



Effects of Gopher Tortoise (*Gopherus polyphemus*) Exclusion on Plant Assemblages in a Longleaf Pine Forest

Authors: Lloyd, Robin B., Henning, Jeremiah A., and Chupp, Adam D.

Source: Journal of Herpetology, 57(4) : 367-372

Published By: Society for the Study of Amphibians and Reptiles

URL: <https://doi.org/10.1670/22-067>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Effects of Gopher Tortoise (*Gopherus polyphemus*) Exclusion on Plant Assemblages in a Longleaf Pine Forest

ROBIN B. LLOYD, JR.,¹ JEREMIAH A. HENNING, AND ADAM D. CHUPP

Department of Biology, University of South Alabama, Mobile, Alabama, 36688, USA

ABSTRACT.—Herbivory serves as a critical top-down mechanism within plant communities by regulating biodiversity, productivity, and ecosystem function. Although top-down impacts of mammalian herbivores have garnered significant attention in the literature, fewer studies have investigated the role of herbivorous reptiles, which can serve as crucial herbivores for some ecosystems, in regulating plant communities. In southeastern coastal plain longleaf pine forests of the United States, Gopher Tortoises (*Gopherus polyphemus*) are a keystone species that may suppress plant productivity and promote local diversity within hyperdiverse understory plant communities. In January 2019, we established permanent tortoise exclusion plots with corresponding accessible control plots within an active Gopher Tortoise population at Splinter Hill Bog Preserve in southwestern Alabama. We measured the response of plant species diversity, composition, and productivity through a single growing season to quantify short-term impacts of tortoise exclusion on understory plant communities. We found that tortoise exclusion plots had 35% more plant cover, with a 15% reduction in plant richness, 6% reduction in evenness, and 12% reduction in Shannon's diversity, relative to control plots. Within a single growing season, tortoise exclusion explained 5% of the variation within overall plant community composition. Our results provide clear evidence on the role of Gopher Tortoise herbivory for the maintenance of plant diversity within species-rich longleaf pine forests of the southeastern United States, even across a single growing season.

Herbivory serves as a critical top-down mechanism within plant communities that regulates biodiversity, productivity, and ecosystem function (Pacala and Crawley, 1992; Terborgh, 2015; Moorhead et al., 2017; Mortensen et al., 2018). Herbivory often influences local-scale spatial ecology of plant communities via direct and indirect impacts (Pacala and Crawley, 1992). Herbivores regulate plant communities directly via consumption of plant biomass. Plant communities are impacted indirectly, however, through changes in resource availability by the removal of dominant, highly productive plant species by herbivores that may facilitate the establishment of rare or subordinate species, potentially increasing richness and community evenness (Pacala and Crawley, 1992; Holt et al., 1994; Becerra et al., 2009; Mortensen et al., 2018).

Herbivory by vertebrates in temperate ecosystems can reduce plant productivity, increase plant diversity, and alter lower trophic levels and soil chemistry (Sala et al., 1986; Ritchie et al. 1998; Schowalter, 2012; Wilson et al., 2012; Moorhead et al., 2017; Ramirez et al., 2021). In North American forests, high density of White-Tailed Deer (*Odocoileus virginianus*), a ruminant herbivore, is often strongly related to reductions in understory plant productivity, diversity, and tree recruitment (Ritchie et al., 1998; Shelton et al., 2014; Habeck and Schultz, 2015). Herbivory by mammals can also have cascading impacts on ecosystem function (Van Der Wal et al., 2004; Moorhead et al., 2017; Ramirez et al., 2021). For example, even small mammal consumption and redistribution of plant biomass have been shown to alter woody biomass and plant community composition, leading to indirect effects on plant tissue chemistry and soil enzyme activities (Moorhead et al., 2017). Although ecological impacts of mammalian and insect herbivores have garnered much attention in the literature (Ritchie et al., 1998; Goheen et al., 2010; Wilson et al., 2012; Hodkinson, 2012), fewer studies have investigated the role of herbivorous reptiles in regulating plant community diversity and composition (King, 1996; Olesen and Valido, 2004; Fourqurean et al., 2010).

Herbivorous reptiles are relatively uncommon because of the physiological constraints imposed by ectothermy on thermoregulation and digestion of nutrient-poor plant materials. However, herbivorous reptiles can serve as the dominant herbivore in a variety of environments, such as arid deserts, forest canopies, tropical rain forests, and marine and freshwater aquatic systems, particularly on islands (Nagy and Shoemaker, 1975; Moll and Jansen, 1995; King, 1996; Olesen and Valido, 2003; Fourqurean et al., 2010; Lovich et al., 2018; Tapia et al., 2022). In the southeastern United States, herbivorous chelonians can be observed in both aquatic (e.g., *Pseudemys floridanus*, *Chelonia mydas*) and terrestrial (e.g., *Gopherus polyphemus*, *Terrapene carolina*) environments (Bonin et al., 2006; Fourqurean et al., 2010). However, we have a minimal understanding on the role of chelonian herbivores as regulators of plant community diversity and composition (Estill and Cruzan, 2001; Tuberville et al., 2005; Lovich et al., 2018).

