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Seed Consumption by Gopher Tortoises (*Gopherus polyphemus*) in the Globally Imperiled Pine Rockland Ecosystem of Southern Florida, USA

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Abstract. – Turtles have been identified as key dispersers of seeds in many ecosystems; however, seed dispersal by turtles (chelonochory) has received far less attention than seed dispersal by birds or mammals. We assessed the role of gopher tortoises (*Gopherus polyphemus*)—a keystone species—as potential seed dispersers by analyzing the seed composition of their diet in a globally imperiled ecosystem: the pine rockland ecosystem of South Florida. The pine rocklands contain high numbers of both endemic and invasive plant species that may be dispersed by tortoises. We collected scat samples from wild gopher tortoises living in the pine rockland habitats in the Richmond Tract (Miami-Dade County, Florida, USA) and examined the samples to identify seeds consumed. We extracted 2484 seeds from 53 samples from at least 10 individual tortoises. Of the 2484 individual seeds, we distinguished 33 morphospecies and identified 23 to the species taxonomic level. The 14 most abundant seed species in the scat constituted $>90\%$ of all seeds eaten by the tortoises. Three of the 14 most abundant seeds were from nonnative plants, but none were among the most disruptive invasive species. Tortoises consumed mostly herbaceous ground cover and fibrous grasses. Given that the tortoises were consuming several ground cover plants and contained a high density of those seeds in their scats, they seemed to be consuming the seeds as bycatch rather than selectively feeding on them, therefore supporting Janzen's "foliage is the fruit" hypothesis. The prevalence of many seeds and a variety of seed species in the tortoise scat suggests that gopher tortoises may be serving the ecological role of a seed dispersal agent for some of the plants they consume within the pine rocklands.

Key Words. – Testudinidae; seed dispersal; pine savanna; endozoochory; Miami-Dade County

Gopher tortoises are the only native species of tortoise found east of the Mississippi River and are considered ecosystem engineers through their ability to create burrows that are used by hundreds of commensal species, earning the gopher tortoise the keystone species label (Auffenberg and Franz 1978, 1982; Alexy et al. 2003; Catano and Stout 2015). From providing shelter for other organisms to controlling populations of competitively dominant grasses, keystone species such as gopher tortoises play a significant role in the maintenance of ecosystem structure and function (Jones et al. 1994; Hooper et al. 2005; Richardson and Stiling 2019a).

Turtles affect the ecosystems in which they occur through various ways, including bioturbation, nutrient cycling, seed dispersal, and many other processes (Lovich et al. 2018). Some turtle species have such profound impacts on resident plant communities through seed dispersal and enhanced seed germination that they have been used in plant recruitment and rewilding studies, such as studies where extant relatives of extinct taxa are introduced in habitats as functional analogues (Griffiths et al. 2011; Sobral-Souza et al. 2017). Although a keystone species, one of the attributes of gopher tortoises less frequently investigated is their ability to disperse seeds, specifically because a large amount of research interest is focused on their burrowing behavior. Various species of birds and mammals have been studied extensively regarding their seed-dispersing abilities, while many other taxa that also disperse seeds—like fish and reptiles—have received less attention (Kinnaird 1998; Correa et al. 2007; Muscarella and Fleming 2007). Reptiles such as anoles, turtles, rattlesnakes, and crocodilians have all been found to disperse seeds, yet there is still a lack of understanding regarding their influence on in situ plant recruitment, as many studies focus mainly on germination enhancement rather than the dispersal process from germination through the fruit set stage (Braun and Brooks 1987; Horn et al.

2011; Platt et al. 2013; Giery et al. 2017; Reiserer et al. 2018).

