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# Increased water yield due to the hemlock woolly adelgid infestation in New England

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**Key Points:**
- In New England, eastern hemlocks have experienced significant foliar loss due to hemlock woolly adelgid (HWA) infestation
- Evapotranspiration flux over a hemlock-dominated forest has significantly decreased
- Water yield has increased due to the infestation, more in the catchment with a higher hemlock cover

**Supporting Information:**
- Supporting Information S1

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**Abstract** Over the past few decades, a hemlock woolly adelgid (HWA) infestation has significantly affected eastern hemlock (*Tsuga canadensis*) in the eastern U.S., and warmer winters are expected to promote a continued northward expansion in the future. Here we report a water yield increase due to the HWA infestation in New England, U.S. Since the first observation in 2002, peak growing season evapotranspiration over a hemlock-dominated area has decreased by 24–37% in 2012 and 2013. Over the same time period, the water yield from the study catchment significantly increased as compared to an adjacent catchment with less hemlock cover. The net increase was estimated to be as much as 15.6% of annual water yield in 2014 based on an ecohydrological modeling analysis. This study indicates that the ongoing hemlock decline is also largely altering hydrological regimes in the northeastern U.S.

## 1. Introduction

Since first documented in Virginia in 1951 [*Stoetzel*, 2002], hemlock woolly adelgid (HWA, *Adelges tsugae*) has infested about half of the eastern hemlock forests in the northeastern U.S. [*Havill et al.*, 2014]. Eastern hemlock, a so-called "*foundation species*" [*Ellison et al.*, 2005], is one of the dominant coniferous species in riparian areas in the region [*Orwig et al.*, 2008; *Webster et al.*, 2012], and its dense canopy creates cool and moist subcanopy microclimates. Therefore, it has been suggested that loss of eastern hemlock and the subsequent replacement by deciduous hardwood species, such as black birch (*Betula lenta*) and red oak (*Quercus rubra*) [*Orwig and Foster*, 1998; *Orwig et al.*, 2012], will have huge implications for carbon, water, and nutrient cycles across different spatial scales [*Daley et al.*, 2007; *Hadley et al.*, 2008; *Guswa and Spence*, 2012; *Brantley et al.*, 2013]. For example, gradual decreases of transpiration and interception are the direct and foremost impacts on the hydrologic cycle as infested hemlocks lose their foliage [*Domec et al.*, 2013]. More open canopies change subcanopy microclimate conditions (such as increases in throughfall, sunlight, and air turbulence on ground surfaces [*Stadler et al.*, 2005; *Siderhurst et al.*, 2010]), which may promote understory evapotranspiration that partially mitigates the effect of reduced transpiration [*Royer et al.*, 2011; *Adams et al.*, 2012; *Anderegg et al.*, 2012; *Bearup et al.*, 2014]. Defoliation of hemlock also alters nutrient stocks and fluxes (due to larger inputs of litterfall and woody debris [*Webster et al.*, 2012] and elevated mineralization and nitrification rates [*Jenkins et al.*, 1999]), leading to increased nitrogen inputs to streams [*Cessna and Nielsen*, 2012] and cascading impacts on downstream water quality.

Shifts in the large-scale hydrologic cycles highly depend on the infestation and the following regeneration patterns over forested landscapes, which may add substantial uncertainty to the prediction of hydrologic responses over the course of an infestation [*Adams et al.*, 2012; *Anderegg et al.*, 2012; *Mikkelson et al.*, 2013; *Bearup et al.*, 2014]. However, most studies thus far have examined the changes in plot-scale hydrologic fluxes (e.g., throughfall, transpiration, and soil moisture) between pre-HWA and post-HWA infestation forests at the tree and plot scales [*Stadler et al.*, 2005; *Daley et al.*, 2007; *Hadley et al.*, 2008; *Guswa and Spence*, 2012; *Domec et al.*, 2013]. Fewer studies have analyzed the transient effect of gradual hemlock declines on catchment-scale water yield, together with the plot-scale changes [*Vose et al.*, 2013].

Understanding the effect of the ongoing HWA infestation on catchment-scale water balances is important in the northeastern U.S., where the main water supply relies on surface water from forested catchments

[*Barnes et al.*, 2009]. *Brantley et al.* [2014] reported that hemlock mortality did not result in water yield increases in a headwater catchment with a low hemlock cover (~6% watershed basal area) in the southern Appalachian Mountains. However, the HWA-induced hemlock decline may well result in considerably different hydrological consequences in this northern region where the forests have higher densities of eastern hemlock than occur in the southern Appalachian Mountains [*Roberts et al.*, 2009; *Albani et al.*, 2010; *Fitzpatrick et al.*, 2012; *Brantley et al.*, 2014] (Figure S1a in the supporting information). The objective of this study is to assess the effect of the ongoing HWA infestation on hydrologic fluxes during the last decade at a mixed hemlock-hardwood catchment within the Harvard Forest Long-Term Ecological Research (LTER) site in central Massachusetts. We analyzed three different types of field data (tree monitoring, eddy-covariance flux, and stream discharge measurements). We incorporated the HWA-induced mortality into an ecohydrological model to estimate the net magnitude of the HWA-induced changes in water yield.

