Plant Ecol (2019) 220:383–391
https://doi.org/10.1007/s11258-019-00921-4

Gopher tortoise herbivory increases plant species richness and diversity

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Received: 31 May 2018 / Accepted: 20 February 2019 / Published online: 25 February 2019

Abstract Mammalian herbivores often alter plant species richness and diversity, but such impacts have not been much investigated in reptiles. This study examined the effects of gopher tortoise (*Gopherus polyphemus*) herbivory on species richness, Gini-Simpson diversity, and dominance, plant abundance, and biomass. Tortoise herbivory was eliminated in five areas through the use of exclosure plots for a period of two years and was compared to five similar areas where tortoises were allowed to feed. Cafeteria feeding trials were also used to quantify dietary preference. Tortoise exclosure plots had lowered species richness, and significantly lowered diversity, but significantly higher dominance than in controls. *Heliotropium polyphyllum,* the most highly preferred local species by tortoises, was the most dominant plant in exclosure and control plots and became even more dominant in exclosure plots. The abundance and biomass of the next two most common plant species, *Fimbristylis cymosa* and *Polypremum procumbens*, which are not preferred by tortoises, were reduced in the exclosures, probably due to increased competition with *Heliotropium*. Several rare plant species were eliminated in the exclosure plots. We conclude that tortoise herbivory may directly influence plant community assembly by reducing preferred plant species and promoting the growth of non-preferred species.

Keywords Vertebrate herbivory · Plant diversity · Plant communities

Introduction

The relationship between vertebrate herbivores and plant forage species diversity has been investigated since the early 1900s (Tansley 1922). Exploring this relationship may help predict the response of plant communities to the loss of major vertebrate herbivores and the addition of new ones. The effects of some vertebrate herbivores have been considered equivalent to an intermediate disturbance that may facilitate high biodiversity levels by pruning back dominant plant species (Huntly 1987; McNaughton 1983; Rambo and Faeth 1999). However, this is not always the case, and vertebrate herbivory can also lead to local plant species extirpations or complete elimination of herbaceous understories (Coomes et al. 2003; Koerner et al. 2014). These effects have received much attention in

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Communicated by Christian Smit.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s11258-019-00921-4) contains supplementary material, which is available to authorized users.

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mammalian herbivores such as lagomorphs (Delibes-Mateos et al. 2008; Huntly 1987; Tansley 1922), ungulates (Augustine and McNaughton 1998; Goheen et al. 2007), gophers (Rogers et al. 2001), and elephants (Riginos and Grace 2008; Valeix et al. 2011).

However, attempts to quantify the effects of non-mammalian vertebrate herbivores on plants and plant communities are generally lacking, even though herbivory in such groups can be common. For example, chelonians, both aquatic and terrestrial, have a variety of herbivorous species, with many species of land tortoises being exclusively herbivorous. Fourqurean et al. (2010) has shown that sea turtles may reduce overall biomass on a monoculture of seagrass, and Griffiths et al. (2013) showed that grazing by Madagascan radiated tortoises (*Cylindraspis spp.*) heavily increased plant biomass, ground cover, and plant abundances.

The goal of this study was to assess the impact of gopher tortoise (*Gopherus polyphemus*) herbivory on plant abundance and biomass, species richness, and biodiversity through experimental exclosure, thereby simulating an absence of tortoises. Previous studies show that gopher tortoises may exert localized disturbances around their burrows (Boglioli et al. 2000), but these effects possibly extend further out. We hypothesized that plant abundance would increase in the absence of tortoises, but species richness and diversity would decrease as a result of lack of disturbances. This species was chosen because of its relatively large size, potential high densities, and ease of location due to the presence of large conspicuous burrows. These burrows provide central locations from which foraging events begin and end. We also looked at dietary preference among the five most common plant species found at the field site to determine if dietary preference may help explain any differences observed in the field.

Methods

Exclosure study site

Tortoise exclosure plots were set up on Egmont Key (27°35′24″N 82°45′46″W) off the west coast of Pinellas County, Florida. With the exception of the tortoises, no other terrestrial vertebrate herbivores (such as deer or rabbits) or granivores (such as rodents) are present on Egmont Key (Witmer et al. 2010). While a small number of Florida box turtles (*Terrapene carolina bauri*) are present on the island, we attribute the results presented in this study to gopher tortoises because box turtles diets tend not to be dominated by the green herbaceous material sought by gopher tortoises (Garner and Landers 1981; Liu et al. 2004; Macdonald and Mushinsky 1988). Box turtles are also smaller than gopher tortoises and not as abundant on Egmont Key (Personal Observation).

