Folia Geobot
https://doi.org/10.1007/s12224-024-09440-1

Florida's fiery subtropical grasslands: Growth forms, belowground organs, and post-fire recovery strategies

Steve L. Orzell · Martin Bitomský · Edwin L. Bridges · Brett Budach · Jitka Klimešová · Jana Martinková · Zachary E. Reed · Seth J. Raynor

Received: 31 August 2023 / Revised: 12 December 2023 / Accepted: 10 January 2024

Abstract Fire-adaptive traits in plants of tropical and subtropical grassy ecosystems have been the subject of considerable global research, but only recently studied in pyrogenic Florida subtropical grasslands. Plant growth forms, belowground organs, and post-fire recovery strategies were studied for 198 grassland specialists in peninsular Florida. Community types (dry-mesic, mesic, wet-mesic, and wet) were sampled with 1m^2 plots along the edaphic-hydrologic gradient and the association between these variables and fire-related plant traits was tested using fourth-corner analysis. Caulescent herbs (43), cespitose graminoids (27), and rosette herbs (31) are the most common growth forms among species sampled. Plants with epigeogenous and hypogeogenous rhizomes dominate the sample plots, including matrix graminoids, shrub geoxyles, and an acaulescent rhizomatous fire-resilient palm (*Serenoa repens*). Most species (163; 82%) exhibit resprouting, including 30 facultative resprouters and 133 obligate resprouters. All woody rhizomatous species are obligate resprouters, and 35 ephemeral herbaceous species are obligate reseeders. Community type was a better predictor of species abundances than hydrology, however, hydrology was significantly associated with species traits measured, particularly rhizome texture, with woody rhizomes prevalent in all but the wet sites. Belowground organs (xylopodia, geoxylic suffructices) and growth form were associated with frequent fire and phylogeny, suggesting fire regime as a driver of community phylogenetic diversity. Persistence, rapid resilience and co-occurrence of geoxyles align Florida subtropical grasslands with other global geoxyle grasslands. The old-growth, pyrogenic grassy ecosystems of peninsular Florida are the center of geoxyle diversification on the southeastern US coastal plain.

Keywords Fire adaptations · Fire season · Grassland · Florida · Geoxyle · Belowground storage organs · Resprouting · Plant traits · Post-fire recovery · Floristics · Subtropical · C4 grasses

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12224-024-09440-1.

S. L. Orzell (✉)
Avon Park Air Force Range, Avon Park, FL, USA
e-mail: 69C3FL@gmail.com

M. Bitomský · J. Klimešová · J. Martinková
Institute of Botany of the Czech Academy of Sciences, Průhonice, Czech Republic

E. L. Bridges
Gig Harbor, WA, USA

B. Budach
Sebring, FL, USA

Z. E. Reed
Tampa, FL, USA

S. J. Raynor
Museum of Natural History, University of Colorado, Boulder, CO, USA

Published online: 03 February 2024

Introduction

Old-growth tropical and subtropical grasslands are biodiverse pyrogenic ecosystems with unique species composition, growth strategies, and disturbance regimes. These grassy ecosystems have received increasing attention due to threats from afforestation, climate change, agricultural expansion, invasive species, and alteration of the fire regime (Veldman et al. 2015; Lehmann and Parr 2016; Bond 2016, 2019). Although the global academic focus has been on hyper-diverse, extensive, and economically important tropical grasslands, there also are smaller, isolated, and evolutionary distinct old-growth subtropical and tropical grassland regions world-wide in need of further study. Among these are the subtropical treeless grasslands in south-central Florida, hereby referred to as Florida Subtropical Grasslands (FSGs). These and other grasslands once covered large parts of the southeastern coastal plain (Noss 2013) and are old, climatically buffered infertile landscapes characterized by fire-adapted heliophytic graminoids, forbs and subshrubs (Peet et al. 2018). The FSGs are part of the North American Coastal Plain biodiversity hotspot (Noss et al 2015; Pullaiah & Bridges, in prep.). Although they resemble other pyrogenic ecosystems of the North American Coastal Plain (e.g. pine savannas), we know little about their fire-adaptations and species traits.

Florida's subtropical grasslands are among the last strongholds for these globally endangered biodiverse ecosystems, with south-central Florida having the largest extent of subtropical humid grasslands in the United States. Until recently, the distinctiveness of Florida grasslands was disputed by some (Abrahamson and Harnett 1990) as an artifact of pine clearcutting. Evidence for extensive grassy, nearly treeless regions in south-central Florida exists in presettlement land and timber surveys, early maps, and historic and contemporary accounts. Indeed, FSGs were delineated in public land surveys of the 1850's (Bridges 2006a, b) prior to settlement and from historical accounts during early settlement (Harshberger 1914; Harper 1921, 1927). According to presettlement surveys, about 7910 km^2 of the state was mapped as prairie (grassland), with an additional 158 km^2 mapped as open pine savanna (Stephenson 2011). Timber cruise surveys by Consolidated Naval Stores Company from 1918-1921 prior to turpentine production and logging in south-central Florida, show large areas devoid of pine timber which coincidentally overlap with the presettlement survey mapped "prairies". Modern accounts of Florida grasslands highlighting landscape, historical, fire regime and biota differences are numerous (Stephenson 2011; Bridges 2006a, b; Platt et al. 2006; Noss 2006, 2013; DeSelm and Murdock 1993). These grasslands were often bordered by pine savannas with a sparse canopy of *Pinus palustris* or *P. densa* over much of central Florida, which we consider collectively as the south-central Florida savanna grassland ecoregion, based on its similar species pool. The three geographically distinct grassland regions in peninsular Florida (Kissimmee River, Desoto-Glades, and Myakka) cover 5000 km^2 of nearly treeless landscapes, and have been referred to as "Florida dry prairie" (Bridges 2006b). The largest contiguous grasslands in south-central Florida were on the uplands above the Kissimmee River floodplain, an area covering 2037 km^2 (Fig. 1).

Both fire and extreme seasonal changes in hydrology interact to maintain the treeless nature of FSGs, on both a broader landscape and finer plant community level. In regions of south-central Florida with poorly-drained, flat, grassy terrain, early lightning season-ignited wildfires spread across vast areas with no major inflammable barriers. These nearly annual or biennial wildfires occurred when rainfall free intervals reached a maxima at the end of the winter dry season, coinciding with annually low groundwater levels and droughty conditions that enabled their spread (Platt et al. 2006). Upon onset of the summer wet season, rising water levels eventually saturate and often inundate the soil, producing conditions that negatively impact pine reproduction (Menges and Marks 2008) and favor herbaceous species (Platt et al. 2006). In peninsular Florida, it was found that plant community types were strongly correlated to edaphic-hydrologic variables on a landscape level (Huck 1987; Orzell and Bridges 2006a). Furthermore, it was determined that hydrology had fine scale differential effects on herbaceous and woody species richness in a Neotropical savanna (de Oliveira Xavier et al. 2019). None of these studies attempted to correlate plant traits with the hydrology gradient in FSGs.

Plant traits that enable survival from fire have been described for fire prone ecosystems world-wide (Clarke et al. 2015; Clarke 2016; Pausas et al. 2016, 2018; Freschet et al. 2021; Guerrero-Ramirez et al. 2020; Wigley et al. 2020; Paula et al. 2009). In Florida, such studies

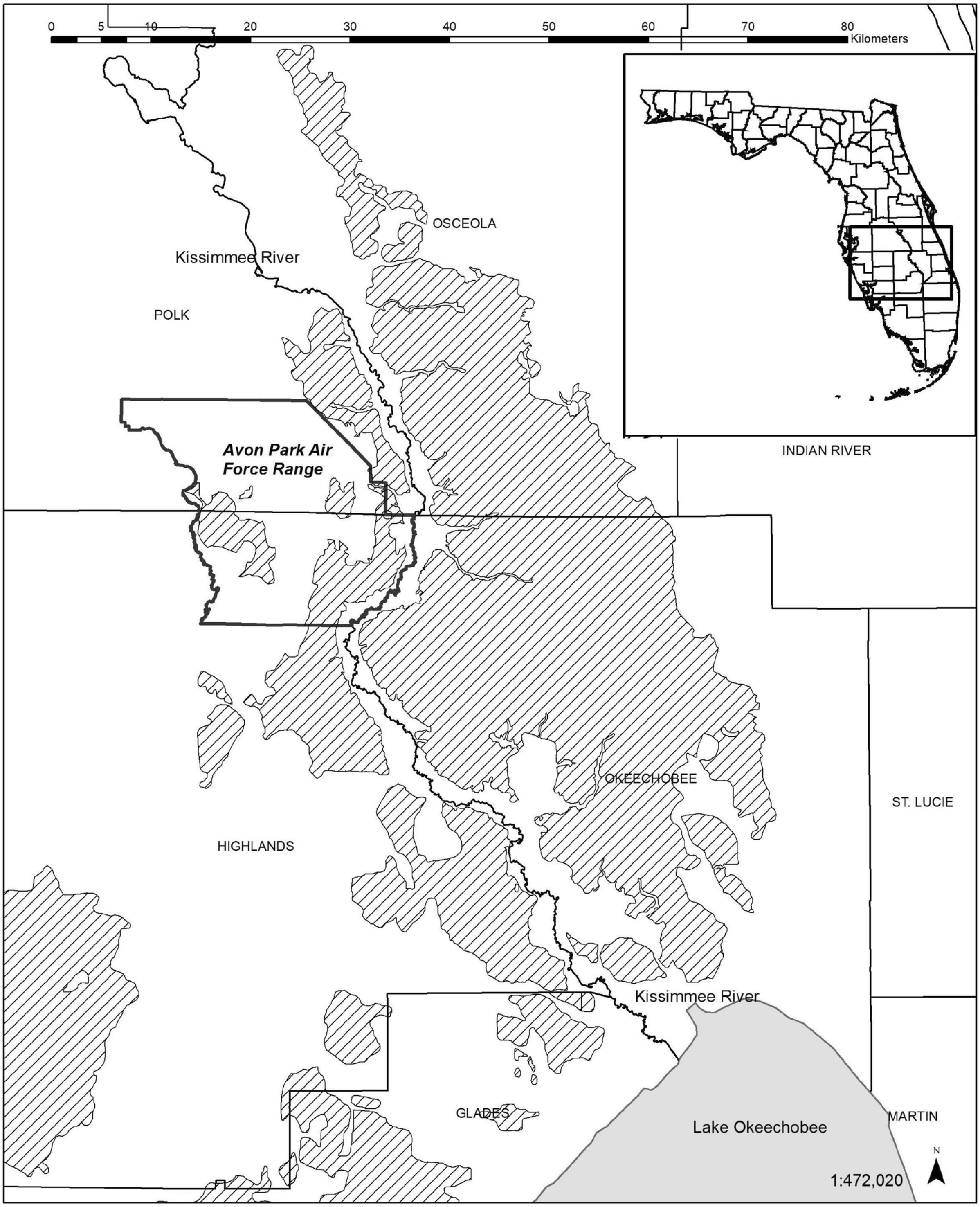


Fig. 1 Location of study site at Avon Park Air Force Range in south-central Florida. The hatching delineates the presettlement extent of subtropical grasslands within the Kissimmee River region that once covered 2,037 km^2 in south-central Florida

have focused on longleaf pine (*Pinus palustris*), a foundation species, wiregrass (*Aristida beyrichiana)*, a keystone groundcover species, and saw-palmetto (*Serenoa repens*) (Abrahamson 1984b, 1995; Abrahamson and Abrahamson 2006; Fill et al. 2012; Wahlenberg 1946; Shibu et al. 2006). Post-fire recovery strategies and belowground organs were studied for Lake Wales Ridge xeric plant communities (Florida scrub and sandhills) (Abrahamson 1984a, b; Menges and Kohfeldt 1995; Maguire and Menges 2011; Menges et al. 2020; Saha et al. 2010) and for a smaller set of species from other Florida plant communities (Hierro and Menges 2002; Maliakal et al. 2000; Abrahamson et al. 2021). Some of these plants also occur in FSGs, particularly the geoxyle shrubs and subshrubs. The largest Florida dataset available for underground storage organs was obtained by Diaz-Toribio and Putz (2021), who assessed non-structural carbohydrates stored in belowground organs of 100 species from xeric pine sandhills and broadly classified belowground organs based on Pate and Dixon (1982), originally developed for southwestern Australia. Plants of FSGs may share many fire-adapted traits with those of other tropical and subtropical grasslands.,

We sought to determine whether 198 grassland specialist of FSGs have similar traits (plant growth form, belowground organs, and post-fire recovery) to other Florida fire-prone ecosystems, or to other subtropical or tropical grassy ecosystems, or if they have fire-adaptation traits unique to FSGs. To do so, we address the following questions:

1) What plant traits and strategies (growth forms, belowground organ types, and post-fire response strategies) occur among FSG plants?
2) Are these plant traits and strategies phylogenetically structured?
3) Do plant communities differ in representation of plant growth forms, belowground organs, or post-fire recovery strategies?
4) Are any of these plant traits or strategies affected by hydrology in FSGs?

