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Assessing Postfire Vegetative Changes and Implications for Management in a Northeast Florida Coastal Strand Ecosystem

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ABSTRACT Coastal ecosystems face numerous well-documented threats that pose significant risk of reduction in the ability of these ecosystems to persevere. Although coastal disturbance processes related to maritime exposure are relatively well known, the past and potential impacts of fire in these ecosystems have not been well studied. Because fire plays such an important role in so many other southeastern ecosystems, and because the areal extent of coastal strand ecosystems has been much reduced, it is important to resolve the role of fire for management of these threatened communities. In 2014, prescribed fire management was undertaken in a protected and relatively intact, 55-ha remnant section of coastal strand in the Guana Tolomato National Estuarine Research Reserve (GTMNERR) adjacent to the Atlantic Ocean in northeast Florida, USA. The fire history for this area was unknown. We compared burned samples to unburned samples to test whether there were differences in patterns of vegetative response to this fire management action. In backdune sites, we found significant dissimilarities in plant community biodiversity indicators between burned and unburned samples, whereas vegetative cover changed significantly in both foredune and backdune sites. We include a review of successional patterns and fire effects for similar sites in the region for comparison, which provisionally suggests a 4–20-yr fire return interval. We conclude that fire management for the backdune component of the coastal strand is an important strategy for this ecosystem to avert succession to maritime hammock.

Key words: Disturbance, fire exclusion, pyrophytic, return interval, succession.

INTRODUCTION Coastal natural communities throughout the world face rapidly intensifying threats, ranging from habitat destruction and fragmentation (Kurz 1942, Richardson 1977, Fernald 1989, Acosta et al. 2000, Isermann 2011), to pathogen-mediated mortality of significant populations of important species (Gramling 2010, Maner et al. 2014), to sea level rise (Nicholls and Cazenave 2010, Noss 2011). Prior to development, the coastal strand ecosystem in Florida, USA, likely ran along the entire east and west coast of the state (Pierce and Curl 1970, Myers and Ewel 1990); however, rapid development continues at an accelerating rate, resulting in increasing losses (Lins 1980, Florida Natural Areas Inventory 1990, Johnson and Barbour 1990, Frazel 2008, GTMNERR Management Plan 2009). In fact, over a 12-yr period (1992–2004), 25% of coastal uplands in private ownership in Florida were developed (Johnson et al. 2005). The Florida Natural Areas Inventory (2010) ranks the coastal strand ecosystem as G3 (globally vulnerable to extirpation)/S2 (state ranked imperiled).

The coastal strand ecosystem is largely characterized by oak–palmetto scrub. It is found along a narrow, vegetated strip paralleling the Atlantic Ocean, and is currently reduced to remnant protected fragments separated from adjacent natural communities by State Road (SR) A1A in much of eastern Florida. In this region, this ecosystem exhibits distinct zonation in response to the influences of the maritime environment, and is therefore divided into two primary components: foredune and backdune. Stable sediments leeward of the high tide line

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extending to the primary stable dune ridge crest support a coastal grassland formation known as the foredune, which is significantly influenced by the presence of low-nutrient soils and by coastal processes, including wind, storms, overwash, sand deposition, and salt spray (Harper 1911, Kurz 1942, Oosting 1954, Hillestad et al. 1975, Johnson and Barbour 1990, Miller et al. 2010). The foredune is dominated by graminoid and forb species including saltmeadow cordgrass [*Spartina patens* (Aiton) Muhl.], sea oats *(Uniola paniculata* L.), and seacoast marshelder *(Iva imbricata* Walter) (Johnson and Barbour 1990).

The backdune, which extends landward of the stable primary dune crest westward to SR A1A is largely sheltered from many of the direct maritime influences by a linear, stabilized dune ridge. This zone is generally characterized by woody species, including saw palmetto [*Serenoa repens* (W. Bartram) Small], yaupon (*Ilex vomitoria* Aiton), cabbage palm [*Sabal palmetto* (Walter) Lodd. ex Schult. & Schult. f.], live oak (*Quercus virginiana* Mill.), and laurel oak (*Quercus laurifolia* Michx.) (Kurz 1942, Florida Natural Areas Inventory 1990, Johnson and Barbour 1990).

In their ecological study of the nearby Cumberland Island National Seashore in Georgia, USA, Hillestad et al. (1975) describe a plant community similar to that of our backdune study area observing, in particular, live oak with a continuous saw palmetto understory. Harper (1914) and Gunter (1921) described what we now know as the coastal strand as being characterized by "vast thickets of saw palmetto." Saw palmetto is a dominant species in the backdune in our and other similar study sites (Richardson 1977, Simon 1986), and might in fact serve as a dune stabilizer, providing "foundation and stability" (Takahashi et al. 2011). Saw palmettos are resilient to fire and can readily facilitate its spread (Abrahamson 1999, Takahashi et al. 2011, Carrington and Mullahey 2013).

Lightning-ignited fire has long been recognized as a significant and essential disturbance process for maintaining most of Florida's natural communities, as well as those of the more widespread Atlantic Coastal Plain of the southeastern United States (Harper 1911, 1914; Komarek 1964; Richardson 1977; Frost 1998; Duncan et al. 2010). Nevertheless, little is known about the specific role of fire in maintaining coastal ecosystems of the region (Komarek 1964, Abrahamson 1984, Simon 1986, Florida Natural Areas Inventory 2010, Duncan et al. 2011). It is clear that in the southeastern USA, the number and size of naturally-ignited fires has decreased since European settlement (Fernald 1989, Frost 1998, Myers and Ewell 1990), and the absence of a natural fire regime has in turn altered fire-dependent natural communities through successional processes resulting in increased dominance of mesophytic hardwood species (Predmore et al. 2007, Nowacki and Abrams 2008).

When the regular fire disturbance pulse is altered, coastal strand succeeds to fire-resistant maritime hardwood hammocks (Laessle and Monk 1961, Austin et al. 1987, Myers and Ewell 1990). Long ago Harper (1911) pointed to the important role of fire and its absence or infrequency in promoting vegetative succession to hammocks on islands and coastal peninsulas. Similarly, Hillestad et al. (1975) proposed a successional vegetative sequence on Cumberland Island, Georgia, which, in the absence of fire, would "release" oak–palmetto forest to oak–scrub forest. These observations were further supported by Veno (1976) and by Turner and Bratton (1987).

Although there is little known about the specific coastal strand ecosystem response to fire, several of the primary backdune plant species responses are quite well-known. Abrahamson (1984) found that oaks (*Quercus* spp.) on the Lake Wales ridge of Florida were resilient to fire, as was saw palmetto (Simon 1986, Abrahamson 1999), with all of these species recovering their preburn dominance as shrubs within 3 yr. The oak and palmetto fire recovery mechanism is primarily by resprouting clonally or from the perennating buds (Menges and Kohfeldt 1995, Abrahamson 1999, Takahashi et al. 2011), whereas saw palmetto can also respond by seeding (Menges and Kohfeldt 1995). Yaupon has been found to resprout vigorously following fire (Mitchell et al. 2014).

