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The legacy of episodic climatic events in shaping temperate, broadleaf forests

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Abstract. In humid, broadleaf-dominated forests where gap dynamics and partial canopy mortality appears to dominate the disturbance regime at local scales, paleoecological evidence shows alteration at regional-scales associated with climatic change. Yet, little evidence of these broad-scale events exists in extant forests. To evaluate the potential for the occurrence of large-scale disturbance, we used 76 tree-ring collections spanning ~840 000 km^2 and 5327 tree recruitment dates spanning ~1.4 million km^2 across the humid eastern United States. Rotated principal component analysis indicated a common growth pattern of a simultaneous reduction in competition in 22 populations across 61 000 km^2. Growth-release analysis of these populations reveals an intense and coherent canopy disturbance from 1775 to 1780, peaking in 1776. The resulting time series of canopy disturbance is so poorly described by a Gaussian distribution that it can be described as "heavy tailed," with most of the years from 1775 to 1780 comprising the heavy-tail portion of the distribution. Historical documents provide no evidence that hurricanes or ice storms triggered the 1775–1780 event. Instead, we identify a significant relationship between prior drought and years with elevated rates of disturbance with an intense drought occurring from 1772 to 1775. We further find that years with high rates of canopy disturbance have a propensity to create larger canopy gaps indicating repeated opportunities for rapid change in species composition beyond the landscape scale. Evidence of elevated, regional-scale disturbance reveals how rare events can potentially alter system trajectory: a substantial portion of old-growth forests examined here originated or were substantially altered more than two centuries ago following events lasting just a few years. Our recruitment data, comprised of at least 21 species and several shade-intolerant species, document a pulse of tree recruitment at the subcontinental scale during the late-1600s suggesting that this event was severe enough to open large canopy gaps. These disturbances and their climatic drivers support the hypothesis that punctuated, episodic, climatic events impart a legacy in broadleaf-dominated forests centuries after their occurrence. Given projections of future drought, these results also reveal the potential for abrupt, meso- to large-scale forest change in broadleaf-dominated forests over future decades.

Key words: closed-canopy forests; deciduous forests; disturbance; drought; frost; gap dynamics; historical documents; mesoscale dynamics; tree-ring analysis.

Introduction

Anthropogenic climate change is altering the structure and function of forested ecosystems and challenging our understanding of how systems react to disturbance. Increased warming has complex effects on ecosystem dynamics through the interaction of drought, species tolerances, insect outbreaks, fire regimes and other perturbations (e.g., Allen and Breshears 1998, Taylor et al. 2006, Worrall et al. 2008, van Mantgem et al. 2009, Allen et al. 2010). Climatic variation drives ecosystem dynamics at large scales in semiarid and boreal forests, where tree species richness is relatively low (e.g., Payette et al. 1985, Savage et al. 1996, Villalba and Veblen 1997, 1998, Allen and Breshears 1998, Brown and Wu 2005, Raffa et al. 2008). An extreme example includes massive forest mortality where one species comprised 95% of the

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composition (Michaelian et al. 2011). While recent disturbances appear to be partly driven by anthropogenic warming, they generally fit the expected disturbance regime in these forests and provide insight into how climate modulates these systems at regional scales.

In contrast to these systems, many forests, especially in temperate, broadleaf forests, experience gap dynamics and partial canopy mortality as the prevailing disturbance regime at stand to landscape scales (Runkle 1982, Yamamoto 1992, Rebertus and Veblen 1993, McCarthy 2001, Gutierrez et al. 2008). These small-scale events are thought to be largely stochastic and not directly tied to climate. Triggered by individual tree mortality, these dynamics could aid in the maintenance of stand composition and structural complexity and play a role in prolonged forest stability at large scales (Runkle 1982, Yamamoto 1992, McCarthy 2001, Gutierrez et al. 2008), an observation that is supported through long-term, simulated forest dynamics (Smith and Urban 1988). Long-term forest stability is primarily achieved through in-filling by lateral branches in small gaps or filling through recruitment of more shade-tolerant species. Temperate forests in humid regions dominated by broadleaf species often have high species diversity, making them resilient to species-specific disturbances like insect outbreaks. In marked contrast with low-diversity coniferous forests, for example, the broadleaf-dominated forests of the eastern United States have no native forest insects that trigger large-scale dieback (Man 2012). And, unlike semiarid or coniferous systems, fire in this region is typically fine-scaled, spatially heterogeneous (Clark and Royall 1996, Parshall and Foster 2002, Guyette et al. 2006, McEwan et al. 2007) and less likely to occur at regional scales (though see McMurry et al. [2007] for an exception). Thus, dynamics in broadleaf-dominated forests are often characterized as asynchronous in space and time and not seen as strongly influenced by climatic variation like other forest types (Schleeweis et al. 2013, Vanderwel et al. 2013). Given future climate forecasts, it is imperative that we understand how broadleaf forests in humid regions might respond to climate change at large spatial scales.

Paleoecological studies have documented regional-scale changes in humid forests driven by climate. Specifically, drought shaped the structure and composition of these systems during the Holocene (Jackson and Booth 2002, Shuman et al. 2004, 2009, Foster et al. 2006, Booth et al. 2012). For example, Booth et al. (2012) recently showed how the decline of American beech during the Medieval Climate Anomaly was triggered by drought and climatic variability in the moist, lake-effect-influenced forests in the Great Lakes region. While paleoecological studies are critical in identifying long-term, regional-scale forest dynamics, they typically can only identify the timing of forest dynamics at decadal to multi-decadal scales and at broad compositional (i.e., genera) levels. How this translates to contemporary systems is less certain. To date, disturbance histories of extant old-growth forests in humid regions primarily identify stand-scale (Runkle 1982, Yamamoto 1992, McCarthy 2001) to moderate-scale dynamics (White et al. 1999, Frelich 2002, Woods 2004, Baker et al. 2005, Worrall et al. 2005, Stueve et al. 2011), although large-scale dynamics have been postulated (e.g., Cho and Boerner 1995). Thus, there is a disparity between paleoecological records of regional-scale forest dynamics and recent forest history reconstructions that primarily document gap dynamics. Bridging this divide for broadleaf-dominated forests could yield important analogues for how forests will respond to climate change at time scales relevant for climate forecasts and human decision making.

Here we develop and analyze two large data sets to investigate the possibility of synchronous, regional-scale disturbance and tree recruitment over the last 500 years of the Common Era (CE) in the humid, broadleaf-dominated region of the eastern United States. We test a null hypothesis of small-scale (gap) dynamics under which disturbance and tree recruitment resemble a stochastic or white-noise process. Explicitly, forest dynamics would not be regionally synchronous and time-series of disturbance and recruitment would not deviate significantly above the long-term background rate. Under the alternative hypothesis, forest dynamics would be regionally synchronous and time-series of disturbance and recruitment would be punctuated by extreme events. We know of no study that has identified severe, synchronous, regional-scale disturbance in temperate humid regions outside of studies covering decadal to centennial time scales (sediment core records). In fact, two tree-ring-based investigations designed to identify regional-scale disturbance did not reveal evidence for synchronous disturbance over the last 300+ years (Rentch 2003, D'Amato and Orwig 2008). The first data set for our investigation, 76 tree-ring records over a $\sim$840 000 km^2 area, is examined for temporal clustering of large-scale canopy disturbance. The second data set, $>$5000 tree recruitment dates from multiple sources that cover $\sim$1.4 million km^2, are examined for evidence of synchronous, large-scale recruitment events.

Identifying the exact triggers of historical disturbance from tree rings or other types of ecological proxies can be difficult given that many factors drive forest dynamics. We thus turned to historical documents to assist in identifying potential drivers of disturbance. Historical documents have been used to clarify the potential impact of climate on human societies (e.g., Endfield 2012) and in physical geographical and ecological studies (e.g., Hooke and Kain 1982). Here, we use historical documents to conduct a "ground-truthing" of events in tree-ring records. Several sources of historical documents were used including a compilation of Atlantic hurricanes (Chenoweth 2006), diaries of frontier settlers, Moravians, in western North Carolina (Fries 1922, 1925, 1926), Thomas Jefferson's Garden Book (1774) and 18th-century newspaper and other accounts (e.g., Ludlum 1963). While many of the Moravian records contain information about births, marriages, deaths, civil unrest, and smallpox, they are also a rich source of information for historical ecology, documenting events that impacted agriculture (like hail storms, oppressive heat, and individual rain events; see *Examples of weather observation from the Moravian Diaries* in Appendix A for examples). We note, however, that their records are of limited spatial coverage and cannot account for possible impacts across our study region. Given their detailed observations of important weather events, spatial coverage of the records, and multiple observers at potentially daily temporal resolution, it is possible that significant, large-scale, weather events were documented, which could complement our understanding of forest dynamics from tree-ring records.

Methods

We investigate the potential for regional scale-disturbance using a network of 76 tree-ring chronologies from the International Tree-Ring Databank (ITRDB) covering ~840 000 km^2 in the broadleaf-dominated region of the humid eastern United States (also called the Eastern Deciduous Forest; Fig. 1a; see Table A1). Tree-ring records from sites in southeastern Kentucky, central Tennessee, and North Carolina indicated the possibility of large-scale disturbance in the late 1770s (see *Temporal and geographic disturbance detection methods* in Appendix A: Fig. A1, and two of these forests in Appendix B). With a larger data set, we sought to test the hypothesis that a regional-scale disturbance event occurred during this period. If there is evidence of a regional event, the larger network will allow us to determine its spatial extent. The network is composed of at least 11 species collected by 15 investigators to study climate, ecology, and fire history. Most trees were targeted for maximum age, drought sensitivity, or fire history, although some were collected via random sampling (Appendix A: Table A1). Most of the collections for climatic reconstruction were not derived from the canonical "open-grown" trees on highly stressed sites (see Fritts 1976), but from closed-canopy forests; 44 of the 49 sites were either visited by a coauthor (N. Pederson) or confirmed to be closed-canopy from the collector (E. Cook, *personal communication*). To avoid inflating results, the Blanton Forest populations were combined during analysis, as two *Quercus* species were intermingled throughout the forest.

Tree-ring chronologies were selected if they met several criteria, including species composition (trees from broadleaf-dominated forests), chronology length (inner ring date pre-1750), geographic location, and the likelihood that they represented old-growth forest. We targeted broadleaf-dominated forest to increase the likelihood that small-scale dynamics was the predominant disturbance regime; we did not, for example, include species such as *Pinus resinosa* or *Pinus rigida*, which would be expected to have more episodic recruitment because of a fire-dominated disturbance regime. We were not able to meet these criteria in all cases. For example, 12 of the 76 chronologies came from conifer-dominated forests with possible episodic recruitment (*Picea rubens*, *Pinus echinata*, *Pinus* spp.; Appendix A: Table A1); *Tsuga canadensis* is an important component of this network, but generally has more of a gap-dynamics life history trait in reaching the forest canopy. To increase the likelihood that potential collections for analysis were not from logged forests, we excluded collections if (1) one-third or more of trees with rapid, early growth were recruited in a single cohort after ca. 1850 or (2) a substantial number of old trees showed major growth releases during this same period (>100% change in growth; see Lorimer [1985], Lorimer and Frelich [1989]). Even though little stand-scale logging occurred in the mountainous and plateau areas of our study region prior to 1850 (Williams 1992: Fig. 6.4), there is the possibility that stands with only natural disturbance were omitted from this analysis. Since many of the collections are from extant old-growth forests, it is less likely that they have been logged because of the common relationship between low site productivity and old trees (Stahle and Chaney 1994). For finer details on discerning expected radial growth patterns and other considerations of our approach, see *Temporal and geographic disturbance detection methods* in Appendix A. The ultimate goal in omitting some trees and collections was to avoid false-positive results that could occur if all data were included in the initial analysis.

To objectively detect if step-change increases in radial increment might resemble a regional-scale canopy disturbance, raw ring widths were standardized using a straight-line fit to remove differences in mean growth rate. The resulting standard chronologies were entered into rotated varimax principal component analysis (RPCA). RPCA identifies the highest loadings of each variable on a single eigenvector while maintaining orthogonality and maximizing variance of retained eigenvectors (Richman 1986). The Monte Carlo "Rule-N" technique was used to determine the number of eigenvectors to use for analysis (Preisendorfer et al. 1981). RPCA retained eight significant eigenvectors, accounting for 62.9% of the common variation (see Table A2 and *Temporal and geographic disturbance detection methods* in Appendix A). We report on the first three for this study. Eigenvector 1 (EV1), accounting for 20.8% of the common variation, represents the temporal decline in ring widths as constrained by allometry (Appendix A: Fig. A2a). Eigenvector 2 (EV2), accounting for 11.1% of the common variance, has a large, step-change in radial increment around 1780 (Fig. 1b). Eigenvector 3 (EV3), accounting for 8.3% of the common variance, reveals an abrupt increase in ring widths in 1840 and 1857 (Appendix A: Fig. A2b, Table A2). As EV1 reflects the commonly observed pattern of large rings when trees are small and there is a good chance that EV3 likely represents the era of European settlement, we focus on investigating the potential for a regional disturbance event among the populations loading strongly on EV2. A complete analysis and discussion of EV3 is beyond the goals of this study.

To investigate whether the step-change in radial increment of EV2 was a regional-scale disturbance event, disturbance history was reconstructed from the 22 chronologies loading positively and significantly onto EV2 ($\geq$0.224, $P \leq 0.05$; following Koutsoyiannis [1977]). Evidence of canopy disturbance in individual raw ring-width series of the 22 chronologies was investigated using conservative methods adopted from a traditional approach. Here, a major canopy disturbance is an increase in radial growth of >99.9% over a 15-year period relative to the prior 15 years; a minor release is an increase in radial growth of 50–99.9% over 15-year periods ([Lorimer and Frelich 1989]; for a deeper discussion on potential pitfalls for these methods, see *Tree and population-level disturbance history analysis* in Appendix A). A release >99.9% is considered an opportunity for an understory tree to reach the canopy (cf. canopy accession; Lorimer and Frelich 1989). While these methods were primarily developed for shade-tolerant species, previous work indicates that these methods are effective for reconstructing disturbance histories using shade-intolerant species (Orwig and Abrams 1994), even in a "gappy forest" (McGuire et al. 2001) dominated by shade-intolerant species (see Pederson et al. 2008). Our method might not detect multiple disturbances in some trees because trees lose some sensitivity to changes in competition as they gain canopy status (Nowacki and Abrams 1997, Rentch et al. 2002, Druckenbrod et al. 2013). However, many trees in our data set recorded more than one disturbance. Further, a test of lower detection thresholds does not alter our findings, but does seem to be sensitive to climate in ways that could result in false positives (see *Detection sensitivity analysis* in Appendix A). Because of the methodology used here, we do not have a complete record of disturbance history. And, given that most ITRDB data are composed of only 20–30 canopy trees per stand, we would not expect to detect all possible disturbances in a particular forest, although increased core replication of the ITRDB collections likely increases the chance of detecting disturbance vs. single-core studies (Copenheaver et al. 2009). Ultimately, our final time-series of canopy disturbance should reflect a lower number of false positives and, more importantly, large canopy gap formation, which should have a more meaningful impact on forest composition and structure than smaller gaps.

Statistical analysis of the disturbance record indicated a heavy tail (i.e., large-disturbance events) that strongly deviated from a Gaussian distribution (see Fig. 2c, d). Therefore, we applied tools from extreme value theory (Davison and Smith 1990, Coles 2001), to analyze the statistical properties of extremes in the disturbance record (i.e., years with many recorded disturbances). In this framework, we use a peak-over threshold approach, based on the generalized Pareto distribution (GPD), to investigate the tail properties of the time-series of canopy disturbance. We fit a GPD to disturbance events above a disturbance rate of 1%. The determination of a suitable threshold for which the asymptotic GPD approximation holds is an essential step that requires the consideration of a trade-off between bias and variance (e.g., Coles 2001). Note that if a threshold is chosen too low, the GPD will fit the exceedances poorly and introduce a bias in the estimates, while if a threshold is chosen too high it will reduce the number of exceedances and thus increase the estimation variance. In practice, threshold choice involves comparing the theoretical behavior of the GPD with the empirical behavior of the data. Tools like the mean residual life plot assist in the threshold choice, and if the observations follow a GPD with a shape parameter <1, the mean exceedance should vary linearly with the threshold. For our application we choose the threshold as a disturbance rate of 1%. The rationale behind this threshold choice is that (1) it fulfills the statistical criteria described here and (2) it allows us to consider more moderate disturbances (that lie clearly above the internal variability of the data record; as a disturbance rate of 1% falls at about the 80th percentile of the record) together with the "high impact" extremes. This model described the high tail much better than the Gaussian distribution. In addition, return intervals (in years T) can be described from the probability of exceeding a disturbance rate x within a time window T directly from the fitted GPD.

