ORIGINAL PAPER

Anisotropic spread of hemlock woolly adelgid in the eastern United States

**Randall S. Morin · Andrew M. Liebhold ·
Kurt W. Gottschalk**

Abstract Simple population models predict that the spread of an invading species through a homogenous habitat should be equal in all directions, but geographic variation in the habitat that affects either reproduction or movement could result in variable rates of spread. We analyse records of the historical range expansion of the hemlock woolly adelgid (HWA) (*Adelges tsugae* Annand) in the eastern United States from 1951 to 2006 to document that this species has spread in an anisotropic fashion. Furthermore, the magnitude and direction of this anisotropy has varied through time. We explore the extent to which this spatial and temporal variation in spread can be explained by geographical variation in climate and by the abundance of hosts, eastern hemlock (*Tsuga canadensis* L.) and Carolina hemlock (*Tsuga caroliniana* Engelm.). We found that a significant component of the spatial anisotropy in HWA spread rate can be explained by the geographical distribution of host trees. January temperatures were negatively associated with spread rates but this may be an artifact of the association between hemlock and cold climates. The current distribution of the adelgid in eastern N. America may be approaching the extent of its potential range to the south and west determined by availability of host hemlock and to the north determined by lethal cold winter temperatures.

Keywords *Adelges tsugae* · Eastern hemlock · *Tsuga canadensis* · Invasive pest · Invasion · Range expansion · Habitat

R. S. Morin (✉)
US Forest Service, Forest Inventory and Analysis,
Northern Research Station, 11 Campus Blvd,
Suite 200, Newtown Square, PA 19073, USA
e-mail: rsmorin@fs.fed.us

A. M. Liebhold · K. W. Gottschalk
US Forest Service, Northern Research Station,
180 Canfield St., Morgantown, WV 26505, USA

Introduction

Invasions by exotic insects and diseases represent one of the most significant threats to the stability and productivity of forest ecosystems around the world (Liebhold et al. 1995; Vitousek et al. 1996; Pimentel et al. 2000). Given trends of increasing global trade and travel, alien species are arriving at increasing rates (Levine and D'Antonio 2003; McCullough et al. 2006). While most invading forest insects and diseases are not particularly abundant and consequently have negligible effects, a few species have become very abundant, and have altered forest ecosystems in profound ways (Niemela and Mattson 1996; Brockerhoff et al. 2006).

Three phases to the biological invasion processes are widely recognised: arrival, establishment, and spread (Mack et al. 2002; Lockwood et al. 2006). While all phases are important, there is often particular interest in understanding and predicting the spread of an alien species once it has established. Predictions of when and where species are likely to expand their ranges are of critical value in planning management activities that target such species.

Considerable effort has gone into the development of theoretical models of invasion spread (Hastings 1996; Shigesada and Kawasaki 1997). These models have considered spread as an emergent process that arises from coupling population growth with movement; any process that influences growth or movement can be expected to affect rates of spread. These models have considerably enhanced our understanding of the spread process but empirical analyses are also needed. Analysis of patterns of spread in historical records for individual species provides critical insight into the spread process (Liebhold and Tobin 2008). Of particular importance is the question of how the habitat effects spread and whether spread has been faster in areas where habitat characteristics promote either population growth or movement.

In this study, we investigate the role of habitat characteristics on spread using the hemlock woolly adelgid (HWA) (*Adelges tsugae* Annand) invasion of eastern N. America as a model system. This insect species is native to East Asia and was first noticed in eastern N. America in the 1950s (Ward et al. 2004). Since then, it has slowly expanded its range; in areas where populations have established, they often reach high densities, causing widespread defoliation and sometimes mortality of hosts, eastern hemlock (*Tsuga canadensis* L.) and Carolina hemlock (*Tsuga caroliniana* Engelm.) (McClure et al. 2001; Orwig et al. 2002). HWA has a complex life cycle that may involve both hemlock and spruce (*Picea* spp.) as hosts, but, in eastern N. America, winged sexuparae have not been observed to develop successfully on any spruce species (McClure et al. 2001). Many agents have been cited as factors in movement of adelgid eggs and crawlers including wind, wildlife, and humans (McClure et al. 2001; Ward et al. 2004). Population densities of adelgids fluctuate in response to density-dependent changes in the nutritional quality of hemlock; populations may multiply rapidly while newly infested trees are still healthy, drop sharply when trees begin to decline, and resurge if the infested trees respond to the drop with new growth (McClure et al. 2001). HWA currently infests about 26% of the range of hemlock in the USA; that area includes about 25% of the total hemlock basal area in that country (Morin et al. 2005).