While not the flagship taxa for seed dispersal research, many studies have found that turtles are important seed dispersers (Rick and Bowman 1961; Liu et al. 2004; Falcón et al. 2018; Richardson and Stiling 2019b). In one of the sentinel chelonochory (seed dispersal by turtles) publications, Galapagos tortoises (*Chelonoidis nigra*) were found to drastically increase germination rates for an endemic sympatric species of tomato: the Galapagos tomato (*Solanum pimpinellifolium*) (Rick and Bowman 1961). Even in the pine rockland ecosystem, where this current study takes place, Florida box turtles (*Terrapene caroliniana bauri*) have been found to enhance germination rates for select plant species that cohabitate their environment (Liu et al. 2004). Although no gopher tortoise seed dispersal studies have taken place in the pine rockland habitat until now, a recent study found that gopher tortoises enhance germination rates and decrease seedling emergence times for plant species that are also found in the pine rockland plant community (Richardson and Stiling 2019b). Furthermore, an even more recent publication suggests that gopher tortoises decrease seedling emergence times for a native drupe found in tropical hardwood hammocks and urban sites across South Florida: the cocoplum (*Chrysobalanus icaco*) (Duquesnel 2020; Hanish et al. 2020).

Within the growing body of research on seed dispersal by reptiles, there is increasing interest in the role of gopher tortoises as seed dispersers (but see Birkhead et al. 2005; Richardson and Stiling 2019b; Hanish et al. 2020). Although studies have investigated the diets of gopher tortoises in different ecosystems (Mushinsky et al. 2003; Birkhead et al. 2005; Halstead et al. 2007; Richardson and Stiling 2019a, 2019b), including their seed consumption, no publication has focused on their feeding ecology within the critically endangered pine rockland ecosystem of South Florida, where one of the southernmost populations of this turtle occurs (Enge et al. 2004; Whitfield et al. 2018). No information is available on the trophic interactions between gopher tortoises and the many species of pine rockland plants. Approximately 58 plant species of the pine rocklands are considered rare, 25 of which are state-listed as threatened or endangered (Possley et al. 2008; Diamond and Heinen 2016).

In this article, we examine the feeding ecology of gopher tortoises in the globally imperiled pine rockland South Florida ecosystem. We identify seed species being consumed—and potentially dispersed—by gopher tortoises, determine the origin (native vs. introduced) and other modes of dispersal for many of those seeds, and discuss cryptic trophic interactions that may be occurring between gopher tortoises and other species in the pine rocklands. Being an herbivorous turtle, we hypothesize that gopher tortoises living in the pine rocklands are consuming a wide variety of herbaceous plants and grasses with grasses being the most represented group in their seed diet based on findings from previous research (Carlson et al. 2003; Mushinsky et al. 2003; Birkhead et al. 2005).

METHODS

Study Site. — Pine rocklands are a globally imperiled ecosystem composed of a sparse, savanna-like canopy of the endemic South Florida slash pine (*Pinus elliottii* var. *densa*) with a diverse understory of saw palmetto (*Serenoa repens*), locustberry (*Byrsonima lucida*), pineland croton (*Croton linearis*), and a variety of other shrubs (Possley et al. 2008; Diamond and Heinen 2016). Pine rocklands are particularly recognized for their diverse ground cover layer of various graminoids and forbs. The pine rockland habitat in this study is characterized by having a thin layer of sandy soil resting on limestone bedrock. The habitat is considered to have evolved as a fire-dependent ecosystem (Possley et al. 2014). Although pine rocklands occupied over 50,500 ha throughout South Florida before the settlement of Miami-Dade County, there is now $< 2\%$ of habitat left outside of Everglades National Park and Big Pine Key (Bradley and Gann 2005; Powell and Maschinski 2012; Fig. 1). Many exotic plant species are established in the pine rocklands, including Brazilian pepper (*Schinus terebinthifolius*), Burma reed (*Neyraudia reynaudiana*), Australian pine (*Casuarina equisetifolia*), and others. Along with exotic species, many endemic and threatened plants are known to occur in this rare habitat. We conducted this study on a $>$ 100-ha tract of pine rockland surrounding Zoo Miami called the Richmond Tract, which is the largest fragment of pine rockland habitat outside of Everglades National Park. There is a resident population of gopher tortoises within the Richmond Tract that is the subject of ongoing studies in population biology and conservation (Whitfield et al. 2018). Many of the telemetered tortoises in this study were located in the northwest corner of Zoo Miami's pine rockland habitat.