We tallied the number of major canopy disturbances per year from the 22 collections and created an index of disturbance magnitude. The magnitude index, based on a method to compare climatic events of differing lengths and intensities (Biondi et al. 2005, Gray et al. 2011), is calculated as

$$M_{\mathrm{I}} = D \times \mathrm{DR} \times \mathrm{MR}$$

where M_{I} is the magnitude index, D is the duration in years, DR is the anomaly of the disturbance rate as the departure from the mean of the percentage of trees disturbed per year from 1685 to 1880, and MR is the percentage of releases qualifying as a "major release" during each event. The magnitude index describes the intensity of each release event. Canopy disturbance analysis is limited to 1685–1880 because it represents the period when tree replication $\geq$ 100 (1685) and precedes large-scale logging (ca. 1880; Williams 1992) when we hypothesize that trees from ITRDB collections would have reduced sensitivity to changes in competition. As many collections from the ITRDB contain trees >200 years of age at the time of sampling, it is not unreasonable to expect that most of these trees, especially species like *Quercus alba* or *Liriodendron tulipifera*, would have reached canopy status within 100–150 years

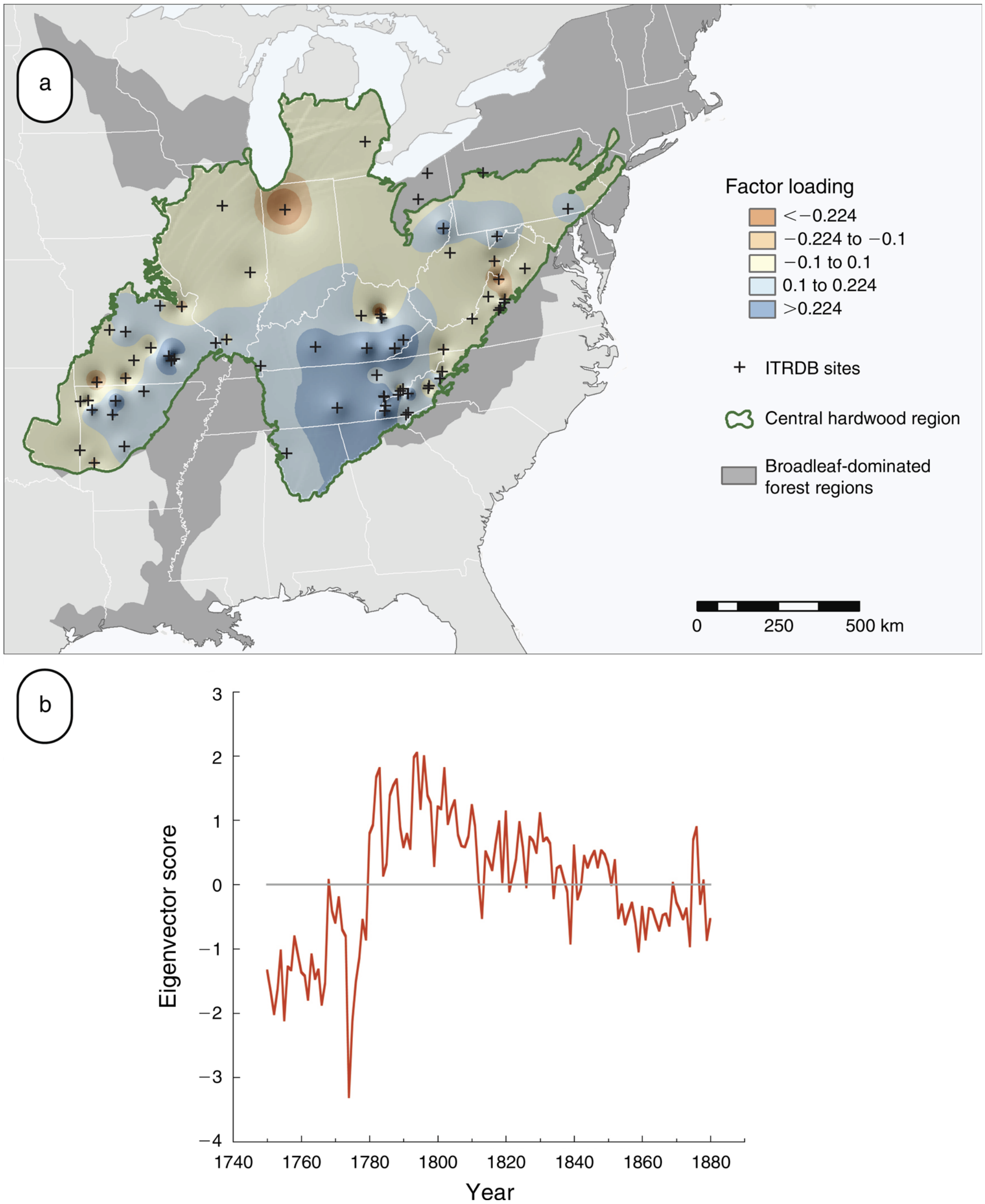

FIG. 1. Spatial loading of populations onto eigenvector 2 (EV2). The central hardwood region is adapted from Fralish and Franklin (2002), and the U.S. Environmental Protection Agency (2003); the broadleaf-dominated forest regions are adapted from Dyer (2006). Plus signs show International Tree-Ring Databank (ITRDB) sites. (b) Time-series of ring width variation of EV2 from 1750–1880 of populations within the dark blue areas in panel a. The gray line in panel b represents the 1750–1880 mean.

prior to sampling; tree-ring sampling in the eastern United States began in earnest during the late 1970s (e.g., Cook and Jacoby 1977, 1983, Cook 1982, Stahle et al. 1985, Stahle and Cleaveland 1988). Reliance on the oldest trees in a reconstruction of disturbance history has the potential to be biased as one moves closer to the period of sampling (McEwan et al. 2014). Thus, we expect the mid-1800s to be the beginning of reduced tree sensitivity to release in our data set, a trend observable in our record.

We then investigated the relationship between canopy disturbance and drought in two ways. First, we made composite drought maps from the North American Drought Atlas (NADA; Cook and Krusic 2004, Cook et al. 2004) for the years prior to the 23 years with elevated disturbance (years with disturbance ≥1.0 SD above the 1680–1880 mean) after we noticed that elevated disturbance often followed regional marker rings. Second, we used superposed epoch analysis (SEA; Swetnam 1993) to examine moisture conditions before, during, and after years with elevated disturbance. Because some of the tree-ring records used for disturbance analysis are used in the NADA, we developed an independent drought proxy (IDP) to test for a relationship between drought and disturbance. IDP is a tree-ring-based proxy of drought using records not used for disturbance analysis from within and around the periphery of the late-1770s disturbance region (see *Creation of the independent drought proxy for superposed epoch analysis* in Appendix A).

We mined published and unpublished data sets of tree establishment dates from old-growth forests dominated by broadleaf species to reconstruct regional-scale recruitment history across the eastern United States (see Supplement). Like our disturbance-detection analysis, forests that would be expected to have episodic recruitment, i.e., pine-dominated forests, were avoided. While some scattered conifers within broadleaf-dominated forests are included in this analysis, recruitment dates for these trees were drawn from broadleaf-dominated forests or conifers with more of a gap-phase life history trait like *Tsuga canadensis* and *Tsuga caroliniana*. We examined a larger area than that of the 76 chronologies for disturbance detection because a review of independent and geographically dispersed studies explicitly discussed a recruitment event, broad compositional change, or stand initiation dates in the late 1600s (Huntington 1914, Haasis 1923, Hough and Forbes 1943, Henry and Swan 1974, Grimm 1983, Guyette et al. 1994, Rentch 2003). Thus, this data set would be another test of regional-scale disturbance in forests dominated by gap dynamics. We only examined recruitment dates prior to 1850 to reduce the influence of widespread regional land-use change associated with land clearing and cutting (Williams 1992). The final data set includes 49 published studies from 56 different stands comprised of 5327 individual tree establishment dates (Appendix A: Fig. A6). These studies used a variety of methods to investigate long-term development of old-growth forests at local scales, although Rentch (2003) is the exception with five sites distributed across ~30 000 km^2. Recruitment dates were tallied from 34 species, not counting "other" and "unknown" categories as other species. The most common species are *Tsuga canadensis* (25.6%) and *Quercus alba* (21.3%). Eight *Quercus* species accounted for 37.6% of the recruitment dates while four *Pinus* species combined for only 6.4%. Recruitment dates are estimates of tree age at stump or coring height. Because these data varied in precision, methodology, recruitment dates, and dates when regeneration reached stump or coring height, dates were placed into four categories: Category 1, from randomized or representative sampling; Category 2, from studies targeting the oldest trees or historical timbers; Category 3, from studies that do not include post-1700 recruitment dates; and Category 4, from studies that have recruitment dates binned at >10 years. We compiled dates by decade because of associated uncertainties in methodology (see *Subcontinental-scale recruitment data* in Appendix A). Raw Category 1 recruitment increases through time (see Appendix A: Fig. A7). This trend was removed using segmented regression (R package segmented; Muggeo 2008) allowing us to detect individual recruitment events from the residuals of this trend as well as an objective assessment of breakpoints or changes in the trajectory of recruitment over time.

Multiple sources of observed weather events were used to conduct ground-truthing of the disturbance events embedded in our tree ring network. Due to the close proximity of the region experiencing the 1770s disturbance event, we relied upon the Moravian records from western North Carolina more than other sources. One value of the Moravian observations is that multiple resident diarists for each year are distributed over an area of at least 400 km^2; visitors to the Moravian settlement would occasionally extend the scale of observations in the diaries. In addition, Moravian records occasionally revealed the intensity and scale of impact. The wind event of 17 March 1776, as one example, was recorded by three observers, but it was noted by one of those observers from a neighboring village to have caused little damage (Fries 1926).

The Moravian records were used in two ways. First, they were used to determine the potential cause of the 1774 "white ring" seen in increment cores across genera (*Liriodendron*, *Carya*, and *Quercus*) collected in Kentucky and Virginia (Fig. A8). White rings are rings with low lignification and have been produced following

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FIG. 2. (a) Frequency of canopy disturbance through time of populations loading >0.224 onto eigenvector 2. The orange filling represents the percentage of major canopy disturbance per year per tree. The blue line with triangles represents tree replication per year. The short dashed line represents one standard deviation (SD) above the 1685–1880 mean, while the long dashed line represents 2 SD above the mean. (b) Map of the spatial extent of the regional-scale 1775–1780 canopy disturbance event. Mapping of the four quartiles of the total accumulation of trees recording disturbance from 1775–1780 indicates severe damage over an ~61 000 km^2 area. Specific site names corresponding to the numbers on this figure are listed in Appendix A: Table A5. Panels (c) and (d) compare the observed percentage of disturbed trees with a Gaussian distribution (least-mean-square fitted to the observations) for 1685–1880. (c) Density (measured as a proportion) plot of the observed percentage of disturbed trees (orange) and theoretical Gaussian distribution (gray). The labels q95, q99, and q99.9 mark the 95%, 99%, and 99.9% quantiles (blue lines), respectively; red line denotes maximum percentage of disturbed trees (6.4%); σ represents the standard deviation. (d) Quantile–quantile plot comparing the observed percentage of disturbed trees with the corresponding Gaussian distribution from panel (a). Black solid line represents the identity line. For convenient reference, the seven years with the highest rate of disturbance are marked to emphasize the uniqueness of the 1775–1778 era.

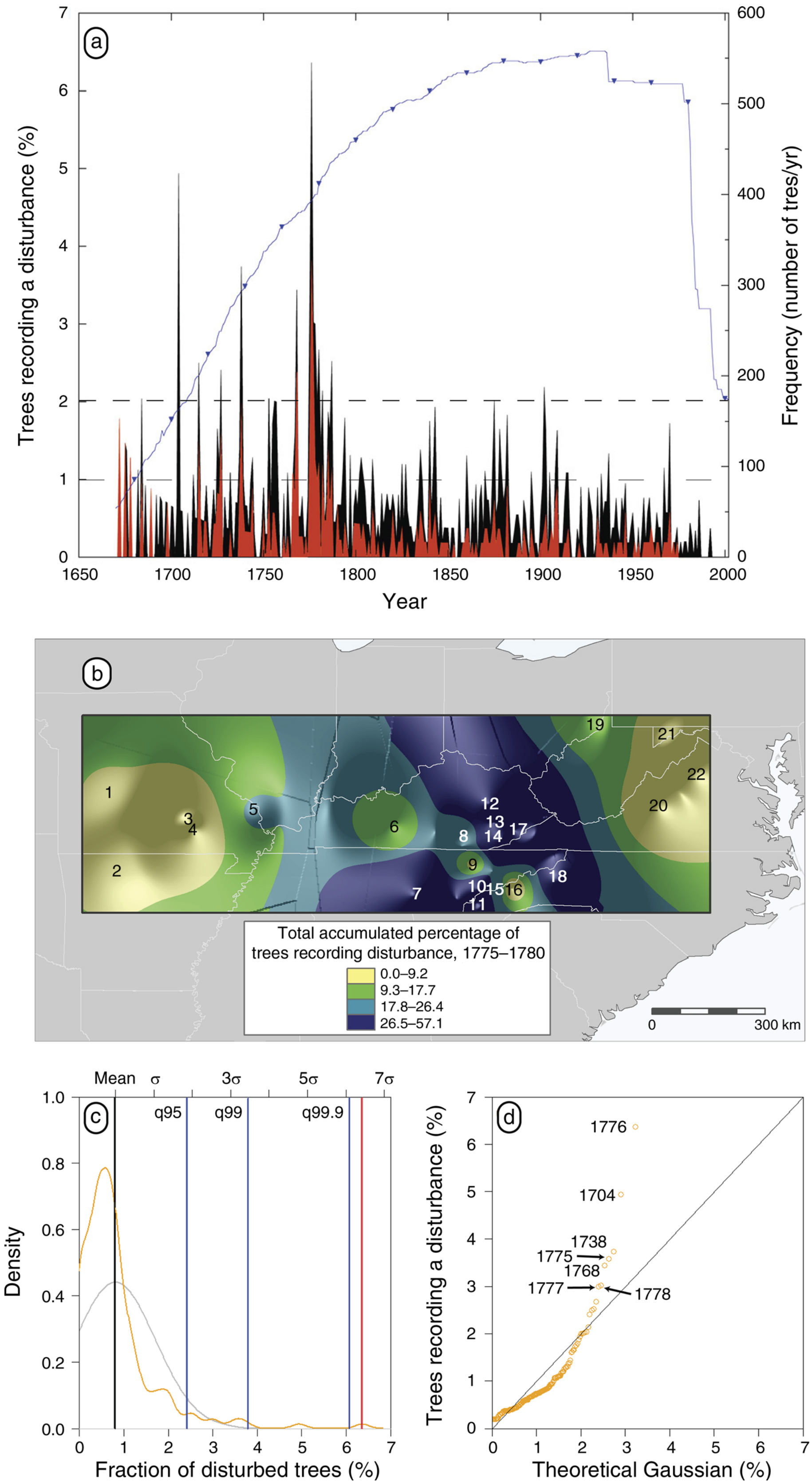
a
Trees recording a disturbance (%)
Frequency (number of tres/yr)
Year
1650
1700
1750
1800
1850
1900
1950
2000
b
Total accumulated percentage of trees recording disturbance, 1775–1780
0.0–9.2
9.3–17.7
17.8–26.4
26.5–57.1
0
300 km
c
Mean
σ
3σ
5σ
7σ
q95
q99
q99.9
Density
Fraction of disturbed trees (%)
d
1776
1704
1738
1775
1768
1777
1778
Trees recording a disturbance (%)
Theoretical Gaussian (%)

TABLE 1. Characteristics of periods with extended canopy disturbance events from 1685–1880.

Elevated disturbance years	Duration (yr)	Anomaly of disturbance rate (departure from mean/yr)	Proportion major release (%)	Magnitude of disturbance index	Sites recording disturbance
1725–1727	3	0.98	61.1	1.79	14.0
1737–1739	3	1.15	67.2	2.33	14.3
1755–1758	6	0.79	22.7	0.72	16.7
1766–1768	3	1.26	69.6	2.63	22.2
1774–1782	9	1.92	52.6	9.07	33.9
1775–1780	6	2.61	56.8	8.92	41.3
1776	1	5.33	62.5	3.33	47.6
1784–1787	4	0.84	57.1	1.92	26.2
1790–1794	5	0.16	33.3	0.27	18.1
1799–1805	7	0.05	44.4	0.16	16.3
1816–1821	6	−0.10	25.0	−0.15	15.1
1834–1836	3	0.28	37.5	0.31	17.5
1840–1843	4	0.53	40.7	0.86	22.6
1870–1872	3	0.20	38.5	0.02	17.5
1877–1883	4	0.29	24.4	0.50	19.0
1685–1880 Annual mean†		0.78 (0.83)	39.6		11.3 (9.8)
Elevated disturbance Mean	4.6 (1.89)	1.92 (0.59)	44.2 (16.1)	1.57 (2.43)	19.4 (5.58)

Notes: Characteristics for the peak year, 1776, and peak event within the 1774–1782 event, 1775–1780, are included to display their exceptionality. The event beginning in 1877 continues until 1883. Thus, its characteristics for the full event are included for completeness. See *Methods* for further discussion of this calculation.

† Values are means with SD in parentheses.

defoliation experiments (Hogg et al. 2002). They are also present during years of gypsy moth defoliation (Pederson 2005). Because the 1774 white ring appeared across genera, we hypothesized that defoliation was caused by a frost event. Second, the Moravian records were used as an independent ground-truthing of hurricanes striking the eastern United States in the year prior to or during elevated canopy disturbance events. These strikes were complied from Ludlum (1963), Rappaport and Ruffman (1999), Landsea et al. (2004), and Chenoweth (2006) and are in Appendix A (Table A4). The Moravian records then became vital in determining if known hurricanes impacted our study region because they lived adjacent to the southeast border of our canopy disturbance region and in an area that would likely experience tropical storm wind.

RESULTS

Disturbance history

Twenty-two collections loaded significantly onto EV2. These collections are composed of six species including, mesic, ravine-bottom *Tsuga canadensis* and *Liriodendron tulipifera*, a high-elevation *Picea rubens* collection, and two *Quercus* species growing on a dry, southeast-facing slope (Appendix A: Table A2). The strongest loadings clustered in the southern Appalachian Mountain–Cumberland Plateau region (Fig. 1a; Table A2; a detailed discussion of the RPCA results are in Appendix A: *Rotated principal component analysis results*). EV2's time-series of radial increment (RPCA scores) reveals below average increment prior to 1780 followed by a 201% increase in average radial increment in 1780–1794 vs. 1765–1779 and a linear decline until 1853 that resembles trees following canopy accession (Fig. 1b).

We detected a total of 866 canopy disturbances over the 1570–2000 CE period from the 558 trees and the 916 time-series of radial increment that comprise the 21 populations loading significantly onto EV2 (Fig. 2a; see Fig. A9 for the raw data; please note that the two Blanton Forest collections were combined prior to this step). The peak period of disturbance was from 1775 to 1780, when 81 disturbances were detected, while the peak year was 1776, when 24 disturbances were detected. We detected 588 disturbances between 1665 and 1880. Despite high tree replication throughout this period, 30 years had no evidence for disturbance and 49 years indicated only one disturbance. Twenty-three years had disturbance rates >1 SD above the long-term (1685–1880) mean, hence called "elevated disturbance" (mean $= 0.79$ disturbance/yr, SD $= 0.83$; Fig. 2a). From these data we identified 13 "extended disturbance" events, or three consecutive years with ≥ 3 disturbances/year (>2.5 SD above the mean; Table 1).

