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Leaf phenology paradox: Why warming matters most where it is already warm

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ABSTRACT

Interactions between climate and ecosystem properties that control phenological responses to climate warming and drought are poorly understood. To determine contributions from these interactions, we used space-borne remotely sensed vegetation indices to monitor leaf development across climate gradients and ecoregions in the southeastern United States. We quantified how air temperature, drought severity, and canopy thermal stress contribute to changes in leaf flushing from mountainous to coastal plain regions by developing a hierarchical state-space Bayesian model. We synthesized daily field climate data with daily vegetation indices and canopy surface temperature during spring green-up season at 59 sites in the southeastern United States between 2001 and 2012. Our results demonstrated strong interaction effects between ecosystem properties and climate variables across ecoregions. We found spring green-up is faster in the mountains, while coastal forests express a larger sensitivity to inter-annual temperature anomalies. Despite our detection of a decreasing trend in sensitivity to warming with temperature in all regions, we identified an ecosystem interaction: Deciduous dominated forests are less sensitive to warming than are those with fewer deciduous trees, likely due to the continuous presence of leaves in evergreen species throughout the season. Mountainous forest green-up is more susceptible to intensifying drought and moisture deficit, while coastal areas are relatively resilient. We found that with increasing canopy thermal stress, defined as canopy-air temperature difference, leaf development slows following dry years, and accelerates following wet years.

1. Introduction

Changes in the speed and timing of leaf development during spring green-up influence biosphere-atmosphere exchange of carbon (Keenan et al., 2014b; Peichl et al., 2015) and water cycles (Fitzjarrald et al., 2001; Hayhoe et al., 2007; Hufkens et al., 2016), length of the growing season (Fridley, 2012; Keenan and Richardson, 2015), and perhaps even species distributions (Fridley, 2012; Polgar et al., 2014). Strong interaction effects on phenology involving temperature, moisture, and plant characteristics at the individual scale (Clark et al., 2014a) suggest that regional phenological change could depend on such climate-ecosystem interactions. These individual-scale changes, combined with widespread impacts of phenological changes observed at the continental scale (Fu et al., 2015b), raise two important questions. First, could climate-ecosystem interactions control, perhaps even dominate, the green-up process across different ecoregions relative to broad scale climate effects? Second, could water availability and canopy thermal stress slow green-up development in ways that could be directly quantified? If so, we might better anticipate the combined effects of warming and drought on leaf phenology (Fu et al., 2014). Answers to these questions require spatio-temporal analysis that admits full uncertainty on continuous phenological development and observations thereof across regions. Clark et al. (2014a) introduced this approach to phenology at the individual scale. We extend it here to the role of interactions at biogeographic scales. Here, we combine field data with remotely sensed observations of forest vegetation indices to quantify how inter-annual variations in environmental variables influence the speed of spring green-up across ecoregions and climatic gradients in the southeastern United States.

Inconsistency in phenology measurement and analysis could be partly responsible for inconsistent interpretations (Cleland et al., 2007; Fu et al., 2015a; Fu et al., 2015b; Polgar and Primack, 2011; Richardson

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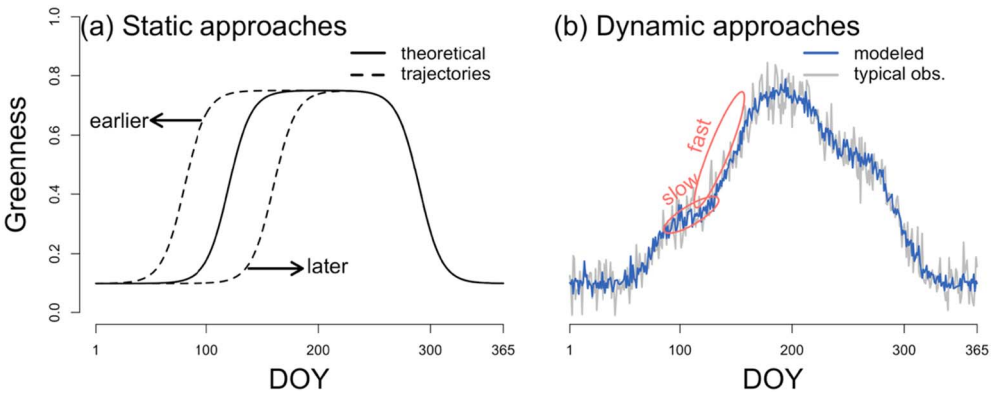

Fig. 1. Static (a) vs. dynamic or continuous development models (CDM) (b) for green-up phenology. Unlike static frameworks, the CDM predicts changing sensitivity over time, while accounting for the dependence structure within time-series data. Dynamics models infer both rate and timing of events, i.e., continuous changes in rate. Figure b shows a simulated dynamic model of phenology. DOY indicates day of year.

et al., 2013; Schwartz et al., 2006; Xie et al., 2015). Phenological trends have been measured by a range of metrics, including a ***date*** of onset of green-up, of minimum greenness, or of peak greenness (Fisher et al., 2006). It can be ***duration***, such as length of growing season (Reyes-Fox et al., 2014). It can be a ***rate***, such as the slope of greenness with respect to time at a specific date (Buitenwerf et al., 2015) or ***continuous*** throughout the development period (Clark et al., 2014b). Some studies have used multiple metrics in combination (Buitenwerf et al., 2015), yet most models have focused on the date or degree days at budburst (Fig. 1a). Despite the large number of studies on leaf phenology (Fisher et al., 2006; Fridley, 2012; Keenan et al., 2014b; Xiao et al., 2006), the interactions involving climate and ecosystem properties remain poorly understood (Beedlow et al., 2013; Cufar et al., 2012; Yue et al., 2015).

Models that can evaluate continuous leaf development are needed to determine the climate-ecosystem interactions that control the growing season. Paradoxically, while green-up starts earlier in warm regions, it is in fact slower (Clark et al., 2014b). In other words, across a region, mean temperature has a positive effect on ***onset*** of green-up, while its correlation with the ***rate*** of green-up is negative. Moreover, global warming is all about temperature anomalies—changes in daily temperatures from one year to the next. If temperature has opposing effects on onset versus rate, then warming effects must be inferred dynamically. The paradoxical slower development in warm regions is accurately quantified by the continuous development model (CDM), because it captures both timing and rate. Unlike degree-day models, which aggregate temperature variation into a single number for a given day, the CDM tracks its changing impacts over time. Because it is continuous, it further separates the effects of mean temperature and the day-to-day anomalies. This dynamic capability can embrace the interactions that involve both static and dynamic variables (Fig. 1-b). CDMs can quantify influence of environmental variables such as warming and droughts and their interactions with ecosystems by quantifying the development process over time.

