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Long-term demography and matrix modeling reveal mechanisms of chestnut oak (*Quercus montana*) population persistence through sprouting and decline

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ABSTRACT

The regeneration class within populations of some canopy tree species can persist within a forest understory for decades, existing as a single dominant stem or replacing dominant stems via sprouting. Trees with the ability to sprout, including oaks, can use multiple strategies to persist in the understory, including long-term persistence and "shrinking" in size as a result of the ability to produce sprouts. This study is the first to examine the long-term effects of sprouting in a population of oaks (Quercus) across all life history stages. We established a 15-year study of the fine-scale demographics in a stand of chestnut oaks (Quercus montana) on the Cumberland Plateau, which enabled us to examine the role of sexual reproduction and sprouting on population persistence. Using a size-class distribution matrix model parameterized from the long-term demography, we project the population 50 years into the future, identifying size classes that represent population bottlenecks. We compare size-class distribution patterns to two other chestnut oak populations in the region. We find that midstory individuals are "shrinking" through stem replacement or dying over time, and it is very rare for an individual to increase in size class. Sprouting (both existence of sprouts and number of sprouts) was associated with the death of a genetic individual. Our matrix model indicated a slow decline of the population over the next 50 years, a pattern reflected in the regional patterns of chestnut oaks. We suggest that the chestnut oaks studied may represent a "remnant population" which slowly declines until either local extinction or the existence of favorable environmental conditions.

1. Introduction

The production of secondary stems, known as sprouting, is a common phenomenon in temperate flowering trees (Bond and Midgley, 2001; Del Tredici, 2001). Sprouts may manifest from the tree collar, lignotubers or rhizomes, roots, or opportunistic branch sprouts (Del Tredici, 2001). Sprouting in trees is generally thought to be a response to tree damage or disturbance (Bellingham and Sparrow, 2000; Plotkin et al, 2013; Aubin et al, 2016). Much of the literature on sprouting concerns stump sprouts and regrowth from logging (e.g. Matula et al 2019), but here we cover the phenomenon of sprouting in the absence of direct anthropogenic disturbance. While understory seedlings and saplings are more likely to sprout than adult trees, over 40% of mature temperate trees can produce collar sprouts, which are sprouts from the base of the trunk. The ability of seedlings and saplings to sprout may allow an individual to survive the stress of shading and competition until environmental conditions improve (Del Tredici, 2001).

Sprouting can allow sapling-sized individuals in a tree population to persist for decades in a closed canopy forest, until they are either released through canopy disturbance or die (Bond and Midgley, 2001). Upon viewing a closed canopy forest with many persistent repressed saplings and seedling-sized individuals, an observer may mistake the high abundance of understory individuals as an indication that the forest is undergoing continuous recruitment and canopy replacement, as described by an inverse-J distribution. This distribution is characterized by a high number of small sized individuals and a low number of very large reproductive individuals (Meyer, 1952).

Though understory individuals may be much more abundant than

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canopy trees, in the case of sprouting trees, these understory individuals may represent numerous cohorts of decades-old individuals that are persisting in the understory rather than growing into the canopy (Del Tredici, 2001; Tryon and Powell, 1984). Among studies of temperate trees, between 58 and 78% of individuals of seedling size are actually resprouts (Liming and Johnston, 1944; Merz and Boyce, 1956; Ward, 1966). These resprouts are individuals where the primary stem died, but generated a replacement stem from the same rootstock, either before the death of the dominant stem or immediately afterwards. Therefore, "old" saplings may exhibit two strategies for persistence based on their species life history (as described in Closset-Kopp et al., 2007). Shade-tolerant stems living in light-limited conditions may persist at the same small size for decades. On the other hand, individuals may "shrink" through sprouting to better survive the current environment. In this case, the dominant stem dies, leaving behind shorter stem sprouts thereby "shrinking" in size. This ability to persist as a result of multiple surviving stems or resprouting has been suggested to delay the death of genetic individuals, resulting in population structural consequences including a persistent understory (Plotkin et al, 2013; Del Tredici, 2001; Paciorek et al., 2000). Certain species (such as Prunus serotina) have been demonstrated to exhibit both strategies in forests-long-term persistence and "shrinking" as a result of the ability to produce sprouts (Closset-Kopp et al., 2007).