Qualitative descriptions have noted anisotropic spread of the adelgid, with populations expanding more quickly to the North and South than to the west (McClure 1990; Souto et al. 1996; McClure and Cheah 1999). Evans and Gregoire (2007) analysed records of HWA spread from 1990 to 2004 and reported that adelgid establishment occurred later in municipalities with colder winter temperatures. However, their analysis did not use records of HWA spread prior to 1990 nor did it directly relate anisotropic spread to other habitat characteristics (e.g. host tree density). Low winter temperatures are known to cause mortality in HWA populations and this may limit the northern distribution in N. America (Parker et al. 1998; McClure and Cheah 1999; Parker et al. 2002; Skinner et al. 2003). The literature does implicate the role of birds (McClure 1987; McClure 1990), but flyways differ for different bird species and *a priori* it would be difficult to identify data for quantifying this relationship from historical spread records. As for quantifying the role of wind direction on spread rates, it is ambiguous during what season wind affects spread and consequently difficult to identify suitable wind direction data. In general, there are many habitat variables that could be tested for effects on spread rates. However, in this study, we chose a parsimonious approach by limiting our analysis to focus on the role of only two habitat variables.

The goal of this study was to use historical records of adelgid spread over its entire history of spread in N. America to quantify anisotropy in spread. We also explore the extent to which this anisotropy can be explained by geographical variation in host hemlock density and mean minimum January temperature.

Methods

Historical rates of anisotropic spread were estimated from maps depicting the advancing distribution of the adelgid (Fig. 1). The expansion of the adelgid's range

Fig. 1 Map of historical (1951–2006) spread of hemlock woolly adelgid in the USA. Boundaries of scale distributions are based upon county-level records assembled by US Forest Service Forest Health Protection
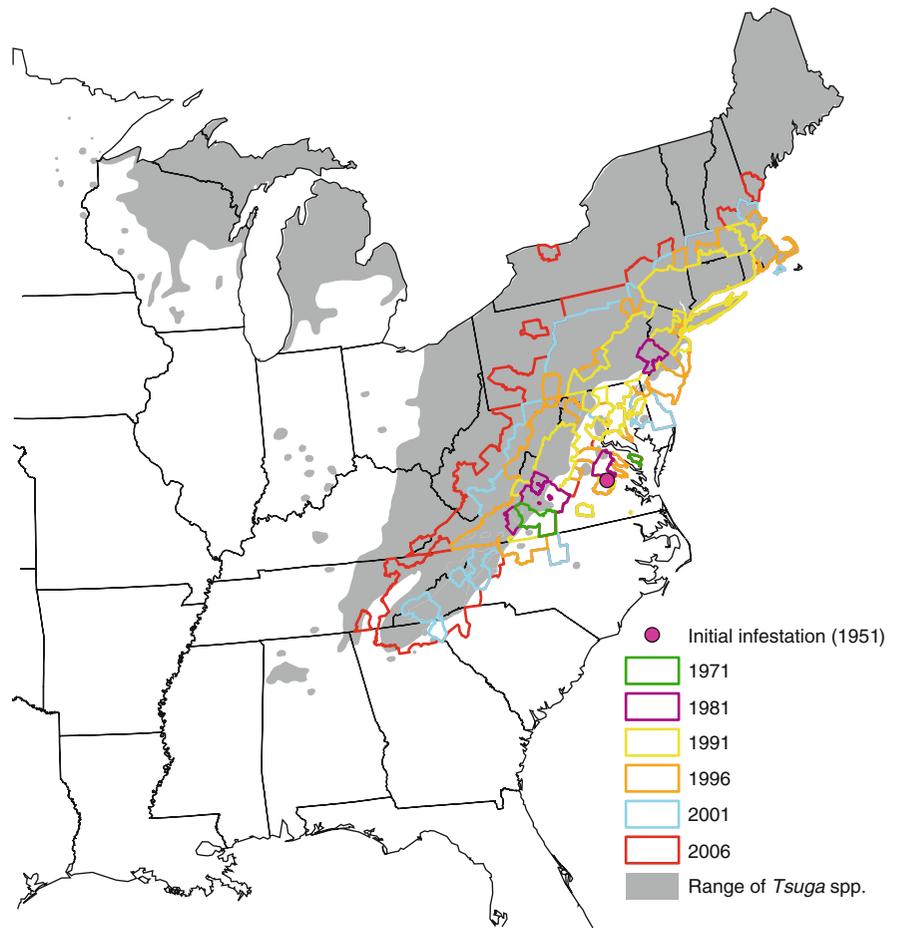
in the USA was derived from county-level records compiled by Forest Service, US Department of Agriculture, Forest Health Protection personnel (Newtown Square, Pennsylvania and Atlanta, Georgia). These records were available for 1951, 1971, 1981, 1991, 1996, and annually from 2001 to 2006. These data were not based on systematic surveys, and therefore there may be minor inconsistencies among years and regions in how HWA populations were detected. While these error sources may affect estimates of spread at the spatial scale of potential discrepancies between years, the effect on spread estimated at the spatial scale of invasion over the full temporal period represented in the data should be negligible.

