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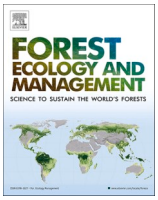

# White oak sapling dynamics across the eastern US: Quantifying a bottleneck to sustainability

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ABSTRACT

The long-term sustainability of white oak (*Quercus alba* L.), an ecologically and economically important species in the eastern United States (US), appears to be threatened by demographic constraints. Earlier research has highlighted widespread bottlenecks in the process of recruiting white oak saplings (2.5 cm - 12.7 cm dbh) into small trees (dbh ≥ 12.7 cm). Thus, the fate of white oak saplings is a key component in understanding whether shortfalls in larger size classes are due to an onset of challenges when white oaks reach the small tree size or are an artifact of unsustainable sapling dynamics. Using Forest Inventory and Analysis (FIA) data, we examined sapling population dynamics, including rates of recruitment into the sapling size class, mortality and removals of sapling sized stems, and outgrowth of saplings into the small tree size class across the eastern US and regionally. Across the eastern US white oak study region, white oak saplings exhibited slightly positive net population growth in 2020, but 13 of the 41 ecological sections that made up our study region had flat or declining sapling populations, and another 7 sections had sapling densities too low to support meaningful trend estimates. Mortality rates for saplings exceeded recruitment for many northern and mid-Atlantic sections, while parts of the Interior and Appalachian Plateaus and Boston Mountains showed stronger sapling accumulation. Compared to saplings of other tree species that were examined, white oak saplings had 1) low mortality rates and 2) a tendency to stall, often for more than 15 years, without growing into the small tree size class. Our results suggest management opportunities may exist for delayed release of white oaks persisting in the sapling stage, particularly in regions where sapling dynamics are slow. Sapling persistence may provide a buffer against regeneration failures, but it does not guarantee eventual canopy recruitment for stalled saplings. Understanding where white oak saplings persist or fail to accumulate offers a more refined lens for diagnosing bottlenecks and promoting sustainable management.

## 1. Introduction

White oak is a foundation species in eastern North American forests (sensu Ellison et al., 2005), valued for its ecological roles and economic importance. It supports diverse wildlife, contributes to forest structure and function, and underpins rural economies through its high-quality timber, especially for cooperage (Fralish, 2004; Hanberry and Nowacki, 2016; Dhungel and Ochuodho, 2024). However, concerns about its long-term sustainability have intensified due to shifting disturbance regimes, aging forest structures, and persistent regeneration challenges (Abrams, 2003; McEwan et al., 2011; Dey, 2014).

Recent analyses of US nationwide forest inventory data revealed troubling demographic trends (Vickers et al., 2025). Despite increasing standing volume, the population of white oak trees ≥ 12.7 cm dbh (diameter at breast height; 1.37 m) is declining, with recruitment failing to offset mortality and harvest losses. Notably, Vickers et al. (2025) reported 70 % of timberland with white oak present in the eastern US faces at least one sustainability threat, with the most widespread being a bottleneck in the influx of saplings (dbh 2.5 cm - 12.7 cm) into small tree size (dbh ≥ 12.7 cm). While seedling establishment was limited in some regions, sapling dynamics appeared to be the more pervasive constraint. Importantly, mortality and harvest rates were not historically anomalous (Shifley and Smith, 1982; Smith and Shifley, 1984), suggesting that insufficient recruitment of small trees was indeed a primary driver of population decline for white oak. Taken together, these findings underscore the existence of two well-recognized demographic bottlenecks

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in oak forests: establishment of seedlings that develop into saplings and ascension of saplings into the overstory (see Loftis and McGee 1993; Dey, 2014; and Johnson et al., 2019 for broader syntheses).

Saplings represent a critical demographic bridge between regeneration and canopy ascecsion, as their performance at this stage determines future stand development and whether regeneration practices were effective (Moser et al., 2006; Fei et al., 2011; Schweitzer and Dey, 2011). Failures at this stage may reflect a mismatch between species traits and contemporary disturbance regimes (Nowacki and Abrams, 2008; Alexander et al., 2021). Yet, despite extensive research on oak ecology and silviculture, oak sapling populations are often sparse and their population dynamics remain an area of research need given their pivotal role in shaping future forest structure (Woodall et al., 2008, Dey and Schweitzer, 2014; Luppold and Bumgardner, 2018). This study addresses that gap by quantifying white oak sapling population dynamics across 41 ecological sections in the eastern US using FIA data. By clarifying the nature of this particular demographic bottleneck, our results will bolster the empirical foundation for future work to develop regionally tailored silvicultural strategies that enhance sustainable white oak recruitment. We focus on four key demographic outcomes for saplings: (1) mortality, (2) removal, (3) persistence within the sapling size class, and (4) outgrowth into the small tree class. Our specific objectives were to:

I. Quantify basic demographic rates (recruitment, mortality, removal, outgrowth) governing changes in the white oak sapling population.
II. Identify regions where recruitment bottlenecks are most acute, defined by low recruitment or high sapling losses.
III. Assess sapling persistence and its implications for management.

## 2. Methods

### 2.1. Study region

Our study region was derived from Vickers et al. (2025), spanning 41 ecological sections in the eastern US where white oak basal area was $\geq$ 0.5 $m^2 ha^{-1}$ in 2020 (Fig. 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 unique ecological characteristics (Cleland et al., 2007, McNab et al., 2007). Ecological sections (hereafter referred to as ecosections) are the foundation of our regional analyses and a reference map is provided in the supplementary material (Supp. Figure 1).