CDM allows us to reconsider the important insights from a range of previous analyses, while combining them to infer climate-ecosystem interactions. Changing temperature, precipitation, moisture and their interactions may or may not affect green-up across ecoregions. Temperature effects on green-up (Cleland et al., 2007; Polgar and Primack, 2011; Schwartz et al., 2006) have been demonstrated with cumulative heat indices (e.g. degree days) (Jing et al., 2016; Kwit et al., 2010), but there could be interactions that regulate its effects. Sensitivity of spring green-up to warming may be limited by unmet vernal chilling and/or photoperiod requirements (Fu et al., 2015b). The effects of warming may vary throughout spring green-up, due to changing physiological sensitivity during plant development. Hydrological stress, as a result of warming or lack of moisture, could also delay leaf development (Wang et al., 2016). Ecoregions in the southeastern (SE) US range from coastal zones to mountainous forests and rolling Piedmont. This region provides an opportunity to examine interactions that involve daily, seasonal, and inter-annual climate variations across ecosystems with a full range of leaf habit, from deciduous to evergreen.

There is growing evidence that temperature effects interact with soil moisture and precipitation. Inter-annual and geographic variation in precipitation may influence spring green-up (Zeppel et al., 2014). In many regions, soils are fully recharged in early spring, and soil moisture deficit remains low. Where moisture is not limiting during green-up there could be little response to spring rainfall (Hernandez-Calderon et al., 2013; Kaye and Wagner, 2014; Rollinson and Kaye, 2012). During hot days and/or drought, stomata closure reduces photosynthesis thereby delaying leaf-out (Yousfi et al., 2015). Green-up may be delayed during multi-year droughts and in regions characterized by spring moisture deficits (Hayden et al., 2010; Kaye and Wagner, 2014).

Strong climate-ecosystem interactions could determine green-up variation across ecoregions, but current evidence does not agree on how. For example, green-up could be more responsive to temperature anomalies at high latitudes and elevations compared with warm low latitudes and elevations (Cufar et al., 2012). Alternatively, green-up may respond most to warming where growing seasons are long at low latitudes and in moderate maritime climates near coastlines (Yue et al., 2015). Individual tree green-up phenology may be more sensitive to warming in southern than northern US forests, potentially due to the compressed seasons in the north. Similarly, experimental data from climate gradients suggest that early spring growth in coastal sites is more sensitive to temperature anomalies than in mountain sites (Beedlow et al., 2013).

Variation in leaf habit across ecoregions could determine how phenology responds to warming (Zhang et al., 2015), but this has not been quantified at the ecosystem scale. On the one hand, evergreens may respond more slowly to climate change than deciduous species, as they tend to display a weak seasonality (Dalmolin et al., 2015). On the other hand, deciduous trees may be less sensitive to daily weather variability because the green-up period is compressed. Leaf habit may also interact with moisture deficit. Green-up phenology and growth of deciduous trees may be more sensitive to deficit than evergreens or mixed forests (Montserrat-Marti et al., 2009). Deciduous species with large leaves could disproportionately respond to changing evapotranspiration demand, light, and incoming energy (Dalmolin et al., 2015). Distinguishing deficit impacts varying with leaf habit can be directly measured by CDM.

We develop a Bayesian state-space approach to quantify dynamic daily changes in forest green-up at landscape scales. State-space models quantify a dynamic development process (Ibanez et al., 2010), including observation error (Burthe et al., 2011; Clark and Bjornstad, 2004), and the model uncertainty (Rizzardi, 2008). The CDM accommodates nonlinear responses of leaf phenology to environment (Korner and Basler, 2010), which changes throughout development. We use this approach to quantify how inter-annual variation in climate affects phenology across six different ecoregions in the southeastern United States. Analyses include the interactions involving temperature and moisture, and how they differ from coastal to interior mountain

environments with different levels of evergreenness. Using the CDM developed for ecosystem scale green-up phenology, this study specifically addresses two key points on: a) how the interactions between climate and ecosystem control spring green-up across a climate gradient and different ecosystems; and b) how moisture limitation and thermal stress could potentially delay spring green-up for different ecosystems.

2. Methods and study design

Climate-ecosystem interactions was determined at the regional scale. Because it spans coastal lowlands to mountainous interior and a range of climates, we analyzed vegetation and climate for the southeastern United States. This region falls within the coverage of the MODIS h11v05 tile, including the states of Georgia, Indiana, Kentucky, Maryland, North Carolina, Ohio, South Carolina, Tennessee, Virginia and West Virginia. To simplify discussion, we use physiographic boundaries as a geographic reference. We selected specific sites for analysis in the physiographic provinces that include the Appalachian Plateau, Blue Ridge, Coastal Plain, Interior Low Plateaus, Piedmont, and Valley and Ridge. The geographically adjacent provinces of Appalachian Plateaus, Interior Low Plateaus, and Valley and Ridge are merged as the reference class to focus on three regions: Blue Ridge Mountains, Coastal Plain and Piedmont. A CDM was developed for and fitted to daily remotely sensed datasets, automated field measurements, and geospatial data.

2.1. Study area

Study sites coincide with the Remote Automated Weather Stations (RAWS) dataset (http://www.raws.dri.edu/). Fig. 2a–c shows the distribution of the study sites with mean climate and phenology time series. Automated weather stations are located in forests, savannahs, shrublands, and grasslands. We analyzed sites with forest cover that could be classified either as deciduous, evergreen or mixed forest. The International Geosphere–Biosphere Programme (IGBP) global vegetation classification scheme was used to select sites with forest cover including deciduous, and mixed forest. No sites were classified as fully evergreen forest. Sites with other land classifications were not used in this study. Sites at which land cover types has changed during the study period were excluded from the model.

2.2. Field data and regional boundaries

Climate data were obtained from the RAWS dataset (available at http://www.raws.dri.edu/), including average daily measurements of air temperature, relative humidity, radiation, precipitation and potential evapotranspiration (estimated based on the Penman-Monteith method (Choudhury, 1997)). The data were obtained from ground stations and summarized as mean annual temperature ($MAT_{p,t}$) and daily anomalies from $MAT_{p,t}$, or $aTemp_{p,t,d}$, for location p in year t on day d. Climate anomalies were taken as the difference between daily values and the historical mean values for the same date and location (Fig. 2a), the $aTemp_{p,t,d}$. Physiographic boundaries were obtained from the physiographic divisions of the conterminous US (available at http://water.usgs.gov/).

