolate outside the ranges of ash. In other words, in order to interpolate temperatures to the edges of the ranges of ash, we needed to use stations outside the ranges of ash.

2.3. Climate data

Across the area of interest, we compiled data from 179 United States weather stations and 315 Canada weather stations (Fig. 1). United States weather station data were obtained from the Northeast Regional Climate Center (National Oceanic and Atmospheric Administration, 2010) and Canada weather station data were obtained from Environment Canada's National Climate Services (Environment Canada, 2012). In the United States, National Weather Service Offices, known as first-order weather stations, report a comprehensive in situ array of weather variables each hour, on the hour, around the clock. They were the only weather stations available with long, reliable periods of record, daily snow depth readings, and hourly temperature readings. Comprising thousands of active locations in the Northeastern United States as of 2012, cooperative network sites are more numerous but make only one observation at the same time each day (National Oceanic and Atmospheric Administration, 2010). Observations at cooperative network sites are generally limited to daily maximum and minimum temperatures, precipitation, snowfall and depth of snow on the ground. Because snow and bark modeling necessitated daily snow depth readings and hourly temperature readings before, during, and after extreme low temperature weather events, we only

used first-order weather stations from the United States. Similarly, we limited our use of Canadian weather station data to those stations with snow depth readings and hourly temperature readings. While these limitations constrained the number of weather stations and the period of time in which we could analyze weather data, they were necessary for snow modeling and bark modeling techniques that required hourly temperature readings (Vermunt, 2011).

2.4. Modeling the effects of snow cover on beneath-bark temperatures

To understand the potential impact changing snow cover has on the temperatures experienced by larvae overwintering beneath bark near the ground, we employed a model that computed temperatures beneath snow with time-dependent depth profiles (Bartlett et al., 2004). The model incorporated the most important physics of snow-ground thermal interactions while remaining simple enough to be driven by the available meteorological observations: hourly surface-air temperatures and daily observations of snow depth. The model broke the air-snow-ground regime into multiple layers; thermal energy conducts through these layers satisfying

$$C^A(T) \frac{\partial T}{\partial t} = \frac{\partial}{\partial z} \left(k \frac{\partial T}{\partial z} \right)$$

within each layer, where $C^A(T)$ is the apparent volumetric heat capacity as a function of temperature T , ∂ is the partial derivative, k is thermal conductivity, t is time, and z is depth. In other words, “delta- T /delta- t ” is the time derivative of temperature (or the rate of change of temperature in time), “delta/delta- z ” is the derivative with respect to depth, and “delta- T /delta- z ” is the depth-derivative of temperature (or the change of temperature with depth). The effect of latent heat exchange at the phase transition was modeled using a homographic approximation of the function $C^A(T)$. Details of the development of this numerical snow-ground thermal model,

including the handling of latent heat and snow thermal parameter evolution are available in Bartlett et al. (2004).

The ratio of the parameters k and $C^A(T)$ [$k/C^A(T)$] defines the thermal diffusivity of the snow and indicates the rate at which temperature concavity is “smoothed out” by the medium. The thermal diffusivity of snow depends on numerous factors including snow-water content, compaction, average mean crystal dimensions, and average crystal connectivity (Yen, 1981; Goodrich, 1982; Sturm et al., 1997). For all locations we used a common set of snow and soil thermal parameters identical to those used in Bartlett et al. (2005) for all sites in North America. Though conceptually simple and ignoring many of the inter-snow processes, the model produced robust results for the temperature at the snow-ground interface and was verified against a broad range of observational sites (Bartlett et al., 2004).

Our model was driven by the observed hourly surface air temperature-time series and the daily observations of snow depth. The model assumes that the snow cover is applied to the ground at the beginning of the snow event and that initially the snow-pack takes on the observed temperature of the air at the beginning of the event. The underlying ground temperature is preconditioned by conducting a time-reversed version (i.e., a flipped version of the observed temperature-time series from the station) of the observed air temperature during the event into the ground. This procedure guarantees a match in the temperature boundary condition at the snow-ground interface at the beginning of the event. This procedure also guarantees that the snow-ground interface is not being warmed excessively by residual heat in the ground. Consequently, the modeled snow-ground interface temperature during the event is the coldest possible. Examination of these coldest possible temperature events seemed the logical course in examining the potential range limitations of EAB.