### 2.2. FIA data

We used publicly available data from the FIA program (https://research.fs.usda.gov/products/dataandtools/fia-datamart). FIA data are collected by periodically visiting a network of permanent field plots that are spatially distributed at an intensity of approximately one plot for every 2428 ha (Westfall et al., 2022). Plots are visited when the area meets FIA's definition of 'forest land'; at least 0.4 ha and no less than 36.6 m wide with $\geq$ 10 % canopy cover by trees of any size, including land that formerly had such tree cover and that will be naturally or artificially regenerated (USDA 2021). 'Timberland,' the focus of our study, is a subset of forestland that is not withdrawn from timber utilization by statute and that can produce $\geq$ 1.4 $m^3 ha^{-1} yr^{-1}$ of industrial wood. Each plot consists of four 7.3 m fixed-radius subplots dispersed at 36.6 m, and each subplot has an offset, nested microplot with a fixed-radius of 2.1 m. The definitions of 'sapling' and 'tree' used here are not arbitrary but rather they are derived from how FIA data are collected. Trees (at least 5-inches [$\geq$12.7 cm] dbh) are tallied on the subplot while seedlings and saplings (1.0–4.9 in. [2.5–12.6 cm] dbh) are tallied on the microplot. As a result, FIA data are often reported using these descriptors as general size classifications.

At the time of data retrieval (2024), we chose the most recent inventory year shared across all states, 2020, for our analyses. For temporal comparisons, we used 2013 data, which was the most recent inventory year that did not overlap in plot visits with the 2020 inventory (Supp. Table 1).

### 2.3. Analyses

For our region-wide analysis of sapling demography, saplings tallied on microplots were expanded to population level estimates using standard FIA methods (Westfall et al., 2022). Those estimates were further

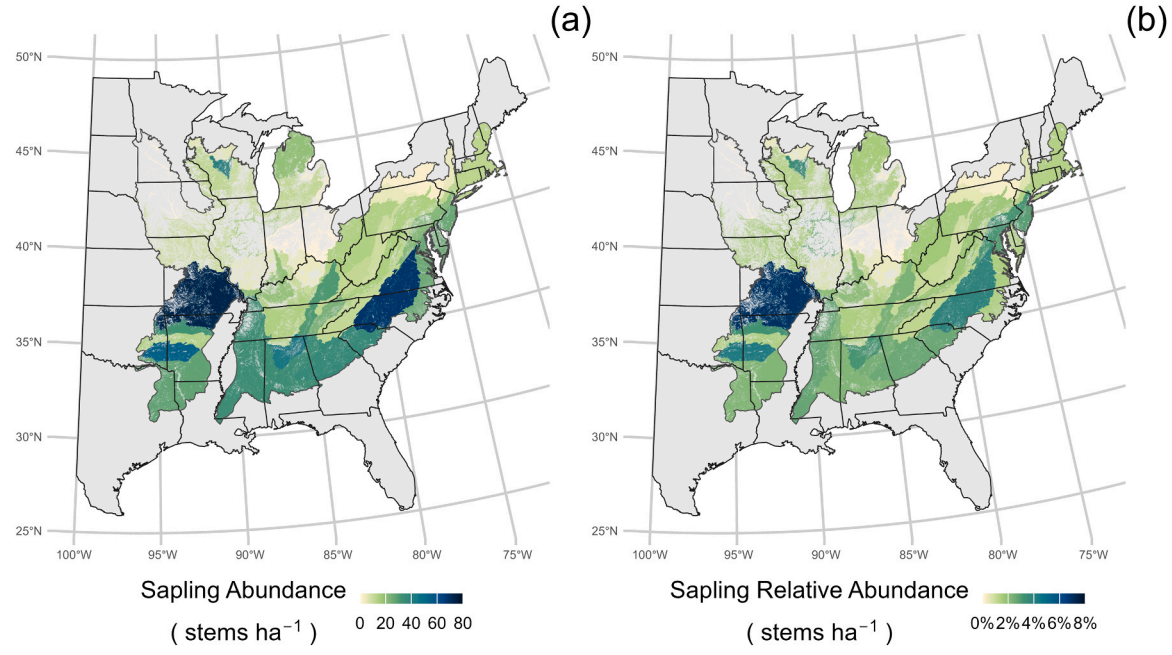


**Fig. 1.** Abundance (a) and relative abundance (b) of white oak saplings (dbh: 2.5 cm - 12.7 cm) on timberland in the eastern US white oak study region (outlined in grey), 2020. The eastern US white oak study region was defined as the 41 ecological sections where white oak basal area was $\geq$ 0.5 $m^2$ $ha^{-1}$ in 2020.

