



The University of West Florida campus ecosystem study: gopher tortoise and longleaf pine populations in an urban interface

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Published online: 27 January 2020

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Abstract

College/university campuses comprise a distinct type of urban interface, with their generally expansive spatial pattern of alternating permanent structures, parking lots, and green spaces. The campus of the University of West Florida (UWF) in Pensacola, Florida, was constructed among second-growth longleaf pine stands recovering from extensive logging in the western-most extent of the Panhandle, with the original campus design deliberately carried out to maintain original contours and minimize tree removal. The extended campus includes a fire-excluded, longleaf-dominated landscape with active gopher tortoise populations confined to power line right-of-ways. This study (1) examined burrowing effects on soils and plant communities, and (2) estimated the age of longleaf pine stems (trees) around campus to assess the influence of human activity on population structure. Gopher tortoise sampling was confined to three discrete areas (types) for each burrow: apron (redistributed soil outside burrow), burrow (soil above burrowed cavity), and matrix (unaltered surrounding area). Within one 0.1 m² quadrat/sample type for each of 16 burrows, density was determined for all vascular species; mineral soil was taken to a 5-cm depth. Air-dried soil was analyzed for pH, organic matter (OM), cation exchange capacity (CEC), extractable macro- and micronutrients, and extractable aluminum. All longleaf stems >2.5 cm diameter at breast height (DBH) were measured for DBH. Stem age was estimated with an allometric equation. Plant density was reduced by burrowing 7-fold on apron versus burrow and matrix sites, which did not vary between each other. Soil variables did not vary between burrow and matrix samples. Apron soils were significantly lower in pH, OM, CEC, and cations. Soil NO₃⁻ was ~3-fold higher in apron soils. Age structure of longleaf pine on campus revealed that nearly 2/3 of all stems are between 75 and 125 years old, consistent with the cessation of extensive logging of longleaf in this region.

Keywords Urban interfaces · Gopher tortoise · Longleaf pine · Fire exclusion

Introduction

Although a human imprint is indelibly etched on virtually all landscapes of the biosphere (Gilliam 2016), urban interfaces represent a unique juxtaposition of human populations and the natural systems that sustain them (Barrington-Leigh and Millard-Ball 2015; Francos et al. 2019). The chronic nature of human intervention in the biosphere has led to a renaming of our current epoch (the Holocene) to the Anthropocene (Ellis 2015). More recently, the expanse of cities into rural areas—urban sprawl—has created an acute threat to sustainability by

hampering vital ecosystem services (Grimm et al. 2015; Oueslati et al. 2015). Thus, an understanding of the dynamics of urban interfaces represents both a necessary challenge and an important research opportunity (Goffman et al. 2017).

Though perhaps not widely acknowledged as such, college/university campuses comprise a distinct type of urban interface, with their often extensive spatial pattern of alternating permanent structures (e.g., classroom and administration buildings, dormitories), parking lots, and green spaces (Turner 1984; Roman et al. 2017). For this, we distinguish between on-campus green spaces versus institutions with separate forested areas, e.g., the Duke Forest and Yale School Forests at Duke and Yale Universities, respectively, which are used expressly for teaching and research. Some campuses were established long enough ago to contain remnants of old growth stands (Copenheaver et al. 2014), whereas others allow for the tracking of urban forest development (Roman et al. 2017). Still others have portions of the campus set aside as

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arboreta, such as the F.R. Newman Arboretum at Cornell University and the Coker Arboretum at the University of North Carolina—Chapel Hill (Henderson 1949). Even Charles Dickens remarked that the Yale University campus was something to “...bring about a kind of compromise between town and country...” (Dickens 1842). Beginning in 2008, the Arbor Day Foundation sponsors a national program—*Tree Campus USA*—to honor colleges/universities for promoting tree health and student/staff engagement toward environmental stewardship.

Establishment of the University of West Florida in Pensacola was approved by the Florida State Legislature in 1963, with doors opening for first classes in 1967. In the intervening period, the campus was constructed among second- and third-growth longleaf pine stands that had recovered from extensive logging in the western-most extent

of the Panhandle region (Knight et al. 2011). The original design was deliberately carried out to spare from cutting as many trees as possible, including longleaf pine, live and other southern oaks, and southern magnolias. In addition, much of the original contour was maintained during construction of buildings and most parking lots (Marse 2007; Jarvis 2008). Of the native species of trees, the most prominent—in terms of physical stature, frequency, and density—is longleaf pine (Fig. 1).

