

1 Running Head: Extreme episodic climate and broadleaf forests

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3 Title: **The legacy of episodic climatic events in shaping temperate, broadleaf forests**

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23

24 **Abstract**

25 In humid, broadleaf-dominated forests where gap-dynamics and partial canopy mortality appears
26 to dominate the disturbance regime at local scales, paleoecological evidence shows alteration at
27 regional-scales associated with climatic change. Yet, little evidence of these broad-scale events
28 exists in extant forests. To evaluate the potential for the occurrence of large-scale disturbance,
29 we used 76 tree-ring collections spanning ca 840,000 km² and 5,327 tree recruitment dates
30 spanning ca 1.4 million km² across the humid eastern US. Rotated principal component analysis
31 indicated a common growth pattern of a simultaneous reduction in competition in 22 populations
32 across 61,000 km². Growth-release analysis of these populations reveals an intense and coherent
33 canopy disturbance from 1775-1780 peaking in 1776. The resulting time-series of canopy
34 disturbance is so poorly described by a Gaussian distribution that it can be described as ‘heavy
35 tailed’, with most of the years from 1775-1780 comprising the heavy-tail portion of the
36 distribution. Historical documents provide no evidence that hurricanes or ice storms triggered the
37 1775-1780 event. Instead, we identify a significant relationship between prior drought and years
38 with elevated rates of disturbance with an intense drought occurring from 1772-1775. We further
39 find that years with high rates of canopy disturbance have a propensity to create larger canopy
40 gaps indicating repeated opportunities for rapid change in species composition beyond the
41 landscape scale. Evidence of elevated, regional-scale disturbance reveals how rare events can
42 potentially alter system trajectory – a substantial portion of old-growth forests examined here
43 originated or were substantially altered more than two centuries ago following events lasting just
44 a few years. Our recruitment data, comprised of at least 21 species and several shade-intolerant
45 species, document a pulse of tree recruitment at the subcontinental scale during the late-1600s
46 suggesting that this event was severe enough to open large canopy gaps. These disturbances and
47 their climatic drivers support the hypothesis that punctuated, episodic climatic events impart a

48 legacy in broadleaf-dominated forests centuries after their occurrence. Given projections of
49 future drought, these results also reveal the potential for abrupt, meso- to large-scale forest
50 change in broadleaf-dominated forests over future decades.

51

52 **Keywords:** Closed-canopy forests, deciduous forests, gap dynamics, disturbance, drought, tree-
53 ring analysis, mesoscale dynamics, frost, historical documents.

54

55 **Introduction**

56 Anthropogenic climate change is altering the structure and function of forested
57 ecosystems and challenging our understanding of how systems react to disturbance. Increased
58 warming has complex effects on ecosystem dynamics through the interaction of drought, species
59 tolerances, insect outbreaks, fire regimes and other perturbations (e.g., Allen and Breshears 1998,
60 Taylor et al. 2006, Worrall et al. 2008, van Mantgem et al. 2009, Allen et al. 2010). Climatic
61 variation drives ecosystem dynamics at large scales in semi-arid and boreal forests, where tree
62 species richness is relatively low (e.g., Payette et al. 1985, Savage et al. 1996, Villalba and
63 Veblen 1997, 1998, Allen and Breshears 1998, Brown and Wu 2005, Raffa et al. 2008). An
64 extreme example includes massive forest mortality where one species comprised 95% of the
65 composition (Michaelian et al. 2011). While recent disturbances appear to be partly driven by
66 anthropogenic warming, they generally fit the expected disturbance regime in these forests and
67 provide insight into how climate modulates these systems at regional scales.

68 In contrast to these systems, many forests, especially in temperate, broadleaf forests,
69 experience gap dynamics and partial canopy mortality as the prevailing disturbance regime at
70 stand to landscape scales (Runkle 1982, Yamamoto 1992, Rebertus, Alan and Veblen 1993,
71 McCarthy 2001, Gutierrez et al. 2008). These small-scale events are thought to be largely
72 stochastic and not directly tied to climate. Triggered by individual tree mortality, these dynamics
73 could aid in the maintenance of stand composition and structural complexity and play a role in
74 prolonged forest stability at large scales (Runkle 1982, Yamamoto 1992, McCarthy 2001,
75 Gutierrez et al. 2008), an observation that is supported through long-term, simulated forest
76 dynamics (Smith and Urban 1988). Long-term forest stability is primarily achieved through in-
77 filling by lateral branches in small gaps or filling through recruitment of more shade-tolerant
78 species. Temperate forests in humid regions dominated by broadleaf species often have high
79 species diversity, making them resilient to species-specific disturbances like insect outbreaks. In

80 marked contrast with low-diversity coniferous forests, for example, the broadleaf-dominated
81 forests of the eastern United States have no native forest insects that trigger large-scale dieback
82 (Man 2012). And, unlike semi-arid or coniferous systems, fire in this region is typically fine-
83 scaled, spatially heterogeneous (Clark and Royall 1996, Parshall and Foster 2003, Guyette et al.
84 2006, McEwan et al. 2007) and less likely to occur at regional-scales (though see McMurry et al.
85 (2007) for an exception). Thus, dynamics in broadleaf-dominated forests are often characterized
86 as asynchronous in space and time and not seen as strongly influenced by climatic variation like
87 other forest types (Vanderwel et al. 2013, Schleeweis et al. 2013). Given future climate forecasts,
88 it is imperative that we understand how broadleaf forests in humid regions might respond to
89 climate change at large spatial scales.

90 Paleoecological studies have documented regional-scale changes in humid forests driven
91 by climate. Specifically, drought shaped the structure and composition of these systems during
92 the Holocene (Jackson and Booth 2002, Shuman et al. 2004, 2009, Foster et al. 2006, Booth et al.
93 2012). For example, Booth et al. (2012) recently showed how the decline of American beech
94 during the Medieval Climate Anomaly was triggered by drought and climatic variability in the
95 moist, lake effect-influenced forests in the Great Lakes region. While paleoecological studies are
96 critical in identifying long-term, regional-scale forest dynamics, they typically can only identify
97 the timing of forest dynamics at decadal to multi-decadal scales and at broad compositional (i.e.,
98 genera) levels. How this translates to contemporary systems is less certain. To date, disturbance
99 histories of extant old-growth forests in humid regions primarily identify stand-scale (Runkle
100 1982, Yamamoto 1992, McCarthy 2001) to moderate-scale dynamics (White et al. 1999, Frelich
101 2002, Woods 2004, Baker et al. 2005, Worrall et al. 2005, Stueve et al. 2011), although large
102 scales dynamics have been postulated (e.g., Cho and Boerner 1995). Thus, there is a disparity
103 between paleoecological records of regional-scale forest dynamics and recent forest history
104 reconstructions that primarily document gap dynamics. Bridging this divide for broadleaf-

105 dominated forests could yield important analogues for how forests will respond to climate
106 change at time scales relevant for climate forecasts and human decision-making.

107 Here we develop and analyze two large data sets to investigate the possibility of
108 synchronous, regional-scale disturbance and tree recruitment over the last 500 years of the
109 Common Era (CE) in the humid, broadleaf-dominated region of the eastern US. We test a null
110 hypothesis of small-scale (gap) dynamics under which disturbance and tree recruitment resemble
111 a stochastic or white-noise process. Explicitly, forest dynamics would not be regionally
112 synchronous and time-series of disturbance and recruitment would not deviate significantly
113 above the long-term background rate. Under the alternative hypothesis, forest dynamics would
114 be regionally synchronous and time-series of disturbance and recruitment would be punctuated
115 by extreme events. We know of no study that has identified severe, synchronous, regional-scale
116 disturbance in temperate humid regions outside of studies covering centennial time scales
117 (sediment core records). In fact, two tree-ring based investigations designed to identify regional-
118 scale disturbance did not reveal evidence for synchronous disturbance over the last 300+ years
119 (Rentch 2003, D'Amato and Orwig 2008). The first data set for our investigation, 76 tree-ring
120 records over a ca 840,000 km² area, is examined for temporal clustering of large-scale canopy
121 disturbance. The second data set, >5000 tree recruitment dates from multiple sources that cover
122 ca. 1.4 million km², are examined for evidence of synchronous, large-scale recruitment events.

123 Identifying the exact triggers of historical disturbance from tree rings or other types of
124 ecological proxies can be difficult given that many factors drive forest dynamics. We thus turned
125 to historical documents to assist in identifying potential drivers of disturbance. Historical
126 documents have been used to clarify the potential impact of climate on human societies (e.g.,
127 Endfield 2012) and in physical geographical and ecological studies (e.g., Hooke and Kain 1982).
128 Here, we use historical documents to conduct a 'ground-truthing' of events in tree-ring records.
129 Several sources of historical documents were used including a compilation of Atlantic hurricanes

130 (Chenoweth 2006), diaries of frontier settlers, Moravians, in western North Carolina (Fries 1922,
131 1925, 1926), Thomas Jefferson’s Garden Book (1774) and 18th century newspaper and other
132 accounts (e.g., Ludlum 1963). While many of the Moravian records contain information about
133 births, marriages, deaths, civil unrest, and smallpox, they are also a rich source of information for
134 historical ecology, documenting events that impacted agriculture (like hail storms, oppressive
135 heat, and individual rain events; See ‘*Examples of weather observation from the Moravian*
136 *Diaries*’ in Appendix A for examples). We note, however, that their records are of limited spatial
137 coverage and cannot account for possible impacts across our study region. Given their detailed
138 observations of important weather events, spatial coverage of the records, and multiple observers
139 at potentially daily temporal resolution, it is possible that significant, large-scale weather events
140 were documented, which could complement our understanding of forest dynamics from tree-ring
141 records.

142

143 **Methods**

144 We investigate the potential for regional scale-disturbance using a network of 76 tree-ring
145 chronologies from the International Tree-ring Databank (ITRDB) covering ca 840,000 km² in the
146 broadleaf-dominated region of the humid eastern US (also called the Eastern Deciduous Forest;
147 Figure 1a; see Table A1). Tree-ring records from sites in southeastern Kentucky, central
148 Tennessee, and North Carolina indicated the possibility of large-scale disturbance in the late
149 1770s (see ‘*Temporal and Geographic Disturbance Detection Methods*’ in Appendix A, Figure
150 A1, and two of these forests in Appendix B). With a larger data set, we sought to test the
151 hypothesis that a regional-scale disturbance event occurred during this period. If there is
152 evidence of a regional event, the larger network will allow us to determine its spatial extent. The
153 network is composed of at least 11 species collected by 15 investigators to study climate,
154 ecology, and fire history. Most trees were targeted for maximum age, drought sensitivity, or fire

155 history, although some were collected via random sampling (Table A1). Most of the collections
156 for climatic reconstruction were not derived from the canonical ‘open-grown’ trees on highly
157 stressed sites (see Fritts 1976), but from closed-canopy forests; 44 of the 49 sites were either
158 visited by a co-author (N. Pederson) or confirmed to be closed-canopy from the collector (E.
159 Cook, personal communication). To avoid inflating results, the Blanton Forest populations were
160 combined during analysis as the two species were intermingled throughout the forest.

161 Tree-ring chronologies were selected if they met several criteria, including species
162 composition (trees from broadleaf-dominated forests), chronology length (inner ring date pre-
163 1750), geographic location, and the likelihood that they represented old-growth forest. We
164 targeted broadleaf-dominated forest to increase the likelihood that small-scale dynamics was the
165 predominant disturbance regime; we did not, for example, include species such as *Pinus resinosa*
166 or *Pinus rigida*, which would be expected to have more episodic recruitment because of a fire-
167 dominated disturbance regime. We were not able to meet these criteria in all cases. For example,
168 12 of the 76 chronologies came from conifer-dominated forests with possible episodic
169 recruitment (*Picea rubens*, *Pinus echinata*, *Pinus* spp.; Table A1); *Tsuga canadensis* is an
170 important component of this network, but generally has more of a gap-dynamics life history trait
171 in reaching the forest canopy. To increase the likelihood that potential collections for analysis
172 were not from logged forests, we excluded collections if: 1) a third or more of trees with rapid,
173 early growth were recruited in a single cohort after ca. 1850 or 2) a substantial number of old
174 trees showed major growth releases during this same period (>100% change in growth; see
175 Lorimer 1985, Lorimer and Frelich 1989). Even though little stand-scale logging occurred in the
176 mountainous and plateau areas of our study region prior to 1850 (Figure 6.4 on pg 161 in
177 Williams (1992), there is the possibility that stands with only natural disturbance were omitted
178 from this analysis. Since many of the collections are from extant old-growth forests, it is less
179 likely that they have been logged because of the common relationship between low site

180 productivity and old trees (Stahle and Chaney 1994). For finer details on discerning expected
181 radial growth patterns and other considerations of our approach, see '*Temporal and Geographic*
182 *Disturbance Detection Methods*' in Appendix A. The ultimate goal in omitting some trees and
183 collections was to avoid false-positive results that could occur if all data were included in the
184 initial analysis.

185 To objectively detect if step-change increases in radial increment might resemble a
186 regional-scale canopy disturbance, raw ring widths were standardized using a straight-line fit to
187 remove differences in mean growth rate. The resulting standard chronologies were entered into
188 rotated varimax principal component analysis (RPCA). RPCA identifies the highest loadings of
189 each variable on a single eigenvector while maintaining orthogonality and maximizing variance
190 of retained eigenvectors (Richman 1986). The Monte Carlo 'Rule-N' technique was used to
191 determine the number of eigenvectors to use for analysis (Preisendorfer et al. 1981). RPCA
192 retained eight significant eigenvectors, accounting for 62.9% of the common variation (see Table
193 A2 and *Temporal and Geographic Disturbance Detection Methods* in Appendix A). We report
194 on the first three for this study. Eigenvector One (EV1), accounting for 20.8% of the common
195 variation, represents the temporal decline in ring widths as constrained by allometry (Figure
196 A2a). Eigenvector Two (EV2), accounting for 11.1% of the common variance, has a large, step-
197 change in radial increment around 1780 (Figure 1b). Eigenvector Three (EV3), accounting for
198 8.3% of the common variance, reveals an abrupt increase in ring widths in 1840 and 1857
199 (Figure A2b, Table A2). As EV1 reflects the commonly observed pattern of large rings when
200 trees are small and there is a good chance that EV3 likely represents the era of European
201 settlement, we focus on investigating the potential for a regional disturbance event among the
202 populations loading strongly on EV2. A complete analysis and discussion of EV3 is beyond the
203 goals of this study.

204 To investigate whether the step-change in radial increment of EV2 was a regional-scale
205 disturbance event, disturbance history was reconstructed from the 22 chronologies loading
206 positively and significantly onto EV2 (≥ 0.224 , $p \leq 0.05$; following Koutsoyiannis 1977).
207 Evidence of canopy disturbance in individual raw ring-width series of the 22 chronologies was
208 investigated using conservative methods adopted from a traditional approach. Here, a major
209 canopy disturbance is an increase in radial growth of $>99.9\%$ over a 15-year period relative to
210 the prior 15 years; a minor release is an increase in radial growth of 50-99.9% over 15-year
211 periods (Lorimer and Frelich 1989; For a deeper discussion on potential pitfalls for these
212 methods, see '*Tree and Population-level Disturbance History Analysis*' in Appendix A). A
213 release $>99.9\%$ is considered an opportunity for an understory tree to reach the canopy (cf.
214 canopy accession; (Lorimer and Frelich 1989). While these methods were primarily developed
215 for shade-tolerant species, previous work indicates that these methods are effective for
216 reconstructing disturbance histories using shade-intolerant species (Orwig and Abrams 1994),
217 even in a 'gappy forest' (McGuire et al. 2001) dominated by shade-intolerant species (see
218 Pederson et al. 2008). Our method might not detect multiple disturbances in some trees because
219 trees lose some sensitivity to changes in competition as they gain canopy status (Nowacki and
220 Abrams 1997, Rentch et al. 2002, Druckenbrod et al. 2013). However, many trees in our data set
221 recorded more than one disturbance. Further, a test of lower detection thresholds does not alter
222 our findings, but does seem to be sensitive to climate in ways that could result in false positives
223 (see '*Detection Sensitivity Analysis*' in Appendix A). Because of the methodology used here, we
224 do not have a complete record of disturbance history. And, given that most ITRDB data are often
225 comprised of only 20-30 canopy trees per stand, we would not expect to detect all possible
226 disturbances in a particular forest, although increased core replication of the ITRDB collections
227 likely increases the chance of detecting disturbance versus single-core studies (Copenheaver et
228 al. 2009). Ultimately, our final time-series of canopy disturbance should reflect a lower number

229 of false-positives and, more importantly, large canopy gap formation, which should have a more
230 meaningful impact on forest composition and structure than smaller gaps.

