RESEARCH PAPER



Do historic log buildings provide evidence of reforestation following depopulation of Indigenous Peoples?

Kristen K. de Graauw 🕒 | Amy E. Hessl



Department of Geology and Geography, West Virginia University, Morgantown, WV, USA

Correspondence

Kristen K. de Graauw, Department of Geology and Geography, West Virginia University, 98 Beechurst Ave, Morgantown, West Virginia 26506, USA. Email: kristen.degraauw@gmail.com

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Abstract

Aim: To test the previously published hypothesis that there was widespread reforestation following the depopulation of Indigenous Peoples in the 16th and 17th centuries.

Location: The central Appalachian Mountains of eastern North America.

Taxon: Quercus alba, Liriondendron tulipifera

Methods: To test for reforestation following depopulation, we used tree-ring evidence of tree recruitment, early radial growth and growth releases from 18 historic log buildings (n = 361 logs) and eight old-growth forest sites (n = 197 trees). We used inner-ring dates to determine if a synchronous recruitment event(s) was present at historic sites but absent from old-growth sites following depopulation. We used cluster analysis to determine if historic logs established in a clearing (fast early growth) or under a canopy (slow early growth). Similarly, we calculated disturbance rates (growth releases per 100 years) to determine if historic logs grew in a clearing (low disturbance) or under a canopy (high disturbance).

Results: Historic log and old-growth forest sites both document a period of elevated recruitment beginning in the 1670s. This event was observed in previous studies and across site types, suggesting that either climate variability or the absence of low-intensity land use (e.g. fire) may have also contributed to forest establishment. Most historic sites (61%-83%) had fast early growth, indicating growth of trees in high-light conditions. The rate of disturbance was lower at historic sites with fast early growth (5.3 events/century, 95% CI [3.6, 7.0]) than at old-growth sites with slow early growth (23.5 events/century, 95% CI [17.5, 29.5]), consistent with the idea that most historic logs were harvested from fast-growing, second-growth forests that established after depopulation.

Main Conclusions: Our results support the hypothesis of reforestation in upland forests of the central Appalachian Mountains following depopulation and suggest that upland forests, at the time of European immigration, were at least in part, a legacy of indigenous land use practices. However, the timing of a regional drought event, depopulation and subsequent recruitment of trees, all within the period of ~1650-1690 CE, warrants further research into interactions between indigenous land use and climate during a pivotal period in North American history.

abandonment, disturbance, forest regrowth, land use, Native American, radial growth, recruitment, succession, tree ring

1 | INTRODUCTION

The relative magnitude of forest management in the Americas prior to European immigration has long been a subject of debate (Denevan, 1992; Doolittle, 1992; Marlon et al., 2008; Vale, 2002). While 19th century accounts suggested that land use impacts of Indigenous Peoples were minimal, with only locally concentrated disturbances occurring until the arrival of European immigrants (Bakeless, 1950; Shetler, 1991), other sources (Denevan, 1992; Doolittle, 1992) support a more widespread impact of indigenous land use on forest structure and composition. Historical sources and sediment records indicate that Indigenous Peoples practiced a variety of land management techniques, including high-intensity activities (e.g. logging) and low-intensity forest management (e.g. understorey burning; Delcourt & Delcourt, 1997; Denevan, 1992; Doolittle, 1992; Lafon, Naito, Grissino-Mayer, Horn, & Waldrop, 2017: Williams, 1989). Recently, it has been proposed that forest regrowth following land abandonment may have been widespread enough to explain the drawdown in global CO2 and associated cooling observed during the coldest part of the Little Ice Age (~1570-1650 CE; hereafter: 'extensive forest regrowth model'; Dull et al., 2010; Koch, Brierly, Maslin, & Lewis, 2019; Lewis & Maslin, 2015; Nevle, Bird, Ruddiman, & Dull, 2011). We use the term land abandonment to describe the cessation of large scale land management from an ecological perspective. Cessation of land use could be caused by a wide variety of factors including changes in land management, migration, or mortality. Evaluating the degree of forest establishment after depopulation of Indigenous Peoples requires careful investigation of the forest history of the Americas and has the potential to alter our fundamental understanding of forest structure and dynamics prior to European contact.

Palaeoecological archives, such as tree-ring records, should record the response of forests to land use change in this magnitude, for example through tree recruitment following land abandonment (Liebmann et al., 2016) or through growth anomalies in establishing and extant trees (McEwan & McCarthy, 2008). Tree rings have been widely used to investigate the effects of forest disturbances, for example through pulses of tree recruitment following secondary succession (Foster, 1988) and rapid changes in growth initiated by canopy gaps (Lorimer & Frelich, 1989; Runkle & Yetter, 1987). However, much of our understanding of forest composition and dynamics in eastern North America prior to European immigration is based on tree-ring data from few, fragmented and spatially restricted old-growth forests (Abrams, Orwig, & Demeo, 1995; Foster, Orwig, & McLaughlin, 1996; Nowacki & Abrams, 1997). Due to deforestation since European arrival, many extant old-growth forests are restricted to dry, rocky, southwest-facing slopes (Therrell & Stahle, 1998) that were less suitable for human occupation, and are therefore not ideally located to record land-use prior to or following depopulation of Indigenous Peoples.

Log buildings, constructed in upland valleys at the time of European immigration, represent a different forest type than remnant old-growth forests (de Graauw, 2017). European immigrants sought flat, fertile land near water for agriculture and pasture, and with ample, straight timber on site for construction of their houses, barns and outbuildings (Kercheval, 1902; Williams, 1989). These are

the same characteristics that describe sites occupied by Indigenous Peoples prehistorically (Coughlan & Nelson, 2018; Gardner, 1983; Kercheval, 1902; McWhorter, 1915; Potter, 1993; Williams, 1989). Thus, indigenous land use legacies might be stored in the timbers of historic log buildings.