Gopher Tortoises (*Gopherus polyphemus*) are herbivores found throughout the upland pine forests of the southeastern Coastal Plain in North America. Gopher Tortoise herbivory and burrow excavation increase habitat heterogeneity by altering light exposure, temperature, soil pH, soil moisture content, and distribution of nutrients in sandhill substrates (Diemer, 1986; Kaczor and Hartnett, 1990; Pike and Mitchell, 2013). Browsing Gopher Tortoises may remove dominant, palatable plant species and increase the relative abundance of rarer species (MacDonald and Mushinsky, 1988); thus, Gopher Tortoises may impact plant community composition and primary production, but there have only been a few attempts to document these impacts (Diemer, 1986; Breininger et al., 1991; McCoy et al., 2006).

Gopher Tortoise herbivory and burrowing provide frequent, low-intensity bouts of disturbance because of low metabolic costs within a relatively small home range (0.004–3.2 ha) (McRae et al., 1981; King, 1996; Guyer et al., 2012). Studies that quantify impacts of herbivory commonly deploy experiments that selectively exclude herbivores, control grazing intensity, or both (Ritchie et al., 1998; Hester et al., 2000; Habeck and Schultz, 2015). Exclusion experiments allow researchers to understand thresholds of grazing intensity, effects on primary productivity, herbivore–herbivore interactions, and impacts on biodiversity and whole-system

¹Corresponding author. E-mail: robin.lloyd@mail.utoronto.ca
DOI: 10.1670/22-067

dynamics (Noy-Meir, 1975; Mitchell and Kirby, 1990; Milchunas and Lauenroth, 1993; Ritchie et al., 1998; Hester et al., 2000; Fourqurean et al., 2010; Habeck and Schultz, 2015; Richardson and Stiling, 2019; Tapia et al., 2022). In the case of Gopher Tortoises, Richardson and Stiling (2019) completed a 2-yr tortoise exclusion on coastal Florida shrubland islands devoid of mammalian herbivores and found a reduction in both plant richness and species diversity with Gopher Tortoise exclusion. Species-rich upland longleaf pine forest provides an ideal system to test how the removal of low-intensity, frequent disturbance by a reptilian herbivore affects 1) univariate measures of richness, evenness, and diversity; 2) aboveground plant community production; and 3) overall effects on plant community composition. We hypothesized that Gopher Tortoise exclusion would increase aboveground plant production, but reduce plant richness, evenness, and diversity as fast-growing, dominant species quickly respond to removal of herbivory. Therefore, a significant shift in overall plant community composition between access and enclosure plots was expected.

MATERIALS AND METHODS

Study Site.—Our study was conducted at Splinter Hill Bog (31.02189897°N, 87.69123339°W; WGS84), a property managed by The Nature Conservancy and located in northern Baldwin County, Alabama. Splinter Hill Bog covers 849.8 ha of wet and dry (sandhill) pine forest communities with sandy-loamy soils. The climate is classified as humid subtropical with hot, humid summers, cold-to-mild winters, and a growing season of 260 d from 5 March to 20 November (Gallup, 1980). In preliminary surveys, active Gopher Tortoise burrows were observed in a large portion of dry sandhill habitats. These habitats are characterized by a semi-open canopy (*Pinus palustris* and *Pinus taeda*) with an understory dominated by grasses (*Andropogon*, *Sorghastrum*, and *Bulbostylis* spp.), herbaceous vines (*Smilax*, *Gelsemium*, and *Ipomoea* spp.), ferns (*Pteridium* spp.), and tree seedlings (*Pinus* and *Quercus* spp.).

Our study focused on a small Gopher Tortoise population at Splinter Hill Bog. During a multivisit consensus survey from April to October 2019 across approximately 2–3 ha of sandhill longleaf pine forest habitat, the population had 27 burrows, including 17 adult burrows (>18-cm burrow width) and 10 juvenile burrows (<18-cm burrow width), based on the classification of Landers et al. (1982). Twenty-three of the 27 burrows were active and exhibited signs of recent tortoise activity (e.g., fresh tracks in the burrow entrance, devoid of leaf litter, spider webs). We estimated that the population was comprised of approximately 10–15 adults, with close to 5 juveniles based on estimations from active burrows (Stober and Smith, 2010).

Herbivore Exclusion Experiment.—In January 2019, 10 active adult burrows were randomly selected as center points for paired access and tortoise exclusion plots (1 × 1 m). Plots were set up permanently for future long-term monitoring of plant communities. Vegetation plots were established during the extended period of dormancy for both tortoises and plants with minimal percent plant cover. Access and enclosure plot locations were randomly selected by angle degree (0–180) in the front-facing direction of each burrow (no plots were placed behind burrow entrances) and distance (3–5 m) from the mouth of each focal burrow. Each enclosure plot consisted of a 20-ga, 2.5-cm mesh chicken wire that was 75 cm high and secured flush with the ground by 1-m-long metal stakes. Each access plot was delineated with four 1-m metal stakes, but no fencing (Figure S1). The short height and intermediate

mesh size of enclosure plot fencing allowed other herbivores, both large (e.g., White-Tailed Deer) and small (e.g., rodents, rabbits), to enter the exclusion plots while excluding Gopher Tortoises, which was confirmed with motion- and heat-activated camera traps (model 119874C, Bushnell). We documented Gopher Tortoises foraging in 9 of the 10 access plots, and Gopher Tortoises represented 85% of all herbivores observed in access plots. No Gopher Tortoises were observed inside enclosure plots; however, we did observe White-Tailed Deer and Eastern Cottontail Rabbits (*Sylvilagus floridanus*) in enclosure plots.

