Disturbance history and stand dynamics in secondary and old-growth forests of the Southern Appalachian Mountains, USA

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BUTLER, S. M. (Family Forest Research Center, University of Massachusetts, Amherst, MA 01003), A. S. WHITE (School of Forest Resources, University of Maine, Orono, ME 04469-5755), K. J. ELLIOTT (Coweeta Hydrologic Laboratory, Center for Forest Watershed Science, Southern Research Station, USDA Forest Service, Otto, NC 28763) AND R. S. SEYMOUR (School of Forest Resources, University of Maine, Orono, ME 04469-5755). Disturbance history and stand dynamics in secondary and old-growth forests of the Southern Appalachian Mountains, USA. J. Torrey Bot. Soc. 141: 189–204. 2014.—Understanding the patterns of past disturbance allows further insight into the complex composition, structure, and function of current and future forests, which is increasingly important in a world where disturbance characteristics are changing. Our objectives were to define disturbance causes, rates (percent disturbance per decade), magnitudes and frequency (time since last disturbance) for both secondary and old-growth mixed-oak stands, and to determine if all mixed oak stands experience similar disturbance history. The study was located in two southern Appalachian forests in western North Carolina, USA: Coweeta Hydrologic Laboratory, a 2,185 ha experimental forest with some history of harvesting, and the Joyce Kilmer Wilderness, a 6,805 ha old-growth forest with no known harvesting. We used dendroecological techniques to evaluate the disturbance histories and create chronologies of these mixed-oak forests. Average decadal disturbance rates ranged from 4.3% to 13.8%, similar to rates common in eastern temperate forests (5% to 20%). The decades of peak recruitment common to several stands were the 1840s, which coincides with the historical accounts of a hurricane; the 1900s through the 1940s, which coincide with logging and elimination of *Castanea dentata* (Marshall) Borkh. by chestnut blight; and the 1960s, which coincides with drought and an elm spanworm infestation. The large peaks of disturbance were often synchronous and widespread, affecting stands across both Coweeta and Joyce Kilmer. However, there were also scattered pulses of disturbance unique to single stands, suggesting that localized events also played a role in the disturbance dynamics. Periods of constant low rates of disturbance present in all stands also indicate the importance of small canopy gaps in these forests. We found that stands similar in disturbance regimes were also similar in species composition. Results from our study provide information on how past disturbances, both regional and local events, have shaped the current forest. This understanding could help inform models to better predict how forests might respond to future climate (e.g., rising temperatures and increasing precipitation variability) and disturbance patterns (e.g., more frequent and severe events).

Key words: dendrochronology, dendroecology, disturbance rates, recruitment events.

Past and present disturbances can strongly influence the composition, structure and diversity of forests. Conversely, characteristics of a forest influence the types, magnitudes, spatial dimensions, and temporal patterns of disturbances. Recognizing this interplay between disturbances and forests is fundamental to understanding how forests have come to their present state and predicting how they might change in the future. Disturbances in the eastern US, including the southern Appalachians, vary in type (including timber harvests, hurricanes, ice storms, fires, insects and diseases), frequency, severity (ranging from low, where overstory trees may be damaged or stressed but incur minimal mortality, to high, where overstory trees suffer extensive mortality and new forest stands are initiated), and spatial extent (from within stands to across landscapes; e.g., Runkle 1982, Elliott and Swank 1994, Elliott et al. 1997, Crow et al. 2002, Lafon and Speer 2002, Elliott and Knoepp 2005, Hart and Grissino-Mayer 2008, White et al. 2011).

The mixed-*Quercus* forests of the Southern Appalachian Mountains provide a rich, albeit complicated, setting for disturbance ecology research. Their very existence, compositionally, is due in part to the loss of *Castanea dentata* (American chestnut) from the Chestnut-Oak type (c.f. Braun 1950) due to the introduced chestnut blight fungus (*Cryphonectria parasitica* Murr.; Keever 1953, Crow 1988, Abrams et al. 1995, Abrams et al. 1997, Harrod and White 1999). *Castanea dentata* was a foundation species, and its loss from the forest canopy had a strong effect on the ecosystem (Ellison et al. 2005). In many places, the in-place mortality was further complicated by salvage cuttings that removed the chestnut boles from the sites. Harvesting occurred for other species as well, both before (Hale 1883) and after the arrival of chestnut blight.

The history of disturbances in southern Appalachian mixed-*Quercus* forests is thus a complex one. To study such a history requires that several choices be made. For example, what forest types are of interest, and are recent human influences to be included? Many studies of disturbance history in the eastern U.S. have focused on old-growth forests of a variety of types (e.g., mesic-hardwood (Lorimer 1980), northern hardwood (Orwig et al. 2001)), and some have included second-growth forests (e.g., xeric *Quercus-Pinus* (Bratton and Meier 1998), mixed-*Quercus* on the Cumberland Plateau (Hart and Grissino-Mayer 2008)). Another question concerns what approach will be used. Many are potentially available (c.f. Egan and Howell 2001), but each must be matched carefully with the questions being asked.

Our major focus was on the disturbance history of the mixed-*Quercus* forest type in the southern Appalachians of western North Carolina as elucidated by dendroecology, a technique that uses tree-ring analysis for a retrospective look at forest disturbances (Abrams et al. 1995, Fraver and White 2005a). We sampled mixed-*Quercus* second-growth forests in Coweeta Hydrologic Laboratory (hereafter Coweeta) and old-growth forests of the same type in Joyce Kilmer Wilderness (hereafter Joyce Kilmer). Our specific objectives were to (1) determine the average disturbance rates, the pattern of disturbance rates over time, severities, and agents for each of nine secondary and old-growth mixed-*Quercus* stands, (2) assess the spatial extent of these disturbances by comparing within-location disturbance characteristics and between-location disturbance characteristics, and (3) determine if there is a relationship between disturbance histories and successional status (old-growth versus secondary-growth), environmental site factors, and current species composition.

Underlying these objectives is a body of questions/assumptions about the role of disturbances in forest stands of any type. For example, we often assume that small random disturbances tend to make disturbance histories more stand-specific whereas larger and/or more targeted disturbances tend to synchronize disturbance histories across stands. The degree of synchrony will depend on the degree of commonality among stands with respect to the presence of vulnerability factors, which vary with type of disturbance. For example, chestnut blight damage would be synchronized across sites to the extent sites had similar amounts of *Castanea dentata*. How the stand recovered from the blight, however, would depend on the species left behind, leading to the assumption that the more similar sites are in terms of their composition and physical environment, the more likely they are to have had similar disturbance histories. That line of thought could lead to the conclusion that disturbances act to keep stand development

parallel or convergent rather than being a disruptive, divergent force.