2.3. Remotely sensed data

Vegetation indices, canopy surface temperature, and land cover type data between years 2001 and 2012 were obtained from the NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) on board the Terra satellite. MODIS data products used in this study are listed in Table 1. MODIS vegetation indices provide valuable insights on land surface processes (Ran et al., 2016) and phenology (e.g. Huemmrich et al. (1999)). The best available MODIS products from NASA's Aqua and Terra satellites (i.e. MOD13A1, MOD13A2, MYD13A1, MYD13A2) offer vegetation indices only every 16 days. This time interval is too wide to capture rapid changes in leaf unfolding during the green-up season (Klosterman et al., 2014). MODIS Enhanced Vegetation Index (*EVI*) has been used extensively to study seasonality in forest dynamics (Hess et al., 2009; Xiao et al., 2006). For this analysis, we calculated daily *EVI* values (Huete et al., 1994) for each site from the daily surface reflectance data of individual thermal and visual bands. The daily EVI data provide extensive insight into green-up status. Our EVI index is given by

$$EVI_{p,t,d} = \frac{2.5(NIR_{p,t,d} - R_{p,t,d})}{NIR_{p,t,d} + 6R_{p,t,d} - 7.5B_{p,t,d} + 1} \quad (1)$$

where NIR, R and B are the near infra-red, red and blue bands, respectively. Again, subscript p, t and d indicate location, year and day. Red and near infrared bands are obtained from MODIS band 1 (620–670 nm) and band 2 (841–876 nm) at 250-m resolution. The blue band is obtained from MODIS band 3 (459–479 nm) at 500-m resolution. MODIS bands data are available from MODIS surface reflectance data (MOD09GQ for bands 1 and 2 and MOD09GA for band 3). Given the coarse spatial resolution of the greenness data, each pixel represents the overall response of the dominant species. Land cover data for each site were obtained from the yearly MODIS land cover type (MCD12Q1 v5.1, yearly, 500-m resolution). The MODIS classification was verified by comparison with the US National Land Cover Dataset (NLCD2011 (Homer et al., 2015)) to exclude inconsistent data (Table S1).

Preseason water deficit status was obtained from the MODIS Global Terrestrial Drought Severity Index (DSI) (Mu et al., 2013; Mu et al., 2011), for December, January and February (DJF) before the green-up season. DSI is a dimensionless metric for relative moisture with respect to normal conditions, accounting for both anomalies in evaporation to potential evaporation ration and variabilities in the Normalized Difference Vegetation Index (NDVI). DSI values are negative during droughts, and positive in wet years. The preseason deficit variable is defined as

$$deficit = \overline{-DSI}_{DJF}$$

where the bar indicates the seasonal average. To estimate canopy hydrological balance, we used the canopy-air temperature differential (Kim et al., 2016; Still et al., 2014),

$$\Delta T_{p,t,d} = C_{p,t,d} - A_{p,t,d},$$

for canopy temperature $C_{p,t,d}$ and air temperature $A_{p,t,d}$, hereafter termed as "thermal stress" (Seyednasrollah, 2017; Seyednasrollah et al., in review). High ΔT (canopy warmer than air) is expected at unmet transpiration demand and low water availability (Mcnaughton and Black, 1973) that accompanies stomatal closure and canopy heating. Daily canopy temperature data were extracted from the MODIS land surface temperature product (MOD11A1 v5) at 1-km resolution. Only daytime temperature data were used in the model, when ΔT is expected to be mostly dominated by stomatal closure. Data with average emissivity error > 0.01 were excluded from the analysis. Only remotely sensed data with the best quality index, minimum average error, and clear sky conditions were used. Data during the green-up period spanned from the onset of green-up until 21 days after leaf maturity. This range (onset and end of the green-up season) varies for each site and year; and was extracted using the MODIS Land Cover Dynamics product (MCD12Q2). The layers "Onset_Greenness_Increase" and "Onset_Greenness_Maximum" were used for the timing of green-up and maturity, summarized by region in Fig. 2d and e. Environmental and phenological variables are shown in the supplementary document.

2.4. Validation

The community green-up response (Fisher et al., 2006; Gressler et al., 2015; Keenan et al., 2014a) is an aggregate of individuals

