

Modeling monthly temperature in mountainous ecoregions: importance of spatial scale for ecological research

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ABSTRACT: Large gridded climate datasets facilitate correlation with landscape patterns (e.g. with species distribution), but point-based ecological data are often disconnected from the spatial extent and resolution of available climate data. Consequently, data users must understand the tradeoffs between spatial and temporal resolution, as well as potential biases arising from the modeling approach when selecting data. The Global Regression Ecoregional Analysis of Temperature (GREAT) model was developed to describe monthly temperature experienced by locations along elevation and latitudinal gradients in the central Appalachians. Model performance was assessed at 30 m and 1 km spatial resolutions, with subsequent analysis of the tradeoffs between extracting temperatures from an *a priori* spatial grid versus modeling temperature for specific locations. Results indicate that temperatures modeled at coarser resolution (1 km) had higher correlation with observed station temperatures because models developed at finer spatial scales (30 m) over-emphasize the influence of topographic variation. Monthly temperatures from the GREAT model were compared with temperatures extracted from the established, spatially weighted gridded products PRISM and Daymet. This comparison showed greater correlation between the spatially weighted modeling approaches than with the global regression-based method. However, monthly temperatures from the GREAT model had the highest correlation with temperatures observed at 14 independent climate stations that were not used in the development of any of the 3 models. The GREAT model allows temperature to be modeled specifically for each station and results in higher model performance than can be achieved with gridded datasets.

KEY WORDS: Scale · Topography · Terrain · Temperature model · Interpolation · PRISM · Daymet · Model validation

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1. INTRODUCTION

Many landscape-scale patterns, e.g. species distribution, are driven by individual responses that operate at fine spatial and temporal scales; however, the climate data used to explain biogeographical patterns primarily exist for coarse spatial scales. For example, climate envelope models often correlate species distribution with temperature and precipitation at the resolution of square kilometers, even though estab-

lishment and growth of individuals that drive that landscape distribution typically occur at resolutions of square meters (Potter et al. 2013). Past analyses have shown that spatial resolution and assumptions of uniformity within climate grid cells used to parameterize distribution models can result in markedly different predictions of suitable habitat across a landscape (Franklin et al. 2013). Furthermore, microclimatic conditions driven by topographic factors, e.g. solar insolation, can disrupt common elevation-tem-

perature assumptions and associated species distributions (Dobrowski 2011). Accessible temperature modeling approaches that allow high spatial resolution or customization to a region of interest are necessary to better explain biogeographic associations with climate and the underlying mechanisms.

Physical relationships between topography and temperature can be used to spatially interpolate geographically and temporally dispersed station data. Site-specific weather stations provide accurate weather at a particular location, but research focused on describing patterns over long periods of time or large geographic regions are rarely able to rely on station data for each location of interest. As a result, many researchers turn to modeled climate datasets and are faced with decisions that include the limitations of model structures, as well as trade-offs between resolution and extent in both space and time. Long-term gridded historical datasets, e.g. the Parameter–elevation Regressions on Independent Slopes Model (PRISM, Daly et al. 1997), go back to 1895, but have monthly information freely available at a 4 km resolution. Another gridded dataset, Daymet (Thornton et al. 1997), provides daily temperature and precipitation extending back to 1980 at a 1 km spatial resolution for much of North America. Both datasets combine geographical weighting of station data with effects of topography, and have been used extensively with landscape-scale studies of vegetation dynamics such as species distribution and phenology (e.g. McKenzie et al. 2003, Ackerly et al. 2010, Lutz et al. 2010, Homer et al. 2013). Similar datasets exist for other regions of the world, e.g. the European monthly (1901–present) CRU (Climatic Research Unit) dataset (Harris et al. 2014) and the daily (1950–present) E-OBS dataset (Haylock et al. 2008). Despite seemingly abundant options for climate data, these data sources often remain too coarse to be useful with many elevation gradient studies, or too restricted in temporal length for use with long-term studies such as those using tree rings.

The need for gridded sub-kilometer spatial resolution climate data grows as scientists seek to link fine-scale patterns of species behavior to large-scale species distribution and ecosystem functioning. We developed a Global Regression Ecoregional Analysis of Temperature (GREAT) model for the central Appalachians to provide a flexible temperature modeling framework that could be applicable both to landscape surfaces and point data common in ecological research. Temperatures from the GREAT model were validated using data from NOAA COOP (Cooperative Observer Network) stations and comparing

these with 2 existing gridded temperature products, PRISM and Daymet (Daly et al. 2008, Thornton et al. 2014). A final model validation evaluated the accuracy of the GREAT model, PRISM, and Daymet at 14 independent weather stations that were not used in the development of any of the models. To investigate how spatial resolution and the extent of topographic information influence the ability to model historical monthly temperatures of specific points on the landscape while holding the modeling approach constant, we used the GREAT model to predict monthly temperature for surrounding areas at 30 m and 1 km resolution throughout the central Appalachian ecoregion. Modeling temperature at specific points using topographic information for the surrounding area is an alternative to the development of spatial resolution grids, and we provide an example of the utility of point-based temperature modeling by comparing grid-extracted and point-based modeled temperatures along 6 elevation gradients in the central Appalachian ecoregion.

2. METHODS

2.1. Study ecoregion and topographic factors

Our temperature model was developed for the south and central region of the Appalachian Mountain range. This region is characterized by generally north–south ridge and valley topographic configurations, and is predominantly covered by forests, although agriculture and urban development are found at lower elevations. We selected US Forest Service ecoregions M221A, M221B, and M221D for climate analysis (Fig. 1, Bailey 1995). *Quercus–Carya* forests dominate the central region, but high elevations and northern latitudes have increased presence of *Acer–Fagus–Betula* and *Picea–Abies* forest types; the southeastern edge contains *Quercus–Pinus* forests (Braun 1950).