Materials and Methods. STUDY AREA DESCRIPTIONS AND HISTORY. Coweeta is located in the Nantahala Mountain Range of western North Carolina, USA within the Blue Ridge Physiographic Province, near the southern end of the Appalachian Mountain chain (35° 03′ N, 83° 25′ W). The 2185 ha research laboratory is owned and operated by the USDA Forest Service and consists of two adjacent, east-facing, bowl-shaped basins: Coweeta Basin and Dryman Fork Basin, both of which have been extensively studied. Elevations range from 675 to 1592 m asl, with steep slopes ranging from 30 to over 100 percent. The relief has a major influence on hydrologic, climatic, and vegetation characteristics (Elliott et al. 1999). Streams flow throughout the year, fed by approximately 2000 mm of precipitation per year, most of which is rain. Mean annual temperature is 12.6 °C and ranges from an average of 11.7 °C in winter to 21.6 °C in summer (Swift et al. 1988). Deep sandy loams are underlain by folded schist and gneiss. Two soil orders are found within Coweeta: immature Inceptisols and older developed Ultisols, including Umbric Dystrochrepts and Typic Haplumbrepts (Thomas 1996). The principal overstory species are of the genera *Quercus*, *Acer*, *Carya*, and *Liriodendron*. Evergreen shrubs (*Rhododendron* and *Kalmia*) combine with deciduous species of *Cornus*, *Robinia*, *Acer*, and *Betula* to form a dense understory cover (Day et al. 1988).

Numerous disturbances and stressors, such as logging, drought, hurricanes, and invasive insects and pathogens, have influenced forest structure, composition, and distribution of species in the Coweeta Basin (Elliott and Vose 2011). The U.S. Forest Service purchased the Basin in 1918 from J.A. Porter Logging Company, but the company reserved the rights to harvest the timber over 38 cm in diameter and continued selective but heavy cutting until 1923 (Douglas and Hoover 1988). Chestnut blight, a fungus introduced to the United States in the late 1800s, was first noted in Coweeta in the early 1920s; by the late 1930s most *Castanea dentata* trees were dead or dying (Elliott and Swank 2008). Droughts, such as those in 1985–1988, 1998–2001 and 2006–2008 are increasingly common (Coweeta Hydrologic Laboratory, http://www.coweeta. uga.edu; Li et al. 2011, Laseter et al. 2012) and can result in canopy gap formation due to hardwood tree mortality (Clinton et al. 1993). Significant mortality of *Pinus rigida* Mill. occurred due to a combination of drought and subsequent attack by the southern pine beetle (*Dendroctonus frontalis* Zimmerman) during the 1985–1988 drought (Elliott and Swank 1994). However, these patterns are described over large areas and spatially explicit disturbance history is unknown.

Joyce Kilmer, like Coweeta, is located in the Blue Ridge Physiographic Province and spans the Nantahala and Cherokee National Forests (35° 02′ to 35° 04′ N, 83° 06′ to 84° 00′ W). The 6805 ha wilderness area is approximately 110 km from the Coweeta Basin. Elevations range from 331 to 1615 m asl. Mean annual precipitation is 2200 mm at high elevation and 1760 mm at low elevation (Newell et al. 1997). Low elevation areas experience higher summer temperatures (25 to 30 °C) than high elevation areas (18 °C), with an average decrease of 1.24 °C for every 305 m of elevation gain (Newell et al. 1997). Soils are coarse-loamy, mixed, mesic Typic Haplumbrepts underlain by Arkosic metasandstone (Lesure et al. 1977). Similar to Coweeta, dominant overstory genera include *Quercus*, *Acer*, *Carya*, and *Liriodendron* (Newell et al. 1997). Spatially explicit disturbance history in mixed-Quercus forests is largely unknown at Joyce Kilmer.

FIELD AND LABORATORY PROCEDURES. Seven stands were chosen to represent the mesic to dry moisture gradient occupied by the mixed-*Quercus* type at Coweeta (Table 1). Stands were selected on the basis of several criteria, including species composition, topographic position (to include a range of topographic positions within the study), and preliminary dating of old trees. Our aim was to sample sites within the mixed-Quercus type, with old trees on a range of topographic positions. In addition, two old-growth stands were selected in the Joyce Kilmer watershed (Table 1). They were old-growth representatives of similar second-growth stands at Coweeta. Both stands were located in the high elevation, mixed-*Quercus* forest described by Newell et al. (1997).

Variable radius plot sampling (also called point sampling) with a wedge prism (2.0 BAF, metric) was used to sample stand composition and structure at five to thirteen points in each

Table 1.   Stand characteristics at Coweeta and Joyce Kilmer. Descriptive characteristics are slope, aspect, elevation, basal area, density, and crown projection area (CPA).

Location	Stand	Slope (degrees)	Aspect	Elevation (m)	Basal area ($m^2 ha^{-1}$)	Density (stems ha^{-1})	CPA ($m^2 ha^{-1}$)
Coweeta	DC	16	N	1234	28.6	426	13016
	DS	28	NW	1204	28.3	345	12204
	DY	21	E	1097	21.7	223	8789
	MG	34	NE	1341	23.2	290	8260
	PM	31	NE	1387	37.6	595	12465
	PR	36	NW	1265	26.4	292	9541
	RK	19	NW	1143	22.6	216	8217
Joyce Kilmer	GD	9	SW	1219	27.8	596	15200
	SB	5	NE	1183	36.0	467	15608

stand. A wedge prism is used to determine which trees are sampled based on their size and distance from a sample point. Points were spaced along transects within each stand; distance between points varied due to differences in stand shape and size. Species, diameter at breast height (DBH, at 1.37 m), and crown class (dominant, codominant, intermediate and overtopped) were recorded for each tree ≥ 10 cm DBH in the prism sample. Small trees and saplings < 10 cm DBH and ≥ 1.37 m height, were recorded by species and DBH in a 0.01 ha circular plot centered on each sample point. Slope, aspect, and elevation were recorded for each stand (Table 1). Nomenclature follows Kirkman et al. (2007).

Tree crown radii, used to predict crown projection areas (CPA) from DBH, were determined for the five most abundant species sampled: *Quercus rubra* L., *Quercus alba* L., *Quercus prinus* L., *Acer rubrum* L., and *Betula lenta* L. Trees were randomly sampled over a range from 10 to 120 cm DBH in four of the sample stands that spanned the range of topographic positions. For each tree sampled, the horizontal distance from bole center to canopy drip line of the longest radius was measured. Three more radii were subsequently measured at 90 degree intervals, each extending from bole center to canopy drip line. CPA was then calculated using the quarter-ellipse method (Lorimer and Frelich 1989), and linear regression models were created for each species to predict CPA from DBH. For less common species, CPA was predicted from published equations from this same region (Bechtold 2003).