We determined the five coldest ambient air temperatures recorded by each weather station that had concurrent hourly ambient air temperatures and daily snow depth readings. Because of a lag effect of temperature changes, modeling the effects of snow depth required at least 6 h of ambient air temperature readings following the coldest ambient air temperature recordings. Subsequent tree bark modeling required at least 48 h of ambient air temperature readings prior to the coldest ambient air temperature recordings. Therefore, for each weather station we utilized at least 55 h of ambient air temperature readings concomitant to each coldest ambient air temperature.

2.5. Modeling the effects of tree bark on estimated EAB-experienced temperatures

Following modeling of beneath-snow temperatures from ambient air temperatures, we modeled subsequent beneath-bark temperatures using a tree bark model based on a Newtonian convective cooling model (Tran et al., 2007; Vermunt, 2011). This beneath-bark temperature modeling was based on the principle of convective cooling, whereby the transfer of heat occurs when a solid and the gas or liquid around it are at different temperatures. Beneath-bark temperature modeling only required the estimation of the cooling constant, K . The beneath-bark temperature model linked current beneath-bark temperature to earlier beneath-bark temperatures and the current temperature of the air with a cooling constant by the equation

$$T_{t+\Delta t} = T_t + K(A_{t+\Delta t} - T_t)$$

where T_t is the beneath-bark temperature of the tree at time t , Δt is a time step of 1 h, A_t is the ambient air temperature of the weather station at time t , and K is a cooling constant that is associated with the physical properties of the tree. We used a cooling constant of

0.11 because in related studies, it was found to be the optimal value of the cooling constant (Vermunt et al., 2012a) and because it was within in a range of values used for similar purposes (Tran et al., 2007). Vermunt's optimal value of K was selected by minimizing the residual sum of squares of a model-building set, while the model with that value of K was run on the testing set.

We used an initial T_0 beneath-bark temperature of 0°C, and allowed the model 48 time steps (hours) to converge. We subsequently refer to beneath-bark temperatures as estimated EAB-experienced temperatures.

2.6. Data analysis

We determined the range of dates that each weather station recorded hourly ambient air temperature and daily snow depth. The average weather station period of record and period of record variance were also determined. We determined the coldest air temperatures, estimated EAB-experienced temperatures, and the number of weather stations recording $\leq -30^\circ\text{C}$ air and estimated EAB-experienced temperatures and $\leq -35.4^\circ\text{C}$ air and estimated EAB-experienced temperatures. Stations recording only one occurrence of the appropriate temperatures throughout their entire periods of record were included in this count. The average number of years per $\leq -30^\circ\text{C}$ EAB temperature divides the total number of years on the period of record by the number of $\leq -30^\circ\text{C}$ EAB temperature events. Temperature intervals refer to the amount of time (years) in between consecutive events that get to the appropriate temperature. Standard deviations and standard errors refer to the average number of year per appropriate temperature.

We used the Fire History Analysis and Exploration System (FHAES, Alpha 1.0; Grissino-Mayer, 1995 and Grissino-Mayer, 1999 and Grissino-Mayer, 2001) to determine differences in means, variances, distributions, and percent of weather stations recording extreme low temperature events between time periods using Student's t -tests, F -tests, and Kolmogorov–Smirnov Goodness-of-Fit (KS) tests. The assumptions of each test were tested and met. Tests were done separately for events recording $\leq -30^\circ\text{C}$ estimated EAB-experienced temperatures and $\leq -35.4^\circ\text{C}$ estimated EAB-experienced temperatures. FHAES is traditionally used to analyze fire scar event data, but it can be used to analyze forest stand regeneration, forest disturbance impacts, and non-fire events recorded in tree rings such as landslides, avalanches, and flooding. Since FHAES can analyze any event data including those not recorded in tree rings, we were able to treat events recording $\leq -30^\circ\text{C}$ estimated EAB-experienced temperatures and $\leq -35.4^\circ\text{C}$ estimated EAB-experienced temperatures as input variables similar to fire scars in FHAES to analyze their occurrence. We determined mean and median cold temperature event intervals for the composite cold temperature event history and used KS tests to determine whether a Weibull distribution fit the data better than a normal distribution and whether mean, median, or Weibull means or medians described the historical cold temperature event interval better (Table 1). This was done separately for events recording $\leq -30^\circ\text{C}$ estimated EAB-experienced temperatures and $\leq -35.4^\circ\text{C}$ estimated EAB-experienced temperatures.