Topographic factors used for temperature modeling originate from 10 m resolution digital elevation models (DEMs) from the National Elevation Dataset (Gesch et al. 2002, Gesch 2007). Monthly solar radiation and upslope area contributing to cool air drainage were calculated from 10 m resolution DEMs, and then resampled to 30 m and 1 km resolution for climate analysis (Fig. 2). Prior to spatial aggregation, elevation in the study region ranged from 4 to 2034 m above sea level. Monthly solar radiation is a primary driver of monthly temperature (Hansen et al. 1997) and was calculated across the study region using the

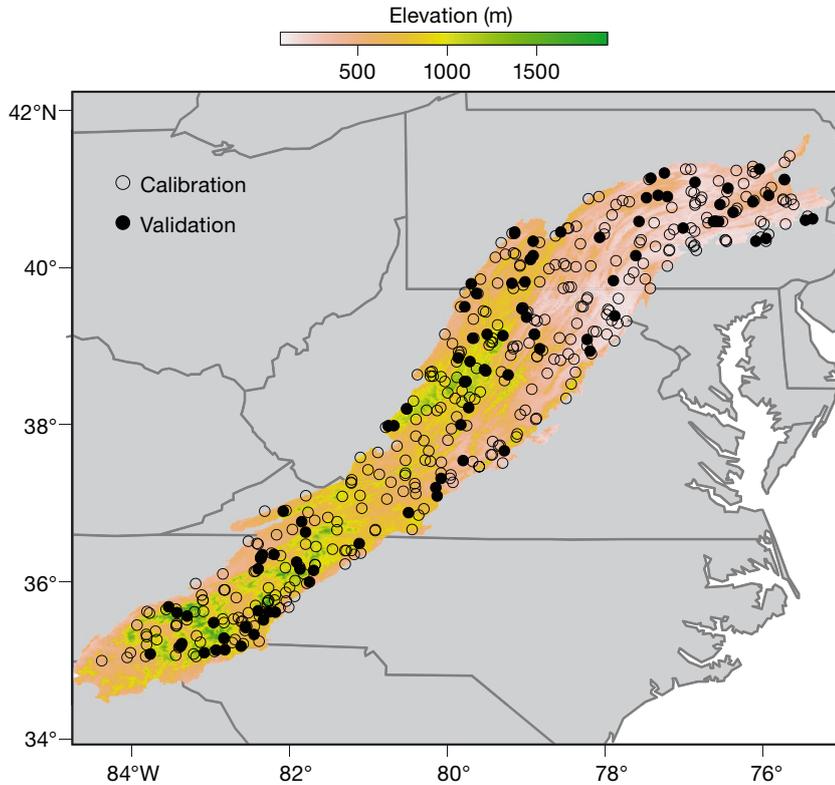
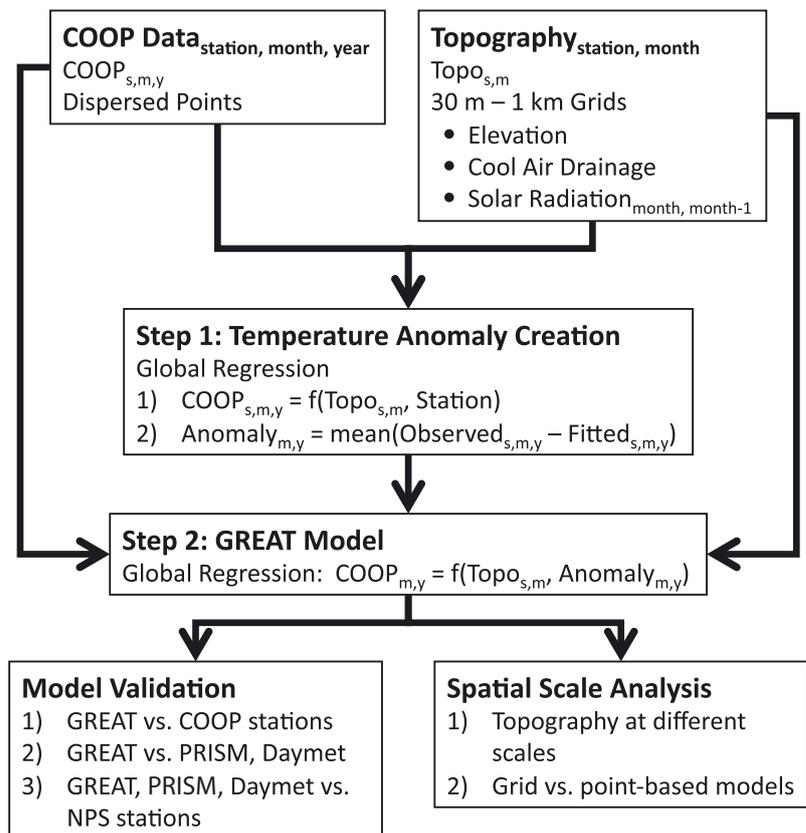


Fig. 1. NOAA COOP (Cooperative Observer Network) stations used for calibration and validation of the GREAT (Global Regression Ecoregional Analysis of Temperature) model

area solar radiation spatial analyst function in ArcMap 10.1 (Rich et al. 1994, Fu & Rich 2002). Because solar radiation varies with latitude, solar radiation calculations were performed separately on 0.3° latitude sections of the central Appalachian study region, with 0.05° overlap between bands. Overlapping sections were then merged to create continuous monthly solar radiation surfaces for the study region. December had the least amount of solar radiation (540–9178 Wh m⁻²), while July had the most solar radiation (5609–226 541 Wh m⁻²). Previous studies have indicated an approximate 1 mo lag between peak solar radiation (summer solstice) and peak maximum temperatures (Legates & Willmott 1990, Huang et al. 2008); thus, both solar radiation in the month of interest and solar radiation in the preceding month were included separately in temperature models. Throughout this manuscript, solar radiation refers to the combination of both factors (Fig. 2). Potential for cool