Data Collection.—Vegetation plots were surveyed in April (24 April 2019–8 May 2019), June (25 June 2019–10 July 2019), August (17 August 2019–28 August 2019), and October 2019 (22 September 2019–6 October 2019). We identified all species present and then visually estimated the percent cover of individual species (to the nearest 0.5%) in each plot. We calculated species richness, evenness as Pielou's evenness index [$J' = \frac{H'}{H'_{max}}$], and their combined effect as Shannon diversity [$H' = -\sum_{i=1}^S p_i \ln p_i$]. We summed all plant species cover as a proxy measurement of plant productivity. As an additional proxy measurement of plant productivity, we measured the height (in centimeters) of every plant in each plot and calculated an average height (ground level to the tallest vegetation) per plot.

Statistical Analysis.—All analyses were conducted using R 3.6.0 (R Development Core Team, 2020) and RStudio 1.2.1335 (R Studio Team, 2019), with relevant packages cited below. To test for differences in plant richness, evenness, diversity, total plant cover, and height across the growing season, we constructed a linear mixed-effects model using the *lmer* function in the *lme4* package (Bates et al., 2015). Within our model, herbivore exclusion, survey month, and their interaction were treated as fixed effects and plot was nested within plot pairing to account for repeated measures and spatial variation of our site. We performed a Wald test to assess the significance of fixed effects by using the *Anova* function (Fox and Weisberg, 2019). We plotted modeled parameter estimates of the herbivore exclusion treatment after accounting for random effects by using the *effects* package (Fox and Weisberg, 2019) with the *ggplot2* package (Wickham, 2016).

We used a permutational multivariate analysis of variance (PERMANOVA) to examine differences in plant species composition because of herbivore exclusion, sampling date, plot pairing, which accounts for heterogeneity in spatial structure across paired plots across our field site, and their interactions by using the *Adonis* function in the *vegan* package (Oksanen et al., 2013). We also performed a PERMANOVA, by using a Bray–Curtis dissimilarity metric (Bray and Curtis, 1957), to explore the combined effect of species abundance changes and turnover within plots. Finally, we visualized the results of PERMANOVA by using nonmetric multidimensional scaling (NMDS) via the *metaMDS* function in the *vegan* package.

To understand the contribution of each plant species to compositional change in response to tortoise exclusion, we conducted a similarity percentage analysis by using the *simper* function in the *vegan* package. The *simper* function calculates the contribution of each species to differences in Bray–Curtis distance between treatment groups and calculates the average abundance per group. The similarity percentage analysis generates a permutation *P*-value based on the probability of getting a larger or equal average contribution in random permutation of the group factor. We conducted 99 permutations during the similarity percentage analysis.

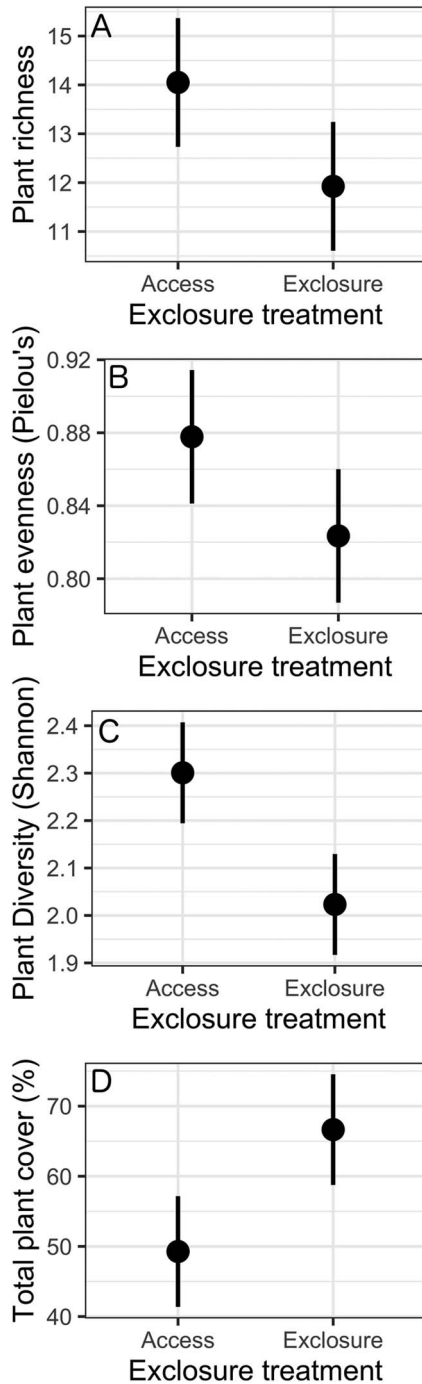


FIG. 1. Model-predicted coefficients for plant species richness (A), plant evenness (B), plant diversity (C), and total plant cover (D) from Gopher Tortoise exclusions and access (control) plots. Modeled coefficients are from linear-mixed effects models after accounting for random effects; error bars reflect 95% confidence intervals.

