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Global change at the landscape level: relating regional and landscape-scale drivers of historical climate trends in the Southern Appalachians

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ABSTRACT: Organisms in montane environments are sensitive to fine-scale climatic variation associated with highly dissected topography, yet few studies have examined the sensitivity of different landscape positions to climate change. We downscaled biologically significant temperature variables to below-canopy 30 m resolution and assessed temporal trends from 1980 to 2011 across elevation and topographic gradients in Great Smoky Mountains National Park (GSMNP; Tennessee and North Carolina, USA) using a previously developed empirical model derived from a 120-sensor temperature network. Additionally, we assessed GSMNP climate trends from 1900 using six historical climate records from the region and an additional eight records from 1980, spanning the Park's elevation gradient. Regional temperatures increased through the 1980s and 1990s, but currently remain at or below those recorded in the early to mid-20th century and are strongly associated with different phases of the North Atlantic Oscillation. In contrast, annual and growing season precipitation steadily rose during the past century. Landscape-scale analysis showed that rates of change for maximum seasonal temperatures, frost-free days (FFD), and growing degree days were strongly mediated by topographic position, with high-elevation ridges having greater rates of maximum temperature increases, whereas high-elevation near-stream positions showed the least amount of increase in FFD and growing degree days. Most importantly, we show how modelled differences in rates of climatic change based on landscape position could have significant ecological effects in this biologically significant region, depending on how organisms respond to particular climate factors. Organisms that depend on growing season length may experience the largest climate effects at the lowest elevations, while those that depend on warm days in spring and autumn for particular phenological processes will experience the largest shifts at high-elevation ridges.

KEY WORDS topographic complexity; downscaling climate; temperature; precipitation; mixed effect model; Great Smoky Mountains

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1. Introduction

The current rate of global climate change is unprecedented over the course of the Holocene (Hof *et al.*, 2011; Marcott *et al.*, 2013), but varies significantly by region (Pachauri and Reisinger, 2007; Portmann *et al.*, 2009). Mountainous regions in particular are expected to experience significant warming in the coming century with major anticipated effects on biodiversity (Nogués-Bravo *et al.*, 2007). Evidence already exists for species range shifts along elevation gradients (Parmesan, 2006; Lenoir *et al.*, 2008; Jump *et al.*, 2009). However, studies have shown conflicting results on the rate and magnitude of climate change at high elevations compared to nearby lower-elevation sites (reviewed in Pepin and Lundquist, 2008). Further, potential interactions of temperature and water balance at low elevations (Urban *et al.*, 2000) or in topographically exposed sites (Fridley, 2009) may lead to complex relationships between the extent of climate warming, elevation, and topography (Beniston, 2003), particularly within forested canopies. In such instances, predictions of suitable habitat, local refugia, and habitat connectivity may be underestimated if the spatial scale of climate data inputs is not matched to what individuals are actually experiencing (Jackson and Overpeck, 2000; Austin and Van Niel, 2011; Dingman *et al.*, 2013; Franklin *et al.*, 2013).

In montane landscapes, near-ground and below-canopy temperatures can be decoupled from atmospheric conditions because of fine-scale variation in slope, aspect, soil and plant water content, and shading from local vegetation (Ashcroft *et al.*, 2008; Fridley, 2009; Albright *et al.*, 2011; Dobrowski, 2011). As a consequence, montane landscape positions may vary considerably in their sensitivity to atmospheric climate trends (Geiger *et al.*, 2003). Moreover, particular climate factors, such as annual or seasonal extremes in minimum or maximum temperatures, may interact with topographic factors in different ways. For example, growing season duration, expressed as the

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amount of time above some minimum threshold temperature, should be relatively insensitive to temporal shifts in maximum (daytime) temperatures. Conversely, climate factors associated with the accumulation of heat, such as growing degree days (GDD), should be most directly associated with the increasing frequency of very hot days and little affected by night-time temperatures. Because topographic variables influence day and night-time temperatures in different ways (Geiger *et al.*, 2003; Fridley, 2009), we expect climate trends in montane regimes to vary in ways specific to the climate factors of interest, yet this seems little investigated in climate studies (Vanwalleghem and Meentemeyer, 2009).

Temperatures also differ significantly between closed-canopy and open-site positions (Morecroft *et al.*, 1998; Friedland *et al.*, 2003), yet by design permanent weather stations represent open-site conditions. Forest-floor temperatures are generally cooler during the day and warmer at night than open sites (Fridley, 2009). Plants and animals in forest environments will therefore experience significantly different environmental conditions than those predicted by open-site climate data. Landscape models should ideally reflect the systematic differences between forested and non-forested sites by translating traditional open-site weather station data to the more buffered understory environment.

Fridley (2009) developed a landscape-scale (30 m) temperature model for Great Smoky Mountains National Park (GSMNP) located in the Southern Appalachian Mountains, United States with the primary objective of understanding how topographic factors mediate near-ground temperatures in a forested landscape. Using a network of below-canopy temperature sensors, Fridley (2009) monitored temperatures at 120 locations arrayed along gradients of elevation and topographic exposure. Sensors recorded temperature continuously every 2 h over a 16-month period (July 2005–October 2006), thus capturing the seasonal variability of the system. A hierarchical spatial model was used to predict daily minimum and maximum sensor temperatures using regional weather station data and geographic information system (GIS)-derived predictor variables reflecting radiative load, site water balance, and cold air drainage. Application of the model to a validation data set of sensors located park-wide demonstrated a major role of topographic factors, including stream proximity and fine-scale differences in incident radiation, in near-ground temperatures (Fridley, 2009, Figures 5–6 therein). Although topographic effects varied by season, reflecting differences in seasonal canopy cover and cooling *versus* warming effects of site water content in summer *versus* winter, the limited deployment duration of the sensor network precluded an assessment of how longer-term regional climate trends are mediated by topography and land cover.

Here, we apply the spatial and seasonal model developed by Fridley (2009) to regional climate trends in the Southern Appalachians since 1980, a date reflecting the availability of high-elevation weather data. Our goal is to use our spatial model of how topography mediates near-ground temperatures in dissected terrain, fit using data collected in 2005 and 2006, to extrapolate how longer-term climate trends may have differed across different landscape positions, and under a forested canopy that strongly buffers near-ground climate. Among the most important findings in the original study were strong interactions between synoptic (regional) temperatures and topographic factors driving near-ground microclimates; such interactions in the model suggest some landscape positions are more sensitive to regional warming than others and could be detected by feeding the model long-term climate data. We assume that topographic factors shown to mediate near-ground temperatures in 2005 and 2006 operate the same today as they have in decades past. We hypothesize that certain landscape positions, such as less-exposed, near-stream locations, would experience smaller changes in seasonal and annual climate compared with those experienced in the greater GSMNP region.

