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ORIGINAL ARTICLE

Convergence in drought stress, but a divergence of climatic drivers across a latitudinal gradient in a temperate broadleaf forest

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ABSTRACT

Aim Information about climate stressors on tree growth is needed in order to assess the impacts of global change on forest ecosystems. Broad-scale patterns of climatic limitations on tree growth remain poorly described across eastern North American deciduous forests. We examined the response of broadleaf tree species to climate in relation to their taxonomy, functional traits and geographical location.

Location Eastern North America (32–45° N; 70–88° W).

Methods We used a network of 86 tree-ring width chronologies from eight species that cover a wide range of ecological and climatic conditions. Species were analysed individually or combined according to taxa and wood anatomical functional traits. We identified climate stressors through correlations between growth and climate (from 1916 to 1996). We also explored patterns in the climate responses of these species with two clustering techniques.

Results We found strong correlations between water availability and growth for all species. With few exceptions, this drought stress was independent of taxonomy or wood anatomical functional group. Depending on latitude, however, different climatic drivers governed this common drought response. In the cool, northern part of our network, forest growth was most strongly limited by precipitation variability, whereas maximum temperature was a stronger limiting factor than precipitation in the wetter and warmer southern parts.

Main conclusions Our study highlights the sensitivity of broadleaf temperate forests to drought stress at annual to decadal scales, with few species-specific differences. The roles of temperature and precipitation on drought-sensitivity differ at opposing ends of our subcontinental-scale network. The impact of future environmental changes on these forests will ultimately depend on the balance between temperature and precipitation changes across this latitudinal gradient.

Keywords

Climate change, climatic sensitivity, forest ecology, gradient analysis, maximum temperature, North America, tree growth, tree-ring network analysis.

INTRODUCTION

The future trajectories of forest productivity, composition and the global carbon cycle will greatly depend upon how different tree species respond to climate, competition with neighbours and local environmental conditions. Humid temperate forests are generally thought to experience minimal limitations from climate (Boisvenue & Running, 2006), especially compared to ecosystems in regions that are drier or that have greater climatic variability, where drought can cause widespread forest mortality (Allen *et al.*, 2010; Anderegg *et al.*, 2013). The importance of tree sensitivity to climate in modulating forest carbon dynamics (Ciais *et al.*, 2005) and shaping communities through forest decline has, however, been highlighted around the globe, including regions that are not typically considered drought-limited (Allen

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et al., 2010; Anderegg *et al.*, 2013). One important step towards understanding the impacts of environmental changes on forest productivity and development is an accurate estimation of the response of trees to climate (Bugmann & Cramer, 1998). Another important step is the identification of groups of tree species with similar climatic limitations. This level of identification could improve our ability to model the impacts of climate change, especially in diverse ecosystems (Woodward & Cramer, 1996).

Broad-scale dendrochronological studies show that some species can be temperature-limited at their upper latitudinal and elevational range margins (Pederson *et al.*, 2004; Frank & Esper, 2005; Salzer *et al.*, 2009; Babst *et al.*, 2013), whereas drought-limitation increases towards drier regions and lower elevations (Cook *et al.*, 2001; Büntgen *et al.*, 2007; Vicente-Serrano *et al.*, 2013). Several studies have identified plant functional types based upon common responses to climate in eastern North America (Graumlich, 1993; Cook *et al.*, 2001), which suggests that phylogenetic differences are more important than ecological differences or intersite variation. Analyses of several European tree-ring networks have also shown that phylogenetics and environmental conditions control the response of trees to climate (Büntgen *et al.*, 2007; Babst *et al.*, 2013). In contrast, temperature-limited conifers in the Alps show little interspecific differences in their response to climate (Frank & Esper, 2005). These results indicate that, although tree-ring networks can reflect some representation of their biomes, they also highlight some species-specific responses to climate. One important difference between Europe and eastern North America is the distribution of precipitation by latitude. In Europe, temperature and precipitation follow opposite latitudinal trends: in general, cold and humid sites are located north of warm and dry sites. In contrast, mean annual precipitation and temperature in eastern North America both increase from north to south, thus creating distinct environmental conditions in which to test biogeographical patterns described for other parts of the world (Graumlich, 1993; Cook *et al.*, 2001; Frank & Esper, 2005; Büntgen *et al.*, 2007; Babst *et al.*, 2013).

We focus our study on the deciduous temperate forests of eastern North America. This biome, bounded by tropical forest to the south and boreal forests to the north (Dyer, 2006), is characterized by high tree species diversity (Keith *et al.*, 2009). In these forests, climate is believed to be only moderately limiting for tree growth because of the abundant and even distribution of precipitation throughout the year. Nonetheless, these forests can experience severe droughts (Cook & Jacoby, 1977; Stahle *et al.*, 1985; Pederson *et al.*, 2013) and soil moisture stress can reduce their carbon-fixing potential (Brzostek *et al.*, 2014). Although the drought-sensitivity of trees has been documented (Tardif *et al.*, 2006; Speer *et al.*, 2009; LeBlanc & Terrell, 2011; Pederson *et al.*, 2012a, and references therein), the strength and extent of climate responses has not been investigated with a multispecies approach across the latitudinal extent of these diverse deciduous forests.

Space-for-time studies at broad scales, such as those provided by long-term observational studies, give insight into factors influencing tree growth and rates of mortality. There might, however, be serious shortcomings in these studies because of the specific period analysed or the duration of the period under analysis. Precipitation over recent decades is higher than in the previous four centuries in the northern end of the eastern deciduous forest, an area that has not experienced a severe or extended drought since the 1960s (Pederson *et al.*, 2013). The increase in precipitation and the absence of prolonged droughts in recent decades may limit our ability to detect the importance of drought on tree growth and mortality (see Lorimer, 1984).

In this study, we use an extensive multispecies tree-ring network of deciduous species along a 1700-km latitudinal gradient covering most of these species' distribution ranges. We hypothesized that the influence of climate on tree growth across this temperate and humid region is characterized by different species- or genus-specific responses. This follows from prior research which has suggested that the influence of phylogeny on the climate responses of trees is more important where climate exerts only moderate limitations (Cook *et al.*, 2001). Differences in ring porosity (ring-porous or diffuse-porous ring structures) in our network allowed us to explore climate responses across wood anatomical groups. We also explored the impact of environmental conditions and the existence of any latitudinal trends on these responses. Our specific objectives were: (1) to analyse the growth responses of broadleaf trees to climate; (2) to investigate the influence of species or genus, wood functional traits and geographical location on the climate–growth relationship; and (3) to explore the potential influence of climate on future changes in growth and composition in humid temperate forests.