Seed Collection. — We collected fecal samples from $\geq$ 10 individual tortoises by following the tortoises in an ongoing telemetry study. We followed tortoises fitted with radio transmitters and held tortoises until defecation occurred, up to 15 min. If the tortoises did not defecate in that span of time, we released them at their point of capture. In addition to using scat collected from specific tortoises, we also opportunistically collected droppings of unknown tortoises throughout the rocklands, hence the lack of a specific number of individual tortoises. Our samples include at least 10 tortoises followed via radio telemetry as well as scats collected on the ground from an unknown number of telemetered and nontelemetered tortoises. We collected all tortoise scat samples between November 2015 and June 2017, and once the samples were collected, we either examined them immediately or froze them shortly after collection for examination at a later date.

Seed Identification/Analysis. — We counted the number of seeds belonging to each morphospecies using

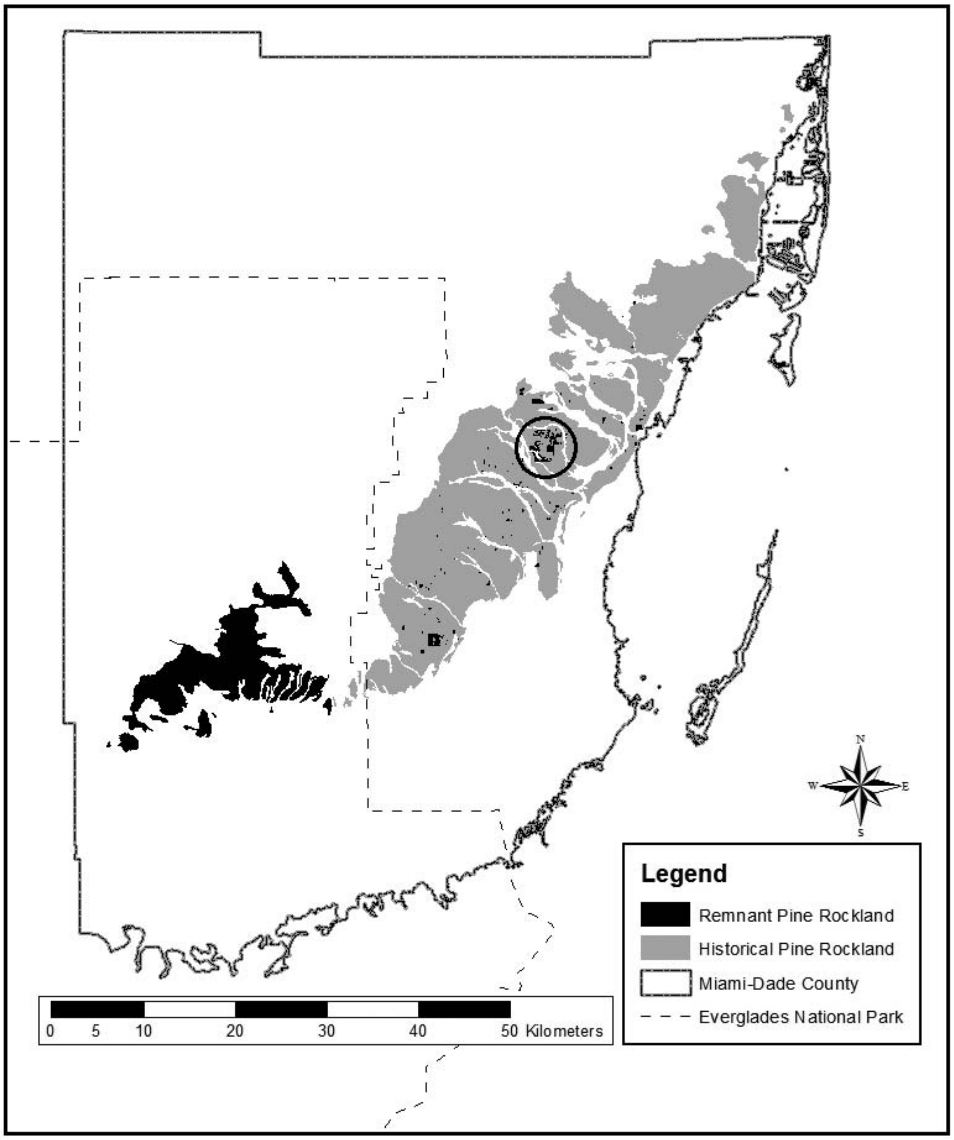

Figure 1. Map of historical versus remnant pine rockland in South Florida. The study site, known as the Richmond Tract pine rockland, is circled in the solid black line.

several resources: the Institute for Regional Conservation's Floristic Inventory of South Florida, Plant Profiles from the US Department of Agriculture's Natural Resources Conservation Service, and the Atlas of Florida Plants from the University of South Florida's Institute for Systematic Botany. Each of these sites come from governmental, academic, or nongovernmental research organizations that have pine rockland plant specimens archived online. When online resources could not result in a confident identification, seed species were verified through comparison with fresh plant material collected at the study site. Any seeds that were unrecognizable were labeled as "unknown."