RESULTS

Plant Richness, Evenness, and Diversity.—We observed a total of 41 plant species in our 20 plots across the four sampling periods (Tables S1, S2). We found that tortoise exclusion led to a 15% reduction in plant richness ($\chi^2 = 6.674$; $df = 1$, $P = 0.01$; Fig. 1A), which equates to the loss of approximately two species per plot, although species identities differed by exclusion plot (Table S1, S2). In addition, we observed a significant exclusion \times sampling period interaction ($\chi^2 = 10.72$; $df = 3$, $P = 0.013$), indicating that

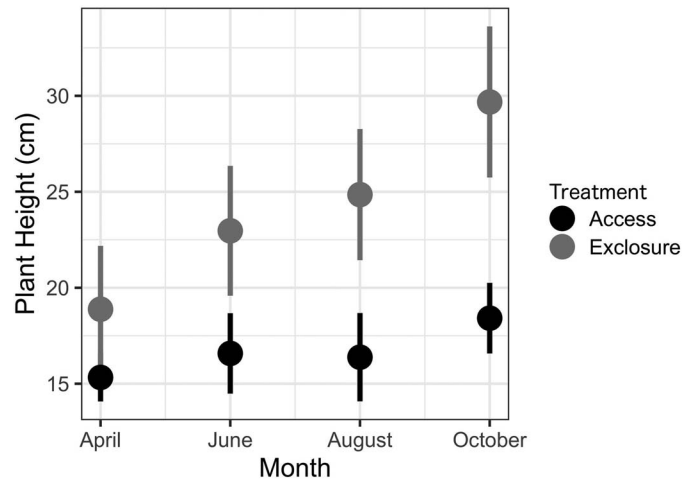


FIG. 2. Average plant height (cm) over the 2019 growing season in Gopher Tortoise access (black) and exclusion (gray) plots. Each point represents the average of 10 plants during a survey period; error bars reflect 95% confidence intervals.

the effect of tortoise exclusion on plant species richness became more pronounced as the growing season progressed. Tortoise exclusion also led to a 6% reduction in plant evenness ($\chi^2 = 5.657$; $df = 1$, $P = 0.02$; Fig. 1B). We observed a 12% reduction in Shannon diversity because of tortoise exclusion ($\chi^2 = 19.62$; $df = 1$, $P < 0.0001$; Fig. 1C). We found no evidence that tortoise exclusion impacted plant evenness ($\chi^2 = 2.669$; $df = 3$, $P = 0.19$; Table S3) or diversity ($\chi^2 = 2.667$; $df = 3$, $P = 0.45$) differently across sampling periods, that is, no significant interaction effect. Thus, reduction of plant diversity following Gopher Tortoise exclusion is the result of a simultaneous loss in plant richness and shifts in the dominance of species within our plots.

Total Relative Plant Cover and Height.—Tortoise exclusion led to a 35% increase in total cover within our plots ($\chi^2 = 9.627$; $df = 1$, $P = 0.002$; Fig. 1D; Table S3), an effect that became stronger throughout the growing season (exclusion \times sampling period: $\chi^2 = 14.45$; $df = 3$, $P = 0.002$). Similarly, excluding Gopher Tortoises increased average plant height by 45% ($\chi^2 = 17.912$; $df = 1$, $P < 0.0001$; Table S4) and that effect became stronger through time ($\chi^2 = 35.010$; $df = 1$, $P < 0.0001$; Figs. 2, S2; Table S3).

Community Composition.—Overall, Gopher Tortoise exclusion had a weak, albeit significant, effect on plant community composition, accounting for approximately 5% of the observed variation of community composition (Figs. 3, S3; Tables 1, S4, S5). Plot pairing, that is, spatial heterogeneity across our field site, explained the highest amount of variation ($\sim 48\%$) in plant community composition (Table 1), and the interaction between tortoise exclusion and plot location explained an additional 22% of the variation in plant community composition (Table 1). The significant interaction term indicates the effect of Gopher Tortoise herbivory differed across the spatial layout of our plots (Fig. 3; Table 1). Sampling period explained approximately 3% of the variation in plant composition, suggesting we had limited shift in overall community composition within a plot across the growing season (Table 1). The change in plant composition across the growing season did not interact with tortoise exclusion (Table 1); however, we did find that change in composition across the growing season weakly interacted with plot pairing, that is, the spatial heterogeneity of our field site (Table 1).

Our similarity percentage (SIMPER) analysis and NMDS revealed that *Sorghastrum secundum* ($P = 0.04$), *Geobalanus*

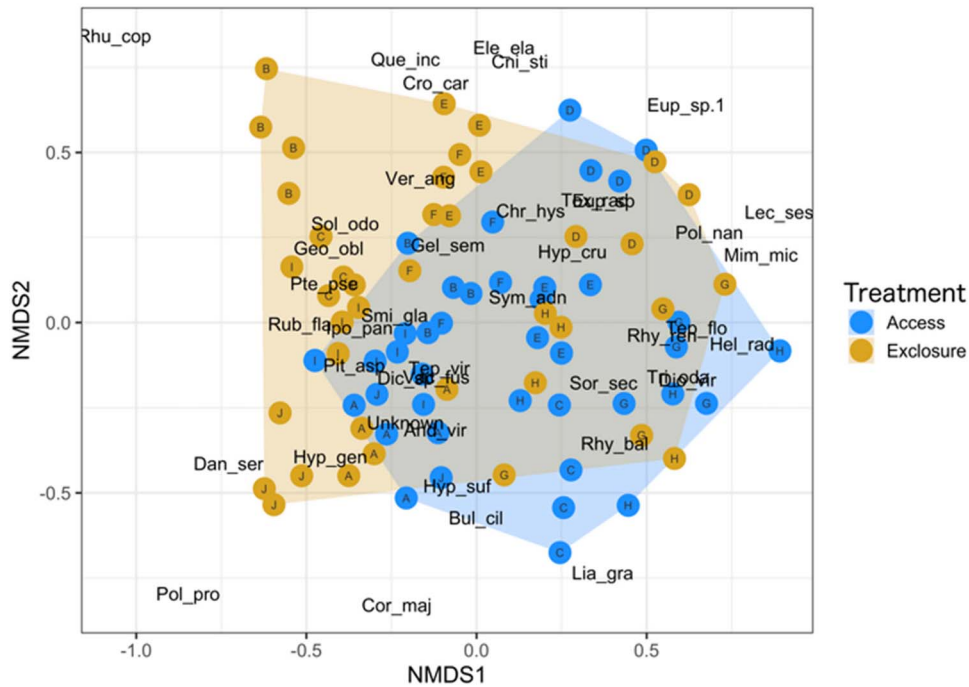


FIG. 3. Nonmetric multidimensional scaling of Bray-Curtis dissimilarities (abundance-weighted) for Gopher Tortoise access (blue) and exclusion plots (gold) during October 2019. Reference Table S5 for species abbreviations in figure.