231 Statistical analysis of the disturbance record indicated a heavy tail (i.e., large disturbance
232 events) that strongly deviated from a Gaussian distribution (see Figure 2c, d). Therefore, we
233 applied tools from extreme value theory (Davison and Smith 1990, Coles 2001), to analyze the
234 statistical properties of extremes in the disturbance record (i.e., years with many recorded
235 disturbances). In this framework we use a peak-over threshold approach - based on the
236 generalized Pareto distribution (GPD) - to investigate the tail properties of the time-series of
237 canopy disturbance. We fit a GPD to disturbance events above a disturbance rate of 1%. The
238 determination of a suitable threshold for which the asymptotic GPD approximation holds is an
239 essential step that requires the consideration of a trade-off between bias and variance (e.g., Coles,
240 2001). Note that if a threshold is chosen too low, the GPD will fit the exceedances poorly and
241 introduce a bias in the estimates, while if a threshold is chosen too high it will reduce the number
242 of exceedances and thus increase the estimation variance. In practice, threshold choice involves
243 comparing the theoretical behavior of the GPD with the empirical behavior of the data. Tools
244 like the mean residual life plot assist in the threshold choice, and if the observations follow a
245 GPD with a shape parameter <1 , the mean exceedance should vary linearly with the threshold.
246 For our application we choose the threshold as a disturbance rate of 1%. The rationale behind
247 this threshold choice is that (i) it fulfills the statistical criteria described above, and (ii) it allows
248 us to consider more moderate disturbances (that lie clearly above the internal variability of the
249 data record; as a disturbance rate of 1% \sim 80th-percentile of the record) together with the ‘high
250 impact’ extremes. This model described the high tail much better than the Gaussian distribution.
251 In addition, return intervals (in years T) can be described from the probability of exceeding a
252 disturbance rate x within a time window T directly from the fitted GPD.

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

$$257 \quad M_I = D * DR * MR$$

258 where M_I = the magnitude index, D = duration in years, DR = anomaly of the disturbance rate as
259 the departure from the mean of the percent of trees disturbed/yr from 1685-1880, and MR = the
260 percent of releases qualifying as a ‘major release’ during each event. The magnitude index
261 describes the intensity of each release event. Canopy disturbance analysis is limited to 1685-
262 1880 because it represents the period when tree replication ≥ 100 (1685) and precedes large-scale
263 logging (ca 1880; Williams 1992) when we hypothesize that trees from ITRDB collections
264 would have reduced sensitivity to changes in competition. As many collections from the ITRDB
265 contain trees >200 years of age at the time of sampling, it not unreasonable to expect that most of
266 these trees, especially species like *Quercus alba* or *Liriodendron tulipifera*, would have reached
267 canopy status within 100-150 years prior to sampling; tree ring sampling in the eastern US began
268 in earnest during the late 1970s (e.g., Cook and Jacoby 1977, 1983, Cook 1982, Stahle et al.
269 1985, Stahle and Cleaveland 1988). Reliance on the oldest trees in a reconstruction of
270 disturbance history has the potential to be biased as one moves closer to the period of sampling
271 (McEwan et al. 2013). Thus, we expect the mid-1800s to be the beginning of reduced tree
272 sensitivity to release in our data set, a trend observable in our record.

273 We then investigated the relationship between canopy disturbance and drought in two
274 ways. First, we made composite drought maps from the North American Drought Atlas (NADA;
275 Cook and Krusic 2004, Cook et al. 2004) for the years prior to the 23 years with elevated
276 disturbance (years with disturbance ≥ 1.0 standard deviation (SD) above the 1680-1880 mean)
277 after we noticed that elevated disturbance often followed regional marker rings. Second, we used

278 superposed epoch analysis (SEA; Swetnam 1993) to examine moisture conditions before, during,
279 and after years with elevated disturbance. Because some of the tree-ring records used for
280 disturbance analysis are used in the NADA, we developed an independent drought proxy (IDP)
281 to test for a relationship between drought and disturbance. IDP is a tree-ring based proxy of
282 drought using records not used for disturbance analysis from within and around the periphery of
283 the late-1770s disturbance region (see ‘*Creation of the Independent Drought Proxy for*
284 *Superposed Epoch Analysis*’ in Appendix A).

285 We mined published and unpublished datasets of tree establishment dates from old-
286 growth forests dominated by broadleaf species to reconstruct regional-scale recruitment history
287 across the eastern United States (see Supplement A). Like our disturbance detection analysis,
288 forests that would be expected to have episodic recruitment, i.e., pine-dominated forests, were
289 avoided. While some scattered conifers within broadleaf-dominated forests are included in this
290 analysis, recruitment dates for these trees were drawn from broadleaf-dominated forests or
291 conifers with more of a gap-phase life history trait like *Tsuga canadensis* and *Tsuga caroliniana*.
292 We examined a larger area than that of the 76 chronologies for disturbance detection because a
293 review of independent and geographically-dispersed studies explicitly discussed a recruitment
294 event, broad compositional change, or stand initiation dates in the late-1600s (Huntington 1914,
295 Haasis 1923, Hough and Forbes 1943, Henry and Swan 1974, Grimm 1983, Guyette et al. 1994,
296 Rentch 2003). Thus, this data set would be another test of regional-scale disturbance in forests
297 dominated by gap dynamics. We only examined recruitment dates prior to 1850 to reduce the
298 influence of widespread regional land-use change associated with land clearing and cutting
299 (Williams 1992). The final dataset includes 49 published studies from 56 different stands
300 comprised of 5,327 individual tree establishment dates (Figure A6). These studies used a variety
301 of methods to investigate long-term development of old-growth forests at local scales, although
302 Rentch et al. (2003) is the exception with five sites distributed across ca 30,000 km².

303 Recruitment dates were tallied from 34 species, not counting ‘other’ and ‘unknown’ categories as
304 other species. The most common species are *Tsuga canadensis* (25.6%) and *Quercus alba*
305 (21.3%). Eight *Quercus* species accounted for 37.6% of the recruitment dates while four *Pinus*
306 species combined for only 6.4%. Recruitment dates are estimates of tree age at stump or coring
307 height. Because these data varied in precision, methodology, recruitment dates, dates when
308 regeneration reached stump or coring height, dates were placed into four categories: Category 1 -
309 from randomized or representative sampling; Category 2 - from studies targeting the oldest trees
310 or historical timbers; Category 3 - from studies that do not include post-1700 recruitment dates;
311 and Category 4 - from studies that have recruitment dates binned at > 10 years. We compiled
312 dates by decade because of associated uncertainties in methodology (see ‘*Subcontinental-scale*
313 *Recruitment Data*’ in Appendix A). Raw Category 1 recruitment increases through time (see
314 Figure A7). This trend was removed using segmented regression (R package segmented;
315 Muggeo 2008) allowing us to detect individual recruitment events from the residuals of this trend
316 as well as an objective assessment of breakpoints or changes in the trajectory of recruitment over
317 time.

318 Multiple sources of observed weather events were used to conduct ground-truthing of the
319 disturbance events embedded in our tree ring network. Due to the close proximity of the region
320 experiencing the 1770’s disturbance event, we relied upon the Moravian records from western
321 North Carolina more than other sources. One value of the Moravian observations is that multiple
322 resident diarists for each year are distributed over an area of at least 400 km²; visitors to the
323 Moravian settlement would occasionally extend the scale of observations in the diaries. In
324 addition, Moravian records occasionally revealed the intensity and scale of impact. The March
325 17, 1776 wind event, as one example, was recorded by three observers, but it was noted by one
326 of those observers from a neighboring village to have caused little damage (Fries 1926).

327 The Moravian records were used in two ways. First, they were used to determine the
328 potential cause of the 1774 ‘white ring’ seen in increment cores across genera (*Liriodendron*,
329 *Carya*, and *Quercus*) collected in Kentucky and Virginia (Figure A8). ‘White rings’ are rings
330 with low-lignification and have been produced following defoliation experiments (Hogg et al.
331 2002). They are also present during years of gypsy moth defoliation (Pederson 2005). Because
332 the 1774 white ring appeared across genera, we hypothesized that defoliation was caused by a
333 frost event. Second, the Moravian records were used as an independent ‘ground-truthing’ of
334 hurricanes striking the eastern US in the year prior to or during elevated canopy disturbance
335 events. These strikes were compiled from Ludlum (1963), Rappaport and Ruffman (1999),
336 Landsea et al. (2004), Chenoweth (2006) and are in Appendix A (Table A4). The Moravian
337 records then became vital in determining if known hurricanes impacted our study region because
338 they lived adjacent to the southeast border of our canopy disturbance region and in an area that
339 would likely experience hurricanes strikes.

340

341 **Results**

342 *Disturbance History*

343 Twenty-two collections loaded significantly onto EV2. These collections are composed
344 of six species including, mesic, ravine-bottom *Tsuga canadensis* and *Liriodendron tulipifera*, a
345 high elevation *Picea rubens* collection, and two *Quercus* species growing on a dry, southeast-
346 facing slope (Table A2). The strongest loadings clustered in the southern Appalachian Mountain-
347 Cumberland Plateau region (Figure 1a; Table A2; a detailed discussion of the RPCA results are
348 in ‘Rotated Principal Component Analysis Results’ in Appendix A). EV2’s time-series of radial
349 increment (RPCA scores) reveals below average increment prior to 1780 followed by a 201%
350 increase in average radial increment from 1780-1794 versus 1765-1779 and a linear decline until
351 1853 that resembles trees following canopy accession (Figure 1b).

352 We detected a total of 866 canopy disturbances over the 1570-2000 CE period from the
353 558 trees and the 916 time-series of radial increment that comprise the 21 populations loading
354 significantly onto EV2 (Figure 2a; see Figure A9 for the raw data; please note that the two
355 Blanton Forests were combined prior to this step). The peak period of disturbance was from
356 1775-1780, when 81 disturbances were detected, while the peak year was 1776, when 24
357 disturbances were detected. We detected 588 disturbances between 1665-1880. Despite high tree
358 replication throughout this period, 30 years had no evidence for disturbance and 49 years
359 indicated only one disturbance. Twenty-three years had disturbance rates > 1 SD above the long-
360 term (1685-1880) mean, hence called '*elevated disturbance*' (mean = 0.79 disturbance/yr, SD =
361 0.83; Figure 2a). From these data we identified 13 '*extended disturbance*' events, or three
362 consecutive years with ≥ 3 disturbances/year (> 2.5 SD above the mean; Table 1).

363 Of the 588 canopy disturbances from 1685-1880, 60.4% are classified as minor canopy
364 disturbance (Figure 2a). For the 23 years with elevated disturbance, the minor:major canopy
365 disturbance ratio is closer to 1:1 (51.0% vs. 49.0%, respectively). This ratio swings in favor of
366 major disturbances for years with disturbance rates ≥ 2 SD (48.2% vs. 51.8%). We also found a
367 positive association between severity and disturbance extent. That is, when disturbance was
368 widespread, it was also more severe. Seven of the 13 extended events had a greater proportion of
369 major canopy disturbance than the 1685-1880 mean (Table 1) and individual years and periods
370 with elevated disturbance also appear to be widespread. For example, the annual mean
371 percentage of sites with disturbance from 1685-1880 is 11.3% (SD = 9.8), but during periods of
372 elevated disturbance, the mean of sites recording disturbance was 19.4 (range = 14.0-33.9, SD =
373 5.58; Table 1). Disturbance was recorded in 33.9% of all sites from 1774-1782, > 3 SD above the
374 mean, and in 41.3% of all sites from 1775-1780 (Table 1). The spatial extent of disturbance
375 peaked in 1776 when it was found in 47.6% of all sites. The total accumulated percentage of
376 trees recording disturbance during the 1775-1780 event ranged from 0-57.1% (average = 19.7%,

377 SD = 17.7%). Mapped quartiles of the total amount of disturbance recorded from 1775-1780
378 indicate severe damage over ca 61,000 km² (Figure 2b). The four collections with less damage
379 during this event include two *Liriodendron tulipifera* and two *Quercus alba* populations. The
380 magnitude index for extended, elevated disturbance events for the 1770s events was 3.4-3.9
381 times greater than the next two most severe events (1737-1739, 1766-1768) (Table 1).

382 The time-series of canopy disturbance from 1685-1880 is not well described by a
383 Gaussian distribution. In fact, the distribution of canopy disturbances is ‘heavy tailed’ (Figure 2c,
384 d). Notably, all years from 1775-1778 are included in the list of the top seven most disturbed
385 years (Figure 2d) and show a disturbance rate $\geq 3\%$, which is \geq the 98th-percentile of our data set.
386 These years are well out in the ‘heavy tail’ of the disturbance rate distribution (Figure A10).
387 Return intervals for disturbance rates of 2%, 4%, and 6% of disturbed trees per year ranged from
388 40, 250, and ~930 years, respectively. Uncertainty around return intervals greatly flares out
389 beyond the 4% rate because of small sample size (Figure A11).

390 We found that elevated canopy disturbance is significantly correlated with a low index of
391 inferred drought during the prior year (Figure 3a). Drier conditions prevail during four of the five
392 years prior to elevated disturbance. The southern Appalachian Mountain region experienced
393 three intense droughts between 1742 and 1775 with the 1772-1775 drought, spatially expressed
394 across much of the temperate US, as the most intense (Figure 3b, c). Composite maps of North
395 American drought for the year prior to elevated disturbance, the 1772-1775 drought, and a
396 statistical model of the 1772-1775 drought reveals pan-continental drying over most of the U.S.
397 and wetter than average conditions in the Pacific Northwest and northern Great Plains
398 (Figures 3d, A12). These findings indicate that regional-scale drought is associated with elevated
399 disturbance across the 1775-1780 disturbance region.

400

401 *Tree Recruitment across the Eastern Deciduous Forest*

402 Recruitment data from studies using plot level or representative sampling (Category 1)
403 have 2,277 dates from trees that recruited between 1460 and 1850. Of these trees, 14.5% (n =
404 330 trees) recruited between 1650-1699, with more than half of these trees recruiting from 1670-
405 1689 (n = 168). In sharp contrast, only 86 trees (3.8%) recruited from 1600-1649, or less than
406 half of those recruiting between 1670 and 1689. Of the 620 recruitment dates collected through
407 representative or plot-level sampling in old-growth forests before 1944 (e.g., Gates and Nichols
408 1930, Williams 1936, Hough and Forbes 1943), 21.1% recruited from 1650-1699 versus 8.5%
409 from 1600-1649 and 10.8% from 1500-1649 (Table 2). Segmented linear regression on Category
410 1 data indicates a significant break in recruitment around 1599 CE (± 10.6 yrs). Residuals from
411 this regression indicate a large and prolonged period of recruitment from 1640-1699, followed by
412 below average recruitment from 1700-1729, and decadal-scale fluctuation through 1849 (Figure
413 4a). The three greatest positive departures in recruitment occur in the 1670s (a residual departure
414 of +1.36), 1680s (+0.79), and 1780s (+0.79). Data from targeted sampling (Category 2) or
415 collections made during the early-1900s that do not have data after 1699 (Category 3), reveal
416 similar jumps in recruitment during the latter half of the 17th century (Table 2). Within Category
417 2, the peak in recruitment of the 461 historical timber dates is centered on 1660-1699 (35.4% of
418 total sample) with 15.6% recruited from 1670-1689 versus 18.4% during the preceding 119
419 years. Despite deliberate attempts by 15 different tree-ring scientists over the last 30 years to
420 core the oldest living trees in various forests, only 5.1% of the 730 trees recruited between 1500
421 and 1649. In comparison, 7.5% of the 730 trees recruited between 1670-1689.