To describe a tree population with such a complex life history-both the ability to stay one size for perpetuity, and the ability to shrink-we turn to matrix modeling. Matrix modeling is both a simple and powerful tool to describe the demographic transitions of individuals through size classes (Caswell, 2001; Sebert-Cuvillier et al., 2007). This approach has been used in other sprouting tree species, including black cherry (P. serotina), Quercus eduardii, and Quercus potosina to project population growth and the impact of sprouting vs sexual reproduction (Alfonso-Corrado et al., 2007; Sebert-Cuvillier et al., 2007). Of interest to us are oak species (Quercus), which have the potential to exhibit both the ability to persist at a small size and the ability to produce sprouts, but are widely experiencing regeneration failure in the Eastern Deciduous Forest of North America (Abrams, 1992; Del Tredici, 2001; Tyler et al., 2006). Using a fine-scale demographic study combined with a modeling approach, we investigate the future of a population of persistent oaks that have little to no recruitment upward from seedling to canopy and subcanopy trees.

This study examines chestnut oak (Quercus montana), a xeric ridgeloving white oak native to the eastern United States (Nixon and Muller, 1997). Like other species of oaks in eastern forests, chestnut oaks are declining in dominance (Mikan et al., 1994). Given the oak's disturbance-tolerant physiology and life strategies, patterns of regeneration failure have been linked to the history of fire suppression and mesophication in the Eastern United States (Abrams, 1992). Oaks have been characterized as fire-adapted given their investment in underground resources and ability to produce sprouts in response to disturbance (Abrams, 2003; Green et al., 2010). It has been suggested that oaks require disturbances, including fire, to maintain their dominance in temperate forests (Abrams, 2003; Foster et al., 2002). Chestnut oak, like other white oak species, is a prolific producer of vegetative sprouts (Del Tredici, 2001), which may promote population persistence in the face of widespread environmental changes such as fire suppression (Heggenstaller et al. 2012).

Given the long generation times characteristic of oak populations, individuals may persist through unfavorable environmental conditions with stored resources, which may be facilitated by sprouting. While there are multiple studies on sprouting in chestnut oaks after clearcutting and other human disturbances (Sands and Abrams, 2009; Tworkoski et al., 1990; Wendel, 1975), little is known about natural patterns and consequences of sprouting in a mature or old growth forests (but see Powell and Tryon, 1979).

We aim to answer the following questions regarding the population dynamics of chestnut oak in the upland forests of the Cumberland Plateau in SE Tennessee: (1) what is the probability that an acorn will become an adult tree?; (2) what role does sprouting play in population persistence; (3) based on current demographic trends, will this population persist into the future?; (4) are there landscape-level trends of chestnut oak decline? To answer these questions, we use a combination of long-term field data to investigate the fine-scale demography of chestnut oak over 15 years, modeling to project the population 50 years into the future, and regional long-term data to examine landscape-scale patterns of chestnut oak size class-distributions over 37 years. This study is the first to examine the long-term effects of sprouting on a population of oaks across all life history stages and will provide greater resolution to size-class transition bottlenecks.

2. Materials and methods

2.1. Fine-scale demographics

We studied chestnut oaks in a one ha (100×100 m) plot of forest on the southwestern edge of the Cumberland Plateau, Tennessee, USA (35.219, -85.962; 585 masl) on the campus of the University of the South. The plot was located in an upland forest stand that was chosen as typical of mixed-oak communities on the southern Cumberland Plateau as part of a long-term study of plateau forest dynamics (Evans et al., 2019; Reid et al., 2008). Chestnut oak is the dominant tree in the plot represented by 60% of all canopy individuals, followed in dominance by white oak (Q. alba) (15%), scarlet oak (Q. coccinea) (9%), and hickory (Carya spp.) (6%). The subcanopy is composed of sourwood (Oxydendrum arboreum), sassafras (Sassafras albidum), blackgum (Nyssa sylvatica), and red maple (Acer rubrum) (Evans et al., 2019). The soils in the study area are well-drained and characteristic of the southern Cumberland Plateau composed of Hartsells fine sandy loam and Muskingum stony fine sandy loam (Soil Survey Staff, 2019). This area is known for acidic and nutrient-poor thin soils (pH 4.5 \pm 0.3) (Evans et al., 2019). The highest average temperatures are recorded in July and August (28.0 °C), with the lowest average temperature in January (-1.4 °C). The average annual precipitation is 155 cm, with most precipitation between December and March (Evans et al., 2016a). The forest is considered old second-growth (Evans et al. 2019). According to University forest management and stand inventory records, the study site experienced very limited selective logging for Quercus alba in 1952, and for Quercus coccinea, Nyssa sylvatica and Carya spp in 1954, but has received no timber harvesting since that time.