A novel approach was applied to determine the level of anisotropy in the historical spread of HWA. Historical boundaries of adelgid extent were used to estimate the rate of spread in "bearing intervals" in order to quantify the level of anisotropy. A

geographical information system was used to locate the intersection of the range boundary with a series of radii emanating at 1-degree intervals from the centroid of the county that was initially infested in Virginia in 1951. The distance from the original infestation to the range boundary at each time interval was then calculated. These data were then binned into 16 groups to provide the best separation of spread at the longest distances; this resulted in 22.5-degree bearing intervals (e.g. 0–22.5 degrees, 22.5–45 degrees, etc.). Average distances were calculated for each combination of 7 years (1971, 1981, 1991, 1996, 2001, and 2006) and nine bearing intervals (distances for the other seven bearing groups were not calculated because they largely coincided with ocean) (Fig. 2). An average rate of spread was estimated for each bearing interval by the slope of the linear regression of these distances as a function of the year for each group of reference points (Tobin et al. 2007).

Fig. 2 Bearing groups used in linear models for anisotropic spread estimation
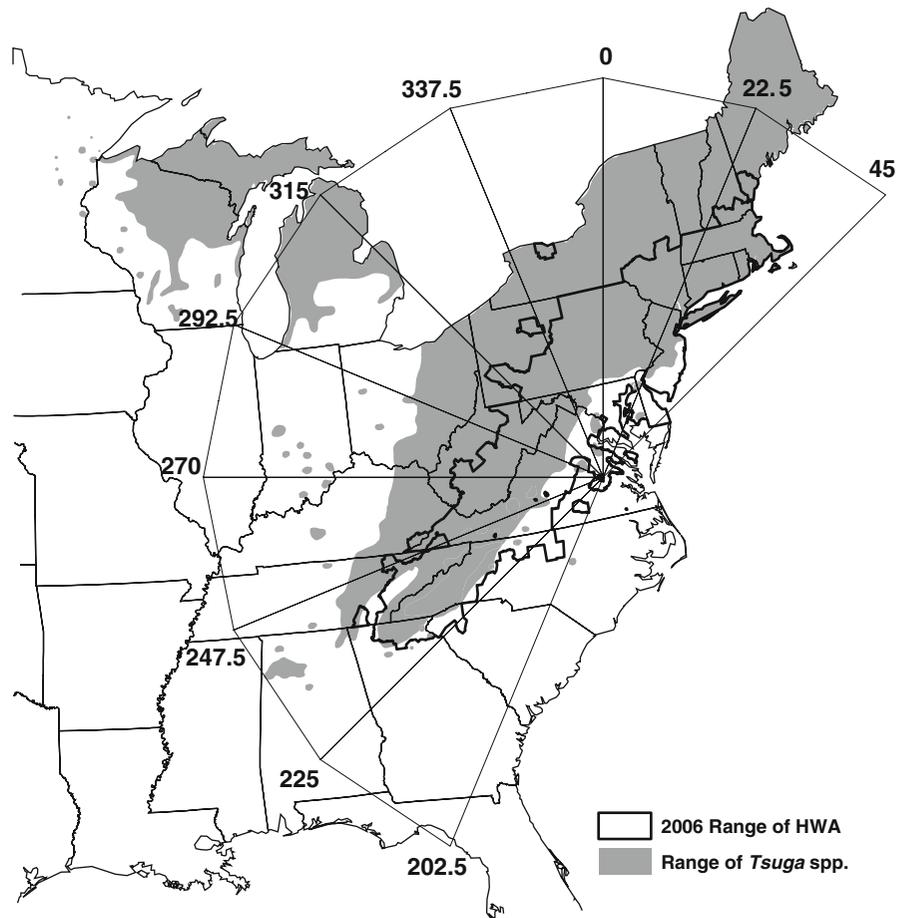

In an attempt to explain anisotropy in the spread of HWA, environmental variables were calculated for areas between successive historical boundaries (from 1971, 1981, 1991, 1996, 2001, and 2006) within each bearing interval. The US Forest Service has conducted surveys of overstory forest composition in the eastern USA as part of the "Forest Inventory and Analysis" (FIA) programme since the 1940s (see http://www.fia.fs.fed.us). These data were available as part of the "Eastwide database" and consisted of data from 93,611 plots located in 37 states in the eastern USA (Hansen et al. 1992). Basal area (m^2/ha) of all tree species was estimated at each plot during inventories conducted from 1985 to 1999. The geographic distribution of combined eastern and Carolina hemlock basal area was interpolated on a 1 km^2 grid from forest inventory plots and adjusted for forest density (Morin et al. 2005; Fig. 3). Hemlock basal area was averaged within polygons coinciding with each time interval-bearing interval combination. Similarly,

spatially interpolated climatic data (Analysis Service, Oregon State University, http://www.ocs.oregonstate.edu/prism/, created 4 Feb 2004; Fig. 4) were used as the source for estimates of mean minimum January temperature for each time interval-bearing interval combination.

