Long-term Understory Vegetation Dynamics and Responses to Ungulate Exclusion in the Dry Forest of Mona Island

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Abstract - Mona Island protects one of the most important remnants of Caribbean dry forests and hosts a high diversity of rare and endangered plant and animal species. Feral ungulates (goats and pigs) were introduced to the island ~500 y ago, and their populations may be threatening the conservation of Mona Island's native biodiversity. In this study, we used permanent fenced and unfenced plots at 4 different depression-forest sites on Mona Island to assess long-term (10-y) understory vegetation dynamics and the potential responses of this vegetation stratum to ungulate exclusion. Depression forests on Mona Island are of particular interest because they hold the highest diversity of tree species on the island and are critical nesting habitats for the endangered *Cyclura cornuta stejnegeri* (Mona Island Rock Iguana). Overall, our results showed that understory vegetation at depression forests on Mona Island is very diverse and highly dynamic. In terms of composition and abundance, the understory of Mona Island is characterized by a high abundance of grasses and herbs and a high diversity of trees and shrubs. Long-term understory responses to ungulate exclusion were highly variable over time and included significant increases in the abundance of woody species as well as significant increases in the richness of non-woody species. Our results provide valuable information about the dynamics of understory vegetation in Caribbean dry forests that should be useful in planning for the conservation and restoration of these habitats.

Introduction

Tropical forest understories support a distinct array of species compared to the canopy and represent an integral and important part of the tropical plant community (Gentry and Emmons 1987). However, studies evaluating the structure and functional characteristics of understory plant communities in tropical sites have focused on wet forests and rainforests; less data is available from dry forests (but see Fajardo et al. 2005, Killeen et al. 1998, Lott et al. 1987, Quigley and Platt

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2003). Worldwide, tropical dry forests are among the most threatened ecosystems due to their small size, habitat loss, species invasion, and high density of human settlements within them (Murphy and Lugo 1986, Quesada et al. 2009). Historically, tropical dry forests have been subject to anthropogenic disturbances that are more persistent and extensive than those that affect tropical humid forests (Janzen 1988, Miles et al. 2006, Murphy and Lugo 1986). In the Caribbean region, tropical dry forests occur mostly on porous limestone substrates with shallow soils in areas with highly seasonal rainfall. The resulting conditions expose these communities to greater water stress and nutrient limitations than non-calcareous dry forests with similar rainfall (Lugo et al. 2006). Caribbean dry forests are also exposed to periodic large-scale disturbances such as hurricanes (Imbert and Portecop 2008, Rojas-Sandoval et al. 2014). Compared to tropical and subtropical wet forests and rainforests, Caribbean dry forests are characterized by a poorly developed understory stratum, a dominance of trees and shrubs with a multi-stemmed growth-form, and a lack of both cover and diversity of herb species when compared to tropical wet forests (Cintrón and Rogers 1991, Murphy and Lugo 1986).

Mona Island protects one of the most important remnants of Caribbean dry forests documented thus far. Natural habitats within this island are characterized by a high diversity of rare and endangered plant and animal species (Cintrón and Rogers 1991). However, despite the conservation status of the island's natural resources, the presence of exotic mammals, especially *Sus scrofa* L. (Feral Pig) and *Capra aegagrus hircus* Erxleben (Feral Goat), on Mona Island threatens the preservation of native species and ecosystems (García et al. 2000, López 2011, Rojas-Sandoval and Meléndez-Ackerman 2011a). On oceanic islands, plant communities are highly vulnerable to the effects of exotic mammals because plants have evolved in the absence of these kinds of herbivores; consequently, insular plant species often lack defenses such as thorns and toxic chemicals (Carlquist 1974, Chynoweth et al. 2013, Cole and Litton 2014, Cole et al. 2012, Fernández-Lugo et al. 2013, Glen et al. 2013, Murphy et al. 2014). Previous studies have shown that exotic mammals are responsible for extensive negative impacts on insular floras, including changes in the structure and composition of plant communities, increases in soil-erosion rates, and increases in exotic plant-invasion rates (Cabin et al. 2000). The International Union for the Conservation of Nature (IUCN) includes Feral Pigs and Feral Goats on their list of 100 of the world's worst invasive alien species (Lowe et al. 2004). Indeed, Feral Goats have been identified as the primary hazard to about 26% of the threatened insular plant species worldwide (Chynoweth et al. 2013, Fernández-Lugo 2013, Glen et al. 2013, Walter and Gillett 1998).

