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Community Analyses of Urban and Suburban Forested Natural Areas in Shelby County, Tennessee, Reveal Old-Growth Attributes

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ABSTRACT

European colonization of eastern North America resulted in widespread loss of old-growth eastern deciduous forest, altering native plant and animal biodiversity. Though recent studies have revealed remnant old-growth forests, it remains uncertain how widespread forests with old growth characteristics are throughout the southeastern United States. This is especially true near urban centers where historical disturbance was likely most pronounced. Yet, small patches of forest with old growth characteristics persist as urban or suburban forested natural areas where they are important reservoirs of biodiversity and provide crucial ecosystem services. Here, we investigate several upland deciduous forest communities in Shelby County, Tennessee, to assess whether urban and suburban forested natural areas exhibit species assemblage and structural features consistent with commonly-accepted criteria for old-growth forest, and how they may have been shaped by diverse land use histories across an urban to suburban gradient. We found community composition broadly similar between urban and suburban forested natural areas, but also significant differences in species assemblage based on tree densities and basal areas, likely due to unique land use and disturbance histories. Forests also meet some, but not all, commonly employed criteria for western and mixed mesophytic old-growth forest, including individual tree ages >200 years, consistent with ongoing successional trajectories toward old-growth forest. Nevertheless, the urban and suburban forested natural areas of southwest Tennessee harbor important plant biodiversity in a region that has experienced intensive post-colonial anthropogenic disturbance and likely warrant continued thoughtful management and restoration to attain "new" old-growth status.

Key words: community structure, old growth, tree cores, upland forest, urban forested natural area.

INTRODUCTION

Old-growth forests, comprising intact, structurally complex stands of trees that may also be old, are accepted as being important reservoirs of biodiversity and crucial components of healthy forested landscapes (Braun 1950; Martin 1992; Davis 1996; Spies 2004; McGee 2018). Though "old-growth forest" is an ambiguous descriptor with varied criteria, such forests generally comprise a diversity of microhabitats characterized by uneven age distributions with vertically complex canopy structure, common standing dead trees ("snags"), and generally abundant coarse woody debris (Davis 1996; Franklin and Van Pelt 2004; Burrascano et al. 2013). These forests are also important conservation

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targets as they represent reservoirs of flowering and non-flowering plant, bird, invertebrate, lichen, and fungal biodiversity, as well as providing ecosystem services such as carbon sequestration, aquifer recharge, nutrient cycling, air purification, and aesthetic value (Runkle 1991; Martin 1992; Haney and Schaadt 1996; Trombulak 1996; Greenberg et al. 1997; Frank et al. 2009).

Drastic reductions in forest cover throughout eastern North America until the mid-1900s has been attributed, at least in part, to the forced removal of indigenous populations and the transition from pre-colonial land-use practices (e.g., relatively low intensity agriculture and timber harvest, intermittent fires) to post-European colonization land-uses involving intensive timber harvesting, conversion to intensive agriculture, and disruptions of wildfire regimes (e.g., cessation of low-intensity fires, suppression, etc.; Delcourt and Delcourt 1987; Hanberry et al. 2020). The large-scale alterations to forests of eastern North America led to the widely held opinion that old-growth forests were functionally extirpated from eastern North America (Davis 1996). However, recent studies have revealed the presence of remnant patches of forest that satisfy most operational definitions for “old-growth forest” representing some elements of pre-colonization forest communities (e.g., Stahle and Chaney 1994; Dunwiddie et al. 1996; Foster et al. 1996; Frelich and Reich 1996; Davis 2003; Diggins and Kershner 2005; Diggins 2013).

Although pre-European colonization forests were largely extirpated over the last ~400 years, at least some elements (e.g., old and ancient trees, complex canopy structure, high biodiversity) of these forest communities persist, and are likely contributing to the recovery of eastern deciduous forests over the last 50–75 years (Keeton et al. 2018). However, the recovery of forests is also likely due to a diversity of communities proceeding along various successional trajectories since the cessation of widespread agricultural and timbering activities in the mid1900s. Thus, many eastern forests may now exhibit structural and species composition attributes of old-growth forest (i.e., “new” old growth), but remain relatively underappreciated for their contributions to ecosystem health.

Most field surveys identifying or characterizing eastern old-growth forest communities have focused on the northeastern United States and parts of the Appalachian Mountains (e.g., Runkle 1991; Davis 1996), with comparatively little effort throughout parts of the southeastern United States (but see Woodbridge et al. 2025). Thus, it remains uncertain how widespread forests with old growth characteristics are throughout the southeastern United States, including in western and mixed mesophytic forests of the Mississippi Embayment in southwest Tennessee. This is especially true near urban centers where historical forest disturbance is likely to have been most pronounced and occurred earliest after European colonization even though many eastern cities incorporated swaths of intact forest as urban forested natural areas (i.e., parks, preserves, open areas, buffers, and nearby forest product resources) as they expanded over the last 100+ years (Loeb 2011; Meier 2018; Pregitzer et al. 2021).

Since the early 1800s, like other parts of eastern North America, the forests of southwest Tennessee have been shaped by varying levels of hardwood timber harvest, conversion to agricultural lands, and on-going agriculture-related woodlot and grazing disturbances (Guldin et al. 1990; Young et al. 2007; Brown 2017). For example, Memphis and surrounding areas of southwest Tennessee experienced rapid post-colonial population growth and the expansion of plantation agriculture from the early- to mid-1800s (Jeter 1955; Cowell and Gallien 1997; Dowdy 2019). The generally flat topography and rich alluvial soils of the Mississippi Delta and adjacent loess bluffs, combined with easy access to shipping on the Mississippi River, encouraged largescale clearing of forests for conversion to agriculture (Miller and Neiswender 1987a, Kupfer and Kirsch 1998). And despite coordinated efforts at conservation and redevelopment (Van West 2001; Citizens to Preserve Overton Park v. Volpe 1971), the diverse and abundant mesophytic forests (Braun 1950) also contributed to the city becoming widely regarded as a “hardwood timber capital” with a high concentration of hardwood lumber mills supplying markets nationwide through the mid-1900s (Dowdy 2019).

As with other eastern forests, such intensive resource extraction resulted in changes to forest dynamics, species assemblages, and structural features (Rhemtulla et al. 2009; Thompson et al. 2013). For example, past forest community composition studies have documented shifts from chestnut (*Castanea* spp.)-oak (*Quercus* spp.)-hickory (*Carya* spp.) to beech (*Fagus grandifolia* Ehrh.)-maple

(*Acer* spp.) assemblages (i.e., shade tolerant species) and an apparent failure of oak species replacement among the forest canopy (i.e., a lack of oak saplings in forest understories leading to mesophication; Nowacki and Abrams 2008; Hanberry et al. 2020; Alexander et al. 2021). In urban/suburban environments like the matrix of developed and forested habitat in southwest Tennessee, changes to wildlife activity, fire suppression, and recreational disturbance likely also resulted in altered forest dynamics (Guldin et al. 1990).