The longleaf pine ecosystem of the southeastern United States represents somewhat of an ecological paradox. In contrast to other forest types in eastern North America, wherein high plant diversity is closely linked to the number of dominant overstory species (Fig. 2), plant diversity of longleaf pine ecosystems is among the highest of the eastern forest types. Yet, longleaf pine stands are typically dominated by single



Fig. 1 Longleaf pines amid campus buildings, sidewalks, and green spaces at the University of West Florida. These pines were part of the second- and third-growth forest landscape within which the UWF campus was constructed

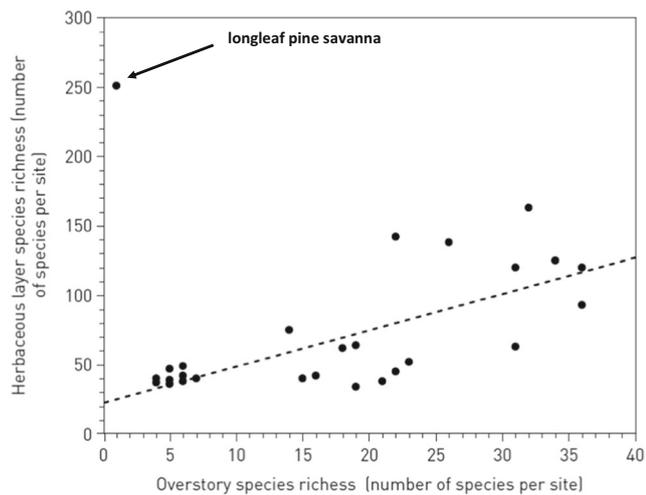


Fig. 2 Species richness of overstory versus herbaceous layer among forest sites. Figure modified from Gilliam (2014), used by permission

overstory species (Gilliam 2014). This is largely connected to another paradox, which is the essential role of a disturbance usually considered destructive in forest ecosystems—fire.

Fire has been a component of ecosystems of the southeastern Coastal Plain throughout the late Quaternary (i.e., 0.5 to 1 million years), resulting in the selection for plant species that are both fire tolerant and fire dependent, and that produce aboveground biomass that is highly inflammable (Kirkman and Jack 2018). It has been recognized for over a century that longleaf pine depends on fire for regeneration. Savannas characteristically have open canopies with widely spaced, scattered trees (Platt 1999). Under a frequent fire regime, this open matrix of the longleaf savanna not only facilitates successful germination of longleaf seeds, but also allows the coexistence of numerous ground cover species, leading to the pattern depicted in Fig. 2. Although longleaf pine ecosystems once covered 25–35 million ha throughout the southeastern U.S., at the current time less than 3% is still extant and much of what remains is quite degraded (Gilliam and Platt 2006). Such losses have been due to intensive human alterations, such as turpentine operations and logging after railroads were constructed in the southeast, and to an effective fire suppression effort that began in the region around 1920.

An animal species that is commonly associated with longleaf pine ecosystems, especially in the far southeastern United States, is the gopher tortoise (*Gopherus polyphemus* Daudin), the only North American tortoise found east of the Mississippi River. Its home range occurs in portions of six states of the southeastern Coastal Plain of the U.S., including Louisiana, Mississippi, Alabama, South Carolina, and Georgia. The state with the largest numbers of the gopher tortoise, however, is Florida; populations occur in all 67 counties of the state (Mushinsky et al. 2006).

Unfortunately, many populations have become isolated and their numbers reduced greatly to small fractions of their

former range and numbers (Berish and Leone 2014). In the southern portion of the state, south of Lake Okeechobee, the gopher tortoise probably always occurred in relatively small isolated populations, mostly along the coastline (Knight et al. 2011). Scattered populations of tortoises occur in the relatively high elevation hammock islands within the northern Everglades. They generally thrive in fire-maintained longleaf pine savannas, but have also been found in urban interfaces, so long as the surrounding vegetation is of an open structure. As a result, they decline in longleaf pine stands experiencing long-term fire exclusion, the result of the filling in of the otherwise open matrix with fire-sensitive hardwood species (Castellón et al. 2018). McCoy et al. (2006) reported widespread declines in gopher tortoise activity throughout Florida, citing numerous causes, including the decreased herbaceous cover and increased canopy development associated with fire exclusion.

