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Using changes in basal area increments to map relative risk of HWA impacts on hemlock growth across the Northeastern U.S.A

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Abstract Eastern hemlock (*Tsuga canadensis*) is a critical species in eastern North American forests, providing a multitude of ecological and societal benefits while also acting as a foundation species in many habitats. In recent decades, however, hemlock has become threatened by hemlock woolly adelgid (HWA; *Adelges tsugae*), an invasive sap-feeding insect from Asia. In addition to causing the more commonly assessed metrics of foliar damage, crown decline, and hemlock mortality, HWA also decreases hemlock growth and productivity. Dendrochronological methods provide a more nuanced assessment of HWA impacts on hemlock by quantifying variable rates of radial-growth decline that follow incipient infestation. This information is necessary to better understand the variable response of hemlock to HWA, and identify the characteristics of stands with the highest potential for tolerance and recovery. To quantify decline, we calculated changes in hemlock yearly radial growth using basal area increment (BAI) measurements to identify periods of growth decline from 41 hemlock stands across New England covering a range of infestation density, duration and hemlock vigor. The onset of growth decline periods were predominantly associated with either HWA infestation or drought. However, the magnitude of change in BAI values pre- and post-decline was significantly related to HWA infestation density and crown impacts, indicating that radial growth metrics can be used to identify locations where HWA infestations have incited significant reductions in hemlock health and productivity. Additional site characteristics (slope, hillshade, and January minimum temperatures), were also significantly associated with hemlock health and productivity decline rates. In order to develop a model to identify stands likely to tolerate HWA infestation, these metrics were used to build a logit model to differentiate high- and low-BAI-reduction stands with 78% accuracy. Independent validation of the model applied to 15 hemlock sites in Massachusetts classified high and low BAI reduction classes with 80% accuracy. The model was then applied to GIS layers for New England and eastern New York to produce a

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spatially-explicit model that predicts the likelihood of severe hemlock growth declines if/when HWA arrives. Currently 26% of the region's hemlock stands fall into this high risk category. Under projected climate change, this could increase to 43%. This model, along with knowledge of current HWA infestation borders, can be used to direct management efforts of potentially tolerant hemlock stands in eastern North America, with the intention of minimizing HWA-induced hemlock mortality.

Keywords *Adelges tsugae* · Decline statistic · Dendrochronology · Hemlock decline · Radial growth · Risk mapping · Spatial model · *Tsuga canadensis*

Introduction

Eastern hemlock (*Tsuga canadensis*) provides an array of economic, ecological, and cultural benefits. In eastern North American forests, this species can regulate both terrestrial and aquatic environments by producing dense canopies that heavily shade the understory (Ellison et al. 2005; Orwig et al. 2012). Due to hemlock's ability to regulate multiple ecosystem processes, provide wildlife habitat, and impact soil acidity, it is often referred to as a foundation species across its range (Ellison et al. 2005), which extends from southern Canada to Alabama and west to Minnesota. While the species is often valued for its long lifespan (500+ years), it is also subject to multiple environmental stressors.

Since the mid-twentieth century, hemlock's continued survival has been increasingly threatened by the hemlock woolly adelgid (*Adelges tsugae*; HWA), an invasive insect from Asia. This sap-feeding insect targets hemlock twigs and branches; the feeding prevents new growth and desiccates current-year needles, resulting in needle loss (McClure 1987). Hemlock mortality can occur in as little as 4 years following infestation (McClure 1991a, b, 1995); however, under certain conditions, it can survive for more than 10 years (Orwig and Foster 1998; Orwig et al. 2002). Since HWA's arrival in the eastern U.S., the insect has spread to at least 17 states and provinces at a rate of 7.6–20.4 km per year (Trotter et al. 2013), causing widespread hemlock crown damage and mortality throughout its range.

While HWA and eastern hemlock have been the foci of numerous studies, a comprehensive landscape-scale model evaluating hemlock's growth response to HWA-incited stress is lacking. Orwig and Foster (1998) assessed the forest's response to HWA based on hemlock mortality rates; however, their work centered on community and landscape-level responses. Other studies have examined the association between site characteristics and HWA-incited hemlock crown damage and mortality (Orwig et al. 2002; Pontius et al. 2010; Eschtruth et al. 2013). Yet previous studies have often overlooked the potential use of annual growth variation in individual hemlock trees, which is directly influenced by abiotic and biotic stressors such as HWA. Also, unlike subjective canopy metrics, annual radial growth is a direct measure that may be able to more accurately quantify nuanced differences in decline response. Such metrics can provide a basis for evaluating severity of HWA infestation impacts on hemlock growth without having to rely on subjective assessments or wait for mortality to occur. However, there are no known studies focused on hemlock's growth response to HWA or how additional stressors may impact hemlock response.

Detailed research has been conducted on annual radial growth response to defoliators and other insect pests (for example, Swetnam et al. 1985; Speer et al. 2001; Rolland et al. 2001; Orwig 2002). These studies typically compare the growth of a defoliator host with the growth of a non-host in order to isolate the defoliator signal. Further, many of these dendrochronology studies use a "conservative standardization" approach, which removes the biological trend by fitting a growth curve to the chronology using nonlinear regression (Biondi and Qeadan 2008). While this can be effective for large sample sizes and long chronologies, this standardization method can overlook individual tree-level responses and does not distinguish between age-related versus growth-related trends or other, non-host specific stresses affecting a tree.

One alternative to the above approaches is a size adjusted, ring-area measurement referred to as basal area increment (BAI), which is ideal for smaller sample sizes, shorter chronologies, and samples where the biological age is unknown (Biondi and Qeadan 2008). This ring-area approach is well suited for assessing tree-level responses to biological stress agents.

Our study used BAI to quantify radial growth changes in mature hemlock to assess the impact of HWA across a range of site characteristics and stress agents. BAI has often been used to assess growth performance and decline (LeBlanc 1990; Duchesne et al. 2002; DeMaio 2008), while accounting for age related allometric growth (Cook and Innes 1989), and to detect declines in growth that raw ring widths can miss.

By evaluating the interactions among (1) HWA-incited stress, (2) non-HWA-induced stress, and (3) site characteristics on hemlock BAI we developed a comprehensive landscape model that predicts the likelihood of rapid hemlock growth decline in response to HWA. This empirical model was based on significant statistical relationships with ecologically relevance to HWA population dynamics and hemlock radial growth.

Currently, reports vary with regard to which factors most strongly influence hemlock vulnerability to HWA; potential significant factors reported in the literature include elevation, slope, aspect, topographic position, annual precipitation, and winter minimum temperatures. In Shenandoah National Park, Virginia, lower elevations were associated with increased HWA-incited crown decline and mortality (Bair 2002). Additionally, south and southwest facing slopes were reported to increase hemlock vulnerability to HWA and other environmental stressors (Bonneau et al. 1999; Souto and Shields 2000; Mayer et al. 2002; Orwig et al. 2002; Pontius et al. 2006). Ridge tops, excessively well-drained soils, and a shallow depth-to-bedrock layer have also been associated with increased HWA-incited hemlock damage (Bonneau et al. 1999; Pontius et al. 2006). These studies have a common theme: sites with warmer winter temperatures and exposure to additional environmental stressors such as moisture limitation, typically experience greater HWA-incited hemlock growth decline and mortality. Furthermore, the large variability observed in hemlock mortality rates (McClure 1991a, b, 1995; Orwig and Foster 1998; Orwig et al. 2002; Eschtruth et al. 2006, 2013) emphasizes a need for detailed studies examining variability in hemlock's annual response not only to HWA, but to other factors that may influence rates of growth decline.

Specifically, this study intends to develop a spatial predictive models that identifies where hemlock are at greatest risk of rapid HWA-incited growth decline and how this may change under a warming climate. To achieve this goal, our specific research objectives were to:

1. develop a decline metric, based on changes in radial growth, to quantify hemlock's decline response to stresses;
2. relate this growth decline metric to the magnitude of stress associated with HWA infestation and drought;
3. build a model to quantify the additional influence of site factors leading to HWA-incited growth decline, and
4. develop a spatially-explicit model that maps hemlock growth decline probability across the landscape based on significant model parameters.

To achieve these objectives, a combination of dendrochronological methods and landscape modeling are used to relate changes in annual hemlock growth to factors site and climate characteristics across the landscape. The resulting model can be a critical hemlock management tool that allows land managers to identify which stands are at greatest risk and prioritize management efforts accordingly.

