

LETTER

Climate remains an important driver of post-European vegetation change in the eastern United States

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The influence of climate on forest change during the past century in the eastern United States was evaluated in a recent paper (Nowacki & Abrams, 2014) that centers on an increase in 'highly competitive mesophytic hardwoods' (Nowacki & Abrams, 2008) and a concomitant decrease in the more xerophytic *Quercus* species. Nowacki & Abrams (2014) concluded that climate change has not contributed significantly to observed changes in forest composition. However, the authors restrict their focus to a single element of climate: increasing temperature since the end of the Little Ice Age ca. 150 years ago. In their study, species were binned into four classifications (e.g., *Acer saccharum* – 'cool-adapted', *Acer rubrum* – 'warm-adapted') based on average annual temperature within each species range in the United States, reducing the multifaceted character of climate into a single, categorical measure. The broad temperature classes not only veil the many biologically relevant aspects of temperature (e.g., seasonal and extreme temperatures) but they may also mask other influences, both climatic (e.g., moisture sensitivity) and nonclimatic (e.g., competition).

Understanding the primary drivers of forest change is critically important. However, using annual temperature reduces the broad spectrum of climatic influence on forests (e.g., Jackson & Overpeck, 2000; Jackson *et al.*, 2009) to a single variable. *Tsuga canadensis* illustrates one example of the complex interaction between trees and temperature. In the southern part of its range, *Tsuga canadensis* growth is weakly, but positively correlated with early growing-season temperature. However, this relationship becomes stronger and shifts to later in the season toward the northern part of its range (Cook & Cole, 1991). Moreover, *Tsuga canadensis* growth is significantly and negatively correlated with just May temperatures during the current growing season in the northeastern United States (Cook, 1991; Cook & Cole, 1991; Vaganov *et al.*, 2011), while in the southeastern United States it is strongly and negatively correlated with summer (June–August) temperatures (Hart *et al.*, 2010). Trees can also be sensitive to diverse and often interacting climate variables at various stages of their life cycles (Jackson *et al.*, 2009). Interactions between precipitation and temperature are clearly important (Harsch & Hille Ris Lambers, 2014; Martin-Benito & Pederson, accepted), and often lead to counterintuitive responses. For example, some plant species that would have been expected to move north and ups-

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lope with increasing temperature have in fact moved south during periods of warming, both recently and in the Holocene (Webb, 1986; Jackson & Overpeck, 2000; Crimmins *et al.*, 2011; Harsch & Hille Ris Lambers, 2014).