Chestnut oak individuals were tracked in the one ha study plot yearly from 2000 to 2015. For the purpose of sampling, the plot was divided into twenty-five 20 \times 20 m subplots. Each individual \geq 0.5 m tall was tagged and classified by height using the following labeling system: B (0.5–1 m), C (1–1.5 m), D (1.5–2 m), E (2–4 m), F (subcanopy – above 4 m tall, crown not receiving direct sunlight), and G (canopy – crown in direct sunlight and not overtopped). If a tracked individual became an A, we continued to track it throughout the duration of the study.

The presence and abundance of sprouts were characterized for each tagged chestnut oak individual (≥ 0.5 m tall) in the one ha fine-scale demography plot (Fig. 1). The presence and number of sprouts—stems connected to the leading stem—was measured on a yearly basis. Further, stem replacement (whether there was change in the tallest stem due to death or overtopping) and damage to the dominant stem was recorded yearly. Damage categories included top snap, bottom snap, frost, and deer browse. We used logistic regression to examine whether there was a relationship between sprouting or number of sprouts and the death of a genetic individual.

Eight 1 m diameter circle plots were established in each 20×20 m subplot of the ha (n = 200 circle plots) in 2006 and surveyed in the years 2006–2015 to characterize ha-wide acorn, seedling, A, and B abundance (Fig. 2). In this study, seedlings are <1 year old chestnut oaks, which is evident by attachment to an acorn. Seedlings, A-sized individuals and B-



Fig. 1. Two chestnut oak individuals denoted by tag number with multiple shoots from the root collar. The dominant stem is the tallest stem.



100 meters

Fig. 2. Schematic of 1 ha plot design (100×100 m) with 25 subplots (20×20 m). Inset shows the random distribution of circle plots (n = 200) within a subplot.

sized individuals were not measured in 2011 in the circle plots. A subset of the data was measured in 2012–2013 and scaled up based on the proportion of the plots the sample represented for each year independently. In 2012, 6 of the 25 subplots were measured, representing 24% of all circle plots. In 2013, 4 of the 25 subplots were measured, representing 16% of all circle plots.

2.2. Population matrix model

Using the mean yearly transition probabilities for the size classes over 15 years, we parameterized a discrete and size-classified matrix model using the "popbio" package in R (Stubben and Milligan, 2007).

Reproduction per G-sized individual and transition probability from the A to B size class were estimated using the circle plot census data. We estimated the reproduction per individual G using the recorded number of seedlings <1 year old in circle plots scaled up to a hectare level (2656 on average) and divided by the starting number of G-sized individuals. This calculation estimated that, on average, each G-sized individual produced 23 new A-sized individuals each year. The total mean number of A-sized individuals was scaled to the hectare level based on the circle plots, resulting in a total of 27,125 individuals. The yearly A-sized individual survival rate was estimated to be 85%, based on a past study of chestnut oak survival rates in a closed forest on the Cumberland Plateau (Green et al., 2010). We set the A to B size class transition probability as 0.001%, which reflected the patterns recorded from the circle plots. This probability may be an overestimate; it is important to note that the majority of A to B transitions detected in circle plots were of individuals that were first recorded as B-sized or larger that subsequently shrank to A-size before growing again.

We assume that individuals cannot increase more than two size classes per year. We used the following matrix equation:

$$n_{t+1} = An_t$$

where n_t is an initial population at year t of different size classes and A is a matrix of transition probabilities; the output is the population of different size classes at year t + 1. The population was simulated 50 years from the year 2015, and lambda was calculated. The confidence interval for lambda was calculated using the Delta Method (Bowles et al., 2015; Skalski et al., 2007). A life cycle diagram was generated to depict all possible demographic transitions for chestnut oaks.

The assumptions for this model include no environmental



Fig. 3. Plot locations within Tennessee (A) and along the Cumberland Plateau (B). Detail of the fine-scale demographic plot (C). Imagery: Google, Landsat / Copernicus.