Methods

Study sites

In order to develop a robust calibration model, in 2007 our study sampled 41 long-term HWA monitoring plots (20 m × 20 m) from a regional, long-term hemlock monitoring network established by Pontius et al. (2006), henceforth referred to as calibration plots (Fig. 1). Plots were selected from the larger monitoring network if HWA had been reported in the area for at least 5 years, a time period during which vulnerable stands would have time to develop severe infestations (McClure 1991a, b, 1995; Orwig and Foster 1998; Orwig et al. 2002). Therefore, we assume that plots without severe HWA infestations or hemlock decline symptoms demonstrate some level of tolerance to HWA infestation rather than a lack of opportunity for HWA infestation development and impact. These calibration plots were distributed across the following states: New York (22), Connecticut (12), Pennsylvania (3), Massachusetts (2), and New Jersey (2) and

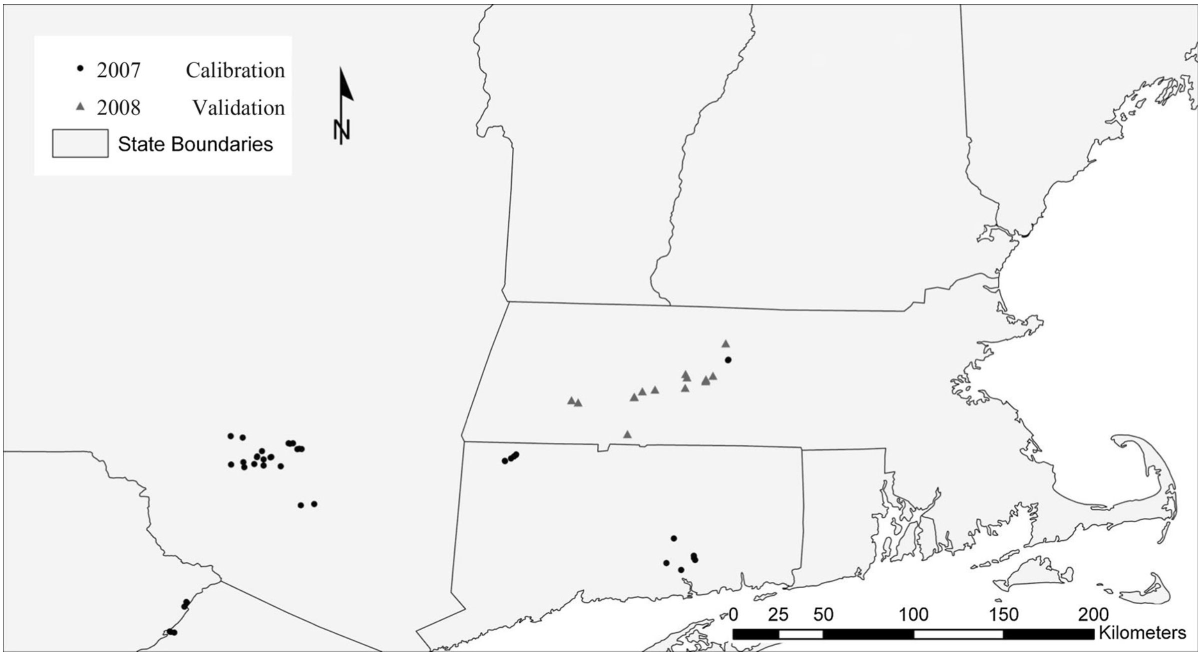

Fig. 1 Locations of sites sampled in 2007 and 2008

included a range of HWA infestation densities and hemlock decline symptoms. In 2008 we developed an independent validation dataset by sampling an additional 15 plots located along the northern front of HWA-incited growth decline (central Massachusetts; Fig. 1). These 15 plots were used to assess the model's ability to predict the likelihood of HWA-incited growth reductions at the northern edge of current infestations.

Existing data and field sampling

Our study made use of the data previously collected by Pontius et al. (2006) on the 41 calibration plots and five validation plots. The stands were dominated by mature hemlock (DBH >8 inches), with canopy dominant trees tagged for yearly foliar chemistry analyses, HWA population assessments (percentage of terminal branches infested with HWA) and canopy decline symptoms (canopy decline rating, CDR) between 2001 and 2006. CDR values were calculated from four measurements aggregated into an equally weighted summary index (Pontius et al. 2014) based on: (1) Percent of terminal branches with new growth, (2) Percent crown transparency, (3) Percent fine twig dieback, and (4) Live crown ratio (LCR, USDA Forest Service 1997). CDR values range from 0 (ideal health) to 10 (dead). Tree-level CDR was averaged by plot to produce a plot-level mean assessment of hemlock canopy condition. Similarly, long-term HWA monitoring on our 41 calibration plots provided mean percent hemlock infestation levels in each year between 2001 and 2007. Lastly, all trees greater than 5 cm diameter at breast height (dbh) were measured to calculate plot total and percent hemlock basal area. The 10 remaining validation plots followed the same methods for selecting hemlock trees, but HWA infestation levels were not assessed. Stand basal area was measured using a 2 m BAF prism.

Spatial data

To enable spatial modeling, data were collected from online GIS databases based on previously reported factors influencing hemlock vulnerability to HWA (Table 1; Parker et al. 1998, 1999; Bonneau et al. 1999; Souto and Shields 2000; Orwig et al. 2002, 2012; Skinner et al. 2003; Pontius et al. 2006, 2010; Eschtruth et al. 2013). We obtained 30-year normals for January minimum temperatures and annual precipitation (1971–2000 and 1981–2010) for the northeastern United States (PRISM Climate Group 2015, Oregon State University, http://prism.oregonstate.edu). January minimum temperatures were used because they

Table 1 Stand characteristic values including minimum, maximum, mean, and standard deviation values of all calibration and validation sites sampled; 41 and 15 sites, respectively

Stand characteristic	Calibration sites (n = 41)				Validation sites (n = 15)			
	Min	Max	Mean	SD	Min	Max	Mean	SD
Avg. annual temperature (°C)	5.00	9.44	7.47	1.39	7.22	9.44	8.26	0.51
Annual precipitation (cm)	114.30	149.86	133.50	9.67	114.30	139.70	122.43	6.60
Elevation (m)	41.17	736.27	395.42	208.21	53.82	356.98	194.90	69.50
Normalized aspect*	0.00	1.00	0.58	0.33	0.01	0.99	0.52	0.39
Slope (%)	2.66	78.79	23.11	18.08	3.07	31.37	19.39	9.62
Summer Hillshade	155.67	251.67	229.74	19.52	208.00	253.75	232.48	14.56
Winter Hillshade	0.00	190.75	95.21	42.72	37.00	166.75	93.49	37.30
Avg. 1971–2000 Jan. min. temp. (°C)	−13.01	−7.08	−10.57	1.54	−11.86	−9.51	−10.95	0.57
Avg. 1981–2010 Jan. min. temp. (°C)	−12.58	−7.77	−10.08	1.46	−12.08	−8.93	−10.78	0.81
HWA infestation levels (%)**	0.00	75.11	21.41	21.98	–	–	–	–

Values were used in model development

* Values transformed according to Beers et al. (1966)

** Data provided for 40 of 41 calibration sites. Data lacking on 13 of 15 validation sites and is not presented

are generally the lowest recorded temperatures of the year in our region, and low winter temperatures are known to limit the survival of HWA (Parker et al. 1998, 1999). Additionally, 30 m Digital Elevation Models (DEMs) were obtained for the area of interest (NRCS 2015). The DEMs were then used to calculate percent slope, aspect, summer and winter hillshade in ArcGIS 10.2 (ESRI 2014). Aspect values were normalized between 0 (NE aspect) and 1 (SW aspect) using the following modified version of Beers' equation (Beers et al. 1966): aspect = 1 − [(cosine (0.7845-radians) + 1)/2]. Hillshade values ranged from 0 (darkest) to 255 (brightest) and were used to approximate the amount of solar radiation (temperature load) at a given point based on a fixed position of the sun (Iverson and Prasad 2003). Adams, Massachusetts was selected as the central-most point in our dataset, for latitude, sun angle, and azimuth to calculate hillshade values for solar noon of the summer solstice (June 21 for summer hillshade, elevation = 70.8°, azimuth = 183.9°) and solar noon of the winter solstice (December 21 for winter hillshade, elevation = 23.9°, azimuth = 182.3°).