MATERIALS AND METHODS

Study area

Our study area comprises a 1700-km transect along the eastern deciduous forest of North America, 32–45° N and 70–88° W (Fig. 1a). In general, temperature increases from north to south, with the lowest mean annual temperatures occurring in the Adirondack Mountains in the north and the highest temperatures occurring in the piedmont of Georgia (Fig. 1). Annual precipitation also increases from north to south, from less than 1000 mm in parts of New York State to more than 2000 mm in the mountains of North Carolina (Fig. 1b). Despite differences in temperature and precipitation, the study region is characterized by broad common patterns in the temporal and spatial variability of precipitation and moisture availability (Karl & Koscielny, 1982). Nevertheless, during the last few decades, precipitation has increased in the northern region and decreased in the southern region (Melillo *et al.*, 2014). Our study region includes four of the eight main forest types across the region (Dyer, 2006): the 'northern

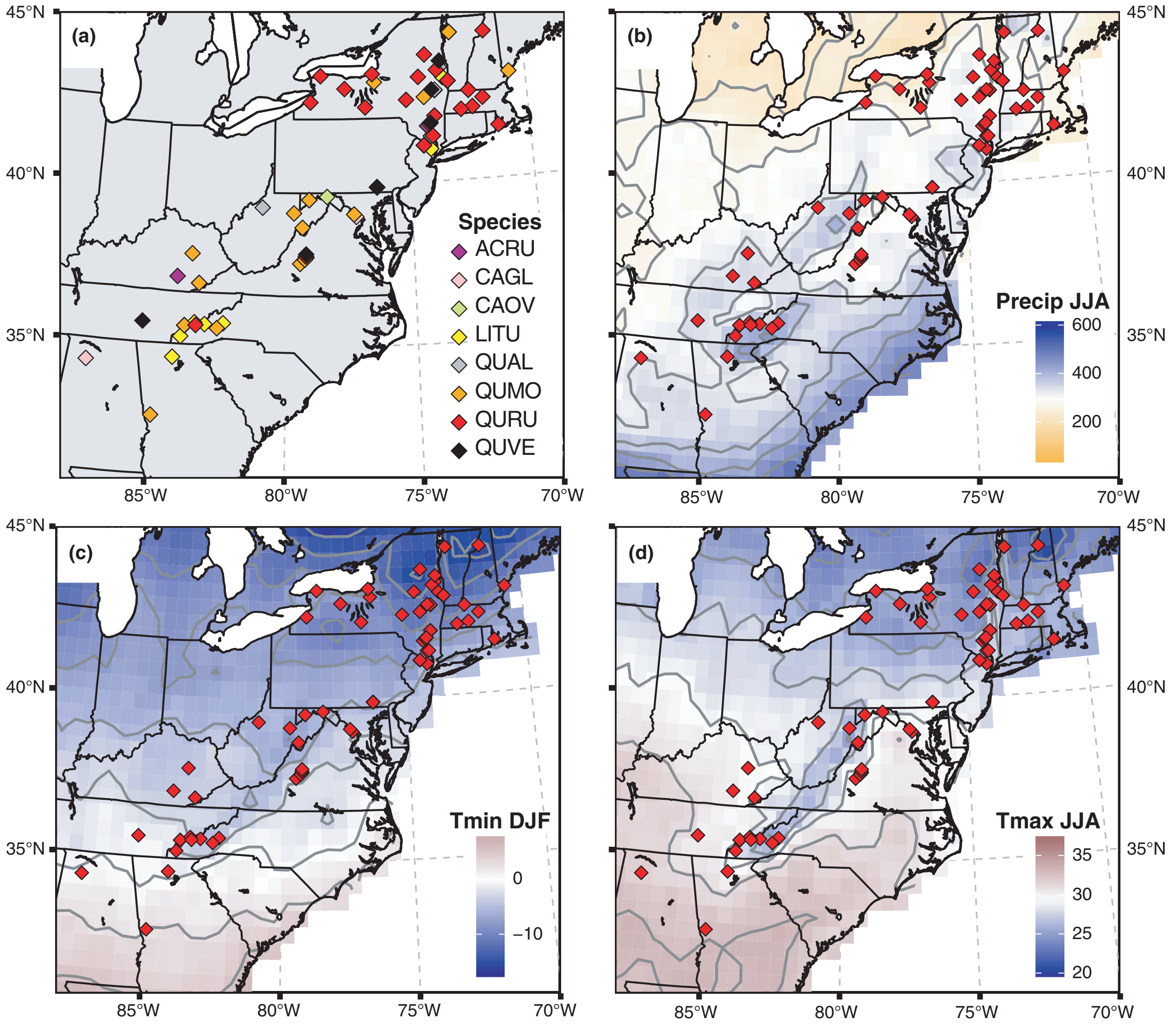

Figure 1 Map of eastern North America containing the network of 86 tree-ring width chronologies of eight species and average climate conditions. (a) Spatial distribution of chronologies per species. At some sites, more than one species were sampled, and their points overlap: see Table S1 (in Appendix S1) and Fig. S1 (in Appendix S2) for detailed locations. Species abbreviations: ACRU, *Acer rubrum*; CAGL, *Carya glabra*; CAOV, *Carya ovata*; LITU, *Liriodendron tulipifera*; QUAL, *Quercus alba*; QUMO, *Quercus montana*; QURU, *Quercus rubra*; QUVE, *Quercus velutina*. (b) Average total precipitation (in mm) for June, July and August (Precip JJA). (c) Mean minimum temperature for December, January and February (Tmin DJF, in °C). (d) Mean maximum temperature for June, July and August (Tmax JJA, in °C).

hardwoods–hemlock', 'beech–maple–basswood', 'mesophytic' and 'southern mixed' forests.

