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Changes to southern Appalachian water yield and stormflow after loss of a foundation species

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ABSTRACT

Few studies have examined how insect outbreaks affect landscape-level hydrologic processes. We report the hydrologic effects of the invasive, exotic hemlock woolly adelgid (HWA) in a headwater catchment in the southern Appalachian Mountains. The study watershed experienced complete mortality of an evergreen tree species, *Tsuga canadensis* (L.) Carr. (eastern hemlock), after infestation was first detected in 2003. Hemlock mortality resulted in a ~6% reduction in basal area in the watershed, and this loss was primarily concentrated in riparian zones. We used a paired-watershed approach to quantify changes in water yield and peak stormflow using streamflow data from the infested watershed and a nearby watershed with significantly lower hemlock basal area. We hypothesized that yield would increase shortly after hemlock infestation but decrease over the longer-term. We found that annual yield did not increase significantly in any year after infestation but decreased significantly by 12·0 cm (~8%) in 2010. Monthly yield also decreased after infestation, but changes were limited to the dormant season. The decline in yield is likely to persist as hemlock is replaced by species with higher transpiration rates. Peakflow increased significantly after infestation during the two largest flow events in the post-infestation period. Changes in stormflow during extreme events may have been temporary as another evergreen, *Rhododendron maximum*, may have mitigated some of the changes after hemlock loss. Thus, streams draining watersheds where eastern hemlock has been lost due to HWA infestation demonstrate permanent reductions in yield and transient increases in peakflow during large-flow events. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS *Adelges tsugae*; flow duration curves; forest health; frequency pairing; hemlock woolly adelgid; paired watersheds; storm hydrograph; *Tsuga canadensis*; water yield

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INTRODUCTION

Forests play a critical role in regulating hydrologic processes in headwater catchments by moderating the timing and magnitude of streamflow (Burt and Swank, 2002; Ice and Stednick, 2004; Ford *et al.*, 2011; Vose *et al.*, 2011). Hydrologic processes in forests are particularly sensitive to disturbances that reduce tree vigour or leaf area and thus decrease evapotranspiration (Bethlahmy, 1974; Ford and Vose, 2007; Edburg *et al.*, 2012; Brantley *et al.*, 2013). Most efforts at studying the effects of disturbance on watershed hydrology have focused on quantifying the effects of forest-harvesting practices on watershed yield (Bosch and Hewlett, 1982; Stednick, 1996; Brown *et al.*, 2005; Ford *et al.*, 2011) and storm runoff (Reinhart, 1964; Hewlett and Helvey, 1970; Hornbeck, 1973; Burt and Swank, 2002; Alila *et al.*, 2009; Green and Alila, 2012). Reviews by Bosch and Hewlett (1982) and Brown *et al.* (2005) have shown that, in general, harvesting <20% of the basal area shows no detectable increase in water yield; but water yield increases thereafter as the percentage of basal area harvested increases. Reported results of storm runoff responses to harvesting are more variable. Some studies show large increases in peakflow (Figure 1) after harvest (e.g. Partridge and Sopper, 1973; Ziemer, 1981; Burton, 1997; Green and Alila, 2012), and others show little or no effect after harvest (e.g. Reinhart 1964; Rothacher, 1973; Troendle *et al.*, 2001; Moore and Scott, 2005). Some of the disagreement in the effects of harvesting on peakflow may stem from the methods used to detect differences in flow metrics after harvest, as most of these studies used the chronological pairing (CP) method that has fallen under increasing criticism in recent studies (Alila *et al.*, 2009; Alila and Green, 2014a, 2014b).

Fewer studies have quantified the effects of insect outbreaks on yield and stormflow compared with the effects of forest harvest on streamflow, although the

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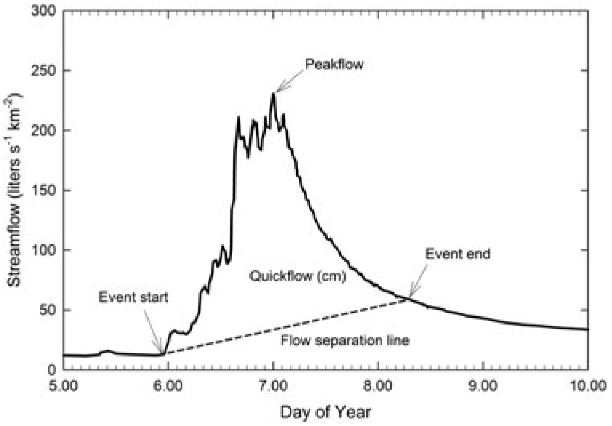

Figure 1. Example hydrograph for a large storm (Jan 2009; 12·85 cm total rainfall). Storm events were identified using a flow separation line with a slope of 0·54651 s^{-1} km^{-2}. Peakflow is the maximum flow rate observed during the event.

concepts are similar, as both result in a reduction of tree density and forest leaf area. Insect outbreaks have increased in recent decades and are now considered among the most serious threats to forest health in North America with some examples affecting millions of hectares of forest in the United States (Allen *et al.*, 2010; Orwig *et al.*, 2012; Edburg *et al.*, 2012; Ayres *et al.*, 2014). Depending on the scale and duration of the disturbance, effects of insect outbreaks on ecosystem function may parallel those of other large-scale disturbances, such as logging or fire, which decrease canopy density or alter species composition and thus reduce evapotranspiration (Bethlahmy, 1974; Swank *et al.*, 1981; Riscassi and Scanlon, 2009). Common examples of functional changes in the hydrologic cycle resulting from insect outbreaks include altered rates of transpiration (Daley *et al.*, 2007; Ford and Vose, 2007; Brantley *et al.*, 2013), changes in soil moisture and runoff (Bethlahmy, 1974) and changes in streamflow responses to storm events (Schwarze and Beudert, 2009).