Increment core processing

In 2007 (calibration plots) and 2008 (validation plots), field crews extracted increment cores from seven canopy dominant hemlock trees at each study plot. These mature trees were selected in order to minimize impacts to growth caused by competition, shading or crowding. Two cores per tree were collected at 180° angles, perpendicular to the slope, along with tree height, dbh, and height to live canopy base. Cores were dried, mounted, and sanded (to 800 grit) using standard dendrochronological procedures (Stokes and Smiley 1996). Annual ring-widths (RW) were measured using WinDendro (Regent Instruments Inc. 1996) and a sliding-stage measuring table (Velmex Inc.). After measuring all cores, one core per tree was selected for final analysis based on the longest series length and the lack of defects such as compression wood or rot. Crossdating was statistically verified using COFECHA software (Grissino-Mayer et al. 1997).

Raw RW were converted to BAI, our ring-area metric of growth for analyses (Eq. 1). This requires calculation of diameter inside bark (DIB), which was estimated by multiplying hemlock's bark ratio of 0.934 (Dixon and Keyser 2013) times the tree's DBH. Yearly BAI was averaged across trees to produce a plot-level annual BAI measurement.

$$BAI_{TY-n} = \pi\left(r_{TY} - \sum_{n=0}^{x} RW_{TY-n}\right)^2 - \pi\left(r_{TY} - \sum_{n=0}^{x} RW_{TY-n+1}\right)^2 \quad (1)$$

BAI = basal area increment for year in subscript, TY = terminal year (e.g. last year of annual growth on increment core), r = radius of the tree, calculated as diameter inside bark (DIB)/2, RW = annual ring-width.

Individual tree ages ranged from 51 to 301 years in calibration plots, and 39–157 years in validation plots. To maintain a robust stand-wide signal, chronologies across all plots were assessed back to 1967, the earliest common year across all trees.

Analysis

Growth decline detection and quantification

To detect periods of declining hemlock growth, defined as periods of reduced BAI, we developed a metric to characterize the magnitude of change within a chronology while also accounting for variability (Decline-score or D-score, Eq. 2). The D-score uses the same formula as an independent two-sample t test based on the 3 year average BAI before and after each sample year. The standard error is calculated by using the square root of the pooled variance (Eq. 3) and multiplying by the square root of 2/n where n = 3 for the years included in the smooth. Dividing by the standard error results in lower values for portions of the chronology that were highly variable and likely did not result from stress-induced decline trends. The relatively short 3-year averages allow us to detect shorter trends that develop rapidly, such as typical growth reduction patterns following initial HWA infestation (McClure 1991a, b). However, this metric will likely miss slower declines that likely result from lower-level, chronic stress. As such, this approach filters out low-level stress and allows us to better identify stress events or agents that are likely to have more dramatic impacts on tree growth.

$$D\text{-}score_X = \frac{\left\{\left[\frac{(BAI_{X-3}+BAI_{X-2}+BAI_{X-1})}{3}\right]-\left[\frac{(BAI_X+BAI_{X+1}+BAI_{X+2})}{3}\right]\right\}}{\left[\sqrt{VAR_X}*\sqrt{\frac{2}{3}}\right]} \tag{2}$$

X = year for which D-score is being calculated, BAI = basal area increment for year in subscript, VAR_X = the pooled variance (Eq. 3).

$$VAR_X = \frac{\frac{\sum_{i=x-3}^{x-1}\left(BAI_i-\frac{\sum_{i=x-3}^{x-1}BAI_i}{3}\right)^2}{2}+\frac{\sum_{i=x}^{x+2}\left(BAI_i-\frac{\sum_{i=x}^{x+2}BAI_i}{3}\right)^2}{2}}{2} \tag{3}$$

The D-score generates a yearly standardized index that can be compared across temporal periods on individual cores, as well as across trees and species. A positive D-score indicates a decrease in average BAI (declining growth); similarly, a negative D-score indicates an increase in average BAI (increasing growth). D-scores were calculated for each year of the chronology, except the first two and last 2 years (Fig. 2a).

To quantify duration and severity of growth declines, percent decline in BAI (BAI_{decl}) was calculated for each chronology (Fig. 2b). The year with the largest D-score value was recorded as the onset of decline. BAI_{prior} (Eq. 4) was calculated as the 3-year BAI average prior to the onset of decline. We also identified the subsequent 3-year period with the lowest average BAI, then calculated the mean for this period (BAI_{min}, Eq. 5). BAI_{decl} was then calculated by subtracting BAI_{min} from BAI_{prior}, and dividing the difference by BAI_{prior} (Eq. 6). The decline period is defined as the years between BAI_{prior} and BAI_{min} (Fig. 2) representing the period during which the tree experienced persistent, declining increment growth. The decline period includes BAI_{min} but excludes BAI_{prior}.

$$BAI_{prior} = \frac{(BAI_{YD-3}+BAI_{YD-2}+BAI_{YD-1})}{3} \tag{4}$$

BAI = Basal Area Increment, YD = First year of decline (year of maximum D-score).

$$BAI_{min} = \frac{(BAI_{YL-1}+BAI_{YL}+BAI_{YL+1})}{3} \tag{5}$$

BAI = Basal Area Increment, YL = Year of lowest subsequent BAI following maximum D-score.

$$Percent\ BAI\ Decline\ (BAI_{decl}) = \frac{(BAI_{prior}-BAI_{min})}{BAI_{prior}} \times 100$$
$$BAI_{prior} = \frac{(BAI_{YD-3}+BAI_{YD-2}+BAI_{YD-1})}{3}$$
$$BAI_{min} = \frac{(BAI_{YL-1}+BAI_{YL}+BAI_{YL+1})}{3} \tag{6}$$

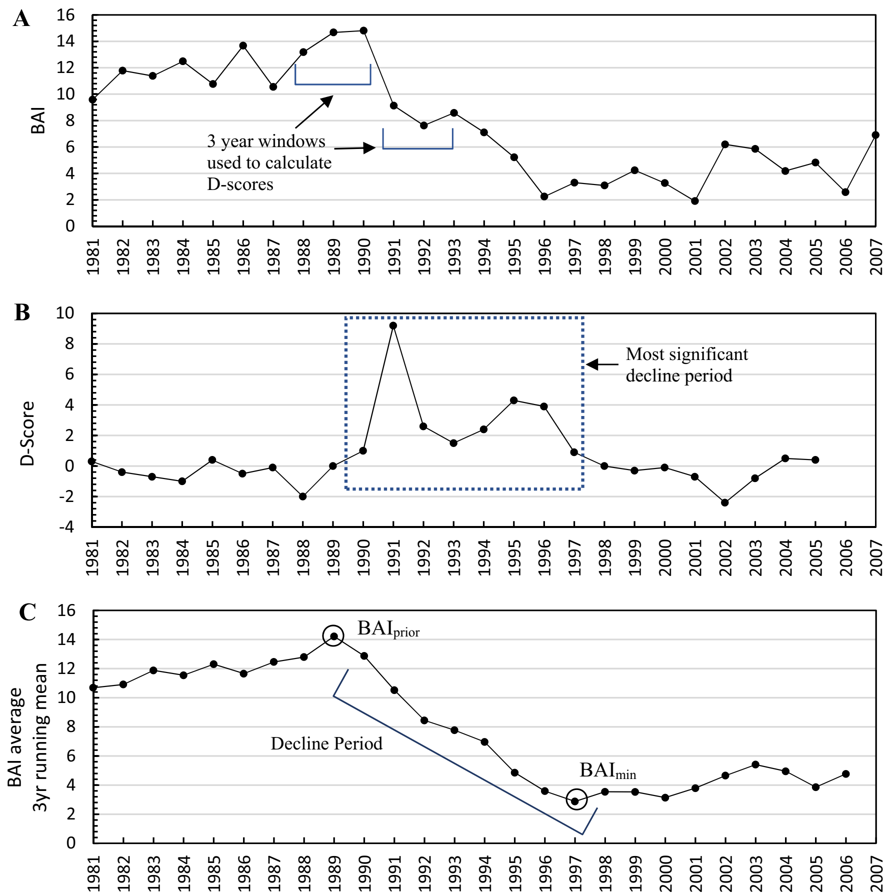

Fig. 2 Examples of parameters used for growth decline detection and quantification using example core: BB101B. **a** Example D-score calculation using the difference between consecutive 3-year moving average smooths. The D-score is assigned a year label based on the first calendar year of the second window. **b** A decline period occurs when D-scores are positive for at least three consecutive years, followed by 2 years of negative D-scores. D_{max} is defined as the year with the greatest D-score magnitude. In this example, D_{max} occurs in 1991. **c** Graph depicting a decline period, which excludes BAI_{prior} (Eq. 3) but includes BAI_{min} (Eq. 4), or 1990–1997 in this example. The period represents the years during which the tree experienced persistent declining growth

Logit models

Logit models generate probabilities of an event occurring (i.e. risk). In this study, logit model probabilities were combined with spatial mapping methods to predict the risk of rapid hemlock growth decline, i.e., BAI_{decl}. We took a "niche mapping" approach, with a goal of identifying locations likely to withstand HWA infestation. This led us to develop a model with two categories we call high- and low-BAI-reduction. This binary design allows us to differentiate potential "HWA tolerant" locations from other locations where hemlock may be more susceptible. A location was classified as high-BAI-reduction (susceptible) if the site's BAI_{decl} exceeded the median BAI_{decl} of all calibration sites. Sites with BAI_{decl} less than the median were classified as low-BAI-reduction (tolerant).