Sampling and tree-ring width chronology development

We focused our analyses on a network of 86 tree-ring chronologies developed from 58 sites. The mix of eight deciduous tree species includes four oaks – two in the white oak subgenus *Leucobalanus* (*Quercus alba* L. and *Quercus montana* Willd.) and two in the black oak subgenus *Erythrobalanus* (*Quercus rubra* L. and *Quercus velutina* Lam.) – pignut hickory [*Carya glabra* (Mill.) Sweet], shagbark hickory [*Carya ovata* (Mill.) K.Koch], yellow-poplar or tulip-tree (*Liriodendron tulipifera* L.) and red maple (*Acer rubrum* L.) (see Table S1 in Appendix S1 of Supporting Information). We relied on chronologies that were previously developed for dendroecological studies (Pederson *et al.*, 2004; Pederson, 2005) or climate reconstructions (Maxwell *et al.*, 2011; Pederson *et al.*, 2012a,b, 2013), as well as chronologies from the International Tree-Ring Data Bank, or chronologies newly developed for this work (see Table S2 in Appendix S1). Some of these species have frequently been used in dendroecology and dendroclimatology, particularly species of *Quercus* (Meko *et al.*, 1993), whereas others, such as *Liriodendron* and *Carya*, have only recently been used for drought reconstruction (Maxwell *et al.*, 2011; Pederson *et al.*, 2013).

We selected mature forest sites with as little anthropogenic disturbance as possible since *c.* AD 1900 (Pederson, 2005). For most collections developed in the last decade, one or two increment cores were collected from each tree, in a trade-off between core replication and latitudinal coverage (Pederson, 2005). Within each site, trees were selected following a typical dendrochronological sampling strategy, in which old-looking trees were targeted (Fritts, 1976), or a modified strategy that specifically included younger trees (Pederson, 2005; Pederson *et al.*, 2012a). This modification was made to allow a more representative sampling of the forest (Table S2). At five sites, trees were randomly sampled, and at two sites the random selection of trees was distributed across different diameter classes (Table S2).

Network sites covered different portions of the distribution range of each species (see Fig. S1 in Appendix S2). Sites of *Q. montana* and *L. tulipifera* covered their entire latitudinal range, whereas most sites of *Q. rubra*, *A. rubrum* and *C. ovata* were located in the northern half of each species' range. The number of chronologies per species varied from four for *A. rubrum* and *C. ovata* to 22 for *Q. rubra* (Table S1).

Individual ring-width series were standardized to remove size-related trends and other non-climatic influences on radial growth. The variance in each ring-width series was stabilized by adaptive power transformation to produce homoscedastic indices (Cook & Peters, 1997) and later standardized using a spline function with a 50% variance cut-off equal to two-thirds of the series length, using ARSTAN (Cook, 1985). At the site level, individual ring-width series for each species were combined into annual chronologies using a biweight robust estimation of the mean (Cook, 1985). Using chronologies with and without previously removing their significant autocorrelations did not change the results qualitatively for any analyses, so ARSTAN chronologies (i.e. retaining population-level autocorrelation) were used for further analysis. The ARSTAN chronology was developed to reduce growth anomalies below the stand level while retaining growth anomalies common to the population, which are hypothesized to be driven more by climate than by ecology (Cook, 1985). The common period for all chronologies and analyses was AD 1916–1996, a compromise that included as many sites and species as possible while covering the longest possible period (Table S1).

Climate data

Two gridded global climate datasets for the period 1901–2009 with a 0.5° × 0.5° resolution were used: CRU TS 3.10 for maximum, mean and minimum temperature (Mitchell & Jones, 2005) and GPCC.v5 for precipitation (Rudolf *et al.*, 2011). For each site, data from the closest four grid points were averaged and subsequently used. From the temperature and precipitation datasets, we calculated the SPEI (standardized precipitation–evapotranspiration index) using the package SPEI (Beguería *et al.*, 2014) in R (R Core Team, 2014). SPEI is a multiscalar climatic drought index (i.e. it can be calculated for different temporal scales) that considers precipitation and the effect of temperature on drought severity through the inclusion of evapotranspiration (Vicente-Serrano *et al.*, 2010). Here, we used the Thornthwaite equation to estimate potential evapotranspiration (Thornthwaite, 1948) and calculated SPEI for 6- and 12-month periods.

Data analysis

Because of our subcontinental scale and the number of species in the network, we conducted a principal components analysis (PCA) using all 86 ARSTAN chronologies to explore groups of common growth variation (Graumlich, 1993; Meko *et al.*, 1993; Cook *et al.*, 2001). Because all tree-ring indices are scaled to a mean of one and stable variance, we performed the PCA on the covariance matrix of the complete set of 86 tree-ring width indices for the period AD 1916–1996 in R (R Core Team, 2014). The significance of each eigenvalue was estimated using the Rule N with Monte Carlo randomizations (Overland & Preisendorfer, 1982).

To identify the climate-forcing patterns across sites and species along our transect, the response of chronologies to climate variables was calculated for an 18-month time window (i.e. from the previous May to the current October). The 18-month window is important because of substantial lags in the climate's influence on growth due to the use of non-structural carbon and other genetic traits (Fritts, 1976; Carbone *et al.*, 2013). We also analysed the response of all chronologies to SPEI at 6-month and 12-month time-scales to consider the short-term and long-term effects of drought (Vicente-Serrano *et al.*, 2010).

We analysed the spatial distribution of correlation coefficients between ring-width index and common seasonal climate variables: June, July and August (JJA) precipitation; JJA maximum temperature; December, January and February (DJF) minimum temperature; and July SPEI6. July SPEI6 represents the standardized difference between precipitation and potential evapotranspiration from February to July. Because spatial autocorrelation in our data would violate the assumption of independence of residuals and invalidate standard hypothesis-testing, models were fitted using generalized least-squares estimation in the package NLME (Pinheiro *et al.*, 2009) and considering three spatial autocorrelation structures in R (R Core Team, 2014): no autocorrelation, Gaussian autocorrelation and spherical autocorrelation (Pinheiro & Bates, 2000).

We identified groups of chronologies by their common responses to climate using self-organizing maps (SOMs; Kohonen, 2001). SOMs apply artificial neural networks, complementary to PCA for the identification of general patterns (Reusch *et al.*, 2005), and have been used in synoptic climatology (Crane & Hewitson, 2003) and dendrochronology (Babst *et al.*, 2013). SOMs allow the number of resulting groups (nodes) to be controlled, as a compromise between using numerous nodes, which results in low generalization, and using few nodes, which increases the variance within nodes (Crane & Hewitson, 2003). We grouped chronologies into four SOM nodes based on all correlation coefficients of growth with monthly precipitation and maximum temperature using the KOHONEN package in R (Wehrens & Buydens, 2007). Using four SOM nodes provided enough records per node (around 20 records) such that the clusters can be defined by their main climate response patterns while also allowing high similarity of records within each node. Maximum temperature was chosen because most chronologies showed a higher correlation with this variable than with mean temperature, as has been observed in previous studies of other broadleaf species (Tessier *et al.*, 1994).

