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1 Running Head: Extreme episodic climate and broadleaf forests

2

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

4

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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 km<sup>2</sup> and 5,327 tree recruitment dates  
 30 spanning ca 1.4 million km<sup>2</sup> 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 km<sup>2</sup>. 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 Historical documents provide no evidence that hurricanes or ice storms triggered the  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.

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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 km<sup>2</sup> 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 km<sup>2</sup>, 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 18<sup>th</sup> 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 km<sup>2</sup> 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 ( $\geq 0.224$ ,  $p \leq 0.05$ ; 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%  $\sim$  80<sup>th</sup>-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  $\geq 100$  (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  $\geq 1.0$  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 km<sup>2</sup>.

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 km<sup>2</sup>; 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 hurricane 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  $\geq 3$  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  $\geq 2$  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 km<sup>2</sup> (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 98<sup>th</sup>-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 ( $\pm 10.6$  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 17<sup>th</sup> 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 km<sup>2</sup>). 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 4<sup>th</sup> and 5<sup>th</sup> 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-18<sup>th</sup> 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, 20<sup>th</sup>-century droughts are known to have lead to tree mortality (Jenkins and  
 542 Pallardy 1995, Pedersen 1998), suggesting the more severe mid-18<sup>th</sup> 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 km<sup>2</sup> 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 km<sup>2</sup> 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  $\geq 2$  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 preceding 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 20<sup>th</sup> 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 17<sup>th</sup> 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-17<sup>th</sup> 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-17<sup>th</sup> 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 17<sup>th</sup>  
 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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- 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<br>Disturbance | Duration | Anomaly of<br>Disturbance | Proportion |           | Sites Recording<br>Disturbance |
|-------------------------|----------|---------------------------|------------|-----------|--------------------------------|
|                         |          | Rate                      | Release    | Magnitude |                                |
| Departure from          |          |                           |            |           |                                |
|                         | 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)   |        |        |        |        |        |

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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<br>1 Studies<br>(1930-1943) |      |
|-----------|------------|------|-----------------------|------|------------|------|------------|-------|------------|------|------------|------|------------|------|--|------|
|           | # Trees    | %    | # Trees               | %    | # Trees    | %    | 20-yr Bins |       | 25-yr Bins |      | 50-yr Bins |      | # Trees    | %    | # Trees                                    | %    |
|           | n = 2277   |      | n = 1236 <sup>a</sup> |      | n = 1105   |      | n = 270    |       | n = 209    |      | n = 230    |      | n = 709    |      | N = 620                                    |      |
| 1450-1499 | 1          | 0.04 | 0                     | 0    | 0          | 0    | 0          | 0     | 0          | 0    | 0          | 0    | 0          | 0    | 1 <sup>c</sup>                             | 0.2  |
| 1500-1549 | 3          | 0.1  | 5                     | 0.4  | 3          | 0.3  | 0          | 0     | 0          | 0    | 1          | 0.4  | 1          | 0.1  | 1 <sup>c</sup>                             | 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 --

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|-----------|-----|-----|-----|------|-----|------|----|------|---|------------------|-----|------|-----|-----|-----|------|
| 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 <sup>d</sup> | n/a | -    | n/a | -   | n/a |      |

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

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**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 km<sup>2</sup> 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 17<sup>th</sup> 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

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