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ORIGINAL PAPER

# Bourbon Barrels and Bottlenecks: a Nuanced Look at Thirty Years of White Oak Population Dynamics

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**Abstract**
White oak (*Quercus alba* L.) is an ecologically and economically important tree species, common in upland hardwood forests throughout the eastern United States (US). This study examines the population dynamics of this foundational species over the past 30 years, highlighting both range-wide and regional metrics of change. Using data from the USDA Forest Service Forest Inventory and Analysis program, we analyzed changes in age and size distributions, as well as recruitment, mortality, and growth rates. We found a significant shift towards an older, mature-dominant population, with a notable decline in young age classes. Despite substantial increases in standing volume, net annual recruitment for trees with a diameter at breast height (dbh) ≥ 5 in. was negative—a concerning result for long-term sustainability if persistent. Regional analyses highlighted variation as most areas showed no signs of overutilization, but some exhibited volume reductions over the last 30 years and currently unsustainable growth-to-drain ratios. Other areas, spanning almost ¾ of the study region exhibited either seedling or sapling scarcity suggesting recruitment- or establishment-based bottlenecks that challenge long-term sustainability. Our results underscore the importance of management strategies to address challenging demographic rates. Efforts to mitigate the risks and effects of population decline and maintaining the myriad benefits white oak provides to eastern US forests, especially in the context of climate change and shifting species ranges, benefit from a deeper understanding of the ecological and socioeconomic factors driving these results.

**Keywords** Silviculture · Sustainability · Regeneration · Recruitment · Forest management

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## Introduction

White oak (*Quercus alba* L.) is one of the most economically and ecologically important tree species in the eastern United States (US). Present on about 1/3rd of the 311 million acres of forestland in the eastern US, the white oak range stretches north to southern Canada and Maine, west to Minnesota and the eastern edge of the Plains, south to Texas, and east to north Florida (Rogers 1990; USDA 2024). White oak exhibits climatic plasticity and is found on a variety of soils and sites, from rich coves to dry ridges (Rogers 1990). Contemporary inventories estimate that only loblolly pine (*Pinus taeda* L.) and yellow-poplar (*Liriodendron tulipifera* L.) exceed the standing sawtimber volume of white oak in the eastern US (USDA 2024).

Ecologically, white oak is considered a foundational species (Hanberry & Nowacki 2016), providing critical habitat for a wide range of wildlife species, and greatly influencing forest structure and environment (Fralish 2004; Ellison et al. 2005). Because of its high canopy and crown architecture, white oak forests typically have higher understory light levels than forests dominated by maples (*Acer* spp.) and/or American beech (*Fagus grandifolia* Ehrh.), and, consequently, white oak forests support a more diverse and robust understory herb layer (Fralish 2004). Furthermore, white oak is currently considered one of the most important hard mast species in the eastern US (Feret et al. 1982; Kirkpatrick and Pekins 2002), with increased importance following the functional extinction of the American chestnut (*Castanea dentata* (Marsh.) Borkh.; Anagnostakis 2001). A diverse array of game and non-game wildlife species depends on white oak acorns including white-tailed deer (*Odocoileus virginianus*), ruffed grouse (*Bonasa umbellus*), and many others (Pekins and Mautz 1988; Whitaker et al. 2007; McShea et al. 2007). In addition, white oak provides a significant food resource for at least 138 herbivorous insects and the insectivores that feed on them (Corff and Marquis 1999; Lill and Marquis 2003; Lichtenberg and Lichtenberg 2002). Finally, white oaks provide structural habitat, cavities, and exfoliating bark, critical for species of concern including wood ducks (*Aix sponsa*), neotropical migratory songbirds, and forest dwelling bats (Hansen 1965; Wagner et al. 2015; Lacki and Schwierjohann 2001).

White oak is one of the most economically important hardwood species in North America (Abrams 2003; Luppold and Bumgardner 2004). Logs and lumber have been in high demand for both domestic and international markets despite economic challenges such as the 2008–2009 recession (Luppold and Bumgardner 2013; Stringer et al. 2019). Commercially valued for numerous products, white oak is one of few species with wood properties required for tight cooperage (barrels or casks) and is used for wine and aged spirits production worldwide (Chatonnet and Dubourdie 1998; Gollihue et al. 2018; Kim et al. 2024). Less abundant, related native species are also used for this purpose (e.g., *Q. muehlenbergii* Engelm.), but white oak is the only native species of economic significance. The abundance and utility of this resource is one of the many reasons that oaks, and chief among them white oak, have been instrumental for providing food, shelter, and transportation to human civilization for millennia (Logan 2006; Gil-Pelegrín et al. 2017).

Forest disturbances can have both direct effects and long-term indirect consequences in oak forests by catalyzing species and/or structural composition shifts (Vickers et al. 2023). In the eastern US, the threat of landscape-scale shifts from oak-dominance to dominance by late-successional mesic species is pervasive (Nowacki and Abrams 2008). Non-native pests such as oak wilt (*Ceratocystis fagacearum;* Haight et al. 2011) and spongy moth (*Lymantria dispar*; Morin and Liebhold 2016) can cause damage and mortality of white oak trees but neither are causing widespread losses (Fei et al. 2019). However, that threat is exacerbated when there are insufficient seedlings and saplings to replace canopy oaks (Dey 2014; Vickers et al. 2023), a condition commonly found in mature oak forests across the eastern US (Miller and McGill 2019; Dey et al. 2019; Vickers et al. 2019b).

While broad oak declines are well-documented (Abrams 2003; Moser et al. 2006; Fei et al. 2011), it remains unclear whether white oak forests follow the same trajectory. The growing awareness and interest in white oak sustainability (e.g., White Oak Initiative, U.S. House Bill 5582, U.S. House Resolution 471) is creating additional incentive to understand its population dynamics and demographic challenges (U.S. House of Representatives 2023; 2025). Smaller-scale studies (Thomas-Van Gundy & Morin 2021; Dhungel et al. 2024) suggest demographic shifts, and some evidence points to declining recruitment (McEwan et al. 2011; Luppold & Bumgardner 2018). Pillars of oak sustainability include ensuring successful regeneration establishment and recruitment of established cohorts into the canopy (Dey 2014) yet gaps remain in assessing the scope and scale of demographic challenges to these essential processes. This study directly addresses this gap through analyses which: (1) characterize long-term change in white oak abundance, volume, and structure across the eastern US; (2) assess patterns of regeneration, recruitment, and population dynamics at a regional scale; and (3) identify nature, severity, and immediacy of areas where population trends suggest demographic bottlenecks pose risks to white oak sustainability. While this study identifies key demographic rates for white oak, establishing or attributing causal relationships to these patterns is beyond its scope.

