Predicting the impact of hemlock woolly adelgid on carbon dynamics of eastern United States forests

Marco Albani, Paul R. Moorcroft, Aaron M. Ellison, David A. Orwig, and David R. Foster

Abstract: The hemlock woolly adelgid (HWA; *Adelges tsugae* Annand) is an introduced insect pest that threatens to decimate eastern hemlock (*Tsuga canadensis* (L.) Carriere) populations. In this study, we used the ecosystem demography model in conjunction with a stochastic model of HWA spread to predict the impact of HWA infestation on the current and future forest composition, structure, and carbon (C) dynamics in the eastern United States. The spread model predicted that on average the hemlock stands south and east of the Great Lakes would be infested by 2015, southern Michigan would be reached by 2020, and northeastern Minnesota by 2030. For the period 2000–2040, the ecosystem demography model predicted a mean reduction of 0.011 Pg C·year^{-1} (Pg C = 10^{15} g C), an 8% decrease, in the uptake of carbon from eastern United States forests as a result of HWA-caused mortality, followed by an increased uptake of 0.015 Pg C·year^{-1} (a 12% increase) in the period 2040–2100, as the area recovers from the loss of hemlock. Overall, we conclude that while locally severe, HWA infestation is unlikely to have a significant impact on the regional patterns of carbon fluxes, given that eastern hemlock represents a limited fraction of the standing biomass of eastern forests and that it has relatively low productivity compared with the tree species that are likely to replace it.

Résumé : Le puceron lanigère de la pruche (*Adelges tsugae* Annand) est un insecte ravageur introduit qui menace de décimer les populations de pruche du Canada (*Tsuga canadensis* (L.) Carrière). Dans cette étude, nous avons utilisé le modèle démographique des écosystèmes conjointement avec un modèle stochastique de propagation du puceron lanigère pour prédire l'impact de l'infestation de cet insecte sur la composition, la structure et la dynamique du carbone (C) dans l'est des États-Unis. Le modèle de propagation prédit, qu'en moyenne, les peuplements de pruche situés au sud et à l'est des Grands Lacs seront infestés vers 2015, que le sud du Michigan sera touché vers 2020 et le nord-est du Minnesota vers 2030. Pour la période allant de 2000 à 2040, le modèle d'écosystème prédit une réduction moyenne de 0,011 Pg C·an^{-1} (Pg C = 10^{15} g C), soit une diminution de 8 % de l'absorption de carbone par les forêts de l'est des États-Unis due à la mortalité causée par le puceron lanigère, suivie d'une augmentation de l'absorption de 0,015 Pg C·an^{-1} (une augmentation de 12 %) au cours de la période allant de 2040 à 2100, à mesure que la région se remet de la perte des pruches. Globalement, nous arrivons à la conclusion que, bien qu'elle soit sévère localement, il est peu probable que l'infestation du puceron lanigère ait un impact significatif sur les patrons régionaux des flux de carbone étant donné que la pruche du Canada représente une faible proportion de la biomasse sur pied dans les forêts de l'est et que la productivité de cette essence est relativement faible comparativement aux espèces d'arbre les plus susceptibles de la remplacer.

[Traduit par la Rédaction]

Introduction

Changes in forest structure and canopy composition or wholesale losses of forestlands as a result of invasive insects, conversion to agriculture, and urbanization inevitably alter the amount of carbon (C) stored or taken up across the landscape. In the eastern United States (US), there are >200 × 10^6 m^3 of eastern hemlock (*Tsuga canadensis* (L.) Carrière), the dominant late-successional conifer in this region (Smith et al. 2001). Because hemlock is one of the most shade-tolerant and long-lived trees in its range, it plays a unique role in forest ecosystems (Rogers 1978; Abrams and Orwig 1996; Ellison et al. 2005), creating habitats with characteristic soil chemistry, microclimate, and ecosystem dynamics. Currently, hemlock is being killed rapidly by an invasive insect, the hemlock woolly adelgid (HWA; *Adelges tsugae* Annand), and by preemptive salvage logging in anticipation of additional adelgid infestations (Kizlinski et al. 2002; Orwig et al. 2002; Brooks 2004). In its wake, hemlock is being largely replaced in the short term by hardwood species, including black birch (*Betula lenta* L.) and red maple (*Acer rubrum* L.) (Orwig and Foster 1998; Small et al.

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2005; Eschtruth et al. 2006; Sullivan and Ellison 2006). However, because HWA has caused damage to eastern forests on a large scale only since the late 1980s, there is currently no empirical evidence regarding the long-term future species composition of formerly hemlock-dominated forests.

The ecological effects of this large-scale stand replacement include reduced habitat for wildlife dependent on hemlock (Brooks 2001; Snyder et al. 2002; Tingley et al. 2002), changed patterns of runoff of water and nutrients (Foster et al. 1997; Jenkins et al. 1999; Stadler et al. 2005, 2006; Orwig et al. 2008), and altered regional fluxes of carbon between land and atmosphere (Hadley et al. 2008).

In this study, we used a spatially explicit model of regional forest dynamics to provide a 100 year forecast of the impact of HWA infestation on the temporal and spatial dynamics of eastern US forests and the resulting patterns of carbon fluxes in this region. County-level infestation records were used to calibrate a simple stochastic spread model, which was used to predict the regional-scale spread of adelgid infestation over the next 100 years. The spatial pattern of mortality predicted by the stochastic spread model was then applied to a regional simulation of forest ecosystem dynamics by using the Ecosystem Demography model (ED) (Moorcroft et al. 2001; Hurtt et al. 2002). A complicating factor is that the impacts of HWA on eastern forests are occurring against a backdrop of historical and ongoing changes in the land-use change and forest harvesting disturbance regimes across the region. Accordingly, the impacts of HWA-induced hemlock mortality were quantified here by comparing the transient ecosystem dynamics of eastern forests in the presence and absence of HWA-pathogen-induced hemlock mortality.

Background

HWA was first observed in the eastern US in the early 1950s in Virginia (Souto et al. 1996). Its populations expanded dramatically in the mid-1980s (Preisser et al. 2008), and it currently occurs east of the Appalachian Mountains, from southern Maine to northern Georgia, and new infestations have been detected as far west as northwestern New York, Kentucky, and Tennessee (USDA Forest Service 2008). There are no effective native predators of the HWA; introduced biological control agents have not yet been effective over large scales, and eastern hemlock shows no resistance to infestation or recovery after chronic infestations (McClure 1995, 1996; Orwig et al. 2002). Consequently, the expansion of HWA's range has been followed by the rapid and extensive mortality of hemlock (Orwig et al. 2002). In southern and mid-Atlantic states, the onset of HWA-induced hemlock mortality occurs rapidly — in some cases, near complete hemlock loss occurs within 3–4 years (McClure 1991). In northern states, evidence suggests that cold temperature extremes reduce HWA survivorship during the winter (Parker et al. 1998, 1999; Paradis and Elkinton 2005; Shields and Cheah 2005), slowing the rate of infestation and the resulting time-course of hemlock mortality (Orwig et al. 2002). However, residual HWA populations recover quickly, and HWA may develop increased cold tolerance as it spreads north and east into regions with lower winter temperatures (McClure and Cheah 1999; Butin et al. 2005).

Methods

Our approach to predicting the regional-scale impacts of HWA infestation was to develop a quantitative model of HWA regional spread and link its predicted spatio-temporal pattern of HWA-induced hemlock mortality to a regional-scale forest ecosystem model. By comparing model simulations with and without HWA-induced hemlock mortality, we calculated the predicted impact of HWA infestation on future forest composition and structure and on carbon dynamics in the eastern US.