Stepwise logistic regression was used to identify the subset of climate and site variables that were able to most accurately differentiate calibration plots into high- or low-BAI-reduction classes. Logit model variables were retained if the *p*-value was less than 0.1. Once a final model was selected, model parameters and coefficients were used to estimate probabilities of being assigned as a high- or low-BAI-reduction (for full equation, see Eq. 7). This empirical model was then evaluated to ensure that significant factors retained in the final model were ecologically relevant to HWA population dynamics and hemlock radial growth patterns. The model was validated by calculating validation plot probabilities for growth decline in comparison to observed decline rates.

Spatially-explicit models

The final validated logit model was used to generate GIS risk maps by applying the coefficients of significant site variables to GIS data layers across New

England and eastern New York, resulting in logit probabilities for each cell. Because the final model included January minimum temperatures as a significant predictor of HWA-incited reductions in BAI, we further explored the influence of potential climate-induced changes in winter temperatures by evaluating model simulations with varied January minimum temperature as follows: (1) historical January minimum temperatures defined as 1971–2000 norms, (2) current January minimum temperatures defined as 1981–2010, and (3) future January minimum temperatures (assuming a 2 °C increase over current January minimum temperatures). These climate periods were specifically selected to represent significant temporal events. The 1971–2000 period coincides with HWA establishment and increased hemlock infestation levels: these conditions developed prior to sampling. The 1981–2010 period reflects conditions at the time of sampling. Lastly, the 2 °C increase from the 1981–2010 period reflects potential future conditions, which allows us to better estimate future regions at potential high-risk of HWA-incited reductions in BAI. Two degrees was selected as a conservative measure of projected temperature increases from recent IPCC models (projected to be roughly 1.1–2.9 °C under a lower emissions scenario and 2.0–5.4 °C under a higher emissions scenario (Christensen et al. 2013)). Slope and summer hillshade layers had a cell size of 30 m while the 1971–2000 and 1981–2010 January minimum temperature layers had a cell size of 800 m. Resulting risk maps were created with 800 m cells.

BAI_{decl} relationship to crown damage, HWA infestations, and drought

BAI_{decl} is based on changes in annual radial growth and is influenced by multiple factors and stress agents. We established links between potential stress agents and BAI_{decl} periods if (1) the magnitude of BAI_{decl} was related to the magnitude of the stress, and/or (2) a stress consistently coincided with the onset of growth decline periods in multiple stands. To assess if identified BAI_{decl} periods were also related to other metrics of decline, we compared BAI_{decl} to CDR as a measure of crown damage and to HWA infestation levels on a tree basis (Pontius and Hallett 2014).

To further examine relationship between BAI_{decl} periods and stress occurrence, the timing of decline onset was used to categorize plots into those where (1) stress was concurrent with the decline period (stress occurred prior to the median year of the growth decline) or (2) not associated with the decline period (stress occurred after the median year of the decline period). A 2 × 2 contingency table was created with BAI-reduction level (high or low) as one factor and HWA infestation timing (concurrent or not associated) as the second factor (Fig. 3). Drought is another stress commonly associated with declining growth in hemlock. There was a significant and widespread drought in the sampled region during 1998–2002 (Fig. 4). Therefore, a second 2 × 2 table was created using BAI-reduction level as one factor and drought timing (median of BAI_{decl} before 1999 or after 1998) as the second factor. A Pearson Chi square analysis used to assess associations among decline levels and stress timing. Statistical analyses utilized SYSTAT (SYSTAT v. 12, 2007) and R (R Core Team 2015).

Results

Site data summary

On calibration plots, elevation ranged from 41 m to 736 m, while site position ranged from relatively flat (<5%) to steep slopes (86%) (Table 1). Hillshade values (winter and summer) ranged from 0 to 254. The annual precipitation ranged from 114 cm to 150 cm and was evenly distributed throughout the year. Using the 1971–2000 climate data, average annual temperatures ranged from 5 to 9.5 °C. Average January minimum temperatures ranged from –13.01 to −7.08 °C and averaged −10.57 °C (see Online Resource 1). From 1981 to 2010, average January minimum temperatures ranged from −12.58 to −7.77 °C and averaged −10.08 °C.

Data from the validation plots fit within the range of the variables described above, although elevation and temperature ranges were smaller: validation plot elevations ranged from 54 m to 357 m and 1971–2000 January minimum temperatures ranged from –11.86 °C to −9.51 °C, and averaged −10.95 °C. The 1981–2010 average January minimum temperatures ranged from −12.08 °C to −8.93 °C, and averaged −10.78 °C (Table 1; also see Online Resource 1).

On both the calibration and validation plots, eastern hemlock was the dominant species, with a majority of

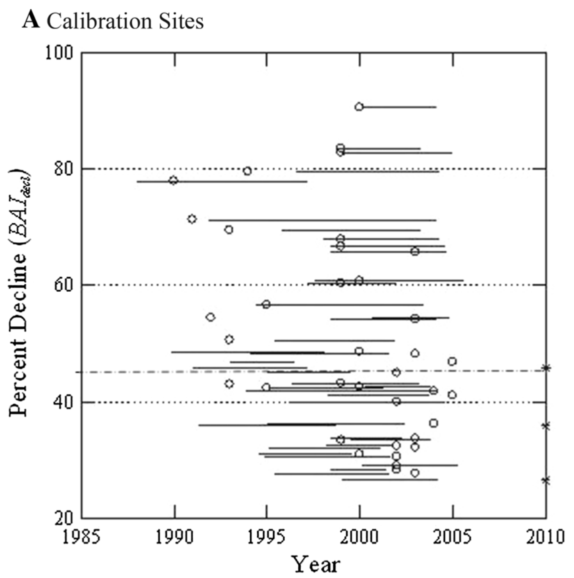

Fig. 3 Graph depicting the relationship between BAI_{decl} (Eq. 6) values for each site's most significant growth decline period and HWA infestations: **a** 41 calibration sites and **b** 15 validation sites. The decline period is represented with *solid lines* demarking average BAI_{decl}. The *horizontal line* of *dashes* represents the calibration sample median: $BAI_{decl} = 45\%$. *Open circles* indicate the year HWA was first reported at each calibration site. An *asterisk* indicates sites where HWA was not documented in the stand prior to 2006 (time of calibration plot sampling)

plots (>85%) containing greater than 50% hemlock basal area. Other associated species included red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), black birch (*Betula lenta*), sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) (see Online Resource 2).

The first year of reported HWA infestation is provided for calibration plots and two validation plots.[1] The earliest year of detection was 1990; however, most sites documented infestations between 1995 and 2005. Infestation levels across all years sampled ranged from 0 to 75% (see Online Resource 3), and were highly variable as year-to-year weather fluctuations affected HWA population size. Because HWA is likely in a stand for a number of years prior to detection, and all of our stands were in regions where HWA was detected prior to sampling, it is a reasonable assumption that HWA could have developed detectable infestations in all plots if conditions were favorable. Plots with low or undetectable levels of HWA within infested regions are assumed to have conditions that don't favor the high HWA infestation levels associated with rapid growth decline (Pontius et al. 2006).

Growth decline detection and quantification

Cores from 271 hemlock trees on 41 calibration sites and 101 hemlock trees on 15 validation sites were analyzed for growth decline trends. Interseries correlation ranged from 0.033 to 0.729 on calibration plots, but averaged 0.484. Interseries correlation ranged from 0.041 to 0.616 on validation plots, and averaged 0.463. Cores from sites with low correlations were visually inspected for errors in crossdating or measurement, and adjusted if needed. Once complete, five of the 41 calibration sites fell below the 99% confidence interval minimum interseries correlation (0.3281), while only one validation plot fell below this value. All plots were used in analyses, assuming that stands with low interseries correlations occur naturally across the landscape resulting from natural variability within sites due to competition and microsite characteristics.