A recent example of such a disturbance is the outbreak of the exotic invasive insect hemlock woolly adelgid (HWA, *Adelges tsugae* Annand), which has caused widespread mortality of eastern hemlock [*Tsuga canadensis* (L.) Carr.] throughout much of eastern North America (Orwig *et al.*, 2012). Eastern hemlock is considered a foundation species in riparian and cove habitats in the southern Appalachian Mountains (Ellison *et al.*, 2005). Hemlock stands are characterized by a dense, evergreen canopy that creates a unique microenvironment within a broader forest landscape that is otherwise dominated by deciduous tree species (Orwig *et al.*, 2012). In the southern Appalachians, eastern hemlock is often limited to ~10% of basal area within a given watershed, but these trees are often concentrated along riparian corridors (Ellison *et al.*, 2005). Although eastern hemlock rarely dominates within a given watershed, it serves several distinct ecohydrological roles: It is an evergreen tree that maintains year-round transpiration rates, it is a riparian tree that has high transpiration rates in the spring (Ford and Vose, 2007) and it forms a dense evergreen canopy in riparian zones, which increases interception rates. Eastern hemlock mortality results in reduced annual stand-level transpiration (E_t) in the short term; but 10–20 years after infestation, eastern hemlock loss is expected to result in higher growing season and annual stand transpiration because hemlock is being replaced by species with higher leaf-level transpiration rates (Daley *et al.*, 2007; Ford and Vose, 2007; Brantley *et al.*, 2013). In winter, transpiration rates are expected to decline permanently if hemlock is replaced primarily with deciduous species (Brantley *et al.*, 2013). No other native evergreen will likely fill the ecohydrological role of eastern hemlock after widespread mortality (Ford and Vose, 2007; Brantley *et al.*, 2013); and the observed changes in stand-level evapotranspiration may result in permanent alteration of the seasonal dynamics of streamflow. How HWA-induced eastern hemlock mortality affects water fluxes at the watershed scale in small headwater catchments remains unknown; but understanding those effects is critical to managing potential impacts of eastern hemlock loss on streamflow.

Our objectives were to determine the effects of eastern hemlock loss on water yield and stormflow in a mixed deciduous southern Appalachian headwater catchment that has experienced near-complete mortality of hemlock as a result of HWA infestation. We hypothesized that the effects of eastern hemlock loss on water yield would vary by season, with small effects annually, and initial increase in yield followed by a decrease in yield, and more pronounced effects in the dormant season due to the elimination or loss of the evergreen leaf habit coupled with relatively mild winters that allow year-round transpiration. We also hypothesized that streamflow during storms would be characterized by higher peakflow (maximum streamflow during a storm) post-infestation and that these changes would be most pronounced and persistent during the dormant season.

METHODS

Site description

The study was conducted at the USDA Forest Service Coweeta Hydrologic Laboratory, a 2185-ha forested watershed in the Nantahala National Forest in Macon County, North Carolina, United States (35·06N, 83·43W). The climate in Coweeta Basin is classified as marine, humid temperate (Swift *et al.*, 1988). Annual temperature and precipitation range from 12·8 °C and 1795 mm year^{-1} at the valley floor, which is at 685 m above sea level (ASL) to 9·8 °C and 2359 mm year^{-1} at higher elevations (1398 m ASL). The Coweeta Basin contains numerous headwater catchments, 16 of which are currently monitored for streamflow (Laseter *et al.*, 2012). Two closely located (~1·1 km apart) watersheds (WS14 and WS2), similar in elevation, slope and disturbance history but differing in pre-HWA eastern hemlock tree cover, were selected (Table I). WS14, henceforth the infested watershed, has a northwest aspect and an elevation range of 707–992 m ASL. WS2, henceforth the reference watershed, has a south aspect and an elevation range of 747–990 m ASL. Soils in both watersheds are moderately permeable, well-drained and moderately deep to very deep (Thomas, 1996). The saprolite layer beneath the solum may be up to 6 m deep (Thomas, 1996).

Both the reference and infested watersheds are characteristic of mature, second-growth hardwood forests, and both have remained relatively undisturbed since 1927 (Swank and Crossley, 1988). Notable disturbances include loss of American chestnut in the 1930s in both watersheds and eastern hemlock loss over the last decade (Elliott and Vose, 2011). The infested watershed was characterized by a major eastern hemlock component in the riparian corridor (e.g. 6% of basal area overall and 26% of basal area in the riparian corridor, Table I), whereas the reference watershed had significantly less eastern hemlock (e.g. <2% of basal area overall and 4% of basal area in the riparian corridor, Table I). In these mixed deciduous forested watersheds, eastern hemlock was the most common canopy evergreen before infestation. HWA infestation was first noticed in the study watersheds in late 2004. As of 2010, eastern hemlock mortality throughout the Coweeta basin, including both study watersheds, was nearly 100% for stems ≥2·5 cm, based on permanent plot surveys (K. J. Elliott, *unpublished data*).