In each stand at five randomly chosen points, increment cores were extracted from all trees tallied with the prism. Cores were taken to the pith (when possible) at 1.0 m above the ground and parallel to topographic contours. Approximately 80 trees per stand were cored.

In the lab, cores were air dried, mounted, and sanded using progressively finer sandpaper in preparation for analysis (Stokes and Smiley 1996). Ring widths were measured to the nearest 0.01 mm using a dissecting microscope, VELMEX sliding stage (VELMEX Inc., Bloomfield, NY) and MeasureJ2X© software. Cores were visually cross-dated within species and stands by using marker years and then checked with the computer cross-dating program COFECHA (Holmes 1983). For trees where the core missed the pith, the center date was estimated using Applequist's (1958) commonly used concentric ring pith locators, which are based on ring curvature and width of the innermost rings. We used the estimated age of cores that did not hit the pith if there were 20 or fewer rings missing. Cores that missed the pith by more than 20 years were not used for age data ("age" refers to the number of rings at coring height (1.0 m), not total age since germination).

DISTURBANCE DETECTION. Past disturbances often can be detected by the pattern of radial growth in surviving trees or in the recruitment (establishment) of new trees. Abrupt, large, and sustained increases in radial growth (growth release) occur in surviving trees and rapid early growth occurs in small stems that are recruited into the gaps created by a disturbance (Lorimer and Frelich 1989). Releases and gap recruitment are the consequence of mortality in the canopy, which frees up space or resources (Frelich 2002). Trees in the same age class could be of non-gap origin or of gap origin.

Various criteria for detecting releases have been used across a variety of forest types and

species (e.g., Chokkalingam 1998, Black and Abrams 2004, Fraver and White 2005a). We used the percent increase method, a commonly used method of release detection. The equation for this method was formalized by Nowacki and Abrams (1997):

$$\% \, GC = [(M_2 M_1)/M_1] \times 100$$

where $\% \, GC$ is the percent growth change for any given year within a series, M_1 is the average radial growth during the selected window of time prior to, and including, a given year and M_2 is the average radial growth during the selected window of time after a given year. The window of time used for this study was ten years. $\% \, GC$ must exceed an arbitrary threshold (e.g., 100%) to qualify as a release.

However, a single $\% \, GC$ threshold can be overly sensitive at slow rates of prior growth and overly stringent at high rates (Black and Abrams 2004, Fraver and White 2005b), thus requiring adjustment. For slow growing trees (defined for this study as those having a radial growth < 1.0 mm yr^{-1} before a potentially releasing event), a release was defined as at least a 100% growth increase and a post-release growth rate greater than 0.5 mm yr^{-1}. Setting the post-release growth rate threshold at 0.5 mm reduced the inclusion of false-positive releases; i.e., those percent increases that are high but whose absolute growth is far less than one would expect for a stem growing in a gap. At the other end of the spectrum, when a tree was growing at moderate to high rates (defined here as ≥ 1 mm yr^{-1}), a 100% increase in growth might have been impossible for the tree to achieve, because the tree was already growing well and thus was less restricted by competition from neighboring trees. Therefore, a release was identified when the faster-growing trees showed at least a 60% increase in growth, thus reducing the number of false-negative releases.

In addition to meeting minimum growth thresholds, releases also had to be sustained. A release was considered to be sustained when the percent growth change exceeds the threshold growth change (for preceding 10 years) for 7 out of 10 years following the event (Fraver and White 2005b). Finally, determining if the release was abrupt or gradual was done by visually inspecting each graphed chronology (Fraver and White 2005b). If the growth rate after the release was approximately the same

as it was prior to the suppression preceding the release, indicating the tree's crown did not expand (i.e., it simply regained its prior space), the disturbance was counted as a recovery. Recovery events still reflect disturbances to the ecosystem and were counted as such. All release and recovery events occurring in a single tree were included in determining disturbance history.

Gap recruited trees were identified from the population of trees whose pith was intersected or whose innermost ring was estimated to be 10 or fewer years from the pith. A tree was considered gap recruited when it had an average growth rate of at least 1.0 mm per year for the first five years measured, as well as a pattern of growth typical of a gap recruited tree as described by Lorimer and Frelich (1989) and Frelich (2002). Once all disturbances were identified, stand-level temporal patterns of the events ("disturbance chronologies") were created.

DISTURBANCE CHRONOLOGIES. Disturbance chronologies typically describe the percentage of the stand canopy area disturbed in each decade. For each decade, CPAs of released trees (including recovered trees) and gap recruited trees were summed and divided by the total CPA of trees still alive from that decade (Fraver et al. 2009). This proportion was converted to a percentage and is hereafter referred to as the decadal disturbance rate. Disturbance chronologies were truncated when the sample size became too small (< 10 trees) to be assumed reliable further back in time (Fraver et al. 2009). Chronologies were created for each stand using all current canopy trees. Peaks in disturbance in each stand were identified as those decades whose disturbance rate was 50% or higher than the stand's average decadal disturbance rate.

STANDARDIZED GROWTH CHRONOLOGIES. Once decadal disturbance rates were calculated for each stand, evidence of species-specific disturbances across stands were investigated by creating standardized growth chronologies for the five most abundant species sampled (*Acer rubrum*, *Betula lenta*, *Quercus alba*, *Quercus prinus* and *Quercus rubra*) using the program ARSTAN (Cook and Krusic 2011). First, raw ring widths were plotted over time for each tree, creating a tree-ring series. Next, we used ARSTAN to fit a horizontal line through the mean ring width for each tree-ring

series. Then, the raw ring widths were divided by fit values, thus standardizing the series for each tree, yielding a mean tree-ring index of one and a constant variance, while preserving most of the temporal pattern of variation in growth (Jonsson et al. 2009). Standardized ring width series for all trees of the same species were averaged using a robust bi-weight mean, which reduces the effects of outliers and extreme values (Cook et. al. 1990). Standardized chronologies were cut off when the sample size became small (< 10 trees) further back in time (Jonsson et al. 2009, Fraver et al. 2009).

We examined growth reductions to look for across-stand disturbances that affected a given species or group of species. Growth reductions can indicate disturbance events that affected trees in the stand by preventing growth or damaging the canopy, but not killing the tree or opening the canopy. Growth reductions were identified when at least three years of consecutive ring width index values were 0.8 or lower. Because standardized growth chronologies address a population of trees instead of individual trees, a threshold of three years was used to highlight a decrease in growth across trees in the stand. These growth reductions identify short-term decreases in growth, but do not address long-term or gradual declines in growth due to canopy closure (Chokkalingam 1998). Instead, the abrupt decreases in growth are likely due to disturbance events.