In spite of its conservation ranking, there exists a paucity of information about managing the highly threatened coastal strand ecosystem (Simon 1986, Lau and Dodd 2015). In addition to the many threats described previously, coastal natural communities worldwide share widely similar xeric vegetative structure and patterns of zonation (Doing 1985, Acosta et al. 2000, Isermann 2011). Given the sheer magnitude of threats to this ecosystem, a better understanding of the specific, and relatively unknown, community responses to disturbance pulses such as fire is critical. Understanding the role of fire, and the systemic responses to it, is essential for natural areas managers tasked with sustaining these threatened coastal ecosystems.

The Guana Tolomato Matanzas National Estuarine Research Reserve (hereafter, GTMNERR) in northeastern Florida manages a significant, protected example of the coastal strand ecosystem. Fire is being used as a management tool by the GTMNERR in an attempt to restore this disturbance process to enhance biodiversity and reduce succession in many of the Reserve's natural communities (GTMNERR Management Plan 2009). In January 2014, GTMNERR managers conducted a prescribed burn in a 55-ha portion of the coastal strand, dividing the site nearly in half by a firebreak. This burn presented an opportunity to examine the effects of fire in this natural community.

This research was undertaken to contribute to a better understanding of the vegetative response to fire in this and similar highly threatened coastal ecosystems. We hypothesized that: (1) plant species cover and abundance would differ between burned and unburned treatments; (2) burning would increase plant species diversity; (3) tree species size would differ between burned and unburned treatments as a result of fire mortality; and, (4) soil characteristics would differ between burned and unburned treatments.

METHODS

Study Area

Our study area is the northern component of the GTMNERR on the Atlantic coast of north Florida, running from 30°07′37.68″N, 81°20′51.84″W to 30°04′05.43″N, 81°20′01.63″W. The climate is classified as subtropical marine, with a mean annual temperature of 21.3°C. Mean annual precipitation is 124.5 cm, with the maximum rainfall occurring between June and October and the minimum between November and February (Florida Climate Center 2016).

The geology is of Pleistocene origin (Gunter 1921) with Holocene sediments composed largely of sand and shell material underlain by a Hawthorn group clay aquitard (GTMNERR Management Plan 2009). The soils are characterized as Fripp–Satellite–Paola complex and Beaches, which are excessively well-drained (Soil survey of St. Johns County, Florida 1999; GTMNERR Management Plan 2009). Stabilized primary dunes dividing the foredune (vegetated area from the crest eastward) and backdune (from the crest westward to A1A) can reach heights of 12 m (GTMNERR Management Plan 2009).

Our study area is linear (approximately 6.5 km in length), varying in width from 90 to 145 m for a total area of approximately 55 ha. Floristically, the foredune component of the study site is characterized by grassland beach dune vegetation east of the primary dune ridge (Stout 1979, Doing 1985), with the backdune zone immediately west of the dune ridge characterized as coastal scrub (Florida Natural Areas Inventory 1990, Johnson and Barbour 1990). State Road (SR) A1A bounds the site along its entire west side, and the Atlantic Ocean forms the eastern boundary. SR A1A was constructed in the mid- to late 1920s by teams of men and mules as a dirt road (Florida Memory 2016). This effectively bisected the coastal strand, leaving a narrow, vegetated ribbon east of the road, now a high traffic, two-lane paved road.

In January 2014, a prescribed fire treatment was applied to both foredune and backdune components of the southern portion (22.5 ha) of the study area, whereas the adjacent northern sector (32.6 ha) was left unburned, allowing us to compare control vs. fire treatment effects in this ecosystem. We examined the study area according to the two ecozones: foredune and backdune. The delineation was made on the basis of primary dune topography and the abrupt demarcation in vegetative structure from grassland to woody scrub, as indicated above.

We sampled soils in the backdune and vegetation in both of these ecozones between SR A1A and the vegetated swale above the mean high tide line postburn during each of three sampling periods: the mid-growing season (May, 2015), late growing season (September–October, 2015), and early growing season (March–April, 2016). We alternated locations and treatments so that each postfire sampling period was distributed approximately equally across sample locations (foredune and backdune), treatments (burned and unburned), and seasonal variation (Gibson and Looney 1992). Our investigation therefore took place between 1 and 2 yr postburn. Previous investigators (Stout 1979, Lau and Dodd 2015) described the backdune as an "impenetrable thicket," and we found field work in this ecotype similarly challenging and time-consuming. Our backdune surveys therefore encompassed a more limited sample area than the foredune. All raw data have been deposited at www.castaneajournal.org.

Vegetation

Plant species abundance, cover, and tree size data were collected to assess the vegetative response to burning on the foredune and backdune subcommunities. Our vegetative survey methodology was adapted from the Carolina Vegetation Survey (CVS) (Peet et al. 1998, 2012), and used the "module" sampling unit concept. We sampled 10 modules in each of our four treatment combinations (burned foredune, unburned foredune, burned backdune, and unburned backdune) for a total of 40 modules. For the 20 foredune modules, we sampled a total of 2.0 ha, whereas the 20 backdune modules totaled an area of 0.4 ha. Each module was oriented north to south, paralleling the shoreline, primary dune ridge, and SR A1A. This orientation was designed to assess vegetative differences within the natural community type as a factor of fire treatment rather than reflecting differences across zones.

Each of the modules comprised a 100 m by 10 m (foredune, 1,000 m^2) or 50 m by 4 m (backdune, 200 m^2) belt transect and four 1 m^2 quadrats. We placed the short (10 m or 4 m) transect lines in each module perpendicular (east–west orientation) to the long (100 m or 50 m) transect lines (oriented north–south, parallel with the primary dune line). The midpoints of both the long and short transects intersected at a 90-degree angle. We then placed each of the four quadrats, used to conduct stem counts (abundance data), at opposite, terminal corners on each side of the short transect end points. Within each quadrat we recorded stem counts for each species and combined the four quadrat counts into a total stem count by species for each module.

We collected cover data by first identifying each species and then estimating cover class following the CVS 1–10 cover scale categories (<0.1%, 0.1–1, 1–2, 2–5, 5–10, 10–25, 25–50, 50–75, 75–95, 95–100%) (Peet et al. 1998). We collected tree size data by measuring diameter at breast height (dbh) for all mid-story and canopy trees $\geq$2 cm in the backdune modules. Because there were no individuals with woody stems $\geq$2 cm in the foredune modules, these data were not collected (Supplemental Material 1).

Soils

We collected and characterized soil samples to determine whether soil characteristics differed by treatment, and might therefore explain any differences in floristic species composition, distribution, or dominance. Soil samples were only analyzed for the backdune zone because there is negligible soil development in the foredune habitats. In the field, soil color was determined using a Munsell Color Chart (2000) for each of three soil samples per module and Global Positioning System (GPS) sample locations were recorded.

For each of the 20 backdune modules we collected approximately 1.0 L of soil from three within-module sample locations. These three samples were combined, and then analyzed for particle size distribution, pH, percent organic matter, and total carbon content in the lab. The analysis methodologies followed those of the Natural Resource Conservation Service (Soil Survey Staff 2014). We analyzed both pH in water and pH in salt. This combination is a common practice; the salt analysis enables a reduction in measured pH, which enables a finer-scaled classification of the soil (Soil Survey Staff 2014). We conducted these soil analyses during the winter of 2016, 2 yr postburn (Supplemental Material 2).