422

423 **Discussion**

424 Our records of forest dynamics – two large, species-rich, and geographically-extensive
425 data sets – indicate that: 1) the dynamics of broadleaf forests in a temperate, humid region occur
426 synchronously across different scales, from the stand to subcontinental level and 2) extended

427 events of canopy disturbance are often of greater severity. These findings more closely resemble
428 our alternative hypothesis where forest dynamics can be regionally synchronous and punctuated
429 by extreme events. Discovering that larger canopy gaps are often formed during synchronous
430 large-scale events in broadleaf-dominated forests is broadly relevant because it provides a
431 mechanism for rapid, large-scale change. That is, a greater number of larger canopy openings in
432 light-limited forests offer increased opportunities for a compositional shift in the canopy at the
433 time of major disturbance. Our large-scale analysis also reveals a greater spatial extent of
434 previously reported disturbances. The large and severe 1775-1780 event is a period of increased
435 disturbance observed at the stand scale in western North Carolina (Fig 7 in Lorimer 1980) and
436 landscape scale in central Tennessee (Figs 7 & 8 in Hart et al. 2012) and central Pennsylvania
437 (see Table 3 in Nowacki and Abrams 1997). This large-scale event precedes the highest peak in
438 tree recruitment in our data set from 1700-1849 (Figure 4a). Further, two other periods of
439 extended disturbance discovered in our study, 1737-1739 and 1755-1758 (Table 1), are evident
440 in a landscape-scale study (Hart et al. 2012). While the resulting time-series of disturbance still
441 resembles a white-noise process, we find synchronous disturbance at multi-annual to nearly
442 decadal time-scales. Our findings go beyond the limitations of local studies and reveal forest
443 dynamics at both the landscape and mesoscale (from decades to centuries over 100 to 100,000
444 km²). As such, they are relevant for anthropogenic climate change and have important
445 implications for forest management.

446 We have also statistically identified a plausible trigger for these disturbance events:
447 drought-induced canopy mortality. These findings support observations of drought-induced
448 forest dynamics and sensitivities conducted at short time scales and local to regional scales
449 (Hough and Forbes 1943, Clinton et al. 1993, Jenkins and Pallardy 1995, Olano and Palmer
450 2003) across different forest types including humid regions (Allen et al. 2010, Choat et al. 2012).
451 In doing so, we bridge the spatial and temporal gaps between local and sediment studies by

452 providing insights from paleoecological records while revealing broad-scale patterns not seen in
453 stand-scale or landscape-level studies.

454 Disturbance in humid to wet temperate regions can be characterized by frequent, small,
455 low-severity disturbance events with occasional large-scale, intense disturbance (Lorimer 1989,
456 White et al. 1999). Most studies in extant forests in humid regions have not revealed regional-
457 scale events perhaps because of a predominant focus on local to landscape scales. Experimental
458 forest modeling suggests small-scale analysis reduces the ability to detect large-scale change
459 (Smith and Urban 1988). Our results reveal dynamical processes at small and large-scales over
460 the last 400 years (cf., Jackson 2006) and demonstrate the legacy of large-scale, intense
461 disturbance events centuries after their occurrence in broadleaf-dominated forests, a finding
462 similar to previous work (e.g., Lorimer 1980, Frelich and Lorimer 1991, Nowacki and Abrams
463 1994, Hanson and Lorimer 2007). The distinction here is that we document events at regional to
464 subcontinental spatial scales and show that some of these events can occur repeatedly within the
465 maximum longevity of many canopy species. The infrequent, but meso to large scale
466 disturbances are important because they can create the “substrate” that the more frequent, but
467 less-intense, small-scale dynamics act upon. While it is known that historical events resonate for
468 centuries and millennia through the structure and dynamics of forested ecosystems (e.g., Lorimer
469 1989, Sprugel 1991, Swetnam and Betancourt 1998, Foster et al. 1999, Williams and Jackson
470 2007, Turner 2010), we have identified large-scale events from 230-360 years ago at high
471 resolution that are still reverberating in the structure of today’s old-growth broadleaf-dominated
472 forests.

473 Interestingly, some old trees in today’s old-growth forests in the eastern US are the result
474 of historical events (Tables 1, 2; Figures 1b, 2a, b) that occurred during a drier era than the more
475 moist conditions that prevailed during the period of repeated measures and field studies (Figure
476 5). Dry conditions have the potential to alter other processes like increased fire or insect

477 outbreaks (e.g., Raffa et al. 2008, Lynch and Hessler 2010) and feed into forest dynamics in direct
478 and indirect ways. The rare, but coherent, spatially broad, and severe events identified here can
479 provide greater opportunities for regeneration as canopy gap formation increases. Alternatively,
480 these species-rich forests, interacting with historical contingencies and a wide range of possible
481 future scenarios, could abruptly change into substantially different types than the current forest
482 (Williams and Jackson 2007).

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

490

491 *Triggers for Elevated Canopy Disturbance*

492 Triggers of elevated canopy disturbance at large scales across a humid and diverse region
493 are likely complex. Our data support early and more research linking tree mortality to drought
494 across forest types and land-use histories (e.g., Lorimer 1984, Olano and Palmer 2003, Mueller
495 et al. 2005, Pederson et al. 2008, 2012b, Anderegg et al. 2012). The association between
496 disturbance extent and disturbance intensity indicating the mortality of canopy trees dovetails
497 with observations that tall and large canopy trees are more susceptible to drought-induced
498 mortality (e.g., Hursh and Haasis 1931, Hough and Forbes 1943, Floyd et al. 2009, Hartmann
499 2011). Trees in closed-canopy forests primarily compete for canopy access and solar radiation
500 (Hartmann 2011). Competition for solar radiation likely pushes tree height near the maximum
501 height possible within the context of microsite and other prevailing environmental conditions.

502 Because tree height limits leaf-specific hydraulic conductance (McDowell et al. 2008), it is likely
503 that canopy trees in closed-canopy forests live closer to the margin of water balance for survival
504 and are more susceptible to drought-induced mortality. This has been directly observed within
505 our larger study region: the “*extreme drought of 1930*” in Pennsylvania led to “*mortality of the*
506 *larger or overstory trees both of hemlock and of the subsequently exposed beech*” (Hough and
507 Forbes, 1943, page 311). Further, repeated drought increases the mortality risk of trees (Pedersen
508 1998, McDowell et al. 2008). Therefore, it is not too surprising that the 1775-1780 disturbance
509 event is preceded by three intense droughts during the previous three decades (Figure 3b). Our
510 data suggests that drought plays an important role in canopy dynamics of broadleaf-dominated
511 forests in the eastern US.

512 While the 1772-1775 drought was severe, it is not the most severe over the last 450 years
513 (Figure 3b). Therefore, a variety of additional triggers likely interacted with drought to generate
514 the broad-scale patterns of disturbance and canopy dynamics. For instance, colonial-era
515 documents reveal an early onset of leaf-out in 1774 and the commencement of farming two
516 weeks early across the southeastern U.S. (e.g., Thomas Jefferson’s Garden Book, 1774, Fries
517 1925). Heavy frosts after the cold nights of May 4th and 5th 1774 made green leaves look “*black*
518 *and dead*” (Fries 1925). Additional accounts confirm cold air, frost, or damage to plant tissue
519 throughout the southeastern US up to southeastern Pennsylvania (*The Pennsylvania Gazette*
520 (Philadelphia, PA) May 11, 1774, p. 2; Virginia Gazette (Williamsburg, VA) May 12, 1774, p. 4;
521 *Essex Gazette* (Salem, MA) June 7, 1774, p. 176). A frost was observed to have killed “*every*
522 *tender thing*” near coastal South Carolina (Rudisill 1993). These observations confirm tree-ring
523 evidence of a frost event in the southern Appalachian Mountain region (Figure A8) and extend it
524 throughout the southeastern US.

525 Following repeated drought during the mid 1700s, the 1774 frost event and subsequent
526 defoliation must have reduced available energy from surviving, but drought-stressed trees.

527 Widespread frost events in April 2007 (Gu et al. 2008, Augspurger 2009) and May 2010
528 (Hufkens et al. 2012) lead to tissue and shoot dieback and necrosis in ways similar to 1774 (see
529 Figure A13a). Refoliation in 2007 did not occur for more than a month in some cases
530 (Augspurger 2009), especially for *Liriodendron tulipifera* (Gu et al. 2008; see Figure A13b), and
531 was estimated to be 46-99% of 'normal' for seven species, with 40 to ca. 90% coming from a
532 second flush (Gu et al. 2008, Augspurger, 2009). In 2010, net carbon assimilation of *Acer*
533 *sacharrum* was reduced following leaf necrosis and delayed canopy development (Hufkens et al.
534 2012). If these frosts were similar in intensity to the 1774 frost, preceding climatic conditions
535 prior to 1774 likely predisposed canopy trees to higher rates of mortality (sensu Manion 2003).
536 The mid-18th century was one of the driest periods in the southeastern US of the last 300 years
537 (Cook et al. 1988, Pederson et al. 2012a). Trees adapt to aridity by: 1) shedding leaves, 2)
538 reducing the root/sapwood to leaf area ratio, and 3) experiencing a reduction in height through
539 crown dieback (McDowell et al. 2008). Drought-stressed trees recovering from the severe 1774
540 frost could struggle with alteration of the carbon sink or carbon metabolism (cf., Adams et al.
541 2013). Lesser, 20th-century droughts are known to have lead to tree mortality (Jenkins and
542 Pallardy 1995, Pedersen 1998), suggesting the more severe mid-18th century droughts could have
543 resulted in greater mortality (Figure 3b). The rate of disturbance in our data during the late 1770s
544 was up to 7.8 times greater than the mean (Figure 2), a rate even greater than that observed in a
545 tropical everwet forest during the strong, El Niño drought of 1998 (Potts 2003). Based upon
546 these observations, we postulate that the 1770s period of elevated disturbance was likely
547 triggered by several interacting factors, including drought and frost.

548 Following decades of dry conditions, however, fire is another potential contributor to
549 elevated disturbance of the late 1770s. Fire occurs more often and burns a larger area in a humid
550 region during drier conditions (Lynch and Hessl 2010) and in areas with a great range of daily
551 precipitation variability (Lafon and Quiring 2012). Fire was generally rare, spatially restricted, or

552 absent from 1775-1780 in or near the event region (Guyette et al. 1994, Aldrich et al. 2010,
553 Feathers 2010, Flatley et al. 2013, McEwan et al. 2013). As an example, Flatley et al. (2013)
554 reports ‘area-wide’ fires in 1773 and 1775 in only one of three forests they investigated. These
555 findings suggest a lack of broad-scale fire during the 1770s. Fire is not recorded in the mid-
556 1700s in broadleaf-dominated forests, although it is was recorded before and after this period
557 (Guyette et al. 1994, McEwan et al. 2013). Guyette et al., (2006) show an increase in fire during
558 the 1770s, but also note that “*Fire frequency was highly variable in both time and space even at*
559 *regional scales*” (Guyette et al. 2006; pg 20). The broadest fire in this region occurred in 1780
560 (Guyette et al. 2002), which is after the peak of the 1770s disturbance event. Due to the low
561 incidence of spatially-extensive fire across our study region during the 1770s, a pattern supported
562 by paleo studies (Clark and Royall 1996, Parshall and Foster 2003), and the ability of drought to
563 kill overstory trees, it would seem repeated, intense drought leading up to the mid 1770s was a
564 primary contributor to elevated canopy mortality with frost-induced defoliation and potentially
565 fire as secondary contributors.

566 Windstorms are another important canopy disturbance that have been well documented
567 across our study region (Lorimer 1977, White 1979, Foster and Boose 1992, Everham and
568 Brokaw 1996, Peterson 2000, 2007, Stueve et al. 2011). Windstorms can leave a lasting impact
569 in forests beyond the stand scale. To wit, a squall line increased mortality over roughly 0.027
570 km² in the Amazon (Negrón-Juárez et al. 2010), while a conservative estimate of windstorms in
571 the midwestern US was extrapolated to damage forests over ca 1,500 km² over a 26-year period
572 (Stueve et al. 2011). In contrast with line storms or tornadoes, which are local in scale,
573 hurricanes have the potential to affect large regions. From a compilation of hurricanes striking
574 the eastern U.S. during each elevated disturbance event in our study (Table A4), we find that five
575 elevated disturbance events coincide with relatively high landfall years (1766-1768, 1834-1836,
576 1840-1843, 1870-1872, 1877-1883); ‘relatively high’ here is ≥ 2 hurricanes per year. However,

577 the simple occurrence of a hurricane making landfall might not translate into an ecological
578 impact because of insufficient intensity or a failure to penetrate inland. Focusing on the most
579 important of these reconstructed events, 1775-1780, the Moravian records hold no evidence of
580 forest damage from wind during the hurricane season. There are three hints that low-pressure
581 systems might have moved through western North Carolina during this period, however. First, it
582 was noted on August 30, 1775 that, "*For some time it has been raining every day*" and that by
583 September 4 there has been large-scale clearing of the atmosphere, "*It is clear, but the air feels*
584 *like fall*" (Fries 1925, pg 883). The track of this storm appears to have traveled far to the east of
585 the 1775-1780 event region (Rappaport and Ruffman 1999). Then, in 1778, a year with
586 hurricanes in August and October (Table A4), there are observations of "*a hard storm from the*
587 *north-east*" on August 11 (Fries 1926, pg 1244) and that a "*strong wind from the north-east*
588 *cleared the sky*" on October 11 (Fries 1926, pg 1248). No forest damage is reported with these
589 observations. Observations of winds from the northeast, but with less than tropical-storm
590 strength, matches model predictions of tropical storm decay into this region (Kaplan and
591 DeMaria 1995). And, observations of winds from the northeast causing no damage are in
592 contrast to the windstorms of note between 1774 and 1779. The March 1775 the storm "*fell over*
593 *a strip about 14 miles long and four wide*" (Fries 1925, pg 873). Similarly, the March 1776
594 windstorm was reported to be more local: "*Br. Praezal returned from Bethabara; the storm was*
595 *not nearly so severe there, and had done no particular damage*" (Fries 1926, pg 1057). It is
596 beyond the scope of this investigation to quantify the paths of all windstorms and their impacts
597 within our network. While geographically limited, the Moravian records suggest only one wind
598 event at the landscape scale and no late-season windstorms of the years we reviewed (the
599 Moravians diaries contain no evidence of hurricane-like storms during the 1766-1768 event).
600 Nevertheless, windstorms are a potential factor affecting historical canopy disturbance.