We propose that if upland forests experienced massive recruitment of trees on land abandoned by Indigenous Peoples, tree rings from historic logs should capture those land-use changes through evidence of: (a) synchronous recruitment dates; (b) early radial growth patterns and (c) growth release events. Synchronous recruitment events, identified by peaks in establishment, are indicative of largescale disturbance events (e.g. logging, fire and windthrow) that clear previously forested areas and allow a new cohort of trees to establish (Abrams et al., 1995; Lorimer, 1980; Oliver, 1981). Early radial growth may be indicative of light availability at the time of establishment. Fast early growth among groups of trees reflect stand-clearing disturbance events that allow trees to ascend to canopy positions (Buttrick, 1917; Lorimer & Frelich, 1989; Lorimer, Frelich, & Nordheim, 1988; Rentch, Fajvan, & Hicks, 2003). Growth releases occur in understorey trees when a gap is created by local disturbance or senescence of a canopy-dominant tree (Lorimer & Frelich, 1989; Rentch et al., 2003; Rubino & McCarthy, 2004) and indicate closed-canopy conditions. Therefore, trees initiating in open fields should have lower rates of disturbance (fewer growth releases) than old-growth forests where competition for light is intense (Lorimer & Frelich, 1989; Lorimer et al., 1988; Rentch et al., 2003).

Here, we compare recruitment, early radial growth and growth releases in historic logs versus old-growth forests in the central Appalachian Mountains to test for extensive reforestation following depopulation and land abandonment. We include old-growth forests because many currently protected old-growth sites are unsuitable for human occupation and would likely not have experienced strong effects of abandonment on recruitment or growth. We hypothesize that compared to old-growth forests, historic logs will have evidence of land abandonment through (a) synchronous recruitment following depopulation, (b) rapid early growth and (c) few growth releases.

2 | MATERIALS AND METHODS

2.1 | Climate and vegetation

The study area is in the central Appalachian Mountains of eastern North America along the border of West Virginia and Virginia, USA. Sites are located in the Ridge and Valley and Appalachian Plateau physiographical provinces (Figure 1), which are both generally characterized by deep valleys flanked by narrow, forested mountain ridges (Fralish, 2003). We selected this study area because it provides: (a) distinctly different topographical sites (upland valleys (historic buildings) versus hillslopes (old-growth forests)), (b) numerous previously undated historic log buildings for sampling and (c) a region not historically recognized as densely

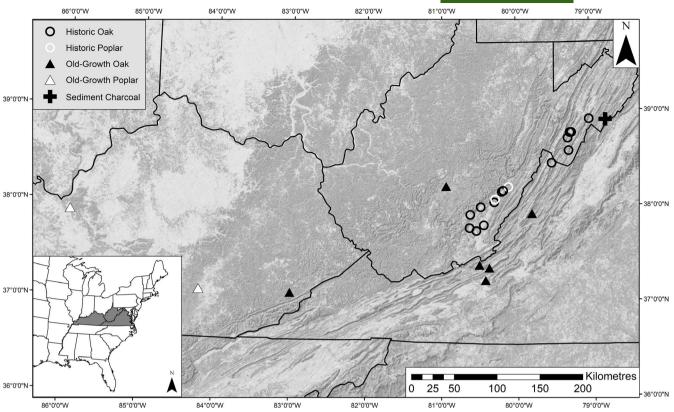


FIGURE 1 Locations of 18 historic log buildings (circles) and eight old-growth sites (triangles) within the central Appalachian region, USA. Black symbols represent white oak (*Quercus alba*) sites and white symbols represent tulip poplar (*Liriodendron tulipifera*) sites. The sediment charcoal site (Lynch and Clark (2002) as cited in Lafon et al., 2017) is represented by a black cross

populated by Indigenous Peoples. Thus, if there is evidence of reforestation here, then it is also likely to be found in more densely populated regions.

The region is characterized by temperate climate, with average temperatures ranging from –6.6 to 4.4°C (January) to 15.6 to 26.7°C (July), and average precipitation ranging from 50.9 to 152.4 mm annually (NCEI, 2019). The region is part of the mesophytic Appalachian oak section of the eastern deciduous forest and is dominated by oaks (*Quercus* spp.), hickories (*Carya* spp.), tulip poplar (*Liriodendron tulipifera*) and pines (*Pinus* spp.; Braun, 1950; Dyer, 2006). Gap-phase dynamics are common in mature stands (Rentch et al., 2003; Runkle & Yetter, 1987), whereas windthrow and (human-ignited) fire are historically common disturbance processes (Abrams, 1992; Delcourt & Delcourt, 1997; Hessl, Saladyga, Schuler, Clark, & Wixom, 2011).

2.2 | Land use history

Although archaeological evidence of late prehistoric (1000–1700 CE) to historic (post-1700 CE) occupation of Indigenous Peoples in the study area is sparse (McMichael, 1968; Spencer, 2016), the general region (including West Virginia, Virginia and Maryland) was inhabited by Iroquoian, Algonquian and Siouan speaking peoples (Kercheval, 1902; McMichael, 1968; Potter, 1993; Swanton, 1943; Wall & Lapham, 2003). Indigenous peoples of this region likely sought

fertile river valleys for agriculture and villages, used girdling and fire to clear land and used stone tools to fell smaller trees for housing, palisades and fuel (Denevan, 1992; Munoz, Mladenoff, Schroeder, & Williams, 2014; Potter, 1993; Springer et al., 2010; Williams, 1989). European immigrants began inhabiting the study area between the 1740s and 1760s (Brooks, 1911; Dayton, 1942; Kercheval, 1902), and their descriptions of the landscape vary. While many European accounts detail dense forests, some describe large clearings attributed to indigenous land use (see Denevan, 1992 and Williams, 1989 and references therein). In what is now West Virginia, one European traveller in 1752 noted 'a great many cleared fields', and another in 1769 noted 'stands of trees uniform in growth', and about 100 years old, 'some of which were growing up through the cobblestone floors used by the Indians' (Maxwell, 1910; Williams, 1989). The depopulation of most Indigenous Peoples from the study area likely occurred in the 1600s (Jones, 2014); however, some Indigenous Peoples were still inhabiting the region alongside European immigrants into the 1770s (Kercheval, 1902).