On Mona Island, Feral Goats and Feral Pigs were introduced early in the 16th century (Ruiz and Chabert 1989, Wiewandt 1977). Previous studies estimated original populations of ~300–700 pigs (density = 0.05–0.13 individuals/ha) and ~1500–3000 goats (density = 0.27–0.61 individuals/ha) on the island (Ruiz and Chabert 1989, Wiewandt 1977). Researchers have also suggested that composition and regeneration of native plant communities on Mona are strongly impacted by these ungulates (Cintrón 1991, Meléndez-Ackerman et al. 2008, Rojas-Sandoval et al. 2014). Through

their activities, Feral Goats and Feral Pigs may also directly or indirectly influence animal species of conservation concern, such as *Cyclura cornuta stejnegeri* Barbour & Noble (Mona Island Rock Iguana), an endangered species endemic to the island. The main threats to this species include habitat modification by Feral Goats and egg predation by Feral Pigs (Peréz-Buitrago et al. 2008).

In 1997 and 1999, The Department of Natural and Environmental Resources of the Commonwealth of Puerto Rico fenced fixed areas within depression forests on Mona Island to protect critical nesting sites for the Mona Island Rock Iguana. This state agency requested collaboration from the University of Puerto Rico to monitor depression-forest vegetation for changes following the establishment of these enclosures. Depression forests on Mona Island are small and dispersed patches of dense forests growing in sinkholes and terrain depressions characterized by deeper soils and the tallest canopy heights (3–5 m tall) of the different vegetation associations that occur on the island (Cintrón and Rogers 1991, Martinuzzi et al. 2008). On Mona Island, fenced and unfenced areas of the same size have been monitored annually for vegetation changes since 1997.

In this study, we used long-term (10-y) understory-vegetation data gathered in fenced and adjacent unfenced areas to assess the long-term vegetation dynamics and the potential responses of this stratum to ungulate exclusion. Our specific aims were to: (1) describe the long-term dynamics of understory vegetation in terms of temporal and spatial changes in plant abundance and species composition, and (2) evaluate the responses of understory vegetation to ungulate exclusion in relation to the temporal and spatial changes in plant abundance and species richness by different functional groups (woody vs. non-woody species). Because little is known about the dynamics of understory vegetation in tropical dry forests, the results of our study may lead to a better understanding of this forest stratum and may provide valuable information for the conservation and restoration of Caribbean dry forests.

Field-site Description

Mona Island (5517 ha) is primarily a limestone plateau located in the Caribbean Sea between Puerto Rico and Hispaniola (18°05'N, 67°54'W). About 90% of the island is covered by a an association of semideciduous shrubs and small trees classified as "lowland dry limestone semideciduous forest" (Martinuzzi et al. 2008). Interspersed within this forest are the small and scattered patches of depression forests (Cintrón and Rogers 1991). Previous reports of stem densities at this site ranged from 2000 to 3000 trees/ha (Cintrón and Rogers 1991, Rojas-Sandoval et al 2014). Mean annual rainfall over 54 y for this island is 807.8 mm (range = 285–1518 mm) with a dry season extending from December to April, and a rainy season that coincides with the Atlantic hurricane season from May to November. Mean annual temperature is 25.6 °C, with highest temperatures occurring during July–September (Rojas-Sandoval and Meléndez-Ackerman 2011b). Human settlements have been documented on Mona Island since pre-Columbian times until 1973, when the entire island was declared a natural reserve and all remaining human settlements were removed (Wadsworth 1973).

Methods

Data collection

Our study focused on vegetation data from permanent paired plots (ungulates present vs. ungulates excluded) located at 4 mature depression-forest sites: Farallon, Indio, Pelota, and Phyllanthus. One 20 m × 15 m fenced plot (fence dimensions: height = 220 cm, mask width = 70 mm, wire gauge = 1.8 mm) and 1 adjacent but unfenced plot of equal dimensions (control plot) were established at each site. Plots located in Farallon and Indio were established in 1997, and the plots in Pelota and Phyllanthus were established in 1999. Fenced and unfenced plots were divided into 1 m^2 × 1 m^2 subplots, and we monitored understory vegetation in 20 randomly located 1-m^2 subplots within each plot. We performed understory vegetation surveys within each plot by tagging all seedlings, juveniles, and adult plants <1 m height and identifying them to species level following Alder and Synnott (1992). We also classified each species according to life-form (i.e., vines, grasses, herbs, cacti, shrubs, or trees), growth type (perennial or annual), and origin (native or exotic) based on data from the USDA-NRCS (2014) Plant Database. We initiated understory-vegetation surveys in 2000 and repeated them annually until 2010. We deposited specimen vouchers for all species at the UPR-RP herbarium (University of Puerto Rico, Río Piedras, PR).