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

611

612 *Tree Recruitment Across the Eastern Deciduous Forest*

613 Our recruitment data reveals a subcontinental-scale event in a forest type where this scale
614 of event would be less expected. This finding synthesizes nearly a century of reported stand
615 origin dates scattered across the literature. Given the temporal distribution of these studies over
616 the last 90 years and that the forests from which these data are collected can be characterized by
617 continuous, small-scale dynamics, the date of stand origin would be expected to shift back in
618 time according to the time of sample collection. We found, in fact, that a disproportionate
619 amount of recruitment occurs during the mid to late 1600s, even in the oldest studies with
620 recruitment dates. These findings resemble recent evidence of a regional-scale synchrony of
621 understory forest dynamics in a broadleaf-dominated forest (Gravel et al. 2010). Our findings
622 suggest that synchronized tree recruitment at large scales can be an important process in
623 broadleaf-dominated ecosystems.

624 While it is possible that the late 1600s recruitment pulse is an artifact of tree longevity,
625 four lines of evidence argue against this idea. First, 21 tree species in Category 1 recruited

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

649

650 *Potential Triggers of the 17th Century Recruitment Pulse*

651 Though recruitment is often associated with wet conditions, drought could lead to tree
652 recruitment (Shuman et al. 2009). In this scenario, formation of canopy gaps from drought-
653 induced mortality would increase the amount of solar radiation penetrating the understory to
654 stimulate potential recruitment. A return to mesic conditions following drought could aid
655 recruitment. Hydroclimatic records with decadal-scale resolution from Quebec to Ohio and Lake
656 Michigan indicate drier conditions during the early to mid-17th century (Bégin and Payette 1988,
657 Wolin 1996, Lichter 1997, Loope and Arbogast 2000, Greenlee 2006, Argyilan et al. 2010,
658 Hubeny et al. 2011). The dating uncertainties of these records are a limitation, but a record in this
659 region reports a “*high probability*” of trees growing below current water levels “*as early as AD*
660 *1663*” (Shuman et al. 2009, pg. 2796). These geologic records suggest regional drought from ca.
661 1640-1680 that could have caused wide-scale increased canopy tree mortality.

662 Despite some asynchrony, tree-ring records across the eastern U.S. indicate drier
663 conditions during the mid-1600s. Each record contains severe drought between 1630 and 1650
664 (Figure 4b). A mid-Mississippi River Valley record indicates the mid-17th century to be the driest
665 since 1600 CE (Cook et al. 2010) while a northeastern US record indicates six severe droughts
666 between 1629 and 1700 (Pederson et al. 2013). Of these six droughts, five rank as the 10 most
667 severe droughts since 1531 CE, with 1661-1667 and 1630-1636 ranked second and third,
668 respectively. Other annually-resolved proxies support these records over a large region (St.
669 George et al. 2009, Maxwell et al. 2011). Interestingly, all of these tree-ring proxies generally
670 substantiate some geologic evidence for a mid-1600s drought sandwiched between two pluvials,
671 prolonged periods of above-average moisture (Wolin 1996, Lichter 1997, Loope and Arbogast
672 2000, Argyilan et al. 2010). The switch from pluvial conditions following drought during the 17th
673 century likely has far-reaching ecological consequences. If trees adapt to aridity by root and
674 shoot dieback (McDowell et al. 2008), then pluvial conditions likely stimulate the opposite.
675 Therefore, an abrupt, severe drought following a pluvial could exacerbate drought stress by

676 making it difficult to maintain pluvial-level biomass, elevating mortality, increasing solar
677 radiation to the forest floor, and possibly increasing opportunities for tree recruitment.

678 Like many aspects of macroecology, the exact cause of regional-scale disturbance cannot
679 be ascribed to a single trigger (McEwan et al. 2011). Low tree replication prior to the mid 1600s
680 forces us to consider circumstantial evidence. The combination of fire and drought cannot be
681 ruled out. Several studies found charcoal or asserted that drought and fire led to stand origin
682 during the mid-1600s (Huntington 1914, Hough and Forbes 1943, Henry and Swan 1974, Foster
683 1988). The most consistent fires in northwestern Vermont, for example, occurred in 1586, 1595,
684 1635, and 1670 (Mann et al. 1994), which coincides with some of the driest periods in the
685 northeastern U.S. (Pederson et al. 2013). While sample replication is low in the heart of our
686 study region, fire is more often recorded from 1660-1680 than during the mid 1700s (Mann et al.
687 1994, Guyette and Dey 1995, Dey and Guyette 2000, Guyette et al. 2002, 2006, Guyette and
688 Spetich 2003, McMurry et al. 2007, Stambaugh et al. 2011).

689 Given that forests in the Western Hemisphere were in a ‘managed landscape’ prior to
690 European settlement (Crosby 1986, Mann 2005, Krumhardt 2010), it is possible that the
691 catastrophic decline in indigenous populations contributed to the recruitment pulse. However, the
692 locations of recruitment data and resettlement patterns post-population collapse are in opposition
693 to one another. Recruitment data used here are primarily from old-growth forests in mountainous
694 areas (Figure A6; see raw recruitment data in Supplement A). Most of today’s old-growth forests
695 grow on sites with low productivity and commercial viability (Therrell and Stahle 1998). Most
696 indigenous populations were observed in large and fertile river valleys at the time of European
697 settlement (Cronon 1983, Williams 1992, Davis 2000). In the southern Appalachian Mountain
698 region, people moved into flatter, moister river valleys following the population collapse (Davis
699 2000). Supporting this, an estimation of natural vegetation inferred from human demographics
700 indicates forests to be broadly recovered by 1600 CE over much of our study region (Figure

701 A14; Krumhardt 2010). The uncertainties regarding land-use and human demographics are large
702 at this time (Milner and Chaplin 2010), but they suggest broad forest recovery at least 50-years
703 prior to our reconstructed recruitment pulse.

704

705 *Climate Change Implications*

706 Secular trends in anthropogenic climate change are expected to have significant impacts
707 on eastern US forests (Iverson and Prasad 2001, McKenney et al. 2011), although change could
708 occur relatively slowly due to hysteresis and canopy persistence (e.g., Loehle 2000). However, as
709 observed here, rare or low probability events could have immediate and long-term ramifications
710 for ecosystem structure and function. The severe frost event of 1774 following repeated droughts
711 over large spatial scales altered the trajectory of forest structure through synchronous canopy
712 disturbance. These changes in forest structure generated historical contingencies that can be
713 observed today. Severe droughts in the eastern US, like the 1960s drought that increased *Acer*
714 *rubrum* mortality (Lorimer 1984), can occur as a result of internal variability of the climate
715 system (Seager et al. 2012) making stochastic climate dynamics an important aspect of forest
716 dynamics. Further, Pacific Ocean sea surface temperatures seems to have been a trigger for the
717 1772-1775 drought (Figure 3d) and, thus, ocean-atmosphere dynamics may have created a legacy
718 in eastern US forests where this part of the climate system has less of an influence on the average
719 climatology. These events illustrate how hard-to-predict, singular scenarios can shape forests for
720 decades to centuries in regions where the average scenario might not.

721 Understanding how the effects of long-term climate trends and extreme events interact is
722 a major challenge for ecological forecasting, not the least because extreme events such as
723 droughts have often been perceived as a minor risk in humid regions such as eastern North
724 America (e.g., McMahon et al. 2010, Vanderwel et al. 2013, Schleeweis et al. 2013). Future
725 droughts could turn out to be analogous to the 16th century megadrought (Stahle et al. 2000), the

726 most synchronous drought across our study region over the last 450 years (Figure 4b). If future
727 warming exacerbates drought stress in trees and other stressors including elevated air pollution
728 (Dietze and Moorcroft 2011), non-native pests and pathogens (Aukema et al. 2010), or a
729 combinations of stressors (e.g., Waller 2013), widespread tree mortality and subsequent canopy
730 turnover could drive rapid rates of change in temperate forests across humid eastern North
731 America.

732

733 **Summary**

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

741 Our results can aid future simulations attempting to forecast carbon sinks or rates of
742 ecological change under a changing climate (e.g., Millar et al. 2007) at the scales relevant to the
743 management of forests across a region with high ecosystem functionality (Freudenberger et al.
744 2012). Large-scale, synchronous, and climatically-influenced disturbances over the last four
745 centuries are still detectable, and thus, important in today's old-growth forests. These events
746 point to the possibility that severe events can push ecosystems to new structures and/or
747 compositions (Jackson 2006, Williams and Jackson 2007, Jackson et al. 2009, Frelich and Reich
748 2010), even by distal climate systems that do not typically have an influence on a particular
749 region. As local and regional climate and ecologies are influenced by Anthropogenic climatic
750 change, historical events and species diversity will interact in complex ways as the future forest

751 develops. Evidence here indicates that broadleaf-dominated forests could change abruptly from
752 small to subcontinental scales in the coming decades.

753

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769 **Literature Cited**

- 770 Adams, H. D., M. J. Germino, D. D. Breshears, G. A. Barron-Gafford, M. Guardiola-
771 Claramonte, C. B. Zou, and T. E. Huxman. 2013. Nonstructural leaf carbohydrate dynamics
772 of *Pinus edulis* during drought-induced tree mortality reveal role for carbon metabolism in
773 mortality mechanism. *New Phytologist* 197:1142–1151.
- 774 Aldrich, S. R., C. W. Lafon, H. D. Grissino-mayer, G. G. Deweese, and J. A. Hoss. 2010. Three
775 centuries of fire in montane pine-oak stands on a temperate forest landscape. *Applied*
776 *Vegetation Science* 13:36–46.
- 777 Allen, C. D., and D. D. Breshears. 1998. Drought-induced shift of a forest–woodland ecotone:
778 Rapid landscape response to climate variation. *Proceedings of the National Academy of*
779 *Sciences of the United States of America* 95:14839–14842.
- 780 Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T.
781 Kitzberger, A. Rigling, D. D. Breshears, and E. H. (Ted) Hogg. 2010. A global overview of
782 drought and heat-induced tree mortality reveals emerging climate change risks for forests.
783 *Forest Ecology and Management* 259:660–684.
- 784 Anderegg, W. R. L., J. A. Berry, D. D. Smith, J. S. Sperry, L. D. L. Anderegg, and C. B. Field.
785 2012. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-
786 off. *Proceedings of the National Academy of Sciences of the United States of America*
787 109:233–237.
- 788 Argyilan, E. P., S. L. Forman, and T. A. Thompson. 2010. The Holocene variability of Lake
789 Michigan water level during the past 1000 years. *The Holocene* 20:723–731.
- 790 Augspurger, C. K. 2009. Spring 2007 warmth and frost: phenology, damage and refoliation in a
791 temperate deciduous forest. *Functional Ecology* 23:1031–1039.

- 792 Aukema, J. E., D. G. McCullough, B. Von Holle, A. M. Liebhold, K. Britton, and S. J. Frankel.
793 2010. Historical Accumulation of Nonindigenous Forest Pests in the Continental United
794 States. *BioScience* 60:886–897.
- 795 Baker, P., S. Bunyavejchewin, C. D. Oliver, and P. S. Ashton. 2005. Disturbance history and
796 historical stand dynamics of a seasonal tropical forest in western Thailand. *Ecological*
797 *Monographs* 75:317–343.
- 798 Bégin, Y., and S. Payette. 1988. Dendroecological evidence of lake-level changes during the last
799 three centuries in subarctic Quebec. *Quaternary Research* 30:210–220.
- 800 Biondi, F., T. J. Kozubowski, and A. K. Panorska. 2005. A new model for quantifying climate
801 episodes. *International Journal of Climatology* 25:1253–1264.
- 802 Booth, R. K., S. T. Jackson, V. A. Sousa, M. E. Sullivan, T. A. Minckley, and M. J. Clifford.
803 2012. Multi-decadal drought and amplified moisture variability drove rapid forest
804 community change in a humid region. *Ecology* 93:219–226.
- 805 Brown, P. M., and R. Wu. 2005. Climate and disturbance forcing of episodic tree recruitment in
806 a southwestern ponderosa pine landscape. *Ecology* 86:3030–3038.
- 807 Burns, R. M., and B. H. Honkala. 1990. *Silvics of North America: 1. Conifers; 2. Hardwoods.*
808 Washington, D.C. 877 pp. USDA Forest Service Agriculture Handbook 654.
- 809 Chenoweth, M. 2006. A reassessment of historical Atlantic Basin tropical cyclone activity,
810 1700–1855. *Climatic Change* 76:169–240.
- 811 Cho, D.-S., and R. E. J. Boerner. 1995. Dendrochronological analysis of the canopy history of
812 two Ohio old-growth forests. *Vegetatio* 120:173–183.
- 813 Choat, B., S. Jansen, T. J. Brodribb, H. Cochard, S. Delzon, R. Bhaskar, S. J. Bucci, T. S. Feild,
814 S. M. Gleason, U. G. Hacke, A. L. Jacobsen, F. Lens, H. Maherali, J. Martínez-Vilalta, S.
815 Mayr, M. Mencuccini, P. J. Mitchell, A. Nardini, J. Pittermann, R. B. Pratt, J. S. Sperry, M.

816 Westoby, I. J. Wright, and A. E. Zanne. 2012. Global convergence in the vulnerability of
817 forests to drought. *Nature* 491:752–5.

818 Clark, J., and P. Royall. 1996. Local and regional sediment charcoal evidence for fire regimes in
819 presettlement north-eastern North America. *Journal of Ecology* 84:35–382.

820 Clinton, B. D., B. L. R., and W. T. Swank. 1993. Canopy gap characteristics and drought
821 influences in oak forests of the Coweeta Basin. *Ecology* 74:1551–1558.

822 Coles, S. 2001. An introduction to statistical modeling of extreme values. 224 pp. Springer-
823 Verlag, London.

824 Cook, E., and G. Jacoby. 1977. Tree-ring-drought relationships in the Hudson Valley, New
825 York. *Science* 198:399–401.

826 Cook, E., M. Kahlack, and G. Jacoby. 1988. The 1986 drought in the southeastern United States:
827 How rare an event was it? *Journal of Geophysical Research* 93:14,257–14,260.

828 Cook, E. R. 1982. Tree-Ring Data Networks: comment. Pages 6–7 *in* M. K. Hughes, P. M.
829 Kelly, J. R. Pilcher, and V. C. LaMarche Jr., editors. *Climate from Tree Rings*. Cambridge
830 University Press, London.

831 Cook, E. R., and G. C. Jacoby. 1983. Potomac River streamflow since 1730 as reconstructed by
832 tree rings. *Journal of Climate and Applied Meteorology* 22:1659–1672.

833 Cook, E. R., and P. J. Krusic. 2004. *The North American Drought Atlas*.
834 <http://iridl.ldeo.columbia.edu/SOURCES/.LDEO/.TRL/.NADA2004/.pdsi-atlas.html> .

835 Cook, E. R., C. a Woodhouse, C. M. Eakin, D. M. Meko, and D. W. Stahle. 2004. Long-term
836 aridity changes in the western United States. *Science* 306:1015–8.

837 Cook, E., R. Seager, R. R. J. Heim, R. S. Vose, C. Herweijer, and C. A. Woodhouse. 2010.
838 Megadroughts in North America: placing IPCC projections of hydroclimatic change in a
839 long-term palaeoclimate context. *Journal of Quaternary Science* 25:48–61.

840 Copenheaver, C. a., B. a. Black, M. B. Stine, R. H. McManamay, and J. Bartens. 2009.
841 Identifying dendroecological growth releases in American beech, jack pine, and white oak:
842 Within-tree sampling strategy. *Forest Ecology and Management* 257:2235–2240.

843 Cronon, W. 1983. *Changes in the Land: Indians, Colonists, and the Ecology of New England*.
844 235 pp. Hill and Wagner.

845 Crosby, A. W. 1986. *Ecological Imperialism: The Biological Expansion of Europe, 900-1900*.
846 390 pp. Cambridge University Press, Cambridge, United Kingdom.

847 D’Amato, A. W., and D. A. Orwig. 2008. Stand and landscape-level disturbance dynamics in
848 old-growth forests in western Massachusetts. *Ecological Monographs* 78:507–522.