2.3 | Tree-ring dating of sites

We collected samples from 18 historic log buildings (1700s–1800s CE) in upland valleys in West Virginia and Virginia (Figures 1 and 2) based on the following criteria: 1) constructed with hand tools to

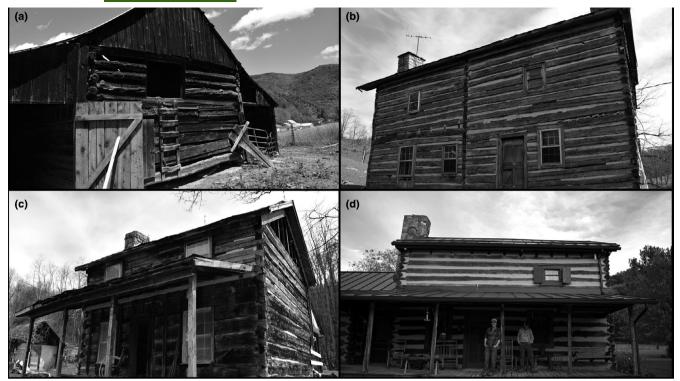


FIGURE 2 Examples of historic log buildings used in this study: (a) Whiskey Barn (WBQ), white oak (*Quercus alba*), inferred construction in 1844; (b) Carraway House (CY), white oak, inferred construction in 1804; (c) Sisler Cabin (SC), tulip poplar (*Liriodendron tulipifera*), inferred construction in 1869; (d) Stump Cabin (SCQ), white oak, inferred construction in 1784. Photos: K. de Graauw

ensure the trees were felled on site; 2) ≥10 logs available for sampling and 3) buildings constructed with species with existing regional reference chronologies for crossdating. We selected eight old-growth sites for comparison based on the following criteria: (a) mean series length >150 years; (b) the same species represented in historic logs and (c) sites in proximity to historic log buildings (Figure 1; see also Table S1.1, Appendix S1 in Supporting Information). The historic log buildings used in this study reflect European immigrants' preference for home sites and therefore represent upland valleys suitable for human occupation. Likewise, the old-growth forests used here were collected from long-lived trees in remote locations. Additionally, we collected samples from ten white oak (Quercus alba) trees in a forested stand that established in an abandoned field (c. 1930s-1940s) adjacent to one of our historic sites to provide a reference for the early radial growth pattern of trees establishing in abandoned fields (hereafter: 'reference site'; Figure S2.1, Appendix S2). We removed all duplicate cores (additional samples from the same tree/log) from each chronology to reduce the risk of representing a historic log, oldgrowth tree or reference site tree more than once in our analyses. Whenever possible, we retained the core with the most rings for use in analyses.

To identify felling dates of historic log buildings, we collected 14 mm core samples from ≥2 logs per wall that displayed outer edge characteristics (e.g. bark, rounding). Cores were taken from the basal end of logs to obtain the maximum number of inner rings. Logs are often harvested ~30 cm above the tree base (Quigley, 1954), whereas cores are often collected from live trees at breast height (~140 cm;

Speer, 2010), producing some uncertainty in estimates of inner ring dates from both historic logs and live trees. All core samples were mounted and sanded using progressively finer sanding grits (100–800 ANSI-grit) to display cellular structure and ring boundaries. We measured ring widths to the nearest 0.001 mm using a Velmex sliding-stage micrometre and the program Tellervo (Brewer, Murphy, & Jansma, 2011). We statistically crossdated all tree-ring series using the program COFECHA (Holmes, 1983) and compared each series with regional tree-ring chronologies from the International Tree Ring Data Bank (ITRDB; https://www.ncdc.noaa.gov/data-access/paleo climatology-data/datasets/tree-ring). All outer rings of historic log samples were inspected to determine terminal ring attributes and felling years (Bannister, 1962; Nash, 1999).

2.4 | Recruitment

We used the innermost rings of historic logs and old-growth trees to assess whether there was a recruitment pulse in historic logs following abandonment that was absent from old-growth forests. Inner ring dates are not germination dates but instead represent age at coring height (Villalba & Veblen, 1997) and are hereafter referred to as recruitment dates. We used pith indicators, concentric circles of varying sizes on transparency sheets, to estimate the number of missing rings (pith offset; PO) of historic log samples in which pith was not sampled. To estimate the PO of historic samples lacking curvature, we shifted inner ring dates by a fixed PO of 20 years (EPO).

Actual inner ring (pith) dates are unknown for old-growth sites (these data were not reported by the original authors) so only innermost ring dates (no pith offset; NPO) were used in this case.

Trees may have been selected for construction based on similar log sizes, though this does not always constrain the ages of samples to one age group (de Graauw, 2017; Pederson, 2010). To assess if recruitment dates were a function of selection bias, we: (a) compared the series length (number of rings) of historic logs to diameter; (b) compared ages of trees with felling dates to assess whether samples were ageing through time (i.e. trees felled for 1700s buildings would have fewer rings than trees felled for 1800s buildings) as logs were successively felled from forests following abandonment and (c) compared felling dates and diameter of each log as an additional test of the age/size relationship.