The Old Forest State Natural Area in Overton Park, Memphis, Tennessee, has been characterized as "old-growth forest" due to the presence of old trees, high woody perennial and herbaceous plant diversity—including regionally rare species—uneven age distributions among trees, and well-defined vegetation layers (Guldin et al. 1990; Heineke 2009). Despite changing land-use patterns and significant post-colonial anthropogenic disturbances, the old growth designation implies that the Old Forest State Natural Area represents unique old-growth forest that provides habitat for native forest species and a suite of ecosystem services in the heart of a bustling city. However, the old growth designation also raises questions about whether nearby urban and suburban forested natural areas in southwest Tennessee may also exhibit species assemblage and structural features consistent with old-growth forest. Here, we conduct field sampling of upland eastern deciduous forest communities in Shelby County to assess whether 1) urban and suburban forested natural areas exhibit species assemblage and structural features consistent with old-growth forest similar to the Old Forest State Natural Area, and 2) to assess whether forest community structure is consistent with commonly-accepted criteria for old-growth forest across a gradient of urban and suburban forested natural areas despite legacies of diverse land use histories.

MATERIALS AND METHODS

Forest Community Surveys

We targeted five relatively large upland mixed-hardwood urban and suburban forested natural areas in southwest Tennessee (Shelby County) for woody perennial community surveys. We identified areas that were likely to represent western and mixed mesophytic old-growth forest community elements based upon classical descriptions (Braun 1950), preliminary observational surveys, and historical documentation (e.g., histories as parkland, intact canopies in historical aerial photography; Shelby County Assessor 2024). The surveyed sites were: Meeman-Shelby Forest State Park (MSF; 35.343°, −90.045°), T.O. Fuller State Park (TOF; 35.061°, −90.117°), Lucius Burch State Natural Area in Shelby Farms Park (LB; 35.123°, 89.836°), Nesbit Park (NP; 35.224°, −89.870°), and the Old Forest State Natural Area in Overton Park (OP; 35.146°, −89.986°). The land-use history of the Old Forest State Natural Area is relatively well documented over the last ~150 years. The forest is characterized by old-growth forest community elements such as large and old canopy trees, uneven tree age and stage class distributions, and high proportions of "snags" (standing dead wood) and coarse woody debris (CWD; Guldin et al. 1990; Heineke, 2009; Bridges, 2019). We included plot surveys of this forest to assess whether the other forests, with comparatively less well-documented land-use histories, contained similar old-growth forest elements and to better understand differences in urban and suburban forested natural area community structure. Each study site comprised upland mixed deciduous forest and has a recent history of mixed recreational uses (e.g., hiking, biking, and horseback riding), agricultural applications (e.g., farming, grazing), and timber resource extraction. All study areas occur within an urban-suburban matrix of housing, agriculture, and impermeable road surfaces, though housing in proximity to Meeman-Shelby Forest State Park is much sparser than other forests and may better be considered "rural." Each of the studied forests varied in area of upland forest: MSF=ca. 1308 ha, LB=ca. 357 ha, NP=ca. 135 ha, TOF=ca. 240 ha, OP=ca. 57 ha.

At each study site, we employed a stratified random sampling design to establish 25×25 m sampling plots in upland habitat. Potential survey areas were pre-identified using the desktop version of Google Earth (Google Maps Platform 2025). Haphazard points were placed into areas of intact canopies in aerial imagery and topography likely to harbor upland forest. On site, we ground-truthed the *a priori* evaluations of upland forest communities from Google Earth and adjusted as necessary to remain in upland forest while seeking to ensure dispersion among sampling plots (>25 m apart) and representation of the studied urban/suburban forested natural area (Figure 1). Once representative forest communities were identified, a flying disc was thrown blindly to mark the corner of a sampling plot. GPS coordinates were recorded to establish an initial plot corner (**Supplemental Table 1**). From the corner, we extended a 25 meter tape in a random direction that best avoided trails and impassable obstacles to define the first side of the sampling plot. The other sides of the square plot were established using a magnetic compass to maintain parallel edges. In all cases, we attempted to avoid placing plots within 10 m of forest edges and hiking trails, though this was sometimes unavoidable due to the density of recreational activities and remnants of past land use (e.g., old fence lines, farm roads, trails). The number of survey plots at each study site generally scaled with urban/suburban forested natural area size (i.e., more plots in larger forests) with a total of 98 plots established across the five study sites (MSF: 30 plots, LB: 24 plots, TOF: 16 plots, NP: 17 plots, OP: 11 plots).

Within each sampling plot, we measured the diameter at breast height (1.3 m above ground level, dbh) of all woody plant stems ≥1 cm using a diameter tape. Measurements were made for trees, shrubs, and lianas, and included all stems of multi-stemmed individuals, as well as snags (standing dead wood) that were ≥1 cm in diameter. We also measured the length and width of coarse woody debris (CWD) within each plot ≥20 cm in diameter to estimate the volume of CWD. All measured stems were identified to species except for snags and CWD, which were maintained as separate categories in our dataset. When species identities were uncertain, we referenced iNaturalist (iNaturalist 2025), the USDA PLANTS Database (USDA 2025), and field guides to trees and shrubs of the region (e.g., Little 1980; Duncan and Duncan 2000; Kirkman et al. 2007).

Stand Structure and Community Composition Analyses

We calculated species richness (*S*) and Shannon-Wiener diversity (*H'*) values for each forest. Additionally, we calculated stem densities and basal areas (from dbh measures) for each species recorded in each sampling plot and used these measures to compute total and species-specific mean stem densities and basal area per hectare for each forest. Stem density and total basal area were computed without the inclusion of snags. We also estimated the total volume of coarse woody debris in each plot by assuming each measured item represented a cylinder. Although we noted the presence of several red oak species in our surveys (e.g., *Quercus nigra* L. *Quercus velutina* Lam., *Quercus pagoda* Raf., *Quercus falcata* Michx.), field identifications were often too uncertain and we combined observations into a broader functional group (e.g., "red oak" [*Quercus* subgen. *Erythrobalanus*], exclusive of *Q. nigra*). Similarly, *Toxicodendron radicans* (L.) Kuntze was noted as occurring at all sites, but we did not count stems or measure diameters due to the potential for severe contact dermatitis. We also eliminated species that were very rare (i.e., occurred in <3 plots) from the dataset if they could not be combined into other functional groups (but included these species for species richness, diversity, and old growth assessments). The adequacy of our sampling effort to document species diversity was assessed via a mean species accumulation curve using the random addition option in the *specaccum* function in the R (v3.5.1; R Core Team, 2023) package vegan (v2.5-7; Oksanen et al. 2020) via RStudio (v1.3.1056-1; RStudio Team, 2020).