2.7. Geospatial analysis

We performed spatial interpolation of modeled minimum bark temperature, concurrent ambient air temperature, and snow depth using the ArcGIS Geostatistical Analyst software package (Johnston et al., 2001) and an ordinary kriging interpolator with a twelve nearest neighbors approach (Fig. 2). All 494 first-order station observations were used for training data which was converted to a grid with a 10-by-10-km cell spatial resolution and masked to exclude areas outside the area of interest. Each FIA plot was linked

Table 1
Basic statistical information for weather stations used in this study.

	Total/overall	Canada	USA
Number of weather stations	494	315	179
Weather station start	1945	1953	1945
Weather station stop	2012	2012	2012
Average station period of record, years	34.91	28.38	46.41
Station period of record variance, years	2 to 67	5 to 59	2 to 67
Coldest air temperature, °C	-50.00	-50.00	-43.90
Coldest EAB temperature, °C	-39.97	-39.97	-37.26
Number of stations ≤ -30 °C air temperature	338	245	93
Percent of stations ≤ -30 °C air temperature	68	78	52
Number of stations ≤ -30 °C EAB temperature	146	133	13
Percent of stations ≤ -30 °C EAB temperature	30	42	7
Mean ≤ -30 °C EAB temperature interval	1.20	1.20	5.22
Median ≤ -30 °C EAB temperature interval	1.00	1.00	5.00
Weibull median ≤ -30 °C EAB temperature interval	NA	NA	NA
Average number of years per ≤ -30 °C EAB temperature	14.3	13.00	36.00
Standard deviation ≤ -30 °C EAB temperature	0.58	0.58	3.15
Total number of ≤ -30 °C EAB temperature intervals	46	46	9
Standard error ≤ -30 °C EAB temperature	0.09	0.09	1.05
Percent of years with temperatures ≤ -30 °C EAB temperature only using stations experiencing ≤ -30 °C	78	78	15
Percent of total years with temperatures ≤ -30 °C EAB temperature	69	78	15
Number of stations ≤ -35.4 °C air temperature	226	186	40
Percent of stations ≤ -35.4 °C air temperature	46	59	22
Number of stations ≤ -35.4 °C EAB temperature	31	29	2
Percent of stations ≤ -35.4 °C EAB temperature	6	9	1
Mean ≤ -35.4 °C EAB temperature interval	2.80	2.80	NA
Median ≤ -35.4 °C EAB temperature interval	1.00	1.00	NA
Weibull median ≤ -35.4 °C EAB temperature interval	2.13	2.13	NA
Average number of years per ≤ -35.4 °C EAB temperature	25.80	25.30	37.00
Standard deviation ≤ -35.4 °C EAB temperature	2.91	2.91	NA
Total number of ≤ -35.4 °C EAB temperature intervals	15	15	NA
Standard error ≤ -35.4 °C EAB temperature	0.75	0.75	NA
Percent of years with temperatures ≤ -35.4 °C only using stations experiencing ≤ -35.4 °C EAB temperature	27	27	3
Percent of total years with temperatures ≤ -35.4 °C EAB temperature	24	27	3

to a pixel and attributed to the bark and ambient temperature predictive surface map cell values by the location of the plot center. The area of interest (de facto range map of green, white, and black ash) comprised 670,867,565 ha. We used a total of 20,656 FIA plots in this analysis. All data were projected using the North America Albers Equal Area Conic projection, NAD 83.