categorized as recruitment, mortality, or removals based on the past and present status of the tallied saplings (excluding removals due to changes in land use or status). Removals quantify saplings killed due to silvicultural activity whereas mortality assumes natural causes. 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. To facilitate comparisons between ecosections we expressed these annual estimates on a per hectare basis and as a percentage of the total population using a previous time estimate of saplings per hectare (SPH) as a denominator. In the same manner, we estimated outgrowth as the annual percentage of saplings that cross the $>$ 12.7 cm diameter threshold into the small tree size class. We calculated two additional metrics from the individual demographic components described above: 1) net annual population change for saplings, which was defined as recruitment into the sapling size class less the sum of sapling mortality and removals and 2) annual recruitment-to-losses ratio, which was defined as recruitment divided by the sum of sapling mortality and removals. The recruitment-to-losses ratio is conceptually similar to the growth:drain ratio often used in forest sustainability analysis for volume or biomass. Annual demographic rate estimates were compared between 2013 and 2020 for the entire eastern US white oak study region and among ecosections for 2020. To provide broader ecological context for our white oak focal analyses, we estimated the same demographic rates for common associates in the study region, including: red maple (*Acer rubrum* L.), sugar maple (*A. saccharum* Marshall), hickory (as a genus; *Carya* spp.), yellow-poplar (*Liriodendron tulipifera* L.), northern red oak (*Quercus rubra* L.), and black oak (*Q. velutina* Lam.). All data for 'white oak' refers to the single species alone (*Q. alba* - FIA species code 802), not the broader 'select white oak' species group sometimes reported by FIA.

We also examined the length of time a white oak sapling remained in the sapling size class, known hereafter as 'residence time', by first identifying plots with live saplings in 2020 that were visited during previous inventory cycles (with or without saplings). We then calculated the percentage of those white oak saplings in 2020 that were also alive and present as a sapling at each previous plot visit. We used this residence time metric as a temporal proxy. While a 5-year cycle was most common for this study's temporal window, FIA inventory cycles span 5–7 years in the eastern US (Westfall et al., 2022). Due to state-level variation in inventory administration, four inventory cycles was the maximum possible number of remeasurements in our dataset, though not uniformly possible in all ecosections. Data from three inventory cycles was available across the entire study region. In our analysis, we referred to saplings that were present, as a sapling, across at least three inventory cycles as 'resident saplings.' We summed plot remeasurement period at the ecosection level to approximate a 'least age' range for resident saplings. That range was 10–13 years after plots were visited 3 times (three cycles) and 15–18 years for those visited four times (four cycles).

We used the stat_cor function in the ggpubr package (Kassambara, 2023) for R statistical software (R Core Team, 2024) to calculate pearson correlaton coefficients and their associated p-values ($\alpha = 0.05$). Those were used to determine the strength and direction of relationships between the proportion of resident saplings, net sapling population change, and the individual components of population change, at the ecosection scale for the 2020 data. Only ecosections with at least 10 sample plots were used here.

## 3. Results

### 3.1. Quantify basic demographic rates (recruitment, mortality, removal, outgrowth) governing changes in the white oak sapling population

Across the study region, the net annual rate of population change for white oak saplings was slightly positive (0.5 % $yr^{-1}$) in 2020 (Table 1). Recruitment into the sapling size class was 4.0 % $yr^{-1}$ while mortality was 2.3 % $yr^{-1}$, and removals were 1.2 % $yr^{-1}$. This combination indicates a 1.1 recruitment-to-losses ratio, which is slightly above the critical threshold of 1.0 where recruitment into the sapling size class exactly matches the combined sapling losses from mortality and removals. Outgrowth of white oak saplings into the small tree size class was 0.9 % $yr^{-1}$. The mortality rate varied with tree size. White oak mortality was greatest in smaller size classes and declined as tree size increased (Fig. 2). Mortality rates for the smallest stems entering the sapling size class were 2.5 % $yr^{-1}$, decreasing to about 1.4 % $yr^{-1}$ for stems transitioning from saplings to small tree size, and stabilizing around 0.5 % $yr^{-1}$, beyond diameters of about 28 cm.

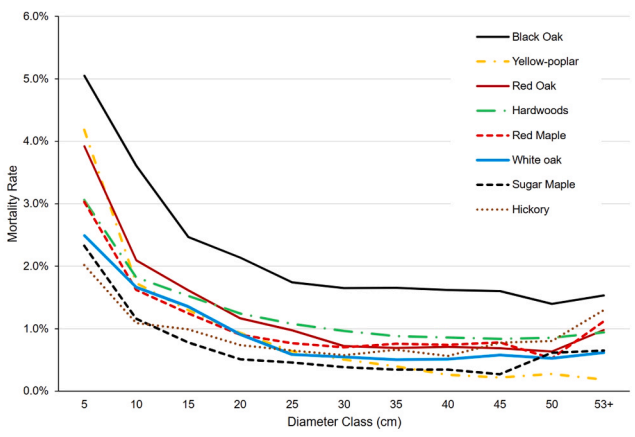


**Fig. 2.** Annual mortality number of trees as a proportion of total trees (mortality rate) by diameter class for select species on timberland in the eastern US white oak study region, 2020.