DISTURBANCE HISTORY ALONG COMPOSITIONAL AND ENVIRONMENTAL GRADIENTS. We used a Mantel test to evaluate whether the degree of stand similarity based on species composition and abundance was similar to that based on disturbance histories at Coweeta (Quinn and Keough 2003, Fraver et al. 2009). We used Sorenson's (Bray-Curtis) distance measure to calculate similarity of each pair of plots based on species composition using basal area and density of the six most common species (*Acer rubrum, Betula lenta, Quercus alba, Quercus prinus, Quercus rubra, Carya* spp.). Again using Sorenson's distance measure, we calculated a second distance matrix using stand-level decadal disturbance rates transformed by arcsine square root as the basis for calculating the degree of similarity between all possible pairs of plots. In this case, each decade was analogous to species; the matrix from which the Sorenson distance was calculated was sample plot by decade disturbance rate rather than sample plot by species abundance. The Mantel test was used to correlate the two matrices, thus determining whether plots with similar vegetation composition also tended to have similar temporal patterns of disturbances. Mantel tests were also conducted to determine if correlations existed between distance matrices based on decadal disturbance rates and ones based on topographic variables (slope and elevation, individually analyzed). All Mantel tests were performed in PC-ORD (McCune and Mefford 1999).

Results. DISTURBANCE RATES AND PATTERNS. All stands were uneven aged. Most decades had fairly low disturbance rates but occasional peaks in recruitment and release did occur; peaks varied from synchronous to asynchronous (Fig. 1, 2). Mean decadal disturbance rates ranged from 4.3 to 13.8% across the nine stands at Coweeta and Joyce Kilmer (Table 2).

PEAK DECADES OF DISTURBANCE. The decades of peak recruitment common to several stands were the 1840s, which coincides with the historical accounts of a hurricane; the 1900s through the 1940s, which coincide with logging and elimination of *Castanea dentata* by chestnut blight; and the 1960s, which coincides with drought and an elm spanworm infestation. Other peaks in disturbance include the 1820s, 1850s–1870s, and 1980s.

The most pronounced peak in disturbance in the 1840s occurred in Coweeta stand MG (20.2% canopy area disturbed; Fig. 1), based on a combination of recovery events, releases and gap recruited trees. In the 1900s, stand DS had 15.9% canopy area disturbed and PR had 9.8% canopy area disturbed (Fig. 1). Peaks in disturbance in the 1910s included Coweeta stands PM and PR (adjacent stands with 25.5% and 15.9% canopy area disturbed, respectively) and in the 1920s included stands DC, DS, and DY. These peaks ranged from 17.2% to 41.5% of canopy area disturbed (Fig. 1). Every stand in Coweeta had a peak in disturbance in the 1930s (ranging from 47.9% in stand RK to 13.4% in stand PR; Fig. 1). Coweeta stands DY, PM and RK also showed disturbance peaks in the 1940s (ranging from 19.5% in PM to 14.6% in DY). Because the peaks in the 1920s–1940s were found throughout our Coweeta sample sites, they were likely watershed wide. Stand DC showed a peak in disturbance in the 1960s, consisting mostly of

Fig. 1. Disturbance history for forest stands at Coweeta (DC, DS, DY, MG, PM, PR and RK) and Joyce Kilmer (GD and SB) from the 1750s to the 1990s expressed as canopy area disturbed (%). Disturbance categories include gap origin (recruited trees), major disturbances (releases), and recovery events (see text for definitions). Sample depth is the number of trees contributing to that decade.

recovery events and releases (17.9% canopy area disturbed; Fig. 1).