To determine ash distribution, abundance, and availability, we used ArcGIS software to combine geospatial raster datasets of a United States ash basal area map (Wilson et al., 2012), FIA ash plot data, and the interpolated bark temperature and coincident air temperature prediction surface maps into a single raster layer. Using these four combined geospatial datasets, we obtained and

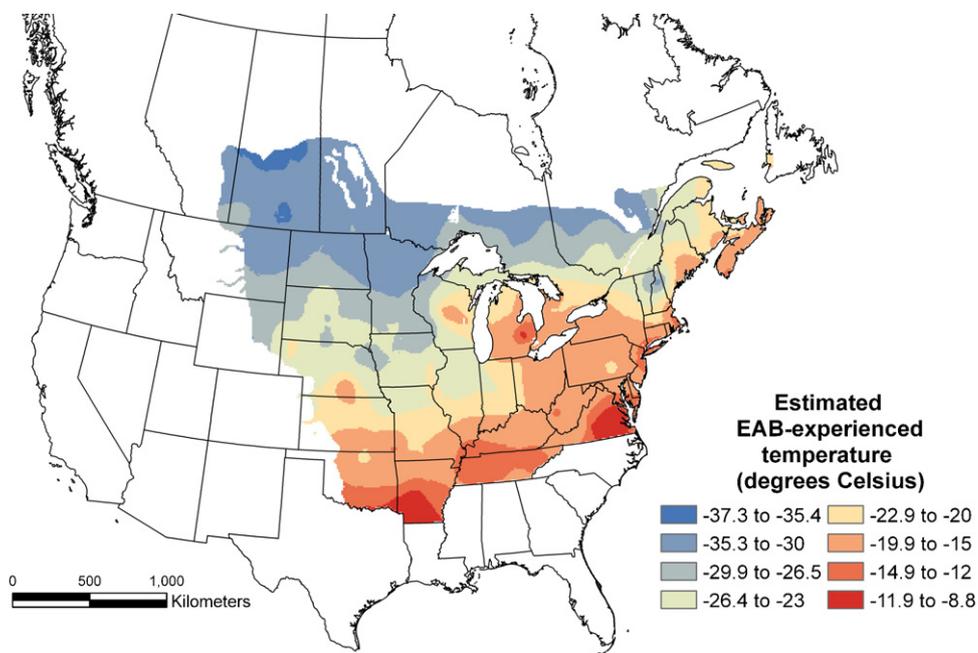


Fig. 2. Coldest estimated EAB-experienced temperatures in the United States and Canada.