We also analysed the direction and extent of climate change in the GSMNP region during the past century based solely on changes in air temperature as measured by permanent weather stations. This analysis served to put the topographic drivers of climate change since 1980 in context and also allowed us to investigate larger, regional-scale drivers of climate change that may interact with local-scale factors over time. In this longer-term analysis, we were particularly interested in links between climate variability and the North Atlantic Oscillation (NAO), a recurrent teleconnection named for the distribution of atmospheric pressure between the Arctic and mid-Atlantic regions (Hurrell *et al.*, 2003). Variability in the NAO affects the Atlantic thermohaline circulation and alters poleward heat transport and sea surface temperatures (Hurrell *et al.*, 2003). Further, variability in the NAO has been found to have significant effects on terrestrial ecosystems, in both the timing of spring budbreak and growing season length (Hurrell *et al.*, 2003). However, while it has been shown that the NAO has large effects on climate patterns in Europe (e.g. Stenseth *et al.*, 2002) relatively little research has connected the NAO to global change issues in North America (Durkee *et al.*, 2008; Warren and Bradford, 2010).

2. Methods

2.1. Study area

GSMNP encompasses 2090 km^2 in the Southern Appalachian mountains of Tennessee and North Carolina (United States) and is one of the most biologically diverse regions outside the tropics in North America (Shanks, 1954; Whittaker, 1956). Extreme climatic gradients in both temperature and rainfall (Shanks, 1954; Busing *et al.*, 2005) along with a transition from southern piedmont to boreal forest across a distance of <15 km have putatively allowed GSMNP to serve as an important historical refuge for plant and animal species during periods of rapid climate change (Braun, 1950; Whittaker, 1956; Delcourt and Delcourt, 1998). Elevation within the park ranges from 256 m in valleys along the western border to 2024 m at the highest point (Clingmans Dome). The principal

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Table 1. Weather stations included in analysis of GSMNP climate trends. Stations included in longer-term analysis are indicated in bold. Thermometers are 1–2 m above ground level.

Station name	Elevation (m)	Latitude (°N)	Longitude (°W)	Duration of record
Knoxville Exp. Stn.	253	35.882	83.957	1966–2011
Sevierville	275	35.883	83.583	1955–2011
Knoxville McGhee Tyson Airport	293	35.818	83.986	1911–2011
Newport 1 NW	316	35.983	83.201	1900–2011
Tapoco	338	35.456	83.940	1961–2011
Waterville 2	439	35.774	83.098	1930–2011
Gatlinburg 2 Sw	443	35.688	83.537	1922–2011
Andrews–Murphy Airport	517	35.195	83.865	1909–2005
Oconaluftee	622	35.526	83.309	1959–2011
Franklin	648	35.180	83.393	1946–2011
Cullowhee	668	35.326	83.191	1910–2011
Cataloochee	808	35.638	83.096	1965–2011
Waynesville 1 E	810	35.487	83.968	1900–2011
Mt. LeConte[a]	1937	35.650	83.433	1977–2011

[a]Temperature only, no precipitation data.

driver of temperature variation in GSMNP is elevation, with temperatures 10–15 °C cooler at the highest points compared with the lowest elevations during the growing season (Shanks, 1954). Precipitation is generally higher in summer (July–August) and winter (November–January), with environmental lapse rates mediated by air, ground water content, and heavy cloud cover at high elevations (Busing *et al.*, 2005). High relative humidity persists across elevations, with near-ground air saturated for most of the year under forest canopies (Fridley, 2009).

2.2. Weather station data

An initial set of 115 weather stations from the National Park Service Appalachian Highlands Network (Davey *et al.*, 2007) located within 30 km of the GSMNP boundary were considered for analysis. We obtained daily maximum and minimum temperature and daily precipitation records for all stations (J. D. Fridley, 2010; unpublished report to the National Park Service). Station records were excluded if they did not extend back from 2011 to at least 1980 (the majority did not capture this temporal extent) or if the record included significant amounts (e.g. multiple year gaps) of missing data. Records from 14 stations were suitable for analysis of the time period extending back to 1980 (Table 1). Six of the fourteen stations had records extending back as far as the 1920s or earlier (Table 1). The six long-term records were used for a separate analysis spanning 1900–2011.

Eleven of the fourteen stations were operated by the National Weather Service (NWS) Cooperative Observer Program. Current and archived data of daily minimum and maximum temperature and total daily precipitation were obtained from the National Climate Data Center website (http://www.ncdc.noaa.gov). The Andrews–Murphy Airport station is part of the Automated Weather Station Observation System. The Knoxville McGhee Tyson Airport station has a separate Automated Surface Observing System. Data for both these stations were obtained through the NC State Climate Office (http://www.nc-climate.ncsu.edu). We account for potential differences between station equipment and calibration by including station as a random effect in modelling.

Data from the highest elevation station (Mt. LeConte) were obtained from a combination of the NWS Cooperative Observer Program and records from the privately operated LeConte Lodge. Records from the NWS station were available from 1987 to 2011, and records from the LeConte Lodge extended back to 1977. These records were obtained with assistance from GSMNP staff (K. Langdon, personal communication, 2010) and consisted of daily notes written on calendars from a minimum to maximum thermometer and manually tipping rain gauge, subsequently digitized. The two data sets were combined for this analysis, so that the combined single record met the duration criterion of continuous data from 1980 to 2011. For unknown reasons, data from the period of overlap were not identical between the Lodge and NWS records. We used the period of overlap (1987–2011) to build a transfer function that was then used to recalibrate the LeConte Lodge data prior to 1987 to the NWS data. This approach was only used with the daily maximum and minimum temperature data, where there was a consistent trend in discrepancies that could be well accounted for with the transfer function ($R^2 > 0.95$). Discrepancies between the Lodge and NWS precipitation data were frequent and inconsistent so these data were excluded from precipitation analyses.