Fuel Characteristics

In an effort to help natural areas managers in fire management planning, we attempted to develop a fuel model for this coastal strand site. To this end, in November, 2014, we collected vegetation samples along five transects exclusively within the unburned treatment of the study area as follows. We established five, 50-m transects in a west-to-east direction within the backdune. A random numbers generator was used to locate three, 0.5-m^2 quadrats along each transect. We cut all vegetation originating in each quadrat from its maximum height to ground level, constituting the live samples. Samples were bagged separately for each transect. These live-fuel samples were weighed in the lab, then placed in an oven to dry at a temperature of 105°C for 24 hr and reweighed, generally following the methods of Stronach and McNaughton (1989). We calculated the difference between live and dried fuel weights to yield fuel moisture content. We averaged fuel loads in g/m^3 over the five transects, then extrapolated out to the total area representing the unburned treatment area, which represents the fuel load of this unburned coastal strand in g/m^3. We then calculated coastal strand fuel load and compared this with the fuel loads of fuel models from Anderson (1982).

Fire History

In an effort to determine fire history, and establish whether the coastal strand ecosystem has historically naturally burned with lightning ignition, we obtained and analyzed geospatial data (ArcMap 10.3.1) from the Florida Forest Service (FFS) on their available fire records for St. Johns County, Florida, between 1981 and 2015 (Taylor and Cummins, pers. comm.).

Data Analyses

We separated foredune from backdune modules for all analyses.

Plant Data. We began our plant analyses with NMDS (nonmetric multidimensional scaling) ordinations on plant species data using Primer 7 (version 2014) to test whether there were clear separations (differences) in plant species cover or abundance by treatment (burned or unburned). These analyses use the Bray–Curtis similarity index, which represents the distance (similarity or dissimilarity) between sample characteristics (such as species abundance or cover class) and an environmental factor (treatment: burned or unburned) in multidimensional ordination space (Clarke and Warwick 2014). For the NMDS analyses, both the cover and abundance (stem count) data were used. We then used analysis of similarity (ANOSIM) on cover and abundance data sets to determine whether dissimilarities between samples and treatments were significant. Once we determined that burned modules clearly separated from unburned modules in several of the NMDS analyses, we then conducted similarity percentage (SIMPER) analyses using Primer 7 (version 2014) on the abundance data to determine which plant species were responsible for most of the dissimilarities between burned and unburned modules.

Biodiversity analyses between burned and unburned treatments also used Primer 7 (version 2014). These calculations are “based on the taxonomic distinctness or relatedness of the species making up a quantitative sample or species list” (Clarke and Warwick 2014). The Shannon diversity index, Simpson, Brillouin and Fisher’s indices, Margalef’s richness, and Pielou’s evenness were calculated using the cover and abundance data.

For midstory and canopy tree diameter data we used two-way ANOVA to test for differences in mean dbh among the five dominant tree species and between burned or unburned treatments (2 × 5 factorial ANOVA) using Microsoft Excel (version 2013). We did not test for fire-induced mortality in tree species for two reasons. The first is that we had no opportunity to collect prefire data, and the second is that for red bay, which would be expected to be a foundation species, many of these individuals had been killed by the invasive ambrosia beetle (*Xyleborus glabratus*)-mediated fungal infection (Ellison et al. 2005, Goldberg and Heine 2009, Shields et al. 2011), so we were unable to discern whether mortality was due to fire or to infection.

Soil Data. For soil data, Microsoft Excel (2013) was used for parametric statistical analyses (Student’s *t*-tests) of the soil chemistry and particle size data to test whether there were any differences in soil characteristics between burned and unburned treatments.

Soil and Vegetation Data. We tested whether there were similarities between plant and soil characteristics in burned and unburned treatments in the following manner. We analyzed soil characteristics (soil chemistry and soil particle data sets) and plant cover and abundance data sets with Primer 7 (version 2014) NMDS, using all combinations of these four data sets to test whether there were clear separations (differences) by treatment (burned or unburned).

RESULTS

Plants

We recorded 40 species for the backdune locations, and 41 from the foredune area (Tables 1 and 2). The backdune list encompasses a range of woody and herbaceous species. Arboreal taxa include 13 tree species, of which five are oaks (genus *Quercus*) (Table 1). Among the herbaceous forms, the sunflower family (Asteraceae) is conspicuous by the presence of seven species. We also recorded several perennial or biennial herbs and five taxa of vines, particularly the

Table 1. Backdune Samples Plant Species List, Guana Tolomato National Estuarine Research Reserve (GTMNERR) (*not native). Sources: EOL 2017; Wunderlin et al. 2016.

Family	Species	Common Name	Life Form
Arboreal taxa:			
Anacardiaceae	*Rhus copallinum*	Winged sumac	shrub
Aquifoliaceae	*Ilex opaca*	American holly	shrub, tree
Aquifoliaceae	*Ilex vomitoria*	Yaupon holly	shrub
Arecaceae	*Sabal palmetto*	Cabbage palm	tree
Arecaceae	*Serenoa repens*	Saw palmetto	shrub
Asteraceae	*Baccharis halimifolia*	Salt bush, groundsel tree	shrub
Euphorbiaceae	*Triadica sebifera**	Chinese tallowtree	tree
Fabaceae	*Erythrina herbacea*	Coral/Cherokee bean	shrub
Fagaceae	*Quercus geminata*	Sand live oak	tree
Fagaceae	*Quercus chapmanii*	Chapman's oak	shrub, tree
Fagaceae	*Quercus laurifolia*	Laurel oak	tree
Fagaceae	*Quercus myrtifolia*	Myrtle oak	shrub, tree
Fagaceae	*Quercus virginiana*	Live oak	tree
Lamiaceae	*Callicarpa americana*	American beautyberry	shrub
Lauraceae	*Persea borbonia*	Red bay	tree
Magnoliaceae	*Magnolia grandiflora*	Southern magnolia	tree
Oleaceae	*Cartrema americana*	Wild olive	tree
Rosaceae	*Prunus caroliniana*	Carolina laurelcherry	tree
Rosaceae	*Rubus trivialis*	Southern dewberry	subshrub, rambler
Rutaceae	*Zanthoxylum clava-herculis*	Hercules club	tree
Vitaceae	*Ampelopsis arborea*	Peppervine	liana
Vitaceae	*Parthenocissus quinquefolia*	Virginia creeper	liana
Vitaceae	*Vitis aestivalis*	Summer grape	liana
Vitaceae	*Vitis rotundifolia*	Muscadine grape	liana
Herbaceous taxa:			
Amaranthaceae	*Amaranthus australis*	Southern amaranth	annual herb
Asteraceae	*Ambrosia artemisiifolia*	Common ragweed	annual herb
Asteraceae	*Bidens alba*	Beggarticks	annual herb
Asteraceae	*Cirsium horridulum*	Purple thistle	annual/biennial herb
Asteraceae	*Erechtites hieraciifolius*	American burnweed	annual herb
Asteraceae	*Eupatorium capillifolium*	Dogfennel	perennial herb
Asteraceae	*Mikania scandens*	Climbing hempvine	vine
Asteraceae	*Solidago sempervirens*	Seaside goldenrod	perennial herb
Passifloraceae	*Passiflora incarnata*	Purple passionflower	vine
Phytolaccaceae	*Phytolacca americana*	American pokeweed	perennial herb
Solanaceae	*Physalis walteri*	Walter's groundcherry	perennial herb
Solanaceae	*Solanum carolinense*	Carolina horsenettle	perennial herb
Solanaceae	*Solanum chenopodioides*	Black nightshade	perennial herb
Smilacaceae	*Smilax auriculata*	Earleaf greenbrier	vine
Smilacaceae	*Smilax bona-nox*	Saw greenbrier	vine
Smilacaceae	*Smilax rotundifolia*	Roundleaf greenbrier	vine

greenbriers (*Smilax* spp.). We noted that pines were absent from the tree taxa, and no grasses or sedges were observed for this ecozone (Table 1). The foredune plant species composition is simpler in both structure and composition, with only three shrub species, no trees, and multiple graminoids (Table 2). The dominant species were the graminoids, with the Poaceae family most abundant and widespread.