An open area was selected on Egmont Key with pine trees and other woody vegetation and with a relatively uniform ground cover. At least 15 active burrows (as defined by Mushinsky et al. (2006)) were seen in the area. The immediate surrounding areas were monocultures of 3–5-m-tall palms (Arecaceae) with the ground covered by shed palm fronds. As the areas dominated by palms are not ideal for the growth of herbaceous forage, we suspect tortoises whose burrows are in these areas enter the field site to forage. Tortoises were observed in the general area upon each visit and occasionally observed basking and feeding in the control plots. Scats were also frequently found in control plots and the areas surrounding the plots. Sand dunes and sandy beaches dominate the areas of the island beyond the palm monocultures. The only other open area we have witnessed is a manicured lawn outside the park ranger station ~ 0.5 km north of the field site.

Experimental design

The design consisted of five blocks each with three 2 m × 2 m treatments: (1) an exclosure consisting of four walls made from metal flashing; (2) a fenced control plot made from two perpendicular sides of flashing; and (3) an additional control delineated only by metal survey flags to account for any potential effects of the exclosure material. Each block was placed approximately 5 meters apart.

Plots were established on March 13, 2015 and we recorded plant counts per species at the start of the experiment, and every four months subsequent until March 17, 2017. For each census we counted the number of individuals (each stem was considered an individual in clonal species) and calculated five metrics: the total number of individuals across all species; species richness as a count of individual species; the Gini-Simpson index, measured as $1 - \sum_{i=1}^{s} p_i^2$ where p_i is the proportion of the total number of individuals that belong to species i and S is the number of species; and dominance, the number of individuals of the most abundant species divided by the total number of individuals. At the conclusion of the study, all plants were collected, split into aboveground and belowground sections, and weighed.

We also conducted a cafeteria-style dietary preference study utilizing captive tortoises at the Lowry Park Zoo (Tampa, FL) using the five most common species observed on Egmont Key (*Heliotropium polyphyllum*, *Fimbristylis cymosa*, *Polypremum procumbens*, *Waltheria indica*, and *Phyllanthus abnormis*). Equal amounts of aboveground plant material (by approximate volume) were weighed and presented at the same time to 8 tortoises individually. Tortoises were allowed to feed freely until they lost interest and did not ingest food for 15 min. Final masses for each plant were then obtained. Concurrently with each feeding trial, we had equal amounts of each plant outside the tortoise pen to account for evaporative water loss. The difference in mass obtained for these controls was added into the final weight for the plants consumed by tortoises to obtain the true mass lost from grazing.

Statistical analysis

As error distributions for each metric was non-normal (except for diversity), generalized linear mixed effects models (GLMMs), with the measured metric as a fixed effect and block number as a random effect, were used for all comparisons in the exclosure experiment. The distribution used for each comparison is listed in Table 2 in Appendix 1. We first tested for differences between the two control types (fenced and ground) for each of the five metrics measured. As none were found during any point in the experiment, these were collapsed into a single treatment for subsequent analyzes to increase sample size. This collapsed treatment is henceforth referred to as "control" (Table 3 in Appendix 2). Values for each metric were compared: (1) between exclosures and controls at the start of the experiment to ensure no differences were inherently present; (2) between the start and end for each treatment; and (3) between exclosures and controls at the end. Community structure between exclosures and controls were assessed using analysis of similarities (ANOSIM). Plant weights were compared between treatments using t tests.

To analyze dietary preference, we used Manly's α index without food replacement (Manly 1974). This index is calculated with the formula:

$$\frac{\ln\left(\frac{n_{i0}-r_i}{n_{i0}}\right)}{\sum_{j=1}^{m}\ln\left(\frac{n_{i0}-r_i}{n_{i0}}\right)}, \quad i = 1, \ldots, m,$$

where n_{i0} is the mass of food type i at the beginning of a foraging event, r_i is the mass consumed, and m is the number of food types. A plant species is considered a preferred part of the diet when α is greater than $1/m$, an avoided part of the diet when α is less than $1/m$, and randomly selected when α is equal to $1/m$. All analyzes were performed in R version 3.2.3 (R Development Core Team 2015). ANOSIM was conducted using the "vegan" package.