Linear regression analysis was employed to model the relationship of mean spread distance in each bearing interval as a function of host basal area and minimum January temperature averaged over the corresponding bearing interval. In order to investigate temporal variation in this relationship, Pearson correlation coefficients were calculated for spread distances and the environmental variables among bearing intervals in each time period. Additionally, we used restricted maximum likelihood analysis to portion out the simultaneous effects of host basal area and temperature by fitting a linear mixed model of spread distance with bearing class as a repeated measure and host basal area and temperature as covariates (PROC
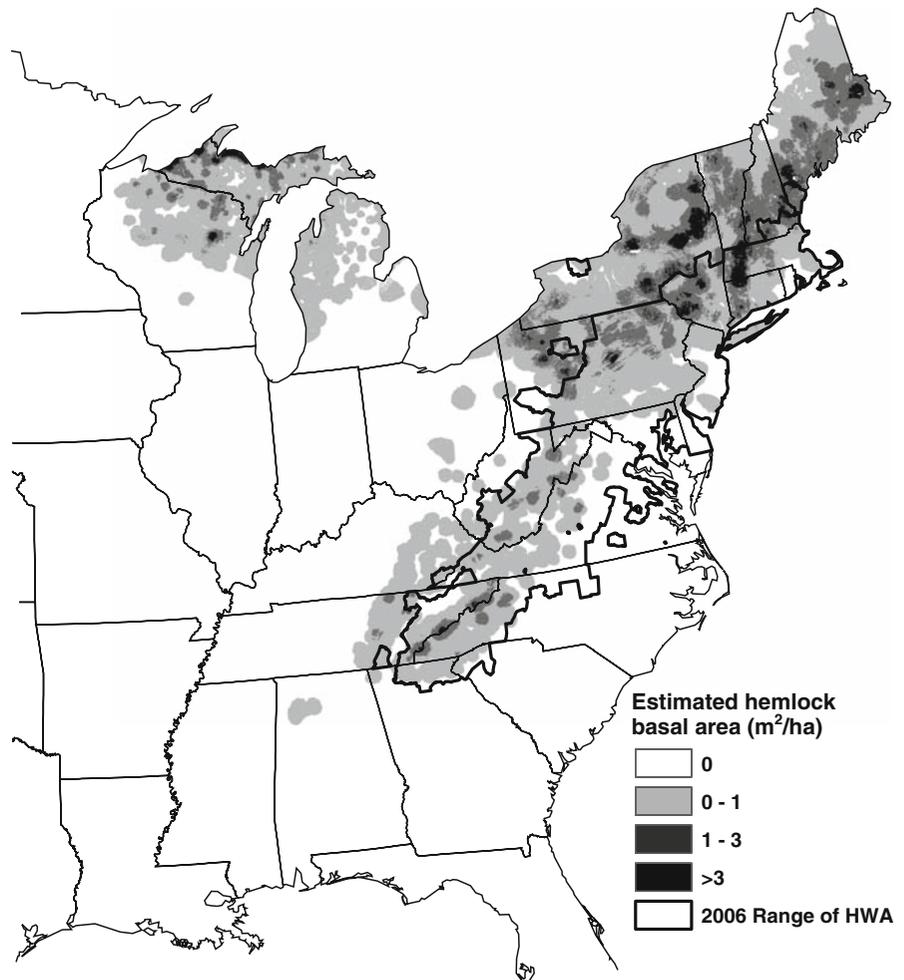
MIXED, SAS Institute Inc. 2004). We selected this technique based on the abundance of covariance structures available with this estimation method. We used the Kenward–Rogers denominator degrees of freedom method as it has been shown to be the most robust degrees of freedom method with repeated measures. After visually inspecting profile plots, we decided that the spatial power function most appropriately modelled the repeated measures portion of our analysis (Littell et al. 2006). This covariance structure assumes higher correlations between adjacent bearing intervals in the framework of repeated measures not equally spaced in time.

Results and discussion

A map of historical HWA spread is shown in Fig. 1. For many years after its introduction to the United States in 1951, HWA was limited to a small private garden in an urban area in Richmond, Virginia (Ward et al. 2004). Dispersal of adelgids from this original infestation was slow and characterised by long-range transport into forested areas in counties surrounding Richmond. Shigesada et al. (1995) reported that the coupling of short distance dispersal with long-distance dispersal (termed "stratified dispersal") can cause much greater rates of spread than would occur with either form of dispersal alone. Under this mechanism, new colonies are founded by long-distance dispersal well ahead of the infested population front; these colonies expand via short-distance dispersal and ultimately coalesce. The existence of "outlying" populations has been common in historical spread of hemlock woolly adelgid (Fig. 1) and provides evidence of stratified dispersal. These outlying populations are presumably the result of