NMDS Ordinations

Cover and Abundance. For the backdune cover data, the NMDS ordination showed clear separation between burned and unburned samples (3D stress = 0.12) (Figure 1a). The ANOSIM analyses indicated that the dissimilarity in cover class between burned and unburned groups was significant for the backdune (R = 0.366, df = 19; p = 0.02). NMDS analyses for the foredune cover data showed a moderate separation (Figure 1b), with the ANOSIM results showing significant dissimilarity between treatments (R = 0.204, df = 19, p = 0.03).

The backdune NMDS abundance data analyses showed a clear separation between burned and unburned treatments (3D stress = 0.12) (Figure 2a), with ANOSIM analyses returning a signifi-

Table 2. Foredune Samples Plant Species List, Guana Tolomato National Estuarine Research Reserve (GTMNERR) (*not native). Sources: EOL 2017; Wunderlin et al. 2016.

Family	Species	Common Name	Life Form
Arboreal taxa:			
Asteraceae	*Baccharis halimifolia*	Groundsel Tree	shrub
Arecaceae	*Serenoa repens*	Saw Palmetto	shrub
Sapotaceae	*Sideroxylon tenax*	Buckthorn	shrub/tree
Herbaceous taxa:			
Brassicaceae	*Cakile lanceolata*	Coastal searocket	annual herb
Poaceae	*Cenchrus spinifex*	Coastal sandbur	annual/perennial graminoid
Fabaceae	*Chamaecrista nictitans* var. *aspera*	Sensitive Pea	annual/perennial herb
Asteraceae	*Cirsium horridulum*	Purple thistle	biennial/perennial herb
Euphorbiaceae	*Cnidoscolus stimulosus*	Tread-softly; Stinging nettle	annual
Commelinaceae	*Commelina erecta*	Whitemouth dayflower	annual
Asteraceae	*Conyza canadensis*	Canadian horseweed	annual/biennial herb
Fabaceae	*Crotalaria rotundifolia*	Rabbitbells; Rattlebox	perennial herb
Euphorbiaceae	*Croton punctatus*	Beach tea	perennial herb
Cyperaceae	*Cyperus compressus*	Poorland flatsedge	annual/perennial graminoid
Amaranthaceae	*Dysphania ambrosioides**	Mexican tea	annual herb/subshrub
Euphorbiaceae	*Euphorbia exserta*	Spurge	perennial herb
Poaceae	*Eustachys glauca*	Saltmarsh fingergrass	perennial graminoid
Asteraceae	*Gaillardia pulchella*	Firewheel; Blanket flower	annual/biennial herb
Rubiaceae	*Galium hispidulum*	Coastal bedstraw	perennial herb
Asteraceae	*Helianthus debilis*	East Coast dune sunflower	annual/perennial herb
Araliaceae	*Hydrocotyle bonariensis*	Largeleaf marshpennywort	perennial herb
Fabaceae	*Indigofera spicata**	Trailing indigo	herb/subshrub
Fabaceae	*Indigofera hirsuta**	Hairy indigo	herb/subshrub
Convolvulaceae	*Ipomoea imperati*	Beach morning glory	perennial vine
Polemoniaceae	*Ipomopsis rubra*	Standingcypress	biennial herb
Asteraceae	*Iva frutescens*	Bigleaf sumpweed	perennial herb
Asteraceae	*Iva imbricata*	Seacoast marshelder	perennial herb/subshrub
Lamiaceae	*Monarda punctata*	Spotted beebalm	annual/biennial/perennial herb
Onagraceae	*Oenothera humifusa*	Seabeach evening primrose	perennial herb
Cactaceae	*Opuntia pusilla*	Cockspur pricklypear	perennial subshrub
Cactaceae	*Opuntia stricta*	Erect pricklypear	perennial subshrub
Passifloraceae	*Passiflora incarnata*	Purple passionflower	perennial herb/vine
Phyllanthaceae	*Phyllanthus odorata**	Chamber bitter	annual herb
Solanaceae	*Physalis walteri*	Walter's groundcherry	perennial herb
Plantaginaceae	*Plantago lanceolata**	Narrowleaf plantain	annual/biennialherb
Asteraceae	*Pluchea camphorata*	Camphorweed	annual/perennial herb
Lamiaceae	*Salvia lyrata*	Lyreleaf sage	perennial herb
Smilacaceae	*Smilax bona-nox*	Saw Greenbriar	vine
Asteraceae	*Solidago fistulosa*	Pinebarren goldenrod	perennial herb
Poaceae	*Spartina patens*	Saltmeadow cordgrass	perennial graminoid
Poaceae	*Uniola paniculata*	Seaoats	perennial graminoid
Agavaceae	*Yucca filamentosa*	Adam's needle	perennial herb/subshrub

cant difference in the backdune treatment groups (R = 0.296, df = 19, p = 0.03). NMDS ordination of the foredune abundance data showed no clear separation between treatment groups (Figure 2b) and the ANOSIM analyses were insignificant (R = 0.074, df = 19, p = 0.08).

SIMPER analyses, which are based on testing the "Bray-Curtis similarities between samples" (Clarke and Warwick 2014), enabled a further test for whether there were species composition differences between burned and unburned treatments. SIMPER analysis on the backdune abundance data identified five species—climbing hempvine [*Mikania scandens* (L.) Willd.], American pokeweed (*Phytolacca americana* L.), yaupon, Carolina laurelcherry [*Prunus caroliniana* (Mill.) Aiton], and saw palmetto—as those contributing most to the dissimilarities between treatment groups (burned and unburned) (Table 3a). Climbing hempvine and American pokeweed were found only in the burned treatment modules, whereas saw palmetto was more abundant in the unburned treatment modules.