Results

Exclosures

Comparisons between the number of individual plants, species richness, diversity, and dominance did not significantly differ between controls and exclosures at the start of the experiment, and values for control plots did not differ between start and end (Table 1). The number of individual plants also did not significantly differ between controls and exclosures at the conclusion of the study.

Species richness dropped in exclosures where tortoises were not feeding, though this drop was not statistically significant ($\chi^2 = 2.7188$, $df = 1$, $p = 0.0991$. Similarly, at the conclusion of the study, species richness was lower in exclosure than in control plots, though not significantly so ($\chi^2 = 3.1325$, $df = 1$, $p = 0.0767$) (Table 1, Fig. 1a).

The Gini-Simpson diversity index values followed similar trends to that observed in species richness. In exclosures, diversity dropped overtime ($\chi^2 = 13.478$, $df = 1$, $p = 0.0002$) (Fig. 1b). Diversity was also significantly lower in exclosures than in controls at the end of the experiment ($\chi^2 = 37.097$, $df = 1$, $p < 0.0001$). As diversity dropped, dominance significantly increased in exclosures over time ($\chi^2 = 16.295$, $df = 1$, $p < 0.0001$) and also increased

Table 1 Comparisons between and within exclosures and controls at the beginning and end of the exclosure experiment

	Plot	Mean	SE	Plot	Mean	SE	χ^2	*p*
Number of individuals	Exclosure: start	206.75	67.28	Exclosure: end	217	71.67	0.012	0.911
	Control: start	260.88	61.09	Control: end	267	60.33	0.524	0.468
	Control: start	260.88	61.09	Exclosure: start	206.8	67.28	1.102	0.293
	Control: end	267	60.33	Exclosure: end	217	71.67	0.351	0.553
Richness	Exclosure: start	8	0.58	Exclosure: end	5	0.41	2.718	0.099
	Control: start	7.4	0.26	Control: end	7.8	0.35	0.131	0.717
	Control: start	7.4	0.26	Exclosure: start	8	0.58	0.137	0.771
	Control: end	7.8	0.35	Exclosure: end	5	0.41	3.132	0.076
Gini-Simpson index	Exclosure: start	0.67	0.04	Exclosure: end	0.38	0.064	13.478	< 0.001
	Control: start	0.62	0.04	Control: end	0.65	0.02	0.567	0.451
	Control: start	0.62	0.04	Exclosure: start	0.67	0.04	0.756	0.384
	Control: end	0.65	0.02	Exclosure: end	0.38	0.064	37.097	< 0.001
Dominance	Exclosure: start	0.5	0.05	Exclosure: end	0.77	0.05	16.295	< 0.001
	Control: start	0.49	0.05	Control: end	0.51	0.03	0.062	0.803
	Control: start	0.49	0.05	Exclosure: start	0.5	0.05	0.012	0.911
	Control: end	0.51	0.03	Exclosure: end	0.77	0.05	26.734	< 0.001