Data analysis

Vegetation dynamics. We assessed the dynamics of understory vegetation in terms of spatial and temporal changes in abundance and species richness of different life-forms occurring in fenced and unfenced plots. To do this, we estimated the abundance and species richness of each life-form (i.e., herbs, grasses, vines, shrubs and trees) as its percentage contribution to the total number of understory individuals and species in fenced and unfenced plots for the 4 depression-forest sites and for 2 specific vegetation surveys: the 2000 survey (baseline) and the 2010 survey (performed after 10 y of ungulate exclusion in the case of fenced plots or 10 y of vegetation monitoring in the case of unfenced plots). We used likelihood ratio tests (*G*-test) to determine if there were significant changes in the percentage contribution by each life-form class to understory plant cover between 2000 and 2010.

To analyze temporal changes in plant-community composition, we conducted a non-metric-multidimensional scaling ordination (NMS). This ordination model was performed using the slow-and-thorough autopilot mode of PC-ORD with the Bray–Curtis distance measure and a stability threshold of 0.0001 (McCune and Grace 2002). For the randomization procedure, 100 runs were carried-out to determinate the probability of finding an equally good solution with randomized data. We then used the NMS ordination data to create a successional-vector overlay to depict the temporal trends of the vegetation community throughout the 10 y of vegetation monitoring from 2000 to December 2010. All multivariate analyses were performed with PC-ORD version 5.0 (McCune and Mefford 2011); we omitted species that occurred on less than 5% of the plots from the analysis (McCune and Grace 2002).

Effects of ungulate exclusion. We used repeated-measures MANOVAs to evaluate changes over time as a factor of ungulate exclusion in plant abundance and species

richness. For this analysis, we separated plant species into 2 functional groups: woody and non-woody species. We grouped all species classified as shrubs and trees as woody, and all species classified as grasses, herbs, and vines as non-woody. To reduce within-site variation due to initial differences between plots (see Results below), each variable was normalized to represent the change in plant abundance and species richness relative to the baseline value. For each site and treatment, we divided the mean plant abundance and mean species richness estimated for each functional group at each year by the mean value estimated for the baseline year. To reduce potential between-site variation, we averaged normalized data from the 4 depression-forest sites to obtain a mean value for each normalized variable for each year. Analyses were run with functional group (woody and non-woody) and treatment (fenced and unfenced) as main effects.

We used correlation analyses to test for associations among changes in plant abundance and species richness relative to the baseline for non-woody and woody species with environmental variables related to temperature (°C) and rainfall (mm). We estimated values for mean annual temperature, monthly mean temperature, monthly mean minimum temperature, monthly mean maximum temperature, mean annual rainfall, and monthly cumulative rainfall. Records for temperature (°C) and rainfall (mm) were obtained from an automated meteorological station with a CR23X data logger (Campbell Scientific Inc., Logan, UT, USA) located on the island. In the case of monthly variables, we estimated mean and cumulative value for a period of 30 d before the date in which each vegetation survey was performed (Fig. 1). All tests were performed using JMP 7.0 (SAS Institute 2007).
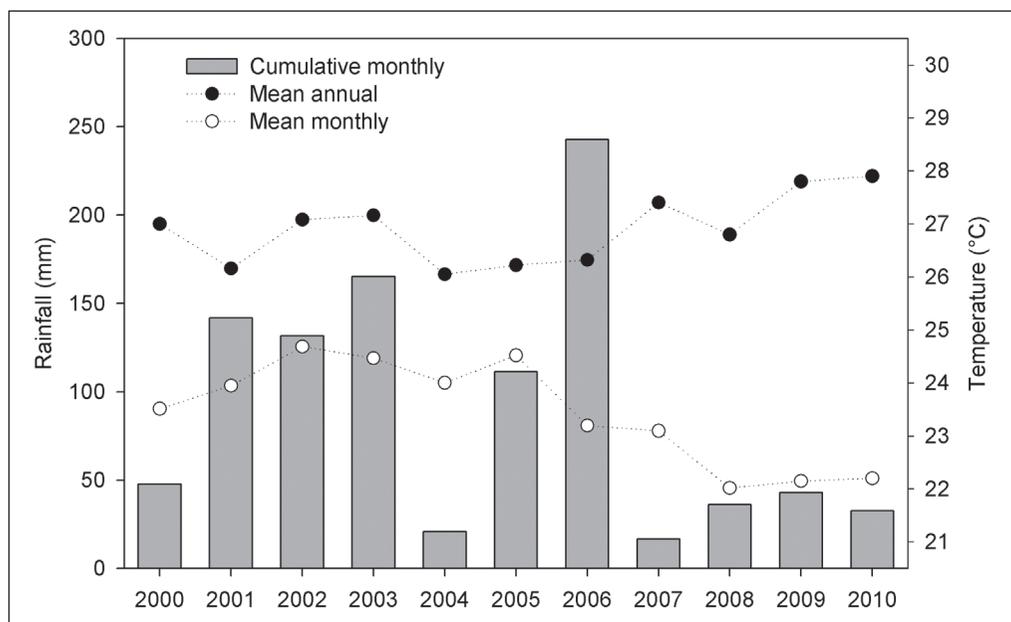

Figure 1. Mean monthly temperature (ºC) and monthly cumulative rainfall (mm) on Mona Island during the study. Monthly values were estimated using data for the 30-days before the date on which each vegetation survey was performed.