The foredune analyses of the abundance data using SIMPER returned four species with major

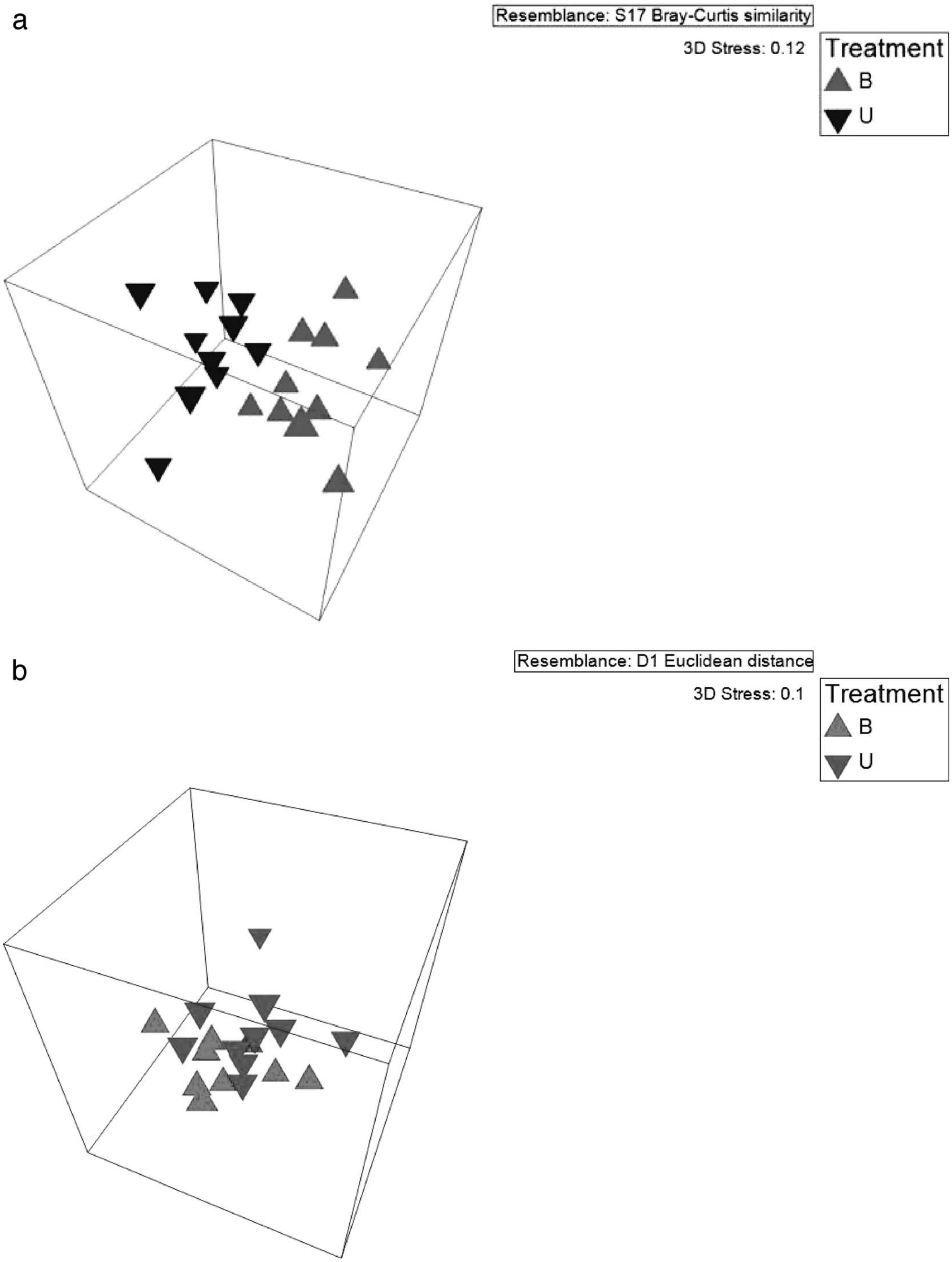
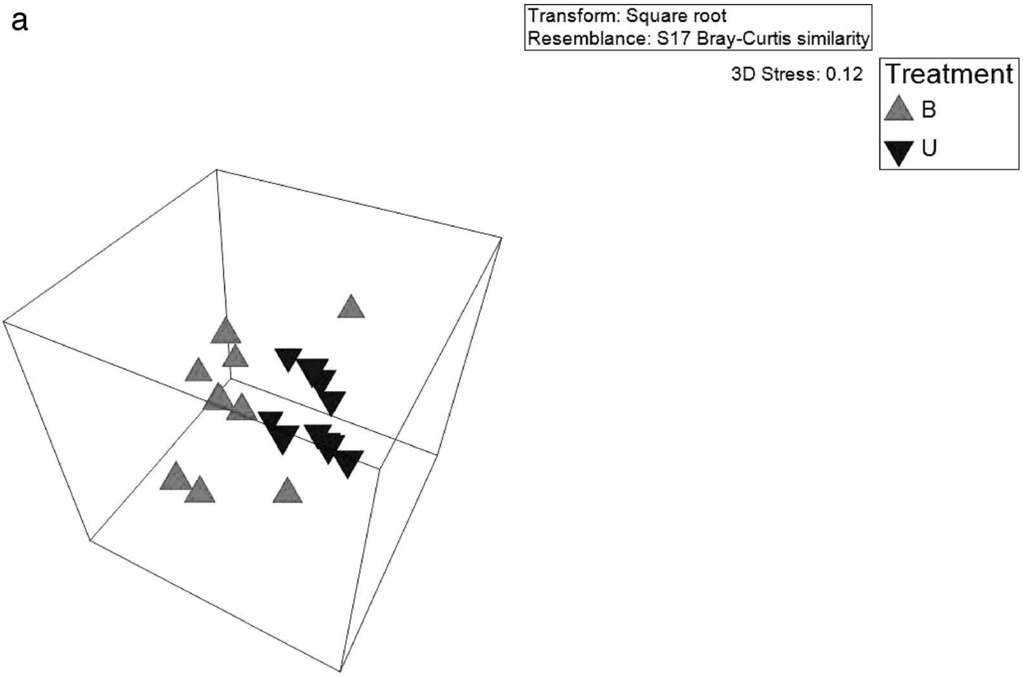


Figure 1. **(a)** Backdune NMDS analysis of similarity for cover (R = 0.366, df = 19; p = 0.02; 3Dstress value: 0.12). **(b)** Foredune NMDS analysis of similarity for cover (R = 0.204, df = 19, p = 0.03; 3Dstress value: 0.10). Calculated using Primer 7 on species abundance (stem count) data collected at the GTMNERR coastal strand, Florida, 2015–2016. B = Burned treatment; U: Unburned treatment.