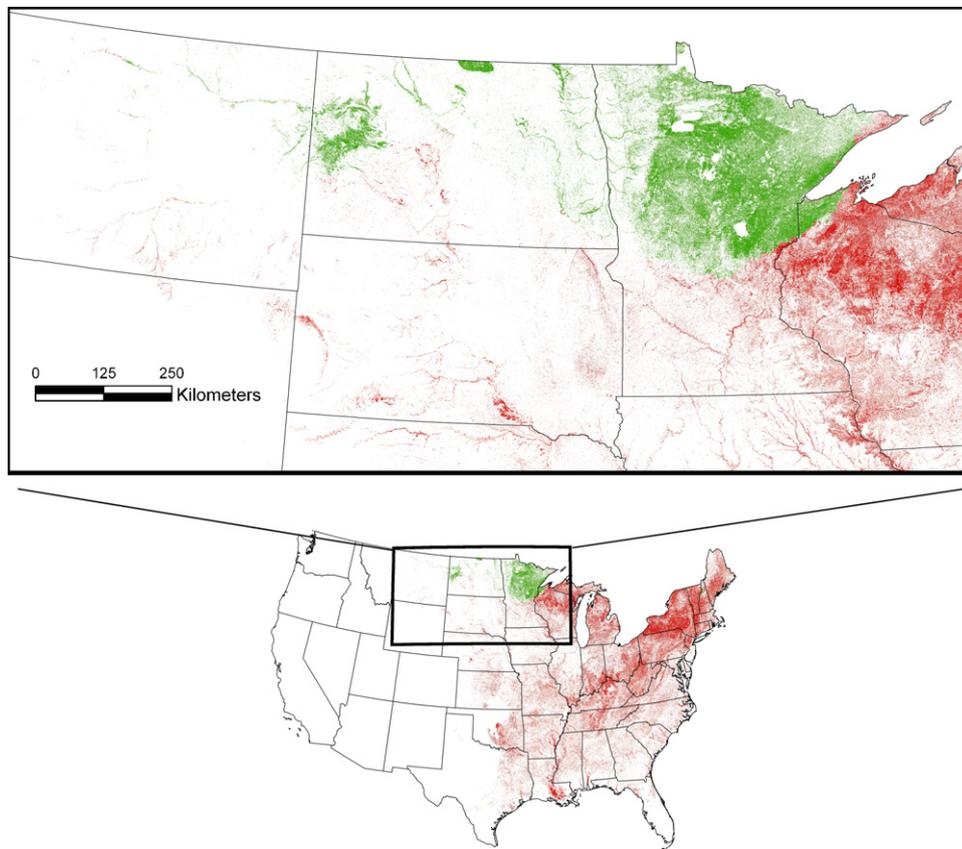


Fig. 3. Identification of areas in the United States where ash could survive EAB indefinitely. Locations in green indicate areas where ash is present and experiences estimated EAB-experienced temperatures $\leq -30^{\circ}\text{C}$, and locations in red indicate areas where ash is present and experiences estimated EAB-experienced temperatures $> -30^{\circ}\text{C}$. Ash presence based on Wilson et al. (2012). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

summarized per-area of interest pixel counts and calculated the resulting ash area percentages that encountered estimated EAB-experienced temperatures $\leq -30^{\circ}\text{C}$ and $\leq -35.4^{\circ}\text{C}$. Because there was no equivalent dataset for Canadian ash, we were only able to carry out this analysis for the United States (Fig. 3).

Due to the possibility of variable lengths of data from weather stations biasing a comparison of locations, we performed spatial interpolation of modeled minimum bark temperature, concurrent ambient air temperature, and snow depth in two additional analyses: One, we analyzed only weather stations with periods of record ≥ 30 years (159 stations), and two, we analyzed only weather stations with the same periods of record (74 stations; none located in Canada). Because the limitations of our modeling system constrained the number of weather stations and the period of time in which we could analyze weather data, we were left with limited station coverage. Considering these two additional analyses further constrained the number of stations we were able to use, there were insufficient data to conduct such an analysis of the entire study area for both additional analyses. For example, for the first additional analysis, a maximum of six Canadian weather stations shared the same period of record start year, end year, and length. Where there was weather station coverage, results of all additional analyses were qualitatively similar to Figs. 2 and 3.

3. Results

According to FIA data from 2010, the three major species of North American ash total over 8.94 billion trees and saplings, and represent an estimated volume of over 724.94 million m^3 in the United States. Throughout their ranges in the United States, these three species account for nearly 14% of all woody species stems and

over 12% of total basal area and volume for all stems ≥ 2.54 cm dbh. These estimates exclude urban trees growing along streets, in yards, and other linear features that FIA does not consider to be forest land. According to the Canadian Forest Service, green, white, and black ash-leading stands comprise an estimated volume of over 36.11 million m^3 in Canada and cover an estimated area of 385,000 ha (Canada's National Forest Inventory, 2012). Ash is common to the urban environment and can represent 5–20% of the street trees in many Canadian and Midwestern United States cities (Haack et al., 2002).