Vegetation measurements

Tree surveys were conducted in each watershed to characterize the relative importance of eastern hemlock in the forest community. In 2010, we surveyed a total of 30 permanent plots, 0·08 ha (20 m × 40 m) in area, in the infested watershed (~4% of watershed area) with six of these located in riparian corridors. In 2011 and 2013, we surveyed a total of twelve 0·08-ha plots in the reference watershed (~8% of watershed area) with four of these plots located in riparian zones. In each plot, diameter at breast height (DBH) of all woody stems ≥2·5 cm DBH was measured to the nearest 0·1 cm and recorded by species. We used DBH and species-specific allometric equations developed on site to estimate the leaf area index (square metre of leaf area per square metre of ground area) contribution of each species in each watershed (i.e. all plots) and in riparian zones prior to HWA-induced mortality (Table I; McGinty, 1972; Santee and Monk, 1981; Martin *et al.*, 1998; Ford and Vose, 2007; B. D. Kloeppel, *unpublished data*; C. F. Miniat, *unpublished data*).

Quantifying water yield responses

Streamflow from both watersheds was measured using permanent weirs that record stream head every 5 min (Swift *et al.*, 1988). To detect potential hydrologic responses to eastern hemlock mortality, we used the paired-watershed approach (Wilm, 1944, 1949). This approach uses pre-disturbance streamflow data from two watersheds similar in physical characteristics (e.g. elevation and slope) and pre-disturbance cover to parameterize the regression equation

$$\hat{Y}_i = b_0 + b_1 X_i \tag{1}$$

where X_i is the observed streamflow in the reference watershed for period i and $\hat{Y}_i$ is the expected streamflow for the infested watershed under undisturbed conditions for the same period. In this case, i can represent a specific year or month or a discrete stormflow event. Following disturbance (e.g. logging or insect infestation), the regression equation is used to predict the response variable (e.g. water yield or

Table I. Community composition of infested (WS14) and reference (WS2) watersheds.

	Infested watershed				Reference watershed			
	Riparian area		Watershed		Riparian area		Watershed	
Dominant species	Basal area (%)	LAI (%)	Basal area (%)	LAI (%)	Basal area (%)	LAI (%)	Basal area (%)	LAI (%)
Tsuga canadensis	**26·4**	**24·2**	**6·3**	**5·8**	**3·9**	**4·5**	**1·8**	**1·7**
Rhododendron maximum	15·8	16·7	11·4	11·5	12·7	12·6	4·1	3·7
Liriodendron tulipifera	14·4	12·7	6·3	5·5	5·6	4·4	8·5	6·0
Betula lenta	13·7	9·9	4·4	3·3	6·7	4·3	2·2	1·3
Acer rubrum	9·5	13·7	11·7	17·2	16·2	21·1	16·0	19·1
Quercus montana	3·2	4·1	17·7	22·0	3·7	4·1	16·1	16·0
Quercus rubra	2·8	3·7	5·3	6·8	5·9	6·9	2·6	2·7

Dominant species (those representing >5% of basal area in the watershed) in the infested watershed are listed in descending order of basal area in the riparian area of WS14. Note that eastern hemlock (*Tsuga canadensis*) are standing dead trees. Leaf area index (LAI) was based on allometric equations between leaf area and diameter at breast height (1·37 m).

peakflow), which is then compared with observed streamflow parameters (Y_i) of interest during the post-disturbance period.

The annual water yield relationship between the reference (WS2) and infested (WS14) watersheds for the calibration period (1938–2003) was highly significant ($n = 63$; $r^2 = 0{\cdot}99$; $P < 0{\cdot}001$). The equation was used to predict post-infestation (after 2004) yield in WS14 from 2005 to 2012 (PROCMODEL, SAS v9.3, SAS Institute, Cary, NC). A separate model was created for monthly water yield using monthly streamflow data from May 1937 to Aug 2003. To model monthly yield, we separated the data by calendar month and created 12 separate regression equations. Using separate regression equations for each month helped account for variations in yield relationships between the two watersheds among months and eliminated serial autocorrelation, which is often observed in monthly streamflow among consecutive months. Monthly water yield models were highly significant for all months (all $r^2 > 0{\cdot}91$; $P < 0{\cdot}001$), and they were used to predict monthly post-infestation yield in WS14 from Mar 2004 to Apr 2012.

We also predicted changes in post-infestation stormflow characteristics. Specifically, we focused on peakflow during storm events. Storm events were identified using standard flow separation procedures described by Hewlett and Hibbert (1966) and Hibbert and Cunningham (1966) and use a flow separation line with a slope of $0{\cdot}5465\,\mathrm{l\,s^{-1}\,km^{-2}}$ (Hewlett and Helvey, 1970; Figure 1). Pre-treatment stormflow data for the analysis spanned the period from May 1937 to Aug 2003 ($n = 2397$ recorded storm events). As with the monthly yield analysis, separate regression models relating peakflow in each watershed were developed for each month, with each month having $n > 150$ events over the pre-treatment period. The post-treatment period included all recorded stormflow events from May 2004 to Apr 2012 ($n = 214$ recorded storm events).

