

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

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Abstract Global climate change has already affected the abundances, range limits, and interactions of many species. The hemlock woolly adelgid (*Adelges tsugae*), an invasive insect introduced to eastern North America from Japan, has decimated stands of eastern hemlock (*Tsuga canadensis*) and Carolina hemlock (*T. caroliniana*) from Georgia to Connecticut. However, its spread across central and northern New England has been slowed substantially by its inability to tolerate cold winter temperatures. Using data from previous lab and field studies collected over the past 17 years, including adelgid spread and overwintering mortality, we first characterize the temperature conditions that may limit adelgid spread. We then show how, in the future, rising winter temperatures due to climate change are likely to remove the conditions currently limiting adelgid spread, and facilitate the northward expansion as more suitable habitat becomes available.

Keywords *Adelges tsugae* · Climate change · Hemlock · Invasive species · Woolly adelgid

1 Introduction

Over the past century, temperatures over much of North America have warmed. These warming temperatures are thought to be responsible for observed changes in the characteristics of species currently limited by cold temperatures, including their distribution

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and abundance, phenology, and morphology (Logan and Bentz 1999; Parmesan and Yohe 2003; Root et al. 2003; Stireman et al. 2005). Over the coming century, warming temperatures and changing precipitation patterns due to climate change are expected to continue to promote the spread of pests and other invasive species whose northern extent is currently limited by cold temperatures, resulting in the disruption of ecological communities (Ayres and Lombardero 2000; Volney and Fleming 2000; Logan et al. 2003). One insect species likely to benefit from warmer temperatures is the hemlock woolly adelgid (HWA; *Adelges tsugae*; Annand 1921), an invasive insect that is already decimating stands of both eastern and Carolina hemlock (*Tsuga canadensis*, *T. caroliniana*) throughout the eastern USA (Orwig and Foster 1998).

The adelgid is an aphid-like insect that feeds on the phloem of hemlock trees by inserting its stylet into twigs, usually at the base of needles on the undersides of branches. It is hypothesized that the insect injects toxic saliva (Young et al. 1995), which weakens the tree, causing needle loss, reduced growth, and eventual death within 4 to 6 years of infestation (McClure 1991). Hemlock woolly adelgid is parthenogenetic and completes two generations per year; this high rate of reproduction contributes substantially to its overall impact.

The adelgid was accidentally introduced to Virginia from Osaka, Japan in the early 1950s (Souto et al. 1996; Havill et al. 2006). Once introduced, HWA spread slowly along the east coast of the USA. It arrived in Connecticut in the mid-1980s (McClure 1990) and within a decade had spread north to the border of Massachusetts, killing thousands of trees throughout the state (Orwig and Foster 1998). Its current distribution extends from northern Georgia to southern coastal Maine, with inland populations found as far north as the southern border of Vermont and New Hampshire. Single towns in Michigan (Deborah McCullough, personal communication) and upstate New York on Lake Ontario became infested just this past year (US Department of Agriculture [USDA 2005]).

Interestingly, the interval between first infestation and tree death appears to vary from location to location. For example, McClure (1991) described a 4- to 6-year infestation period that involved cycles of adelgid growth and tree decline in Connecticut, which often resulted in tree death. In contrast, many hemlocks in Massachusetts have harbored infestations for 10 years or more without dying, and these infestations are not widespread. For example, HWA was first documented in Amherst, MA in 1995, yet as of 2006 the vast majority of hemlock trees in this town are still not infested (Elkinton, personal observation). Further, many towns in the inland-central and western part of the state have no known infestations despite the insect having been present in Massachusetts for 17 years. At the northern range of adelgid in New England, cold winters are thought to explain the observed slow rate of spread of HWA and the long survival of infested hemlocks.

Many field and laboratory studies have documented the vulnerability of adelgid to cold winter temperatures (Parker et al. 1998, 1999; Gouli et al. 2000; Skinner et al. 2003; Shields and Cheah 2004; Butin et al. 2005). Shields and Cheah (2004) have shown that overwintering mortality varies greatly over a broad geographical scale and that adelgid in the south (North Carolina) experience significantly less mortality than those in the north (Connecticut and Massachusetts). Field surveys and experimental cold shock experiments have demonstrated that colder temperatures result in larger amounts of mortality, and that susceptibility to cold increases later in the season (February and March). Similar results were obtained by Gouli et al. (2000) in a study that examined adelgid hemolymph (blood) before and after exposure to cold shock. They found that temperatures of -20 and -25°C significantly decreased the overall number of intact cells and affected the proportions of different cell types. After exposure to -30°C for 2 h, there were no intact cells in the

hemolymph and all adelgid had died. Other studies by Parker et al. (1998, 1999) and Skinner et al. (2003) show that after exposure to -30°C , 3% of the adelgid in the experiment had survived. The death of all adelgid occurred between -30 and -35°C . Most recently, Butin et al. (2005) used a common garden study at a field site in Massachusetts with HWA collected from Maryland and Massachusetts to show that there was a genetic component to cold hardiness.