RESULTS

Principal components analysis

The first five principal components exceeded the 95% confidence intervals based on the Rule N. Together, these first five principal components explained 50.1% of the total variance in tree-ring network (PC1, 23.6%; PC2, 11.5%, PC3, 5.8%; PC4, 5.0%; PC5, 4.1%). No clustering of species or genus (e.g. *Quercus* or *Carya*) was evident from the scatter-plot of loadings of the first two components (Fig. 2a) or the other three components (results not shown). All loadings on PC1 were positive (except one *Q. montana* site), clustered together irrespective of species, and showed no correlation with either latitude or longitude (Fig. 2b). The second principal component yielded two clear clusters and was strongly correlated with latitude: most of the chronologies north of 40° N gave negative loadings whereas those to the south gave positive loadings (Fig. 2b).

Climate correlations

Correlations between climate variables and tree-ring indices revealed that all species were climatically sensitive across the study area (Fig. 3). Drought was the strongest climate signal across our network (July SPEI6; Fig. 3). *Quercus rubra* was the least responsive species to precipitation, whereas most chronologies of *Q. velutina*, *Q. alba*, *Q. montana* and *L. tulipifera* showed stronger correlations. Five species, *L. tulipifera*, *Q. velutina*, *C. glabra*, *C. ovata* and *Q. alba*, showed significant correlations with precipitation or drought the previous summer in at least 50% of their sites (Fig. 3, Fig. S2). Two features about temperature sensitivity were observed. First, sites of all species showed strong negative correlations with summer temperatures, most strongly expressed in *Q. alba* and *Q. velutina*. The weakest negative response to summer maximum temperatures corresponded to *Q. rubra*, which was the only species with a consistent positive response to summer minimum temperatures (40% of sites). Second, certain species and sites were positively correlated with maximum and/or minimum temperatures during the previous autumn or winter (Fig. 3). The species most responsive to winter maximum temperatures were *L. tulipifera* (70% of sites) and *C. glabra* (30% of sites). *Carya ovata* (50% of sites) and *Q. montana* (38% of sites) also responded positively to winter minimum temperatures (see Fig. S2 in Appendix S2).

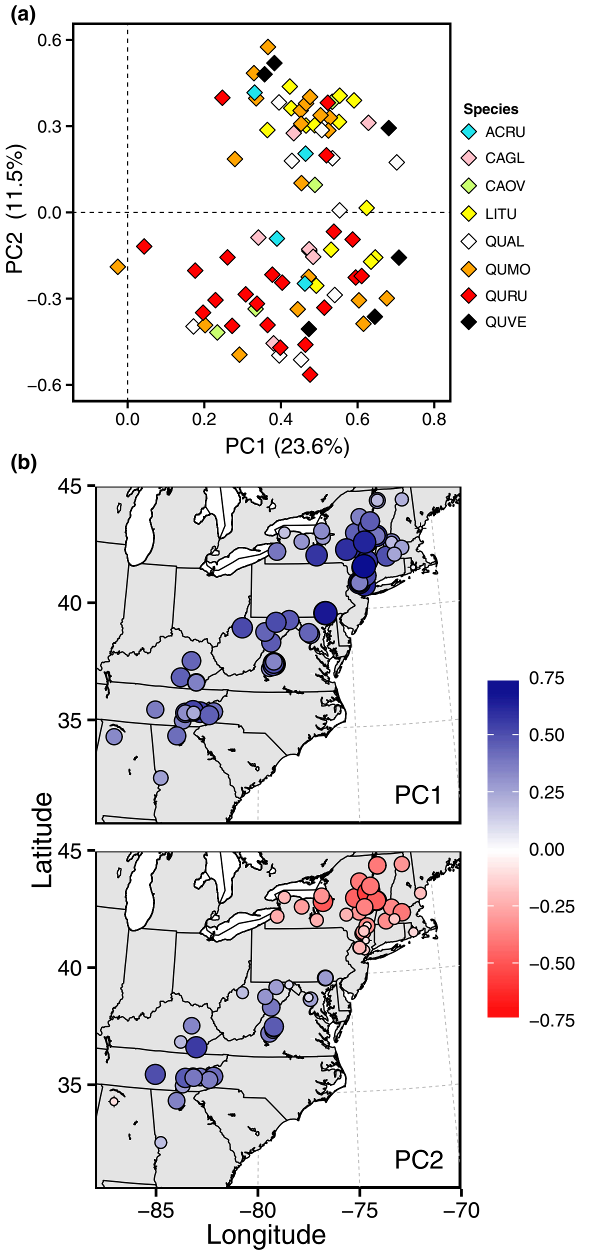

Figure 2 Scatter-plot and spatial distribution of the loadings of each tree-ring width chronology on the first two principal components. All calculations are based on the 1916–1996 common period. (a) Scatter-plot of the loadings of the first two principal components including all sites. Different colours denote different species. Species abbreviations: ACRU, *Acer rubrum*; CAGL, *Carya glabra*; CAOV, *Carya ovata*; LITU, *Liriodendron tulipifera*; QUAL, *Quercus alba*; QUMO, *Quercus montana*; QURU, *Quercus rubra*; QUVE, *Quercus velutina*. (b) Spatial distribution of the loadings of each chronology within the tree-ring network on the first and second principal components. Symbol size is proportional to the loading of the sites on PC1 or PC2. A plus sign is plotted behind each point to show sites where loadings are very small.