We tested for differences in tree species composition (with abundance based on density and basal area), snag composition (density), and coarse woody debris composition (volume) per hectare between forest communities using permutational MANOVA (PERMANOVA). The PERMANOVA was implemented with the *adonis2* function with Bray-Curtis distances in the R package vegan via RStudio. For these comparisons, we excluded snags and stems <10 cm in diameter from our dataset to reduce the influence of potentially ephemeral recruiting individuals (Leck and Outred 2008) and tested for differences in variance among sites using an ANOVA with the *betadisper* function in the R package vegan. Additionally, individual differences in tree species density and basal area were analyzed with univariate Kruskal-Wallis ANOVA and Dunn's post-hoc tests. To visualize the

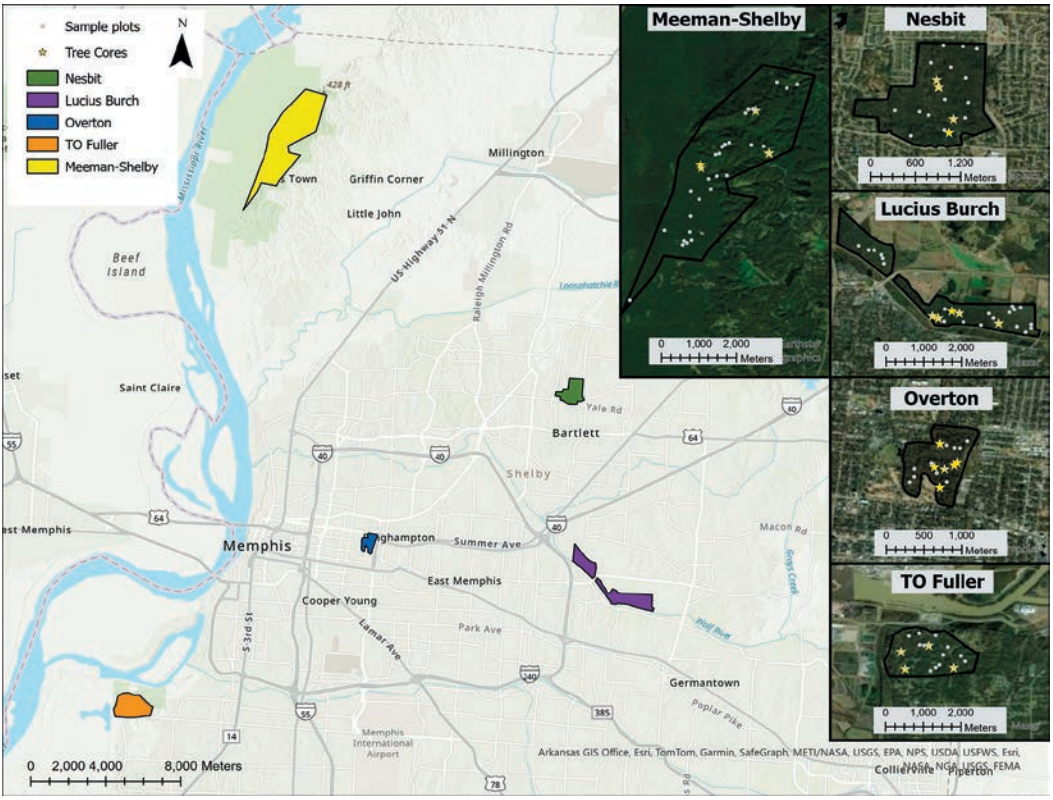

Figure 1. Map of the Shelby County area in southwest Tennessee with the outlines of the studied urban and suburban forested natural areas highlighted. Detailed insets show the distribution of individual survey plot locations within each studied forest (**Supplemental Table 1**). Stars in insets indicate locations of cored trees (Table 1). Inset outlines correspond to highlighted areas in overview map. Meeman-Shelby=Meeman-Shelby Forest State Park, Nesbit=Nesbit Park, Lucius Burch=Lucius Burch State Natural Area, Overton=Old Forest State Natural Area in Overton Park, TO Fuller=T.O. Fuller State Park. Coordinate System: NAD 1983 StatePlane Tennessee FIPS 4100 feet.

similarities between plots at each forest community we also conducted a nonmetric multidimensional scaling (NMDS) ordination in R using the metaMDS function with the autotransform option (i.e., square-root transform and Wisconsin double-standardized data using Bray-Curtis dissimilarities when appropriate; McCune and Grace 2002) in the R package vegan. Ordinations were conducted on datasets that included all measured stems as well as datasets that only included stems ≥10 cm and visualized using the R package ggordiplot. We also constructed tree diameter class histograms to evaluate whether the studied urban/suburban forested natural areas comprised trees with even- or uneven-age-class distributions.

Old Growth Assessments

To examine whether forests contained elements consistent with old-growth forest beyond comparisons to the Old Forest State Natural Area, we compared attributes of the forests to old-growth forest criteria for eastern deciduous forests. Many criteria and operational definitions for “old-growth forest” have previously been published, with many overlapping in some way (e.g., Davis 1996; Gaines et al. 1997; Greenberg et al. 1997; Hale et al. 1999; Diggins and Kershner 2005; Barndt et al. 2023; Pelz et al. 2023). We selected a set of measurements that were straightforward to obtain and generalizable to aid comparisons among other studies of old-growth forests following Greenberg et al. (1997): total stem densities (stems ≥10 cm dbh) between 168–455/ha, total basal area (stems ≥10 cm dbh) between 26–68 m^2/ha, snag density (snags ≥10 cm dbh) between 10–70/ha, coarse woody debris/downed logs (≥20 cm diameter) between 66–410 m^3/ha , and number of trees ≥75 cm dbh between 8.5–44.3/ha. We additionally evaluated the forests with some overlapping criteria following Gaines et al. (1997): basal area of trees ≥12.7 cm dbh at least 9.18 m^2/ha, density of snags ≥10 cm dbh at least 9.88/ha, density of trees ≥76.2 cm dbh at least 14.83/ha, and presence of trees at least 140 years old.

We used increment borers to obtain cores from 25 of the largest trees occurring in, or adjacent to, our plots to estimate ages for the current largest size class (coordinates of cored trees in Table 2). Sampled species included *Fraxinus americana* L., *Liriodendron tulipifera* L., *Quercus alba* L., *Quercus falcata*, *Quercus michauxii* Nutt., *Quercus nigra*, and *Taxodium distichum* (L.) Rich. Cores were extracted using a 71 cm long, 5.15 mm diameter Hagloff 3-thread increment borer. Dried cores were mounted to grooved boards and sanded by hand with progressively finer grit beginning with 120-grit and ending with 1,500-grit until a fine polish was achieved (Stachowiak et al. 2016). Tree rings were evaluated using an 80× dissecting microscope. When increment cores did not contain pith center, rings per centimeter for the innermost 20 rings were calculated and multiplied by the estimated missing core length.

RESULTS

Forest Community Surveys

All forests exhibited human-mediated disturbance (e.g., hiking trails, old fence lines, dirt roads, cut stumps, dikes and levees, derelict farm equipment, etc.). Plots in Meeman-Shelby Forest State Park tended to be further away from forest edges, whereas plots in the Old Forest State Natural Area and T.O. Fuller State Park tended to be near hiking trails. A few plots at each study site were situated near, or included, hiking trails representing “edge” habitat due to spatial limitations in how plots could be situated in representative upland forest habitat. Given the stratified random sampling design and representative sampling of each forest (Figure 1), there did not appear to be a systematic bias in the sampling of “edge” habitats. Thus, while the inclusion of trails and forest edges could increase representation of younger or non-typical forest elements in our study, these plots represent a small fraction of the overall sample size, and their inclusion in our study likely provides a more accurate characterization of these relatively small urban/suburban forested natural areas embedded in a highly fragmented landscape.