Of the 588 canopy disturbances from 1685–1880, 60.4% are classified as minor canopy disturbance (Fig. 2a). For the 23 years with elevated disturbance, the minor : major canopy disturbance ratio is closer to 1:1 (51.0% vs. 49.0%, respectively). This ratio swings in favor of major disturbances for years with disturbance rates ≥ 2 SD (48.2% vs. 51.8%). We also found a positive association between severity and disturbance extent. That is, when disturbance was widespread, it was also more severe. Seven of the 13 extended events had a greater proportion of major canopy disturbance than the 1685–1880 mean (Table 1) and individual years and

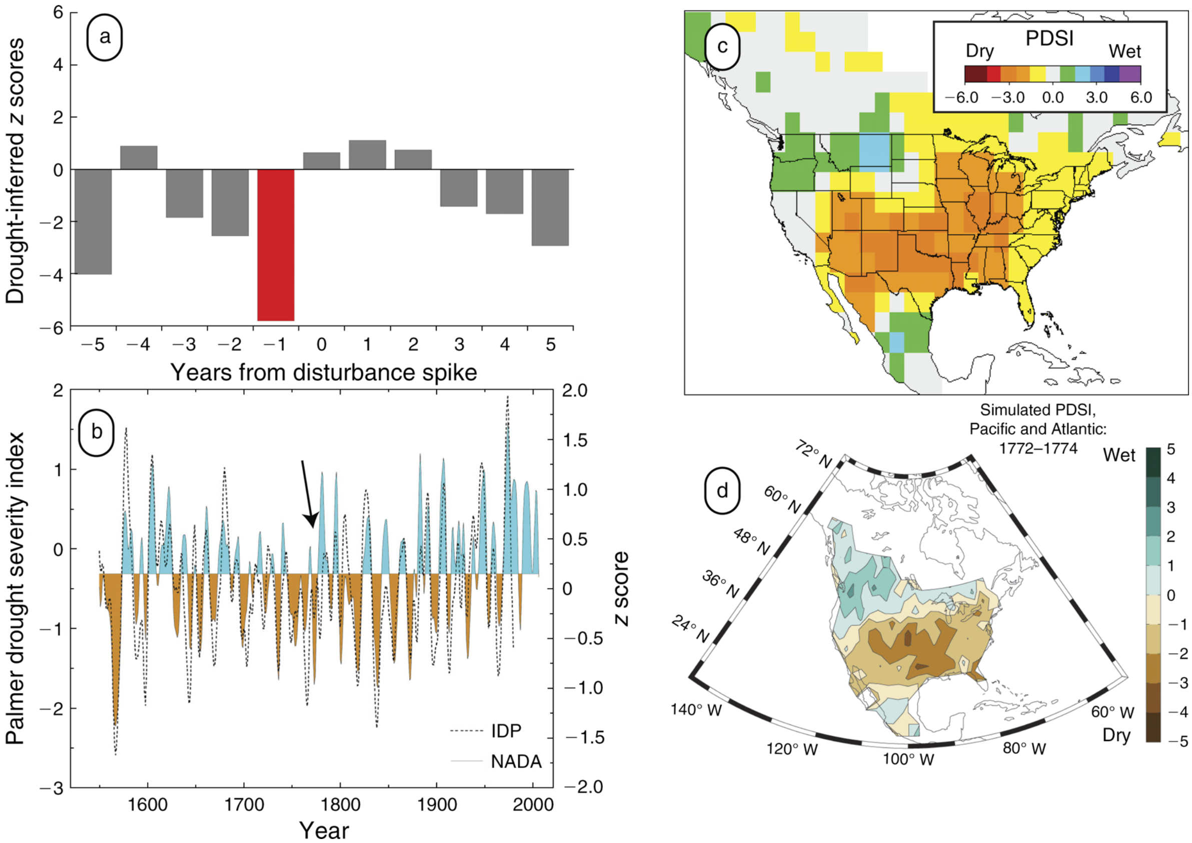

FIG. 3. Relation between climate and disturbance. Superposed epoch analysis of years with disturbance 1 SD or greater above the mean vs. (a) independent drought proxy (IDP). The red bar represents the only year where disturbance is significantly correlated to drought as represented by the IDP ($P < 0.05$). (b) Smoothed reconstruction of drought from 1550–2006 (9-yr spline). The filled curve is derived from the North American Drought Atlas (NADA; Cook et al. 2010) while the dashed line is the IDP. The arrow marks the end of the 1772–1775 drought. (c) NADA composite map of 1772–1775 drought just prior to the 1776 disturbance spike. (d) A 2000 member ensemble simulation for 1772–1775 drought as forced by Pacific and Atlantic sea surface temperatures.

periods with elevated disturbance also appear to be widespread. For example, the annual mean percentage of sites with disturbance from 1685–1880 is 11.3% (SD = 9.8), but during periods of elevated disturbance, the mean of sites recording disturbance was 19.4 (range = 14.0–33.9, SD = 5.58; Table 1). Disturbance was recorded in 33.9% of all sites from 1774–1782, >3 SD above the mean, and in 41.3% of all sites from 1775–1780 (Table 1). The spatial extent of disturbance peaked in 1776 when it was found in 47.6% of all sites. The total accumulated percentage of trees recording disturbance per site during the 1775–1780 event ranged from 0 to 57.1% (average = 19.7%, SD = 17.7%). Mapped quartiles of the total amount of disturbance recorded from 1775–1780 indicate severe damage over ca 61 000 km^2 (Fig. 2b). The four collections with less damage during this event include two *Liriodendron tulipifera* and two *Quercus alba* populations. The magnitude index for extended, elevated disturbance events for the 1770s events was 3.4–3.9 times greater than the next two most severe events (1737–1739, 1766–1768) (Table 1).

The time-series of canopy disturbance from 1685–1880 is not well described by a Gaussian distribution. In fact, the distribution of canopy disturbances is heavy tailed (Fig. 2c, d). Notably, all years from 1775–1778 are included in the list of the top seven most-disturbed years (Fig. 2d) and show a disturbance rate ≥3%, which is ≥ the 98th percentile of our data set. These years are well out in the heavy tail of the disturbance rate distribution (Fig. A10). Return intervals for disturbance rates of 2%, 4%, and 6% of disturbed trees per year ranged from 40, 250, and ~930 years, respectively. Uncertainty around return intervals greatly flares out beyond the 4% rate because of small sample size (Fig. A11).

We found that elevated canopy disturbance is significantly correlated with a low index of inferred drought during the prior year (Fig. 3a). Drier conditions prevail during four of the five years prior to elevated disturbance. The southern Appalachian Mountain region experienced three intense droughts between 1742 and 1775 with the 1772–1775 drought, spatially expressed across much of the temperate United States, as the most intense (Fig. 3b, c). Composite maps of

TABLE 2. Comparison of tree recruitment categories from 1500–1849.

Era	Category 1, n = 2277		Category 2, n = 1236†		Category 3, n = 1105		Category 4: 20-yr bins, n = 270		Category 4: 25-yr bins, n = 209		Category 4: 50-yr bins, n = 230‡	
	No. trees	%	No. trees	%	No. trees	%	No. trees	%	No. trees	%	No. trees	%
1450–1499	1	0.04	0	0	0	0	0	0	0	0	0	0
1500–1549	3	0.1	5	0.4	3	0.3	0	0	0	0	1	0.4
1550–1599	20	0.9	27	2.2	4	0.4	3	1.1	0	0	9	3.9
1600–1649	86	3.8	95	7.7	105	9.5	6	2.2	5	2.4	13	5.6
1650–1699	330	14.5	301	24.4	814	73.7	15	5.55	11	5.3	23	10.0
1700–1749	425	18.7	318	25.7			26	9.63	22	10.5	60	26.1
1750–1799	626	27.5	272	22.0			78	28.89	78	37.3	51	22.2
1800–1849	786	34.5	218	17.6			142	52.59	93	44.5	73	31.7
Other eras for comparison												
Pre-1650	110	4.8	127	10.3	112	10.1	13	4.81	5	2.4	23	10.0
1670–1689	168	7.4	127	10.3	413	37.4	4	1.48	6	2.4¶		

Notes: See *Methods* for category details. Total number of trees is shown by *n*. Empty cells indicate that there is no data.
† Dates decline after ca. 1735 because of sampling methods.
‡ Tyrrell and Crowe (1994) age categories crossed some of the time periods used in this table. Thus, there is some uncertainty in total numbers per 50-year period.
§ Gates and Nichols (1930) first recruitment date could have been 1500. To be conservative, we are using it in pre-1500 and 1500–1549 class.
¶ Represents 1675–1699.

North American drought for the year prior to elevated disturbance, the 1772–1775 drought, and a statistical model of the 1772–1775 drought reveals pan-continental drying over most of the United States and wetter than average conditions in the Pacific Northwest and northern Great Plains (Figs. 3d, A12). These findings indicate that regional-scale drought is associated with elevated disturbance across the 1775–1780 disturbance region.

Tree recruitment across the eastern deciduous forest

Recruitment data from studies using plot level or representative sampling (Category 1) have 2277 dates from trees that recruited between 1460 and 1850. Of these trees, 14.5% (n = 330 trees) recruited between 1650–1699, with more than one-half of these trees recruiting from 1670–1689 (n = 168). In sharp contrast, only 86 trees (3.8%) recruited from 1600–1649, or less than one-half of those recruiting between 1670 and 1689. Of the 620 recruitment dates collected through representative or plot-level sampling in old-growth forests before 1944 (e.g., Gates and Nichols 1930, Williams 1936, Hough and Forbes 1943), 21.1% recruited from 1650 to 1699 vs. 8.5% from 1600 to 1649 and 10.8% from 1500 to 1649 (Table 2). Segmented linear regression on Category 1 data indicates a significant break in recruitment around 1599 CE (± 10.6 yr). Residuals from this regression indicate a large and prolonged period of recruitment from 1640 to 1699, followed by below average recruitment from 1700 to 1729, and decadal-scale fluctuation through 1849 (Fig. 4a). The three greatest positive departures in recruitment occur in the 1670s (a residual departure of +1.36), 1680s (+0.79), and 1780s (+0.79). Data from targeted sampling (Category 2) or collections made during the early-1900s that do not have data after 1699 (Category 3), reveal similar jumps in recruitment during the latter half of the 17th century (Table 2). Within Category 2, the peak in recruitment of the 461 historical timber dates is centered on 1660–1699 (35.4% of total sample) with 15.6% recruited from 1670 to 1689 vs. 18.4% during the preceding 119 years. Despite deliberate attempts by 15 different tree-ring scientists over the last 30 years to core the oldest living trees in various forests, only 5.1% of the 730 trees recruited between 1500 and 1649. In comparison, 7.5% of the 730 trees recruited between 1670–1689.

DISCUSSION

Our records of forest dynamics—two large, species-rich, and geographically extensive data sets—indicate that (1) the dynamics of broadleaf forests in a temperate, humid region occur synchronously across different scales, from the stand to subcontinental level and (2) extended events of canopy disturbance are often severe. These findings more closely resemble our alternative hypothesis where forest dynamics can be regionally synchronous and punctuated by extreme events. Discovering that larger canopy gaps are often formed during synchronous large-scale events in broadleaf-dominated forests is broadly relevant because it provides a mechanism for rapid, large-scale change. That is, a greater number of larger canopy openings in light-limited forests offer increased opportunities for a compositional shift in the canopy at the time of major disturbance. Our large-scale analysis also reveals a greater spatial extent of previously reported disturbances. The large and severe 1775–1780 event is a period of increased disturbance observed at the stand scale in

TABLE 2. Extended.

Category 4, $n = 709$		Early category 1 studies, 1930–1943, $n = 620$	
No. trees	%	No. trees	%
0	0	1§	0.2
1	0.1	1	0.2
12	1.7	13	2.1
24	3.4	53	8.5
49	6.9	131	21.1
108	15.2	162	26.1
207	29.1	138	22.2
308	43.4	113	18.2
41	5.8	67	10.8

western North Carolina (Lorimer 1980: Fig. 7) and landscape scale in central Tennessee (Hart et al. 2012: Figs. 7 and 8) and central Pennsylvania (Nowacki and Abrams 1997: Table 3). This large-scale event precedes the highest peak in tree recruitment in our data set from 1700 to 1849 (Fig. 4a). Further, two other periods of extended disturbance discovered in our study, 1737–1739 and 1755–1758 (Table 1), are evident in a landscape-scale study (Hart et al. 2012). While the resulting time-series of disturbance still resembles a white-noise process, we find synchronous disturbance at multi-annual to nearly decadal time scales. Our findings go beyond the limitations of local studies and reveal forest dynamics at both the landscape and mesoscale (from decades to centuries over 100 to 100 000 km^2). As such, they are relevant for anthropogenic climate change and have important implications for forest management.

We have also statistically identified a plausible trigger for these disturbance events: drought-induced canopy mortality. These findings support observations of drought-induced forest dynamics and sensitivities conducted at short time scales and local to regional scales (Hough and Forbes 1943, Clinton et al. 1993, Jenkins and Pallardy 1995, Olano and Palmer 2003) across different forest types including humid regions (Allen et al. 2010, Choat et al. 2012). In doing so, we bridge the spatial and temporal gaps between local and sediment studies by providing insights from paleoecological records while revealing broad-scale patterns not seen in stand-scale or landscape-level studies.

Disturbance in humid to wet temperate regions can be characterized by frequent, small, low-severity disturbance events with occasional large-scale, intense disturbance (Lorimer 1989, White et al. 1999). Most studies in extant forests in humid regions have not revealed regional-scale events perhaps because of a predominant focus on local to landscape scales. Experimental forest modeling suggests small-scale analysis reduces the ability to detect large-scale change (Smith and Urban 1988). Our results reveal dynamical processes at small and large scales over the last 400 years (cf., Jackson 2006) and demonstrate the legacy of large-scale, intense, disturbance events centuries after their occurrence in broadleaf-dominated forests, a finding similar to previous work (e.g., Lorimer 1980, Frelich and Lorimer 1991, Nowacki and Abrams 1994, Hanson and Lorimer 2007). The distinction here is that we document events at regional to subcontinental spatial scales and show that some of these events can occur repeatedly within the maximum longevity of many canopy species. The infrequent, but meso- to large-scale disturbances are important because they can create the "substrate" that the more frequent, but less-intense, small-scale dynamics act upon. While it is known that historical events resonate for centuries and millennia through the structure and dynamics of forested ecosystems (e.g., Lorimer 1989, Sprugel 1991, Swetnam and Betancourt 1998, Foster et al. 1999, Williams and Jackson 2007, Turner 2010), we have identified large-scale events from 230–360 years ago at high resolution that are still reverberating in the structure of today's old-growth, broadleaf-dominated forests.

Interestingly, some old trees in today's old-growth forests in the eastern United States are the result of historical events (Tables 1, 2; Figs. 1b, 2a, b) that occurred during a drier era than the more moist conditions that prevailed during the period of repeated measures and field studies (Fig. 5). Dry conditions have the potential to alter other processes, like increased fire or insect outbreaks (e.g., Raffa et al. 2008, Lynch and Hessl 2010), and feed into forest dynamics in direct and indirect ways. The rare, but coherent, spatially broad, and severe events identified here can provide greater opportunities for regeneration as canopy gap formation increases. Alternatively, these species-rich forests, interacting with historical contingencies and a wide range of possible future scenarios, could abruptly change into substantially different types than the current forest (Williams and Jackson 2007).

It is important to note that these results also suggest that local dynamics and other endogenous factors are at play. Four populations within the 1775–1780 event region have low amounts of canopy disturbance (Fig. 2b). Two populations are *Liriodendron tulipifera* whose requirement for relatively large gaps for successful recruitment might have made them less sensitive to changes in competition if they had reached canopy status prior to the 1770s. Although we have evidence for large-scale, synchronous disturbance, not all populations were similarly affected, which could be due to the many factors influencing forest dynamics.

Triggers for elevated canopy disturbance

Triggers of elevated canopy disturbance at large scales across a humid and diverse region are likely complex. Our data support early and more recent research linking tree mortality to drought across forest types and land-use histories (e.g., Lorimer 1984, Olano and Palmer

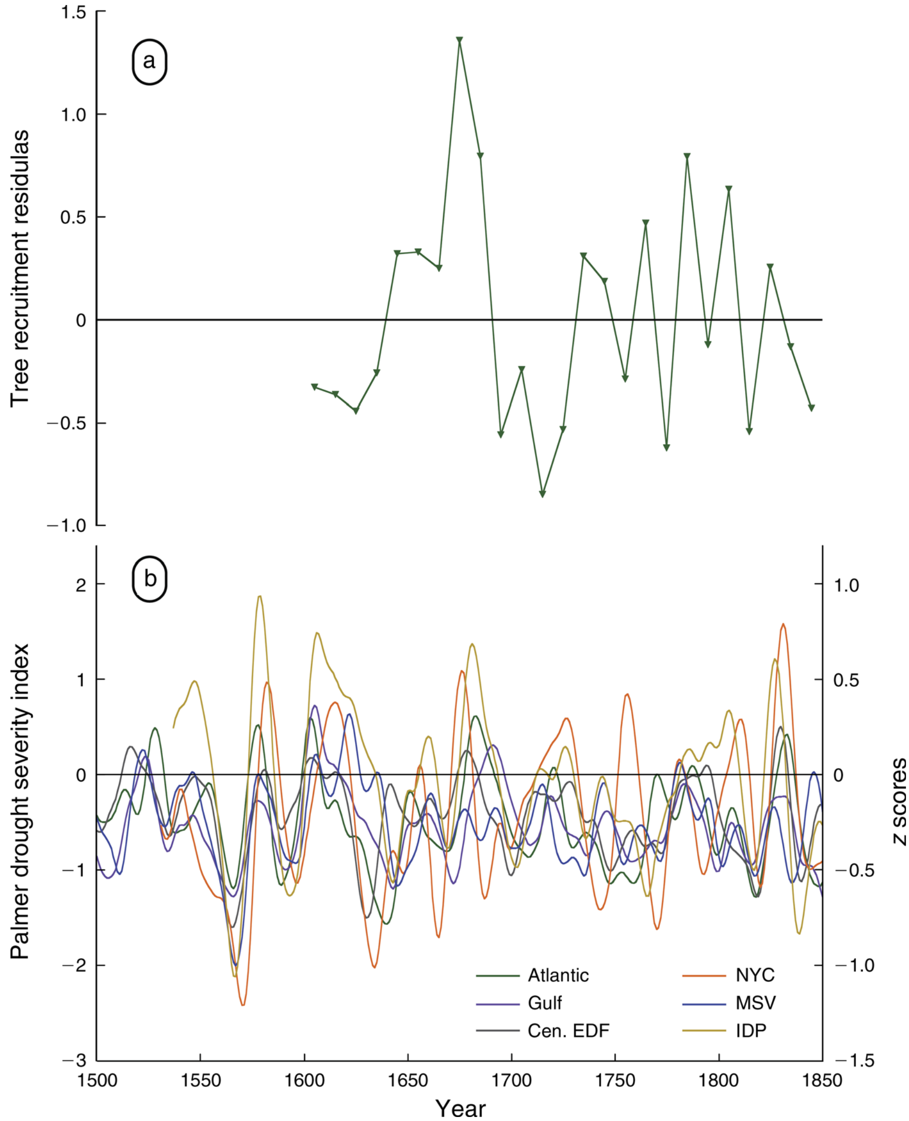

FIG. 4. Forest recruitment and climate across the broadleaf-dominated forests of the eastern United States. (a) Residual of tree initiation dates from 1500–1850 after removing demographic trends (n dates = 2276). (b) Drought proxies for Atlantic Coast (Atlantic; Georgia to Virginia), Gulf Coast (Gulf; Georgia to Louisiana), center of the Central Eastern Deciduous Forest region (Cen. EDF), northeastern United States (NYC; New Jersey to central Massachusetts and western New York State), Mississippi Valley (MSV; Louisiana to Illinois), and the independent drought proxy (IDP; see Appendix A for more information on IDP). The Atlantic, Gulf, Cen. EDF, and MSV records are from the NADA. NYC is from Pederson et al. (2013). Despite the inclusion of trees used in our disturbance analysis, the Cen. EDF record is included to show that drought variation in that record is not dramatically different from records from surrounding areas.