849 Davis, D. E. 2000. *An Environmental History of the Southern Appalachians*. 320 pp. The
850 University of Georgia Press, Athens, Georgia, U.S.A.

851 Davison, A. C., and R. L. Smith. 1990. Models for exceedances over high thresholds. *Journal of*
852 *the Royal Statistical Society. Series B (Methodological)* 52:393–442.

853 Dey, D. C., and R. P. Guyette. 2000. Anthropogenic fire history and red oak forests in south-
854 central Ontario. *Forestry Chronicle* 76:339–347.

855 Dietze, M. C., and P. R. Moorcroft. 2011. Tree mortality in the eastern and central United States:
856 patterns and drivers. *Global Change Biology* 17:3312–3326.

857 Druckenbrod, D. L., N. Pederson, J. Rentch, and E. R. Cook. 2013. A comparison of times series
858 approaches for dendroecological reconstructions of past canopy disturbance events. *Forest*
859 *Ecology and Management* 302:23–33.

860 Dyer, J. M. 2006. Revisiting the deciduous forests of eastern North America. *BioScience* 56:
861 341-352.

862 Endfield, G. H. 2012. Complexity, causality and collapse: social discontinuity in history and
863 prehistory. Pages 355–374 in J. Matthews, editor. Handbook of Environmental Change
864 Sage: Vol 2. SAGE Publications, London.

865 Essex Gazette. 1774, June 7. Extract of a Letter from Baltimore, dated May 21. Essex
866 Gazette:176. Salem, MA.

867 Everham, E., and N. Brokaw. 1996. Forest damage and recovery from catastrophic wind. The
868 Botanical Review 62:113–185.

869 Feathers, I. C. 2010. Fire History from Dendrochronological Analyses at Two Sites near Cades
870 Cove, Great Smoky Mountains National Park, U.S.A. MS Thesis. University of Tennessee.

871 Flatley, W. T., C. W. Lafon, H. D. Grissino-Mayer, and L. B. Laforest. 2013. Fire history and its
872 relation to climate and land use in three Southern Appalachian landscapes in the Eastern
873 U.S. Ecological Applications 23:1250–1266.

874 Floyd, M. L., M. Clifford, N. S. Cobb, D. Hanna, R. Delph, P. Ford, and D. Turner. 2009.
875 Relationship of stand characteristics to drought-induced mortality in three southwestern
876 piñon-juniper woodlands. Ecological Applications 19:1223–1230.

877 Foster, D., and E. Boose. 1992. Patterns of forest damage resulting from catastrophic Patterns of
878 forest wind in central New England, USA. Journal of Ecology 80:79–98.

879 Foster, D., M. Fluet, and E. Boose. 1999. Human or natural disturbance: landscape-scale
880 dynamics of the tropical forests of Puerto Rico. Ecological Applications 9:555–572.

881 Foster, D. R., W. W. Oswald, E. K. Faison, E. D. Doughty, and B. C. S. Hansen. 2006. A
882 climatic driver for abrupt mid-Holocene vegetation dynamics and the hemlock decline in
883 New England. Ecology 87:2959–66.

884 Fralish, J.S., and Franklin, S.B. 2002. Taxonomy and Ecology of Woody Plants in North
885 American Forests. 612 pp. New York, NY. John Wiley and Sons.

886 Frelich, L. E. 2002. *Forest Dynamics and Disturbance Regimes Studies from Temperate*
887 *Evergreen-Deciduous Forests*. 280 pp. Cambridge University Press, Cambridge, United
888 Kingdom.

889 Frelich, L., and C. Lorimer. 1991. Natural disturbance regimes in hemlock-hardwood forests of
890 the Upper Great Lakes Region. *Ecological monographs* 61:145–164.

891 Freudenberger, L., P. R. Hobson, M. Schluck, and P. L. Ibisch. 2012. A global map of the
892 functionality of terrestrial ecosystems. *Ecological Complexity* 12:13–22.

893 Fries, A. L. (ed.). 1922. *Records of the Moravians in North Carolina, Volume 1, 1752-1771*.
894 North Carolina Historical Commission, Raleigh, NC.

895 Fries, A. L. (ed.). 1925. *Records of the Moravians in North Carolina, Volume 2, 1752-1775*.
896 Pages 808–839. North Carolina Historical Commission, Raleigh, NC.

897 Fries, A. L. (ed.). 1926. *Records of the Moravians in North Carolina, Volume 3, 1776-1779*.
898 North Carolina Historical Commission, Raleigh, NC.

899 Fritts, H. C. 1976. *Tree Rings and Climate*. 567 pp. Academic Press, New York.

900 Gates, F. C., and G. E. Nichols. 1930. Relation between age and diameter of the trees in the
901 primeval northern hardwood forest. *Journal of Forestry* 28:395–398.

902 Gravel, D., M. Beaudet, and C. Messier. 2010. Large-scale synchrony of gap dynamics and the
903 distribution of understory tree species in maple–beech forests. *Oecologia* 162:153–161.

904 Gray, S. T., J. J. Lukas, and C. a. Woodhouse. 2011. Millennial-length records of streamflow
905 from three major Upper Colorado River tributaries. *Journal of the American Water*
906 *Resources Association* 47:702–712.

907 Greenlee, D. M. 2006. Dietary variation and prehistoric maize farming in the middle Ohio
908 Valley. Pages 215–233 *in* J. E. Staller, R. H. Tykot, and B. E. Benz, editors. *Histories of*

909 Maize: Multidisciplinary Approaches to the Prehistory, Linguistics, Biogeography,
910 Domestication, and Evolution of Maize. Academic Press, Waltam, MA.

911 Grimm, E. 1983. Chronology and dynamics of vegetation change in the prairie-woodland region
912 of southern Minnesota, U.S.A. *New Phytologist* 93:311–350.

913 Gu, L., P. J. Hanson, W. Mac Post, P. Kaiser, Dale, B. Yang, R. Nemani, S. G. Pallardy, and T.
914 Meyers. 2008. The 2007 Eastern US spring freeze: Increased cold damage in a warming
915 world? *BioScience* 58:253–262.

916 Gutierrez, A. G., J. C. Aravena, N. V. Carrasco-Farias, D. A. Christie, M. Fuentes, and J. J.
917 Armesto. 2008. Gap-phase dynamics and coexistence of a long-lived pioneer and shade-
918 tolerant tree species in the canopy of an old-growth coastal temperate rain forest of Chiloe´
919 Island, Chile. *Journal of Biogeography* 35:1674–1687.

920 Guyette, R. P., and D. C. Dey. 1995. A presettlement fire history of an oak-pine forest near Basin
921 Lake, Algonquin Park, Ontario. Ontario Forest Research Institute, Forest Research Report
922 No. 132. Saulte Ste. Marie, Canada.

923 Guyette, R. P., D. C. Dey, and M. C. Stambaugh. 1994. Fire and human history of a barren-forest
924 in southern Indiana. *American Midland Naturalist* 149:21–34.

925 Guyette, R. P., D. C. Dey, M. C. Stambaugh, and R.-M. Muzika. 2006. Fire scars reveal
926 variability and dynamics of eastern fire regimes. Pages 20–39 *in* M. B. Dickinson, editor.
927 *Fire in Eastern Oak Forests: Delivering Science to Land Managers*. US Dept. of
928 Agriculture, Forest Service, Northern Research Station, General Technical Report NRS-P-1,
929 Newtown Square, PA.

930 Guyette, R. P., R. M. Muzika, and D. C. Dey. 2002. Dynamics of an anthropogenic fire regime.
931 *Ecosystems* 5:472–486.

- 932 Guyette, R. P., and M. A. Spetich. 2003. Fire history of oak–pine forests in the Lower Boston
933 Mountains, Arkansas, USA. *Forest Ecology and Management* 180:463–474.
- 934 Haasis, F. W. 1923. Significance of a 255-year age class in an eastern Kentucky forest. *Journal*
935 *of Forestry* 21:700–704.
- 936 Hanson, J. J., and C. G. Lorimer. 2007. Forest structure and light regimes following moderate
937 wind storms: Implications for multi-cohort management. *Ecological Applications* 17:1325–
938 1340.
- 939 Hart, J. L., S. L. Clark, S. J. Torreano, and M. L. Buchanan. 2012. Composition, structure, and
940 dendroecology of an old-growth *Quercus* forest on the tablelands of the Cumberland
941 Plateau, USA. *Forest Ecology and Management* 266:11–24.
- 942 Hartmann, H. 2011. Will a 385 million year-struggle for light become a struggle for water and
943 for carbon? - How trees may cope with more frequent climate change-type drought events.
944 *Global Change Biology* 17:642–655.
- 945 Henry, J. D., and J. M. A. Swan. 1974. Reconstructing forest history from live and dead plant
946 material - an approach to the study of forest succession in southwest New Hampshire.
947 *Ecology* 55:772–783.
- 948 Hogg, E. H., M. Hart, and V. J. Lieffers. 2002. White tree rings formed in trembling aspen
949 saplings following experimental defoliation. *Canadian Journal of Forest Research* 32:1929–
950 1934.
- 951 Hooke, J. M., and R. J. P. Kain. 1982. *Historical Change in the Physical Environment*. 260 pp.
952 Butterworth Scientific, London.
- 953 Hough, A. F., and R. D. Forbes. 1943. The ecology and silvics of forests in the High Plateau of
954 Pennsylvania. *Ecological Monographs* 13:299–320.

955 Hubeny, J. B., J. W. King, and M. Reddin. 2011. Northeast US precipitation variability and
956 North American climate teleconnections interpreted from late Holocene varved sediments.
957 Proceedings of the National Academy of Sciences of the United States of America
958 108:17895–17900.

959 Hufkens, K., M. a. Friedl, T. F. Keenan, O. Sonnentag, A. Bailey, J. O’Keefe, and A. D.
960 Richardson. 2012. Ecological impacts of a widespread frost event following early spring
961 leaf-out. *Global Change Biology* 18:2365–2377.

962 Huntington, E. 1914. *The Climatic Factor as Illustrated in Arid America*. 341 pp. Carnegie
963 Institution of Washington, Washington, D.C.

964 Hursh, C. R., and F. W. Haasis. 1931. Effects of 1925 summer drought on southern Appalachian
965 hardwoods. *Ecology* 12:380–386.

966 Irland, L. C. 2000. Ice storms and forest impacts. *Science of the Total Environment* 262:231–
967 242.

968 Iverson, L. R., and A. M. Prasad. 2001. Potential changes in tree species richness and forest
969 community types following climate change. *Ecosystems* 4:186–199.

970 Jackson, S. T. 2006. Vegetation, environment, and time: The origination and termination of
971 ecosystems. *Journal of Vegetation Science* 17:549–557.

972 Jackson, S. T., and R. K. Booth. 2002. The role of Late Holocene climate variability in the
973 expansion of yellow birch in the western Great Lakes region. *Diversity and Distributions*
974 8:275–284.

975 Jenkins, M. A., and S. G. Pallardy. 1995. The influence of drought on red oak group species
976 growth and mortality in the Missouri Ozarks. *Canadian Journal of Forest Research*
977 25:1119–1127.

- 978 Kaplan, J., and M. DeMaria. 1995. A simple empirical model for predicting the decay of tropical
979 cyclone winds after landfall. *Journal of Applied Meteorology* 34:2499–2512.
- 980 Koutsoyiannis, A. 1977. *Theory of econometrics: an introductory exposition of econometric*
981 *methods*. 681 pp. MacMillan Press, Ltd., New York.
- 982 Krumhardt, K. M. 2010. *Methodology for worldwide population estimates: 1000 BC to 1850;*
983 *Technical Report 3*. 19 pp. Lusanne, Switzerland.
- 984 Lafon, C. W. 2006. Forest disturbance by ice storms in *Quercus* forests of the southern
985 Appalachian Mountains, USA. *Ecoscience* 13:30–43.
- 986 Lafon, C. W., and S. M. Quiring. 2012. Relationships of Fire and Precipitation Regimes in
987 Temperate Forests of the Eastern United States. *Earth Interactions* 16:1–15.
- 988 Lafon, C. W., and J. H. Speer. 2002. Using dendrochronology to identify major ice storm events
989 in oak forests of southwestern Virginia. *Climate Research* 20:41–54.
- 990 Landsea, C. W., C. Anderson, N. Charles, G. Clark, J. Dunion, J. Fernandez-Partgas, P.
991 Hungerford, C. Neumann, and M. Zimmer. 2004. The Atlantic Hurricane Database Re-
992 analysis Project: Documentation for 1851-1910 Alterations and Additions to the HURDAT
993 Database. Pages 178–221 *in* R. Murnane and K. Liu, editors. *Hurricanes and Typhoons,*
994 *Past, Present and Future*. Columbia University Press, New York.
- 995 Lemon, P. C. 1961. Forest ecology of ice storms. *Bulletin of the Torrey Botanical Club* 88:21–
996 29.
- 997 Lichter, J. 1997. Radiocarbon Dating of Lake Michigan Beach-Ridge and Dune Development.
998 *Quaternary Research* 48:137–140.
- 999 Loehle, C. 2000. Forest ecotone response to climate change: sensitivity to temperature response
1000 functional. *Canadian Journal of Forest Research* 30:1632–1645.

- 1001 Loope, W. L., and A. F. Arbogast. 2000. Dominance of an ~150-year cycle of sand-supply
1002 change in Late Holocene dune-building along the eastern shore of Lake Michigan.
1003 *Quaternary Research* 54:414–422.
- 1004 Lorimer, C. 1977. The presettlement forest and natural disturbance cycle of northeastern Maine.
1005 *Ecology* 58:139–148.
- 1006 Lorimer, C. G. 1980. Age structure and disturbance history of a Southern Appalachian virgin
1007 forest. *Ecology* 61:1169–1184.
- 1008 Lorimer, C. G. 1984. Development of the red maple understory in northeastern oak forests.
1009 *Forest Science* 1:3–22.
- 1010 Lorimer, C. G. 1985. Methodological considerations in the analysis of forest disturbance history.
1011 *Canadian Journal of Forest Research* 15:200–213.
- 1012 Lorimer, C. G. 1989. Relative effects of small and large disturbances on temperate hardwood
1013 forest structure. *Ecology* 70:565–567.
- 1014 Lorimer, C. G., and L. E. Frelich. 1989. A methodology for estimating canopy disturbance
1015 frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research*
1016 19:651–663.
- 1017 Ludlum, D. W. 1963. *Early American Hurricanes, 1492-1870*. 198 pp. American Meteorological
1018 Society, Boston, MA.
- 1019 Lynch, C., and A. Hessler. 2010. Climatic Controls on Historical Wildfires in West Virginia, 1939-
1020 2008. *Physical Geography* 31:254–269.
- 1021 Man, G. 2012. *Major Forest Insect and Disease Conditions in the United States: 2011*. 50 pp.
1022 USDA Forest Service FS-1000.
- 1023 Manion, P. 2003. Evolution of concepts in forest pathology. *Phytopathology* 98:1052–1055.
- 1024 Mann, C. C. 2005. *1491: New Revelations of the Americas Before Columbus*. 480 pp. Knopf.

1025 Mann, D. H., F. B. Engstrom, and J. L. Bubier. 1994. Fire history and tree recruitment in an
1026 uncut New England forest. *Quaternary Research* 42:206–215.

1027 Maxwell, R. S., A. E. Hessler, E. R. Cook, and N. Pederson. 2011. A multispecies tree ring
1028 reconstruction of Potomac River streamflow (950–2001). *Water Resources Research* 47:1–
1029 12.

1030 McCarthy, J. 2001. Gap dynamics of forest trees: A review with particular attention to boreal
1031 forests. *Environmental Reviews* 9:1–59.