Since the mid-1960s, the plot-level maximum BAI_{decl} ranged from 27 to 91% on calibration sites and 30–75% on validation sites. The median BAI_{decl} on calibration plots was 45%; this threshold value was used to classify plots as either high-BAI-reduction ($n = 20$, $BAI_{decl} > 45\%$) or low-BAI-reduction sites

[1] Year of infestation is unknown for 13 of 15 validations plots. However, the plots were within the known distribution of HWA infestations.

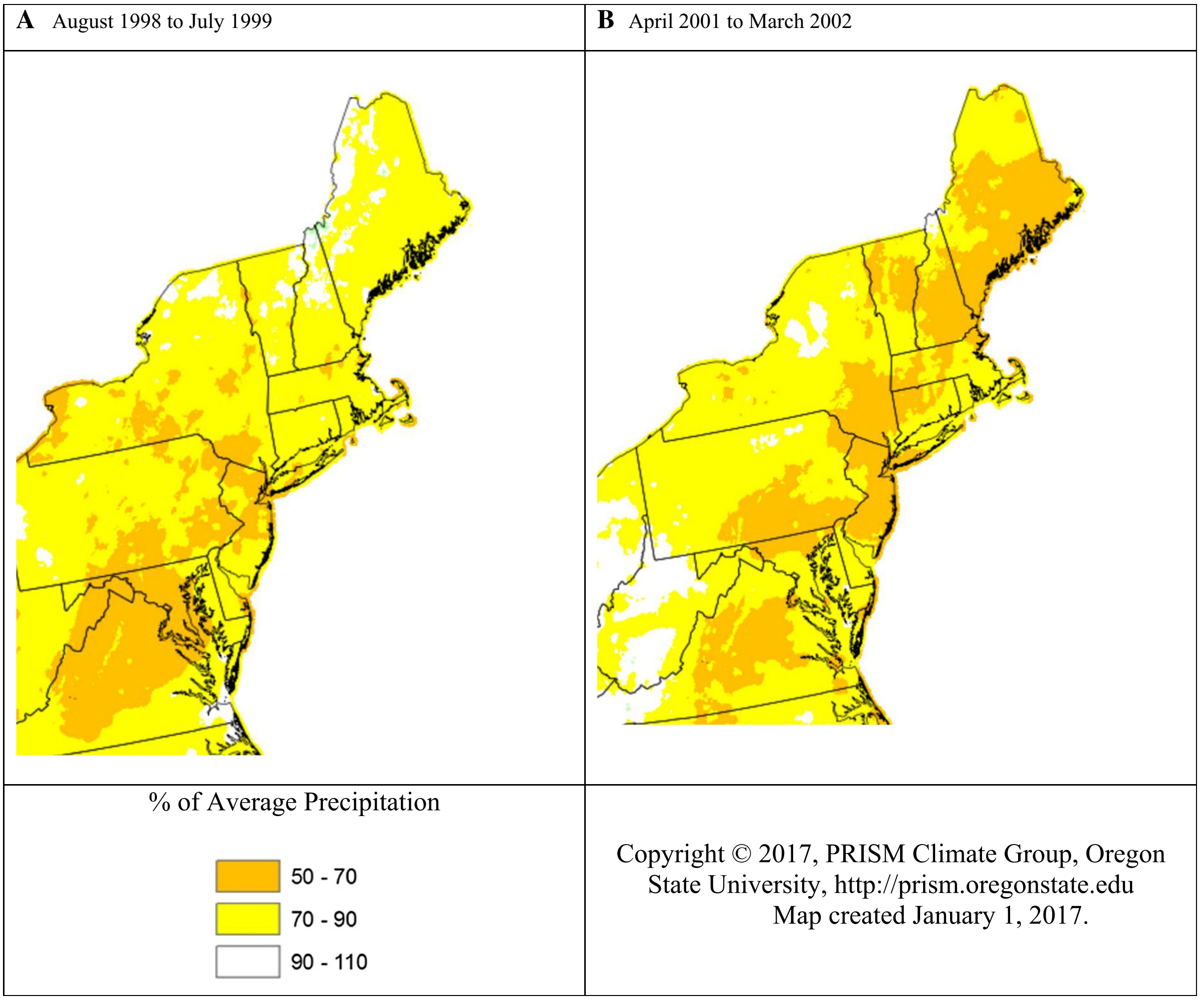

Fig. 4 Drought periods in the northeastern United States from 1998 to 2002. The *map* shows percentage of average precipitation

(n = 21, $BAI_{decl} < 45\%$). This resulted in an average BAI_{decl} of 64% (±3.1) for high-BAI-reduction sites and 36% (±1.3) for low-BAI-reduction sites. The same median BAI_{decl} value was used to classify validation plots into high-BAI-reduction (n = 8) and low-BAI-reduction sites (n = 7).

On calibration sites the average length of growth decline periods was 6.1 years, with a minimum length of 3 years and a maximum of 12 years (Fig. 3). The average length of the decline period on validation sites was comparable at 6.6 years, with a minimum length of 4 years and a maximum length of 11 years.

Logit models

Logistic regression was used to identify site factors that distinguish between high- and low-BAI-reduction plots. Site variables including slope, winter and summer hillshade, normalized aspect, annual precipitation, average annual temperature, and January minimum temperature were considered for inclusion in the model. Stepwise logistic regression identified slope, hillshade (summer) and January minimum temperature as significant predictors at $\alpha = 0.10$ (Eq. 7, Table 2).

$$\textit{Probability of high-BA-reduction} = \frac{1}{1+e^{-(\beta_0+\beta_1[Slope]+\beta_2[FutureJanMinT]+\beta_3[HillshadeSum])}} \quad (7)$$

B_0 = intercept, B_1 *through* B_3 = regression coefficients of logit model parameters (Table 2).

Using model parameters, plots were classified as high-BAI-reduction (logit probability $\geq$0.5), or low-BAI-reduction (logit probability <0.5). The selected model correctly classified 14 of 20 high-BAI-reduction and 18 of 21 low-BAI-reduction calibration sites (Table 3a) for an overall accuracy of 78%. Most errors (six of the nine incorrectly predicted sites) were associated with plots on the margin of the high/low BAI reduction threshold, i.e., BAI_{decl} values were 40–50%.

Model parameters were then applied to the 15 validation sites. The model correctly predicted six of eight high-BAI-reduction and six of seven low-BAI-reduction sites (Table 3b), resulting in 80.00% classification accuracy, which further validated the model. Errors for validation sites were associated with a wider range of BAI_{decl} values; only one of three incorrectly predicted sites had BAI_{decl} values between 40 and 50%.

Our results suggest that sites with steeper slopes, brighter hillshade values, and warmer January minimum temperatures (Table 2) increase the likelihood of having a substantial BAI_{decl} (>45%; Table 3) following HWA infestation (see also Online Resource 1). This model should only be used for locations currently dominated by hemlock with site and stand characteristics similar to those used in the calibration data set.

Model simulation risk maps

Applying the resulting logit equation on a pixel by pixel basis to spatial coverages of slope, hillshade and historical temperature norms (Fig. 5,

Table 2 Logistic regression parameters and statistics based on data from 41 calibration sites to predict the probability of falling within the high-BAI-reduction class

Parameter	Coefficient	Robust standard error	Z-score	*p*-value
Intercept	−10.021	7.871	−1.273	0.203
Jan. min. temp.	0.764	0.297	2.572	0.010
Summer Hillshade	0.072	0.033	2.220	0.026
Slope	0.069	0.040	1.745	0.081

The cutoff between classes (high-BAI-reduction, low-BAI-reduction) was 0.5

Table 3 Cross tabulations of classified sites as high-BAI-reduction (BAI_{decl} > 45%) or low-BAI-reduction (BAI_{decl} < 45%)

	Actual class	
	Low-BAI-reduction	High-BAI-reduction
A Cross tabulation of calibration sites based on BAI_{decl} and logit model. Overall accuracy = 78.05%		
Predicted class		
Low-BAI-reduction	18	6
High-BAI-reduction	3	14
% Correct	85.71%	70.00%
B Cross tabulation of validation sites based on BAI_{decl} and logit model. Overall accuracy = 80.00%		
Predicted class		
Low-BAI-reduction	6	2
High-BAI-reduction	1	6
% Correct	85.71%	75.00%

Significant logistic regression model parameters (average slope, summer hillshade, and January minimum temperature; Table 2) were used to assign sites into the two classes (cutoff = 0.50)

