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Burrow Characteristics and Habitat Associations of Gopher Tortoises in Urban Pine Rockland Reserves (Miami, Florida, USA)

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The Gopher Tortoise is a keystone species and a species of conservation concern in the southeastern United States, but the biology of tortoises at the extreme southeastern limit of the range is poorly understood. We examined physical characteristics and habitat associations of Gopher Tortoise burrows in pine rockland natural preserves in the highly urbanized Miami-Dade County (Florida, USA). We measured width, depth, and orientation of burrows at two sites. We compared a suite of 11 habitat features (e.g., canopy cover, understory density, ground cover, soil depth, and soil compaction) at random points and at Gopher Tortoise burrows in each of the two sites. Burrow widths were similar between sites and included burrows of both adults and juveniles—evidence that both populations are reproducing. Burrows were very short (most <2 m) compared to burrow lengths reported from other sites (>4 m), likely because soil depth is very shallow in extreme south Florida. We used multidimensional scaling and analysis of similarity to detect differences in habitat variables among sites, among point types (random points and burrows), and between active and inactive burrows. Low leaf litter cover, high grass cover, low canopy cover, and deep soil were among the major variables associated with all burrows and active burrows. The habitat associations of the burrows were similar to studies from other areas, yet the short burrows and association with the deepest available soils appear to be a strong response to the unique geology of pine rockland habitats. We discuss vegetative associations of Gopher Tortoises in the context of management in urban natural areas and implications for protection of Gopher Tortoises at the southern limit of their geographic range.

THE Gopher Tortoise (*Gopherus polyphemus*) is a threatened keystone species indigenous to much of the southeastern United States, where it is the only native tortoise. Gopher Tortoises have a major function in their habitats as ecosystem engineers because the burrows they dig in sandy soil increase soil aeration, affect plant community structure, and are used as refuge by hundreds of other animal species (Young and Goff, 1939; Hansen, 1963; Lips, 1991; Dziadzio and Smith, 2016). Burrow commensals include both threatened and endangered species and obligate commensal species found nowhere else (Young and Goff, 1939; Lips, 1991). Gopher Tortoises have experienced major population declines associated with direct human consumption and expansion of agriculture and urban areas (Auffenberg and Franz, 1982; Schwartz and Karl, 2005; Smith et al., 2006). While only the northwestern populations of Gopher Tortoises are listed as threatened under the U.S. Endangered Species Act (hereafter, "ESA"), they are listed as state threatened species throughout most of their range, and they are protected as a threatened species by Florida's Fish and Wildlife Conservation Commission ("FWC"). The U.S. Fish and Wildlife Service ("USFWS") is currently conducting a range-wide review of their status for inclusion under the ESA (Berry and Aresco, 2014).

At the southeastern end of their range (Fig. 1), there exists distinct confusion over the distribution and ecology of the species, and data deficiencies regarding biology and status of tortoises in the area may inhibit effective conservation planning. There are two particular challenges for Gopher Tortoises living at the southern end of their range: unique geology and intense urbanization. The predominant habitats of the Greater Everglades ecosystem in south Florida are seasonally flooded marshes and swamps, which are dissimilar to occupied habitats in the remainder of the range (upland pine savannas with deep sandy soils; Auffenberg and Franz, 1982). Upland habitats in extreme south Florida include open-canopy pine rocklands and closed-canopy hardwood hammocks, but these are limited in distribution to the Miami Rock Ridge (O'Brien, 1998; Jones and Koptur, 2017). The Miami Rock Ridge is a limestone extension of the Atlantic Coastal Ridge, which has been nearly entirely converted to urban and suburban ecosystems within the past century (Fig. 1). Small and isolated natural areas remain intact but are nested entirely within an urban matrix. Close proximity to dense human populations presents substantial challenges for tortoises, as they are highly susceptible to auto collisions (Deimer, 1989; Mushinsky et al., 2006) and displacement by people (Whitfield et al., 2018). Finally, natural areas within an urban matrix face particular challenges for application of prescribed fires (Possley et al., 2008; Jones and Koptur, 2017).

Currently, few data exist for the distribution or abundance of Gopher Tortoises at the far southern end of their range. European settlers in Miami in the late 19th and early 20th century describe hunting and eating Gopher Tortoises (Monroe, 1943; Worth, 2012). Simpson (1920) reported on the natural history of the Miami area in the early 20th