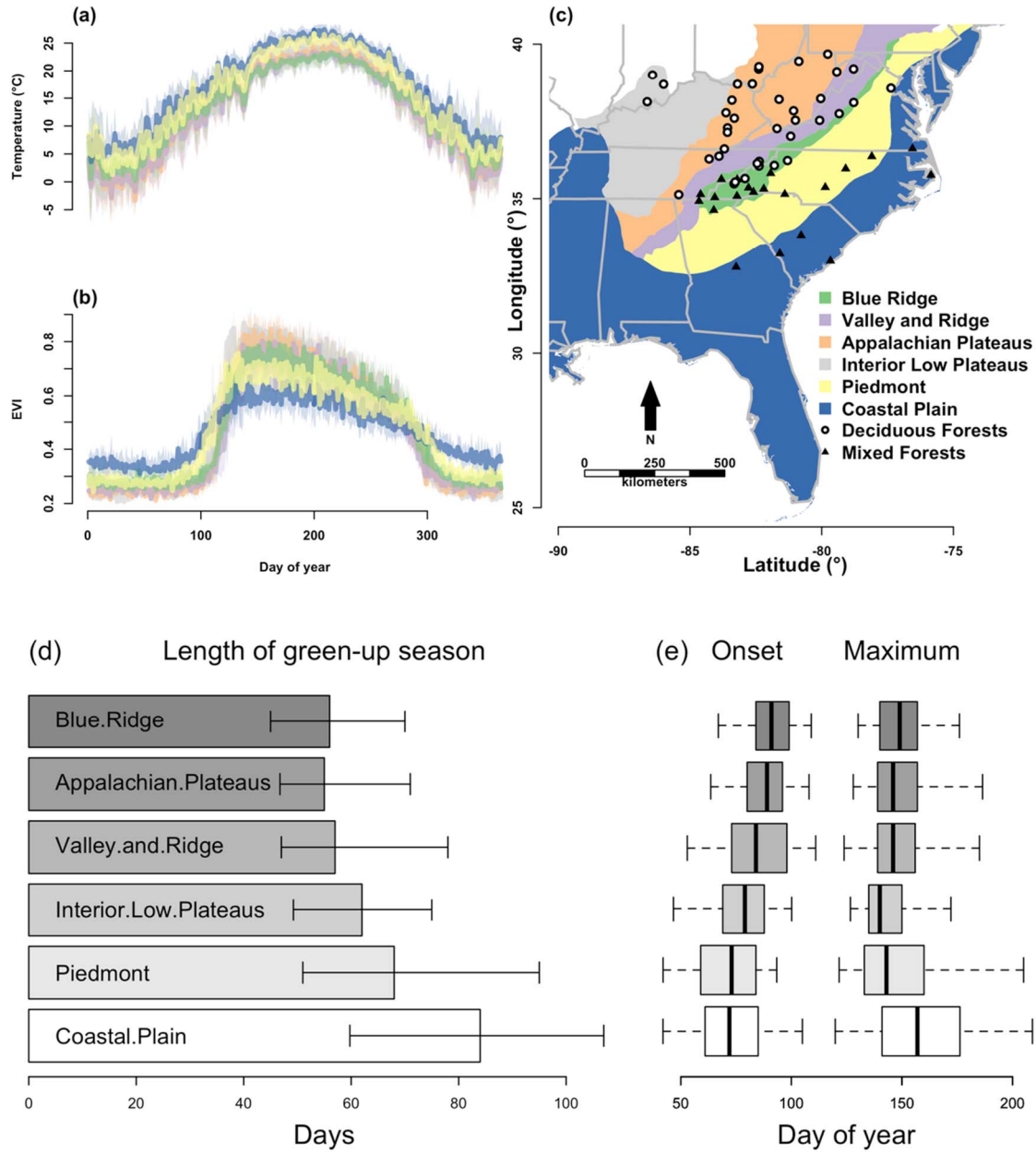

Fig. 2. Historical variation of forest (a) air temperature (from RAWS dataset) and (b) greenness (as *EVI*) by region. (c) Study sites and ecoregions. Deciduous forests are open circles. Mixed forests are filled triangles. (d) Length of the green-up season by region. (e) Variation in green-up onset and maximum greenness. The onset and maturity (maximum greenness) dates are extracted from MODIS product MCD12Q2 for years 2001 to 2012. Whiskers in (d) and (e) are 95th percentiles. Boxes show 50th percentiles.

Table 1
List of MODIS datasets used in the study. The daily MODIS reflectance data from year 2000 to 2014 were downloaded in the original Sinusoidal projection. The grid data were re-projected to the Equirectangular system.

Product	Spatial res.	Temporal res.	Use
MOD09GQ	250 m	1–2 days	Red and NIR bands
MOD09GA	500 m	1–2 days	Blue bands
MOD11A1	1 km	Daily	Land surface temperature
MCD12Q1	500 m	Yearly	Land cover data
MCD12Q2	500 m	Yearly	Land cover dynamics, onset and maturity
NLCD2011	30 m	–	Land cover verifications
MODIS Global Terrestrial Drought Severity Index	0.05 degree	Monthly	Drought severity index (Mu et al., 2013; Mu et al., 2011).

(Penuelas et al., 2009), which can be observed on the ground (Keenan et al., 2014a). Ground truth data (MacBean et al., 2015) is particularly important in remote sensing studies. We tested the near daily spaceborne observations of *EVI* against the ground-truth leaf area index (*LAI*) at four sites in North Carolina, USA. Test field data were collected every 5–7 days over spring 2008 green-up using a LAI-2000 Plant Canopy Analyzer (LI-COR, Lincoln, NE, USA), and the comparison of *LAI* and *EVI* show close agreement (Fig. S5).

2.5. Model

We developed a hierarchical Bayesian state-space model for continuous development of leaf unfolding to infer the main effects and interactions that control spring green-up. The hierarchical structure consists of data, process, and parameters (Berliner, 1996). Data include predictors and the response, greenness (*EVI*). The process stage describes phenological development. Consider phenological development

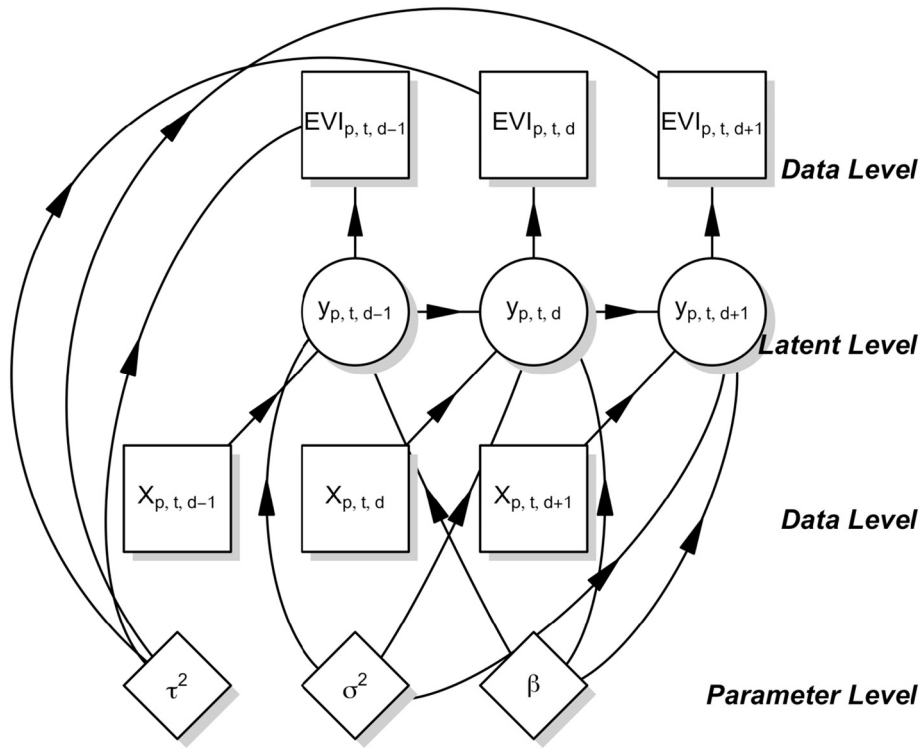

Fig. 3. Model graph: the data model consists of observations of greenness $EVI_{p,t,d}$ and predictors $X_{p,t,d}$ for site p, year t, and day d. The process model is the time series of true greenness (latent states, $y_{p,t,d}$). Parameters include coefficients β, process variance σ^2, and observation error τ^2. Latent phenology states are $y_{p,t,d}$.

state $y_{p,t,d}$ per site p, year t, and day d (Fig. 3): Greenness can increase, or not, in the interval (d, $d + 1$), initially at expected rate $\mathbf{x}_{p,\ t,\ d}\boldsymbol{\beta}$, but declining as development approaches full leaf expansion. This is not to say that the environment no longer affects greenness following spring green-up. Rather, the variation, after which spring green-up is completed, is not part of the green-up process. The submodels for each stage are organized by the graph in Fig. 3.