All station records were tested for inhomogeneities. Inhomogeneities in climate records are caused by non-climatic factors, such as changes in station equipment, recording techniques, or location, and may obscure true climate trends (Peterson *et al.*, 1998). To test for discontinuities or gradual drifts in each station record, we used a jackknife approach to iteratively create reference series of the daily minimum and maximum temperature records and the daily precipitation records that contained all but one focal station. The mean and standard deviation were calculated for the reference series. We then compared each of the individual station records with the reference

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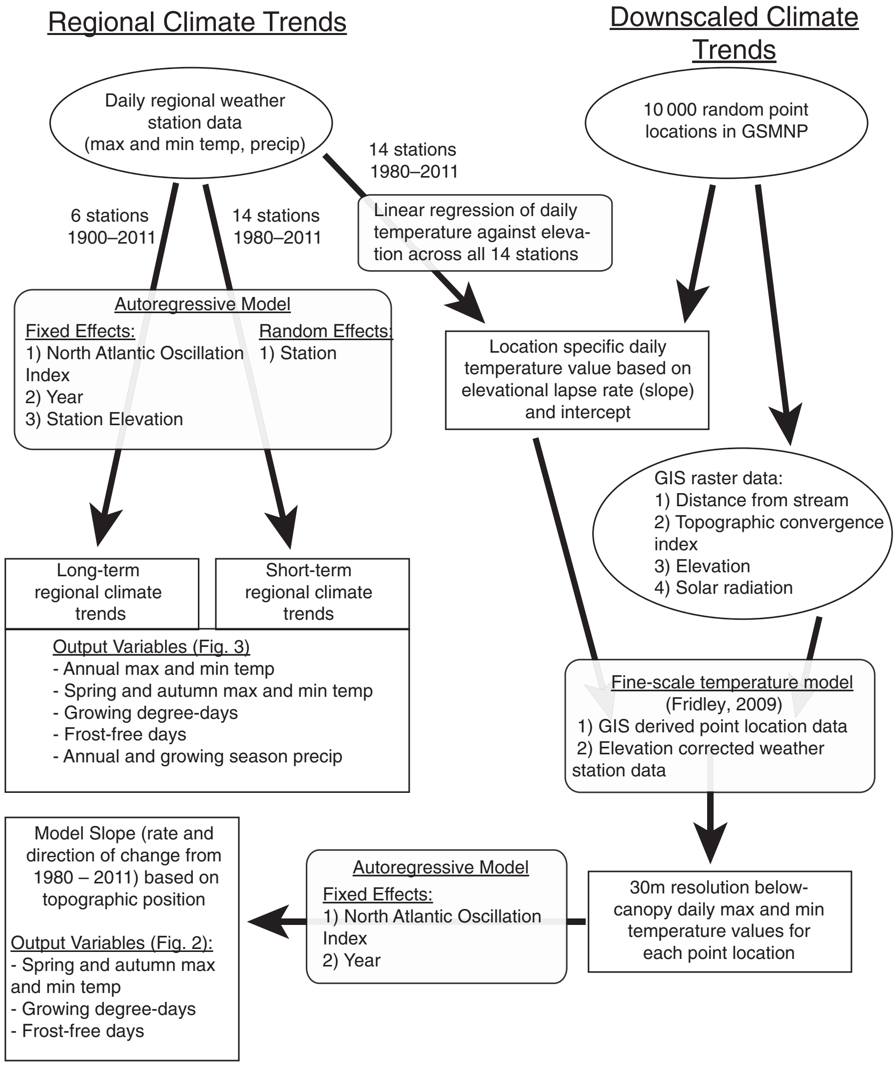

Figure 1. Flowchart of analysis. Data inputs, modelling steps, and outputs are shown for both the regional and downscaled analysis.

series and looked for systematic outliers where, for a given date, the station record fell outside two standard deviations of the reference data. We also calculated the Pearson correlation between the reference time series and the removed station to assess overall agreement between records. Finally, we again used jackknifing to iteratively remove one station at a time from long and short-term models. Coefficients from each jackknifed model were compared with the full model to determine if the removed station had an effect on the direction or significance of the overall result. All inhomogeneity analysis was conducted using the R package 'bootstrap', version 2015.2 (Tibshirani and Leisch, 2015).

2.3. Landscape-level downscaling of climate trends

To assess the influence of fine-scale topographic position on climate trends, we randomly selected 10 000 point locations from within GSMNP on a 10 m × 10 m raster GIS grid. A small percentage of points (<4%) were missing raster values for topographic variables, because of unequal spatial extents of input rasters, reducing the total number of sampled points to 9684. The selected points spanned the entire park extent and represented the full range of the elevation and exposure gradients present in the study area (Figure S1, Supporting Information).

Daily maximum and minimum temperature values from the 14 weather stations spanning 1980–2011 were regressed against station elevation to produce daily baseline temperatures (model intercept) and lapse rates (model slope) (average R^2 value across all days = 0.604, standard deviation = 0.269). We did not use the long-term data set of six stations extending back to 1900 because of its lack of a high-elevation station. Daily intercepts and lapse rates were used to model the daily maximum and minimum temperature at the elevation specific to each of our selected points (Fridley, 2009) (Figure 1). These temperatures represent the open-site temperature of that landscape position, based solely on elevation.

Adjusted point-specific daily temperature values were then used in conjunction with GIS-based factors describing topographic drivers of site-thermal regimes, including distance-from-stream, topographic convergence index (TCI), and potential site radiation (Fridley, 2009). Distance-from-stream serves as a proxy

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of the streamside-to-ridge top exposure gradient, which is a complex gradient involving surface irradiance, slope shape, and soil-moisture drainage. Elevation, TCI [used as a water balance proxy, (Beven and Kirkby, 1979)], and daily and annual shortwave radiation (including hillshading effects) were also calculated for each point as the input into the fine-scale (30 m resolution) model developed by Fridley (2009) for GSMNP (Figure 1). Radiation values were calculated as daily intercepted solar irradiance using the 'r.sun' algorithm, which incorporates date, latitude, slope orientation, slope angle, and shading from local topography (Neteler and Mitasova, 2004), using default parameters for atmospheric turbidity and ground albedo coefficients (3.0 and 0.2, respectively). While the model framework accounts for seasonal interactions of these variables, an important assumption of the model is that relative spatial water distribution, radiative load, and overall canopy cover remain static across years.

Our model predicts below-canopy daily maximum and minimum temperature, based on the parameters listed above, within a mixed-hierarchical structure (for model specifications, see supplement of Fridley, 2009). The model was built using below-canopy temperature measurements collected from 120 Thermochron I-button temperature sensors arrayed along transects that encompassed the full elevation and exposure gradients, along with accounting for aspect and watershed factors. I-buttons were deployed at a height of 1 m on the north facing side of a tree and further protected from rain and radiation by enclosing them within a polyvinyl open-bottomed cap. These measures served to minimize exposure and radiation differences, while still accurately capturing site temperatures (Fridley, 2009). For full model details see Fridley (2009).

