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Variation of Florida scrub vegetation along gradients of soil pH and landscape age on a barrier island complex[1, 2]

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Abstract. Florida scrub is a fire-maintained shrub vegetation of well-drained, sandy soils associated with ridge systems that originated as coastal dunes. It is unique to Florida and supports many rare plants and animals. Between 1992 and 2005, we sampled 30 stands of long-unburned scrub with 196 line-intercept transects (15 m length) across the Merritt Island-Cape Canaveral barrier island complex where dune ridges range from relatively recent to $>$ 30,000 years old with a range of soil leaching and reaction. These data allow us to determine the relationships of landscape age and soil reaction on community composition. We recorded community composition in $\leq$ 0.5 m and $>$ 0.5 m height strata. We determined mapped soil type for all transects; for 151 transects we determined soil pH of the 0–15 cm and 15–30 cm layers. Hierarchical cluster analysis of stands ($N = 30$) and transects ($N = 196$) using 41 species (of 53) present in $\geq$ 2 transects gave two groups: coastal scrub with *Quercus virginiana* (shrub form) and *Serenoa repens* as dominant species on the most alkaline soils, and oak-saw palmetto scrub with *Quercus chapmanii, Quercus geminata, Quercus myrtifolia*, and *S. repens* on the strongly to somewhat acidic soils. Direct gradient analysis indicated that dominant species except *S. repens* varied from acidic to alkaline soils. Indicator species analysis identified seven species that indicated acidic soils and five that indicated alkaline soils ($P < 0.01$). Nonmetric multidimensional scaling (NMS) ordination at the stand level separated the two groups along the first axis, and NMS ordination of the transect data showed the gradient of coastal to oak-saw palmetto scrub. Position of transects on the first axis was related to soil pH class, and to measured pH of the 0–15 cm and 15–30 cm layers. Soils show a progressive leaching of shell material from the surface horizons followed by podsolization; this process takes $\geq$ 4,000 years. Our results indicate substantial differences between the community composition of scrub vegetation on recent alkaline soils compared to leached acidic soils.

Key words: barrier island, chronosequence, coastal dunes, Florida scrub, podsolization, *Quercus*, soil pH

Climate structures vegetation distribution at the global scale (*e.g.*, Walter 1979, Woodward 1986). At regional and local scales, microclimate, soil moisture availability, and other edaphic factors frequently determine distribution (Bailey 1996). Soil reaction (pH) and carbonate content have long been recognized as important to the distribution of plant species and communities (*e.g.*, Kurz 1920, Salisbury 1920). Soil pH represents a complex gradient where calcium (Ca), magnesium (Mg), potassium (K), and molybdenum (Mo) deficiencies may occur in acid soils along with toxic concentrations of aluminum (Al), hydrogen ion (H^+), manganese (Mn), and iron (Fe), but in alkaline soils Fe, Mn, and phosphorus (P) deficiencies are common (Epstein 1972, Marschner 1986, Fitter and Hay 1987, Tyler and Falkengren-Grerup 1998). In acid soils, nitrification is inhibited and available nitrogen (N) is low, occurring primarily as ammonium-nitrogen (NH_4-N; Marschner 1986).

Studies at the regional scale recognize the importance of soil pH in the distribution of plants in grasslands (Wagner *et al*. 2017), coastal vegetation (Angiolini *et al*. 2013, Munoz Valles *et al*. 2015), forests (Peet *et al*. 2003, Diekmann *et al*. 2015, Michaelis *et al*. 2016, Reinecke *et al*. 2016), woodlands (Santos-Filho *et al*. 2013, Viani *et al*. 2014), shrublands (Li *et al*. 2016), alpine vegetation (Schmidtlein and Ewald 2003), and roadside vegetation (Schaffers and Sykora 2000). The inclusion of soil pH improved montane plant distribution models over models that included only climate and topography (Dubuis *et al*. 2013).

Development of soils of coastal dunes typically begins with parent material of sand and shell that lacks organic matters, is low in available N, but

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high in carbonates and alkaline in pH (Ranwell 1972). This is also the case on dunes formed on large, freshwater lakes (Olson 1958, Lichter 1998). Initial soil development on these dunes involves leaching of Ca and Mg carbonates, increases in organic matter and N, and decreases in pH (Salisbury 1925, Olson 1958, Lichter 1998, Tackett and Craft 2010, Rossi and Rabenhorst 2016). On many dune systems, soils develop podzol (spodosol) characteristics after carbonates are leached (Thompson 1992, Lundstrom *et al.* 2000, Sauer *et al.* 2008, Eger *et al.* 2011, Turner *et al.* 2012, Martinez *et al.* 2018). Incipient podzol development can occur in $<$ 100 years to 1,000 years with mature podzols developing in 1,000–6,000 years (Sauer *et al.* 2007), but in areas of high precipitation podzol formation can occur more rapidly (Sauer *et al.* 2007, Eger *et al.* 2011).

Florida scrub is a relict shrub community associated with former coastlines and paleo-dunes (Laessle 1967, Myers 1990). Florida scrub is one of the most endangered ecosystems in the USA (Noss and Peters 1995) due to habitat loss for development and agriculture (Myers 1990, Weekley *et al.* 2008). The community type occurs on well-drained, acidic, infertile sandy soils where scrub oaks (*Quercus geminata* Small, *Quercus myrtifolia* Willd., *Quercus chapmanii* Sarg., *Quercus inopina* Ashe), *Ceratiola ericoides* Michx, repent palms (*Serenoa repens* (W. Bartram) Small, *Sabal etonia* Swingle ex Nash), and ericaceous shrubs predominate (Myers 1990), with or without a pine canopy. Florida scrub and the adjacent scrubby flatwoods are characterized by periodic, intense, stand-replacing fire (Abrahamson and Hartnett 1990, Myers 1990) and are habitat for many rare, endemic plants (Christman and Judd 1990, Menges 1999, Stout 2001) and rare, threatened, or endangered fauna (Myers 1990, Menges 1999).

Former coastlines and paleo-dunes that originated as coastal dunes have experienced high levels of leaching. Here we present data on vegetation composition and soil pH from the Merritt Island-Cape Canaveral barrier island complex that spans the transition from recent alkaline coastal dunes to much older acidic and leached systems. Improved dating of the barrier island complex (Rink and Forrest 2005, Burdette *et al.* 2009, 2010) has allowed soil development and vegetation composition to be assessed more closely over longer time scales. Chronosequences of soil and vegetation development offer valuable insights when used appropriately (Huggett 1998, Walker *et al.* 2010, Turner and Laliberte 2015).

Materials and Methods. The Merritt Island-Cape Canaveral barrier island complex is located on the east coast of central Florida (28°38′N, 80°42′W) and much of it is within the federal properties of Kennedy Space Center, Merritt Island National Wildlife Refuge, Canaveral National Seashore, and Cape Canaveral Air Force Station (Fig. 1). The climate is warm and humid; precipitation averages 134 cm/yr (Foster *et al.* 2015), but year-to-year variability is high (Mailander 1990). The wet season extends from May to October. The mean annual air temperature from 1920 to 2011 was 22.3 °C with high temperatures occurring in July (28.0 °C) and low temperatures (15.5 °C) occurring in January (Foster *et al.* 2015).