Stand Structure and Community Composition Analyses

We recorded 68 species across all forests (after combining some groups; **Supplemental Table 2**). Our species accumulation curve indicated that our sampling effort was sufficient to approximate true species diversity (**Supplemental Figure 1**). Individually, the forests had generally high species richness and diversity values (Table 1). Removing non-native species reduced species richness at all sites but increased the diversity value at Lucius Burch State Natural Area, likely due to the prevalence of non-native *Ligustrum sinense* Lour. at this site (Table 1). The 10 most abundant species per hectare across study sites were generally consistent with expectations for oak-hickory or beech-maple associations of eastern deciduous forests: *Asimina triloba* (L.) Dunal, *Ligustrum sinense*, *Ostrya virginiana* (Mill.) K. Koch, *Ulmus alata* Michx., *Fagus grandifolia*, *Carya tomentosa* (Lam.) Nutt., *Liquidambar styraciflua* L., *Lindera benzoin* (L.) Blume, *Acer saccharum* Marshall, and *Vitis* spp. Similarly, the 10 species comprising the greatest basal areas per hectare across study sites were also consistent with expectations for oak-hickory or beech-maple associations of eastern deciduous forests, but included elements of southern mixed deciduous forest: *Liriodendron tulipifera*, *Quercus rubra* L. (and other red oaks), *Liquidambar styraciflua*, *Quercus alba*, *Taxodium distichum*, *Fraxinus americana*, *Carya tomentosa*, *Ulmus rubra* Muhl., *Platanus occidentalis* L., and *Fagus grandifolia*.

With snags excluded, all forests had more than 300 stems/ha and basal areas greater than 35 m^2/ha for stems ≥10 cm dbh (Table 1). Snag densities for stems ≥10 cm ranged widely but exceeded

Table 1. The studied urban and suburban forested natural areas satisfy most (bolded), but not all, commonly employed operational criteria for potential old-growth forest selected from prior studies. LB=Lucius Burch State Natural Area, MSF=Meeman-Shelby Forest State Park, NP=Nesbit Park, OP=Old Forest State Natural Area in Overton Park, TOF=T.O. Fuller State Park.

Metric	Range	Mean	LB	MSF	NP	OP	TOF
Species Richness (*S*) (w/o non-natives)	–	–	39 (37)	35 (34)	35 (34)	35 (30)	43 (42)
Diversity (*H'*) (w/o non-natives)	–	–	1.69 (2.90)	2.52 (2.51)	2.74 (2.68)	1.74 (1.52)	3.00 (2.95)
Basal area (m^2/ha; ≥10 cm dbh; ±1SE)* (m^2/ha; ≥12.7 cm dbh; ±1SE)**	26-68* ≥9.18**	38±11*	**38.80** (2.64) **38.19** (2.66)	**50.96** (2.91) **50.05** (2.93)	**46.09** (3.29) **45.42** (3.27)	**40.85** (6.58) **40.18** (6.59)	**40.96** (2.65) **40.13** (2.65)
Density (no./ha; ≥10 cm dbh; ±1SE)	168–455*	322±85*	**338.00** (16.99)	**391.47** (20.22)	**459.29** (27.84)	**317.09** (26.23)	**378.00** (18.70)
Snag density (no./ha; ≥10 cm dbh; ±1SE)	10–70*, ≥9.88**	31±19*	**14.67** (3.46)	**18.67** (3.52)	**81.88** (20.25)	**10.18** (2.43)	**33.00** (8.19)
Coarse woody debris volume (m^3/ha.; logs ≥20 cm diameter; ±1SE)	66–410*	155±113*	18.25 (4.55)	20.05 (4.47)	18.72 (8.20)	48.85 (12.23)	21.57 (6.97)
Trees ≥75 cm dbh (no./hectare; ±1SE)* ≥76.2 cm dbh (no./hectare, ±1SE)**	8.5–44.3* ≥14.83** *	27.8±12	**17.33** (3.10) **16.67** (3.54)	**32.00** (3.76) **29.33** (3.76)	**16.00** (5.13) **15.06** (5.22)	**32.00** (6.82) **29.09** (6.76)	**20.00** (3.1) **19.00** (3.34)
Number of 10 cm size classes (≥10 cm dbh)	1-22*	17*	12	13	11	15	11
Minimum age of oldest age class (years)	–	140**	120–140	**220–240**	120–140	**220–240**	120–140

*Greenberg et al. 1997, **Gaines et al. 1997/Barndt et al. 2023

Table 2. Study site, latitude/longitude, species identity, diameter, and estimated age for all cored trees. Cored trees were distributed among sites and were either located within or near study plots (Figure 1). Ages marked with an asterisk were adjusted with additional ring counts projected from average rings/year over the 20-year-span closest to center to account for missing pith centers. Ages marked with double asterisks are from recently fallen trees. Ages marked with carets represent minimum ages due to hollow centers. LB=Lucius Burch State Natural Area, MSF=Meeman-Shelby Forest State Park, NP=Nesbit Park, OP=Old Forest State Natural Area in Overton Park, TOF=T.O. Fuller State Park.

Study Site	Latitude	Longitude	Species Identity	DBH (cm)	Estimated Age (year)
LB	35.1246	–89.8380	*Taxodium distichum*	72	140
LB	35.1239	–89.8444	*Quercus nigra*	119	89*
LB	35.1221	–89.8285	*Quercus michauxii*	107	140
LB	35.1251	–89.8398	*Liriodendron tulipifera*	86	67*
LB	35.1233	–89.8430	*Liriodendron tulipifera*	115	74*
MSF	35.3433	–90.0498	*Liriodendron tulipifera*	120	129*
MSF	35.3442	–90.0498	*Quercus falcata*	135	128*
MSF	35.3573	–90.0368	*Liriodendron tulipifera*	122	77
MSF	35.3468	–90.0336	*Quercus falcata*	103	86
MSF	35.3468	–90.0336	*Liriodendron tulipifera*	135	224^
NP	35.2222	–89.8693	*Liriodendron tulipifera*	94	73
NP	35.2261	–89.8710	*Quercus alba*	126	112*
NP	35.2270	–89.8713	*Quercus falcata*	91	125*
NP	35.2261	–89.8710	*Quercus falcata*	99	91
NP	35.2205	–89.8698	*Liriodendron tulipifera*	86	69
OP	35.1460	–89.9860	*Fraxinus americana*	136	132
OP	35.14376	–89.9866	*Quercus falcata*	110	132
OP	35.14649	–89.9849	*Quercus pagoda*	130	187**
OP	35.14625	–89.9872	*Quercus falcata*	140	185**
OP	35.14649	–89.9849	*Liriodendron tulipifera*	121	227^
OP	35.14908	–89.9866	*Liriodendron tulipifera*	105	177
TOF	35.0624	–90.1277	*Quercus alba*	103	122
TOF	35.0639	–90.1211	*Liriodendron tulipifera*	103	90
TOF	35.0585	–90.1152	*Liriodendron tulipifera*	108	70*
TOF	35.0582	–90.1267	*Liriodendron tulipifera*	106	86

10 snags/ha (Table 1). Coarse woody debris volumes for logs ≥20 cm in diameter were below 50 m^3/ha (Table 1).