## 2. Materials and Methods

### 2.1. Study Site

The study site includes two adjacent headwater catchments, the Bigelow-Brook catchment (BBC) and the Nelson-Brook catchment (NBC), within the Harvard Forest Long-Term Ecological Research (LTER) site (Figure S1b). The forest has a cool and moist temperate climate with an annual mean temperature of 8.5°C, varying from 20°C in July to −7°C in January. Mean annual precipitation is approximately 1100 mm, 25% of which falls as snow, evenly distributed throughout the year (http://harvardforest.fas.harvard.edu/). Dominant tree species are northern red oak (*Quercus rubra*), red maple (*Acer rubrum*), eastern hemlock (*Tsuga canadensis*), black birch (*Betula lenta*), and white pine (*Pinus strobus*). The two study catchments are comparable in sizes (65.9 ha BBC and 40.5 ha NBC), elevations (340–410 m and 350–390 m above sea level in BBC and NBC, respectively), and soil types (mostly well-drained sandy-loam with about 3 m depth formed from the gneiss and schist bedrock [*National Resources Conservation Service (NRCS)*, 2009]). They differ greatly, however, in the areal proportion dominated by hemlock (defined as >50% overstory cover [*Orwig et al.*, 2012]) with a proportion of 41.1% in the BBC and 18.7% in the NBC. HWA was first observed at the Harvard Forest in 2002 (Orwig pers. observ.) and had infested 1% of hemlock trees examined in 2004 within the study catchments ($n = 400$) [*Barszcz*, 2004].

### 2.2. HWA Infestation Monitoring

Foliar loss condition and mortality (alive or dead) of all trees greater than or equal to 5 cm diameter breast high (DBH) were visually determined in 1999, 2009, and 2014 after peak growing season each year within the long-term hemlock-monitoring plot (Figure S1b; $n = 499$) (Harvard Forest data archive ID-HF031). The amount of foliar loss was categorized into five vigor indices with one referring to 0–25% foliar loss, 2 to 26–50%, 3 to 51–75%, 4 to 76–99%, and 5 to a dead hemlock. We calculated the mean and standard deviation of the vigor indices for each tree size class (interval at every 15 cm DBH) to examine the differences in the effects of the infestation depending on tree size. The HWA infestation status (presence or absence of HWA on two branches) was recorded for hemlock trees within the long-term hemlock-monitoring plot in 2009 ($n = 49$) and in 2014 ($n = 41$) (ID-HF031). We used the trees examined in both 2009 and 2014 to evaluate the changes in HWA infestation status ($n = 29$).

### 2.3. Evapotranspiration Flux and Water Yield Change Data Analysis

Half-hourly evapotranspiration (ET) has been measured at a flux tower within Harvard Forest since June 2004 (Figure S1b; Ameriflux site: US-Ha2; ID-HF103; data through July 2014 were used in this study). We removed the data from rainy days and also from the day after a rainy day to prevent any unpredictable bias resulting from rainfall [*Loescher et al.*, 2005]. We analyzed the data only from the 190–240° wind directions where about 83% of the basal area is composed of eastern hemlock [*Daley et al.*, 2007]. In this study, we define "daytime" between 11:00 A.M. and 3:30 P.M. each day and "peak growing season" as day of year between 170 and 250 (more description is available in Figure S2). After filtering, the average data coverage is 12% during the peak growing season.

The change in the ET flux over time was examined in two different ways, a mean-variance analysis and a non-linear ET response model. First, we calculated the daily mean values of the daytime ET data ($ET_{daytime}$). We performed the Kruskal-Wallis test followed by the Tukey-Kramer test to determine the years when the peak growing season $ET_{daytime}$ was statistically different. ET data in 2014 were not included in the analysis because of its limited availability for the entire peak growing season (as of September 2016). Second, we examined whether the changes in the ET data were driven by climatic variability. It has been reported that photosynthetically active radiation (PAR) and vapor pressure deficit (VPD) exert the primary controls on eastern hemlock ET during the peak growing season in this study site [*Hadley et al.*, 2008]. We assessed the ET response to PAR and VPD, respectively (Figure S3), during the peak growing seasons over the calibration period (2004–2007), and selected the best response for each variable based on two measures (mean square error and coefficients of determination, $R^2$). We developed a Jarvis-type multiplicative model by multiplying the best responses so that the model can represent the simultaneous nonlinear effects of both PAR and VPD on ET [*Granier and Loustau*, 1994]. We calibrated the model coefficients during the peak growing seasons over the calibration period and applied the calibrated model to the individual years from 2008 to 2013. The agreement between the measured and modeled ET was examined each year by using the reduced-major axis regression.

We performed a paired catchment analysis by using monthly stream discharge data from BBC and NBC (ID-HF070). We used NBC (the less hemlock-dominated catchment) as the reference catchment to estimate the changes in the BBC stream discharge (target catchment) based on the regression relationship between the stream discharge of the two catchments in the period before the HWA infestation significantly changed the ET flux. We applied ordinary least squares regression between the two discharge data in the period before the ET flux showed a significant decrease. Following *Watson et al.* [2001], we analyzed heteroscedasticity, seasonality, autocorrelation, and normality in the regression model (Figure S4). After removing a lag-1 autoregressive component (AR1), we calculated the 95% prediction intervals from the AR1-removed residuals. We considered the residuals exceeding the 95% prediction intervals as significant deviations [*Lane and Mackay*, 2001; *Watson et al.*, 2001; *Brown et al.*, 2013]. Annual water yield deviations were calculated by summing the monthly deviations on a vegetation year basis. Vegetation year represents the period from the beginning of the growing season to the end of the following dormant season (from 1 May to 30 April of the following year) [*Troch et al.*, 2009], which effectively minimizes the effect of soil water storage changes for an annual-scale mass balance analysis [*Patric and Reinhart*, 1971; *Hwang et al.*, 2014; *Kelly et al.*, 2016].

