Declining water yield from forested mountain watersheds in response to climate change and forest mesophication

PETER V. CALDWELL, CHELCY F. MINIAT, KATHERINE J. ELLIOTT, WAYNE T. SWANK, STEVEN T. BRANTLEY* and STEPHANIE H. LASETER
USDA Forest Service, Southern Research Station, Center for Forest Watershed Research, Coweeta Hydrologic Lab, 3160 Coweeta Lab Road, Otto, NC 28734, USA

Abstract
Climate change and forest disturbances are threatening the ability of forested mountain watersheds to provide the clean, reliable, and abundant fresh water necessary to support aquatic ecosystems and a growing human population. Here, we used 76 years of water yield, climate, and field plot vegetation measurements in six unmanaged, reference watersheds in the southern Appalachian Mountains of North Carolina, USA to determine whether water yield has changed over time, and to examine and attribute the causal mechanisms of change. We found that annual water yield increased in some watersheds from 1938 to the mid-1970s by as much as 55%, but this was followed by decreases up to 22% by 2013. Changes in forest evapotranspiration were consistent with, but opposite in direction to the changes in water yield, with decreases in evapotranspiration up to 31% by the mid-1970s followed by increases up to 29% until 2013. Vegetation survey data showed commensurate reductions in forest basal area until the mid-1970s and increases since that time accompanied by a shift in dominance from xerophytic oak and hickory species to several mesophytic species (i.e., mesophication) that use relatively more water. These changes in forest structure and species composition may have decreased water yield by as much as 18% in a given year since the mid-1970s after accounting for climate. Our results suggest that changes in climate and forest structure and species composition in unmanaged forests brought about by disturbance and natural community dynamics over time can result in large changes in water supply.

Keywords: climate change, evapotranspiration, forest hydrology, mesophication, streamflow, water yield

Received 14 December 2015 and accepted 4 March 2016

Introduction
Climate change (Melillo et al., 2014) and forest disturbances (Ice et al., 2004; Adams, 2013; Brantley et al., 2013, 2014; Bearup et al., 2014) are threatening the ability of forested mountain watersheds to provide the clean, reliable, and abundant fresh water necessary to support aquatic ecosystems and a growing human population (Postel & Richter, 2003; Viviroli et al., 2007). Forests in the densely populated eastern USA are especially important for provisioning human water supply. Recent estimates suggest that southeastern forests deliver surface drinking water to an estimated 2130 communities serving 48.7 million people (Caldwell et al., 2014). In particular, reanalysis of the data in Caldwell et al. (2014) shows that streamflow originating from the forest-dominated Southern Appalachian region supplies a large proportion of water to several major cities in the south (Table 1), and in total, the region provides drinking water to more than ten million people. The recent drought of 2007–2008 highlighted the vulnerability of these major population centers to changes in streamflow originating in the southern Appalachians, magnifying decades-long tensions among the states of Georgia, Alabama, and Florida for water releases from Lake Lanier (a reservoir on the Chattahoochee River originating in the southern Appalachians supplying water to Atlanta, Georgia). The drought cost the region an estimated $88 million and more than 1200 jobs due to reduced commercial activity (Bleakly Advisory Group Inc. et al., 2010). Despite the threats to water supply from forested mountain watersheds, we know little about the extent to which climate, forest structure, and forest species composition interact over many decades to affect streamflow. This knowledge-gap is due in-part to a paucity of long-term climate, streamflow, and vegetation datasets in unmanaged forest environments (Vose et al., 2011).

Water yield (Q) from a watershed is the basis of river flows, and over long time-scales is the balance of precipitation (P) inputs less evapotranspiration...
(ET) in watersheds with negligible groundwater losses. Thus, changes in either $P$ or ET will affect $Q$. Like $Q$, ET is regulated by water inputs (i.e., $P$) as well as atmospheric conditions affecting evaporation and plant water use including air temperature ($T$), vapor pressure deficit, wind speed, and net solar radiation (Monteith, 1965); thus increases in $T$ could increase ET and reduce $Q$. Potential evapotranspiration (PET) represents the net effect of all of the atmospheric conditions that influence ET and $Q$, as it is the amount of water evaporated from a wet surface with no resistance (Jensen et al., 1990). ET in a forested watershed is the sum of transpiration (water removed from the soil and used by plants during photosynthesis) and evaporation of precipitation intercepted by the forest canopy, stems, and soil litter layer. Forest structure (e.g., leaf area, stem density, basal area) influences both canopy interception of precipitation and tree water use. In addition, tree water use differs widely among species due to several tree architectural and physiological characteristics. Among these, xylem anatomy and sapwood area are two of the strongest predictors of stand water use (Wullschleger et al., 2001). Species with a ring-porous xylem anatomy have less functional sapwood area and thus transpire less water for a given stem diameter than species with a diffuse-porous xylem, semi-ring porous xylem, and tracheid xylem anatomies (Ford et al., 2011a,b) (Fig. S3). As a result, changes in climate, forest structure, and species composition could impact ET and $Q$ from forested mountain watersheds.

Here, we quantified changes in $Q$, and examined the relative contributions of changes in climate, forest structure, and forest species composition to the changes in $Q$ in six unmanaged, reference watersheds at the USDA Forest Service Coweeta Hydrologic Laboratory in western North Carolina, USA (Table 2; Fig. 1). Established in 1934, Coweeta is uniquely positioned to evaluate the effects of climate and forest changes on $Q$ in the region, having maintained climatic, streamflow, and vegetation records in several small, unmanaged watersheds for more than 75 years. Previous studies at Coweeta have shown that $T$ has been increasing at a rate of $0.5 \, ^\circ\text{C}$ per decade since the 1980s; and while the mean annual $P$ has not changed, $P$ in extremely wet (e.g., 90th percentile) and extremely dry (e.g., 25th percentile) years has increased and decreased over time, respectively (Ford et al., 2011b; Laseter et al., 2012) (Fig. S1). In addition to changes in climate, several forest disturbances ubiquitous across the southern Appalachian region have altered forest structure and species composition and have potentially affected $Q$. These include logging in the early 20th century, drought, hurricanes, and insect and disease outbreaks. Most notable among these was the introduction of the Chestnut Blight fungus [Endothia parasitica (Murr.) P.J. And. & H.W.] in the 1920s–1930s that led to widespread mortality of Carya dentata (Marsh. Borkh.) in eastern North American forests. In a process known as mesophication, disturbances and climate change over the 20th century have changed forest species composition from dominance by drought- and fire-tolerant xerophytic species to drought-and fire-intolerant mesophytic species across the eastern USA (Nowacki & Abrams, 2008, 2015; Pederson et al., 2015). In the southern Appalachians, species composition changed from dominance by C. dentata with ring-porous xylem in the 1930s, to drought-tolerant, xerophytic Quercus spp. with ring-porous xylem in the mid-century, and finally to dominance by drought-intolerant, mesophytic species (e.g., Acer rubrum L., Liriodendron tulipifera L.) with diffuse-porous xylem by the end of the century (Nelson, 1955; Elliott & Swank, 2008; Elliott & Vose, 2011; Ford et al., 2012) (Fig. S2). Based on their xylem anatomy and water use (Meyer, 1927; Day & Monk, 1974; Bauerle et al., 2006; Ford et al., 2011a,b; Brantley et al., 2013), these changes in species composition could have induced long-term changes in ET and $Q$. We used statistical time-series models to determine whether $Q$ and ET in high- and low-elevation replicate headwater watersheds in the Coweeta Basin are changing over time. We then examined the relative influences of changes in $P$, PET, and forest structure and species composition on the observed changes in $Q$ and ET. We hypothesize that $Q$ has decreased due to climate change