Results

Understory diversity

In 2000, the baseline understory-plant community for the pooled depression-forest sites contained a total of 102 species distributed in 40 families. After 10 y, the understory plant community increased to 122 plant species distributed across 41 families with an overall contribution across different life forms as follows: 36.9% herbs, 29.5% shrubs, 12.3% trees, 9% grasses, 7.4% vines, and 4.9% cacti (Appendix 1). One hundred-eleven species (91%) were native and 11 species (9%) were introduced to Mona Island. Three of the species—*Oeceoclades maculata* (Lindl.) Lindl., *Megathyrsus maximus* (Jacq.) R. Webster, and *Prosopis juliflora* (Sw.) DC.—are listed as invasive on Mona Island. Perennials and annuals accounted for 86% and 14% of the species in the understory, respectively. Four families—Fabaceae (13 species), Euphorbiaceae (11 species), Malvaceae (10 species), and Poaceae (9 species)—were dominant at these forest sites. The most abundant plant species in the understory of our depression-forests sites were: *Spermacoce confusa* Rendle (Rubiaceae), *Sidastrum multiflorum* (Jacq.) Fryxell (Malvaceae), *Setaria utowanaea* (Scribn. ex Millsp.) Pilg. (Poaceae), and *Myrcianthes fragrans* (Sw.) McVaugh (Myrtaceae) (see Table S1 in Supplemental File 1, available online at http://www.eaglehill.us/CANA-online/suppl-files/cSP1-C123d-Rojas-Sandoval-s1). Fifteen of the 122 species were only found within fenced plots and, importantly, 4 of them— (*Malachra fasciata* (Jacq.), *Tillandsia utriculata* L., *Trichostigma octandrum* (L.) H. Walt., and the endemic cactus *Harrisia portoricensis* Britton—are species of conservation concern listed as endangered or threatened under US Federal Regulation (Appendix 1).

Life-form dynamics

The relative contributions of the different life forms to plant abundance inside and outside fenced plots were highly variable over space and time (Fig. 2a, b; see also Fig. S1 in Supplemental File 1, available online at http://www.eaglehill.us/CANAonline/suppl-files/cSP1-C123d-Rojas-Sandoval-s1). The baseline data recorded in 2000 indicated that 3 out of 4 unfenced plots (Indio, Pelota, and Phyllanthus) were dominated by grasses and herbs, and the unfenced plot in Farallon was dominated by trees. After 10 y, we detected significant increases in the abundance of trees in unfenced plots in Farallon ($G = 5.54$, df =1; $P = 0.01$), Indio ($G = 38.23$, df = 1; $P < 0.001$) and Pelota ($G = 8.78$, df = 1; $P = 0.003$). In Phyllanthus, the abundance of grasses increased from 46% in 2000 to 80% in 2010 ($G = 8.88$, df = 1; $P = 0.002$). We also detected decreases in the abundance of herbs from 77% to 39% in Pelota ($G = 12.68$, df = 1; $P < 0.001$) and from 37% to 10% in Phyllanthus ($G = 16.50$, df =1; $P < 0.001$). In fenced plots, contributions of the different life forms to understory abundance changed over time in Farallon and Phyllanthus (Fig. 2a, b; see also Fig. S1 in Supplemental File 1, available online at http://www.eaglehill.us/CANAonline/suppl-files/cSP1-C123d-Rojas-Sandoval-s1). Baseline measurements recorded in 2000 showed that the fenced plots in Farallon and Phyllanthus were dominated by grasses and trees, respectively. However, after 10 y of ungulate exclusion, we found an increase of more than 50% in the abundance of herbs at

Farallon ($G = 54.48$, df = 1; $P < 0.001$) and a reduction of more than 30% in the abundance of trees at Phyllanthus ($G = 30.62$, df = 1; $P < 0.001$, Fig. 2a, b), a site which was dominated by grasses when monitored in 2010.

