Variation in Winter Survival of the Invasive Hemlock Woolly Adelgid (Hemiptera: Adelgidae) Across the Eastern United States

R. TALBOT TROTTER, III[1] AND KATHLEEN S. SHIELDS

Forest Service, U.S. Department of Agriculture, Northern Research Station, 51 Mill Pond Rd., Hamden, CT 06514

Environ. Entomol. 38(3): 577–587 (2009)

ABSTRACT The hemlock woolly adelgid (*Adelges tsugae* Annand) is a small, aphid-like insect native to East Asia and western North America. First documented in the eastern United States in Richmond, VA, in 1951, it has spread to at least 17 states, where it causes increased mortality among both eastern and Carolina hemlocks (*Tsuga canadensis* Carrière and *T. caroliniana* Engelmann., respectively). Previous work has suggested low temperatures may limit northward spread of the adelgid. Using recent surveys of *A. tsugae* mortality across the infested latitudinal gradient of the eastern United States, we show there is a significant positive relationship between minimum winter temperatures and winter survival at the landscape scale. The strength and nature of this relationship, however, varies through time, with absolute minimum winter temperatures explaining almost one half of the tree-level variance in survival in the spring of 2004 but only 9% in 2003. Post hoc analyses of the data suggest the explanatory power of temperature can be improved in ongoing studies by examining seasonal temperature profiles. Previous studies have also suggested adelgid survival may be density dependent, and although these data support this observation, contemporary density is a poor predictor of adelgid survival at the landscape scale. Using landscape estimates of minimum winter temperature, we show two simple methods of estimating landscape-scale adelgid survival rates. Both methods suggest much of the range of *T. canadensis* in the eastern United States, and the entire range of *T. caroliniana* falls in areas where winter temperatures will not impose critical limits on *A. tsugae* populations.

KEY WORDS invasive species, climate, landscape, *Adelges tsugae*, hemlock

Invasive species are a major threat to natural, agricultural, and urban ecosystems and carry ecological (Cobb et al. 2006, Stadler et al. 2006, Towns et al. 2006, Drenovsky and Batten 2007) and financial costs (GAO 2000, Pimental et al. 2000). Managing invasive species requires an understanding of the processes that govern their arrival (Haack 2001, 2006; Work et al. 2005; Jerde and Lewis 2007), establishment (Liebhold and Bascompte 2003), and spread (Dobson and May 1986, Hengeveld 1988, Andow et al. 1990, Liebhold et al. 1992, Shigesada et al. 1995, Fagan et al. 2002, Evans and Gregoire 2007, Tobin et al. 2007). However, understanding the biology behind these processes can be difficult because of complex interactions between the biotic and abiotic factors that influence the dynamics and distribution of a species. The influences of stochastic factors such as mating success, weather, unintentional human-assisted transport, and dispersal (Allee 1938, Johnson et al. 2006) further complicate the system and, as noted by Jerde and Lewis (2007), the specific biological information needed to predict species dynamics is often lacking.

The hemlock woolly adelgid (*Adelges tsugae* Annand), however, may offer a unique opportunity to examine the simplified invasion dynamics of an already established, high-impact species. This small, aphid-like herbivore is native to East Asia (McClure 1996, McClure and Cheah 1999, Havill et al. 2006) and western North America (Havill et al. 2006, Havill and Foottit 2007). In the eastern United States, however, *A. tsugae* was unintentionally introduced from Japan (Havill et al. 2006) sometime before 1951, when it was first documented on ornamental hemlocks in Richmond, VA (Gouger 1971). In the 1980s, *A. tsugae* was recognized as a threat to eastern and Carolina hemlocks (*Tsuga canadensis* Carrière and *T. caroliniana* Engelmann.) as populations moved north through New Jersey, Long Island, and southern Connecticut (McClure 1991), and ultimately all of the New England states. Moving through the northeastern United States at an average rate of just over 8 km/yr (Evans and Gregoire 2007), populations of *A. tsugae* dramatically increased hemlock mortality, killing trees in as little as 4–5 yr (McClure 1991, Orwig and Foster 1998), although trees have been known to survive >10 yr of infestation (Paradis et al. 2008). To the south, the impact of *A. tsugae* on hemlocks has been more severe, with populations moving as far south as northern Georgia. Moving across the landscape at >15 km/yr (Evans and Gregoire 2007), adelgid infestation can kill

[1] Corresponding author, e-mail: rttrotter@fs.fed.us.

trees in as little as 2–3 yr and can eliminate the hemlock in a stand (R.T.T., personal observation). Currently, *A. tsugae* can be found in at least 17 states in the eastern United States.

There are four primary reasons commonly cited for the rapid spread and severe impact of the hemlock woolly adelgid, each of which makes managing the species challenging but simplifies the rules governing its distribution. First, the adelgid has a bivoltine, parthenogenic life history (McClure 1989, 1996). Although the adelgid is cyclically parthenogenic in its native ranges, with both holocyclic (cycles which include sexual generations on the primary host) and anholocyclic (cycles which do not include sexual generations, typically on the secondary host) generations (Havill and Foottit 2007), suitable primary spruce (*Picea* spp.) hosts are not known to occur in the eastern United States (McClure 1989). In the absence of a suitable primary host, reproduction is limited to asexual generations on secondary hosts in the genus *Tsuga.* The lack of dependence on sexual reproduction may buffer populations against a stochastic environment and reduce the importance of Allee effects (Allee 1938), and with the spring and winter generations producing ≈22 and 49 eggs (respectively) per individual (McClure 1989), small populations may grow quickly. The second likely reason for the rapid expansion of the adelgid is a lack of natural enemies. To date, no native predators have been shown to exert significant negative pressure on *A. tsugae* populations in the eastern United States, and no parasites of *A. tsugae* have been observed (Montgomery and Lyon 1996, Wallace and Hain 2000). Although classical biological control efforts focused on the use of *Laricobius nigrinus, L. osakensis, Tetraphleps* spp., *Sasajiscymnus tsugae, Scymnus sinuanodulus, Scymnus camptodromus, Scymnus ningshanensis,* and fungal pathogens are underway, introductions have been recent (*S. tsugae* starting in 1995, *Scymnus* species starting in 2006, see Onken and Reardon 2005 for details), and none have yet been shown to suppress adelgid populations in the wild. Third, movement of the adelgids on the landscape may be assisted by mammals, birds, and humans, increasing their potential dispersal range (McClure 1990). Finally, the rapid movement of *A. tsugae* through the eastern United States is facilitated by an apparent lack of resistance or tolerance by native *T. canadensis* and *T. caroliniana* (McClure et al. 2001, Lagalante et al. 2006). Although the suitability of hemlocks for adelgid growth can decline as a result of increasing adelgid density (McClure 1991), constitutive or induced resistance mechanisms have not been documented.