Once species were identified, we performed a descriptive statistical analysis that included species and seed counts per scat as well as total seed counts and total species counts across all samples. We also calculated the seed density, which we define as the average number of seeds per scat sample in which seeds of that species are present.

RESULTS

We extracted 2484 seeds from 53 scat samples. Of the 53 scat samples, 26 were from 10 marked tortoises, and the other 27 were from unknown and potentially unmarked tortoises through opportunistic collection. Ten species were categorized to morphospecies, and the remaining 23 were identified to the species taxonomic level. The 14 most abundant species constituted over 90% of the cumulative tortoise seed diet (Table 1; Fig. 2). The most common species consumed was needleleaf witchgrass (*Dichanthelium aciculare*), a native grass that is common at the site and that accounted for 16.1% of all seeds. The other most abundant plants present in the seed diet of gopher tortoises were the nonnative ribbed paspalum

Table 1. The 14 most abundant seed species comprising over 90% of the seeds found in tortoise diets in Zoo Miami's pine rocklands. * = nonnative species.

Seed species	No. of seeds	% of all seeds	Cumulative % of all seeds
Needleleaf witchgrass (*Dichanthelium aciculare*)	401	16.14	16.14
Ribbed paspalum (*Paspalum malacophyllum*)*	358	14.41	30.56
Blue crowngrass (*Paspalum caespitosum*)	345	13.89	44.44
Largeflower Mexican clover (*Richardia grandiflora*)*	234	9.42	53.86
Egyptian crowfoot grass (*Dactyloctenium aegyptium*)*	218	8.78	62.64
Caribbean stylo (*Stylosanthes hamata*)	151	6.08	68.72
Hairy spurge (*Euphorbia hirta*)	108	4.35	73.07
Southern crabgrass (*Digitaria ciliaris*)	98	3.95	77.01
Alyce clover (*Alysicarpus vaginalis*)	96	3.86	80.88
Jack in the bush (*Chromolaena odorata*)	83	3.34	84.22
Eastern prickly pear cactus (*Opuntia austrina*)	48	1.93	86.15
Cuban jute (*Sida rhombifolia*)	41	1.65	87.80
Rattlebox (*Crotalaria* sp.)	37	1.49	89.29
Beggar's tick (*Bidens alba*)	36	1.45	90.74

(*Paspalum malacophyllum*; 14.4% of all seeds) and native blue crowngrass (*Paspalum caespitosum*; 13.9% of all seeds), followed by many other herbs and forbs (Table 1; Fig. 2).