## Methods

### Study Region

Our preliminary study region spanned forests east of the 100th W meridian in 37 eastern US states to ensure inclusion of the totality of the US white oak geographic range. Preliminary analysis indicated that white oak was not present as trees (dbh ≥ 1 inch (2.5 cm)) in contemporary forests of four of the western-most states (KS, NE, ND, SD) of our preliminary study region. Our study region was narrowed to ecological sections within the remaining 33 states (Fig. 1) where white oak basal area was ≥ 2 $ft^2ac^{-1}$ (0.5 $m^2ha^{-1}$). Ecological sections are one tier in a nation-wide hierarchical classification created by the USDA Forest Service to delineate areas of climate, physiography, and geologic substrate with distinctive vegetation and other

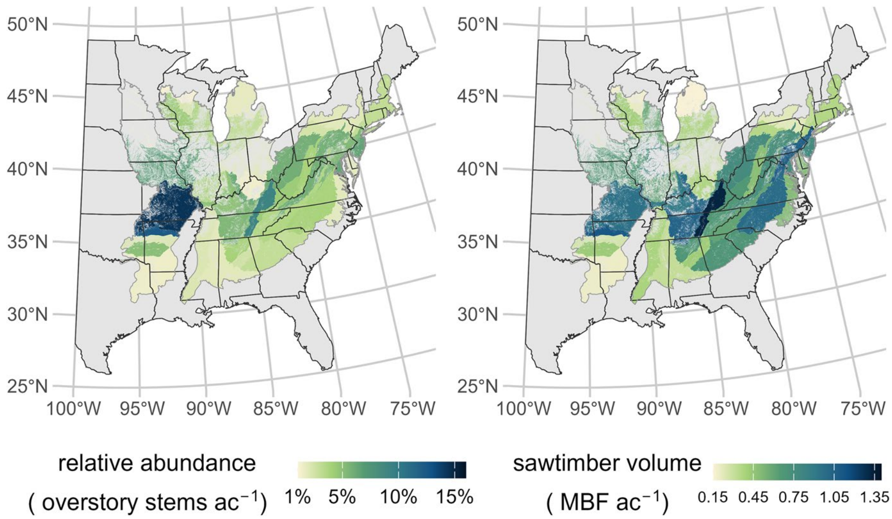



**Fig. 1** Region of study (outlined in grey) within 33 states of the eastern US includes the 41 ecological sections where white oak basal area was ≥ 2 $ft^2ac^{-1}$ in 2020. Left: relative abundance (stems per acre) within the overstory, which includes trees in dominant and codominant crown classes. Right: net sawlog wood volume per acre (thousands of board feet, International ¼ in rule) of sawtimber trees (dbh ≥ 11 in). Note, unit-area measures (e.g., stems $ac^{-1}$) reported use *all* timberland in a specified area as the area basis, rather than timberland with white oak present

unique ecological characteristics (Cleland et al 2007; McNab et al 2007). Because ecological sections are the foundation of our regional analyses, a reference map is provided (Supplemental Fig. 1).

## Data

The data used for this project was retrieved from the USDA Forest Service Forest Inventory and Analysis (FIA) program (https://www.fs.usda.gov/research/products/dataandtools/tools/fia-datamart). The FIA nationwide forest inventory is a uniform grid of sample locations across the US, each sample representing approximately 6,000 ac (2,428 ha) (USDA Forest Service 2023). Since ca. 2000, an annualized forest inventory has been used by FIA where a portion of sample locations are measured every year such that all sample locations are visited over a ca. 5–7 year period, the length of which varies by state (see Bechtold and Patterson 2005). The data is collected from a 'plot' that occupies 1-ac (0.4 ha) and is composed of four circular subplots (24 ft, 7.3 m) each containing a circular microplot (6.8 ft, 2.1 m) within. Attributes of trees ≥ 5 in (12.7 cm) dbh are measured on subplots, whereas trees 1–5 in are measured on microplots. Seedlings (dbh < 1 in), which include hardwoods with a height ≥ 12 in (30.5 cm) and softwoods ≥ 6 in (15.2 cm) are also tallied on microplots. Inventories are conducted on 'forestland,' which is defined as areas of at least 1 ac with ≥ 10% canopy cover by trees of any size, including land that formerly had such tree cover and that is planned to be regenerated by natural or artificial methods (see Reams et al. 2005). 'Timberland,' the focus of our study, is a subset of forestland comprised of unreserved forestland that can produce ≥ 20 $ft^3$ $ac^{-1}$ $yr^{-1}$ (1.4 $m^3$ $ha^{-1}$ $yr^{-1}$) of wood among other criteria (USDA Forest Service, n.d.). Prior to ca. 2005, only timberland was inventoried and, of the 435.5 million ac (176.2 million ha) of contemporary forestland across the 33 eastern states in our study region, about 84% qualifies as timberland (USDA Forest Service 2024). During that time, seedling data was absent or otherwise incongruent across states and therefore only reliable in more recent years of the annualized inventory data (ca. 2005-present).

The most recent annuallized inventory data common to all 33 states in our study region (as of November 2024) was inventory year 2020. Hereafter, we refer to the 2020 data as either 2020 or contemporary forest conditions. We obtained data from the 2013 inventory to examine recent change in population change components (sensu Eriksson 1995) which, for trees with dbh ≥ 5 in, included recruitment (ingrowth), mortality, removals, and survivor growth. To capture longer temporal changes in populations we relied on older FIA inventories that were collected periodically and asynchronously across states, and differed in plot layout from the current design, with those differences varying by FIA administrative region. Our earliest temporal window for a given state was the inventory closest to the nominal year 1990. Prior to this temporal window, inventory data was increasingly inconsistent in availability and methodology at the scale of our study. The closest inventory year varied across states (range: 1983–1995, mode: 1986, mean: 1988). Hereafter, we refer to this dataset as 1988 for convenience. The inventory years within these timeframes for each state used are listed in the supplemental material (Supplemental Table 1).

Tree volume, biomass and carbon estimates coming from the annualized forest inventory (ca. 2000 to present) were estimated using the National Scale Volume and Biomass framework (NSVB, Westfall et al. 2024) while estimates derived from periodic inventory data were made using an earlier system of equations and biomass expansion factors (see Jenkins et al. 2003 and Woodall et al. 2011 for details). Westfall et al. 2024 showed minor differences in merchantable wood cubic-foot volume nationwide from this methodological difference (1.6% increase). In a comparison made using 2019 data from within our study area, sawlog volume estimates increased 4.0% when comparing pre- to post-NSVB methods. Given this increase was only a small portion of the large increase in volume that occurred over the time period of the study, we felt these methodological differences across inventory eras, within the context of our analysis, were outweighed by their informative contribution to temporal change (e.g., Luppold and Bumgardner 2018).

## Analyses

We identified white oak plots as those containing at least one white oak tree (dbh ≥ 1 in) present and timberland with white oak present as the acreage represented by white oak plots. We defined an overall frequency rate for white oak as the proportion of white oak plots among *all* inventoried timberland plots. We defined frequency rates for white oak seedlings and saplings (dbh 1–4.9 in) as the proportion of white oak plots that contained at least one white oak seedling or sapling, respectively. All data summarized here for 'white oak' refers to the single species alone (FIA species code 802), not the 'select white oak' species group sometimes reported by FIA.

Our range-wide analyses of white oak population demographics included age and diameter distributions. Age distributions for all timberland and timberland with white oak present were calculated from the stand age (STDAGE) data reported by FIA for timberland using 20-year bins from ages 0–120 and everything older combined into a single bin. White oak diameter distributions were calculated for basal area and tree abundance using one inch diameter classes with everything larger than 30 in (76.2 cm) combined.

Our region-wide temporal analyses compared frequency rates, abundances, and diameter distributions from the 1988 and 2020 dataset. Relative measures (abundance, basal area, volume) were calculated as the ratio of white oak values alone to the total for all species. Sawtimber volume was defined as net sawlog wood volume of sawtimber trees (dbh ≥ 11 in, 27.9 cm) in board feet (International ¼ inch rule) as reported by FIA (FIA Population Attribute 21, see Burrill et al. 2024). Temporal change in those metrics was calculated by subtracting 1988 values from 2020 values. Because of the temporal limitation with seedling data, a temporal seedling analysis was not conducted.