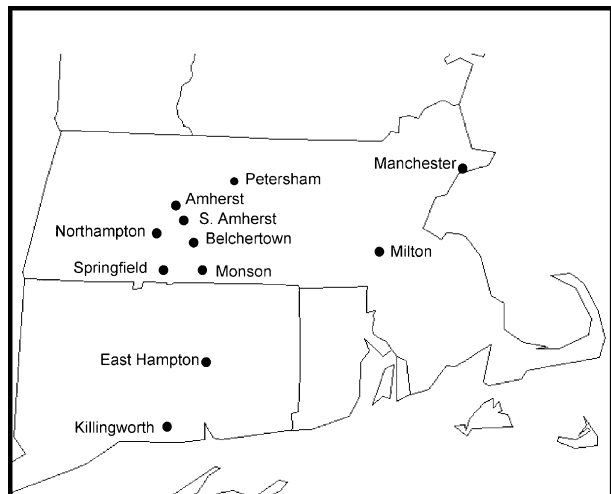
Here, we document the effect of temperature on overwintering mortality of HWA at several additional sites in Massachusetts, and synthesize the body of available literature from studies conducted over the past 17 years to analyze the effect of winter temperature on the rate of spread across the Northeastern USA. Based on the cold temperature thresholds identified in the literature, we then explore the implications of climate change on the future spread of HWA northward across the region.

2 Methods

2.1 HWA field sampling methods

We examined the effects of overwintering temperature on adelgid survival by sampling 12 naturally occurring hemlock stands in Massachusetts and Connecticut in early April 2004, 2005, and 2006 (Fig. 1). On each sampling occasion, several branches about 0.3 m long were cut from two to 12 mature hemlock trees at each site. Trees and branches within 2 m of the ground were selected randomly, with a preference for ones that harbored HWA. All branches were examined to identify the proportion of branchlets on the branch containing adelgid, the length of the most recent growth for each branchlet, and the number of living and dead adelgid (after McClure 1991). Live adelgid are reddish-brown in color, occasionally move their legs, and produce a red droplet of hemolymph when pierced with forceps. When squeezed, live adelgid tend to regain their original shape. In contrast, dead adelgid are black, brittle when squeezed, or produced a clear droplet of liquid when pierced.

Fig. 1 Adelgid overwintering mortality sampling locations in Connecticut and Massachusetts for the winters of 2003–2004, 2004–2005, and 2005–2006



2.2 Analysis of HWA colonization records in MA

Hemlock woolly adelgid first reached Springfield, MA in 1989 (Fig. 2), and dates of the first recorded infestation in each of the 351 towns in the state of Massachusetts were recorded by the Massachusetts Department of Conservation and Recreation (Fig. 2). We obtained a crude estimate of year-to-year variation in the rates of HWA spread between 1994 and 2004 by calculating the proportion of newly infested towns to towns not yet infested, for each year. Prior to 1994, the infestation was confined to a small number of towns near Springfield, Massachusetts and the number of newly infested towns was limited by the small geographical size of the source population. The analysis began in 1994 as by then, a large area had become infested and spread was occurring along a broad front in the southern portion of the state. We then determined whether a statistical relationship existed between the proportion of available towns that became newly infested each year and several measures of overwintering temperatures observed during the previous winter.

2.3 Statistical analysis

Daily mean and minimum temperature data for December through March were collected from the closest weather station to each field site and downloaded from Weather Source (<http://www.weather-source.com>). To estimate the effects of winter temperature on mortality, we fit the data using a mixed model (the Mixed Procedure SAS V9.3 [SAS 2003]) of the form $Y_{st} = \beta_0 + \beta_1 X_{st} + R_t + e_{st}$, where Y_{st} and X_{st} are the mortality rate and one of eight different measures of winter temperature, respectively. At location s in year t , β_1 is the slope of the winter temperature X , R_t contains a random year effect in year t and e_{st}