When comparing the species richness of the different life-forms outside and inside fenced plots over time (baseline vs. after 10 y), we found that species richness varied over time, but not as dramatically as abundance (Fig. 2c, d; see also Fig. S2 in Supplemental File 1, available online at http://www.eaglehill.us/CANAonline/suppl-files/cSP1-C123d-Rojas-Sandoval-s1). Our results showed that at the time of the baseline survey and after 10 yrs of monitoring or exclusion, the understory of both fenced and unfenced plots across sites were characterized by having a greater number of tree and shrub species relative to the number of herb, vine, and grass species. However, when we compared the baseline and the 10-y survey, we detected significant reductions in shrub (35% decline; $G = 32.36$, df = 1; $P < 0.001$) and tree (40% decline; $G = 55.45$, df = 1; $P < 0.001$) species richness for unfenced plots in Farallon and Phyllanthus, respectively (Fig. 2c, d).

Temporal changes in vegetation composition

The first 2 axes of the NMS ordination explained 77.8% of the variability in the original data matrix (r^2 for axis 1 = 0.36, r^2 for axis 2 = 0.56; $P < 0.04$). The
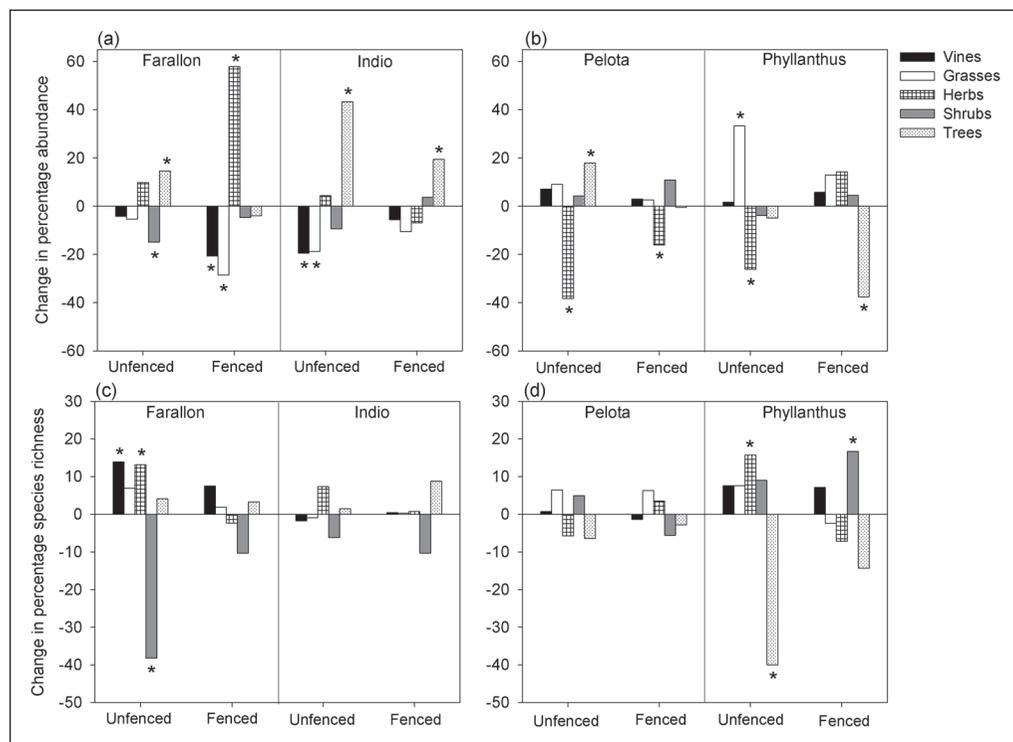

Figure 2. Change in percentage abundance (a, b) and percentage species richness (c, d) for different life forms within unfenced and fenced plots between the 2000 and 2010 surveys. Bars marked withan asterisk (*) denote significant changes ($P < 0.05$) in the percentage between the 2 surveys (see the main text).

distribution of the points in multivariate space showed that there were strong initial differences in plant-community composition among sites and treatments (fenced vs. unfenced; Fig. 3). This ordination analysis also reflected a highly dynamic vegetation composition for all depression-forest sites. Regardless of treatment, individual plots exhibited different plant-composition trajectories, and by the end of the study in 2010, all plots differed in plant composition relative to their initial conditions. Despite these differences, we observed that both fenced and unfenced plots within a given depression site were more similar to each other than they were to plots from other sites, and that plots in Farallon and Indio (regardless of treatment) were more similar to each other than they were to plots in Pelota and Phyllanthus (Fig. 3).