### 2.4. Ecohydrological Model Simulation

We applied a mechanistic ecohydrological model (Regional Hydro-Ecologic Simulation System, RHESSys [*Tague and Band*, 2004]) to assess the magnitude of net changes in water yield due to the infestation. The model couples plot-scale ecosystem processes with watershed-scale surface and subsurface flows within a spatially distributed modeling framework. We estimated the HWA impact on canopy conductance ($f_{HWA}$) from the mean of peak growing season daytime ET. We incorporated this function as an additional multiplicative form when calculating canopy conductance by using a Jarvis equation in the model. A detailed description of incorporating HWA into RHESSys is provided in Text S1 in the supporting information [*Somers et al.*, 1980; *Sperry et al.*, 1998; *The MathWorks*, 2000; *Hwang et al.*, 2009; *Domec et al.*, 2013; *McDowell et al.*, 2013]. The growth of understory vegetation was not implemented in the model as the black birch was not yet sufficiently established for the simulation period. We calibrated and validated hydrological parameters in the model with monthly stream discharge and further validated the model with field-measured leaf area index (LAI) values. A detailed description of the calibration and validation is provided in Text S2 [*Beven and Binley*, 1992; *Davidson and Savage*, 1999; *Munger and Wofsy*, 1999; *White et al.*, 2000; *Cohen et al.*, 2006; *Dingman*, 2009; *NRCS*, 2009]. We then assessed the net changes in water yield due to the infestation by comparing the simulated results with and without the prescribed canopy conductance function $f_{HWA}$.

## 3. Results

### 3.1. HWA Infestation Progress

In the long-term hemlock-monitoring plot, HWA was found on 17.2% and 96.5% of the sampled hemlock trees in 2009 and 2014, respectively. Saplings and pole trees (DBH $<$ 30 cm) had lost more than 50% of their foliage by 2009 (vigor index of 2.08 and 1.48, respectively), significantly higher than the preinfestation foliar loss (vigor index of 1.28 and 1.06 in 1999) (Table S2 and Figure S7a in the supporting information). Defoliation

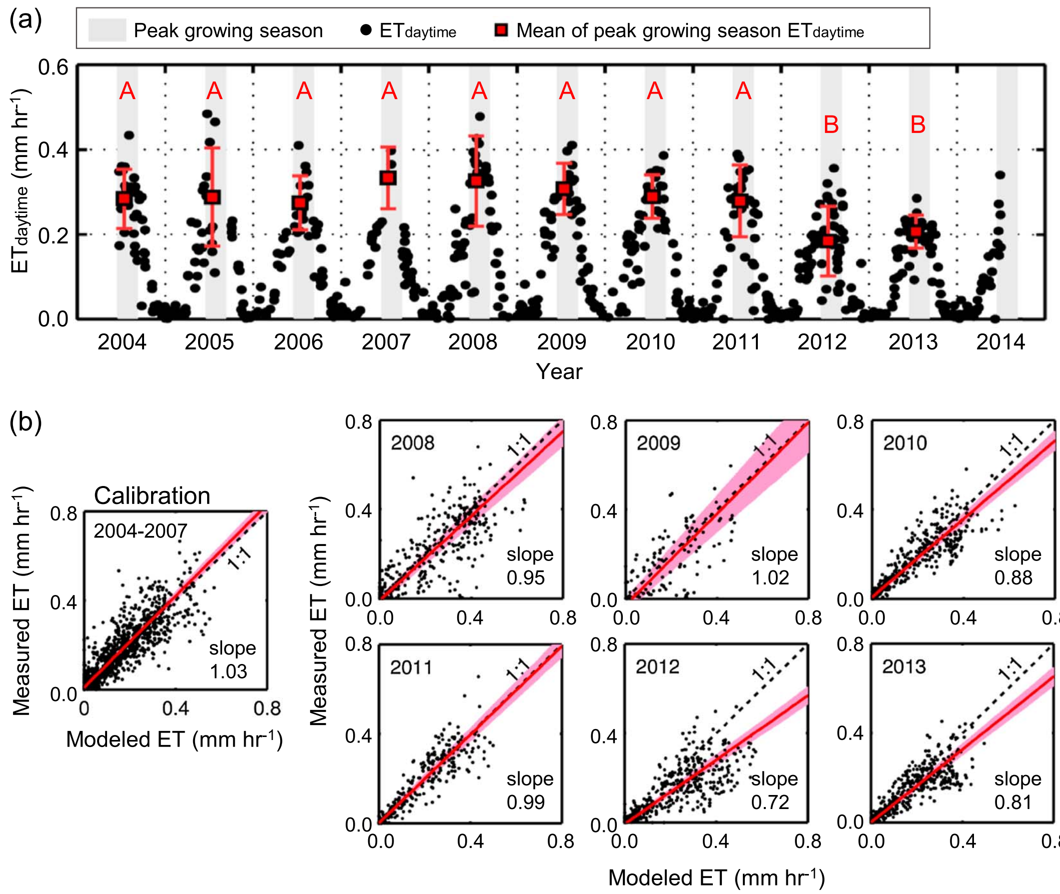


**Figure 1.** Changes in the evapotranspiration (ET) flux. (a) The mean daytime (11:00–15:30 local time) ET flux ($ET_{daytime}$; black dots) of the hemlock-dominated area (190–240° wind directions) and the mean and standard deviations during peak growing season (170–250 day of year; red squares and vertical bars, respectively). The different superscript letters indicate statistical differences at 5% significance level (Kruskal-Wallis test followed by Tukey-Kramer test). (b) Peak growing season ET data and the modeled ET using the Jarvis-type multiplicative model of PAR and VPD data during the calibration period (early infestation period: 2004–2007) and in each following year. The regression fits (red solid lines) and 95% confidence intervals (pink-shaded areas) were calculated by using the reduced major axis (RMA) regression. Regression model results are summarized in Table S4.

of the large trees (DBH > 30 cm) was not noticeable in 2009 (vigor index between 1.0 and 1.14), but it became more prevalent in 2014, with about 50% foliage loss on average (vigor index between 1.65 and 2.0). However, there was no significant increase in overall mortality among the sampled trees over the course of foliage loss between 2009 and 2014 as compared to the period between 1999 and 2009 (about ~8% per year; Figure S7b).