2003, Mueller et al. 2005, Pederson et al. 2008, 2012*b*, Anderegg et al. 2012). The association between disturbance extent and disturbance intensity indicating the mortality of canopy trees dovetails with observations that tall and large canopy trees are more susceptible to drought-induced mortality (e.g., Hursh and Haasis 1931, Hough and Forbes 1943, Floyd et al. 2009, Hartmann 2011). Trees in closed-canopy forests primarily compete for canopy access and solar radiation (Hartmann 2011). Competition for solar radiation likely pushes tree height near the maximum height possible within the context of microsite and other prevailing environmental conditions. Because tree height limits leaf-specific hydraulic conductance (McDowell et al. 2008), it is likely that canopy trees in closed-canopy forests live closer to the margin of water balance for survival and are more susceptible to drought-induced mortality. This has been directly observed within our larger study region: the "extreme drought of 1930" in Pennsylvania led to "mortality of the larger or overstory trees both of hemlock and of the subsequently exposed beech" (Hough and Forbes 1943: 311). Further, repeated drought increases the mortality risk of trees (Pedersen 1998, McDowell et al. 2008). Therefore, it is not too surprising that the 1775–1780 disturbance event is preceded by three intense droughts during the previous three decades (Fig. 3b). Our data suggests that drought plays an important role in canopy dynamics of broadleaf-dominated forests in the eastern United States.

While the 1772–1775 drought was severe, it was not the most severe (Fig. 3b). Therefore, a variety of additional triggers likely interacted with drought to generate the broad-scale patterns of disturbance and canopy dynamics. For instance, colonial-era documents reveal an early onset of leaf-out in 1774 and the commencement of farming two weeks early across the southeastern United States (e.g., Thomas Jefferson's Garden Book 1774, Fries 1925). Heavy frosts after the cold nights of 4 and 5 May 1774 made green leaves look "black and dead" (Fries 1925). Additional accounts confirm cold air, frost, or damage to plant tissue throughout the southeastern United States up to southeastern Pennsylvania (Pennsylvania Gazette [Philadelphia, Pennsylvania] 11 May 1774, page 2; Virginia Gazette [Williamsburg, Virginia] 12 May 1774, page 4; Essex Gazette [Salem, Massachusetts] 7 June 1774, page 176). A frost was observed to have killed "every tender thing" near coastal South Carolina (Rudisill 1993). These observations confirm tree-ring evidence of a frost event in the southern Appalachian Mountain region (Fig. A8) and extend it throughout the southeastern United States.

Following repeated drought during the mid 1700s, the 1774 frost event and subsequent defoliation must have reduced available energy from surviving, but drought-stressed, trees. Widespread frost events in April 2007 (Gu et al. 2008, Augspurger 2009) and May 2010 (Hufkens et al. 2012) lead to tissue and shoot dieback and necrosis in ways similar to 1774 (see Fig. A13a). Refoliation in 2007 did not occur for more than a month in some cases (Augspurger 2009), especially for *Liriodendron tulipifera* (Gu et al. 2008; see Appendix A: Fig. A13b), and was estimated to be 46–99% of normal for seven species, with 40% to ~90% coming from a second flush (Gu et al. 2008, Augspurger 2009). In 2010, net carbon assimilation of *Acer sacharrum* was reduced following leaf necrosis and delayed canopy development (Hufkens et al. 2012). If these frosts were similar in intensity to the 1774 frost, preceding climatic conditions prior to 1774 likely predisposed canopy trees to higher rates of mortality (sensu Manion 2003). The mid-18th century was one of the driest periods in the southeastern United States of the last 300 years (Cook et al. 1988, Pederson et al. 2012*a*). Trees adapt to aridity by (1) shedding leaves, (2) reducing the root/sapwood to leaf area ratio, and (3) experiencing a reduction in height through crown dieback (McDowell et al. 2008). Drought-stressed trees recovering from the severe 1774 frost could struggle with alteration of the carbon sink or carbon metabolism (cf., Adams et al. 2013). Lesser, 20th-century droughts are known to have led to tree mortality (Jenkins and Pallardy 1995, Pedersen 1998), suggesting the more severe mid-18th century droughts could have resulted in greater mortality (Fig. 3b). The rate of disturbance in our data during the late 1770s was up to 7.8 times greater than the mean (Fig. 2), a rate even greater than that observed in a tropical ever-wet forest during the strong, El Niño drought of 1998 (Potts 2003). Based upon these observations, we postulate that the 1770s period of elevated disturbance was likely triggered by several interacting factors, including drought and frost.

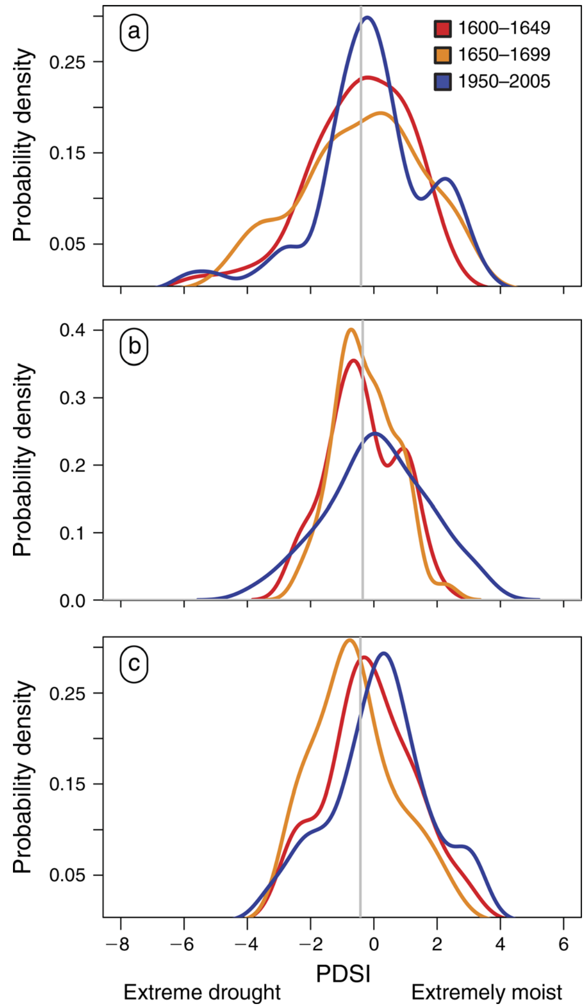

FIG. 5. Probability density functions of reconstructed drought (PDSI) for 1600–1649 (red), 1650–1699 (orange), and 1950–2005 (blue) for three broad regions: (a) northeastern United States, (b) central hardwood region of Fig. 1a, and (c) central Mississippi River Valley. Panels a, b, and c are adapted from the original data used to construct Fig. 4. These plots show that, during the 17th century, more years tended to be dry while, during the period of observation (repeated measures and many ecological field studies), tends to be substantially wetter and close to extremely moist conditions, conditions that are nearly absent during the 17th century.

Following decades of dry conditions, however, fire is another potential contributor to elevated disturbance of the late 1770s. Fire occurs more often and burns a larger area in a humid region during drier conditions (Lynch and Hessl 2010) and in areas with a great range of daily precipitation variability (Lafon and Quiring 2012). Fire was generally rare, spatially restricted, or absent from 1775–1780 in or near the event region (Guyette et al. 1994, Aldrich et al. 2010, Feathers 2010, Flatley et al. 2013, McEwan et al. 2014). As an example, Flatley et al. (2013) reports area-wide fires in 1773 and 1775 in only one of three forests they investigated. These findings suggest a lack of broad-scale fire during the 1770s. Fire is not recorded in the mid 1700s in broadleaf-dominated forests, although it is was recorded before and after this period (Guyette et al. 1994, McEwan et al. 2014). Guyette et al. (2006) show an increase in fire during the 1770s, but also note that "Fire frequency was highly variable in both time and space even at regional scales..." (Guyette et al. 2006: 20). The broadest fire in this region occurred in 1780 (Guyette et al. 2002), which is after the peak of the 1770s disturbance event. Due to the low incidence of spatially extensive fire across our study region during the 1770s, a pattern supported by paleo studies (Clark and Royall 1996, Parshall and Foster 2002), and the ability of drought to kill overstory trees, it would seem repeated, intense drought leading up to the mid 1770s was a primary contributor to elevated canopy mortality with frost-induced defoliation and potentially fire as secondary contributors.

Windstorms are another important canopy disturbance that have been well documented across our study region (Lorimer 1977, White 1979, Foster and Boose 1992, Everham and Brokaw 1996, Peterson 2000, 2007, Stueve et al. 2011). Windstorms can leave a lasting impact in forests beyond the stand scale. A squall line increased mortality over roughly 27 km^2 in the Manaus region and an estimated 4.5×10^6 km^2 across the Amazon (Negrón-Juárez et al. 2010), while a conservative estimate of windstorms in the midwestern United States was extrapolated to damage forests over $\sim$1500 km^2 over a 26-year period (Stueve et al. 2011). In contrast with line storms or tornadoes, which are local in scale, hurricanes have the potential to affect large regions. From a compilation of hurricanes striking the eastern United States during each elevated disturbance event in our study (Table A4), we find that five elevated disturbance events coincide with relatively high landfall years (1766–1768, 1834–1836, 1840–1843, 1870–1872, 1877–1883); "relatively high" here is two or more hurricanes per year. However, the simple occurrence of a hurricane making landfall might not translate into an ecological impact because of insufficient intensity or a failure to penetrate inland. Focusing on the most important of these reconstructed events, 1775–1780, the Moravian records hold no evidence of forest damage from wind during the hurricane season. There are three hints that low-pressure systems might have moved through western North Carolina during this period, however. First, it was noted on 30 August 1775 that, "For some time it has been raining every day" and that by 4 September there has been large-scale clearing of the atmosphere, "It is clear, but the air feels like fall" (Fries 1925: 883). The track of this storm appears to have traveled far to the east of the 1775–1780 event region (Rappaport and Ruffman 1999). Then, in 1778, a year with hurricanes in August and October (Table A4), there are observations of "a hard storm from the north-east" on 11 August (Fries 1926: 1244) and that a "strong wind from the north-east cleared the sky" on 11 October (Fries 1926: 1248). No forest damage is reported with these observations. Observations of winds from the northeast, but with less than tropical-storm strength, matches model predictions of tropical storm decay into this region (Kaplan and DeMaria 1995). And, observations of winds from the northeast causing no damage are in contrast to the windstorms of note between 1774 and 1779. The windstorm of March 1775 caused damage "over a strip about 14 miles long and four wide" (Fries 1925: 873). Similarly, the March 1776 windstorm was reported to be more local: "Br. Praezal returned from Bethabara; the storm was not nearly so severe there, and had done no particular damage" (Fries 1926: 1057). It is beyond the scope of this investigation to quantify the paths of all windstorms and their impacts within our network. While geographically limited, the Moravian records suggest only one wind event at the landscape scale and no late-season windstorms of the years we reviewed (the Moravians diaries contain no evidence of hurricane-like storms during the 1766–1768 event). Nevertheless, windstorms are a potential factor affecting historical canopy disturbance.

Ice storms are another common canopy disturbance in this region that can cause limb breakage, snapped stems, and treefall (Lemon 1961, Irland 2000, Proulx and Greene 2001, Wonkka et al. 2013) over large areas (Millward and Kraft 2004, Vanderwel et al. 2013). While the impact of ice storms can be severe, they also trigger a mixed response, ranging from tree death to a positive growth response in surviving trees (Lafon and Speer 2002). Within the Southern Appalachian region, up to 40% of the trees in a stand were observed to have been killed (Lafon 2006). However, there is no mention of a severe ice storm in the Moravian records preceeding or during the 1775–1780 event (Fries 1925, 1926). Ice storms could have been a trigger in our reconstruction of disturbance, but we are lacking evidence of it being an agent for the most severe and widespread event in our records.

Tree recruitment across the eastern deciduous forest

Our recruitment data reveals a subcontinental-scale event in a forest type where this scale of event would be less expected. This finding synthesizes nearly a century of reported stand origin dates scattered across the literature. Given the temporal distribution of these

PLATE 1. (Upper) The *Quercus montana* being cored in the Blanton Forest of Kentucky (USA) reflect the subcontinental- and regional-scale dynamics discovered through our investigation. Most of the cored *Quercus* on a dry, southeast-facing slope were recruited to coring height during the late 1600s; none before 1670. We observed this recruitment event in data from across much of the eastern U.S. Many of the cored *Quercus* trees in the Blanton Forest were simultaneously released from competition in the synchronous, large-scale event of the late 1770s in the Southern Appalachian Region. (Lower) Overlooking the old-growth forest at the bottom of Savage Gulf, Tennessee at dusk. Many of the *Tsuga canadensis* cored in this ravine experienced a significant and synchronous reduction in competition at the same time as the *Quercus* trees in the Blanton Forest of Kentucky. The forests on the plateau above this raving at Savage Gulf also experienced increased canopy disturbance (Hart et al. 2012), which independently helps to confirm the regional-scale disturbance in the late 1770s. These photos and others are available in color in Appendix B. Photo credits: N. Pederson.

studies over the last 90 years and that the forests from which these data are collected can be characterized by continuous, small-scale dynamics, the date of stand origin would be expected to shift back in time according to the time of sample collection. We found, in fact, that a disproportionate amount of recruitment occurs during the mid to late 1600s, even in the oldest studies with recruitment dates. These findings resemble recent evidence of a regional-scale synchrony of understory forest dynamics in a broadleaf-dominated forest (Gravel et al. 2010). Our findings suggest that synchronized tree recruitment at large scales can be an important process in broadleaf-dominated ecosystems.

While it is possible that the late 1600s recruitment pulse is an artifact of tree longevity, four lines of evidence argue against this idea. First, 21 tree species in Category 1 recruited between 1650 and 1699, including shade-intolerant, fast-growing species like *Betula lenta*, *Castanea dentata*, *Liriodendron tulipifera*, and *Pinus strobus* as well as shade-tolerant, slower-growing species like *Acer saccharum*, *Fagus grandifolia*, and *Tsuga canadensis* (Burns and Honkala 1990). Given variations in longevity, shade tolerance, the spatial extent of our recruitment data set, and light limitations in this forest type, a recruitment pulse seems to require an exogenous factor opening the canopy, not an intrinsic factor such as longevity. Second, conventional wisdom on maximum tree age has proven to be underestimated for many species, sometimes by a century or two (Pederson 2010). Thus, the longevity of 255-year-old trees described in 1923 as comprising most of the recruitment between 1660 and 1674 (Haasis 1923) should not be a factor as most of the species in that study can live longer than 250 years. Third, the late 1600s recruitment pulse is evident in data collected >75 years ago from old-growth forests (Huntington 1914, Haasis 1923, Gates and Nichols 1930, Williams 1936, Hough and Forbes 1943). These early studies identify a slightly higher percentage of trees before 1650 vs. our database (Table 2). But, all authors, save Williams (1936), note a recruitment pulse during the mid to late 1600s when discussing their results. Fourth, dates from tree-ring investigations targeting old trees during the 20th century or historical timbers cut in the late 1700s to mid 1800s (Category 2) show a similar recruitment pulse (Fig. A7). In fact, there is nearly a tripling of recruitment from 1650–1699 vs. pre-1650 in Category 2 and the number of trees from 1650 to 1699 in the tree-ring data set is five times greater than the prior 50 years (Fig. A7). Although there is uncertainty in these data due to different methods, source material, and potential selection biases between the different sources of data, the striking consensus from these data is that the late 1600s was an important era of subcontinental scale tree recruitment in broadleaf forests of temperate eastern North America.

Potential triggers of the 17th-century recruitment pulse

Though recruitment is often associated with wet conditions, drought could lead to tree recruitment (Shuman et al. 2009). In this scenario, formation of canopy gaps from drought-induced mortality would increase the amount of solar radiation penetrating the understory to stimulate potential recruitment. A return to mesic conditions following drought could aid recruitment. Hydroclimatic records with decadal-scale resolution from Quebec to Ohio and Lake Michigan indicate drier conditions during the early to mid 17th century (Bégin and Payette 1988, Wolin 1996, Lichter 1997, Loope and Arbogast 2000, Greenlee 2006, Argyilan et al. 2010, Hubeny et al. 2011). The dating uncertainties of these records are a limitation, but a record in this region reports a "high probability" of trees growing below current water levels "as early as AD 1663" (Shuman et al. 2009: 2796). These geologic records suggest regional drought from ~1640–1680 that could have caused wide-scale increased canopy tree mortality.

Despite some asynchrony, tree-ring records across the eastern United States indicate drier conditions during the mid 1600s. Each record contains severe drought between 1630 and 1650 (Fig. 4b). A mid-Mississippi River Valley record indicates the mid-17th century to be the driest since 1600 CE (Cook et al. 2010) while a northeastern U.S. record indicates six severe droughts between 1629 and 1700 (Pederson et al. 2013). Of these six droughts, five rank as the 10 most severe droughts since 1531 CE, with 1661–1667 and 1630–1636 ranked second and third, respectively. Other annually resolved proxies support these records over a large region (St. George et al. 2009, Maxwell et al. 2011). Interestingly, all of these tree-ring proxies generally substantiate some geologic evidence for a mid-1600s drought sandwiched between two pluvials, prolonged periods of above-average moisture (Wolin 1996, Lichter 1997, Loope and Arbogast 2000, Argyilan et al. 2010). The switch from pluvial conditions following drought during the 17th century likely has far-reaching ecological consequences. If trees adapt to aridity by root and shoot dieback (McDowell et al. 2008), then pluvial conditions likely stimulate the opposite. Therefore, an abrupt, severe drought following a pluvial could exacerbate drought stress by making it difficult to maintain pluvial-level biomass, elevating mortality, increasing solar radiation to the forest floor, and possibly increasing opportunities for tree recruitment.

Like many aspects of macroecology, the exact cause of regional-scale disturbance cannot be ascribed to a single trigger (McEwan et al. 2011). Low tree replication prior to the mid 1600s forces us to consider circumstantial evidence. The combination of fire and drought cannot be ruled out. Several studies found charcoal or asserted that drought and fire led to stand origin during the mid-1600s (Huntington 1914, Hough and Forbes 1943, Henry and Swan 1974, Foster 1988). The most consistent fires in northwestern Vermont, for example, occurred in 1586, 1595, 1635, and 1670 (Mann et al. 1994), which coincides with some of the driest periods in the northeastern United States (Pederson et al. 2013). While sample replication is low in the heart of our study region, fire is more often recorded from 1660–1680 than during the mid 1700s (Mann et al. 1994, Guyette and Dey 1995, Dey and Guyette 2000, Guyette et al. 2002, 2006, Guyette and Spetich 2003, McMurry et al. 2007, Stambaugh et al. 2011).