Daily minimum and maximum temperatures generated from the model for each of our sample points were used to calculate eight temperature summary variables commonly accepted as important broad-scale drivers of organismal biology, ecosystem function, and watershed dynamics (Hijmans *et al.*, 2005). First, we calculated the 95th and 5th quantiles of annual maximum (MXT) and minimum temperature (MNT), respectively (trends for these two variables were not significant and are not shown). Autumn maximum and minimum temperature were calculated as the average daily minimum and maximum temperature values from September to November. Similarly, spring maximum and minimum temperatures were calculated from April to June. Frost-free days (FFD) were calculated annually as the sum of days in which the minimum temperature was >0 °C. Growing degree days (daily heat accumulation) were calculated annually as the cumulative averages of the daily minimum and maximum temperature minus a base temperature of 10 °C.

For each location, climate variables were regressed against time and the NAO index to determine the magnitude of change for each response variable (Figure 1). The NAO index is a dimensionless measure calculated as the difference between normalized sea level pressure at Gibraltar and southwest Iceland (Jones and Wheeler, 1997). Monthly index values from 1900 to 2011 were downloaded from the University of East Anglia's Climate Research Unit online data depository (http://www.cru.uea.ac.uk/cru/data/nao/).

To summarize landscape-level climate trends across elevation and topographic gradients, we determined elevation and log-transformed distance-from-stream (as a proxy of the streamside-to-ridge top exposure gradient) values for each of our 9684 selected locations from raster digital elevation model (DEM) layers and plotted fitted slopes of linear temporal trends in each response variable. We then smoothed these values along elevation and stream distance axes using a loess model (degree = 2, span = 0.5). To assess topographic influence on the magnitude of change, slopes were plotted as contours on bivariate plots of elevation and logged stream distance, similar to classic Whittaker (1956) diagrams of vegetation distribution along elevation and exposure gradients.

2.4. Regional climate trend analysis

Daily maximum and minimum temperature values from the 14 weather stations were used to calculate the same eight temperature variables used in the landscape-scale analysis. Note that the regional analysis only incorporated air temperature as recorded by the permanent weather stations and not the suite of topographic variables included in the landscape-scale analysis (Figure 1). The Cataloochee weather station was excluded from FFD and GDD analysis because of large amounts of missing daily data. In addition to the temperature variables, we included total annual precipitation (TAP) (calculated as the sum of daily precipitation values) and precipitation during the growing season (growing season precipitation, GSP) (calculated as the sum of precipitation from May through October, inclusive) in the analysis.

The variables were calculated for the short-term period (1980–2011) using all 14 weather station records, and the long-term period (1900–2011) using the subset of six weather stations where long-term data were recorded. For each variable, we calculated the anomaly from the mean for each weather station by subtracting the mean from each annual value. The average anomaly across all weather stations was then calculated. To visualize temporal trends, a 5-year moving average of the anomaly was computed using the 'rollapply' function in the R time series package 'zoo', version 1.7-12 (Zeileis and Grothendieck, 2005). We also fit a generalized additive model (GAM) with a spline smoother to the annual data for each variable using the R package 'mgcv', version 1.8-3 (Wood, 2011) as a flexible means of summarizing long-term climate trends (see Supporting Information).

Autoregressive models were used to statistically assess short-term and long-term climate trends for the combined weather station data (Figure 1). We used linear mixed models via the R package 'nlme', version 3.1-118 (Pinheiro *et al.*, 2015), including station as a random effect. Station elevation and year were included as linear fixed effects. NAO index data were also included as a fixed effect. A lag-1 coefficient was included in all models to account for

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Table 2. Standardized coefficients for autoregressive models of ten climate variables from 1980 to 2011. Each model included elevation, year, and NAO index as fixed effects. Weather station was included as a random effect, along with lag-1 temporal autocorrelation. Interaction terms were not significant. All 14 stations listed in Table 1 were used except Mt. LeConte for precipitation variables and Cataloochee for frost-free days and growing degree-day variables.

	Coefficient			
Response variable	Intercept	Elevation	Year	NAO
Maximum temperature (95th quantile)	30.980***	−2.829***	−0.105	−0.305***
Minimum temperature (5th quantile)	−7.796***	−2.137***	0.684***	0.931***
Maximum autumn temperature	23.138	−2.610***	0.121*	0.001
Minimum autumn temperature	9.277***	−1.863***	0.284***	0.250***
Maximum spring temperature	22.169***	−2.794***	0.177**	−0.279***
Minimum spring temperature	7.730***	−2.034***	0.374***	−0.145**
Frost-free days	254.974***	−15.467*	5.449**	5.433***
Growing degree days	2189.040***	−444.785***	44.901**	5.821
Annual precipitation	1269.127***	15.498	50.268**	79.690***
Growing season precipitation	615.201***	6.803	27.283**	35.143***

*$P < 0.1$, **$P < 0.05$, ***$P < 0.001$.

temporal autocorrelation between years. Interaction terms were tested with likelihood ratio tests but found to be insignificant in all cases and are therefore not included in the final models. Higher-order terms were also excluded from the models, as visual examination of the data did not justify their inclusion. Further, the increased complexity of adding higher-order terms would obscure the primary focus of the study, which was to assess linear trends in the data. All final models were run with standardized independent variables so that direct comparisons of effect sizes of predictors could be made.

3. Results

3.1. Station accuracy

Tests for inhomogeneities in station records showed no single-station discrepancies. Jackknife results of the mean daily values showed no signal of a systematic departure in any of the records from the reference series that would indicate a non-climatic source. Pearson correlation coefficients between stations and reference series were all significant suggesting overall homogeneity in the records. Jackknife results of iteratively removing stations from regression models resulted in no coefficients changing in significance. A small percentage (4%) of coefficients changed in direction; however, in none of these instances was the coefficient significant in the model [e.g. six of the eight discrepancies in the short-term jackknifed model results were the NAO term in the model for maximum autumn temperature changing from + to −, where the coefficient with all stations included was extremely close to zero (0.001) and non-significant (Table 2)]. Based on these diagnostics, we proceeded with all selected stations included in the subsequent analysis.

3.2. Landscape-level trends

Downscaled, below-canopy temperatures showed a strong positive trend from 1980 to 2011 overall (Figures 2 and 3), but differed substantially in their extent and direction of change across elevation and exposure gradients (Figure 2). Spring and autumn maximum temperature had the greatest amount of change at high-elevation positions and increased to a greater extent in exposed ridge-top locations (Figure 2, top left panels). High-elevation sites showed rates of increase of maximum temperatures >0.4 °C decade^{-1} higher than lower-elevation sites. The influence of position along the exposure gradient decreased with elevation (Figure 2). In contrast, spring and autumn minimum temperatures increased the most at low elevations (Figure 2, bottom left panels). Position along the exposure gradient had no systematic effect on the rate of change for minimum temperatures. The contrasting patterns between maximum and minimum temperatures indicates that at high elevations, and particularly those of more sheltered topographic locations, the range of temperatures (maximum−minimum) is broadening as maximum temperature increases at a faster rate than minimum temperature. Conversely, at low elevations, the temperature range is becoming narrower as maximum temperature increases at a lower rate than the increase in minimum temperature.