oblongifolius ($P = 0.02$), *Pteridium pseudocaudatum* ($P = 0.01$), and *Toxicodendron radicans* ($P = 0.01$) were significantly more abundant within the exclusion plots relative to the access plots and contributed most to changes in compositional differences between access and exclusion plots (Figs. 3, S3; Table S6).

DISCUSSION

Following a single growing season of Gopher Tortoise exclusion, we found a 35% increase in total plant cover, 45% increase in plant height, 15% reduction in plant species richness, and 12% reduction in plant diversity. Although short-term, Gopher Tortoise exclusion had measurable impacts on the understory plant communities of the heterogeneous, highly diverse upland pine forests. Our results also suggest that Gopher Tortoise exclusion led to an increase in small stature woody species (*G. oblongifolius* and *T. radicans*), grasses (*S. secundum*), and ferns (*P. pseudocaudatum*), many

of which are known dietary components of Gopher Tortoises (MacDonald and Mushinsky, 1988; Mushinsky et al., 2003). Our results suggest that the persistence of Gopher Tortoises may be useful for maintaining the heterogeneous and biodiverse understory plant assemblages of coastal upland pine forests (Kaczor and Hartnett, 1990; Breining et al., 1991; McCoy et al., 2006).

The effects of tortoise exclusion on plant richness and diversity over 6 mo are comparable with longer term studies in scrub-shrub habitats (Richardson and Stiling, 2019). After 2 yr of Gopher Tortoise exclusion in a coastal Florida shrubland, Richardson and Stiling (2019) found a 37% reduction in plant richness (nine plant species total) and a 38% reduction in Gini-Simpson diversity. Although our 15% reduction in richness and 12% in plant diversity were approximately half the effect size found by Richardson and Stiling (2019), we suspect that future studies will reveal that effects of tortoise exclusion will increase with time. Significant impacts of herbivore exclusion experiments after 1 yr of exclusion are rare in the literature, and significant effects build up after multiple years (Shelton et al., 2014; Moorhead et al., 2017; Frank et al., 2018; Schäfer et al., 2019; Bloodworth et al., 2020). In longleaf pine forests in southern Alabama, White-Tailed Deer exclusion had no effect on plant diversity and cover after 4 yr of exclusion (Brockway and Lewis, 2003). As a potential working hypothesis to explain the differences between Gopher Tortoise and mammal exclusion, most mammalian herbivores have significantly larger home ranges relative to Gopher Tortoises. For example, White-Tailed Deer have home ranges up to 1,000 ha and Eastern Cottontail Rabbits have home ranges of 4–8 ha, whereas Gopher Tortoise home ranges are typically limited to 0.004–3.2 ha (Trent and Rongstad, 1974; Bowers, 1993; Gálvez-Bravo et al., 2011; Guyer et al., 2012). The strong effects of Gopher Tortoise exclusion may be driven by the more concentrated impacts of Gopher Tortoise herbivory relative to the diffuse impacts of grazing mammals (McRae et al., 1981; Bowers, 1993).

TABLE 1. Plant community composition as affected by tortoise exclusion (trt); plot-level variation (pair); sampling period (rep); and interactions among tortoise exclusion, plot spatial structure, and sampling period. PERMANOVAs were conducted with 999 permutations by using the Bray-Curtis (abundance-weighted) dissimilarity index on estimated plant cover. Significance codes: 0 "****" 0.001 "***" 0.01.

	df	F.Model	R ²	P	
trt	1	14.4561	0.0483	0.001	***
pair	9	16.1077	0.4852	0.001	***
rep	1	10.2576	0.0343	0.001	***
trt:pair	9	7.4666	0.2244	0.001	***
trt:rep	1	0.9727	0.0033	0.471	
pair:rep	9	1.4154	0.0454	0.010	**
trt:pair:rep	9	0.9816	0.0295	0.526	
Residuals	40		0.1336		
Total	79		1.0000		

We found that plot spatial location, or site-level spatial heterogeneity, explained 48% of the variation in plant community composition, substantially more than tortoise exclusion, which explained approximately 5% of plant community variation. Comparing across all plots, plant species richness ranged between 7 and 24 individual species and percent cover varied between 0.5 and 55% coverage, yielding high amounts of spatial heterogeneity among our plots. We found that 24% of observed plant species were found in only one or two plots, and only 13 species were found in more than half of our plots. High spatial heterogeneity is commonly reported within understory communities of upland longleaf pine forests (Drew et al., 1998; Kirkman et al., 2001; Agrawal et al., 2006; Mitchell et al., 2006; Blaustein, 2008).