Fig. 2. Workflow for the development of the GREAT model and subsequent analyses. GREAT model regression equation development consisted of 2 stages: (1) development of a single anomaly record for each month and year for the entire ecoregion using topography and COOP station data; and (2) modeling monthly temperature at each COOP station using topography and the anomaly record. The resulting linear regression equation was then used to model temperature either at individual points or across a gridded ecoregion, and validated with COOP calibration stations, other gridded products, and independent NPS (National Park Service) weather stations



air drainage was calculated as upslope area using the flow accumulation hydrology function in ArcMap 10.1 (Jenson & Domingue 1988) on a sink-filled 30 m DEM. The original function calculates the number of upslope cells, which were then transformed into upslope area in km^2 . Due to the large range of upslope areas observed in the study region, cool air drainage area was truncated so that the maximum contributing area for cool air drainage was 100 km^2 . The distribution of cool air drainage area was highly skewed, with 98% of the study region being characterized by a potential cool air drainage area of $<1 \text{ km}^2$, so this factor was log-transformed for analyses.

The central Appalachian ecoregion contains 386 stations in the NOAA COOP stations that contained a minimum of 24 mo of observations between 1900 and

2013; these were used for the GREAT model development (Fig. 2). Mean pairwise correlation of temperatures among these stations was $0.99 \pm 0.03 \text{ SD}$ (variation in data hereafter reported as SDs except in the Supplement), although mean correlations for individual months ranged from 0.65 ± 0.34 in August to 0.85 ± 0.28 in December. NOAA COOP stations ranged in elevation from 86.5–969 m (Fig. 3). Monthly solar radiation ranged from $11\,769\text{--}81\,554 \text{ Wh m}^{-2}$ in December and $138\,748\text{--}220\,773 \text{ Wh m}^{-2}$ in July (Fig. 3). The median cool air drainage area of COOP stations was 0.004 km^2 , and the cool air drainage area of 11 stations was rescaled to 100 km^2 for temperature modeling (Fig. 3). We randomly excluded 10% (39 stations) of the 386 stations from the initial model development, to be used for model validation.

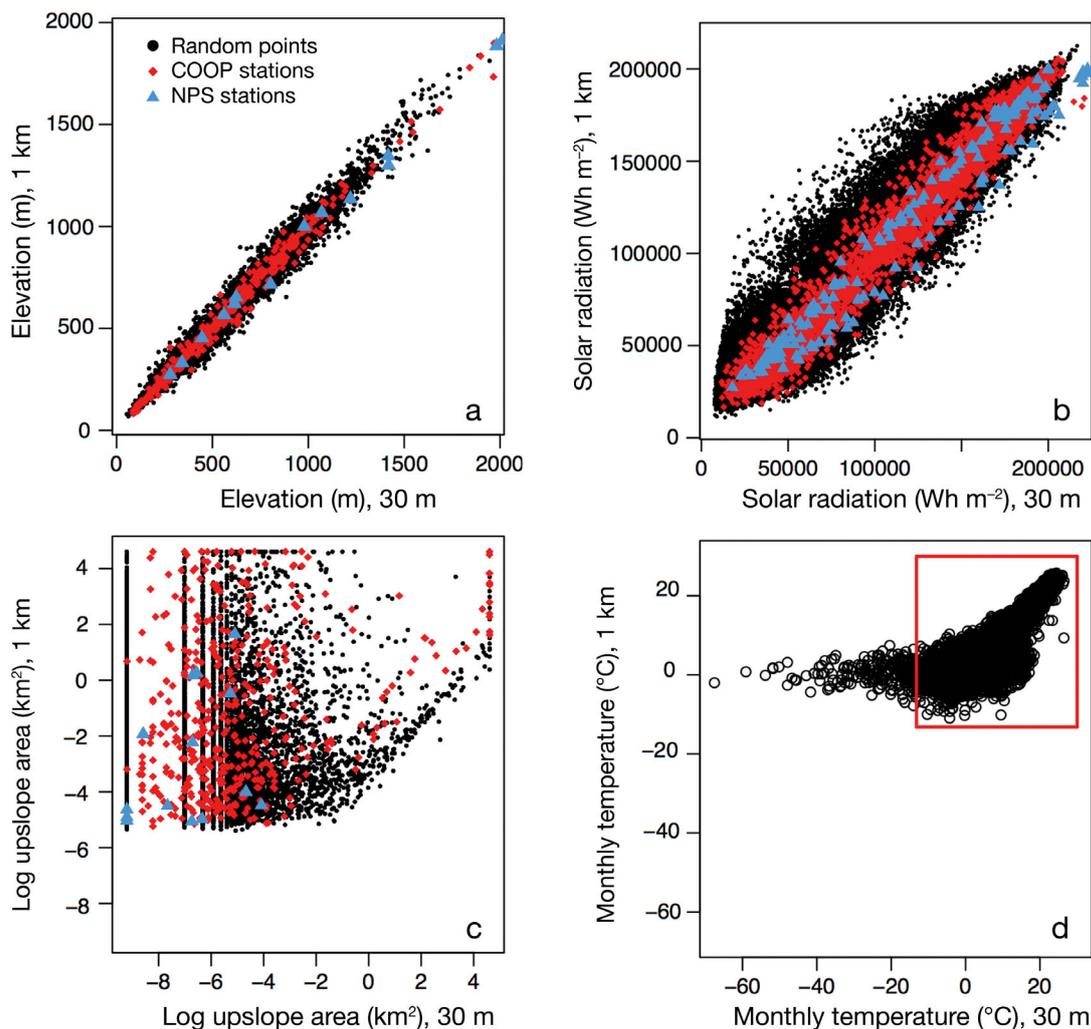


Fig. 3. Correlation between the 30 m and 1 km spatial resolutions for topographic parameters (a,c) and monthly solar radiation (b) used to model monthly temperature at 10 000 random points throughout the study region, NOAA COOP stations used to parameterize and validate the GREAT model, and the NPS stations used in model validation. Monthly temperature (d): mean monthly temperature for 1981–2010; red box: the full range of monthly temperatures observed in the COOP station record

We modeled climate at 3 spatial resolutions: 30 m, 800 m, and 1 km. Values for topographic factors at spatial resolutions >30 m were calculated as the mean of 30 m resolution values. For example, monthly solar radiation extracted for a COOP station for use in the development of the 1 km GREAT model was calculated as the mean value of solar radiation from the 30 m resolution grid over a 1 km² circular area centered on the station. For model validation in which the GREAT model was compared to existing gridded products such as PRISM, topography was first mean-aggregated to the appropriate scale (800 m or 1 km) from the 30 m grids, and then resampled so that grid cells between the 2 datasets were aligned.