To detect differences between observed and predicted streamflows, we used frequency-pairing (FP) methods previously detailed by Alila *et al.* (2009). Most studies of post-disturbance watershed hydrology (e.g. Reinhart, 1964; Hornbeck, 1973; Partridge and Sopper, 1973; Ziemer, 1981; Swank *et al.*, 2001) have used CP, pairing flow events in time, to quantify changes in yield or stormflow. CP has methodological shortcomings that have generally been ignored in the forest hydrology literature (Alila *et al.*, 2009; Alila and Green, 2014a, 2014b). Applying CP to forest hydrology leads to inaccurate estimates of the change in magnitude of streamflow because CP cannot account for antecedent soil moisture conditions and thus does not isolate the effects of the disturbance on flow. On the other hand, FP, which is pairing flow based on frequency distributions of flow events, controls for both storm attributes (e.g. rainfall amount) and soil conditions. While FP has been used sparingly in the forest hydrology literature, it is a well-established method in the broader hydrology and climatology literature (e.g. Booth, 1990; Bonsal *et al.*, 2001). More detailed arguments for the use of FP over CP in forest hydrologic studies can be found in Alila *et al.* (2009) as well as in Alila and Green (2014a, 2014b).

We compared the empirical cumulative distribution functions (CDFs, F_Y) for observed and predicted water yields and peak stormflows as

$$F_Y\left[\hat{Y}_i\right] = p \tag{2}$$

where p is an estimate of the probability of occurrence for a ranked event $Y_{(i)}$ during any period i. Streamflow parameters (i.e. yield or peakflow) were ranked, and an exceedance probability, $1 - p$, was estimated for each ranked event using

$$1 - F_Y\left[\hat{Y}_\mathrm{i}\right] = \frac{m - 0{\cdot}40}{n + 0{\cdot}20} \tag{3}$$

where m is the rank for a given event and n is the total number of events in the distribution. This function provides an empirical estimate of the quantile for a given flow value (Cunnane, 1978; Stedinger *et al.*, 1993). The CDFs were then used to construct flow duration curves to assess changes in untransformed water yield and peakflow by comparing the change in magnitude for a given probability or the change in probability for a given magnitude (Alila *et al.*, 2009; Green and Alila, 2012). These methods were used to compare whether the CDFs of observed and predicted streamflows were significantly different for annual yield, monthly yield in both the dormant and growing seasons and peakflow during storm events in both the dormant and growing seasons.

Confidence limits for each probability of occurrence were estimated using a pair of Monte Carlo simulations. These estimated the variability associated with both the predictive uncertainty in Equation (1) (Var_1) and the uncertainty associated with the sampling variability at each rank (Var_2; Alila *et al.*, 2009). The first Monte Carlo simulation to estimate predictive uncertainty in Equation (1) was accomplished by using the following steps on the raw discharge data: (1) introduce random errors for each estimate of $\hat{Y}_i$ by randomly sampling from a t distribution with $n - 2$ degrees of freedom; (2) calculate updated discharge estimates incorporating the random error ($\widetilde{Y}_\mathrm{i}$); (3) rank the updated estimates; (4) repeat steps 1–3 for 10 000 iterations. Results of the simulation provide an estimate of the mean, $\widetilde{Y}_\mathrm{i}$, and an estimate of the variance around $\widetilde{Y}_\mathrm{i}$ for each rank (Var_1). A second Monte Carlo simulation was used to estimate the uncertainty imposed by the sampling variability on the quantile estimates at each rank as follows: (1) fit a Poisson–Pareto distribution to the expected discharge data, $\widetilde{Y}_\mathrm{i}$; (2) randomly sample from the distribution in step 1; (3) re-estimate the distribution parameters; (4) re-estimate quantile values from each rank using exceedance probabilities from Equation (3); and (5) repeat steps 1–4 for 10 000 iterations. Results from the second Monte Carlo simulation provide an estimate of the mean, $\widetilde{Y}_i$, and an estimate of the variance around $\widetilde{Y}_i$ for each rank (Var_2).

Confidence limits for each ranked event are then given by

$$Y_m \pm z_{1-\frac{\alpha}{2}}\sqrt{(Var_1\,[Y_m] + Var_2\,[Y_m])} \qquad (4)$$

We corrected for the loss of variability in the upper tails by using the raw, expected post-disturbance values from Equation (1) rather than the estimates calculated from the Monte Carlo simulation (Alila *et al.*, 2009). We also created a probability density function for each CDF by creating a histogram of the flow distributions (PROC UNIVARIATE, SAS v9.3, SAS Institute, Cary, NC) and compared changes in the median and interquartile range of the distribution. For visual comparison, we plotted histograms of observed and predicted flow distribution in SigmaPlot (version 12.0, Systat Software Inc., Chicago, IL, USA) using a spline curve.