<table>
<thead>
<tr>
<th>City, State</th>
<th>Human population served</th>
<th>Percentage of water supply originating in the southern Appalachian mountain region (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greater Atlanta, Georgia area*</td>
<td>2 100 000</td>
<td>8–13</td>
</tr>
<tr>
<td>Charlotte, North Carolina</td>
<td>788 000</td>
<td>40</td>
</tr>
<tr>
<td>Greenville, South Carolina</td>
<td>350 000</td>
<td>57–100</td>
</tr>
<tr>
<td>Knoxville, Tennessee</td>
<td>236 000</td>
<td>57</td>
</tr>
</tbody>
</table>

*Dekalb and Gwinnett counties and the city of Atlanta.
in March and were the focus of this study (Fig. 1; Table 2). Watersheds in paired watershed experiments (Wilm, 1944) unmanaged since the 1920s to serve as control (i.e., reference) watersheds to demonstrate the impact of forest management. While many of the gaged watersheds have served as treatment (south-facing) and south (north-facing) sides of the basin. Water yield is typically high during extreme drought due to relatively high P and the large storage capacity of deep soils (Thomas, 1996). Nested within the Coweeta Basin are several smaller watersheds, 16 of which are currently instrumented to measure water yield. Most of these gaged watersheds lie on the north (south-facing) and south (north-facing) sides of the basin. While many of the gaged watersheds have served as treatment watersheds to demonstrate the impact of forest management practices on water quantity and quality, six have been left unmanaged since the 1920s to serve as control (i.e., reference) watersheds in paired watershed experiments (Wilm, 1944) and were the focus of this study (Fig. 1; Table 2).

### Materials and methods

#### Study area

The east-facing 1626 ha Coweeta Basin is located in western North Carolina, USA (Fig. 1) in the Appalachian Highlands Region, Blue Ridge Province (Fenneman, 1917). Elevation in the basin ranges from 626 m above mean sea level at the valley bottom to 1592 m on the western boundary. Climate is classified as marine, humid temperate (Peel et al., 2007). Mean T and annual P at the valley bottom at CS01 are 12.6 °C and 1794 mm yr⁻¹ (Ford et al., 2011b). Most P occurs as rain in frequent, small, low intensity storms in all seasons (Swift et al., 1988). Air temperature and P are highly influenced by elevation with T decreasing approximately 5 °C per 1000 m elevation gain (Bolstad et al., 1998) and P increasing approximately 5% per 100 m (Swift et al., 1988). Water yield is typically highest in March–April and lowest in September–October, and is perennial even during extreme drought due to relatively high P and the large storage capacity of deep soils (Thomas, 1996). Nested within the Coweeta Basin are several smaller watersheds, 16 of which are currently instrumented to measure water yield. Most of these gaged watersheds lie on the north (south-facing) and south (north-facing) sides of the basin. While many of the gaged watersheds have served as treatment watersheds to demonstrate the impact of forest management practices on water quantity and quality, six have been left unmanaged since the 1920s to serve as control (i.e., reference) watersheds in paired watershed experiments (Wilm, 1944) and were the focus of this study (Fig. 1; Table 2).

### Table 2 General characteristics of reference watersheds at the Coweeta Hydrologic Laboratory in Otto, NC, USA. Mean annual precipitation (P) and water yield (Q) based on data collected over water years (WY, May–April) during the common period of record (1956–2013) across all watersheds. Watersheds and rain gage locations are shown in Fig. 1

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Units</th>
<th>02</th>
<th>14</th>
<th>18</th>
<th>27</th>
<th>34</th>
<th>36</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area</td>
<td>ha</td>
<td>12.26</td>
<td>61.03</td>
<td>12.46</td>
<td>39.05</td>
<td>32.70</td>
<td>48.60</td>
</tr>
<tr>
<td>Mean elevation</td>
<td>m</td>
<td>849</td>
<td>878</td>
<td>823</td>
<td>1254</td>
<td>1020</td>
<td>1288</td>
</tr>
<tr>
<td>Mean basin slope</td>
<td>%</td>
<td>53</td>
<td>50</td>
<td>55</td>
<td>57</td>
<td>54</td>
<td>62</td>
</tr>
<tr>
<td>Aspect</td>
<td></td>
<td>SSE</td>
<td>NW</td>
<td>NW</td>
<td>NE</td>
<td>SE</td>
<td>ESE</td>
</tr>
<tr>
<td>Year of first complete flow record</td>
<td>WY</td>
<td>1937</td>
<td>1938</td>
<td>1938</td>
<td>1948</td>
<td>1956</td>
<td>1944</td>
</tr>
<tr>
<td>Nearest rain gage</td>
<td></td>
<td>SRG20</td>
<td>SRG41</td>
<td>SRG96</td>
<td>SRG31/SRG55*</td>
<td>SRG40</td>
<td>SRG02</td>
</tr>
<tr>
<td>Mean precipitation (P)</td>
<td>mm yr⁻¹</td>
<td>1849</td>
<td>1842</td>
<td>2028</td>
<td>2316</td>
<td>1971</td>
<td>2036</td>
</tr>
<tr>
<td>Mean water yield (Q)</td>
<td>mm yr⁻¹</td>
<td>819</td>
<td>997</td>
<td>1019</td>
<td>1694</td>
<td>1122</td>
<td>1683</td>
</tr>
<tr>
<td>Mean evapotranspiration (ET = P – Q)</td>
<td>mm yr⁻¹</td>
<td>1030</td>
<td>845</td>
<td>1009</td>
<td>622</td>
<td>849</td>
<td>352</td>
</tr>
<tr>
<td>Q/P</td>
<td></td>
<td>0.44</td>
<td>0.54</td>
<td>0.50</td>
<td>0.73</td>
<td>0.57</td>
<td>0.83</td>
</tr>
</tbody>
</table>

*Precipitation averaged across standard rain gages (SRG) shown.