Gopher tortoises are sometimes referred to as a *keystone species*, that is, a single species with wide-ranging effects on its community that are disproportionate to the number of individuals. On the other hand, the loss of a keystone species typically results in drastically deleterious responses for the ecosystem (Paine 1966), which is not always the case for gopher tortoises and longleaf pine ecosystems. That is, despite the high species richness and level of endemism often associated with gopher tortoise burrows, the ecosystem generally maintains its structure and function with or without the gopher tortoise. Accordingly, another appropriate term for the gopher tortoise is *ecosystem engineer*. By definition, ecosystem engineers are species that alter the availability of resources for other species by altering biotic and abiotic factors, and modifying, maintaining, and creating habitats (Jones et al. 1994). Kinlaw and Grasmueck (2012) provided extensive evidence of the engineering role of burrowing, wherein they constructed cavity casts to demonstrate the depths and shapes of burrows, along with their use by other species.

Although numerous studies have examined the dynamics and ecological genetics of gopher tortoises populations (Knapp et al. 2018), fewer have demonstrated the unique effects that burrowing by gopher tortoises has on plant communities and soil fertility. Kaczor and Hartnett (1990) found substantial differences in herb community cover and composition from gopher tortoise activity, along with generally lower soil fertility, soil organic matter, and acidity. In particular, they found that gopher tortoise-mediated disturbances increase seed recruitment of *Pityopsis graminifolia* (narrowleaf silkgrass), a common rhizomatous member of the Asteraceae.

Because of the fire exclusion that is often dictated by the urban interface (Francos et al. 2019), the longleaf pine stands of nature trails adjacent to the UWF campus proper have had their open matrix filled with dense hardwood species. Thus, the only appropriate habitat available for successful

establishment of gopher tortoise burrows (i.e., open canopy with herbaceous cover) is coincidental with right-of-way areas, a phenomenon that has been reported at several sites (Hermann et al. 2002; Baskaran et al. 2006). Previous surveys at the UWF have identified numerous active gopher tortoise burrows, all of which are found in the open vegetation structure of power line right-of-ways.

The purpose of this study was to examine gopher tortoise and longleaf pine populations in the urban interface of a college campus. More specifically, we addressed the following questions: (1) what is the effect of burrowing by gopher tortoises on herbaceous plant communities? (2) how does soil fertility respond to redistribution by burrow creation? (3) what is the age structure of longleaf pine on the UWF campus?

Methods

Study site

This study was carried out on the campus and property of the University of West Florida (UWF), Pensacola, Florida (30° 33' N, 87° 11' W). During its initial 4 years beginning in 1963, the campus was constructed in just over 400 ha of second-growth longleaf pine uplands, with mixed southern oak species, particularly *Quercus virginiana* (live oak). As described by the designer, construction of the campus, especially roads and parking lots, was “designed to fit into the natural landscape...significant trees were left in place...woven into the natural contours” (Jarvis 2008).

Field sampling

Outside the UWF campus proper (i.e., permanent buildings, parking lots, and roads), UWF property comprises a network of walking trails, some of which lead to power line right-of-ways. Within these open areas, 16 gopher tortoise burrows were identified and established as study units. For each unit, three distinct habitat types were sampled: apron (soil redistributed by burrowing), burrow (area just above the burrowed hole), and matrix (unaltered area adjacent to the burrow). One square 0.1 m² quadrat was placed in each sample type within which all vascular plants were identified and measured for plant density. Plant identifications were confirmed with specimens from the UWF Herbarium (UWFP—James Burkhalter, curator). Mineral soil was taken to a 5-cm depth within each sample type per burrow unit with a 2-cm diameter soil corer. Soil was air-dried to a constant weight and shipped to the University of Maine Soil Testing Service and Analytical Laboratory for determination of cation exchange capacity (CEC), organic matter (OM—loss on ignition), and pH (CaCl₂ buffer). Available NH₄⁺ and NO₃⁻ were determined colorimetrically by Flow Injection Analysis following

KCl extraction. Macronutrients (P, Ca, Mg, K), micronutrients (Fe and Mn), and Al were determined via inductively coupled plasma optical emission spectrometry following extraction with NH₄Cl.