The observed *EVI* values are related to the latent states (*y*) with a Gaussian distribution:

$$EVI_{p,t,d} \sim N\left(y_{p,t,d}, \tau^2\right)$$

Change in phenological state ($dy_{p,\ t,\ d}$) from day d to d + 1,

$$y_{p,t,d+1} = y_{p,t,d} + dy_{p,t,d}$$

depends on environmental predictors in a design vector $\boldsymbol{X}_{p,\ t,\ d}$, fitted coefficients $\boldsymbol{\beta}$, and process error, with variance σ^2. The rate can be positive continuous, but with point mass at zero,

$$dy_{p,t,d} = \begin{cases} \delta_{p,t,d},\ \delta_{p,t,d} \geq 0 \\ 0,\ \delta_{p,t,d} < 0 \end{cases}$$

$$\delta_{p,t,d} \sim N\left(\mu_{p,t,d}, \sigma^2\right)$$

$$\mu_{p,t,d} = \mathbf{X}_{p,t,d-1}\beta\left(1 - y_{p,t,d}/y_{p,t,max}\right)$$

where $\delta_{p,\ t,\ d}$ can be positive or zero, σ^2 is the process stochasticity and $y_{p,\ t,\ max}$ is the asymptotic limit for greenness by the end of the green-up season. The censoring at zero follows the Tobit model, used when continuous variables may admit discrete zeros (Clark et al., 2017; Sahu et al., 2010). Given a Gaussian prior distribution for β, and uniform prior distributions for σ^2 and τ^2, the overall model can be expressed as:

$$[\beta, \sigma^2, \tau^2, \mathrm{y}, \mathrm{y}_{\max} \mid \mathrm{X}, EVI]$$
$$\propto \prod_p \prod_y \prod_d N\left(EVI_{p,t,d} \mid y_{p,t,d}, \tau^2\right) \left[\frac{1}{\sigma}\phi\left(\frac{\delta_{p,t,d} - \mu_{p,t,d}}{\sigma}\right)\right]^{I(\delta_{p,t,d} > 0)} \left[1 - \Phi\left(\frac{\mu_{p,t,d} - \delta_{p,t,d}}{\sigma}\right)\right]^{I(\delta_{p,t,d} \leq 0)}$$
$$\times N\left(\beta \mid \beta_0, V_b\right) Unif\left(\sigma^2 \mid 0, \infty\right) Unif\left(\tau^2 \mid 0, \infty\right) Unif\left(\mathrm{y}_{\max} \mid 0, 1.\right)$$

where ϕ and Φ are the standard normal density and distribution functions, β_0 and V_b are the mean vector and covariance for the prior distribution of β. The indicator function $I(\cdot) = 1$ when its argument is true and zero otherwise. Non-informative priors are used for β ($\beta_0 = 0$, $V_b = \infty$) and *Unif* indicate the uniform distribution as prior for σ and τ. A Metropolis–Hastings algorithm with Gibb's sampling through the "rjags" package in R is used to fit the posterior distributions of β, σ, τ and *y*. Sensitivity maps were generated as predictive distributions of derivatives (as shown in the supplementary document), marginalizing over the posterior distributions of coefficients. The model was tested and has performed well with simulated data. Diagnostics and the list of predictors used are presented in supplementary document and Table S3, respectively.

To test the model against realistic green-up data, we predicted the time series of greenness for all study sites. We used climate and site data as inputs along with the posterior distributions of parameters from the fitted model to predict the entire time series for all site-seasons. For each site-season, we predicted greenness from the initial value through 21 days after full green-up. We drew 500 samples for each time step, leading to 500 predicted time series for each site-season. The model predictions for a representative site (Duke Forest) are shown in Fig. S6a for three seasons with contrasting moisture regimes (2002, 2009 and 2011). The accumulated error from previous time steps increases the uncertainty later in the season. Observation error from the satellite data contributes additional uncertainty. Despite multiple sources of uncertainty, the model reliably predicts observations at all sites (in-sample

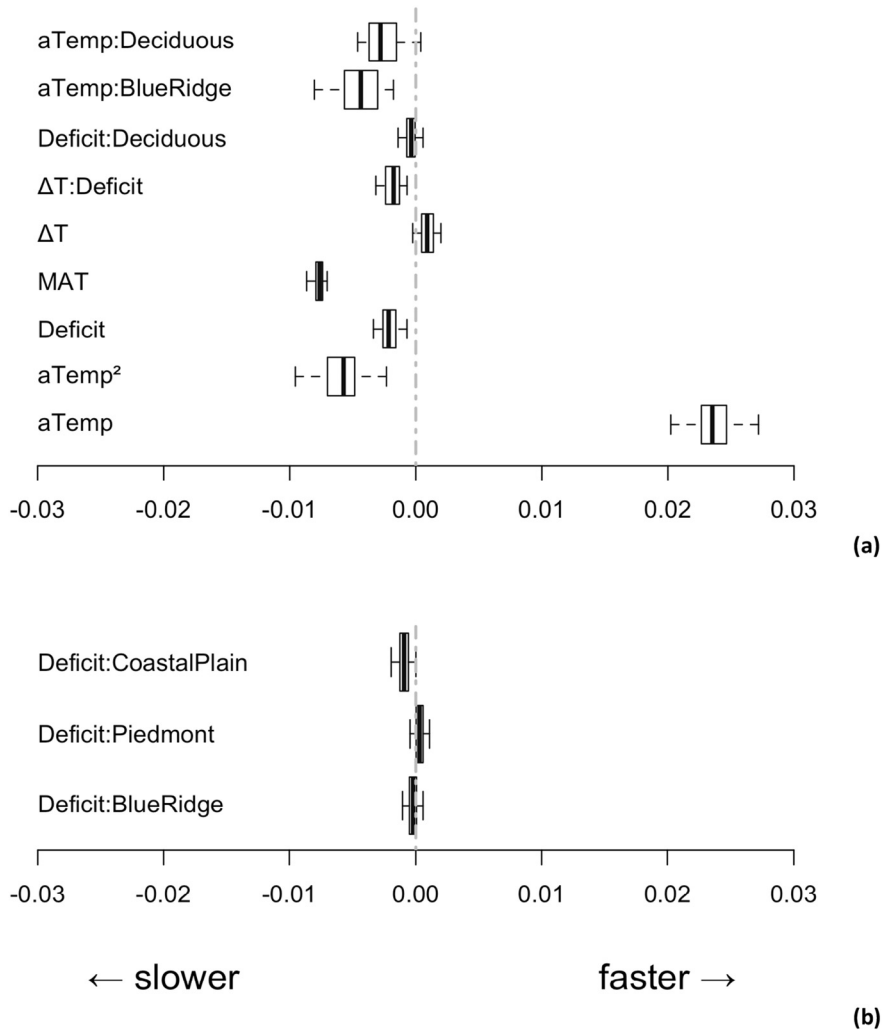

Fig. 4. Posterior distributions of model predictors. Positive values accelerate leaf development, and negative slow leaf development. (a) main effects and climate interactions, (b) interactions of moisture deficit with ecoregions. The main variables include aTemp: daily temperature anomaly, MAT: mean annual temperature, Deficit: preseason moisture deficit, and ΔT: spring thermal stress. The boxes and whiskers represent 50% and 95% of the posterior distributions. Predictors not including zero in their 95th percentile are significant.

data Fig. S6b and an out-of-sample season (Duke Forest, 2012, Fig. S6c). The root-mean-square error between predictions and observed greenness values was 0.13% of the range of greenness values. The R-squared value was 0.76. The average error between modeled and observed greenness was 0.12.