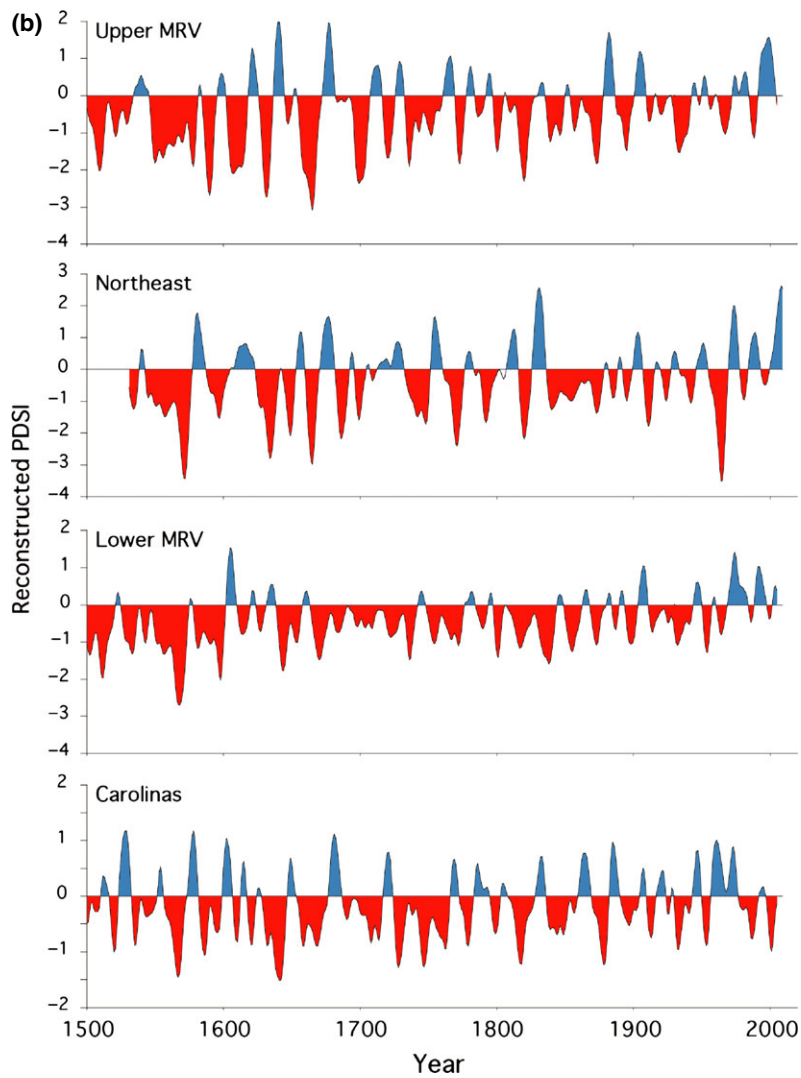
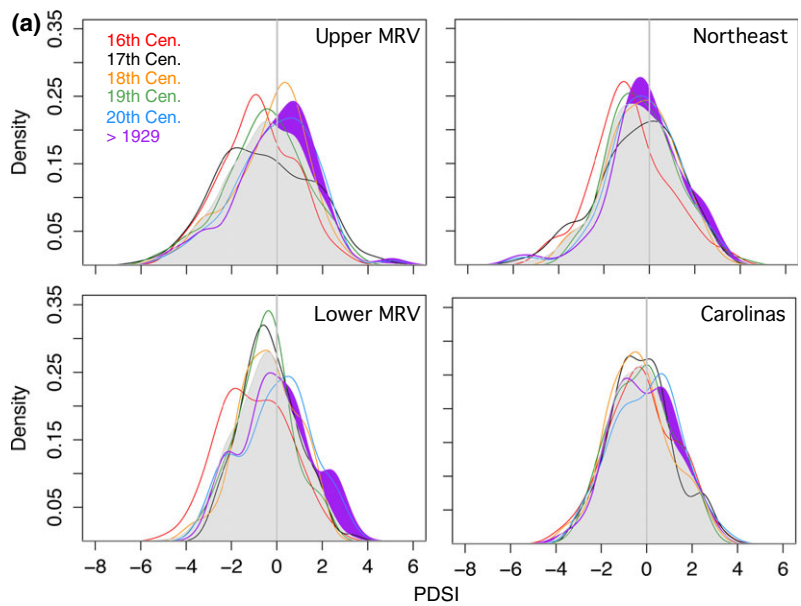
We argue here that moisture availability has strongly influenced forest dynamics and suggest that elimination of climate as a driver of recent forest change in eastern North America is premature. Important to this discussion is the fact that our current reference point, the late 20th century, is among the *wettest* periods since 1500 CE over much of the eastern United States (Pederson *et al.*, 2013) (Fig. 1).