Multiple dune ridges occur on the barrier island topography (White 1970) with intervening swales of lower elevation. Scrub vegetation occupies the well-drained ridges, pine flatwoods occupy the more poorly drained flats, and graminoid marshes or woody swamps occupy the lower swales (Schmalzer *et al.* 1999). Scrub communities on Merritt Island are primarily oak-saw palmetto scrub, a shrubland characterized by three species of oaks (*Q. chapmanii*, *Q. geminata*, *Q. myrtifolia*) along with *S. repens* and ericaceous shrubs, and scrubby flatwoods with a similar shrub layer and scattered *Pinus elliottii* Engelm. var. *densa* Little & K.W. Dorman (Schmalzer and Hinkle 1992b, Schmalzer *et al.* 1999). On Cape Canaveral and the outer barrier island, coastal scrub occurs inland from the coastal dunes and strand but on alkaline to circumneutral soils where a coastal, shrubby form of *Quercus virginiana* Mill. predominates (Kurz 1942, Schmalzer *et al.* 1999). Nomenclature follows Wunderlin and Hansen (2011) unless otherwise noted.

Cape Canaveral and Merritt Island form a barrier island complex shaped by the alternating high and low sea stands of the Pleistocene and Holocene (Fig. 1). Cape Canaveral is Holocene in age, with its formation beginning about 7,000 years ago when the rate of sea level rise slowed after the end of the Wisconsin glaciation (Brooks 1972, Davis 1997). Cape Canaveral formed as part of a prograding barrier island complex (White 1958, 1970) with alternating periods of deposition and erosion (Chaki 1974). This prograding forma-

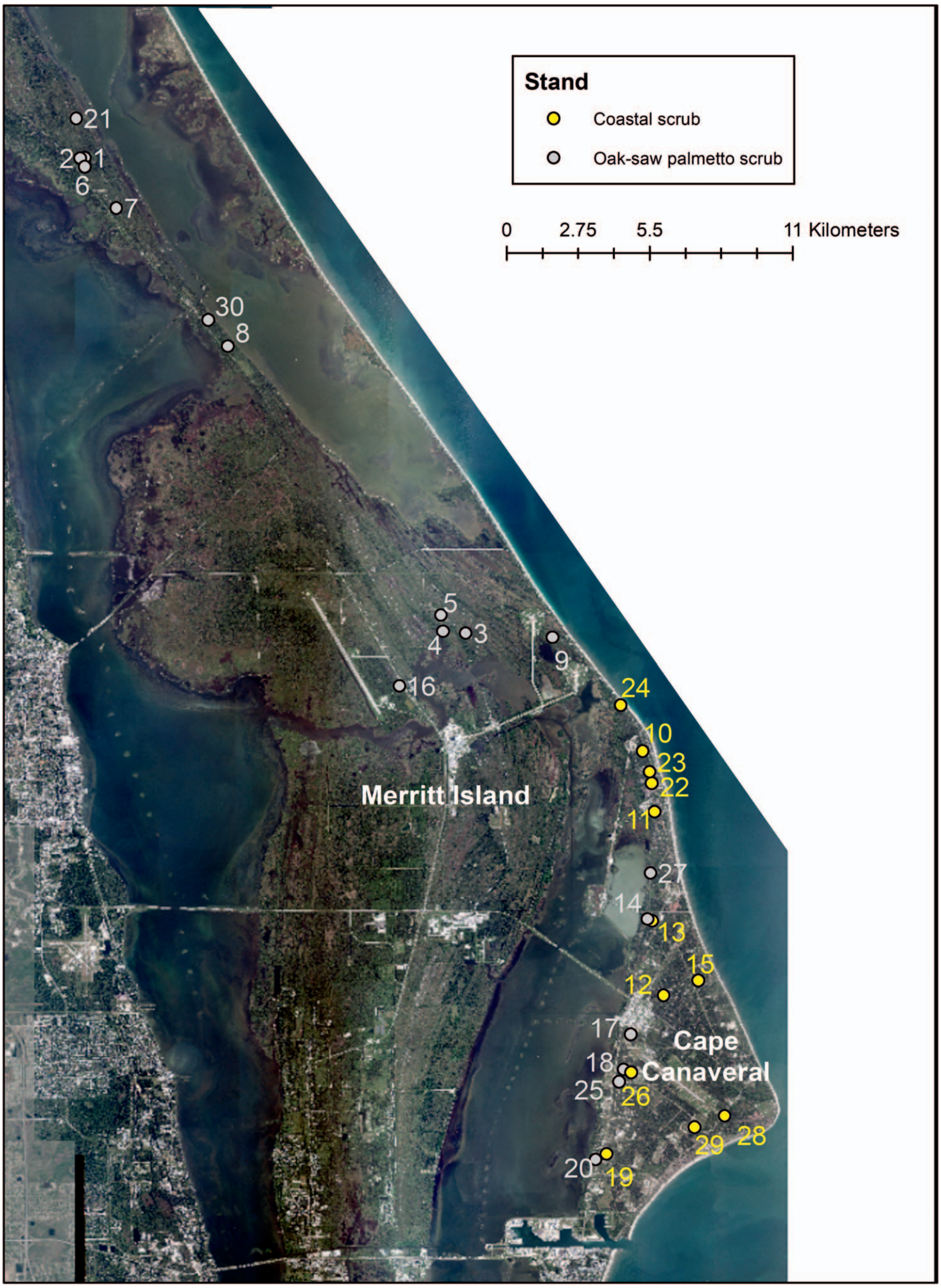

Fig. 1. Location of 30 long-unburned scrub stands on the Merritt Island-Cape Canaveral barrier island complex that were sampled before restoration.

tion extends south of Cape Canaveral then transitions to a structure indicating overwash (Mayhew and Parkinson 2007). The Mosquito Lagoon barrier beach is also characterized by overwash and landward regression (Mehta and Brooks 1973). Merritt Island also formed as a prograding barrier island complex, earlier than Cape Canaveral (White 1958, 1970). Multiple dune ridges represent successive stages in this growth. The eastern portion of Merritt Island is substantially younger than the west (Brooks 1972) and retains ridge-swale topography (Brown *et al.*

1962). Surface strata are primarily unconsolidated white to brown quartz sand containing beds of sandy coquina of Pleistocene and Holocene age (Cooke 1945, Brown *et al*. 1962).

Parent material for soils of this barrier complex are primarily sands of mixed terrestrial and biogenic origin. The terrestrial material originated from southern rivers carrying sediments eroded from highly weathered Coastal Plain and Piedmont soils; these sediments are quartzose with low feldspar content (Milliman 1972). The biogenic carbonate fraction of the sand is primarily of mollusk or barnacle origin (Milliman 1972). Adams (2018) suggested that the barrier island complex may have formed as the paleodelta of a formerly south-flowing St. Johns River.