1032 McDowell, N., W. T. Pockman, C. D. Allen, D. D. Breshears, N. Cobb, T. Kolb, J. Plaut, J.
1033 Sperry, A. West, D. G. Williams, and E. a Yezzer. 2008. Mechanisms of plant survival and
1034 mortality during drought: why do some plants survive while others succumb to drought?
1035 *The New Phytologist* 178:719–39.

1036 McEwan, R. W., J. M. Dyer, and N. Pederson. 2011. Multiple interacting ecosystem drivers:
1037 toward an encompassing hypothesis of oak forest dynamics across eastern North America.
1038 *Ecography* 34:244–256.

1039 McEwan, R. W., T. F. Hutchinson, R. P. Long, D. R. Ford, and C. B. McCarthy. 2007. Temporal
1040 and spatial patterns in fire occurrence during the establishment of mixed-oak forests in
1041 eastern North America. *Journal of Vegetation Science* 18:655–664.

1042 McEwan, R. W., N. Pederson, A. Cooper, J. Taylor, R. Watts, and A. Hruska. 2013. Fire and gap
1043 dynamics over 300-years in an old-growth temperate forest. *Applied Vegetation Science*.

1044 McGuire, J. P., R. J. Mitchell, E. B. Moser, S. D. Pecot, D. H. Gjerstad, and C. W. Hedman.
1045 2001. Gaps in a gappy forest: plant resources, longleaf pine regeneration, and understory
1046 response to tree removal in longleaf pine savannas. *Canadian Journal of Forest Research*
1047 31:765–778.

1048 McKenney, D. W., J. H. Pedlar, R. B. Rood, and D. Price. 2011. Revisiting projected shifts in the
1049 climate envelopes of North American trees using updated general circulation models.
1050 *Global Change Biology* 17:2720–2730.

1051 McMahon, S. M., G. G. Parker, and D. R. Miller. 2010. Evidence for a recent increase in forest
1052 growth. *Proceedings of the National Academy of Sciences of the United States of America*
1053 107:3611–5.

1054 McMurry, E. R., M. C. Stambaugh, R. P. Guyette, and D. C. Dey. 2007. Fire scars reveal source
1055 of New England’s 1780 Dark Day. *International Journal of Wildland Fire* 16:266–270.

1056 Michaelian, M., E. H. Hogg, R. J. Hall, and E. Arsenault. 2011. Massive mortality of aspen
1057 following severe drought along the southern edge of the Canadian boreal forest. *Global*
1058 *Change Biology* 17:2084–2094.

1059 Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the
1060 future: managing in the face of uncertainty. *Ecological Applications* 17:2145–51.

1061 Millward, A. A., and C. E. Kraft. 2004. Physical influences of landscape on a large-extent
1062 ecological disturbance: the northeastern North American ice storm of 1998. *Landscape*
1063 *Ecology* 19:99–111.

1064 Milner, G., and G. Chaplin. 2010. Eastern North American Population at ca A.D. 1500.
1065 *American Antiquity* 75:707–726.

1066 Mueller, R. C., C. M. Scudder, M. E. Porter, R. T. Trotter, C. A. Gehring, and T. G. Whitham.
1067 2005. Differential tree mortality in response to severe drought: evidence for long-term
1068 vegetation shifts. *Journal of Ecology* 93:1085–1093.

1069 Muggeo, V. 2008. Modelling temperature effects on mortality: multiple segmented relationships
1070 with common break points. *Biostatistics* 9:613–620.

1071 Negrón-Juárez, R. I., J. Q. Chambers, G. Guimaraes, H. Zeng, C. F. M. Raupp, D. M. Marra, G.
1072 H. P. M. Ribeiro, S. S. Saatchi, B. W. Nelson, and N. Higuchi. 2010. Widespread Amazon
1073 forest tree mortality from a single cross-basin squall line event. *Geophysical Research*
1074 *Letters* 37:1–5.

1075 Nowacki, G. J., and M. D. Abrams. 1994. Forest composition, structure, and disturbance history
1076 of the Alan Seeger Natural Area, Huntington, Pennsylvania. *Bulletin of the Torrey*
1077 *Botanical Club* 121:277–291.

1078 Nowacki, G. J., and M. D. Abrams. 1997. Radial-growth averaging criteria for reconstructing
1079 disturbance histories from presettlement-origin oaks. *Ecological Monographs* 67:225–234.

1080 Olano, J. M., and M. W. Palmer. 2003. Stand dynamics of an Appalachian old-growth forest
1081 during a severe drought episode. *Forest Ecology and Management* 174:139–148.

1082 Parshall, T., and D. Foster. 2003. Fire on the New England landscape: regional and temporal
1083 variation, cultural and environmental controls. *Journal of Biogeography* 29:1305–1317.

1084 Payette, S., L. Filion, L. Gauthier, and Y. Boutin. 1985. Secular climate change in old-growth
1085 tree-line vegetation of northern Quebec. *Nature* 315:135–138.

1086 Pedersen, B. 1998. The role of stress in the mortality of midwestern oaks as indicated by growth
1087 prior to death. *Ecology* 79:79–93.

1088 Pederson, N. 2005. Climatic Sensitivity and Growth of Southern Temperate Trees in the Eastern
1089 US: Implications for the Carbon Cycle. Ph.D. dissertation. Columbia University.

1090 Pederson, N. 2010. External characteristics of old trees in the Eastern Deciduous Forest. *Natural*
1091 *Areas Journal* 30:396–407.

1092 Pederson, N., A. R. Bell, E. R. Cook, U. Lall, N. Devineni, R. Seager, K. Eggleston, and K. P.
1093 Vranes. 2013. Is an Epic Pluvial Masking the Water Insecurity of the Greater New York
1094 City Region? *Journal of Climate* 26:1339–1354.

1095 Pederson, N., A. R. Bell, T. A. Knight, C. Leland, N. Malcomb, K. J. Anchukaitis, K. Tackett, J.
1096 Scheff, A. Brice, B. Catron, W. Blozan, and J. Riddle. 2012a. Long-term perspective on a
1097 modern drought in the American Southeast. *Environmental Research Letters* 7 014034.

1098 Pederson, N., K. Tackett, R. W. McEwan, S. Clark, A. M. Cooper, G. Brosi, R. Eaton, and R. D.
1099 Stockwell. 2012b. Long-term drought sensitivity of trees in second-growth forests in a
1100 humid region. *Canadian Journal of Forest Research* 42:1837–1850.

1101 Pederson, N., J. M. Varner III, and B. J. Palik. 2008. Canopy disturbance and tree recruitment
1102 over two centuries in a managed longleaf pine landscape. *Forest Ecology and Management*
1103 254:85–95.

1104 Peterson, C. 2000. Catastrophic wind damage to North American forests and the potential impact
1105 of climate change. *Science of the Total Environment* 262:287–311.

1106 Peterson, C. J. 2007. Consistent influence of tree diameter and species on damage in nine eastern
1107 North America tornado blowdowns. *Forest Ecology and Management* 250:96–108.

1108 Potts, M. 2003. Drought in a Bornean everwet rain forest. *Journal of Ecology* 91:467–474.

1109 Preisendorfer, R. W., F. W. Zwiers, and T. Barnett. 1981. Foundations of principal components
1110 selection rules. La Jolla, CA.

1111 Proulx, R. J., and D. F. Greene. 2001. The relationship between ice thickness and northern
1112 hardwood tree damage during ice storms. *Canadian Journal of Forest Research* 31:1758–
1113 1767.

1114 Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H.
1115 Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic
1116 amplification: the dynamics of bark beetle. *BioScience* 58:501–517.

1117 Rappaport, E., and A. Ruffman. 1999. The catastrophic hurricane(s): the search for data and
1118 understanding. Pages 787–790 in A. M. Society, editor. Preprints, 23rd Conference on
1119 Hurricanes and Tropical Meteorology. American Meteorological Society, Boston, MA.

1120 Rebertus, Alan, J., and T. T. Veblen. 1993. Structure and tree-fall gap dynamics of old-growth
1121 *Nothofagus* forests in Tierra del Fuego, Argentina. *Journal of Vegetation Science* 4:641–
1122 654.

1123 Rentch, J. 2003. Oak establishment and canopy accession strategies in five old-growth stands in
1124 the central hardwood forest region. *Forest Ecology and Management* 184:285–297.

1125 Rentch, J. S., F. Desta, and G. W. Miller. 2002. Climate, canopy disturbance, and radial growth
1126 averaging in a second-growth mixed-oak forest in West Virginia, U.S.A. *Canadian Journal*
1127 *of Forest Research* 32:915–927.

1128 Richman, M. B. 1986. Rotation of principal components. *Journal of Climatology* 6:293–335.

1129 Rudisill, H. F. (ed.). 1993. *The Diaries of Evan Pugh (1762–1801)*. (H. F. Rudisill, Ed.). St
1130 David’s Society, Florence, SC.

1131 Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North
1132 America. *Ecology* 63:1533–1546.

1133 Savage, M., P. M. Brown, and J. Feddema. 1996. The role of climate in a pine forest
1134 regeneration pulse in the southwestern United States. *Ecoscience* 3:310–318.

1135 Schleeweis, K., S. N. Goward, C. Huang, J. G. Masek, G. Moisen, R. E. Kennedy, and N. E.
1136 Thomas. 2013. Regional dynamics of forest canopy change and underlying causal processes
1137 in the contiguous U.S. *Journal of Geophysical Research: Biogeosciences* 118:1035–1053.

1138 Seager, R., N. Pederson, Y. Kushnir, and J. Nakamura. 2012. The 1960s drought and the
1139 subsequent shift to a wetter climate in the Catskill Mountains Region of the New York City
1140 watershed. *Journal of Climate* 25:6721–6742.

- 1141 Shuman, B., A. K. Henderson, C. Plank, I. Stefanova, and S. S. Ziegler. 2009. Woodland-to-
1142 forest transition during prolonged drought in Minnesota after ca. AD 1300. *Ecology*
1143 90:2792–807.
- 1144 Shuman, B., P. Newby, Y. Huang, and T. Webb. 2004. Evidence for the close climatic control of
1145 New England vegetation history. *Ecology* 85:1297–1310.
- 1146 Smith, T., and D. Urban. 1988. Scale and resolution of forest structural pattern. *Vegetatio*
1147 74:143–150.
- 1148 Sprugel, D. G. 1991. Disturbance, equilibrium, and environmental variability: What is “natural”
1149 vegetation in a changing environment? *Biological Conservation* 58:1–18.
- 1150 St. George, S., D. M. Meko, M.-P. Girardin, G. M. MacDonald, E. Nielsen, G. T. Pederson, D. J.
1151 Sauchyn, J. C. Tardif, and E. Watson. 2009. The tree-ring record of drought on the
1152 Canadian Prairies. *Journal of Climate* 22:689–710.
- 1153 Stahle, D. W., and P. L. Chaney. 1994. A predictive model for the location of ancient forests.
1154 *Natural Areas Journal* 14:151–158.
- 1155 Stahle, D. W., and M. K. Cleaveland. 1988. Texas drought history reconstructed and analyzed
1156 from 1698 to 1980. *Journal of Climate* 1:59–74.
- 1157 Stahle, D. W., M. K. Cleaveland, and J. Hehr. 1985. A 450-year drought reconstruction for
1158 Arkansas, United States. *Nature* 316:530–532.
- 1159 Stahle, D. W., E. R. Cook, M. K. Cleaveland, M. D. Therrell, H. D. Grissino-Mayer, E. Watson,
1160 and B. H. Luckman. 2000. Tree-ring data document 16th century megadrought over North
1161 America. *EOS Transactions* 81:121, 125.
- 1162 Stambaugh, M. C., J. Sparks, R. P. Guyette, and Wilson G. 2011. Fire history of a relict oak
1163 woodland in northeast Texas. *Rangeland Ecology and Management* 64:419–423.

1164 Stueve, K. M., C. H. (Hobie) Perry, M. D. Nelson, S. P. Healey, A. D. Hill, G. G. Moisen, W. B.
1165 Cohen, D. D. Gormanson, and C. Huang. 2011. Ecological importance of intermediate
1166 windstorms rivals large, infrequent disturbances in the northern Great Lakes. *Ecosphere*
1167 2:art2.

1168 Swetnam, T. W. 1993. Fire history and climate change in giant sequoia groves. *Science*
1169 262:885–9.

1170 Swetnam, T. W., and J. L. Betancourt. 1998. Mesoscale disturbance and ecological response to
1171 decadal climatic variability in the American Southwest. *Journal of Climate* 11:3128–3147.

1172 Taylor, S. W., A. L. Carroll, R. I. Alfaro, and L. Safranyik. 2006. Forest, climate and mountain
1173 pine beetle outbreak dynamics in western Canada. Pages 66–94 *in* L. Safranyik and B.
1174 Wilson, editors. *The Mountain Pine Beetle A Synthesis of Biology, Management, and*
1175 *Impacts on Lodgepole Pine*. Natural Resources Canada, Canadian Forest Service, Pacific
1176 Forestry Centre Victoria, Victoria, BC, Canada.

1177 *The Pennsylvania Gazette*. 1774, May 11. No Title. *The Pennsylvania Gazette*:2. Philadelphia.

1178 Therrell, M., and D. Stahle. 1998. A predictive model to locate ancient forests in the Cross
1179 Timbers of Osage County, Oklahoma. *Journal of Biogeography* 25:847–854.

1180 Thomas Jefferson’s Garden Book. 1774. Papers of Thomas Jefferson in the Collections of the
1181 Massachusetts Historical Society. Monticello, VA.

1182 Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. *Ecology*
1183 91:2833–2849.

1184 U.S. Environmental Protection Agency. 2003. Level III Ecoregions of the Conterminous United
1185 States. U.S. EPA Office of Research & Development - National Health and Environmental
1186 Effects Research Laboratory. Corvallis, OR.

1187 van Mantgem, P. J., N. L. Stephenson, J. C. Byrne, L. D. Daniels, J. F. Franklin, P. Z. Fulé, M.
1188 E. Harmon, A. J. Larson, J. M. Smith, A. H. Taylor, and T. T. Veblen. 2009. Widespread
1189 increase of tree mortality rates in the western United States. *Science* 323:521–524.

1190 Vanderwel, M. C., D. a. Coomes, and D. W. Purves. 2013. Quantifying variation in forest
1191 disturbance, and its effects on aboveground biomass dynamics, across the eastern United
1192 States. *Global Change Biology* 19:1504–1517.

1193 Villalba, R., and T. Veblen. 1998. Influences of large-scale climatic variability on episodic tree
1194 mortality in northern Patagonia. *Ecology* 79:2624–2640.

1195 Villalba, R., and T. T. Veblen. 1997. Regional patterns of tree population age structures in
1196 northern Patagonia: climatic and disturbance influences. *Journal of Ecology* 85:113–124.

1197 Virginia Gazette. 1774, May 12. No Title. *Virginia Gazette*:4. Williamsburg, VA.

1198 Waller, M. 2013. Drought, disease, defoliation and death: forest pathogens as agents of past
1199 vegetation change. *Journal of Quaternary Science* 28:336–342.

1200 White, P. 1979. Pattern, process and natural disturbance in vegetation. *The Botanical Review*
1201 45:229–299.

1202 White, P. S., J. Harrod, W. Romme, and J. Betancourt. 1999. The role of disturbance and
1203 temporal dynamics. Pages 281–312 in R. C. Szaro, N. C. Johnson, W. T. Sexton, A. J.
1204 Malk, editors. *Ecological Stewardship Volume 2*. Elsevier Science, Oxford.

1205 Williams, A. B. 1936. The composition and dynamics of a beech-maple climax community.
1206 *Ecological Monographs* 6:317–408.

1207 Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and
1208 ecological surprises. *Frontiers in Ecology and the Environment* 5:475–482.

1209 Williams, M. 1992. *Americans and Their Forests: A Historical Geography*. Page 624. Cambridge
1210 University Press, Cambridge, United Kingdom.