### 3.2. ET Flux and Water Yield Changes

Significant changes in the peak growing season daytime ET flux ($ET_{daytime}$) of the hemlock-dominated area began in 2012 ($p < 0.05$; Figure 1a). $ET_{daytime}$ was $0.29 \pm 0.08$ mm h$^{-1}$ before the change (therefore between 2004 and 2011), then had significantly declined by 37% in 2012 ($0.19 \pm 0.09$ mm h$^{-1}$) and by 24% in 2013 ($0.22 \pm 0.04$ mm h$^{-1}$). With the calibrated Jarvis-type multiplicative model, the two climatic variables (PAR and VPD) accounted for 73% of the variation in the peak growing season ET data during the early infestation period (2004–2007; slope = 1.03, $R^2 = 0.73$, $p < 0.01$; Figure 1b and Table S4). The modeled ET showed fairly good agreements with the measured ET each year until 2011 (slope = 0.88–1.02 and mean slope of 0.96; $R^2 = 0.63$–$0.82$ and $R^2 = 0.49$ in 2009 when data coverage was less than 10%). However, without any noticeable decline in the coefficient of determination metrics, the modeled ET consistently overestimated the ET by 28% in 2012 and 19% in 2013 (slope = 0.72 and 0.81 and $R^2 = 0.67$ and 0.73, in 2012 and 2013, respectively).

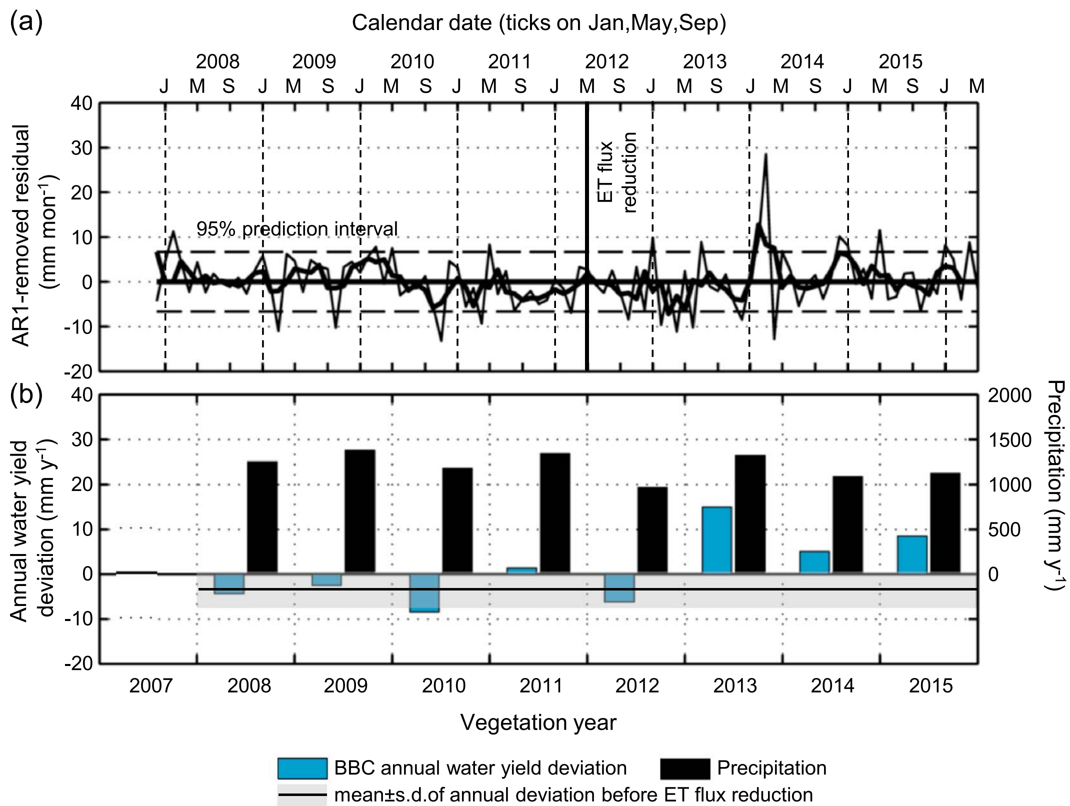


**Figure 2.** (a) Lag-1 autoregressive (AR1)-removed residuals of the monthly water yield (thin solid line) and 3 months averaged residuals for the overall trend (thick solid line) with 95% prediction intervals (dashed lines) and the timing when ET flux begun to decrease (2012 peak growing season; vertical solid line). (b) The deviation of the annual water yield (blue bars) and its variation before the ET flux reduction (the horizontal solid line for the mean value of annual deviations between vegetation years 2008 and 2011 and mean ± standard deviation in the gray-shaded area) and annual precipitation (black bars). Detailed numbers are summarized in Table S5.

Before the ET flux showed a significant reduction (from January 2008 through April 2012; $n = 52$), the monthly stream discharge from the two study catchments was highly correlated with each other ($r^2 = 0.98$, $p < 0.01$; Figure S4a). The residuals in the BBC monthly water yield did not show any noticeable seasonality (Figure 2a) or a correlation with monthly precipitation during the period ($p > 0.1$). Starting in 2013, however, there was a tendency for increasing positive and less negative residuals (Figure 2a). The BBC annual water yield was mostly lower than the modeled values before the ET flux reduction and in the following year (vegetation years 2008–2012; Figure 2b). However, the BBC annual water yield became larger than the prediction intervals after vegetation year 2013.