For our region-wide temporal analysis for individual components of population change we obtained 2013 and 2020 estimates directly from the FIA Evalidator online tool (https://apps.fs.usda.gov/fiadb-api/evalidator). FIA makes estimates of growth, mortality, and removals on an average annual (referred to here simply as 'annual') basis to account for variation in remeasurement periods at the plot level. Sound volume was defined as sound bole wood volume of trees (timber species ≥ 5 in dbh) in cubic ft (FIA Population Attribute 574,175, see Burrill et al. 2024) as reported by FIA. We calculated two volume metrics for the temporal analysis: 1) net annual growth, defined as the sum of survivor growth and ingrowth less mortality, and 2) annual growth-to-drain ratio, which was defined as net growth divided by removals. We calculated two similar metrics for number of trees: 1) net annual recruitment, which was defined as ingrowth less the sum of mortality and removals and 2) annual recruitment-to-losses ratio, which was defined as ingrowth divided by the sum of mortality and harvest removals (excludes removals due to changes in land use or status). Annual components of change estimates for both sound volume and stem abundance were compared within the temporal window across the study region and within ecological sections.

We used the following metrics to assess ecological sections for potential sustainability risks for white oak under contemporary conditions. While identification of both volume and recruitment challenges (Points a and b below) draw on existing forest sustainability metrics or concepts, long-term establishment challenges (Point c) involve greater uncertainty, as they require projecting regeneration dynamics over extended time frames. Our indicators for establishment challenges, though necessarily based on some assumptions, draw on existing research for a pragmatic but non-definitive identification of potential establishment bottlenecks.

a) Near-Term Volume Challenges – Ecological sections were considered a concern if they exhibited:

- Any decline in standing white oak sawlog volume from 1988 to 2020.
- A negative annual net volume growth rate (sound or sawlog) in 2020.
- A growth-to-drain ratio ≤1.0 for white oak volume (sound or sawlog) in 2020.

b) Imminent Sustainability Challenges (Recruitment deficits) – Ecological sections were considered a concern if they showed:

- A non-positive annual recruitment rate, indicating more white oaks are dying or being harvested than entering the system as recruits (i.e., ingrowth).
- A recruitment-to-loss ratio ≤1.0.

c) Long-Term Sustainability Challenges (Establishment deficits)—Ecological sections were considered a concern if they exhibited:

- Mean seedling abundance less than twice the mean tree abundance (dbh ≥1 in), following the framework of Vickers et al. (2019a, 2019b) and recognizing that this is likely an optimistic replacement threshold (Sander et al. 1984; Brose et al. 2008).
- A seedling frequency rate below 20%, reflecting the idea that not every acre must be regeneration-ready simultaneously, but that some dispersal of seedlings across the landscape provides insurance against canopy-replacing disturbances. While the spatial distribution of 'stocked-plots' is a common consideration in stand-level regeneration assessments (e.g., Sander et al. 1984; Steiner et al. 2008), the literature offers no consensus on minimum frequency thresholds at either the stand or landscape scale. Therefore, our use of a 20% threshold is an assumption for analytical purposes, not a prescriptive benchmark.

## Results

Contemporary white oak forests in the eastern US have a skewed, unbalanced age distribution with limited young forest acres but many acres that have attained or are approaching maturity (Fig. 2). The age imbalance for timberland with white oak present was more pronounced compared to all timberland, a pattern that has progressed from unbalanced age classes in 1988. A right-ward shift in both the stand age and tree size distributions (Supplemental Fig. 2) for white oak since 1988 marked a decline in the number of young, small white oaks and an increase in older, larger specimens both in absolute terms and relative to other species. Accompanying these rightward shifts in age and size distributions was a decline in white oak frequency rates (dbh ≥1 in) across the study region, which decreased from 41% of all timberland plots in 1988 to being present on 33% in 2020.

While white oak frequency, absolute abundance, and relative abundance were lower in 2020 than 1988, QMD, total basal area, and sawtimber volume all increased

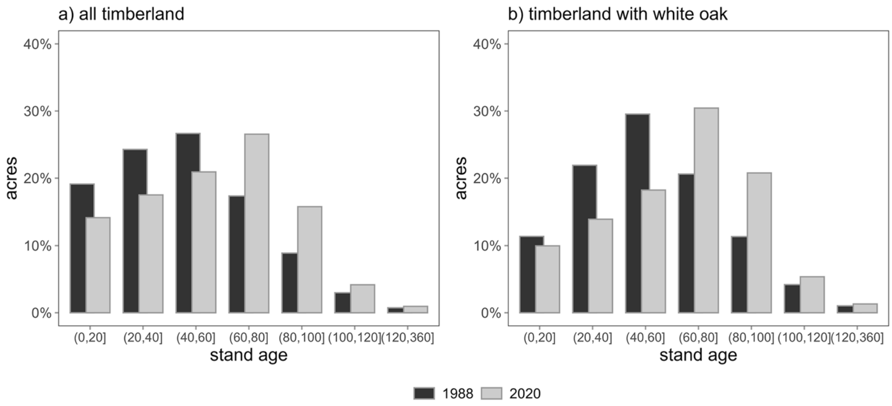



**Fig. 2** Stand age class distributions for all timberland (L) and timberland where white oak is present (R) across the eastern US white oak study region in 1988 (black) and 2020 (grey)

during that same time frame, allowing that some increase in volume was due to the NSVB estimation change (Fig. 3, Table 1). By 2020, white oak sawtimber volume had increased by over 50 million MBF, an almost 80% increase, from 1988. At the region-wide scale, there were no indications of over-utilization or volume supply shortages in recent years as net growth has remained positive and the growth-to-drain is approaching 3.0 for sawlog volume. Nonetheless, the annual volume growth from new recruits into the five-inch diameter class (i.e., ingrowth) has been, essentially, counterbalanced by annual mortality losses in recent years.

The number of trees at least five inches in diameter that were lost on an annual basis due to mortality and removals has exceeded the recruitment (ingrowth) rate of new trees entering this size class in both 2013 and 2020 (Fig. 4). As a result of this, the net annal population growth rate was –0.4% in 2020 for trees at least 5 inches in diameter. The recruitment-to-losses ratio was 0.8 in 2020. Like the growth-to-drain ratio for timber, recruitment-to-losses values below 1.0 indicate that mortality and removals outpace recruitment.

Negative changes from 1988 to 2020 were most acute for young and/or small stems (Fig. 2, Supplemental Fig. 2). White oak saplings (dbh 1-4.9 in.) occurred on 34% of all white oak plots in 1988. By 2020, white oak sapling frequency rate was 22% on white oak plots. For white oak seedlings, the region-wide frequency rate was about 40% on white oak plots in 2020. White oak saplings averaged ≈ 16 $ac^{-1}$ in 1988 and ≈ 11 $ac^{-1}$ in 2020, comprising 3% and 2% of all saplings in those respective years. In 2020, white oak seedlings averaged 75 $ac^{-1}$ or about 4% of all seedlings, similar to the overall relative abundance for white oak saplings and trees ().