Given that forests in the Western Hemisphere were in a managed landscape prior to European settlement (Crosby 1986, Mann 2005, Krumhardt 2010), it is possible that the catastrophic decline in indigenous populations contributed to the recruitment pulse. However, the locations of recruitment data and resettlement patterns post-population collapse are in opposition to one another. Recruitment data used here are primarily from old-growth forests in mountainous areas (Fig. A6; see raw recruitment data in the Supplement). Most of today's old-growth forests grow on sites with low productivity and commercial viability (Therrell and Stahle 1998). Most indigenous populations were observed in large and fertile river valleys at the time of European settlement (Cronon 1983, Williams 1992, Davis 2000). In the southern Appalachian Mountain region, people moved into flatter, moister, river valleys following the population collapse (Davis 2000). Supporting this, an estimation of natural vegetation inferred from human demographics indicates forests to be broadly recovered by 1600 CE over much of our study region (Appendix A: Fig. A14; Krumhardt 2010). The uncertainties regarding land-use and human demographics are large at this time (Milner and Chaplin 2010), but they suggest broad forest recovery at least 50 years prior to our reconstructed recruitment pulse.

Climate change implications

Secular trends in anthropogenic climate change are expected to have significant impacts on eastern U.S. forests (Iverson and Prasad 2001, McKenney et al. 2011), although change could occur relatively slowly due to hysteresis and canopy persistence (e.g., Loehle 2000). However, as observed here, rare or low probability events could have immediate and long-term ramifications for ecosystem structure and function. The severe frost event of 1774 following repeated droughts over large spatial scales altered the trajectory of forest structure through synchronous canopy disturbance. These changes in forest structure generated historical contingencies that can be observed today. Severe droughts in the eastern United States, like the 1960s drought that increased *Acer rubrum* mortality (Lorimer 1984), can occur as a result of internal variability of the climate system (Seager et al. 2012) making stochastic climate dynamics an important aspect of forest dynamics. Further, Pacific Ocean sea surface temperatures seems to have been a trigger for the 1772–1775 drought (Fig. 3d) and, thus, ocean–atmosphere dynamics may have created a legacy in eastern U.S forests where this part of the climate system has less of an influence on the average climatology. These events illustrate how hard-to-predict, singular scenarios can shape forests for decades to centuries in regions where the average scenario might not.

Understanding how the effects of long-term climate trends and extreme events interact is a major challenge for ecological forecasting, not the least because extreme events such as droughts have often been perceived as a minor risk in humid regions such as eastern North America (e.g., McMahon et al. 2010, Schleeweis et al. 2013, Vanderwel et al. 2013). Future droughts could turn out to be analogous to the 16th-century megadrought (Stahle et al. 2000), the most synchronous drought across our study region over the last 450 years (Fig. 4b). If future warming exacerbates drought stress in trees and other stressors, including elevated air pollution (Dietze and Moorcroft 2011), nonnative pests, and pathogens (Aukema et al. 2010), or a combinations of stressors (e.g., Waller 2013), widespread tree mortality and subsequent canopy turnover could drive rapid rates of change in temperate forests across humid eastern North America.

Conclusions

We have identified two synchronous disturbance events at regional to subcontinental scales in old-growth, broadleaf-dominated forests in a humid region. Not only do these records reveal a severe, regional-scale event from 1775–1780, but also disturbances at other spatial scales in the broadleaved-dominated forest of the eastern United States. Importantly, we find elevated canopy disturbance at moderate frequency beyond the stand scale. Thus, our analysis supports the alternative hypothesis that dynamics in broadleaf-dominated forests can be regionally synchronous and punctuated by extreme events.

Our results can aid future simulations attempting to forecast carbon sinks or rates of ecological change under a changing climate (e.g., Millar et al. 2007) at the scales relevant to the management of forests across a region with high ecosystem functionality (Freudenberger et al. 2012). Large-scale, synchronous, and climatically influenced disturbances over the last four centuries are still detectable, and thus, important in today's old-growth forests. These events point to the possibility that severe events can push ecosystems to new structures and/or compositions (Jackson 2006, Williams and Jackson 2007, Jackson et al. 2009, Frelich and Reich 2010), even by distal climate systems that do not typically have an influence on a particular region. As local and regional climate and ecologies are influenced by anthropogenic climatic change, historical events and species diversity will interact in complex ways as the future forest develops. Evidence here indicates that broadleaf-dominated forests could change abruptly from small to subcontinental scales in the coming decades.

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Supplemental Material

Ecological Archives

Appendices A and B and the Supplement are available online: http://dx.doi.org/10.1890/13-1025.1.sm

Ecological Archives **M084-023-A1**

Neil Pederson, James M. Dyer, Ryan W. McEwan, Amy E. Hessl, Cary J. Mock, David A. Orwig, Harald E. Rieder, and Benjamin I. Cook. 2014. The legacy of episodic climatic events in shaping temperate, broadleaf forests. *Ecological Monographs* 84:599–620. http://dx.doi.org/10.1890/13-1025.1

APPENDIX A. Additional information, figures, images, analysis, and discussion material.

Examples of weather observation from the Moravian Diaries during the 1775–1780 Elevated Disturbance Event (Fries 1925, 1926).

Vol 2, 1775, Congregation and Society in Friedberg, pg 860 "*...in March, when a cyclone blew off one side of the roof of the School-House,…"*

Vol 2, 1775, Diary of the Salem Congregation, pg 868, written by Bishop Graff with translated extracts about every 3-4 days including some rain events, hot spells, etc "March 16. *In the morning was a most unusual thunder-storm with hail stones as large as hickory nuts, which badly injured every-thing in that was in the gardens. The wind blew down many fences, especially around the Square, and half of the shed by the store. No one has seen such a storm in many a years."*

Vol 2, 1775, Diary of the Salem Congregation, pg 873 "May 18. *Joseph Bryant was here, and had much to say concerning the great damage done by the terrible hail storm on the 6th of this month. It fell over a strip about 14 miles long and four wide, and was accompanied by a flood which ruined several plantations."*

Vol 2, 1775, Diary of the Salem Congregation, pg 883 "Aug. 30. *For some time* ***it has been raining every day****."*

Vol 2, 1775, Diary of the Salem Congregation, pg 883 "Sept. 4. *It is clear, but the air feels like fall."*

Are the last two entries related to the "*Barbados to Maryland*" hurricane in late August to early September 1775 documented in Chenoweth (2006)?

Vol 2, 1775, Bethania Diary, pg 909, written by Rev. John Jacob Ernst with translated extracts about every month "Mar. 16. *The Liturgy could not be held on account of stormy weather, for the tiles falling from the roof of the Gemein Haus made it dangerous to enter. The wind also blew down several fences."*

Vol 2, 1775, Friedberg Diary, pg 913, written by Rev. Ludolph Bachhof with about 4-5 translated extracts for each month "Mar. 16. *There was a terrible wind storm, and half the roof was blown off the School-House, the fences around the garden and God's Acre were ruined, and nearly all the small houses on the place were unroofed. Shingles were scattered in the garden, the yard, and in the woods for half a mile around. It happened all in a minute, probably in a cyclone, and on the account of the terrible roaring we in the room could not tell what was happening to the house. Some of the windows were blown in, and seeing that the children were frightened I began to sing…."*

Vol 3, 1776, Bagge MS, pg 1041, anon. detailed, essay-like review of the year "*In spring there were severe storms, especially that if the 17th of March, which was like a hurricane; it blew off many roofs and blew down many fences, uprooted the largest trees, overturned a recently built shed for fodder and broke it. Following this there was a long-continuous drought, so that we feared the grain would be ruined, but in spite of this our Father in heaven gave us a good harvest of all kinds of grain, and also of fruit, so that all who live by them are full of content."*

Vol 3, 1776, Salem Diary, pg 1057, written by anon. with translated extracts about every 3-4 days including rain events, hot spells, etc "March 17. *In the afternoon there was a sudden storm, the most severe we ever remember here. During the few minutes that it lasted, the noise was like that of the storm of on year ago yesterday, and it did more damage, for it blew into a heap the stable recently built and roofed on the Single Brothers farm, and a few pieces of wood remained unbroken*;"….[more specific descriptions of damage to houses]…"*Br. Praezal returned from Bethabara; the storm was not nearly so severe there, and had done no particular damage. It cleared up warm, which is just the opposite of what usually happens after such a hard storm."*

Vol 3, 1776, Salem Diary, pg 1057, "March 20. *There was a frost this morning, but we hope it has not hurt the peaches, which are in bloom."*

Vol 3, 1776, Salem Diary, pg 1061, "April 11. *All day there was unfriendly weather, rain mixed with snow, and during the night it cleared and froze, and in the morning there was a frost that has probably done harm."*

Vol 3, 1776, Salem Diary, pg 1072, "August 1. *The weather continued very hot and dry, the corn and vegetables are suffering greatly."*

Vol 3, 1776, Salem Diary, pg 1076-1077, early Sept – early Oct. Rain events are recorded, 1-2 hour rain events on Sept 8-10 and then a full days drain on Oct 3 and evening rainfall event on Oct 4.

Vol 3, 1778, Salem Memorabilia [translated in full], written by anon., pg 1214, " *The weather this year was not particularly favorable, for in spring the buds of the fruit trees were frozen; and in late summer there was a long, wet spell, which injured grained and also the health of the people, but the dear Father provided the necessary food for man and beast, and there were many wild grapes."*

Vol 3, 1778, Salem Diary [less than two thirds translated. The rest concerns the religious services of the congregation], written by anon. with translated entries every 2-3 days, pg 1226, "April 3. *It is evident that many blossoms of the fruit trees have been killed, but we hope not all."* – previous diary entries speak of glazing and some old events in 1778 leading up to April.

Vol 3, 1778, Salem Diary, written by anon., pg 1226, "April 4. *Last night there was a frost again, but not so heavy."*

Vol 3, 1778, Salem Diary, written by anon., pg 1230, "May 7. *In the second hour of the afternoon the horizon was filled with thick heavy clouds, the wind roared, and suddenly there was a storm like a hurricane, without rain, such as no one* *remembers to have seen here. It lasted only five to six minutes but did much damage to the fences around the Square and Gemein Haus garden, to the roof and in the woods. It tore the heavy roof and roof timbers from the wood-shed of the Single Sisters, and threw part of it into the garden behind the Gemein Haus more than a hundred paces away;"*

Vol 3, 1778, Salem Diary, written by anon., pg 1237, "June 24. *Beginning shortly before 9 o'clock in the morning there was an almost total eclipse of the sun. At the peak of the eclipse the sun was under a cloud, and for some minutes it was necessary to light the candles, stars peeped out here and there, and no one can remember to have seen the like before.*

Vol 3, 1778, Salem Diary, written by anon., pg 1238, "July 7. *The heat is very oppressive."*

Vol 3, 1778, Salem Diary, written by anon., pg 1238, "July 13. *In the afternoon there was a severe thunder storm and a terrible wind which broke and blew down the corn and also the trees in the forest; the rain lasted into the night."*

Vol 3, 1778, Salem Diary, written by anon., pg 1244, "Aug 11. *All night there was a hard storm* ***from the north-east****, and there was much rain during the morning. The storm has beaten down the corn, which was very tall and heavily loaded with ears, and has broken some of it. It cleared in the afternoon.*

Vol 3, 1778, Salem Diary, written by anon., pg 1244, "Aug 15. *It rained heavily all day and into the night. The storm of the 11th of this month was very severe in other Counties and did much damage, which will lead to a speedy close of the Assembly."*

Vol 3, 1778, Salem Diary, written by anon., pg 1244, "Aug 20. *For the first time in two weeks we had a day without rain, though a thunder cloud passed by."*

Vol 3, 1778, Salem Diary, written by anon., pg 1248, "Oct 11. *Last night a strong wind* ***from the north-east*** *cleared the sky, but the Wach was again so high from yesterday's rain that no one could cross the Bridge on horse-back."*

--- this diary suggests 1778 to be a wet year

Vol 3, 1779, Salem Diary, written by anon. with translated entries every 2-3 days, pg 1294, "March 5. …*The trees are blooming as never before, but that the weather has caused many bad colds and several of the Single Brethren have had to go to bed. Not one swallow has been seen yet."*

Vol 3, 1779, Salem Diary, written by anon., pg 1295, "March 16. *Yesterday's storm induced a sharp frost which killed most of the peach and cherry blossoms, the apples seem not to be greatly hurt."*

Vol 3, 1779, Salem Diary, written by anon., pg 1299, "April 19. *Last night the frost was much heavier, and all leaves on the sprouts are black. The apples, peaches and grapes which escaped last month are frozen."*

Vol 3, 1779, Salem Diary, written by anon., pg 1308, "June 25. *We hear from everywhere that the wheat was badly hurt by the recent mildew; on the Catawba and further south they will not even mow their fields for there is no grain in the straw….The heat is almost unendurable."*

Vol 3, 1779, Salem Diary, written by anon., pg 1312, "Aug. 26. *For several days the air has been cool, and* ***the wind from the north-east****."*

Vol 3, 1779, Bethania Memorabilia, written by anon., pg 1338, "*The late frost completely ruined the fruit, and did great harm to the winter grain, but on the other hand the corn in this neighborhood did well, for which thanks are due our heavenly Father."*

TABLE A1. Chronologies used in RPCA. Chronologies with an asterisk - * - are from the International Tree Ring Data Bank. Those that are not from one of the authors of this publication or the ITRDB were graciously donated to our study by the investigator listed in the Investigator column. Underlined dates in the column '1st yr 3 Trees' indicates the exceptions for chronologies with at least three trees in 1760. Species codes are: CAOV = *Carya ovata*; CADN = *Castanea dentata*; LITU = *Liriodendron tulipifera*; QUAL = *Quercus alba*; QUMO = *Quercus montana*; QUMU = *Quercus muehlenbergii*; QUST = *Quercus stellata*; PCRU = *Picea rubens*; PIEC = *Pinus echinata*; TSCA = *Tsuga canadensis*; TSCA = *Tsuga caroliniana*.

Site	State	Spp	1st yr 3 Trees	CRN period	Purpose	Investigator
Andrew Johnson Woods*	OH	QUAL	1652	1605-1985	Climate	Cook,E.R.; Update Wiles,G.
Babler State Park*	MO	QUAL	1689	1641-1980	Climate	Duvick,D.N.
Balsam Gap *	NC	PCRU	1654	1609-1983	Climate	Cook,E.R.
Blackfork Mountain*	AR	QUAL	1720	1650-1980	Climate	Stahle,D.W.
Blanton Forest	KY	QUAL	1679	1673-2006	Climate	Pederson,N.

Blanton Forest	KY	QUMO	1676	1670-2005	Climate	Pederson,N.
Blanton Forest	KY	TSCA	1715	1684-2006	Climate	Pederson,N.
Blue Ridge Parkway*	VA	QUAL	1602	1520-2002	Climate	Cook,E.R.;Update Pederson,N.
Blue Ridge Parkway*	VA	QUMO	1659	1587-2002	Climate	Cook,E.R. Update Pederson,N.
Boogerman Trail *	TN	LITU	1765	1736-1995	Ecology	Young,J.;Keeland,R.;Alford,J.
Boogerman Trail*	NC	CADN	1772	1720-1931	Ecology	Young,J.;Keeland,R.;Alford,J.
Buffalo Park Boundary*	AR	QUST	1639	1620-1993	Climate	Stahle,D.W.;Therrell,M.D.
Cedar Knob	WV	QUMO	1498	1660-1981	Climate	Wilson,R.
Clayton Ridge*	MO	QUST	1702	1696-1992	Climate	Stahle,D.W.
Clingman's Dome*	NC	PCRU	1629	1558-1983	Climate	Cook,E.R.
Cranbrook Institute*	MI	QUAL	1597	1581-1983	Climate	Cook,E.R.
Current River Natural Area Recollection*	MO	QUAL	1594	1588-1992	Ecology	Guyette,R.P.
Dysart Woods*	OH	QUAL	1659	1625-1998	Ecology	Rubino,D.L.;McCarthy,B.C.
Ferne Clyffe State Park*	IL	QUAL	1668	1655-1981	Climate	Duvick,D.N.
Fiddler's Green	VA	CAOV	1750	1650-2002	Climate/Ecology	Pederson,N.
Fiddler's Green	VA	LITU	1683	1668-2002	Climate/Ecology	Pederson,N.
Fire Tower Road Cook Forest*	PA	QUAL	1683	1660-1981	Climate	Cook,E.R.
Floracliff Sanctuary	KY	QUMU	1638	1612-2007	Ecology	Pederson,N.
Fox Ridge State Park*	IL	QUAL	1691	1674-1980	Climate	Duvick,D.N.
Gee Creek*	AR	PIEC	1611	1600-2003	Fire Ecology	Stambaugh,M.C.;Guyette,R.P.
Giant City State Park*	IL	QUAL	1658	1652-1981	Climate	Duvick,D.N.
Grandfather Mountain*	NC	PCRU	1696	1560-1984	Climate	Cook,E.R.
Greenbriar*	TN	CADN	1680	1641-1930	Ecology	Young,J.;Blozan,W.
Greenbriar*	TN	QUMO	1735	1654-1994	Ecology	Young,J.;Blozan,W.
Hahatonka*	MO	QUST	1697	1660-1982	Climate	Stahle,D.W.

[a] – while most of the trees sampled were targeted, trees at a few sites were randomly-selected.

Temporal and Geographic Disturbance Detection Methods:

A goal of disturbance detection analysis was to isolate and identify significant canopy disturbance that likely created conditions for the accession of understory trees into the canopy during the 1770s. A priori, we wished to determine if established trees across a larger geographic region responded with a step-change in radial increment as was observed in three populations of trees, including collections of *Quercus alba*, *Quercus montana*, and *Tsuga canadensis*, from southeastern Kentucky to central Tennessee (N. Pederson, *unpublished data*; Fig. A1; Appendix B). An abrupt and sustained increase in ring increment across populations would indicate significant, regional-scale canopy disturbance. Therefore, collections with high rates of recruitment after 1750 were excluded. The addition of young trees with rapid, early-growth in a site chronology during this time period would inflate the average ring width as they entered the chronology. Detection of a step-change increase in ring widths from collections that do not have high rates of recruitment after 1750 would increase the likelihood that a disturbance resulted in the accession of understory trees into the canopy.

Finally, only collections with at least three living trees prior to 1760 were included in this analysis so the potential inclusion of a site for disturbance analysis is not the result of one or two trees being released from competition. The year 1760 is used as a cutoff date so that at least 15 years of growth are present prior to the hypothesized disturbance event of ca. 1775 that followed observations of significant release among four widely-scattered populations (N. Pederson, *unpublished data*; Fig. A1). Detection of canopy disturbance from ring-width series traditionally involves looking at a moving window of ring widths in 15-year segments (Lorimer 1985, Lorimer and Frelich 1989). Three collections of *Liriodendron tulipifera* and *Castanea dentata* with inner ring dates between 1761 and 1772 were included in this analysis to increase species replication or spatial coverage. Only one of these collections, Boogerman Trail *Liriodendron tulipifera*, was used for disturbance detection analysis (see Table A2).