2.2. GREAT model

Mean monthly temperatures in the study region were modeled using a 2-step global regression process (Fig. 2). First, we used a hierarchical linear mixed model to create an ecoregional anomaly record by predicting mean monthly station temperature from solar radiation and elevation. Similar linear model-based approaches have been used at finer spatial scales at other locations in the US (e.g. Brown & Comrie 2002, Huang et al. 2008, Fridley 2009). The model in the present study included fixed effects of month, solar radiation, and elevation as well as a random station effect to account for autocorrelation of observations from the same station. The ecoregional anomaly record was calculated as the mean difference between fitted and observed station temperatures for each month and year.

Following creation of the anomaly record, data from the 347 calibration stations were used to create a full climate model that was used to model monthly temperature across the entire study region (Fig. 2). In these models, monthly climate station temperature was predicted by interactions among the monthly anomaly record and 2 additive components: (1) solar radiation, and (2) interactions between elevation and cool air drainage. Additionally, all fixed effects were fit with month-specific slopes and intercepts. The full temperature model followed the following form:

$$\text{Temperature}_{(\text{month}, \text{year})} = \text{Month}_{(\text{month})} \times \text{Anomaly}_{(\text{month}, \text{year})} \times (\text{solar radiation}_{(\text{month})} \times \text{solar radiation}_{(\text{month}^{-1})} + \text{elevation} \times \text{cool air drainage})$$

We used the GREAT model to predict temperature at 30 m and 1 km spatial resolutions. The anomaly record and fixed effects of the 2 resolutions were fit independently.

2.3. Model validation

2.3.1. NOAA COOP stations (GREAT model)

Model fit at 30 m and 1 km spatial resolutions was assessed using the R² correlation and intercept from simple linear regression of modeled and observed temperature at the 347 COOP calibration stations and 39 COOP validation stations. To aid in intercept interpretation, data were centered on zero by subtracting the mean monthly or station observed temperature from both fitted and observed values.

2.3.2. Temperature model comparison (GREAT model, PRISM, Daymet)

Temperatures modeled using GREAT were compared with those modeled using the 2 established gridded climate models PRISM and Daymet. For these grid-based comparisons, we resampled topographic grids to match the spatial extent and resolution (~800 m) of the 1981–2010 temperature normals developed by the PRISM research group (PRISM Climate Group 2004) and the 1 km resolution Daymet dataset (Thornton et al. 2012). Analysis of the GREAT model versus PRISM compared 30 yr monthly temperature normals as well as a mean annual temperature at 10 000 randomly located points throughout the study region. Comparison between the GREAT model and Daymet were restricted to 2433 of those points that were located inside one 2° × 2° downloadable gridded climate tile in the central region of the study area. Models were compared using the intercepts and R² values from linear regression of temperature values from the different model datasets at the randomly located points.

2.3.3. NPS stations (GREAT model, PRISM and Daymet)

Temperature data from 14 National Park Service (NPS) air quality monitoring stations (Fig. 2, NPS 2013) were used to validate temperatures predicted by the GREAT model at 30 m and 1 km extent point interpolations, as well as temperatures extracted from 4 km resolution monthly PRISM grids and 1 km Daymet grids. The NPS stations are not part of the NOAA COOP network and are not used to parameterize the GREAT, PRISM, or Daymet climate models, thus providing an independent dataset against which the performance of all the models can

be compared. The 14 NPS stations represent the range of topographic conditions found in the study area (Fig. 3) and provide a total of 474 monthly temperature observations between 1990 and 2013, which were used for model validations and comparisons. As with the model comparisons, NPS station model validation used linear regression to evaluate model fit with the observed data.

2.4. Scale analysis

2.4.1. Topographic drivers across spatial scales

We compared the topography at 10 000 randomly located points extracted at 30 m and 1 km resolutions throughout the central Appalachian region to understand how changes in topography across spatial scales influence temperature modeling. This analysis used simple linear regression and paired *t*-test to compare elevation, solar radiation, cool air drainage area, and temperature at these 2 resolutions.

2.4.2. Gridded versus point-based temperature models

Differences in temperature among available models or modeling approaches may not only be an artifact of spatial resolution, but may also be a bias from the use of coarsely gridded data to describe climate in potentially co-located points. We demonstrate this common problem in ecology by describing the temperature profiles of 6 elevation gradients in the central Appalachians (Fig. 4). Gridded climate products capture climate variation in latitude-based climate gradients or elevation gradients spread out over a large geographic area; however, even the finest publicly available data products such as Daymet, often remain too coarse for use in many ecological studies. Studies using elevation gradients as a proxy for climate gradients may have all study locations fall within a single grid cell, even though individual points and elevations have distinct climates (Fig. 4). Within each of the 6 elevation gradients, points were located along 100 m transects at 3 elevations per site for a total of 60 points across the 6 sites. Elevation transects within each site were located on the same side of the mountain so that differences in solar radiation were due to microtopography rather than overall large-scale aspect. Within a site, elevation transects were separated by 150 m elevations, although linear distance between transects varied by site.