To determine the age structure of longleaf pines at UWF, all stems ≥ 2.5 cm diameter at breast height (DBH) were measured for DBH. Sampling for this part of the study was carried out on UWF campus proper, including all parking lots, permanent buildings, and other structures (e.g., athletic facilities), but excluding the areas surrounding the trails that led to gopher tortoise burrows. In all, over 2100 stems were measured. Age for each stem was estimated from an algorithm for age versus DBH created for longleaf pine, based on increment coring and DBH measurement of >400 longleaf pine stems (WJ Platt, personal communication):

$$\text{Age} = 2.9 \times \text{DBH} - 7.7$$

Age structure was determined by constructing histograms of relative numbers of stems within each of 25-year age classes.

Data analysis

To assess variation in plant communities among sample types—apron, burrow, and matrix—density of each species was average across sample type and importance values (IVs) were calculated as relative density (%) in each type. Means for plant density and soil variables were compared among sample types via analysis of variance, followed by least significant difference tests (Zar 2009). To further assess spatial variability of soil variables among sample types, soil data were subjected to principal components analysis using Canoco 5.11, Windows release (Šmilauer and Lepš 2014).

Results and discussion

Gopher tortoise study

Although plant density did not vary significantly between burrow and matrix sample types, which was ~ 17 stems/0.1 m², density averaged ~ 3 stems/0.1 m² the apron samples (Table 1). Matrix/burrow sites were co-dominated by mixed grasses—especially *Andropogon virginicus*—and ruderal forbs, including *Polypremum procumbens*, *Leucospora multifida*, and *Pityopsis graminifolia*. By contrast, apron sites were overwhelmingly dominated by *Pityopsis graminifolia*, with an importance value (IV) of nearly 40% (Table 2).

Similar patterns of contrast among sample types were found for soil analytes. That is, there were no significant differences for any measured soil variable between burrow and matrix samples, but numerous significant differences between means for apron soil versus burrow/matrix soil. In general, means for (1) OM, CEC, Mg, Mn, Fe, and Al were

Table 1 Means (± 1 SE) of soil variables for sampling areas around gopher tortoise burrows

Plant/soil variable	Apron	Change	Burrow	Matrix
Density (plants/0.1 m ²)	2.5 \pm 1.3^a	↓	17.6 \pm 2.4^b	16.9 \pm 2.2^b
Organic matter (%)	1.13 \pm 0.14^a	↓	1.98 \pm 0.18^b	2.20 \pm 0.20^b
Cation exchange capacity (meq/100 g)	0.63 \pm 0.12^a	↓	1.51 \pm 0.29^b	1.51 \pm 0.21^b
pH	6.36 \pm 0.02^a	↑	6.21 \pm 0.04^b	6.18 \pm 0.03^b
NH ₄ -N (μ g/g)	3.21 \pm 1.40		2.11 \pm 0.24	3.08 \pm 0.82
NO ₃ -N (μ g/g)	0.83 \pm 0.23^b	↑	0.23 \pm 0.07^a	0.24 \pm 0.08^a
S (μ g/g)	8.13 \pm 1.73^b	↑	4.08 \pm 0.37^a	3.61 \pm 0.24^a
P (μ g/g)	0.16 \pm 0.02^a	↓	0.36 \pm 0.05^b	0.38 \pm 0.04^b
Ca (μ g/g)	77.3 \pm 23.3	↓?	176.3 \pm 59.6	174.0 \pm 42.8
K (μ g/g)	17.2 \pm 2.8		16.3 \pm 2.2	17.3 \pm 3.3
Mg (μ g/g)	14.3 \pm 1.6^a	↓	21.9 \pm 3.5^b	22.1 \pm 3.6^b
Mn (μ g/g)	3.4 \pm 0.4^a	↓	5.7 \pm 0.7^b	7.2 \pm 0.8^b
Fe (μ g/g)	2.2 \pm 0.2^a	↓	4.9 \pm 0.6^b	5.1 \pm 0.6^b
Al (μ g/g)	40.0 \pm 4.2^a	↓	52.2 \pm 6.1^b	51.8 \pm 4.9^b

Values in bold are for variables exhibiting significant differences among areas, based on analysis of variance. Means for a given variable with the same superscript are not different at $P < 0.05$. For convenience, arrows indicate significant increases (\uparrow) and decreases (\downarrow) for apron means relative to burrow and matrix means

significantly lower in apron soils, (2) pH, NO₃, and SO₄ were higher in apron soils, and (3) NH₄, Ca, and K did not vary significantly among soil types (Table 1).