Methods

Climate and Fire Regime

Our study area, Avon Park Air Force Range (hereafter AP), is located in south-central Florida, (27˚35' N, 81˚16' W; Fig. 1). The 424 km^2 installation lies north of Lake Okeechobee in the Everglades headwater region and was established during World War II for pilot training.

The climate is seasonal humid subtropical, with an annual mild, dry (winter) and hot, wet (summer) season. On average, the wet season lasts on average 134 days (May 21 to October 1) with 89 ± 27 cm yr^{-1} of rainfall, and the dry season lasts on average 231 days (October 2 to May 20) with 42 ± 15 cm yr^{-1} of rainfall (Slocum et al. 2010). The mean annual temperature at the nearest station (Avon Park 2 W; 27° 36'N, 81° 32'W) from 1942-2005 was 22.8° C, with the highest daily mean (27.8° C) in August during the wet season, and the lowest (16.3° C) in January during the dry season. Tropical depressions, storms, and hurricanes can bring strong winds and locally heavy rainfall, especially during August and September from Cape Verde tropical systems (Chen and Gerber 1990) that originate in the Atlantic Ocean. Between 1851 and 2004, fourteen land falling hurricanes have passed within 50 miles or less of Avon Park AFR (Blake et al. 2005).

A hyperseasonal climate allows for rapid fuel accumulation during the wet season and curing of fuels during the dry season. Peninsular Florida is a global hotspot for cloud-to-ground lightning strikes, which are the ignition source for wildfires during the fire season (Platt et al. 2015). Lightning-ignited wildfires during the transition (late April thru mid-June) between the dry season and the wet season historically burned large areas (Platt et al. 2015). This seasonally-cued fire timing is an important evolutionary driver, producing a fire-filtered flora and pyrogenic plant communities. AP has a drought-driven fire regime characterized by high frequency, low severity fires, with annual to biennial lightning-ignited fires prior to human settlement (Huffman 2006). From the early 1940s through the 1980s there was widespread fire suppression in central Florida (Duncan et al. 1999, 2009; Fowler and Konopik 2007). However, during this period AP had an uninterrupted history of lightning- and military-ignited wildfires, followed by frequent prescribed ignitions for natural resource management. This uninterrupted fire history, without any long period of fire suppression, makes it ideal for study of fire adaptations.

Geologic, Edaphic, and Hydrologic Setting

AP is on the Osceola Plain, a poorly to very poorly drained terrace from 15-22 m elevation, with few natural barriers to the spread of wildfires. The surficial geology is mapped as undifferentiated Quaternary sediments of fine to coarse grained sands, sandy clays and clayey sands with admixtures of organics (Green et al. 2019). The soils are acidic, nutrient poor, sandy to sandy clay Spodosols and Alfisols. Poor drainage and impermeable subsurface layers (most commonly the spodic soil horizon) result in soil saturation or shallow inundation during the summer wet season and alternate with long winter dry season droughty soils. These create stressful physiological conditions for plants due to low water retention capacity, oligotrophy, and waterlogging, with seasonally high water tables that impact the distribution of herbaceous and woody species (de Oliveira Xavier et al. 2019) in hyperseasonal grasslands (Sarmiento and Monaterio 1983).

Biodiversity Setting

AP is a cornerstone of conservation in south-central Florida due to its size and, along with nearby conservation lands, provides some protection to over 319,700 hectares of globally significant biodiversity (Stein et al. 2008; Sorrie and Weakley 2006). About 38,000 ha of natural vegetation at AP is subject to recurrent fire. The 116,510 ha of grasslands within south-central and the southern peninsular Florida comprise the largest subtropical grassland region in the United States. AP also contains one of the largest exemplary remnants of longleaf pine (*Pinus palustris*) savannas in the southeastern United States (Sorrie and Weakley 2006; Peet et al. 2018), supports many federally listed species (Stein et al. 2008), and has some of the largest representative landscapes of pyrogenic ecosystems in peninsular Florida.

Vegetation Sampling

We classified 198 vascular plant species of FSGs as to: 1) plant growth forms; 2) belowground organs; and 3) post-fire recovery strategies. We used datasets created from quantitative vegetation plot sampling at burned sites over a 28-year period (1995-2023) and 6 years (2017-2022) of post-fire recovery sampling at AP. The vegetation plot sampling was used in assessment of community level relationships of plant growth forms and belowground organ types. Post-fire recovery sampling data allowed us to classify post-fire recovery strategies.

Quantitative vegetation sampling was timed to correspond with peak post-fire flowering of graminoids and forbs at the end of the wet season. 731 plots were sampled within intact groundcover at AP, in linear transects of 50 to 100 meters, with 1.0 m^2 plots sampled every 5 meters. Transects were placed in areas burned during the year of sampling at sites lacking obvious signs of artificial disturbances or hydrologic impediments. Percent cover was estimated for each species from vertical projection of the aboveground plant material with the square meter, and for unvegetated plot substrate (i.e., bare ground or surface rhizomes). All vascular plant species within each plot were recorded and percentage cover, bare ground and surface rhizomes were visually estimated at each plot. Field data was recorded on a field sampling form that was later computerized into Microsoft Access for processing and analysis. Plant nomenclature follows Weakley et al. (2023).

Hydrology classes were assigned to plots based upon soil sampling, field evaluation of the highest wet season water table levels, published soil series drainage classes, and hydraulic conductivity descriptions. We recognized hydrologic variables at two scales, a coarse plant community with four types, and a finer-scale with nine vegetation types (Table S1). The species composition and environmental characteristics of the first six of these are described in detail by Orzell and Bridges (2006a).

Post-fire Recovery Sampling

We described and classified post-fire recovery traits for FSG vascular plant species. We sampled 14 sites averaging 3.0 ha each on dry-mesic to wet-mesic soil types at AP which were burned at various times between December and July, with sampling starting within one week post-fire at each site.

Following fire, measurements of leaf length, stem height, and/or number of culms were compiled, and phenology data were collected for up to 10 individuals of each species at each site. In the first year post-fire, these were sampled at 7-10 day intervals until about 100 days post-burn, at which point sampling frequency decreased gradually to about once a month by the end of the first growing season, and continued once every two months through the second year post-burn. Sampling began in 2017 and has continued through 2023, with all sites experiencing additional fires, some in different seasons.

At each site, a central photo point was marked using an angled aluminum stake. Four additional stakes were placed 5 meters from the central stake in the four cardinal directions. At the central stake, a camera was placed atop a 75 cm tripod and photos were taken of the surrounding vegetation at each sampling event, with a 2 meter PVC pipe marked at 20cm intervals placed at the directional stakes for each photo. This provided both consistency and scale for photo-documentation of the general aspect and changes in phenology and height of the vegetation.

To classify post-fire recovery strategies we used the systems of Pausas et al. (2016) and Clarke et al. (2015), independently assessing species with each classification in our initial evaluation, based on resprouting and seedling observations from 6 to 18 months post-fire. Pausas et al. (2016) describe four post-fire recovery strategies: obligate resprouters, facultative seeders, obligate seeders, and post-fire colonizers. Clarke et al. (2015) describe five post-fire recovery strategies: resprouters, non-resprouters, variable [resprouters], post-fire seeders, and post-fire non-seeders. By adapting criteria provided in both papers, we ultimately classified the FSG flora into three broad categories: obligate resprouters, facultative resprouters, and obligate seeders (Supplemental Information S1). Obligate resprouters rely on resprouting following fire and often lack fire resistant seedbanks. Facultative resprouters are species which post fire regeneration strategies include both re-seeding recruitment and resprouting recovery. Obligate seeders do not exhibit any resprouting following fire, but instead rely on seeding for post-fire regeneration.

Belowground Storage Organs & Plant Growth Forms Sampling

We collected belowground storage organs of 198 vascular plant species following the protocols in Klimešová et al. (2019), and Pausas et al. (2018), and used the rhizome terminology in Klimešová and Klimeš (2007). Most excavations were made during the winter dry season of 2016-2017, with supplemental excavations in 2021. For each plant species, representative individuals were hand-excavated to the deepest practical depth. We have not unearthed an entire genet of any of the large geoxyle species, since their areal extent, tough woody tissues, and mixed growth with other species make this impractical. Each specimen was photographed on a white or beige background with a ruler or a scale bar with 1 cm increments, before being dried and stored. Using the published literature, photos, and observations at earlier dates, each species was then classified by growth form (Palmquist et al. 2014; Pausas et al. 2018) and type of belowground organ (Klimešová et al. 2019) (Supplemental Information S2 & S3). Definitions of specialized terms are in S2. For belowground organs we also distinguished two rhizome textures (herbaceous and woody), where soft tissue is herbaceous in contrast to hardened lignified/woody tissue. Therefore, we call woody rhizomes woody but also we include lignified rhizome as in saw-palmetto (*Serenoa repens*) as a woody rhizomatous shrub, despite it lacking classic secondary thickening of the vascular cambium. We also classified rhizome extent based three lengths of lateral spread in rhizomes: short (up to 5 cm). medium (from 5 to 25 cm), and long (more than 25 cm). Rhizome type refers to epigeogenous or hypogeogenous rhizomes (Klimešová and Klimeš 2007).

Data Analysis

To examine species based on their belowground organs, plant growth form, and post-burn recovery strategy (Table S1), we calculated their relative occupancy rates (total cover of a category across all sites divided by the total cover of all categories together) when vegetation plots were sampled within 12 months post burn. Overall effects of site characteristics (hydrology and vegetation type, (Table S2) on species abundances were tested using multivariate generalised linear models (Wang et al. 2012; Warton et al. 2012). We fitted the models assuming negative binomial distribution with a logarithmic link function and unknown over dispersion parameter, which has been shown to have desirable properties when analysing multivariate abundance data (Wang et al. 2012; Warton et al. 2012). Statistical inference was based on Akaike's information criterion (AIC), not on P-values (due to very long computation times to estimate these). We considered two or more AIC units as a decisive difference between the model including site characteristics as a predictor and the null model (with no predictors). Because the considered site characteristics provided overlapping information in some cases (Table S1), the explanatory power of all predictors of species abundances was examined using commonality analysis and hierarchical partitioning (Lai et al. 2022). For each predictor, these statistical tools estimate it's unique (separated from joint effects with other predictors) and shared (the effect common to all predictors) contributions. These contributions can be used to calculate the independent effect of a predictor (sensu hierarchical partitioning; Chevan and Sutherland 1991; Lai et al. 2022) to assess the relative importance of predictors with some degree of collinearity.