### Vegetation and disturbance history

Species composition in the ca. 85 year old forest of the Coweeta Basin reflects the disturbance history of the basin and the region (Fig. S2). Like much of the southern Appalachian region, forest products were extracted from the Coweeta Basin in the early 20th century. The entire basin was selectively harvested between 1909 and 1923; all trees greater than 15 inches (38 cm) at the stump were removed (Douglass & Hoover, 1988). The chestnut blight fungus was first observed at Coweeta in the early 1920s. By 1930, most of the previously unlogged C. dentata trees (comprising 36% of the total basal area) were infected (Woods & Shanks, 1959; Elliott & Swank, 2008). Chestnut blight functionally eliminated C. dentata from over 3.5 million ha of upland forests in eastern North America since the early 20th century (Anagnostakis, 1987). By 1942, the forest once dominated by C. dentata ‘consisted mostly of an oak-hickory stand of low quality with scattered openings occupied by mountain-laurel (Kalmitia latifolia L.), rhododendron (Rhododendron maximum L.), and other low, shrubby species’ (Hibbert, 1969). Today C. dentata only occurs as a minor understory species (Elliott & Swank, 2008). Fall cankerworm (Alsophila pomelaria Harris), a spring defoliator, consumed about 33% of the total leaf mass of Quercus species between 1976 and 1978 (Swank et al., 1981) at higher elevations with a measurable growth reduction during those years (Elliott et al., 2015). Drought in the 1980s resulted in the creation of small canopy gaps (mean 172 m²) due to single-tree snags of mostly larger, older oaks on drier slopes and ridges (Clinton et al., 1993) at lower elevations. Little to no tree damage and canopy gap creation from hurricane Opal in 1996 was observed in any of the reference watersheds in the Coweeta Basin based on aerial photographs (W. Swank, unpublished data), although large-scale tree damage across the region was documented (Greenberg & McNab, 1998). The arrival of the hemlock woolly adelgid (HWA, Adelges tsugae Annand) to the region and first observed at Coweeta in 2003 has resulted in an almost complete loss of this riparian species once found in abundance at
high elevation and/or north-facing riparian and cove areas (Ford et al., 2012). The contemporary species composition (Fig. S2) consists of oak-hickory forests at lower elevations and northern hardwoods at higher elevations, both with increasing dominance of mesophytic species (e.g., *A. rubrum*, *L. tulipifera*) in the overstory and *Rhododendron* in the understory (Elliott & Swank, 2008; Elliott & Vose, 2011).

**Field measurements**

Low-elevation watersheds (<1000 m elevation) were instrumented with permanent weir structures in the mid-1930s, and high-elevation watersheds (>1000 m elevation) somewhat later (1944–1956, Table 2), to measure stage above the weir notch on 5-min intervals over the period of record (Fig. 1). The measured stage was used to calculate streamflow using rating equations dependent on the geometry of each weir (Reinhart & Pierce, 1964). Q was calculated on a unit-area basis by dividing streamflow volume by the upstream drainage area measured by field survey (Table 2). Watershed P was estimated by pairing each watershed with the nearest eight inch (20.3 cm) National Weather Service standard rain gage among those distributed across the Coweeta Basin (Table 2; Fig. 1). PET was estimated using a 36 inch (91.4 cm) diameter 18 inch (45.7 cm) deep buried evaporation pan located in the valley bottom at climate station CS01 (Fig. 1). Annual ET was computed using the water balance method by taking the difference between annual P and annual Q, assuming the largely impermeable bedrock underlying the basin results in negligible deep groundwater losses (Douglass & Swank, 1972). ET calculated in this manner on an annual time-step may have errors in some years due to year-to-year changes in storage (e.g., before and after drought periods), however we expect that these effects will only increase the short-term variability (i.e., scatter or noise) in the ET estimates and not affect estimates of changes in ET over long periods of time. Soils are consistently wet in May, thus all annual Q, P, PET, and ET values were calculated on a May to April water year to minimize the effects of interannual changes in soil water storage on ET estimation by the water balance method (Swift et al., 1975).

Field vegetation survey plots of 20 × 40 m were established and measured in 1934 on approximately N-S transects at 200 m intervals. The plots were remeasured in the 1970s (1969–1973), 1990s (1988–1993), and 2010s (2009–2013) (Elliott & Swank, 2008; Elliott & Vose, 2011) resulting in four survey periods at approximately 20–35 year intervals. The vegetation survey plots were originally established to capture broad spatial patterns in vegetation across the entire Coweeta Basin, but not necessarily for individual watersheds within the basin. However, forest community type in the southern Appalachian mountains varies according to topographic position such as high ridge, mid-slope, cove, and riparian areas (Day & Monk, 1974). Plot locations were overlain with watershed boundaries in a Geographic Information System to identify plot and watershed associations. The relationship between topographic position and forest community type permitted an assessment of whether plots located in a given watershed were sufficient in number and sufficiently distributed across topographic positions to characterize the vegetation in the watershed.

We examined the spatial distribution of plots in each watershed with respect to topographic position to determine whether the vegetation plots in each watershed provided a...
reasonable representation of the range of forest types that could be expected in each watershed. Across the six reference watersheds, vegetation survey data from the 30 plots located in WS14 were considered to be reasonably representative of the topographic gradient from ridges, mid-slopes, to riparian areas in multiple locations in the watershed and could be used to relate changes in forest structure and species composition to \( Q \). Vegetation survey data from all other watersheds could not be evaluated in this study because there were either too few plots within the watershed and/or the plots are not located such that they represented the topographic gradient of the watershed. For example, there were only two vegetation survey plots in WS36, WS02, WS18, and WS34 had seven to eight plots, but in all three watersheds the plots were located near the ridge and high slope positions and did not include mid-slope and riparian areas. WS27 had 16 plots arranged in two transects, one in steep, rocky terrain near the ridge at the highest elevation and one near the watershed outlet at lower elevation; these transects were positioned parallel to the slope and thus did not provide representation of the mid-slope topographic position. Although the plots in WS18 were not considered to be representative of the watershed, vegetation survey data from these plots matched the pattern of vegetation across the Coweeta Basin as a whole (Fig. S2) and were included to supplement the vegetation data in adjacent WS14 because they were also surveyed in 1941 and 1953 (total of six survey periods) providing additional temporal resolution during the decline of \( C. \ dentata \).

**Modeling approach**

We developed statistical models to examine long-term changes in annual \( Q \) from the six small, unmanaged forested mountain watersheds at Coweeta representing a range of topographic settings and climate regimes (Table 2; Fig. 1). Autoregressive-Integrated-moving average (ARIMA) time-series models (Ford et al., 2005, 2011b; Laseter et al., 2012) were fitted using the PROC ARIMA procedure in SAS version 9.4 (SAS, 2013) to (i) determine the magnitude and timing of changes in \( Q \), \( P \), PET, and ET for each watershed, and (ii) separate climate from forest impacts on \( Q \). ARIMA time-series models are a type of regression model that can account for serial correlation in the data and can use other independent variables to describe the effect of these factors (e.g., climate and/or vegetation changes) on the dependent variable (e.g., \( Q \)) using transfer functions. When the residuals of the predicted dependent time series are not randomly distributed over time, there are external perturbations affecting the dependent time series that are not included in the model. ‘Interventions’ can be constructed to account for these external perturbations (Box & Tiao, 1975). For example, if a forested watershed was completely harvested and permanently converted to grass pasture, one could expect a sustained step increase in \( Q \) from that watershed assuming a constant climate. In that case, an intervention representing the conversion from forest to pasture could be included in the model using an indicator variable with a coefficient. The indicator was zero for years prior to the harvest and one for years after the harvest, and the estimated regression coefficient for the intervention represents the magnitude of the step change in \( Q \). The year in which the watershed was converted from forest to pasture is the ‘breakpoint’ in the time series, or the time in which the external perturbation represented by the intervention begins to affect the dependent variable \( Q \). Other types of interventions that affect \( Q \) could include a pulse (e.g., temporary storm damage to vegetation) or a ramp representing a gradual change over time (e.g., the aging of a forest stand and associated species changes). For this study, we used ramp interventions because we were interested in examining effects of gradual changes in forest structure and species composition on \( Q \) over the long term. This type of intervention was appropriate because (i) visual inspection of the time series suggested gradual changes in \( Q \), \( P \), and PET over the period of record and (ii) previous studies of the vegetation survey plots in the basin suggested gradual changes in forest structure and species composition since 1934 (Elliott & Swank, 2008; Elliott & Vose, 2011) (Fig. S2).