Fig. 4 Map of mean minimum January temperature (°C) from the Parameter-elevation regressions on independent slopes model (PRISM, Analysis Service, Oregon State University, http://www.ocs.oregonstate.edu/prism/)
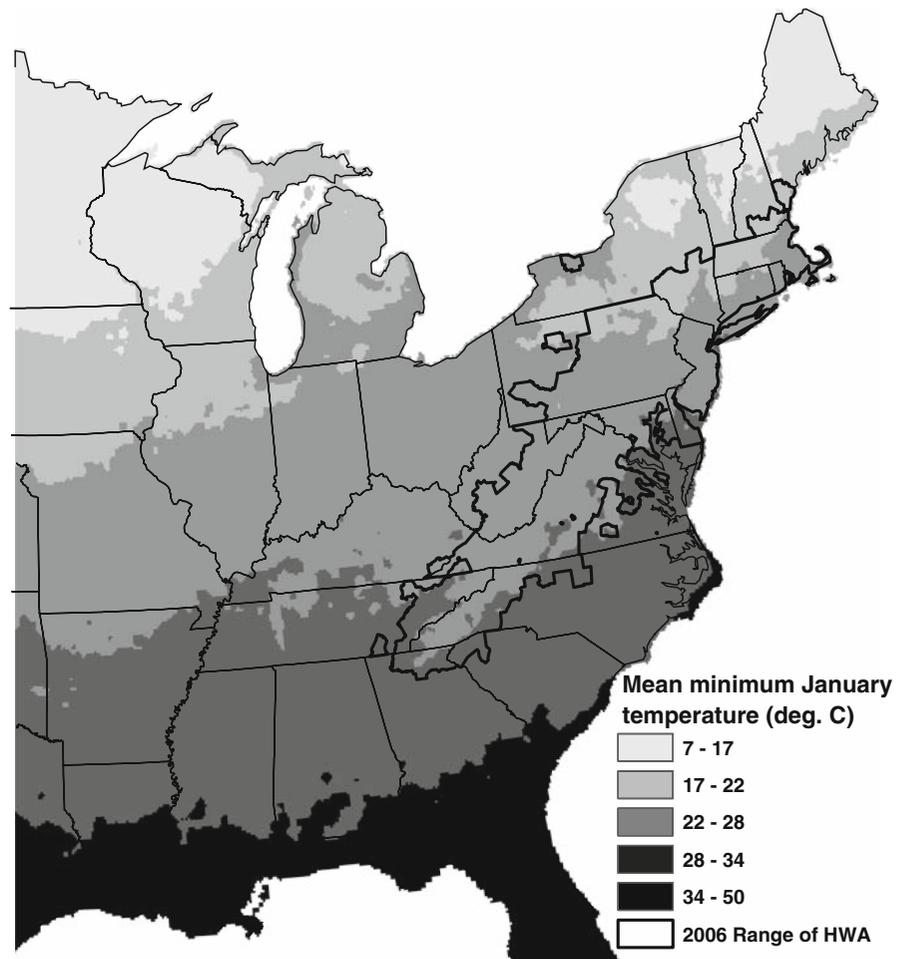
accidental transportation of infested host material into previously uninfested regions.

Estimated spread rates of the adelgid in each of the bearing intervals ranged from 8.9 to 20.4 km/year with the fastest rates towards the northeast (Table 1, Fig. 5, Supplemental material). Previous estimates of hemlock woolly adelgid spread range from 12.5 km/year (Evans and Gregoire 2007) to 20–30 km/year (McClure et al. 2001). A previously advanced explanation for spread anisotropy is that hemlock woolly adelgid spread is facilitated by passive contamination of birds flying along spring and fall migration routes in northeast and southwest directions (McClure 1987, 1990).

Linear regression analysis using spread rates over all years for each bearing interval indicated that spread was positively correlated with hemlock basal area ($R^2 = 0.6852$; $P = 0.0059$; Fig. 6) and negatively

correlated with minimum January temperature ($R^2 = 0.3794$; $P = 0.0774$; Fig. 7). Among bearing intervals, the Pearson correlation coefficient indicated that hemlock basal area was negatively correlated with minimum January temperature ($r = -0.7571$; $P = 0.0182$). Stepwise multiple regression indicated that hemlock basal area was a more important factor related to variation in spread rates than minimum January temperature. Furthermore, hemlock basal area was a significant effect ($P = 0.0013$) in a mixed-model test in which bearing groups were treated as repeated measures using the spatial power function (parameter estimate = 0.9723).