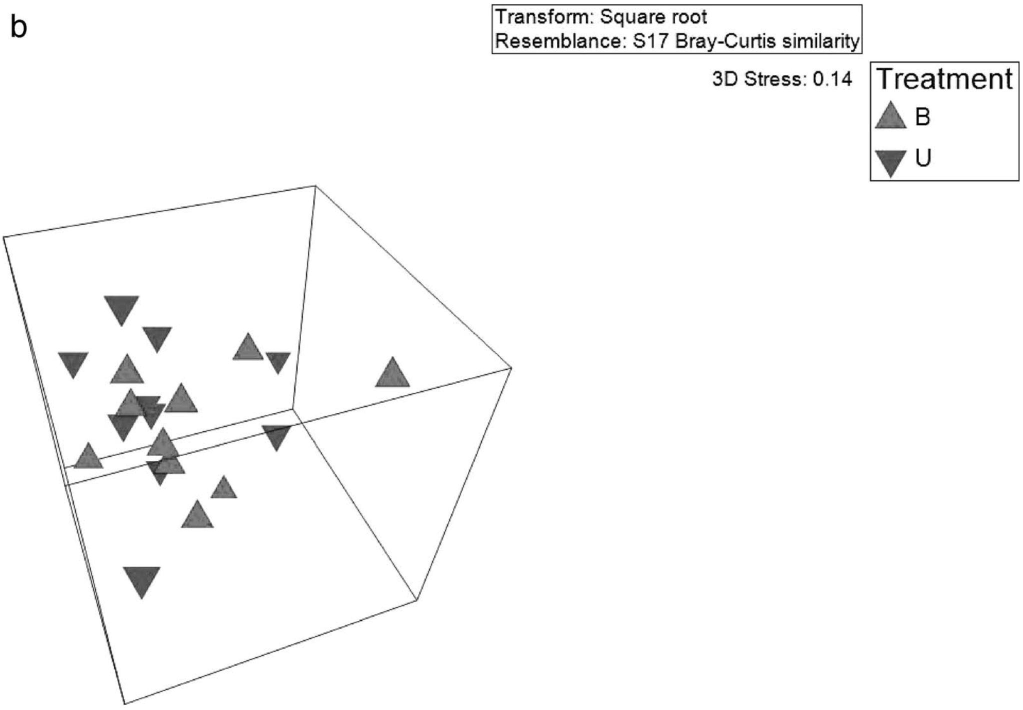


Figure 2. **(a)** Backdune NMDS analysis of similarity for species abundance (R = 0.296, df = 19, p = 0.03; 3Dstress value: 0.12). **(b)** Foredune NMDS analysis of similarity for species abundance (R = 0.074, df = 19, p = 0.08; 3Dstress value: 0.14). Calculated using Primer 7 on species abundance (stem count) data collected at the Guana Tolomato National Estuarine Research Reserve (GTMNERR) coastal strand, Florida, 2015–2016. B = Burned treatment; U = Unburned treatment.

Table 3a. Similarity percentage (SIMPER) (Primer 7) analysis for backdune species between burned and unburned treatments with average dissimilarities of primary species calculated (n = 10 modules for each treatment), from total stem counts on species abundance (using total stem count data from four, 1-m^2 quadrats in each module). Data collected at the Guana Tolomato National Estuarine Research Reserve (GTMNERR) coastal strand, Florida, 2015–2016. Parameters for both SIMPER analyses; Resemblance: S17 Bray-Curtis similarity; Cut off for low contributions: 70.00%.

Species	Mean Abundance Burned	Mean Abundance Unburned	Mean Dissimilarity	% Contribution to Dissimilarity
Mikania scandens	2.07	0	10.71	14.11
Phytolacca americana	0.89	0	5.93	7.81
Ilex vomitoria	0.95	1.01	6.69	8.81
Prunus caroliniana	0.64	0.58	5.42	7.14
Serenoa repens	1.18	1.40	4.16	5.48

contributions to the dissimilarities between treatment groups: saltmeadow cordgrass, sea oats, seacoast marsh elder, and largeleaf marsh pennywort (*Hydrocotyle bonariensis* Comm. ex Lam.) (Table 3b). Saltmeadow cordgrass and sea oats were more abundant in the burned treatment modules, whereas seacoast marsh elder and largeleaf marsh pennywort were more abundant in the unburned treatments.

Biodiversity

Calculated biodiversity means indicate clear differences between burned and unburned treatment groups using the cover data for both backdune (Figure 3a) and foredune (Figure 3b) samples. However, for the same calculations using abundance data, there were no clear differences in biodiversity in either the backdune or the foredune.

Tree Species Stem Diameters

Of the five most abundant species in the backdune (yaupon, laurel oak, live oak, red bay, and magnolia), the two-way ANOVA analysis indicated that there was no relationship between tree species mean dbh and treatment (burned or unburned) (ANOVA; df = 1, F = 5.16, F crit = 7.71; $p < 0.79$). It should be noted that for several species—cabbage palm, wild olive [*Cartrema americana* (L.) G. L. Nesom] and cherry laurel—every individual of that species was found in only one treatment type, so there was no opportunity to compare treatments across these species.

Soil

Of the soil chemical characteristics we analyzed (Table 4), only pH in salt was significantly different between treatments in the backdune (df = 19, p = 0.04) and there were no significant differences in soil particle size distributions between treatments.

Soil and vegetation

We analyzed combinations of the soil characteristics data and plant cover and abundance data sets using NMDS with Primer 7 (2014). None of these analyses showed clear separations between burned and unburned treatments.

Fuel Characteristics

We compared fuel load calculations for the backdune with Anderson's fuel models (Anderson 1982). Analyses indicate that the coastal strand fuel load is closest to Fuel Model 7 (Southern

Table 3b. Similarity percentage (SIMPER) (Primer 7) analysis for foredune species between burned and unburned treatments with average dissimilarities of primary species calculated (n=10 modules for each treatment), from total stem counts on species abundance (using total stem count data from four, 1-m^2 quadrats in each module). Data collected at the Guana Tolomato National Estuarine Research Reserve (GTMNERR) coastal strand, Florida, 2015–2016.

Species	Mean Abundance Burned	Mean Abundance Unburned	Mean Dissimilarity	% Contribution to Dissimilarity
Spartina patens	14.86	12.93	5.58	10.96
Uniola paniculata	10.09	5.35	5.33	10.47
Iva imbricate	2.65	5.42	4.65	9.14
Hydrocotyle bonariensis	6.76	8.05	4.49	8.82