The Akaike’s Information Criterion (AIC) was used to evaluate the parsimony and goodness-of-fit among models of a given dependent variable. The model having the lowest AIC for that variable is the best fitting and most parsimonious model (Johnson & Omland, 2004). Differences in the AIC values among candidate models (\( \Delta_i = AIC_i - AIC_{\text{min}} \)) were used to compute a relative weight (\( w_i \)) of each model relative to the fit of all models:

\[ w_i = \frac{e^{-0.5A_i}}{\sum_{i=1}^{R} e^{-0.5A_i}} \]

with the sum of all \( w_i \) equal to one. The final model selected was the model with the highest \( w_i \) (Burnham & Anderson, 2002; Johnson & Omland, 2004).

We considered four candidate models for each dependent variable, each model making different assumptions regarding the timing and direction of change in the variable over time. The four models included (i) no change in the variable, (ii) gradual change at the beginning of the time series ending in a given year between 1950 and 2000 with no change after that year, (iii) gradual change at the end of the time series beginning in a given year between 1950 and 2000 with no change before that year, and (iv) gradual change both at the beginning and end of the time series, each with potentially different end and start years, respectively. The models that assumed no change in the variable (#1 above) did not include interventions. The models that assumed change in the variable at the beginning, end, or both beginning and end of the time series (#2-4 above) included interventions. For these models, each year between 1950 and 2000 was evaluated as a potential breakpoint year for the beginning or end of change in that variable by testing a model that included an intervention that started or ended in that year. The model among these with the highest \( w_i \) of all of the models of different breakpoint years was selected as the best fitting, most parsimonious model of that candidate model. Lastly, the best fitting models of each of the four candidate models were compared, and the model among these with the highest \( w_i \) was selected as the best
fitting model and therefore best represented the change in that variable over time.

Detecting the magnitude and timing of changes in Q, P, PET, and ET

Models considered when detecting and quantifying changes in Q, P, PET, and ET (Table 3a) included the mean value (model 1), the mean value plus a ramp intervention at the beginning of the time series ending at year $T_{\text{int1}}$ (model 2), the mean value plus a ramp intervention at the end of the time series beginning at year $T_{\text{int2}}$ (model 3), and the mean value with both a ramp intervention ending at year $T_{\text{int1}}$ and beginning at year $T_{\text{int2}}$ (model 4), where $t = \text{time (water year)}$, $\mu$ = the estimated mean value of Q, P, PET, or ET over the period estimation, $X_t$ = ramp intervention from start of time series to $T_{\text{int1}}$, $Y_t$ = ramp intervention from $T_{\text{int2}}$ to end of time series, $Y_t = \left\{ \begin{array}{ll} 0, & t < T_{\text{int2}} \\ t - T_{\text{int2}}, & t \geq T_{\text{int2}} \end{array} \right.$

where $T_{\text{int1}} = \text{breakpoint year for } X_t$, $\alpha_1 = \text{coefficient on ramp intervention } X_t$, representing the slope or rate of change in $Q$, $P$, PET, or ET from start of time series to year $T_{\text{int1}}$, $Y_t$ = ramp intervention from $T_{\text{int2}}$ to end of time series, $a_t = \text{random error}$.

Separating the influences of climate and forest structure and species composition on Q

Autoregressive-integrated-moving average models were fitted to separate the influences of climate and forest structure and species composition on Q. Climate effects were incorporated using P and PET as explanatory variables in the models. We could not explicitly use the vegetation survey data directly in the models because while the vegetation data extended more than 70 years, they lacked sufficient temporal resolution and spatial coverage across all watersheds. In lieu of directly incorporating vegetation data into the models to quantify the effect


Table 3 Models considered for quantifying the magnitude and timing of changes in annual water yield ($Q$), precipitation ($P$), potential evapotranspiration ($PET$), and evapotranspiration ($P - Q$) (a), and separating the impacts of climate and forest structure and species composition on $Q$ (b). Models in (a) are shown using calculations for $Q$ as an example, model form is the same for $P$, PET, and $P - Q$. Climate variables considered in (b) included annual $P$ and annual PET.

<table>
<thead>
<tr>
<th>Model ID</th>
<th>Model form</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Quantifying the magnitude and timing of changes in $Q$, $P$, PET, and ET</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Mean $Q_t = \mu + \alpha_1 + Y_t$</td>
</tr>
<tr>
<td>2</td>
<td>Mean with ramp intervention $X_t$ at beginning of time series ending at $T_{\text{int1}}$ $Q_t = \mu + \alpha_3 \times X_t + \alpha_1$</td>
</tr>
<tr>
<td>3</td>
<td>Mean with ramp intervention $Y_t$ at end of time series beginning at $T_{\text{int2}}$ $Q_t = \mu + \alpha_2 \times Y_t + \alpha_1$</td>
</tr>
<tr>
<td>4</td>
<td>Mean with two ramp interventions $X_t$ and $Y_t$ ending at $T_{\text{int1}}$ and starting at $T_{\text{int2}}$ $Q_t = \mu + \alpha_0 \times X_t + \alpha_1 \times Y_t + \alpha_1$</td>
</tr>
<tr>
<td>(b) Separating the impacts of climate and forest structure and species composition on $Q$</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Precipitation ($P$) only $Q_t = \alpha_2 \times P_t + \alpha_1$</td>
</tr>
<tr>
<td>6</td>
<td>P with ramp intervention $X_t$ at beginning of time series ending at $T_{\text{int1}}$ $Q_t = \alpha_2 \times P_t + \alpha_4 \times X_t + \alpha_1$</td>
</tr>
<tr>
<td>7</td>
<td>P with ramp intervention $Y_t$ at end of time series beginning at $T_{\text{int2}}$ $Q_t = \alpha_2 \times P_t + \alpha_4 \times Y_t + \alpha_1$</td>
</tr>
<tr>
<td>8</td>
<td>P with two ramp interventions $X_t$ and $Y_t$ ending at $T_{\text{int1}}$ and starting at $T_{\text{int2}}$ $Q_t = \alpha_2 \times P_t + \alpha_4 \times X_t + \alpha_5 \times Y_t + \alpha_1$</td>
</tr>
<tr>
<td>9</td>
<td>P and Potential evapotranspiration (PET) only $Q_t = \alpha_2 \times P_t + \alpha_3 \times PET_t + \alpha_1$</td>
</tr>
<tr>
<td>10</td>
<td>P and PET with ramp intervention $X_t$ at beginning of time series ending at $T_{\text{int1}}$ $Q_t = \alpha_2 \times P_t + \alpha_3 \times PET_t + \alpha_4 \times X_t + \alpha_1$</td>
</tr>
<tr>
<td>11</td>
<td>P and PET with ramp intervention $Y_t$ at end of time series beginning at $T_{\text{int2}}$ $Q_t = \alpha_2 \times P_t + \alpha_3 \times PET_t + \alpha_5 \times Y_t + \alpha_1$</td>
</tr>
<tr>
<td>12</td>
<td>P and PET with two ramp interventions $X_t$ and $Y_t$ ending at $T_{\text{int1}}$ and starting at $T_{\text{int2}}$ $Q_t = \alpha_2 \times P_t + \alpha_3 \times PET_t + \alpha_4 \times X_t + \alpha_5 \times Y_t + \alpha_1$</td>
</tr>
</tbody>
</table>
of changes in forest structure and species composition, interventions were added to the Q models to approximate the influence of changes in forest structure and species composition (Box & Jenkins, 1976; Rasmussen et al., 2001; Brockwell & Davis, 2002).