We found significant differences in composition based on stem densities (PERMANOVA: $F_{4,93}$= 9.647, p=0.001) and basal areas/ha (PERMANOVA: $F_{4,93}$=4.792, p=0.001) among forests when rare species and snags were excluded and red oak species were combined into a broader functional group (i.e., “red oak”) because of uncertain species identity. Variance among sites was not homogeneous for densities (*betadisper* ANOVA: $F_{4,93}$=11.733, p<0.001) or basal areas (*betadisper* ANOVA: $F_{4,93}$=9.504, p<0.001).

Similarly, we found significant differences in composition in univariate analyses based on stem densities (χ^2=19.115, p<0.001) and basal area (χ^2=11.131, p=0.025) for all species (stems ≥10 cm dbh) at the studied forests. Post-hoc analyses for stem densities indicated that Nesbit Park was significantly different from the Lucius Burch State Natural Area and the Old Forest State Natural Area, but was not significantly different from other forests. Post-hoc analyses for basal area indicated that Lucius Burch State Natural Area was significantly different from Meeman-Shelby Forest State Park but was not significantly different from other forests (Figure 2).

NMDS ordinations for stem density and basal area per hectare are consistent with the PERMANOVA results and indicate that several of the studied urban forested natural areas are broadly similar, but exhibit some differences in stem density, basal areas, and/or species assemblage

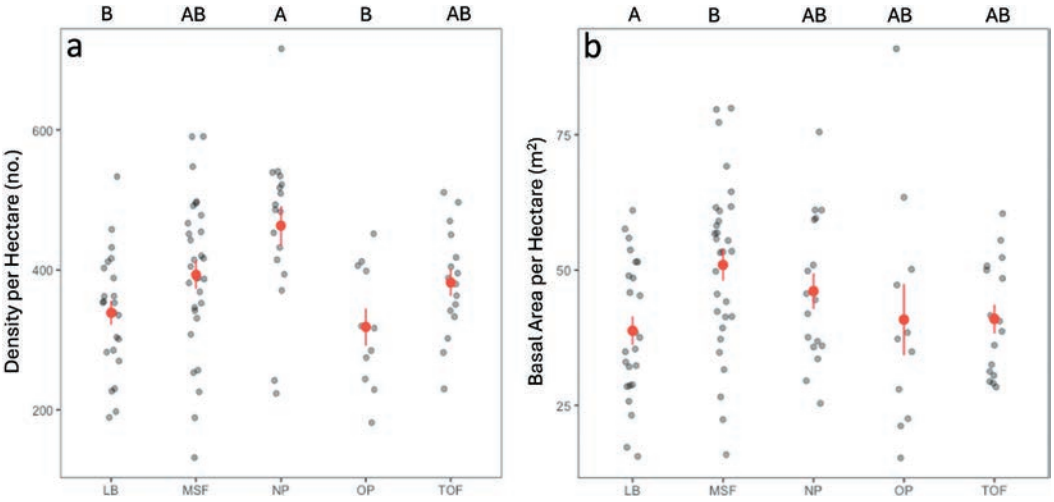

Figure 2. Stripcharts showing a) stem density per hectare and b) basal area per hectare for stems ≥10 cm dbh at each studied urban and suburban forested natural area. Though densities and basal areas were generally similar among studied forests, Nesbit Park was significantly different in density from the Lucius Burch State Natural Area and the Old Forest State Natural Area, and the Lucius Burch State Natural Area was significantly different in basal area from Meeman-Shelby Forest State Park. Points represent individual plots. Rare species and snags were omitted. Means are indicated by darker circles with ±1 SE. Letters above indicate the outcome of Tukey's posthoc analyses where different letters indicate significant differences. LB=Lucius Burch State Natural Area, MSF=Meeman-Shelby Forest State Park, NP=Nesbit Park, OP=Old Forest State Natural Area in Overton Park, TOF=T.O. Fuller State Park.

(Figure 3a). There appeared to be more overlap in basal area among sites than in stem density (Figure 3b). Fourteen species (stems ≥10 cm dbh) occurred in survey plots at all studied forests, including *Liriodendron tulipifera*, *Quercus rubra* (and other red oak species), *Carya tomentosa*, and *Fraxinus americana*. However, sites also exhibited differences in species occurrence. The Old Forest State Natural Area was unique in containing high densities and basal areas of *Asimina triloba* and *Acer negundo* L. relative to other studied forests, while *Taxodium distichum* was only observed at Lucius Burch State Natural Area adjacent to the floodplain of the Wolf River. Lucius Burch State Natural Area also exhibited high densities of non-native *Ligustrum sinense* that occurred minimally at other sites. *Fagus grandifolia* and *Acer saccharum* were especially prevalent (high density and basal area) at T.O. Fuller State Park and Meeman-Shelby Forest State Park, which also exhibited high basal areas of *Quercus alba*. Nesbit Park was characterized by high densities of *Ulmus alata* and *Liquidambar styraciflua*, which were not as large as specimens of this species in other forests. Notably, Lucius Burch State Natural Area exhibited little overlap with other sites in stem density and basal area (Fig. 3). Data used for analyses may be found in **Supplemental Files 1–8**.

Old-Growth Assessments

Excluding snags, the mean stem count of trees ≥10 cm dbh and mean basal area for the studied forests was 376.77 stems/ha (SE=24.59) and 43.53 m^2/ha (SE=2.21), respectively. Individually, the forests met some of the old-growth forest criteria, but none of them satisfied all criteria (Table 1). All forests had stem counts per hectare, basal area per hectare, and snag densities per hectare that exceeded the minimum values considered to represent old-growth forest, and had exceptionally large trees with stem diameters exceeding 75 cm (or 76.2 cm). The greatest densities of large trees occurred at Meeman-Shelby Forest State Park, the Old Forest State Natural Area, and T.O. Fuller State Park, however the densities at all sites were consistent with old-growth forest (MSF=32 trees >75 cm dbh/ha, OP=32 trees >75 cm dbh/ha, TOF=20 trees >75 cm dbh/ha, LB=17.33 trees >75 cm

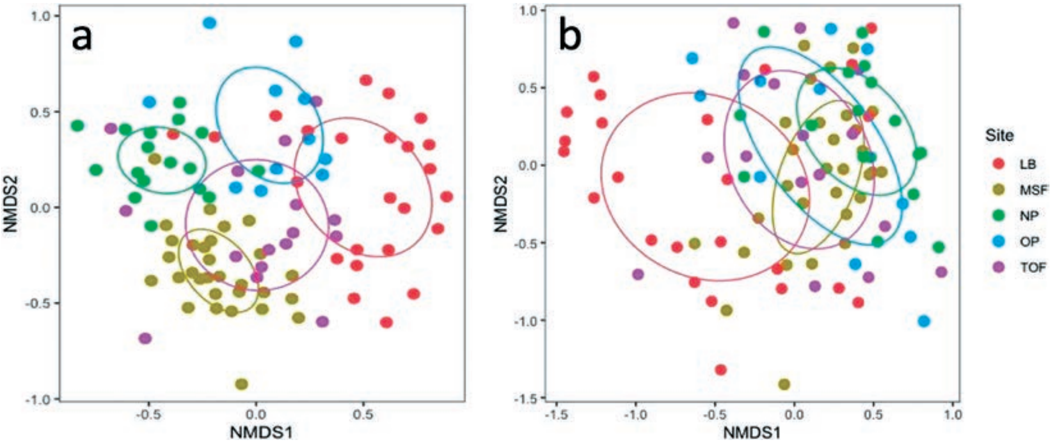

Figure 3. Non-metric multidimensional scaling (NMDS) ordinations showing differences in a) stem densities and b) basal areas among studied urban and suburban forested natural areas. Points that are closer together indicate study plots that are more similar in species composition after removal of stems <10 cm dbh, rare species, and snags. The stem densities and basal areas among the studied forests were significantly different (PERMANOVA; stem densities: $F_{4,93}$=9.647, P=0.001; basal areas: $F_{4,93}$=4.792, P=0.001). LB=Lucius Burch State Natural Area, MSF=Meeman-Shelby Forest State Park, NP=Nesbit Park, OP=Old Forest State Natural Area in Overton Park, TOF=T.O. Fuller State Park.