Similar, though weaker relationships were observed when spatial variation in spread was examined separately for different time periods (Table 2). Most correlations were not significant but the signs of correlation coefficients between spread

Table 1 Estimated rates of adelgid spread (1951–2006) in different directions estimated from linear regression models
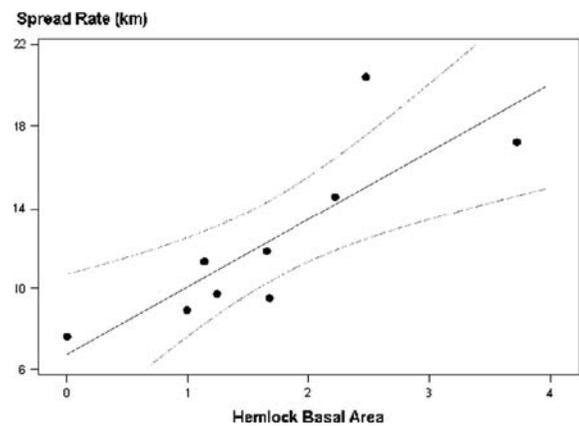
Bearing interval	P	R^2	Spread rate (km/year)	Hemlock basal area (m²/ha)	Mean minimum Jan. temperature (°C)
0–22.5	0.0014	0.9388	17.2	3.7	23.3
22.5–45	0.007	0.8665	20.4	2.5	24.5
202.5–225	0.0034	0.9069	7.6	0	29.4
225–247.5	0.0318	0.7234	11.8	1.7	28.0
247.5–270	0.0022	0.9242	8.9	1.0	26.4
270–292.5	0.0001	0.9882	9.5	1.7	25.1
292.5–315	0.0002	0.9766	9.7	1.2	24.8
315–337.5	0.0004	0.9689	11.3	1.1	24.8
337.5–360	0.0003	0.9737	14.5	2.2	24.3

Also shown for each bearing interval are average hemlock basal area/ha and mean minimum January temperature averaged over the area coinciding withy each bearing interval
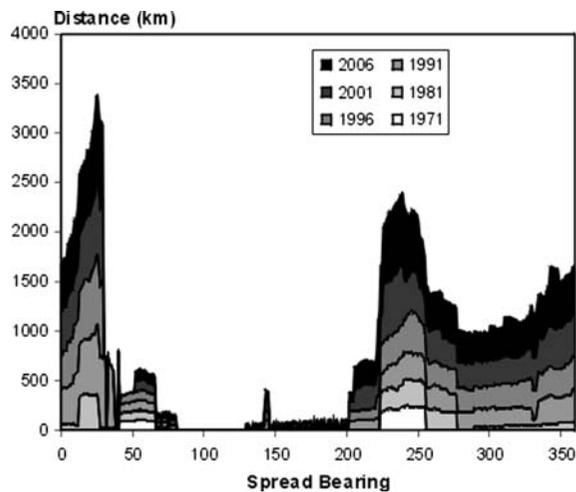
Fig. 5 Distances to adelgid invasion boundaries from the initial (1951) infestation for time groups used for analysis

Fig. 6 Linear regression of spread rate (estimated for each bearing interval) on hemlock basal area. The *solid line* represents the linear regression model, and the *dotted line* is the 95% estimation interval

distance and hemlock basal area were generally positive and coefficients between spread and minimum January temperature were generally negative (Table 2). Again, hemlock basal area and minimum January temperature were generally negatively correlated with each other.

The relationship between HWA survival and cold temperature is well documented; cold winter temperatures can cause considerable mortality and trigger dramatic population declines (Parker et al. 1998, 2002; McClure and Cheah 1999; Skinner et al. 2003). Evans and Gregoire analysed records of HWA spread from 1990 to 2004 and found that both geographical

and temporal variation in spread rates were positively associated with winter temperatures. Our finding of a negative relationship between spread and winter temperature thus appears to be in contradiction to these previous studies. However, our analyses also indicate that the abundance of host trees is the major determinant of spread rate. Thus, the unexpected negative correlation between temperature and spread rate may reflect the influence of host abundance on spread rather than the influence of weather directly on adelgid populations since hemlock abundance was negatively associated with temperature. Interestingly, the negative correlation of temperature with spread
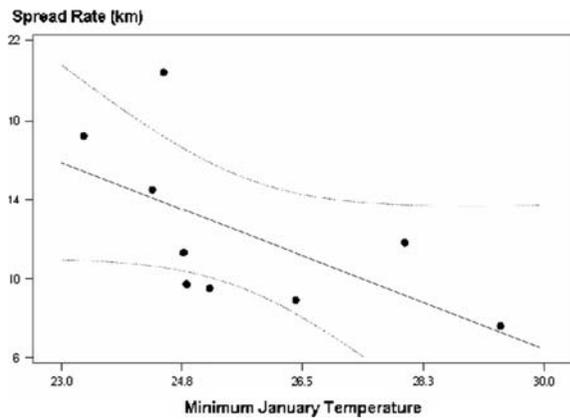
Fig. 7 Linear regression model of spread rate (estimated for each bearing interval) on minimum January temperature. The *solid line* represents the linear regression model, and the *dotted line* is the 95% estimation interval

appears to have diminished over time and this may reflect an opposing positive effect of winter temperatures on adelgid spread as the range has expanded to the north into particularly cold areas.