Peaks in disturbance in the 1840s occurred in Joyce Kilmer stand SB (38.7% canopy area disturbed; Fig. 1) based on a combination of recovery events, releases, and gap recruited trees (Fig. 2). Peaks in disturbance in the 1910s and 1920s occurred in Joyce Kilmer
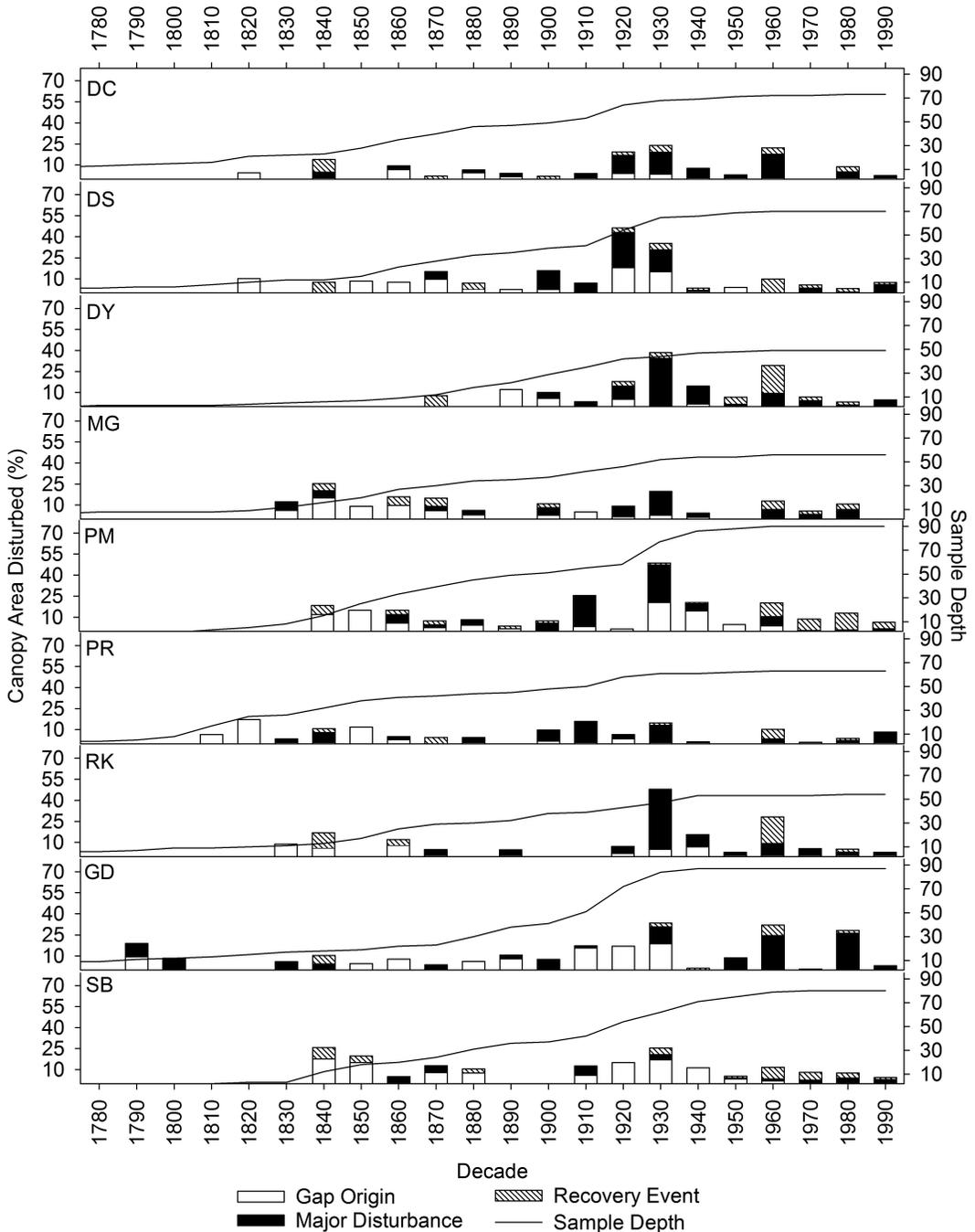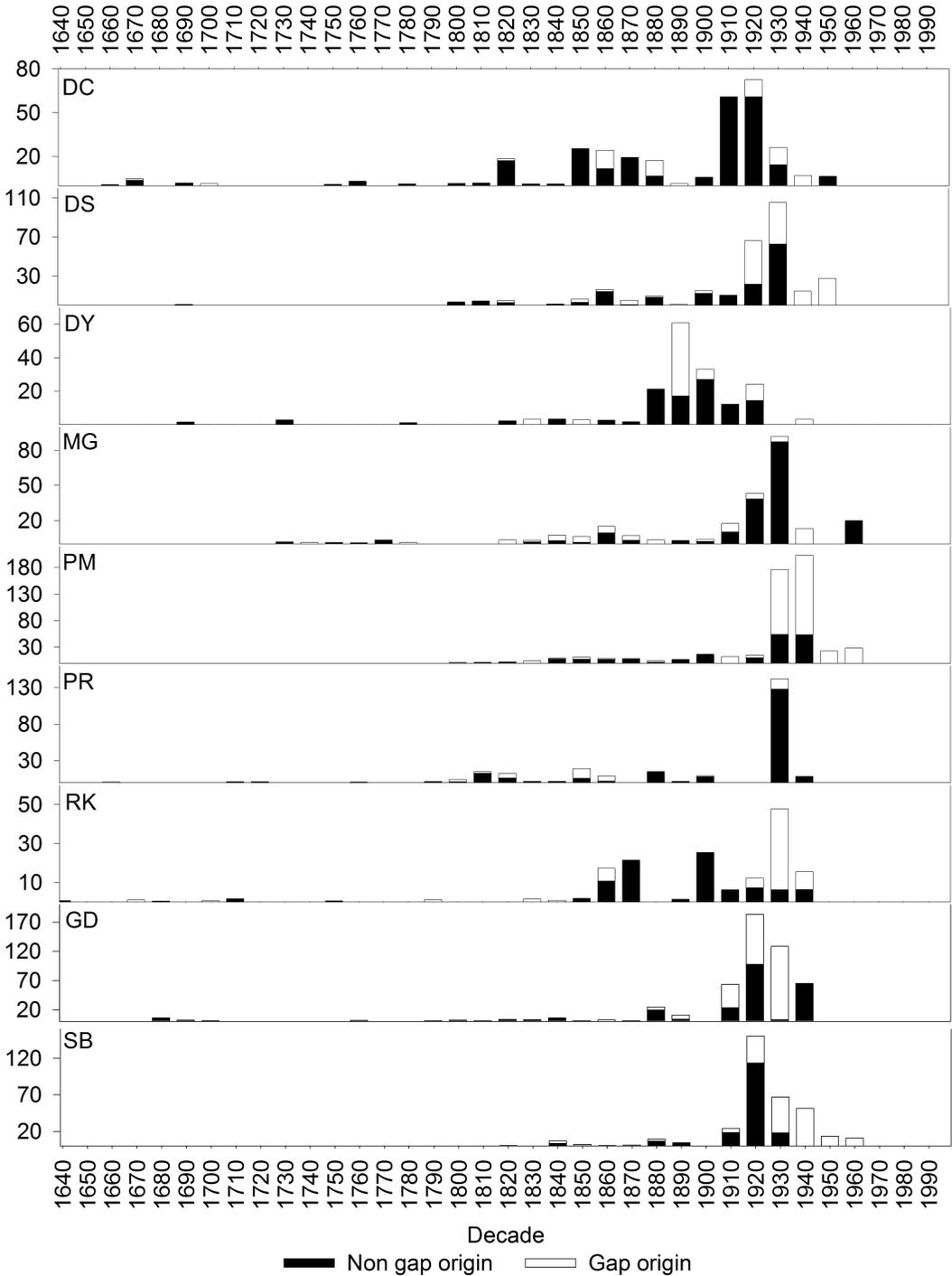
Fig. 2. Recruitment events for forest stands at Coweeta (DC, DS, DY, MG, PM, PR and RK) and Joyce Kilmer (GD and SB) from the 1640s to the 1990s expressed as density (trees per hectare). Recruitment events include non-gap origin and gap origin (recruited trees).

Table 2.   Mean disturbance rates (% of canopy area disturbed) for each stand at Coweeta and Joyce Kilmer. All rates are calculated from the 1990s back to the earliest decade that included at least ten trees. Standard errors are in parentheses.

Location	Stand	Disturbance rate	Earliest decade with ≥ 10 trees	Earliest decade with 1 tree
Coweeta	DC	4.3 (1.2)	1750	1670
	DS	8.8 (2.6)	1820	1680
	JC	8.7 (2.6)	1870	1690
	MG	7.8 (1.4)	1830	1730
	PM	10.8 (3.0)	1840	1800
	PR	6.3 (1.2)	1810	1660
	RK	7.0 (2.6)	1820	1640
Joyce Kilmer	GD	9.8 (2.0)	1790	1680
	SB	13.8 (4.2)	1840	1740

stand GD. Both stands at Joyce Kilmer had a peak in disturbance in the 1930s (67.0% in stand SB and 30.9% in stand GD; Fig. 1), and the occurrence of these peaks of disturbance in stands at Joyce Kilmer as well as at Coweeta suggests that they were region-wide events. Stand GD showed a peak in disturbance in the 1960s, consisting mostly of recovery events and releases (24.8% canopy area disturbed; Fig. 1). Joyce Kilmer stand GD showed a peak in disturbance in the 1980s (26.6% canopy area disturbed; Fig. 1).