Eight candidate models were evaluated (Table 3b) including Q predicted as a function of P only (model 5), P with the three intervention scenarios described above (models 6–8), and PET only (model 9), and P and PET with the three intervention scenarios (models 10–12), where \( X_t \) and \( Y_t \) are defined as above and: \( \alpha_2 = \) coefficient on \( P \) term, representing the contribution of \( P \) to the magnitude \( Q \), \( \alpha_3 = \) coefficient on PET term, representing the contribution of PET to the magnitude \( Q \), \( \alpha_4 = \) coefficient on ramp intervention \( X_t \), representing the slope or rate of change in \( Q \) that is not explained by climate from the start of time series to year \( T_{int1} \), \( \alpha_5 = \) coefficient on ramp intervention \( Y_t \), representing the slope or rate of change in \( Q \) that is not explained by climate from year \( T_{int2} \) to end of time series.

With each scenario, residuals were checked for autocorrelation and white noise to insure random variation and serial independence.

Where interventions improved the fit of the model predicting \( Q \) as a function of climate, the slope of the intervention was interpreted as the change in \( Q \) not caused by climate and likely attributable to changes in forest structure and species composition. We visually compared the direction of changes in basal area and species composition over time to the direction of changes in \( Q \) attributed to changes in vegetation (i.e., the slope of the interventions) in WS14 where vegetation survey plots were most representative of the watershed. We quantified the probable effect of the changes in forest structure and species composition on \( Q \) in each watershed by computing the difference between \( Q \) predicted using the selected intervention models for each watershed (\( Q \) affected by both climate and forest change) and \( Q \) predicted using these models but with intervention coefficients \( \alpha_4 \) and \( \alpha_5 \) set to zero (\( Q \) affected by climate only).

**Results**

Water yield increased in all low-elevation watersheds in the first half of the 20th century and declined in the latter part of the century in north-facing low-elevation watersheds (Fig. 2; Tables 4 and S2). Water yield in south-facing low-elevation WS02 increased by 24.3 mm yr\(^{-1}\) (55%) until 1950, and increased in north-facing low-elevation watersheds by 7.3–8.5 mm yr\(^{-1}\) (31%–36% in WS14 and WS18, respectively), until 1974. Water yield then decreased in these north-facing watersheds by 6.4–6.5 mm yr\(^{-1}\) (–22% for both WS14 and WS18, respectively) after 1974. Although we did not identify significant changes in \( Q \) for high-elevation watersheds, likely because \( Q \) in these watersheds is much more variable than low-elevation watersheds, temporal patterns in \( Q \) followed the same trend and were highly correlated to those of low-elevation watersheds \((R^2 > 0.89, P < 0.0001)\).

Consistent with the changes in \( Q \), ET decreased in all watersheds in the first half of the 20th century and increased in the latter part of the century in all watersheds but high-elevation WS27 (Fig. 3; Tables 4 and S3). Decreases in ET prior to breakpoint years of low-elevation watersheds ranged from 2.3–3.4 mm yr\(^{-1}\) (9% in both WS18 and WS2), and of high-elevation watersheds by 4.3–4.9 mm yr\(^{-1}\) (31% and 12% in WS36 and WS27). Observed decreases in ET for WS34 were not comparable to the other watersheds due to the shorter period of record. Evapotranspiration increased in low-elevation watersheds in the latter part of the 20th century by 3.7–9.3 mm yr\(^{-1}\) (15% and 13% in WS14 and WS2), and in high-elevation watersheds by 6.2–8.7 mm yr\(^{-1}\) (29% and 15% in WS36 and WS34).

Precipitation and PET were strong predictors of \( Q \) variability, but did not completely explain the long-term temporal pattern of changes in \( Q \) and ET. Annual \( P \) increased by 37.3 mm yr\(^{-1}\) (19.7%) until 1946, but the central tendency has not changed since that time.
Table 4  Best fitting models to quantify the magnitude and timing of changes in $Q$, $ET$, $P$, and PET. Models are described in Table 3a. Results for all models are shown in Tables S2–S4.

<table>
<thead>
<tr>
<th>Watershed</th>
<th>Best model</th>
<th>$\mu$ (mm)</th>
<th>$T_{int1}$ (year)</th>
<th>$\omega_0$ (mm)</th>
<th>$P$</th>
<th>$T_{int2}$ (year)</th>
<th>$\omega_1$ (mm)</th>
<th>$P$</th>
<th>AIC</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water yield ($Q$)</td>
<td>2</td>
<td>2</td>
<td>820.2</td>
<td>1950</td>
<td>24.3</td>
<td>0.036</td>
<td>1999</td>
<td>9.3</td>
<td>0.003</td>
<td>900.7</td>
</tr>
<tr>
<td>14</td>
<td>4</td>
<td>1108.5</td>
<td>1974</td>
<td>7.3</td>
<td>0.034</td>
<td>1974</td>
<td>–6.4</td>
<td>0.042</td>
<td>1074.8</td>
<td>0.37</td>
</tr>
<tr>
<td>18</td>
<td>4</td>
<td>1138.3</td>
<td>1974</td>
<td>8.5</td>
<td>0.025</td>
<td>1974</td>
<td>–6.5</td>
<td>0.059</td>
<td>1090.3</td>
<td>0.38</td>
</tr>
<tr>
<td>34</td>
<td>1</td>
<td>1122.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>830.8</td>
<td>0.38</td>
</tr>
<tr>
<td>27</td>
<td>1</td>
<td>1695.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>972.8</td>
<td>0.40</td>
</tr>
<tr>
<td>36</td>
<td>1</td>
<td>1682.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1031.1</td>
<td>0.46</td>
</tr>
<tr>
<td>Evapotranspiration ($ET$)</td>
<td>2</td>
<td>4</td>
<td>1011.6</td>
<td>1967</td>
<td>–3.4</td>
<td>0.004</td>
<td>1999</td>
<td>9.3</td>
<td>0.003</td>
<td>900.7</td>
</tr>
<tr>
<td>14</td>
<td>4</td>
<td>800.3</td>
<td>1974</td>
<td>–3.1</td>
<td>0.001</td>
<td>1980</td>
<td>3.7</td>
<td>&lt;0.001</td>
<td>885.6</td>
<td>0.95</td>
</tr>
<tr>
<td>18</td>
<td>4</td>
<td>967.1</td>
<td>1978</td>
<td>–2.3</td>
<td>0.012</td>
<td>1985</td>
<td>4.0</td>
<td>0.005</td>
<td>902.9</td>
<td>0.78</td>
</tr>
<tr>
<td>34</td>
<td>4</td>
<td>827.3</td>
<td>1959</td>
<td>–59.8</td>
<td>0.033</td>
<td>1999</td>
<td>8.7</td>
<td>0.015</td>
<td>704.2</td>
<td>0.67</td>
</tr>
<tr>
<td>27</td>
<td>2</td>
<td>618.1</td>
<td>1965</td>
<td>–4.9</td>
<td>0.046</td>
<td></td>
<td></td>
<td></td>
<td>787.6</td>
<td>0.45</td>
</tr>
<tr>
<td>36</td>
<td>4</td>
<td>317.6</td>
<td>1978</td>
<td>–4.3</td>
<td>0.001</td>
<td>1998</td>
<td>6.2</td>
<td>0.080</td>
<td>855.6</td>
<td>0.58</td>
</tr>
<tr>
<td>Precipitation ($P$)</td>
<td>2</td>
<td>4</td>
<td>1810.4</td>
<td>1946</td>
<td>37.3</td>
<td>0.084</td>
<td>1997</td>
<td>4.6</td>
<td>0.002</td>
<td>819.9</td>
</tr>
<tr>
<td>Potential Evapotranspiration (PET)</td>
<td>4</td>
<td>879.2</td>
<td>1949</td>
<td>–5.0</td>
<td>0.046</td>
<td>1997</td>
<td>4.6</td>
<td>0.002</td>
<td>819.9</td>
<td>0.699</td>
</tr>
</tbody>
</table>