Fig. 4. The density of acorns, seedlings, A-sized and B-sized individuals scaled to ha from 2006 to 2015 using circle plot data. There is a gap in the data in 2011. Seed rain is irregular as is typical for a masting species like chestnut oak. The density of seedlings and A-sized individuals is steady from 2006 to 2010 and variable between 2012 and 2015. The density of B-sized individuals remains low throughout the study period.

stochasticity over the 50 years including seed rain such that related parameters were averaged over the study period, and the same transition probabilities were used for each timestep.

2.3. Landscape-scale patterns of demography

To examine the long-term landscape-level patterns of chestnut oak abundance, we examined the size-class structure of chestnut oaks in two mature mixed-hardwood forests in central Tennessee (Fig. 3). All individuals 3 cm DBH and larger in 5 ha in Franklin State Forest (Sherwood, TN: 35.095, -85.853, 585 masl) and 3 ha in Fall Creek Falls State Park (Pikeville, TN: 35.667, -85.361; 496 masl) were measured in the

Table 1

Analysis of sprouting of chestnut oak individuals alive in 2015 based on size class (B, C, D, E, F, G). The 95% confidence interval of a parameter is indicated in parentheses. Mean stem sequence indicates whether there was a shift in the dominant stem, with 1 representing the same dominant stem and 2 representing one instance of stem replacement. The mean stem sequence and number of sprouts are derived from individuals alive in 2015, whereas the percent that ever sprouted is derived from sprouting data on all individuals from 2000 to 2015.

Size l	Mean stem	Mean # sprouts	Percent that ever sprouted (2000–2015)
class s	sequence (2015)	(2015)	
B C D E F C	1.35 (1.27–1.44) 1.64 (1.35–1.93) 1.57 (1.08–2.07) 1.18 (0.91–1.45) 1	0.58 (0.37–0.79) 2.07 (0.23–3.92) 4.43 (–0.31–9.17) 3.18 (1.22–5.15) 1.32 (0.63–2.01) 0.42 (0.12, 0.70)	37% 86% 100% 91% 62%

years 1976/1978 and 2015/2016. These two sites were chosen as representative of Cumberland Plateau forests as part of a Tennessee Valley Authority watershed comparison study (Ramseur and Kelly, 1981). Both forests are mixed oak-hickory, with chestnut oaks dominating ridges. Chestnut oak is more common in Franklin State Forest than Fall Creek Falls State Park.

Because chestnut oak measurements at Franklin State Forest and Fall Creek Falls State Park were tree diameters rather than size classes, we used to following method to reclassify the data. Using tree cm DBH data collected from the fine-scale demography plot from 2001 to 2003, 2008, and 2013 as a guide, we developed approximate intervals for the range of diameters represented by the following size classes: E (mean cm DBH: 2.86, standard deviation = 1.92, range = 1–11), F (mean cm DBH: 10.58, standard deviation = 4.97, range = 1.1–34.8), and G (mean cm DBH: 34.1, standard deviation = 11.1, range = 10–64.8). We assigned the following bins: E 3–5 cm DBH, F 5–25 cm DBH, G 25+ cm DBH. We reclassified diameter-based field data at Franklin State Forest and Fall Creek Falls into these size classes to examine changes in the size structure of these two forests from the 1970s to 2010s.

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Table 2

Total number of years (0, 1–3, 4–6, 7+) from 2000 to 2015 that damage was detected on chestnut oak individuals (856 total) compared with the number of individuals that had at least 1 sprout and number that died during this interval.

Years of damage	# individuals in each damage	# at least 1	# died
detected	category	sprout	
0	282 (33%)	110 (39%)	17 (6%)
1–3	417 (48%)	250 (60%)	129
4–6	124 (15%)	110 (89%)	(31%) 40
7+	33 (4%)	32 (97%)	(32%) 7 (21%)

3. Results

3.1. Fine-scale demographics

From 2000 to 2015, we tracked all chestnut oak individuals (≥ 0.5 m tall) in 1 ha, totaling 858 genetic individuals. The total number of live chestnut oak individuals in the study plot increased from 456 to 511 (+12%). The number of individuals in the smallest size class measured (B) increased, and the number of individuals in all other size classes (C, D, E, F, G) decreased.

Of the 456 individuals alive in 2000, by 2015, 49.8% were the same size class, 17.5% were smaller, 5.0% were bigger, and 27.6% were dead. It is possible for an individual to be "smaller" due to either damage and dieback of the dominant stem, or death of the dominant stem with sprouts present.