Native plants constituted 10 of the 14 most common species found in the scat samples. The other 4 included 3 nonnative species and 1 (*Crotalaria* sp.) that was the only species of the 14 with an unknown native status. The 4 most abundant species, 2 native and 2 nonnative, constituted more than 50% of the total gopher tortoise seed diet at 53.8% (Table 1). Of all plant species observed in this study, 57.6% were native with 15.2% being nonnative and 27.3% unidentified. Native species constituted 61.4% of all seeds counted in the tortoise scat samples, while nonnative species constituted 33.1% with unidentified species at 5.5%.

The nonnative grass *P. malacophyllum* was observed in more scat samples ($n = 28$) than any other species (Table 2). However, of all species observed in > 10 scat samples, the native *D. aciculare* had the highest seed density per scat with > 25 seeds per sample, whereas *P. malacophyllum* had the third-highest seed density with > 12 seeds per sample (Table 3). Native species constituted 4 of the 5 highest seed densities per scat sample. Of all plant families, Poaceae was the most frequently consumed at 60.19%. Poaceae was followed by Fabaceae (13.63%), Rubiaceae (10.40%), Euphorbiaceae (8.10%), Asteraceae (4.99%), Malvaceae (1.72%), Cyperaceae (0.50%), and Arecaceae (0.46%). The scats examined contained an average of 46.02 ($\pm$ 58.30) seeds with the highest number of seeds found in a given scat being 295. The maximum number of species found in a scat was 13, while on average there were 3.3 ($\pm$ 2.3) seed species per scat.

DISCUSSION

Gopher tortoises in our study site routinely dispersed many seeds of both native and nonnative plants. Given the broad range of taxa consumed by gopher tortoises in this study, we believe that gopher tortoises have a broad diet and may not be very selective, as evident in the wide variety of plant taxa in their scats (e.g., grasses, cacti, and euphorbs). Tortoise scats contained between 0 and 13 seed species per scat with an average of 3.4 ($\pm$ 2.2) species. We believe that the foraging strategy of gopher tortoises, being central place foragers and exhibiting no turning bias (Halstead et al. 2007), may explain the wide range of seed and species counts per scat. It appears that gopher tortoises feed until satiated with no strong foraging preferences, as is evident in the breadth of their diet and in their foraging tactic analyzed in a previous study (Halstead et al. 2007); however, we do not have relative plant abundance data in this study to explain preferential feeding on the basis of available plant species.

Of all 23 identified species, only 5 were classified as nonnative with 3—Egyptian crowfoot grass (*Dactyloctenium aegyptium*), largeflower Mexican clover (*Richardia grandiflora*), and shrubby false buttonweed (*Spermacoce verticillata*)—being categorized by the Florida Exotic Pest and Plant Council (FLEPPC) as a Category II invasive (FLEPPC 2019). Category II invasive species are nonnative and have become more frequent or abundant without yet showing signs of negatively altering the Florida native plant communities, whereas Category I invasive species have already been found to negatively affect Florida native plant communities (FLEPPC 2019). At the time of this study, none of the seeds consumed by gopher tortoises were listed as Category I. In summary, 18 of the 23 identified species were identified as native (78.30%), while 5 were identified as nonnative (21.70%). A majority of the 14 most common seed species consumed were herbaceous plants (12 species). The other 2 species—*Opuntia austrina* and *Chromolaena odorata*—grow into a cactus and a suffrutescent shrub, respectively. Although not found in high abundance, *C. linearis*, an endemic shrub and the only known host plant for 2 federally listed butterfly species—*Anaea troglodyta* and *Strymon acis bartrami*—made up 0.9% of all seeds consumed by the tortoises with 23 seeds present in the scats.