2.5 | Early growth

We calculated early radial growth using standardized tree-ring series with no offset and two treatments to evaluate the effects of pith offset. First, we standardized the raw ring-width values in each sample, aligned all ring-width series by cambial age (ring number from pith) at the innermost ring (NPO), and created site means for historic sites, old-growth sites and the reference site. We visually compared each of the NPO site means (historic and old-growth sites; Figures S2.2-S2.26, Appendix S2) with the reference site to assess whether early growth was consistent with fast-growing trees in open fields. We separated sites according to two early growth patterns (fast vs. slow growth) based on visual comparison (Table S2.1, Appendix S2). We then used 'kmeans' cluster analysis (stats v3.6.1) in base R (R Core Team, 2013) to quantitatively separate historic and old-growth sites into two groups based on early growth patterns (fast vs. slow growth). We then used those clusters to determine how many sites (historic and old-growth) had fast versus slow early growth in the first 100 years and to determine if trees in the fast-growing sites established earlier, during the period of depopulation, relative to slow-growing sites.

Next, we examined the effects of adjusting series according to PO. Cluster analysis requires values for every observation, therefore, we replaced the missing values created by PO with the mean of the first three (PO3) and first five (PO5) years of standardized mean ring widths. To objectively categorize sites as having either early fast or slow growth, we again used cluster analysis on growth during the first 100 years. We then compared cluster assignments of the three sets of site means (NPO, PO3, PO5).

2.6 | Disturbance reconstruction

We used percent change in radial growth to identify and compare growth releases at historic and old-growth sites (Lorimer & Frelich, 1989). We evaluated multiple disturbance detection methods (Figure S3.1, Appendix S3) using the R package 'TRADER' (v1.2-3; Altman,

Fibich, Dolezal, & Aakala, 2014; R Core Team, 2013). Here, we used a hybrid approach ('mid-canopy growth averaging') because of its ability to capture events recorded by both canopy-dominant and understorey trees. We evaluated growth changes within a window length of 25 years (12 years prior to and after current year) and growth release thresholds (moderate: 35% growth increase; major: 70% growth increase) from radial growth averaging (Lorimer & Frelich, 1989; Nowacki & Abrams, 1997) disturbance detection methods. We combined the outputs (moderate and major releases) to determine if a growth release occurred for each sample in a given year. Results based on other disturbance detection methods are available in Appendix S3 (Figures S3.2–S3.27).

To account for unequal numbers of samples between sites and the increased rate of disturbance with sample size (Figure S3.28, Appendix S3), we used the bootstrap method to resample the disturbance histories of 10 trees 1,000 times at each site, estimate the percentage of trees recording release events in each year and estimate the 95% CLs around those estimates. Using these estimates we compared the disturbance rate (release events per 100 years) of site types (historic vs. old-growth) and cluster types (fast vs. slow) using the 'ANOVA' function (car v3.0-3) in base R (R Core Team, 2013).

3 | RESULTS

3.1 | Tree-ring dating of sites

We identified the felling dates (1784–1874 CE) of 18 historic log buildings (Table 1) located in upland valley settings. 16 buildings were constructed from white oak and two were constructed from tulip poplar (Table 1). Of the eight old-growth sites, six were white oak and two were tulip poplar (Table 2). Series intercorrelations for old-growth sites (mean = 0.579, range = 0.504–0.680) are equivalent to those of historic buildings (mean = 0.592, range = 0.507–0.695; t_{14} = 0.539, p > .001). Comparisons of detrended mean ring-width chronologies for old-growth and historic sites are reported in Appendix S1 (Figures S1.1–S1.3 and S1.4–S1.19 respectively).

3.2 | Recruitment

We estimated PO for 270 (75%) of 361 historic logs. Of those, 1% contained pith, 6% had a PO of <5 rings and 93% had a PO of ~5–15 rings (Table S1.2, Appendix S1). For the remaining 25% of samples, we added a fixed pith offset of 20 years (EPO). Using inner ring dates with no offset (NPO), we observed a period of elevated recruitment across historic sites (≥10% of trees/decade) between 1690 and 1730, with the highest period of recruitment occurring in the 1710s and 1720s (each ~13% of total recruitment; Figure 3a). Using PO and EPO dates, we observed elevated recruitment between 1680 and 1710, with the period of highest recruitment occurring in the 1690s (~15% of total recruitment; Figure 3b). At old-growth sites, using

TABLE 1 Summary of dendroarchaeological dating results (Series IC: series intercorrelations), locations and general landscape type for each historic log building

ID	Building name	Species	Trees	Span	Series IC	Felling date	Coordinates	General landscape
BAR1	Barracks	QUAL	24	1683-1799	0.689	1799	37.80, -80.44	Upland valley
BAR2	Barracks Addition	QUAL	13	1698-1877	0.590	1877	_	-
СВ	Caraway Barn	QUAL	17	1682-1824	0.566	1824	38.04, -80.30	Upland valley
CY	Caraway House	QUAL	22	1680-1804	0.577	1804	_	_
DB	Diamond Barn	QUAL	23	1684-1786	0.668	1786	38.15, -80.20	Upland valley
ווו	James Jarrett House	QUAL	15	1674-1792	0.621	1792	37.77, -80.63	Upland valley
KML	Kee Cabin	LITU	17	1777-1865	0.578	1865	38.20, -80.11	Upland valley
KQ	Kile Homestead	QUAL	16	1691-1833	0.522	1833	38.77, -79.28	Upland valley
MC	Mallow Church	QUAL	16	1586-1794	0.536	1794	38.77, -79.26	Hill
MCF	McCoy Fort	QUAL	17	1684-1871	0.659	1799	37.99, -80.48	Upland valley
MP	Mill Point Barn	QUAL	44	1688-1851	0.625	1851	38.16, -80.18	Hill
РВ	Pitsenbarger Barn	QUAL	18	1714-1840	0.514	1840	38.58, -79.30	Hill
RC	Rimer Cabin	QUAL	16	1675-1840	0.507	1840	38.45, -79.53	Upland valley
SC	Sisler Cabin	LITU	17	1719-1869	0.530	1869	38.07, -80.29	Upland valley
SCQ	Stump Cabin	QUAL	27	1645-1784	0.567	1784	38.91, -79.02	Upland valley
SH	Sydenstricker House	QUAL	28	1690-1831	0.695	1831	37.74, -80.54	Upland valley
WBQ	Whiskey Barn	QUAL	12	1725-1844	0.555	1844	38.71, -79.31	Upland valley
ZH	Zigafuss House	QUAL	19	1675-1874	0.662	1874	37.91, -80.62	Upland valley