The study region spans a vast area and exhibits considerable variation across its 41 distinct ecological sections. In contemporary forests, white oak frequency, relative abundance, and sawtimber volume were most prominent at mid-latitudes (approximately 35–40°), with notable concentrations in the Ozark Highlands, Boston Mountains, and Ouachita Mountains ecological Sects. (223A, M223A,

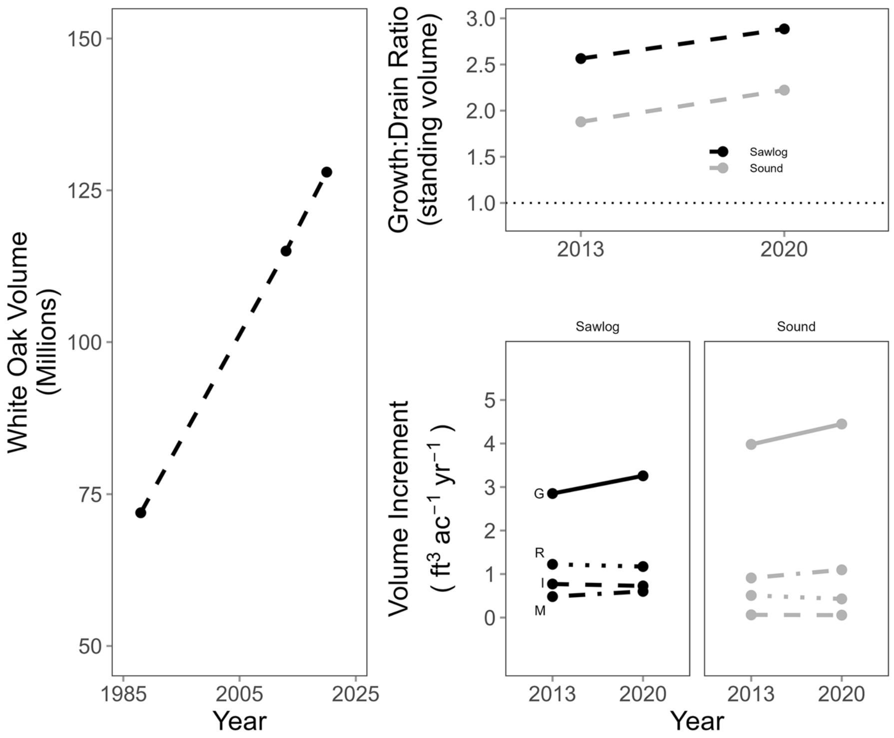



**Fig. 3** White oak volume changes for the eastern US white oak study region. Left: Standing volume from 1988–2020 (Net sawlog wood volume [thousands of board feet International 1/4-inch rule] of sawtimber trees [dbh ≥ 11 inches.]). Top right: Annual Growth to Drain Ratio for standing volume in 2013 and 2020, where the Growth to Drain Ratio is defined as net growth over harvest removals (Sawlog {black line}: sawlog wood volume [cubic feet] of sawtimber trees [dbh ≥ 11 inches]; Sound {grey line}: Sound bole wood volume [cubic feet] of trees [dbh ≥ 5 inches]). Bottom right: Components of annual volume increment in 2013 and 2020 for Sawlog volume {black line} and Sound volume {grey line} (G: survivor growth; R: Removals from harvesting; I: Ingrowth (dbh > 5 inches); and M: Mortality). Note – The shorter temporal window for the panels on the right reflects only data from those plots in more recent annualized forest inventories with updated growth accounting techniques

M231A). Additional high concentrations further east occurred in certain ecological sections of the Interior Low and Cumberland Plateaus (223E, 223B, 221H) and Appalachian Piedmont (221D, 231I) (Fig. 1, Supplemental Table 1). The Boston Mountains had the highest white oak frequency (65%) and, along with the Ozark Highlands, Northern Cumberland Plateau, and Central Appalachian Piedmont, were the only sections to exceed 45%. Relative stem abundance surpasses 5% and canopy stem abundance exceeds 10% only in the Ozark Highlands and Boston Mountains. The Northern Cumberland Plateau led in sawtimber volume per acre and ranks second to the Ozark Highlands in sound volume per ac.

As of 2020, the mean white oak plot age ranged 40 to 90 years across ecological sections, generally increasing from southwest to northeast (Supplemental Fig. 3). Age distributions were negatively skewed in 25 of 41 ecological sections,

**Table 1** Summary of forest attributes across the eastern US white oak study region, 1988 and 2020. Relative measures (abundance, basal area, volume) were calculated as the ratio of white oak values alone to the total for all species

| Study region attribute | 1988 | 2020 |
|---|---|---|
| Total timberland area (millions ac) | 205.6 | 213.7 |
| White oak frequency rate (% FIA plots) | 41% | 34% |
| Total white oak trees ≥ 1 in (billions) | 5.2 | 4.1 |
| Relative abundance (%) | 4% | 3% |
| Total white oak basal area ($ft^2$) ≥ 1 in (billions) | 1.3 | 1.5 |
| Relative basal area (%) | 7% | 7% |
| Total white oak sawtimber volume† (bd ft) ≥ 11 in (billions) | 71.9 | 128.0 |
| Relative sawtimber volume (%) | 12% | 8% |
| Mean white oak Quadratic Mean Diameter (in.) | 6.8 | 8.2 |

†Net sawlog wood volume of sawtimber trees (International 1/4-inch rule)

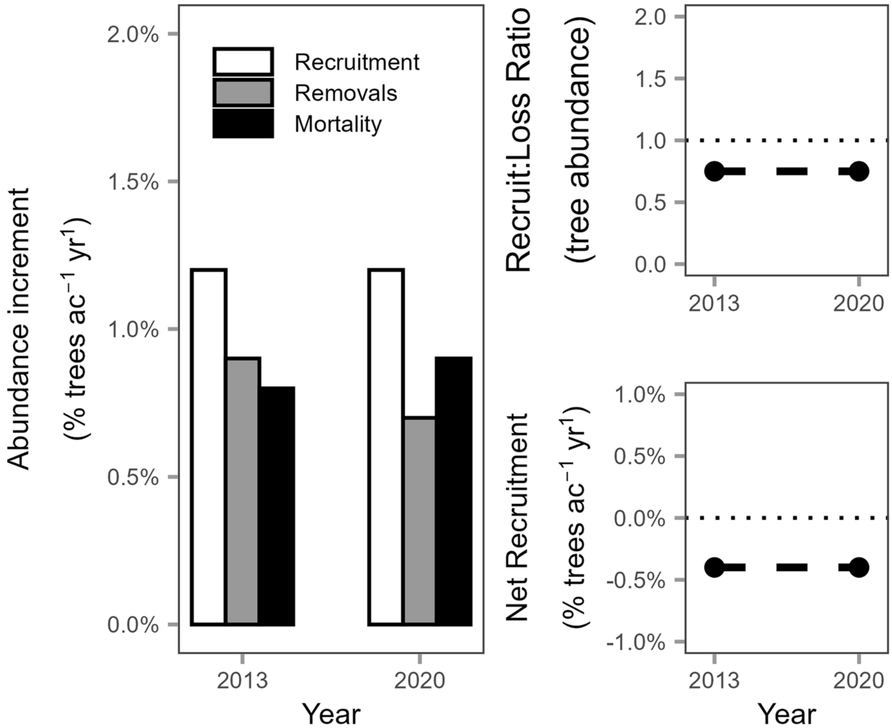



**Fig. 4** White oak abundance of trees with dbh ≥5 inches in the eastern US white oak study region for 2013 and 2020. Left: Components of annual abundance increment across the study region. Top right: Annual recruit-to-loss ratio for standing tree abundance. Bottom right: Annual net recruitment rate, defined as ingrowth trees less mortality and removal trees across the study region. Rates are relative to the initial population. Note, unit-area measures (e.g., stems $ac^{-1}$) reported use *all* timberland in a specified area as the area basis, rather than timberland with white oak present

indicating distributions that tended toward older, more mature white oak plots. Conversely, sections with positive skew reflect a higher presence of younger, less mature white oak plots.