Given the similar parent material, climate, and topographic position, landscape age (time) is a critical factor in soil pedogenesis and properties (Jenny 1941, 1980). While the overall sequence of landscape age from Cape Canaveral (youngest) to mainland Atlantic Coast Ridge (oldest) is well established (White 1958, 1970; Osmond *et al*. 1970; Brooks 1972), more recent studies provide improved quantification. Rink and Forrest (2005) dated a series of sand samples taken at 1 m below the surface. On Cape Canaveral dates ranged from 150 YBP near the area of current sand accumulation on the coast to ca. 4,000 YBP near the west side of the island; in contrast, the one sample from central Merritt Island dated to ca. 43,750 YBP (Rink and Forrest 2005). Along a transect on Merritt Island, Burdette *et al*. (2010) identified subsurface strata (sands) deposited at periods dating between 113.6 *ka* to 133.6 *ka*, 95–105 *ka*, and 69.2–83.6 *ka*; these depositional periods correspond to high sea stands. Burdette *et al*. (2009) dated two Anastasia Formation coquina deposits on Merritt Island, one at Haulover Canal dated from 66.8–91.6 *ka*, and one on central Merritt Island dated from 100.3–119.4 *ka*; these were deposited at high sea stands. Burdette *et al*. (2010) considered the surface strata (ca. 1–2 m) to be an aeolian sand sheet dating to about 15 *ka* formed from remobilized sand on top of older deposits; this corresponds to a period of aeolian activity recorded in the coastal plain of Georgia (Ivester *et al*. 2001) and North Carolina (Mallinson *et al*. 2008).

Soils on Cape Canaveral, False Cape, and the barrier island on the east side of Mosquito Lagoon are younger and less weathered than those of Merritt Island (Huckle *et al*. 1974). Well-drained soils in these areas retain shell fragments in the upper layers, while those inland on Merritt Island do not. The presence of shell fragments influences soil nutrient levels, particularly Ca and Mg, and pH. Schmalzer *et al*. (2001) found that coastal soils had significantly higher total Ca, Mg, sodium (Na), Fe, and Mn concentrations as well as higher soil pH compared to acid scrub soils.

We obtained vegetation data from 196 line-intercept transects (15 m length each) (Mueller-Dombois and Ellenberg 1974) in 30 stands of long-unburned scrub on Merritt Island and Cape Canaveral between 1992 and 2005 (Fig. 1). All stands were on well-drained to moderately well-drained sites. Scrub was sampled before cutting and burning to improve habitat conditions (Schmalzer *et al*. 1994). We recorded vegetation cover data by species in two height strata ($\leq$ 0.5 m and $>$ 0.5 m); cover was measured to the nearest 5 cm. We measured height at four locations (0, 5, 10, 15 m) along each transect. Transect locations were recorded with a differentially corrected GPS system (Trimble, Sunnyvale, CA). We determined mapped soil series and general soil properties from transect locations and the soil survey (Huckle *et al*. 1974) as updated by the National Resources Conservation Service (www.nrcs.usda.gov). For 151 transects in 22 stands, we sampled soils from the 0–15 and 15–30 cm layers; soil pH was determined on a 1:1 soil to water slurry (McLean 1982).

The complete vegetation data set included 196 transects in 30 stands and 53 species. We summarized species composition by stand (IBM SPSS, ver. 25; www.ibm.com). For cluster and ordination analyses, we dropped species with fewer than two occurrences in the $>$ 0.5 m data set to avoid outliers. The reduced $>$ 0.5 m data set had 196 samples and 41 species. We conducted hierarchical cluster analysis (Ward's method, relative Euclidian distance; PCORD, ver. 7; MjM Software Design, Gleneden Beach, OR) at the transect level using species cover and at the stand level using species cover means. We grouped soil series into three classes that differed by soil reaction and degree of leaching based on Huckle *et al*. (1974): acid, acid-neutral, and alkaline. We compared mean percent cover of dominant species across soil classes in a direct gradient analysis. We used indicator species analysis (Dufrene and Legendre 1997; PCORD, ver. 7) to determine species related to acidic or alkaline soil classes. For the indicator species analysis, we combined the acid and acid/neutral soil series based on similar species composition.

We conducted nonmetric multidimensional scaling (NMS) ordination (Kruskal 1964a, 1964b; PCORD, ver. 7) at the stand and transect level using the Sorenson distance measure. Nonmetric multidimensional scaling is considered the most generally effective method for the ordination of community data (McCune and Grace 2002). We examined correlations of NMS axes scores to soil series pH classes and measured soil pH using Spearman's rank order coefficients (IBM SPSS, ver. 25). We compared soil H^+ concentrations across the three soil series pH classes: acid ($N = 72$), acid/neutral ($N = 43$), and alkaline ($N = 36$) with the nonparametric Kruskal-Wallis test (IBM SPSS, ver. 25).

Results. Scrub transects occurred on nine soil series in three soil reaction and leaching categories: alkaline soils with shell material remaining in the upper soil layers (Palm Beach and Canaveral series), acid/neutral soils where the upper part of the soil profile is leached and acidic but shell material remains at depth (Cocoa and Welaka series), and soils that are leached and acidic throughout (Immokalee, Myakka, Orsino, Paola, and Pomello series; Table 1). Seventy-two transects occurred on acid soils, 58 transects on acid/neutral soils, and 66 transects on alkaline soils. Direct gradient analysis indicated that dominant species except *S. repens* as well as several less abundant species differed across soil reaction classes (Fig. 2). *Quercus chapmanii*, *Q. geminata Q. myrtifolia,* and *Lyonia ferruginea* were abundant on acid and acid/neutral soil classes, but absent or in low abundance on alkaline soils (Fig. 2A). *Quercus virginiana* and *Myrcianthes fragrans* (Sw.) McVaugh were absent or in low abundance on acidic soils but abundant on the alkaline soil series (Fig. 2A). Of the less abundant species, *Carya floridana* Sarg. occurred only on acidic soils, but *Persea borbonia* (L.) Spreng. and *Sideroxylon tenax* L. were much more abundant on alkaline soil classes (Fig. 2B)

Cluster analysis of the 30 stands gave two distinct groups (Fig. 3). All 11 stands on acid soil and eight of nine stands on acid/neutral soil were in Group 1 (oak-saw palmetto scrub), and all 11 stands on alkaline soils plus one stand (Stand 13 with 2 transects) on acid/neutral soil were in Group 2 (coastal scrub). Scrub oaks, *S. repens*, and ericaceous shrubs were dominant in stands on all acid soils and most acid/neutral soils, but *Q. virginiana* and *S. repens* were dominant on all alkaline soils (Table 2). Detailed species composition by stand is given in Table S1. Cluster analysis of the 196 transects also gave two groups (dendrogram not shown). Two transects on mapped acid/neutral soil (Stand 13) and one on acid soil were dominated by *Q. virginiana* and grouped with coastal scrub; three transects on alkaline soil that were dominated by *S. repens* with little oak cover grouped with oak-saw palmetto scrub. H^+ concentrations differed among the three soil classes (Kruskal-Wallis test, $P \leq 0.001$; Table 3), with acidic soils having the highest concentrations (lowest pH).