To test whether species with different belowground organs, plant growth forms or post-burn recovery strategies tended to prefer or avoid sites with different hydrology or vegetation type, we performed fourth-corner analysis (Legendre et al. 1997; Dray and Legendre 2008). To study trait-environment links, fourth corner analysis measures the relationship between three matrices, one describing species x site abundances (L matrix), one describing site (environmental) variables (R matrix) and one describing species traits (Q matrix). Significance testing was based on chi-squared (X^2) statistic and 999 permutations, and Holm correction (Holm 1979) for multiple testing was applied. We used the permutation model that permutes both values of sites and species because it does not have inflated type I error (Dray and Legendre 2008). All site and species characteristics were categorical variables (factors). In order to obtain as precise fourth corner results as possible, species belonging to very rare categories were omitted. The arbitrary threshold to keep a category for the analysis was if four and more species belonged to this category. For example, when linking belowground organ to hydrology and vegetation type, only annuals, species with epi- and hypogeogenous rhizomes and species with main root were considered (Table S2).

All analyses and graphics in R 4.2.1 (R Core Team 2022) were used in the packages: *ade4* 1.7-19 (Dray and Dufour 2007) to perform fourth corner analysis, *ggplot2* 3.4.0 (Wickham 2016) and *ggtree* 3.4.2 (Yu et al. 2017) to draw graphics, *mvabund* 4.2.1 (Wang et al. 2012) to perform multivariate generalised linear models, *rdacca.hp* 1.0-8 (Lai et al. 2022) to perform commonality analysis and hierarchical partitioning, and *vegan* 2.6-2 (Oksanen et al. 2022) to compute scores for ordination diagrams. We used Pagel's lamba (Pagel 1999) as a measure of phylogenetic signal, which was estimated using the *fitDiscrete* function (*geiger* 2.0.10, Pennell et al. 2014). Species phylogeny was obtained using the *V.PhyloMaker2* package (Jin and Qian 2022).

Results

Species Level Analysis

The most common belowground organs were rhizomes (81 species with epigeogenous and 60 species with hypogeogenous rhizomes) followed by nonclonal perennial plants with main roots (23 species) and annual herbs (23 species). Clonality in herbs and shrubs is high in 151(76%) of the sampled species. Other types of belowground organs (root sprouters, stolons, stem tubers and bulbs) were represented by one to 4 species each (Table S2a). Among rhizomatous plants, long and short rhizomes were similarly abundant while herbaceous rhizomes were more common than woody ones.

The most common growth forms were herbaceous forbs (98 species), with the most common categories being caulescent herbs (43) and rosette herbs (31). Other non-graminoid herbs include species with elongate (medium to long) rhizomes (often clonal) (7), bulbs (1), corms (2), stem tubers (2), xylopodia (9), and hemiparasites (1) (Table S2b). Graminoids are represented by 70 species, these mostly cespitose (27), having single or few culms (23) or rhizomatous (12). The remaining species are shrubs (19), trees (4), ferns (2), vines (4), and lianas (1) (Supplemental Information S2).

The studied species were mainly characterized by an obligate resprouting strategy (133 species) while facultative resprouters (30) and obligate seeders (33) were less common (Table S2).

Evolutionary and Taxonomic Analysis

Florida subtropical grasslands have a species pool of warm-temperate and Neotropical floristic affinities, from which we assessed 198 species in 49 plant families (Table 1), and found the most diverse families being Poaceae, Asteraceae and Cyperaceae (Supplemental Information S3).

Belowground organs were clearly associated with phylogeny in our species pool (Fig. 2A), reflecting deep phylogenetic differences between monocots and dicots. Epigeogenous rhizomes were highly prevalent in monocots (especially in Poaceae) but quite rare in dicots (except for Asteraceae, (Fig. 2A). Post-burn recovery strategies were relatively evenly distributed across the phylogeny (Fig. 2B). Taxonomic classifications underscored the observed differences in growth forms; graminoids were predominately found among monocots, while herbs were chiefly represented in dicots (Fig. 2C).

Community Level Aanalysis

Species with epigeogenous and hypogeogenous rhizomes dominated the sampled plots (Fig. 3A). In terms of growth form, graminoid matrix, shrub geoxylic (e.g. *Quercus minima*) and shrub rhizomatous (i.e. *Serenoa repens*) were the most dominant groups (Fig. 3B). In terms of post-burn recovery strategy, obligate resprouters dominated (Fig. 3C). Considering rhizomatous species only, more species had short (Fig. 4A) and herbaceous (Fig. 4B) rhizomes but the differences were slight. Including any of the site characteristics (hydrology and vegetation type) improved the model fit of species abundances (Table 2) and 72% or more species showed changes in their abundance according to these site characteristics (AIC improved by at least two units compared to a null model with no predictors). In total, hydrology and vegetation type explained around 16% of variability in species abundances. Unique contributions and independent effects were higher for vegetation type (both coarse and fine resolution, Table 2) while the effect of hydrology was mostly shared with them – this is because finer vegetation type levels were basically a combination of hydrology and coarse vegetation type (Table S1). Although vegetation type was a better predictor of species abundances than hydrology, it was hydrology only that was significantly associated with any species

Table 1 Summary of plant families

Family	N of species	% of species
Poaceae	41	20.7
Asteraceae	27	13.6
Cyperaceae	26	13.1
Ericaceae	8	4.0
Xyridaceae	8	4.0
Fabaceae	5	2.5
Hypericaceae	5	2.5
Lentibulariaceae	5	2.5
Polygalaceae	5	2.5
Apiaceae	4	2.0
Eriocaulaceae	4	2.0
Apocynaceae	3	1.5
Euphorbiaceae	3	1.5
Gentianaceae	3	1.5
Melastomataceae	3	1.5
Plantaginaceae	3	1.5
Aquifoliaceae	2	1.0
Burmanniaceae	2	1.0
Campanulaceae	2	1.0
Commelinaceae	2	1.0
Droseraceae	2	1.0
Juncaceae	2	1.0
Lamiaceae	2	1.0
Onagraceae	2	1.0
Orchidaceae	2	1.0
Orobanchaceae	2	1.0
Pinaceae	2	1.0
Rubiaceae	2	1.0
Alismataceae	1	0.5
Annonaceae	1	0.5
Arecaceae	1	0.5
Chrysobalanaceae	1	0.5
Cistaceae	1	0.5
Dennstaedtiaceae	1	0.5
Ebenaceae	1	0.5
Fagaceae	1	0.5
Haloragaceae	1	0.5
Haemodoraceae	1	0.5
Hypoxidaceae	1	0.5
Iridaceae	1	0.5
Liliaceae	1	0.5
Linaceae	1	0.5
Linderniaceae	1	0.5
Lycopodiaceae	1	0.5
Myricaceae	1	0.5
Nartheciaceae	1	0.5

Table 1 (continued)

Family	N of species	% of species
Sarraceniaceae	1	0.5
Smilacaceae	1	0.5
Vitaceae	1	0.5
TOTAL	**198**	**100.0**

traits measured, namely rhizome texture (Table 3b). Species (Table 4) with woody rhizomes avoided wet sites (Fig. 5). In all cases, the information about evolutionary contingency- lambda model - improved AIC (by 15 units and higher) compared to a non-phylogenetic model. Lambda values (belowground organ = 0.88, post-burn recovery strategy = 0.74 and growth form = 0.97) mostly suggest an association of these traits with phylogeny.

Discussion

Within studied Florida subtropical grasslands, plant communities had similar growth forms, belowground organs and post-fire response strategies but differed in rhizome texture, with rhizomes being the most common belowground bud bearing and storage organ. In communities typical for wet sites, woody rhizomes were absent while both woody and herbaceous rhizomes occurred in communities typical of mesic and dry sites. Herbaceous and woody species are uniquely adapted to cope with hyperseasonal water availability

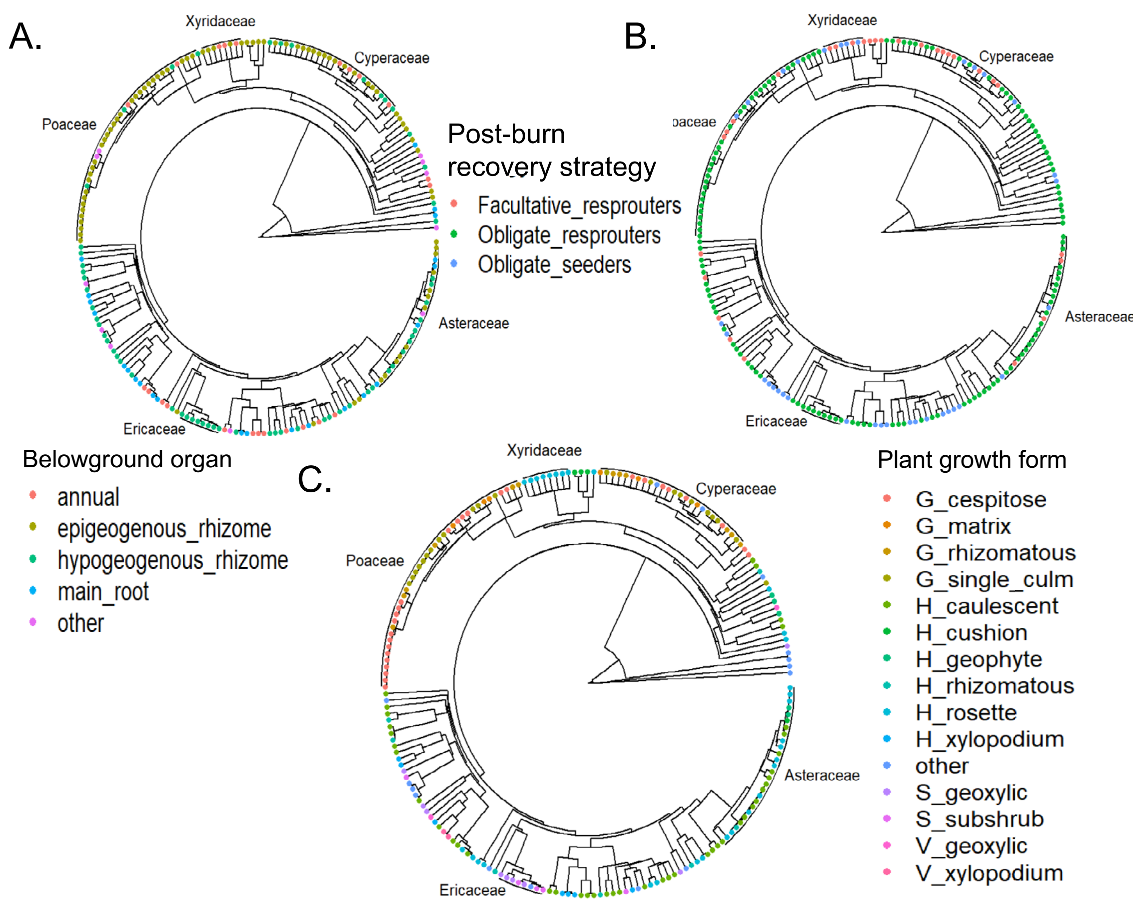


Fig. 2 Species pool phylogenies with the distributions of **A**. belowground organ forms, **B**. post-burn recovery strategy and **C**. plant growth form across the tree. Rare trait categories (represented by less than four species) are merged (the "other" category) to reduce over plotting. Five the most species-rich families of the species pool are indicated to allow orientation. See Supplemental Information S1 and S2 for definitions of terminology