White oak frequency rate declined in 35 of 41 ecological sections from 1988 to 2020, with absolute frequency differences ranging from −4% to −25% (Supplemental Table 3). However, the rate of occurrence increased most in the Wisconsin Central Sands (+ 7%; 222R) and Southern Appalachian Piedmont (+ 7%; 231 A). Only two sections—the Wisconsin Central Sands and Central Ridge and Valley (221J) – showed increases in relative stem abundance.

Only four sections (222U, 222 J, 223G, 222L) had declines in sawtimber volume from 1988 to 2020 (Supplemental Table 3). In contrast, three ecological sections (221H, M223A, 223 A) saw gains of at least 0.5 MBF $ac^{-1}$ in sawtimber volume since 1988, averaging at least 50%. All ecological sections reported positive net sound volume growth (survivor + ingrowth—mortality) in the most recent annual inventory, however when harvest removals are included, the net annual change for the North Central Driftless and Escarpment (222L) and Northern Unglaciated Allegheny Plateau (211G) turn negative (Fig. 5, Supplemental Table 4). Growth-to-drain ratios for sound volume remained above the critical threshold of 1.0 in 38 of 41 ecological section, exceeding 5.0 in 7 sections. Among the three sections at or below the 1.0 threshold, two (211G, 251B) recorded no ingrowth volume for white oak while the third (North Central Glaciated Plains, 251B) had no recorded volume removals.

In contrast to increasing volume, tree abundance metrics were generally opposite. Annual net recruitment (dbh $\geq$ 5 in), a measure of population growth, was positive in only seven ecological sections, primarily in the southern portion of the study region (Fig. 6, Supplemental Table 5). Across these seven sections, the average annual recruitment rate was 0.5% $yr^{-1}$. More broadly, net annual recruitment rates ranged from −2.0% $yr^{-1}$ to 0.8% $yr^{-1}$. In 22 sections, annual recruitment gains offset no more than half of the total losses from mortality and removals.

White oak sapling abundance ranged from 0–29 saplings $ac^{-1}$ around a region-wide average of 11 saplings $ac^{-1}$ (Fig. 7, Supplemental Table 6). Saplings were entirely absent in the Central Till Plains-Beech-Maple section (222H) and comprised less than 1% of saplings in five other sections (211F, 212Q, 222U, 223 F, 251B). The highest relative abundance was recorded in the Ozark Highlands (223A) at 7%, while no other section exceeded 4%. White oak sapling frequency rate ranged from 0 to 37% around the region-wide average of 22%. Overall, 26 ecological sections had a sapling frequency below 20%, meaning white oak saplings were present on fewer than 1 in 5 white oak plots.

White oak seedlings were more widespread than white oak saplings. Seedling frequency was at least 50% in eight sections, while seedlings were absent from white oak plots in only three setions (222U, 251B, 251D). In total, eight ecological sections had white oak seedling frequencies below 20%. Seedling abundance varied widely, from fewer than 2 $ac^{-1}$ in the North Central Glaciated Plains (251B) to 223 $ac^{-1}$ in the Ozark Highlands (223A). However, white oak never accounted for more

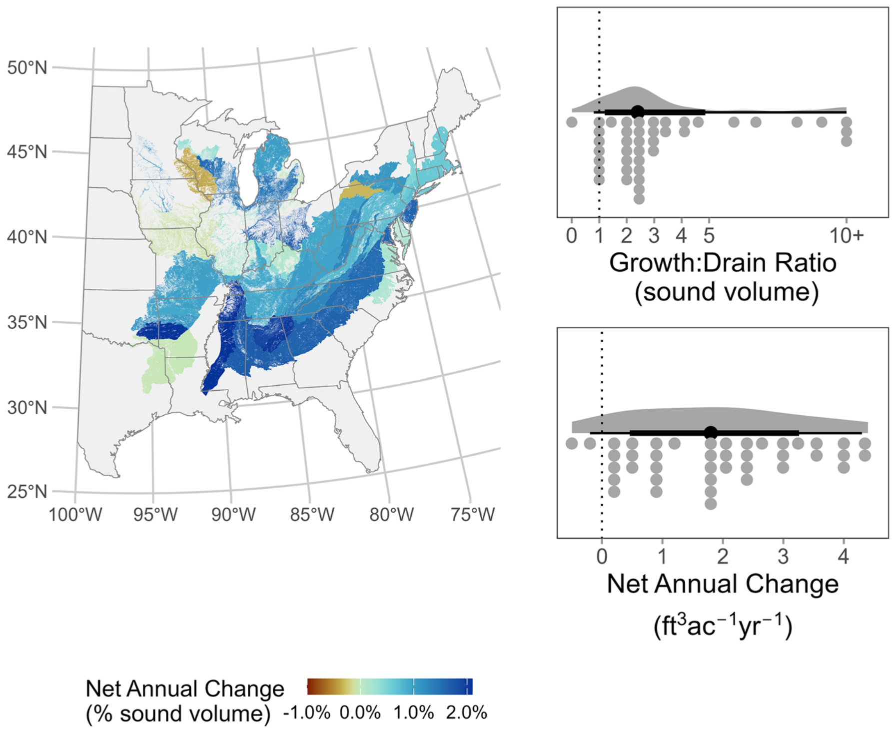



**Fig. 5** White oak sustainability metrics for sound volume of trees ≥ 5 in dbh in the eastern US white oak study region for 2020. Left: Map of net annual change in sound volume by ecological section year, defined as survivor and ingrowth volume less mortality and removal volume. Top Right: Annual growth-to-drain ratio for sound volume, defined as survivor and ingrowth volume less mortality over harvest removal volume. Bottom right: Annual net change in sound volume in cubic feet per acre per year, defined as survivor and ingrowth volume less mortality and removal volume. Rates (%) are relative to the initial population. Note: Both panels on the right depict summary statistics across all ecological sections in the study region such that the heavy point depicts the median value, the heavy band depicts the 33rd-66th percentile, the thin band depicts the 5th-95th percentile, the shaded area depicts the probability density, and the points below the distrubution depict a histogram. Sound = Sound bole wood volume [cubic feet] of trees [≥ 5 in dbh.]). Note, unit-area measures (e.g., stems $ac^{-1}$) reported use *all* timberland in a specified area as the area basis, rather than timberland with white oak present

than 11% of all seedlings (251D), and seedling composition was less than canopy composition in 16 sections.

A total of six ecological sections, collectively covering 9% of the study region and accounting for 8% of the sound volume, exhibited at least one indicator of near-term white oak volume challenges (Fig. 8). The North Central US Driftless and Escarpment Sect. (222L) showed both declines in standing volume and growth-to-drain ratios not exceeding 1.0. These sections were generally concentrated in the midwest portion of the study region.