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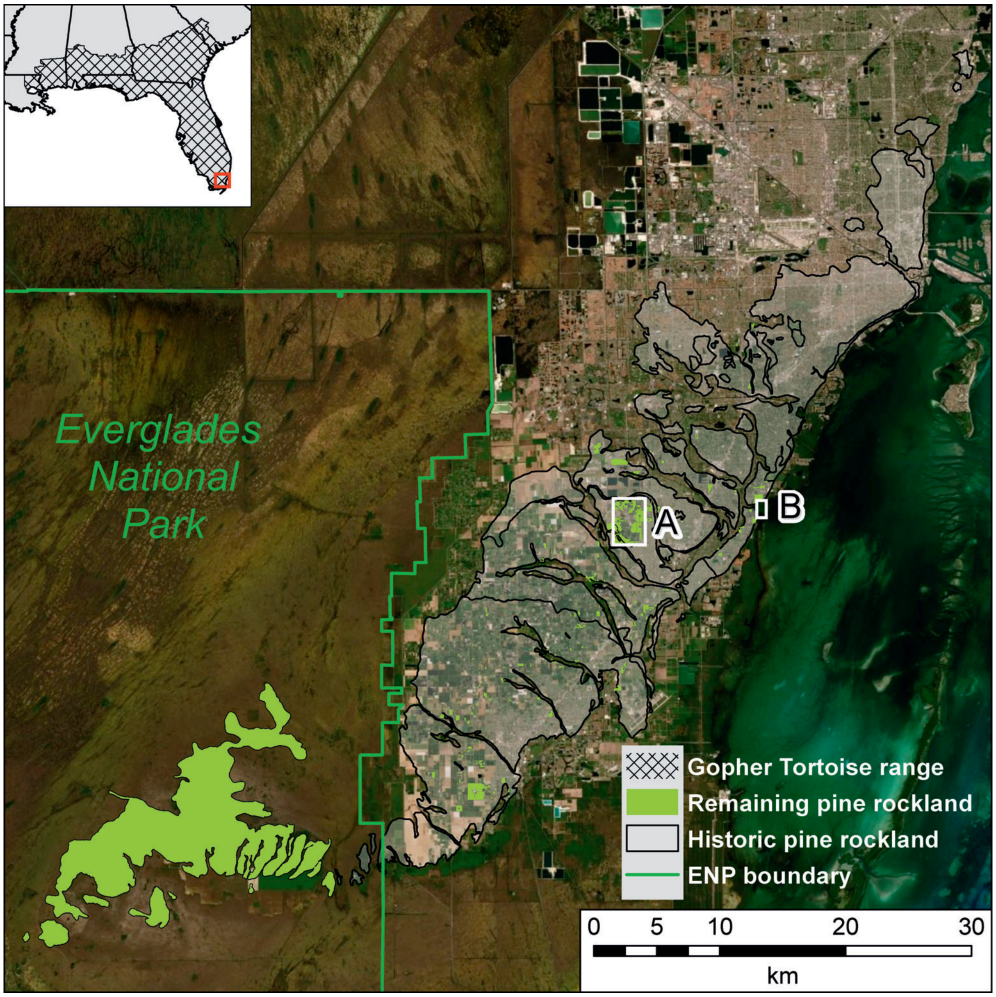

Fig. 1. Locations of two study sites (A, Zoo Miami and B, Deering Estate) in this study within the context of the larger global extent of the Miami pine rocklands and the range of the Gopher Tortoise. The inset at upper left indicates the geographic range of the Gopher Tortoise in the southeastern United States, and the red box in the inset indicates the extent of the main map. The larger map illustrates Miami-Dade County, and the historic and current distribution of the pine rocklands. Inset boxes show the two study sites.

century and expressed surprise at finding Gopher Tortoises and their burrows in Miami because of the inhospitable geology. Carr (1940) described tortoises as occasional inhabitants of south Florida's "limestone flatwoods." Duellman and Schwartz (1958) described Gopher Tortoises as rare and limited in distribution in extreme south Florida, but they collected one specimen from Miami-Dade County. In the 1970s, Auffenberg and Franz (1982) estimated a population of 700 tortoises in Miami-Dade County, though they predicted the tortoises would be extirpated by the year 2000 as a consequence of projected rapid human population growth. Through the 21st century, reports of tortoises in the area are extremely sparse. Enge et al. (2004) reported a single tortoise and a single burrow found in one of six natural areas sampled in Miami, and Krysko et al. (2010) reported a single individual from coastal dunes in Crandon Park in Key Biscayne in Miami-Dade County. Whitfield et al. (2018) reported tortoises from several locations in Miami-Dade County, though many of these appeared to have been displaced by humans, and only one site represented a small tortoise population. Figueroa et al. (2021) reported data from a small population of tortoises from a single natural area in Miami-Dade County. Given the sparce reporting of Gopher Tortoises from the area and extensive urbanization, recent range-wide assessments of the species have excluded the area from the geographic range (Schwartz and Karl, 2005; Smith et al., 2006; Gaillard et al., 2017).

The limited soils in far southern Florida may have profound effects on burrow structure, or perhaps the ability to construct burrows at all (Hoffmeister et al., 1967). Auffenberg and Weaver (1969) reported that *Gopherus berlandieri* in southern Texas take refuge in pallets (shallow constructions similar to burrows, but insufficiently deep to cover the entire tortoise), and Pike and Seigel (2006) reported the use of pallets by juvenile Gopher Tortoises. Plausibly Gopher Tortoises in far southern Florida may construct pallets instead of burrows or may forego burrows altogether in an environment with limited soil yet mild winters. But we are unaware of any populations of Gopher Tortoises that rely solely on pallets or populations that lack burrows entirely.

Here, we present a study of burrow characteristics and habitat associations of Gopher Tortoises in two pine rockland preserves in Miami-Dade County. We have three specific aims: 1) Describe the characteristics of tortoise burrows in south Florida's pine rocklands, environments with limited soil and a relatively high water table. 2) Clarify microhabitat associations of Gopher Tortoise burrows within the pine rocklands and assess whether these are similar to microhabitat associations in other habitat types. 3) Provide a preliminary assessment of population status in extreme south Florida. We expect that information provided herein will help clarify the ecology of tortoises living at the extreme southern edge of their range and will be useful to manage-