RESULTS

Water yield

Annual water yield showed evidence of decline in the infested watershed following HWA infestation. After HWA infestation, ranked annual yield values were lower than predicted for any given probability (Figure 2a). Data from the most recent three years (2010–2012) deviated most from expected, although only one year, 2010, was outside the confidence limits when yield was 12·0 cm (~8%) below expected. Overall, the distribution function for annual yield shifted towards lower yield with the median yield decreasing by 6·8 cm (~9%).

Monthly water yield also showed evidence of decline in the infested watershed following HWA infestation. Ranked monthly water yield values were lower than predicted for any given probability; however, only seven months showed yield values significantly lower than expected (Figure 2b). All months that deviated significantly were in the wettest 10% of the distribution in terms of runoff response (Figure 2). Overall, the median monthly water yield shifted towards lower yield (−0·36 cm or ~5%), and the interquartile range increased by ~3%, suggesting slightly greater variability in the distribution (Figure 2b, inset). When monthly yield data were separated into growing and dormant seasons, all of the observed significant changes in yield and the changes in the distribution function were due to changes in the dormant season. During the growing season, none of the months were outside of the confidence intervals (Figure 2c), and there was virtually no change (<1% change in median yield or interquartile range) in the distribution (Figure 2c, inset). Months that showed significant deviations from expected were not distributed evenly throughout the post-infestation period but occurred within 4 months of each other, one in December 2007 and one in March 2008. Overall, the distribution function for the dormant season shifted towards lower yield with the median yield decreasing by −0·54 cm (~6%) and showing a ~10% increase in the interquartile range, suggesting greater variability in the distribution (Figure 2d, inset).

Storm responses

Peakflow in the infested watershed increased significantly after HWA infestation, but only for the largest flow events. Prior to HWA infestation, relationships between peakflow in the infested watershed and peakflow in the reference watershed for simultaneous events were highly significant for all months ($R^2 > 0{\cdot}81$, $P < 0{\cdot}01$). Peakflow values for any given probability of occurrence fell both above and below the predicted values but were generally not outside the confidence limits (Figure 3a). When data were ranked for the entire year, only two events showed significantly different peakflow than expected (Figure 3a), and both of these events had >95% probability of non-exceedance. No event had significantly lower peakflow than predicted. The largest deviations were increases in peakflow for the two largest peakflow values observed during the post-HWA period, and these occurred in December 2007 and March 2008. The overall distribution of peakflows shifted towards lower values with the median peakflow decreasing by 0·26 l s^{-1} km^{-2} (~4%; Figure 3a, inset). However, the interquartile range increased by ~12% (Figure 3a, inset), indicating a substantial increase in the variability in the distribution.

Results differed when data were separated into growing and dormant seasons. During the growing season, no storm event showed a significant change in peakflow (Figure 3b). The overall distribution of peakflow values shifted very slightly towards lower peakflow with the median peakflow value declining by 0·07 l s^{-1} km^{-2} (~1%; Figure 3b, inset). The interquartile range increased by ~7% (Figure 3b, inset), indicating an increase in variation across the distribution. During the dormant season, the median peakflow shifted towards slightly higher values by 0·28 l s^{-1} km^{-2} (~4%), and the interquartile range increased by ~5% (Figure 3c, inset), indicating an increase in variability.

DISCUSSION

Contrary to our first hypothesis, the loss of eastern hemlock basal area in the infested watershed did not stimulate a