(Tables 4 and S4; Fig. 4a). Annual PET decreased by 5.0 mm yr$^{-1}$ (5.9%) until 1949, and then increased by 4.6 mm yr$^{-1}$ (8.3%) after 1997 (Tables 4 and S4; Fig. 4b). Precipitation and PET together explained 88–94% of the variability in annual $Q$ across the six watersheds (Table 5), while $P$ alone explained 67–88% and PET explained an additional 6–23% (Table S5, cf. models 9 and 5). Although $P$ and PET explained a significant proportion of the variability in $Q$, residuals (i.e., model error) of the $Q$ models, while uncorrelated and normally distributed with a mean of zero (Table S6), had a nonlinear relationship over time (Fig. 5), suggesting that climate did not completely explain the temporal changes in $Q$.

Changes in forest structure and species composition are consistent with the temporal pattern of residuals in the models of $Q$ as a function of climate (Figs 5 and 6), and likely contribute to the observed changes in $Q$ (Fig. 2). The mean total overstory tree basal area in WS14 decreased 15% by 1970 due to the loss of $C$. dentata, but had recovered to within 3% of the 1934 level by 2010. Similar temporal patterns in total basal area were found in WS18, with a consistent decline between 1934 and 1970 and increases since that time. By the 1970s, the forest was dominated by ring-porous $Quercus$ species, but by the end of the 20th century, a diversity of mostly diffuse-porous mesophytic species became dominant (Elliott & Swank, 2008) including $L$. tulipifera, $A$. rubrum, and $Betula$ lenta L. Thus, while the total basal area was similar in 1934 and 2010, the species distribution changed from dominance by $C$. dentata to $Quercus$ species and finally to diffuse-porous, mesophytic species (Fig. 6b, c) resulting in potential changes in transpiration over time (Fig. S3).

Interventions added to the statistical models of $Q$ allowed us to estimate the likely magnitude of the impact of changes in forest structure and species composition on $Q$. When added to the $Q$ models, the interventions: improved model fit while maintaining parsimony (Table S5); minimized the temporal pattern of residuals (Fig. 5); and were consistent with, and thus a proxy for, the effect of the observed changes in forest basal area on $Q$ (Fig. 6). Taking the difference in adjusted $R^2$ values between models that predicted $Q$ as a function of climate and vegetation (Table S5) and models that predicted $Q$ as a function of climate only (Table S5 model 9), we found that the interventions and the changes in forest structure and species composition they represent explained an additional 1–2% of the variability in $Q$ beyond that explained by climate. Declines in forest basal area likely increased $Q$ in all low-elevation watersheds by 3.3–4.2 mm yr$^{-1}$ until 1976, and in high-elevation watersheds by 5.3–6.5 mm yr$^{-1}$ (WS36 and WS27) until 1973 (Table 5; Fig. 7). Again, increases in high-elevation watershed WS34 $Q$ due to forest change in the early 20th century were not comparable to the others because the period of record in this watershed began 18 years later. In the latter part of the 20th century, the changes in forest structure and species composition likely decreased $Q$ in
all low-elevation watersheds and high-elevation WS34. These decreases in $Q$ due to forest change began in the late 1960s to early 1970s, and ranged from 2.4–3.3 mm yr$^{-1}$ (in WS02 and WS14, Table 5). Forest changes in the latter half of the 20th century may have decreased $Q$ by as much as 18% in low-elevation watersheds in a given year vs. what would be expected due to changes in climate only (Fig. 7).

Discussion

Both climate and changes in forest structure and species composition interacted to induce long-term changes in $Q$ from forested watersheds in the southern Appalachian mountains. The variability in $Q$ has been shown to correspond to larger global climate cycles including the El Niño Southern Oscillation and the Pacific Decadal Oscillation (Jones et al., 2012). While projections of trends in $P$ for the region from General Circulation Models remain ambiguous over the 21st century (IPCC, 2013), $T$ is projected to increase with certainty (IPCC, 2013; Melillo et al., 2014) resulting in predicted increases in PET (Milly & Dunne, 2011) and ET (Kirtman et al., 2013). These projections of future $P$, $T$, PET, and ET are consistent with our recent observations in the long-term record suggesting negligible trends in mean $P$ over time (Ford et al., 2011b; Laseter et al., 2012), increases in $T$ since the 1980s (Ford et al., 2011b; Laseter et al., 2012), and increases in PET and ET since 1980 (this study).

We can perhaps expect continued increases in ET and decreases in $Q$ through the 21st century strictly from a climate perspective; however, increases in PET may or may not manifest as proportional increases in ET because ET is also influenced by other factors such as atmospheric CO$_2$, soil moisture stress, leaf area, and ozone concentrations. Plants regulate stomatal conductance to reduce transpiration during extreme hydro-climatic conditions such as low soil moisture, high wind speed, and high vapor pressure deficit. There is considerable uncertainty surrounding ecosystem responses to elevated atmospheric CO$_2$ including changes in ET and/or water use efficiency (WUE: carbon gained per unit water consumed) given tree regulation of stomata during photosynthesis. Studies assessing whether ET or WUE has changed with increasing CO$_2$ have drawn different conclusions depending in part on the scale at which they were conducted (i.e., leaf, stand, or watershed). Reductions in stomatal conductance and transpiration are expected to occur under increased atmospheric CO$_2$ concentration such that photosynthesis is maximized for a given level of water availability (Katul et al., 2010; Manzoni et al., 2013; Palmroth et al., 2013). Global meta-analyses across many forest types
suggest that WUE has increased over roughly the last century (e.g., Penuelas et al., 2011; Van Der Sleen et al., 2015) and in particularly over the last few decades (Keenan et al., 2013). While the latter study shows increasing WUE with rising CO$_2$, it is largely driven by decreased ET and not increased productivity; partially explained by the decrease in stomatal conductance with enhanced CO$_2$ (Herrick et al., 2004; Domec et al., 2009; Leakey et al., 2009). Despite potential changes in forest ET in response to rising CO$_2$, the magnitude of the change in Q due increasing WUE is expected to be small relative to changes in precipitation (Leuzinger & Korner, 2010) and is opposite in direction to the changes in ET due to the variability in ET, and particularly in steep, flashy high-elevation watersheds like those in the southern Appalachians with high Q/P (~0.7) and a large proportion (~20%) of Q occurring during and immediately after storm events (Swift et al., 1988). In contrast, low-elevation watersheds had Q/P of approximately 0.5 (Table 2) and approximately 5% of Q derived from storm events. Changes can be more readily detected for variables with relatively less variability such as ET (Fig. 3) and in fact changes in ET were detected in both low- and high-elevation watersheds. Although changes in Q were not detected in high-elevation watersheds, the best fitting Q models for high-elevation watersheds that included interventions at the beginning and end of the time series had the same 1974 breakpoint as those models for the low-elevation watersheds (model 4, Table S2). This suggests that the temporal patterns in Q observed in low-elevation watersheds may have also been present in the high-elevation watersheds but they may have been masked by the interannual variability. As a result of this variability, these models were not selected as the best fitting, most parsimonious models among those evaluated and we could not justify using these models to represent the changes in Q over time.