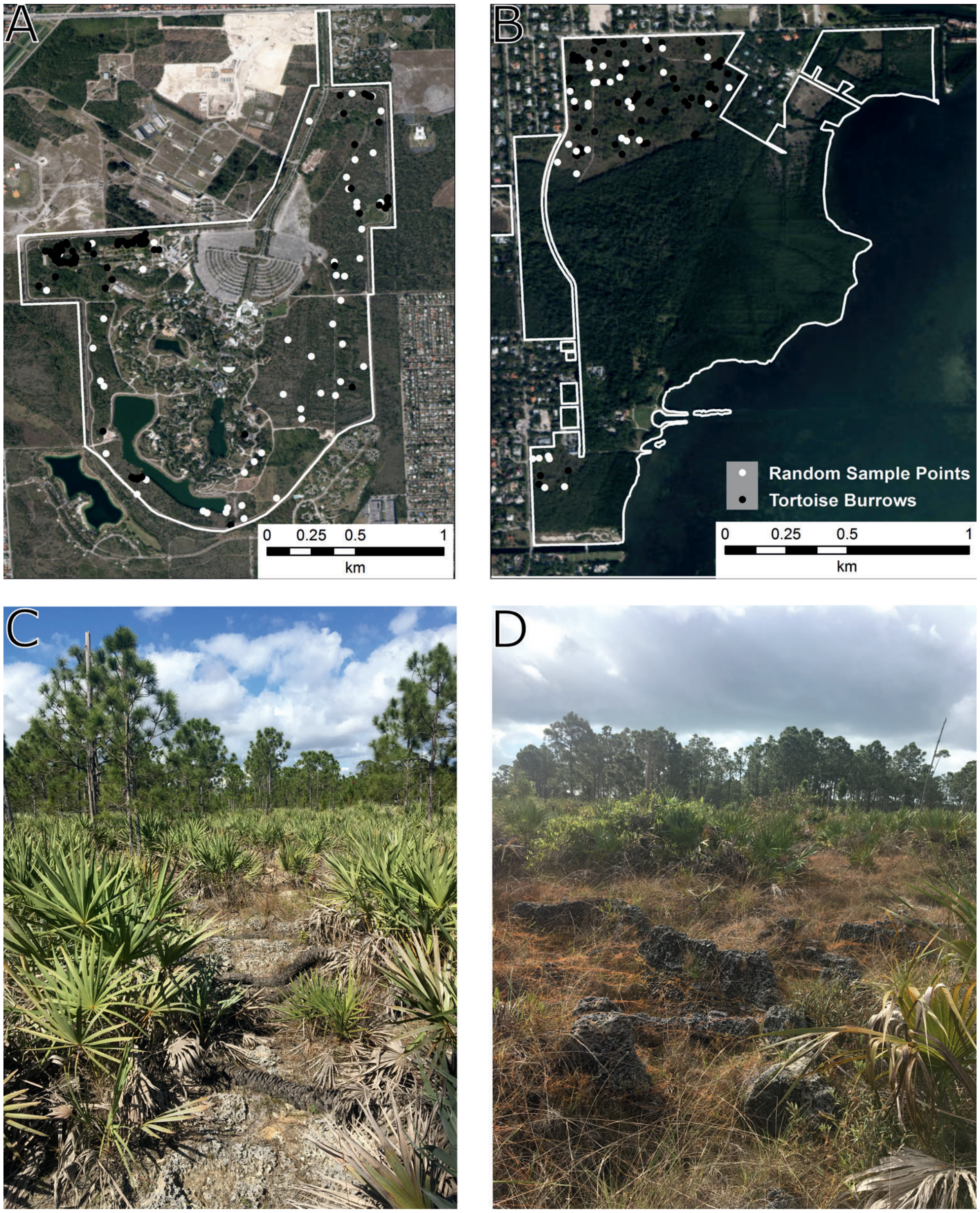

Fig. 2. The two pine rockland sites included in this study are Zoo Miami (A) and the Deering Estate (B). The locations of tortoise burrows sampled in this study and random sampling points are indicated on each map. Zoo Miami is surrounded by adjacent pineland preserves and by extensive urban development. The Deering Estate is bounded by Biscayne Bay to the east and extensive urban development to the north and west. Representative habitats are shown from Zoo Miami (C) and the Deering Estate (D).

ment and conservation planning for Gopher Tortoises in south Florida.

MATERIALS AND METHODS

Study sites.—We conducted this study within two pine rockland preserves within Miami-Dade County (Figs. 1, 2). Pine rocklands are a critically endangered subtropical pine savanna found only within extreme south Florida on the Miami Rock Ridge. Outside of Everglades National Park, less than 2% of this ecological community remains intact (Fig. 1). The substrate underlying the pine rocklands is oolitic limestone, and the ground surface is interspersed with limestone outcroppings and shallow pockets of sandy soil (Osmond et al., 1965; Hoffmeister, 1974; Snyder et al., 1990). The single dominant tree species, *Pinus elliottii* var *densa*, is endemic to south Florida. There is an understory dominated by palms (*Serenoa repens*, *Sabal palmetto*, and *Cocothrinax argentata*) and an extremely diverse understory plant community of grasses, herbs, and shrubs, which includes many endemics (O'Brien, 1998; Possley et al., 2008; Diamond and Heinen, 2016; Trotta et al., 2018). The pine rocklands require fire to maintain an open canopy. In the absence of fire, the ecosystem transitions into tropical hardwood hammock, a closed-canopy subtropical dry forest (Snyder et al., 1990).

Our first field site is a pine rockland preserve owned and managed by Zoo Miami (Fig. 2). This 102 ha pineland is the central component of the larger Richmond Tract, an assemblage of contiguous rockland properties owned by private landowners and local and federal government (Possley et al., 2018). Collectively, the Richmond pine rocklands are the largest contiguous rockland area outside of Everglades National Park. Pine rocklands within Zoo Miami (and much of the Richmond Tract) are protected under Miami-Dade County as Natural Forest Communities (Diamond and Heinen, 2016; Possley et al., 2018). Zoo Miami's pine rocklands are not an uninterrupted block of continuous habitat; rather, there are several variably connected patches of rockland interspersed with patches of different land use types, and variably connected to other rockland patches of the Richmond Tract (Fig. 2). Zoo Miami's pine rocklands are topographically quite flat, with elevation ranging 3–4 m above sea level, and the soil is classified as Opalocka Sand-Rock Outcrop Complex (USDA, 1990).

The Deering Estate at Cutler (hereafter, "Deering"; Figs. 1, 2) is a 184 ha site that contains two disjunct pine rockland parcels. One parcel is in the northern section of the main estate encompassing ~33 ha and one smaller section of ~3 ha is in the "South Addition." The two rocklands are ~1 km apart, separated by a block of hardwood hammock and a wetland restoration area. Soils at Deering are also classified as the Opalocka Sand-Rock Outcrop Complex (USDA, 1990), and as with Zoo Miami, the topography is also flat, ranging from sea level to 4 m above sea level. Deering's other natural areas include other habitats that are not used by tortoises (i.e., remnant slough and mangrove forests).