When we examined the 4 individuals that grew 2 or more size classes over the course of the study, we found that all individuals had sprouted during the study period, and 75% had experienced replacement of the dominant stem once (the tallest stem died or was surpassed by a sprout).

3.2. Circle plots for acorns, seedlings, A-sized, and B-sized individuals

Consistent with the masting nature of chestnut oak, we found that 2008, 2010, 2012, and 2014 were mast years, whereas 2006 and 2009 were low seed rain years. No acorns were detected in 2007, 2011, 2013, or 2015. Scaled up from the 200 circle plots to one ha, there was a yearly mean of 3438 seedlings, 24,625 A-sized individuals, and 125 B-sized individuals (Fig. 4).

Not every mast year translated into elevated seedling densities. For instance, 2008 was a mast year, but the number of seedlings recorded in 2009 was near 0. The 2012 seed rain resulted in the largest peak in seedlings. The A size class was maintained at a stable state from 2006 to

2010 and fluctuated from 2012 to 2015.

3.3. Sprouting, stem replacement, and stem damage within study site

Of the 858 unique chestnut oak individuals measured in the hectare, 502 (59%) sprouted—produced stems in addition to a dominant stem—at least once within the 15-year study. As sprouting and stem replacement were only measured beginning in 2000, it is certain that individuals have a more extensive history of sprouting and stem replacement. Stem replacement refers to the dominant stem either dying with the presence of sprouts, or a sprout growing taller and thereby overtaking the dominant stem. For individuals alive in 2015, 428 (62%) had the same dominant stem, 192 (28%) had undergone stem replacement once, 49 (7%) had undergone stem replacement twice, 13 (2%) three times, and 1 (0.2%) four times.

We examined sprouting patterns by size class in 2015 and found that the D, E, and C size class had the most sprouts on average, whereas G and B has the fewest on average (Table 1). Similar patterns were found in the percent that had sprouted at least once from 2000 to 2015. All D-sized individuals had sprouts over the study period. The mean stem sequence indicated that cycling stems was a common method of persistence in the smaller size classes. Sprouts can exist without the replacement of the dominant stem.

We also examine whether there is an association between dominant stem damage, sprouting, and death (Table 2). In general, as more years of damage were detected, there was a higher likelihood of sprouting and death when compared to individuals with no damage. This indicates that damage, sprouting, and death are linked, although visible damage does not always precede sprouting or death.

The logistic regression of individuals that died (binary) vs individuals that sprouted (binary) indicated that, sprouting, which we earlier showed was associated with tree damage, was associated with tree death (chisquare = 231.95; p < 0.001). We also fit a logistic regression of individuals that died (binary) and maximum # of sprouts (numeric) which also indicated that the more sprouts an individual had, the greater its likelihood of death (chisquare = 27.28; p < 0.001).

The size-class structure in the ha over the years 2000, 2005, 2010, and 2015 (Fig. 5A) shows a decline in midstory size classes C, D, E, and increase in the number of B-sized individuals. To examine the role of stem replacement in population persistence, we ran an alternate scenario that excluded the ability to replace the dominant stem through sprouting. Therefore, any individual that experienced death or overtopping of the dominant stem by a sprout was classified as dead. In the absence of the ability to replace stems, we find that the midstory



Fig. 5. The number of chestnut oaks in each size class from 2000 to 2015 in the 1 ha study plot with natural stem replacement (A), or without stem replacement (B).

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declines more rapidly (Fig. 5B). D-sized individuals are eliminated from the population by 2015. Canopy and subcanopy trees (F, G size classes) are largely unaffected, as stem replacement in these size classes is an extremely rare event. The B size class experiences a slight decline in 2005 and 2010 when the ability to replace the dominant stem is excluded, but the pulse of new B-sized individuals causes an increase in the number of individuals in 2015.

3.4. Population matrix model

We developed a discrete and size-classified matrix model and life cycle diagram to describe the population of chestnut oaks and all possible transitions (Table 3) (Fig. 6). Our starting population lambda was 0.99 (95% Confidence interval: 0.991–0.999). We simulated the population from the year 2015–2065 and found a temporary increase in the number of C-sized individuals, followed by a decline. This increase is the result of individuals that were formerly taller than C "shrinking," a natural phenomenon that occurs either through damage or stem replacement coupled with B-sized individuals growing. Over the course of the 50-year simulation, the abundance of all size classes declined (Fig. 7). The elasticity, a measure of the matrix element that contributes most to population growth, indicated that surviving G-sized individuals were the most important in maintaining population growth (elasticity for G remaining a G element = 0.97).