Species' standardized growth chronologies showed declines in growth in the 1860s for *Quercus prinus* and *Quercus rubra*, 1917–1919 for *Quercus alba*, *Quercus prinus*, and *Quercus rubra,* early 1960s for *Acer rubrum* and *Betula lenta*, and 1989–1991 for *Betula lenta, Quercus prinus* and *Quercus rubra* (Fig. 3). Species' standardized growth chronologies showed similar results at Joyce Kilmer (data not shown).

DISTURBANCE HISTORY, SPECIES COMPOSITION, AND ENVIRONMENT. The Mantel test revealed a significant correlation between species composition and patterns and magnitudes of decadal disturbance rates (standardized Mantel statistic $r = 0.39$, $P = 0.03$). In other words, the more similar two plots were in their tree species composition, the more similar their disturbance rates were over time. In contrast, there was no significant correlation between similarity of disturbance rates and similarity of environmental conditions (slope and elevation).

Discussion. DISTURBANCE RATES AND TEMPORAL PATTERNS. Cohorts of varying sizes and species composition arose throughout each stand's history, likely as a result of various disturbance pulses. The stands were generally uneven-aged,

suggesting that they had not been subjected to stand-replacing disturbances. Old age classes at both Coweeta and Joyce Kilmer (maximum age ranged 200–360 years across all plots) tended to be dominated by Quercus species, with a minor component of Carya species. In general, most stands had constant but low recruitment of Quercus species until the 1920s, 1930s, and 1940s, when *Acer rubrum* and *Betula lenta* increased in abundance. It is not clear if other species were shorter lived and had been in the stands at current densities as long as *Quercus* species, or if these species were recruited for the first time in these decades (Johnson et al. 1994).

Examining peaks in disturbance as determined by radial growth patterns is often used to describe a forest's disturbance history (Lorimer 1980, Orwig et al. 2001, Fraver et al. 2009). Mean decadal disturbance rates at Coweeta and Joyce Kilmer ranged from 4.3 to 13.8% across the nine stands and are comparable to rates found in several temperate forests in this region, even though different methods were used to derive these rates (Runkle 1982, Bratton and Meier 1998; Table 2). Disturbance patterns over time consisted of constantly varying but relatively low decadal rates of disturbance, but all sites had one or more peak decades. Disturbances in the Southern Appalachian Mountains are largely shaped by frequent small gaps associated with single tree deaths interspersed with less frequent multiple tree gaps resulting from larger disturbances, such as windstorms, drought, logging and diseases such as chestnut blight (Hursh and Haasis 1931, Runkle 1982, Clinton et al. 1993, Bratton and Meier 1998).

DISTURBANCE AGENTS. The following section describes peak decades of disturbance, both

Table 3. Species composition at Coweeta and Joyce Kilmer. Density (stems ha^{-1}) and basal area (BA, m^2 ha^{-1}) of trees $\geq$ 10 cm diameter at breast height (DBH, 1.37 m) for each sampled stand.

Location	Stand	A. rubrum		B. lenta		Q. alba		Q. prinus		Q. rubra		Carya spp.		Other	
		Density	BA	Density	BA	Density	BA	Density	BA	Density	BA	Density	BA	Density	BA
Coweeta	DC	61	1.8	12	0.8	83	11.6	31	3.6	39	5.0	68	2.2	131	3.6
	DS	53	2.0	14	0.6	1	4.8	9	0.8	93	12.8	15	1.2	142	6.2
	DY	70	5.7	0	0.0	0	0.0	26	3.3	47	7.3	66	3.7	14	1.7
	MG	3	0.8	101	3.6	0	0.0	1	0.4	61	15.2	0	0.0	124	5.2
	PM	0	0.0	290	10.0	1	0.4	0	0.0	95	20.0	0	0.0	209	7.2
	PR	8	0.8	40	1.6	13	2.4	88	4.8	11	14.4	14	1.2	108	1.6
	RK	14	1.2	40	3.6	28	4.0	17	1.4	42	6.6	14	0.8	63	5.0
Joyce Kilmer	GD	294	9.0	0	0.0	40	4.8	78	5.5	68	6.0	35	0.5	81	2.0
	SB	91	4.7	26	0.7	10	1.0	1	0.3	93	20.0	54	2.7	191	6.7

watershed and region wide and localized at the stand level. In addition, we suggest probable disturbance agents based on historical documentation, common disturbances in eastern temperate forests, and radial growth patterns.

1830s–1840s. In 1835, a hurricane struck Jones Creek (north of Coweeta), causing major blowdown at Coweeta (Douglass and Hoover 1988). The peaks in the 1830s and 1840s may partially be due to damage or mortality from this hurricane. Hurricanes affect the Southern Appalachian Mountains every 1 to 24 years (Greenberg and McNab 1998). These wind events occur at varying scales, causing considerable gaps in the canopy and influencing forest species composition and structure (Greenberg and McNab 1998).

All three components (releases, recoveries, and gap recruitment) of major disturbances in the 1840s occurred in stands located on ridges, while stands at lower elevations primarily experienced recovery events (Fig. 2). Most damage from hurricane Opal (1995) occurred on ridges and upper slopes, where shallow soils, large crowns, and saturated soils made trees more susceptible to windthrow (Clinton and Baker 2000). Joyce Kilmer stand SB experienced a peak in disturbance in the 1840s, with 38.7% canopy area disturbed (Fig. 1). Exposure to varying winds can differ based on slope position. Stand SB is a northeast-facing ridge, while GD, which experienced 10.3% canopy area disturbed in the 1840s, is a southwest-facing slope. Although direction of the hurricane winds cannot be predicted at a fine enough scale to differentiate between close stands without knowing the hurricane's path, varying exposures of the two stands may explain differences in disturbance intensity.

1900s–1940s. The dominant decades of disturbance detected in these stands occurred in the 1900s–1940s. Historical documentation provides insight to potential causes of these peaks, but many of these potential causes overlap in time and space, making distinction of the events difficult. We use the magnitude, extent, and timing of the documented disturbances in these decades to help distinguish the varying peaks in these stands.