Given the absence of known predators, parasites, or pathogens, the lack of apparent resistance by the hosts, and a high dispersal potential, the distribution of *A. tsugae* may be expected to expand quickly to occupy the entire landscape within its ecological envelope. Recognized as early as 1890 by C. H. Merriam, the concept of an ecological envelope argues that the distribution of a species in space and time is determined by the distribution of the biotic and abiotic requirements for that species (Merriam 1890, Dansereau 1957, Akin 1991, Rosenzweig 1995), and the literature includes numerous applications of this concept to predict or describe the distributions of vegetation types and species (Merriam 1890, Good 1953, Dansereau 1957, Neilson 1995, Iverson et al. 1999). With regard to the hemlock woolly adelgid, arrival and establishment have been successfully accomplished, showing that at least some of the eastern United States is within its ecological envelope. This prompts the following question: what is the geographic distribution of that envelope, or more simply, which portions of the landscape are suitable for this species?

Evans and Gregoire (2007) have shown that, based on infestation records from townships and counties, *A. tsugae* populations move south almost twice as fast as they move north, and discuss the potential role of low temperatures in driving this pattern. Other authors have also shown *A. tsugae* can be cold limited (see Paradis et al. 2008), and laboratory studies have shown the importance of the severity (Parker et al. 1999, Skinner et al. 2003) and timing (Skinner et al. 2003) of low temperatures as determinants of adelgid mortality. Based on these patterns, we asked four questions. First, do populations of *A. tsugae* exhibit latitudinal and elevational variation in survivorship? Latitudinal (mediated by altitudinal) differences in survivorship may provide a mechanism for the differences in expansion rate between northern and southern populations observed by Evans and Gregoire (2007). Second, is variation in *A. tsugae* survival significantly related to the minimum winter temperature at a landscape scale? Other studies have conducted similar surveys but have typically been spatially limited to smaller regions (Orwig et al. 2002, Skinner et al. 2003, Paradis et al. 2008) and have focused on the use of individual proximal weather stations rather than spatially continuous temperature estimates. Third, does contemporaneous *A. tsugae* density contribute to variation in survival? Adelgid density may produce a negative feedback on population growth, and the importance of density as an interacting factor with temperature is unknown. Finally, using the observed relationships between landscape factors and hemlock woolly adelgid survival, we ask whether weather-based estimates of landscape-scale *A. tsugae* winter mortality suggest consistent spatial patterns of adelgid survival across the 2 yr of study.

Materials and Methods

From 9 March through 24 April 2003 and from 29 February through 28 April 2004, cooperators from state and national forests, parks, and private land collected branches from eastern hemlock (*T. canadensis*) infested by *A. tsugae* across the latitudinal gradient occupied by the adelgid, with collections from southern locations made earliest. The distribution of collection sites (36 locations in 2003 and 35 in 2004) is shown in Fig. 1. Each cooperator was provided with identical, specific instructions on how to select and

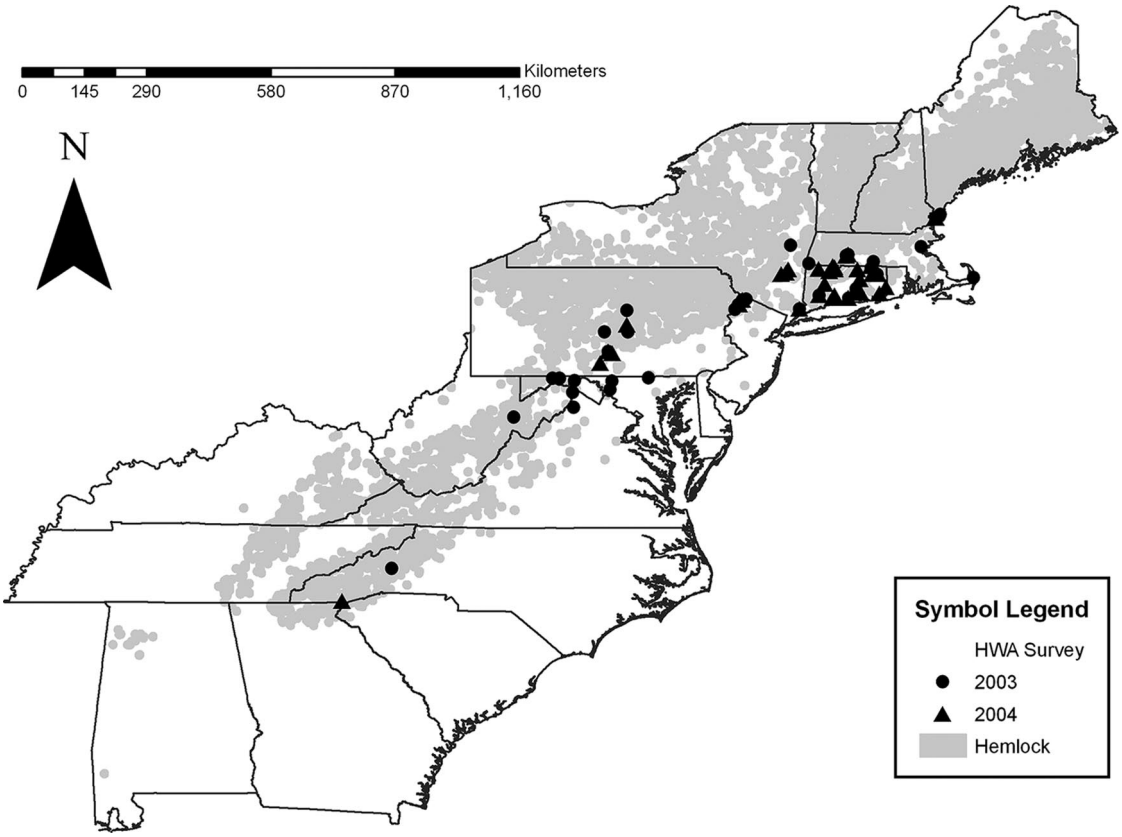

Fig. 1. Distribution of locations surveyed in 2003 (circles) and 2004 (triangles). The distribution of hemlock is shown in gray and is based on scrambled (i.e., publicly available) Forest Inventory and Analysis (USDA Forest Service) locations with 10-km buffers. Map is rendered in a Mercator projection.

collect material, requesting they collect one branch from the readily accessible portion of the canopy (typically breast height) from each of 10 eastern hemlocks with visually apparent infestations of *A. tsugae.* Trees in a site were to be selected within a maximum 2-ha area. Cardinal direction for collection was not specified and was assumed to contribute to random variation. Branches were typically shipped through express mail in plastic bags to Hamden, CT. On arrival branches were removed from the bags and labeled. The ends of the branches were cut, placed in water in plastic buckets to slow desiccation of the foliage, and stored at 5–6°C. Preliminary experiments showed that this temperature was effective at arresting *A. tsugae* development without inducing mortality (K.S.S., unpublished data). We used a first-come, first-served queue in processing samples, and all branches were processed within 7 d of collection. Processing consisted of measuring the length of the most recent (previous) year's growth on branch tips (used to estimate adelgid density) and recording the number of dead and living first instars and dead and living adelgids that were second-stage nymphs or older. Branches were collected before budbreak in spring, so the live outermost stems were those produced in the growing season of the previous calendar year. Only those stems with live buds were included in the study. The numbers of adelgids were summed by branch for a tree-level estimate of survival. The condition of adelgids (live/dead) was determined by looking for movement and a positive hemolymph response (i.e., produced abundant claret-colored fluid) when probed. Those insects that had desiccated, discolored, had no detectable movement, and showed little turgor were considered dead.