Field sampling.—We conducted sampling at Zoo Miami between February and June of 2019, and at Deering between February 2019 and November 2020. No major habitat alterations (i.e., fire or mechanical thinning) were conducted over this time period. We located tortoise burrows in several ways. At Zoo Miami, we found burrows through opportunistic encounters between 2015–2019 and through radiotelemetry of tortoises between 2016–2019. At Deering, we found burrows through complete walkthroughs of the two pine rockland parcels between February and March 2017. Between three and five observers took place in each sampling event. At each site, we sampled randomly generated points and previously located Gopher Tortoise burrows. Random points were created in ArcGIS, constrained by a shape file with the extent of Zoo Miami or Deering. We required that random points were at least 10 m apart, required that random points were at least 10 m from any tortoise burrow, and we removed points that were included within developed areas, on roads or parking lots, hardwood hammocks, or open water. We included points that were within pine rockland habitats, non-native forests (closed-canopy forests dominated by invasive species), and maintained lawns with variable canopy cover, as each of these habitats contained Gopher Tortoise burrows.

Sampling burrow characteristics.—At each burrow, we measured a number of physical characteristics about the burrow. First, at the time of field sampling (2019 and 2020) we categorized burrows as active or inactive. We considered burrows to be active if they were either occupied by a tortoise during surveys, had a well-defined apron with or without tortoise tracks or recently excavated sand, and did not contain leaf litter or debris within the burrow opening. Inactive burrows did not have a clear, visible apron, contained leaf litter within the burrow, contained spider webs within the burrow, or were partially collapsed. While classification of burrow activity can be subjective (Smith et al., 2005), in this study between two and four observers, each with more than one year experience working with Gopher Tortoises in pine rockland habitats, reached consensus on whether burrows were active or inactive; we believe these assessments should be generally reflective of recent activity by tortoises. An active burrow by our definition is an indication that a tortoise has selected habitat within present ecological conditions. An inactive burrow indicates that a site was selected by a tortoise for burrowing, but not necessarily with the present set of habitat conditions, which may have led to either burrow collapse or abandonment by the tortoise.

Tortoise burrows may be non-random in orientation (McCoy et al., 1993), either because of topographic features of the natural landscape (which in our sites, is minimal) or anthropogenic modifications of the landscape (which in our sites, are extensive in the periphery of natural areas). We measured the orientation of each burrow by inserting a 1.2 m probe into the burrow entrance approximately 0.5 m and collecting the direction that the probe is pointing using a compass (McCoy et al., 1993). We measured the width of each burrow entrance using calipers inserted ~20 cm into the burrow entrance (Smith et al., 2005). We measured the length of each burrow by inserting a burrow camera (Gopher Tortoise Burrow Cam, Environmental Management Systems, Canton, GA) with video monitor until the end of the burrow was reached by the camera probe and measuring the length of the BurrowCam from the burrow entrance to the end of the camera probe. We did not collect burrow length measurements for any burrow that was occupied by a tortoise or other large vertebrate(s) because animals were obstructing access to the end of the burrow.

Sampling habitat variables.—At each point (burrow or random point location), we collected data for a suite of 11 habitat variables (canopy cover, vegetation density at ground, vegetation density at 1 m above ground, vegetation density at 2 m above ground, bare ground cover, leaf litter cover, herb cover, grass cover, shrub cover, soil depth, and soil compaction). To evaluate canopy cover, we used a spherical densiometer to estimate canopy cover in each of four cardinal directions (Lemmon, 1956). To evaluate ground cover among our five classes (bare ground, leaf litter, herbs, grasses, and shrubs), we laid a 1 m^2 quadrat centered either over the burrow entrance or at the random point specified by GPS. Within the quadrat, we estimated cover among the five classes to the nearest 10%. To estimate vegetation density, we used a modification of protocols for a Secchi disk (Antsey, 1964; Tyler, 1968) where we established a fixed point at the burrow or random GPS point and generated a random compass direction. We paced away from the fixed point with a Secchi disk, until the Secchi disk is concealed by vegetation from the fixed point, and the distance where Secchi visibility is lost is our estimate of vegetation density. For each burrow or random point, we measured vegetation density at 0 m (ground level), 1 m above ground, and 2 m above ground. To evaluate soil depth, we inserted a 1.2 m soil probe into the soil at the four corners of our 1 m^2 quadrat, until the probe stopped, and we measured the penetration depth of the probe. Because the maximum soil depth we could estimate with this method was 1.2 m, if the soil probe penetrated to the maximum depth, we recorded a depth of 1.2 m. We averaged the four values to produce an estimated soil depth for that burrow or random point. To measure soil compaction, we used a Pocket Penetrometer in each of the four corners of the quadrat and averaged the four values to produce an estimate of compaction for that burrow or random point.

Statistical analysis.—To evaluate whether burrows deviated from random orientations, we used a series of Rayleigh tests in the *circular* package of *R* with compass direction as a response variable, sequentially testing all burrows and several subsets of burrows: Zoo Miami burrows, Deering burrows, active burrows, and inactive burrows. To compare burrow width and burrow length among sites and simple burrow activity categories, we used general linear models specifying burrow status (active or inactive) and site as predictor variables and length of burrows as response variables and an interaction between site and burrow status.

To evaluate differences in 11 habitat variables, habitat features between burrows and random points, and to evaluate differences in habitat features between sites, we used a series of multivariate tests and visualizations using the *vegan* package of *R* (Oksanen et al., 2019). First, we constructed dissimilarity matrices based on the Bray-Curtis index for all points. We performed one non-metric multidimensional scaling (nMDS) using site and point type as factors, and one nMDS using site and burrow activity as predictors. We used Analysis of Similarity (ANOSIM) as a statistical test for each nMDS, and we used SIMPER (a function that calculates the percentage in dissimilarity according to individual attributes in the nMDS) following each ANOSIM to evaluate the contribution of each of our 11 habitat features to differences among groups.