Historical documentations of ice storms indicate a damaging storm in 1915 in western North Carolina (Rhoades 1918). This storm may have contributed to peaks in disturbance
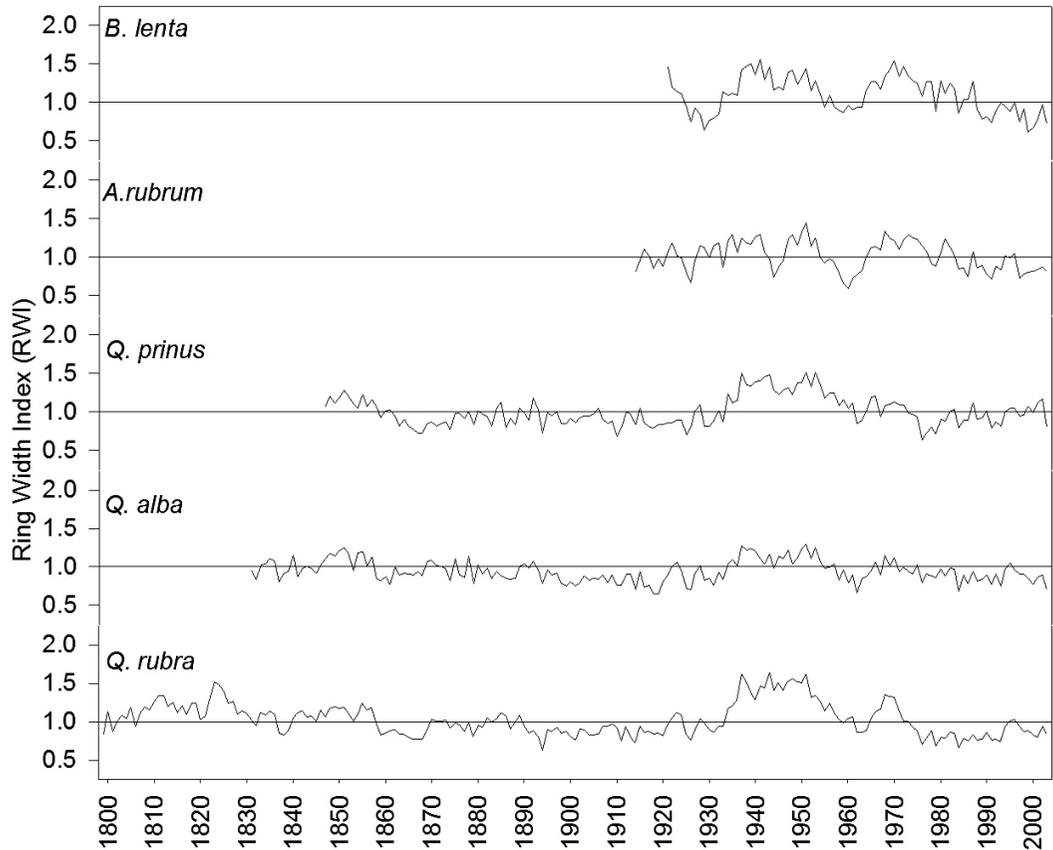
Fig. 3.   Standardized growth chronologies for the five most common species at Coweeta.

in the 1910s in Coweeta and Joyce Kilmer. Species-specific resistance to ice storm damage varies, with susceptibility extent based on forest type, topographic position, aspect, stand age and species size classes (Whitney and Johnson 1982, Boerner et al. 1988, Warrillow and Mou 1999).

In our study, *Castanea dentata* decline likely contributed to peaks in disturbance in the 1930s and 1940s, while the 1920s peak was likely a combination of harvesting and various other stresses. High rates of disturbance occurred in decades preceding the blight in many stands. Spatial and temporal documentation of harvesting patterns and intensity at Coweeta are lacking; however, the timing of these peaks in disturbance and recruitment coincide with the estimated dates of harvesting at Coweeta. Documentation indicates logging occurred at Coweeta in the early 1900s. The W. M. Ritter Company harvested from 1906 to 1918, and J.A. Porter logged from 1919 to 1923 (Douglass and Hoover 1988). The

occurrence of harvesting in the 1920s and *C. dentata* mortality in the 1930s makes separation of these disturbances difficult. Both disturbances show similar patterns of release, with increases in radial growth occurring soon after crown openings (Rentch et al. 2002). However, even after logging subsided, *C. dentata* averaged 10.1 m^2 ha^{-1} in basal area and was the most important species at Coweeta (Elliott and Swank 2008). Therefore, harvested stands still had substantial residual *C. dentata* present to allow further release of surrounding trees following its death a decade later. Indeed, eight of the nine stands had greater disturbance rates in the 1930s than in the 1920s.

In addition to logging in the 1920s, a severe drought (July and August) and a late freeze (late May) were recorded in the southern Appalachians in 1925 (Beal 1926, Hursh and Haasis 1931). Both disturbances killed and injured many upper elevation *Quercus* species in the southern Appalachians (Hursh and

Haasis 1931). We detected narrow rings in many trees in 1925 (Fig. 3). We see some differences between the disturbance events at Coweeta and Joyce Kilmer during the 1920s. While Joyce Kilmer does have disturbance events in the 1920s, the peaks are largely dominated by gap origin trees recruiting. The stands at Coweeta have releases, gap origin recruitment, and recovery events. Other disturbance events, such as drought or late freeze, likely contributed to the gap-origin recruitment patterns we see at both sites during the 1920s.

Because the effects of logging are generally seen within three years of the harvest (Rentch et al. 2002), and harvesting ended at Coweeta in 1923, releases seen in the 1930s and 1940s were likely due to death of *Castanea dentata* as opposed to logging. However, harvesting and death of *C. dentata* were only a decade apart and our study could not identify specific patterns of release unique to either disturbance.

Castanea dentata was an abundant species in the southern Appalachians. In the early 1920s, chestnut blight was found infecting *C. dentata* trees in the Coweeta Basin (Elliott and Swank 2008); however, tree mortality does not occur for several years following the fungal infection (Anagnostakis 1987). In 1934, standing dead and dying *C. dentata* comprised 41% of the basal area of a single, low elevation watershed in Coweeta. Analysis of species composition across permanent plots that spanned the Coweeta Basin found that *C. dentata* was the most important species prior to 1934, based on the sampling of dead and dying trees. It was found in 98% of the plots, comprised 22% of the density, and 36% of the total basal area (Elliott and Swank 2008). By the time of the next sampling in 1953, live *C. dentata* was less than 1% (Nelson 1955).

Stress factors also contributing to peaks in the 1930s include a damaging ice storm (1932) (Abell 1934) and short-term drought (1934; Biocca et al. 1993). In our study, narrow rings were detected for many trees in 1933 and 1934, but sustained decreases in radial growth following 1934 were not typically detected. Growth reductions can occur after an ice storm if damage was incurred on the tree from the ice itself or falling branches from other affected trees (Whitney and Johnson 1984). While the dominating disturbance in the 1930s was likely a combination of gaps created from *Castanea dentata* mortality and damage and

mortality from the ice storm and drought, the documented widespread nature and extensive change in the southern Appalachians resulting from *C. dentata* mortality leads us to believe that the blight was the overriding contributor to the peak in this decade.