Ordination revealed a high degree of similarity among apron soils, with dense clustering in ordination space associated with higher pH and extractable NO₃. There was higher spatial variability among burrow and matrix soils compared to that of apron soils. Principal variability among burrow and matrix soils was associated with extractable Al/base cation gradients and decreasing pH/increasing Mn, P, and OM (Fig. 3).

Clearly, burrowing by gopher tortoises has greatly altered the structure and composition of plant communities, as well as the fertility and chemistry of mineral soil, at UWF. Although there was some degree of spatial variability in species dominance among burrow/matrix areas of the 16 sampled sites, the apron areas were of consistently low plant density (Table 2). Some aprons had no plants, but those with plants were typically dominated by *Pityopsis graminifolia*. This species has been found in conjunction with gopher tortoise burrows in several studies in Florida (Hartnett 1987; Kaczor and Hartnett 1990; Aresco and Guyer 1999) and is often associated with disturbances, such as fire (Brewer and Platt 1994). More specifically, however, its successful establishment from seed has been hypothesized to require small-scale disturbances, such as burrowing (Kaczor and Hartnett 1990). Our results support this hypothesis.

Working in gopher tortoise populations at the University of South Florida Ecological Research Area (Hillsborough County, 28°05'N; 82°00'W), Kaczor and Hartnett (1990) found notable responses of soil resources to burrowing, including an increase in pH, but also decreases in all other

soil analytes exhibiting a significant response, i.e., K, NH₄, NO₃, Ca, Mg, Fe, Mn, OM. Our results were similar to these, but also contrasted in several ways. Similarities include an increase in pH and a general decrease in soil cation fertility (and CEC), OM, micronutrients, and Al. It should be noted for our results that, while not a significant difference, mean Ca was >2-fold lower in apron soils. Thus, it is possible that this was a burrowing effect masked statistically by high spatial heterogeneity among sampled burrows. Contrasts of our results with those of Kaczor and Hartnett (1990) include a lack of response of NH₄ and an increase in NO₃ and extractable S.

Though there was an overall decline in fertility, the most prominent response was a change in the relative balance between essential nutrients. That is, although there were decreases in base cation availability, there were nearly 2-fold increases in availability of N. The principal mechanism for these changes appears to be less about innate changes in intact soil, but rather that soil of lower fertility becomes redistributed from depths to the surface (Kalisz and Stone 1984). Although not measured in this study, burrows can extend down to 2 m (Mushinsky et al. 2006). Net nitrification and the increased levels of soil NO₃ are common responses to a wide variety of soil disturbances (Gilliam et al. 2010).

These responses have important implications for the recolonization of plants to the apron of each burrow. Recolonization can be rapid and dependent on the status and condition of the burrow (Guyer and Hermann 1997). Working in Eglin Air Force Base, which includes expansive longleaf savannas under fire management and is ~62 km east of UWF campus, Goodman et al. (2018) determined that burrows

Table 2 Plant species importance values (%), by site type, associated with gopher tortoise burrows

Species	Apron	Burrow	Matrix
<i>Andropogon virginicus</i>		12.1	17.0
<i>Panicum</i> sp.	7.5	11.0	11.4
<i>Polypremum procumbens</i>	10.0	13.2	7.4
<i>Leucospora multifida</i>		1.4	6.6
<i>Poa</i> sp.		13.5	6.3
<i>Solidago</i> sp.		2.1	6.3
<i>Licania michauxii</i>		1.8	5.9
<i>Pityopsis graminifolia</i>	37.5	7.5	5.9
<i>Rubus trivialis</i>		3.2	5.2
<i>Danthonia sericea</i>	7.5	6.8	4.8
<i>Stellaria media</i>	12.5	2.5	3.7
<i>Tragia smallii</i>		4.3	3.7
<i>Aristida beyrichiana</i>	2.5	1.1	3.3
<i>Lechea mucronata</i>	12.5	3.6	2.6
<i>Alternanthera brasiliana</i>			1.8
<i>Trichostema dichotomum</i>		2.5	1.8
<i>Chrysopsis hyssopifolia</i>			1.5
<i>Pinus palustris</i>		0.7	1.1
<i>Smilax</i> sp.		2.1	1.1
<i>Lupinus villosus</i>		0.4	0.7
<i>Gelsemium sempervirens</i>	7.5	1.1	0.7
<i>Ceanothus americanus</i>		1.4	0.4
<i>Cytisus racemosus</i>			0.4
<i>Plantago lanceolata</i>			0.4
<i>Aster linariifolius</i>		2.1	
<i>Cynodon dactylon</i>		1.1	
<i>Cenchrus echinatus</i>		2.5	
<i>Heterotheca subaxillaris</i>	2.5		
<i>Mimosa pudica</i>		1.4	
<i>Polygonum cuspidatum</i>		0.4	
<i>Rhynchosia reniformis</i>		0.4	
Total	100.0	100.0	100.0