The period of record was 1953–2012 and varied from 5 to 59 years for the 315 weather stations we analyzed in Canada. The period of record was 1945–2012 and varied from 2 to 67 years for the 179 weather stations we analyzed in the United States. The average period of record was 28 years for Canadian weather stations, 46 years for American weather stations, and 35 years for all weather stations. In Canada the coldest recorded ambient air and estimated EAB-experienced temperatures were -50°C and -39.97°C , respectively. These temperatures were recorded in two separate locations; the first was recorded at the Graham A weather station in southwestern Ontario and the second at the Spiritwood West weather station in west-central Saskatchewan. According to estimates from Little (1971) the former lies within the ranges of green and black ash, and the latter lies approximately 50 km outside the northern extent of the range of green ash. In the United States the coldest recorded ambient air and estimated EAB-experienced temperatures were -43.9°C and -37.26°C , respectively. These temperatures were recorded or estimated from the Mount Washington weather station in New Hampshire, located within the ranges of ash. Although this weather station is located on the treeless summit of Mount Washington, ash is located in proximity to

the summit. Sixty-eight and 30% of all weather stations experienced recorded ambient air and estimated EAB-experienced temperatures $\leq -30^{\circ}\text{C}$, respectively. Forty-six and 6% of all weather stations experienced recorded ambient air and estimated EAB-experienced temperatures $\leq -35.4^{\circ}\text{C}$, respectively. Over 69% and nearly 24% of years included in the total period of record documented estimated EAB-experienced temperatures $\leq -30^{\circ}\text{C}$ and $\leq -35.4^{\circ}\text{C}$, respectively.

Our geospatial analysis linking weather station data and FIA plots estimated that 0% of ash in the United States lies within areas experiencing estimated EAB-experienced temperatures $\leq -35.4^{\circ}\text{C}$. Geospatial analysis estimated that roughly 8% of ash trees and saplings, 5% of ash basal area, 4% of ash volume, and 4% of the area where ash was estimated to occur by FIA data lies within areas experiencing estimated EAB-experienced temperatures $\leq -30^{\circ}\text{C}$. In Canada, 47 of the 60 (78%) years on record experienced estimated EAB-experienced temperatures $\leq -30^{\circ}\text{C}$ somewhere within the area of the network of weather stations used for this study (Table 1). In the United States, 10 of the 68 (15%) years on record experienced estimated EAB-experienced temperatures $\leq -30^{\circ}\text{C}$ somewhere within the area of the network of weather stations used for this study. Throughout the ranges of the three major species of North American ash, for 47 of the 68 (69%) years on record there was at least one weather station where the equivalent estimated EAB-experienced temperature was $\leq -30^{\circ}\text{C}$.

4. Discussion

Similar to previous studies, our results indicated the overwhelming majority of the ranges of ash in North America have climates suitable for EAB survival (Cappaert et al., 2005; Gandhi and Herms, 2010; Sobek-Swant et al., 2012b). Unlike previous studies, we identified locations where climates are not suitable for EAB survival; we found that a substantial amount of the ranges of ash endures estimated EAB-experienced temperatures $\leq -30^{\circ}\text{C}$ (Table 1, Fig. 3). Considering literature suggests the majority of overwintering EAB may not be able to survive temperatures $\leq -30^{\circ}\text{C}$ (Venette and Abrahamson, 2010; Crosthwaite et al., 2011) and EAB at low populations often does not cause widespread ash mortality (Wei et al., 2004; Cappaert et al., 2005), our results suggest there is potential for a substantial amount of the ranges of ash to survive EAB indefinitely.

The coldest temperatures experienced by EAB occur in the winter, during time periods in which EAB is inactive and overwintering beneath tree bark. Previous research indicated EAB consistently overwinters 1.5 cm beneath the bark surface (Therese Poland, pers. comm., USDA Forest Service, February 17, 2011). However, it is unclear at what vertical location on the tree bole EAB tends to overwinter. For instance, overwintering EAB has been found to overwinter low on tree boles, such as in aboveground tree roots close to the root collar. Therefore, a conservative estimate of the coldest temperatures experienced by overwintering EAB should take into account the buffering capacity of both snow cover and tree bark.

According to historical climate data, the northern United States and southern Canada occasionally experience extreme low ambient air temperatures $\leq -35.4^{\circ}\text{C}$. This is significant because literature suggests EAB cannot survive temperatures -35.3°C and colder (Wu et al., 2007; Venette and Abrahamson, 2010; Crosthwaite et al., 2011). EAB larvae overwintering in northern United States and southern Canada ash would experience temperatures warmer than this due to the buffering properties of snow and tree bark. Snow provides relatively good insulation and even a small amount can have a pronounced influence on ground temperatures. Like all insulators, snow effectively slows the exchange of energy between the

ground and the air, without completely prohibiting this exchange. Snow effectively introduces time-lags between changes in ambient air temperatures and the timing of when the ground sees those changes.