We predicted the overall sensitivity to warming by considering three scenarios for temperature anomalies: cold (i.e. Temperature lower than mean temperature by one standard deviation), normal and hot (i.e. Temperature higher than mean temperature by one standard deviation). To evaluate the interaction between deficit with thermal stress, we estimated thermal stress sensitivity at three drought regimes based on the Drought Severity Indices (DSI): +1 (wet), 0 (normal) and −1 (dry).

3. Results

The predictors with the largest effect on spring green-up were the daily temperature anomaly for a given year (aTemp), followed by mean annual temperature (*MAT*), preseason moisture deficit (deficit), and thermal stress (ΔT) (Fig. 4). The high aTemp coefficient suggests a dominant control of green-up compare to other predictors. Positive linear and negative quadratic terms indicate limitations at low and high aTemp. Across the entire study area, slow phenological development was associated with high MAT and moisture deficit (Fig. 4-a). Although ΔT did not delay green-up at all sites and ecoregions, the deficit effect was amplified with increasing ΔT (negative ΔT: deficit interaction, negative deficit). The interactions of deficit with ecoregions includes an amplified deficit effect in the Blue Ridge (Fig. 4b), relative to the Coastal Plain and the Piedmont. The interactions of daily temperature anomaly with ecoregion and deciduousness suggest different trends across regions. Our results showed the aTemp effect is comparatively weak in the Blue Ridge and for deciduous trees (negative interaction terms in Fig. 4a).

Based on the direct aTemp effects and its interactions, we quantified the sensitivity of green-up speed to daily temperature anomalies for deciduous and mixed forest sites. Fig. 5a shows sensitivity values for three different daily temperature anomalies regimes at the Blue Ridge, Piedmont and Coastal Plain. Sensitivity decreased with increasing anomalies (cold to hot years). Sites located near the coast and in the Piedmont were more sensitive to increasing daily temperature anomaly than Blue Ridge forests. Deciduous sites showed lower sensitivity to daily temperature anomalies than mixed forests in all ecoregions. Fig. 5b shows how the temperature effect on spring green-up varies with *EVI* during the green-up season for three main ecoregions: Blue Ridge, Piedmont and Coastal Plain. Green-up was most sensitive to daily temperature anomalies early in the growing season, especially in the mountains.

The green-up response to moisture deficit varied across ecoregions

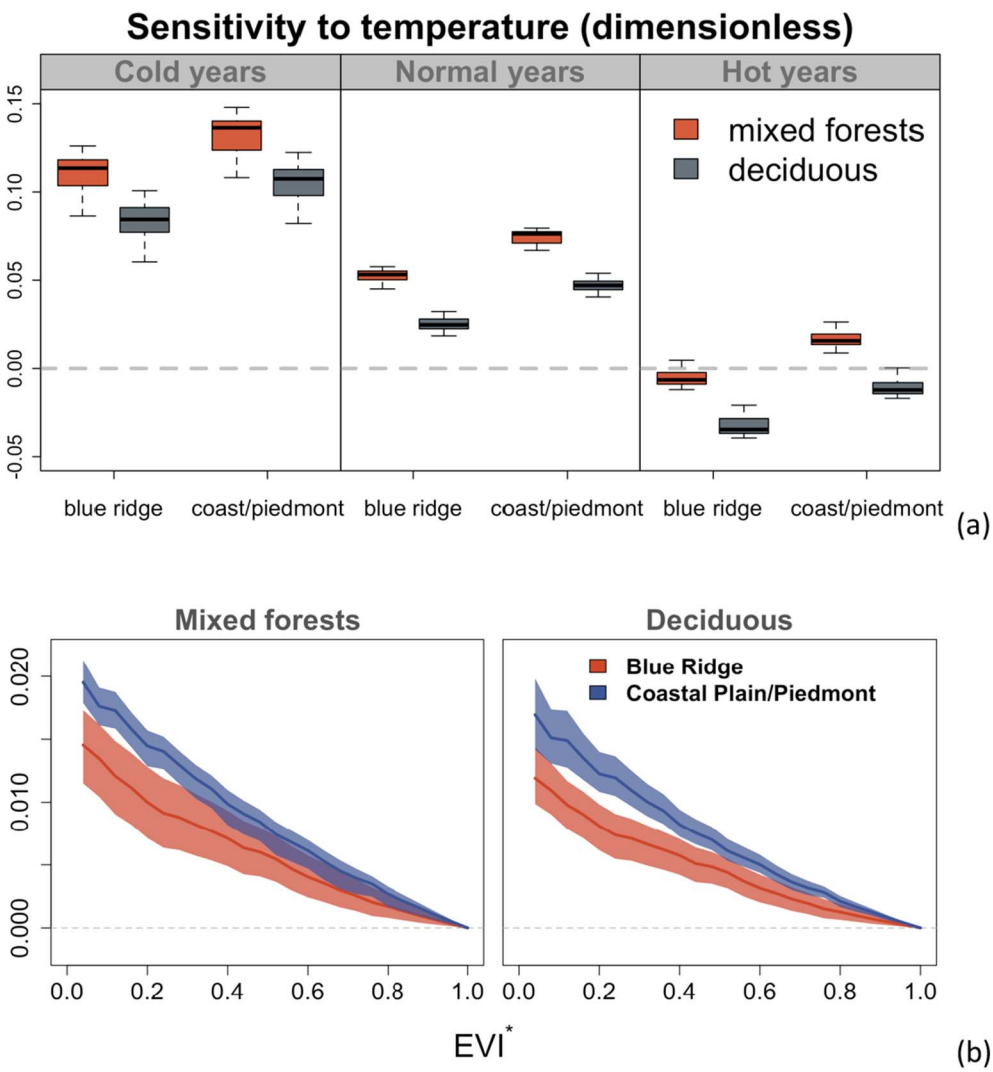

Fig. 5. Sensitivity of the rate of change in greenness to the daily temperature anomaly for the Blue Ridge, Piedmont and Coastal Plain. (a) The seasonal average sensitivity of deciduous and mixed forests to the daily temperature anomaly in Coastal Plain and Blue Ridge mountains in cold years (less than one standard deviation below the historic mean), normal years, and hot years (greater than one standard deviation above the mean). (b) Declines in temperature sensitivity with relative leaf development (EVI^*). EVI^* is defined as $EVI^* = (EVI - EVI_{min}) / (EVI_{max} - EVI_{min})$ and EVI is the observed enhanced vegetation index. Sensitivity values are dimensionless using standard deviations of the predictors and response, with positive meaning accelerating green-up; and negative indicating slowing green-up. Forests in the Coastal Plain and the Piedmont are more sensitive to temperature anomalies than Blue Ridge sites.