1211 Wolin, J. A. 1996. Late Holocene lake-level and lake development signals in Lower Herring
1212 Lake, Michigan. *Journal of Paleolimnology* 15:19–45.

1213 Wonkka, C. L., C. W. Lafon, C. M. Hutton, and A. J. Joslin. 2013. A CSR classification of tree
1214 life history strategies and implications for ice storm damage. *Oikos* 122:209–222.

1215 Woods, K. D. 2004. Intermediate disturbance in a late-successional hemlock-northern hardwood
1216 forest. *Journal of Ecology* 92:464–476.

1217 Worrall, J. J., L. Egeland, T. Eager, R. A. Mask, E. W. Johnson, P. A. Kemp, and W. D.
1218 Shepperd. 2008. Rapid mortality of *Populus tremuloides* in southwestern Colorado, USA.
1219 *Forest Ecology and Management* 255:686–696.

1220 Worrall, J. J., T. D. Lee, and T. C. Harrington. 2005. Forest dynamics and agents that initiate and
1221 expand canopy gaps in *Picea-Abies* forests of Crawford Notch, New Hampshire, USA.
1222 *Journal of Ecology* 93:178–190.

1223 Yamamoto, S.-I. 1992. The gap theory in forest dynamics. *The Botanical Magazine Tokyo*
1224 105:375–383.

1225

1226 Ecological Archives Appendix A contains additional information, figures, images, analysis, and
1227 discussion material to support the main article.

1228

1229 Ecological Archives Appendix B contains photos of two important old-growth forests central to
1230 this investigation.

1231

1232 Ecological Archives Supplement A contains files with raw recruitment data in bins with different
1233 temporal windows, references from which these data are drawn, and reasons for rejecting
1234 potential data from additional references.

1235

1236 Table 1 – Characteristics of periods with extended canopy disturbance events from 1685-1880.
 1237 Characteristics for the peak year, 1776, and peak event within the 1774-1782 event, 1775-1780,
 1238 are included to display their exceptionality. The event beginning in 1877 continues until 1883.
 1239 Thus, its characteristics for the full event are included for completeness. See Methods for further
 1240 discussion of this calculation.

Elevated Disturbance		Anomaly of Disturbance Rate	Proportion Major Release	Magnitude	Sites Recording Disturbance
Duration	Years	Mean/yr	Percent	-	Percent
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
<u>1775-1780</u>	6	2.61	56.8	8.92	41.3
<u>1776</u>	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	-	0.78	39.6	-	11.3
annual mean		(0.83)			(9.8)
(SD)					
Elevated	4.6	1.92	44.2	1.57	19.4
Disturbance	(1.89)	(0.59)	(16.1)	(2.43)	(5.58)
mean (SD)					

1241

Table 2 – Comparison of tree recruitment categories from 1500-1849. See Methods for category details

Era	Category 1		Category 2		Category 3		Category 4						Category 4		Early Category 1 Studies (1930-1943)	
	n = 2277		n = 1236 ^a		n = 1105		20-yr Bins n = 270		25-yr Bins n = 209		50-yr Bins n = 230		n = 709		N = 620	
	# Trees	%	# Trees	%	# Trees	%	# Trees	%	# Trees	%	# Trees	%	# Trees	%	# Trees	%
1450-1499	1	0.04	0	0	0	0	0	0	0	0	0	0	0	0	1 ^c	0.2
1500-1549	3	0.1	5	0.4	3	0.3	0	0	0	0	1	0.4	1	0.1	1 ^c	0.2
1550-1599	20	0.9	27	2.2	4	0.4	3	1.1	0	0	9	3.9	12	1.7	13	2.1
1600-1649	86	3.8	95	7.7	105	9.5	6	2.2	5	2.4	13	5.6	24	3.4	53	8.5
1650-1699	330	14.5	301	24.4	814	73.7	15	5.55	11	5.3	23	10.0	49	6.9	131	21.1
1700-1749	425	18.7	318	25.7	-	-	26	9.63	22	10.5	60	26.1	108	15.2	162	26.1
1750-1799	626	27.5	272	22.0	-	-	78	28.89	78	37.3	51	22.2	207	29.1	138	22.2
1800-1849	786	34.5	218	17.6	-	-	142	52.59	93	44.5	73	31.7	308	43.4	113	18.2

-- Other Eras for Comparison --

Pre-1650	110	4.8	127	10.3	112	10.1	13	4.81	5	2.4	23	10.0	41	5.8	67	10.8
1670-1689	168	7.4	127	10.3	413	37.4	4	1.48	6	2.4 ^d	n/a	-	n/a	-	n/a	

^a = dates decline after ca. 1735 because of sampling methods; ^c 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; ^b 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; ^d represents 1675-1699.

Figure captions

Figure 1 - Spatial loading of populations onto Eigenvector 2. The Central Hardwood Region is adapted from Fralish and Franklin (2002), and US EPA (2003); the Broadleaf-dominated Forest Regions are adapted from Dyer (2006). (b) Time-series of ring width variation of EV2 from 1750-1880 of populations within the dark blue areas in (a). The grey line in (b) represents the 1750-1880 mean.

Figure 2 - (a) Frequency of canopy disturbance through time of populations loading > 0.224 onto Eigenvector 2. The orange filling represents the percent 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 two SD's 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 a ca 61,000 km² area.

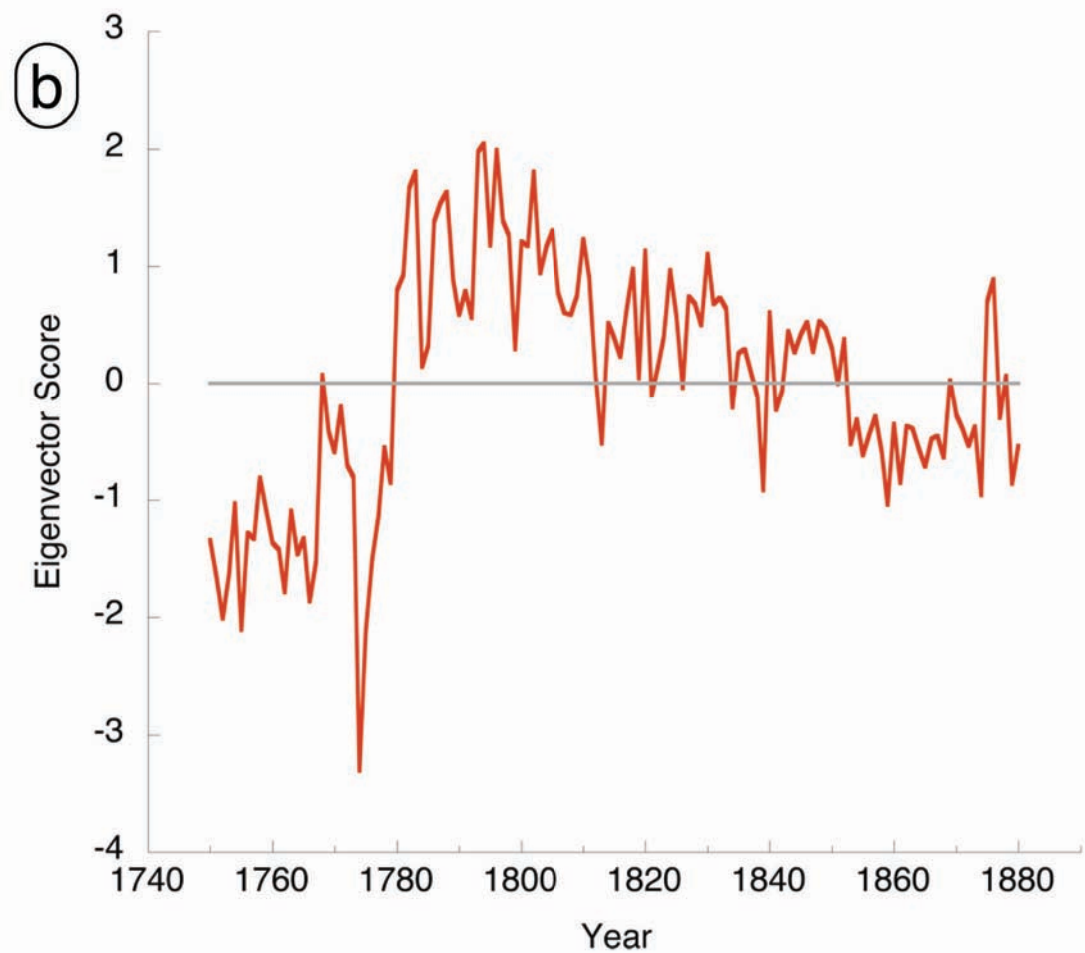
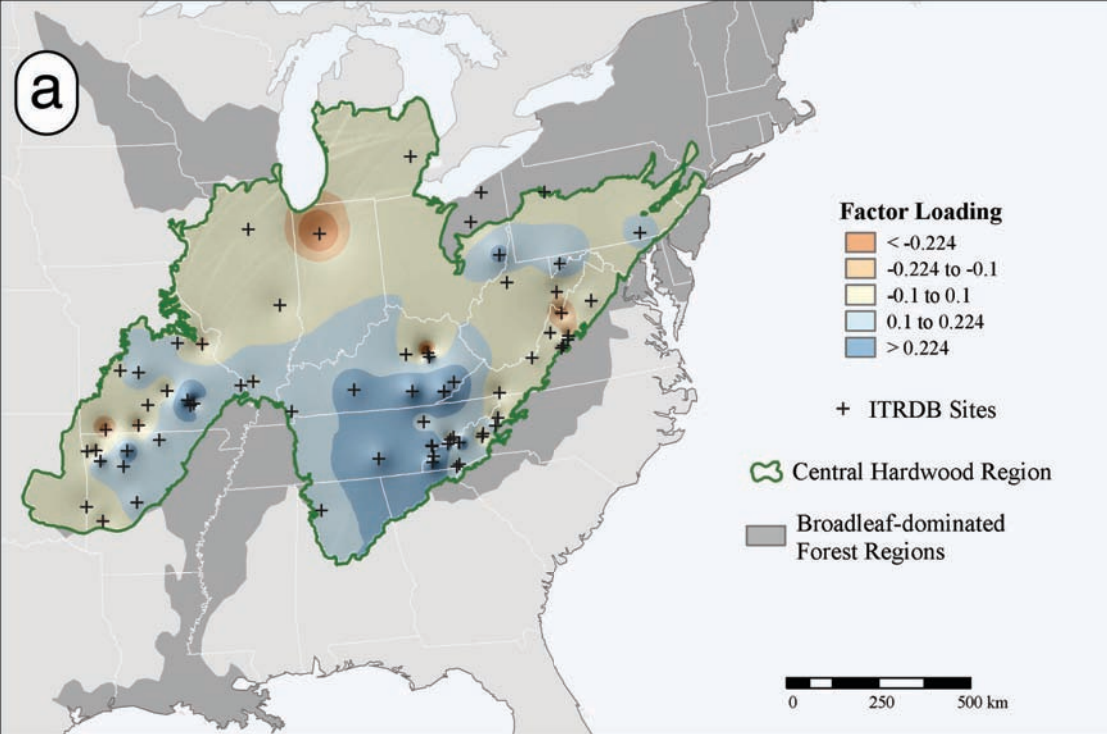
Specific site names corresponding to the numbers on this figure are listed in Appendix A, Table A5. The lower panels in (c) and (d) compare the observed percent of disturbed trees with a Gaussian distribution (least-mean-square fitted to the observations) for 1685-1880. (c) Density plot of the observed percentage of disturbed trees (orange) and theoretical Gaussian distribution (grey). 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%, red line). (d) Quantile-Quantile plot comparing the observed percentage of disturbed trees with the corresponding Gaussian distribution from (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.

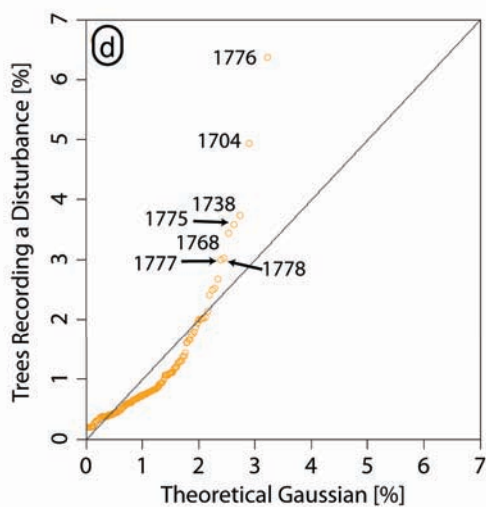
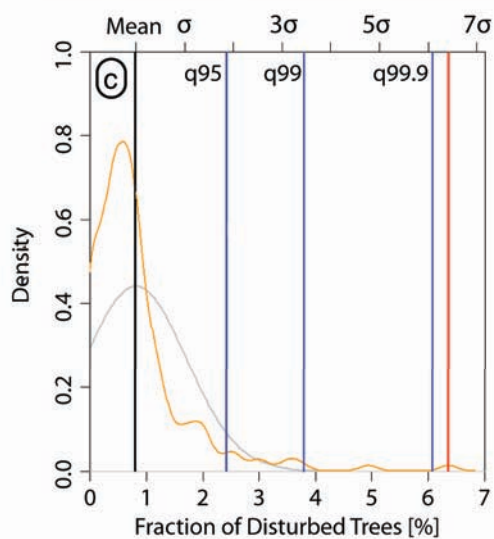
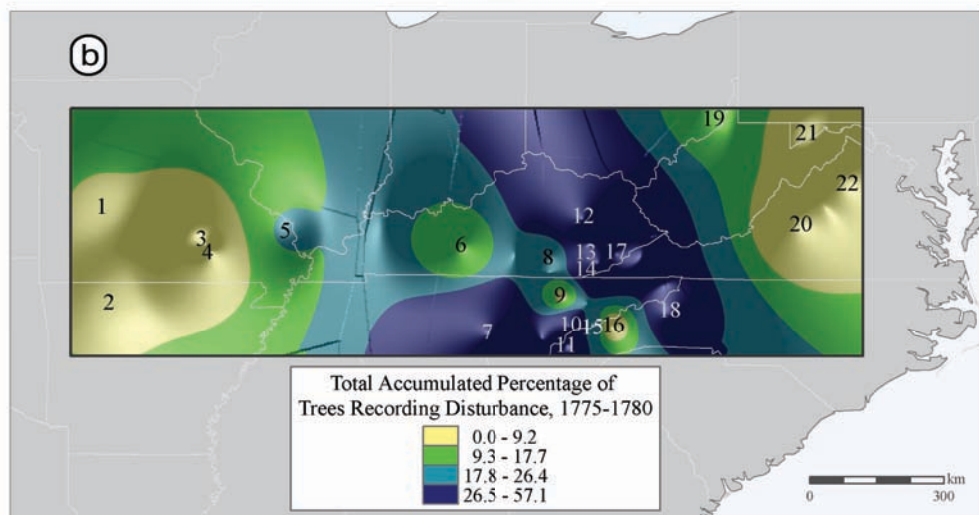
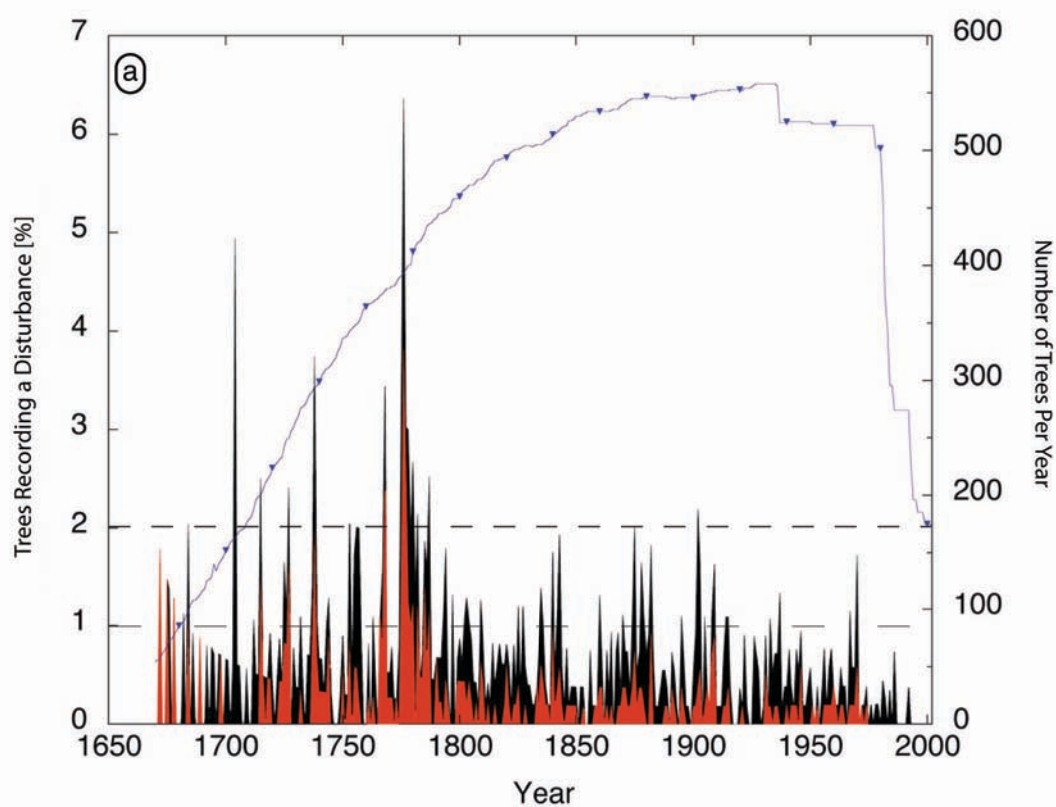
Figure 3 - Relation between climate and disturbance. Superposed epoch analysis of years with disturbance 1 STD or greater above the mean versus (a) independent drought proxy (IDP). Only the red bar is significant $p < 0.05$. (b) Smoothed reconstruction of drought from 1550-2006 (9-yr spline). The filled 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 SST.