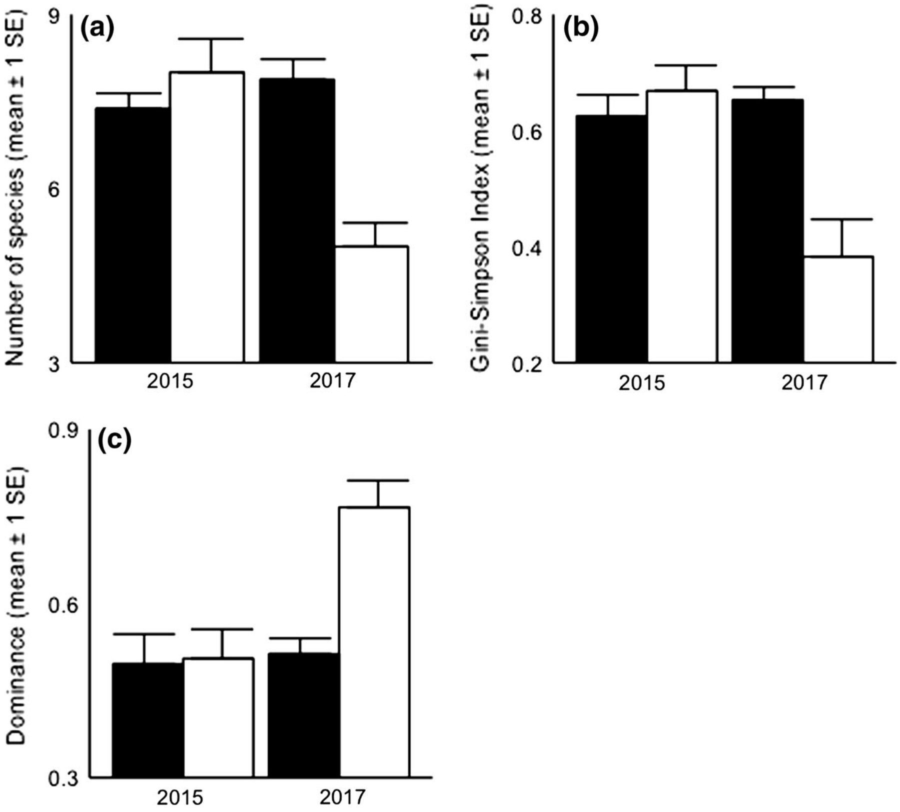

Fig. 1 Means (± 1 SE) for species richness (**a**), the Gini-Simpson diversity index (**b**), and species dominance (**c**) for controls plots (black) and exclosures (white). Species richness dropped and the Gini-Simpson index dropped significantly in tortoise exclosure plots through time, while dominance significantly increased

compared to control plots ($\chi^2 = 27.257$, $df = 1$, $p < 0.0001$) (Fig. 1d).

In both exclosure and control plots at the conclusion of the experiment, *Heliotropium polyphyllum* (Boraginaceae) was the most common species, even more so in exclosures (Fig. 2). *Fimbristylis cymosa* abundance in exclosure plots significantly dropped when compared to control plots ($\chi^2 = 9.2853$, $df = 1$, $p = 0.0020$), and the abundance of *Polypremum procumbens* was also reduced, although not significantly so ($\chi^2 = 0.5248$, $df = 1$, $p = 0.4688$). Several species appear to have been extirpated in tortoise exclosure plots: *Catharanthus roseus* (Apocynaceae), *Mecardonia acuminata* (Plantaginaceae), and *Paspalum setaceum* (Poaceae). Overall community structure as revealed by ANOSIM differed between exclosures and controls (R = 0.357, $p = 0.016$). Full presence/absence data can be found in the electronic supplementary material.

In terms of biomass, at the end of the experiment *H. polyphyllum* dominated aboveground and belowground biomass in exclosure plots. In fact the average belowground biomass of *H. polyphyllum* was much greater than the belowground biomass of all other species combined. Significant differences existed between the two treatments aboveground ($t = 2.738$, $p = 0.04$) but not belowground ($t = 1.598$, $p = 0.172$). In control plots, *F. cymosa* had the highest aboveground biomass, but did not differ significantly from exclosures $t = 1.661$, $p = 0.12$). While *P. procumbens* was the second most dominant plant in both plot types by number, its biomass was not as great as *F. cymosa* (Fig. 3).