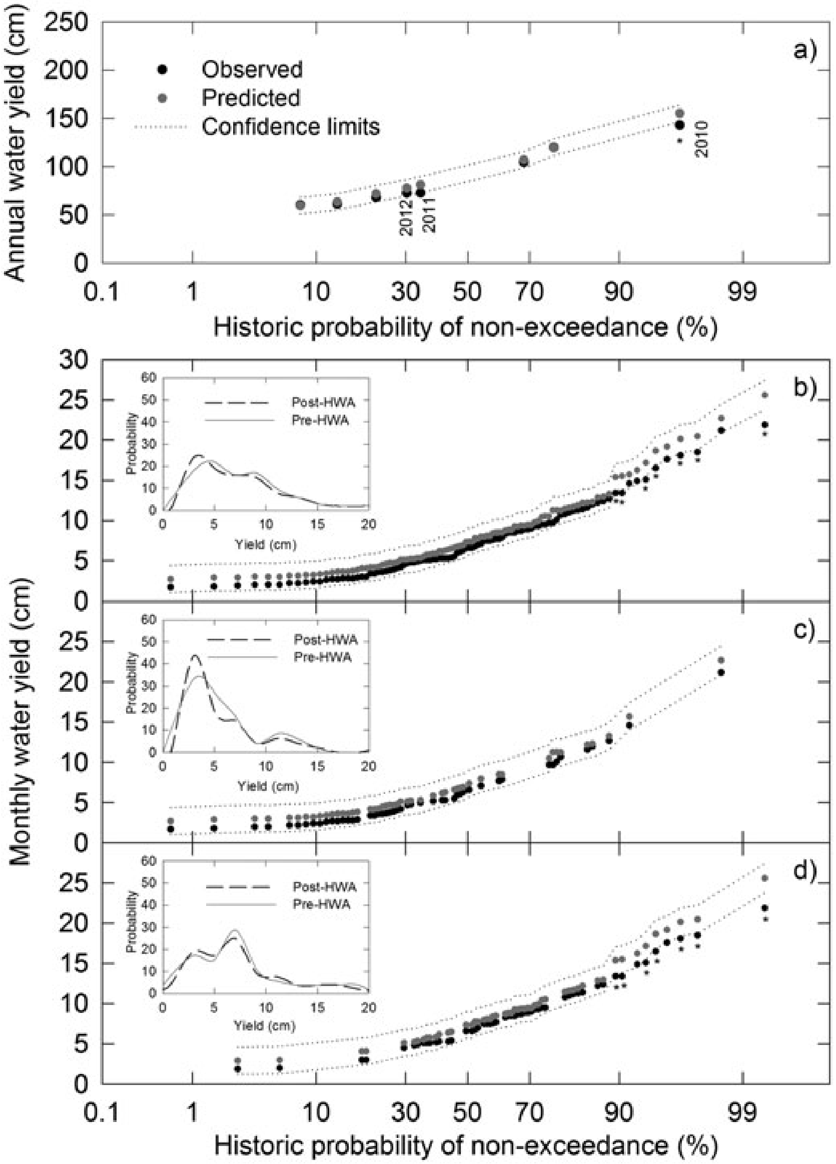

Figure 2. Differences in observed and predicted cumulative distribution functions for annual (a) and monthly (b–d) watershed yield for a watershed that has experienced complete mortality of eastern hemlock after infestation with hemlock woolly adelgid (HWA). Results for monthly yield (b) are further divided into growing (c) and dormant (d) seasons. Insets show changes in the probability density function of yield for each flow duration curve.

short-term increase in water yield. This was probably due to the relatively low proportion of hemlock (~6% of basal area) in the watershed and the rapid response of co-occurring species to the increased light after hemlock mortality (Ford *et al*., 2012). Previous studies indicate that a >20% reduction in tree basal area is required to observe increased annual water yield (Bosch and Hewlett, 1982; Stednick, 1996; Brown *et al*., 2005). Other watersheds with a greater abundance of hemlock may experience short-term increases in water yield after hemlock infestation and mortality. However, even in watersheds where more hemlock has been lost, the magnitude and duration of this response may depend on the rate of subsequent growth of co-dominant vegetation and the ability of the remaining forest community to buffer the disturbance. Previous work at Coweeta postulated an initial 10% increase in annual water yield due to hemlock loss (Ford and Vose, 2007); however, the observed changes in water yield were not detected in this analysis.

The observed changes in water yield were likely a result of a rapid response of co-dominant species with less conservative transpiration rates (Ford *et al*., 2012; Brantley *et al*., 2013). Loss of hemlock may have reduced stand-level E_t temporarily; but because runoff did not correspondingly increase, the additional resources resulting from eastern hemlock mortality likely served as a subsidy for