and with leaf habit (Fig. 6a). Green-up speed was less affected by moisture deficits near the coast, while the Piedmont and the Blue Ridge became slower with increasing moisture deficit. Mixed forest sites at the Blue Ridge and the Piedmont were less sensitive to deficit than deciduous sites, but with larger uncertainty. Green-up was insensitive to thermal stress in years with average moisture balance. It was delayed following dry winters, and accelerated following wet winters (Fig. 6b).

We mapped contrasting responses to warming and drought in the mountains and coastal regions (Fig. 7a and b). To highlight regions of strong effects, only sites for which 95% of posterior distributions exclude zero are shown. Green-up was faster with increasing daily temperature anomalies (aTemp) in all sites. Southern sites in the Piedmont and Coastal Plain were most sensitive to warming. Deciduous sites of the Blue Ridge were least affected by increasing aTemp (Fig. 7a). Sites in the Valley and Ridge and the Appalachian Plateaus ranged from low to moderate temperature sensitivity. Following dry winters, spring deficit delayed green-up everywhere in the southeast, with the greatest impacts in the Blue Ridge mountains (Fig. 7b).

4. Discussion

The daily spring green-up data shed light on the continuous development of leaves across a wide range of climates and how these effects are modified in dominant ecosystem. Using a continuous development model (CDM), we found that mountainous and coastal forests had contrasting responses to increasing temperature anomalies (warming) and intensifying moisture deficit. Increasing temperature anomalies have their greatest accelerating impacts on coastal forests and weakest effects in the mountains. Conversely, forests in the mountains are more negatively affected by spring moisture deficits. All environmental effects are mediated by ecosystem interactions. Our results showed that ecosystem properties such as evergreenness interact with temperature and deficit to control green-up phenology.

4.1. Climate impacts on green-up

The paradox of greatest effects of daily temperature anomalies in the sites that are already warm likely results from the protracted green-up period in warm climates. There is a long window during which green-up can respond. However, green-up response to deficit depends on ecosystem properties—the interactions, a point to which we return below. Temperature effects enter through two variables: mean annual temperature (*MAT*) and inter-annual daily temperature anomalies (aTemp). Our results support findings from previous studies (e.g. Clark et al. (2014a) and Yue et al. (2015)), indicating that warm regions are most sensitive to increasing daily temperature anomalies. While climate controls on phenology is described through *MAT*, the aTemp effect explains how seasonal temperature variability during spring may influence leaf phenology. Changing temperature continues to influence leaf development throughout the green-up season, but the effect is non-

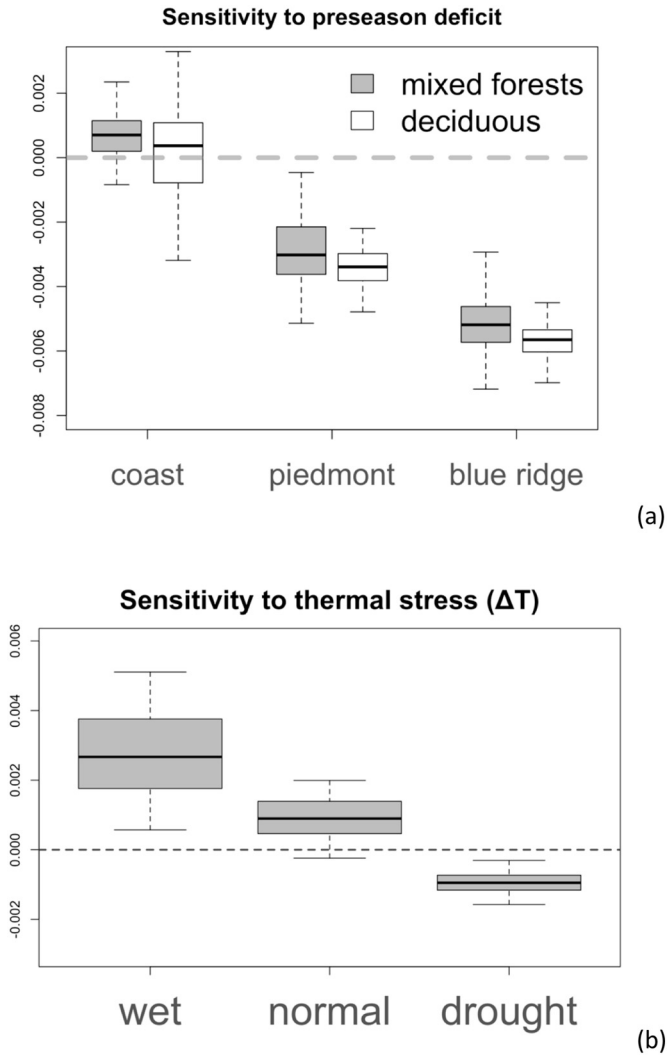

Fig. 6. Sensitivity of change in greenness to (a) preseason deficit and (b) thermal stress (ΔT). In (a) droughts slow green-up most at deciduous sites. In (b) the thermal stress variable shifts from acceleration in wet (DSI > +1) to delay in dry (DSI < 1) years. Sensitivity values are dimensionless using standard deviations of the predictors and response. Moisture deficit has the strongest effect in the mountains. ΔT slows green-up in springs following drought years and accelerates it after wet years.

linear, decreasing in magnitude as anomalies become large (Fig. S7). Preseason deficit can slow leaf development and growth, depending on interactions discussed in the next section.

4.2. Ecosystem interaction with temperature anomalies

Mixed forests are disproportionately sensitive to increasing daily temperature anomalies (aTemp) (Fig. 5a). Presence of leaves year-round allows them to respond to conditions rapidly. A number of studies have documented photosynthesis in conifers during warm days in late winter and spring (Tanja et al., 2003; Yin et al., 2008). Root development could be another important factor causing the distinct trends (Collet et al., 1996).