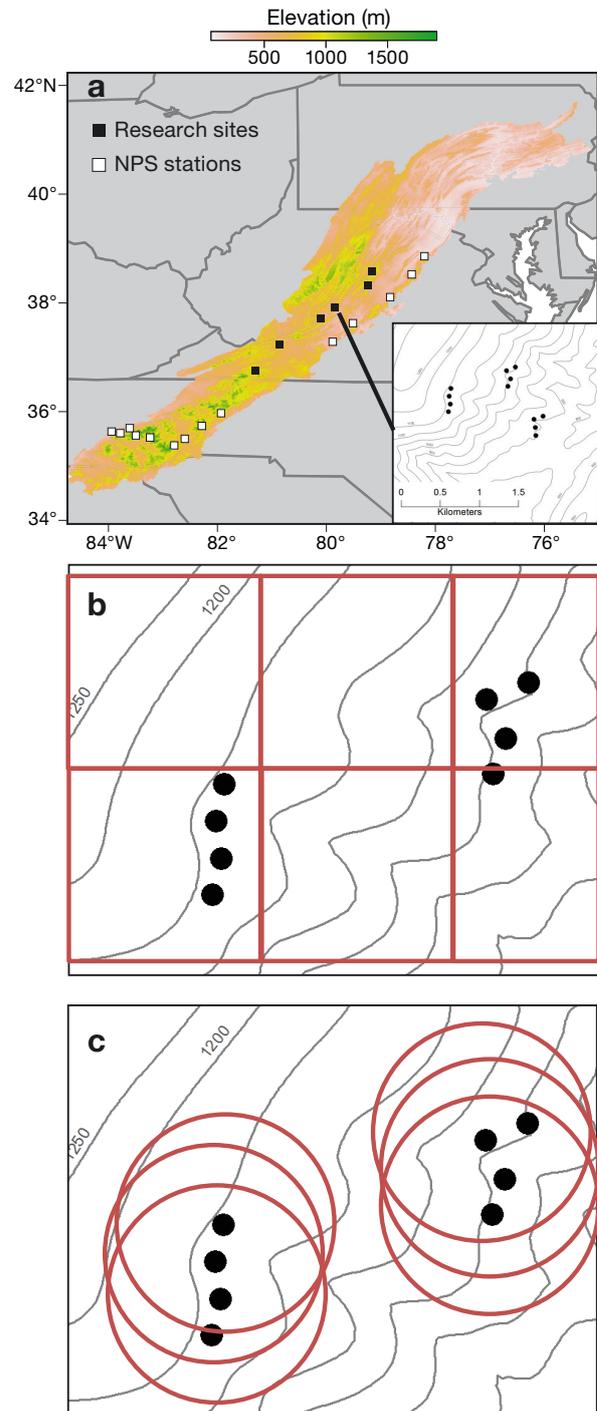


Fig. 4. (a) National Park Service (NPS) air quality weather stations used for independent climate model validation of the 30 m and 1 km regional regression models as well as the PRISM and Daymet gridded climate datasets. Six sites were used for ecological research and contained points (black dots) located along 3 elevation transects per site (a, inset). Points along each elevation transect are spaced 100 linear meters apart and transects are separated by 150 m elevation. These points were used to demonstrate differences between gridded (b) and point-specific (c) temperature modeling. Areas of grid cells and circles are the same (1 km²) for analyses, but are not drawn to scale here

Since no long-term temperature records are available for these sites, climate was calculated for each point in 2 ways: (1) simple extraction from a continuous 1 km resolution climate raster grid; and (2) point-based calculations from topography averaged over a 1 km² circular area centered on each point (Fig. 4). The area used for point-based topographic integration and the area of the grid cells are the same, but a single grid cell or multiple cells may characterize an entire site since grid cell boundaries are independent of point location. For point-based integration of topography, individual points may overlap in the area being used to calculate climate at a given location; however, each point has a unique set of mean topographic conditions since it draws from a slightly different area. Correlation of gridded or point-based climate with topographic factors within a site was assessed using a linear mixed model that included a

random site effect and a fixed elevation effect. In the comparison of the temperature models, actual plot elevation is the elevation extracted from the 30 m DEM. Mixed model pseudo- r^2 correlations were calculated using the `r.squaredGLMM` function in the `MuMIn` package in R (Barton 2013, Nakagawa & Schielzeth 2013).

3. RESULTS

3.1. Model validation

3.1.1. COOP validation: GREAT model

GREAT model correlations with observed temperature increased with spatial aggregation, while model intercepts decreased (Table 1). Monthly temperature correlation from calibration stations at a 1 km resolution ranged from 0.66 to 0.89 and were on average 0.09 ± 0.04 higher than at the 30 m resolution, which had an R^2 range of 0.48 to 0.83. Model improvement was even greater in the validation data: mean monthly correlations increased 0.16 ± 0.08 , with a decrease in the centered intercept of $0.24 \pm 0.13^\circ\text{C}$. April consistently had the lowest correlation among months, and the correlation was particularly low for fine-resolution models (e.g. the 30 m resolution model), where the April correlation coefficient was 0.25 below the mean monthly correlation in the validation stations. This contrasts with the 1 km resolution model, where April correlation was only 0.10 below the mean.