The relationship between *A. tsugae* survival rates and both latitude and altitude was examined using multiple linear regression (SPSS 2005), treating latitude and elevation as independent variables. Latitude and elevation values were recorded in the field by cooperators or were estimated using topographic maps. Data were initially pooled for both years because both latitude and elevation are fixed variables that (ignoring continental drift and mountain formation) do not vary between years.

Weather data were compiled by downloading data for all weather stations within each of the 19 states (shown in Fig. 1) for which monthly minimum temperatures were available through the National Oceanic and Atmospheric Administration's National Climatic Data Center (2007). This yielded 1,263–1,281 stations for November 2002 through March 2003 and

1,267–1,279 stations for November 2003 through March 2004. Station temperature values and positions were used to generate point shapefiles using ArcMap (ESRI 2005). Temperatures were interpolated by month for November 2002 through March 2003 and November 2003 through March 2004 to generate temperature estimate surfaces. Interpolation was based on ordinary cokriging (ESRI 2005). Ordinary cokriging uses geographic autocorrelation, as in ordinary kriging, for the variable of interest (temperature) with cross-correlations of related variables (elevation). Within this study, elevation values for the entire landscape were obtained from Digital Elevation Models (DEM), and based on the relationship between elevation and temperature, were used to improve landscape estimates of temperature. Elevation values were estimated by reducing the resolution of DEMs based on the SRTM (Shuttle-Based Radar Topography) to generate ≈50,000 evenly spaced points with elevation values; these points were used to augment the ≈1,200 stations with temperature values. The surface estimate based on the stations and elevation data was calculated at a pixel size of ≈0.023 degrees (2.56 km) using ArcMap Geostatistical Analyst (ESRI 2005). SRTM DEM data were not available for a region in northeastern Alabama, as marked on the map. Temperature estimates within this region are based on ordinary kriging using only the weather stations. Temperature estimates are based on a minimum of the five nearest stations, and interpolated values were rounded to integers, because the original NCDC data are in integer format. The positions from which *A. tsugae* were collected were overlaid on the temperature distribution maps, and monthly temperature estimates were extracted from the corresponding raster.

The statistical relationships between hemlock woolly adelgid survival and estimated minimum winter temperature and *A. tsugae* density were examined by regression analysis (SPSS 2005). This yielded three models per year; one with both independent variables (estimated minimum winter temperature and observed adelgid density) and one with each individually. Models were compared within years using Akaike's information criterion (AIC) (Akaike 1973, SPSS 2005). Although the literature includes discussion about the relative strengths of both AIC and Bayesian information criterion, also called Schwarz's information criterion (Schwarz 1978), the goals of the two differ, and AIC is intended to address changes in predictive accuracy, as discussed by Forster (2001).

Landscape estimates of *A. tsugae* survival rates were made using two linear models. In the first, the linear relationship is defined by regression (SPSS 2005) of the observed adelgid survival on all of the trees (S_{HWA}), against the estimated minimum winter temperature (T_{MIN}). The resulting map provides an estimate of the average adelgid survival at a given location. The second approach provides a simple, conservative (or worst-case spread scenario) estimate of adelgid survival risk. Because of the high fecundity of these parthenogenetic insects, populations may persist even with very few survivors. Assuming, as we have in the previous model, that the relationship between adelgid survival and minimum winter temperature is linear, the boundary temperatures for survival rates can be estimated by connecting the two points with a line such that all of the remaining points fall below that line. This approach provides a map describing the expected maximum adelgid survival rate at a given location. It is important to note, however, that this approach is subject to error, because variation in the two uppermost points, driven by sampling error, can change this estimated boundary.

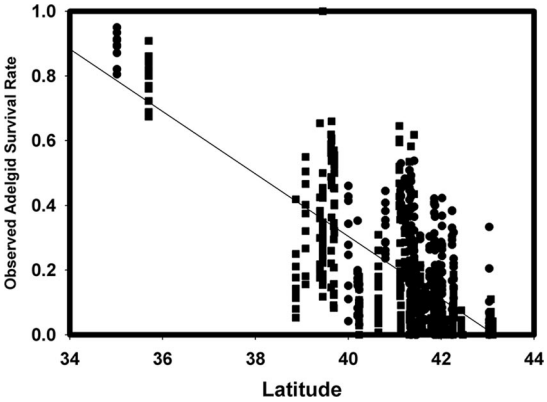

Fig. 2. Tree-level rates of adelgid survival are closely associated with latitude in both 2003 and 2004. The consistency of this relationship for both years suggests latitude is capturing landscape variables related to adelgid survival. Even when the southern locations are removed from the analysis for both years, the relationship is statistically significant ($P < 0.001$, $R^2 = 0.265$).

Results and Discussion

Roles of Latitude, Altitude, Temperature, and Density in Structuring *A. tsugae* Survival on the Landscape. In the combined years of 2003 and 2004, latitude and elevation explained one half of the variation in *A. tsugae* survival (analysis of variance [ANOVA], $R^2 = 0.52$, $F = 385$, $P < 0.001$), with survival increasing as latitude and elevation decreased; however, elevation explained only 2% of the variation in adelgid survival at the landscape scale, whereas latitude alone explained one half of the variation in adelgid survival (ANOVA, $R^2 = 0.50$, $F = 708$, $P < 0.001$; Fig. 2). These data suggest the difference between northern and southern invasion rates observed by Evans and Gregoire (2007) at a similar spatial scale may be driven by differences in survival rate, i.e., reduced populations may exert less propagule pressure on surrounding uninfested regions. Latitude by itself, however, has little biological meaning, but represents environmental gradients such as temperature that affect organisms. Because temperatures vary interannually, it might be expected that the relationship between latitude and *A. tsugae* survival might vary between years. A post hoc analysis of the 2 yr separately, however, indicates that, despite the potential for interannual variation, the predictive power of latitude was similar between years

Table 1. Regression Model

Year	Model	Adjusted R^2	Parameter			AIC	P
			Constant	T_{MIN}	D_{HWA}		
2003	2003-1	0.103	0.256 (0.017)	0.011 (0.002)	−0.008 (0.004)	−1,326.11	<0.001
2003	2003-2	0.094	0.230 (0.012)	0.012 (0.002)		−1,323.54	<0.001
2003	2003-3	0.011	0.208 (0.016)		−0.009 (0.004)	−1,291.24	<0.025
2003	2003-E		0.863	0.044			
2004	2004-1	0.477	0.295 (0.021)	0.031 (0.002)	0.019 (0.006)	−1,318.99	<0.001
2004	2004-2	0.464	0.350 (0.012)	0.031 (0.002)		−1,311.26	<0.001
2004	2004-3	0.009	0.153 (0.027)		0.017 (0.008)	−1,095.16	<0.038
2004	2004-E		1.065	0.065			

(2003: ANOVA, $R^2 = 0.44$, $F = 287$, $P < 0.001$; 2004: ANOVA, $R^2 = 0.54$, $F = 420$, $P < 0.001$; Fig. 2), suggesting latitude is capturing factors relevant to adelgid survival.