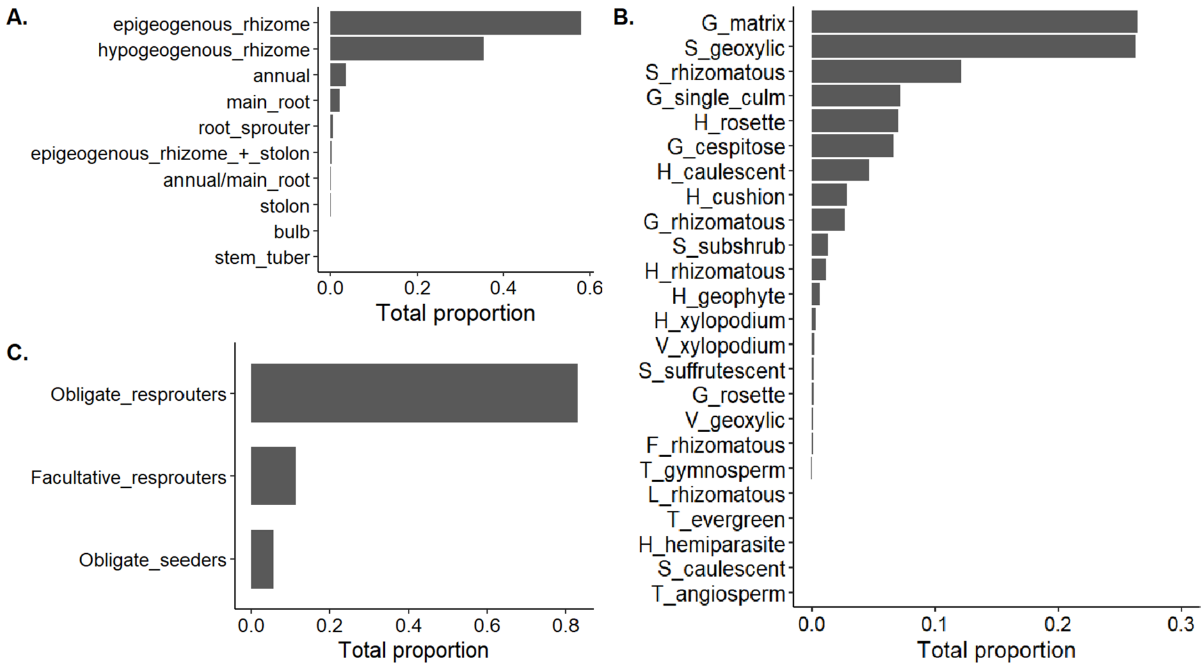


Fig. 3 Total observed proportion (relative occupancy rates) of species belonging to different categories in subtropical Florida grassland plant communities. **A** - belowground organ; **B** - plant growth form; **C** - post-burn recovery strategy. See Supplemental Information S1 and S2 for definitions of terminology

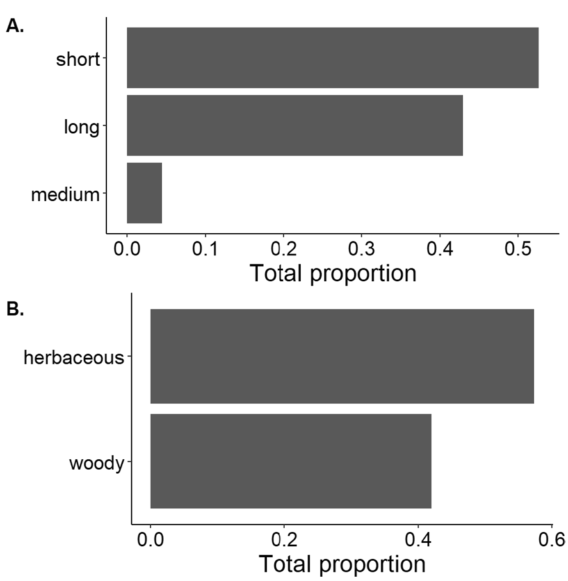


Fig. 4 Total observed proportion (relative occupancy rates) of species belonging to different categories in subtropical Florida grassland plant communities. **A** - rhizome length; **B** - rhizome texture (herbaceous and woody)

and fire (Silva and Batalha 2011). Herbaceous species were more often seeders (annuals) compared to woody species but resprouters prevailed in all community types and among all perennial species (both woody and herbaceous). The studied traits were mainly phylogenetically conservative, i.e. they probably developed recently in the evolutionary history of represented taxonomical groups (monocots vs dicots).

Herbs and Shrubs

The most diverse growth forms in FSGs are caulescent and rosette herbs and cespitose graminoids. In terms of belowground storage organs, epigeogenous and hypogeogenous rhizomes prevail, and obligate resprouters are the most common post-fire recovery strategy. In terms of community dominance, the proportion of growth forms differ from those based on species diversity. Non-dominant small or dwarf interstitial plants (i.e. single culm, rosette, geophytes, matrix graminoids & hemiparasites) are emblematic of grasslands with recurrent fires, declining when fire is less frequent (Palmquist et al. 2014). In south-central peninsular Florida, herbs and shrubs

Table 2 Explanatory power of three community aspects (site hydrology and vegetation type) of plant species abundances. Total variation explained by these community aspects was 0.164. AIC sum = overall model' Akaike's information criterion (the sum of AIC values of all species), AIC improvement = total number of species (and relative number in percentages) in which the tested community aspect improved AIC by at least two units (in comparison with a null model with no predictors), unique contribution = individual effect of a predictor without joint effects with other predictors, shared contribution = total average shared effect of a predictor with other predictors, independent effect = percentage independent effect of a predictor (hierarchical partitioning).

Model metrics	Hydrology	Vegetation type (coarse)	Vegetation type (finer)	Null
AIC sum	105 061	107 268	101 037	110 497
AIC improvement	134 (77%)	126 (72%)	135 (77%)	-
Unique contribution	0.0012	0.0129	0.0528	-
Shared contribution	0.0311	0.0181	0.0482	-
Independent effect (%)	19.7	18.9	61.6	-

Table 3 Significance testing of the fourth corner analysis examining whether plant traits (belowground organ, or post-burn recovery strategy) affected species abundances according to site hydrology and vegetation type

Community aspect	Belowground organ	Plant growth form	Post-burn recovery strategy
a) All species			
Hydrology	$X^2 = 1095$, $P = 0.590$	$X^2 = 3099$, $P = 0.164$	$X^2 = 406$, $P = 0.751$
Vegetation type (coarse)	$X^2 = 1210$, $P = 0.366$	$X^2 = 2245$, $P = 0.355$	$X^2 = 484$, $P = 0.596$
Vegetation type (finer)	$X^2 = 2761$ $P = 0.630$	$X^2 = 5896$, $P = 0.474$	$X^2 = 989$, $P = 0.742$
b) Rhizomatous species only	Rhizome length	Rhizome texture	
Hydrology	$X^2 = 2551$, $P = 0.084$	**$X^2 = 3209$, $P = 0.012$**	
Vegetation type (coarse)	$X^2 = 867$, $P = 0.414$	$X^2 = 836$, $P = 0.414$	
Vegetation type (finer)	$X^2 = 3721$, $P = 0.414$	$X^2 = 4458$, $P = 0.060$	

X^2 chi-squared statistic.

Table 4 Example rhizomatous species with the strongest affiliation to the hydrology

Species	Hydrology
a) Woody rhizome	
Serenoa repens, Quercus minima, Lyonia lucida	Dry-mesic
Asimina reticulata, Ilex glabra, Vaccinium myrsinites	Mesic
b) Herbaceous rhizome	
Andropogon cabanisii, Gymnopogon chapmanianus, Scleria pauciflora	Dry-mesic
Rhexia nuttalii, Rhynchospora fascicularis, Xyris elliottii	Wet-mesic
Dichanthelium leucothrix, Eragrostis elliottii, Fuirena scirpoidea	Wet

with temperate and tropical affinities mix (Long 1974; Long et al. 1969; Orzell and Bridges 2006b) along transition zones producing many geographically unique species assemblages (Allen et al. 2019) in FSGs across subtle edaphic hydrologic gradients (Huck 1987; Carr et al. 2009, 2010). Shrub geoxyles (*Ilex glabra*, *Quercus minima*, *Geobalanus oblongifolius*), a pyrogenic acaulescent palm (*Serenoa repens*), matrix graminoids in the Cyperaceae (*Rhynchospora*, *Scleria*, etc.) and Poaceae (*Aristida, Andropogon,* etc.)

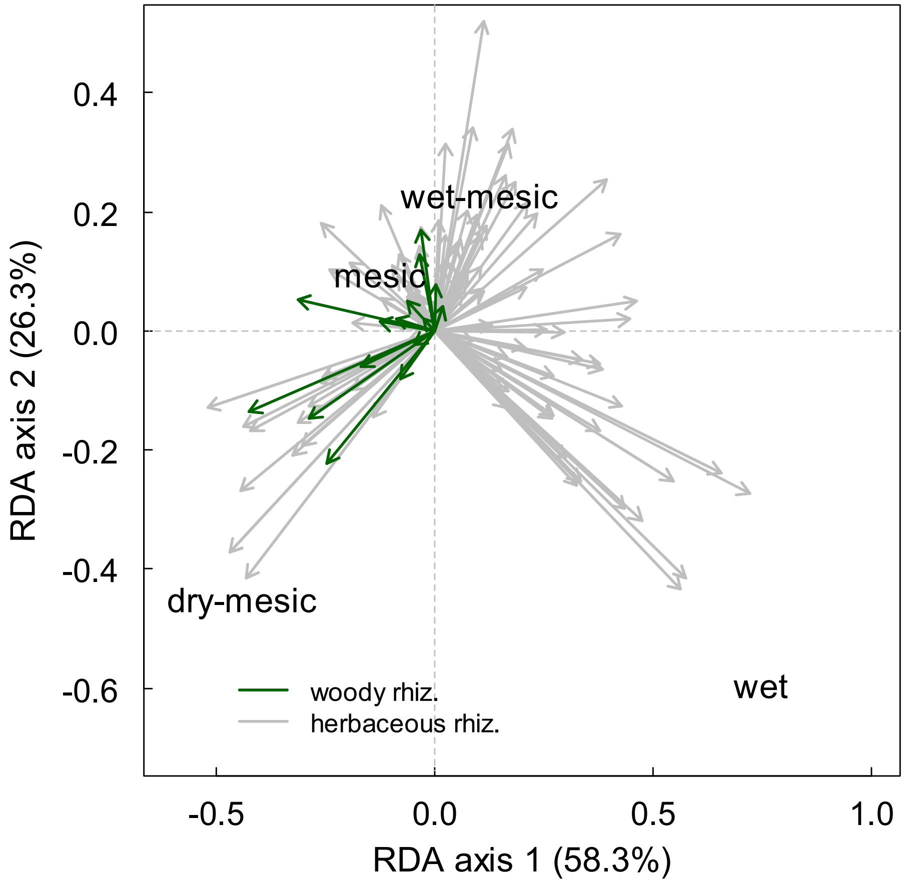


Fig. 5 Ordination diagram of the responses of the abundances of herbaceous and woody rhizomatous species (arrows) by community type and site hydrology

comprise most of the dominant species. Two or three geoxyles are often co-dominant across large parts of the FSG landscape, the so-called geoxyle grasslands, clearly differentiating them from pine savannas. FSGs form unique species associations with forbs, dominant C4 grasses and a diversity of Xyridaceae, Cyperaceae, and Eriocaulaceae species which further serves to differentiate them from floristically similar Florida pine savannas while better aligning them with tropical rather than temperate North American grasslands. *Rhynchospora* is one of the richest genera in the southeastern coastal plain flora in endemics (Sorrie 2008), with 29 species found in FSGs (Orzell and Bridges 2006a), and 13 in our sample. The number of *Xyris* species and their abundance in FSGs differentiates these grasslands from other southeastern US grasslands. FSGs also have a modest diversity of six species of carnivorous plants, representing three families (Droseraceae, Lentibulariaceae, Sarraceniaceae) and four genera (*Drosera*, *Pinguicula*, *Utricularia*, *Sarracenia*). Moist sandy soils are known for their diversity of Ericaceae (Peet et al. 2018) and such is the case in FSGs where Ericaceae is represented by eight species in four genera (*Bejaria*, *Lyonia*, *Gaylussacia*, *Vaccinium*), all shrubby and rhizomatous.