Spatial anisotropy in HWA spread has previously been noted but some uncertainty exists as to its origin (McClure 1990; Souto et al. 1996; McClure and Cheah 1999; Evans and Gregoire 2007). Our analyses here indicate that host hemlock abundance explains a large fraction of the spatial variability in spread. While it is possible that directional bias in passive movement of migratory birds (McClure and Cheah 1999) may contribute to the anisotropic spread of HWA, the simple geographical distribution of hemlock provides a more parsimonious explanation. Additionally, observational evidence supports the

Table 2 Average distance (km) from the centroid of the single county infested in 1951 to the range boundary in each time and bearing group

Bearing interval	Time period					
	1951–1970	1971–1980	1981–1990	1991–1995	1996–2000	2001–2006
0–22.5	0	191,828	478,235	501,936	540,105	576,449
22.5–45	19,170	88,443	455,278	509,922	751,392	817,609
202.5–225	16,283	16,283	111,622	137,995	225,469	269,432
225–247.5	221,556	234,102	253,252	332,724	519,806	660,984
247.5–270	82,040	226,107	240,676	280,239	335,829	429,079
270–292.5	0	63,885	182,851	242,433	262,671	326,577
292.5–315	0	41,425	182,749	231,951	264,966	321,395
315–337.5	0	53,808	170,495	275,280	297,652	387,149
337.5–360	0	69,708	279,443	297,276	415,092	490,044
r_H^a	0.1196	0.188	0.899883905	0.7475	0.6099	0.642
P_H^a	0.9462	0.8028	0.0029	0.0581	0.1881	0.1739
r_T^b	−0.5789	−0.3959	−0.82310428	−0.6912	−0.3548	−0.265
P_T^b	0.639	0.5596	0.0264	0.1782	0.8071	0.8651
r_{HT}^c	−0.7951	−0.7992	−0.92658	−0.8447	−0.6858	−0.5869
P_{HT}^c	0.4148	0.0173	0.0009	0.0083	0.0604	0.1261

Also shown are Pearson correlation coefficients of spread distance over each interval with hemlock basal area (H) and mean minimum January temperature (T), and Pearson correlations between hemlock basal area and mean minimum January temperature

[a] r_H and P_H are respectively, the correlation coefficient of spread rate with mean hemlock basal area/ha and the probability of a larger R

[b] r_T and P_T are respectively, the correlation coefficient of spread rate with mean minimum January temperature and the probability of a larger R

[c] r_{HT} and P_{HT} are respectively, the correlation coefficient of mean hemlock basal area/ha with mean minimum January temperature and the probability of a larger R

relationship between HWA spread and host abundance. For several decades after its introduction in Virginia the adelgid spread very slowly. It was not until HWA reached the natural range of hemlock that acceleration of spread occurred (Fig. 1).

Comparison of the current HWA range with forest inventory data (Fig. 3) suggest that HWA has yet to invade much of the range of hemlock. However, most of the currently uninfested portions of hemlock's range with relatively high host densities also have considerably colder winter temperatures (Fig. 4) which are likely to limit future spread. Thus it is possible that HWA is nearing the limits of potential range in most regions.

Invasion spread is a phenomenon that emerges as a result of the combination of population growth and dispersal and consequently any habitat characteristic that affects either process can be expected to influence spread. While theoretical models indicate that habitat heterogeneity can result in geographical variable rates of spread (Shigesada and Kawasaki 1997; Hastings et al. 2005), there are relatively few empirical examples of this, particularly for invasive insects. Thus, our finding here of a strong association between host abundance and insect spread rate is rather unique though a similar relationship has been described for the spread of horse chestnut leaf miner, *Cameraria ohridella*, in Europe (Gilbert et al. 2004, 2005). Local basal area of hemlock presumably affects the carrying capacity of adelgid populations but this alone would not be expected to affect invasion speed in a system that is dominated by simple reaction-diffusion spread (Shigesada and Kawasaki 1997). However, as stated above, adelgid spread appears to be affected by stratified dispersal and increased carrying capacity can be expected to affect the frequency of long distance dispersal propagules and thereby influence spread.

References

Brockerhoff EG, Liebhold AM, Jactel H (2006) The ecology of forest insect invasions and advances in their management. Can J Forest Res 36:263–268

Evans AM, Gregoire TG (2007) A geographically variable model of hemlock woolly adelgid spread. Biol Inv 9:1387–3547. doi:10.1007/s10530-006-9039-z

Gilbert M, Gregoire JC, Freise JF et al (2004) Long-distance dispersal and human population density allow the prediction of invasive patterns in the horse chestnut leafminer *Cameraria ohridella*. J Ecol 73:459–468. doi:10.1111/j.0021-8790.2004.00820.x

Gilbert M, Guichard S, Freise J et al (2005) Forecasting *Cameraria ohridella* invasion dynamics in recently invaded countries: from validation to prediction. J Appl Ecol 42:805–813. doi:10.1111/j.1365-2664.2005.01074.x

Hansen MH, Frieswyk T, Glover JF et al (1992) The eastwide forest inventory data base: data base description and user's manual. USDA For Serv Gen Tech Rep NC-151. p 53