Past work has shown that temperature (Parker et al. 1999, Skinner et al. 2003, Paradis et al. 2008) and density (McClure 1991) are important moderators of *A. tsugae* population dynamics, and our data provided an opportunity to evaluate both of these factors at a landscape scale. Based on our 2003 and 2004 surveys, both of these parameters are statistically significant predictors of adelgid survival (Regression model parameters Table 1). Despite the statistical significance of density, however, the predictive power and biological significance of the current year's density in determining adelgid survival rates (probably through changes in host quality) is small, and the slope of the relationship reversed between the 2 yr of study. The regression of density against adelgid survival yields low R^2 values (Table 1, equations 2003-3 and 2004-3), and the addition of density to the temperature model results in a negligible improvement in R^2 values (Table 1, equations 2003-2 and 2004-2 compared with equations 2003-1 and 2004-1).

The weak link between adelgid density and winter mortality may be the result of an asynchrony between cause and effect. The density-dependent response shown by McClure (1991) was driven by a 1-yr timelag in host quality, such that this year's population density determines next year's host quality. Within our data, the current year's density was used to explain the current year's adelgid survival. To assess the role of density in landscape patterns of adelgid survival, future studies should include the use of long-term monitoring within stands and across landscapes (perhaps using remotely sensed data as shown by Bonneau et al. 1999 and Pontius et al. 2005) or surrogates for last year's adelgid density (such as foliage density or number of live stems).

Although density was a poor predictor of adelgid survival, minimum winter temperatures were a strong, but inconsistent predictor (Table 1, equations 2003-2 and 2004-2; Figs. 3 and 4, lines marked A). In 2004, the estimated minimum winter temperature explained nearly one half of the variation in adelgid survival (Table 1; Fig. 4). Laboratory studies have experimentally documented the sensitivity of the hemlock woolly adelgid to low temperatures (Parker et al. 1999, Skinner et al. 2003), and the strong link between minimum temperature and adelgid survival in 2004 suggests this is one of the primary variables captured by latitude. However, although latitude explained one half the variation in adelgid survival in 2003, minimum winter temperatures explained <10% (Table 1; Fig. 3). This disconnect between latitude and minimum winter temperatures in 2003 suggests other factors associated with latitude played a more prominent role in determining adelgid survival.

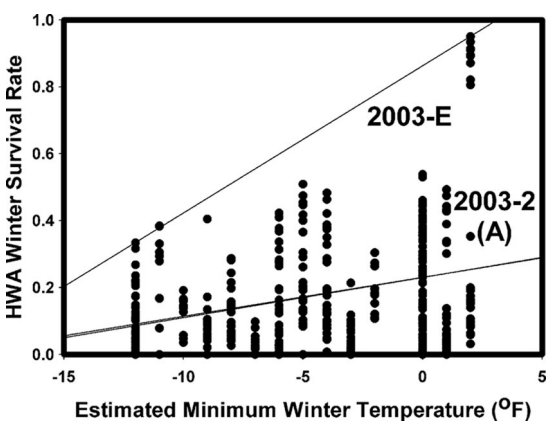

Fig. 3. Estimated minimum winter temperature explains <10% of the variation in adelgid survival in 2003. See Table 1 for parameters.

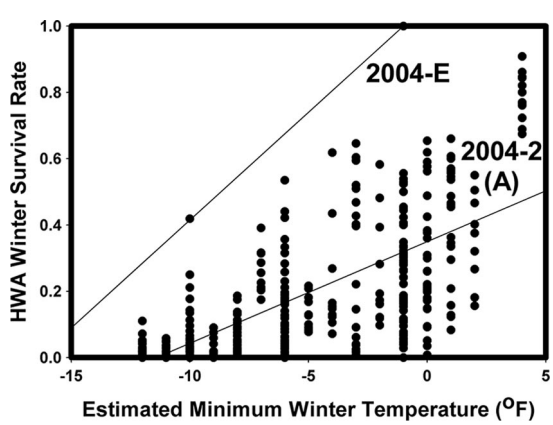

Fig. 4. Estimated minimum winter temperature explains one half the variation in adelgid survival in 2004. See Table 1 for parameters.

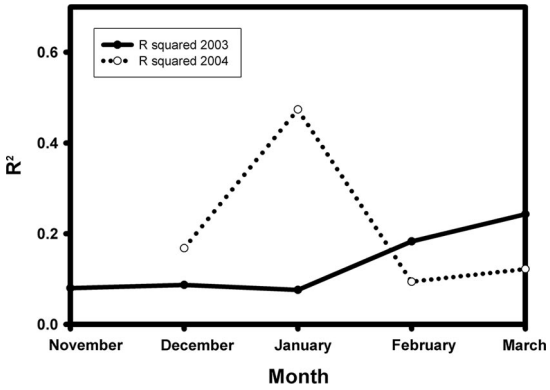

Fig. 5. R^2 values produced using individual months to predict adelgid survival. In 2004, January was a strong predictor of adelgid survival, whereas in 2003, the greatest variation in adelgid survival was explained by estimated minimum temperatures in March. All points are statistically significant at $P < 0.05$, with the exception of November 2004, which is not plotted.

One potential explanation for the variation in the importance of minimum winter temperature between the years is that the seasonal amplitude of the temperature profile differed, i.e., 1 yr was colder than the other. Comparison of temperature estimates at the locations sampled between the 2 yr, however, shows that they did not differ significantly (mean minimum 2003 temperature: -4.49 ± 0.24°C, mean 2004 temperature: -4.79 ± 0.25°C, ANOVA, $F = 0.711$, $P = 0.399$). Alternatively, the timing of temperature events (winter temperature profile) may have played a role. Skinner et al. (2003) showed that low temperatures in March may produce higher adelgid mortality than the same temperatures experienced in January. A post hoc comparison of the relationship between the minimum temperatures by month and adelgid survival (Fig. 5) suggests that the role of temperature is mediated by seasonality. In 2004, both January minimum temperatures and minimum winter temperatures explained about the same amount of variation in adelgid survival; this is not surprising, because they are often synonymous. In 2003, however, minimum temperatures in February and March explained more of the variation in adelgid survival than minimum winter temperatures or January temperatures, although neither separately or combined explained as much variation as latitude. Further work is needed to determine the relationship between seasonal temperature profiles and adelgid survival, and we have established long-term study sites