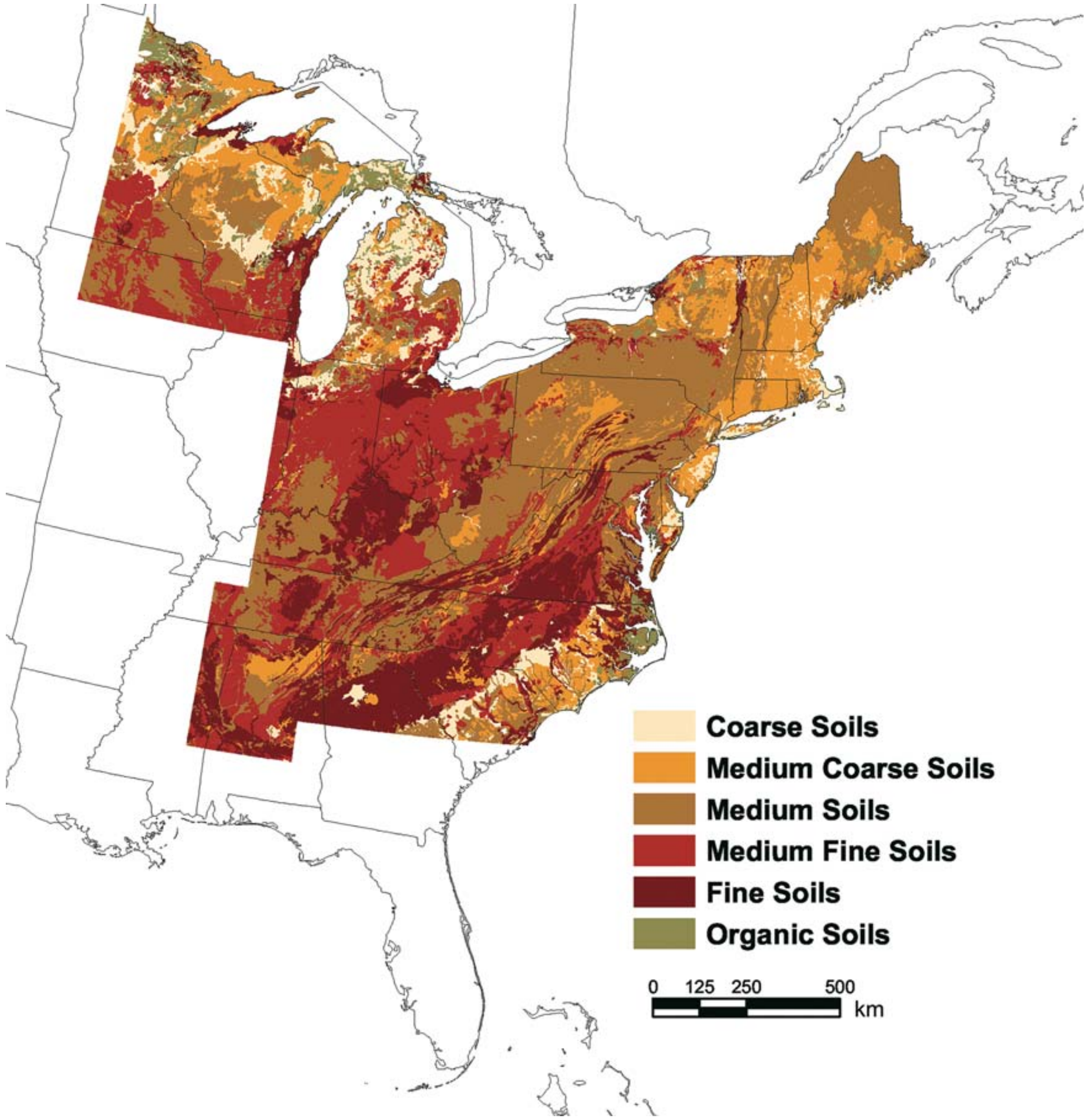
Model framework

The Ecosystem Demography (ED) model (Moorcroft et al. 2001; Hurtt et al. 2002; Albani et al. 2006) is a partial differential equation (PDE)-based approximation of an individual-based, stochastic gap model that formally scales up leaf-level physiological processes to the ecosystem level through the incorporation of vegetation dynamics and natural and anthropogenic disturbances. ED simultaneously simulates leaf physiology, long-term vegetation dynamics, and ecosystem biogeochemistry, and it can incorporate the impacts on terrestrial carbon fluxes caused by climatological forcing, growth enhancement due to atmospheric CO_2 increase, land-use changes, and disturbance dynamics. Here we use ED as parameterized by Albani et al. (2006) — we simulated seven plant functional types: a C_3 grass, three conifer types, and three hardwood types. We changed the parameterization of the late-successional conifer in the model by increasing its specific leaf area from 10 to 11 $m^2 \cdot (kg\ C)^{-1}$ to represent eastern hemlock more accurately. See Supplementary Appendices A–D for further details on the model formulation and parameterization.[2]

Our simulations encompassed the current range of eastern hemlock in the US. The model was implemented on an irregular, polygon-based grid, with each polygon having a unique soil type, climate, disturbance history, and HWA spread scenario (see section Regional Spread of HWA). The basic mapping units were the soil polygons extracted from the USDA State Soil Geographic (STATSGO) database (Miller and White 1998). Each polygon was assigned the soil texture representing the dominant soil texture in the profile (Fig. 1). We then aggregated all polygons that had the same textural class and that were contained within the same cell of the 2.5° data grid of the National Centers for Environmental Prediction/National Center for Atmospheric Research NCEP/NCAR Reanalysis 1 data (Kalnay et al. 1996; Kistler et al. 2001), while a few polygons that spanned more than 2° in latitude or longitude were split at the edge of the NCEP grid cells. The total number of polygons within the simulations domain was 400, with a mean size of 4489 km^2.

[2] Supplementary data for this article are available on the journal Web site (http://cjfr.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5335. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html.

Fig. 1. Soil types of the domain for the ecosystem demography model simulation of hemlock woolly adelgid impact. The simulation domain is divided into 2.5° grid cells for climatic purposes, and each cell is divided into polygons based on the principal soil characteristics. Polygon boundaries are not shown to improve clarity.



Disturbance regime

As noted in the Introduction, the impacts of HWA are occurring in ecosystems that are in transition as a result of past and continuing changes in land-use and forest harvesting. We accounted for these dynamics in this study by overlaying the effects of HWA mortality onto simulations that incorporate the historical and projected future dynamics of land-use change and forest harvesting. Specifically, we used the methodology of Albani et al. (2006), which tracks the transition of land from three land-use types defined in terms of their disturbance origin: agricultural land originating from land-clearing, secondary vegetation originating from agricultural land abandonment or forest harvesting, and primary vegetation originating from natural disturbance. The disturbance history for each polygon was determined by county-level land-use changes and a forest harvesting scenario (Fig. 2). Further details on how disturbance rates were calculated and how the different modes of disturbance were incorporated into the ED model can be found in Supplementary Appendices A and D.

Regional spread of HWA

The timing of the infestation for each polygon was prescribed from a regional spread model. In nature, most adelgid crawlers disperse within 300 m of infested stands, but wind, birds, deer, and human activities can disperse HWA individuals much farther (McClure 1990). It is these rarer, long-distance dispersal events that were of interest to this study, since they will dominate the regional-scale spread of HWA. Because it is difficult to directly observe long-range dispersal events and estimate regional-scale dispersal, we used the observed historical pattern of HWA spread to infer regional-scale probabilities of HWA dispersal.

For the eastern US, the US Forest Service maintains a da-

Fig. 2. Land-use change (left) and forest harvesting scenario (right) used in the simulations.