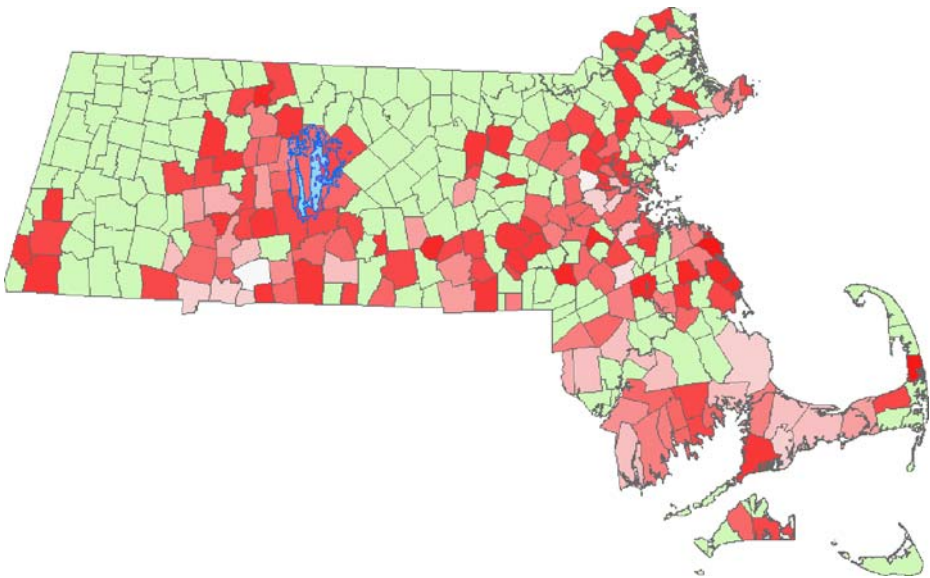


Fig. 2 Colonization of MA towns by Hemlock Woolly adelgid (HWA) from 1989–2004; the years in which towns became infested are indicated by *different shades of red*; the earlier a town became infested, *the lighter the color*. Springfield (south-central MA), the first town to become infested (1989), is *colored white*. Uninfested towns are *green*. (Source: data collected Charlie Burnham, Massachusetts Department of Conservation and Recreation; figure produced by Diana Barszcz.)

is additional noise. This model accounts for random year effects beyond those due to the temperature variable being evaluated, which would include effects of winter temperature not captured by a particular temperature variable, as well as other aspects of inter-annual variability across the region. These year effects need to be accounted for as they induce correlation over locations in a given year. While proportions often need to be modeled using some type of non-linear model, residual analyses showed that a direct linear fit of proportion dead on temperature was sufficient to meet the usual least-squares assumptions, (e.g., equal variance). These residuals showed no evidence of changing variance or serial correlation in the additional noise term. In a mixed model there is not an R-squared calculated to compare models. Here, with just a random year effect one can use $R\text{-squared} = (SSTO - SSE) / SSTO$, where SSTO is the total uncorrected sum of squares and SSE is the sum of the squared residuals resulting from using the coefficients from the mixed model estimation (although this quantity is not guaranteed to be positive as in standard linear regression).

In addition to overwintering mortality, lifetable data such as adelgid density and fecundity were also collected, with the goal of understanding the relative importance of overwintering mortality in comparison to other causes of mortality. Overwintering mortality is typically the largest cause of HWA mortality in our region, and overwintering temperatures also affect fecundity. Details of these studies will be reported elsewhere as data collection and analysis are ongoing. Using these data (unpublished) we also project the conditions under which adelgid population growth will stop – that is, when mortality from all causes balances fecundity and the population is simply replacing itself from year to year and not increasing or decreasing in size. In our data this occurred on average when 91% of the adelgid population died over the winter. In order to determine the temperature conditions under which adelgid populations are expected to stop spreading, we inverted the fitted regression model to obtain an estimated mean and minimum winter temperature $T^* = (0.91 - \beta_0) / \beta_1$ at which the expected mortality equaled 91%. The inverse problem is called regulation in the statistical literature. Standard errors were estimated using the delta method (Graybill and Iyer 1994, Section 6.4; Buonaccorsi 2001).

2.4 Future climate projections

Hemlock woolly adelgid is likely to spread northward over the coming century as winter temperatures across the Northeast continue to warm due to climate change (Hayhoe et al. 2006). To assess potential future HWA spread, we relied on projections from three coupled atmosphere–ocean general circulation models (AOGCMs): NOAA/GFDL CM2.1 (Delworth et al. 2005), UKMO HadCM3 (Pope et al. 2000), and DOE/NCAR PCM (Washington et al. 2000). Climate sensitivity for these models ranges from 1.3–3.3°C, covering the lower part of the Intergovernmental Panel on Climate Change (IPCC) 1.5–4.5°C uncertainty range (Alley et al. 2007), and all climate projections are shown for the three-model average. Based on these global model simulations, high-resolution daily projections for future Northeast temperature and precipitation at one-eighth degree were generated using a statistical bias removal and downscaling technique after Wood et al. (2002), as presented in Hayhoe et al. (2006).