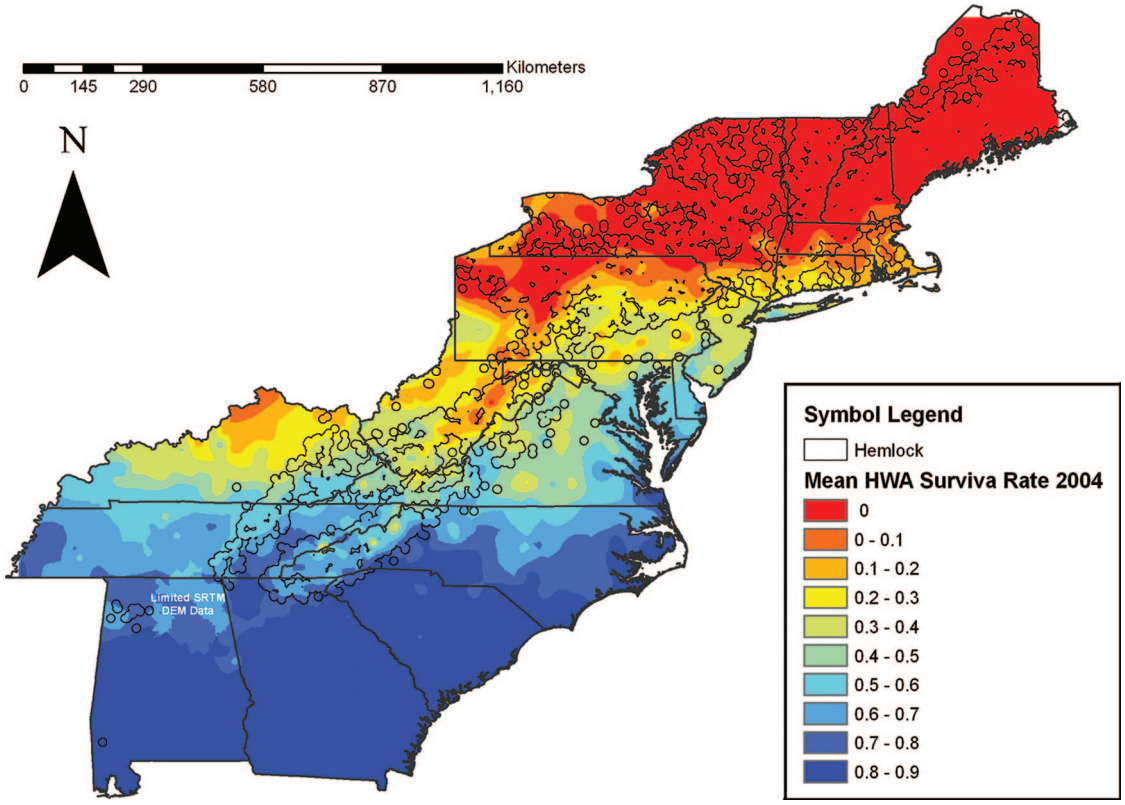

Fig. 6. Estimated average adelgid survival in the eastern United States in 2004 based on equation 2004-2. In 2003, minimum winter temperatures explained <10% of the variation in adelgid survival and were not used to produce landscape estimates. The area labeled "limited SRTM DEM data" indications the region of Alabama for which DEM data were not available. Temperature estimates in this subregion are based on ordinary kriging using only the station data.

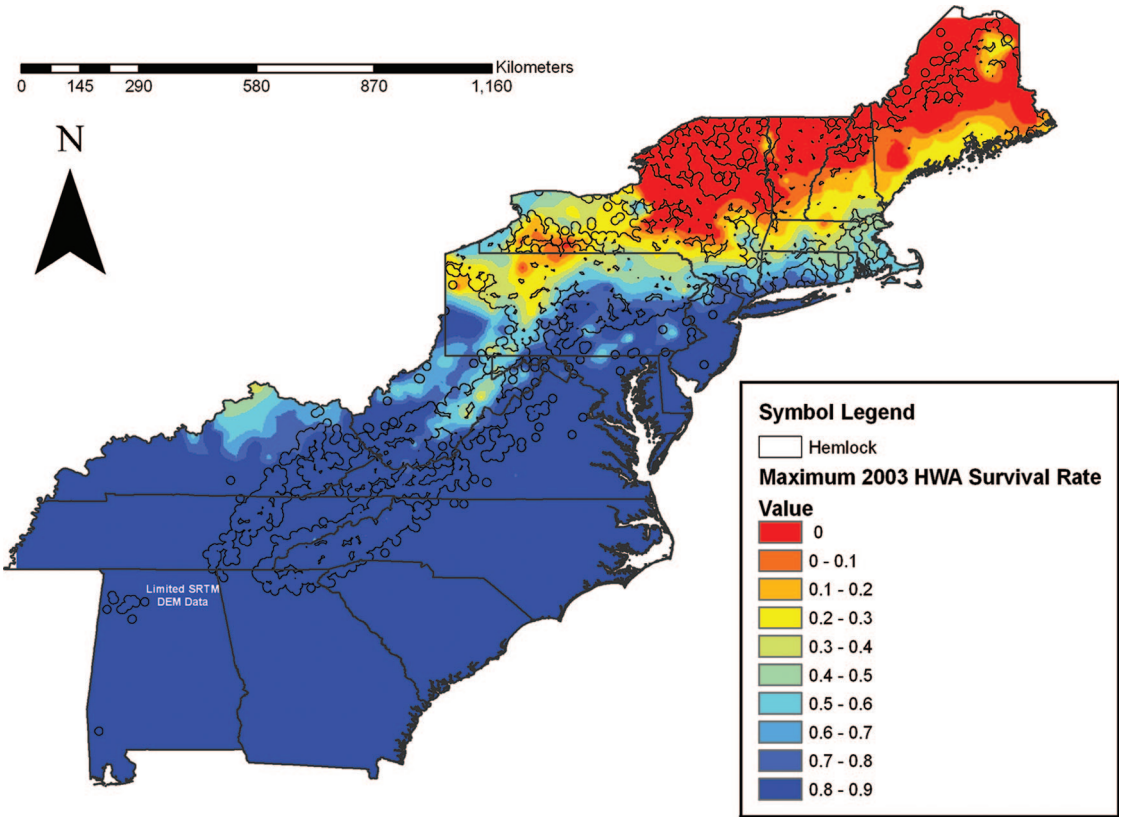

Fig. 7. This map, produced using equation 2003-E, shows a high degree of similarity with the 2004 map. This suggests that, taken at a landscape scale and based on extensive collections, survival between years may follow similar patterns. Further collections should be made to examine the implied large-scale consistency in the distribution of hemlock woolly adelgid survival.

with in situ sensors recording high temporal resolution weather data across the latitudinal gradient occupied by *A. tsugae* to address this knowledge gap.

Estimating Temperature-Driven Patterns of *A. tsugae* Survival in the Eastern United States. Using the relationship between minimum winter temperature and adelgid survival described by equation 2004-2 (Table 1; Fig. 4, line marked A), we used the interpolated minimum winter temperatures to develop a landscape estimate of the mean rate of *A. tsugae* survival in the eastern United States (Fig. 6). This procedure was not done using the 2003 data, because the explanatory power of equation 2003-2 was weak. Density was also omitted based on the asynchrony between cause and effect discussed previously. The resulting map shows a strong north-to-south gradient in adelgid survival and the influence of topography (and its influence on temperature) shown by the Appalachian Mountains. This spatial estimate of adelgid survival may be useful for estimating the relative impact in a region assuming impact is related to mean rates of adelgid survival.