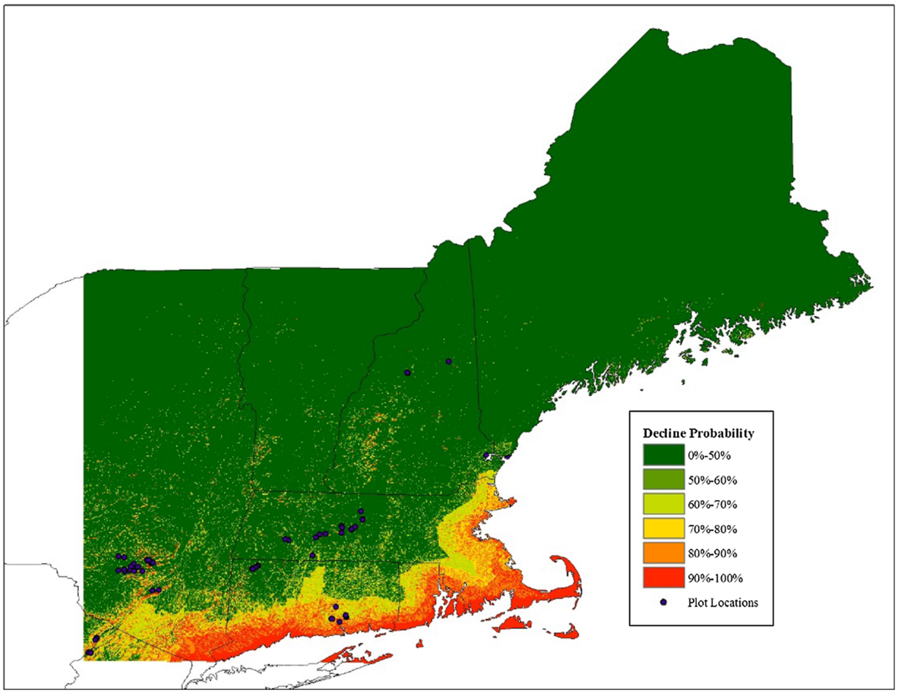

Fig. 5 Historical climate risk *map* shows probable locations of declining sites ($BAI_{decl} > 45\%$) using logit coefficients (Table 2) applied to three parameters across the New England region: *1* slope, *2* summer hillshade, and *3* 1971–2000 January minimum temperature. A *color* gradient indicates the probability quartile (0–50, 50–60, 60–70, 70–80, 80–90, 90–100%) that a given location has site conditions favoring hemlock growth decline post-HWA infestation

1971–2000) show a concentration of high-BAI-decline risk locations primarily in southern New England (4,504,192 hectares, or 17.4% of the region). Replacing historical January minimum temperatures with current norms (Fig. 6, 1981–2010), the total high-BAI-decline risk area increases to 6,826,752 hectares (26.4% of the region), including almost all of Connecticut and Rhode Island as well as large swaths extending up through the Catskills, NY. Using a projected 2 °C increase in minimum January temperatures (Fig. 7), results in high-BAI-decline risk areas across the entirety of southern New England, along with the coast of Maine and large swaths of New Hampshire and Vermont (total area = 11,101,568 hectares, or 43.0% of the region; Table 4).

BAI_{decl} relationship to crown damage, HWA infestations, and drought

BAI_{decl} was significantly ($p < 0.01$) correlated with CDR ($r^2 = 0.732$; Fig. 5), and HWA infestation levels ($r^2 = 0.612$; Fig. 8). This indicates that BAI_{decl} is quantitatively linked to visible hemlock decline and stress associated with HWA infestation. Average CDR values were 5.6 (±0.2) for high-BAI-reduction sites and 4.3 (±0.1) for low-BAI-reduction sites. HWA infestation levels averaged 34% (±4.6) for high-BAI-reduction sites and 7.2% (±3.0) for low-BAI-reduction sites.

The relationships between BAI_{decl} decline periods and the timing of HWA infestation are shown in Fig. 3 (see also Online Resource 3). Documented HWA infestations typically preceded the median year of the of a decline period for high-BAI-reduction plots (14 of 20), but not for low-BAI-reduction plots (6 of 21, $X^2 = 7.04$, $p < 0.01$) (Fig. 3). This is not surprising considering that HWA is typically only documented in locations where visual hemlock canopy decline is apparent. It is likely that low-BAI reduction sites maintained low-level infestations for significant periods of time.

The 1998–1999 drought occurred prior to the decline median year in 12 of 20 high-BAI-reduction calibration plots and 11 of 21 low-BAI-reduction calibration plots ($X^2 = 0.241$, $p = 0.357$, Fig. 3). In contrast, the 1998–1999 drought occurred prior to the decline median year in 8 of 8 high-BAI-reduction sites and 3 of 7 low-BIA-reduction sites on the validation plots ($X^2 = 6.234$, $p < 0.01$, Fig. 3). Because of the low expected frequency (<5) in the validation plots 2 × 2 contingency table, Fisher's exact test probability was used, showing a significant association between BAI-decline levels and stress timing ($p = 0.0256$).

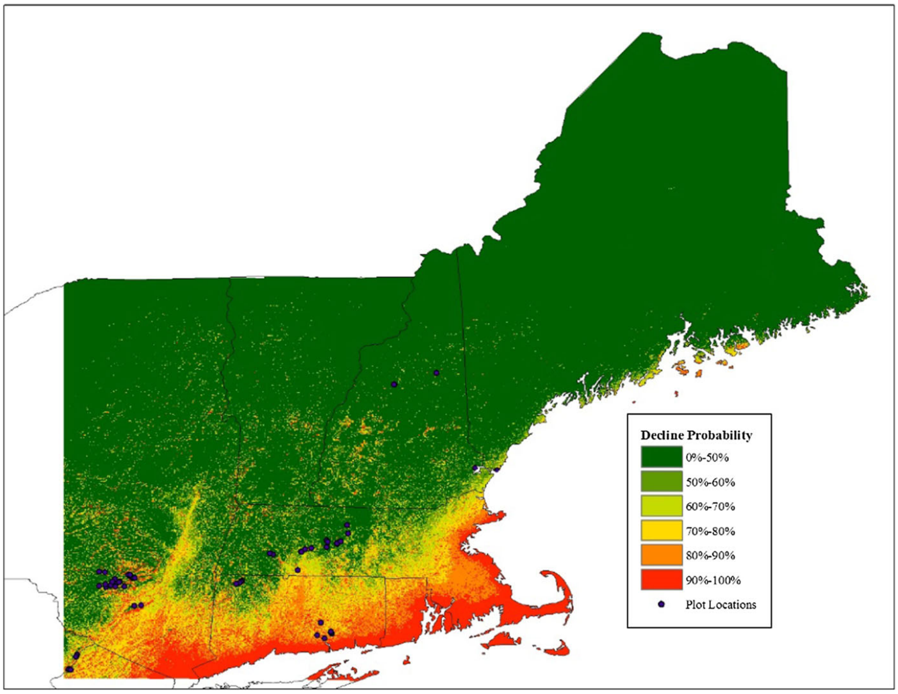

Fig. 6 Present climate risk *map* shows probable locations of declining sites ($BAI_{decl} > 45\%$) using logit coefficients (Table 2) applied to three parameters across the New England region: *1* slope, *2* summer hillshade, and *3* 1981–2010 January minimum temperature. A *color* gradient indicates the probability quartile (0–50, 50–60, 60–70, 70–80, 80–90, 90–100%) that a given location has site conditions favoring hemlock growth decline post-HWA infestation