Thirty-four unique sections, spanning 72% of the study region and containing 70% of the sound volume, met at least one indicator of imminent sustainability challenges related to contemporary recruitment rates. Specifically, these sections had

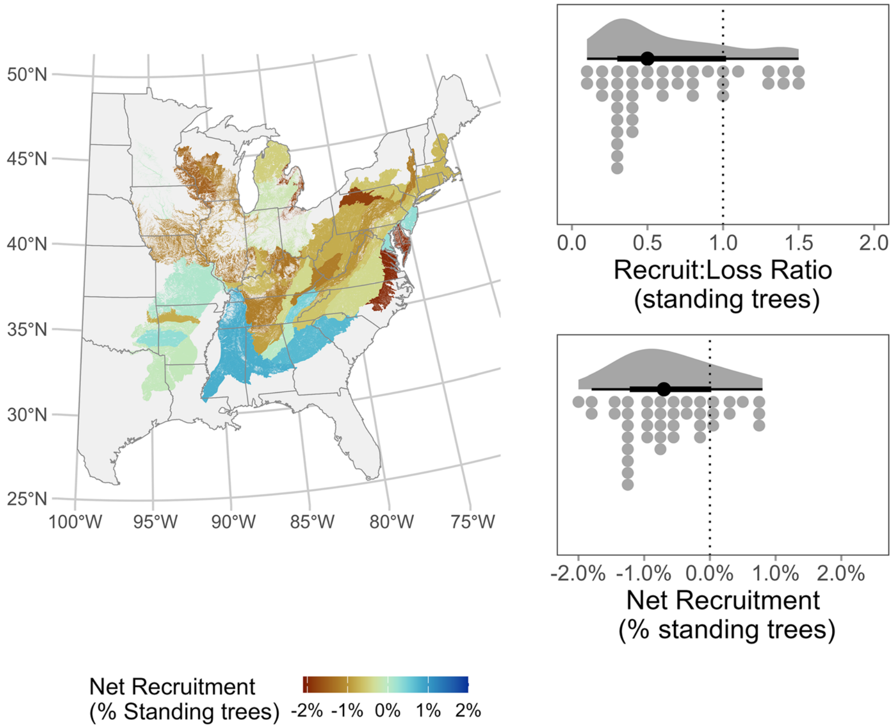


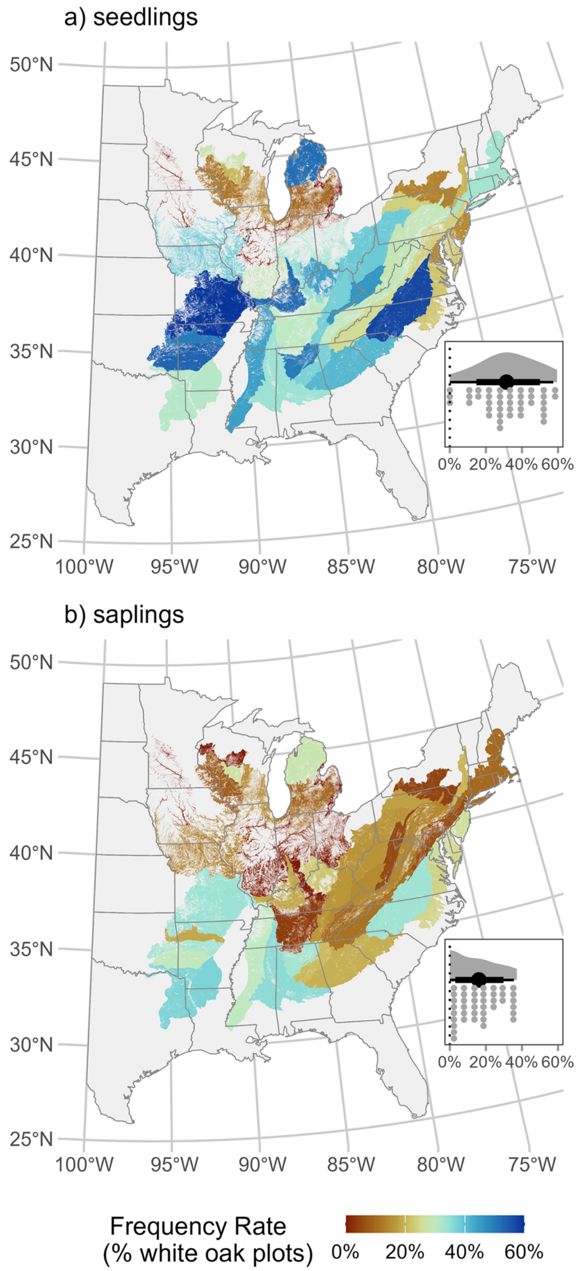

**Fig. 6** White oak sustainability metrics for abundance of trees ≥5 inches dbh in the eastern US white oak study region for 2020. Left: Map of net annual change in tree abundance by ecological section. Top Right: Annual recruitment-to-loss ratio for standing tree abundance, defined as ingrowth abundance over mortality and harvest removal abundance. Bottom right: Annual net change in tree abundance defined as ingrowth abundance less mortality and removal abundance. Rates (%) are relative to the initial population. Note: Both panels on the right depict summary statistics across all ecological sections in the study region such that the heavy point depicts the median value, the heavy band depicts the 33rd-66th percentile, the thin band depicts the 5th-95th percentile, the shaded area depicts the probability density, and the points below the distrubution depict a histogram

either non-positive annual recruitment rates – indicating that more white oaks were being lost to mortality or harvest than were entering the system as new recruits – or recruitment-to-losses ratios not exceeding 1.0.

Ten sections, covering approximately 16% of the study region and 10% of the white oak sound volume, met at least one indicator of long-term sustainability challenges related to establishment. Six sections had mean white oak seedling abundances below twice their mean white oak tree abundance, while eight had seedling frequency rates below 20%. Notably, Sects. 222L, 222U, 232 A, and 251B met both establishment-related indicators.

Four sections—the South Central Great Lakes (222 J), North Central US Driftless and Escarpment (222L), Lake Whittlesey Glaciolacustrine Plain (222U), and Central Till Plains-Oak Hickory (223G)—collectively spanning about 4% of the study region and comprising 4% of the white oak sound volume, met indicators for

**Fig. 7** Average white oak seedling (top) and sapling (bottom) frequency rates in the eastern US white oak study region for 2020 by ecological section. For each attribute, insets depict summary statistics across all ecological sections in the study region such that: heavy point depict median value, heavy bands depict the 33rd-66th percentile, thin bands depict the 5th-95th percentile, shaded area depict the probability density, and points depict histogram




near-term volume challenges, imminent recruitment related challenges, and longer-term establishment related challenges.

Conversely, six ecological sections, accounting for 29% of the standing white oak sawtimber volume and occupying approximately 26% of the study region,