To estimate population boundaries, a different approach is needed. With mean reproductive rates of 22 and 49 eggs per female (McClure 1989) in spring and winter generations (respectively), a stable population (neither increasing nor decreasing) requires the survival of only 2% of the winter generation and 4.5% of the spring generation. These estimates are of the same order of magnitude as those presented by Paradis et al. (2008), who indicated a 9% adelgid survival rate of the winter population results in a stable population. Even when mean adelgid survival rates are below this value, the survival rates on individual trees may be higher, sustaining local populations. If we assume that the relationship between adelgid survival and minimum winter temperature is linear (an assumption that merits further study), and if we assume that the trees collected fall in the ecological envelope defined by temperature, a simpler way to define that envelope is by connecting the two points such that the remaining points fall below that line, producing a temperature envelope that captures the remaining data. Doing this for data from both 2003 and 2004 yields surprisingly similar results (Table 1, equations 2003-E and 2004-E; Figs. 3 and 4, lines marked E) and similar landscape estimates of maximum adelgid survival (Figs. 7 and 8) based on the respective year's weather. The agreement between the two maps suggests that, although *A. tsugae* survival may vary from year to year (as would be expected based on variation in the weather), it should be possible to estimate the ecological limits for the species using this approach as the boundary of the envelope

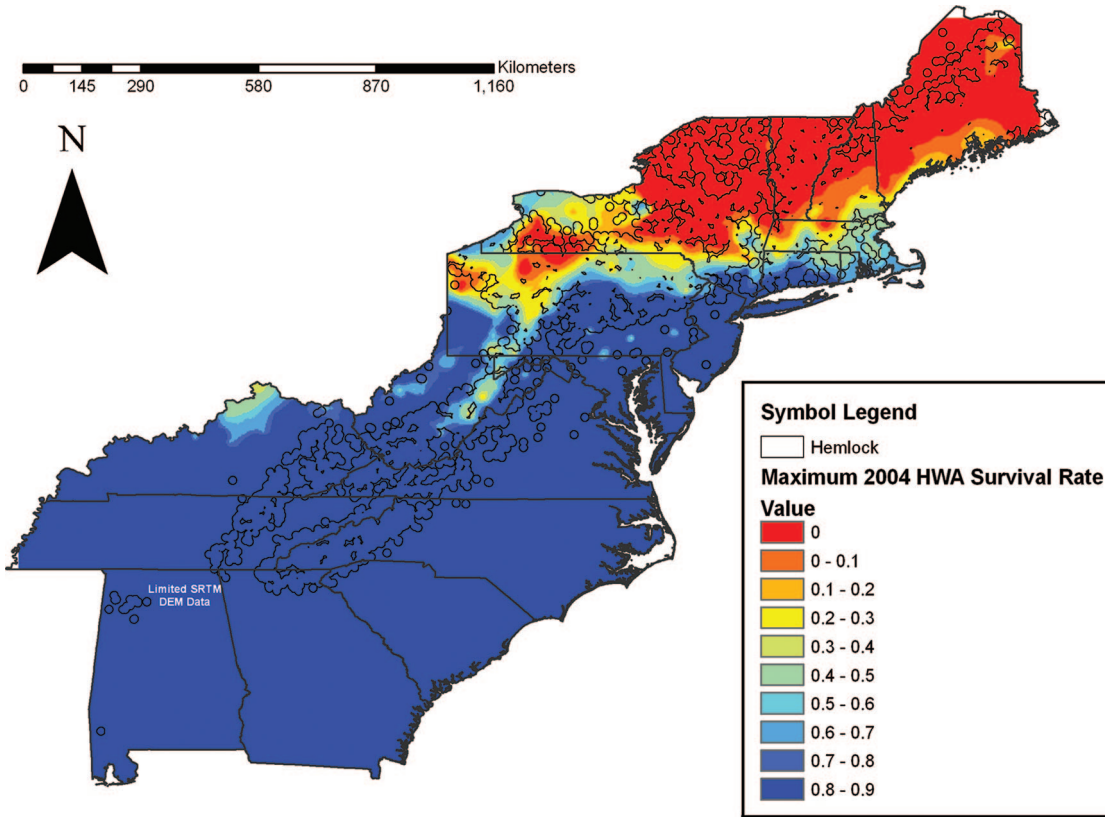

Fig. 8. This map, produced using equation 2004-E, shows a high degree of similarity with the 2003 map. These suggest that, taken at a landscape scale and based on extensive collections, survival between years may follow similar patterns. Further collections should be made to examine the implied large-scale consistency in the distribution of hemlock woolly adelgid survival.

is a characteristic of the species rather than the environment. Continuing to refine these estimates will require combining knowledge about the sensitivity of *A. tsugae* to temperature profiles with an improved understanding genotypic variation and selective pressures as discussed by Butin et al. (2005), and changes in the distribution of temperatures, as described by Paradis et al. (2008).

***Adelges tsugae* Climatic Suitability Modeling: Limits and Utility.** These maps provide a starting point for estimating the potential distribution of *A. tsugae* in the eastern United States. However, it is important to note that each of these maps are models based on estimates of both the weather (through interpolation) and adelgid response (through linear modeling), and there are four key issues to consider in their use.

First, the pixel size used to generate these maps is large (≈2.5 km). While well suited for the landscape analysis, it is too coarse to estimate local survivorship where variables such as slope, aspect, and soil type may play larger roles. Second, these maps are based on temperatures observed in the years studied, and the locations of boundaries will shift with annual changes in the weather. Although climatic normals may provide an estimate of general boundaries as described by Paradis et al. (2008), contemporary risk should be estimated using contemporary weather data, and the use of multiple years as shown in Fig. 9 can provide an estimate of the expected interannual variation in the location of the population boundary. Third, although the models provide an estimate of winter survival, only one of the two annual generations experiences winter. The spring generation is not subject to winter temperatures, and populations may quickly recover from winter impacts (McClure 1996). Finally, the relationship between the minimum winter temperature and adelgid survival has been assumed to be linear. Under laboratory conditions, the survival limit for adelgids was shown to be −35°C (Parker et al. 1999, Skinner et al. 2003). Extrapolation of the lines produced by equations 2003-E and 2004-E, however, both indicate that the temperature at which *A. tsugae* survival should drop to 0 is about −20°C, whereas data presented by Paradis et al. (2008) suggest the minimum temperature is −40°C. These discrepancies suggest that (1) some or all of the relationship between minimum winter temperatures and adelgid survival may be nonlinear, one of the many risks associated with extrapolation beyond available data, (2) the realized ecological tolerances of the adelgid may be narrower in natural settings where temperature effects are com-