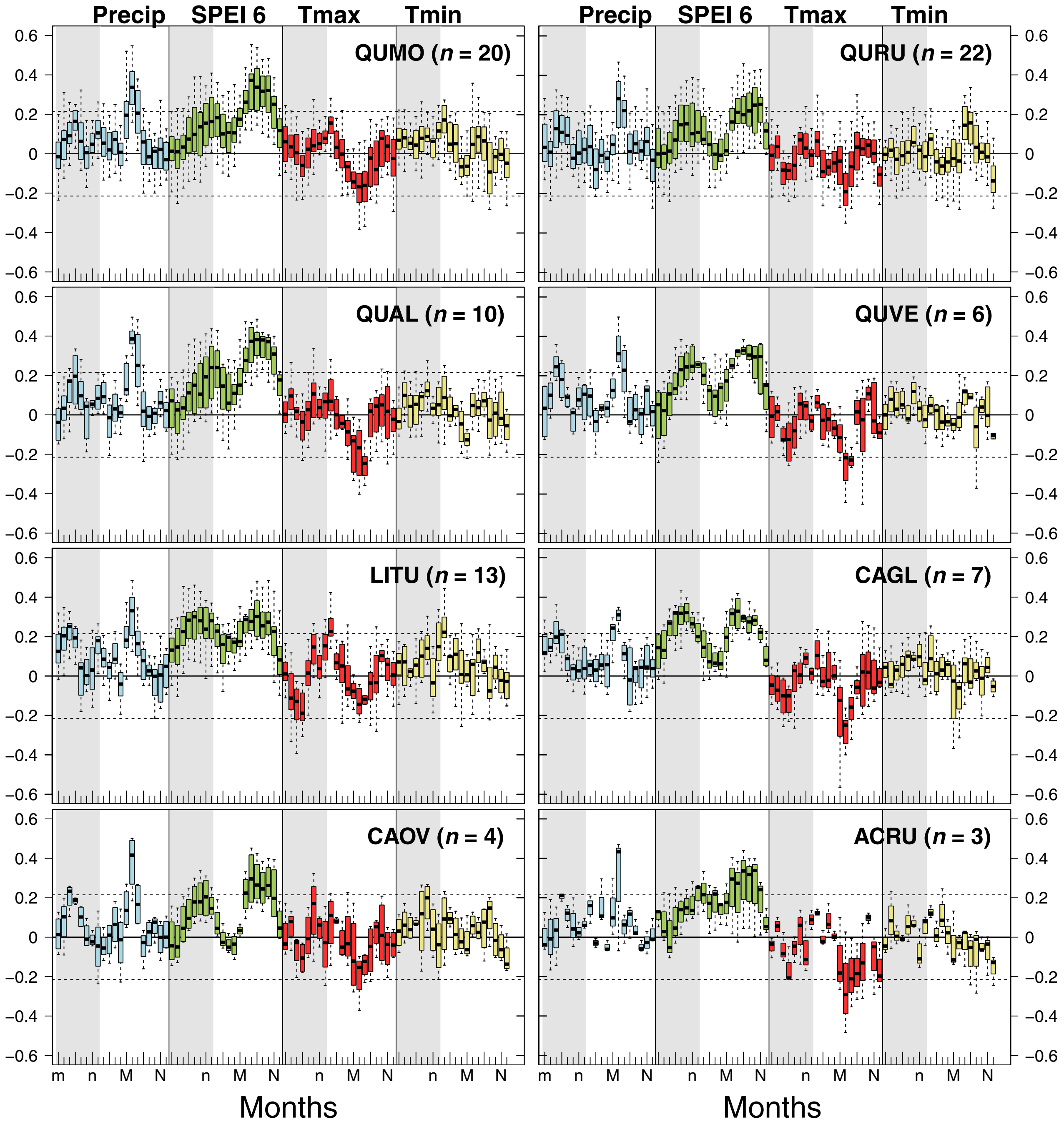

Figure 3 Correlations between tree-ring width chronologies and mean monthly climate (precipitation; SPEI6, standardized precipitation–evapotranspiration index over 6 months; maximum temperature; minimum temperature) for each of the eight species for the period 1916–1996. Box-and-whisker plots show the median, lower and upper quartiles (25% and 75%) and the minimum and maximum values of the correlations for each month (left axis). Dashed horizontal lines indicate the $P = 0.05$ significance level for a two-tailed test. Shaded areas and lower-case letters represent months of the calendar year prior to the growing season: M, May; N, November. Species abbreviations: ACRU, *Acer rubrum*; CAGL, *Carya glabra*; CAOV, *Carya ovata*; LITU, *Liriodendron tulipifera*; QUAL, *Quercus alba*; QUMO, *Quercus montana*; QURU, *Quercus rubra*; QUVE, *Quercus velutina*.

Spatial distribution of correlations

The response to SPEI6 showed no significant latitudinal trend, although non-significant coefficients were more abundant in the northern part (Fig. 4a). As precipitation decreases from south to north, so the positive response to summer precipitation becomes stronger ($r = 0.34$, $P = 0.0017$) (Fig. 4b). In contrast, correlations with summer maximum temperatures were more strongly negative in the south ($r = 0.28$, $P = 0.0239$; Fig. 4c). Correlations with

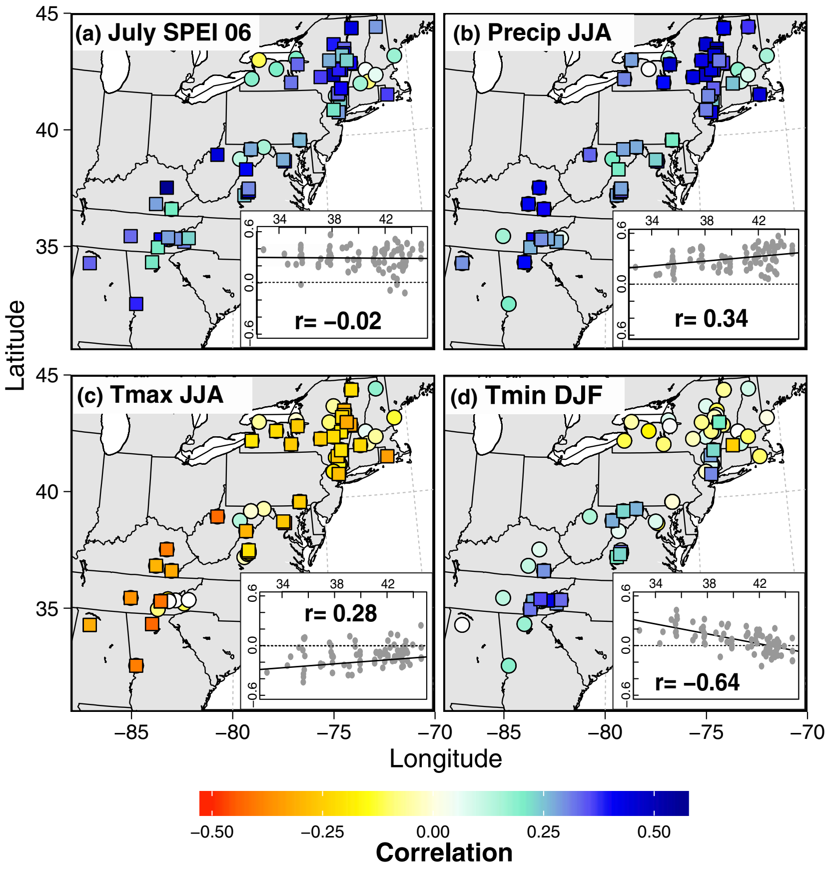

Figure 4 Spatial distribution of the correlations between tree radial growth and monthly climate variables for the period 1916–1996. Correlations were calculated between annual indices of tree-ring widths and monthly climate variables: (a) current July standardized precipitation–evapotranspiration index over 6 months (July SPEI6), (b) summer (June, July and August) precipitation (JJA), (c) summer maximum temperature, and (d) winter minimum (December, January and February) temperature (DJF). Squares (circles) show sites with significant (not significant) coefficients ($P < 0.05$). Inset scatter-plots show the relationship between correlation coefficients and latitude and their associated correlations (all significant at $P < 0.05$, except July SPEI6).