Indicator species analysis comparing two groups, acidic (including acid/neutral; $N = 130$ transects) and alkaline ($N = 66$ transects), was significant ($P = 0.0002$) with 12 species having indicator values significant at $P \leq 0.01$ (Table 4). Seven species indicated acidic soils, and five species indicated alkaline soils (Table 4).

Nonmetric multidimensional scaling ordination at the stand level separated the oak-saw palmetto scrub from the coastal scrub along the first axis (Fig. 4); NMS ordination of the transect data showed the gradient of coastal to oak-saw palmetto scrub (Fig. 5A). Position of transects on the first axis was related to soil pH class, $r_s = -0.793$, $P < 0.001$ (soil series coded as acid, acid/neutral, alkaline) and to measured pH of the 0–15 cm layer ($r_s = -0.616$, $P < 0.001$) as well as to pH of the 15–30 cm layer ($r_s = -0.623$, $P < 0.001$).

Species characteristic of coastal scrub (*e.g.*, *Q. virginiana, M. fragrans, P. borbonia, S. tenax*) occurred to the left of the first axis of the species ordination (Fig. 5B). *Serenoa repens*, abundant in both types, occurred towards the center. Characteristic oak-saw palmetto scrub species (*Q. chapmanii, Q. geminata, Q. mytrifolia, Lyonia* spp., *Vaccinium* spp.) were located right of center. *Ceratiola ericoides* and *Carya floridana*, occurring or particularly abundant in only one stand each (Table 1), ordinated farther to the right.

Discussion. Scrub on the Cape Canaveral-Merritt Island barrier island complex occurs across a chronosequence of landscape age, soil leaching and development, and changes in soil pH and

Table 1. Characteristics of scrub soil series on the Merritt Island-Cape Canaveral barrier island complex. Data are from Huckle *et al.* (1974) and nrcs.usda.gov.

Soil series	Classification	Description
Canaveral	Hyperthermic, uncoated Aquic Quartzipsamment (Entisol)	Moderately well-drained to somewhat poorly drained sandy soil mixed with shell. Amount of shell increases below 30 cm. Neutral (pH 6.6–7.3) to moderately (pH 7.9–8.4) alkaline throughout.
Cocoa	Siliceous, hyperthermic Psammentic Hapludalf (Alfisol)	Well-drained sandy soil underlain by coquina. Medium acid (pH 5.6–6.0) to mildly alkaline (pH 7.4–7.8) in all layers.
Immokalee	Sandy, siliceous, hyperthermic Arenic Alaquod (Spodosol)	Nearly level, poorly drained sandy soil with spodic (Bh) horizon at 84–140 cm. Strongly (pH 5.1–5.5) to very strongly (pH 4.5–5.0) acid throughout.
Myakka	Sandy, siliceous, hyperthermic Aeric Alaquod (Spodosol)	Nearly level, poorly drained sandy soil with spodic (Bh) horizon at 56–89 cm. Strongly (pH 5.1–5.5) to very strongly (pH 4.5–5.0) acid throughout.
Orsino	Hyperthermic, uncoated Spodic Quartzipsamment (Entisol)	Nearly level, moderately well-drained sandy soil lacking a continuous spodic (Bh) horizon. Very strongly (pH 4.5–5.0) to moderately (pH 5.6–6.0) acid throughout.
Palm Beach	Hyperthermic, uncoated Typic Quartzipsamment (Entisol)	Nearly level and gently sloping, excessively drained soils formed in marine sand and shell; shell material present in 0–8 cm layer. Mildly (pH 7.4–7.8) to strongly (pH 8.5–9.0) alkaline throughout.
Paola	Hyperthermic, uncoated Spodic Quartzipsamment (Entisol)	Nearly level to strongly sloping, excessively drained sandy soil lacking a continuous spodic (Bh) horizon. Very strongly (pH 4.5–5.0) to moderately (pH 5.6–6.0) acid throughout.
Pomello	Sandy, siliceous Oxyaquic Alorthod (Spodosol)	Nearly level, moderately well to somewhat poorly drained sandy soil with spodic (Bh) horizon at 79–157 cm. Strongly (pH 5.1–5.5) to very strongly (pH 4.5–5.0) acid throughout.
Welaka	Hyperthermic, uncoated Spodic Quartzipsamment (Entisol)	Nearly level, well drained sandy soil with a Bw horizon at 46–140 cm and a 2C horizon of mixed shell and sand at 140 cm. Extremely acid (pH $<$ 4.5) to slightly acid (pH 6.1–6.5) in the A and B horizons and moderately alkaline (pH 7.9–8.4) in the 2C horizon.

associated soil properties. Dominant species in scrub vegetation change across this sequence of landscape age, soil development, and soil pH. Multiple analyses (cluster, direct gradient analysis, NMS ordination, and indicator species) indicate differences between the coastal scrub of alkaline sands and the oak-saw palmetto scrub of acid and acid/neutral sands confirming earlier qualitative information (Kurz 1942, Schmalzer *et al.* 1999). There is a turnover of dominant species across the landscape age and soil pH gradient that is consistent with what is known of their soil and site preferences. Fire is a critical ecological factor in scrub vegetation along this chronosequence.

On Cape Canaveral, soil development on well-drained soils is a function of leaching over time and incipient podsolization in similar parent material. Shell material is found progressively deeper in the Palm Beach to Canaveral to Welaka series sequence but is still present at depth indicating that it was originally in the surface but has been leached over a period of 4,000–7,000 years (Brooks 1972, Rink and Forrest 2005). Classification of the Welaka series as Spodic Quartzipsamment (Entisol; Table 1; Huckle *et al.*