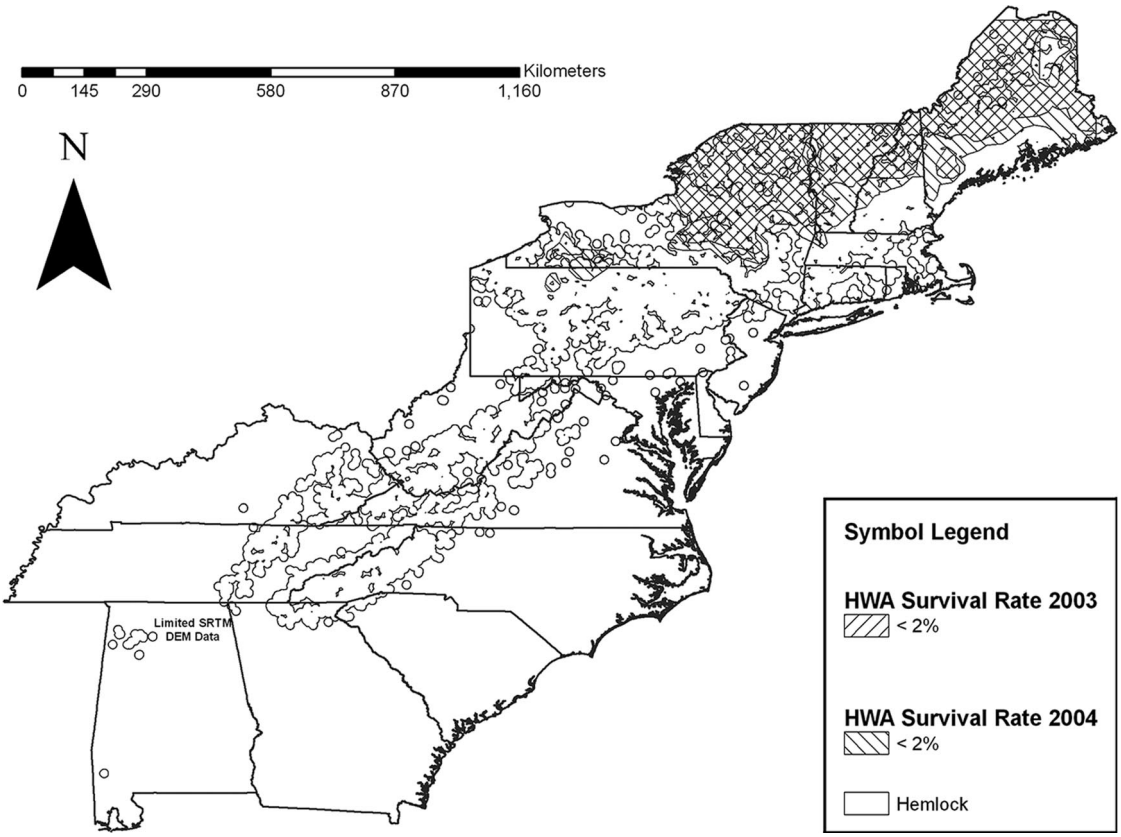

Fig. 9. Regions where the estimated adelgid survival were <2% in both 2003 and 2004 occupy similar regions of the northeastern United States. These boundaries suggest those areas that may be climatically resistant to the hemlock woolly adelgid.

pounded by other biotic and abiotic factors, or (3) some combination of these and other factors.

Although necessarily limited for the reasons stated, these maps begin the process of describing the potential range of the invasive *A. tsugae.* They identify sources of variation that can be tracked across the landscape and highlight some of the biological and ecological data that remains to be collected and described. For example, although there is no evidence that predation impacts population dynamics (Montgomery and Lyon 1996, Wallace and Hain 2000), past predator surveys have been regional, and surveys across the full adelgid distribution remain to be made. Pathogens are not currently known to control adelgid populations, but work by Gouli et al. (1997) and Costa et al. (2005) suggests the environment may already harbor fungi that can attack *A. tsugae.* Host quality also needs further study. Although both *T. canadensis* and *T. caroliniana* are highly susceptible to *A. tsugae,* that susceptibility may vary as a function of secondary compounds driven by the genetics of the host plants and by variation in the environment. Work by Lagalante et al. (2006) has shown that changes in terpenoid composition and concentration in new foliage coincides with the aestivation of first instar sistens. The affects of timing and abundance of these plant compounds (whether genetically based, the result of adelgid herbivory, or the result of the local biotic or abiotic environment) on adelgid development remains to be examined. Further study of each of these factors should be a high priority, because they may provide tools for mitigating *A. tsugae* populations.

Acknowledgments

We thank C. Cheah, M. Montgomery, D. Mikus, A. Sior, J. Denham, R. Cowles, J. Compton, M. Meyer, T. Lupp, C. Firme, R. Evans, J. Unger, D. Ouelette, J. Bofinger, and others who assisted with the collection of material and N. Havill, P. Tobin, R. Haack, K. McManus, and two anonymous reviewers for comments provided on previous versions of the manuscript.

References Cited

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle, pp. 267–281. *In* B. N. Petrov and F. Csaki (eds.) Proceedings of the 2nd International Symposium on Information Theory. Akademia Kiado, (1973) Budapest, Hungary.

Akin, W. E. 1991. Global patterns: climate, vegetation, and soils. University of Oklahoma Press, Norman, OK.

Allee, W. C. 1938. The social life of animals. Norton, New York.

Andow, D. A., P. M. Kareiva, S. A. Levin, and A. Okubo. 1990. Spread of invading organisms. Landscape Ecol. 4: 177–188.

Bonneau, L. R., K. S. Shields, and D. L. Civco. 1999. A technique to identify changes in hemlock forest health over space and time using satellite image data. Biol. Invasions 1: 269–279.

Butin, E., A. H. Porter, and J. Elkinton. 2005. Adaptation during biological invasions and the case of *Adelges tsugae.* Evol. Ecol. Res. 7: 887–900.

Cobb, R. C., D. A. Orwig, and S. Currie. 2006. Decomposition of green foliage in eastern hemlock forests of southern New England impacted by hemlock woolly adelgid infestations. Can. J. For. Res. 36: 1331–1341.

Costa, S. D., B. L. Parker, V. Gouli, M. Brownbridge, M. Skinner, and S. Gouli. 2005. Insect-killing fungi as a component of hemlock woolly adelgid integrated pest management, p. 155. *In* B. Onken and R. Reardon (eds), Third Symposium on Hemlock Woolly Adelgid, 1–3 February 2005, Asheville, NC. U.S. Department of Agriculture Forest Service, Morgantown, WV.

Dansereau, P. 1957. Biogeography: an ecological perspective. The Ronald Press Company, New York.

Dobson, A. P., and R. M. May. 1986. Patterns of invasions by pathogens and parasites, pp. 58–76. *In* H. A. Mooney and J. A. Drake (eds.), Ecology of biological invasions of North American and Hawaii. Ecology studies 58. Springer, New York.

Drenovsky, R. E., and K. M. Batten. 2007. Invasion by *Aegilops triuncialis* (barb goatgrass) slows carbon and nutrient cycling in a serpentine grassland. Biol. Invasions 9: 107–116.

ESRI ArcMap. 2005. Version 9.1, ArcInfo license. ESRI, Redlands, CA.

Evans, A. M., and T. G. Gregoire. 2007. A geographically variable model of hemlock woolly adelgid spread. Biol. Invasions 9: 368–382.

Fagan, W. F., M. A. Lewis, M. G. Neubert, and P. van den Driessche. 2002. Invasion theory and biological control. Ecol. Lett. 5: 148–157.

Forster, M. R. 2001. The new science of simplicity, pp. 83–117. *In* A. Zellner, H. Keuzenkamp, and M. McAleer (eds.), Simplicity, inference and modelling. Cambridge University Press, Cambridge, United Kingdom.

[GAO] General Accounting Office. 2000. Invasive species, federal and selected state funding to address harmful, nonnative species. GAO, Washington, DC.

Good, R. 1953. The geography of the flowering plants. Longmans, Green and Co., New York.

Gouger, R. J. 1971. Control of *Adelges tsugae* on hemlock in Pennsylvania. Sci. Tree Topics 3: 1–9.