3.1.2. Model comparison: GREAT model, PRISM, Daymet

The 2 well-vetted gridded climate datasets, PRISM and Daymet, correlated higher with each other at different spatial resolutions than with the GREAT model at the same resolutions. Correlation between monthly temperatures from Daymet and PRISM were consistently high due to similar spatial weighting of the NOAA COOP stations used in both models (mean $R^2 = 0.95 \pm 0.01$, range 0.93–0.96). Overall monthly correlation of the GREAT model with Daymet and PRISM was similar (PRISM $R^2 = 0.66 \pm 0.13$, Daymet $R^2 = 0.67 \pm 0.10$). Despite the tight correlation of monthly temperatures between Daymet and PRISM, the month of greatest and least correlation with the GREAT model varied. The GREAT model had the highest correlation with PRISM in December ($R^2 =$

Table 1. Correlations and intercepts from linear regressions of predicted and observed temperature from the GREAT model at different spatial scales. Data from the 347 calibration and 39 validation NOAA COOP stations are shown. All temperatures were centered by subtracting the mean monthly temperature from both predicted and observed values

	30 m		1 km	
	R^2	Intercept	R^2	Intercept
Calibration month				
Jan	0.79	6.30×10^{-11}	0.87	0.0101
Feb	0.82	-3.36×10^{-10}	0.85	0.0082
Mar	0.67	-8.43×10^{-11}	0.79	0.0133
Apr	0.48	3.88×10^{-11}	0.66	0.0176
May	0.58	3.85×10^{-11}	0.70	0.0184
Jun	0.59	1.45×10^{-11}	0.69	0.0101
Jul	0.66	5.20×10^{-11}	0.73	0.0039
Aug	0.61	1.70×10^{-10}	0.71	0.0101
Sep	0.56	3.22×10^{-11}	0.69	0.0110
Oct	0.66	2.17×10^{-11}	0.75	0.0054
Nov	0.78	1.05×10^{-10}	0.82	-0.0014
Dec	0.83	-2.26×10^{-11}	0.88	0.0036
Stations	0.80–1.00	-2.79–3.14	0.80–1.00	-2.84 – -2.90
Validation month				
Jan	0.61	0.2436	0.89	0.0982
Feb	0.69	0.4270	0.84	-0.0799
Mar	0.59	0.2333	0.80	-0.1358
Apr	0.37	0.0398	0.68	-0.1879
May	0.58	-0.0466	0.74	-0.1851
Jun	0.62	-0.0020	0.71	-0.0982
Jul	0.73	0.0466	0.78	-0.0375
Aug	0.66	0.0043	0.75	-0.0992
Sep	0.57	0.0360	0.74	-0.1107
Oct	0.67	0.1319	0.79	-0.0530
Nov	0.70	0.3131	0.80	0.0141
Dec	0.72	0.2911	0.89	-0.03533
Stations	0.95–1.00	-2.79–2.14	0.96–1.00	-2.68 – -1.99

0.85) and the lowest in May ($R^2 = 0.49$), while correlation with Daymet was highest in July ($R^2 = 0.81$) and lowest in March ($R^2 = 0.49$). On average, the GREAT model predicted mean monthly temperature to be $0.14 \pm 1.1^\circ\text{C}$ warmer than the PRISM prediction ($p < 0.01$) and $0.39 \pm 0.87^\circ\text{C}$ warmer than the Daymet prediction ($p < 0.01$).

3.1.3. NPS model validation: GREAT model, PRISM, Daymet

When the 30 m and 1 km GREAT model, PRISM, and Daymet were validated against 14 independent NPS stations that were not used in the calibration of any of the models, the 1 km GREAT model was the only one to predict mean monthly temperatures that were not significantly different from the observed values ($p = 0.16$). Both the 30 m GREAT and Daymet models predicted monthly temperatures that were 0.20°C (GREAT: ± 1.4 , Daymet: ± 1.2) cooler than observed in the station data, while PRISM predicted temperatures that were $0.88 \pm 1.7^\circ\text{C}$ warmer than observed ($p < 0.01$). The 1 km GREAT model had a mean monthly correlation of $R^2 = 0.80 \pm 0.16$, with correlations being highest in the summer and lowest in winter, where the GREAT model generally predicted warmer temperatures than observed (Fig. 5). In contrast, Daymet had the highest correlations in the winter and spring, with mean monthly $R^2 = 0.72 \pm 0.13$. Correlations of PRISM with the observed monthly temperatures (mean $R^2 = 0.74 \pm 0.06$) did not show a clear seasonal trend, but consistently over-predicted summer temperatures.

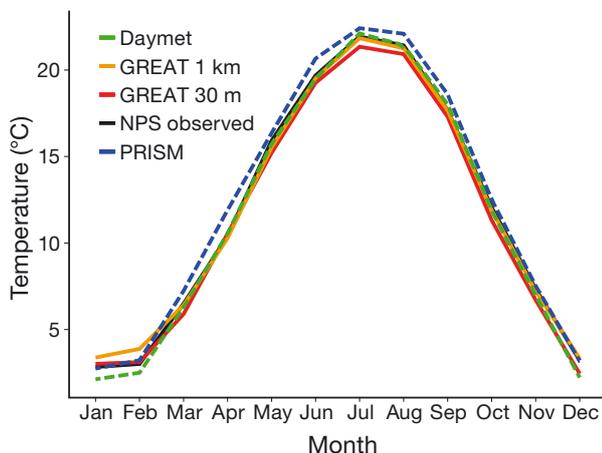


Fig. 5. Validation of the GREAT model (at 30 m and 1 km resolution), the PRISM and Daymet climate grids against mean monthly temperature at 14 independent NPS climate stations

3.2. Scale analyses

3.2.1. Topographic drivers across spatial scales

Topographic factors that influence the spatial distribution of temperature varied widely in their correlation between fine (30 m) and coarse (1 km) spatial resolutions. Elevation is the topographic factor with the greatest consistency and correlation across spatial resolutions. Mean grid cell elevations extracted for 10 000 random points from 30 m and 1 km resolutions had an R^2 of 0.98 (Fig. 3). Elevation from the 30 m grids was on average only 0.05 m lower than that from the 1 km grids ($p < 0.01$), but this varied greatly spatially ($SD = 39.9$ m). Solar radiation, which is the largest factor driving temperature in the GREAT model, also showed high correlation between 30 m and 1 km resolutions ($R^2 = 0.95$), with similar patterns of high spatial variability; solar radiation at the 1 km resolution was on average 155.8 ± 12376 Wh m^{-2} higher than that in the 30 m resolution grids (Fig. 3). Estimates of cool air drainage based on upslope area at 30 m and 1 km resolutions showed very little correlation ($R^2 < 0.01$), and the 1 km resolution had on average 1.3 ± 87.5 km^2 larger drainage area than the 30 m resolution (Fig. 3).