### 3.3. Simulation Results

The simulated leaf area index (LAI) gradually decreased with the HWA impact on canopy conductance ($f_{HWA}$), which agreed with the measured LAI (Figure 3a). The net impact of the HWA infestation on the simulated LAI was about 26% in 2014 summer, which is comparable with the visually monitored foliage loss (25–50%; Figure S7a). The change in the simulated monthly stream discharge due to $f_{HWA}$ is noticeable after 2013, especially higher increase in heavy rainfall events (Figure S8). The simulated monthly stream discharge corresponds to the measured discharge in BBC better with $f_{HWA}$ than without $f_{HWA}$ (Table 1). The annual water yield was underestimated more when simulated without $f_{HWA}$ (more negative percent bias; Figure 3b). Our results show that the HWA infestation has gradually reshaped the hydrologic budget of the infested catchment. The simulated ET of BBC with $f_{HWA}$ gradually decreased since 2010 (Figure 3c), while the simulated ET without $f_{HWA}$ was primarily driven by the water use of hardwood species (which is shown in the measured LAI pattern of hardwood species in Figure S9). The magnitude of the HWA impact on the BBC water yield can be seen clearly at the annual scale (on a vegetation year basis; Figure 3c). The net increases in the annual

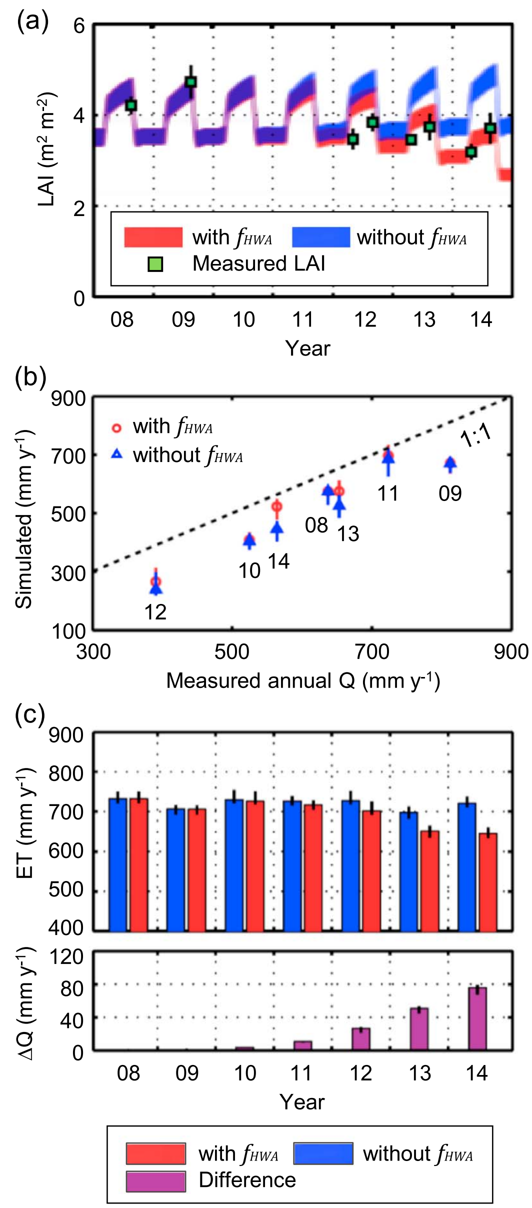


**Figure 3.** Model simulation results. (a) Leaf area index (LAI) measurements within the hemlock-dominated area (Figure S1b, mean value in square and one standard deviation bar) and LAI simulated with the HWA-impact on canopy conductance ($f_{HWA}$) (red-shaded area showing 95% confidence interval) and without $f_{HWA}$ (blue-shaded area). (b) Comparison between the measured annual water yield in the Bigelow-Brook catchment (BBC) from 2008 to 2014 and the simulated water yield with $f_{HWA}$ (red circle) and without $f_{HWA}$ (blue triangle). The symbol shows the median value of the accepted simulations (labeled with the year), and the vertical bar shows the 95% confidence intervals. (c, top) Simulated annual evapotranspiration (ET) flux with $f_{HWA}$ (red bar) and without $f_{HWA}$ (blue bar; the vertical bar shows the 95% confidence intervals). (bottom) The difference between the simulated annual water yield with $f_{HWA}$ and without $f_{HWA}$ (purple bar). The detailed numbers are summarized in Tables S6 and S7.

water yield due to $f_{HWA}$ have grown incrementally since 2010 to 76.5 mm in 2014 (15.6% increase from the simulated result without $f_{HWA}$).

## 4. Discussion

In this study, we analyzed the hydrological effects of the ongoing hemlock woolly adelgid (HWA) infestation, in central Massachusetts, U.S., using independent field measurements (tree monitoring, eddy-covariance flux, and stream discharge) and a mechanistic ecohydrological model. Our results show that the amount of decreased ET (by 24–37%) is comparable with the HWA-induced foliar loss (by 25–50%), and the ET reduction could not be accounted for by the interannual variability of climate forcings (PAR and VPD). A paired catchment analysis revealed the differing response in annual water yield along with the reduction in ET between the two catchments, indicating a higher water yield increase in the study catchment (BBC) associated with the larger area of infestation. Ecohydrological simulation with the prescribed HWA impact also agreed better with the measured stream discharge and leaf area index. The simulation results showed the net change of water yield as 15.6% in 2014 (76.5 mm increase as compared to the simulation without the HWA impact).

We noticed that the HWA infestation spread and the resulting effects have progressed more slowly in the study site than in more southern regions. While it took about 10–12 years for 50% foliar loss and 24–37% ET decreases to occur in the study site, it only took 6–7 years in Delaware to have 67.6–95.6% of infestation level [*Eschtruth et al.*, 2006] and only 4 years to have a 60% foliar loss and 45% reduction in summer transpiration in the southern Appalachian Mountains [*Domec et al.*, 2013]. This is likely due to the cold winter

**Table 1.** Improvements in Behavior Model Simulations of Monthly Stream Discharge With the HWA Impact on Canopy Conductance ($f_{HWA}$) (May 2010 to April 2015)[a]

| Simulation | NSE | $NSE_{log}$ | RSR | PBIAS |
|---|---|---|---|---|
| With $f_{HWA}$ | 0.73 | 0.65 | 0.52 | −13.25% |
| Without $f_{HWA}$ | 0.69 | 0.61 | 0.55 | −19.16% |

[a]The median values of four performance measures (NSE: Nash-Sutcliffe efficiency, $NSE_{log}$: Nash-Sutcliffe efficiency for log-streamflow, RSR: ratio of the root mean square error to the standard deviation of measured data, PBIAS: percent bias [*Moriasi et al.*, 2007]) show a better model performance (higher NSE and $NSE_{log}$ and lower RSR and PBIAS) with incorporating $f_{HWA}$. The total number of the behavioral model runs is 101 out of 3000 calibration runs.

temperatures in New England that restrain HWA survival and fecundity and therefore slow down the infestation as it spreads into more northern regions [*Paradis et al.*, 2008; *Fitzpatrick et al.*, 2012]. Therefore, the HWA-induced impacts on local hydrological cycles of the eastern hemlock forests in the northern U.S. would be promoted for the next few decades as warming winters are expected to continue in the future.