Although Gopher Tortoises directly impact plant assemblages by defoliation, they also influence plants by burrow excavation, urine and feces deposition, and routine trampling of vegetation during foraging and frequent burrow-to-burrow migrations (Diemer, 1986; Kaczor and Hartnett, 1990; Pike and Mitchell, 2013). The small size of our exclosures (1 m²) likely fails to account for the full impacts of Gopher Tortoises on understory plant communities. Larger exclosures may be better equipped to assess impacts other than direct ingestion of plant material, coupled with experimental manipulation to isolate and quantify impacts of alternative disturbances, such as trampling effects, nutrient deposition, and burrow construction. In other herbivore species that live in social networks and burrow systems, large areas are used in quantifying impacts to the surrounding plant communities and not necessarily herbivore exclusion. For example, European rabbits (*Oryctolagus cuniculus*) and their warren (burrow) systems were used to show that rabbit activity promoted vegetation productivity and diversity by increases in soil disturbance and resources provided by latrines in (15.5-m²) open influence areas (Gálvez-Bravo et al., 2011). Similarly, Gopher Tortoises have a life history that relies on complex interacting social networks and frequent movements among multiple burrows that require a larger area to assess the full impacts of how these reptiles impact the forest floor understory (McRae et al., 1981; Boglioli et al., 2003; Guyer et al., 2012).

We found that exclusion of Gopher Tortoise herbivory had effects on plant diversity and productivity that are like large and small mammalian herbivores. Although reptilian herbivores are relatively rare in most ecosystems and have been traditionally underrepresented in the herbivory literature, some studies have shown reptilian herbivory to impact arid deserts (Nagy and Shoemaker, 1975), tropical rain forests (Moll and Jansen, 1995), and coastal upland forest (King, 1996; Olesen and Valido, 2003) through seed dispersal, pollination, increases in diversity, and alterations in plant biomass. Future studies should investigate the role of Gopher Tortoises in maintaining biodiversity of longleaf pine understories in comparison with other commonly used management strategies, such as prescribed burning (Pacala and Crawley, 1992). Gopher Tortoises may work in conjunction with fire to promote and maintain biodiversity in the understory of longleaf pine ecosystems. Although arguments for Gopher Tortoises as a keystone species have largely focused on the animal assemblages that access Gopher Tortoise burrows (Guyer and Bailey, 1993; Catano and Stout, 2015), our results suggest that Gopher Tortoises have a role as regulators of plant diversity and productivity through herbivory as well. Gopher Tortoises may be important in maintaining the productivity and diversity of longleaf pine understory communities; however, human development and habitat loss are having negative effects on Gopher Tortoise populations throughout their range. Our results highlight the

importance of continued protections and conservation efforts for Gopher Tortoises in the southeastern United States.

Acknowledgments.—We thank the University of South Alabama Biology Department, Alabama Audubon, and the Gopher Tortoise Council for financial support. We thank the Nature Conservancy for access to the Splinter Hill Bog Nature Preserve and W. Barger at the Alabama Department of Conservation and Natural Resources for assistance with plant species identification. Finally, we owe many thanks to the following field technicians: C. Adams, A. Allen, C. Baggett, C. Barnes, M. Boudreaux, M. Broome, D. Dean, S. Kerr, B. Meador, E. Melby, C. Smelley, P. Walston, and R. Well.

LITERATURE CITED

- AGRAWAL, A. A., J. A. LAU, AND P. A. HAMBÄCK. 2006. Community heterogeneity and the evolution of interactions between plants and insect herbivores. *Quarterly Review of Biology* 81:349–376.
- BATES, D., M. MÄCHLER, B. BOLKER, AND S. WALKER. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- BECERRA, J. X., K. NOGE, AND D. L. VENABLE. 2009. Macroevolutionary chemical escalation in an ancient plant–herbivore arms race. *Proceedings of the National Academy of Sciences of the United States of America* 106:18062–18066.
- BLAUSTEIN, R. J. 2008. Biodiversity hotspot: the Florida panhandle. *BioScience* 58:784–790.
- BLOODWORTH, K. J., M. E. RITCHIE, AND K. J. KOMATSU. 2020. Effects of white-tailed deer exclusion on the plant community composition of an upland tallgrass prairie ecosystem. *Journal of Vegetation Science* 31:899–907.
- BOGLIOLI, M. D., C. GUYER, AND W. K. MICHENER. 2003. Mating opportunities of female gopher tortoises, *Gopherus polyphemus*, in relation to spatial isolation of females and their burrows. *Copeia* 2003:846–850.
- BONIN, F., B. DEVAUX, AND A. DUPRÉ. 2006. *Turtles of the World*. Johns Hopkins University Press, USA.
- BOWERS, M. A. 1993. Influence of herbivorous mammals on an old-field plant community: years 1–4 after disturbance. *Oikos* 67:129–141.
- BRAY, J. R., AND J. T. CURTIS. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27:326–349.
- BREININGER, D. R., P. A. SCHMALZER, AND C. R. HINKLE. 1991. Estimating occupancy of Gopher Tortoise (*Gopherus polyphemus*) burrows in coastal scrub and slash pine flatwoods. *Journal of Herpetology* 25:317–321.
- BROCKWAY, D. G., AND C. E. LEWIS. 2003. Influence of deer, cattle grazing and timber harvest on plant species diversity in a longleaf pine bluestem ecosystem. *Forest Ecology and Management* 175:49–69.
- CATANO, C. P., AND J. J. STOUT. 2015. Functional relationships reveal key-stone effects of the gopher tortoise on vertebrate diversity in a longleaf pine savanna. *Biodiversity and Conservation* 24:1957–1974.
- DIEMER, J. E. 1986. The ecology and management of the Gopher Tortoise in the southeastern United States. *Herpetologica* 42:125–133.
- DREW, M. B., L. K. KIRKMAN, AND A. K. GHOLSON, JR. 1998. The vascular flora of Ichauway, Baker County, Georgia: a remnant longleaf pine/wiregrass ecosystem. *Castanea* 63:1–24.
- ESTILL, J. C., AND M. B. CRUZAN. 2001. Phylogeography of rare plant species endemic to the southeastern United States. *Castanea* 66:3–23.
- FOURQUREAN, J. W., S. MANUEL, K. A. COATES, W. J. KENWORTHY, AND S. R. SMITH. 2010. Effects of excluding sea turtle herbivores from a seagrass bed: overgrazing may have led to loss of seagrass meadows in Bermuda. *Marine Ecology Progress Series* 419:223–232.
- FOX, J., AND S. WEISBERG. 2019. *An R Companion to Applied Regression*. 3rd ed. Sage, USA.
- FRANK, G. S., R. A. RATHFON, AND M. R. SAUNDERS. 2018. Ten-year responses of underplanted northern red oak to silvicultural treatments, herbivore exclusion, and fertilization. *Forests* 9:571.
- GÁLVEZ-BRAVO, L., A. LÓPEZ-PINTOR, S. REBOLLO, AND A. GÓMEZ-SAL. 2011. European rabbit (*Oryctolagus cuniculus*) engineering effects promote plant heterogeneity in Mediterranean dehesa pastures. *Journal of Arid Environments* 75:779–786.
- GALLUP, J. R. 1980. Climatic features and length of growing season in Alabama. *Bulletin of the Agricultural Experiment Station*, Auburn University, USA.