**Table 1**
Demographic components of annual population change for saplings (2.5 cm $\geq$ dbh $<$ 12.7 cm) of select species on timberland in the eastern US white oak study region, 2013 and 2020.

| | 2020 | | | | | | 2013 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SPECIES | SPH | %RECR | %MORT | %REMV | NRsap | RLsap | SPH | %RECR | %MORT | %REMV | NRsap | RLsap |
| white oak | 27.6 | 4.0 % | 2.3 % | 1.2 % | 0.5 % | 1.1 | 26.7 | 5.5 % | 2.3 % | 1.3 % | 1.9 % | 1.5 |
| black oak | 11.3 | 4.0 % | 4.2 % | 1.0 % | −1.2 % | 0.8 | 12.5 | 5.1 % | 4.2 % | 1.3 % | −0.4 % | 0.9 |
| n. red oak | 10.7 | 4.0 % | 3.4 % | 0.6 % | 0.0 % | 1.0 | 11.8 | 4.6 % | 2.8 % | 0.8 % | 1.8 % | 1.6 |
| hickory | 50.7 | 3.4 % | 1.8 % | 1.2 % | 0.4 % | 1.1 | 50.0 | 4.1 % | 1.8 % | 1.3 % | 1.0 % | 1.3 |
| red maple | 118.9 | 3.4 % | 2.6 % | 1.2 % | −0.4 % | 0.9 | 118.3 | 4.5 % | 2.3 % | 1.1 % | 1.1 % | 1.3 |
| sugar maple | 42.0 | 2.0 % | 1.9 % | 0.4 % | −0.4 % | 0.8 | 42.2 | 2.9 % | 1.7 % | 0.5 % | 0.7 % | 1.3 |
| yellow-poplar | 35.6 | 6.9 % | 3.9 % | 1.3 % | 1.8 % | 1.3 | 33.8 | 7.6 % | 4.1 % | 1.2 % | 2.4 % | 1.5 |

Where: SPH = saplings $ha^{-1}$, %RECR = annual rate of recruitment into the sapling size class as a proportion of the total initial sapling population (saplings $ha^{-1}$), %REMV = annual rate of sapling removals as a proportion of the total initial sapling population (saplings $ha^{-1}$), %MORT = annual rate of sapling mortality as a proportion of the total initial sapling population (saplings $ha^{-1}$), NRsap = annual net population change rate for saplings (recruitment - mortality - removals) as a proportion of the total initial sapling population (saplings $ha^{-1}$), RLsap = annual recruitment-to-losses ratio (recruitment / mortality + removals) for saplings.

White oak saplings averaged ca. 28 SPH in 2020, while common associates ranged from 11 SPH to 119 SPH (Table 1). Average sapling abundance for most species was similar from 2013 to 2020. Northern red oak and black oak, two oaks that are common and co-occur with white oak across much of the study region, had the same recruitment rate as white oak overall but displayed differing sapling demography in 2020. Northern red oak had higher mortality rates than white oak at 3.4 % $yr^{-1}$, but lower removals (0.6 % $yr^{-1}$). Sapling mortality rates for black oak were higher still (4.2 % $yr^{-1}$), and exceeded recruitment, producing a declining population rate of −1.2 % $yr^{-1}$.

Hickory (as a genus) and red maple both had slightly lower recruitment rates than white oak (3.4 % $yr^{-1}$). However, hickory had a lower sapling mortality rate than both red maple and white oak, resulting in a recruitment-to-losses ratio identical to white oak, while red maple's population was slightly declining at −0.4 % $yr^{-1}$ in 2020.

Sugar maple had among the lowest recruitment and mortality rates (2.0 % $yr^{-1}$, 1.9 % $yr^{-1}$ respectively in 2020) of the common associates we examined. In contrast, yellow-poplar had the highest recruitment rate (6.9 % $yr^{-1}$ in 2020), and was second only to black oak in mortality rate (3.9 % $yr^{-1}$). In the case of yellow-poplar, the rate of recruitment more than compensated for the high mortality rates, producing the most positive sapling population growth of the common associates examined in both 2013 and 2020. White oak outgrowth rates were similar to northern red oak and black oak, but lower than yellow-poplar (Table 2). Outgrowth rates for hickory, red maple, and sugar maple were notably lower than that of the oaks and yellow-poplar.

Across all size classes, white oak mortality rates were lower than an average rate that included all hardwood species (Fig. 2). Among the associates examined, differences in mortality rates were most pronounced as saplings, ranging from 2 % $yr^{-1}$ for the smallest hickory saplings to 5.1 % $yr^{-1}$ for the smallest black oak saplings. Mortality for all species examined generally converged on rates ≤ 1 % $yr^{-1}$ once they reached a dbh of about 23 cm. A notable exception to this trend was black oak, which had higher mortality rates than the other species across all sizes and was never less than 1.4 % $yr^{-1}$.

From 2013–2020, sapling population dynamics showed some temporal variability. For white oak and common associates, recruitment rates were universally lower in 2020 than in 2013, while mortality and removal rates remained similar (Table 1). All species exhibited lower net population growth rates and reduced recruitment-to-loss ratios in 2020 compared to 2013. Notably, red maple and sugar maple were the only species that shifted from positive to negative net population growth rates over this period. Sapling outgrowth rates were virtually unchanged from 2013 to 2020 for the species examined (Table 2).