Abbreviations: LITU: tulip poplar (Liriodendron tulipifera); QUAL, white oak (Quercus alba).

Sites BAR1 and BAR2 are located on the same site, as are sites CB and CY. Site RC is adjacent to the early growth reference site.

TABLE 2 Summary of old-growth site characteristics used in this study

ID	Site name	Species	Trees	Span	Series IC	Coordinates	General landscape
CFQ	Carnifex Ferry	QUAL	20	1670-2013	0.544	38.21, -80.94	Mountain slope
FGT	Fiddler's Green	LITU	22	1677-2002	0.680	37.89, -85.93	Mountain slope
KY003	Lilly Cornett Tract	QUAL	40	1660-1982	0.625	37.10, -84.20	Mountain slope
KYLD	KY London District	LITU	13	1649-2007	0.504	37.08, -83.00	Mountain slope
VA011	Mountain Lake	QUAL	26	1552-1983	0.602	37.38, -80.50	Mountain slope
VA017	Patty's Oaks	QUAL	23	1569-1982	0.517	37.92, -79.80	Mountain slope
VA029	Craig Creek	QUAL	20	1722-2001	0.592	37.35, -80.37	Mountain slope
VA037	Stadium Woods	QUAL	33	1697-2011	0.565	37.22, -80.42	Upland valley

Abbreviations: LITU, tulip poplar (*Liriodendron tulipifera*); Series IC, Series Intercorrelations; QUAL, white oak (*Quercus alba*). See Table S1.1, Appendix S1 in Supporting Information for data sources.

only inner ring dates, there was a similar recruitment event between 1670 and 1740, though a lower percentage of trees recruited in those decades (≥5% of trees/decade; Figure 3c). Prior to the 1670s, there is comparatively little evidence of recruitment at either historic or old-growth sites.

Analyses of the relationship between series length and tree diameter suggest there is a weak but positive correlation for historic logs ($R^2 = .071$, $p \le .001$) reflecting a weak selection bias in tree

age, given the range of log diameters in the sample (range = 18.5–40.2 cm). Historic oak series increase in length (age over time; R^2 = .172, $p \le .001$), consistent with an ageing forest (Figure 3d). Two early sites (MC and SCQ), where trees were among the oldest at the time of felling, are outliers in this overall trend (Figure 3d). There is a similar weak but positive relationship between felling date and log size (R^2 = .071, $p \le .001$) that could partially explain increasing series length with time.

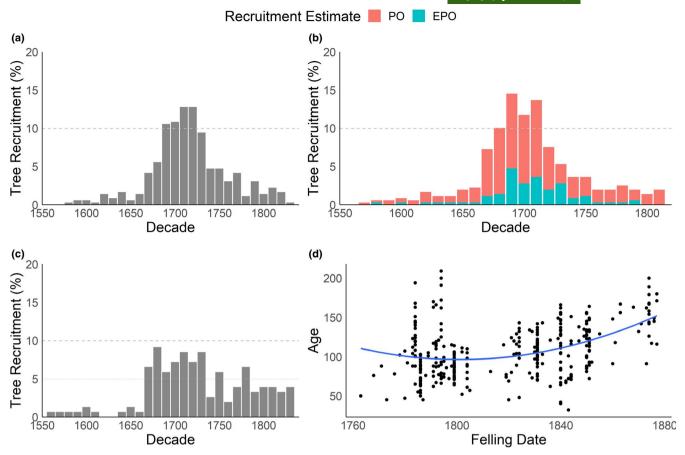


FIGURE 3 Percent of historic logs (a) and old-growth trees (c) recruiting in each decade (1550–1940) using unadjusted innermost ring dates. Percent of historic logs recruiting (b) in each decade (1550–1810) using estimated number of rings to pith (pith offset (PO)) and estimated pith offset (EPO), a 20-year shift of inner rings in samples lacking curvature. The curvilinear relationship between ages of individual logs from all historic white oak (*Quercus alba*) sites and felling dates ($R^2 = .172, p \le .001$) (d)

3.3 | Early growth

Early radial growth at the reference site (Table 1) was characterized by 45 years of fast initial growth (y-intercept = ~2.0, growth declining exponentially; Figure 4a). Using the NPO dataset, cluster analysis independently separated historic and old-growth sites into either: (a) rapid early growth (y-intercept = ~2.0, growth declining exponentially for ~80 years; Figure S2.27, Appendix S2; Figure 4b) associated with high-light conditions in second-growth forests or (b) slow early growth (y-intercept = ~1.5, growth declining exponentially for ~20 years; Figure 4c) typical of understorey trees in low-light conditions under the closed canopy of a mature forest. The mean recruitment date of all series from sites in the fast-growth cluster (1719 CE, 95% CI [1713, 1725]) was older than the mean recruitment date of all series from sites in the slowgrowth cluster (1748 CE, 95% CI [1740, 1756]; t_{553} = 5.9, $p \le .001$; Figure 4d), indicating that trees that recruited earlier were more likely to have fast early growth.