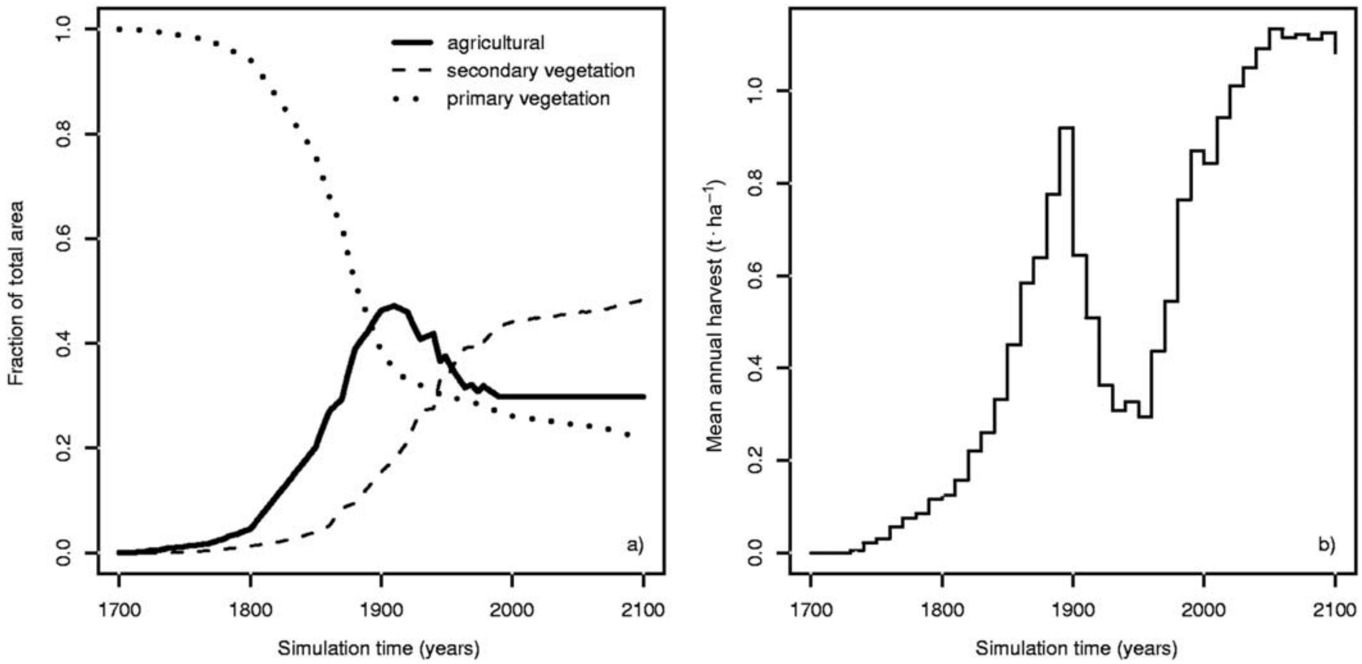
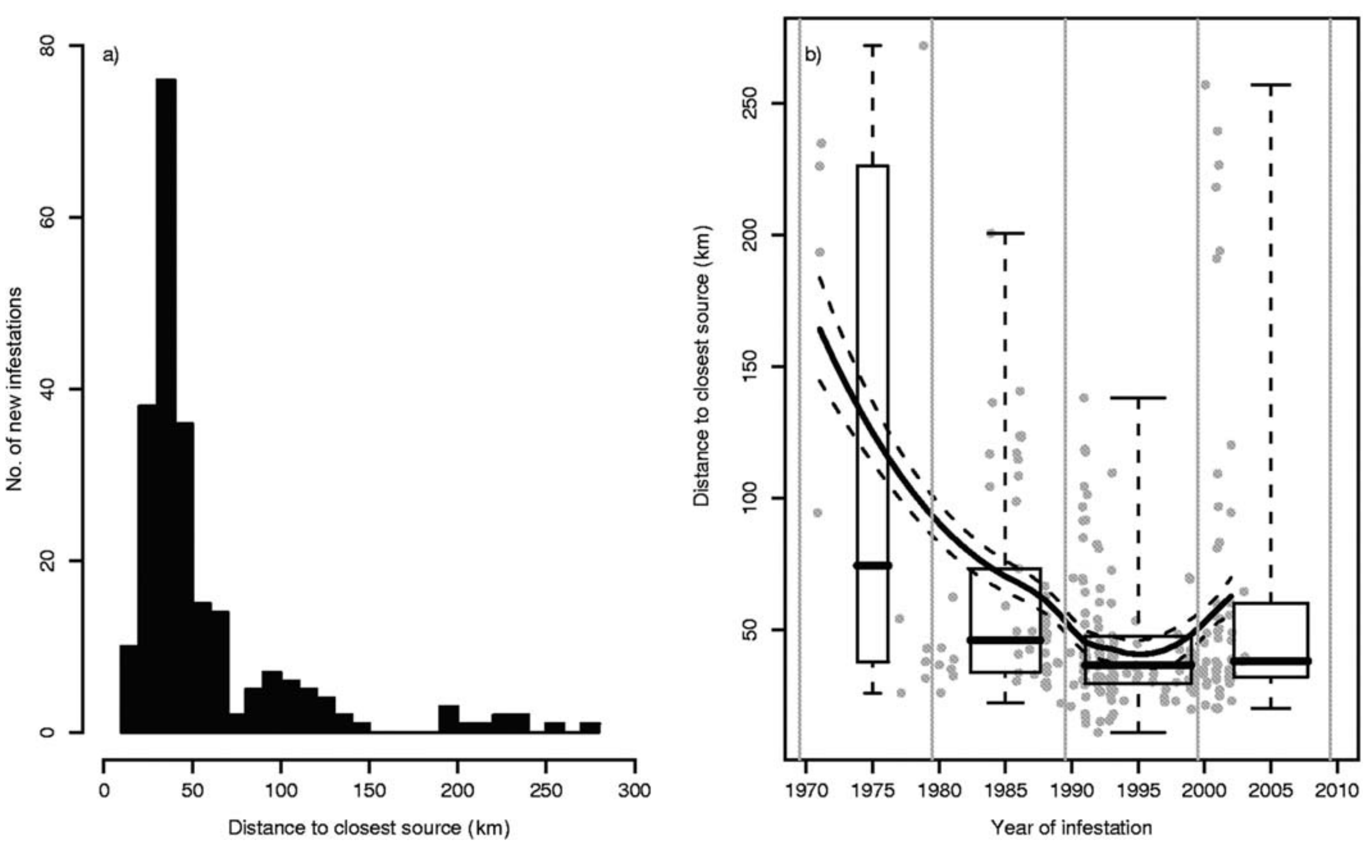
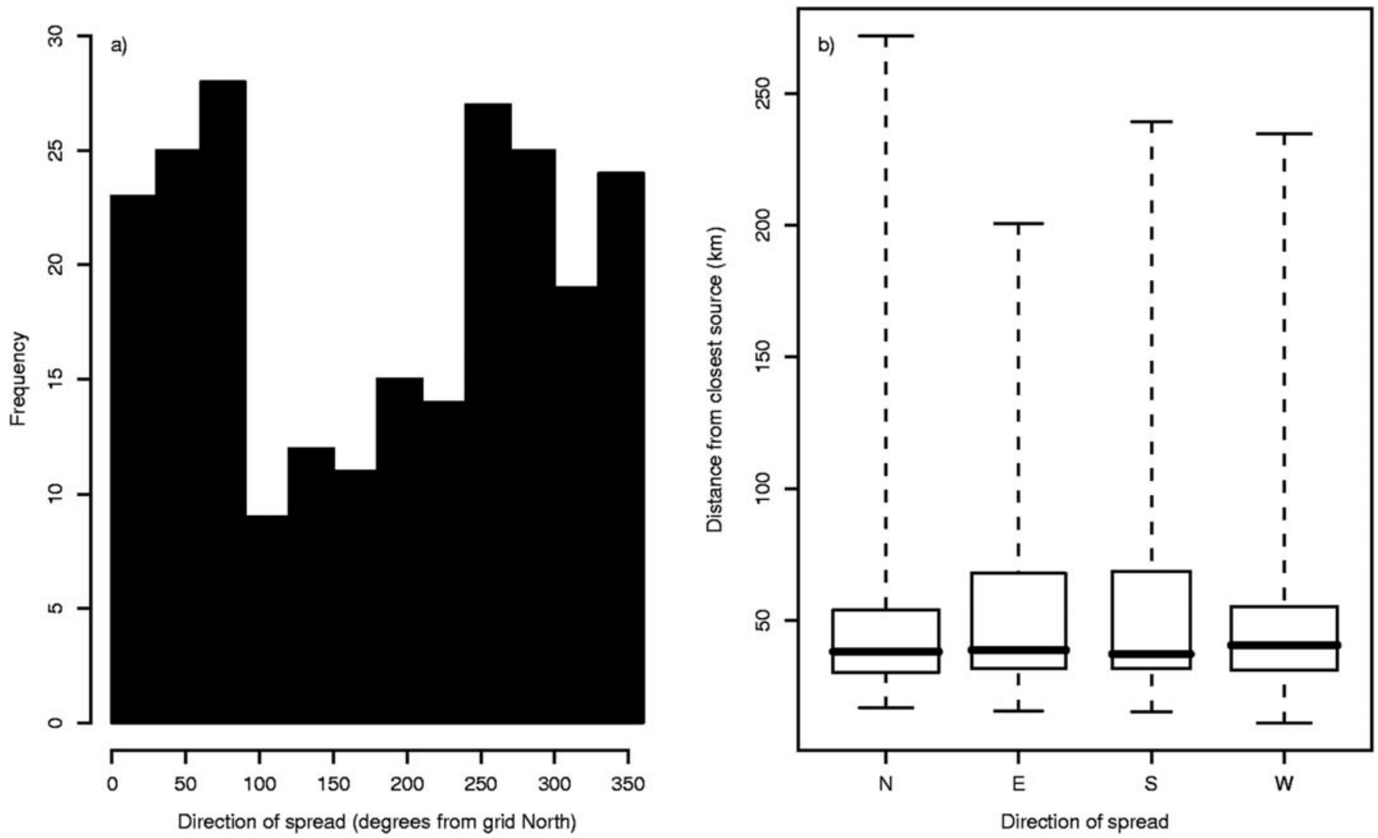


Fig. 3. (*a*) Histogram of new hemlock woolly adelgid infestations as a function of distance from the closest US source. (*b*) Box plots of distance to closest US source as a function of the of time of infestation at the destination for all newly infested counties (grey circles), 1970–2003. The solid line is a loess fit with a span of 0.75. Data are summarized by decade.



tabase of the year in which HWA infestations are first observed in each county (Ann K. Stekatee, USDA Forest Service, personal communication). We used these data to identify counties infested in year *t* and the closest infested county in year *t*–1 for each of the newly infested counties. The geographic coordinates of the centroid of each county were used to compute a distance matrix of distances between each county. We used Euclidean distances and com-

Fig. 4. (*a*) Histogram of the direction of the vectors connecting the closest source to each new infestation. (*b*) Box plots of distances from the closest source by direction from the closest source, 1983–2003. N indicates newly infested polygons that are between 315° and 45° of the azimuth from the closest source; E, between 45° and 135°; S, between 135° and 225°; and W, between 225° and 315°.



pass directions and did not account for spatial configuration of the counties beyond the location of their centroids or for the possible effects of physical barriers to dispersal, such as major rivers and mountain ranges.