### 3.2. *Identify regions where recruitment bottlenecks are most acute, defined by low recruitment or high sapling losses*

Though the annual net population growth for white oak saplings was 0.5 % $yr^{-1}$ across the eastern US white oak study region in 2020, population growth in individual ecosections ranged from −4.4 % $yr^{-1}$ to 4.6 % $yr^{-1}$ (Fig. 3, Supp. Table 2). Among the 35 ecosections where white oak sapling populations could support meaningful trend estimates for individual ecosections, net population growth was highest in the

**Table 2**
Annual outgrowth rates for saplings (dbh: 2.5 cm - 12.7 cm) of select species on timberland in the eastern US white oak study region, 2013 and 2020.

| SPECIES | 2020 | 2013 |
|---|---|---|
| white oak | 0.9 % | 1.0 % |
| black oak | 0.9 % | 1.1 % |
| n. red oak | 1.1 % | 1.1 % |
| hickory | 0.6 % | 0.6 % |
| red maple | 0.5 % | 0.6 % |
| sugar maple | 0.6 % | 0.6 % |
| yellow-poplar | 1.3 % | 1.2 % |

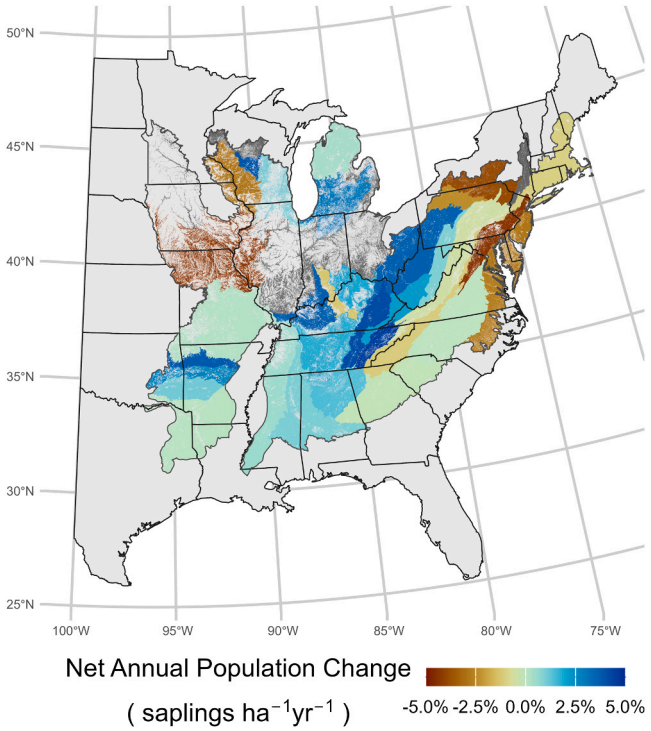


**Fig. 3.** Net annual population change for white oak saplings (dbh: 2.5 cm - 12.7 cm), on timberland in the eastern US white oak study region, by ecological section, 2020.

Central Ridge and Valley (221 J), parts of the Allegheny/Cumberland Plateau (221 H, 221E), Wisconsin Central Sands (222 R), Boston Mountains (M223A), and the Interior Low Plateau-Shawnee Hills (223D). These regions also had high rates of recruitment into the sapling class (Fig. 4).

Thirteen sections showed evidence of flat or declining sapling populations in 2020, ten in 2013. Another seven sections had sapling densities too low to support meaningful trend estimates. Ten sections, including the Northern Appalachian Piedmont (221D), Northern Glaciated Allegheny Plateau (211 F), Central Dissected Till Plains (251 C), Northern Atlantic Coastal Plain (232 A), North Central U.S. Driftless and Escarpment (222 L), Northern Unglaciated Allegheny Plateau (211 G), Interior Low Plateau-Transition Hills (223B), Lower New England (221 A), Blue Ridge Mountains (M221D), and Northern Ridge and Valley (M221A) had recruitment rates less than mortality rates in 2020 with the average deficit being 2.2 percentage points. Six sections showed this pattern in 2013. The Northern Appalachian Piedmont (221D), Central Dissected Till Plains (251 C), and North Central US Driftless and Escarpment (222 L) were the only ecosections where both recruitment and mortality were markedly worse (≥ 1 std. dev.) than other sections in 2020. Removals tended higher in the southeastern US, particularly in parts of the Coastal Plain and Piedmont (Fig. 4, Supp. Table 2). Four ecosections (232 H - Middle Atlantic Coastal Plains and Flatwoods, 231 A - Southern Appalachian Piedmont, 231I - Central Appalachian Piedmont, 231E - Mid Coastal Plains-Western), all of which were in the southeastern US, had removal rates that pushed the recruitment to losses ratio to or below the critical 1.0 though recruitment easily outweighed mortality.

### 3.3. *Assess sapling persistence and its implications for management*

White oak saplings displayed potential for longevity as 54 % of the white oak saplings were resident saplings (Table 3), meaning they had persisted, as saplings, for *at least* three inventory cycles (≥ 10–13 years). This phenomenon was widespread - half or more of the pool of white oak