RESULTS

We sampled 97 burrows at Zoo Miami (of which 39 were active and 57 were inactive) and 67 burrows at Deering (of which 29 were active and 37 were inactive). One burrow at each site was unclassified as active or inactive. Seven burrows were occupied at Zoo Miami, and nine were occupied at Deering. We sampled 50 random points at Zoo Miami and 50 random points at Deering.

Burrow characteristics.—There was no trend in burrow orientation for burrows overall (Fig. 3A, Rayleigh Test t = 0.126, $P = 0.253$), for burrows at Zoo Miami (Rayleigh Test t = 0.080, $P = 0.581$), for burrows at Deering (t = 0.208, $P = 0.120$), for active burrows (Rayleigh Test t = 0.141, $P = 0.327$), or for inactive burrows (Rayleigh Test t = 0.134, $P = 0.253$). Burrow entrances at Zoo Miami were slightly wider than burrow entrances at Deering Estate (Fig. 3B, $F_{1,127} = 6.55$, MS = 646.52, $P = 0.012$), and active burrows were wider than inactive burrows ($F_{1,126} = 8.09$, MS = 798.27, $P = 0.005$), but there was no interaction between site and burrow activity pattern on burrow width ($F_{1,127} = 0.0004$, MS = 0.04, $P = 0.983$). Burrows at Deering were longer than burrows at Zoo Miami (Fig. 3C, $F_{1,126} = 25.55$, MS = 17.30, $P < 0.0001$), and active burrows were longer than inactive burrows ($F_{1,126} = 130.3$, MS = 8.82, $P < 0.0005$), but there was no interaction between site and activity class on burrow length ($F_{1,126} = 0.13$, MS = 0.08, $P = 0.724$).

Habitat associations.—There were differences in habitat features between random points and burrows (Fig. 4A, ANOSIM, R = 0.257, $P = 0.001$), and there were differences in habitat features between sites (Fig. 4B, ANOSIM, R = 0.119, $P = 0.001$). Of our 11 habitat variables, seven differed between random points and burrows (Table 1A). Compared to random points, burrows had less leaf litter, lower canopy cover, deeper soils, greater understory visibility at 2 m, lower understory visibility at 1 m, lower understory visibility at ground level, and greater soil compaction.

We also found differences in habitat features between active and inactive burrows (Fig. 4B, ANOSIM, R = 0.070, $P = 0.002$). Of our 11 habitat variables, only three differed among active and inactive burrows (Table 1B). Compared to inactive burrows, active burrows had greater soil depth, greater coverage of bare ground, and less canopy cover (Table 1B). There were no associations with other cover types, understory visibility at any height, or soil compaction (Table 1B).

DISCUSSION

We described burrow characteristics and habitat associations of Gopher Tortoises at two pine rockland preserves in urban natural areas at the southern extent of their geographic range. Burrows were relatively abundant in these two pine rockland preserves. The burrows constructed by tortoises in this ecosystem were shorter than in most other habitats, and short burrows appear to be a limitation of the habitat on tortoises in this environment. Indeed, mean soil depth for random points was <50 cm at both sites. Clearly this is a restriction for burrow site availability for tortoises living within pine rocklands. Still, most habitat associations of the tortoises that we detected (affinity for open canopy, deep sandy soil, grass cover) were similar to associations seen elsewhere in the species' range (Jones and Dorr, 2004; Baskaran et al., 2006; Kowal et al., 2014; Lau and Dodd, 2015).

Burrow characteristics.—The size distribution of burrows at both sites was fairly typical for Gopher Tortoise populations, and size distributions of burrows reflect age distributions of tortoises in the populations. Both of our sites had populations where most burrows were adult-sized. Using a cutoff of 22 cm in width as an indication of an adult burrow (Doonan and Stout, 1994), 59.2% of burrows were from adults at Deering, and 64.4% of burrows were from adults at Zoo Miami. However, both populations had juvenile burrows across a range of sizes. Some studies have raised concern about high juvenile mortality and potential reproductive failure in tortoise populations (Epperson and Heise, 2003; Pike and Seigel, 2006). Fortunately, the presence of juvenile burrows in both sites was firm evidence of reproduction, although we lack population-level data on fecundity and recruitment at these sites. Future research on southern populations should focus on understanding demography of these populations, as they are at the forefront of impacts from both urbanization and climate change.

The burrows we describe here were far shorter than burrows reported elsewhere in the range. Hansen (1963) measured 14 burrows in central Florida and reported mean length of 4 m. Ulstsch and Anderson (1986) measured 15 burrows in northern Florida and southern Georgia and reported a mean length of 3.7 m. Very few of the burrows we measured at either site were more than 2 m in length, and at Zoo Miami, very few burrows were longer than 1 m. Gopher Tortoises have been suggested to use pallets—described by Auffenberg and Weaver (1969) as burrow-like structures that are insufficiently deep for a tortoise to entirely conceal itself—yet we are unable to find any documentation of Gopher Tortoises using this definition of pallet in any literature for any site. However, many of the burrows we describe here appear consistent with Auffenberg and Weaver's (1969) original description. Still, during >4 y of observations of tortoises at Zoo Miami, including weekly