FFD and GDD both showed similar overall patterns, with the rate of increase decreasing with elevation (Figure 2, right panels). GDD was strongly affected by topographic position and its interaction with elevation, where near-stream locations have experienced a lower rate of increase than ridges of comparable elevation except at the low extreme of the elevation gradient. The influence of topography was not as strong for FFD but was significant at the highest elevations, where protected near-stream locations show the least amount of change since 1980, similar to GDD.

3.3. Regional analysis

Major trends across ten climate variables (Figure 3, Figures S2−S11) can be summarized as: (1) a dominant influence of the NAO index on nearly all climate variables, modelled since 1980 (Table 2) or 1900 (Table 3), (2) weaker but significant annual increases in most

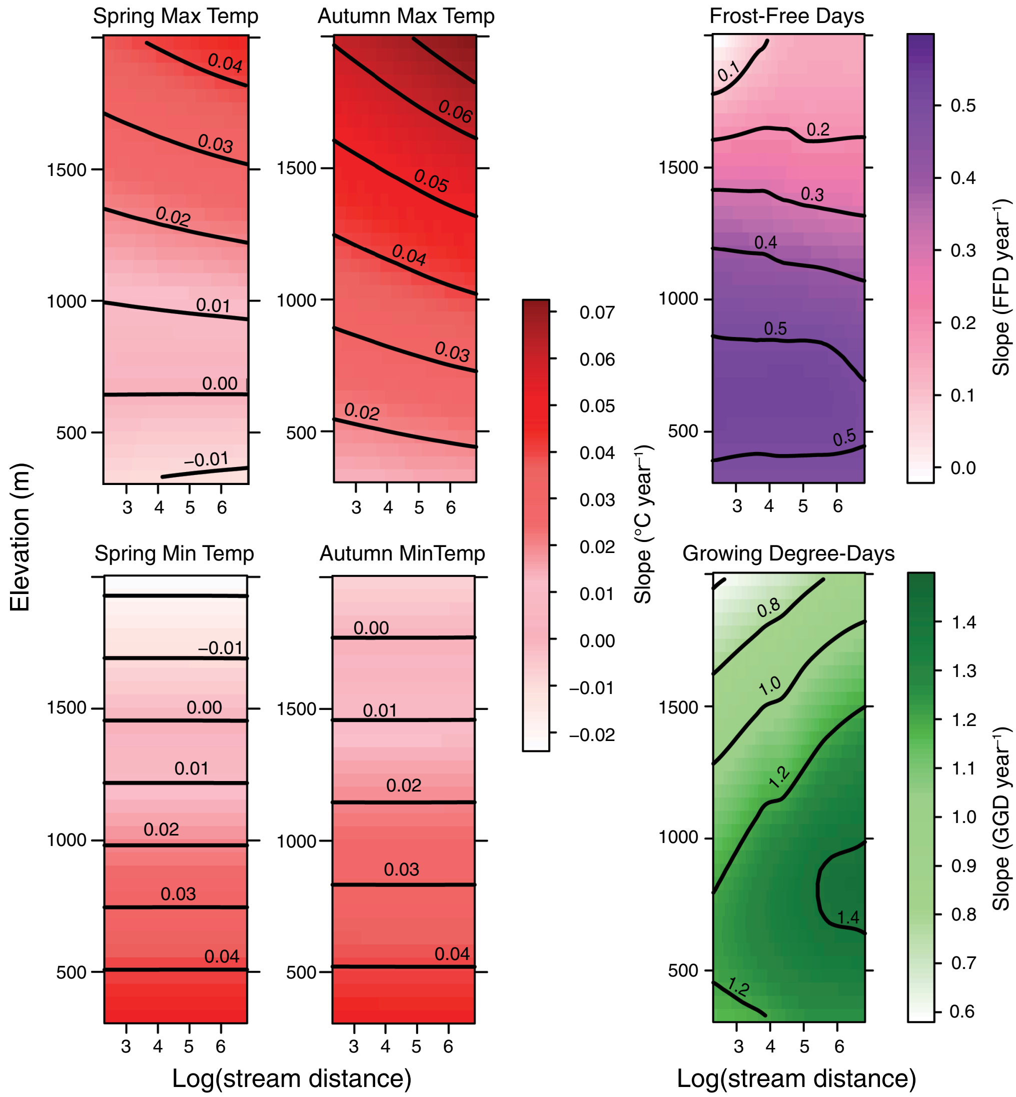

Figure 2. Variation in rate of change (temporal slope, 1980–2011) as a function of topographic position for six downscaled climate variables: spring and autumn minimum and maximum temperatures, FFD, and GDD. Slopes are shown across the full range of elevation and distance-from-stream (proxy for cove-to-ridge) gradients that are present in GSMNP. Slopes were calculated as the time coefficient from regression models of each variable against time (1980–2011) and the NAO index. Darker shading indicates a higher rate of change across the measured time period. Isolines indicate specific slopes along the gradients.

temperature variables since 1980 (Table 2), but not when examined over the 20th century (Table 3), and (3) a strong and steady increase in annual precipitation over the 20th century of about 100 mm (Table 3, Figure 3(i)). Curves fit by GAM were about equally split between linear or nearly linear and complex functions through time, for both post-1900 and post-1980 time series (Figures S2–S11).

Temperature variables all showed similar declines with elevation (lapse rates *ca.* $-5\,°\mathrm{C\,km}^{-1}$). MXT showed no clear trend in the short- or long-term records (Figure 3(a)). All six stations included in the long-term analysis have comparable temperatures in the 1930s to 1950s to the present. MNT increased since 1980, except for the highest elevation station, Mt. LeConte, where MNT has decreased (Figure S3). However, current MNT values are comparable with the mid-20th century values, which were followed by a cold period through the 1960s and 1970s before warming again in the 1980s (Figure 3(b)).