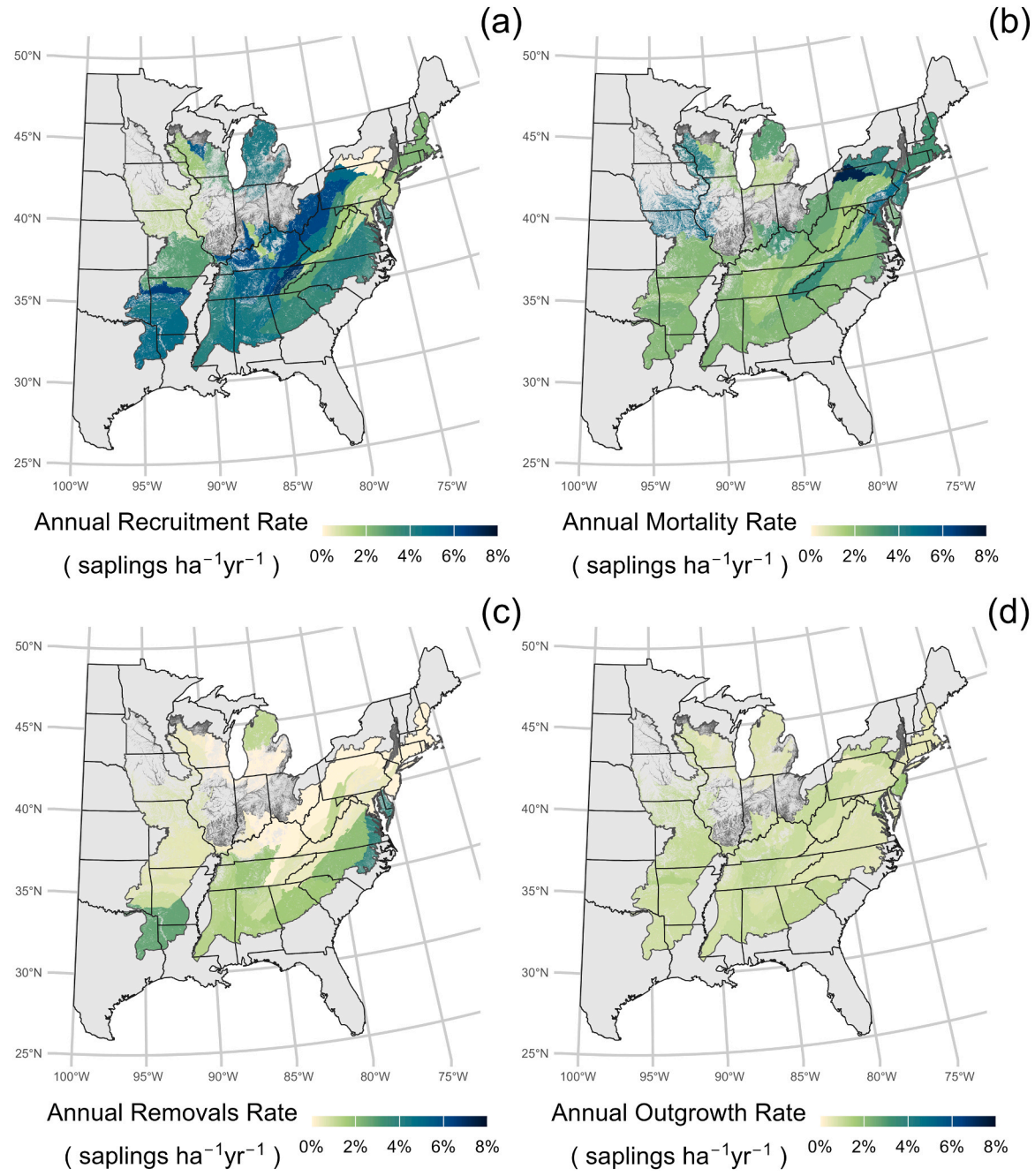


**Fig. 4.** Demographic components of annual population change for white oak saplings (dbh: 2.5 cm - 12.7 cm) on timberland in the eastern US white oak study region, by ecological section, 2020. (a) Annual rate of recruitment into the saplings size class, (b) annual rate of mortality within this sapling size class, (c) annual rate of removals within the sapling size class, and (d) annual rate of outgrowth from the sapling size class into the small tree size class (dbh $\geq$ 12.7 cm).

saplings were residents in 20 of the 29 individual ecosections in our study region where saplings densities could support meaningful long-term residency estimates (Fig. 5, Supp.Table 3). The resident sapling proportion varied from about 28 % in the Interior Low Plateau-Shawnee Hills (223D) to 95 % in the Northern Atlantic Coastal Plain (232 A). Among ecosections with measurement histories spanning four inventory cycles, 30 % of the white oak saplings persisted as saplings throughout the measurement window ($\geq$ 15–18 years). A smaller proportion of white oak saplings persisted for at least three inventory cycles (54 %) compared to sugar maple (72 %) and hickory (64 %) but more than yellow-poplar (32 %). The resident sapling proportion for white oak was more similar to the other oaks and red maple (Table 3).

Unsurprisingly, at the ecosection scale, overall recruitment and mortality rates were both strongly correlated with the net population growth rate but in opposing directions (Supp. Figure 2). Removal rate in the sapling layer was not significantly correlated with net population rate. Neither of those three demographic processes (recruitment, mortality, removals) were statistically correlated with sapling outgrowth rates. However, the resident sapling proportion had a strong negative correlation with net population growth rate for saplings (Supp. Figure 3), suggesting that high rates of white oak sapling persistence is not indicative of a sustainable and productive population. The proportion of resident saplings was negatively correlated with recruitment rate, positively correlated with mortality rate, but not significantly correlated with either removal or outgrowth rates.