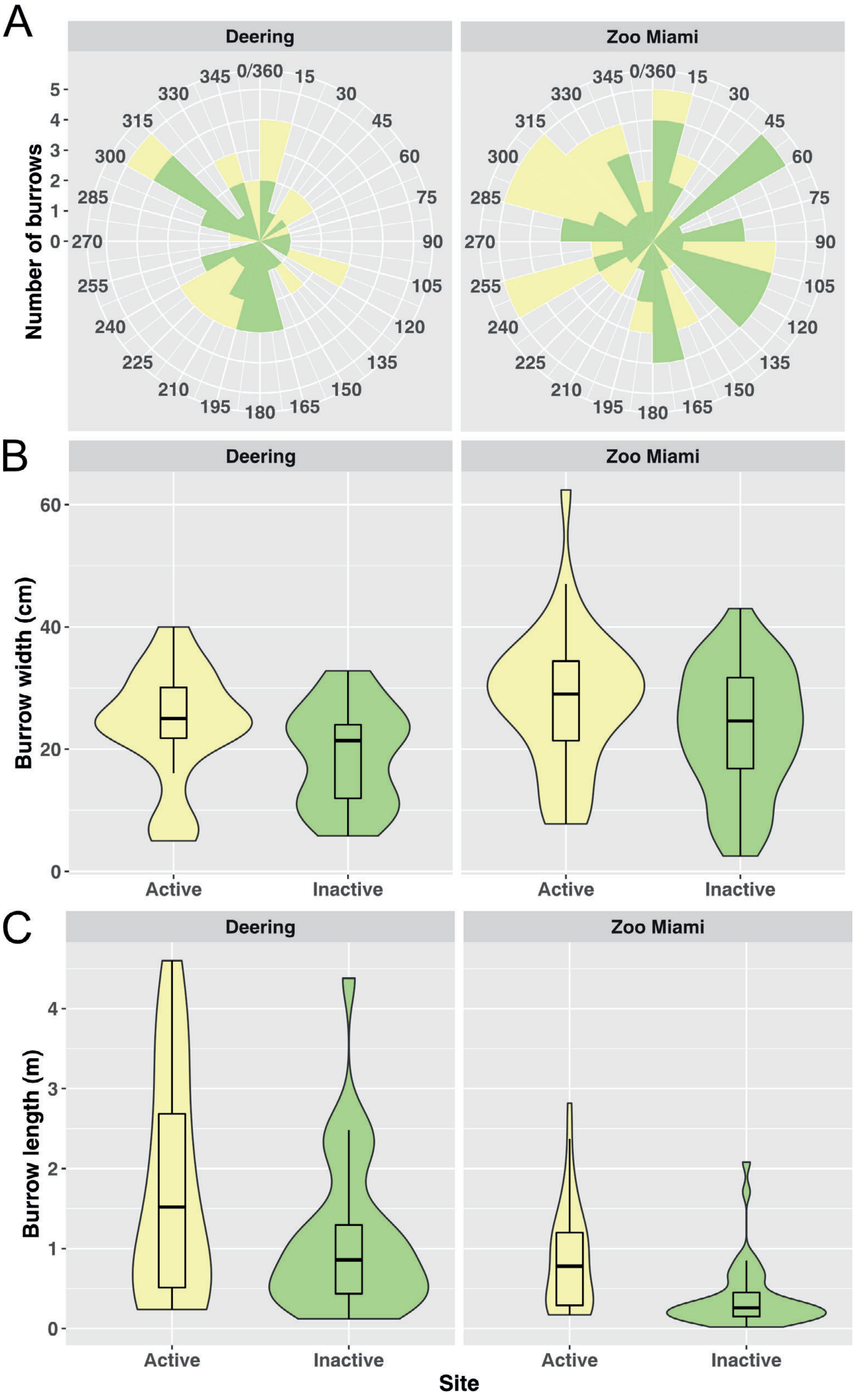

Fig. 3. Characteristics of Gopher Tortoise burrows at two sites in Miami-Dade County, Florida, USA. (A) Polar plots for Gopher Tortoise burrow orientations. There was no trend in direction of burrow opening at either site. (B) Burrow openings were wider at Zoo Miami than at the Deering Estate, and in both sites active burrows were wider than inactive burrows. (C) Burrows were far longer at the Deering Estate than at Zoo Miami, and active burrows were far longer than inactive burrows at both sites.

radiotelemetry for ~3 y, we very rarely observe tortoises using such pallets (B. Chin, unpubl. data). Instead, at least for Gopher Tortoises, we suggest that pallets are burrows for which construction has been aborted because further excavation is precluded by limestone rock. We do not believe such pallets are used as primary refugia by tortoises.

Regardless of the function or use of pallets, even the longest burrows we report are shorter than typical burrows found elsewhere. The short burrows may be an important feature of the ecology of tortoises in pine rocklands. Short burrows likely provide less protection from environmental extremes, though south Florida experiences far less extreme