dbh/ha, NP=16 trees >75 cm dbh/ha; Greenberg et al. 1997). After excluding shrubs, lianas, non-native species, and stems <10 cm dbh, more than 8% of trees fell within or above the 60 cm dbh size class at all forests (Figure 4). When all stems were included, no site had greater than 5% of trees in the ≥60 cm dbh size class due, in part, to large densities of small-stemmed *Ligustrum sinense* and *Asimina triloba*.

All sites had snag densities (for snags ≥10 cm dbh) exceeding the minimum old growth criteria of 10 snags/ha (Greenberg et al. 1997; Table 1), though most snags had relatively small diameters. Nesbit Park had a snag density that exceeded the upper range of the criteria for old-growth forest (>70 snags/ha.; Greenberg et al. 1997), with several plots that had very high snag densities. Most of the snags appeared to be dead *Juniperus virginiana* L., which was not found in any other study site. In contrast, none of the studied urban/suburban forested natural areas satisfied old growth criteria for volume of coarse woody debris having volumes less than the lower threshold of 66 m^3/ha (Greenberg et al. 1997; Table 1).

The stem cores we took from representative large trees at the studied urban/suburban forested natural areas indicate ages ranging from ca.70–225 years from species such as *Fraxinus americana*, *Quercus* spp., *Taxodium distichum*, and *Liriodendron tulipifera* (Table 2). Two cores sampled from *Liriodendron tulipifera* in Meeman-Shelby Forest State Park and the Old Forest State Natural Area indicated ages of ca. 225 years old (i.e., established in 1799). In contrast, large representative trees at T.O. Fuller State Park, Nesbit Park, and Lucius Burch State Natural Area were estimated to be much younger. Large *Quercus* spp. and *Liriodendron tulipifera* were estimated to be 70–120 years at T.O. Fuller State Park, 70–125 years at Nesbit Park, and 70–140 years at Lucius Burch State Natural Area. Large *Taxodium distichum* sampled at Lucius Burch State Natural Area were ca. 140 years old.

DISCUSSION

Eastern deciduous forests with structural features consistent with old-growth forest are rare, and even more so near population centers where historic disturbance regimes have been substantially altered (Davis 1996; Leverett 1996; Davis 2003; Loeb 2011). Yet, small patches of eastern deciduous forest, some of which exhibit old growth characteristics, persist as urban or suburban forested

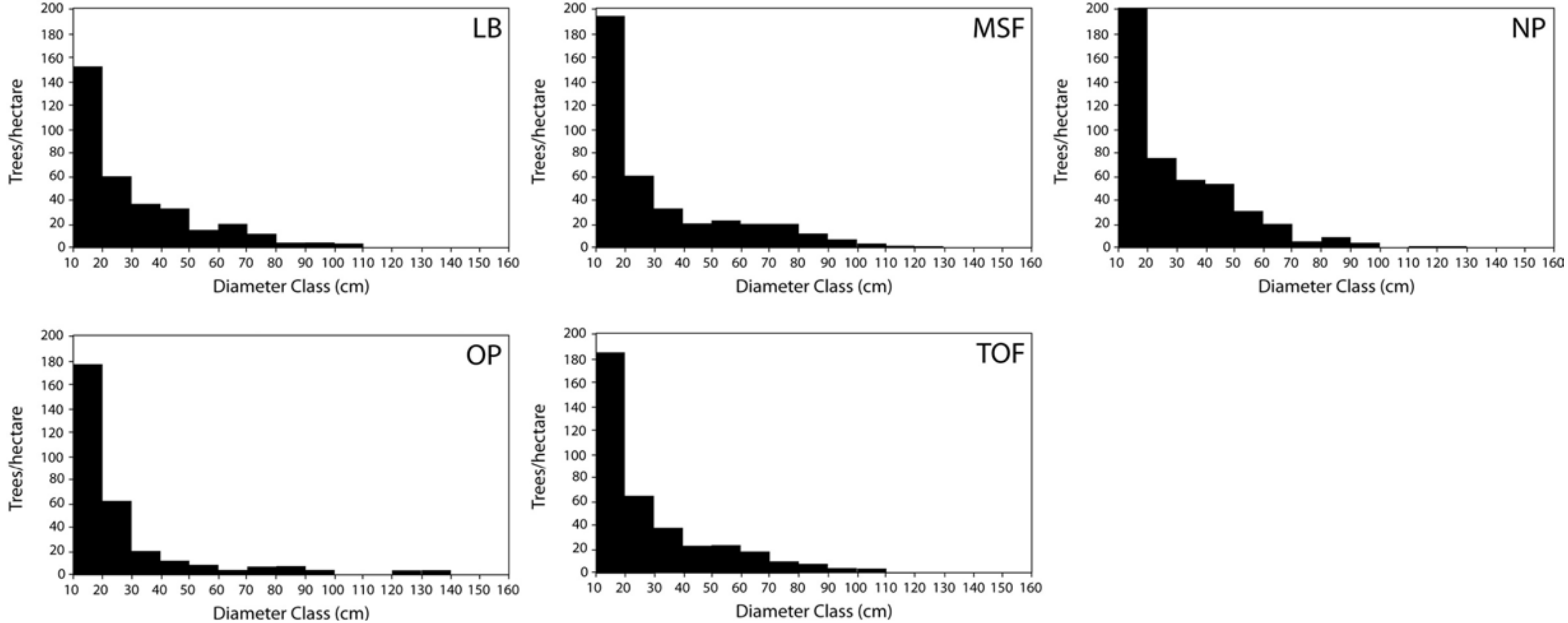

Figure 4. Tree diameter distributions at each of the studied urban and suburban forested natural areas. Site abbreviations in each panel correspond to those in other figures. Stems <10 cm were excluded to reduce the influence of potentially ephemeral recruiting individuals. Stem diameter distributions in all forests generally conform to the expected negative exponential shape exhibited by forests with a wide range of tree ages and size classes and had >5% of stems in the ≥60 cm dbh size class, suggesting that sites contain elements of mature or old-growth forest.

natural areas where they are important reservoirs of biodiversity and provide crucial ecosystem services (Conner and Sharitz 2005; King et al. 2009; McGee 2018). We found that several urban and suburban forested natural areas in and near Memphis exhibit some features consistent with old-growth forest, harbor appreciable tree and shrub diversity, and likely provide indispensable ecosystem services to urban and suburban parts of southwestern Tennessee. While generally similar, we also found that these forests exhibit differences in community composition, with different species assemblages based upon tree densities and basal areas likely reflecting different land-use histories and patterns of development and disturbance over the last two centuries (Shankman 1990; Cowell and Gallien 1997). The forests are either continuing to recover from unique post-colonial anthropogenic disturbances on a trajectory toward old-growth forest (e.g., "new old growth"), or they continue to experience levels of anthropogenic disturbance that hinder the transition to formalized definitions of old-growth forest. Thoughtful management approaches to maintain—and enhance—species diversity, stand structure, and community composition of these urban and suburban forested natural areas would likely have major beneficial impacts on regional ecosystem health. Taken together, these observations suggest that old-growth forest may be more common than previously thought in urbanized areas and should be more widely studied.