Effects of ungulate exclusion on species abundance and richness

Repeated-measures MANOVA detected significant differences in the change in plant abundance relative to the baseline between functional groups ($F_{1,2} = 28$, 71; $P = 0.03$) and treatments ($F_{1,2} = 20$, 46; $P = 0.04$) over time ($F_{10,10} = 3$; 39, $P = 0.004$). However, there were no functional group or treatment × time interaction effects ($F < 0.92$, $P > 0.17$ in all cases). Overall, there was considerable temporal variation in the change in plant abundance relative to the baseline, with woody species at fenced plots showing the greatest changes, and non-woody species at unfenced plots experiencing the lowest amount of change (Fig. 4a, b). For both functional groups, these temporal variations were more pronounced in fenced plots than in unfenced plots. We also observed that changes in the abundance of woody species in fenced plots were significantly higher than changes in unfenced plots through most of the 10 y analyzed (Fig. 4b).
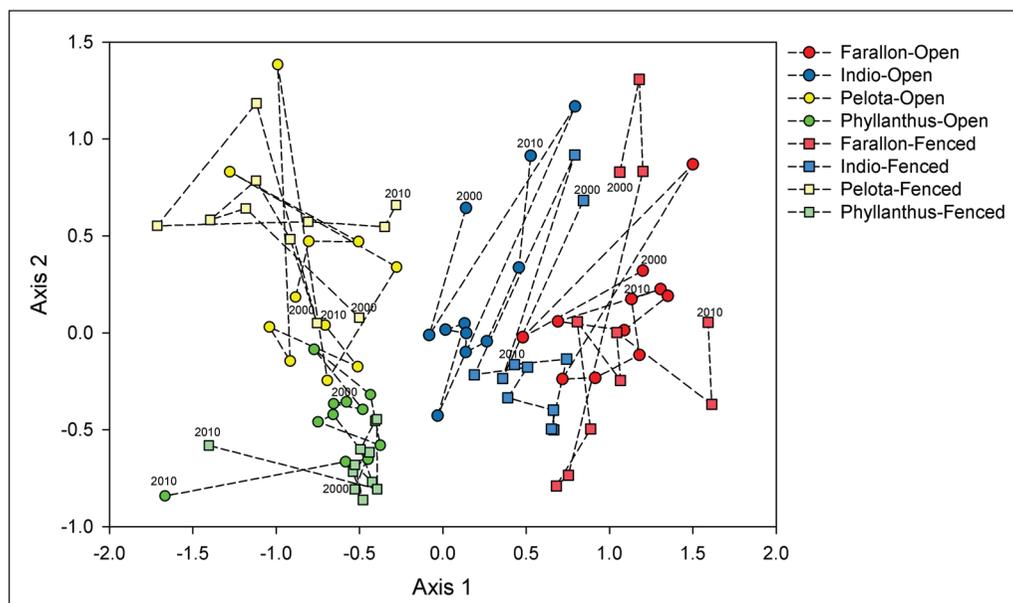

Figure 3. Non-metric multidimensional scaling (NMS) ordination with successional vector overlays for plant-community composition within fenced and unfenced plots established in 4 depression-forests site on Mona Island.

We also detected significant differences in species richness between functional groups ($F_{1,2}$ = 22.03, P = 0.02), between treatments ($F_{1,2}$ = 13.63, P = 0.04), and across time ($F_{10,10}$ = 5.37, P = 0.001), but interaction effects (F < 0.12, P > 0.97) were not detected. Similar to plant abundance, the MANOVA showed that changes in species richness relative to baseline were highly variable across time for both woody and non-woody species. The analysis also demonstrated that responses to ungulate exclusion, in terms of changes in species richness relative to baseline, were more conspicuous for non-woody species than for woody species (Fig. 4c, d). Our data showed that for non-woody species, ungulate exclusion caused a steady increase in species richness resulting in values at the end of the study in 2010 that were double the baseline values (Fig. 4c).