Our result is the first report of the water yield increase due to the ongoing HWA infestation in New England. Previous studies suggested that the infestation would result in a water yield decrease based on plot-scale measurements that only reflect either preinfestation or postinfestation states (i.e., hemlock- or hardwood-dominated forests) [*Daley et al.*, 2007; *Guswa and Spence*, 2012]. In this study, however, we show the transient increase in water yield during the early infestation stage by using both data and modeling analyses. Our results indicate that the catchment-scale hydrologic behavior is tightly coupled with the vegetation dynamics at the study site. Therefore, the growth rate and the water use of trees replacing hemlock will drive long-term and seasonal patterns of water yield over the course of the infestation in this region.

This study also presents a contrasting result with the report from the southern Appalachians, where the near-complete hemlock mortality led to decreases in water yield over several years [*Brantley et al.*, 2014]. This suggests that impacts of HWA infestation on hydrological cycles will vary depending on the regional factors, such as hemlock distributions, co-occurring understory species, and climatic conditions. Therefore, further research is needed to predict the infestation-associated changes in amount and timing of water yield across the wide range of conditions over the eastern U.S. Given the importance of surface water as a primary water resource in New England, it is critical to understand the implication of these ongoing hemlock declines and follow regeneration patterns on changes in forested-catchment water yield.

## 5. Conclusion

This study investigates the effect of the ongoing HWA infestation on evapotranspiration flux and water yield in the central region of Massachusetts, U.S. The peak growing season evapotranspiration over the hemlock-dominated area has significantly decreased by 24–37% from 2012 to 2013 with a 25–50% foliage loss caused by the infestation. A paired catchment analysis and ecohydrological modeling confirm that annual water yield has significantly changed in the meantime (15.6% of the net increase in 2014). Warmer winter temperatures are accelerating the northward spread of HWA into regions where eastern hemlock is even more abundant [*Albani et al.*, 2010]. This study, therefore, highlights the need to improve our understanding of the dynamics between the large-scale infestation and the hydrological cycles in New England, where local water supply systems are strongly dependent on surface water generation.

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## References

Adams, H. D., C. H. Luce, D. D. Breshears, C. D. Allen, M. Weiler, V. C. Hale, A. M. S. Smith, and T. E. Huxman (2012), Ecohydrological consequences of drought- and infestation- triggered tree die-off: insights and hypotheses, *Ecohydrology*, *5*(2), 145–159, doi:10.1002/eco.233.

Albani, M., P. R. Moorcroft, A. M. Ellison, D. A. Orwig, and D. R. Foster (2010), Predicting the impact of hemlock woolly adelgid on carbon dynamics of eastern United States forests, *Can. J. For. Res.*, *40*(1), 119–133, doi:10.1139/X09-167.

Anderegg, W. R. L., J. M. Kane, and L. D. L. Anderegg (2012), Consequences of widespread tree mortality triggered by drought and temperature stress, *Nat. Clim. Change*, *3*(1), 30–36, doi:10.1038/nclimate1635.

Barnes, M. C., A. H. Todd, R. W. Lilja, and P. K. Barten (2009), Forests, water and people: Drinking water supply and forest lands in the Northeast and Midwest United States, NA-FR-01-08: United States Department of Agriculture Forest Service Northeastern Area State and Private Forestry Newtown Square, 71 p.

Barszcz, D. (2004), Incidence of hemlock woolly adelgid (Adelges tsugae) at Harvard Forest, in *Abstracts From the 12th Annual Harvard Forest Summer Research Program*, 6 pp., Petersham, Mass, Harvard Forest.

Bearup, L. A., R. M. Maxwell, D. W. Clow, and J. E. McCray (2014), Hydrological effects of forest transpiration loss in bark beetle-impacted watersheds, *Nat. Clim. Change*, *4*(6), 481–486, doi:10.1038/nclimate2198.

Beven, K. J., and A. Binley (1992), The future of distributed models: Model calibration and uncertainty prediction, *Hydrol. Process.*, *6*(3), 279–298, doi:10.1002/hyp.3360060305.

Brantley, S. T., C. R. Ford, and J. M. Vose (2013), Future species composition will affect forest water use after loss of eastern hemlock from southern Appalachian forests, *Ecol. Appl.*, *23*(4), 777–790, doi:10.1890/12-0616.1.

Brantley, S. T., C. F. Miniat, K. J. Elliott, S. H. Laseter, and J. M. Vose (2014), Changes to southern Appalachian water yield and stormflow after loss of a foundation species, *Ecohydrology*, *8*, 518–528, doi:10.1002/eco.1521.

Brown, A. E., A. W. Western, T. A. McMahon, and L. Zhang (2013), Impact of forest cover changes on annual streamflow and flow duration curves, *J. Hydrol.*, *483*, 39–50, doi:10.1016/j.jhydrol.2012.12.031.

Cessna, J. F., and C. Nielsen (2012), Influences of hemlock woolly adelgid-induced stand-level mortality on nitrogen cycling and stream water nitrogen concentrations in southern Pennsylvania, *Castanea*, *77*(2), 127–135, doi:10.2179/11-025.