Based on historical data (Figs. 3 and 4), we estimated the probability of infestation as a function of distance from the closest infested county using a logistic regression model. Infestation events prior to 1983 were excluded because of the substantially different distribution of distances from the closest source during this period (Fig. 3) and because of the likelihood that this distribution was primarily due to underreporting during the early stages of spread, as HWA was considered no more than an annoying ornamental pest (Souto et al. 1996). There is a significant north–south bias in the direction of HWA spread (Fig. 4*a*); however, this reflects the north-to-south distribution of hemlock rather than directionality in the rate of spread. As shown in Fig. 4*b*, the mean distance to nearest source is independent of direction, and accordingly, the spread model only considered the distance from the closest source to calculate the predicted pattern of spread. The model was fitted to the recorded pattern of infestation events that occurred between 1983 and 2003 using the glm package in R (R Development Core Team 2004).

Forecasts of HWA dispersal were restricted to the US counties that fall within the US forest inventory eastern hemlock range map of Godman and Lancaster (1990) and to a few additional counties in which HWA infestations have been recorded by the USDA. For each of these counties, the distance *d* from the closest infested county was computed, counting each new infestation of a county as an infestation event, while all other counties were counted as

Fig. 5. Mean annual fraction of newly infested counties (points) by distance from possible sources in 10 km bins, and logistic regression of probability of new infestation in 1 year versus distance from closest possible source (solid line). Dotted lines represent 2 standard errors. Note that each fractional bin represents a very different number of observations. Estimates of both parameters are significantly different from 0 ($P < 1\times10^{-13}$), and the proportion of variance explained by the regression (r^2) = 0.3.

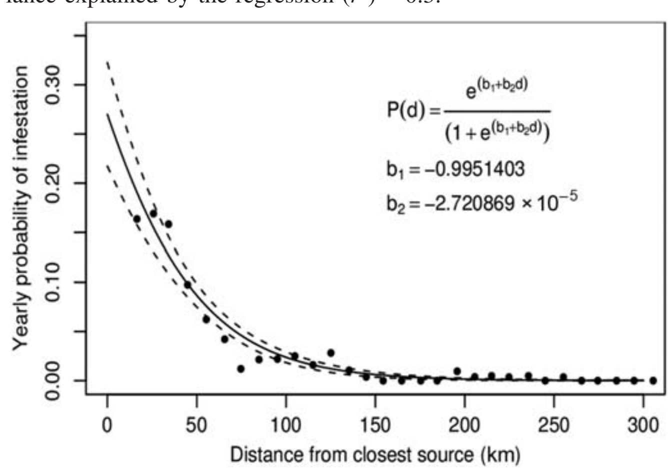
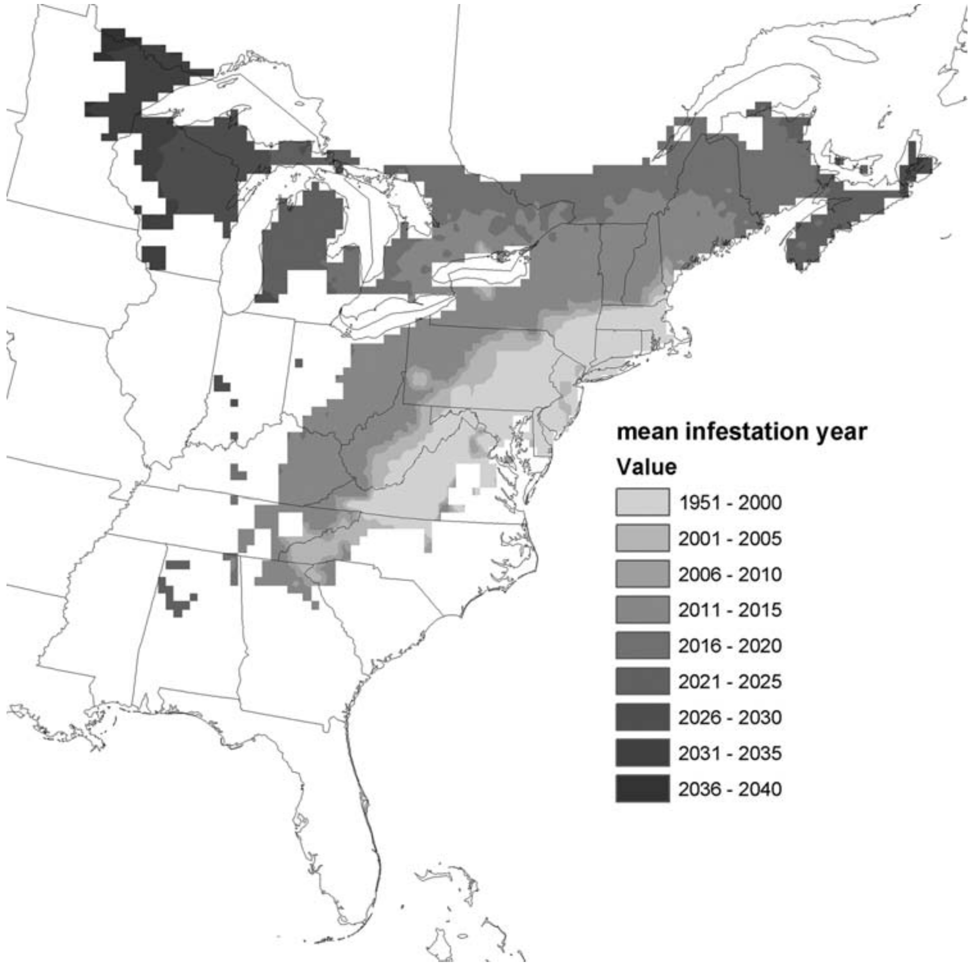


Fig. 6. Mean year of hemlock woolly adelgid infestation (1951–2040) computed from 100 runs of the stochastic spread model.



noninfestation events. We aggregated all these observations and fit a logistic regression of the annual probability of infestation P as a function of distance d as follows:

$$[1] \qquad P(d) = \frac{e^{(b_1+b_2d)}}{1+e^{(b_1+b_2d)}}$$

where the parameters b_1 and b_2 together determine the probability of nearby locations becoming infested, and the rate at which the probability of infection declines with distance from a potential source of HWA infestation. Equation 1 was then used to model the future spread of the infestation. A stochastic spread model was implemented on a raster map of the hemlock range at 25 km resolution. At each time step, a Bernoulli random variable was drawn for each grid cell with probability P calculated from eq. 1, which converts the Euclidean distance of each grid cell to the closest source of infestation into a corresponding probability of infestation. The model then recalculated the distribution of infested grid cells and the distance to the closest infestation source, accounting for the new infestations that occurred during the time step.

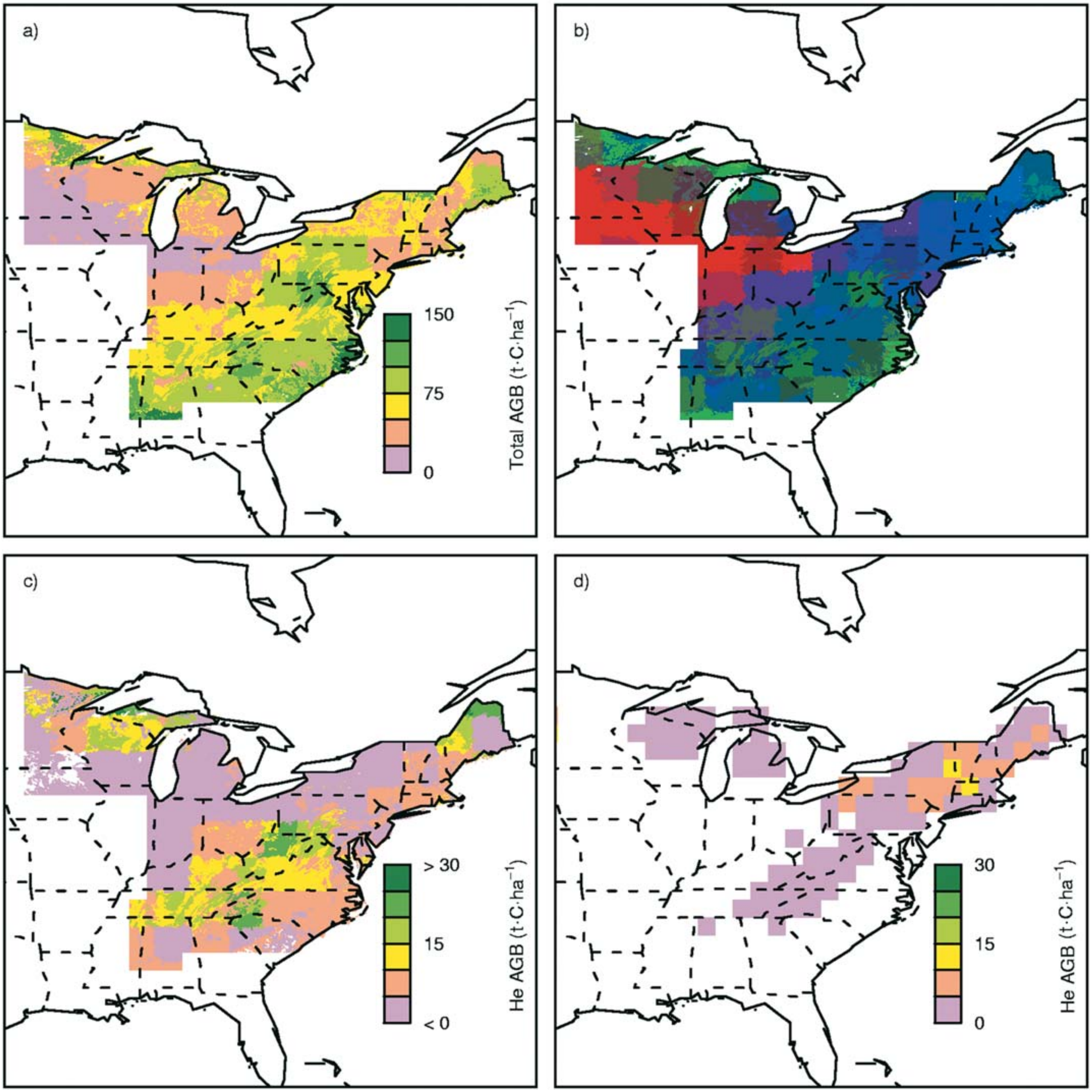
The model was initialized with the distribution of HWA infestation for the year 2004 and run for 96 time steps until 2100. One hundred replicates of the stochastic model were performed, and an average spread scenario was then computed by calculating the mean year of infestation for each grid cell obtained from 100 realizations of the spread model, which was sufficient to yield a stable mean year of infestation for all locations in the simulation region. The impact of HWA is represented as a time-dependent additional mortality term $\mu_{\mathrm{HWA}}(t)$ that is applied to the late-successional conifer plant functional type. The shape and magnitude of this additional mortality term was specified from the study of Orwig et al. (2002), which indicated that the HWA-induced mortality rate typically increases linearly from 0% to 50% in 20 years following the onset of HWA infestation.