Adhering to the rationale above, rotate principal component analysis (RPCA) was used to elucidate the disturbance signal across populations. Like above, retained collections were further distilled for the specific RPCA here to ensure that potential disturbance detection through RPCA is more likely the result of canopy disturbance. Each collection was treated in the following manner prior to RPCA: (1) ring-width series beginning in 1760 or later were removed to provide 15 years of ring width data prior to the hypothesized ca. 1775 disturbance event and (2) each series was standardized using a straight-line fit through the mean to remove differences in radial increment. Removal of individual growth rates using a straight-line fit results in a chronology with less bias. Series of ring widths that are significantly different than the mean could potentially inflate or deflate changes in growth from canopy disturbance at the population level. The standard chronology from this standardization retains much of the annual to multi-decadal information present in the raw ring-width chronology.

We extended the window for PCA from 1673–1918 to see if the 1750–1880 window pre-selected the 1770s event. There are 23 fewer tree-ring collections in this analysis and the ca 1770s event shows up as EV4 instead of EV2. In fact, the EV4 time-series from the 1673–1918 analysis crosses the mean at ca 1777, not 1780 as in the 1750–1880 PCA. In the 1673–1918 analysis, EV1 indicates a significant increase in raw ring widths in the 1840s, much like EV3 in the original analysis. EV2 in the 1673–1918 analysis shows the negative exponential decline in ring widths like EV1 in the original analysis. EV3 in the 1673–1918 PCA reveals a step change in ring width in ca 1738, an event we pick up in our disturbance analysis. So, a different window changes the EV position of the various events, but it does not lead to different overall conclusion in our study. All events in the 1673–1918 PCA are found using the 1750–1780 PCA. And, the 1750–1780 window allows for increased tree and species replication.

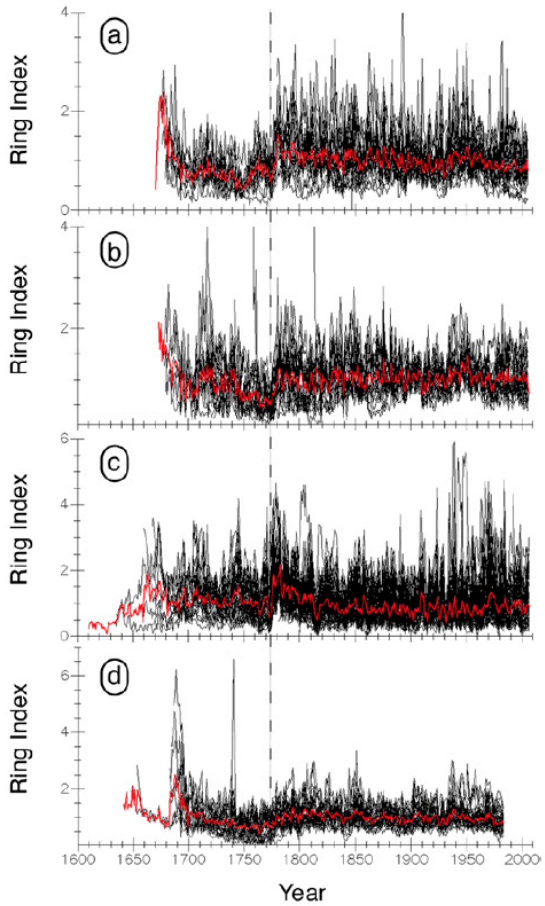

FIG. A1. Initial evidence of abrupt, regional disturbance. Spaghetti plots of four tree populations: Blanton Forest, KY (a) *Quercus montana* and (b) *Q. alba*, (c) Savage Gulf, TN *Tsuga canadensis* and (d) Joyce Kilmer Memorial Forest, NC *Q. alba*. The thin black lines represent radial growth time-series for each population. The thick line in each population represents mean radial growth. The vertical line represents the year 1774. Time-series within each population were detrended using a straight-line fit to only remove individual differences in growth rates.

TABLE A2. All Species eigenvector loadings > 0.10 on the first eight varimax eigenvalues (EV) for the common period 1750–1880. **Bold values** are > 0.224 or the 95% confidence limit. EV 1-8 represent 62.9% of the common variation. Populations are ordered by state, species, and population name to convey some of the geographic and species patterns in the rotated RPCA.

Populations	**Species**	**EV 1**	**EV 2**	**EV 3**	**EV 4**	**EV 5**	**EV 6**	**EV 7**	**EV 8**
	--- Percent variance for each EV listed immediately below ---								
		20.8	**11.1**	8.3	6.0	5.4	4.1	3.9	3.3
	--- Eigenvector loadings for each chronnology ---								
London Forest, KY	LITU	0.072	**0.599**	-0.129	0.220	0.138	0.168	-0.202	-0.258
Red River Gorge, KY	Pispp	**0.514**	-0.569	**0.334**	0.167	0.072	0.096	0.035	-0.065
Blantonton For., KY	QUAL	-0.450	**0.688**	0.138	0.168	0.051	0.174	0.124	0.065

Rotated Varimax Eigenvectors 1 and 3

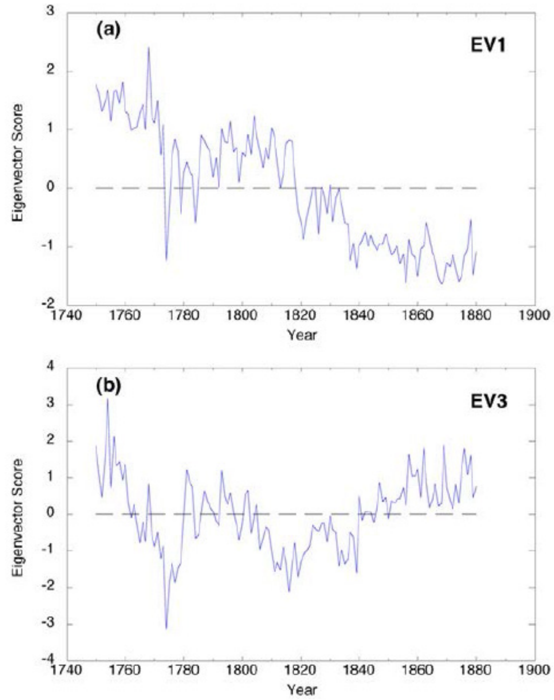

FIG. A2. Time-series of ring width variation of (a) EV1 from 1750-1880 showing the decline in ring widths as tree diameter increases. This pattern is centered on southern Appalachian Mountain region of the 76-chronology network (Table A3). (b) Time-series of ring width variation of EV3 from 1750–1880 showing a step-change in radial increment in 1840 and 1857. This event is centered on Ohio, Indiana and Illinois (Table A3). Horizontal dashed lines represent the long-term mean.

Tree and Population-level Disturbance History Analysis

Once collections with potential canopy disturbance were identified with RPCA, raw ring widths from each of the 22 collections, totaling 558 trees, were analyzed to identify growth release. Individual time-series of ring widths removed for RPCA analysis were re-inserted for this analysis. All but two collections have at least two cores/tree. Increased core replication refines disturbance detection (Copenheaver et al. 2009). The disturbance detection was based upon traditional methods (Lorimer 1980, Lorimer and Frelich 1989). To detect growth release we used ring-width intervals no shorter than 15 yrs or thresholds less than 50% to differentiate those events from the extended droughts that preceded pluvial events over the last 500 years in the eastern U.S. (see Stahle et al. 2000, Cook et al. 2010, McEwan et al. 2011, Maxwell et al. 2011, Pederson et al. 2013). Shorter periods or lower thresholds could possibly trigger detection of "disturbance" in the growth record when the trees might be reacting to a transition from a megadrought to a pluvial (more below). Extended droughts are more typical from 1600–1900 than the 20th century when the disturbance detection method was tested to ensure disturbances were not the result of moist conditions following drought (Lorimer and Frelich 1989).

Next, each series was visually checked for "false positive" releases during periods of slow radial growth (cf. Fraver and White 2005) or associated with an anomalously large "spike" ring (Fig. A3). Therefore, the disturbances retained should reflect: (a) independent step-change in ring widths and (b) events that allow for a new mean level in growth for nearly two decades that is above the prior 15 yrs (Fig. A3). We recognize that this methodology might not retain all small-scale, canopy disturbance events, especially from canopy trees that are less responsive to canopy disturbance (Nowacki and Abrams 1997). Fine-temporal scale disturbance is not a main goal of this investigation. The final time-series of disturbance history was analyzed at the annual time-step because (1) all series were crossdated and (2) the lag between disturbance and growth response is often two years or less (Rentch et al. 2002).

Examples of False Positives in the Detection of Canopy Disturbance

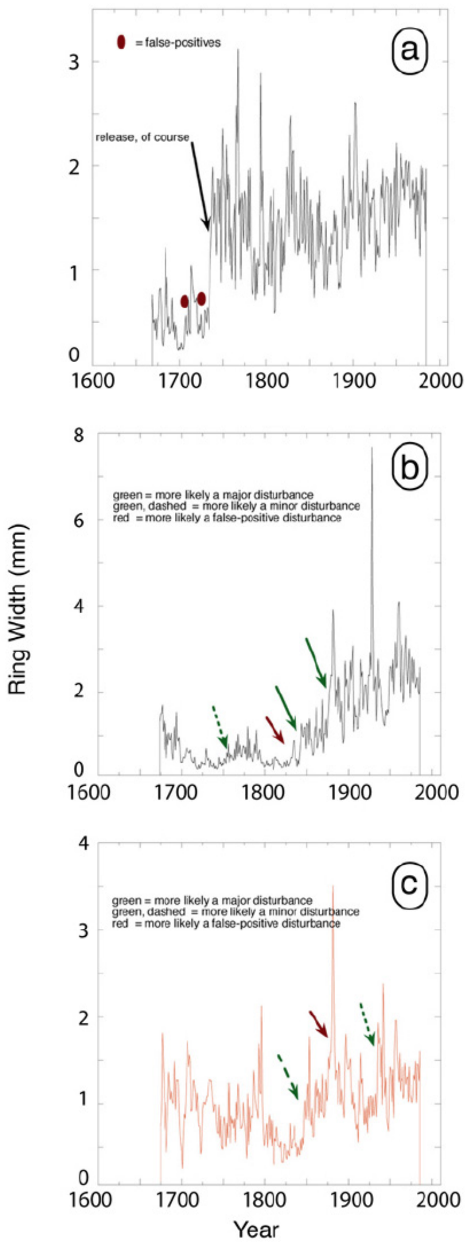

FIG. A3. Examples of detected disturbances and false-positive detections. (a) True- and false-positive examples of disturbance. (b) Minor disturbance during a period of low radial growth and a false positive driven by a release event years after first detection. (c) Minor disturbances and a false-positive result driven by a spike ring.

Detection Sensitivity Analysis'

Recent methods of disturbance detection adopt shorter windows and lower thresholds of changes in growth in ring widths because of the lowered sensitivity of canopy trees to competition (e.g., Nowacki and Abrams 1997). The method used in our analysis was originally developed to reduce detections of growth releases that were the result of an improved moisture balance using the 20th century data (Lorimer and Frelich 1989). Further work along this thread of research posits that, "*sequential 10-yr ring-width averages may effectively neutralize both short-term (i.e., drought) and long-term trends associated with climate"* Nowacki and Abrams, 1997). However, because extended droughts were more common from 1600–1900 than the 20th century (Pederson et al. 2013), we suspected these lower thresholds might not be insensitive to climatic change. To examine potential complications between climate change and radial-growth response using 10-year windows and the recommended 25% threshold from Nowacki and Abrams (1997), we tested this method on four series of meteorological data and a reconstruction of moisture conditions (Pederson et al. 2013). Results indicate that lower thresholds are sensitive to climate in ways that could result in false positives. First, the transition from the end of the 16th century megadrought in 1577 to subsequent above average moisture conditions in the northeastern US equates to a 148%

increase reconstructed May-Aug average Palmer Drought Severity Index (PDSI). Similarly, reconstructed PDSI increased 81.0% and 133.2% following the severe 1630–1636 and 1661–1667 droughts, respectively. When using these thresholds on instrumental data in the Hudson Valley following the mid-1960s drought, the worst drought of the 20th century in the northeastern US (Seager et al. 2012) and one of the most intense since 1531 (Pederson et al. 2013), we calculate a 144.1% increase in Jun-Aug average PDSI, a 41.7% increase in precipitation, and a 71.8% increase in average Jun-Sep average flow (m^3/sec) at the Green Island gauge on the Hudson River. When we test these thresholds over the greater Northeastern US region as established by the National Climate Data Center, a larger region where climate is not likely spatially homogeneous, we calculate a 21.1% increase in total Jun-Aug precipitation following the mid-1960s drought. Therefore, these results depend on the highly variable nature of moisture balance and extreme events. And, while a percentage increase in moisture availability does not necessarily translate in a direct increase in growth, decades of research in this region indicate moisture availability as a primary constraint on radial growth (e.g., Schumacher and Day 1939, Fritts 1962, Cook 1991, Orwig and Abrams 1997, Leblanc and Terrell 2011, Pederson et al. 2012). Because of our decisions here, we do not have a complete record of disturbance history. And, because of the collection methods of the ITRDB data sets, often 20-30 trees per stand, we would not expect to detect all possible disturbances in a forest for each year. Our record, however, should reflect a lower number of false-positive disturbances and, most importantly, the creation of large canopy gaps that likely have a more meaningful impact on forest composition and structure than smaller canopy gaps

Finally, we re-analyzed a portion of our data set from the Southern Appalachians using the 25%, 10-year thresholds and compared it to results from the same set of trees using thresholds in the manuscript. We re-analyzed the data using the Blanton Forest oak collection, which loaded first on EV2, two collections that loaded in the middle of EV2, Scott's Gap in TN and Dysart Woods in OH, and one collection that loaded second to last on EV2. In this approach, we analyze populations with the 'regional disturbance signal' and those with less of that 'signal' to examine differences in the two methodologies. Another reason these collections were chosen was to get better representation of species with varying growth rates, sensitivities, and life-history traits. The four collections are composed of chestnut oak, post oak, white oak, and tulip-poplar. They represent 81 trees and 134 time-series, which is 14.5% and 14.6% of the original tree and time-series sample, respectively

We followed the same detection methods as described in the manuscript. Disturbances detected in periods of growth of ~ 0.5 mm/yr were not counted nor were releases detected after abrupt declines in growth that last only about a decade.

Differences between the two methods are generally what one would expect: the 25%, 10 yr threshold detects more disturbances and the average size of release can be higher (likely because of averaging over shorter periods). See Figs. A4 and A5 below. Overall, the main structure of the subset of our original data is virtually the same as when analyzed with the lower thresholds.

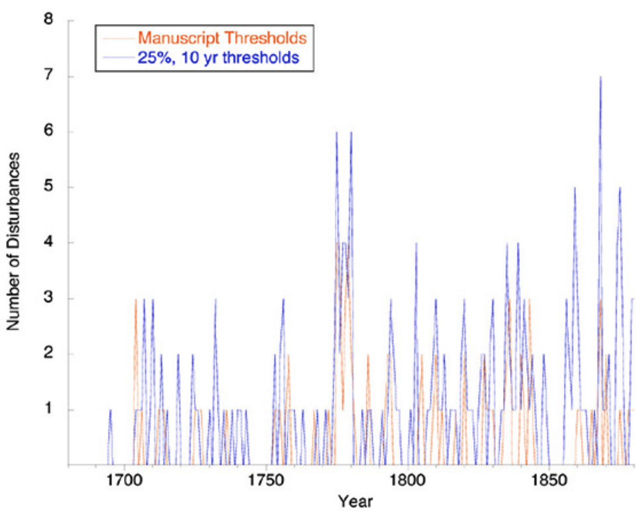

FIG. A4. Number of disturbances detected per year from 1680–1880 using the methods of the original manuscript (orange line) and using the 25%, 10 yr detection method (blue line). In this subsample, disturbance detection methods do not substantially change the structure of the 1770s disturbance event. Sample size might be too small to adequately test other years of elevated disturbance.

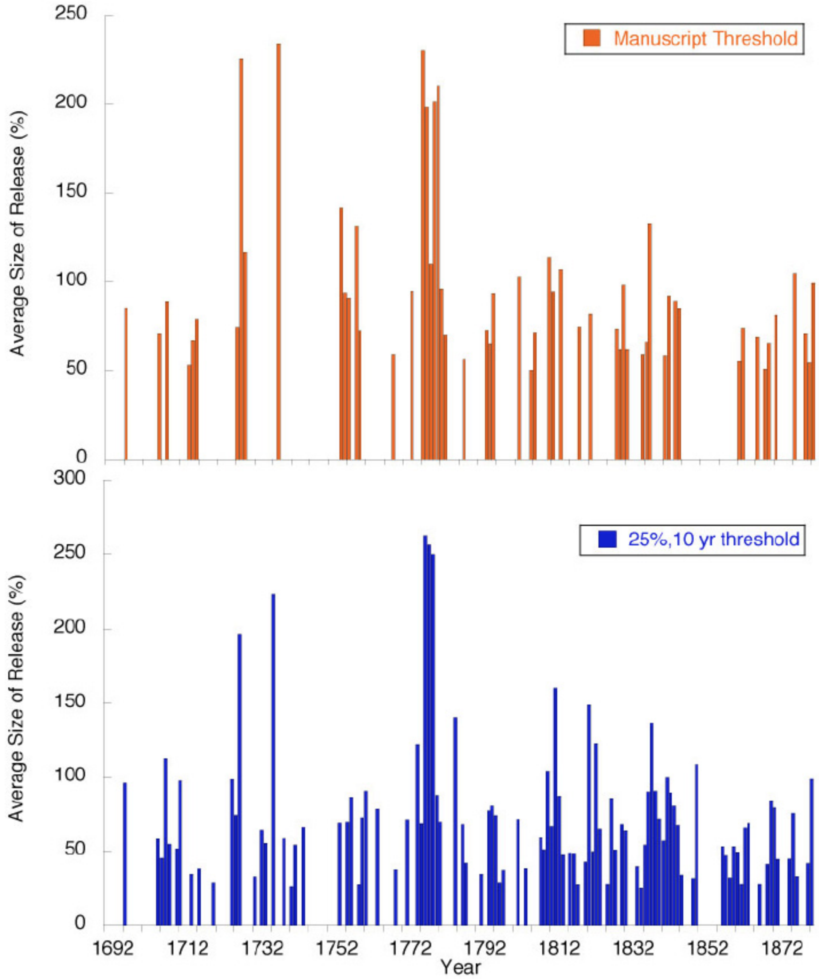

FIG. A5. Average size of growth release detected per year from 1680–1880 using the methods of the original manuscript (orange bars, top panel) and using the 25%, 10 yr detection method (blue bars, bottom panel). In this subsample, disturbance detection methods do not substantially change the structure of the 1770s disturbance event and there are some similarities with other years.