When we tested for associations among vegetation and environmental variables, we detected that changes in the abundance of non-woody species relative to the baseline were associated with the monthly cumulative rainfall in fenced (r^2 = 0.45, F = 7.51; P = 0.02) and unfenced plots (r^2 = 0.65, F = 17.37; P = 0.002). Similarly, changes in the abundance of woody species were correlated with mean annual
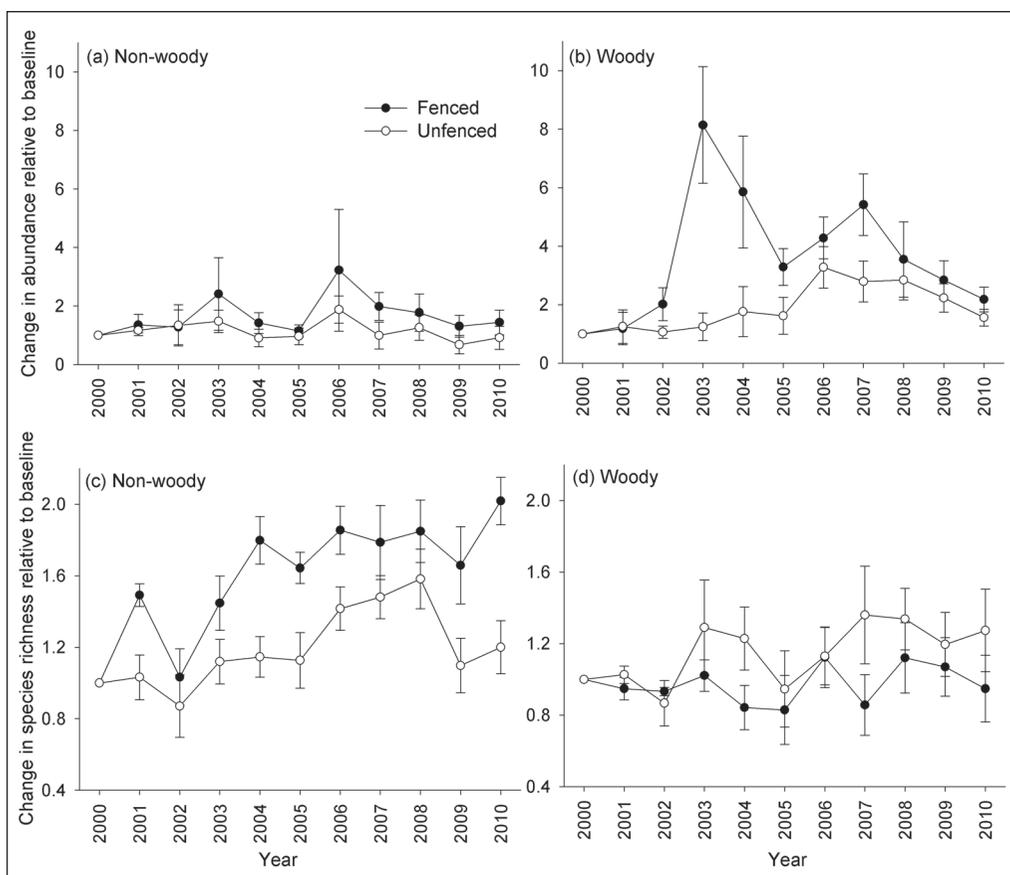

Figure 4. Change in abundance (a, b) and species richness (c, d) relative to the baseline value for non-woody and woody species within fenced and unfenced plots as a function of time. Values are mean (± SE) among the 4 depression-forest sites.

rainfall in fenced plots ($r^2 = 0.30$, $F = 4.36$; $P = 0.05$) and with monthly cumulative rainfall in unfenced plots ($r^2 = 0.37$, $F = 5.27$; $P = 0.04$). None of the remaining environmental variables measured was associated with changes in the abundance of non-woody or woody species ($r^2 < 0.13$, $F < 1.40$; $P > 0.26$ in all cases). In contrast to plant abundance, changes in species richness were not associated with any of the environmental variables analyzed ($r^2 < 0.11$, $F < 1.29$; $P > 0.20$ in all cases).

Discussion

Our combined results showed that the understory of depression forests on Mona Island is very diverse and highly dynamic. The diversity and floristic composition of the understory of Mona Island is similar to that described for other dry forests (Gentry 1995, Lugo et al. 2006, Quigley and Platt 2003). As in many other continental and Caribbean dry forests, Fabaceae was the dominant family on Mona Island, followed by species-rich families such as Euphorbiaceae, Malvaceae, and Poaceae (Gentry 1995). In terms of species composition, our results showed that the understory of Mona Island is very diverse and dominated by non-woody species (i.e., herbs and grasses). This result contrasts with a previous study performed on Mona Island's depression forests 25 y ago that described these forests as having low herbaceous species diversity (Cintron and Rogers 1991). Our data showed that in the understory of Mona Island, 2 herbs and one grass species, *Spermacoce confusa*, *Ayenia insulicola* Cristobal, and *Setaria utowanaea*, respectively, were the most abundant plant species among the depression forests we studied, whereas Cintron and Roger's (1991) study reported two woody species, *Ephorbia petiolaris* Sims and *Phyllanthus epiphyllanthus* L. as the most abundant species. This difference in the current dominance of non-woody species compared to the previous dominance of woody species could be related to hurricane disturbances. Like many other Caribbean dry forests, the dry forest of Mona Island is often subjected to large-scale disturbances such as hurricanes and tropical storms which may influence its forest dynamics (Imbert and Portecop 2008, Rojas-Sandoval et al. 2014, Van Bloem et al. 2005). Indeed, hurricanes are considered to be among the primary drivers influencing the structure and composition of Caribbean forests (Lugo 2008). Previous studies have also demonstrated that an overabundance of non-woody vegetation is indicative of early succession at disturbed sites (Griscom and Ashton 2011, Seidl et al. 2011). In 1998, Hurricane Georges, a category-3 storm, hit Mona Island with sustained winds of 185–193 km/h and gusts up to 240 km/h (Bennett and Mojica 1998). Therefore, the overabundance of non-woody species we observed in the understory of Mona Islands could be an indicator that this forest is still undergoing post-hurricane early succession (Rojas-Sandoval et al. 2014).

