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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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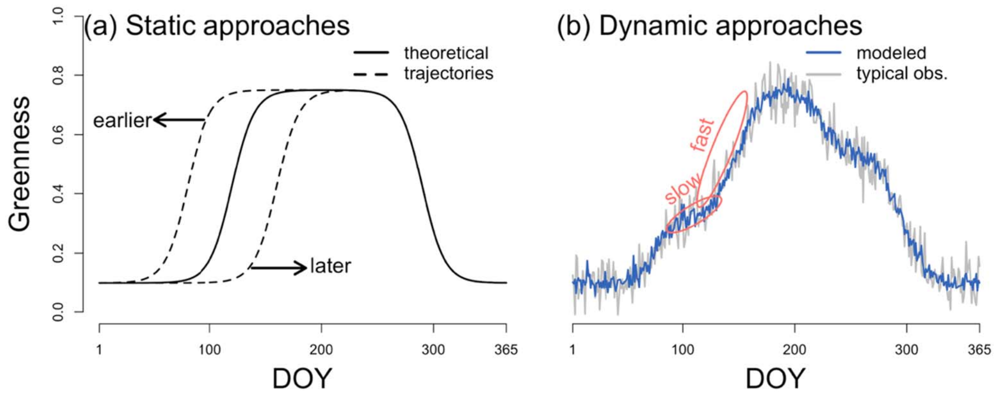

Fig. 1. Static (a) vs. dynamic or continuous development models (CDM) (b) for green-up phenology. Unlike static frameworks, the CDM predicts changing sensitivity over time, while accounting for the dependence structure within time-series data. Dynamics models infer both rate and timing of events, i.e.,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