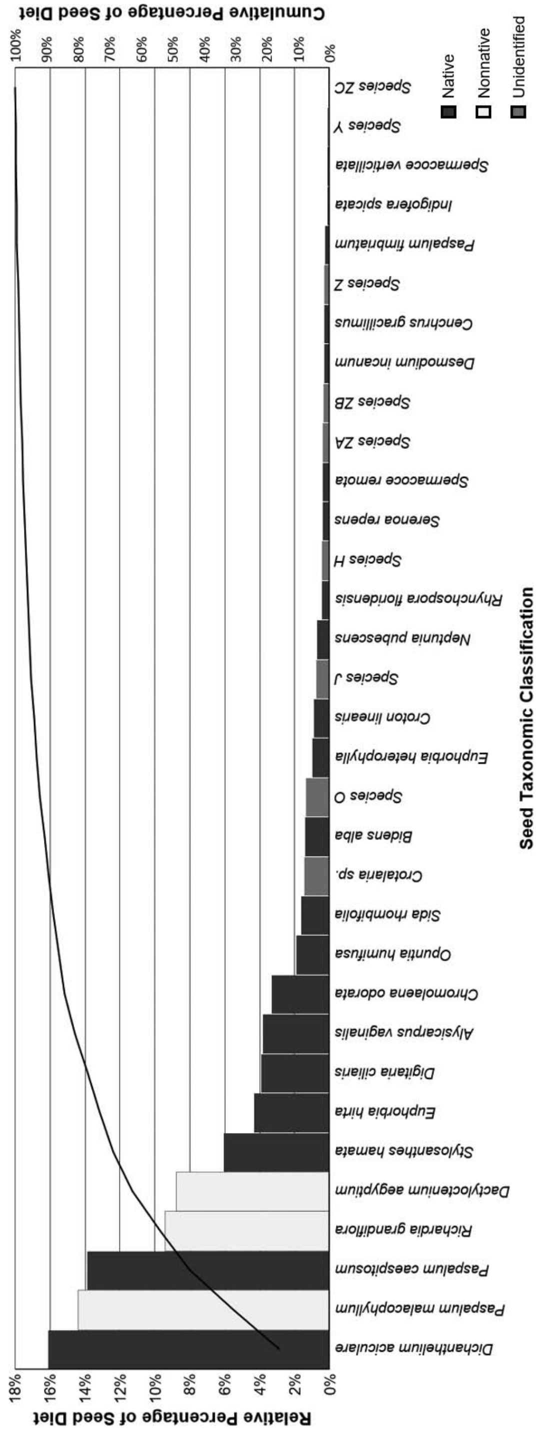

Figure 2. Relative seed abundance from all tortoise fecal samples. The 12 most abundant seed species compose nearly 90% of all seeds found in the tortoise diet. Curved line illustrates the cumulative percent comprising the total seed diet of gopher tortoises in this study.

Previous studies have shown that gopher tortoises do, to some extent, serve as seed dispersal agents in central Florida and corroborated our findings that gopher tortoises mostly consume grasses (Carlson et al. 2003; Mushinsky et al. 2003; Birkhead et al. 2005; Richardson and Stiling 2019a, 2019b). In addition to these feeding observations, other studies have examined the mean passage time of plant material in the gopher tortoise gut and determined it to be approximately 13 d (Bjorndal 1987). This long gut retention time may enhance seed dispersal for pine rockland species consumed by tortoises before a fire has swept through the landscape, possibly facilitating recolonization in this habitat after a burn (Guzmán and Stevenson 2011).

A recent study indicated that gopher tortoises are playing a significant role in plant community dynamics, via herbivory, by controlling competitively dominant grasses and thereby enhancing growing conditions for less competitive, rare herbaceous plants (Richardson and Stiling 2019a). Another study in Pinellas County, Florida, found that gopher tortoise seed ingestion enhanced germination rates and decreased seedling emergence times for 2 fleshy-fruited, native plants: *Opuntia humifusa* and *Physalis angustifolia* (Richardson and Stiling 2019b). Our results suggest that gopher tortoises living in pine rocklands are eating a wide variety of plants, many of which are grasses and some of which are fleshy-fruited species that may experience enhanced germination via gut passage through the gopher tortoise. Additionally, a point pattern analysis on the spatial distribution of adult cocoplum (*C. icaco*) plants revealed a nonrandom distribution with evidence suggesting dispersal by gopher tortoises in movement pathways frequented by these chelonians (Hanish et al. 2020). This study was the first of its kind to reveal the nonrandom relationship between gopher tortoise movement behavior and plant recruitment patterns of a large-seeded plant that it disperses. The gopher tortoise seed dispersal literature has been increasingly finding that this species may be the primary frugivore in many communities where it occurs, meriting even further investigation into this ecological function.