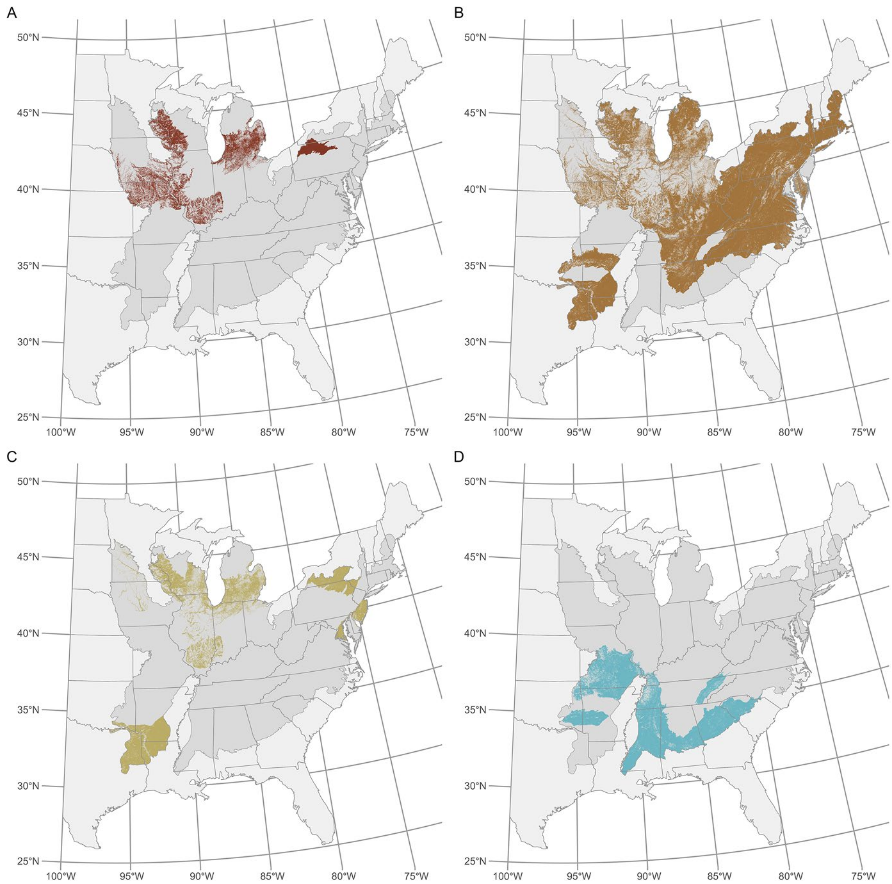



**Fig. 8** Regional white oak sustainability challenges based on contemporary demographics in the eastern US white oak study region (A-D). A) Ecological sections with near-term white oak volume challenges under contemporary conditions including 1) a decline in standing white oak sawlog volume from 1988 to 2020, 2) any negative annual net growth rates (sound or sawlog) for white oak in 2020, or 3) growth-to-drain ratios not exceeding 1.0 for white oak volume (sound or sawlog) in 2020. B) Ecological sections facing imminent sustainability challenges due to contemporary recruitment rates including 1) non-positive annual recruitment rate for white oak, or 2) A recruitment-to-losses ratio not exceeding 1.0. C) Ecological sections facing long-term sustainability challenges driven by regeneration rates including 1) seedling frequency rate less than 20%, or 2) mean seedling abundance was less than twice the mean tree abundance (dbh ≥ 1 in). D) Ecological sections that did not meet any criteria for near-term, imminent, or long-term sustainability challenges based on volume, recruitment, and regeneration metrics outlined above

predominantly in the southern portion of the study region, did not meet any indicators of sustainability challenges based on contemporary volume, recruitment, or regeneration demographics.

## Discussion

The sustainability of white oak has received heightened attention recently, drawing interest from popular media and even the US Congress. Much of this attention stemmed from a growing popularity of bourbon and a recognition of white oak's importance to expanded production- yet the broader concerns surrounding white oak sustainability extend well beyond the distilling sector (Zhang et al. 2024; https://whiteoakinitiative.org). Challenges associated with oak regeneration, historical factors leading to current forest conditions, and long-term implications of current forest dynamics all contribute to the concern about future resource availability. These concerns are well-founded in a large body of literature documenting both the past dominance of oak forests and the issues that threaten their persistence (McWilliams et al. 2002; Abrams 2003; Fei et al. 2011).

Our findings both validate and temper concerns about white oak sustainability. A key challenge in assessing this resource is distinguishing contemporary conditions from their long-term implications (McRoberts et al. 2004; Wear & Greis 2013). While standing volume remains high and continues to grow, demography points to a future decline. Over the past 30 years, white oak volume has increased across the eastern US range, and in nearly all regions therein. Although some regions show signs of sustainability concerns, those regions amounted to less than 10% of the white oak acreage (or volume) and were generally coincident with older average ages (Supplemental Fig. 3). Widespread over-utilization was not evident from the region-wide growth-to-drain ratio nor has it been since at least the 1980's (McWilliams et al. 2002). This suggests that, barring extraneous factors (e.g., Conrad et al. 2019), white oak volume will likely continue to increase in the near-term.

However, demography within contemporary white oak forests suggest that some degree of population reduction is inevitable over time. White oak volume growth was driven by increasing size of large diameter trees, not an influx of small or young trees over the past 30 years. The unbalanced size and age structures, which are a byproduct of past land-uses (Foster et al. 1998; Thompson et al. 2013), have an underrepresentation of younger forests relative to the abundance of older cohorts, making future reductions in white oak standing volume a near certainty at some point (Greenberg et al. 2011; Shifley et al. 2014). This is consistent with McEwan and others' (2011) report that both northern red oak and white oak were underrepresented in smaller size classes relative to their proportion of the status as canopy trees. The region-wide negative population growth for trees larger than 5 in dbh appears minor (−0.38% · yr⁻1), but even at this low rate, a back-of-the-envelope compound interest projection { $A = P \cdot e^{(rt)}$} that assumes a constant decline rate and no ecological feedbacks, suggests white oak abundance could shrink by about one-third over the next century if unaddressed. Some studies have projected when resource availability may reach a critical tipping point in the future (e.g., Dhungel et al. 2024 for Kentucky), but sophisticated methodologies that enable environmental, economic, social, and silvicultural variations to be analyzed across spatial scales are not fully developed. Moreover, the long lifespan and slow growth of white oak mean that any substantial losses due to forest health issues could have lasting consequences. Modeling and simulation approaches to better predict potential risks and inform proactive mitigation strategies would be fruitful lines of future research.

Our results show that for white oak, recruitment bottlenecks were far more widespread and limiting than establishment bottlenecks. In total, regions that represent 10–16% of the current white oak volume or acreage indicated future sustainability challenges related to seedling establishment such as low seedling frequency or abundance. This finding, of course, is contingent on the indicators and assumptions used, and would benefit from further empirical researchAnalyses across the eastern US have consistently shown that advance reproduction in the understory of mature forests is often insufficient to secure desirable regeneration outcomes (Miller and McGill 2019; Vickers et al. 2019a, b; Miller et al. 2023). This issue is particularly pronounced for oaks and has been recognized as a major threat to oak forest health and sustainability (Vickers et al. 2023). However, our findings suggest that white oak establishment may be less concerning than the broader patterns observed for oaks as a genus. In contrast to other oaks that share its range, white oak is more shade tolerant, has a much higher root:shoot ratio, and exhibits especially slow juvenile height growth (Rogers 1990; Rebbeck et al. 2011, 2012). Moreover, white oak seedlings have been shown to persist in the understory of forests for decades especially via resprouting following top dieback (Minckler 1957; Tryon & Powell 1984; Rentch et al. 2003). The regions with establishment challenges largely coincide with areas known to have excessive deer browse (McWilliams et al. 2018).

Recruitment concerns were widespread. Recruitment deficits occurred in regions that represent 70–72% of current white oak acreage or volume and were particularly pronounced in core parts of the white oak range, including most of the Central Hardwood Region (Hicks 1998; Fralish 2003). These findings align with broader forest dynamics such as mesophication where historical disturbances, especially fire, that once favored oak have been suppressed (Alexander et al. 2021), allowing shade-tolerant species to dominate the understory (Nowacki & Abrams 2008; McEwan et al. 2011; Woodbridge et al. 2022). The resulting conditions limit white oak recruitment and ingrowth, reinforcing the decline in younger cohorts (Hutchinson et al. 2016; Lhotka et al. 2018; Hackworth et al. 2020). An exception to this was the Ozark Highlands, where the generally lower site productivity and absence of American beech and yellow-poplar along with reduced importance of red maple probably allow white oak to maintain a stronger presence compared to other regions where these competitors are more abundant (Dey et al. 2009; Johnson et al. 2019). Given white oak's central role in both forest ecosystems and regional economies, understanding its population dynamics in the Central Hardwood Region is crucial, with significant implications for both (McShea et al. 2007; Dhungel & Ochuodho 2024; Harris et al. 2024).