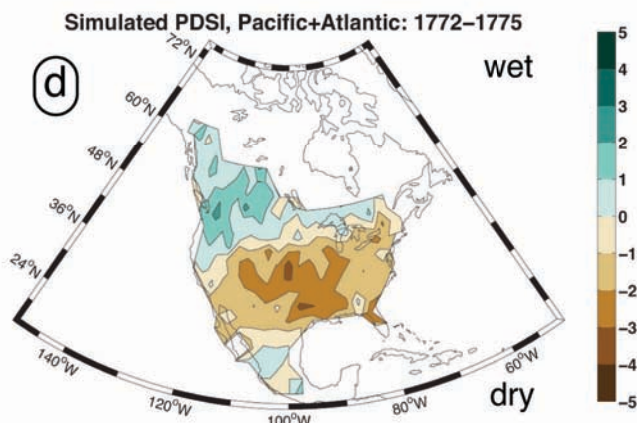
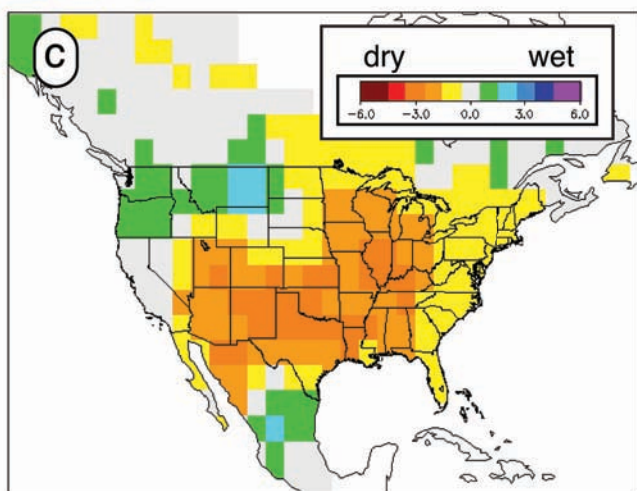
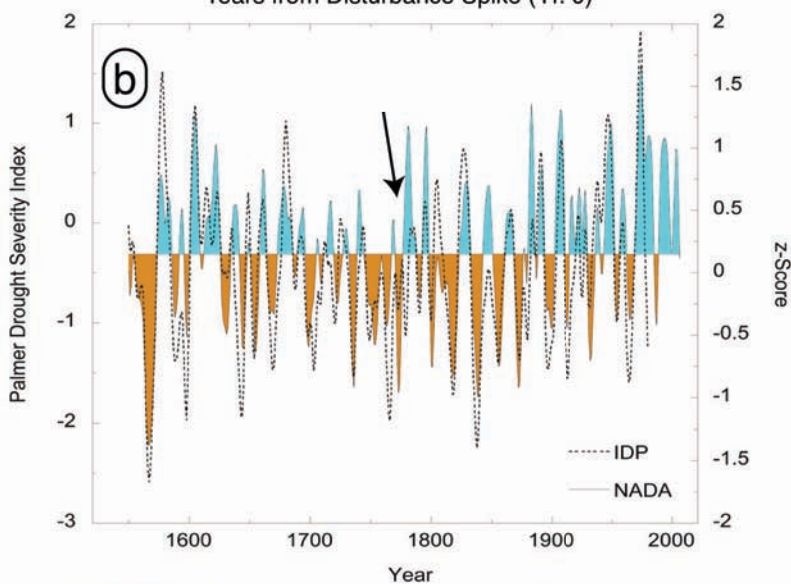
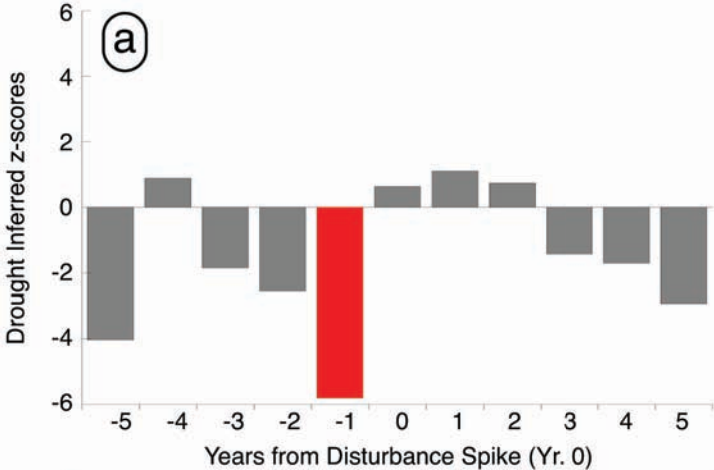
Figure 4 - Forest recruitment and climate across the broadleaf-dominated forests of the eastern US. (a) Residual of tree initiation dates from 1500-1850 after removing demographic trends (n dates = 2276). (b) Drought proxies for Atlantic Coast (Atlantic; GA to VA), Gulf Coast (Gulf; GA to LA), center of the Central Eastern Deciduous Forest region (Cen. EDF), northeastern US (NYC; NJ to central MA and western NY State), Mississippi Valley (MSV; LA to IL), and the Independent Drought Proxy (IDP; see Appendix A for more information on IDP). The Atlantic, Gulf, Cen. EDF, 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.

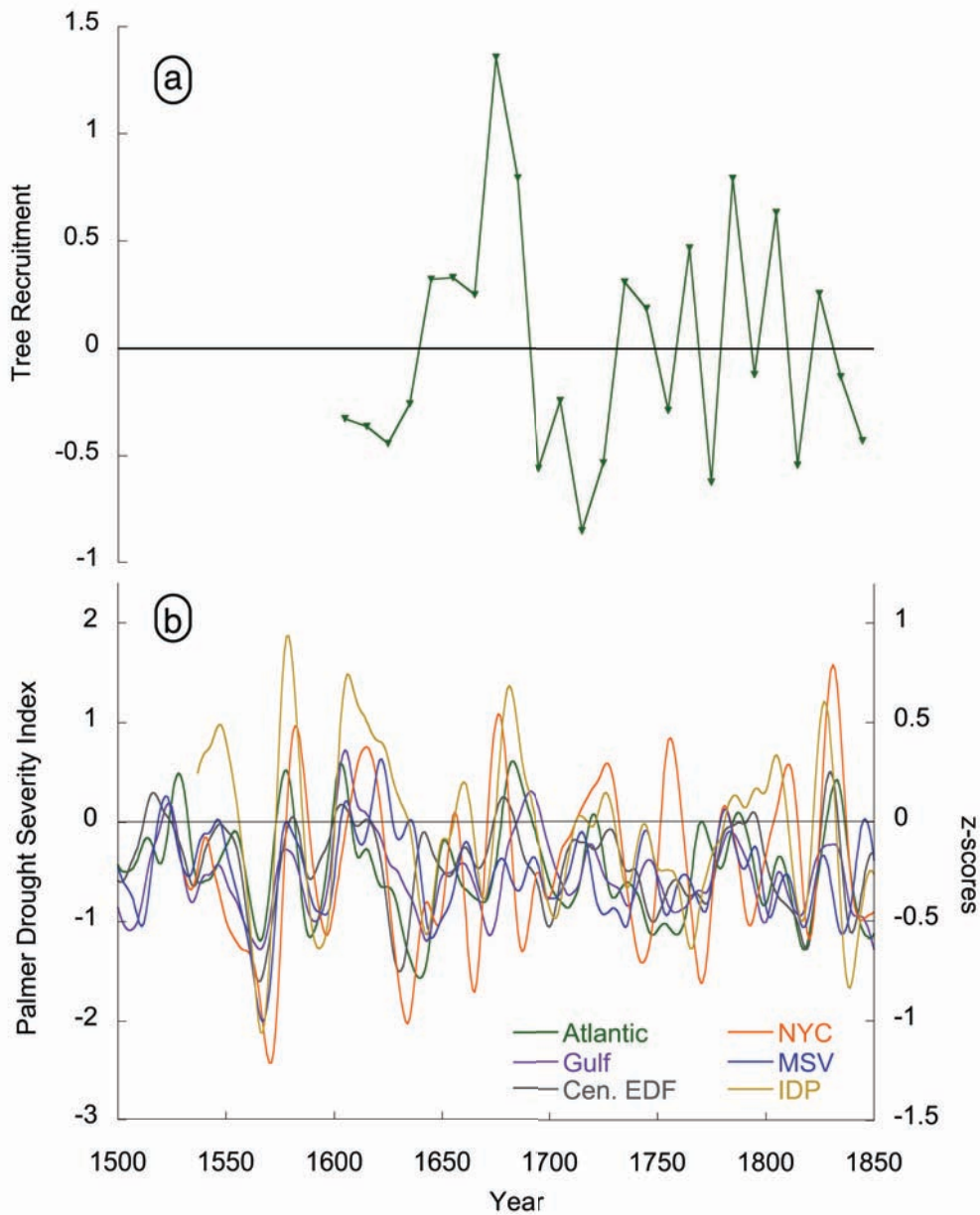
Figure 5 – Probability density functions of reconstructed drought (PDSI) for 1600-1649 (red), 1650-1699 (orange), and 1950-2005 (blue) for three broad regions: (a) northeastern US, (b) Central Hardwood Region of Figure 1a, and (c) central Mississippi River Valley. (a), (b), and (c) are adapted from the original data used to construct Figure 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

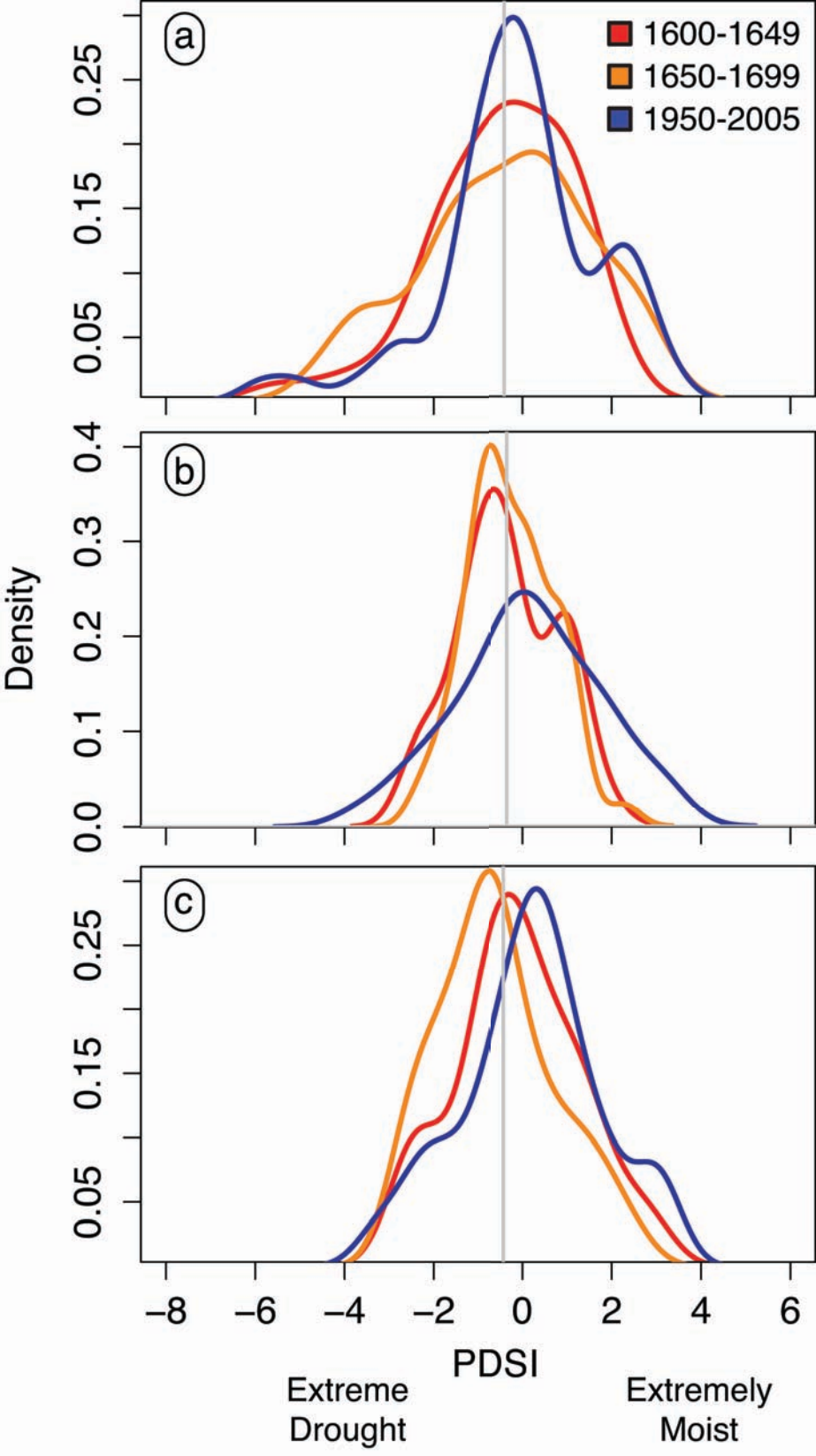
extremely moisture conditions, conditions that are nearly absent during the 17th century.











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Appendix 2. Photographs of two important old-growth forests reflecting the complexity in structure impacted by the events in the late 1600s and late 1770s documented in our. Photo credit: Neil Pederson.



FIG. 2_1: 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. 2_2: 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. 2_3: 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. 2_4: 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. 2_5: 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. 2_6: 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. 2_7: 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.