**Table 3**
Percentage of initial saplings by number of inventory cycles the stem remained present, as a sapling, by species, 2020. Saplings span 2.5 cm – 12.7 cm dbh. Due to state-level variation in inventory timing and onset, 4 cycles was the maximum possible and not possible in some sections.

| SPECIES | Sapling Residence Time | | | Sample size (n) | |
|---|---|---|---|---|---|
| | 2 cycles | 3 cycles | 4 cycles | plots | saplings |
| white oak | 76 % | 54 % | 30 % | 2367 | 4064 |
| black oak | 72 % | 51 % | 28 % | 999 | 1513 |
| n. red oak | 75 % | 53 % | 31 % | 1034 | 1565 |
| hickory | 80 % | 64 % | 38 % | 4180 | 7155 |
| red maple | 78 % | 59 % | 27 % | 6814 | 17,087 |
| sugar maple | 86 % | 72 % | 47 % | 2742 | 5687 |
| yellow-poplar | 57 % | 32 % | 9 % | 2237 | 5845 |

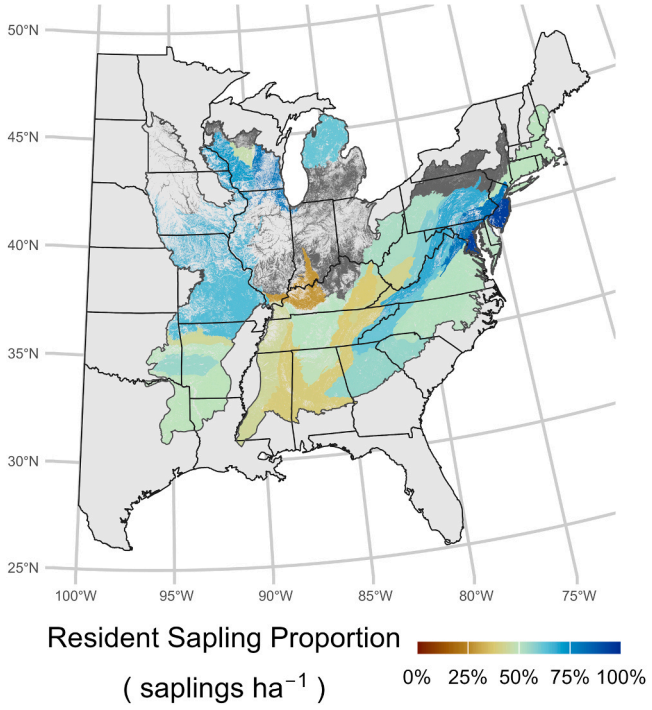


**Fig. 5.** Proportion of white oak saplings (dbh: 2.5 cm - 12.7 cm) that were classified as 'resident saplings' on timberland in the eastern US white oak study region, by ecological section, 2020. Resident saplings were defined as saplings that remained in the sapling size class for at least three FIA inventory cycles, each typically spanning ca. 5–7 years.

## 4. Discussion

Overall, white oak saplings exhibited modestly positive population growth at the scale of the study region, contrasting with the declining trend observed for white oak in larger size classes in the same region (Vickers et al., 2025). However, this apparent stability in the sapling population warrants closer scrutiny. The white oak sapling population is not an abundant one, averaging ca. 27 SPH in 2013. In this context, a 0.5 % annual population growth rate results in an increase of 1 SPH in 7–8 years. Moreover, a sapling outgrowth rate of ca. 1.0 % $yr^{-1}$, as was the case in our study, translates to the development of one small tree per hectare developing from a sapling every four years or so. In contrast, red maple, a species with a far more abundant sapling population (ca. 118 SPH in 2013), exhibited a slightly negative population growth rate (-0.4 % in 2020). Yet even with that decline, the red maple sapling pool remained robust in the time it took white oak saplings to grow from 27 to 28 SPH, with ca. 119 red maple SPH enduring. Further, despite having only about half the sapling outgrowth rate of white oak (0.5 % $yr^{-1}$ vs 0.9 % $yr^{-1}$), red maple will produce a new small tree every 1–2 years, owing to its high sapling abundance. It is evident, then, that a stable white oak sapling population can still fail to ensure long-term canopy replacement when saplings are not abundant and rates of outgrowth into larger size classes are modest (Abrams, 2003; McEwan et al., 2011; Dey, 2014). This highlights the importance of a more nuanced understanding of white oak life history including the residence time, mortality risk, and outgrowth potential in the sapling stage (Harcombe, 1987).

Our findings reinforce the importance of considering sapling-stage dynamics when evaluating white oak sustainability, as this size class is often a bottleneck to sustainable management of oak forests (Nowacki and Abrams, 1992; Schweitzer and Dey, 2011; Hackworth et al., 2020). Although sapling population growth rates across the study region were modestly positive, regional variation was considerable. In this study, 13 ecosections had flat or declining sapling populations and 11 of them were among the 34 sections Vickers et al. (2025) identified as facing imminent sustainability challenges due to recruitment deficits into the small tree size class. Unsurprisingly, the seven sections where white oak sapling densities were too low to support meaningful demographic trend estimates were also among those identified. This strong alignment indicates that problematic sapling dynamics are often a precursor to broader demographic shortfalls in larger size classes. Concomitantly, seedling recruitment declined between 2013 and 2020 across all species examined, including white oak. These concurrent patterns suggest increasing demographic pressure, potentially driven by elevated herbivory (McWilliams et al., 2018), altered disturbance regimes (Nowacki and Abrams, 2008), and compounding effects of invasive species or land-use history (Foster et al., 1998; Thomas-Van Gundy et al., 2014; Alexander et al., 2021).