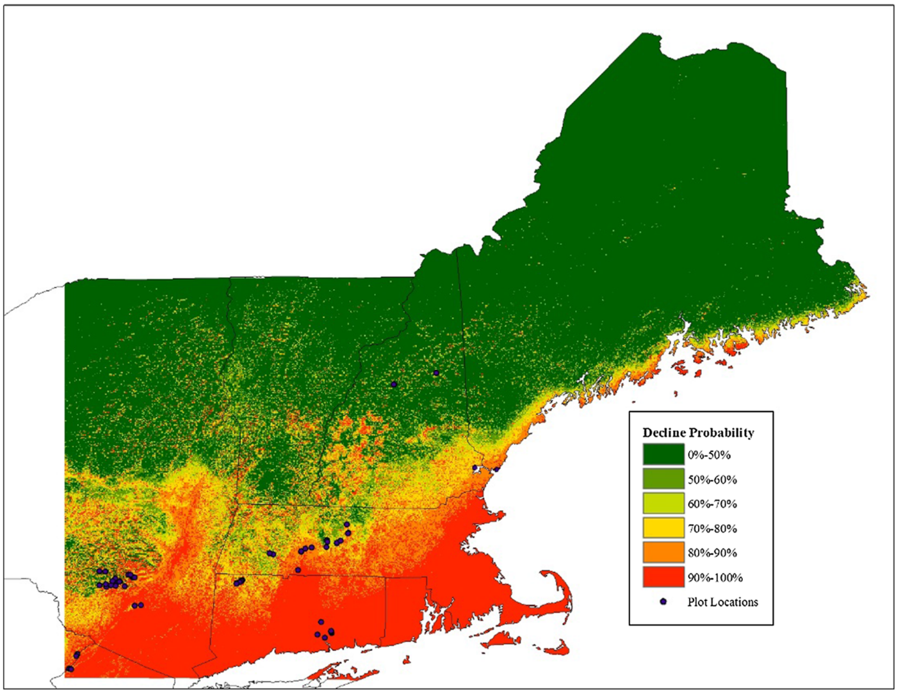

Fig. 7 Future climate risk *map* shows probable locations of declining sites ($BAI_{decl} > 45\%$) using logit coefficients (Table 2) applied to three parameters across the New England region: *1* slope, *2* summer hillshade, and *3* 1981–2010 January minimum temperature normals +2 °C. A *color* gradient indicates the probability quartile (0–50, 50–60, 60–70, 70–80, 80–90, 90–100%) that a given location has site conditions favoring hemlock growth decline post-HWA infestation

Discussion

These results suggest that the proposed BAI_{decl} metric is associated with stress onset and can be used to quantify the relative response of hemlock to HWA infestation and drought events. Rentch et al. (2009) also found that LCR, crown density, foliar transparency and crown dieback were relatively accurate

Table 4 Hemlock growth decline risk, per hectare, according to past (1971–2000), present (1981–2010), and future (1981–2010 +2 °C) climatic conditions

Probability of growth decline	Hectares affected 1971–2000	Hectares affected 1981–2010	Hectares affected 1981–2010 +2 °C
0–50%	21,335,296	19,012,736	14,737,920
50–60%	549,376	1,050,624	1,165,632
60–70%	835,840	1,028,736	1,240,640
70–80%	638,912	1,185,088	1,489,024
80–90%	828,992	1,254,784	2,056,576
90–100%	1,651,072	2,307,520	5,149,696
Total hectares	25,839,488	25,839,488	25,839,488

Six probability uartiles (0–50, 50–60, 60–70, 70–80, 80–90, 90–100%) demonstrate the likelihood that a given location has site conditions favoring high hemlock growth decline post-HWA infestation

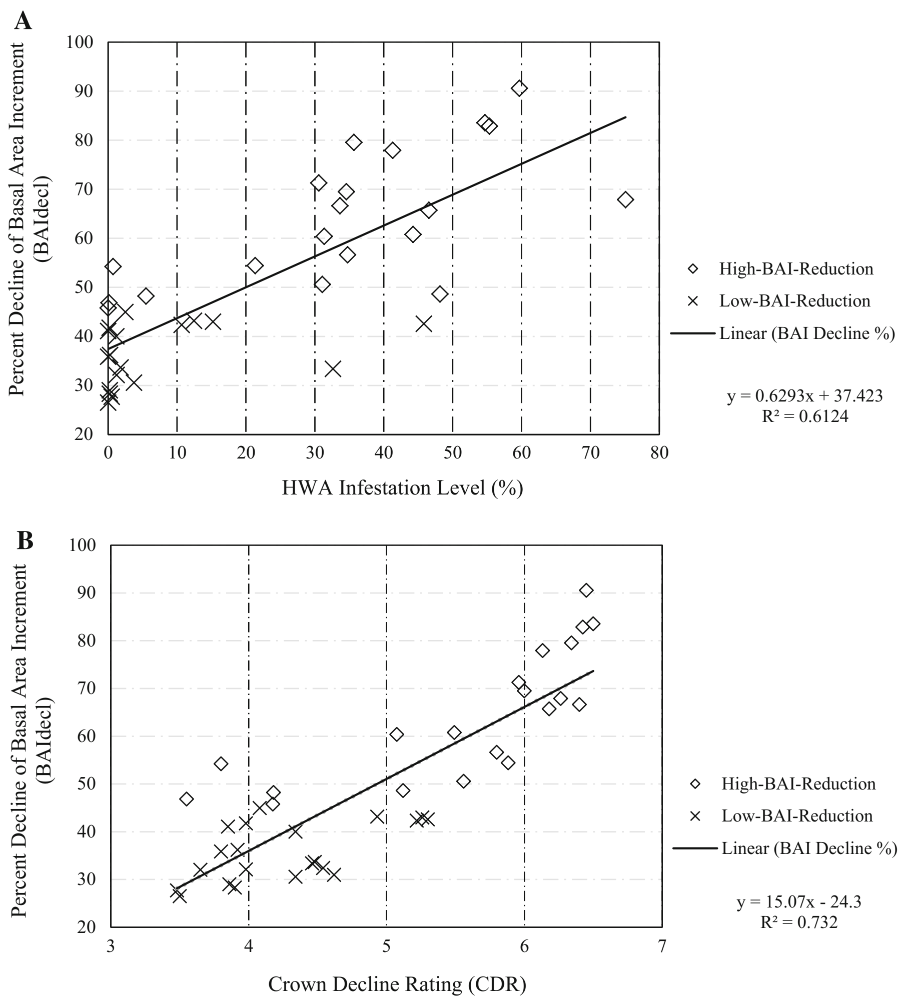

Fig. 8 Comparison of BAI_{decl} with **a** HWA infestation levels and **b** CDR. *Solid lines* indicate regression results; **a** $r^2 = 0.6124$ and **b** $r^2 = 0.732$. High-BAI-reduction sites are those with $BAI_{decl} > 45\%$, the median value for calibration sites

predictors of hemlock growth decline. The CDR metric used in this study incorporated both foliar transparency and LCR, which can be used as early to mid-range predictors of tree stress (Pontius and Hallett 2014).

Similar to our results, others have also reported that HWA infestations result in variable rates of crown and growth decline and that HWA is not the only driver adversely affecting hemlock health in the region. In 48 HWA-infested stands that Orwig et al. (2012) sampled in Massachusetts, two stands exhibited >50% hemlock mortality, one stand exhibited >30% mortality, and the remaining 45 stands <30% mortality. However, only eight of those 48 stands had high densities of HWA. Evans et al. (2011) sampled 49 stands from Maine to Alabama, of which 25 were infested with HWA as of 2008. They defined hemlock decline as the percent dieback of the tree's crown. Across all 49 stands, an average of 37% of the total hemlock basal area experienced moderate decline (>25% dieback) or greater, but only 13 of those stands reported moderate decline or greater for 75% of the hemlock basal area. Their more severely affected stands were located in the mid-Atlantic and southeastern United States, where warmer winter temperatures are less likely to control HWA populations.

Eschtruth et al. (2013) found that the length of time a tree was exposed to HWA infestation, warmer winter temperatures prior to mortality, and water deficits in the current year were the most significant factors affecting hemlock mortality. These findings support our empirical model with warmer winter temperatures and hillshade as a proxy for moisture stress as the likely drivers influencing hemlock growth decline and mortality.

Our study also demonstrated that BAI_{decl} is a useful metric to identify which sites are most adversely affected by HWA infestations. Across validation plots, high-BAI-reduction sites ($BAI_{decl} > 45\%$, average = 64%) consistently demonstrated incipient HWA infestations prior to the median year of the identified decline period in 14 of 20 locations. Similarly, high-BAI reduction plots had significantly higher HWA infestations levels. The mean percent infestation on these high-BAI-reduction plots was 34%, with 18 of 20 with infestation levels of 20% or more. This indicates that HWA levels >20% can consistently increase BAI_{decl} values to above 45%. If, however, HWA levels are maintained below 20%, resulting declines in radial growth of hemlock is less severe ($BAI_{decl} < 45\%$).

The onset of drought was only associated with the onset of BAI_{decl} in high-BAI-reduction validation plots (Figs. 3, 4). It is not clear why the relationship was not also apparent for high-BAI-reduction calibration plots. It is possible that the drought of 1998–1999 and 2001–2002 was more severe in the location of the validation plots, whereas the large geographical range of the calibration plots encompasses a wider range of drought conditions.