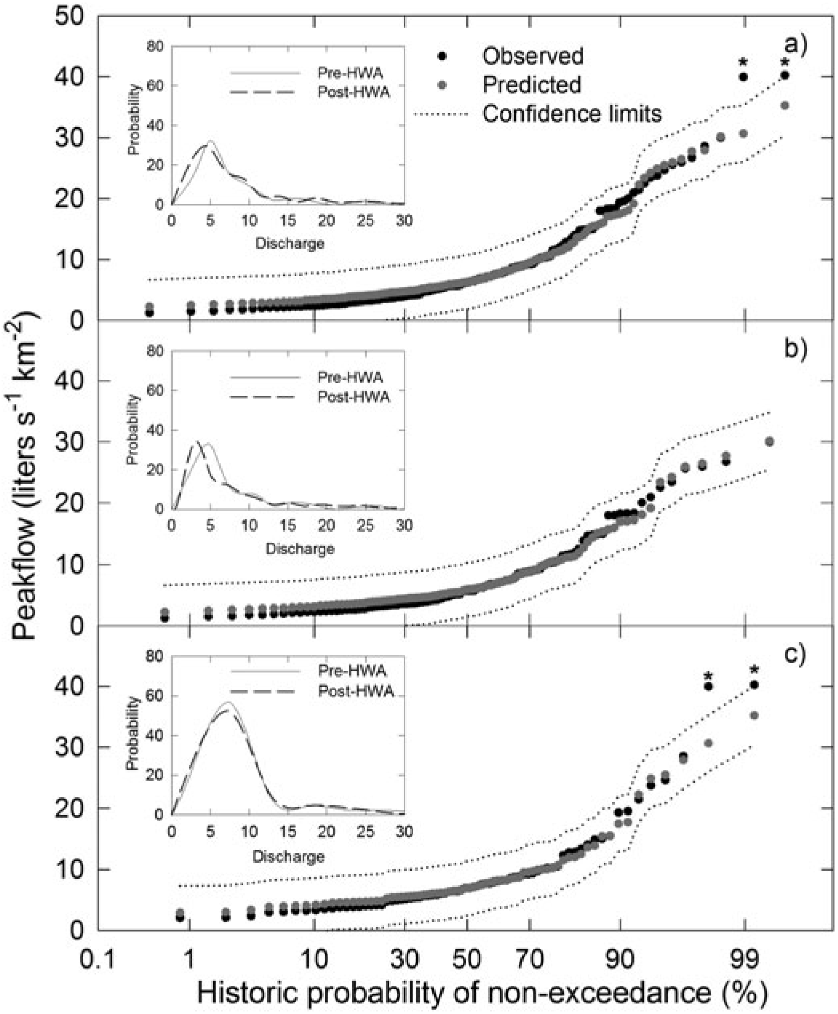

Figure 3. Differences in observed and predicted cumulative distribution functions for peakflow for a watershed that has experienced complete mortality of eastern hemlock after infestation with hemlock woolly adelgid (HWA). Results are further divided into growing (b) and dormant (c) seasons. Insets show changes in the probability density function for each flow duration curve.

co-occurring species in the first years post-infestation (Stednick, 1996; Ford *et al.*, 2012). Declining hemlock stands experienced substantially increased light levels after HWA infestation, resulting in enhanced growth of co-occurring canopy and sub-canopy woody species (Ford *et al.*, 2012; Brantley *et al.*, 2013). Deciduous species including *Acer rubrum* L., *Betula lenta* L. and *Liriodendron tulipifera* L. are major components of eastern hemlock-dominated areas, and these species have much greater transpiration rates than hemlock (Ford and Vose, 2007; Ford *et al.*, 2011; Vose *et al.*, 2011). The evergreen shrub *Rhododendron maximum* L. is also a major component in the understorey of these watersheds, especially in the infested watershed (Table I), and growth of this species has responded strongly to hemlock canopy loss (Ford *et al.*, 2012). Previous large-scale manipulations at Coweeta have clearly documented the importance of the evergreen understorey (*R. maximum* and *Kalmia latifolia* L.) in overall water budgets (Johnson and Kovner, 1956). Although we anticipated sustained increases in dormant season yield due to the loss of a canopy evergreen species, however, the positive growth response of the understorey evergreen species likely increased evapotranspiration in response and thus decreased dormant season yield. In our study, observed changes in monthly water yield occurred most often in March and April when *R. maximum* often shows the highest transpiration rates (Brantley *et al.*, 2013). Increased light levels likely allowed *R. maximum* to transpire water that would otherwise have been used by eastern hemlock in the dormant season, compensating for the loss of transpiration by hemlock. As *R. maximum* and other co-occurring deciduous species increased in leaf area after hemlock canopy loss (Ford *et al.*, 2012; Brantley *et al.*, 2013), yield declined significantly, suggesting a net increase in evapotranspiration (i.e. increases of E_t, soil evaporation and/or interception). Whether these relatively small decreases in yield are of hydrological significance remains to be seen as these watersheds continue to change as a result of HWA infestation.

Stream responses to storms showed significant changes after HWA infestation for only extreme events, partially supporting our second hypothesis. Even with vigorous statistical analysis and the large sample sizes used in this study, making inferences from such results must be performed cautiously, especially when the only observed differences are at the tails of the distribution (Alila *et al.*, 2009; Green and Alila, 2012). However, several observations suggest that the changes observed in the extreme storms are physically relevant. First, the fact that no changes were detected at the tail end in Figure 3b supports the conclusion that the changes seen in Figure 3a and c were a result of physical change in the watershed and not an artefact of the modelling technique. Second, we would note that the timing of these two events is evidence that the observed changes were due to hemlock canopy loss and mortality. These events occurred in Dec 2007 and Mar 2008, the same period when hemlock canopy loss was beginning to peak and widespread hemlock mortality began to occur (Ford *et al.*, 2012). Lastly, we note that these two largest flow events were not a result of the two largest rainfall events during the post-infestation period. While the event in Mar 2008 occurred as a result of a large rainfall event (7·85 cm), there were 16 larger storm events during the post-HWA period that did not produce flows as large. Additionally, the event in Dec 2007 occurred as the result of a fairly moderate storm (2·51 cm) event. However, this event followed 2 days with total rainfall of 3·38 cm, so it is possible that the soils were already saturated.

Because our results are focused on loss of a dominant evergreen species, which contributes to year-round evapotranspiration, we had expected that effects would be greater in the dormant season, and while our results are limited to the most extreme events, that is what we observed. Several authors have suggested that watershed responses to forest disturbances could vary seasonally (Hewlett and Helvey, 1970; Ziemer, 1981; Wright *et al.*, 1990); however, there is little agreement as to whether the growing season or the dormant season should produce a greater response. Ziemer (1981) hypothesized that differences in stormflow after disturbance should be greater during the growing season because greater differences in soil moisture between treated and untreated watersheds would be observed at this time, and this pattern has been observed in much of the forest hydrology literature (Chang, 2003). An alternative to this hypothesis is that increases in peakflow from disturbance would be greater in the dormant season because dormant season soil moisture is higher because of reduced evapotranspiration and soils are more likely to be saturated (i.e. soils have a reduced storage capacity for incoming precipitation). According to this hypothesis, pre-event soil saturation increases the proportion of precipitation that exits, increasing both peakflow and quickflow during storm events (Hewlett and Helvey, 1970; Wright *et al.*, 1990; Swank *et al.*, 2001). In the current study, we expected that a primary effect of hemlock loss would be a short-term decrease in stand-level transpiration (Ford and Vose, 2007; Brantley *et al.*, 2013), which would lead to increased soil moisture; this should be a sustained increase, especially in the dormant season when hemlock is the dominant physiologically active species in the canopy. However, we did not find increases in soil moisture in previous work carried out in nearby hemlock stands, likely because stands dominated by hemlock are in areas of convergent topography (Ford *et al.*, 2012) and species co-occurring with hemlock before disturbance had higher leaf-level transpiration rates than hemlock that compensated for loss of hemlock transpiration (Brantley *et al.*, 2013).