winter minimum temperature decreased in strength from south to north ($r = -0.64$, $P < 0.0001$; Fig. 4d). These latitudinal relationships were significant (except SPEI6) regardless of the spatial autocorrelation structure considered.

Self-organizing maps

Four nodes allowed for sufficient generalization but still provided enough detail in the climatic responses of each node (Fig. 5). The first three nodes were characterized by a strong positive response to summer precipitation, although it was stronger in chronologies within nodes 1 and 2 (Fig. 5c). Node 1 had a negative response to spring–summer temperature and a stronger response to precipitation later into the summer than nodes 2 and 3. Compared to node 1, node 2 had a higher summer precipitation response and a weaker and shorter response to temperature during spring and early summer. Node 3 grouped chronologies with a positive winter temperature signal, a positive correlation with summer precipitation and, to a lesser extent, a negative correlation with summer temperature. Chronologies with no response to summer temperature, but positive correlations with warm winters, grouped into node 4. Node 4 also showed the weakest response to summer precipitation. All nodes showed similar effects of the previous summer's precipitation (positive) and temperature (negative).

As with the results of the PCA, none of the SOM nodes were dominated by a single species (Fig. 5b), although two nodes revealed a strong latitudinal component (Fig. 5a). We did, however, observe a certain pattern of species falling within one of the nodes. The highly responsive node 1 included chronologies from all species except *C. ovata* and was entirely located in the southern half of the network (i.e. south of 40° N). In contrast, chronologies within node 2 were only located north of 40° N and belonged to *Quercus* and *Carya*; none of the chronologies within node 2 were *A. rubrum* or *L. tulipifera*. The majority of chronologies in node 3 clustered along the Hudson River valley (14/20 chronologies), and *L. tulipifera* was the most abundant species within this node (6/20 chronologies). Node 4 included chronologies of five species distributed along the entire latitudinal transect. These results emphasize the high degree of geographical dependence of the climatic response within our network and the separation of sites north and south of 40° N.

The geographical distribution of correlation coefficients was similar to the north–south pattern found for the PCA applied to all chronologies (Fig. 2b). We analysed the distribution of correlations between maximum temperature and precipitation at each of the 58 sites and yearly values of PC1 and PC2 (see Fig. S3 in Appendix S2) to determine whether these spatial distributions of PC1 and PC2 were related to the climate responses of trees. PC1 was most strongly and positively correlated with JJA precipitation (mean, 0.383; range, 0.073–0.550),