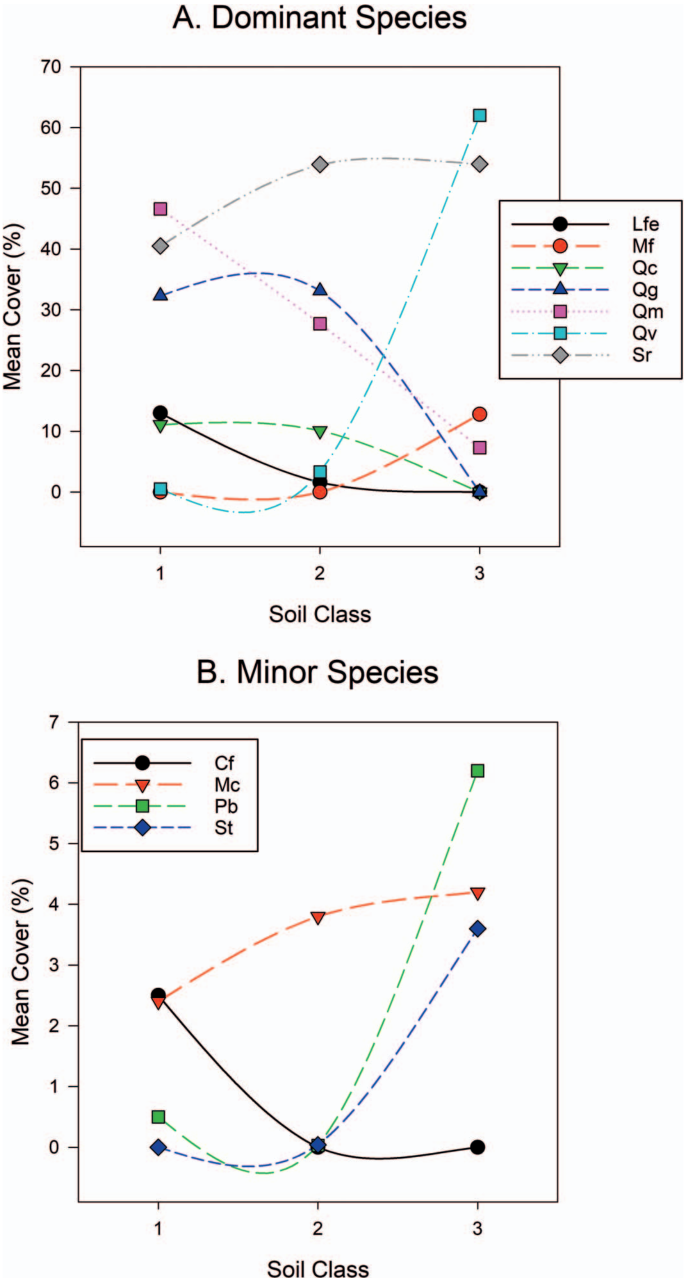

FIG. 2. Direct gradient analysis of mean percent cover of scrub species along a soil series gradient. Soil series are grouped as 1 = Acid (Immokalee, Myakka, Orsino, Paola, and Pomello; $N = 72$), 2 = Acid/Neutral (Cocoa, Welaka; $N = 58$), and 3 = Alkaline (Canaveral, Palm Beach; $N = 66$). A. Dominant species. B. Less abundant species. Species codes are: Cf = *Carya floridana*, Lfe = *Lyonia ferruginea*, Mc = *Myrica cerifera*, Mf = *Myrcianthes fragrans*, Pb = *Persea borbonia*, Qc = *Quercus chapmanii*, Qg = Quercus *geminata*, Qm = *Quercus myrtifolia*, Qv = *Quercus virginiana*, Sr = *Serenoa repens*, St = *Sideroxylon tenax*.

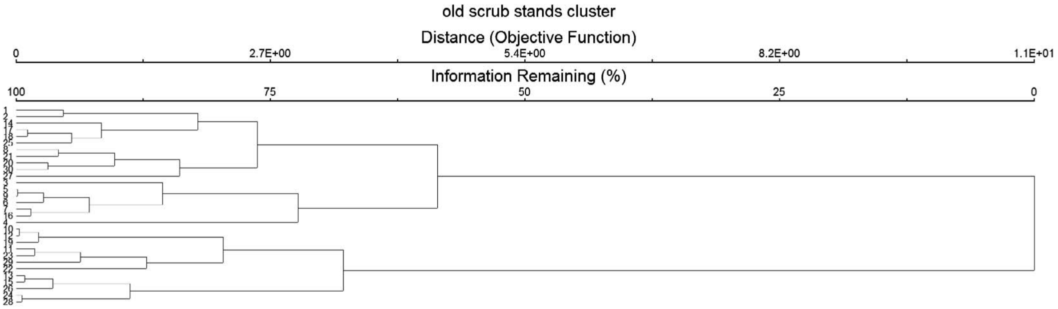

FIG. 3. Cluster analysis (Ward's method, relative Euclidean distance) dendrogram of 30 scrub stands using mean cover $>$ 0.5 m of 41 species present in $>$ 1 transect. Oak-saw palmetto scrub and coastal scrub are separated at the 50% information remaining level.

1974) is consistent with studies showing that leaching of carbonates is required for podzol formation (Thompson 1992, Lundstrom *et al.* 2000, Sauer *et al.* 2008, Eger *et al.* 2011, Turner *et al.* 2012, Martinez *et al.* 2018).

There is then a hiatus between the younger Cape Canaveral and older Merritt Island landscapes with underlying sand (sampled *ca.* 2–5 m depth) and coquina on Merritt Island dating to high sea stands at about 113.6–133.6 *ka*, 95–105 *ka*, and 69.2–83.6 *ka* (Burdette *et al.* 2009, 2010), but there are also indications of aeolian activity at 15 *ka* that formed the surface 1–2 m (Burdette *et al.* 2010). If the wind-blown sand had fewer carbonates than coastal deposits, then leaching and podsolization may have proceeded more rapidly; however, Merritt Island scrub soils have had at least twice as much time for leaching as those on Cape Canaveral. Scrub soils on Merritt Island are all Spodosols or Entisols with some podsolization with the exception of the Cocoa series, which formed in marine or aeolian sand over coquina and retains shell material at depth (Table 1; Huckle *et al.* 1974). Even so, the upper layers of Cocoa soils are acidic (Table 2).

Spodosols (podzols) on the southeastern Coastal Plain (Markewich and Pavich 1991) and subtropical and tropical areas (Schaetzl and Harris 2011) are associated with seasonally high, fluctuating water tables, which affect the movement of carbon (C) and metals in the soil (Banik *et al.* 2016). On the driest ridges where the water table is deep, leaching occurs but not complete podsolization. In our study area, only the Palm Beach, Paola, and Cocoa soils on the driest ridges have water tables that are consistently deep (1.8–3.0 m; Huckle *et al.* 1974).

Expected soils reaction based on mapped soil types (Huckle *et al.* 1974) and measured soil pH are in good agreement (Table 2). One exception is Stand 13, which is mapped as Welaka soil, an acid/neutral type, but had soil pH similar to the more alkaline Canaveral soil. This is probably a minor error in the soil map as the nearby Stand 14 is more acidic and consistent with the Welaka series. Mapped soil units may contain inclusions of other soil types and are limited by the scale of mapping (Soil Science Division Staff 2017).

The transition from coastal scrub to oak-saw palmetto scrub occurs where carbonates are leached from the upper soil horizons. This transition occurs on the western side of Cape Canaveral (Fig. 1). On the substantially older Merritt Island landscape, scrub oaks and *S. repens* remain dominant on even more deeply leached soils and the abundance of ericaceous scrub increases.

Oak-saw palmetto scrub and coastal scrub are well separated in cluster analysis (Fig. 2) and in the stand level ordination (Fig. 3). In the U.S. National Vegetation Classification (Faber-Langendoen *et al.* 2014, 2018), oak-saw palmetto scrub falls within the *Q. geminata*-*Q. myrtifolia*-*Q. chapmanii* Scrub Alliance and at the Association level resembles the *Q. myrtifolia*-*Q. geminata*-Q. *chapmanii* Shrubland Association and the Q. *myrtifoia*-*Q. geminata*-*Lyonia lucida*-*L. ferruginea* Shrubland Association (Mohan and Evans 2008, Weakley 2102, Nordman and Weakley 2014). Coastal scrub is generally similar to the *Q. virginiana*-*S. repens* (*Ilex vomitoria*) Shrubland Association, a type not well defined in the national classification (Summer 2007).