Results

Pattern of HWA spread

The modeled annual probability of infestation decreases by ~50% for each 30 km distance from a possible infestation source (Fig. 5). The relatively low r^2 value for the relationship between probability of infestation and distance from the closest source ($r^2 = 0.3$) indicates significant unexplained variance in the probability of infestation; however, the relationship is highly significant statistically ($P < 1\times10^{-13}$). The spatial extent of infestation is driven primarily through the occurrence of rare, long-distance dispersal events, and the stochastic spread models predict a patchy pattern of new infestations (Fig. 6). When the times to infestation are averaged they yield a narrow band surrounding the initial

Fig. 7. Predicted forest conditions in 1985. (*a*) The total aboveground biomass (AGB) for all plant functional types (PFTs); (*b*) a RGB map of fractional distribution of area between the three land-use types, with green representing primary vegetation, blue secondary vegetation, and red agricultural land; and (*c*) the fraction of the AGB in the hemlock (He) PFT. For comparison, panel *d* shows the actual mean He AGB, as measured by the US Forest Inventory.

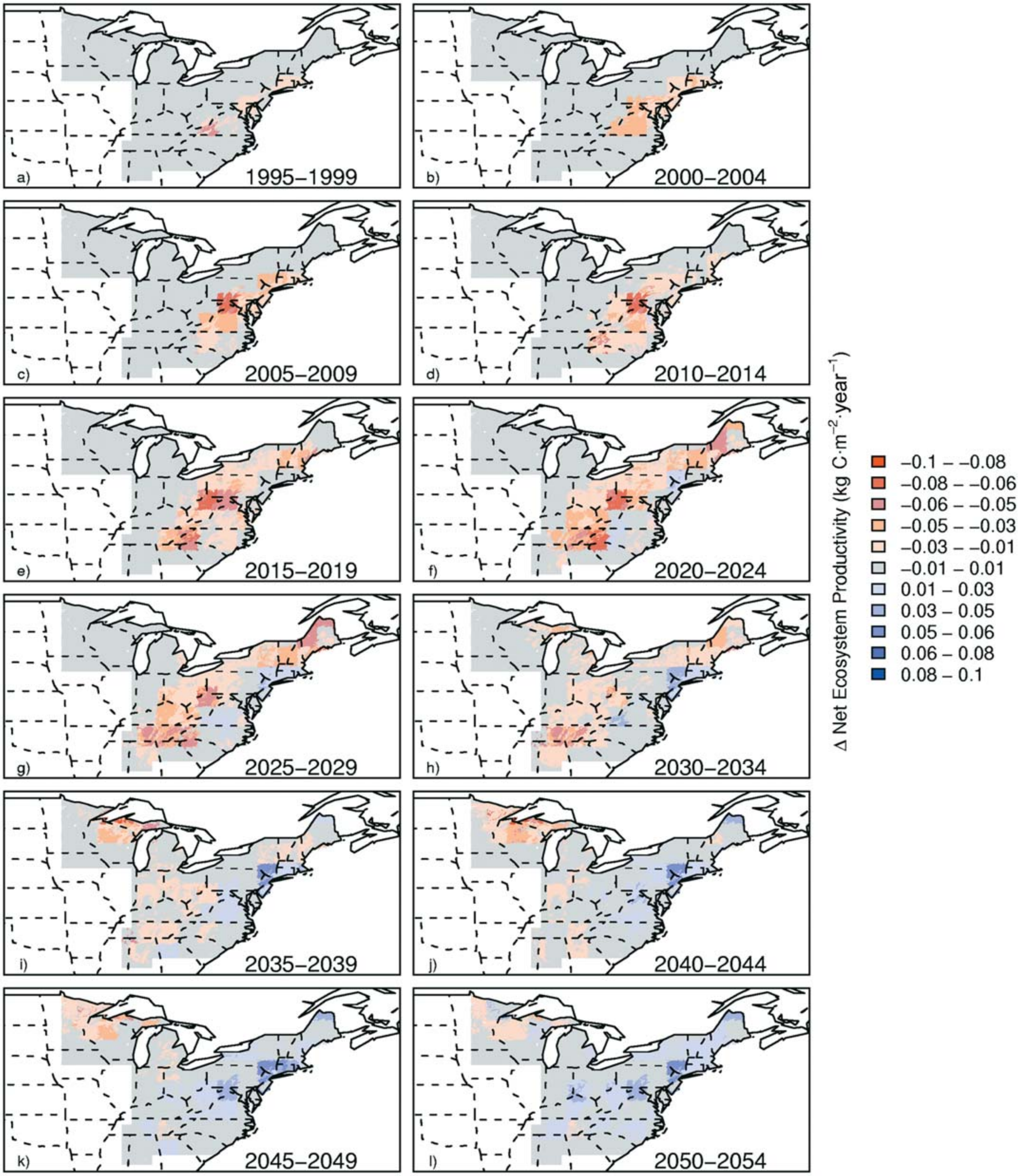


infested area that are infested on average during the first 5 years of the simulation, but thereafter the infestation proceeds rapidly. Most locations east of Lake Huron and south of the US–Canada border have a mean infestation year between 2010 and 2015, while all locations east of Lake Michigan have a mean infestation year before 2025, and by 2040, all locations within the simulation domain are infested.