Fine-resolution parameterizations of the GREAT model resulted in greater spatial variation in temperature and a larger proportion of anomalous temperature values than coarse-resolution models. At the 1 km resolution, only 19 monthly temperatures at 3 points from the 1981–2010 time period fell below the range of temperatures observed in the NOAA COOP stations used to calibrate the model ($< 0.01\%$ of the data). In contrast, at the 30 m resolution, 2.3% of the 10 000 random points had at least one predicted monthly temperature that was below the range observed in the station data. The greater prevalence of extreme cold temperatures in the 30 m resolution model is driven by the interaction between cool air drainage effect and elevation. In the 30 m resolution model, the cool air drainage \times elevation interactions decreased monthly temperature, whereas these effects increased temperature and provided a moderating effect at the 1 km resolution (Table S1 in the Supplement at www.int-res.com/articles/suppl/c064/p099_supp.pdf). Neither model predicted temperatures that were above those observed in the COOP record. Monthly temperatures correlated well between the 2 spatial resolutions ($R^2 = 0.95$), and temperatures from the 1 km resolution were $< 0.01 \pm 1.9^\circ\text{C}$ warmer than those from the 30 m resolution model. There was no significant difference between

mean monthly temperatures modeled at the 2 resolutions ($p = 0.90$), although the 1 km model predicted a narrower range of temperatures and was less prone to prediction of extreme minimum winter temperatures (Fig. 3).

3.2.2. Gridded versus point-based temperature models

Using grids to estimate the temperature of closely spaced locations reduces the spatial variation represented in a climate dataset. Point-based extrapolation of temperature over a 1 km² area resulted in each of the 60 points along elevation gradients having a unique mean annual temperature, whereas extracting temperature from a 1 km gridded climate dataset resulted in only 20 different temperatures in the same 60 points (Fig. 6). Because grid cell boundaries have no relation to the location of points within a site, many sites were spread across multiple grid cells. Although $R^2 = 0.88$ between grid cell and point elevation, the grid cell grouping of points within a site was not necessarily based on elevation, which can drive mismatches between point and grid cell temperatures. Grid-based and point-based temperature models showed similarly low correlations be-

tween actual point elevation and temperature (grid-based marginal $R^2 = 0.06$; point-based marginal $R^2 = 0.04$). On average, grid-based temperatures were slightly warmer than point-based mean monthly temperatures ($0.14 \pm 1.1^\circ\text{C}$), although differences ranged from 3°C cooler to 4°C warmer. However, mean annual temperatures were not significantly different ($p = 0.29$) between the 2 methods.

4. DISCUSSION

Temperature at a given location is influenced by the topography over a relatively large area; therefore coarser-resolution models, such as the 1 km GREAT model, better predict monthly and annual temperature than models at finer resolutions (30 m). This is consistent with the decision of widely vetted climate products like PRISM and Daymet to provide climate data at spatial resolutions of 1 km or greater. In the central Appalachian ecoregion, the high spatial resolution (30 m) GREAT model over-emphasized the effects of topography on temperature, particularly solar radiation and cool air drainage, and produced temperature extremes not seen in meteorological observations. Mechanistic parameterization of temperature models based on direct empirical observations of convection, conduction, adiabatic lapse rate or cool air drainage may improve model accuracy. Convection and conduction result in smoother climate surfaces across the landscape; however, accurate modeling of these effects as well as of adiabatic lapse requires consideration of additional parameters such as humidity and wind speed, which increase model complexity and require information that is seldom readily available. Coarse-resolution models may not explicitly include conduction or convection in their structure, but averaging of topographic factors over a large area minimizes the role of microtopography and reduces sharp temperature differences among grid cells. Spatial smoothing of topographic model inputs or the resulting climate grids, as well as spatial weighting of calibration climate stations, can also result in smoother temperature surfaces and mimic the effects of conduction and convection. However, using large areas such as 1 km² to smooth fine-resolution gridded datasets over large geographic extents can be computationally intensive and prohibitive. In the present study, we did not vary the scale of topographic effects within the spatial resolution of a model. Optimizing the spatial resolution of influence for each topographic factor could have resulted in better parameterization of cool air drainage effects. For

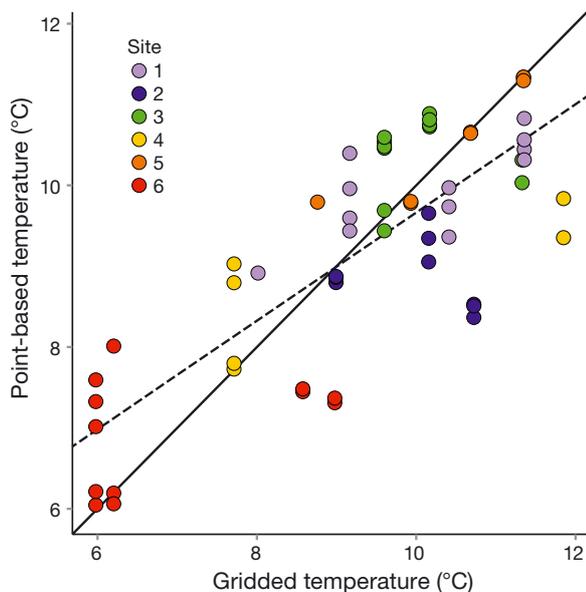


Fig. 6. Comparison of mean annual temperature at 60 plots along elevation gradients in 6 research sites ordered north (Site 1) to south (Site 6) (Fig. 2). Gridded temperature was extracted from 1 km resolution climate grids, while point-based temperature was derived from the mean topographic conditions from a circular 1 km² area centered on each plot. (—) 1:1 relationship between gridded and interpolated temperature; (---) best fit line from linear regression ($R^2 = 0.63$)

example, elevation and current month solar radiation may influence temperature at fine scales, but effects such as cool air drainage and lagged solar radiation are likely to influence temperature over broader areas. As with spatial smoothing and conduction, consideration of varying spatial scales of influence of individual topographic parameters has the potential to increase model accuracy, but comes at a potentially prohibitive computational cost.