Four oak (*Quercus*) species are important across the coastal scrub to oak-saw palmetto scrub

Table 2. Summary of soils and vegetation of 30 stands of long-unburned scrub on the Merritt Island-Cape Canaveral barrier island complex before restoration.

Stand number	Description	Number of transects	Soil series[1]	Soil pH class[2]	Dominant species[3]	pH 0–15 cm[4]	pH 15–30 cm[5]
1	Shiloh 1–north	10	Paola	Acid	Sr, Qg, Qm, Lf	3.84	4.53
2	Shiloh 1–interior	4	Paola	Acid	Sr, Qg, Lf, Mc	3.74	4.52
3	Happy Creek sand road	6	Paola/Pomello	Acid	Qm, Qg, Qc, Lf	4.19	4.33
4	Happy Creek–south of tower	4	Pomello/Orsino	Acid	Cf, Sr, Qm, Qg, Qc	4.84	5.11
5	Happy Creek–north of tower	12	Pomello/Orsino	Acid	Qm, Sr, Qg, Qc	4.12	4.48
6	Shiloh 1–south	10	Paola	Acid	Sr, Qm, Qg, Lf	4.08	4.67
7	Shiloh 2	10	Paola	Acid	Qm, Sr, Qg, Lf	4.24	4.71
8	Haulover	8	Cocoa/Myakka	Acid/Neutral	Sr, Qg, Qm	4.27	4.52
9	39A/B	7	Paola/Immokalee	Acid	Qm, Sr, Qg, Qc	4.22	4.62
10	LC41	5	Palm Beach	Alkaline	Sr, Qv	7.92	8.53
11	CCAFS LC40	11	Palm Beach/ Canaveral	Alkaline	Sr, Qv, Mf, Pb	6.58	7.29
12	CCAFS Heavy Launch Road	10	Canaveral	Alkaline	Qv, Sr, Qm, (Vr)	5.15	5.39
13	CCAFS Test Road–east	2	Welaka	Acid/Neutral	Qv, Sr, (Vr)	5.42	4.93
14	CCAFS Test Road–west	8	Welaka	Acid/Neutral	Qg, Sr, Qm, (Vr)	3.76	4.14
15	CCAFS Complex 19	5	Canaveral	Alkaline	Qv, Sr, Qm (Vr)	4.56	4.70
16	SLF Roller-chopped	5	Immokalee	Acid	Qm, Sr, Lf, Qg	3.59	3.95
17	CCAFS C-37/38	10	Welaka	Acid/Neutral	Qg, Sr, Qm	4.73	4.69
18	CCAFS C-68	5	Welaka	Acid/Neutral	Sr, Qm, Qg, Qc	4.91	5.04
19	CCAFS C-116	5	Palm Beach	Alkaline	Sr, Qv, Qm	3.83	4.18
20	CCAFS C-101	5	Welaka	Acid/Neutral	Sr, Qm, Qg, Qc	5.68	5.21
21	Shiloh Roller-chopped	4	Paola	Acid	Sr, Qg, Qm, Ll	3.75	4.26
22	Coastal Scrub–south	5	Palm Beach	Alkaline	Sr, Mf, Qv, Mc	NA	NA
23	Coastal Scrub–center	5	Palm Beach	Alkaline	Sr, Qv, Mf	NA	NA
24	Coastal Scrub–north	5	Palm Beach	Alkaline	Qv, Sr, St, (Sa)	NA	NA
25	CCAFS C-69	5	Welaka	Acid/Neutral	Sr, Qg, Qc, Qm	4.51	4.69
26	CCAFS C-48	5	Canaveral	Alkaline	Qv, Sr, Qm (Vr)	NA	NA
27	CCAFS C-7	5	Pomello/Welakka	Acid/Neutral	Sr, Ce, Qg, Qm	NA	NA
28	CCAFS C-87	5	Canaveral	Alkaline	Qv, Sr, Mf, Mc	NA	NA
29	CCAFS C-89	5	Canaveral	Alkaline	Qv, Sr, Pb, Mc	NA	NA
30	Haulover Canal	10	Cocoa	Acid/Neutral	Sr, Qm, Mc, Qc	NA	NA

[1] Series from Huckle *et al.* (1974).

[2] Soil pH classes from Huckle *et al.* (1974).

[3] Dominant species from transect sampling. Codes are: Ce = *Ceratiola ericoides*, Cf = *Carya floridana*, Lf = *Lyonia ferruginea*, Ll = *Lyonia lucida*, Mc = *Myrica cerifera*, Mf = *Myrcianthes fragrans*, Pb = *Persea borbonia*, Qc = *Quercus chapmanii*, Qg = *Quercus geminata*, Qm = *Quercus myrtifolia*, Qv = *Quercus virginiana*, Sa = *Smilax auriculata*, Sr = *Serenoa repens*, Vr = *Vitis rotundifolia*. Parenthesis indicates vines.

[4] Mean soil pH, 0–15 cm, calculated from H^+ concentrations.

[5] Mean soil pH, 15–30 cm, calculated from H^+ concentrations.

gradient, *Q. virginiana* in coastal scrub and *Q. chapmanii, Q. geminata*, and *Q. myrtifolia* in oak-saw palmetto scrub. *Quercus virginiana* and *Q. geminata* are considered sister taxa but taxonomically distinct (Nixon *et al.* 1997, Manos *et al.* 1999, Cavender-Barres *et al.* 2004b, Cavender-Barres and Pahlich 2009); *Q. virginiana* is more widespread (Nixon *et al.* 1997). Where sympatric, *Q. geminata* typically occurs on drier soils of lower nutrient availability than *Q. virginiana* (Cavender-Barres *et al.* 2004a). In North Florida, Cavender-Barres *et al.* (2004a) found that sites occupied by *Q. virginiana* and *Q. geminata* differed in average soil moisture to 1 m depth, soil pH, Ca content, and exchangeable NH_4-N, nitrate-nitrogen (NO_3-N), and P; *Q. virginiana*

Table 3. Comparison of H^+ ion concentration (expressed as pH) in the three soil series classes. Acid soil series include Immokalee, Myakka, Orsino, Paola, and Pomello; acid/neutral include Cocoa and Welaka; alkaline series include Canaveral and Palm Beach. Differences are significant across the groups (Kruskal-Wallis, $P \leq 0.001$).