Shrubs are not as species-rich in FSGs as herbs, an important difference in comparison with tropical grasslands that are characterized by numerous woody taxa (e.g. Brazilian tropical grassland Cerrados, Pausas et al. 2018). This perhaps is an effect of the relatively small size and climatic isolation of Florida subtropical grasslands (or suboptimal conditions) thereby the niche of resprouting shrubs is occupied by fewer species. In this respect, FSGs are more similar to the Rio de la Plata grasslands of southern Brazil, Uruguay and central-eastern Argentina, which cover a sizeable area (750,000 km^2). This grassland region and FSGs both harbor a diverse herbaceous flora, but lack diversity of tropical woody species, especially tropical shrubs, a hallmark of Cerrado savanna grasslands (Overbeck and Pfadenhauer 2007; Simon et al. 2009).

Saw-palmetto (*Serenoa repens*), a monotypic genus in the Arecaceae (subfamily Coryphoideae) endemic to the southeastern United States Coastal Plain, has multiple adaptations to recurrent fire (Fig. 6). First, although its leaves are exposed aboveground to fire, most of its biomass is a semi-subterranean, epigeogenous rhizome that is protected from the direct effects of fire. The long petioles, which position the flammable leaf canopy away from the apical meristem, serve to dissipate heat during leaf combustion. When fire is long-excluded, *S. repens* can assume an ascendant small tree growth form (Fisher and Tomlinson 1973). Second, the rhizome is often covered with persistent, closely packed charred leaf bases, and thereby is insulated from fire by thickened hypodermal tissue (Fisher and Jayachandran 1999). Third, the rhizomes contain abundant storage of carbohydrates for resprouting, a common trait in resprouters (Diaz-Toribio and Putz 2021). Fourth, resprouting is both from terminal apical meristems and epicormic buds, the latter derived from axillary buds (i.e., suckering *sensu* Fisher and Tomlinson 1973). Resprouting from epicormic buds is a post-fire evolved recovery strategy in high fire frequented ecosystems (Pausas and Keeley 2014, 2017). The apical bud of *Serenoa repens* is not killed by most fires due to insulation by leaf bases (Abrahamson 1995; Abrahamson and Abrahamson 2006; Fisher and Tomlinson 1973). Insulation of apical buds (McPherson and Williams 1998) is a trait similar to that found in other fire-tolerant monocots, such as the "grass trees" of Australia (*Xanthorrhoea* spp.) (Lamont et al. 2004).

Serenoa repens exhibits very rapid post-fire leaf regeneration (Abrahamson 1984b; Menges and Kohfeldt 1995; Hierro and Menges 2002; Abrahamson 2007) due to its carbohydrate reserves (Hough 1965, 1968). Its leaves are larger in area, but are reduced in number when compared to sympatric groundcover species in FSGs, however, its leaf size is smaller than most other coryphoid palms (Abrahamson 2007). Our post-burn data show that *S. repens* resprouts with emerging new fronds in as

Fig. 6 Saw-palmetto (*Serenoa repens*) is often dominant in peninsular Florida fire prone ecosystems. Note the semi-subterranean, epigeogenous rhizomes which easily reach several meters in length. The blackened rhizome and re-sprouting leaves are 21 days since burning. Photo by Steve Orzell

little as 7-14 days post burn. Its rapid post-fire leaf recovery contributes to long-term persistence under recurrent fire, with some clonal genets of *S. repens* over 10,000 years old, and possibly much older (Takahashi et al. 2011, 2012). Similarly Liesenfeld and Vieira (2018) found post-fire resprouting greater in clonal Neotropical palms. Despite these fire adaptations, we consider *Serenoa repens* to be an aeroxyle (e.g., Pausas et al. 2018) since aeroxyles can resprout both apically and epicormically. Other dwarf acaulescent, fire-adapted palms include *Allagoptera campestris, Sabal etonia, Sabal miamiensis*, and *Syagrus petraea.* The Mediterranean dwarf palm (*Chamaerops humilis*), with its underground rhizomes and upright stems radiating from a clumped base, is adapted to recurrent fire in shrublands and also has apical buds which are protected by persistent leaf bases (Garcia et al. 2018; Pausas 2016). Dowe (2010) noted similar adaptations to fire retained leaf bases, insulation of the terminal bud in some palms from Australia, including *Livistona humilis, L loriphylla*, and *L. muelleri*.

Another typical component of tropical and subtropical savannas grasslands are geoxyles. In addition to their dominance in savanna grasslands they also occur in xeric sandy uplands. However, they are rarely mentioned in the Florida and the southeastern coastal plain literature (Abrahamson et al. 2021; Noss 2018; Peet et al. 2018). Many global studies (Bond and Parr 2010; Pennington and Hughes 2014; Gomes et al. 2019, 2021; Lamont et al. 2017; Meller et al. 2021, 2022; Corkalo 2023; Rickenback 2022) provide phylogenetic evidence for fire adaptation in geoxyles (Simon et al. 2009; Simon and Pennington 2012; Maurin et al. 2014). Their aerial stems are highly susceptible to annual or biennial fires, while their well-protected extensive belowground suffrutices with carbohydrate reserves afford rapid resprouting from bud banks (Fig. 7) (Pausas et al. 2018). The geoxylic suffrutex has been considered an evolutionary response to recurrent fire (Peet et al. 2018). Geoxyles contribute to ecosystem function, persistence, and resource storage; their clonal underground storage organs promote resilience through rapid resprouting

Fig. 7 Runner oak (*Quercus minima*) a geoxyle: a - 60 days post burn, note the flush of young leaves; b – partially excavated woody geoxylic suffrutex of *Q. minima*, pole with 20 cm incremental marks for scale. Photo by Steve Orzell

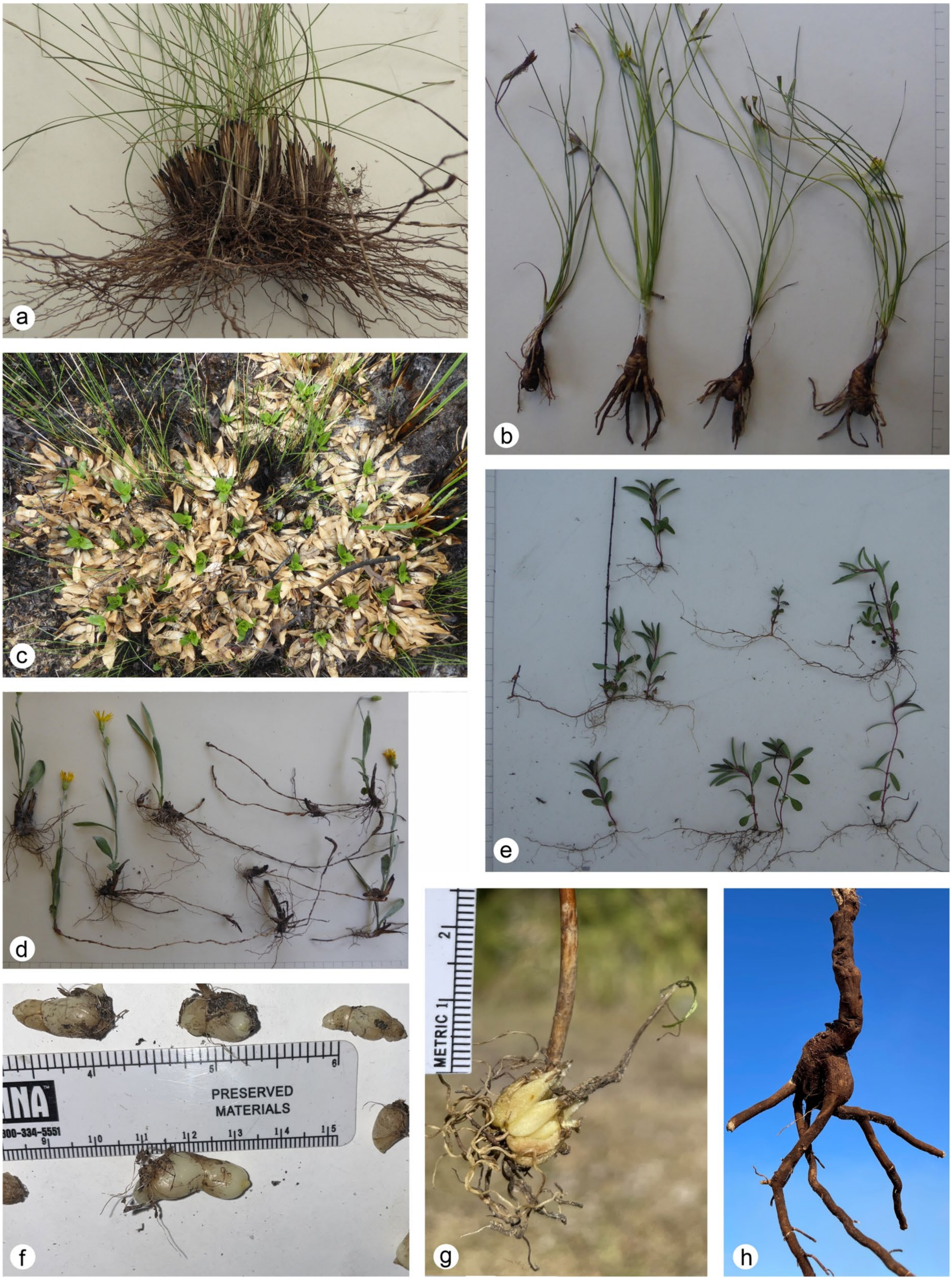
in fire-prone open ecosystems (Tsakatos et al. 2022; Meller et al. 2021).

Phylogenetically, the geoxyle flora of FSGs has evolved in multiple lineages and often have trees or tall shrubs as congeners (White 1976; Maurin et al. 2014; Gomes et al. 2019; Pennington and Hughes 2014; Girolda et al. 2017). While geoxyles in tropical grasslands originated in tropical or subtropical plant lineages (Pennington and Hughes 2014), in Florida there are geoxyles derived from mostly temperate families (Ericaceae, Fagaceae, and Aquifoliaceae), mostly tropical families (Chrysobalanaceae and Annonaceae), and families with no clear temperate or tropical affinity (Myricaceae). While geoxyles are considered typical of savanna regions characterized by high precipitation (Zupo et al. 2021) our study shows that they avoid wet and long-term flooded habitats within those regions (see results concerning woody rhizomes). Within the southeastern US coastal plain, peninsular Florida is the center of geoxyle diversity and evolution, where humid subtropical grasslands and savannas are maintained by some of the highest fire return intervals in the world. Frequent fire and high precipitation, both advantageous for geoxyles (Zupo et al. 2021), prevail in peninsular Florida more than elsewhere in the southeastern US.