Forest structure and composition prior to infestation

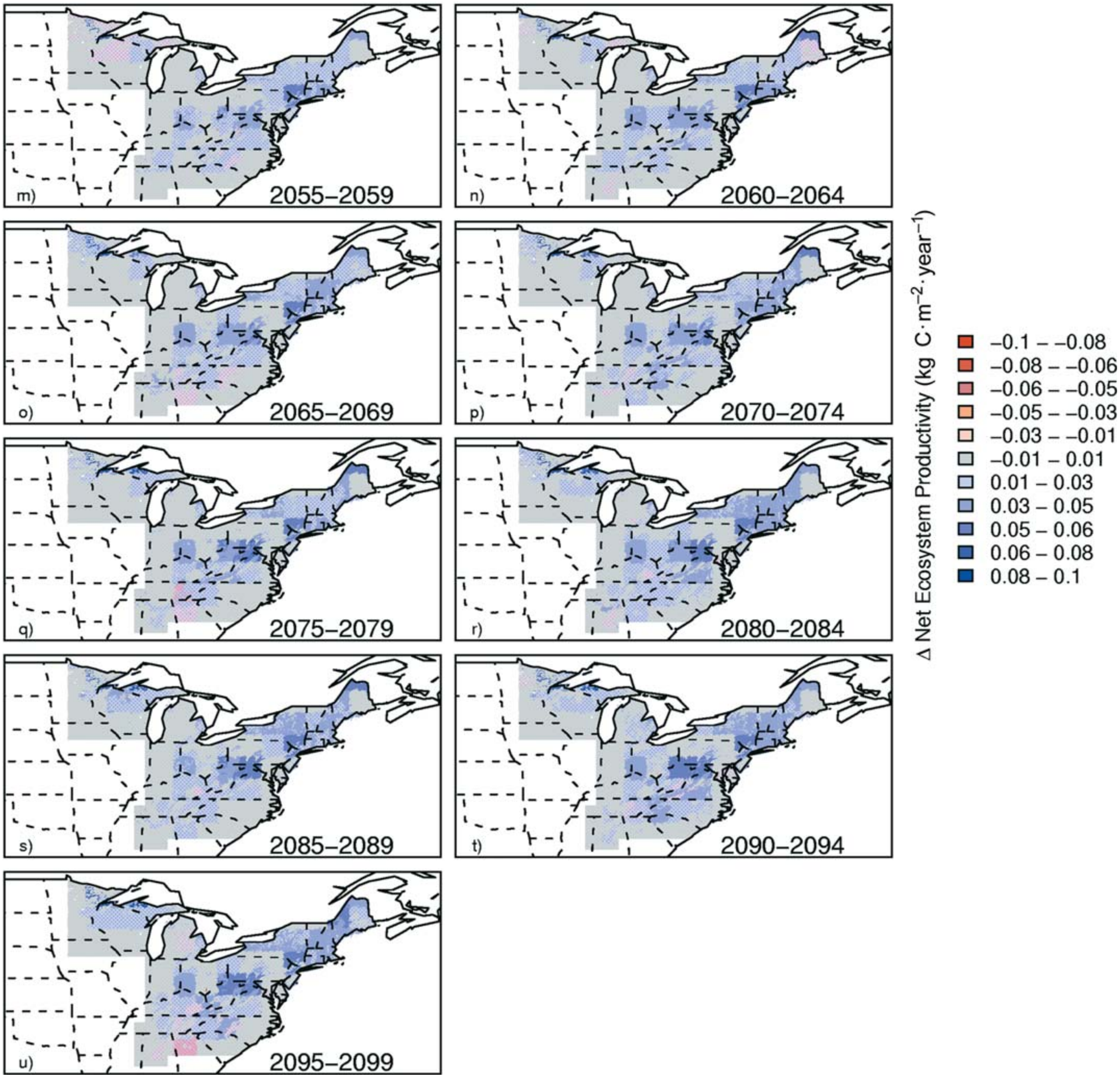
Simulated total aboveground biomasses (Fig. 7*a*) for 1985 on most of the forest-dominated polygons were between 50 and 125 t C·ha^{-1}, with lower levels in the agriculturally dominated polygons of the US Midwest (Fig. 7*b*). The model estimated the total forest aboveground biomass of the modeling domain at 10.3 Pg C (Pg C = 10^{15} g C), a number that

Fig. 8. Predicted impact of hemlock woolly adelgid (HWA) on net ecosystem productivity.



is close to the Forest Inventory and Analysis (FIA)-based measurement of 10.4 Pg C. The modeled spatial distribution of hemlock (Fig. 7*c*) was also generally consistent with the FIA measurements (Fig. 7*d*), with hemlock reaching its highest densities in New England, the northern Great Lake states, and along the Appalachians. However, in the simulation the late successional conifer plant functional type comprised 1.1 Pg of the total aboveground biomass across the region, while in the FIA measurements hemlock comprised 0.3 Pg C of the total aboveground biomass with an addi-

Fig. 8 (*concluded*).



tional 0.8 Pg C of the other late-successional conifer species, such as balsam fir (*Abies balsamea* (L.) Mill.) and black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.). To account for this discrepancy, we scaled the amount of the late-successional conifer functional type within each polygon experiencing HWA infestation in proportion to the observed spatial distribution of hemlock biomass as measured by the US Forest Inventory censuses taken during the mid 1980s and early 1990s.

Carbon dynamics

Changes in net ecosystem productivity (NEP) follow the infestation pattern and are mediated by the local abundance of hemlock. We estimated the impact of simulated HWA as the difference in mean NEP between model runs with and without the infestation — negative values indicate a reduction in NEP caused by the infestation. For the period 1995–1999, the impact of HWA is limited to the northern Atlantic states and southwestern Virginia, with ΔNEP ranging from –0.01 to –0.05 kg C·m^{-2}·year^{-1} (Fig. 8*a*). Between 1999 and 2014 NEP is forecast to be reduced in the rest of Virginia and in West Virginia, North Carolina, Pennsylvania, New Jersey, New York, and southern New England (Figs. 8*b*–8*d*). Between 2015 and 2024, following the western and southern expansion of the infestation, the model predicts HWA-caused reductions in NEP from northern Georgia to Maine. However, the north Atlantic areas that were previously impacted are forecast to rebound, with their NEP ap-

Fig. 9. Predicted 10 year running means of the regional mean annual carbon uptake with (dotted line) and without (solid line) hemlock woolly adelgid infestation. Dynamics since 1700 (*a*) and annual means for 1980–2100 (*b*).

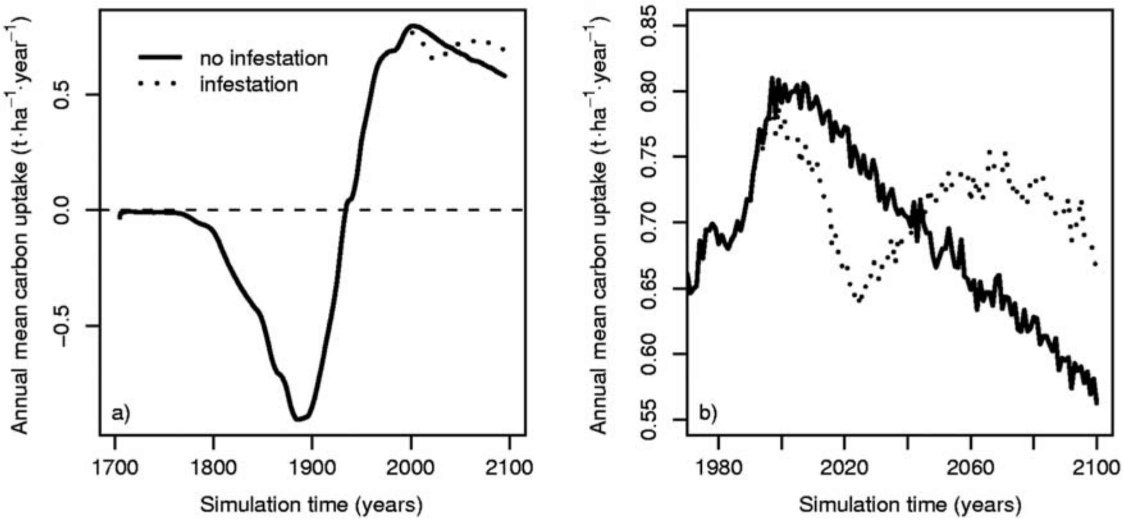


Table 1. Changes in the regional mean rate of carbon (C) uptake arising from hemlock woolly adelgid (HWA) infestation.

Time period	Rate of C uptake in the absence of HWA (t C·ha^{-1}·year^{-1})	Change in C uptake following HWA infestation (t C·ha^{-1}·year^{-1})	% Change in C uptake due to HWA infestation
1980–1989	0.693	–0.00	0.0
1990–1999	0.769	–0.01	–0.9
2000–2009	0.798	–0.04	–4.8
2010–2019	0.779	–0.07	–8.9
2020–2029	0.750	–0.10	–12.8
2030–2039	0.717	–0.04	–5.8
2040–2049	0.694	+0.01	+1.8
2050–2059	0.674	+0.06	+8.6
2060–2069	0.648	+0.08	+13.0
2070–2079	0.630	+0.10	+15.6
2080–2089	0.610	+0.11	+18.2
2090–2099	0.585	+0.11	+18.9

proaching the NEP they would have had in the absence of HWA infestation (Figs. 8*e* and 8*f*). By 2030, the impact of the infestation reduces NEP in upper Michigan, while the northeast will start to show positive NEP as it rebounds from the infestation (Figs. 8*g* and 8*h*). Beyond 2050, the negative effects of HWA on NEP should all but disappear, and some eastern areas will continue to show positive NEP as they recover the lost aboveground biomass (Figs. 8*l*–8*u*).