Based upon these results, we do not see a substantive difference in disturbance detection methods. But, what do we mean by substantive? Here we go back to what has the greatest potential to change the forest. It would seem, though we cannot be positive, that years of elevated disturbance rates and years with greater disturbance intensity, as interpreted by larger growth releases, would be most important to forest change and development in a light-limited forest. The addition of more and potentially smaller disturbances during our period of focus seems less important in the larger picture of how forests might change synchronously at large scales. We acknowledge that this method doesn't give a complete disturbance history. However, given the goal of our study, a failure to detect some disturbances shouldn't diminish the ability to identify the potential for synchronous disturbance at large scales.

Creation of the Independent Drought Proxy for Superposed Epoch Analysis

We assessed the relationship between regional disturbance events and drought using a proxy we created called the Independent Drought Proxy (IDP). The IDP was developed because 66 chronologies used in our RPCA analysis are a part of the North American Drought Atlas (NADA) (Cook and Krusic 2004, Cook et al. 2004, Cook and al. 2008). The IDP is an intentionally independent proxy constructed from 26 chronologies that were within or adjacent to the region for disturbance analysis (see Table A1 and Fig. 1a), but are not part of the NADA reconstruction (Table A3). These chronologies, comprised of three drought-sensitive species, are recently developed datasets, or were downloaded from the International Tree Ring Databank (ITRDB). Many of the IDP chronologies that fall within our study are derived from the highly-sensitive species, *Liriodendron tulipifera* (Pederson et al. 2013). The chronologies on the periphery of our study region or not used in our disturbance analysis are *Juniperus virginiana and Taxodium distichum*, two highly drought-sensitive species (Stahle et al. 1988, Stahle and Cleaveland 1992, Maxwell et al. 2011). Each chronology was detrended following the goals and techniques of Pederson et al. (2004). Briefly, the goal of standardization was to retain as much low frequency information as possible while removing abrupt changes in ring widths likely to be related to changes in tree-to-tree competition or crown damaging disturbances like windstorms or ice storms. All 26 chronologies were combined into a time-series of ring-width anomalies using a PCA. Due to the short duration of some tree-ring records, a nested approach was used to create the longest possible record of ring-width anomalies (cf. Meko 1997, Cook et al. 2003, Wilson et al. 2007). The final IDP series covers 1537–1980. The first principal component was retained as an index of past drought as it correlates at 0.648 ($p < 0.0001$) vs. a regional time-series of drought derived from NADA from 1537–1980.

TABLE A3. Chronologies used for the independent drought proxy for SEA investigation. 1 = ITRDB data; 2 = unpublished data; 3 = shared, published data.

Chronology	Spp	Location	CRN Length	No. Series	Investigator
Hemmed In Hollow, AR	JUVI	36.04 N, 93.18 W	1359-1992	50	11Stahle et al.
Big Cypress St. Park, LA	TADI	32.15 N, 92.58 W	997-1988	70	1Stahle et al.
Little Maumelle River, AR	TADI	34.50 N, 92.30 W	1532-1985	32	1Stahle et al.
Moro Bayou, AR	TADI	33.46 N, 92.20 W	1262-1985	44	1Stahle et al.
Egypt, AR	TADI	34.50 N, 92.30 W	1417-1980	41	1Stahle et al.
Upper Current River, MO	JUVI	37.25 N, 91.34 W	1410-1991	50	1Stahle et al.
Black Swamp, AR	TADI	35.09 N, 91.18 W	1133-1980	61	1Stahle et al.
Bayou Deview, AR	TADI	35.09 N, 91.18 W	1019-1985	60	1Stahle et al.
Mayberry Slough, AR	TADI	35.33 N, 91.15 W	998-1990	61	1Stahle et al.
Cache River, IL	TADI	37.16 N, 89.03 W	1468-1985	39	1Stahle et al.
Ocmulgee River, GA	TADI	32.03 N, 83.18 W	1202-1984	41	1Stahle et al.
Cold Hill District, KY	LITU	36.98 N, 84.32 W	1633-2007	26	2Tackett & Cooper
Amicalola, GA	LITU	34.57 N, 84.22 W	1537-2009	62	2Pederson et al.
Forge Creek, TN	LITU	35.54 N, 83.84 W	1500-2006	20	2Pederson et al.
Scott's Gap, TN	LITU	35.36 N, 83.55 W	1684-1981	27	1Duvick et al.
Boogerman Trail, TN	LITU	35.36 N, 83.05 W	1736-1995	21	1Young et al.
Altamaha River, GA	TADI	31.37 N, 81.48 W	929-1985	60	1Stahle et al.
Four Holes Swamp, SC	TADI	33.11 N, 80.25 W	1041-1985	42	1Stahle et al.

Black River, SC	TADI	33.48 N, 79.52 W	549-1993	80	1Stahle et al.
Smoke Hole, WV	JUVI	38.83 N, 79.29 W	517-2007	135	3Maxwell & Wixom
Cedar Knob, WV	JUVI	38.39 N, 79.22 W	481-1998	177	3Cook et al.
Fiddler's Green, VA	LITU	37.46 N, 79.14 W	1668-2002	34	2Pederson et al.
Black River, NC	TADI	34.19 N, 78.13 W	365-1985	89	1Stahle et al.
Black Water River, VA	TADI	36.47 N, 76.53 W	932-1985	73	1Stahle et al.
Nottoway River, VA	TADI	36.47 N, 77.08 W	1171-1984	53	1Stahle et al.
Lassiter Swamp, NC	TADI	36.27 N, 76.37 W	1524-1984	25	1Stahle et al.

Subcontinental-scale Recruitment Data

To investigate tree recruitment history and the hypothesis that recruitment would not deviate significantly above the long-term background rate in the forest type across our study region, we performed an initial literature search utilizing the "Bibliography of Dendrochronology," (Grissino-Mayer n.d.), a database containing over 11,500 dendrochronological citations, to identify age data from old-growth forests in the forested region of Fig. 1a of the main manuscript. The keywords "old growth," "virgin," and "age structure," resulted in 624 unique references. Titles and abstracts were used to restrict references to the eastern U.S., which reduced the list to 215. Additional references from our collective knowledge on references having age data from increment cores, cross-sections, or stumps increased the initial list to 230 potential. These references were evaluated and accepted if: (1) they presented age data and reported at least one individual with an establishment date prior to 1800 and (2) presented data in a graphical or tabular format that enabled a tally of trees. We assumed that the presence of trees before 1800 would increase the likelihood of data from an old-growth forest. Seven references presented data in 20, 25, or 50-year bins and were analyzed separately from the remaining references. We avoided all obvious presentations of estimated ages.

As we were primarily interested in the dynamics of upland broadleaf-dominated forests, we excluded vegetation types such as high elevation spruce-fir forests, swamp forests, oak savanna, pine forests, and cedar glades where disturbance regimes would be expected to be more episodic. These criteria resulted in the elimination of 166 references. An additional 15 papers were rejected because they contained data duplicated in other publications. The final list of decadally-binned data contained 42 published studies across most of the broadleaf-dominated forests in temperate eastern US Fig. A4). Four of these studies reported data from multiple sites >15 km apart that we treated as separate entries, resulting in a final tally of 52 sites. We augmented this list with previously unpublished data from 30 sites from colleagues or our own collections. The ITRDB represented another potential source of data; however, since those data can be truncated for dendroclimatological analysis prior to submission, we only included ITRDB data after direct discussion with the person who submitted the data. To reduce recruitment pulses likely attributable to settlement and land-use change, we only examined recruitment prior to 1850. Recruitment data across most sites were reported by species. The final data set is comprised of 5,327 individual trees representing at least 34 species; 10.5% were categorized as 'Other' or were unknown. See supplemental Excel spreadsheet, 'eMASTER_LIST_10_RecruitmentDates.xls', with the list of references and data sources used here, rejected references, specific reasons for rejection, and recruitment data extracted for each acceptable reference.

Before final analysis of the 5,327 recruitment dates, data were split into categories depending on collection methodology or data presentation. Differences in collection methodology or data presentation could skew final results. Category 1 contains recruitment dates from studies using randomized selection methods or collections aimed to be representative of a forest's species composition and structure. The 2,277 trees in this category likely best represent the range of ages in a forest. Category 2 is comprised of 1,236 trees from targeted studies or collections from a narrow window of time and includes dendroclimatological collections, collections seeking to sample the oldest trees, or dates of beams from historic structures. Category 3 represents 1,105 recruitment dates from two early-20th century forestry studies (Huntington 1914, Haasis 1923). Data from these studies were categorized separately because no data are presented post-1710, thereby exaggerating a hypothesized recruitment event in the late-1600s (see main text). Category 4 contains 709 recruitment dates from studies that grouped trees into 20-, 25-, or 50-yr bins. Data from Categories 2 and 3 are used only to examine our hypothesis because they represent an incomplete picture of recruitment and have limited value or potentially biased view of tree recruitment post-1700. For example, in direct opposition to the trend in Categories 1 and 4, the resulting age structure in Category 2 declines from the 1700s through the 1840s (Fig. A5, Table 2).

Several factors contribute to the uncertainty of the older data sets including: unknown sampling heights, lack of early cross-dated material, number of hollow trees, etc. However, sample and site replication should reduce potential biases among investigators. Replication of the number of studies, principal investigators, study methods, and study goals should reduce any significant bias of one study or investigator.

Locations of EDF Recruitment Data

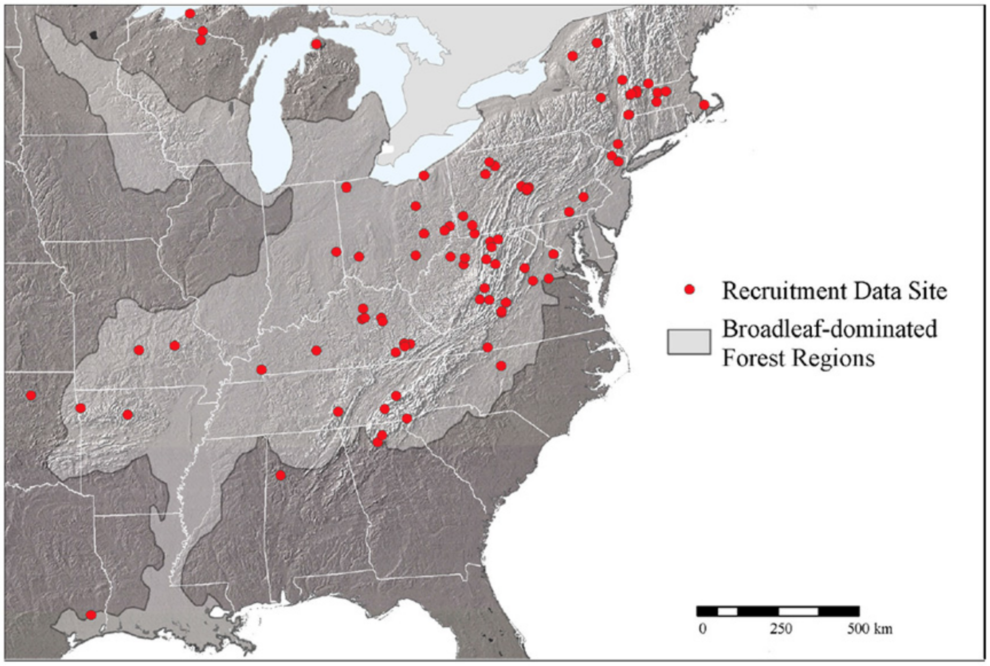

FIG. A6. Locations of sites used to collect recruitment dates from old-growth forests across the broadleaf-dominated forest of the temperate eastern US. Most of the sites are found in mountainous areas or occupy sites with low-productivity or commercial value. The Broadleaf-dominated Forest Regions (light-gray shading) are adapted from Dyer (2006). Elevation data is not available for Canada.

Raw Recruitment Across the EDF

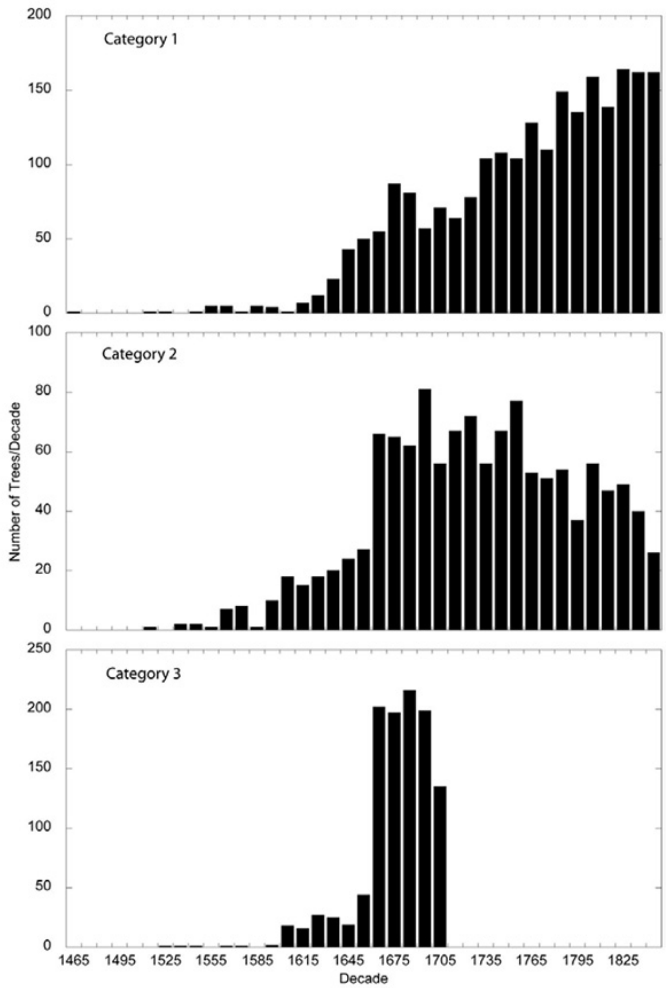

FIG. A7. Number of trees recruited per decade for Categories 1–3. Note: the *y*-axes scales differ because of the differing number of trees in each category.

Examples of White Rings in Two Genera

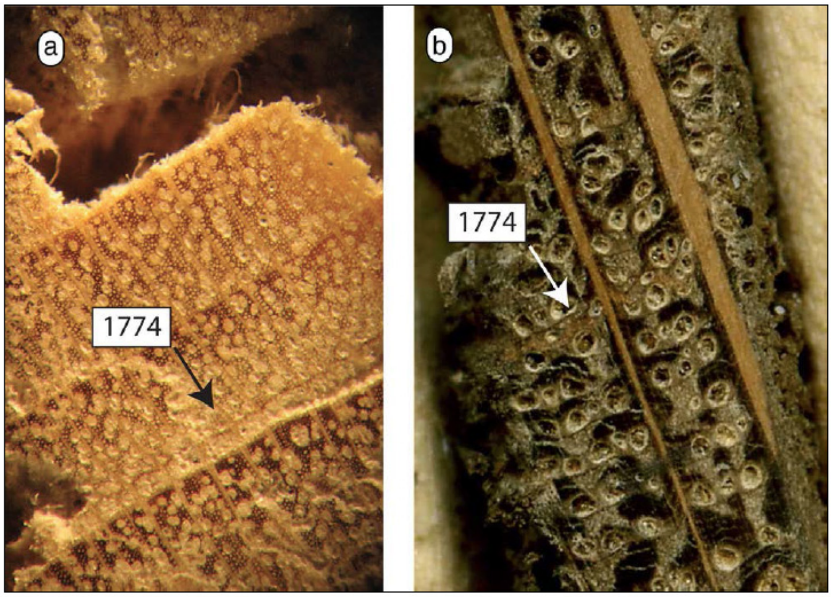

FIG. A8. Evidence of defoliation in 1774 from (a) a white ring in *Liriodendron tulipifera* from Fiddler's Green, VA and (b) a discolored ring *Quercus montana* from Blanton Forest, KY. Photo credit: Neil Pederson.

TABLE A4. Occurrence of Hurricanes prior to elevated disturbance events. Notes below synthesize works documenting hurricanes striking eastern North America. Hurricanes observed off the coast are not listed below nor are hurricanes that strike eastern North America during growing season of the last year of an elevated disturbance event. It is assumed that surviving trees from those events will not trigger increased growth rates reflecting canopy disturbance until the following growing season.

Event	Notes
1725-1727	A hurricane is reported in August, 1724 from South Carolina to Pennsylvania. It struck Chesapeake Bay and James River in Virginia (Machos n.d., Roth and Cobb 2001). Otherwise, no hurricane is documented in eastern US during the event until September 1727 (Chenoweth 2006). **Hurricane Landfall Rate from 1725-1727 on the Eastern US:** 0.33 hurricanes/year
1737-1739	A hurricane from "*West of Grand Cayman to Pensacola, Florida*" is documented in September 1736 (Chenoweth 2006). **Hurricane Landfall Rate 1737-1739 on the Eastern US:** 0.33 hurricanes/year
1755-1758	Hurricanes are documented from "*Lesser Antilles to off North Carolina*" in September 1754, "*Eastern New England and Nova Scotia*" in September 1757, and "*West of Jamaica to Florida to New Jersey coast*" in October 1758 (Chenoweth 2006). **Hurricane Landfall Rate 1755-1758 on the Eastern US:** 0.75 hurricanes/year
1766-1768	Hurricanes are documented in "*South Carolina*" in October 1765, from the "*Gulf of Mexico to Texas*" in September 1766, "*Atlantic to off Virginia to west of New York City*" in September 1766, "*Lesser Antilles to Puerto Rico to off South Carolina*" in October 1766, "*South of Haiti and Jamaica to Pensacola, Florida*" in October 1766, "*Havana to east of Florida*" in October 1766, "*Off North Carolina to southeast Massachusetts*" in September 1767, and "*Gulf of Mexico to SE US coastal waters to 35N 73W*" in October 1767 (Chenoweth 2006). **Hurricane Landfall Rate 1766-1768 on the Eastern US:** 2.66 hurricanes/year
1774-1782	Hurricanes are documented from "*North Carolina to Virginia*" in August 1773, "*Barbados to Maryland*" in late August to early September 1775, "*Guadeloupe to Louisiana*" in September 1776, "*Bahama Banks to New England* "in August 1778, "*Tobago to Pensacola, Florida*" in September and October 1778, in "*New Orleans*" in August 1779, "*Louisiana*" in August 1780, "*Near Jamaica to Gulf of Mexico to 44°50'N 42°28'W*" in October 1780, and "*South Carolina and North Carolina*" and "*West of Jamaica to New Orleans*" in August 1781 (Chenoweth 2006). **Hurricane Landfall Rate 1774-1782 on the Eastern US:** 1.25 hurricanes/year
1784-1787	Hurricanes are documented from "*West of Jamaica to New England*" in October 1783, "*Dominica to Jamaica to Pensacola, Florida*" in July and August 1784, "*Charleston, South Carolina*" and "*Leeward Islands to Bahamas to NC to Canada*" in September 1785, "*Charleston, South Carolina*" in September 1786, (Chenoweth 2006). **Hurricane Landfall Rate 1784-1787 on the Eastern US:** 1.25 hurricanes/year
1790-1794	Hurricanes are documented in "*New Orleans*" in August 1789, from "*Western Cuba to Florida Panhandle*" in June 1791, "*Western Cuba to South Carolina*" in October 1792, and "*Northern Leewards to Bahamas to Louisiana*" in August 1793 (Chenoweth 2006). **Hurricane Landfall Rate 1790-1794 on the Eastern US:** 0.80 hurricanes/year
1799-1805	Hurricanes are documented in "Charleston, *South Carolina*" in September 1799, from "*Leeward Islands to Louisiana*" in August 1800, "*South Carolina*" in October 1800, and "*Nassau to Gulf of Mexico*" in July 1801, "*Mobile, Alabama*" in August 1801, "*North Carolina*" in August-September 1803, "*Norfolk, Virginia*" in October 1803, "*Barbados to New England*" and "*Cuba to South Carolina*" in September 1804, and "*North of Puerto Rico to southeast New England*" in October 1804 (Chenoweth 2006). **Hurricane Landfall Rate 1799-1805 on the Eastern US:** 1.83 hurricanes/year
1816-1821	Hurricanes are documented from "*Martinique to New England*" in September 1815, "*West of Jamaica to South Florida to 3128N 6823W*" in June 1816, "*Martinique to eastern Cuba to South Carolina*" in September 1816, "*Tobago to Pennsylvania*" in August 1817, "*Yucatan to Texas to Mississippi*" in September 1818, "*Bahamas to Mississippi*" in July 1819, "*Florida to North Carolina*" in September 1820, and "*Dominica to Haiti to South Carolina*" from September to October 1820 (Chenoweth 2006). **Hurricane Landfall Rate 1816-1821 on the Eastern US:** 1.33 hurricanes/year
1834-1836	Hurricanes are documented in "*South Carolina*" in August 1833, "*Western Louisiana*" and "*South Carolina*" in September 1833, "*South Carolina*", from "*Gulf of Mexico to Western Louisiana*" and "*Central Leeward Islands to Western Louisiana*" in September 1834, "*16°55'N 53°45'W to Rio Grande, Texas*" in August 1835, "*Barbados to*