However, another 10 of the ecosections identified by Vickers et al. (2025) as having recruitment deficits nonetheless showed net growth of at least 1.5 % $yr^{-1}$ in the sapling population. This, combined with modest sapling outgrowth rates across all sections, underscores that demographic challenges for oaks often intensify from seedlings to saplings to small trees (Swaim et al., 2016; Vickers et al., 2019; Beasley et al., 2022). This is exacerbated where historical disturbance regimes, especially fire, have been altered such that contemporary conditions limit white oak development (Hutchinson et al., 2016; Alexander et al., 2021; Woodbridge et al., 2022).

Compared to common upland oak associates such as northern red oak and black oak, white oak demonstrated more favorable sapling dynamics. Northern red oak saplings experienced higher mortality rates, while black oak saplings exhibited a declining sapling population as even higher mortality rates surpassed recruitment. White oak sapling mortality rates more closely resembled those of hickory and sugar maple—species characterized by slower juvenile growth and higher shade tolerance (Rogers, 1990; Rebbeck et al., 2011; Pile Knapp et al., 2021). These outcomes are consistent with known differences in shade tolerance and competitive dynamics under fire-excluded conditions (Johnson et al., 2019; Patterson et al., 2022) and suggest that white oak may be more tolerant of prolonged suppression than other upland oaks (Dillaway et al., 2007; Rebbeck et al., 2011, 2012). However, the proportion of white oaks that became 'resident' saplings was similar to northern red oak and black oak, which was surprising given their higher sapling mortality rates. The resident sapling proportions for yellow-poplar and sugar maple, which represent opposite ends of the shade tolerance gradient among species commonly found across much of the study region, were consistent with expectations based on silvics and sapling mortality rates (Burns and Honkala, 1990).

A central finding of this study was the prevalence of resident white oak saplings across much of the study region. In many ecosections, a substantial proportion of white oak saplings remained in the sapling stage for at least 15 years, and probably longer, given their unknown history before the initial measurements in our dataset. White oak seedlings can persist for decades in a forest understory (Minkler, 1957; Tryon and Powell, 1984; Rentch et al., 2003) and these extended

residence times may buffer against episodic regeneration failure (Warner and Chesson, 1985; Kelly and Bowler, 2002). It may also provide a potential point of silvicultural leverage to improve the odds of successful canopy recruitment (Schlesinger, 1978; Dale and Sonderman, 1984; Vogel et al., 2022).

However, stalled development into larger size classes also presents challenges as prolonged suppression can negatively affect stem form, reduce growth potential, and limit responsiveness to release (Minkler, 1957; McGee and Bivens, 1984; Miller et al., 2011). Moreover, the prevalence of resident saplings, combined with low rates of population growth and outgrowth, suggests that the establishment of saplings may be relatively infrequent, with non-residents often cycling ephemerally in and out of the population without advancing. Thus, persistence alone does not guarantee canopy recruitment, which reinforces the role of timely disturbance or active management to facilitate continued development once saplings are established (Loftis, 2004; Ward, 2013; Dey, 2014).

Our results suggest the importance of regionally calibrated silvicultural strategies (e.g., Brose et al., 2008). Sections where resident saplings were common tended to have less dynamic sapling populations overall. Management of white oak in that circumstance may have more temporal flexibility (Loewenstein et al., 2000; Loewenstein, 2005; Dey et al., 2009), especially if sapling persistence coincides with 'intrinsic accumulator' site characteristics i.e., drier sites and/or those where non-oaks do not readily displace oaks through succession (sensu Johnson et al., 2019, pg 128). In contrast, where sapling populations are declining—due either to elevated mortality or insufficient recruitment, more immediate or intensive actions such as competition control, prescribed fire, or browse mitigation, may be considered depending on site-specific constraints (Craig et al., 2014; Dey et al., 2019; Rudolph et al., 2025). We suggest further research into the stand- and tree-level characteristics associated with the successful advancement of white oak saplings, the accumulation of resident saplings, and the responsiveness of resident saplings to canopy openings.

## 5. Conclusion

Our findings highlight the critical importance of the sapling stage, where bottlenecks can delay or derail canopy recruitment. Although white oak saplings show modestly positive population growth at broad scales, sapling abundance remains low and elevated sapling mortality or inadequate seedling recruitment constrain sustainability in many areas. Out of the 41 ecosections we examined, 13 showed white oak sapling populations in stasis or decline and 7 had too few to support meaningful trend estimates. Eighteen of those ecosections were among those identified in a prior study as facing recruitment deficits into larger size classes. The variability in sapling residence time, growth, and mortality underscores the importance of regionally tailored silvicultural strategies—those that prioritize timely release in dynamic systems and perhaps others that allow for more flexible, opportunistic management in systems with slower dynamics. Longevity in the sapling stage presents both opportunity and risk: without timely intervention, persistent saplings may stagnate and lose the capacity to respond to openings in the canopy.

## Declaration of Competing Interest

The authors have no competing interests to declare.

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During the preparation of this work the lead author used ChatGPT in order to check punctuation, grammar, and readability. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123232.

## Data availability

Data will be made available on request.

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