Autumn maximum and minimum temperatures showed slight increases for most stations since 1980 but typically plateaued in the 1990s (Figure 3(c) and (d)). In the long-term data set, autumn temperatures generally were highest in the early part of the 20th century and decreased through the 1930s to the 1970s, and current autumn temperatures are no different than early 20th century values. Spring maximum and minimum temperatures showed a similar pattern to autumn temperatures (Figure 3(e) and (f)). However, increases in both maximum and minimum temperatures since 1980 were more pronounced in the spring than autumn, rising by over a degree at many stations. As with the other temperature variables, current temperatures were comparable with early and mid-20th century values, with no clear long-term trend evident for the majority of stations (Figure 3(e) and (f)).

FFD and GDD have significantly increased since 1980 but both plateaued in the 1990s (Figure 3(g) and (h)).

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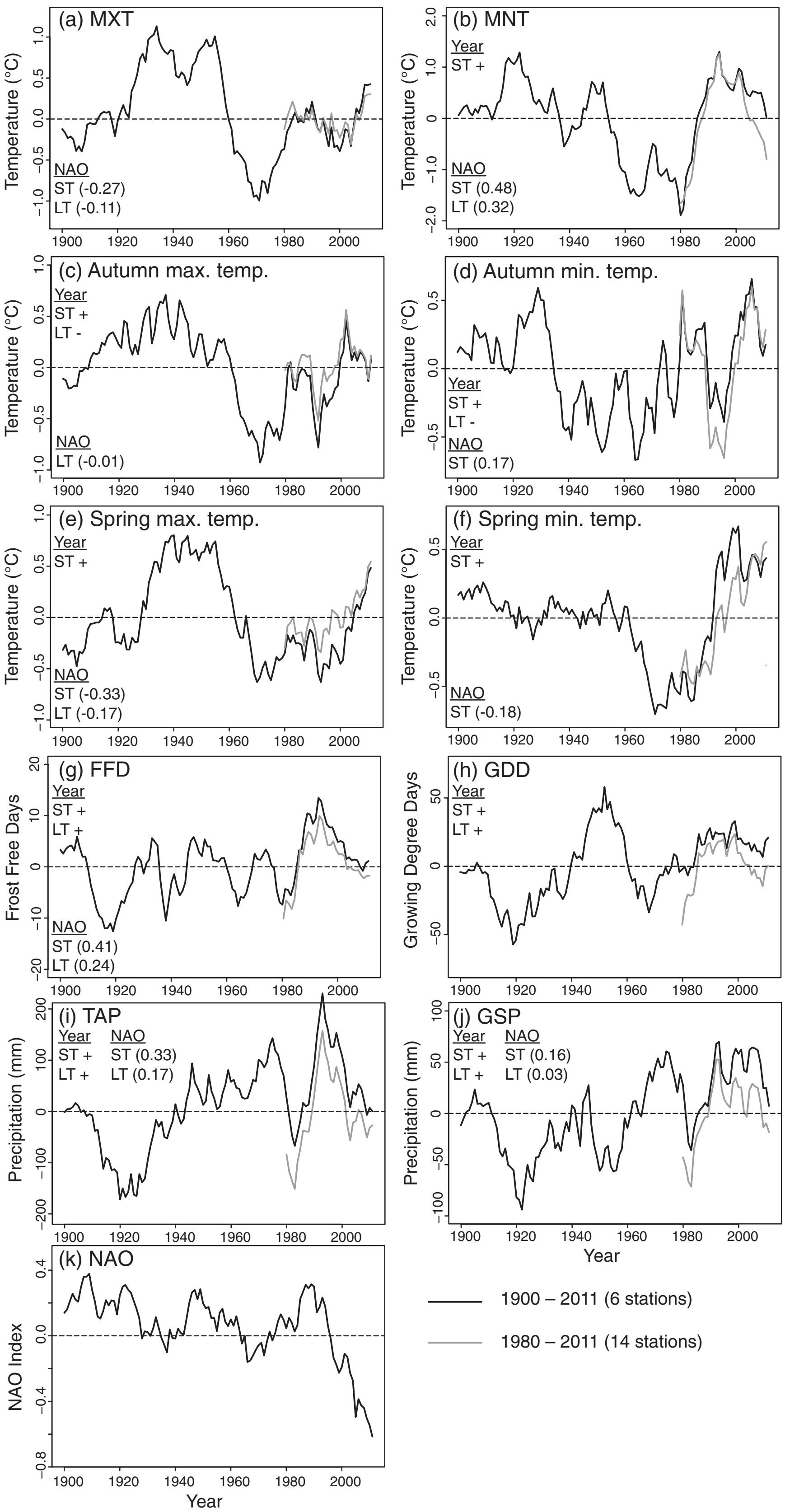

Figure 3. Anomaly from mean for regional climate variables: (a) 95th quantile of MXT, (b) 5th quantile of MNT, (c) autumn maximum temperature, (d) autumn minimum temperature, (e) spring maximum temperature, (f) spring minimum temperature, (g) FFD, (h) GDD, (i) TAP, and (j) GSP. (k) NAO index from 1900 to 2011. For panels (a–j), a significant linear trend of the respective variable to time (year) is shown by ST (short term; black) and LT (long term; grey). The + or −sign indicates the direction of the relationship. Significant relationships between each variable and NAO index are also denoted with ST and/or LT, and correlations are given in parenthesis.

Table 3. Standardized coefficients for autoregressive models of ten climate variables from 1900 to 2011. Each model included elevation, year, and NAO index as fixed effects. Weather station was included as a random effect, along with lag-1 temporal autocorrelation. Interaction terms were not significant. The six long-term stations (bolded) listed in Table 1 were used in each model.

Response variable	Coefficient			
	Intercept	Elevation	Year	NAO
Maximum temperature (95th quantile)	31.719***	−1.184***	−0.023	−0.164**
Minimum temperature (5th quantile)	−7.631***	−1.090**	−0.012	0.461***
Maximum autumn temperature	24.378***	−0.749**	−0.469***	−0.151**
Minimum autumn temperature	9.821***	−1.273**	−0.190**	−0.062
Maximum spring temperature	23.085***	−0.639**	−0.024	−0.213***
Minimum spring temperature	8.233***	−1.272**	−0.031	−0.018
Frost-free days	255.006***	−13.847	4.965**	3.606**
Growing degree days	2316.039***	−185.062**	59.239***	−2.343
Annual precipitation	1256.671***	−12.703	70.055***	47.492***
Growing season precipitation	600.517***	−6.426	29.808***	12.371*

*$P < 0.1$, **$P < 0.05$, ***$P < 0.001$.

In the long-term analysis both variables have increased significantly, with there being 19 more days per year without frosts at mid elevations and a 10% increase in GDD since 1900.