Rhizomes, Moisture and Ffire

Belowground stems (rhizomes) with adventitious roots are the most common belowground organs not only in the subtropical savanna of Florida but also in grasslands with temperate flora (Klimešová and Klimeš 2008). Herbs and shrubs place their stems belowground to protect their bud bank and to store carbohydrates to utilize during periods of seasonal adversity (cold or dry) and disturbance (grazing or fire). These organs enable movement through the community, clonal multiplication, and fast regeneration (Klimešová et al. 2018). In the open pyrogenic ecosystems of peninsular Florida, frequent fires, a seasonal climate, hyperseasonal hydrology, and historical mammalian herbivory probably shaped and selected for belowground diversification (Figs. 8 & 9) and clonality. Belowground bud banks provide for post-fire regeneration for many grassland species and disproportionately account for belowground biomass allocation, an adaptive strategy in grasslands with

Fig. 8 Woody plant belowground organs: **a** –Temperate plant family clonal geoxyle of *Ilex glabra* (Aquifoliaceae) with woody hypogeogenous rhizome, pole marked at 20cm increments, photo by James Cheak, **b** –Tropical plant family clonal geoxyle of *Geobalanus oblongifolius* (Chrysobalanaceae), a monotypic genus endemic to the southeastern US with woody hypogeogenous rhizome, photo by Brett Budach


a
b
c
d
e
PRESERVED
MATERIALS
f
METRIC
g
h

◂**Fig. 9** Herbaceous plant belowground organs: **a** – *Aristida beyrichiana* (Poaceae) a caespitose or bunch C4 grass with its short rhizomes, epigeogenous rhizome (EB), **b** - *Hypoxis juncea* (Hypoxidaceae) main root (EB), **c** - *Litrisa carnosa* (Asteraceae) epigeogenous rhizome, cushion or rosette with centrally located apical meristemic growth protected from scorching in a recent fire (EB), **d** - *Pityopsis tracyi* (Asteraceae) hypogeogenous rhizome (EB), **e** - *Rhexia mariana* (Melastomataceae) root sprouter (EB), **f** – *Calopogon pallidus* (Orchidaceae) geophyte with a stem tuber (SO), **g** – *Lilium catesbaei* (Liliaceae) geophyte with bulb (BB), **h** – *Asclepias connivens* (Apocynaceae) main root, xylopodium (BB). Photos credits: EB (Edwin Bridges), BB (Brett Budach), SO (Steve Orzell)

recurrent fire (Fidelis et al. 2014; Buisson et al. 2019; Kang et al. 2013).

Rhizome type correlated with soil moisture in previous studies from central Europe. While belowground formed rhizomes (hypogegoenous) prefer wet soil with fine structure, the rhizomes formed at the soil surface (epigeogenous) can also withstand dry and stony soil (Klimešová et al. 2012; Sosnová et al. 2010). In the present study hydrology was also found to be significantly associated with species traits, but only with rhizome texture partitioning of herbaceous versus woody rhizomatous species, not with rhizome length or rhizome type. Woody rhizomes may be prone to rot in wet conditions while herbaceous rhizomes may be short-lived and escape rotting, moreover, herbaceous rhizomes may be suitable for water storage, which allows herbs to persist in drying soils and to resprout during dry periods (Silva and Rossatto 2019).

Both belowground organs and growth form were associated with phylogeny. In general, two trait syndromes related to frequent fire and phylogeny can be seen in our dataset. The five most species-rich families were Poaceae (41), Asteraceae (27), Cyperaceae (26), Ericaceae (8), and Xyridaceae (8). In terms of belowground organs, a high prevalence of epigeogenous rhizomes in Poaceae, a family usually with highly flammable species (Cui et al. 2020). In contrast, Asteraceae were mostly rhizomatous herbs and species from this family tend to be less flammable (Cui et al. 2020). Both Poaceae and Asteraceae are two of the most species-rich families of angiosperms in Florida (Allen et al. 2019; Weakley et al. 2023), suggesting that both low and high shoot flammability are successful strategies in fire-prone ecosystems. Within Asteraceae, the subtribe Liatrinae is diverse in the southeastern US, with 19 species known from Florida's pyrogenic ecosystems, of which at least seven are known from FSGs. Zanzarini et al. (2022) attribute maintenance of the openness in savanna grasslands to highly flammable grasses. Rapid resprouting from belowground organs post-fire enables forbs and shrubs to exploit recently burned habitat created by flammable grasses, and there is strong evidence of selection for C4 grasses driven by fire regime (Scheiter et al. 2012). In the tribe Andropogonae flammability traits are associated with high fire frequency (Visser et al. 2012), and are phylogenetically clustered, so diversification of *Andropogon* and *Schizachyrium* in peninsular Florida, where 20 taxa are tentatively recognized, is not surprising. With the phylogenetic signal in these traits, fire regime could be a crucial driver of the spatial patterns of community phylogenetic diversity observed in Florida (Allen et al. 2019).

Post fire Regeneration Strategies

When comparing post-fire recovery strategies and growth forms of subtropical savanna grasslands in Florida, resprouting is the main but not exclusive post-fire regeneration strategy. It is accompanied by re-seeding, resisting fire, or a combination of recovery modes. Resprouting is most the prevalent strategy among dominant species in Florida's pyrogenic (scrub and savanna grasslands) ecosystems (Maliakal et al. 2000; Hierro and Menges 2002; Abrahamson 1984a). Extensive belowground biomass with carbohydrate and water reserves in frequently burned Florida ecosystems promotes resprouting and clonal growth (Abrahamson et al. 2021, Olano et al. 2006; Diaz-Toribio and Putz 2021; Zhou 2023). The post fire regeneration study which is most comparable to FSGs is from dry wiregrass pineland on the Lake Wales Ridge (Maliakal et al. 2000), sharing 34 species with our study. Maliakal et al. (2000) found 89% resprouters and 11% obligate seeders, close to our FSGs values of 82% and 18% respectively. Neotropical grassy ecosystems (savannas & grasslands) maintained by frequent fire, such as the Brazilian Cerrado and subtropical south Brazilian grasslands, share many growth forms, post-fire strategies, and belowground organ types with FSGs. As in FSGs the forbs, cespitose grasses, shrubs, and rhizomatous geophytes are mainly resprouters (ca 90%, Overbeck and Pfadenhauer 2007; Fidelis et al. 2021; Pilon et al.

2021, Zupo et al. 2021) while only about 10% of species were reseeders (Overbeck and Pfadenhauer 2007; Pilon et al. 2021). Reseeders are typically ephemeral herbs that germinate during the wet season in fire-created gaps, however some may germinate from the existing seed bank with or without fire.

Conclusion

The urgency to recognize, protect, and manage the remaining worldwide pyrogenic old-growth grasslands has taken center stage in recent years. They are strongholds for herbaceous plant species richness, where belowground biomass promotes rapid post-fire resprouting and fine fuel replacement, and long-term community persistence. While FSGs grasslands share many plant traits with tropical grasslands, FSGs have a significantly lower diversity of tropical and subtropical woody specialists that are prevalent in other Neotropical grasslands in comparison to FSGs. We hope that our application of terminology on plant growth form, belowground organs, and post-fire recovery strategies will foster continued research in subtropical grasslands of the southeastern US coastal plain. Our sub-sample of these grassy ecosystems should be viewed as a foundation to build knowledge about fire-adapted traits of plants from elsewhere in Florida and the southeastern US, where there are grasslands with unique species assemblages from those in south-central Florida.

Acknowledgements Financial support was provided by the United States Air Force to Avon Park Air Force Range (APAFR). Staff at APAFR, and collaborators are appreciated, including Jean Huffman, Gary Reese, John Schadler, Catherine A. Lauvaux, Alex Griffel-Dalager, James Cheak, Eric Ungberg, Scott Ward, Todd Angel, Sam Crawford, Alexandre Ferraro, Bill Platt, Matt Slocum, the late Paul Ebersbach, Brent Bonner, and Kevin Porteck. The APAFR Wildland Fire Module staff conducted prescribed burns that enabled post-burn recovery studies. Robert Aldredge and Marshall Williams of the United States Fish and Wildlife Service facilitated contract agreements. Scott Zona, Jill Josomovich, Kris Pitcher, and Helen Nesius provided editorial comments on the manuscript and Alena Bartušková assisted with the figures. M. Bitomský was supported by the Programme for the Promotion of Prospective Human Resources – Postdocs (PPLZ) of the Czech Academy of Sciences. JM and JK were supported by Praemium Academiae awarded by the Czech Academy of Sciences. This study was conducted in accordance with legislation in Florida and the United States of America.

Author Contributions SO, EB - study design; SO, EB, BB, JM, JK, SR, ZR – data collection; SO, EB, BB, MB, JK - writing of manuscript; MB, SO, EB, BB, SR, ZR - data analysis. The first draft of the manuscript was written by SO.

Declarations

Competing Interest The authors have no competing or financial interest to declare that are relevant to the content of this manuscript. All the authors read and approved the manuscript.

References

Abrahamson WG (1984a) Post fire recovery of Florida Lake Wales Ridge vegetation. *Amer J Bot* 71:9-21.

Abrahamson WG (1984b) Species responses to fire in the Florida Lake Wales Ridge. *Amer J Bot* 71:35-43.

Abrahamson WG (1995) Habitat distribution and competitive neighborhoods of two Florida palmettos. *Bull Torrey Bot Club* 122:1-14.

Abrahamson WG (2007) Leaf traits and leaf life spans of two xeric-adapted palmettos. *Amer J Bot* 94:1297-1308.

Abrahamson WG, Abrahamson CR (2006) Post-fire canopy recovery in two fire-adapted palms, *Serenoa repens* and *Sabal etonia* (Arecaceae). *Florida Scientist* 69:69-79.

Abrahamson WG, Abrahamson CR, Keller MA (2021) Lessons from four decades of monitoring vegetation and fire: maintaining diversity and resilience in Florida's uplands. *Ecol Monog* 91: e01444.

Abrahamson WG, Harnett DC (1990) Pine flatwoods and dry prairies. Pp. 103-150. In Myers RL(eds). Ecosystems of Florida. University of Central Florida. Orlando.

Allen JM, Germain-Aubrey CC, Barve N, Neubig KM, Majure LC, Laffan SW, Mishler BD, Owens HL, Smith SA, Whitten WM, Abbott JR, Soltis DE, Guralnick R, Soltis P (2019) Spatial phylogenetics of Florida vascular plants: the effects of calibration and uncertainty on diversity estimates. *iScience* 11:57–70.

Blake ES, Rappaport EN, Jarrell JD, Landsea CW (2005) The deadliest, costliest, and most intense United States tropical cyclones from 1851 to 2004 (and other frequently requested hurricane facts). NOAA Technical

Memorandum NWS TPC-4, National Hurricane Center. Miami, Florida. pp 48

Bond WJ (2016) Ancient grasslands at risk. *Science* 351:120-122.

Bond WJ (2019) *Open ecosystems: ecology and evolution beyond the forest edge*. Oxford University Press. pp 178

Bond WJ, Parr CL (2010) Beyond the forest edge: Ecology, diversity and conservation of the grassy biomes. *Biol Cons* 143:2395-2404.

Bridges EL (2006a) Historical accounts of vegetation in the Kissimmee River dry prairie landscape. pp 43-63. In Noss RF (eds) *Land of fire and water: The Florida Dry Prairie Ecosystem. Proceedings of the Florida Dry Prairie Conference.* E. O. Painter, DeLeon Springs, Florida.

Bridges EL (2006b) Landscape ecology of Florida dry prairie in the Kissimmee River region. pp 14-42. In Noss RF (eds) *Land of fire and water: The Florida Dry Prairie Ecosystem. Proceedings of the Florida Dry Prairie Conference.* E. O. Painter, DeLeon Springs, Florida. pp 14-42.

Buisson E, Stradic SL, Silveira FAO, Durigan G, Overbeck GE, Fidelis A, Fernandes CW, Bond WJ, Hermann JM, Mahy G, Alvarado ST, Zamloumis NP, Veldman JW (2019) Resilience and restoration of tropical and subtropical grasslands, savannas, and grassy woodlands. *Biol Rev* 94:590-609.

Carr SC, Robertson KM, Platt WJ, Peet RK (2009) A model of geographical, environmental and regional variation in vegetation composition of pyrogenic grasslands of Florida. *J Biogeog* 36: 1600-1612.

Carr SC, Robertson KM, Peet RK (2010) A vegetation classification of fire-dependent pinelands of Florida. *Castanea* 75:153-189.

Chen E, Gerber JF (1990) *Climate*. In Myers RL, Ewel JJ (eds) *Ecosystems of Florida*. University of Central Florida Press. Orlando, Florida pp 11-35.

Chevan A, Sutherland M (1991) Hierarchical partitioning. *Am Stat* 45:90-96.