Forest Community Surveys

Our surveys are among the first comprehensive attempts to document forest community ecology and the distribution of potential old-growth forest in a highly fragmented landscape with a history of intensive anthropogenic disturbance surrounding Memphis. Prior forest community surveys in the area have focused on characterizing species assemblages for a subset of the forested areas that occur on loess bluffs adjacent to the Mississippi River (Miller and Neiswender 1987a, 1987b), whether these communities are distinct from other eastern hardwood forest assemblages (Braun 1950; Miller and Neiswender 1987a, 1987b; Kupfer and Kirsch 1998), and how successional histories have shaped diversity and structural features in response to agricultural disturbance (Shankman 1990; Cowell and Gallien 1997). Other prior studies emphasized the high biodiversity and uniqueness of the Old Forest State Natural Area in Overton Park (Guldin 1987; Guldin et al. 1990; Heineke 2009). The results of our study are broadly consistent with these prior efforts, but show that some of the largest urban and suburban forested natural areas around Memphis exhibit high biodiversity and complex structural features. This suggests that even in an area characterized by intensive agriculture and resource extraction over the last 200+ years, relatively small pockets of diverse forest can act as repositories for important biodiversity and provide valuable ecosystem services.

Our survey efforts, though relatively modest and with some compromises on species identities, appear to have adequately approximated the diversity of species and relevant structural features (**Supplemental Figure 1**). We observed similar canopy and subcanopy species diversity as other studies (e.g., Miller and Neiswender 1987b; Guldin et al. 1990; Cowell and Gallien 1997; Heineke 2009). While additional effort could prove fruitful in documenting biodiversity in the larger forests, our sampling efforts in large plots distributed throughout each of the forests captured important dimensions of these biological communities. Critically, these surveys facilitated the discovery of some old and ancient trees, and may motivate greater community interest in researching, conserving, and managing urban and suburban forested natural areas throughout the southeastern United States to limit biodiversity loss, enhance connectivity, and enrich ecosystem services in urban and suburban areas.

Stand Structure and Community Composition Analyses

The community composition of all studied urban and suburban forested natural areas was similar to the Old Forest State Natural Area. All forests had relatively high species richness (35–42 species), and had relatively high basal areas of typical upland western mesophytic forest species, including *Liriodendron tulipifera*, *Quercus rubra*, *Quercus alba*, *Carya tomentosa*, *Fraxinus americana*, *Fagus grandifolia*, and *Liquidambar styraciflua*. Though we observed unequal variance in species composition among the forests, the studied forests exhibited some important differences from each other, and the Old Forest State Natural Area. Rarer species, including some non-native species, also differentiated the studied forests. Notably, the Old Forest State Natural Area was distinguished by a high density of *Acer negundo*, but stood out for the exceptionally high density of *Asimina triloba* (greater than any other studied forest; Guldin et al. 1990; Heineke 2009; Bridges 2019). Meeman-Shelby Forest State Park and T.O. Fuller State Park, both situated on loess bluffs adjacent to the Mississippi River, were distinguished by high basal areas of *Fagus grandifolia*, *Acer saccharum,* and *Quercus alba*.

Nesbit Park was characterized by high densities of *Liquidambar styraciflua* and *Ulmus alata*. Lucius Burch State Natural Area was unique from all other forests by containing the only (and large) representatives of *Taxodium distichum*, a species often found in bottomland or floodplain habitats. While this species has previously been documented in floodplains at Meeman-Shelby Forest State Park (Miller and Neiswender 1987b), we did not survey these areas. The presence of *T. distichum* at Lucius Burch State Natural Area may reflect a past ecosystem history of periodic flooding from the nearby, now-channelized Wolf River (Figure 1). Although non-native *Ligustrum sinense* was found at all sites, the densities at Lucius Burch State Natural Area were exceptional. In several places an apparent "invasion front" could be observed. While there is no active management of this species currently occurring in this forest, removal efforts may positively impact overall forest health (A.J. Trently pers comm). These patterns suggest our sites exhibit similar species assemblages and stand structure, but also exhibit some unique characteristics despite occurring within 10–20 km of each other, likely owing to differences in land use history, edaphic and hydrologic features, aspect, etc. (Figure 1).

Human-mediated disturbances (e.g., agriculture, timber harvest, recreation, etc.) have also likely played an important role in shaping species assemblages and stand structures in forest sites. Much of the forested upland area at Meeman-Shelby Forest State Park was harvested for timber and agriculture into the early- and mid-1900s (Miller and Neiswender 1987a; Kupfer and Kirsch 1998), and except for the Old Forest State Natural Area, plantation agriculture and smaller-scale farming was pervasive with remnants of this history persisting today in the form of old fence lines, dirt roads, dikes and levees, cut stumps, and derelict farm equipment. High densities of *Juniperus virginiana* at Nesbit Park is also consistent with a legacy of agriculture as this species is often observed as a pioneer species in old fields in west Tennessee until it is overtopped by hardwood species (personal obs.). Hiking and recreation trails also occur in all the studied forests, and paved roads persist in the forests. We did not specifically attempt to quantify the effects of these historical and continuing disturbances on species assemblages or structural features of the studied forests. It seems unlikely such disturbances have been inconsequential, but it remains unclear in what ways current species assemblages and forest structural features have been influenced by these disturbances.

Old Growth Assessments

Collectively, our forest sites satisfy most of the selected criteria for western and mixed mesophytic old-growth forest, though none satisfied all of the criteria for old-growth forest. We documented several large trees with diameters more than 76 cm, and the percentage of large trees with diameters ≥60 cm exceeded 5% of all stems (when stems <10 cm DBH were excluded) for all studied forests (Table 1). This is consistent with the designation of the studied urban/suburban forested natural areas as including elements of old-growth forest (Gaines et al. 1997; Greenberg et al. 1997; Hale et al. 1999; Fassnacht et al. 2015; Barndt et al. 2023), and suggests these forests may be resilient to the intensive post-colonial anthropogenic influences. Interestingly, the stem diameter distributions at all sites are consistent with characterization as uneven-aged forest (Ashton and Kelty 2018; Figure 4), and this seems like an appropriate designation based on stem densities, basal areas, snag densities, and coarse woody debris volumes. However, in addition to large *Quercus* spp., many of the largest trees we documented were *Liriodendron tulipifera*. Younger mixed mesophytic forests with large trees tend to be dominated by *L. tulipifera* and other less shade-tolerant species (Clebsch and Busing 1989; Lienard et al. 2015). Thus, it remains unclear if the studied forests are on a trajectory toward continued development to old-growth forest with the current trees representing the newest oldest age class (e.g., “new” old growth), but the potential for conserving biodiversity and enhancing ecosystem services make these urban/suburban forested natural areas prime targets for restoration efforts similar to the removal of non-native and invasive species at the Old Forest State Natural Area in Overton Park (Trently 2015).