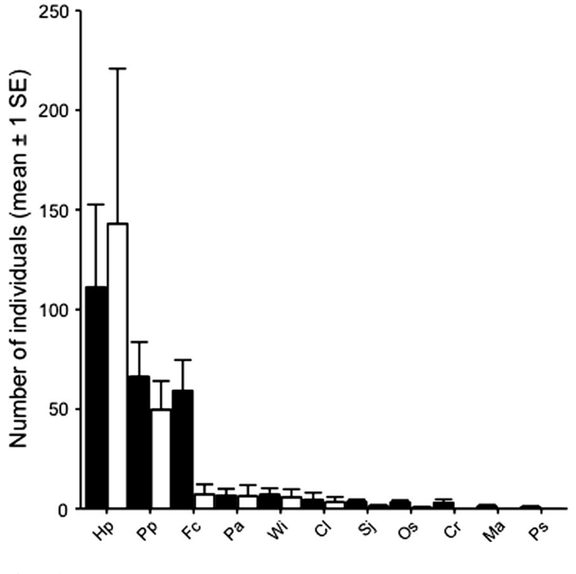

Fig. 2 In tortoise exclosure plots (white), *Heliotropium polyphyllum* became more abundant in comparison to control plots (black). Abundance of *Fimbristylis cymosa* drastically dropped in exclosures, and *Catharanthus roseus*, *Mecardonia acuminata*, and *Paspalum setaceum* were extirpated in exclosure plots. Species abbreviations are as follows: *Cr*, *Catharanthus roseus*; *Cl*, *Cyperus ligularis*; *Fc*, *Fimbristylis cymosa*; *Hp*, *Heliotropium polyphyllum*; *Ma*, *Mecardonia acuminata*; *Os*, *Oenothera simulans*; *Pp*, *Polypremum procumbens*; *Pa*, *Phyllanthus abnormis*; *Ps*, *Paspalum setaceum*; *Sj*, *Stachytarpheta jamaicensis*; *Wi*, *Waltheria indica*

Cafeteria feeding trials

Heliotropium polyphyllum appeared to be selected for ($\alpha = 0.34 \pm 0.12$), while *Fimbristylis cymosa* was selected against ($\alpha = 0.083 \pm 0.053$). All other plants offered were neither selected for nor against as the confidence intervals overlap 0.2 (Fig. 4).

Discussion

Contrary to our original hypothesis, lack of tortoise herbivory did not cause a change in plant abundance in plots where tortoises were excluded from feeding. However, it did impact other aspects of the plant community diversity. Species richness dropped in exclosure plots as compared to control plots, though not significantly so. However, Gini-Simpson diversity significantly decreased, while dominance increased in the absence of tortoises, supporting our original hypothesis concerning effects on biodiversity.

Heliotropium polyphyllum was the dominant species in terms of numbers and belowground biomass across both plot types. The extent of its dominance was greater in exclosure plots than in control plots. *F. cymosa* had greater biomass in control plots. As *H. polyphyllum* is preferred by tortoises over the other four most common plant species, it is likely that tortoises normally graze heavily on this plant, keeping it in lower abundances than would be observed in the absence of tortoise grazing. This consumption allows competitive release for other plant species and they increase in abundance and biomass. In exclosure plots, the increase in *H. polyphyllum* may explain the drastic decrease in abundance of *Fimbristylis cymosa* and the extirpation of some the more rare plants.