The 3 most abundant seed species are all grasses and compose ~ 44.4% of the total number of seeds in the diet of gopher tortoises. Surprisingly, the gopher tortoises in this research project were not consuming *Paspalum notatum*, which was one of the more abundant species present in gopher tortoise diets from a study conducted by Carlson et al. (2003). Through field observations, *P. notatum* was abundant on the edges of pine rockland habitat yet did not appear in any of the samples collected during the time of this study. We believe that this may be a result of the tortoises either feeding in the core habitat rather than on the edges or feeding in areas where *P. notatum* had been mowed. Instead, another nonnative grass species that is found in only a handful of sites in Florida, *P. malacophyllum*, was very abundant in the gopher tortoise diets and constituted 14.41% of all seeds

Table 2. The 10 most prevalent seed species according to their frequency among gopher tortoise scat samples. * = nonnative species.

Seed species	No. of samples with this species	% of samples with this species
Ribbed paspalum (*Paspalum malacophyllum*)*	28	51.85
Blue crowngrass (*Paspalum caespitosum*)	20	37.04
Needleleaf witchgrass (*Dichanthelium aciculare*)	16	29.63
Alyce clover (*Alysicarpus vaginalis*)	16	29.63
Hairy spurge (*Euphorbia hirta*)	11	20.37
Cuban jute (*Sida rhombifolia*)	8	14.81
Largeflower Mexican clover (*Richardia grandiflora*)*	7	12.96
Species O (unidentified)	7	12.96
Paintedleaf (*Euphorbia heterophylla*)	6	11.11
Species J (unidentified)	6	11.11

retrieved although uncommon in South Florida; this species has been recorded in only a few sites in Miami-Dade County (Gann et al. 2019). In the study site, *P. malacophyllum* was present but not as abundant as *P. notatum*. The 2 *Paspalum* species were not found to co-occur in the habitat, which may indicate that the gopher tortoises feed in areas of the habitat where *P. malacophyllum* is found more abundantly than *P. notatum*.

Many of the seeds consumed by the tortoises have other mechanisms for dispersal: anemochory (wind dispersed), epizoochory (externally dispersed by animals), myrmecochory (ant dispersal), and so on. Among seeds with dispersal mechanisms besides endozoochory (ingestion and deposition by animals) were *C. odorata* (anemochory), *Bidens alba* (epizoochory), *Desmodium incanum* (epizoochory), *Cenchrus gracillimus* (epizoochory), and *C. linearis* (myrmecochory). Therefore, it is probable that gopher tortoises facilitate seed dispersal for some species in this study even if the seeds have other modes of dispersal. It should be noted, however, that although the tortoises may disperse these seeds to new sites, the seeds may or may not successfully establish themselves. For seeds bearing dispersal syndromes of anemochory or epizoochory, the gopher tortoise may be dispersing them shorter distances than wind, birds, and mammals would, but previous studies have shown that although dispersal distance is a component of effective seed dispersal, the quality of the deposition site is another important determinant of dispersal success (Jordano et al. 2007; Schupp et al. 2010). Therefore, one cannot exclude the possibility of effective seed dispersal by gopher tortoises compared with other vectors, simply as a result of differences in dispersal distances.