Though our study was focused on urban and suburban forests, studies of other eastern deciduous forests in the Appalachian Mountains suggest the deciduous forest patches of southwest Tennessee may exhibit similar features to old- and second-growth forest in less urbanized areas (Woodbridge et al. 2025). For example, old-growth and second-growth forests in southeastern Kentucky exhibit similar total basal areas, but the old-growth forest comprised fewer large diameter trees (Muller 1982). In the southern Appalachian Mountains, the density of large trees (≥75 cm dbh) ranged from 8.5 to 44.3 per ha (mean=27.8±12.0 per ha) across old growth mixed mesophytic forest stands (Greenberg et al. 1997) though stands with as few as seven trees per hectare with diameters ≥75 cm could indicate old-growth forest (Martin 1992). In some cases, uneven-aged second-growth mesophytic forests may resemble old-growth mesophytic forests by having similar negatively exponential size-class distributions to those we observed (Figure 4), however old-growth forests typically have more old and large diameter trees with a greater range of tree sizes compared to second-growth forests (Lorimer 1980, 1985; Palmer 1987). The forests we studied had diameter distributions that are consistent with mature uneven-aged forests (Pond and Froese 2015). The negative exponential shapes of the size class distributions indicate a wide range of size classes/ages suggesting that our forests have more structural complexity than even-aged forests, and that they may be on a trajectory toward old-growth forest (Goodburn and Lorimer 1998).

Some large trees in the Old Forest State Natural Area have previously been aged via increment borers, ring counts from stem sections removed after treefall, and diameter-age projections. These age estimates suggest trees with the largest diameters (>150 cm dbh) exceed 150–200 years in age (Guldin 1987; Guldin et al. 1990; Heineke 2009; Bridges 2024 pers comm). Although we only cored 25 trees across our study sites, we found trees at least 140 years old in most of the studied forests. Also, two trees exceeded 220 years old indicating a likelihood that many more of the large, uncored trees in our survey plots exceed the old growth criteria of 140 years of age (Gaines et al. 1997; Barndt et al. 2023). Beyond indicating that at least some of the large trees at our sites are old, and concordant with other tree-ring chronologies for old forests throughout eastern North America (Cook et al. 1996; Stahle 1996; Grissino-Mayer 2009), our core sampling also reveals intriguing potential associations with historical periods that might help explain the successional trajectories of our sites. At a broad level with a relatively small sample size, the studied forests appear to be characterized by approximately four broad cohorts (70–90 years old, 120–140 years old, 170–190 years old, and 220–240 years old). These ages are roughly concordant with characterizations of widespread historical alterations to land use throughout eastern North America. The mid-1900s saw the end of major tree harvesting in eastern deciduous forests (Rhemtulla et al. 2009), peak hardwood timber harvests occurred in the late-1800s/early-1900s (Dowdy 2019), pre- and post-civil war land clearing for agriculture occurred in the mid-1800s, and European colonization of the Mid-South began in earnest in the early 1800s. Thus, the oldest age class we sampled is suggestive of pre-colonization forest remnants.

Each of the forests has relatively complex overstory age structures, but only the Old Forest State Natural Area and Meeman-Shelby Forest State Park had representatives of the oldest cohorts (170–190 years old, and 220–240 years old). The complexity of the overstories is consistent with characterizations of the studied urban and suburban forested natural areas as exhibiting old-growth western and mixed mesophytic forest features. Interestingly, the oldest cores were from *Liriodendron tulipifera.* While *L. tulipifera* can live 300+ years, it is typically categorized as a shade-intolerant species with relatively rapid growth rates (Burns and Honkala 1990).

Typical species in prior studies of ancient trees using ring dating tend to be *Quercus* spp., *Taxodium distichum*, *Tsuga* spp., and *Pinus* spp. (e.g., Stahle 1996), which exhibit a range of life-history trajectories. Our core samples from old representatives of *Liriodendron tulipifera* indicate that they experienced slow growth (especially early in their life histories) suggesting complex forest gap dynamics in the past that may have contributed to slow early growth with sudden release in the early European colonization period. This suggests that generalized species-specific life history characterizations may not always be informative for making old-growth forest inferences, and that additional ancient trees may exist in the studied urban and suburban forested natural areas.

While the studied forests almost certainly experienced disparate land-use histories over the last 150–200 years involving selective timber harvest, agricultural applications, livestock grazing, recreational activities, etc. (Brown 2017; Kupfer and Kirsch 1998; Cowell 1997), it remains surprising that they exhibit differences in species composition, size, and density given their proximity to each other. One factor potentially contributing to some of these differences is human-mediated interventions and alterations to herbivore pressure associated with reforestation, non-native species introductions, and urbanization. For example, non-native species have been actively managed and removed in the Old Forest State Natural Area and deer browse has likely not occurred in this urban forest for several decades (Trently 2015). Though this forest occurs centrally within Memphis and has experienced intensive anthropogenic impacts and non-native species pressure over at least the last 100 years, non-native species removal efforts have likely altered tree species regeneration in response to periodic canopy gaps while reshaping understory species composition (Johnson and Handel 2016). Similarly, the lack of deer may have shaped species recruitment in unintended ways, contributing to the unique understory and overstory composition in the Old Forest State Natural Area relative to other sites due to the lack of selective browsing in the understory.

Similar interventions and alterations to browsing mammal populations appear to have occurred, though possibly not with the same intensity, at the other studied forests. Indeed, at least two sites (Lucius Burch State Natural Area and Nesbit Park) contained, or were adjacent to, active agricultural lands within the last 100 years, as indicated in historical aerial photographs (Shelby County Assessor 2024), while one of the forests (T.O. Fuller State Park) is adjacent to an active river port with busy rail and trucking depots, and industrial applications (e.g., steel manufacturing, electricity generation). Such disturbances may have promoted the introduction or establishment of non-native species in these forests with greater intensity compared to the Old Forest State Natural Area and Meeman-Shelby Forest State Park. All three of these forests, but especially Lucius Burch State Natural Area, had high incidences of privet (*Ligustrum sinense*), suggesting unique understory and canopy dynamics (Johnson and Handel 2016). In contrast, Meeman-Shelby Forest State Park is more rural than the other forests, occurring 5–10 km from typical urban development. Though we observed non-native species in this forest, the strongest determinants of community structure are likely the loess bluff topography and the history of timber extraction and agriculture (Miller and Neiswender 1987b; Shankman 1990; Cowell and Gallien 1997). Although we removed non-native species observations from our dataset prior to some analyses, their presence has likely altered the understory species composition with cascading effects on the canopy species composition that might have indirectly influenced our analyses. Nevertheless, given the similar species assemblages, complex structural features, and old growth elements currently present in the studied urban and suburban forested natural areas, continued thoughtful conservation and management of these forests should be considered to maintain these valuable repositories of biodiversity and to promote post-disturbance trajectories to enhance these features.

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