To visualize the model results, we compared the 2000, 2015, and model-predicted 2065 size class distributions (Fig. 8). The model follows the trend of decreases in the C, D, E, F, and G size classes. The model also predicts that the number of individuals in the A and B size-classes will decline over the course of the 50 years.

3.5. Landscape-scale patterns of demography

We found that chestnut oaks are declining across the landscape, as indicated by the size class distribution from the 1970s to 2010s in Franklin State Forest and Fall Creek Falls. The total number of chestnut oaks in the E, F, and G-size class per ha falls from 144 to 63 in Franklin State Forest and 49 to 40 in Fall Creek Falls (Fig. 9). We observed similar general patterns between the two forests over time. In 1978 Franklin State Forest, there were more subcanopy trees than canopy trees. However, by 2015, the E size class (subcanopy) declined by 96% percent (27–1), and the G size class (canopy) grew by 100% percent (16–32). This indicates that individuals grew into canopy trees over the studied time period but were not replaced in the understory. In 1976 Fall Creek Falls, the smallest size classes made up the largest proportion of individuals (though at a smaller scale). By 2016, the number of canopy chestnut oaks had increased, while the number of midstory individuals decreased.

4. Discussion

We set out to track the fine-scale demography of chestnut oaks from acorn to canopy tree over 15 years. We found that, while trees produced seedlings through masting of acorns, the likelihood of a seedling surviving and growing to become a sapling was extremely low. Understory individuals increased in density, while the midstory contracted and subcanopy/canopy layer remained stable. The increase in the density of understory individuals resulted from midstory individuals "shrinking" in size class through stem replacement and smaller individuals growing into the B-size class. These patterns indicate that the chestnut oak population is not successfully producing new genetic individuals that

Table 3

Mean transition probabilities from 2000 to 2015. The standard error is indicated in parentheses. An asterisk (*) indicates that the probability was estimated based on circle plot data. A dagger (†) indicates the probability is based on Green et al. 2010. The model included G reproduction of A individuals, with an estimated 23 new A individuals produced each year per G individual.

Ending size after 1 year (n2)									
		А	В	С	D	Е	F	G	
Starting size (n1)	Α	0.85†	0.001*						
	В	0.013 (0.011)	0.81 (0.014)	0.02 (0.006)					
	С	0.06 (0.016)	0.09 (0.016)	0.76 (0.023)	0.07 (0.012)				
	D	0.06 (0.016)	0.03 (0.01)	0.08 (0.026)	0.76 (0.039)	0.06 (0.018)			
	Е	0.006 (0.018)	0.03 (0.009)	0.01 (0.004)	0.02 (0.008)	0.87 (0.022)	0.01 (0.004)		
	F	0.001 (0.002)	0.004 (0.002)	0.001 (0.001)		0.01 (0.002)	0.97 (0.005)	0.004 (0.001)	
	G						0.004 (0.001)	0.99 (0.002)	



Fig. 6. Chestnut oak life cycle diagram with transition probabilities. The arrows in the life cycle diagram indicate the probability of moving up or down size classes remaining the same size class, or dying. F_n is the number of individuals in the n size class. $P_{n1,n2}$ is the probability that an n1 size class individual becomes an n2 size class individual in one time step (1 year). The fecundity of G-sized individuals is f_g .



Fig. 7. Simulation results of the chestnut oak matrix model from 2015 to 2065 (50 years) indicating the total number of individuals in each size class predicted per ha. Note that the y-axis differs between size classes.

grow into the midstory. Rather, the increase in total number of individuals from 2000 to 2015 is a result of trees that have been present in the understory for years—possibly for decades—growing into the B size class (Liming and Johnston, 1944; Merz and Boyce, 1956; Ward, 1966; Heggenstaller et al., 2012) and which may have formerly been taller before shrinking in size. Given these growth strategies, it is clear that the age of genetic individuals in the stand is much older than the age of the current dominant stem (Heggenstaller et al., 2012; Closset-Kopp et al., 2007). This reserve of surviving "old" small individuals may eventually replace the canopy trees in the population, rather than new seedlings, resulting in a less genetically dynamic population over time.