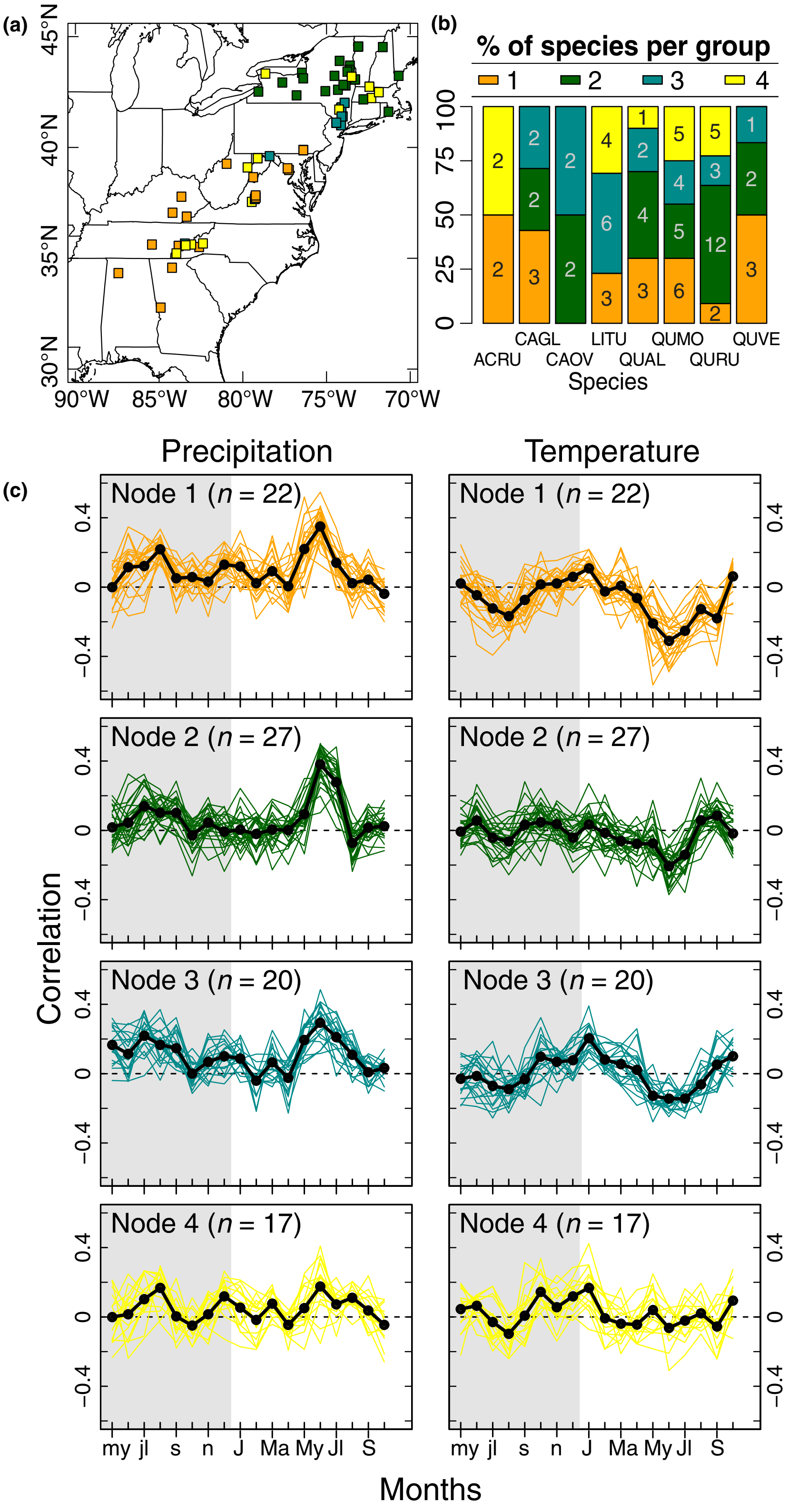

Figure 5 Four nodes derived by self-organizing maps (SOM) applied to correlations of monthly climate variables with tree-ring width indices at all sites in the tree-ring network. (a) Spatial distribution of the four SOM nodes over eastern North America. (b) Percentage and total number of sites of each species classified in each of the four SOM nodes. Species abbreviations: ACRU, *Acer rubrum*; CAGL, *Carya glabra*; CAOV, *Carya ovata*; LITU, *Liriodendron tulipifera*; QUAL, *Quercus alba*; QUMO, *Quercus montana*; QURU, *Quercus rubra*; QUVE, *Quercus velutina*. (c) Climate responses (correlations) of indices in each node (coloured lines) and mean response (thick black line and black circles) and total number of sites in each node. Shaded areas and lower-case letter represent months of the calendar year prior to the growing season (J, Ma, My, Jl, S, N: January, March, May, July, September, November).

being significant for 88% of the sites. These coefficients were in turn correlated with latitude ($r = 0.560$, $P < 0.05$), increasing from south to north. Only five sites north of 40° N fell outside this general pattern, similar to results for direct correlations (Fig. 4). The strength of the relationships between JJA temperature and PC2 (mean, 0.049; range, −0.241–0.263) were highly dependent on latitude ($r = 0.905$, $P < 0.05$). The sign of these coefficients changed around 40° N, similar to the PC2 loadings of the chronologies (Fig. 2b).

DISCUSSION

Our results demonstrate that drought is the main climatic factor at ecosystem and subcontinental scales that limits the growth of trees in the temperate broadleaf forests of eastern North America. The common response of trees in these forests (Fig. 2) is influenced by a high level of shared hydroclimate variability across eastern North America (Karl & Koscielny, 1982). Importantly, the latitudinal pattern of drought response is driven by different climatic factors (Figs 2, 4 & 5). The lower amounts of precipitation in the cooler north increase drought-sensitivity despite lower evapotranspiration, whereas warmer temperatures in the south increase summer evaporative demand, thus depleting soil water faster despite the more abundant precipitation. This regional segregation is in line with more extensive but less species-rich tree-ring networks covering the continental United States (Meko *et al.*, 1993). LeBlanc & Terrell (2001) showed similar latitudinal patterns for *Q. alba* across the eastern United States. Our multispecies analysis at subcontinental scale unveils similar levels of drought stress on broadleaf species in these forests as a consequence of latitudinal trends in temperature and precipitation.

We were also able to use our network of broadleaf deciduous species to explore the influence of taxonomy on climate responses. The general lack of clustering around taxa (i.e. species or genus) in our network (Figs 2a & 5b) supports a common climate signal across species, in line with studies that analysed only conifers (Frank & Esper, 2005) or broadleaf species (Tessier *et al.*, 1994). This is in contrast to studies that included both evergreen and deciduous species to identify functional responses of tree growth to climate (Graumlich, 1993; Cook *et al.*, 2001). Our results also slightly contradict the hypothesis that phylogenetic differentiation is more important than site influences in areas where climate imposes only moderate growth limitations on trees. This hypothesis is upheld in a tree-ring network located at the western edge of the eastern United States forest biome where precipitation is generally lower than areas further east (Cook *et al.*, 2001), as well as a network in the northern portion of the eastern forest biome where temperatures are cooler than in southern regions (Graumlich, 1993). Differences in sampling strategy and replication at different sites could also be a factor in our results, although tree replication versus core replication (Fritts, 1976) and the use of different sampling strategies (Pederson *et al.*, 2012a) only revealed small differences in population chronologies. The differences between our results and previous studies (Graumlich, 1993; Cook *et al.*, 2001) could arise from several factors. Our gradients of precipitation and temperature are wider than in the more climatically homogeneous network of Graumlich (1993) and the Cook *et al.* (2001) network, which extended across a strong longitudinal precipitation gradient with little difference in latitude. Our wide latitudinal range (32–45° N) also encompasses a range of growing-season lengths (Zhu *et al.*, 2012) that can affect the impact of climate on trees. In the southern part of our network (SOM node 1), the influence of summer temperature (May to September) on trees was much stronger than in the north (SOM node 2), which might result from an earlier onset and later termination of growth at lower latitudes regardless of species-specific phenology. Different growing-season lengths between sites and the strong climate gradients could have obscured the species-specific climate responses that might be observed at smaller scales, although PCA applied separately to the regions above and below 40° N also showed no clustering of taxa (results not shown). Finally, the inclusion of both broadleaf and coniferous species in previous studies (Graumlich, 1993; Cook *et al.*, 2001) might have influenced species clustering. It is possible that a better replication of some species (e.g. *A. rubrum*) or covering the complete distribution ranges of other species (e.g. *Q. rubra*) would allow for an improved understanding of climatic forcing on tree growth.

Species responses

Despite the more moderate climate in our study area than the network analysed by Cook *et al.* (2001), where drought becomes more severe from east to west, *Quercus* in our network did not show the taxonomic distinction between sections *Erythrobalanus* (black oaks: *Q. velutina* and *Q. rubra*) and *Leucobalanus* (white oaks: *Q. alba* and *Q. montana*) reported by Cook *et al.* (2001). In a Mediterranean climate, deciduous *Quercus* species in sections *Leucobalanus* and *Mesobalanus* also shared a common response to summer precipitation and temperature (Tessier *et al.*, 1994). These findings suggest that taxonomic classification might be less important for climatic sensitivity than location along geographical gradients.