Cluster analysis of the NPO data assigned most historic sites (61%) to the fast-growth cluster (Figure 4e) and all old-growth sites (100%) to the slow-growth cluster (Figure 4f). Using the PO3 and PO5 treatments, most historic sites were assigned to the fast-growth

cluster (67%–83%) and most old-growth sites were assigned to the slow-growth cluster (87.5%–100%; Tables S2.1 and S2.2, Figures S2.28 and S2.29, Appendix S2). In subsequent analyses, we use cluster assignments for NPO because it provides equivalent treatment of data from historic sites with those of old-growth sites, for which we were unable to estimate PO.

3.4 | Disturbance rate

To determine if there were differences in disturbance rate (bootstrapped release events per 100 years), we used one-way ANOVA and Tukey HSD on cluster (fast and slow) and site type (historic and old growth). Because no old-growth sites were assigned to the fast-growth cluster, there was no 'fast old-growth' group. There was a significant difference in mean disturbance rate between combined cluster and site type groups ($F_{2,23}=15.49,\ p\le.001$). Levene's test indicated equal variances ($F_{2,23}=3.23,\ p=.058$). There was no difference in mean disturbance rate between the 'slow old-growth' group and the 'slow historic' group (p>.001), nor was there a difference in mean disturbance rate between the 'slow historic' group and the 'fast historic' group (p>.001). However,

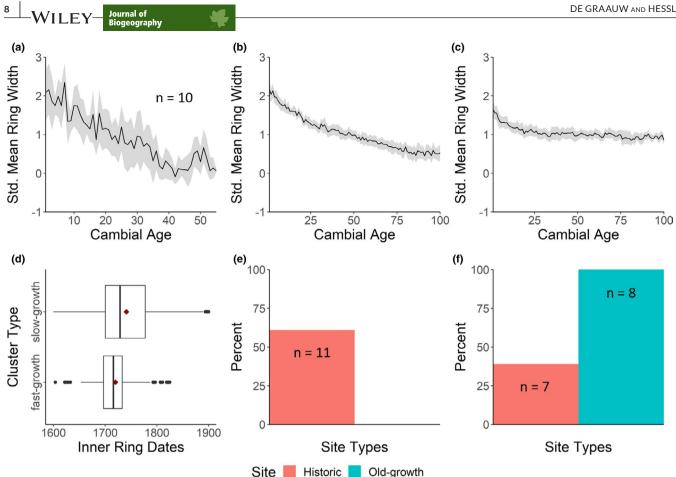


FIGURE 4 Mean early growth (standardized mean ring widths with 95% confidence limits, aligned by cambial age at innermost ring with no pith offset (NPO)) at the modern reference site (a) over the first 55 years, and of all sites assigned to fast (b) and slow (c) growth clusters using cluster analysis over the first 100 years of growth. Inner ring dates (NPO) (d) of series from sites assigned to the two early growth clusters (fast vs. slow). Mean (red diamonds) and median (black lines) disturbance rates are shown, and boxes indicate the 25th and 75th percentiles. Percent and number of historic and old-growth sites assigned to the fast growth cluster (e) and slow growth cluster (f)

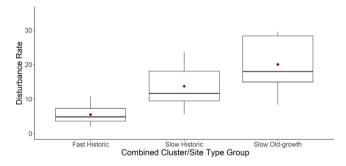


FIGURE 5 Comparison of mean disturbance rate (bootstrapped release events per 100 years with 95% confidence limits) of combined cluster (fast and slow) and site (historic and old growth) groups. There was no 'fast old-growth' group identified in cluster analysis. Red diamonds indicate the mean disturbance rate, black lines indicate the median disturbance rate and boxes indicate the 25th and 75th percentiles

the mean disturbance rate was lower in the 'fast historic' group (5.3 events/century, 95% CI [3.6, 7.0]) than in the 'slow old-growth' group (23.5 events/century, 95% CI [17.5, 29.5]; $p \le .001$; Figure 5). See Appendix S3 for actual and bootstrapped release events with 95% confidence limits for all sites (Figures S3.29-S3.54), combined bootstrapped releases by site type (Figures S3.55 and S3.56), and a comparison of bootstrapped release events by site type over the common period (Figure S3.57).

DISCUSSION

It has been proposed that widespread depopulation of Indigenous Peoples in the Americas beginning in 1492 might have led to extensive reforestation in subsequent decades (Dull et al., 2010; Koch et al., 2019; Lewis & Maslin, 2015; Nevle et al., 2011). We expected that if forests experienced widespread changes in recruitment and density due to land abandonment, logs sampled from historic buildings located in upland sites would be most likely to capture those changes through a pulse in recruitment, fast early growth and low rates of disturbance in second-growth stands. Indeed, our data, though limited in geographical scope, largely support the idea of reforestation following the depopulation of Indigenous Peoples in our study region, though the exact land use changes driving forest regrowth remain uncertain.

4.1 | Recruitment in historic log record

We identified a recruitment pulse at historic log sites that is independent of building age. Few trees recruited at historic log sites until the 1670s and there was a period of elevated recruitment from the 1690s to the 1730s (Figure 3a). One of the highest periods of recruitment, during the 1710s, included the greatest number of logs for which we were unable to estimate PO (i.e. samples with no curvature). This suggests their actual pith dates were at least two decades prior to the inner ring dates in the 1710s, likely recruiting in the 1690s or earlier (Figure 3b). The period of heightened recruitment at historic sites is independent of maximum log ages (150-year-old individuals), as buildings with trees felled in both the 1780s and 1880s recruited in the 1690s-1710s. While most historic oak series increased in length (aged over time), consistent with an ageing forest. SCO and MC were among the oldest sites (felling dates of 1784 and 1794 respectively) and the oldest trees (max series length of 168 and 209 years respectively; Figure 3d). These sites might reflect extant forested areas from the time of indigenous occupation.