Midstory decline, seen both in the one ha study plot and the longterm landscape studies, may be partly an artifact of anthropogenic disturbances which led to chestnut oak recruitment. In the 20th century, the removal of other species as a result of both selective logging and invasive pathogens may have played a key role in allowing chestnut oak to increase in dominance within Plateau upland forest communities. American chestnut (*Castanea dentata*) was once a dominant tree on ridgetops, but populations were decimated in the early 1900s by both logging and chestnut blight (Hepting, 1974), leading to the dominance of chestnut oaks in these sites (Keever, 1953; Korstian and Stickel, 1927; Mowbray and Oosting, 1968; Woods and Shanks, 1959). Similarly, dogwood (*Cornus florida*) was more abundant in the midstory on the Cumberland Plateau, but declined as a result of dogwood anthracnose (Hiers and Evans, 1997). As these tree species from both the midstory and canopy of Plateau forests declined, chestnut oak individuals increased in abundance and recruited upwards until canopy closure. All upland forests are recovering from some sort of disturbance, both



Fig. 8. The number of individual chestnut oaks in each size class in the year 2000, 2015, and 2065 (as predicted by the matrix model) in the study plot. The A-sized individuals are scaled estimates from circle plots, and data was not collected for this size-class in 2000. The size classes are defined as follows: A (<0.5 m), B (0.5–1 m), C (1–1.5 m), D (1.5–2 m), E (2–4 m), F (subcanopy), and G (canopy).



Fig. 9. Size class distributions of chestnut oaks scaled per ha at Fall Creek Falls (A) and Franklin State Forest (B). Note the difference in scale.

natural and anthropogenic, and they are very slow to respond. Evans et al. (2019) found that communities on the Cumberland Plateau, including those unaffected by logging, are shifting in composition and losing species, indicating that they may not be resilient in the face of change.

The second study objective was to examine the role of sprouting in chestnut oak persistence-specifically whether sprouting was associated with tree damage or death. It has been hypothesized that sprouting evolved as a response to disturbance, allowing a tree to persist despite damage to the dominant stem (Bellingham and Sparrow, 2000; Bond and Midgley, 2001; Del Tredici, 2001). Our results supported this idea, with sprouting more likely to occur in trees with recorded damage. The average size class of chestnut oaks in the population shrank in size, and this shrinking was associated with damage, including deer browse, to the dominant stem. As midstory chestnut oak individuals shifted to the B size-class over time, they became susceptible to deer browse in an area where deer overpopulation has had a documented impact on tree sapling density (Evans et al., 2016b). In the damage trends we recorded, we found a sharp peak in deer browse in 2013, affecting 52% of all B and Csized individuals. In other years, the percentage of chestnut oak B and Csized individuals affected by deer browse ranged from 0 to 19%. Deer are increasingly being implicated as a factor among multiple drivers leading to oak regeneration failure, with browsing pressure decreasing the chance of understory trees growing into the midstory (Marquis et al., 1976; McEwan et al., 2011; Nuttle et al., 2013; Petersson et al., 2019). Further, the vegetative sprout strategy manifested by chestnut oak in the understory may fail in the face of deer browse if individuals are forced to remain within the browse zone over time (see Royo et al. 2016). Unsurprisingly, trees that experienced more damage were also more likely to die, indicating that sprouting may be a short-term mechanism of persistence before death (a similar result found in the tropics by Paciorek et al., 2000). Despite its association with tree death, sprouting remains crucial to the persistence of understory and midstory chestnut oaks in this harsh, dry and nutrient poor landscape.

The matrix model showed two main patterns: a short-term increase in C-sized individuals, and then general decline in all size classes. A similar matrix model study in invasive black cherry (*P. serotina*) found that the ability to resprout was not a major driver of population dynamics, but did lead to underestimates of tree age and growth (Paciorek et al., 2000; Sebert-Cuvillier et al., 2007). The long-term ecological consequences of the chestnut oak population structure will lead to a slow but eventual shrinking of the population. At face value, one might

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conclude this population of chestnut oaks is a "healthy" population with the possibility of canopy replacement given its "inverse J" shape (Haq et al., 2019; Meyer, 1952). This assumes that some proportion of understory trees will become midstory trees, and a smaller proportion of midstory trees will become canopy trees. Our data contradicts the idealized model of tree population structure, as we do not detect growth through size classes despite the "healthy"-appearing size structure. Instead, we find evidence for size class dynamics that do not reflect the typical progression of continuous upward recruitment given the ability to sprout and shrink in size. However, this alone is not evidence of regeneration failure—as the survival rates of canopy trees is high, and acorn production is not a limiting factor, successful recruitment may occur in pulses or through the growth of single rare individuals into the canopy (Tyler et al., 2006).