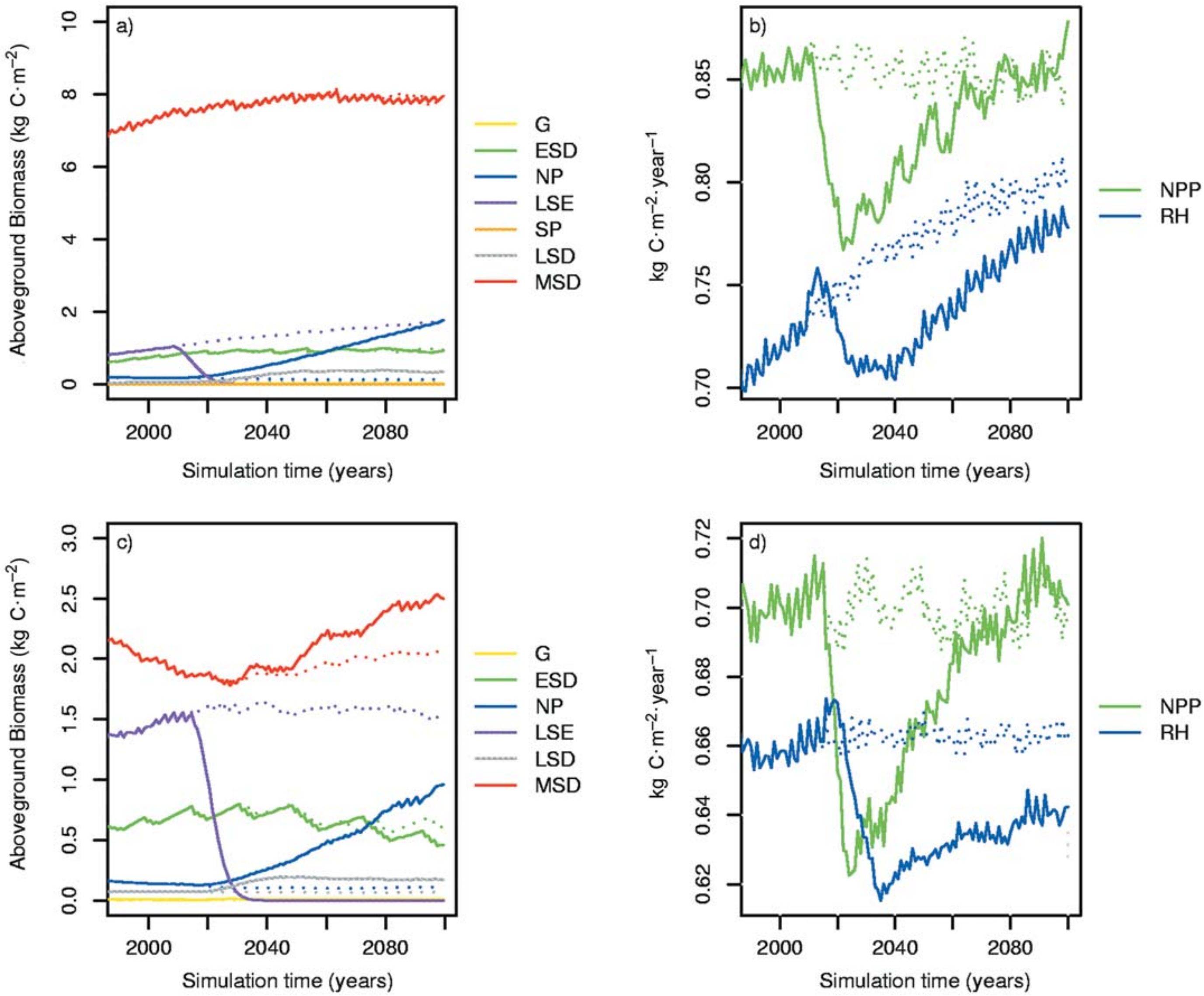
The average effect over the simulation domain follows a similar temporal pattern (Fig. 9 and Table 1). In the second half of the 20th century, the regional mean carbon uptake rose rapidly, as the region recovered from the land-clearing and higher forest harvesting rates of the 18th and 19th centuries (Fig. 9). In the absence of HWA infestation, the model forecasts a peak in the regional mean rate of carbon uptake of 0.8 t C·ha^{-1}·year^{-1} between 2000 and 2010 and a steady decline to 0.57 t C·ha^{-1}·year^{-1} by 2100. When the HWA infestation is added into the simulation, the reduction in uptake rates is accelerated in 1995–2025, so that the regional mean carbon uptake is reduced to 0.65 t C·ha^{-1}·year^{-1} in 2025, which is 0.1 t C·ha^{-1}·year^{-1} less than it would have been in the absence of HWA infestation. The negative impact of the infestation peaks after 2025, as the predicted uptake increases to 0.75 t C·ha^{-1}·year^{-1} by 2070 and then declines again to 0.66 t C·ha^{-1}·year^{-1} by 2100.

When the fluxes are integrated over the entire region for the period 2000–2040, the model forecasts (*i*) a total reduction in carbon uptake of 0.45 Pg C due to the HWA infestation, (*ii*) an mean annual reduction of 0.011 Pg C·year^{-1}, and (*iii*) an 8% reduction in the total uptake forecast for the period. During the recovery phase, from 2040 to 2100, the model predicts that the total uptake in the presence of the HWA infestation would be 0.89 Pg C, or 12% larger than it would have been in the absence of infestation.

Changes in forest structure and composition following infestation

The dynamics of recovery in carbon uptake arise as a consequence of successional dynamics. As hemlock is killed by HWA, other plant functional types in the model increase in abundance. Figure 10 shows the successional dynamics for two different areas: a medium texture soil site in central

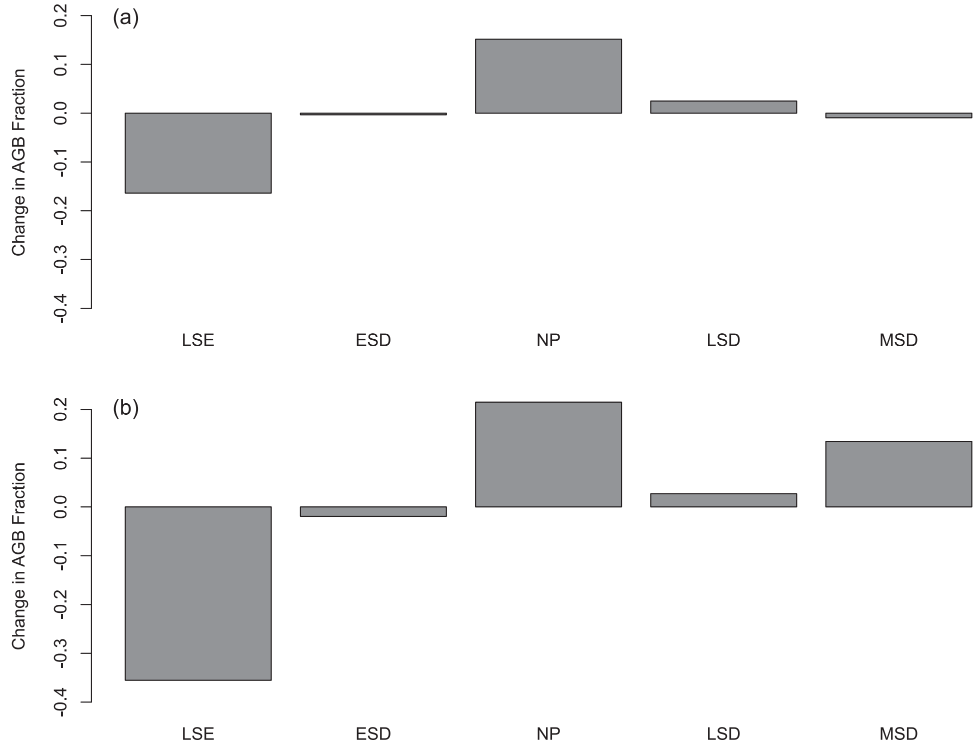
Fig. 10. Forecasts of site-level impact of hemlock woolly adelgid (HWA) infestation on aboveground biomass trajectories (*a*, *c*) and carbon fluxes (*b*, *d*) for a medium soil polygon in central Massachusetts (*a*, *b*) and for a medium–coarse soil polygon in central New Hampshire (*c*, *d*). In Figs. 10*a* and 10*c*, the plant functional type codes are as follows: G, grass; ESD, early successional deciduous; NP, northern pines; LSE, late successional evergreens; SP, southern pines; LSD, late successional deciduous; and MSD, midsuccessional deciduous. In Figs. 10*b* and 10*d*, carbon flux is represented by NPP, net primary productivity, and RH, heterotrophic respiration. Solid lines are for model runs with HWA infestations; dotted lines are for model runs without HWA infestations.



Massachusetts, where hemlock is a relatively minor component (10% of aboveground biomass), and a medium–coarse texture soil polygon in central New Hampshire, where hemlock represents 33% of the aboveground biomass. In central Massachusetts, the removal of hemlock by HWA between 2010 and 2020 (Fig. 10*a*) is followed by increases in the aboveground biomass of the northern pines and late successional hardwoods (Fig. 10*a*). At the end of the century, in the presence of HWA, the fraction of the stand aboveground biomass that is northern pine increases from 1.2% to 16.3%, while the aboveground biomass of late successional hardwoods increases from 0.7% to 3.1% (Fig. 11*a*). Concomitant with the decline of hemlock, there is a short pulse of heterotrophic respiration and a larger drop in net primary productivity (NPP) (Fig. 10*b*). The drop in NPP is followed by a drop in heterotrophic respiration, as lower aboveground biomass lowers leaf and root turnover and mortality. As the northern pines and late successional hardwoods increase in abundance and leaf area, both NPP and heterotrophic respiration recover (Fig. 10*b*).