Diffusivity is an important thermal parameter for arriving at the thermal length for a specific frequency of temperature change. Because snow can have wide ranging values of thermal diffusivity, we modeled the thermal impact of snow on the ground with a relatively straightforward solution to the heat equation for the snow pack. Tree bark affects ambient air temperatures similarly to snow in that it introduces a lag and decrease in the amplitude of temperature oscillations. In other words, the air temperature tends to change more rapidly than the beneath-bark temperature, leading to differences between air and beneath-bark temperature in both positive and negative directions at different times. However, the extreme beneath-bark minima are theoretically always warmer than air minima. Ultimately, the combined effect of snow and bark promotes a warmer microclimate beneath tree bark.

Theoretically, EAB would experience the coldest beneath-bark temperatures during the dormant larval phase since it overwinters inside ash trees (Haack et al., 2002; Crosthwaite et al., 2011). Since the coldest extreme low temperatures most often occur during early-morning hours before sunrise, solar insolation (e.g., one side of a tree experiencing warmer temperatures than the other because it faces sunlight) may not play an important role in the estimation of EAB-experienced temperatures. Moreover, there exists no evidence indicating that prolonged exposure to extreme low temperatures increases EAB mortality risk. While there may be other minor influences on temperatures experienced by EAB, the two major influences on beneath-bark temperatures EAB would likely experience are snow and bark. Therefore, we used these two major influences to drive our modeling of estimated EAB-experienced temperatures.

Our estimated EAB-experienced temperatures are most likely conservative estimates. In other words, hourly temperature and daily snow data collection began later and sometimes ended earlier than the earliest and latest date weather stations collected data. For each weather station we only used up to 67 years of data instead of up to 173 years of the full record because our modeling necessitated hourly temperature and daily snow data. Thus, estimates from each weather station used a relatively short time span compared to the total life of each weather station. Therefore, we likely missed extreme low temperatures as cold as or colder than those that we used, and our estimated EAB-experienced temperatures are probably absolute maxima of the extreme low beneath-bark temperatures. EAB likely experience temperatures as cold as or colder than those we estimated for locations in the northern United States and Canada, and they likely experience these temperatures more frequently.

The limitations of our modeling system provided already rigid constraints to our sample size. Therefore, the addition and interpretation of a fixed time period study analyzing the frequency of these extreme cold temperature events was not plausible. Weather stations with shorter periods of record would be expected to have a lower probability of experiencing extreme cold temperature events, therefore appearing more favorable for EAB survival. However, inclusion of these weather stations likely led to an underestimation of the frequency of these events. In other words, it is likely for the events to occur at the same or higher frequency than that which we observed.

Our estimates are conservative and may address questions about future climate warming effects on extreme low temperatures. In addition, although literature suggests an increase in future global mean temperature, the same literature suggests an increased incidence of future extreme weather events (Intergovernmental Panel on Climate Change, 2007). With wider temperature

fluctuations, there is more potential for EAB to deacclimate to extreme low temperature events, thus raising their supercooling points and making them more susceptible to hard-freezing and subsequent temperature-related mortality (*sensu Sobek-Swant et al., 2012a*).

5. Conclusions

Previous work suggests EAB will eventually decimate ash throughout North America (Herms et al., 2010; Sobek-Swant et al., 2012b). However, our findings and related work support the conclusion that parts of the northern ranges of ash have the potential to survive EAB indefinitely (Cappaert et al., 2005; Venette and Abrahamson, 2010; Crosthwaite et al., 2011). Exposure to temperatures -30°C and colder could hold the EAB population to densities to which ash trees can tolerate infestation, thus limiting ash mortality from EAB. Future forests at the northern ranges of ash may support low levels of EAB but ash may persist indefinitely, while it is decimated by EAB elsewhere.

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