Soil group	Mean pH 0–15 cm	Mean pH 15–30 cm
Acid ($N = 72$)	3.99	4.46
Acid/Neutral ($N = 43$)	4.28	4.54
Alkaline ($N = 36$)	4.53	4.89

Table 4. Indicator species analysis comparing species on acidic ($N = 130$) and alkaline soil series ($N = 66$) for 41 species and 196 transects. Alkaline soil series include Canaveral and Palm Beach; acidic soil series include Cocoa, Immokalee, Myakka, Orsino, Paola, Pomello, and Welaka. Shown are the 12 species with indicator values significant at $P \leq 0.01$ in Monte Carlo tests with 4,999 permutations. Overall analysis was significant ($P = 0.0002$).

Species	Soil group	Indicator value	Significance (P)
Galactia elliottii	Acid	12.3	0.005
Lyonia ferruginea	Acid	39.2	0.0002
Lyonia lucida	Acid	13.8	0.005
Myrcianthes fragrans	Alkaline	37.9	0.0002
Persea borbonia	Alkaline	14.5	0.003
Quercus chapmanii	Acid	64.6	0.0002
Quercus geminata	Acid	90.0	0.0002
Quercus myrtifolia	Acid	79.3	0.0002
Quercus virginiana	Alkaline	91.3	0.0002
Sideroxylon tenax	Alkaline	25.6	0.0002
Vaccinium stamineum	Acid	15.4	0.003
Vitis rotundifolia	Alkaline	33.4	0.005

occurred on moister, higher pH, and more nutrient rich sites. *Quercus virginiana* grew faster and allocated less to root biomass than *Q. geminata* (Cavender-Barres *et al.* 2004a). In our study, coastal scrub with *Q. virginiana* dominant occurred on excessively drained to moderately well-drained soils; oak-saw palmetto scrub also occurred across a range of excessively to moderately drained soils. The difference between coastal scrub and oak-saw palmetto scrub related to soil leaching and soil pH. This contrasts to the North Florida study (Cavender-Barres *et al.* 2004a) where soil moisture and soil pH and nutrients varied together from upland scrub and sandhill sites to lower slope mesic hammocks. Hammocks with *Q. virginiana* also occur on the Merritt Island-Cape Canaveral landscape (Stout 1980, Schmalzer and Foster 2016) on mesic soils more similar to North Florida sites (Cavender-Barres *et al.* 2004a).

Quercus myrtifolia and *Q. chapmanii* overlapped environmentally with *Q. geminata* but differed from *Q. virginiana* and other hammock oaks in North Florida (Cavender-Barres *et al.*

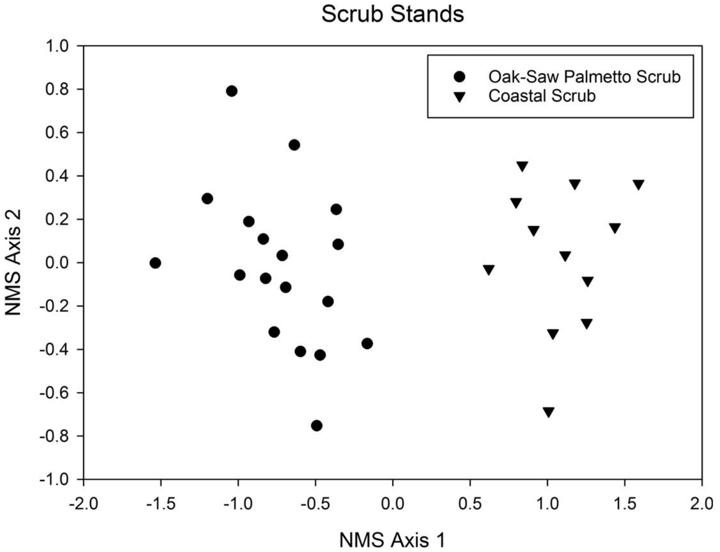

FIG. 4. Nonmetric multidimensional scaling (NMS) ordination of 30 scrub stands using mean cover > 0.5 m of 41 species present in > 1 transect. The final solution had two dimensions after 47 iterations, with a final stress of 9.16, a final instability less than 0.00001, and comparisons to Monte Carlo tests indicated that the reduction in stress was significant (P = 0.02).

2004a). These oaks co-occur in our study on acid and acid/neutral soils. *Quercus geminata* is a live oak (*Quercus* section *Quercus* subsection *Virentes*), *Q. chapmanii* is a white oak (*Quercus* section *Quercus*), and *Q. myrtifolia* is a red oak (*Quercus* section *Lobatae*; Nixon *et al.* 1997). These species differ phylogenetically but share functional traits including resprouting from rhizomes and short stature; this pattern is consistent with Cavender-Barres *et al.* (2004b) who found phylogenetic overdispersion of oaks in North Florida communities (*i.e.*, communities were more likely to contain members of different oak clades than only members of one clade).

Quercus myrtifolia occurs in some stands of coastal scrub but with much lower cover than *Q. virginiana* (Table 2). These stands are primarily on Canaveral series soils where shell material is somewhat leached from surface layers (Table 1). On the Lake Wales Ridge communities characterized by *Carya floridana* (southern ridge sandhill) and *Ceratiola ericoides* (rosemary scrub) occur (Abrahamson *et al.* 1984, Myers 1990). These species occur on the Merritt Island-Cape Canaveral barrier island complex but are less common (Schmalzer *et al.* 1999).

Ericaceous shrubs (*Lyonia* spp., *Vaccinium* spp.) are absent from coastal scrub on alkaline soils (Table 2, Fig. 5B, Table S1). Species in the Ericaceae are frequently found on acid soils (Tucker 2009). The association of ericaceous plants with ericoid mycorrhiza is important to mobilizing nutrients including N and P, and to tolerating metal toxicity in acidic soils (Cairney and Burke 1998, Cairney and Meharg 2003), which appears to contribute to their success on acidic sites.

Serenoa repens occurs widely in coastal strand (Johnson and Barbour 1990), scrub (Myers 1990), and flatwoods (Abrahamson and Hartnett 1990, Carrington and Mullahey 2013) vegetation in Florida. It decreases in abundance on the driest scrub sites (Schmalzer and Hinkle 1992b). Its