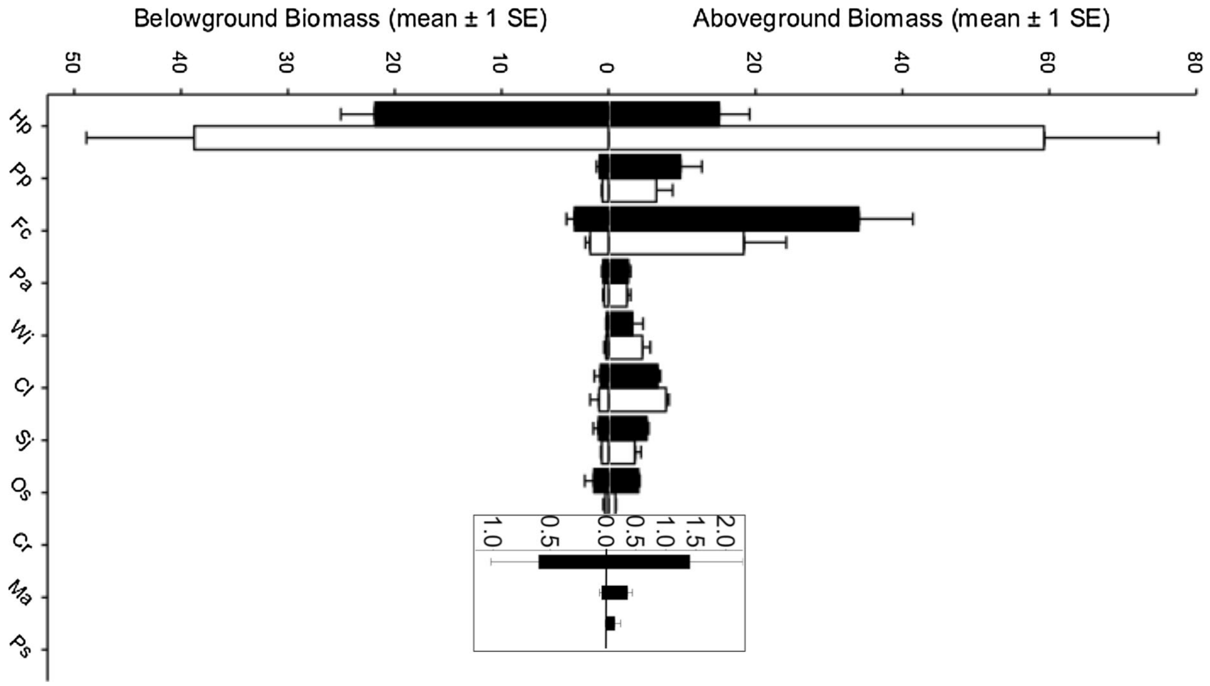

Fig. 3 Biomass of plants across control (black) and exclosure (white) plots. *Catharanthus roseus*, *Mecardonia acuminata*, and *Paspalum setaceum* are magnified in the inset. Abbreviations follow those from Fig. 2

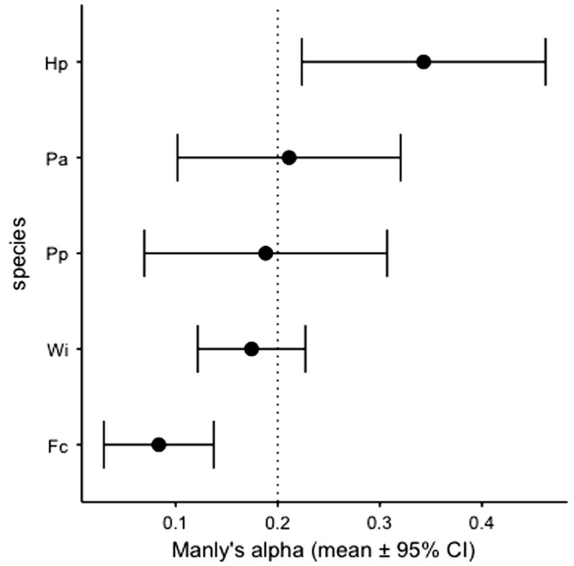

Fig. 4 Dietary preferences (as measured by Manly's α values) for the five most common plants observed in the exclosure experiment. Values with error bars overlapping 0.2 are neither selected for nor against, those to the right of 0.2 are preferred, and those to the left of 0.2 are selected against

The belowground biomass of *H. polyphyllum* in control plots is more extensive than the aboveground biomass. These plants maintain a strong root system, despite being grazed back by tortoises (Fig. 3). We have observed tortoises biting and tearing entire plants (foliage and roots) of other species from the ground, but the extensive root system of *H. polyphyllum* may help ensure its perseverance, permitting recovery following extensive herbivory.

Our study adds to the growing number of papers that document the strong effects of vertebrate herbivores on their forage plants and also shows that reptiles, as well as mammals, may have significant effects on their plant communities. It remains unclear why some herbivores facilitate increased biodiversity and others lower it. Differences may result from several mechanisms such as herbivore density or browsing intensity, or other biotic and abiotic interactions. Barrett and Stiling (2006) showed that plant biodiversity was inversely related to key deer density in the Florida Keys in that highly preferred plant species were significantly lower in density on high deer density islands, while avoided forage species were more abundant on high deer density islands. These impacts were not as pronounced on low deer density islands. Herbivory is but one of a myriad of interactions which help shape plant communities.

Other factors that may influence plant communities include nutrient levels, landscape heterogeneity, and local climate (Gaujour et al. 2012; Ricklefs 1977). The evolution of herbivore–plant systems may also help explain these differences. Native herbivore–native plant interactions tend to produce stable, more diverse communities (Goheen et al. 2007), while invasive herbivores tend to have greater impacts (Coomes et al. 2003; Noymeir 1988). This could be related to a lack of evolved plant defenses against invasive herbivores or an unnaturally high density of some invasive species. Tortoise density on Egmont Key is high relative to other areas (Mushinsky et al. 2006) and the aggressive nature of *H. polyphyllum* results in high dominance values in the absence of tortoises.