Cohen, W. B., D. P. Turner, S. T. Gower, and S. W. Running (2006), Bigfoot land cover surfaces for North and South American sites, 2000–2003, Data set from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tenn. [Available at [http://www.daac.ornl.gov.]

Daley, M. J., N. G. Phillips, C. Pettijohn, and J. L. Hadley (2007), Water use by eastern hemlock (*Tsuga canadensis*) and black birch (*Betula lenta*): Implications of effects of the hemlock woolly adelgid, *Can. J. For. Res.*, *37*(10), 2031–2040, doi:10.1139/X07-045.

Davidson, E. A., and K. E. Savage (1999), Soil respiration, temperature and moisture at Harvard Forest EMS tower since 1995, Harvard Forest Data Archive: HF006. [Available at http://harvardforest.fas.harvard.edu:8080/exist/xquery/data.xq?id=hf006.]

Dingman, S. L. (2009), *Physical Hydrology*, 2nd ed., Waveland Press, Long Grove, Ill.

Domec, J.-C., L. N. Rivera, J. S. King, I. Peszlen, F. Hain, B. Smith, and J. Frampton (2013), Hemlock woolly adelgid (*Adelges tsugae*) infestation affects water and carbon relations of eastern hemlock (*Tsuga canadensis*) and Carolina hemlock (Tsuga caroliniana), *New Phytol.*, *199*(2), 452–463, doi:10.1111/nph.12263.

Ellison, A. M., et al. (2005), Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems, *Front. Ecol. Environ.*, *3*(9), 479–486, doi:10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2.

Eschtruth, A. K., N. L. Cleavitt, J. J. Battles, R. A. Evans, and T. J. Fahey (2006), Vegetation dynamics in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid infestation, *Can. J. For. Res.*, *36*(6), 1435–1450, doi:10.1139/x06-050.

Fitzpatrick, M. C., E. L. Preisser, A. Porter, J. Elkinton, and A. M. Ellison (2012), Modeling range dynamics in heterogeneous landscapes: Invasion of the hemlock woolly adelgid in eastern North America, *Ecol. Appl.*, *22*(2), 472–486, doi:10.1890/11-0009.1.

Granier, A., and D. Loustau (1994), Measuring and modelling the transpiration of a maritime pine canopy from sap-flow data, *Agric. For. Meteorol.*, *71*(1–2), 61–81, doi:10.1016/0168-1923(94)90100-7.

Guswa, A. J., and C. M. Spence (2012), Effect of throughfall variability on recharge: Application to hemlock and deciduous forests in western Massachusetts, *Ecohydrology*, *5*(5), 563–574, doi:10.1002/eco.281.

Hadley, J. L., P. S. Kuzeja, M. J. Daley, N. G. Phillips, T. Mulcahy, and S. Singh (2008), Water use and carbon exchange of red oak- and eastern hemlock-dominated forests in the northeastern USA: Implications for ecosystem-level effects of hemlock woolly adelgid, *Tree Physiol.*, *28*(4), 615–627, doi:10.1093/treephys/28.4.615.

Havill, N. P., L. C. Vieira, and S. M. Salom (2014), Biology and control of hemlock woolly adelgid, USDA Forest Service Publication FHTET-2014-05, USDA For. Serv. Publ. FHTET-2014-05.

Hwang, T., L. E. Band, and T. C. Hales (2009), Ecosystem processes at the watershed scale: Extending optimality theory from plot to catchment, *Water Resour. Res.*, *45*, W11425, doi:10.1029/2009WR007775.

Hwang, T., L. E. Band, C. F. Miniat, C. Song, P. V. Bolstad, J. M. Vose, and J. P. Love (2014), Divergent phenological response to hydroclimate variability in forested mountain watersheds, *Global Change Biol.*, *20*(8), 2580–2595, doi:10.1111/gcb.12556.

Jenkins, J. C., J. D. Aber, and C. D. Canham (1999), Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests, *Can. J. For. Res.*, *29*(5), 630–645, doi:10.1139/x99-034.

Kelly, C. N., K. J. McGuire, C. F. Miniat, and J. M. Vose (2016), Streamflow response to increasing precipitation extremes altered by forest management, *Geophys. Res. Lett.*, *43*, 3727–3736, doi:10.1002/2016GL068058.

Lane, P. N. J., and S. M. Mackay (2001), Streamflow response of mixed-species eucalypt forests to patch cutting and thinning treatments, *For. Ecol. Manage.*, *143*(1–3), 131–142, doi:10.1016/S0378-1127(00)00512-0.

Loescher, H. W., H. L. Gholz, J. M. Jacobs, and S. F. Oberbauer (2005), Energy dynamics and modeled evapotranspiration from a wet tropical forest in Costa Rica, *J. Hydrol.*, *315*(1–4), 274–294, doi:10.1016/j.jhydrol.2005.03.040.

McDowell, N. G., et al. (2013), Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework, *New Phytol.*, *200*(2), 304–321, doi:10.1111/nph.12465.

Mikkelson, K. M., L. A. Bearup, R. M. Maxwell, J. D. Stednick, J. E. McCray, and J. O. Sharp (2013), Bark beetle infestation impacts on nutrient cycling, water quality and interdependent hydrological effects, *Biogeochemistry*, *115*(1–3), 1–21, doi:10.1007/s10533-013-9875-8.

Moriasi, D. N., J. G. Arnold, M. W. Van Liew, R. L. Bingner, R. D. Harmel, and T. L. Veith (2007), Model evaluation guidelines for systematic quantification of accuracy in watershed simulations, *Trans. ASABE*, *50*(3), 885–900, doi:10.13031/2013.23153.

Munger, W. J., and S. C. Wofsy (1999), Biomass inventories at Harvard Forest EMS tower since 1993, Harvard Forest Data Archive: HF069. [Available at http://harvardforest.fas.harvard.edu:8080/exist/xquery/data.xq?id=hf069.]