Regions that did not exhibit sustainability concerns according to the metrics used in our analysis were generally farther south than most definitions of the Central Hardwood Region allow. Excluding the Ozark Highlands (223A), which is predominately in southern Missouri, and the Central Ridge and Valley section of eastern Tennessee (221 J), both of which are firmly in the Central Hardwood Region, the better faring areas comprise a relatively modest portion of the current white oak volume (14%) and acreage (19%). However, all ecological sections that did not exhibit sustainability concerns are projected to decrease in white oak abundance under potential future climate scenarios (https://www.fs.usda.gov/nrs/atlas/tree/v3/802; Iverson et al. 2019). Beyond the differences previously outlined for the Ozark Highlands, we do not posit a definitive explanation for why the remainder of these regions appear to be faring better. This warrants further investigation, and potential factors include differences in forest composition and structure (Granger & Buckley 2021; Hart et al. 2023), prevailing management practices (Fox et al. 2007), land-use and disturbance patterns (Orwig & Abrams 1993; Masek et al. 2013) or abiotic conditions (Au et al. 2020; Jonko et al. 2024).

Across the white oak study region, landowners are overwhelmingly smaller private (largely family) landowners. These landowners are shown to be less likely than larger forest landowners to have written management plans, receive professional forest management advice, be enrolled in forest cost-share programs, or harvest timber from their land (Butler et al. 2020). The silvicultural techniques that foster oak often require a thorough understanding of stand history, trajectory, and potentially multiple, well-planned, intensive entries (e.g., Brose et al. 2008; Greenler & Saunders 2019; Patterson et al. 2022). These needs are at odds with the cited tendency for smaller, often family-owned forests to not seek professional land management assistance and their lack of written management plans (Butler et al. 2020). These smaller, private forest landowners which predominate in the eastern US (Butler et al. 2021) may be less likely to commit to the more complicated management necessary to regenerate oak (Knoot et al. 2010). Instead, there has been the tendency toward making forest land management decisions that do not favor oak establishment or retention, favoring instead simpler and more economically profitable alternatives (Knoot et al. 2010). Additionally, small landowners' desires to maintain aesthetic qualities of the forest (Sass et al. 2023) may conflict with the repeated, sometimes intensive, silvicultural interventions needed to maintain oaks in the stand.

Timber quality is another key aspect of white oak sustainability that warrants further investigation. Although our results indicate that total white oak sound volume remains high, more detailed assessments would be informative, as significant differences may emerge when considering specific timber grades (Dhungel et al. 2024). A study in Kentucky and Tennessee indicated the percent of total hardwood tree volume in higher quality, field-recorded tree grades had decreased over time (Brandeis et al. 2017). Another study showed that trees were increasingly likely to be left in partially harvested stands as their tree grade decreased in quality, i.e. higher quality trees were preferentially harvested and lower quality trees left in the stand (Brandeis 2017; Luppold & Bumgardner 2018). Selective harvesting (i.e., high-grading), which removes the highest-value trees while leaving lower-quality stems, is ubiquitous across the white oak range (Fajvan et al. 1998; Belair & Ducey 2018; Curtze et al. 2022), and will likely be a major factor in future availability of high-quality sawtimber (Ward et al. 2005; Castle et al. 2018).

## Conclusions

Given the concerns highlighted in this study, actions to bolster white oak sustainability warrant consideration. Geographic variation in the nature, severity, and immediacy of challenges suggest that some ecological sections are more vulnerable than others. Regions with well-balanced recruitment and sawtimber volume, as well as frequent establishment, may simply require maintenance to ensure positive trajectories continue, while regions facing demographic constraints may require more intensive interventions. Regardless, the lack of any forest management, which is common across much of the deciduous forestland of the eastern US, poses a threat to white oak sustainability (Moser et al. 2006; Shifley et al. 2014). A large body of research supports the application of low- to intermediate-severity disturbances, including surface disturbance from fire and canopy disturbance for release, to maintain white oak forests (Larsen and Johnson 1998; Abrams 2003; Johnson et al. 2019). Silvicultural prescriptions are developed for site-specific conditions and results can likewise vary; however, past studies have documented successful white oak regeneration using regeneration harvests that range in intensity from clearcutting (e.g., Kabrick et al. 2008), to shelterwoods (e.g., Brose et al. 1999), to uneven-aged selection methods (e.g., Loewenstein et al. 2000). While the success of these specific practices may vary according to conditions across the white oak range, there is consistency that the absence of canopy disturbance is a root cause of white oak regeneration and recruitment concerns.

Regions with establishment challenges face the least immediate threat but also the least readily addressed. Excessive deer browse is known to be a factor limiting the accumulation of seedlings in much of the area identified (McWilliams et al. 2018; Sample et al. 2023). If excessive deer browse is not thought to be the limiting factor, management to increase seedling establishment should occur years in advance of a planned regeneration harvest. Given the cyclical nature of white oak acorn production, masting events can be infrequent but important events to overcome acorn predation. Outside mast years, site preparation practices such as scarification (Lhotka & Zaczek 2003) or prescribed burning (Greenler et al. 2020) may increase the establishment of white oak seedlings, while midstory removal treatments that provide moderate light increases can improve survival to aid accumulation of advance reproduction. In cases with severe problems in natural establishment of oak seedlings, underplanting may be an option to develop advance reproduction when planning for regeneration harvests (Dey et al. 2012; Craig et al. 2014). Further research into silvicultural options for overcoming establishment challenges is worthwhile.

For those regions with recruitment challenges – which was most of the study region – we echo the two fundamental requirements for successful oak silviculture as summarized by Loftis (2004): the presence of competitive reproduction and the provision of timely and sufficient release. In these regions, white oak may benefit from more active management and an increased prioritization of tending treatments, including thinning and competition control through various mechanisms (i.e., mechanical, chemical, pyric) that align with its silvics (Rudolph et al. 2025). A key uncertainty is whether white oak stems with stalled development—or those likely to stall due to their surroundings—warrant silvicultural investment, and if so, the optimal timing of release (Schlesinger 1978; Dale & Sonderman 1984; McGee & Bivens 1984). Ongoing research, particularly on crop-tree release methods (Ward 2013; Vogel et al. 2022), aims to address these questions.

We recommend proceeding thoughtfully in the 10–11% of the study region where near-term volume challenges were evident. When growth-to-removals ratios are below 1.0, harvest decisions are particularly consequential for long-term forest productivity and sustainability goals. Harvesting methods that promote regeneration or maintain adequate residual growing stock and align with the silvics of key species are more likely to ensure white oak sustainability, especially when implemented through coordinated efforts between forest managers, researchers, policymakers, and industry stakeholders. Addressing demographic bottlenecks, improving regeneration success, and mitigating emerging threats is critical to maintaining the long-term viability of white oak forests for timber production, carbon storage, wildlife habitat, and other ecological functions.

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**Authors' contributions** **LAV**: Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization; **BOK**: Writing – review & editing, Methodology, Funding acquisition, Conceptualization; **TG**: Writing – review & editing, Methodology, Formal analysis; **TJB**: Writing – review & editing, Methodology; **JML**: Writing – review & editing, Methodology, Conceptualization, Funding acquisition; **RSM**: Writing – review & editing, Methodology; **KLS**: Writing – original draft, Conceptualization; **JWS**: Writing – review & editing, Project administration, Funding acquisition, Conceptualization.

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**Data Availability** Initial data publicly available from https://research.fs.usda.gov/products/dataandtools/tools/fia-datamart; further data available upon request.

## Declarations

**Conflict of Interests** None declared.

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