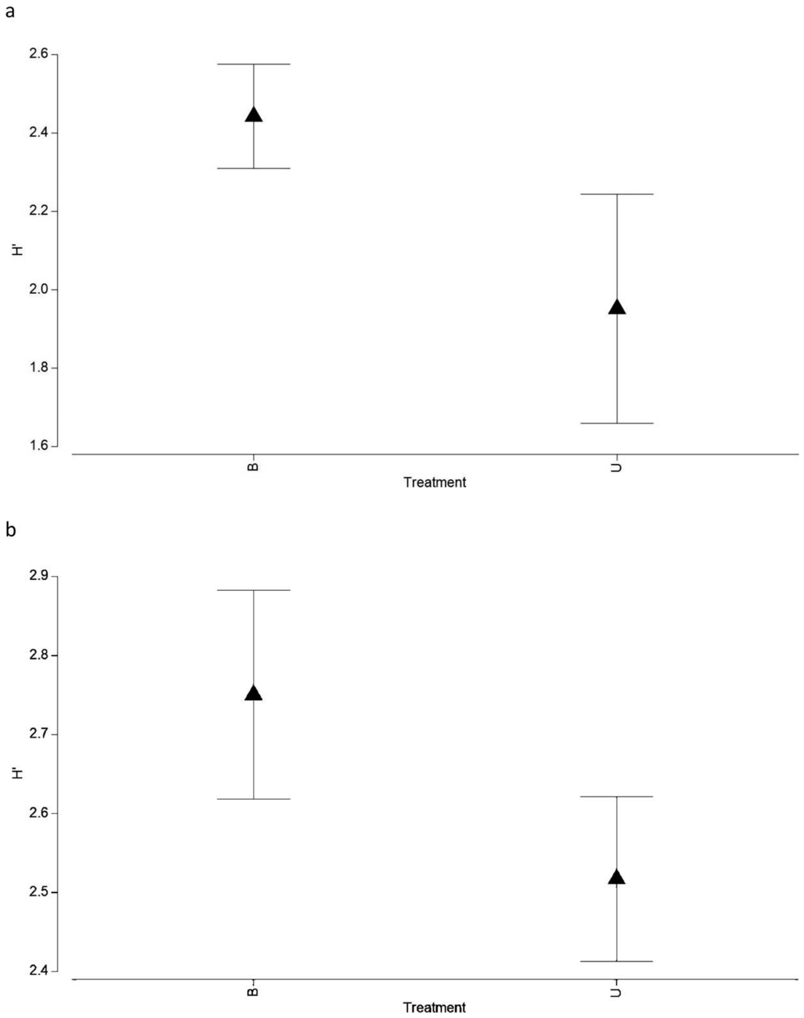


Figure 3. **(a)** Backdune biodiversity analysis (Shannon diversity, H'), with standard error bars. Calculated using Primer 7 on cover data collected at the Guana Tolomato National Estuarine Research Reserve (GTMNERR) coastal strand, Florida, 2015–2016. **(b)** Foredune biodiversity analysis (Shannon diversity, H'), with standard error bars. Calculated using Primer 7 on cover data collected at the GTMNERR coastal strand, Florida, 2015–2016.

rough) but is also comparable to Fuel Model 4 (Chapparal). Mean dead fuel moisture was 40.9% with a range from 24.8% to 63.8% and a standard deviation of 14.5%. It should be noted that our drying temperature was higher (105°C vs. 95°C) than Stronach and McNaughton's (1989) and our drying time was limited to 24 hr, which might have impacted both carbon and moisture levels.

Fire History

ArcGIS analyses of the FFS records indicated that, for this 34-yr period, 15 lightning-ignited fires occurred east of the Guana River in close proximity to the study area (Taylor and Cummins, pers. comm.). These wildfires all occurred during the summer growing season (June–August). Three of these fires were immediately adjacent to the study site, although just on the west side of SR A1A (the study site is just east of A1A). These three lightning-ignited fires ranged in area between 0.04 and 8 ha before being suppressed.

DISCUSSION Our goal was to describe the vegetative response to fire in this threatened ecosystem to help inform natural areas manag-

Table 4. Particle size data, soil chemistry and particle size, and analyses performed for backdune soils at the Guana Tolomato National Estuarine Research Reserve (GTMNERR) coastal strand, Florida, 2015–2016. B = Burned; UB = Unburned.

Particles	Coarse	Medium	Fine	Very Fine
Mean UB	8.28	15.27	67.92	5.52
Mean B	7	19.1	64.62	5.57
df	19	19	19	19
SD UB	5.72	6.56	12.11	2.70
SD B	3.82	7.87	10.34	2.66
p	0.23	0.09	0.22	0.39

Chemistry	Mineral	Organic	Carbon H+	Conc. H_20 H+	Conc. salt
Mean UB	89.99	9.84	4.99	6.25 E−06	2.72 E−05
Mean B	88.68	10.68	5.66	0.00	1.01 E−05
df	19	19	19	19.00	19
SD UB	9.61	9.78E+00	4.81	0.000005	5.55 E−06
SD B	4.45	5.35	2.23	0.000025	1.01 E−05
p	0.324606	0.388456	0.324606	0.2416202	0.0348713

ers in their efforts to conserve and protect what remains of these fragmented coastal ecosystems. As such, we present both our results and a review of fire return intervals in similar ecosystems.

Vegetative Fire Response

When we tested for dissimilarity and biodiversity using the cover data, we found that there was a significantly different vegetation profile in response to fire in both the backdune and foredune of this coastal strand site. These results support our hypotheses that plant species diversity would increase and that cover would differ between burned and unburned treatments. These results also parallel prior investigators' conclusions (Abrahamson 1984, Turner and Bratton 1987, Davison and Bratton 1988) that introducing prescribed fire to the coastal strand ecosystem at GTMNNERR resulted in a significant change in vegetative cover. The moderately low R values obtained with ANOSIM analyses might reflect a resilience to fire in this ecosystem; this could be a topic for further investigation.

When we tested for dissimilarity and biodiversity using the abundance data, we obtained differing results between the backdune and foredune. Significant dissimilarity was found only for the backdune, which converges with the cover data analyses and supports our hypothesis that abundance differs between treatments. However, no significant biodiversity differences were found in either zone using the abundance data set for analyses. We therefore find our results for the foredune abundance data set inconclusive and offer the following possible explanations.

We note that the duration of the sampling effort might have influenced our results; although our sampling effort began early in the first growing season following the prescribed fire in 2014, it wasn't completed until 26 mo postburn. As such, it is possible we missed some of the immediate vegetative response to fire, especially in the faster-growing foredune species. The ambiguity in our abundance analyses for the foredune might be a reflection of the differences in rate of fire recovery mechanisms of the dominant species in each ecozone. Whereas woody tree and shrub species dominate the backdune, the foredune is graminoid-dominated, with species that appear to employ faster fire recovery mechanisms than those dominating the backdune. Our anecdotal observations that saw palmetto cover was reduced and that herbaceous species cover and abundance increased in the burned treatment was supported by the SIMPER analyses (Table 3a) and might reflect the different rate of fire recovery mechanisms of these important species.

Tree sizes as measured by dbh were also no different between treatments, causing us to reject our hypothesis that they would differ. Similarly, we detected only one difference in the soil analyses that might explain any of the significant vegetation results; thus, our hypothesis that there would be differences in soil characteristics between burned and unburned treatments was not well supported. It should also be noted that the soil sampling occurred in the second year following the burn, and it is therefore possible that most fire-related soil differences were no longer detectable. The only significant difference in soil chemistry between treatments was that soil pH in salt was higher for the burned treatment. This could be explained by the persistence of calcite, which is less soluble than other compounds that might affect soil pH (Ulery et al. 1993).

There were no records of differential management within our study area (Frazel 2008); we therefore initially assumed that our study zones were basically similar preburn. However, once we began data collection, we observed that two of our backdune unburned vegetation sample modules were seemingly in the process of succeeding to mesic oak hammock. Large canopy height live oak individuals dominated, with few saw palmettos and fewer herbaceous species in these modules. Shrub and fine fuels that could carry fire were limited; therefore, these two modules might reflect a successional trend toward a fire-resistant oak-dominated mesic hammock (Laessle and Monk 1961, Austin et al. 1987). It should be further noted that our treatments were not replicated, and that these samples represented 2 of the 10 unburned modules (out of a total of 40 total modules; 10 in each of four treatment combinations). We are uncertain why these two modules were different from all the other backdune sample modules and are therefore unclear as to the extent they might have affected our overall results in the backdune. We therefore interpret our results with restraint.