remain functional up to 5 years, generally collapsing after that, with longevity typically varying with soil texture (Guyer and Hermann 1997; Castellón et al. 2018). The extreme coarse-textured nature of sandy soils at UWF suggests that collapse may occur within 3–4 years.

The ubiquitous dominance/co-dominance of *Andropogon virginicus* in both matrix and burrow samples indicates that these study sites are in a relatively uniform state of secondary succession (Keever 1983; Christensen and Gilliam 2003). The contribution of burrowing in this context is to create discrete patches of 1–2 m² that re-initiate secondary succession, as well as increasing the degree of spatial heterogeneity that maintains high plant diversity (Hutchings et al. 2003), and enhancing the success of early-successional species, such as

Pityopsis graminifolia, that both develop from seed and require the open habitat of aprons.

Longleaf pine study

Sampling longleaf pine populations on UWF campus proper (i.e., excluding the areas encompassing the nature trails that lead to the gopher tortoise burrows) yielded 2165 stems measured for DBH. When estimated for age, the age-class distribution indicates that >80% of all stems were between 50 and 125 years old (Fig. 4). The oldest tree was just under 200 years of age. When adjusted for actual area sampled, stem density was ~64 stems/ha. Although this value is understandably a lower density than natural stands (e.g., 120–140 stems/ha—Gilliam and Platt 1999, Gilliam et al. 2006), it is in line with tree densities in other urban settings, i.e., 40 to 100 stems/ha (Roman et al. 2017).

Considering the long-unburned condition typically associated with urban interfaces (Francos et al. 2019), it is not surprising that the age-class pattern for UWF resembled that of old-growth longleaf pine stands under chronic fire exclusion and contrasted sharply with stands under a frequent fire regime (Fig. 3). Although this may appear to bode poorly for the future of longleaf at UWF, longleaf pine is a long-lived

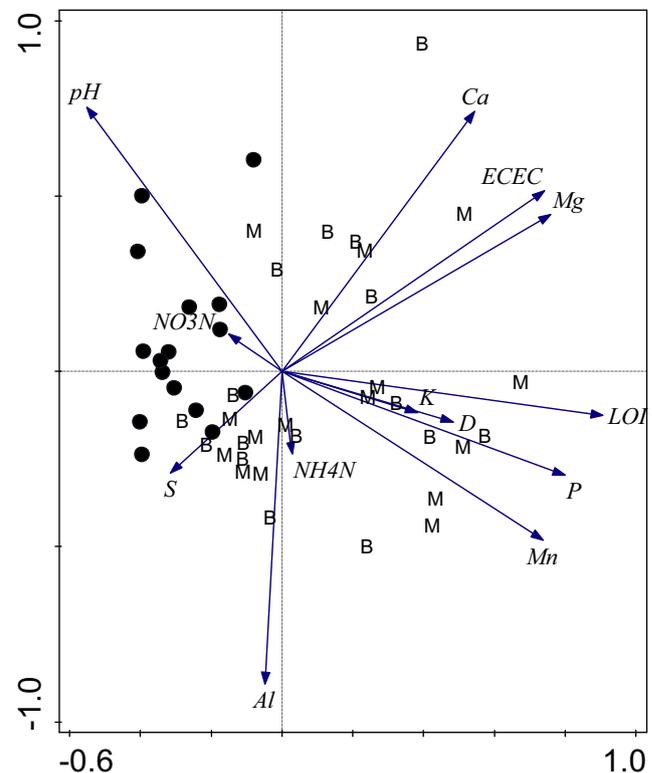


Fig. 3 Principal components analysis of soil variables and plant density ('D') for matrix ('M'), burrow ('B'), and apron (closed circles) samples. For vectors, element symbols are extractable concentrations of stated elements, 'ECEC' is effective cation exchange capacity, and 'LOI' is loss-on-ignition organic matter

species, with stems >400 yr old reported for the Boyd Tract, an old-growth site in North Carolina (Gilliam et al. 1993). Thus, it is likely that, in the absence of major disturbances (e.g., tropical storms/hurricanes), these pines should remain as a prominent part of the campus landscape well into the distant future. Indeed, there are sections of the campus that are unreachable by the mowing activities of the UWF physical plant wherein successful establishment of longleaf juveniles—which were not included in our sampling—is occurring. Indeed, it is strongly suggested that these areas be permanently protected from mowing.