TAP and GSP increased steadily since 1900, by 10 cm annually per station (almost a 10% increase) and more than 80 cm for the low elevation Andrews–Murphy Airport station (Figures S9 and S10). In the short-term analysis, TAP and GSP plateaued in the mid-1990s (Figure 3(i) and (j)). There was no apparent increase of precipitation with elevation in either the short- or long-term data sets (Tables 2 and 3).

The NAO index was a significant driver of nearly all climate variables, for both short- and long-term data sets (Tables 2 and 3). Years of high NAO index had high precipitation, high minimum temperatures, low maximum temperatures, and a lower incidence of frost. GDD was the only variable not related to NAO index for either the short or long-term data sets (Tables 2 and 3).

4. Discussion

4.1. Landscape-level climate trends

Our analysis of climate trends as a function of landscape position in a forested montane region suggests topography mediates microclimatic variation, but in a way specific to particular climate variables. Although the importance of landscape heterogeneity in mediating regional climates and its resulting effects on species-distribution patterns has been widely recognized (Araújo *et al.*, 2005; Keil *et al.*, 2013), our study demonstrates that minimum and maximum temperatures, as well as growing season-related variables, may exhibit different temporal trends as a function of elevation and exposure. Of the modelled climate summary variables, autumn and spring maximum temperatures, FFD, and GDD appeared most sensitive to topographically based downscaling of daily temperatures beneath a forest canopy, meaning that variation in these variables was not well explained by open-site weather stations.

Because topographic influences on near-ground heat balance are complex and work differently for day *versus* night-time influences (Geiger *et al.*, 2003; Fridley, 2009), seasonal and annual climate summary variables can exhibit contrasting trends across montane landscapes, including strong interactions with elevation as shown here. Although some studies have shown greater rates of temperature increase at high elevations (Pepin and Lundquist, 2008), contrasting results (e.g. Vuille and Bradley, 2000) and a lack of any clear relationship between elevation and the magnitude of temperature trends (e.g. You *et al.*, 2008) have also been shown. Our model results show clear increases in the magnitude of change for seasonal maximum temperatures with elevation. However, seasonal minimum temperatures showed the opposite result, with rates of increase greater at low elevations. The model also predicted a strong topographic effect associated with stream distance on maximum temperature variables, which are driven in part by radiative loading (Fridley, 2009). Conversely, the model showed no systematic change along a stream-to-ridge gradient for minimum temperature variables. This may be because of the countering effects of ridge exposure and near-stream cold temperature buffering that offset each other along the gradient (Fridley, 2009).

The combined result of the patterns observed for maximum and minimum seasonal temperatures is that at high elevations the model predicts that the range of temperatures experienced by the vegetation is increasing, while at low elevations the range is decreasing, which may have important implications for species distributions in GSMNP. Of course, absolute temperature shifts must be considered in relation to their biological significance to any particular organism or community.

Low elevation species may be able to migrate upwards based on increases in maximum temperatures, but be limited in their ability to do so by cold temperatures, which are not predicted to increase at the same rate. Further, the model predicts FFD and GDD to increase less with increased elevation, and growing season length in particular has been shown to be important in setting upper-elevational limits on species distributions.

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Siefert *et al.* (2015) found similar results in the Great Smoky Mountains, with summer temperatures and growing season length being the factors most associated with the upper-elevation limit of 28 tree species. If widely true of species in GSMNP, the lack of a strong trend in growing season duration at high elevations may strongly limit expected near-term community-level changes there. At the same time, warmer-adapted species from elsewhere in the southeast United States may successfully colonize low elevations over the coming decades as freezing conditions become rare, thereby 'squeezing' the distributions of species common to mid-elevation locations.

An important caveat in interpreting our results is that the model does not account for changes across years in factors, such as water distribution, radiative loading, or canopy cover. Extrapolation to years that are extreme in comparison with the 2005 and 2006 observation years, such as prolonged drought that may alter the mean water balance at certain landscape positions, are therefore not well accounted for. Likewise, large shifts in canopy cover, such as die-off of large hemlock (*Tsuga canadensis*) that has occurred in GSMNP since 2010, extensive blowdowns, or other canopy disturbances, are not accounted for. These factors, however, have more influence on predicting temperature for a specific year, rather than for analysing long-term trends as we do here.

4.2. Regional trends

An important finding from our short- *versus* long-term trend analysis is that climate trends seen over the past 30 years in GSMNP are not indicative of century-long climate trajectories. For many of the summarized temperature-related variables, current values are no different or even lower than levels from the early and middle points of the past century. Of course, if recent trends continue, GSMNP would likely experience atmospheric conditions that have been absent in the region since the hypsithermal (*ca.* 8000–4000 years ago) within the next century (Kutzbach and Webb, 1991). Nonetheless, general temperature regimes experienced by the Park's biota today are not unusual in the context of strongly fluctuating 20th century conditions. Further, Hansen *et al.* (2014) report biodiversity in GSMNP as being at relatively low risk from impacts of climate change, especially in light of more pressing issues of human land-use change in the region.

Some aspects of annual temperature regime have shifted, however, and may have important ecological impacts. Notable in this context is the long-term increase in spring and autumn temperatures, which have direct implications on phenology and flowering time (Badeck *et al.*, 2004), thus affecting growing season duration. Earlier warming may also lead to increased wildfires (Westerling *et al.*, 2006) and insect outbreaks (Bale *et al.*, 2002), which has implications for ecosystem functioning through changes in successional stage and species composition. Rising autumn temperatures may have less of an effect on growing season length, since the end of the growing season is thought to be triggered by photoperiod (Nitsch, 1957; Li *et al.*, 2003) (but see Heide, 2003), but the increase in FFD is likely to be significant for those species whose behaviour is primarily driven by low temperatures (Körner, 2003).

We also found a strong positive precipitation trend in GSMNP since 1900 consistent with other regions of the eastern United States since the 1970s (Easterling *et al.*, 2000). Increased GSP may alleviate summer water deficits (Burgess *et al.*, 1998; Weltzin *et al.*, 2003), thus potentially allowing more mesic species to colonize drier ridges (Whittaker, 1956). Species composition may also shift as a result of increased seedling and sapling survival because of less drought-induced mortality (Hanson and Weltzin, 2000) or influences of increased precipitation on nutrient cycling (Johnson *et al.*, 2000).