For autochorous seeds (seeds with no particular mechanism of dispersal), dispersal by gopher tortoises would likely enhance dispersal distance and germination success by delivering them farther from the parent plant, likely reducing the risk of density-dependent mortality (Janzen 1970; Connell 1971) and providing seeds with organic substrate in the form of excrement, compared with the native nutrient-limited pine rockland soil (Nguyen 2011). With gopher tortoises potentially consuming seeds of endangered or threatened plants in the pine rocklands, their role in aiding seed dispersal could have significant impacts on conservation by maintaining plant community structure and even genetic diversity within this critically endangered habitat. Nongraminoid seeds consumed by the tortoises in this study were mainly mature, while graminoids were often still green and immature. Seeds of *C. gracillimus*, also known as slender sandbur, are notorious for having sharp spike-like structures. Multiple seeds of *C. gracillimus* were retrieved from 1 tortoise scat but appeared immature, as they were still attached to the rachis when extracted from the scat. As a result, we believe that gopher tortoises may be inadvertently ingesting graminoid seeds as bycatch or are indeed foraging selectively on those parts for better nutrition. By gopher tortoises feeding on competitively dominant plants (see Richardson and Stiling 2019a) and consuming premature reproductive structures, they may relieve some competition pressure for other plants in the vicinity. We believe that this may be occurring in the pine rocklands given that the tortoises appear to opportunistically graze, consuming new growth, including flowers, buds, and immature seeds.

Gopher tortoises in this study consumed nearly 2 dozen seeds of pineland croton (*C. linearis*). As mentioned earlier, this species is a pine rockland endemic plant that

Table 3. The 5 most abundant species in relation to their density found in gopher tortoise scat samples. * = nonnative species.

Seed species	Average no. of seeds per sample present	% of all seeds	% of samples with this species
Needleleaf witchgrass (*Dichanthelium aciculare*)	25.06	16.14	29.63
Blue crowngrass (*Paspalum caespitosum*)	17.25	13.89	37.04
Ribbed paspalum (*Paspalum malacophyllum*)*	12.79	14.41	51.85
Hairy spurge (*Euphorbia hirta*)	9.82	4.35	20.37
Alyce clover (*Alysicarpus vaginalis*)	6.00	3.86	29.63

serves as the only known host plant for the federally endangered Florida leafwing (*Anaea troglodyte floridalis*) and Bartram's hairstreak (*S. a. bartrami*) butterflies (Salvato 2003; Salvato and Salvato 2010). The conservation implications of gopher tortoises dispersing the seeds of this ecologically significant plant could be substantial if future research reveals an increase in dispersal distance and/or germination rates of *C. linearis* seeds after passing through the tortoise gut. Any findings that would suggest such outcomes would further support the notion that effective seed dispersal may be an additional keystone attribute that gopher tortoises exhibit (Schupp et al. 2010) in addition to their ecosystem-engineering burrow-making behavior in the pine rocklands. Because the Richmond Tract is considered the most suitable site for introductions of Florida leafwing butterflies (Possley et al. 2016), we believe that further research into potential tritrophic interactions of gopher tortoises, host plants, and the butterflies they support is warranted since we found multiple *C. linearis* seeds in their scats.

Provided that gopher tortoises are absent from many of the pine rockland fragments of South Florida, better understanding the interconnectedness of this well-established keystone species with the pine rockland plant community could inform management decisions guided by the various ecological functions of the tortoises. At the time of this study, the most recent management plan for the Richmond Tract pine rocklands, where this gopher tortoise population resides, does not consider any influences of gopher tortoises on the plant community (Possley et al. 2018). Another site that contains pine rockland habitat along with resident gopher tortoise populations, the Deering Estate, does not even consider the tortoise populations in their management plan (Miami-Dade County Natural Areas Management Working Group 2004). Seed dispersal of threatened plant species by gopher tortoises could be an impetus for further research that could lead to increased protection of gopher tortoises—being a candidate for federal listing under the Endangered Species Act in the eastern portion of its range—as well as their consideration in pine rockland and butterfly conservation. Continuing research on the seed dispersal ecology of this tortoise is important in understanding not only keystone effects but also other inconspicuous mutualisms that it may be participating in within the nearly eradicated pine rocklands.

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