Our study is not the first to investigate hemlock vulnerability and response to HWA infestation patterns using dendrochronology (DeMaio 2008; Rentch et al. 2009; Walker 2012). However, our growth decline metric using a moving 3-year average of annual basal area increment growth represents a novel approach for evaluating growth declines related to HWA or other environmental stressors. Walker (2012) studied the change in mean RW pre- and post-HWA infestation, however his approach did not account for changes in RW due to increased tree diameter or incorporate the influence of other growth related factors. In contrast, Rentch et al. (2009) used a mean standardized ring-width index (RWI) to evaluate hemlock growth. While RWI is often used in dendrochronological studies, it can mask growth trends of individual trees (Johnson and Abrams 2009). These individual trends can be seen in BAI curves (Johnson and Abrams 2009), which we used to evaluate hemlock growth decline. The yearly D-score we developed also allowed us to estimate when hemlock growth decline began, how long it persisted, and whether or not it coincided with periods of known HWA infestation.

Once we had identified sites with declining hemlock growth, we could analyze which site variables best predict growth declines. When using crown conditions associated with HWA infestations instead of hemlock growth decline, Pontius et al. (2010) found slope and aspect accounted for 35% of the variability in their hemlock decline model, capturing similar landscape characteristics as those selected in our BAI-based model. While Pontius et al. did not include climate metrics, Eschtruth et al. (2013) found average January minimum temperatures to be a good predictor of hemlock survival post-HWA infestation. The three significant predictor variables identified by our analyses (slope, summer hillshade, and January minimum temperatures) support these previous studies and have clear biological explanations relating them to declining hemlock growth.

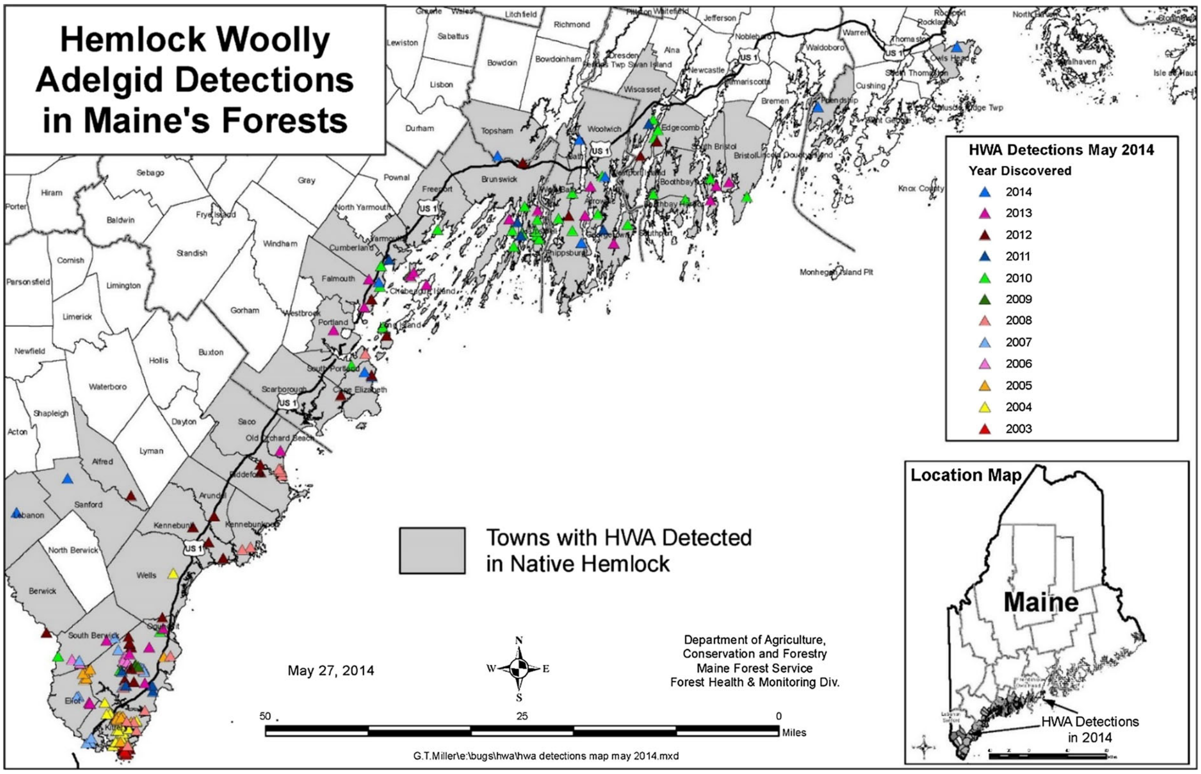

Fig. 9 Maine Forest Service *map* depicting towns with current (as of May 2014) HWA infestations

Low January minimum temperatures result in high HWA mortality and reduced HWA populations, thus restricting impact and spread. Further, average January minimum temperature (−11 °C) on our 15 validation plots was similar to another 123 sites Orwig et al. (2012) sampled in central Massachusetts. Many studies support the observation that HWA populations are limited by extreme winter temperatures (Parker et al. 1998, 1999; Skinner et al. 2003; Shields and Cheah 2004; Costa et al. 2008; Orwig et al. 2012).

Slope and hillshade affect site moisture levels and are commonly used as drought stress indicators. Sites on steeper slopes have increased soil drainage, and sites with greater hillshade values receive greater solar radiation, which increases evapotranspiration. Trees stressed by such exposure may be at higher risk of HWA damage (McClure 1998; Sivaramakrishnan and Berlyn 2000; Rentch et al. 2009).

Using slope, hillshade, and January minimum temperatures, all shown to be significant predictors of hemlock growth declines, we produced spatially-explicit risk maps using historical, current, and projected temperature data (Figs. 5, 6, 7) to highlight probable hemlock decline regions under each climate scenario. To further evaluate the validity of this product, a 2014 map of current HWA infestations in Maine (Fig. 9) was compared to the current risk map. The first observed HWA infestation in southern ME was documented in 2003. Since then, there has been substantial time for HWA to spread and impact hemlock stands across southern ME based on historical rates of spread (McClure 1995; Morin et al. 2009). However, the infestations documented by the Maine Forest Service since 2003 have been restricted only to those areas mapped here as high-BAI-reduction sites. While it is possible that HWA infestations do occur in other locations, it is likely that these have not been mapped because they have not impacted hemlock in those regions, warranting field visits. This provides some independent validation of the model's utility in identifying locations that may experience decline near the HWA infestation front. Continued monitoring of hemlock in the state will indicate if damaging HWA infestations are restricted to the predicted area or if more time will allow HWA to develop to damaging levels outside of the current predicted area of high risk.

Changing temperatures could be a factor allowing HWA to develop damaging infestations outside of the current predicted area of high risk. According to the historical climate risk map (1971–2000 January minimum temperature; Fig. 5), high risk areas of hemlock growth decline (>70% likelihood) were limited to New York's east coast, the southern half of Connecticut, Rhode Island, eastern Massachusetts, and coastal New Hampshire. The current risk map (1981–2010 January minimum temperature; Fig. 6) showed an increase in high risk areas including New York's Hudson River Valley, the northern half of Connecticut, and more of New Hampshire and Maine's coastal regions. But most significantly, the future climate risk map (1981–2010 January minimum temperature +2 °C; Fig. 7) indicated a drastic increase in risk of hemlock growth decline, particularly moving into northern New York, Vermont, New Hampshire, and further inland in Maine. More precisely, high-BAI-reduction risk areas increased from 3.1 million hectares (past), to 4.7 million hectares (present), to 8.7 million hectares (future). If temperatures continue to increase, the future climate risk map demonstrates that hemlock growth decline will become increasingly likely across a majority of New England.

Conclusion

The dendrochronology-based growth decline metric we developed (BAI_{decl}) is a sensitive metric that can be used to quantify hemlock damage, identify periods of growth decline, and identify likely stress agents involved with decline, such as incipient HWA infestation or drought. Using this growth decline metric, we determined that sites with steeper slopes, increased exposure to solar radiation, and warmer January minimum temperatures have a greater probability of experiencing rapid hemlock growth decline in the study region.

Applying our findings to a spatially-explicit predictive model of probable high-BAI-reduction hemlock stands revealed that hemlock stands in southern New England, along the coast, and on the steep slopes of mountainous regions have a higher probability of exhibiting rapid and severe HWA-induced decline characteristics. Land managers can use these maps to help prioritize management strategies for addressing locations where hemlock is likely to decline in growth, as well as identifying locations where hemlock is likely to tolerate HWA infestations. However, the projected increase in January minimum temperatures will result in HWA-incited hemlock growth decline further north and inland than was previously predicted.

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