Rotated Principal Component Analysis Results

Rotated varimax principal component analysis (RPCA) retained eight eigenvectors (EV) that accounted for 62.9% of the common variation. EV1, accounting for 20.8% of the common variation, is comprised of six species (*Liriodendron tulipifera*, *Picea rubens*, *Quercus alba*, *Quercus montana*, *Quercus stellata*, *Tsuga canadensis*) and 22 chronologies loading ≥ 0.224 (p = 0.05, degrees of freedom = 75) and geographically grouped in the southern portion of our study area (Table A2). The resulting time-series of eigenvector scores reflects the common negative exponential decline in ring width commonly found in ring-width series of trees growing in low competitive environments (Fig. A2a; also see (Fritts 1976). EV2, accounting for 11.1% of the common variance, is comprised of six species from 22 chronologies loading ≥ 0.224 and found primarily in the southern Appalachian Mountain, northern Cumberland Plateau and Mississippi River Valley (Fig. 1a). EV3, accounting for 8.3% of the common variance, is comprised of seven species and 20 chronologies loading ≥ 0.224 and geographically grouped in the northern portion of our study area centered on Ohio, Indiana and Illinois. The resulting time-series of EV3 shows a decline in radial increment starting in the 1750s, generally below average radial increment from the 1770s until 1840. Starting in 1840 radial increment steps above the mean and shows an abrupt and sustained increase in 1857 (Fig. A2b). Detailed disturbance analysis of the collections loading strongly onto this eigenvector is outside the scope of this study, although a preliminary analysis indicates elevated disturbance in the mid-1840s and then a smaller spike in disturbance in the late-1850s (N. Pederson, unpublished data). The next five eigenvectors account for 3.3–6.0% of the common variance, are composed of 4–5 species from 11–21 chronologies and can be generally characterized by geography and genetic characteristics such as genera (EV4, 5 spp, 13 chronologies (CRNs); EV5, 4 spp (mostly *Quercus stellata*), 17 CRNs; EV6, 6 spp, 13 CRNS; EV7, 4 spp, 11 CRNs; EV8, 4 spp (mostly *Quercus alba*) 21 crns). See Table A2 for RRPCA results.

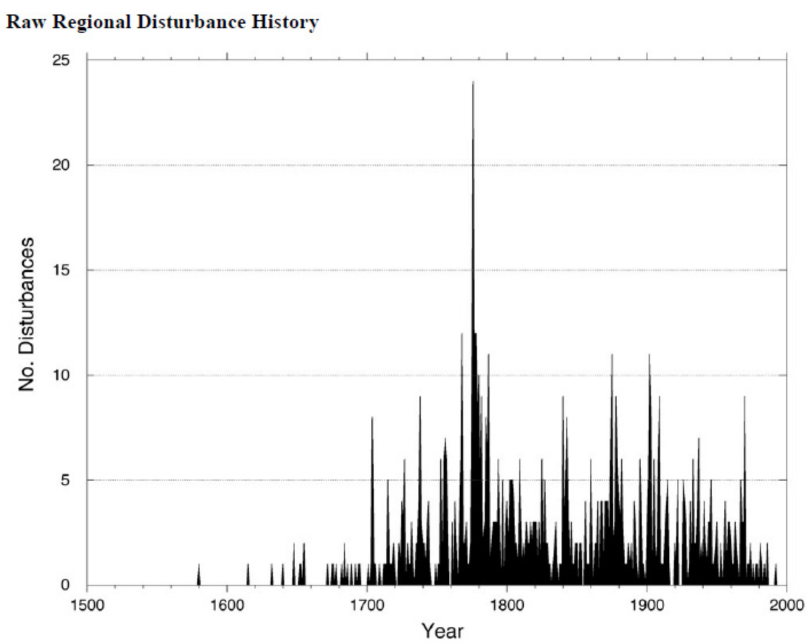

FIG. A9. Annual number of canopy disturbances through time across the southern Appalachian, northern Cumberland Plateau and mid Mississippi River Valley region.

TABLE A5. Table of population names corresponding to the map in Fig. 2b. The Blanton Forest populations were combined into one data point for analyses given the two species were intermingled throughout the forest.

Figure #	Population Name	State	Species	Total Accumulation of Percentage of Trees Recording Disturbance from 1775-1780
1	Pomme de Terre	MO	QUST	9.1
2	Buffalo Park Boundary	AR	QUST	8.3

3	Current River Natural Area Recollection	MO	QUAL	6.6
4	Mill Mountain	MO	QUST	4.3
5	Ferne Clyffe State Park	IL	QUAL	18.2
6	Mammoth Cave Recollect	KY	QUAL	9.5
7	Savage Gulf	TN	TSCA	57.1
8	London	KY	LITU	19.1
9	Norris Dam State Park	TN	QUAL	8.0
10	Scotts Gap	TN	LITU	43.5
11	Joyce Kilmer Wilderness	NC	QUAL	31.6
12	Whittleton RidgeY	KY	QUMO	50.0
13	Blanton Forest	KY	QUMO	46.3
14	Blanton Forest	KY	QUAL	46.3
15	Clingman's Dome	NC	PCRU	23.6
16	Boogerman Trail	TN	LITU	0.0
17	Lilley Cornett Tract	KY	QUAL	29.3
18	Linville Gorge	NC	QUAL	31.6
19	Dysart Woods	OH	QUAL	12.5
20	Irish Creek	VA	QUMO	0.0
21	Savage Mtn	MD	QUMO	6.3
22	Watch Dog/Massenhutten Mountain	VA	QUMO	0.0

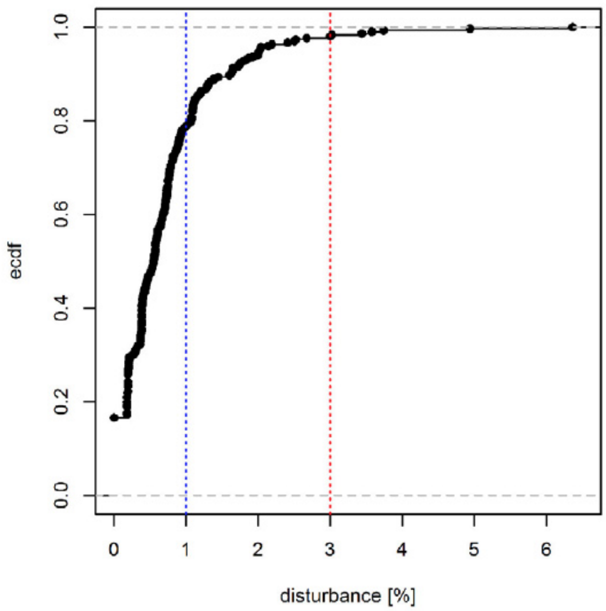

FIG. A10. Empirical cumulative density function (ecdf) of the canopy disturbance rate (disturbance in percent) over the time period 1680–1880. The blue dashed line marks a disturbance rate of 1%, equivalent to the threshold in the GPD application in this study (compare Fig. 2c). The red dashed line marks a disturbance rate of 3%, which is only exceeded for seven events. Four out of these seven events fall in the time period 1775–1778.

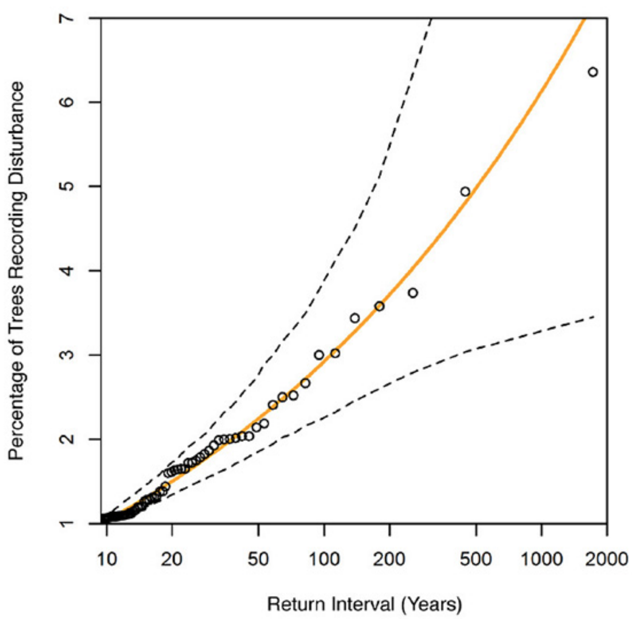

FIG. A11. Return intervals of disturbance rates between 1685 and 1880 for years with a percentage of trees recording more than 1% as predicted by a generalized Pareto distribution based upon Figure 2d. Hollow circles represent individual years. For example, the uppermost circle is the year 1776, the peak year of disturbance in our data set. The solid orange line is fitted to the observations while the dashed lines represent 95% confidence limits. It is important to note that the return interval estimates have great uncertainty beyond a 4% disturbance rate due to limitations in time series length, data coverage, and the targeted nature of tree selection that potentially causes a substantial time-varying, long-term trend.

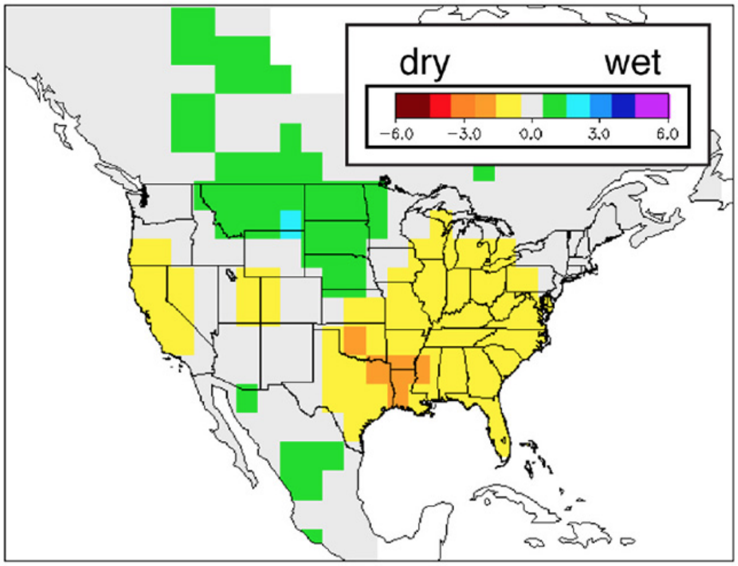

FIG. A12. Composite map of drought from the North American Drought Atlas (Cook et al. 2008) of the year prior to years with elevated disturbance (1 STD or greater above the mean; n = 23).

Examples of the Impact of the 2007 Frost Event on *Liriodendron tulipifera*

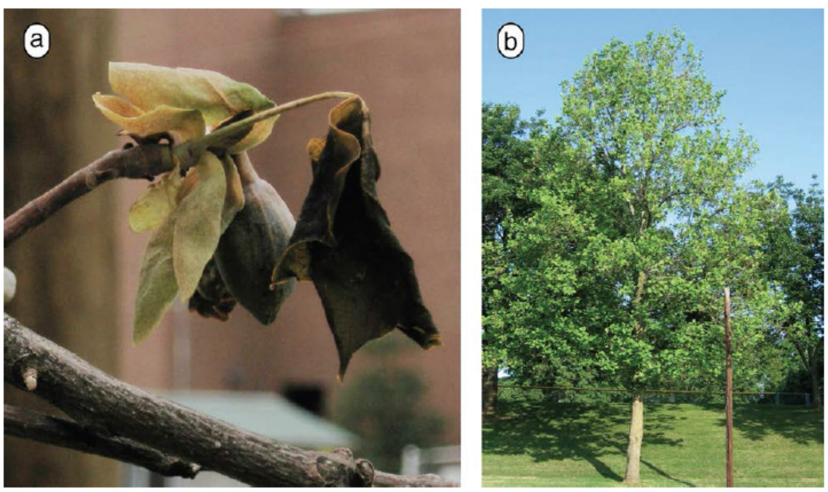

FIG. A13. Impact of 2007 frost event on *Liriodendron tulipifera* in Richmond, KY. (a) Necrosis of green organs on April 7, 2007. (b) The first sign of near-complete recovery of crown of the same tree occurred on May 24th, 2007. Images: N. Pederson.

Reconstructed Land-use and Forest Recovery from 1450-1700

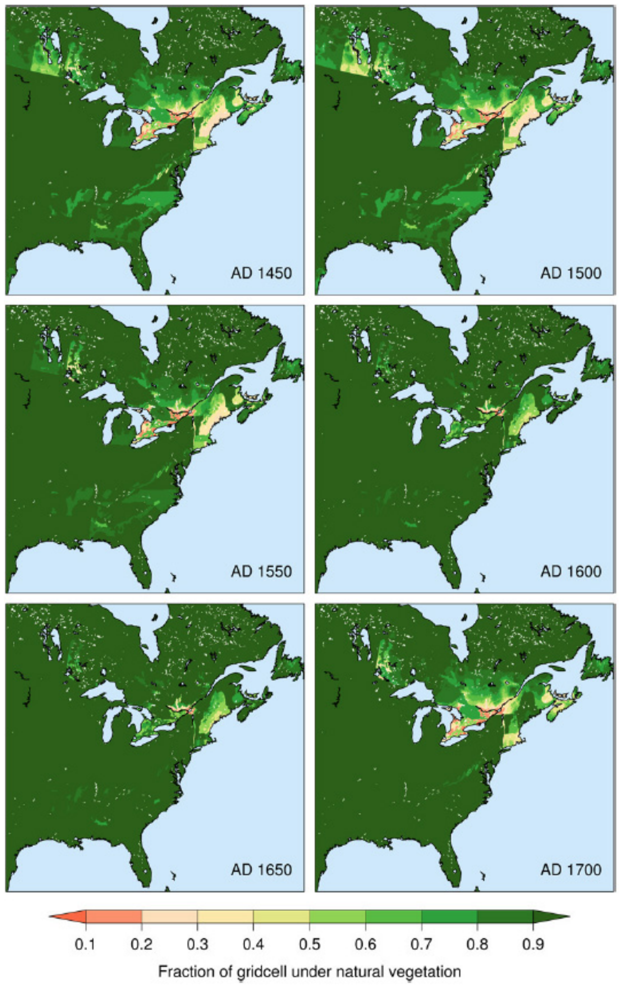

FIG. A14. Reconstructed land-use and forest recovery across the eastern US from 1450–1700 by the ARVE Group (Krumhardt 2010). These 50-year swaths of changing land-use are derived from as derived from demographic data and reflect an estimated amount of natural vegetation via land-management as population densities change in space and time. Outside of Maine, the Connecticut River Valley, the mid Mississippi River Valley, the Black Belt of Alabama and Mississippi, and small pockets in the southern Appalachian Mountains, forests appear to be broadly recovered by 1600. These data represent one of the first analyses at this kind using demographic data and, thus contains great uncertainty. Future revisions could alter these insights observed in this map.

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Neil Pederson, James M. Dyer, Ryan W. McEwan, Amy E. Hessl, Cary J. Mock, David A. Orwig, Harald E. Rieder, and Benjamin I. Cook. 2014. The legacy of episodic climatic events in shaping temperate, broadleaf forests. *Ecological Monographs* 84:599–620. http://dx.doi.org/10.1890/13-1025.1

APPENDIX B. Photos of two important old-growth forests central to this investigation.

FIG. B1. Panoramic stitch of a rich portion of the old-growth forest in Blanton Forest, Kentucky. This portion of the forest is dominated by *Quercus*, but also contains *Carya* and *Magnolia* species. None of the *Quercus* trees cored (>40) pre-date the 1660s. Photo credit: Neil Pederson.

FIG. B2. Coring a large *Quercus alba* in a stand dominated by *Quercus alba* in the old-growth forest in Blanton Forest, Kentucky. Photo credit: Neil Pederson.

FIG. B3. Coring a large *Quercus montana* in a stand dominated by *Quercus alba* and *Quercus montana* in the old-growth forest in Blanton Forest, Kentucky. Photo credit: Neil Pederson.

FIG. B4. Overlooking a tributary of Savage Gulf, Tennessee at dusk. Only *Tsuga canadensis* was cored in this old-growth forest, but a substantial component of broadleaf forest is present in this ravine. Photo credit: Neil Pederson.

FIG. B5. Overlooking a tributary of Savage Gulf, Tennessee dominated by *Tsuga canadensis*. The *Tsuga canadensis* contain a strong growth release in the late 1770s that matches the growth release found in several forests within the region. Note: this picture was taken just before hemlock woolly-adelgid was identified in this old-growth forest. Some trees have since been treated for this insect. Photo credit: Neil Pederson.

FIG. B6. Panoramic of the interior of the old-growth forest in Savage Gulf, Tennessee. The twisty stem leaning to the left is an old *Quercus montana* that could be 200-300+ years old. Photo credit: Neil Pederson.

FIG. B7. Coring old-growth *Tsuga canadensis* in Savage Gulf, Tennessee. Much of the slopes and bottoms of the ravine are characterized by talus. Photo credit: Neil Pederson.

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