1960s. Declining radial growth of *Quercus* species across the southern Appalachians was reported for the 1950s and 1960s (Tryon and True 1958, Tainter et al. 1984, Phipps and Whiton 1988, Tainter et al. 1990), including the Wayah Bald district of the Nantahala Mountains in western North Carolina USA (Biocca et al. 1993). Climate data for Coweeta showed below average precipitation for three consecutive years in the early 1950s, and four years well below average through the 1960s (Laseter et al. 2012). In general, trees recover quickly from short-term droughts; however, if the low precipitation initiates an onset of further stresses or an increase in susceptibility (e.g. insect infestations, wind stress from hurricanes and storms, fungal pathogens), prolonged decreases in radial growth may occur (Tainter et al. 1990). Interactions between drought and insect defoliation may account for the peaks of disturbance in the 1960s. We found indications of growth suppressions in *Acer rubrum* and *Betula lenta* chronologies in the late 1950s and early 1960s (Fig. 3).

In the southern Appalachians, elm spanworm (*Ennomos subsignarius* Hubner) defoliated 1.6 million acres of forest from 1954–1964s (peaking in 1960; Drooz et al. 1976). Elm spanworm primarily defoliates *Quercus, Carya, Juglans nigra* L., *Fraxinus americana* L., *Nyssa sylvatica* Marshall, and *Acer rubrum* (Fedde 1964, Drooz 1980). In 1960, the insect's egg masses were found throughout Coweeta (Grzenda et al. 1964). The entire Coweeta Basin was sprayed with DDT in 1961, and the upper ridges and slopes were subsequently sprayed in 1962. The effect of the DDT sprayings on controlling the outbreak was not reported (Grzenda et al. 1964). The outbreak ended in 1964, largely due to elm spanworm egg parasitism by *Telenomus* species (Ciesla 1963). This insect defoliation likely contributed to peaks in disturbance in the 1960s.

1980s. A major drought was recorded at Coweeta from 1985–1988 (Clinton et al. 1993), which likely contributed to peaks of distur-

bance in these stands. Regionally, this drought was the most severe in over a century (Cook et al. 1988, Pederson et al. 2012). During the peak year (1986), precipitation was 31% below average. Gaps were surveyed following the drought, and Clinton et al. (1993) found 74% of the gaps were created by standing dead trees, and 67% were on ridges and mid-slopes.

Disturbance History and Species Composition. We found significant relationships between decadal disturbance rates and species composition; the more alike sites were compositionally, the more alike they were in their disturbance histories. Elliott et al. (1999) found that environmental variables explained only 50% of the variation in species composition across Coweeta. They hypothesized that disturbance might account for additional variation not explained by site factors. Our correlations between disturbance matrices and species composition support their hypothesis.

Species recruitment and survival characteristics might be more related to disturbance intensity than environmental characteristics (Ruffner and Abrams 2003). Species capable of recruiting across environmental gradients (e.g., *Acer rubrum*) may be better competitors and more likely to recruit after intense disturbances that affect the canopy enough to increase the amount of light that reaches the forest floor. Similarly, shade intermediate-tolerant species (e.g., *Quercus, Betula, Carya*) may prefer different disturbance regimes where competition is reduced, preventing competing species from establishing (Crow 1988). The disturbance characteristics may dictate if species composition changes with varying disturbances (Harmon et al. 1982, Clebsch and Busing 1989, Frelich et al. 1993, Fraver and White 2005b). Species composition and disturbance patterns may also be correlated because of species-specific disturbances, such as insect outbreaks (Fraver et al. 2009). For example, the distribution of *Castanea dentata* likely influenced the percent canopy area disturbed in the 1920s–1940s.

Conclusions. The decadal disturbance rates at Coweeta and Joyce Kilmer since the mid-1700s (4.3%–13.8%) fall within the range typically found in eastern temperate forests (5%–20%; Runkle 1982). Similar patterns of disturbance appeared across all stands, with decades of consistently low rates of distur-

bance intermixed with less frequent peaks of more intense events. The large peaks of disturbance were often synchronous and widespread, affecting stands across both Coweeta and Joyce Kilmer. However, there were also scattered pulses of disturbance unique to single stands, suggesting that localized events also played a role in the disturbance dynamics. Periods of constant low rates of disturbance present in all stands also indicate the importance of small canopy gaps in these forests. We found that stands similar in disturbance regimes were also similar in species composition. This may be due to species-specific disturbances or disturbance events causing similar changes in species composition across stands. We did not, however, find that stands with similar disturbance patterns also had similar topographic characteristics, which may be due to the relatively similar environmental characteristics of the stands or the widespread nature of the disturbances pulses.

There was less of a difference in disturbance histories between second- and old-growth stands than might be expected. While we did see periods of high disturbance rates in decades during which logging occurred at Coweeta (1910s–1920s), these peaks of disturbance are not completely absent from old-growth stands at Joyce Kilmer that were not logged. Other disturbances in those decades, such as a severe drought in the 1920s, likely caused disturbance peaks in the unlogged stands. In addition, chestnut blight overlapped with logging disturbances, making these two hard to distinguish. Thus, we conclude that there is no clear pattern in their disturbance histories that distinguishes the old-growth and second-growth stands in this study because (a) the logging at Coweeta was somewhat masked by its overlap with another, even larger disturbance event (chestnut blight) that occurred in Joyce Kilmer as well Coweeta, (b) many other disturbances and stresses, such as drought and insect outbreaks, occurred at both sites, and (c) small, random events that occurred at the stand level would not necessarily be linked to other stands regardless of whether they were old-growth or second-growth, and thus would not distinguish between them. If logging was more periodic, and if the foundation species *Castanea dentata* had not been so devastated by the exotic blight, the old-growth forests and second-growth forests might differ more in composi-

tion and species abundance, which our results suggest would correspond to greater differences in their disturbance histories.

Understanding how past disturbances, both regional and local events, have shaped forests can help us gauge how forests might respond to future disturbance patterns in a changing world. For example, disturbance rates, intensities, and frequencies are predicted to change with climate change (He et al. 1999, Peterson et al. 2014). How forests will respond to increasing frequency of disturbance events, changes in climate (i.e., rising temperatures and increasing precipitation variability (Li et al. 2011)), and their interaction is the focus of considerable recent and ongoing research (e.g., Bond-Lamberty et al. 2014, McLauchlan et al. 2014, Mitchell et al. 2014, Peterson et al. 2014, Sommers et al. 2014).

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