A similar pattern is seen in the simulations for the New Hampshire site (Figs. 10*c* and 10*d*), but here hemlock represents a larger component of the aboveground biomass and the total leaf area. Here, the loss of hemlock is followed not only by colonization of northern pines and late successional deciduous trees but also by midsuccessional deciduous species (Fig. 10*c*). At end of the century, in the presence of HWA, the fraction of the stand aboveground biomass that is northern pine increases from 2.5% to 20.5%, the fraction of late successional hardwoods increases from 1.5% to 3.6%,

Fig. 11. Changes in relative abundance (in terms of fraction of aboveground biomass (AGB)) of the dominant plant functional types in 2100 following hemlock woolly adelgid infestation in (*a*) a medium soil polygon in central Massachusetts, and (*b*) and a medium–coarse soil polygon in central New Hampshire. See Fig. 10 for plant functional type codes.



and the fraction of midsuccessional hardwoods increases from 47% to 60% (Fig. 11*b*). The latter are more productive than hemlock, especially in high-light conditions, and thus the rate of recovery of NPP is faster than that in central Massachusetts (Fig. 10*d*).

Discussion

Our analysis of the rate of HWA spread based on the observed spatial pattern of new infestations over the last 20 years suggests that most hemlock stands in the eastern US will be reached by the pest within the next 30 years, unless extreme cold winter temperatures in the northern range of eastern hemlock are able to check the spread of this insect (Paradis et al. 2008; Dukes et al. 2009). This analysis indicates that the next 15 years will be particularly crucial, as it is during this period that the HWA infestation will reach the areas with the highest densities of hemlock biomass, specifically western Pennsylvania, upstate New York, Vermont, New Hampshire, and southeastern Maine (Fig. 6).

The results imply that the impact of HWA is then likely to be most dramatic in southern New England and upstate New York. Here hemlock is a large component of forest biomass, background harvesting rates are relatively low, and the process of recovery from past land use is significantly more advanced than in other parts of the eastern US (Albani et al. 2006).

Our simulations of regional forest dynamics forecast that while the impact of hemlock removal by the HWA will have substantial consequences at local scales (Fig. 10), its impact on the regional C cycle is likely to be small (Fig. 9). There are three reasons for this. Firstly, eastern hemlock is a relatively minor component of the forests of the eastern US. Secondly, even where hemlock is abundant, its productivity is low, and thus on a per tree and per area basis it contributes less to regional NEP than hardwoods. Thirdly, the simulations indicate a relatively rapid recovery of both aboveground biomass and NEP after the infestation, since hemlock is replaced by early and mid-successional hardwoods and other conifers.

There are several limitations that need be taken into account when evaluating the accuracy of the model simulations presented here. Firstly, as noted earlier (see section Regional Spread of HWA), while the probability of infestation varies markedly with distance to closest source, there is substantial unexplained variance in the pattern of HWA infestation. This finding is reflective of the inherently stochastic nature of biology invasion processes (Melbourne and Hastings 2009), and implies that the predictions concerning the precise spatial pattern of HWA spread that will occur over the coming century are subject to a large degree of uncertainty. Secondly, the absence of an explicit surface energy balance model in the ED model means that the simulations do not incorporate the impact of hemlock loss on soil respiration rates in HWA-affected areas during the summer months because of drier soil conditions following the loss of the canopy (e.g., Cobb et al. 2006 and Orwig et al. 2008). Thirdly, while the scaling of the HWA impacts within each polygon accounts for differences between the predicted abundance of the late successional conifer plant functional type and the observed hemlock abundance within each polygon, it does not account for errors arising from incorrect abundances and spatial distributions of other species within the late-successional class or for inaccuracies in the

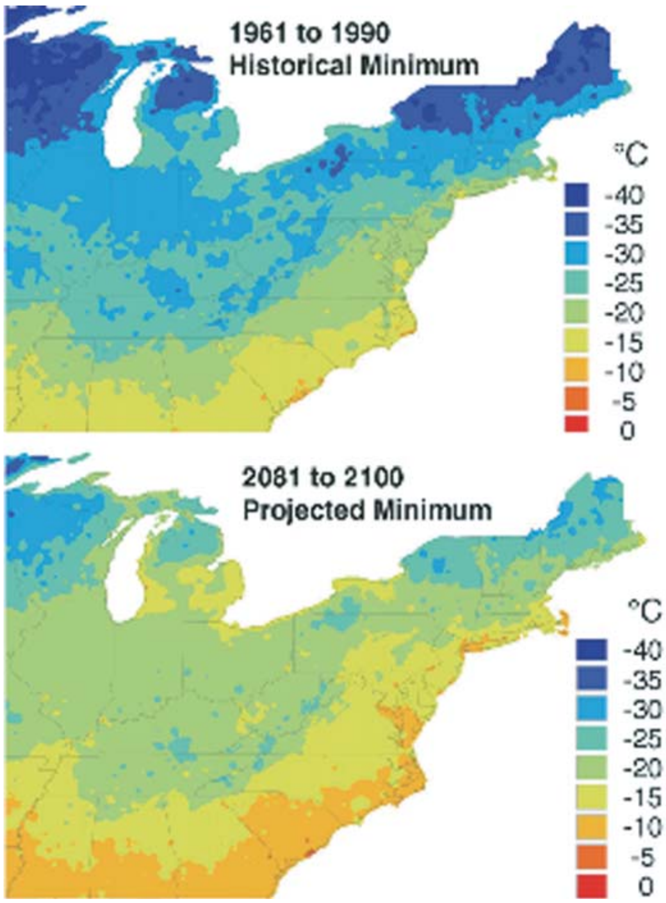


Fig. 12. Spatial distribution of minimum wintertime temperatures in the northeastern United States during 1961–1990 (upper panel). Predicted spatial distribution of minimum wintertime temperatures during 2081–2100 based on the projections of nine coupled atmosphere–ocean general circulation models (lower panel). From Dukes et al. 2009.

relative abundance of the other plant functional types. In particular, these inaccuracies in predicted composition could potentially affect the rate and composition of the successional recovery within infected stands. Fourthly, the simulations did not incorporate a reduction of rate of HWA-induced hemlock mortality as a result of colder temperatures at higher latitudes. Evidence suggests that recent cold temperatures in New England have reduced HWA populations (e.g., Paradis and Elkinton 2005; Shields and Cheah 2005), reducing the impact of HWA infestation in northern regions.

Understanding the determinants of the lower temperature threshold of HWA is critical for improving predictions of its future impact on eastern forests. Laboratory studies indicate that the lower temperature threshold for HWA survival is –35 °C (Parker et al. 1999); however, HWA is currently only found in places whose winter minimum temperatures are above –28.8 °C (Skinner et al. 2003). If the –35 °C threshold applies, then under current conditions only hemlock the northernmost parts of Maine, New Hampshire, and Vermont would be unaffected by HWA. In contrast, if the 28.8 °C threshold applies, then hemlock populations in Maine, New Hampshire, Vermont, Wisconsin, upstate New York, and northern and central Michigan will be unaffected by HWA. However, two additional considerations argue against this latter scenario. Firstly, predictions of a CO_2-induced temperature increase across the region indicate that by 2100, the –28.8 °C winter minimum temperature threshold will have migrated northward and be nearer to the current position of the –35 °C isotherm (Dukes et al. 2009, see Fig. 12). Secondly, genetic studies indicate that HWA is evolving greater resistance to cold shock as it has expanded its range northward (Butin et al. 2005). Another source of uncertainty is whether the spread rate of the infestation will accelerate because of the higher density of hosts, as has been hypothesized for other invading insects, such as gypsy moth (*Lymantria dispar* (L.)) (Liebhold et al. 1992).

Another issue of interest not explicitly included in the simulations is the impacts of the salvage logging operation that frequently precede or follow HWA infestation (Brooks 2004; Foster and Orwig 2006). While HWA mortality is limited to hemlock trees, salvage logging in a mixed stand is rarely confined exclusively to hemlock but also tends to affect commercial species present in the salvaged stands, such as white pine (*Pinus strobus*) (Kizlinski et al. 2002). As a result, salvage logging is likely to have a larger impact than HWA on regional carbon dynamics. If salvage logging captures most of the HWA-caused mortality, this will reduce the negative impact of HWA on local-scale carbon balance. On the other hand, if HWA-induced logging leads to increased regional harvesting rates rather than to just offsetting the harvesting of healthy stands, it will reduce the regional rates of carbon storage, moving more forest carbon to the wood products pool. However, with the exception of the Kizlinski et al. (2002) study, there is currently little quantitative information on relative impacts of HWA mortality and hemlock salvage logging operations.

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