Finally, we compared the size-structure of chestnut oaks in one ha to a broader dataset of chestnut oaks across Tennessee from the 1970s to 2010s. While we have no information on the fine-scale demography of these larger populations, we detected similar size structure patterns over this longer time-scale. This pattern of a drastically declining midstory reflects that found by Mikan et al. (1994) in the Pennsylvania Piedmont. The authors suggest that chestnut oaks in the canopy will soon be replaced by tolerant species such as red maple (Acer rubrum), as maples were dominant in the understory and midstory. Further, oaks are thought of as having negative neighborhood effects - less likely to replace themselves after disturbance (Frelich and Reich, 1999). A study of community changes over 19 years on the southern Cumberland Plateau found some reshuffling in species dominance and declines in certain midstory species, especially oaks including chestnut oak. Red maple was one of the most abundant understory and midstory species, showing a pattern of increasing dominance over the 19 years (Evans et al., 2019). It is possible that a large gap or fire may release the persistent understory into the canopy (Abrams, 2003; Signell and Abrams, 2006), but the canopy tree deaths detected in this 15 year study did not result in recruitment hotspots. It should also be noted that fire does not significantly improve chestnut oak seedling establishment and growth in the understory (Royse et al., 2010), a key bottleneck we found to recruiting new genetic individuals.

In this study, we documented the change in population structure of chestnut oaks over 15 years in the presence of small natural disturbances including canopy tree death. Over the course of the study, we detected 4 chestnut oak canopy individual deaths and 2 deaths of other canopy species. Even with these canopy gaps, we did not observe recruitment by chestnut oak seedlings or saplings into these gaps. Over the study period, the abundance of genetic individuals in the B size class (understory) increased, while the abundance of midstory and canopy individuals decreased, a pattern also shown in the landscape study. Chestnut oaks and many other temperate tree species are adapted to natural disturbance regimes which are no longer maintained (Abrams, 1992; Mikan et al., 1994; Nowacki and Abrams, 1997; Signell and Abrams, 2006). The combined suppression of disturbance and changing climate of the southern Cumberland Plateau may contribute to the changing size class distribution in chestnut oaks. As this species occupies dry, rocky ridges, drought spikes and drying trends may have drastic negative effects on the survival of individuals or competitors. An alternative explanation to regeneration failure in these populations is that the processes that lead to chestnut oak regeneration, and particularly the role of sprouting, occur at a time scale outside of the scope of this study. We documented a tree population that is treading in place with the potential for a very slow eventual decline - very few new genetic individuals are being recruited into the population, and trees are dying or getting smaller over time. Using the model projections, we determined that the maximum percent of new genetic individuals in the G-size class would be 10% after 30 years – indicating that the reproductive individuals in the canopy will continue to be dominated by the same genetic individuals. These populations of chestnut oaks may represent "remnant populations," which slowly decline in the face of unfavorable conditions until extinction

(Eriksson, 2000, 1996). The canopy trees present ascended in a different century and were likely adapted to environmental conditions and disturbance regimes that no longer exist. In the face of changing regimes, it is unknown whether this strategy of persisting through asexual means will result in the long-term persistence of chestnut oaks on the Cumberland Plateau.

CRediT authorship contribution statement

Callie A. Oldfield: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing - original draft, Visualization. Jonathan P. Evans: Conceptualization, Methodology, Investigation, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition. Sarah C. Oldfield: Software, Formal analysis, Writing - review & editing, Visualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

JE conceived the ideas and designed methodology; JE and CO collected the data; CO and SO analysed the data; CO led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data archiving

The fine-scale demography dataset has been archived and is accessible at: Oldfield, Callie; Evans, Jon; Oldfield, Sarah (2020), "Long-term Chestnut Oak (Quercus montana) demography", Mendeley Data, V1, doi: 10.17632/sffnwf2d23.1.

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