Future simulations were forced by the IPCC Special Report on Emission Scenarios (SRES; Nakićenović et al. 2000) higher (A1fi) and lower (B1) emissions scenarios. At the higher end, rapid introduction of new technologies, extensive economic globalization, and a fossil-fuel-intensive energy path cause CO₂ emissions to climb throughout the century, reaching almost 30 Gt/year or six times 1990 levels by 2100. Emissions under the B1

scenario are lower, based on a world that transitions relatively rapidly to service and information economies. Carbon dioxide emissions in the B1 scenario peak at just below 10 Gt/year (around two times 1990 levels) at mid-century and decline slowly to below current-day levels. Together, these scenarios represent the range of IPCC non-intervention emissions futures with atmospheric CO₂ concentrations reaching approximately double and triple pre-industrial levels, at 550 ppm (B1) and 970 ppm (A1fi), by 2100.

3 Results

3.1 Statistical and observed relationships between overwintering and HWA mortality

We considered eight different measures of winter temperature to determine their potential relationship to HWA mortality (Table 1). Six of these were the average minimum or mean temperatures for the months of February, March, or the entire winter season (defined here as December, January, February, and March [DJFM]); we also considered the number of days per winter with temperatures below -10°C , and the absolute minimum winter temperature, or the temperature of the coldest day of the year. We examined February and March separately from the other winter months as laboratory studies have shown that adelgid can be more susceptible to cold temperatures later in the season (Parker et al. 1998).

A significant relationship ($P < 0.05$) was found between adelgid overwintering mortality and seven of the eight measures of winter temperature considered (Table 1). The eighth measure, average daily minimum temperature in March, had a marginally significant correlation with overwintering mortality ($P = 0.057$).

In order to compare our results to those of Parker et al. (1999) and Skinner et al. (2003), we regressed overwintering mortality and the coldest day of the year at each location ($P = 0.042$; $R^2 = 0.253$). We found that all adelgid are likely to die after exposure to a mean winter temperature of -5°C , or 93 days in which the average daily minimum temperature is below -10°C , or an absolute minimum winter temperature of -40°C . The number of days the average daily minimum temperature was below -10°C ($P = 0.031$, $R^2 = 0.277$) was also chosen because it involves not only minimum temperature, which previous studies have shown is important, but is also reflective of the duration of cold (Fig. 3).

Table 1 Statistical relationships between overwintering mortality and eight winter temperature indices

	Temperature coefficient (st err)	Intercept (st err)	R^2	P value
Number of days with daily minimum temperature $< -10^{\circ}\text{C}$	0.006 (0.003)	0.436 (0.140)	0.277	0.031
Average daily mean winter (DJFM) temperature	-0.078 (0.026)	0.507 (0.105)	0.43	0.008
Average daily minimum winter (DJFM) temperature	-0.042 (0.017)	.0349 (0.165)	0.243	0.025
Temperature of the coldest day of the year	-0.021 (0.010)	0.158 (0.242)	0.253	0.042
Average daily mean temperature (Mar)	-0.072 (0.030)	0.740 (0.164)	0.043	0.028
Average daily mean temperature (Feb)	-0.062 (0.024)	0.484 (0.149)	0.106	0.017
Average daily minimum temperature (Mar)	-0.040 (0.019)	0.471 (0.171)	0	0.057
Average daily minimum temperature (Feb)	-0.036 (0.015)	0.343 (0.174)	0.154	0.024

The mixed model P and R^2 values are shown, where R^2 is calculated based on the error sum of squares resulting from the fit obtained using the mixed model with year effects $Y_{st} = \beta_0 + \beta_1 X_{st} + R_t + e_{st}$, and the P value tests for significance of the temperature coefficient.

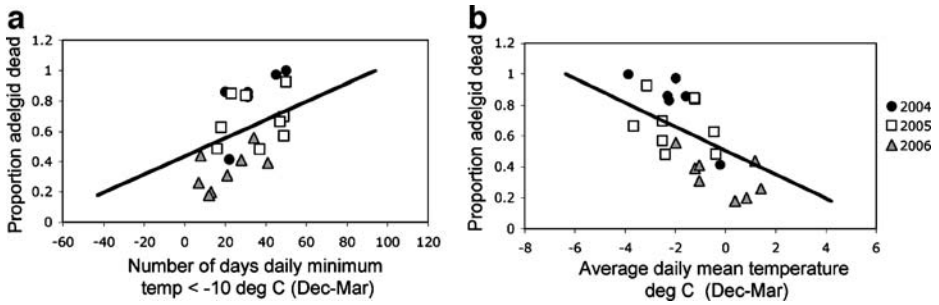


Fig. 3 Relationship between adelgid overwintering mortality and **a** number of days the average daily minimum temperature was $< -10^{\circ}\text{C}$ during December through March ($P=0.031$; $R^2=0.277$), and **b** the average daily mean temperature for December through March ($P=0.008$; $R^2=0.430$). Black circles are data points from the winter of 2004, white squares 2005, and gray triangles 2006. The regression line was fit using a linear mixed model, which adjusted for annual time trends in the data

Using the lifetable data mentioned above (Section 2.3), we estimated the amount of overwintering mortality necessary to keep the adelgid population from expanding to be 91%. We found this to be likely to occur when the mean winter temperature is -5°C , the absolute minimum winter temperature is -35°C , or when there are at least 79 days in which the average daily minimum temperature is below -10°C . Results of the lifetable study are not presented in detail here because data collection and analysis are ongoing.