4.3. Linkages to NAO

Our analysis confirms that temperature and precipitation in GSMNP are significantly associated with NAO, consistent with other studies of climate patterns in North America (Hurrell *et al.*, 2003; Durkee *et al.*, 2008). The NAO has been in a positive phase overall since the 1970s resulting in overall warmer and wetter winters in the eastern United States (Hurrell *et al.*, 2003). NAO has a warming influence on autumn temperatures and precipitation in GSMNP, but a cooling effect on spring minimum and maximum temperatures. Our results suggest that links between the NAO and growing season climate variables are related but less consistent than cold-season variables. The duration of positive phases of the NAO that have dominated since the 1980s are unprecedented in the observational and paleoclimate record (Hurrell and Dickson, 2004). Atmospheric drivers of climate variability, including the NAO, are expected to become more intense over the coming decades (Jones and Mann, 2004).

4.4. Lack of long-term warming trends

Our analysis suggests GSMNP is not experiencing the same extent of climate change as many other montane regions, such as in western North America. This is likely because of the lack of significant recent warming observed across much of the southeastern United States (Pachauri and Reisinger, 2007; Meehl *et al.*, 2012), irrespective of elevation. Warren and Bradford (2010) also found that temperatures in the Southern Appalachians showed no overall warming trend, with temperatures plateauing in recent decades. Other studies have shown less increases in minimum and maximum temperatures in the eastern United States *versus* western regions (Portmann *et al.*, 2009; Meehl *et al.*, 2012), as well as proportionally less increase in FFD (Easterling, 2002). This lack of warming or 'warming hole' (Pan *et al.*, 2004; Kunkel *et al.*, 2006) has been linked to North Atlantic sea surface temperature phase changes and the Interdecadal Pacific Oscillation (Meehl *et al.*, 2012).

Another hypothesis for the difference in warming rates between the eastern and western United States is terrain height, with more mountainous regions in the west warming more quickly than lowland eastern regions

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(Meehl *et al.*, 2012). However, our analysis, along with that of Warren and Bradford (2010), included high-elevation weather stations and showed the same lack of an overall strong warming trend as lowland sites. Furthermore, at the high-elevation site of Mt. LeConte (1937 m a.s.l.), annual extreme temperatures have remained constant or have slightly decreased since 1980. Seasonal temperature variables show inconsistent results with maximum autumn and spring temperatures increasing since the 1980s, while minimum temperatures remained constant or slightly decreased. We note, however, that the non-significant interaction between elevation and year in our analysis may stem from a lack of high-elevation sites. The paucity of quality long-term high-elevation climate data is a serious issue in regional climate modelling in mountainous landscapes such as GSMNP.

5. Conclusions

Our results highlight the importance of downscaling climate data to scales that are relevant to the organisms in question, because the strength of regional climate trends is sensitive to site elevation and exposure. In montane landscapes such as GSMNP, fine-scale microclimate variation has important implications for how species respond to regional climate change trends, depending on how they respond to particular climate variables. Although regional temperature increases were minor when considered across climate fluctuations of the past century, strong changes in thermal regimes of the past few decades for particular landscape positions are likely to have differentially affected the ecology of low *versus* high-elevation species, and those of mesic protected coves *versus* exposed ridges. Thus, even moderate levels of regional temperature change will affect species distributions and community assemblages in such heterogeneous landscapes. Finally, steady long-term increases in precipitation, in an ecosystem that already receives among the highest rainfall amounts in eastern North America, suggest ecosystem properties related to hydrology should remain a focus of monitoring efforts.

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Supporting Information

The following supporting information is available as part of the online article:

Figure S1. (a) Spatial distribution of 9684 randomly selected points, within Great Smoky Mountains National Park, used in the landscape-scale analysis. (b) Frequency distribution of sampled points by elevation. (c) Frequency distribution of sampled points by logged distance from stream.

Figure S2. A 95th quantile of MXT for (a) six weather stations (bolded in legend) spanning the period 1900–2011 and (b) fourteen weather stations spanning the period 1980–2011. Annual values were calculated from daily MXT values. Dashed lines are 5-year moving window averages. Solid lines are fitted values from a GAM.

Figure S3. A 5th quantile of MNT for (a) six weather stations (bolded in legend) spanning the period 1900–2011 and (b) fourteen weather stations spanning the period 1980–2011. Annual values were calculated from daily MNT values. Dashed lines are 5-year moving window averages. Solid lines are fitted values from a GAM.

Figure S4. Maximum autumn temperature for (a) six weather stations (bolded in legend) spanning the period 1900–2011 and (b) fourteen weather stations spanning the period 1980–2011. Annual values were calculated as the average of September, October, and November daily maximum temperature values. Dashed lines are 5-year moving window averages. Solid lines are fitted values from a GAM.

Figure S5. Minimum autumn temperature for (a) six weather stations (bolded in legend) spanning the period 1900–2011 and (b) fourteen weather stations spanning the period 1980–2011. Annual values were calculated as the average of September, October, and November daily minimum temperature values. Dashed lines are 5-year moving window averages. Solid lines are fitted values from a GAM.

Figure S6. Maximum spring temperature for (a) six weather stations (bolded in legend) spanning the period 1900–2011 and (b) fourteen weather stations spanning the period 1980–2011. Annual values were calculated as the average of April, May, and June daily maximum temperature values. Dashed lines are 5-year moving window averages. Solid lines are fitted values from a GAM.

Figure S7. Minimum spring temperature for (a) six weather stations (bolded in legend) spanning the period 1900–2011 and (b) fourteen weather stations spanning the period 1980–2011. Annual values were calculated as the average of April, May, and June daily minimum temperature values. Dashed lines are 5-year moving window averages. Solid lines are fitted values from a GAM.

Figure S8. FFD for (a) six weather stations (bolded in legend) spanning the period 1900–2011 and (b) fourteen weather stations spanning the period 1980–2011. Annual values were calculated as the total number of days where the minimum daily temperature was >0 °C. Dashed lines are 5-year moving window averages. Solid lines are fitted values from a GAM.

Figure S9. GGD for the period of February 1 to May 31 for (a) six weather stations (bolded in legend) spanning the period 1900–2011 and (b) fourteen weather stations spanning the period 1980–2011. Annual values were calculated as the average of the minimum and maximum daily temperature minus a base temperature of 10 °C. Dashed

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lines are 5-year moving window averages. Solid lines are fitted values from a GAM.

Figure S10. TAP for (a) six weather stations (bolded in legend) spanning the period 1900–2011 and (b) fourteen weather stations spanning the period 1980–2011. Annual values were calculated as the sum of all precipitation for the year. Dashed lines are 5-year moving window averages. Solid lines are fitted values from a GAM.

Figure S11. GSP for (a) six weather stations (bolded in legend) spanning the period 1900–2011 and (b) fourteen weather stations spanning the period 1980–2011. Annual values were calculated as the sum of all precipitation for May through October. Dashed lines are 5-year moving window averages. Solid lines are fitted values from a GAM.

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