Clarke, PJ, Lawes MJ, Murphy BP, Russell-Smith J, Nano CEM, Bradstock R, Enright NJ, Fontaine JB, Gosper CR, Radford I, Midley JJ, Gunton RM (2015) A synthesis of postfire recovery traits of woody plants in Australian ecosystems. *Sci Total Environm* 534: 31-42.

Clarke PJ (2016) Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytol* 197:19-35.

Corkalo M (2023) Structure and composition of woody belowground biomass of geoxyle in grasslands and open woodlands in south-central Angola. Master's Thesis, University of Zagreb. pp 87

Cui X, Paterson AM, Wyse SV, Alam MA, Maurin KJL, Pieper R, Cubino JP, O'Connell DM, Donkers D, Bréda J, Buckley HL, Perry GLW, Curran T (2020) Shoot flammability of vascular plants is phylogenetically conserved and related to habitat fire-proneness and growth form. *Nature Plants* 6:355–359.

de Oliveira Xavier R, Leite MB, Dexter K, Matos DMS (2019) Differential effects of soil waterlogging on herbaceous and woody plant communities in a Neotropical savanna. *Oecologia* 190:471-483.

DeSelm HR, Murdock N (1993) Grass-dominated communities. pp. 87-141 In Martin WH, Boyce SG, Echternacht AC (eds) Biodiversity of the southeastern United States upland terrestrial communities. John Wiley & Sons, Inc. New York.

Diaz-Toribio MH, Putz FE (2021) Underground carbohydrate stores and storage organs in fire-maintained longleaf pine savannas in Florida, USA. *Amer J Bot* 108:1-11.

Dowe JL (2010) *Australian Palms: Biogeography, Ecology and Systematics*. CSIRO Publishing, Melbourne. pp 290.

Dray S, Dufour AB (2007) The ade4 package: implementing the duality diagram for ecologists. *J Stat Softw* 22:1–20.

Dray S, Legendre P (2008) Testing the species traits-environment relationships: the fourth-corner problem revisited. *Ecology* 89: 3400-3412.

Duncan BW, Boyle S, Breininger DR, Schmalzer PA (1999) Coupling past management practice and historic landscape change on John F. Kennedy Space Center, Florida. *Landscape Ecol* 14: 291-309.

Duncan BW, Shao GF, Adrian FW (2009) Delineating a managed fire regime and exploring its relationship to the natural fire regime in East Central Florida, USA: A remotesensing and GIS approach. *Forest Ecol and Managem* 258: 132-145.

Fidelis A, da-Glória BA, Pillar VD, Pfadenhauer J (2014) Does disturbance affect bud bank size and belowground structures diversity in Brazilian subtropical grasslands? *Flora* 209: 110-116.

Fidelis A, Rodrigues CA, Dairel M, Blanco CC, Pillar VD, Pfadenhauer J (2021) What matters for vegetation regeneration in Brazilian subtropical grasslands: seeders or resprouters. *Flora* 279:151817.

Fill JM, Welch SM, Waldron JL, Mousseau TA (2012) The reproductive response of an endemic bunchgrass indicates historical timing of a keystone process. *Ecosphere* 3:1-12.

Fisher JB, Jayachandran K (1999) Root structure and arbuscular mycorrhizal colonization of the palm *Serenoa repens* under field conditions. *Plant and Soil* 217:229-241.

Fisher JB, Tomlinson PB (1973) Branch and inflorescence production in saw palmetto (*Serenoa repens*). *Principes* 17:10-19

Fowler C, Konopik E (2007) The history of fire in the southeastern United States. *Human Ecol Rev* 14:165-178.

Freschet CT, Pages L, Iverson CM, Comas LH, Rewald B, Roumer C, Klimešová J, Zadworny M, Poorter H, Postma JA, Adam TS, Bagniewska-Zedworna A, Bengouph AG, Blancaflor ER, Brunner I, Cornelissen JH, Garnier E, Gessler A, Hobbie SE, Meier IC, Mommor L, Picon-Cochard C, Rose L, Ryser P, Scherer-Lorenzen M, Valverde-Barrantes OJ, Weemstra M, Weigelt A, Wurburger N, York LM, Batterman SA, Gomesda Moraes M, Janeček S, Lambers H, Salmon V, Tharayil N, McCormack ML (2021) A starting guide to root ecology: strengthening ecological concepts and standardizing root classification, sampling, processing, and trait measurements. *New Phytol* 232:973-112.

Garcia Y, Castellanos MC, Pausas JG (2018) Differential pollinator underlies plant reproductive resilience after fires. *Ann Bot* 122:961-971.

Girolda AB, Scariot A, Hoffman WA (2017) Trait shifts associated with the subshrub life-history strategy in a tropical savanna. *Oecologia* 185:281-291.

Gomes AL, Revermann R, Goncalves FMP, Lages F, Aidar MPM, Finckh M, Jurgens N (2019) Tree or not tree: differences in plant functional traits among geoxyles and related tree species. *S Afri J Bot* 127: 176-184.

Gomes AL, Revermann R, Goncalves FMP, Lage F, Aidar MPM, Mostajo GAS, Finckh M (2021) Suffrutex grasslands in south-central Angola: belowground biomass, root structure, soil characteristics and vegetation dynamics of the "underground forests" of Africa. *J Trop Ecol* 37:136-146.

Green R. C. et al. (2019) Text to accompany geologic map of USGS Bartow 30 X 60 minute quadrangle, central Florida. *Florida Geol Surv* OFR-108.

Guerrero-Ramirez NR, Mommer L, Freschet GT, Iverson CM, McCormack ML, Kattge J, Poorter H, van der Plas F, Bergmann J, Kuyper TW, York LM, Bruelheide H, Laughlin DC, Meier IC, Roumet C, Semchenko M, Sweeney CJ, van Ruijren J, Valverde-Barrantes OJ, Aubin I, Catford JA, Manning P, Martin A, Miller R, Minden V, Pausas JG, Smith SW, Soudzilovskaia NA, Ammer C, Butterfield B, Craine J, Cornelissen JH, de Vries FT, Isaac ME, Kramer K, König C, Lamb EG, Onipchenko VG, Peñuelas J, Reich PB, Rillig MC, Sack L, Shipley B, Tedersoo L, Valladares F, Van Bodegom P, Weigelt P, Wright JP, Weigelt A (2020) Global root traits (GRoot) database. *Global Ecol & Ecol* 30:25-37.

Harper RM (1921) Geography of central Florida. Florida Geological Survey 13th Annual Report: 71-307.

Harper RM (1927) Natural resources of southern Florida. Florida Geol Surv 18th Annual Report: 27-206.

Harshberger JW (1914) The vegetation of South Florida south of 27 30 north, exclusive of the Florida Keys. Wagner Free Institute of Philadelphia VII Part 3:51-189.

Hierro JL, Menges ES (2002) Fire intensity and shrub regeneration in palmetto-dominated flatwoods of central Florida. *Florida Scientist* 65:51-61.

Holm S (1979) A simple sequentially rejective multiple test procedure. *Scand J Stat* 6:65–70.

Hough WA (1965) Palmetto and gallberry regrowth following winter prescribed burn. *Georgia For Res Pap.* No 31.

Hough WA (1968) Carbohydrate reserves of saw palmetto: seasonal variation and effects on burning. *For Sci* 14: 399-403.

Huck RB (1987) Plant communities along an edaphic continuum in a central Florida watershed. *Florida Scientist* 50:111-128.

Huffman JM (2006) Historical fire regime in southeastern pine savannas.PhD Baton Rouge. Louisiana State University. 77 p.

Jin Y, Qian H (2022) V.PhyloMaker2: An updated and enlarged R package that can generatevery large phylogenies for vascular plants. *Plant Divers* 44:335–339.

Kang M, Dai C, Jiang Y, Yuan Z, Chen HYH (2013) Biomass and its allocation in relation to temperature, precipitation, and soil moisture in Inner Mongolia grasslands China. PLOS One 7:e69561.

Klimešová J, Klimeš L (2007) Bud banks and their role in vegetative regeneration – A literature review and proposal for simple classification and assessments. *Persp Plant Ecol Evol Syst* 8:115-129.

Klimešová J, Klimeš L (2008) Clonal growth diversity and bud banks of plants in the Czech flora: an evaluation using the CLO-PLA3 database. *Presilia* 80:255-275.

Klimešová J, Doležal J, Prach K, Košnar (2012) Clonal growth forms in Artic plants and their habitat preferences: a study from Petuniabukta, Spitsbergen. *Polish Polar Research* 33:412-442.

Klimešová J, Martinková J, Herben T (2018) Horizontal growth: An overlooked dimension in plant traits space. *Persp Plant Ecol Evol & Syst* 32:18-21.

Klimešová J, Martínková J, Pausas JG, de Moraes MG, Herben T, Yu FH, Vesk PA, de Bello F, Janeček S, Altman J, da Glória BA, Bartušková A, Crivellaro A, Doležal J, Ott JP, Paula S, Schnablová R, Schweingruber FH, Ottaviani G (2019) Handbook of standardized protocols for collecting plant modularity traits. *Persp Plant Ecol Evol Syst* 40:1-21.

Lai J, Zou Y, Zhang J, Peres-Neto PR (2022) Generalizing hierarchical and variation partitioning in multiple regression and canonical analyses using the rdacca.hp R package. *Methods Ecol Evol* 13:782–788

Lamont BB, Wittkuhn R, Korczynskyj D (2004) Turner Review No. 8 Ecology and ecophysiology of grasstrees. *Aust J Bot* 52:561-582.

Lamont BB, He T, Pausas JG (2017) African geoxyles evolved in response to fire; frost came later. *Evol Ecol* 31:603-617.

Legendre P, Galzin PR, Harmelin-Vivien ML (1997) Relating behavior to habitat: solutions to the fourth-corner problem. *Ecology* 78:547–562.

Lehmann CER, Parr CL (2016) Tropical grassy biomes: linking ecology, human use, and conservation. *Phil Trans R Soc B* 371:20160329.

Liesenfeld MVA,Vieira G (2018) Postfire palm resprouting in the Amazonian forests: are underground stems and advantage? *Perspectives Rurales Nueva Epoca* 16:11-23.

Long RW (1974) The vegetation of southern Florida. *Florida Scientist* 37: 33-45;

Long RW, Lakela O, Broome CR (1969) Some preliminary statistics of the flora of southern Florida. *Rhodora* 71:495-501.

Maguire AJ, Menges ES (2011) Post-fire growth strategies of resprouting Florida scrub vegetation. *Fire Ecol* 7:12-25.

Maliakal SK, Menges ES, Denslow JS (2000) Community composition and regeneration of Lake Wales Ridge wiregrass flatwoods in relation to time since fire. *J Torrey Bot Soc* 127:125-138.

Maurin O., Davies TJ, Burrows JE, Daru BH, Yessoufou K, Muasya, AM, van der Bank M, Bond WJ (2014) Savanna fire and the origins of the 'underground forests' of Africa. *New Phytol* 204:201-214.

McPherson K, Williams K (1998) Fire resistance of cabbage palms (*Sabal palmetto*) in the southeastern USA. *For Ecol & Mgt* 109:197-207.

Meller P, Stellmes M, Fidelis A, Finckh M (2021) Correlates of geoxyle diversity in Afrotropical grasslands. *J Biogeo* 49:339-352.

Meller P, Frazao R, Lages F, Jurgens N, Finckh M (2022) Tipping the scales: how fire controls the balance among functional groups in Angolan grasslands. *Afr. J Range & Forage Sci* 39:55-69.

Menges ES, Kohfeldt N (1995) Life history strategies of Florida scrub plants in relation to fire. *Bull Torr Bot Club* 122:282-297.

Menges ES, Marks PL (2008) Fire and flood why are south-central Florida seasonal ponds treeless. *American Midl Nat* 159:8-20.