3.2 Adelgid spread records for MA

A significant relationship was found between the proportions of newly infested towns and mean winter temperature ($P=0.026$; $R^2=0.439$), the number of days below -10°C ($P=0.048$; $R^2=0.367$), and absolute minimum winter temperature ($P=0.029$; $R^2=0.429$; Fig. 4). Our results suggest that it is unlikely that new towns will become infested during a winter with at least 77 days in which the average daily minimum temperature is below -10°C , or when winter temperature falls below an absolute daily minimum of -34°C , or below an average daily mean temperature of -5°C (Table 2).

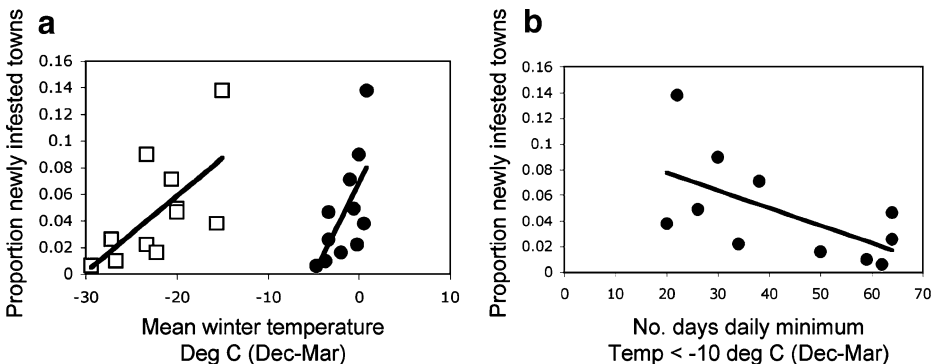


Fig. 4 Regression analysis of the proportion of newly infested towns in MA with temperature. **a** Relationship between the proportion of newly infested towns and mean winter temperature (black circles; $P=0.026$; $R^2=0.439$); absolute minimum winter temperature (white squares; $P=0.029$; $R^2=0.429$). **b** Relationship between the proportion newly infested towns and the number of days the average daily minimum temperature was $< -10^{\circ}\text{C}$ ($P=0.048$; $R^2=0.367$)

Table 2 Conditions under which adelgid population expansion is not expected, based on three temperature indices

	100% adelgid mortality: 3 years of overwintering mortality data	91% adelgid mortality: 3 years of overwintering mortality data ^a (st err)	Proportion of newly infested MA towns [TL1]	Previous lab studies
Number of days with daily minimum temperature < −10°C	93	79 (50.3)	77	N/A
Temperature of the coldest day of the year	−40°C	−35°C (26.5)	−34°C	−30 to −35°C
Average daily mean winter (DJFM) temperature	−5°C	−5°C (2.6)	−5°C	N/A

^a Based on ongoing lifetable studies, an average of 91% overwintering mortality is required to stop adelgid populations from expanding; that is, when mortality from all causes balances fecundity and the population is simply replacing itself from year to year and not increasing or decreasing in size.

3.3 Projected future HWA spread under climate change

The significant statistical relationships identified between multiple indices of winter temperatures and HWA mortality above suggest that long-term trends in regional winter temperatures – particularly a general warming trend, as has already been observed across the Northeast over the past three decades, and is likely to continue in the future due to human-induced climate change (Hayhoe et al. 2006) – would be likely to affect HWA ranges across the region. For that reason, we next evaluated the projected changes in winter temperatures that can be expected across the region over the coming century, under higher and lower scenarios of future emissions from human activities.

To explicitly simulate projected HWA spread under future climate change, we selected the winter temperature measure with the best fit to overwintering mortality, mean (DJFM) winter temperature ($P=0.008$; $R^2=0.43$; Table 1). Further support for use of this metric was provided by the fact that the ‘threshold’ temperature of −5°C predicted by the 3-year overwintering mortality study and Massachusetts spread were the same; and that this variable had the smallest standard error in our estimate of the point at which adelgid should stop spreading (Table 2).