Synthesis and future recommendations

Although the gopher tortoise and longleaf pine studies on the UWF campus may appear as separate endeavors, they are connected regarding future recommendations. Confinement of gopher tortoise populations to the right-of-way areas arose from the chronic fire exclusion that is characteristic of urban interfaces (Francos et al. 2019), and which has occurred in this region since the cessation of logging between 1870 and 1930 (Knight et al. 2011). For the longleaf stands of the nature trails area, this has led to the filling in of the otherwise open matrix with dense hardwoods, relegating gopher tortoise populations to the open vegetation structure of the right-of-ways. On the other hand, our data for burrowing effects mirror those of studies in more natural settings (Kaczor and Hartnett 1990; Hermann et al. 2002), namely that soil fertility is greatly altered in ways that increases spatial heterogeneity, maintaining a patchwork of microsites of varying successional stage.

Future recommendations for these areas focus on the manual/mechanical clearing of hardwood trees and shrubs of longleaf stands immediately adjacent to power line right-of-ways. This would not only allow gopher tortoise populations to move into newly-open areas, but would also provide a

unique research opportunity to study and monitor such activity.

For the campus proper, the filling in process of the stands of the nature trails has been prevented by the construction of the campus itself, with permanent structures, parking lots, walk ways, and green spaces which are mowed with regular frequency. The result has been somewhat of a paradox, i.e., that pines within these campus areas, despite their unburned state, resemble the stand structure of longleaf stands under a frequent fire regime (Fig. 1). What is lacking, primarily as a result of maintaining of green-space campus lawns, is longleaf regeneration. Not only are intact grassy lawns un conducive to pine seed germination, but mature female cones are continually removed as part of green space maintenance.

Accordingly, future recommendations focus on creating open patches within campus lawns to create opportunities for cone deposition/accumulation and seed germination. Furthermore, not only could these patches be protected from human intervention with small fences, but educational signage also could be added to inform interested individuals about the life cycle of the tree species that once dominated the southeastern United States, occupying a prominent position in the culture and ecology of the region surrounding the campus of the University of West Florida.

Acknowledgements We are indebted to numerous undergraduates at the University of West Florida (UWF), led by Alexandra Fox, Daniel Morris, and Phil Darby, for identifying burrow locations for the gopher tortoise study. We also thank the UWF Office of Undergraduate Research for financial support via the Summer Undergraduate Research Program and the Hal Marcus College of Science and Engineering for further funding for soil analyses. We also thank Jim Burkhalter, curator, UWF Herbarium (UWFP), for his expertise on the flora of Florida.

Compliance with ethical standards

Conflict of interest The authors have no conflict of interest to declare.

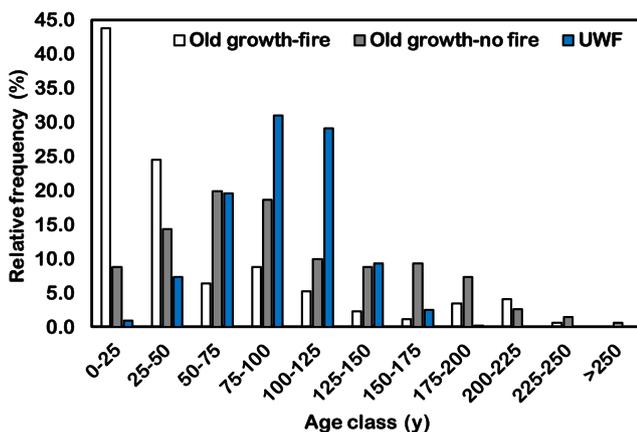


Fig. 4 Age-class frequency distributions for a frequently burned old-growth longleaf stand (Wade Tract, Thomas County, Georgia), a chronically unburned stand (Boyd Tract, Moore County, North Carolina), and UWF campus. Data for old growth stands taken from Gilliam and Platt (1999)

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