Hastings A (1996) Models of spatial spread: is the theory complete? Ecology 77:1675–1679. doi:10.2307/2265772

Hastings A, Cuddington K, Davies KF et al (2005) The spatial spread of invasions: new developments in theory and evidence. Ecol Lett 8:91–101. doi:10.1111/j.1461-0248.2004.00687.x

Levine JM, D'Antonio CM (2003) Forecasting biological invasions with increasing international trade. Conserv Biol 17:322–326. doi:10.1046/j.1523-1739.2003.02038.x

Liebhold AM, Tobin PC (2008) Population ecology of insect invasions and their management. Annu Rev Entomol 53:387–408. doi:10.1146/annurev.ento.52.110405.091401

Liebhold AM, Macdonald WL, Bergdahl D et al (1995) Invasion by exotic pests: a threat to forest ecosystems. For Sci Mon 30:49

Littell RC, Milliken GA, Stroup WW et al (2006) SAS for mixed models, 2nd edn. SAS Institute, Cary

Lockwood JL, Hoopes ML, Marchetti MP (2006) Invasion ecology. Blackwell, UK

Mack RN, Barrett SCH, deFur PL et al (2002) Predicting invasions of nonindigenous plants and plant pests. National Academy of Sciences, Washington, DC

McClure MS (1987) Biology and control of hemlock woolly adelgid. Connecticut Agricultural Experiment Station, Bulletin 851, p 9

McClure MS (1990) Role of wind, birds, deer, and humans in the dispersal of hemlock woolly adelgid (Homoptera: Adelgidae). Environ Entomol 19(1):36–43

McClure MS, Cheah CAS-J (1999) Reshaping the ecology of invading populations of hemlock woolly adelgid, *Adelges tsugae* (Homptera: Adelgidae), in eastern North America. Biol Inv 1:247–254. doi:10.1023/A:1010051516406

McClure MS, Salom SM, Shields KS (2001) Hemlock wooly adelgid. USDA For Serv FHTET-2001–03

McCullough DG, Work TT, Cavey JF et al (2006) Interceptions of nonindigenous plant pests at US ports of entry and border crossings over a 17-year period. Biol Inv 8:611–630. doi:10.1007/s10530-005-1798-4

Morin RS, Liebhold AM, Gottschalk KW et al (2005) Mapping host-species abundance of three major exotic forest pests. USDA For Serv Res Pap NE-726

Niemela P, Mattson WI (1996) Invasion of North American forests by European phytophagous insects. Biosci 46:741–753. doi:10.2307/1312850

Orwig DA, Foster DR, Mausel DL (2002) Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. J Biogeogr 29:1475–1487. doi:10.1046/j.1365-2699.2002.00765.x

Parker BL, Skinner M, Gouli S et al (1998) Survival of hemlock woolly adelgid (Homoptera: Adelgidae) at low temperatures. For Sci 44(3):414–420

Parker BL, Skinner M, Gouli S et al (2002) Cold temperatures. Will they limit range expansion? In: Onken B, Reardon R, Lashom J (eds) Proceedings hemlock woolly adelgid in the United States symposium. East Brunswick, 5–7 February 2002. University and USDA Forest Service, pp 269–273

Pimentel D, Lach L, Zuniga R et al (2000) Environmental and economic costs of nonindigenous species in the United States. BioSci 50:53–65. doi:10.1641/0006-3568(2000)050[0053:EAECON]2.3.CO;2

SAS Institute Inc (2004) SAS OnlineDoc® 9.1.2. SAS Institute, Cary

Shigesada N, Kawasaki K (1997) Biological invasions: theory and practice. Oxford University Press, UK

Shigesada N, Kawasaki K, Takeda Y (1995) Modeling stratified diffusion in biological invasions. Am Nat 146:229–251. doi:10.1086/285796

Skinner M, Parker BL, Gouli S et al (2003) Regional responses of hemlock woolly adelgid (Homoptera: Adelgidae) to low temperatures. Environ Entomol 32(3):523–528

Souto D, Luther T, Chianese B (1996) Past and current status of HWA in eastern and Carolina hemlock stands. In: Salom SM, Tignor TC, Reardon RC (eds) Proceedings of the first hemlock woolly adelgid review. USDA For Serv, Morgantown, pp 9–15

Tobin PC, Liebhold AM, Roberts EA (2007) Comparison of methods for estimating the spread of a non-indigenous species. J Biogeogr 34:305–312. doi:10.1111/j.1365-2699.2006.01600.x

Vitousek PM, D'Antonio CM, Loope LL et al (1996) Biological invasions as global environmental change. Am Sci 84:468–478

Ward JS, Montgomery ME, Cheah CAS-J et al (2004) Eastern hemlock forests: guidelines to minimize the impacts of hemlock woolly adelgid. NA-TP-03-04, USDA Forest Service, Northeastern Area State and Private Forestry, Morgantown, 28 pp