Multiple lines of evidence indicate that moisture availability has been and continues to be a critical factor in forest dynamics of eastern North America. Early growing-season moisture availability is critical for seedling germination and establishment, particularly for fall-dispersed species, with spring drought events often filtering species based on germination phenology (De Steven, 1991). Mature trees can persist in the canopy for decades to centuries in the face of significant temperature increases, inhibiting replacement by other trees and imparting substantial inertia (Davis & Botkin, 1985; Loehle, 2000). Severe and repeated drought has been shown to increase tree mortality and open the canopy (Clinton *et al.*, 1993; Parshall, 1995; Pedersen, 1998; Jackson & Booth, 2002; Klos *et al.*, 2009; Shuman *et al.*, 2009; Booth *et al.*, 2012; Cavin *et al.*, 2013; Pederson *et al.*, 2014). Responses of mesic forests to changes in effective moisture span multiple time scales. For example, dendroecological and forest inventory data reveal tree growth and forest compositional responses from years to decades (e.g., Pederson *et al.*, 2012; Gustafson & Sturtevant, 2013), and parallel trends in Holocene water-level and pollen records reveal that forest composition closely tracked effective moisture changes over centuries to millennia (e.g., Booth *et al.*, 2012; Marsicek *et al.*, 2013). The similarities of findings across time scales support the importance of moisture as a control on forest processes whether they apply over decades or millennia. Drought-induced mortality creates opportunities for canopy accession by understory trees, including species that were not canopy dominants before the drought.

For canopy trees, moisture is widely documented as an important control of tree growth (Davis, 1912; Douglas, 1920; Lyon, 1936; Fritts, 1962; Cook, 1991; Stahle & Cleaveland, 1992; Orwig & Abrams, 1997; Rubino & McCarthy, 2000; Tardif *et al.*, 2006; Kardol *et al.*, 2010; Leblanc & Terrell, 2011; Anning *et al.*, 2013; Brzostek *et al.*, 2014; Clark *et al.*, 2014; Voelker *et al.*, 2014). Even trees in mesic settings show growth responses to moisture variability at interannual to decadal timescales over the last 200 years (Pederson *et al.*, 2012). For mesophytes like *Acer rubrum* or *Liriodendron tulipifera*, growing-season moisture is the most important climatic driver of growth (Hart *et al.*, 2012; Martin-Benito & Pederson, accepted). In comparison to *Quercus*, growing-season moisture is generally more important for the growth of mesophytic species (Pederson *et al.*, 2013; Brzostek *et al.*, 2014; Clark *et al.*, 2014; Maxwell *et al.*, 2014; Martin-Benito & Pederson, accepted with minor revision). Moisture may be the strongest climate-related driver of forest dynamics not only in eastern North America, but in most regions of the globe (Allen *et al.*, 2010).

In their evaluation of forest change in the transition from the Little Ice Age to the present, Nowacki & Abrams (2014) focus exclusively on an inferred increase in annual temperature. However, multiple paleoclimatic records indicate an increase in moisture availability during this same transition that could be as ecologically important as warming (Stahle *et al.*, 1988, 2013; Stahle & Cleaveland, 1992; Cook *et al.*, 2010; Hubeny *et al.*, 2011; McEwan *et al.*, 2011; Pederson *et al.*, 2013; Newby *et al.*, 2014). The long-term trend of increased moisture has persisted to the present in most areas (Fig. 1b); for example, regional-scale water table levels in the northeastern United States are at their highest since the 1950s (Weider & Boutt, 2010). The North American Drought Atlas (Cook & Krusic, 2004) shows that 1930–2005 is one of the wettest periods since 1500 CE over much of the eastern United States (Fig. 1a). The frequency of moderately to extremely wet years (PDSI value ≥ 2) is unusually high during this 75 year period despite significant droughts in the central region (1930s, 1950s, and 1980s), the 1960s drought in the Northeast, and recent drying in the Southeast (Fig. 1b).

Fig. 1 Panel (a): Probability density functions of PDSI over the last 500 years (Cook & Krusic, 2004; Pederson *et al.*, 2013). Purple = distribution since 1930; Gray = long-term distribution. PDSI values > 2 are significantly different from the 20th century mean of 0. Upper MRV = Upper Mississippi River Valley; Northeast = eastern NY State and western New England; Lower MRV = Lower Mississippi River Valley; Carolinas = Coastal North and South Carolina. Panel (b): A stack of 500 years of reconstructed PDSI for each region analyzed above. Each curve is an adaptation of the annual reconstruction smoothed with an 11 year spline. The long-term mean is set at the 20th century mean of zero. The year 1930 is denoted by the light-gray, vertical line. Periods above the 20th century mean are filled blue and indicate wetter conditions. Periods below that line are filled red and indicate drier conditions.