Average mean winter (DJFM) temperatures are projected to warm significantly over the coming century. As shown in Fig. 5, present-day winter temperatures (averaged over the climatological period 1961–1990) currently range from about +4°C in the southern and coastal areas of the Northeast, down to −12°C in northern Maine. Within a few decades (2010–2039), average winter temperatures are projected to warm by about 1.5–2°C. By mid-century, a warming of 3–4°C is expected under the higher emissions scenario and 2–3°C under the lower. By the end of the century (2070–2099), following a higher vs. a lower emissions pathway results in dramatic differences, with winter temperatures warming by 4–6°C under A1fi as compared with 3–4°C under B1.

Similar changes are seen for the other measures of winter temperature described in Table 1. For example, on average, the climatological (30-year average) absolute minimum winter temperature or “coldest day of the year” currently ranges from about −15°C in the southern coastal part of the Northeast down to −38°C in the northern part of Maine. Within just a few decades, these values are projected to warm by about 2–4°C. By the end of the

century, increases are projected, averaging about 8°C under A1fi as compared to about 5–6°C under B1.

As discussed above in Section 3.1, we have determined that adelgid populations are expected to stop expanding at a daily mean winter temperature of -5°C . Based on the projected changes in winter mean temperatures across the Northeast, we therefore map the location of the climatological -5°C isotherm for the historical reference period (1961–1990) as well as its projected location for the three future time periods under the higher and lower emission scenarios. Based on the statistical relationships seen in the observed data, we interpret these maps as a proxy for climatological limitations on wide-spread HWA infestation and subsequent hemlock mortality over the coming century.

During the historical reference period 1961–1990, almost half of the Northeast region remained northward of the HWA-limiting -5°C winter mean temperature isotherm. These areas include upper-state New York and most of the states of Vermont, New Hampshire, and Maine but not, however, the state of Massachusetts which, as we discussed earlier, became infested in 1989. Over the coming century, the -5°C isotherm is projected to move upward (in terms of elevation) as well as northward, as temperatures warm (Fig. 6). By mid-century, nearly half of the area currently protected by the -5°C isotherm could be exposed to HWA infestation. By the end of the century, under the higher emissions scenario, virtually all of the Northeast will experience average winter temperatures above -5°C , which we interpret here as suggesting that the entire Northeast could be susceptible to widespread HWA infestation at that point. Under the lower scenario, however, isolated sections of upper-state New York, Vermont, and New Hampshire, as well as the northern half of the state of Maine will still remain above the -5°C isotherm (i.e., protected from wide-spread HWA infestation).

4 Discussion

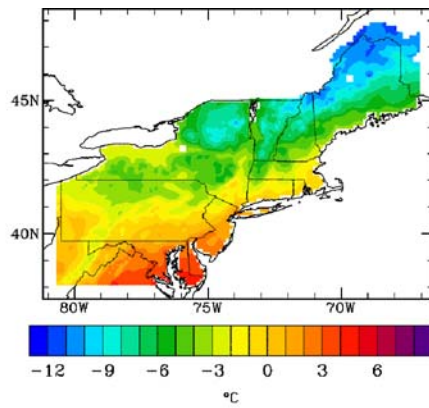
4.1 Implications of the future range of HWA for hemlock in the Northeast

The hemlock woolly adelgid has already caused widespread mortality and near-eradication of hemlock in the southern parts of its range in North America, including Shenandoah National Park (Young et al. 2002) and southern Connecticut (Orwig and Foster 1998). Based on these projections, the forests of northern New England (particularly Vermont, New Hampshire, and Maine) may face the same fate by the end of the century. Because hemlock is a much more dominant component of forests in northern New England, the impact of HWA spread is likely to be even more severe than in the south.

Mean and minimum temperature data, such as were used here, are useful in making broad-scale projections about future potential ranges of species. However, different aspects of winter severity may be responsible for overwintering mortality in different years, as demonstrated by Stenseth and Mysterud (2005). Detailed projections can be further complicated by other factors, including environmental aspects of the region (such as forest structure, composition, and fragmentation), as well as the impact of individual extreme cold events on HWA mortality. To further investigate the latter, we are planning laboratory cold shock experiments to isolate the specific aspects of temperature to which the adelgid are most susceptible to, whether duration of cold, rate of cooling, and/or time of year.