Gouli, S., B. L. Parker, and M. Skinner. 1997. Isolation of fungi associated with hemlock woolly adelgid (Homoptera: Adelgidae). J. Inv. Pathol. 70: 76–77.

Haack, R. A. 2001. Intercepted Scolytidae (Coleoptera) at U.S. ports of entry: 1985–2000. Integr. Pest Manag. Rev. 6: 253–282.

Haack, R. A. 2006. Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions. Can. J. For. Res. 36: 269–288.

Havill, N. P., and R. G. Foottit. 2007. Biology and evolution of Adelgidae. Annu. Rev. Entomol. 52: 325–349.

Havill, N. P., M. E. Montgomery, G. Yu, S. Shiyake, and A. Caccone. 2006. Mitochondrial DNA from hemlock woolly adelgid (Hemiptera: Adelgidae) suggests cryptic speciation and pinpoints the source of the introduction to eastern North America. Ann. Entomol. Soc. Am. 99: 195–203.

Hengeveld, R. 1988. Mechanisms of biological invasions. J. Biogeogr. 15: 819–828.

Iverson, L. R., A. M. Prasad, B. J. Hale, and E. K. Sutherland. 1999. Atlas of current and potential future distributions of common trees of the eastern United States. Northeastern Research Station GTR NE-265. U.S. Department of Agriculture Forest Service, New Town Square, PA.

Jerde, C. L., and M. A. Lewis. 2007. Waiting for invasions: a framework for the arrival of nonindigenous species. Am. Nat. 170: 1–9.

Johnson, D. M., A. M. Liebhold, P. C. Tobin, and O. N. Bjørnstad. 2006. Allee effects and pulsed invasion by the gypsy moth. Nature (Lond.) 444: 361–363.

Lagalante, A. F., N. Lewis, M. E. Montgomery, and K. S. Shields. 2006. Temporal and spatial variation of terpenoids in Eastern Hemlock (*Tsuga canadensis*) in relation to feeding by *Adelges tsugae.* J. Chem. Ecol. 32: 2389–2403.

Liebhold, A. M., and J. Bascompte. 2003. The Allee effect, stochastic dynamics and the eradication of alien species. Ecol. Lett. 6: 133–140.

Liebhold, A. M., J. A. Halverson, and G. A. Elmes. 1992. Gypsy moth invasion in North America: a quantitative analysis. J. Biogeogr. 19: 513–520.

McClure, M. S. 1989. Evidence of a polymorphic life cycle in the hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae). Ann. Entomol. Soc. Am. 82: 50–54.

McClure, M. S. 1990. Role of wind, birds, deer, and humans in the dispersal of hemlock woolly adelgid (Homoptera: Adelgidae). Environ. Entomol. 19: 36–43.

McClure, M. S. 1991. Density-dependant feedback and population cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis.* Environ. Entomol. 20: 258–264.

McClure, M. S. 1996. Biology of *Adelges tsugae* and its potential for spread in the northeastern U.S., pp. 16–25. *In* S. M. Salom, T. C. Tigner, and R. C. Reardon (eds.), Proceedings of the First Hemlock Woolly Adelgid Review, Oct 12, 1995, Charlottesville, VA. US Department of Agriculture Forest Service, Morgantown, WV.

McClure, M. S., and C.A.S.-J. Cheah. 1999. Reshaping the ecology of invading populations of the hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae), in eastern North America. Biol. Invasions 1: 247–254.

McClure, M. S., S. M. Salom, and K. S. Shields. 2001. Hemlock woolly adelgid. U.S. Department of Agriculture Forest Service, Morgantown, WV FHTET-2001–03.

Merriam, C. H. 1890. Results of a biological survey of the San Francisco Mountains region and desert of the Little Colorado in Arizona. North Am. Fauna 3: 1–136.

Montgomery, M. E., and S. M. Lyon. 1996. Natural enemies of adelgids in North America: their prospect for biological control of *Adelges tsugae,* pp. 89–102. *In* S. M. Salom, T. C. Tigner, and R. C. Reardon (eds), Proceedings of the First Hemlock Woolly Adelgid Review, 12 October 1995, Charlottsville, VA. USADA Forest Service, Forest Health Technology Enterprise Team, Morgantown, WV.

National Climatic Data Center. 2007. (http://www.ncdc.noaa.gov). NCDC Climate Data Online.

Neilson, R. P. 1995. A model for predicting continental-scale vegetation distribution and water balance. Ecol. Appl. 5: 362–385.

Onken, B., and R. Reardon (compilers). 2005. Proceedings of the Third Symposium on Hemlock Woolly Adelgid in the Eastern United States, 1–3 February 2005, Ashville, NC. U.S. Department of Agriculture Forest Service, Morgantown, WV.

Orwig, D. A., and D. R. Foster. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, U.S.A. J. Torr. Bot. Soc. 125: 60–73.

Orwig, D. A., D. R. Foster, and D. L. Mausel. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. J. Biogeogr. 29: 1475–1487.

Paradis, A., J. Elkinton, K. Hayhoe, and J. Buonaccorsi. 2008. Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. Mitig. Adapt. Strat. Glob. Change 13: 541–554.

Parker, B. L., M. Skinner, S. Gouli, T. Ashikaga, and H. B. Teillon. 1999. Low lethal temperature for hemlock woolly adelgid (Homoptera: Adelgidae). Environ. Entomol. 28: 1085–1091.

Pimental, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50: 53–65.

Pontius, J., R. Hallett, and M. Martin. 2005. Using AVIRIS to assess hemlock abundance and early decline in the Catskills, New York. Remote Sens. Environ. 97: 163–173.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, NY.

Schwarz, G. 1978. Estimating the dimension of a model. Ann. Stat. 6: 461–464.

Shigesada, N., K. Kawasaki, and Y. Takeda. 1995. Modeling stratified diffusion in biological invasions. Am. Nat. 146: 229–251.

Skinner, M., B. L. Parker, S. Gouli, and Takamaru Ashikaga. 2003. Regional responses of hemlock woolly adelgid (Homoptera: Adelgidae) to low temperatures. Environ. Entomol. 32: 523–528.

SPSS. 2005. SPSS Base 14.0 users guide. SPSS, Chicago, IL.

Stadler, B., T. Müller, and D. A. Orwig. 2006. The ecology of energy and nutrient fluxes in hemlock forests invaded by hemlock woolly adelgid. Ecology 87: 1792–1804.

Tobin, P. C., A. M. Liebhold, and E. A. Roberts. 2007. Comparison of methods for estimating the spread of a nonindigenous species. J Biogeogr. 34: 305–312.

Towns, D. R., I.A.E. Atkinson, and C. H. Daugherty. 2006. Have the harmful effects of introduced rats on islands been exaggerated? Biol. Invasions 8: 863–891.

Wallace, M. S., and F. P. Hain. 2000. Field surveys and evaluation of native and established predators of the Hemlock Woolly Adelgid (Homoptera: Adelgidae) in the Southeastern United States. Environ. Entomol. 29: 638–644.

Work, T. T., D. G. McCullough, J. F. Cavey, and R. Komsa. 2005. Arrival rate of nonindigenous insect species into the United States through foreign trade. Biol. Invasions 7: 323–332.

Received 26 August 2008; accepted 16 March 2009.