Though we collected samples at the basal end of logs whenever possible, we cannot account for the height at which logs were felled. Yet, the pattern of recruitment that we observe is consistent with the timing of depopulation in the region (c. 1600s; Jones, 2014; Wall & Lapham, 2003), especially given the time required for forest establishment following land abandonment, estimated at ~15–20 years in eastern North America (Harrison & Werner, 1984; Myster, 1993; Oliver, 1981).

While the timing of recruitment is consistent with abandonment, the pattern of recruitment at old-growth sites is similar to that of historic logs, suggesting that recruitment may not have been driven exclusively by land abandonment. At old-growth sites, we observed an absence of recruitment until the 1670s followed by elevated recruitment until the 1740s (Figure 3c). These dates are likely biased towards more recent decades since we were not able to estimate how close samples were to the pith or the height at which samples were taken (Villalba & Veblen, 1997). Recognizing that old-growth sites were predominantly located on low-productivity sites that were less suitable for agriculture (Table 2), this synchronous event at both site types (historic and old growth) is not consistent with agricultural clearing. It is, however, consistent with a recruitment event previously documented throughout eastern North America in live trees, historic logs and archaeological samples (Pederson et al., 2014 and references therein; Trouet, Dominguez-Delmas, Pearson, Pederson, & Rubino, 2018). Evidence of this recruitment pulse across both site types suggests that recruitment may have been associated with regional climate variability rather than, or in addition to, land abandonment. Pederson et al. (2014) suggest that mortality, following a sub-continental drought allowed for elevated recruitment during a subsequent pluvial period.

Another possible explanation for the period of recruitment observed in both historic buildings and old growth sites is the

cessation of both high-intensity (agriculture) and low-intensity land use by Indigenous Peoples. There is ample evidence of fire activity in eastern North America prior to European immigration that may reflect indigenous land management practices (e.g. Black, Ruffner, & Abrams, 2006; Delcourt & Delcourt, 1997; Guyette, Muzika, & Dey, 2002; Springer et al., 2010). The absence of fire following depopulation might have led to increases in forest recruitment across site types; however, studies of modern fire cessation have shown mesic species tend to recruit under these conditions, not fire-adapted species such as oaks (Flatley, Lafon, Grissino-Mayer, & LaForest, 2015; Nowacki & Abrams, 2008). A high-resolution sediment charcoal record from a montane lake near our study area (Trout Pond; Figure 1) indicates fire occurred regularly over the last 1,000 years (Lynch & Clark, 2002 as cited in Lafon et al., 2017). Notably, there is a 2- to 3-decade long period beginning in ~1650 CE in which no charcoal accumulation occurs, and it is the longest charcoal-free span in the 1000-year record. This anomaly in the otherwise charcoal-rich record from Trout Pond coincides with the period of recruitment we see in historic and old-growth trees and with the proposed period of depopulation in this region, suggesting a variety of indigenous land management techniques, including fire in the old-growth sites, could have been employed and then abandoned ~1650 CE. A similar fire-free period was documented in ~1675 CE in Indiana and was attributed to the depopulation of Indigenous Peoples from that area (Guyette, Dey, & Stambaugh, 2003), though tree recruitment and growth were not evaluated.

4.2 | Early growth in historic log record

Our analysis of early radial growth trends supports the hypothesis that most, though not all, historic trees were felled from rapidly growing (second-growth) forests. Most historic sites (between 11 and 15 of 18) fell within the fast-growth cluster (Figure 4e; Table S2.2, Appendix S2), typical of trees growing in high-light conditions. All eight old-growth sites, and seven historic sites, were slow-growing (Figure 4f). Furthermore, the series in the fast-growth cluster had earlier recruitment dates than those in the slow-growth cluster (Figure 4d), suggesting that the trees that recruited after depopulation were faster-growing than trees that recruited later when light availability may have attenuated. If there was a period of rapid initial growth in old-growth sites, it is likely that we did not capture it, since there was no evidence that samples were close to, or included, pith. Similarly, initial growth at historic sites may have been more rapid than our results indicate since we cannot account for the height at which logs were felled. Nevertheless, our results suggest most, though not all, historic sites were composed of trees that established in high-light conditions, consistent with the pattern of growth we observed in our reference site. In contrast, all old-growth sites were composed of trees that established in low-light conditions, consistent with mature forests. Despite synchronous recruitment across historic and old-growth sites, these patterns of early radial growth suggest that historic trees initiated under higher levels of light-availability than old-growth trees during the same period.

4.3 | Growth releases in historic log record

Our results support the hypothesis that historic sites with fast early growth had fewer growth releases than old-growth sites, a pattern consistent with the expectation that fast-growing trees in high light conditions would have fewer growth releases than slowgrowing trees in closed-canopy forests (Buttrick, 1917; Lorimer & Frelich, 1989; Lorimer et al., 1988; Rentch et al., 2003). However, among the historic sites, there was no significant difference in fast-growth versus slow-growth sites. These results suggest that the sites themselves, located in upland areas, may have experienced less disturbance than other locations, such as hillslopes, regardless of previous land management. For example Foster (1988) observed that the rate of disturbance increased with increasing topographical position and exposure to wind. Additional work on disturbance rates and their relationship with successional stage and topographical position (upland valleys vs. hillslopes) is required to assess the utility of this measure in evaluating past land use.