The ARIMA time-series modeling approach also allowed us to separate the effects of climate and changes in vegetation on Q. The magnitude and sign of $P$ and PET coefficients in the models that predicted Q as a function of climate and vegetation change using interventions (Table 5) provide support for the adequacy of the model structure, as they generally align with previously published information on hydrological processes across these watersheds (see Appendix S1).

### Table 5: Models used to separate the impacts of climate and forest structure and species composition on water yield (Q) for each watershed (WS). Models are described in Table 3b. Results for all models are shown in Tables S5. All model parameters are significant at $p < 0.010$

<table>
<thead>
<tr>
<th>WS</th>
<th>Model</th>
<th>$P$</th>
<th>$r_2$</th>
<th>$r_3$</th>
<th>$T_{int1}$ (year)</th>
<th>$r_4$ (mm)</th>
<th>$Y_1$</th>
<th>$T_{int2}$ (year)</th>
<th>$r_5$ (mm)</th>
<th>Adj. $R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>9</td>
<td>0.83</td>
<td>-0.82</td>
<td>1972</td>
<td>4.2</td>
<td>1972</td>
<td>-2.4</td>
<td>1972</td>
<td>893.3</td>
<td>0.882</td>
</tr>
<tr>
<td>14</td>
<td>9</td>
<td>0.85</td>
<td>-0.65</td>
<td>1974</td>
<td>4.0</td>
<td>1974</td>
<td>-3.3</td>
<td>1974</td>
<td>879.1</td>
<td>0.994</td>
</tr>
<tr>
<td>18</td>
<td>12</td>
<td>0.86</td>
<td>-0.55</td>
<td>1976</td>
<td>3.3</td>
<td>1976</td>
<td>-2.9</td>
<td>1976</td>
<td>907.7</td>
<td>0.827</td>
</tr>
<tr>
<td>27</td>
<td>10</td>
<td>0.96</td>
<td>-0.59</td>
<td>1965</td>
<td>6.5</td>
<td>1965</td>
<td>-2.6</td>
<td>1965</td>
<td>786.1</td>
<td>0.650</td>
</tr>
<tr>
<td>34</td>
<td>12</td>
<td>0.86</td>
<td>-0.56</td>
<td>1967</td>
<td>16.9</td>
<td>1967</td>
<td>-2.6</td>
<td>1967</td>
<td>701.2</td>
<td>0.836</td>
</tr>
<tr>
<td>36</td>
<td>10</td>
<td>1.10</td>
<td>-0.65</td>
<td>1973</td>
<td>5.3</td>
<td>1973</td>
<td>-2.6</td>
<td>1973</td>
<td>635.2</td>
<td>0.664</td>
</tr>
</tbody>
</table>

Changes in forest structure and species composition, while explaining a smaller proportion of the variability than climate, likely had considerable impacts on the magnitude of annual $Q$, particularly in dry years. For example, in 2001 when annual $P$ was 31% below the 1938–2013 mean, the forest change effect decreased $Q$ by 18% compared to what would have been expected based on climate and had the forest structure and species composition remained unchanged since the 1970s (WS02, Fig. 7). During the 2007–2008 drought that stressed water supplies in the Southeast, $Q$ from low-elevation reference watersheds was 325–375 mm (33–41%) below the 1938–2013 average. During that time, changes in forest structure and species composition may have decreased $Q$ by 85–110 mm (13–18%) relative to what would have been expected based on climate and had the forest structure and species composition remained unchanged since the 1970s (Fig. 7). In other words, $Q$ during the 2007–2008 drought could have been 13–18% higher, had the forest remained unchanged. Forest change may explain more of the variability in $Q$ than the 1–2% predicted by our statistical models because in the absence of complete knowledge of the relationships and feedbacks between climate, topography, vegetation, and ET, we assumed gradual, linear forest change effects while actual forest effects on ET may have occurred non-linearly over shorter time periods (Fig. 6).

The Chestnut Blight had a major impact on stand composition and structure, and likely also impacted $Q$. The reductions in ET and increases in $Q$ in the first half of the 20th century coincided with the decline of *C. dentata* and the associated reduction in basal area and biomass (Fig. 6). In 1934, *C. dentata* was found across the Coweeta Basin, and represented 36% of the total basal area (Elliott & Swank, 2008; Elliott & Vose, 2011). *C. dentata* mortality can partially explain the increasing $Q$ in the first half 20th century, when basal area was lower through 1950s than in 1934, as it took some time before replacement species could achieve the stem size (sapwood area and corresponding water conductance) to transport the amount of water previously used by large *C. dentata* trees. The increases in ET and reductions in $Q$ since the 1970s correspond to the establishment of mesophytic, diffuse-porous species after dominance by xerophytic, ring-porous *Quercus* species in the wake of *C. dentata* loss (Fig. 6). In addition, the forest has aged resulting in increases in transpiration (Fig. S3) and accumulated biomass resulting in increases in canopy interception of $P$. Evapotranspiration, total basal area, and the change in ET due to forest changes recovered to 1930s levels by the end of the 20th century (Figs. 3, 6, and 7), suggesting that the *C. dentata*-dominated forest had similar water use to the contemporary stand dominated by mesophytic species. *C. dentata* is often classified as a ring-porous species (e.g., Panshin & DeZeeuw, 1980), however Dudley (1886) suggested that the xylem shares characteristics...
with semi-ring porous species that transpire more water for a given stem size than their ring-porous counterparts (Fig. S3). Indeed, historical and recent evidence suggests that *C. dentata* may have functioned more similarly to mesophytic species (*A. rubrum* and *L. tulipifera*) than other ring-porous *Quercus* species in terms of water use (Meyer, 1927; Bauerle et al., 2006), photosynthetic response (Joesting et al., 2007), growth rate (Mcewan et al., 2006), and biomass allocation (Wang et al., 2006).