The Massachusetts HWA colonization records suffer from several sources of inaccuracy or bias: a town is recorded as having adelgid present only after it was noticed by a member of the public who then telephoned the Massachusetts Department of Conservation and

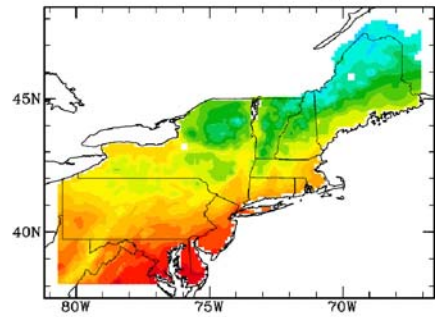
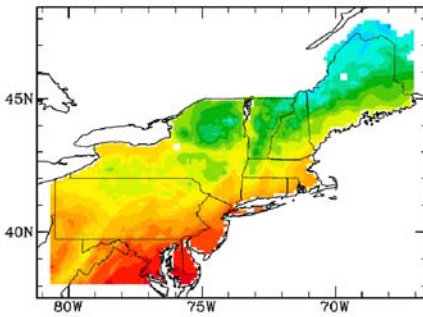
1961-1990



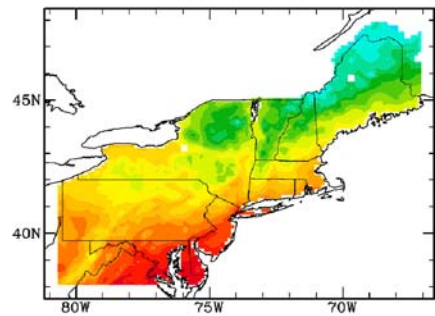
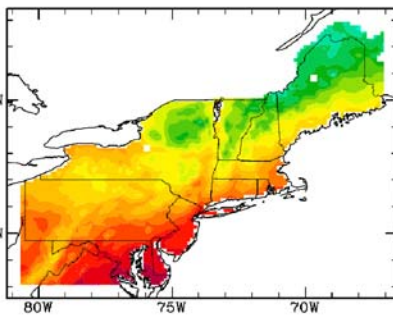
Higher Emissions (A1fi)

Lower Emissions (B1)

2010-2039



2040-2069



2070-2099

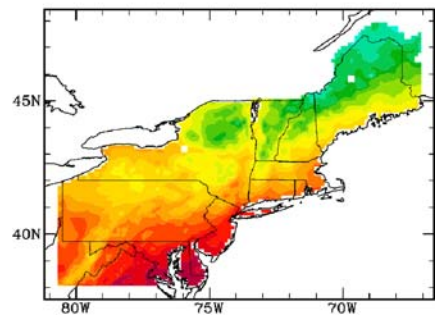
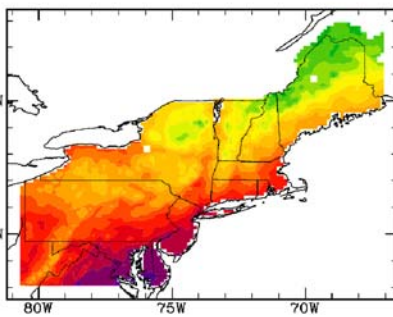


Fig. 5 Average historical (1961–1990) and projected future mean winter (DJFM) temperatures across the Northeast, as simulated by the HadCM3, GFDL CM2.1 and PCM1 models for the Special Report on Emissions Scenarios (SRES) higher (A1fi) and lower (B1) emission scenarios, statistically downscaled to one-eighth degree resolution

Recreation. Nevertheless, we believe that these data approximate the actual distribution of HWA because the presence and absence of adelgid closely matches that obtained from an intensive survey for HWA in hemlock stands in Massachusetts in 2006 (Preisser et al. unpublished). This survey confirms that HWA is not currently present in many northern and western towns in Massachusetts.

4.2 Effects of hemlock loss on Northeast forests

As a late-successional, long-lived, and shade tolerant species, hemlock is an integral part of present-day Northeastern forests, providing cool dense shade, thick acidic litter layers, low light availability, and slow rates of nitrogen cycling. The removal of hemlock from the landscape in some areas has already resulted in changes in forest structure and composition (Orwig and Foster 1998; Orwig et al. 2002) as well as ecosystem function (Jenkins et al. 1999). These modifications to the environment are likely to have wide-ranging effects on the distributions and interactions of wildlife, including many species that are closely associated with hemlock (Yamasaki et al. 2000; Tingley et al. 2002; Ross et al. 2003).

Ecosystem responses to adelgid infestation have been studied at several scales by Jenkins et al. (1999), Kizlinski et al. (2002), and Stadler et al. (2005). Heavily infested hemlocks experience severe defoliation and a lack of new growth resulting in increased light availability, higher soil temperature, and a greater amount of precipitation reaching beneath trees. Phytophagous pests such as Lepidoptera larvae and aphids initiate considerable levels of nutrient increase in precipitation falling through the canopy and reaching the soil. The subsequent increase in levels of dissolved organic carbon