A long-term, broad-scale increase in moisture should favor species with physiological affinities for moisture. Indeed, many of the traits used to characterize the fire sensitivity of mesophytic species are traits that make them vulnerable to drought (Abrams, 1990, 1996; Bond & Midgley, 2001; Hallik *et al.*, 2009). *Liriodendron tulipifera* experienced higher mortality than *Quercus* during the short, but severe 1980s drought in the southeastern United States (Elliott & Swank, 1994). Conversely, the strong response of mesophytic species to moisture would confer a competitive advantage over *Quercus* during times of sufficient moisture.

Nowacki & Abrams (2014) assert that global-change forecasts largely predict reduction and contraction of mesophytic species and increase and expansion of drought-tolerant species and that so far, observed trends are opposite. They also identify the need for such models to include better ecophysiological requirements and disturbance to improve their predictive power and relevance. We agree on the latter count, and note that many such improvements are already being implemented (Iverson *et al.*, 2011; Matthews *et al.*, 2011; Xu *et al.*, 2012; Gustafson & Sturtevant, 2013; Brandt *et al.*, 2014). In addition, Gustafson & Sturtevant (2013) find that drought-induced mortality can be detected in the region from forest inventory data. Other considerations are required for the lack of predicted habitat loss for mesophytic species. First, the southeastern United States has experienced little warming outside of the cool season (Melillo *et al.*, 2014). In fact, temperatures from 1971 to 2000 during the growing season were cooler vs. 1911–1940 over a most of the eastern United States (fig. 3 in McEwan *et al.*, 2011). If warming had occurred during the growing season, we might have expected greater change in the Southeast because the growth of broadleaf species are more limited by high summer temperatures than populations to the north (Martin-Benito & Pederson, accepted). Warmer winters and a lack of warming during the growing season would have likely benefited, not aggravated, the growth of mesophytic species in the southern portion of the eastern United States (Martin-Benito & Pederson, accepted). Second, physiological drought and extreme events are projected to become increasingly frequent and severe across the eastern United States by middle of the 21st century (Melillo *et al.*, 2014). Third, these projected droughts and extreme events have been largely absent since the 1930s (Fig. 1). Finally, the long-lived nature of trees ensures that even as climate is expected to shift to favor drought-tolerant species (Melillo *et al.*, 2014), large-scale changes will be delayed in the absence of major disturbance events. Therefore, conditions promoting an

increase in drought-tolerant species may eventually overtake the increase in mesophytic species, but it might not occur until later in the 21st century. Modeling responses of mesophytic species to future droughts is challenging given that many calibrations are based on observations during one of the wettest periods of the past several centuries (Fig. 1a). Regardless, it is important to include moisture in analyses of past, current, and future trends in vegetation composition.

Forest dynamics in a changing climate will be influenced by multiple interacting factors (McEwan *et al.*, 2011). We agree with Nowacki & Abrams (2014) that altered disturbance regimes, largely instituted by humans, have been an important driver of compositional change in eastern forests (cf. Foster & Aber, 2004), even predominating in the century following land clearance and agricultural abandonment. Changes in land use and moisture are both necessary to explain past and ongoing changes, but neither is independently sufficient. Given the varied influences of temperature, it is premature to rule it out as an influence for past changes, and it will certainly play a role in the future as growing-season temperature increases impart moisture stress to trees, from seedlings to adults. Humans are altering forests in an environment of changing temperature, precipitation, and natural disturbance regimes, and these, in turn, are interacting with newly arriving or spreading pests and pathogens. A multivariate approach that includes quantitative measures and examines interactions across multiple scales should aid understanding of the past and future evolution of forests. Future analyses of climate as a driver of forest change should include a spectrum of ecologically meaningful and independent measures of climate variation that are relevant to the establishment, growth, and mortality of trees.

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