In addition to the Chestnut Blight, other forest disturbances and stresses have occurred in the latter half of the 20th century, but were less extensive and were episodic in nature and thus likely had minimal long-term impacts on the changes in ET and Q we quantified in this study. Fall cankerworm resulted in a brief decrease in *Q* in early winter (November–January) until 1977, but changes in annual *Q* were not detected (Swank et al., 1988). The decrease in *Q* was attributed to increases in ET drive by stimulation of leaf production during defoliation. The drought-induced canopy gaps during the 1980s were mostly constrained to drier slopes and ridges (Clinton et al., 1993). ET rates in these topographic positions are relatively low compared to coves and riparian areas where trees have access to higher soil moisture (Ford et al., 2011a), thus it is unlikely that the drought-induced canopy gaps on ridges and steep slopes would result in a significant change in *Q* at the watershed scale. Further, rapid regeneration in the canopy gaps by *A. rubrum* (Clinton & Boring, 1994) likely mitigated any decrease in ET due to the oak mortality. The loss of *Tsuga canadensis* in riparian areas due to hemlock woolly adelgid (HWA, *Adelges tsugae* Annand) and consequent reduction in interception has contributed to increases in peak flows, but no significant changes in the magnitude of annual *Q* (Brantley et al., 2016).
et al., 2014). However, following *T. canadensis* loss, *R. maximum* density increased (Ford et al., 2012). This evergreen understory species has high leaf area and potentially high canopy interception of *P* but relatively low daily water use (Brantley et al., 2013). Also following hemlock loss diffuse-porous species increased in basal area (Ford et al., 2012) with higher daily water use compared to hemlock. These changes in species growth and recruitment after HWA have initially offset any observable increase in annual *Q*, but may result in decreases in annual *Q* over the long term given that replacement species transpire more water (Brantley et al., 2013).

The results of this study suggest opportunities for further research relating changes in forest structure and species composition to *Q*. We could not explicitly use our vegetation survey data in the *Q* models because they lacked sufficient temporal resolution and spatial coverage across all watersheds. Instead, we constructed interventions and added them to the models to approximate the influence of vegetation changes, and qualitatively related these interventions to changes in forest structure and species composition. The paired watershed approach (Wilm, 1944) used in many forest hydrology experiments at Coweeta and other experimental forests, could be used to isolate and quantify the effect of forest mesophication on *Q* by selectively removing mesophytic species from a treatment watershed and comparing *Q* to a second untreated reference watershed. Examining the effects of mesophication at a larger scale is also warranted. Forest mesophication has been documented across the eastern USA (Nowacki & Abrams, 2008, 2015; Pederson et al., 2015) with potential implications to water supply and downstream aquatic ecosystems. A modeling approach similar to the one used here could employ publically available *Q* (e.g., US Geological Survey gauging stations) and vegetation data (e.g., US Forest Service Forest Inventory and Analysis) to shed light on the extent to which forest mesophication has affected *Q* in larger watersheds across the region.

Milly et al. (2008) concluded that ‘stationarity is dead’ and this study provides additional evidence that we can no longer expect historical flow regimes to continue to serve as a guide for the management of water resources in the future. Indeed, *Q* is changing from local to global scales (Lins & Slack, 1999; Mccabe & Wolock, 2002; Dai et al., 2009; Stahl et al., 2010; Rice et al., 2015) with implications for water supply, hydropower, and flood risk, as well as aquatic ecosystems and the industries that depend on them. Climate and land-use change have long been linked to nonstationarity in hydrological records. This study is among the first to show that in addition to climate, gradual and subtle changes in forest structure and species composition in reference watersheds can also result in hydrological states beyond the envelope of the past. As Milly et al. (2008) argued, ‘in a nonstationary world, continuity of observations is critical.’ Long-term records of climate, vegetation, and hydrology such as those collected at Coweeta will become increasingly valuable as we face a continuously changing world.

Prior to this work, large, abrupt changes to forest basal area or species composition were needed to induce a detectable change in *Q* (Bosch & Hewlett, 1982; Brown et al., 2005). Now with the rise of ecohydrology as a discipline, we can work across scales of the hydrologic cycle from sapwood to the stream, and link this multiscale analysis with the ecophysiology of individual species. Only with this interdisciplinary approach and with long-term data, we can start to see the effect of changes in species composition that plays out over decades and is caused by climate change as well as pests and pathogens acting on a fraction of the forest tree species. Looking forward, state-of-the-art

vegetation models calibrated to regional climate data and projected increases in climate variability (IPCC, 2013; Melillo et al., 2014) suggest continued drought-related forest disturbances in the future that could shift contemporary mesophytic forests comprised of diffuse-porous species (Mcewan et al., 2011) toward xerophytic forests comprised of more drought-tolerant ring-porous Quercus species (Iversion et al., 2004; Clark et al., 2014; Elliott et al., 2015; Mcdowell & Allen, 2015). However, vegetation models based on modeling individual species and their climate-envelopes do not consider competition among individuals, or climate-competition interactions, and may result in great uncertainty in future species distributions (Clark et al., 2014). There remains considerable uncertainty in the future trajectory of climate and species range shifts, but clearly the combined effects of climate and forest vegetation changes will have significant impacts on water yield from forested lands.

Acknowledgements

We thank all scientists, technicians, and students who have contributed to the long-term climate and hydrology data at Coweeta. We also thank Eric Davidson, Paul Barten, Julia Jones and two anonymous reviewers for their thoughtful reviews on previous versions of this manuscript. Funding for this research was provided by the USDA Forest Service, Southern Research Station; the National Science Foundation (NSF), Long-Term Ecological Research (LTER) program (award #DEB-0823293); and the USDA, Agriculture and Food Research Initiative Foundational Program (award #2012-67019-19484). Any opinions, findings, conclusions, or recommendations expressed in the material are those of the authors and do not necessarily reflect the views of the USDA or the NSF.

References

Adams MA (2013) Mega-fires, tipping points and ecosystem services: managing for the USDA or the NSF. Those of the authors and do not necessarily reflect the views of the USDA, Agriculture and Food Research Initiative Foundational Program (award #2012-67019-19484). Any opinions, findings, conclusions, or recommendations expressed in the material are those of the authors and do not necessarily reflect the views of the USDA or the NSF.


Ford CR, Lasetter SH, Swank WT, Vose JM (2011b) Can forest management be used to sustain water-based ecosystem services in the face of climate change? Ecological Applications, 21, 2049–2067.


Declining Water Yield from Forests


Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Changes in the observed climate record at the Coweeta Hydrologic Laboratory, reproduced from (Ford et al., 2011b).

**Figure S2.** Changes in basal area by species across the entire Coweeta Basin, modified from Vose and Elliott (2016).

**Figure S3.** Mean observed daily water use (DWU) estimated from sap flux density measurements in trees of varying species and diameter at breast height (DBH) in reference watersheds at Coweeta, reproduced from (Ford et al., 2011b).

**Table S1.** Summary of tree species found in vegetation survey plots of WS14 and WS18.

**Table S2.** ARIMA model results for quantifying changes in water yield ($Q$).

**Table S3.** ARIMA model results for quantifying changes in evapotranspiration ($P - Q$).

**Table S4.** ARIMA model results for quantifying changes in precipitation ($P$) at SRG19 (low elevation) and pan evaporation (PE) measured at climate station CS01.

**Table S5.** ARIMA model results for model predicting annual water yield ($Q$) as a function of precipitation ($P$) and pan evaporation (PE).

**Table S6.** Statistical tests on residuals of ARIMA models predicting annual water yield ($Q$) as a function of precipitation ($P$) and pan evaporation (PE).

**Appendix S1.** Supplementary discussion: interpreting coefficients in models predicting $Q$ as a function of climate and vegetation.