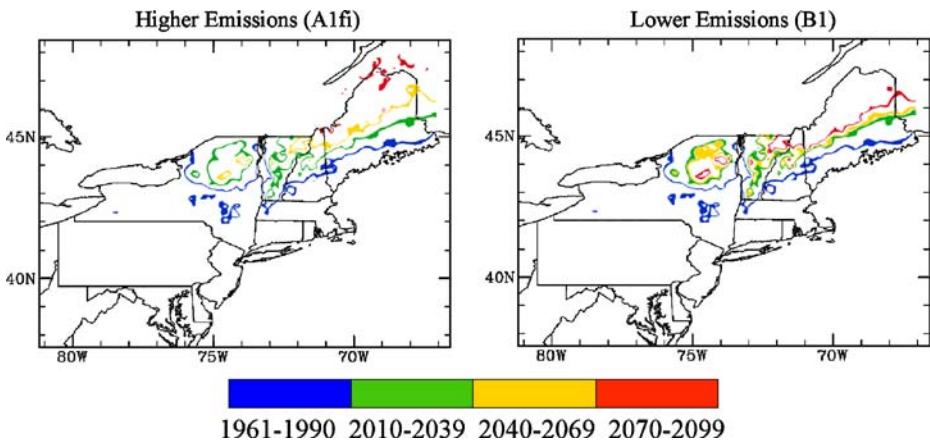


Fig. 6 Historical (1961–1990, blue) and projected future near-term (2010–2039, green), mid-century (2040–2069, yellow) and end-of-century (2070–2099, red) range for HWA in the Northeast using a mean winter (December, January, February, March) temperature of -5°C based on temperature projections averaged over three atmosphere ocean general circulation models (AOGCMs; HadCM3, GFDL CM2.1 and PCM 1) for the Special Report on Emissions Scenarios (SRES) **a** higher (A1fi) and **b** lower (B1) emissions scenarios

and nitrogen in soil have the potential to elevate soil respiration, accelerate decomposition, and increase amounts of nitrate runoff. These changes in ecosystem processes are likely to cause higher amounts of soil erosion, freshwater pollution, shifts in resource availability and changes in plant species distributions. For example, relatively homogenous stands of black birch have already arisen in areas that have experienced hemlock dieback (Orwig and Foster 1998; Orwig et al. 2002).

The impacts of hemlock decline on wildlife are equally dramatic (Evans et al. 1996; Snyder et al. 1998; Yamasaki et al. 2000; Tingley et al. 2002; Ross et al. 2003). Several mammals as well as eight bird species are closely associated with hemlock forests. Among them are the black-throated green warbler, a species that depends solely on hemlock for feeding and nesting sites in some areas of its range. Other bird species that have exhibited a reduction in density in heavily damaged hemlock stands include the blackburnian warbler (*Dendroica fusca*), blue-headed vireo (*Vireo solitarius*), hermit thrush (*Catharus guttatus*), and ovenbird (*Seiurus aurocapillus*). In contrast, other bird species such as the eastern wood-pewee (*Contopus virens*), white-breasted nuthatch (*Sitta carolinensis*), red-eyed vireo (*V. olivaceus*), and tufted titmouse (*Baeolophus bicolor*) have increased in density following hemlock decline. While the overall number of birds in New England forests may not decrease, bird diversity, community structure, and species interactions are likely to undergo profound changes.

In addition to bird assemblages, the diversity and community structure of aquatic invertebrates is also affected by the presence of hemlock. Streams within hemlock forests have a greater diversity of aquatic invertebrates compared to those within hardwood forests, and some species, such as *Hydropsyche ventura*, *Polycentropus* sp., and *Natarsia* sp. are exclusively found in association with hemlock (Snyder et al. 2002). Other aquatic species such as brook trout were three times more likely to be found in streams surrounded by hemlock, which provide cooler water temperatures and more stable flows (Evans et al. 1996; Snyder et al. 1998; Ross et al. 2003). Clearly, as the distribution of hemlock changes via HWA damage, communities of many organisms and their interactions will be altered.

5 Conclusions

Hemlock's role as an important and unique component of northeastern forests means that HWA-linked hemlock loss could have major and irreversible impacts on forest ecosystems in the eastern USA (Ellison et al. 2005). Impacts include the disruption of close associations of hemlock with insects and birds, as well as changes in forest structure and composition, nutrient cycling, and logging practices.

Population expansion of HWA is clearly influenced by temperature. As temperatures in the Northeast continue to rise, we expect extensive range expansions of the adelgid. By the end of the century under higher emissions, HWA infestation could be expected across the entire Northeast; under lower emissions, however, only approximately half of the region currently protected (in terms of mean winter temperature lying below -5°C) would be exposed to HWA infestation. While the exact location of HWA infestations depends on other characteristics in addition to temperature, these projections make it clear that continued spread of HWA across the Northeast is likely over the coming century; however, at the same time, reducing emissions of greenhouse gases and hence the expected degree of warming over the coming century has the potential to greatly reduce the extent of forests likely to experience damage from HWA, particularly at higher elevations and in the northern parts of the region.

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