Increases in peakflow after the loss of a dominant, riparian conifer could also result from differences in interception in plants bordering the streams rather than changes in soil moisture due to a decline in transpiration. Experimental thinning experiments have shown increases in throughfall and corresponding changes in hydrology across a variety of forest types (e.g. Aussenac *et al.*, 1982; Baümler and Zech, 1997). Reduced interception in woody species bordering the stream after hemlock canopy loss would increase precipitation directly entering stream channels and contribute significantly to increased peakflow (Hewlett and Nutter, 1970). Conifers are known for relatively high interception rates compared with deciduous trees because of high branch and stem surface areas (Swank, 1968; Link *et al.*, 2004). Eastern hemlock stands, in particular, have dense canopies with high leaf area index (Brantley *et al.*, 2013), which contributes to high near-stream interception rates during storms. Loss of hemlock would have temporarily reduced dormant season leaf area and may have reduced interception. This change may have persisted if only deciduous species had replaced hemlock; however, the positive growth response of *R. maximum* may have dampened some of the impacts (Ford *et al.*, 2012; Brantley *et al.*, 2013), making any shift in stream storm responses transient and difficult to detect.

Whether increases in stormflow during the two largest flow events were a result of decreased interception or decreased transpiration, the observed changes would likely persist if hemlock were replaced primarily by deciduous species. However, long-term changes in stream responses may depend heavily on the future importance of the sub-canopy evergreen shrub *R. maximum*, which is a major component in the infested watershed and is common throughout southern Appalachian forests. Like eastern hemlock, *R. maximum* is concentrated in riparian zones where it may have a greater effect on watershed hydrologic processes than species located upslope (Hewlett and Nutter, 1970; Jencso *et al.*, 2010). *R. maximum* is also known to suppress regeneration of common deciduous tree species that are likely to replace hemlock (Clinton and Vose, 1996; Wurzburger and Hendrick, 2007).

CONCLUSIONS

We consider the observed changes in yield and stormflow an indication of the importance of hemlock in this forest. The fact that there was any significant effect of hemlock loss on peakflow suggests that hemlock has an important role in both regulating water yield and mediating stormflow during large-flow events; and these findings support previous studies that postulate a unique ecohydrological role for eastern hemlock (Ellison *et al.*, 2005; Daley *et al.*, 2007; Ford and Vose, 2007; Brantley *et al.*, 2013). Although eastern hemlock represented a relatively small proportion of tree basal area throughout the entire infested watershed, the concentration of hemlock along riparian corridors may help explain the observed changes in watershed hydrology. Riparian zones play a critical role in connectivity between upslope material inputs and streams. Several studies have shown that even relatively small disturbances in riparian areas can affect hydrologic and nutrient stream inputs (Hewlett and Nutter, 1970; Yeakley *et al.*, 2003; Jencso *et al.*, 2010; Burt *et al.*, 2010). Loss of the dominant tree species in riparian zones could have implications for attenuation of high flows, an important function of healthy forests (Burt *et al.*, 2010). Hemlock is rarely a dominant species in southern Appalachian forests; but it is often concentrated in riparian areas. The distinct landscape position of eastern hemlock is important in relation to its role across these forests, and future research should consider the effects of variation in the spatial distribution of tree mortality on hydrologic processes.

Understanding the impacts that insect outbreaks have on forest hydrologic cycles is challenging; but such an understanding is critical to managing forests, as pressures on high-quality surface water supply increase (Vose *et al.*, 2011). The relative lack of studies quantifying changes in watershed processes from insect disturbances reflects this challenge and helps highlight the importance of long-term research across a range of forest habitats (Argerich *et al.*, 2013). Understanding how the loss of a foundation species with a distinct landscape position and a unique ecohydrological role will affect watershed processes is of particular importance. The fact that hemlock loss had a measureable impact on yield and may have temporarily impacted peakflow during extreme storm events suggests that riparian trees have a greater role in regulating watershed processes compared with non-riparian trees. Our future studies will concentrate on investigating whether a loss of a similar proportion of eastern hemlock from these catchments will not only increase peakflow but also have greater effects on yield. Other watersheds with a larger hemlock component and/or a higher proportion of yield derived from stormflow may experience measureable, short-term increases in water yield and be at an even greater risk of high flows if widespread hemlock mortality occurs. These factors should be considered in prioritizing future research efforts as well as hemlock restoration or other mitigation strategies.

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