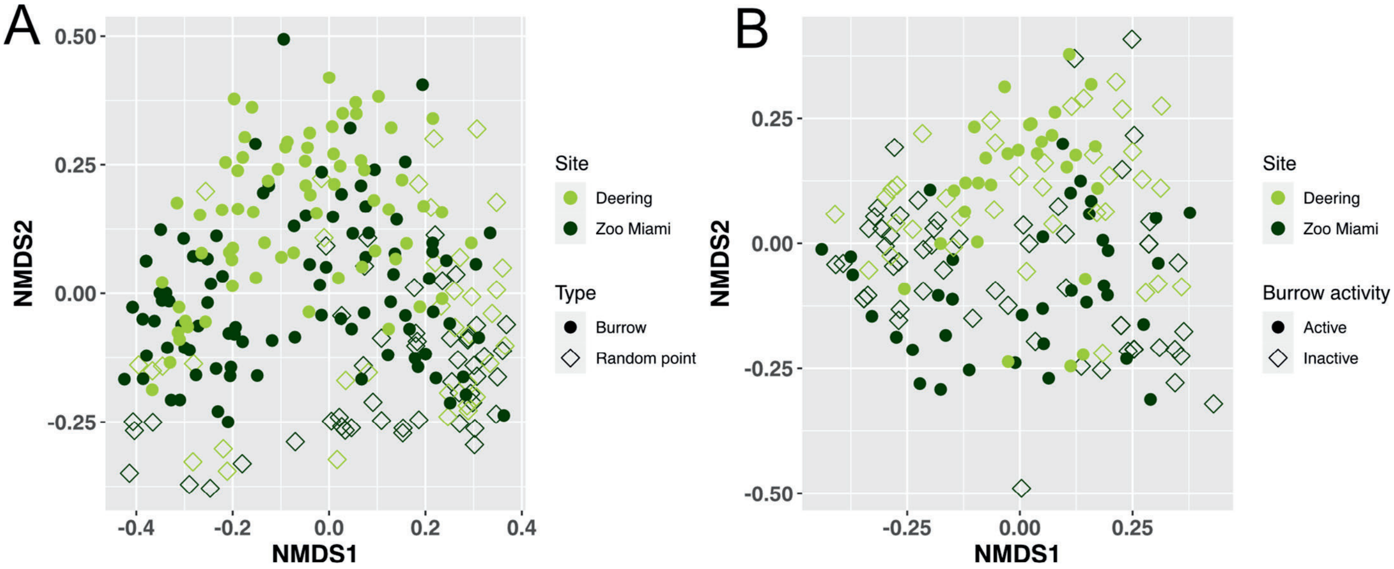

Fig. 4. Non-metric multidimensional scaling (nMDS) plots illustrating differences among sampling point types. (A) Differences in habitat features between burrows and random points. (B) Differences in habitat features between two sites—Deering or Zoo Miami. While there is considerable overlap among point types, there are significant differences in habitat variables measured between point types (burrows and random points) and between sites (Zoo Miami and the Deering Estate).

Table 1. Similarity Percentage (SIMPER) results for differences (A) between random points and Gopher Tortoise burrows and (B) between active and inactive burrows from 11 habitat variables included in Analysis of Similarity (ANOSIM). Variables are ranked from greatest contribution to dissimilarity between groups to least contribution to dissimilarity between groups. "Contribution" indicates the relative contribution of a habitat variable to dissimilarity between random points and burrows. SD indicates the standard deviation of the contribution. Means values for random points and points at burrows are provided.

(A) Burrows vs. Random Points

Variable	Mean burrows (±S.D.)	Mean random point (±S.D.)	Contribution	SD	*P*
Leaf litter cover	25.9 (±28.5)	46.1 (±30.2)	0.105	0.076	0.001***
Grass cover	31.3 (±31.3)	25.7 (±31.7)	0.096	0.083	0.815
Canopy cover	16.4 (±19)	38.2 (±26.9)	0.086	0.062	0.001***
Soil depth	28.7 (±17.7)	14.9 (±16.9)	0.058	0.046	0.001***
Shrub cover	14.4 (±19.3)	17.7 (±17.5)	0.055	0.050	0.409
Bare ground	19.2 (±20.1)	5.1 (±11.6)	0.054	0.053	0.156
Secchi visibility 2 m	16.8 (±13.2)	20.1 (±17.4)	0.045	0.037	0.021*
Herb cover	9 (±13.1)	5.1 (±8.6)	0.028	0.035	0.888
Secchi visibility 1 m	7.6 (±5.3)	9.2 (±12)	0.020	0.025	0.019*
Secchi visibility 0 m	3.2 (±3.5)	5.3 (±9.1)	0.010	0.020	0.014*
Soil compaction	0.7 (±0.6)	1.4 (±1.3)	0.003	0.003	0.001***

(B) Active vs. Inactive Burrows

Variable	Mean active burrows (±S.D.)	Mean inactive burrows (±S.D.)	Contribution	SD	*P*
Soil depth	52.6 (±35.6)	39 (±28.5)	0.094	0.073	0.002**
Grass cover	24.6 (±24.4)	34.9 (±32.8)	0.090	0.073	0.965
Leaf litter cover	17.1 (±20.6)	25.3 (±28.5)	0.071	0.066	1
Bare ground	31.6 (±19.1)	11.9 (±14.5)	0.067	0.050	0.001***
Shrub cover	20.3 (±22.1)	19.8 (±24.3)	0.064	0.059	0.964
Canopy cover	18.9 (±21.8)	3 (±14.4)	0.051	0.048	0.014*
Secchi 2 m	16.5 (±13.1)	17.3 (±12.2)	0.035	0.029	0.367
Herb cover	6.2 (±9.1)	7.7 (±14.3)	0.027	0.037	0.955
Secchi 1 m	5.9 (±4.4)	7.5 (±5.3)	0.014	0.013	0.372
Secchi 0 m	2.3 (±1.3)	3 (±3.8)	0.005	0.008	0.995
Soil compaction	0.7 (±0.9)	0.8 (±2)	0.002	0.005	0.679

cold than the northern portion of the species' range. Short burrows could provide less protection from fires, although it is unclear what burrow depths would be required for a thermal escape from high temperatures produced by fires. Short burrows (and certainly pallets) may provide less space for burrow commensals. Finally, short burrows may make tortoises more susceptible to predation, or may have made tortoises in extreme south Florida particularly susceptible to hunting pressure by humans in Miami's early history (Monroe, 1943; Worth, 2012).

Habitat associations.—Tortoise burrows at our sites were associated with open canopy, sparse understory, grass cover, and deep soils. These characteristics are similar to those reported elsewhere. Tortoise burrows have been positively associated with deep sandy soils (Jones and Dorr, 2004; Kowal et al., 2014), negatively associated with soil clay content (Baskaran et al., 2006), positively associated with bare ground (Ashton et al., 2008), and negatively associated with mid-story vegetation density (Jones and Dorr, 2004; Kowal et al., 2014). Some recent studies have also shown that landscape features at larger spatial scales than those we examined (i.e., elevation and slope, land cover categories, distance to roads, distance to water) may have greater predictive power in determining tortoise associations (Kowal et al., 2014; Lau and Dodd, 2015) than the fine spatial scale habitat variables we describe. However, our two sites have very little variation in topography (<2 m within and between sites) and have virtually no meaningful slope.