Menges E S, Smith, S A, Olano, J M, Schafer, J L, Clarke, G, Main, K (2020) Effects of frequent fire and mowing on resprouting shrubs of Florida scrub USA. *Fire Ecol* 16:1-17.

Noss RF (2006) Introduction to Florida "Dry" Prairie. Pp. 1-2. In Noss RF (eds) *Land of fire and water: the Florida Dry Prairie Ecosystem. Proceedings of the Florida Dry Prairie Conference*. Painter, DeLeon Springs, Florida.

Noss RF (2013) *Forgotten grasslands of the South: Natural history and conservation*. Island Press. pp 317

Noss RF (2018) *Fire ecology of Florida and the southeastern coastal plain*. University of Florida Press, Gainesville, Florida. pp 336

Noss RF, Platt WJ, Sorrie BA, Weakley AS, Means DB, Costanza J, Peet RK (2015) How global biodiversity hotspots may go unrecognized: lessons from North American coastal plain. *Diversity & Distributions* 13:1-9.

Oksanen J, Simpson GL, Blanchet FG et al. (2022) vegan: community ecology package. R package version 2.6-2. https://CRAN.R-project.org/package=vegan. Accessed 23 Feb 2023

Olan JM, Menges ES, Martinez E (2006) Carbohydrate storage in five resprouting Florida scrub plans across a fire chronosequence. *New Phytol* 170: 99-106.

Orzell SL, Bridges EL (2006a) Species composition and environmental characteristics of Florida dry prairies from the Kissimmee River region of south-central Florida. pp 100-135. In Noss RF (eds) *Land of fire and water. The Florida Dry Prairie Ecosystem. Proceedings of the Florida Dry Prairie Conference.* Painter, DeLeon Springs, Florida.

Orzell SL, Bridges EL (2006b) Floristic composition of the south-central Florida dry landscape. pp 64-99. In Noss RF (eds) *Land of fire and water. The Florida Dry Prairie Ecosystem. Proceedings of the Florida Dry Prairie Conference.* Painter, DeLeon Springs, Florida.

Overbeck GE, Pfadenhauer J (2007) Adaptive strategies in burned subtropical grassland in southern Brazil. *Flora* 202: 27-49.

Pagel M (1999) Inferring the historical patterns of biological evolution. *Nature* 401:877–884.

Palmquist KA, Peet RK, Weakley AS (2014) Changes in plant species richness following reduced fire frequency and drought in one of the most species rich savannas in North America. *J Veg Sci* 25: 1426-1437.

Pate JS, Dixon KW (1982) Plants with fleshy underground storage organs a Western Australia survey. *In* Pate JS, McComb J. *eds The biology of Australia plants. 412.* University of Western Australia.

Paula, S.A. et al. 2009. Fire-related traits for plant species of the Mediterranean basin. *Ecology* 90:1420-1440.

Pausas JG (2016) Post-fire resprouting of *Chamaerops humilis*. 18 March 2106 Fire Blog. https://jgpausas.blogs.uv.es/?s=Post+fire+resprouting+Chamaerops+humilis. Accessed 2 Mar 2023

Pausas JG, Keeley JE (2017) Epicormic resprouting in fire-prone ecosystems. *Trends Plant Sci* 22:1008-1015

Pausas JG, Keeley JE (2014) Evolutionary ecology of resprouting and seeding in fire prone ecosystems. *New Phytol* 204: 55-65

Pausas JG Pratt RB, Keeley JK, Jacobsen AL, Ramirez AR, Vilgrosa A, Paula S, Kaneakua-Pia IN, Davis SD (2016) Towards understanding resprouting at the global scale. *New Phytol* 209:945-954.

Pausas JG, Lamont BB, Paula S, Appezzato da Gloria B, Fidelis A (2018) Unearthing belowground bud banks in fire prone ecosystems. *New Phytol* 217: 1435-1448.

Peet RK, Platt WJ, Costanza JK (2018) Fire-maintained pine savannas and woodlands of the southeastern United States coastal plain. In Barton AM, Keeton WS (eds) *Ecology and Recovery of Eastern Old-Growth Forests*. Island Press pp 40-62.

Pennell MW, Eastman JM, Slater GJ, Brown JW, Uyeda JC, Fitzjohn RG, Alfaro ME, Harmon L (2014) geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics* 30:2216–2218. https://doi.org/https://doi.org/10.1093/bioinformatics/btu181

Pennington RT, Hughes CE (2014) The remarkable congruence of New and Old World savanna origins. *New Phytol* 204:4-6.

Pilon NAL, Cava MGB, Hoffman WA, Abreu RCR, Fidelis A, Durigan G (2021) The diversity of post-fire regeneration strategies in the cerrado ground layer. *J Ecol* 109:154-166.

Platt WJ, Huffman JM, Slocum (2006) Fire regimes and trees in Florida Dry Prairie landscapes. pp 3-13. In Noss RF (eds) *Land of fire and water. Proceedings of the Florida Dry Prairie Conference.* Painter, DeLeon Springs, Florida.

Platt WJ, Orzell SL, Slocum MG (2015) Seasonality of fire weather strongly influences fire regime in south Florida savanna-grassland landscapes *PLOS One* 10:e0116952.

Pullaiah, T, and EL Bridges. In prep. Biodiversity of the North American Coastal Plain Hotspot. Apple Academic Press and CRC Press.

R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rickenback J (2022) Savannas at the forest boundary: an understudied biome at risk. PhD Dissertation. University of Edinburgh & Royal Botanic Garden, Edinburgh pp 236

Saha S, Catenazzi A, Menges, ES (2010) Does time since fire explain plant biomass allocation in the Florida USA scrub ecosystem. *Fire Ecol* 6:13-25.

Sarmiento G, Monaterio M (1983) Life forms and phenology. In Bourliere F (eds) *Ecosystems of the World. 13. Tropical Savannas*. Elsevier Scientific Publicaiton Company, Amsterdam, pp 79-108.

Scheiter S, Higgins SI, Osborne CP, Bradshaw C, Lunt D, Ripley BS, Taylor LL, Beerling D. (2012) Fire and fire adapted vegetation promoted C4 expansion in the late Miocene. New Phytol 195:653-666.

Shibu J, Jokela EJ, Miller DL (2006) *The Longleaf Pine Ecosystem: Ecology, Silviculture and Restoration*. Springer-Verlag, New York 438 pp.

Silva IA, Batalha MA (2011) Plant functional types in Brazilian savannas: The niche partitioning between herbaceous and woody species. *Persp Plant Ecol Evol & Syst* 13: 201-206.

Silva BHPD, Rossatto DR (2019) Are underground organs able to store water and nutrients? A study case in non-arboreal species from the Brazilian Cerrado. *Theor Exp Plant Physiol* 31: 413-421.

Simon MF, Grether R, de Queiroz LP, Skema C, Pennington RT, Hughes CE (2009) Recent assembly of the Cerrado, a Neotropical plant diversity hotspot, by in-situ evolution of adaptations to fire. *Proc Nat Acad Sci* 106:359-364.

Simon MF, Pennington RT (2012) Evidence for fire adaptation to fire regimes in the tropical savannas of the Brazilian Cerrado. *Intl J Plant Sci* 173:711-723.

Slocum MG, Platt WJ, Beckage B, Orzell S (2010) Accurate quantification of seasonal rainfall and associated climate-wildfire relationships. *J Applied Meterology & Climatology* 49: 2559-2573.

Sorrie BA (2008) Diversity, endemism, and phytogeography of North American coastal plain sedges. In Naczi RFC, Ford, BA (eds) *Sedges: uses, diversity, and systematics of the Cyperaceae*. Monographs in Systematic Botany Volume 108. Missouri Botanical Garden Press pp 103-117.

Sorrie BA, Weakley AS (2006) Conservation of the endangered *Pinus palustris* ecosystem based on coastal plain centres of plant endemism. *App Veg Sci* 9:59-66.

Sosnová M, Diggelen RV, Klimešová J (2010) Distribution of clonal growth forms in wetlands. *Aquatic Bot* 92: 33-38.

Stein BA, Scott C, Benton N (2008) Federal lands and endangered species: the role of military and other federal lands in sustaining biodiversity. *BioScience* 58: 339-347.

Stephenson KE 2011. Distribution of grasslands in 19^{th} century Florida. *The American Midl Nat* 165: 50-59.

Takahashi MK, Horner LM, Kubota T, Keller NA, Abrahamson WR (2011) Extensive clonal spread and extreme longevity in saw palmetto, a foundation clonal plant. *Molec Ecol* 20:3730-3742.

Takahashi MK, Kubota T, Horner LM, Keller NA, Abrahamson WG (2012) The spatial signature of biotic interactions of a clonal and non-clonal palmetto in a subtropical plant community. *Ecosphere* 3:1-12.

Tsakatos JL, Ottaviani G, Chelli, S, Rea A, Elder S, Dobrowolski MP, Mucina L (2022) Plant clonality in a soil-impoverished open ecosystem: insights from southwest Australian shrublands. *Ann Bot*: 130:981-990.

Veldman JW, Buisson E, Durigan G, Fernandes GW, Le Stradic S, Mahy G, Negreiros D, Overbeck GE, Veldman R, Zaloumis NP, Putz FE, Bond WJ (2015) Towards an old-growth concept for grasslands, savannas, and woodlands. *Front Ecol Environ* 13:154-162.

Visser V, Woodward I, Freckleton RP, Osborne CP (2012) Environmental factors determining the phylogenetic structure of C4 communities. *J Biogeog* 39: 232-246.

Wahlenberg WG (1946) Longleaf pine: its use, ecology, regeneration, protection, growth and management. Charles Lathrop Pack Forestry Foundation, Washington D.C. 429pp.

Wang Y, Naumann U, Wright ST, Warton DI (2012) mvabund – an R package for model-based analysis of multivariate abundance data. *Methods Ecol Evol* 3:471–474.

Warton DI, Wright ST, Wang Y (2012) Distance-based multivariate analyses confound location and dispersion effects. *Methods Ecol Evol* 3:89–101.

Weakley, AS, Lee M, Ward S, Ludwig JC, Sorrie B, Poindexter D, LeBlond R, Kees J, McCormick CA, Oberreiter S, Ungberg E, Lance R, Ballard H, Carter R, Pyne M, Knapp W, Bradley K, Zona S, Barger W, Musselman L, Schafran P, Spaulding D, Nelson J, Keith E, Fleming G, Estes D, Majure L, Medford H, Bridges E, Folk R, Murrell Z, Peet R, Townsend J, Nesom G, Floden A, Horn J, Schilling E, Triplett J, Murphy T, Irick Z, McClelland RKS, Alford M, Brock M et al. (2023) *Flora of the Southeastern United States*, 2023 ed. North Carolina Botanical Garden, Chapel Hill, North Carolina. Available from: https://fsus.ncbg.unc.edu/index.php

White F (1976) The underground forests of Africa: a preliminary review. *The Garden's Bull Singapore* 24:57-71.

Wickham H (2016) *ggplot2: elegant graphics for data analysis*. 2nd ed., Springer, New York.

Wigley BJ et al. 2020. Corrigendum to: A handbook for the standardized sampling of plant functional traits in disturbance prone ecosystems with a focus on open ecosystems. *Australian J Bot* 68:473-531.

Yu G, Smith DK, Zhu H, Guan Y, Lam TT (2017) GGTREE: an R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. *Methods Ecol Evol* 8:28–36.

Zanzarini V, Anderson AN, Fidelis A. (2022) Flammability in tropical savannas: Variation among growth forms and seasons in Cerrado. *Biotropica* 54:979-987.

Zhou Y (2023) Root traits in response to frequent fires: Implications for belowground carbon dynamics in fire-prone savannas. *Front Plant Sci* 14: 1106531.

Zupo T, Daibes LF, Pausas JG, Fidelis A (2021) Post-fire regeneration strategies in a frequently burned Cerrado community. *J Veg Sci* 32:e12968