National Resources Conservation Service (NRCS) (2009), Soil Survey Geographic (SSURGO) database, USDA NRCS [National Resources Conservation Service]. [Available at http://sdmdataaccess.nrcs.usda.gov/.]

Orwig, D. A., and D. R. Foster (1998), Forest response to the introduced hemlock woolly adelgid in southern New England, USA, *J. Torrey Bot. Soc.*, *125*(1), 60–73, doi:10.2307/2997232.

Orwig, D. A., R. C. Cobb, A. W. D'Amato, M. L. Kizlinski, and D. R. Foster (2008), Multi-year ecosystem response to hemlock woolly adelgid infestation in southern New England forests, *Can. J. For. Res.*, *38*(4), 834–843, doi:10.1139/X07-196.

Orwig, D. A., J. R. Thompson, N. A. Povak, M. Manner, D. Niebyl, and D. R. Foster (2012), A foundation tree at the precipice: Tsuga canadensis health after the arrival of *Adelges tsugae* in central New England, *Ecosphere*, *3*(1), 10, doi:10.1890/ES11-0277.1.

Paradis, A., J. Elkinton, K. Hayhoe, and J. Buonaccorsi (2008), Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America, *Mitigation Adapt. Strategies Global Change*, *13*(5–6), 541–554, doi:10.1007/s11027-007-9127-0.

Patric, J. H., and K. G. Reinhart (1971), Hydrologic effects of deforesting two mountain watersheds in West Virginia, *Water Resour. Res.*, *7*, 1182–1188, doi:10.1029/WR007i005p01182.

Roberts, S. W., R. Tankersley, and K. H. Orvis (2009), Assessing the potential impacts to riparian ecosystems resulting from hemlock mortality in Great Smoky Mountains National Park, *Environ. Manage.*, *44*(2), 335–345, doi:10.1007/s00267-009-9317-5.

Royer, P. D., N. S. Cobb, M. J. Clifford, C. Y. Huang, D. D. Breshears, H. D. Adams, and J. C. Villegas (2011), Extreme climatic event-triggered overstorey vegetation loss increases understorey solar input regionally: Primary and secondary ecological implications, *J. Ecol.*, *99*(3), 714–723, doi:10.1111/j.1365-2745.2011.01804.x.

Siderhurst, L. A., H. P. Griscom, M. Hudy, and Z. J. Bortolot (2010), Changes in light levels and stream temperatures with loss of eastern hemlock (*Tsuga canadensis*) at a southern Appalachian stream: Implications for brook trout, *For. Ecol. Manage.*, *260*(10), 1677–1688, doi:10.1016/j.foreco.2010.08.007.

Somers, G. L., R. G. Oderwald, W. R. Harms, and O. G. Langdon (1980), Predicting mortality with a Weibull distribution, *For. Sci.*, *26*(2), 291–300.

Sperry, J. S., F. R. Adler, G. S. Campbell, and J. P. Comstock (1998), Limitation of plant water use by rhizosphere and xylem conductance: Results from a model, *Plant Cell Environ.*, *21*(4), 347–359, doi:10.1046/j.1365-3040.1998.00287.x.

Stadler, B., T. Müller, D. A. Orwig, and R. Cobb (2005), Hemlock woolly adelgid in New England forests: Canopy impacts transforming ecosystem processes and landscapes, *Ecosystems*, *8*(3), 233–247, doi:10.1007/s10021-003-0092-5.

Stoetzel, M. B. (2002), History of the introduction of *Adelges tsugae* based on voucher specimens in the Smithsonian Institute national collection of insects, in *Hemlock Woolly Adelgid in the Eastern United States Symposium*, edited by B. Onken, R. Reardon, and J. Lashomb, 12 pp., USDA Forest Service and New Jersey Agricultural Experiment Station Publication. New Jersey Agricultural Experiment Station and Rutgers University, East Brunswick, New Brunswick, N. J.

Tague, C. L., and L. E. Band (2004), RHESSys: Regional hydro-ecologic simulation system—An object-oriented approach to spatially distributed modeling of carbon, water, and nutrient cycling, *Earth Interact.*, *8*(19), 1–42, doi:10.1175/1087-3562(2004)8<1:RRHSSO>2.0.CO;2.

The MathWorks (2000), MATLAB 8.1 and Statistics Toolbox 8.1.

Troch, P. A., G. F. Martinez, V. R. N. Pauwels, M. Durcik, M. Sivapalan, C. Harman, P. D. Brooks, H. Gupta, and T. E. Huxman (2009), Climate and vegetation water use efficiency at catchment scales, *Hydrol. Process.*, *23*(16), 2409–2414, doi:10.1002/hyp.7358.

Vose, J. M., D. N. Wear, A. E. Mayfield, and C. Dana Nelson (2013), Hemlock woolly adelgid in the southern Appalachians: Control strategies, ecological impacts, and potential management responses, *For. Ecol. Manage.*, *291*, 209–219, doi:10.1016/j.foreco.2012.11.002.

Watson, F., R. Vertessy, T. McMahon, B. Rhodes, and I. Watson (2001), Improved methods to assess water yield changes from paired-catchment studies: Application to the Maroondah catchments, *For. Ecol. Manage.*, *143*(1–3), 189–204, doi:10.1016/S0378-1127(00)00517-X.

Webster, J. R., K. Morkeski, C. A. Wojculewski, B. R. Niederlehner, E. F. Benfield, and K. J. K. J. Elliott (2012), Effects of hemlock mortality on streams in the southern Appalachian Mountains, *Am. Midland Nat.*, *168*(1), 112–131, doi:10.1674/0003-0031-168.1.112.

White, M. A., P. E. Thornton, S. W. Running, and R. R. Nemani (2000), Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: Net primary production controls, *Earth Interact.*, *4*(3), 1–85, doi:10.1175/1087-3562(2000)004<0003:PASAOT>2.0.CO;2.