Our results do not support common climatic influences within ring-porous (*Quercus* and *Carya*) or diffuse-porous species (*Liriodendron* and *Acer*), but the fact that none of the diffuse-porous species showed a strong correlation with June and July precipitation and summer heat stress (node 2) could suggest an influence of certain wood anatomical traits on climate sensitivity. Diffuse-porous *Fagus* and ring-porous *Quercus* in Europe differ in their resistance to xylem embolism, their phenology, their cambial development and their dynamics of stored carbohydrates (Barbaroux & Bréda, 2002). It seems possible that these differences result in significantly different climate responses (Babst *et al.*, 2013). The definition of functional groups based on ring porosity could be useful for simulations of plant responses to environmental conditions (Bugmann & Cramer, 1998; Cook *et al.*, 2001), but there were too few diffuse-porous species in our network to draw any definite conclusion in this regard.

The strength and extent of climate correlations nonetheless revealed interspecific differences. *Quercus* species are physiologically and morphologically adapted to drought (Abrams, 1990). Although *Q. velutina* is considered more drought-resistant than other broadleaf species (Hinckley *et al.*, 1978, 1979), all six chronologies analysed for this species in our network were drought sensitive. *Quercus alba* and *Q. montana* followed *Q. velutina* in terms of drought sensitivity, which is similar to previous studies (Fekedulegn *et al.*, 2003; Speer *et al.*, 2009). Similar climate correlations for *Q. alba* and *Q. rubra* (LeBlanc & Terrell, 2011), even at their northern distribution limit in southern Quebec (Tardif *et al.*, 2006), support a lack of taxonomy-based differences in climate response in broadleaf species. Despite adaptations of *Q. rubra* to low resource availability (including drought) and its weaker response to climate than the other North American oaks (Fekedulegn *et al.*, 2003; Speer *et al.*, 2009), *Q. rubra* showed similar latitudinal trends in climate responses to other species in our network. A denser network of *Q. rubra* towards its southern range would be desirable to better understand its drought response.

Our results agree with previous efforts and have important implications regarding the ecological amplitude of broadleaf tree species: tree growth is not necessarily limited by cold temperatures at the northern distributional limit of species (Tardif *et al.*, 2006; Griesbauer & Scott Green, 2010). In comparison, temperature limitations are stronger for coniferous species towards their northern limits (Cook *et al.*, 1998; Pederson *et al.*, 2004; Bhuta *et al.*, 2009; Babst *et al.*, 2013). Drought stress is strongly limiting in the northern sites of our network, which could favour the persistence of northern oak populations (Tardif *et al.*, 2006). On the other hand, we find that the southern distribution edge may be strongly influenced by heat stress or water availability despite abundant precipitation. Climate may limit life-cycle processes not considered in our study (e.g. fruiting, ability to establish and juvenile survival) more than radial growth. Moreover, extreme events (e.g. deep freezing) could also play an important role in limiting species distributions, but may not have been frequent enough to be recorded in interannual growth variability during the period of our study.

Across our network, the growth of *L. tulipifera* was enhanced by previous warm autumn–winter temperatures, but was rarely decreased by summer heat stress. This finding is in line with previous work suggesting that *L. tulipifera* has greater thermal requirements than other species in eastern North America (Canham & Thomas, 2010). Chronologies of *Q. montana*, *C. glabra* and *C. ovata* also showed this non-growing-season temperature response, as found by Pederson *et al.* (2004). The response of growth to cool-season temperatures decreased with increasing latitude, coinciding with the earlier onset of growth at lower latitudes. The effect of winter temperatures on deciduous trees must involve different mechanisms from those in evergreens, because winter photosynthesis can be ruled out. Positive effects of temperature on bud-burst (Heide, 2006; Delpierre *et al.*, 2009) and winter dormancy (Heide, 2006) might promote growth after warm winters (Orwig & Abrams, 1997). This response was particularly strong and positive in the higher elevations of the southern Appalachians, a cooler area within the southern warm region, and in the Hudson River valley, a warmer area within the northern cool region. These locations might be cold enough to delay the onset of the growing season some years but warm enough to advance it other years, which could make the trees sensitive to winter temperature variability. This sensitivity could also be related to earlier snow-melt, which increases soil moisture and affects the dynamics of fine roots (Tierney *et al.*, 2003). Ultimately, our results support the important effect of winter temperature in ecotone positioning (Neilson, 1993) and forest carbon uptake (Delpierre *et al.*, 2009).

There is still no agreement about the role of drought in humid temperate forests (Boisvenue & Running, 2006), despite numerous accounts and evidence of the drought-induced limitations on growth for trees in these forests (Hursh & Haasis, 1931; Cook & Jacoby, 1977; Orwig & Abrams, 1997; Speer *et al.*, 2009; LeBlanc & Terrell, 2011; Pederson *et al.*, 2012a,b) and the global vulnerability of trees to drought (Allen *et al.*, 2010). Drought-induced limitations across our network suggest that drought should be considered one of the most important drivers of forest dynamics at broad scales, because it can decrease the carbon-fixing potential of forests (Brzostek *et al.*, 2014) and induce widespread forest mortality (Hursh & Haasis, 1931). Disturbance analyses in eastern North America have, however, typically focused on intense and frequent disturbance agents (e.g. wind, fire or insects) at moderate spatial scales rather than more diffuse and widespread agents, such as drought (Vanderwel *et al.*, 2013).

Our findings indicate that the impact of climate change on forests across the eastern United States might depend on latitude more than on species composition. In the north-east, where precipitation is a stronger limiting factor than temperature, drought stress might actually be reduced if the current increase in precipitation (Pederson *et al.*, 2013; Melillo *et al.*, 2014) continues, such that it overrides the negative effect of warming temperatures (Dai, 2013). Recent increases in forest growth in this area (McMahon *et al.*, 2010) could have been caused by the increasing precipitation over recent decades. In time, these increases could be limited or turn into growth declines if the effect of warmer temperatures is greater than that of increased precipitation (Ciais *et al.*, 2005).

Recent cooling in the south-east (Lu *et al.*, 2005) might have partly alleviated the negative effects of decreased precipitation (Melillo *et al.*, 2014), resulting in no trends of drought stress (Dai, 2013). Future warming is, however, likely to increase drought in these forests through increased evapotranspiration (Melillo *et al.*, 2014). Further analyses are required to disentangle the influences of all potential factors, but our results demonstrate that the effects of drought in humid temperate forests need to receive greater attention.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Descriptive tables of the tree-ring width chronologies analysed (Tables S1 & S2).
Appendix S2 Supplementary figures (Figs S1–S3).

BIOSKETCHES

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