Regardless of leaf habit (deciduous or evergreen), forests in the Coastal Plain and in the Piedmont are more sensitive to daily temperature anomalies than sites in the mountains. This is true for all temperature regimes: cold (negative temperature anomalies), normal and warm (positive temperature anomalies) (Fig. 5a). Low temperature sensitivity could be explained by the compressed season and rapid rate of green-up in mountainous regions, where leaves quickly green-up (Wang et al., 2015). For instance, *EVI* at a typical coastal site increases from 0.25 to 0.6 in 150 days, while at a typical site in the mountains, *EVI* ranges from 0.1 to 0.9 in only 60 days. When development is already fast, it may have limited capacity to change its rate. Moreover, the adaptive value of accelerating development where it is already fast could likewise be limited. With varying daily temperature anomaly, the sensitivity of the rate of leaf development to aTemp changes. In colder (negative temperature anomalies) seasons, forests respond quicker (fast development) to increasing aTemp than in normal seasons. However, leaf development is relatively insensitive to aTemp in years when temperature is already high. Despite the strong variability of climate and moisture across ecoregions, we found a monotonic response to aTemp during green-up at all sites (Fig. 5-b). Green-up is most sensitive to increasing aTemp at the beginning of the season in all ecoregions. The sensitivity to warming decreases with increasing *EVI*, as leaves reach full development. The Coastal Plain and Piedmont respond similarly to raising daily temperature and to a greater degree than the Blue Ridge mountains. Furthermore, high temperature anomalies may damage foliar tissues (Hufkens et al., 2012) in coastal areas. The finding is consistent with studies that used multidimensional metrics to compare phenological trends across ecoregions (Buitenwerf et al., 2015).

The effects of temperature anomalies include strong geographical patterns across the Southeast, with highest sensitivity in the southern sites where it is already warm and lowest in the mountains (Fig. 7-a). Due to warm climates and evergreenness, forests located in the Coastal Plain and the Piedmont are more sensitive to temperature anomalies than sites in the mountains. Evergreenness effect on spring green-up might be related to both interspecific physiological differences of evergreen and deciduous forests and dissimilarities in species compositions across sites. Studies that focus on individual trees of evergreen and deciduous may help to understand the underlying controls (Lu et al., 2016). In the mountains and northern plateaus sensitivity is most variable. Sites in the southern Blue Ridge show higher sensitivity than the northern Blue Ridge.

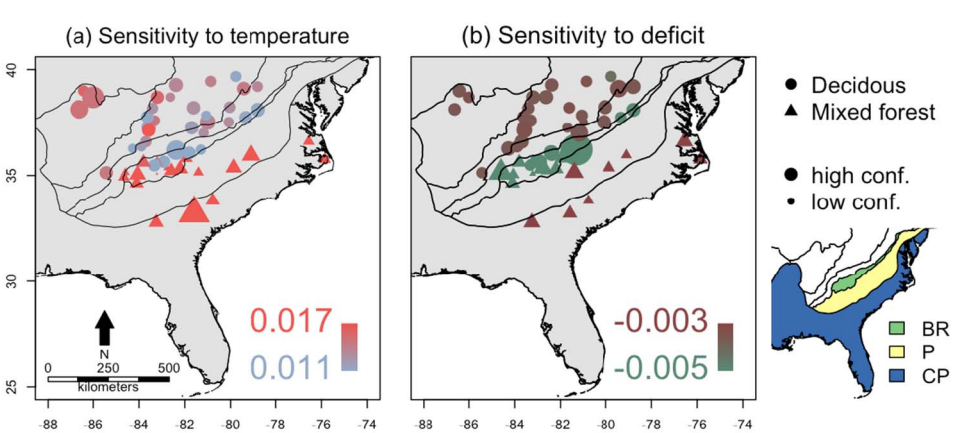

Fig. 7. Geographic sensitivity of green-up to temperature and preseason deficit across the southeast. Circles and triangles indicate deciduous and mixed forests. Large symbols indicate small variance and high confidence. Near the coast, temperature has the greatest and most confident acceleration effect on green-up phenology. In the mountains, deficit has the strongest and most confident slowing effect on green-up. Acronyms indicate as follows BR: Blue Ridge, P: Piedmont, and CP: Coastal Plain.

4.3. Ecosystem interactions with preseason deficit

The impact of preseason deficit depends on climate and evergreenness (Fig. 6a). Deciduous forests responded more to increasing hydrological spring deficit than mixed forests. The response varied across regions. The Coastal Plain is relatively insensitive to deficit. The Blue Ridge shows highest sensitivity, followed by the Piedmont. Differences might be partly explained by regional hydrology (Elliott et al., 2006; Sayer and Newbery, 2003). The water table is commonly inaccessible in the mountains (Hwang et al., 2014), but directly accessed by trees on the coastal plain (Fan et al., 2013). The large uncertainty of the results for deciduous forests in the coastal areas is due to lack of data from deciduous sites in those regions. Similarly, the results show larger credible intervals of sensitivity to temperature anomalies for mixed forest sites in the Piedmont and the mountains, where deciduous trees are more common (Fig. 7a).

The impact of thermal stress suggests contrasting trends following wet versus dry years. Following droughts, soil moisture limitation may cause stomatal closure and increase thermal stress, thus reduce photosynthesis and slow green-up. Conversely, following a wet year, increasing thermal stress is correlated with accelerated leaf development. When soil moisture is high, additional energy received may promote carbon uptake and growth (Fig. 6b). This effect may also be interpreted as the controlling effects of surplus evaporative energy interacting with available moisture. While increasing deficit slows green-up across the Southeast, mountainous areas are most susceptible to water shortage. The Piedmont and coast are least impacted by deficit (Fig. 7b). Drought sensitivity in the mountainous regions might also be related to snowmelt in those regions, however additional data collection is necessary for further investigations.

5. Conclusion

Interactions involving the local mean temperature with the temperature anomalies means that the effect of “warming” on phenology will shift as vegetation responds to temperature trends. We showed that the interpretation of warming effects based on anomalies can lead to opposite conclusions from analyses of geographic patterns. Long-term remotely sensed spring green-up analyzed using a continuous development model (CDM) showed that important interactions extend to temperature, moisture deficit, ecosystems, and leaf habit. Unlike static modeling of phenology, where an entire season may be represented by only a few variables, the continuous development model (CDM) allowed us to design the model based on the biological and environmental forcing to directly quantify the effects on seasonal green-up in forests. Strong responses to temperature anomalies in coastal zones involve not only high mean temperatures there, but also evergreeness and moisture. Green-up in mountainous sites and for deciduous trees is disproportionately slowed by deficit relative to coastal forests where water table is higher and evergreens are common. This is due to the fact that evergreen needles could maintain an efficient hydrologic balance during dry seasons.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rse.2018.02.059.

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