4.4 | Evaluating the extensive forest regrowth model

The idea that the depopulation of Indigenous Peoples in the Americas beginning in 1492 led to widespread reforestation, carbon drawdown and global-scale cooling (Dull et al., 2010; Koch et al., 2019) hinges on three assumptions: (a) the timing of depopulation in the 1500s was coincident with CO₂ drawdown, (b) Indigenous Peoples' land use was intensive enough to result in cleared (or thinned) and subsequently reforested areas and (c) the spatial extent of their impact was sufficient to affect global CO2 levels. While European diseases undoubtedly affected Indigenous Peoples, there is spatiotemporal complexity in the spread of disease, dictated by population sizes, interaction and physical geography (Jones, 2014; Ramenofsky, Wilbur, & Stone, 2003), which suggests depopulation of Indigenous Peoples in North America following European contact likely occurred between 1518 and 1789 CE (Jones, 2014). Estimates of the timing of depopulation within our study area range from 1600 to 1677 CE (Jones, 2014), overlapping with the timing of modelled depopulation, reforestation and carbon drawdown (~1570-1650 CE).

Our analysis of recruitment, early growth and growth releases suggests that (a) a major recruitment event coincided with the estimated timing of depopulation in this region and (b) trees in most, but not all, historic log buildings were felled from second-growth forests, whereas trees in all old-growth sites had early growth and growth releases consistent with that of mature, closed-canopy forests. While the timing of depopulation and reforestation in this

region is not contemporaneous with the nadir of carbon drawdown in the extensive forest regrowth model (~1610 CE), it is consistent with the subsequent period of low atmospheric CO₂ (~1650-1750 CE). Our study region is small, however, and is not an area recognized for dense indigenous populations. Depopulation and reforestation in other locations, particularly the neo-tropics, would have had a much larger effect on atmospheric CO2 and would have occurred earlier, coincident with the CO₂ minimum ~1610 CE (Dull et al., 2010). Furthermore, our study of reforestation is limited to upland valleys and does not reflect the forested landscape as a whole. Other regions in eastern North America, with known histories of high-intensity land use, such as floodplains, which some indigenous cultures may have preferred as agricultural sites, may reveal stronger signals of clearing and regrowth (Bird, Wilson, Gilhooly, Steinman, & Stamps, 2017; Munoz, Schroeder, Fike, & Williams, 2014; Stinchcomb, Messner, Driese, Nordt, & Stewart, 2011). Similar studies conducted in areas such as the Mississippi River Valley, where human populations were higher (e.g. Munoz, Schroeder, et al., 2014) would improve our understanding of the timing of depopulation, reforestation and carbon drawdown.

Finally, it is likely that indigenous land management was diverse and included high- and low-intensity techniques (Black et al., 2006; Doolittle, 1992; Gremillion, 2015) reflective of the diversity of cultures and peoples present at the time of contact. As a result, depopulation may have led to a variety of ecological responses, even in similar locations (e.g. McEwan & McCarthy, 2008). Many of these land management techniques may be difficult to detect in the rings of historic logs alone but may be uncovered through exploration of multiple data sources such as high-resolution charcoal, archaeological records and ethnographical materials.

5 | CONCLUSIONS

Our study contributes empirical evidence from eastern North America to assess whether depopulation of Indigenous Peoples resulted in reforestation of abandoned land. While our results of forest recruitment, early radial growth patterns and growth releases generally support the idea of reforestation following depopulation, the timing of these events in our study area is later than the nadir of reforestation and carbon drawdown in the extensive forest regrowth model (~1610 CE). However, our evidence of reforestation (c. 1670s) in an area not recognized for dense indigenous populations, suggests that earlier reforestation following depopulation may have occurred in more densely populated regions.

Additionally, the forest recruitment event that we observed across historic and old-growth sites has been documented elsewhere in eastern North America. It is possible that a previously recognized sub-continental drought and subsequent pluvial (Pederson et al., 2014) contributed to the recruitment event observed in this region, however, early radial growth and growth releases were different among most historic sites and all old-growth sites, suggesting that the drought/

pluvial event alone may not account for the open-growth conditions at historic sites. Comparisons of recruitment and growth in areas where the regional drought event and depopulation were not contemporaneous may help to disentangle these events.

Finally, the novel data and techniques employed here yielded new insights about Indigenous Peoples' impacts on forests in a place where archaeological and ethnographical data were limited. If these results are replicated in a broader region, it would suggest that upland forests at the time of European immigration may have been a legacy of indigenous land-use practices, an inference that substantially alters our understanding of eastern deciduous forest dynamics. We suggest future research focus on: (a) targeting older log buildings (constructed c. 1600s-1700s CE) that would fully cover the period of depopulation; (b) selecting areas for which archaeological records of Indigenous Peoples, their land use strategies, and the timing of depopulation are better documented (e.g. Liebmann et al., 2016) and (c) combining palaeoecological data sources with historical, ethnographical and archaeological approaches to better define the nature of indigenous land-use practices prior to contact. The timing of a regional drought event, depopulation and subsequent mass recruitment of trees, all within the period of ~1650-1690 CE, is compelling and warrants further research into interactions between indigenous land use and climatic events during a pivotal period in North American history.

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DATA AVAILABILITY STATEMENT

Log building samples are housed in the WVU Department of Geology and Geography archival room and tree-ring data are available on the International Tree Ring Data Bank (ITRDB; see Appendix S1, Table S1.1).

ORCID

Kristen K. de Graauw https://orcid.org/0000-0002-7901-9518

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BIOSKETCH

Kristen K. de Graauw is a physical geographer who investigates past human-environment interactions through forest ecology and dendroarchaeology. Amy E. Hessl is a physical geographer who combines historical and palaeoecological evidence to understand past environments.

Author contributions: K.K.d.G. and A.E.H. conceived the ideas; K.K.d.G. collected the data; K.K.d.G. and A.E.H. analyzed the data; K.K.d.G. and A.E.H. equally contributed to the writing.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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