However, we are concerned about the potential effects of fire exclusion on the threatened coastal strand ecosystem. Although the plant species lists compiled by Gunter (1921) and Oosting (1954) are largely comparable to ours (Tables 1 and 2), Gunter (1921), who described coastal strand species very near our study site, noted the absence of the wild cherries/plums (*Prunus* spp.). Interestingly, one such species, Carolina laurelcherry, was fairly well represented in our backdune samples. The laurelcherry, which is fire sensitive, could reflect the "mesophication" (Nowacki and Abrams 2008) process in the backdune at the GTMNERR. "Mesophication" ("development of cool, moist understory conditions") of ecosystems is a process whereby fire-dependent species are replaced by fire-sensitive species when a fire regime is interrupted, resulting in altered microclimatic changes that favor more shade-tolerant, fire-sensitive species (Nowacki and Abrams 2008).

Several investigators (Laessle and Monk 1961, Austin et al. 1987) note that in the absence of fire, the oaks grow larger, forming a closed canopy that reduces the presence of other species and leads to a fire-resistant, oak-dominated, mesic hammock. Kitzberger et al. (2012) concluded that there is a risk of reduction in flammability as this community ages, which could result in a positive feedback loop that reduces "its probability to spread fire." Davison and Bratton (1988) found that "little canopy mortality occurred in areas where live oak was dominant, but mortality was also dependent on size of individuals of the species." Kane et al. (2008) examined the combustion characteristics of dried leaves of several southeastern oak species and separated them into two groups: fire facilitators and fire impeders. They classified live oak in the "fire impeder" cluster (Kane et al. 2008).

Richardson (1977) states that fire is the "principal factor" in inhibiting succession on the Atlantic coastal ridge of southeastern Florida. Stout (1979) noted that coastal scrub shares species assemblage characteristics with "xeric flatwoods, xeric sand pine scrub or xeric coastal hammock." Laessle and Monk (1961) and Austin et al. (1987) observed that with frequent fire, a low dense vegetative thicket is perpetuated. We observed that the backdune species assemblage and structure resembles that of other "oak scrub" sites in the southeastern USA, with an understory largely dominated by pyrophytic saw palmetto (Abrahamson 1984, Breininger and Schmalzer 1990, Schmalzer and Hinkle 1992, 1996). The 2014 burn in our study site exhibited intense fire behavior, consistent with the pyrogenic nature of saw palmetto (Abrahamson 1984, Davison and Bratton 1988) and the observations of other investigators (Gunter 1921, Stout 1979, Fernald 1989).

While sampling, we observed a quick saw palmetto response to the fire. In fact, in the burned area the intense fire consumed nearly all of the aboveground saw palmetto biomass and the trunks appeared deeply charred. However, early in the growing season immediately following the fire, the palmetto resprouted vigorously and flowered profusely, similar to observations of other investigators (Abrahamson 1984, 1999, Simon 1986, Frost 1998). Conversely, we did not observe saw palmetto flowering in our unburned sites. Although we did not collect data on seed recruitment, this could also be a topic for future research in this ecosystem. Saw palmettos, with their robust resilient rhizomes, are likely one of the most important plant species to manage in this ecosystem, particularly in view of their role in maintaining dune stability. Saw palmetto might be equally essential for maintaining the coastal strand ecosystem by promoting the spread of periodic fire, and would therefore be considered a foundational species.

Although there is no direct evidence yet available that fires naturally occurred in the coastal strand aside from observable fire scars on a number of the larger cabbage palms, we infer that lightning caused the ignition of vegetation in the coastal strand and might have spread readily before widespread development along most of SR A1A. The lightning strike map produced by Komarek (1964) clearly indicates a significant number of "lightning caused fires" occurring in a single year, 1962, in the coastal area near or within our study site. In fact, one fire, on December 5, 1987 (Taylor and Cummins, pers. comm.), burned from upper Guana Lake (very near our study area) east all the way to the dunes in our study area, demonstrating the natural movement of fire across the landscape. This is the last known occurrence of fire in our study area prior to the 2014 prescribed fire. Naturally-occurring fire might well have been essential to sustaining the coastal strand ecosystem by inhibiting succession to oak-dominated mesophytic hammock.

Fire Management Review and Further Investigations

Oosting (1954) was the first to outline a successional process in which disturbance(s) maintained the coastal strand ecosystem in its scrubby form, limiting succession toward a live oak/maritime hammock. Although Laessle and Monk (1961) did not define "frequent" fire in recommending fire to maintain or perpetuate coastal strand ecosystems, Austin et al. (1987) reported that the strand ecosystem in southeast Florida burned on a 4–5-yr interval. Scrub ecosystems on a larger Atlantic barrier island complex, the Merritt Island region, were modeled for fire return intervals by Duncan et al. (2011). They inferred that a cyclical pattern for the largest fires of approximately 11 yr was likely explained by the combined effects of cumulative "fuel loadings and climatic variability" (the ENSO, or El Niño–Southern Oscillation, cycle).

Although Austin et al. (1977) suggest that fires occurred as often as every 4–5 yr in the coastal strand, longer fire return intervals in similar inland systems are more typically described. Scrub fire return intervals of 15–20 yr in Florida (Johnson 1982) and 20–30 yr on Cumberland Island, Georgia (Turner and Bratton 1987) were documented, while a 10–25-yr cycle was indicated for Merritt Island, Florida, oak scrub (Schmalzer and Hinkle 1992, 1996). Richardson (1977) notes that although fire in inland scrub locations occurs on an average of between 20 and 40 yr, when burned more frequently, those communities tend to shift to an oak-palmetto type, closely resembling the composition of the coastal strand community in our study site.

More information is needed on the specific effects of fire on faunal species dependent on these coastal ecosystems, and the dynamic interactions among plant species, fauna, and fire. This research provides a clearer picture of the response of the GTMNERR coastal strand vegetation to fire as well as a potential baseline for a long-term monitoring effort. Future research directions could also include a specific focus on testing fire return intervals for this ecosystem, a focus on "mesophication," and spread dynamics, patch size, and spatial dynamics of fire in this and other remnant coastal ecosystems. Coastal scrubs similar in structure and dominated by fire dependent species in other locations might similarly benefit from reintroduction of fire and sustained fire management; this is another topic for future investigations. Planned research will also consider the individual and combined effects and thresholds created by the actions of fire and storm events.

Fire Management Recommendations

We recommend the use of prescribed fire in the backdune of the coastal strand ecosystem in the study region. When we compare our results with other investigations, similar patterns emerge, which we assert supports the reintroduction of fire as a management strategy for sustaining the coastal strand ecosystem in the GTMNERR.

Based on our results in the backdune and review of the relevant literature, we recommend as a starting point that a fire return interval of between 4 and 20 yr be considered by fire managers of the northeast Florida coastal strand ecosystem. We do caution, however, that in the absence of a firm understanding of an appropriate fire return interval, the risk of destabilizing the dune system with too-frequent or too-intense fires should be considered by fire managers. We are much less confident about recommending fire management for the foredune, for which our results were largely equivocal. Other investigators have described the many maritime disturbance influences which limit succession in the foredune component of this ecosystem, likely to an equivalent or greater extent than fire (Doing 1985, Florida Natural Areas Inventory 1990, 2010).

In conclusion, other investigators' research on successional patterns in ecosystems with similar plant associations, a history of lightning-ignited fires, and our findings on fuel loads and vegetative responses to fire, together support fire management action as an important tool for sustaining this highly threatened ecosystem by impeding succession to a maritime oak hammock.

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