The soil associations we described emphasize adaptation to a unique geology. Soil depth was among the strongest predictors of burrow presence—which is not surprising because the ecosystem is interspersed with sandy pockets and exposed limestone on the ground. Deep sandy pockets are very limited in the pine rocklands, both within our study sites and across the extent of the pine rocklands as an ecosystem. Towards the northern portion of the pine rocklands, soils are considerably deeper, and the northern portions of the pine rocklands essentially transition into sand scrub habitats found elsewhere in Florida. However, the southern rocklands (south of Richmond) are depauperate of sand, and within Everglades National Park (ENP) are nearly sand-free. This likely explains why the large patch of pine rocklands in ENP is lacking a population of Gopher Tortoises.

The habitat associations we describe have important implications for the management of tortoises. Many of the vegetative features in the habitat (canopy cover, leaf litter cover, understory density) can be managed through prescribed fires. However, soil depth is not a feature that is typically altered by land managers. We suggest that management for Gopher Tortoises in pine rockland should capitalize on deep sandy pockets where they are available and prioritize prescribed fires in these areas.

Gopher Tortoise ecology and conservation in extreme south Florida.—Our study is one of very few empirical studies of tortoises at the extreme southern limit of their geographic range (but see Enge et al., 2004; Whitfield et al., 2018; Figueroa et al., 2021). Kushlan and Mazotti (1984) studied a coastal population of tortoises at Cape Sable (Everglades National Park, Monroe County, Florida), an isolated formation of coastal dunes on the extreme southwest of Florida's mainland. This is likely the most climatically similar site to the localities we describe, although the geology and ecology of the Cape Sable population is quite different with regard to vegetation and soils, and with responses to intense tropical storms and hurricanes. Still, Waddle et al. (2006) documented dramatic declines in this population between the 1980s and 2000 and suggested that storm surge from repeated hurricanes had destabilized the sand dunes used by Gopher Tortoises there. While both Zoo Miami and Deering were heavily impacted by hurricanes (including Hurricane Andrew and Hurricane Irma), the geology of these sites is apparently not as susceptible to storm impacts as is Cape Sable, as the limestone matrix interspersed with sand may prevent destabilization of sand formations.

While we were able to identify a considerable number of burrows at each site, few of the burrows we observed were occupied. Only seven burrows at Zoo Miami were occupied and only nine at Deering were occupied. Past researchers have attempted to estimate the number of tortoises based on the number of burrows, but use of such "correction factors" often leads to inaccurate assessments of population size (Burke, 1989; Breininger et al., 1991; McCoy and Mushinsky, 1992). Still, these two sites appear to represent small and isolated, but reproductive populations. More formal efforts to estimate population size will be critical to understanding management scenarios for the tortoises.

The continued presence of Gopher Tortoises in pine rocklands is particularly surprising given the isolation of these preserves within a dense urban matrix. These tortoises face direct impacts from habitat loss, risk of injury or mortality by automobile collision, and direct displacement by people. In fact, despite extensive ongoing conversion of natural areas to low-density urban habitats, the state wildlife agency has (to our knowledge) never required surveys or issued removal permits for Gopher Tortoises within the entirety of Miami-Dade County.

The rocky soils of the pine rocklands have been considered low quality tortoise habitat by both past biologists (Auffenberg and Franz, 1982) and by state wildlife agencies (FWC, 2012), yet we are unaware of any empirical evidence for this claim. As we show, the rocky substrate appears to limit burrow depth; yet it is unclear that deep burrows are necessary in a subtropical climate or that such shallow burrows directly lead to a fitness disadvantage. In contrast, the frost-free climate of south Florida allows nearly year-round tortoise activity (Moore et al., 2009) and may shorten time to maturity (Mushinsky et al., 1994) or enable higher reproductive rates (Ashton et al., 2007) than in the more northern portions of the range.

It may appear surprising that a state-threatened species that constructs rather conspicuous burrows could go nearly unreported in an urban area for two decades (Enge et al., 2004; Krysko et al., 2010). However, such data deficiencies are common for fauna within the pine rocklands of south Florida. The Florida Bonneted Bat (*Eumops floridanus*), a south Florida endemic found in pine rocklands that is now listed under the ESA, was only formally described as a species in 2004 (Timm and Genoways, 2004). The rockland endemic Rim Rock Crowned Snake (*Tantilla oolitica*) has been documented by biologists fewer than 40 times (Hines, 2011; USFWS, 2015). The pine rockland endemic Miami Tiger Beetle (*Cicindelidia floridana*) was undetected from 1934 until its rediscovery in 2007 (Brzoska et al., 2011) and is also now protected under the ESA (USFWS, 2016). Two butterfly species and more than ten pine rockland plant species have been added to the ESA since 2010 (Salvato, 2003; Possley et al., 2016; Trotta et al., 2018). A large and distinctive pine rockland trapdoor spider, *Ummidia richmond*, was only formally described in 2021, and is apparently also a south Florida endemic that occurs primarily in pine rocklands (Godwin and Bond, 2021). A data gap concerning Gopher Tortoises within natural areas embedded in urban Miami is not exceptional; rather, this is typical of a more expansive data deficiency regarding terrestrial fauna in extreme south Florida—and pine rocklands in particular. In this environment, discoveries and rediscoveries of threatened species are surprisingly commonplace.

The tortoise populations we examine in this study were anticipated to be extirpated by the beginning of this century (Auffenberg and Franz, 1982) and have been mostly overlooked by both tortoise biologists and management agencies (Schwartz and Karl, 2005; Smith et al., 2006; FWC, 2012). This is surprising because Gopher Tortoise populations on the western extent of the geographic range have long been protected by the ESA in response to loss of habitat, and because the extent of habitat loss in the southern portion of the range has been far more rapid and extreme. The status of southern populations of Gopher Tortoises should be reexamined, as the severe and ongoing decline in this portion of the species range will likely require increased management attention to avoid extirpation.

DATA ACCESSIBILITY

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