Point-based models of temperature derived from global regression models, such as the GREAT model, provide an alternative to gridded climate datasets for capturing spatial patterns in temperature at a scale relevant to biological processes. When a given location is not representative of the mean topographic or climate conditions of the grid cell it is located in, there may be disparity between modeled and actual temperature. This may be a contributing factor for the higher correlation of the 1 km resolution GREAT model with the NPS validation stations than those of PRISM or Daymet, which are both gridded products. In field research, such as our example of an elevation gradient-based study design, gridded datasets mask some inherent plot-based variation in temperature arising from topography. Gridded climate products may be appropriate for characterizing study location temperatures when locations are geographically dispersed, or when between-site variation is greater than potential temperature variation within a grid cell. However, in topographically complex regions such as the central Appalachians, coarse-resolution temperature datasets should be downscaled with caution.

PRISM and Daymet both use spatial weighting of the COOP station data as the base area temperature, which is then adjusted using topography (Daly et al. 1997, Thornton et al. 1997). Although spatial weighting of COOP station data should increase modeled monthly temperature accuracy, PRISM showed a stronger seasonal bias in model fit than the GREAT and Daymet models. This may be because PRISM does not explicitly consider solar radiation, which is a known driver of spatial and temporal temperature patterns (Lookingbill & Urban 2003, Bertoldi et al. 2010, Holden et al. 2011), and instead assumes elevation as the driving factor of local temperature variation (Daly & Bryant 2013). Validation of all 3 models against independent station data indicates that because the central Appalachian ecoregion shares a common climatic influence at monthly time scales, spatial weighting of station temperatures is not necessary to model temperature in this ecoregion. The GREAT model is able to overcome potential gains in

model fit from spatial weighting by instead facilitating rapid, point-based temperature estimation using an ecoregional global regression equation.

Land cover is a factor that is not commonly included in climate models, but has the potential to greatly influence climate model accuracy. Different land cover types, such as forest or urban land uses, have unique albedo and evapotranspiration values that lead to phenomena such as urban heat islands and regional cooling (Taha 1997, Bala et al. 2007). Differences in monthly model accuracy may be affected by land cover type. The GREAT model had higher correlations with observed temperature in the winter, when the vegetation of the region has senesced and little evapotranspiration occurs. This reduces the difference between weather stations located in urban and rural environments. Lower model correlation in the spring and summer months may be driven by differences in vegetation–temperature feedbacks, where a greater range of temperatures is observed in forested or agricultural regions due to evaporative cooling. In the winter months, above and below canopy temperatures are likely to be more uniform or the ground slightly warmer due to absorption of solar radiation. However, in the summer, below canopy temperatures can be considerably cooler than above or open canopy conditions due to the effects of shading (Pritchard & Comeau 2004, Ritter et al. 2005). While it might be possible to create empirical corrections for open and closed canopy conditions, these relationships would be hard to spatially predict during spring leaf out, when canopy phenology is influenced by temperature and the dominant tree species (Richardson et al. 2006). Effects of land cover on spatial temperature patterns could be modeled for recent time periods where there is extensive land cover information (Jin et al. 2013), but these data are unavailable for modeling historical temperature in most areas.

The GREAT model provides a flexible framework for predicting temperature patterns across space and time at an ecoregional extent. The model can be developed for any ecoregion using freely available digital elevation maps and weather data networks, such as the NOAA COOP stations. However, several considerations need to be made before using this approach. First, climate stations must come from a cohesive climate region and be subject to similar influences of topography. The central Appalachian ecoregion contains similar ridge and valley topography throughout its range, but its large latitudinal extent may have contributed to poor GREAT model performance during transitional climate months such as April. While climate stations throughout the re-

gion consistently showed high temperature correlations, April was also the month with the lowest correlation among climate station temperatures. Climate modeling over a narrower geographic region would likely increase model performance during this time period. Second, climate stations should represent the range of topographic conditions over which one wishes to interpolate climate. In the central Appalachians, climate stations were skewed towards high light locations, with the minimum monthly solar radiation at stations being more than twice the lowest level observed on the landscape. Poor parameterization of low-light conditions, such as those found in narrow valleys and north slopes, contributed to the high occurrence of unreasonably low temperature predictions in our 30 m resolution model. Despite these potential model limitations, the flexibility of a global regression-based model developed for a specific ecoregion better facilitates modeling the climate of specific locations than is possible using coarse-resolution gridded climate datasets.

5. CONCLUSIONS

Continental-scale gridded climate datasets facilitate comparisons of temperature and precipitation over large areas, but pose several challenges for ecological research. Development of an ecoregion-specific climate model may increase accuracy of modeled temperatures and provide greater flexibility for characterization of climate in specific locations. Validation of climate models against independent temperature data not included in model parameterization is essential to assess the suitability of a particular modeling approach or spatial resolution used. Climate models need to reflect the specific spatial and temporal resolution of interest, either through point interpolation or high-resolution grids. Point-based models of climate rather than temperature extraction from gridded datasets capture differences in microclimates while minimizing the risk of over-emphasizing topographic influences and producing unrealistic temperature estimates. High-resolution, region-specific climate models are necessary to accurately represent climate at biologically relevant spatial scales, but climate models for each cell need to consider influences of the surrounding topography to ensure model accuracy.

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