- GOHEEN, J. R., T. M. PALMER, F. KEESING, C. RIGINOS, AND T. P. YOUNG. 2010. Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. *Journal of Animal Ecology* 79:372–382.
- GUYER, C., AND M. A. BAILEY. 1993. Amphibians and reptiles of longleaf pine communities. *Proceedings of the Tall Timbers Fire Ecology Conference* 18:139–158.
- GUYER, C., V. M. JOHNSON, AND S. M. HERMANN. 2012. Effects of population density on patterns of movement and behavior of Gopher Tortoises (*Gopherus polyphemus*). *Herpetological Monographs* 26:122–134.
- HABECK, C. W., AND A. K. SCHULTZ. 2015. Community-level impacts of white-tailed deer on understory plants in North American forests: a meta-analysis. *AoB Plants* 7:plv119.
- HESTER, A. J., L. EDENIUS, R. M. BUTTENSCHÖN, AND A. T. KUITERS. 2000. Interactions between forests and herbivores: the role of controlled grazing experiments. *Forestry* 73:381–391.
- HODKINSON, I. 2012. *Insect Herbivory*. Springer Science and Business Media, The Netherlands.
- HOLT, R. D., J. GROVER, AND D. TILMAN. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist* 144:741–771.
- KACZOR, S. A., AND D. C. HARTNETT. 1990. Gopher tortoise (*Gopherus polyphemus*) effects on soils and vegetation in a Florida sandhill community. *American Midland Naturalist* 123:100–111.
- KING, G. M. 1996. *Reptiles and Herbivory*. Springer Science and Business Media, The Netherlands.
- KIRKMAN, L. K., R. MITCHELL, R. C. HELTON, AND M. B. DREW. 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. *American Journal of Botany* 88:2119–2128.
- LANDERS, J. L., W. A. McRAE, W. A. McRAE, AND J. A. GARNER. 1982. Growth and maturity of the gopher tortoise in southwestern Georgia. *Bulletin of the Florida State Museum* 27:82–110.
- LOVICH, J. E., J. R. ENNEN, M. AGHA, AND J. W. GIBBONS. 2018. Where have all the turtles gone, and why does it matter? *BioScience* 68:771–781.
- MACDONALD, L. A., AND H. R. MUSHINSKY. 1988. Foraging ecology of the Gopher Tortoise, *Gopherus polyphemus*, in a sandhill habitat. *Herpetologica* 44:345–353.
- MCCOY, E. D., H. R. MUSHINSKY, AND J. LINDZEY. 2006. Declines of the gopher tortoise on protected lands. *Biological Conservation* 128:120–127.
- McRAE, W. A., J. L. LANDERS, AND J. A. GARNER. 1981. Movement patterns and home range of the gopher tortoise. *American Midland Naturalist* 106:165–179.
- MILCHUNAS, D. G., AND W. K. LAUENROTH. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63:327–366.
- MITCHELL, F. J. G., AND K. J. KIRBY. 1990. The impact of large herbivores on the conservation of semi-natural woods in the British uplands. *Forestry* 63:333–353.
- MITCHELL, R. J., J. K. HIERS, J. J. O'BRIEN, S. B. JACK, AND R. T. ENGSTROM. 2006. Silviculture that sustains: the nexus between silviculture, frequent prescribed fire, and conservation of biodiversity in longleaf pine forests of the southeastern United States. *Canadian Journal of Forest Research* 36:2724–2736.
- MOLL, D., AND K. P. JANSEN. 1995. Evidence for a role in seed dispersal by two tropical herbivorous turtles. *Biotropica* 27:121–127.
- MOORHEAD, L. C., L. SOUZA, C. W. HABECK, R. L. LINDROTH, AND A. T. CLASSEN. 2017. Small mammal activity alters plant community composition and microbial activity in an old-field ecosystem. *Ecosphere* 8:e01777.
- MORTENSEN, B., B. DANIELSON, W. S. HARPOLE, J. ALBERTI, C. A. ARNILLAS, L. BIEDERMAN, E. T. BORER, M. W. CADOTTE, J. M. DWYER, AND N. HAGENAH. 2018. Herbivores safeguard plant diversity by reducing variability in dominance. *Journal of Ecology* 106:101–112.
- MUSHINSKY, H. R., T. A. STILSON, AND E. D. MCCOY. 2003. Diet and dietary preference of the juvenile Gopher Tortoise (*Gopherus polyphemus*). *Herpetologica* 59:475–483.
- NAGY, K. A., AND V. H. SHOEMAKER. 1975. Energy and nitrogen budgets of the free-living desert lizard *Sauromalus obesus*. *Physiological Zoology* 48:252–262.