Large-bodied animals also destroy and kill plants in ways other than defoliation. Elephants will topple entire trees (Ssali et al. 2013), and trampling or wallowing will also cause localized destruction of plants (Olff and Ritchie 1998). As gopher tortoises are not as large as many mammalian herbivores and do not roam in herds, any impact of trampling is likely negligible. But even smaller bodied animals that burrow may have small-scale impacts in the areas immediately surrounding the burrows (Huntly and Reichman 1994; Smith and Foggin 1999), and this appears to be true for gopher tortoises as well (Boglioli et al. 2000).

Vertebrate herbivores may also exert pressure on plant communities through zoochory, the dispersal of plant seeds by animals (Jordano et al. 2011). This dispersal may result from intentional consumption of fleshy fruits (Delrio and Restrepo 1993; Janzen 1983) or the ingestion and dispersal of seeds evolved for wind dispersal or other non-animal-assisted dispersal syndromes (Janzen 1984; Stiles 1989). Both mechanisms may serve to alter seed germination rates and percentages (Traveset 1998; Traveset and Verdu 2002). Several fleshy-fruited plants are found on Egmont Key, most of them with fruit obtainable by tortoises, but none were observed in any of the plots or in the immediate vicinity. All plants at our field site contain small dry fruits, which may be intentionally or unintentionally ingested and dispersed, or possibly destroyed during gut passage. The impacts of this ingestion and its ramifications for plant community assembly are currently being investigated.

Finally, our results have conservation implications. Without gopher tortoises on Egmont Key, plant diversity would probably be greatly reduced and some species may go locally extinct. While we have investigated the impacts of gopher tortoises on one small location within their range, these tortoises are found across a wide range of habitat types (Mushinsky et al. 2006). Further research will be required to determine if tortoises strongly influence plant diversity across other habitat types they occupy and where other herbivores such as deer and rabbits are present.

Acknowledgements Thanks to Tom Watson and the rest of the Egmont Key State Park staff for keeping an eye on things; Alison Gainsbury, Chris Grimaldi, Stephen Hesterberg, Elizabeth Salewski, Keith Stokes, and Jake Zydek for field assistance; and the Lowry Park Zoo Herps department for use of their tortoises. This study was funded by The Odessa Garden Club and USF Provost's Office. This research was conducted under USF IACUC permit 739.

Appendix 1

See Table 2.

Table 2 Distribution family used in generalized linear models for comparing ground controls (G), fenced controls (C), and exclosures (E) for each metric measured for tortoise exclosure experiments

Metric	Comparison					
	C vs G start	C vs G end	E vs grouped C start	E vs grouped C end	E start vs end	Grouped C start vs end
Number of individuals	Negative binomial	Negative binomial	Negative binomial	Negative binomial	Negative binomial	Negative binomial
Species richness	Poisson	Poisson	Poisson	Poisson	Poisson	Poisson
Gini-Simpson Diversity	Gaussian	Gaussian	Gaussian	Gaussian	Gaussian	Gaussian
Dominance	Beta	Beta	Beta	Gaussian	Beta	Beta
Evenness	Beta	Gaussian	Beta	Beta	Beta	Beta

Appendix 2

See Table 3.

Table 3 Comparisons between fenced control and ground control for the beginning and end of the exclosure experiment

	Plot	Mean	SE	Plot	Mean	SE	χ^2	*p*
Number of individuals	Fenced control: start	221	39.06	Ground control: start	300.75	121.77	0.836	0.361
	Fenced control: end	258	115.89	Ground control: end	276	59.14	0.023	0.880
Richness	Fenced control: start	7.5	0.5	Ground control: start	7.25	0.25	0.017	0.896
	Fenced control: end	8	0.41	Ground control: end	7.75	0.63	0.016	0.900
Gini-Simpson index	Fenced control: start	0.65	0.06	Ground control: start	0.6	0.05	0.488	0.485
	Fenced control: end	0.65	0.02	Ground control: end	0.66	0.05	0.047	0.829
Dominance	Fenced control: start	0.45	0.08	Ground control: start	0.54	0.07	0.792	0.374
	Fenced control: end	0.53	0.02	Ground control: end	0.5	0.05	0.368	0.544

As no comparisons were significantly different, both control types were lumped into one for the final analyzes

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