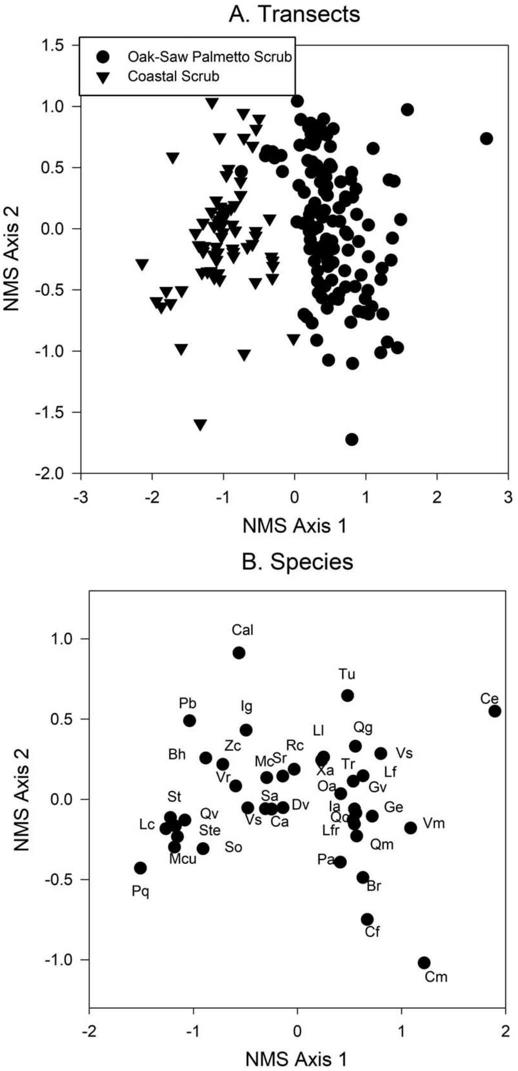

FIG. 5. Nonmetric multidimensional scaling (NMS) ordination of 196 scrub transects using cover > 0.5 m of 41 species present in > 1 transect. The final solution had two dimensions after 91 iterations, with a final stress of 16.74, a final instability less than 0.00001, and comparisons to Monte Carlo tests indicated that the reduction in stress was significant ($P = 0.04$). A. Transects. B. Species. Species codes are: Br = *Bejaria racemosa*, Bh = *Baccharis halimifolia*, Ca = *Callicarpa americana*, Cal = *Chiococca alba*, Ce = *Ceratiola ericoides*, Cf = *Carya floridana*, Cm = *Clitoria mariana*, Dv = *Diospyros virginiana*, Ge = *Galactia elliottii*, Gv = *Galactia volubilis*, Ia = *Ilex ambigua*, Ig = *Ilex glabra*, Lc = *Lantana camara*, Lf = *Lyonia ferruginia*, Lfr = *Lyonia fruticosa*, Ll = *Lyonia lucida*, Mc = *Myrica cerifera*, Mcu = *Myrsine cubana*, Mf = *Myrsianthes fragrans*, Oa = *Osmanthus americanus*, Pa = *Pteridium aquilinum*, Pb = *Persea borbonia*, Pq

←

= *Parthenocissus quinquefolia*, Qc = *Quercus chapmanii*, Qg = *Quercus geminata*, Qm = *Quercus myrtifolia*, Qv = *Quercus virginiana*, Rc = *Rhus copallinum*, So = *Solidago odora*, St = *Sideroxylon tenax*, Ste = *Schinus terebinthifolia*, Tr = *Tillandsia recurvata*, Tu = *Tillandsia usneoides*, Vr = *Vitis rotundifolia*, Vs = *Vitis shuttleworthii*, Xa = *Ximenia americana*, Zc = *Zanthoxylum clava-herculis*.

occurrence in the center of the species ordination is consistent with this widespread distribution and abundance on the Merritt Island-Cape Canaveral landscape. *Myrsianthes fragrans*, one of the species associated with coastal scrub, is of subtropical distribution reaching its northern limits of distribution along the coast north of Merritt Island-Cape Canaveral (Wunderlin and Hansen 2011). The preferential occurrence of subtropical species on shell mounds or other calcareous substrate at or near their northern range limits has long been observed (Small 1923, Norman 1976, Stalter and Kinkaid 2004).

Some differences do occur within the acid and acid/neutral soils. Cocoa soil, formed over coquina, is higher in total Ca, Mg, K, Mn, and Fe, compared to acid scrub soils (Schmalzer *et al*. 2001). Differences within acidic scrub soils may be important to some species. Within acidic scrub soils of the Lake Wales Ridge, Menges *et al*. (2007) found that some rare scrub species showed preferences for xeric yellow sands, xeric white sands, or xeric scrubby flatwoods soils. Data from Schmalzer *et al*. (2001) showed that soils series considered yellow sands (Paola, Astatula, Orsino) had greater concentrations of total Fe and Al compared to white sands (Pomello).

Fire is a critical factor in the ecology of scrub vegetation. The vegetation of much of Merritt Island-Cape Canaveral was open scrub, flatwoods, and marshes up to the 1940s (Duncan *et al*. 2004). This vegetation structure was maintained by fire from frequent lightning strikes (Duncan *et al*. 2010) and burning for range management (Duncan *et al*. 1999). Fire suppression and landscape fragmentation (Duncan and Schmalzer 2004) reduced fire frequency across the landscape (Duncan *et al*. 2009). Prescribed burning has replaced lightning fires in part but often differs in seasonality and extent (Duncan *et al*. 2009). Oak-saw palmetto scrub recovers rapidly after fire by sprouting of the dominant species (Schmalzer and Hinkle 1992a, Schmalzer 2003). Responses of coastal scrub to burning are not well documented. Simon (1986) found that *Q. virginiana, M. fragrans, S. repens*, and other coastal strand species recovered rapidly after burning. Blonder *et al*. (2018) have suggested that fire is important to maintained coastal strand vegetation, which shares some species with the coastal scrub studied here. Our data (Schmalzer and Foster, unpublished) indicate that *Q. virginiana, M. fragrans*, and other characteristic coastal scrub species resprout vigorously after fire.

With fire suppression, changes in scrub vegetation are primarily structural with increases in vegetation height and cover of the dominant *Quercus* spp. but no indication of directional change in species composition (Schmalzer and Hinkle 1992b, Schmalzer and Foster, unpublished). This is consistent with findings reported on long-unburned scrub vegetation of the Lake Wales Ridge (Givens *et al*. 1984, Menges *et al*. 1993).

Fire reduces litter and above-ground biomass, volatilizes C and N and to a lesser extent other nutrients, recycles mineral nutrients, alters soil microbial activity, and affects biogeochemical cycling (Christensen 1987). In Florida scrub, Abrahamson (1984) reported a short-term increase in Ca after a scrub fire but no change in pH and only minor increases in P, K, and Mg. In a scrub fire on Merritt Island, Alexis *et al*. (2007) found that the combined litter and vegetation pools lost 63.4% and 74.6% of their initial C and N stocks, respectively, but soil C and N stocks were not changed significantly. Short-term increases in soil extractable NH_4-N and phosphate occurred after fire in a saw palmetto flatwoods (Schafer and Mack 2010) but not in scrubby flatwoods (Schafer and Mack 2013). Across a post-fire age sequence, Schaefer and Mack (2014, 2018) found indications that N and P colimited scrubby flatwoods at intermediate and longer times after fire. Fire regimes could affect soil development. In some regions (*e.g.*, Great Lakes states) fire limits podsolization by reducing litter and thus, humic acids, but subtropical Alaquods, as in Florida, are an exception (Schaetzl and Harris 2011). In these soils leaching and some degree of podsolization occurs even with relatively frequent burning.

Dominant species in scrub vegetation change across this sequence of landscape age, soil development, and soil pH consistent with what is known of their soil and site preferences. Ecosystem degradation and retrogression have been demonstrated on some very long chronosequences (Peltzer *et al*. 2010, Turner and Laliberte 2015). Such changes are not apparent in our sites, but reduced productivity and greater nutrient limitations could be a factor on the older scrub ridges of the Florida mainland.

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