- NOY-MEIR, I. 1975. Stability of grazing systems: an application of predator-prey graphs. *Journal of Ecology* 63:459–481.
- OKSANEN, J., F. G. BLANCHET, R. KINDT, P. LEGENDRE, P. R. MINCHIN, R. B. O'HARA, G. L. SIMPSON, P. SOLYMOS, M. H. H. STEVENS, AND H. WAGNER. 2013. Package 'vegan.' Community ecology package, version 2.1–295.
- OLESEN, J. M., AND A. VALIDO. 2003. Lizards as pollinators and seed dispersers: an island phenomenon. *Trends in Ecology and Evolution* 18:177–181.
- OLESEN, J. M., AND A. VALIDO. 2004. Lizards and birds as generalized pollinators and seed dispersers of island plants. Pp. 229–249 in J. M. Fernández-Palacios and C. Morici (eds.), *Ecología Insular/Island Ecology*. Centro Universitario de Estudios Sociales, Spain.
- PACALA, S. W., AND M. J. CRAWLEY. 1992. Herbivores and plant diversity. *American Naturalist* 140:243–260.
- PIKE, D. A., AND J. C. MITCHELL. 2013. Burrow-dwelling ecosystem engineers provide thermal refugia throughout the landscape. *Animal Conservation* 16:694–703.
- RAMIREZ, J. I., P. A. JANSEN, J. DEN OUDEN, L. MOKTAN, N. HERDOIZA, AND L. POORTER. 2021. Above-and below-ground cascading effects of wild ungulates in temperate forests. *Ecosystems* 24:153–167.
- R DEVELOPMENT CORE TEAM. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Austria. Available at: <https://www.R-project.org/>.
- R STUDIO TEAM. 2019. RStudio: Integrated Development for R. Available at: <https://www.rstudio.com/products/rstudio>.
- RICHARDSON, J. C., AND P. STILING. 2019. Gopher tortoise herbivory increases plant species richness and diversity. *Plant Ecology* 220:383–391.
- RITCHIE, M. E., D. TILMAN, AND J. M. H. KNOPS. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* 79:165–177.
- SALA, O. E., M. OESTERHELD, R. J. C. LEÓN, AND A. SORIANO. 1986. Grazing effects upon plant community structure in subhumid grasslands of Argentina. *Vegetatio* 67:27–32.
- SCHÄFER, D., D. PRATI, P. SCHALL, C. AMMER, AND M. FISCHER. 2019. Exclusion of large herbivores affects understory shrub vegetation more than herb vegetation across 147 forest sites in three German regions. *PLoS One* 14:e0218741.
- SCHOWALTER, T. D. 2012. Insect herbivore effects on forest ecosystem services. *Journal of Sustainable Forestry* 31:518–536.
- SHELTON, A. L., J. A. HENNING, P. SCHULTZ, AND K. CLAY. 2014. Effects of abundant white-tailed deer on vegetation, animals, mycorrhizal fungi, and soils. *Forest Ecology and Management* 320:39–49.
- STOBER, J. M., AND L. L. SMITH. 2010. Total counts versus line transects for estimating abundance of small gopher tortoise populations. *Journal of Wildlife Management* 74:1595–1600.
- TAPIA, W., H. B. GOLDSPIEL, AND J. P. GIBBS. 2022. Introduction of giant tortoises as a replacement “ecosystem engineer” to facilitate restoration of Santa Fe Island, Galapagos. *Restoration Ecology* 30:p.e13476.
- TERBORGH, J. W. 2015. Toward a trophic theory of species diversity. *Proceedings of the National Academy of Sciences of the United States of America* 112:11415–11422.
- TRENT, T. T., AND O. J. RONGSTAD. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. *Journal of Wildlife Management* 38:459–472.
- TUBERVILLE, T. D., J. D. WILLSON, M. E. DORCAS, AND J. W. GIBBONS. 2005. Herpetofaunal species richness of southeastern national parks. *Southeastern Naturalist* 4:537–569.
- VAN DER WAL, R., R. D. BARDGETT, K. A. HARRISON, AND A. STIEN. 2004. Vertebrate herbivores and ecosystem control: cascading effects of faeces on tundra ecosystems. *Ecography* 27:242–252.
- WICKHAM, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, USA.
- WILSON, J. B., R. K. PEET, J. DENGLER, AND M. PÄRTEL. 2012. Plant species richness: the world records. *Journal of Vegetation Science* 23:796–802.

Accepted: 3 September 2023.

Published online: 12 December 2023.

SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online at <http://dx.doi.org/10.1670/22-067.s1>.