Our combined results also demonstrated the occurrence of high spatial variation in the understory layer. At our study site, spatial variation occurs at very short distances, and fenced and unfenced plots right next to each other are quite different in terms of plant abundance and composition. This pattern of high spatial heterogeneity is not uncommon in water-stressed environments such as tropical dry forests in which highly seasonal rainfall patterns generate microenvironmental

conditions that are more severe and variable than in other forest types (Bullock and Solis-Magallanes 1990, Gerhardt and Hytteborn 1992, Medina and Cuevas 1990). One potential way to understand the high heterogeneity prevalent in Mona Island's dry forests may be to evaluate the ideal plot size and location using geostatistical analyses as well as increasing the number of plots across different areas within and between depression-forest sites.

In terms of vegetation responses, the dynamics of Mona Island's understory vegetation, regardless of treatment, were also highly variable through time, and this variation was partly related to precipitation patterns. The strong association between precipitation and the changes in plant abundance may explain many of the vegetation responses observed after the exclusion treatment. Our results showed that for both woody and non-woody species, the relative changes in plant abundance were primarily influenced by changes in precipitation in both fenced and unfenced plots. Overall, our results are consistent with previous studies which suggest that processes related to vegetation regeneration following ungulate exclusions can be strongly affected by water availability or changes in microclimatic factors (Cabin et al. 2002a, 2002b; McEachern et al. 2009; Thaxton et al. 2010). Plant responses to precipitation are often common in tropical dry forests, where water availability is considered the most important factor influencing the growth and survival of plants (Murphy and Lugo 1986). In this regard, many studies in arid and semiarid ecosystems have shown that precipitation is the most important factor in triggering pulses of plant germination, growth, establishment, and reproduction (Cheeson et al. 2004, Holmgren et al. 2006, Ogle and Reynolds 2004, Reynolds et al. 2004, Rojas-Sandoval et al. 2012). In our case, the remarkable increase in the abundance of woody species in fenced plots after precipitation events was driven by sharp increases in seed germination and seedling recruitment of 3 of the most common species in the understory of Mona Island: the trees *Myrcianthes fragrans* and *Bourreria succulenta* and the shrub *Sidastrum multiflorum* (see Table S1 in Supplemental File 1, available online at http://www.eaglehill.us/CANAonline/suppl-files/cSP1-C123d-Rojas-Sandoval-s1).

A limitation of this study is that data for understory vegetation were not collected prior to the establishment of fences. Consequently, we cannot unequivocally attribute differences in understory vegetation composition and abundance to the exclusion. However, one important outcome that has emerged from this study is that vegetation regeneration in the understory layer following exclusion seems to be inherently slow on Mona Island. One hypothesis to explain this pattern of slow recovery could be related to the level of degradation of these sites prior to the exclusion treatment. Studies in Hawaiian dry forests have shown that vegetation recovery following exclusion is inversely related to the amount of degradation experienced by the area prior to fencing (Cabin et al. 2002a, Loope and Scowcroft 1985). In those studies, highly degraded areas frequently showed little or no recovery even after long-term exclusion periods. Prior research has also suggested that a number of site-specific ecological factors such as soil conditions are likely to create ecological limitations that may influence potential recovery after ungulate

exclusion (Courchamp et al. 2003). Soil-nutritional and biophysical characteristics are highly variable on the island (E. Meléndez-Ackerman et al. 2016 [this issue]) and this variability contributes to differences in species composition at a small scale. Another hypothesis is that the effects of ungulate herbivory (a small-scale, continuous disturbance) on native plant communities may be interacting with effects of large-scale disturbances such as hurricanes and tropical storms which may also influence forest dynamics in additon to the effects of ungulates (Rojas-Sandoval et al., 2014). Consequently, some of the changes in vegetation composition and abundance that we observed within our study sites were likely to be also related to post-hurricane successional dynamics (Rojas-Sandoval et al. 2014).

At a global scale, the eradication and control of introduced alien species has been a major management goal in insular biodiversity conservation (Courchamp et al. 2003, Glen et al. 2013, Simberloff 2000). However, restoration through the removal or exclusion of invasive species is not necessarily a linear process leading to species recovery and often may require supplemental strategies that can facilitate the regeneration of native plant species (Cabin et al. 2000a, b). For instance, studies in diverse ecosystems and situations have shown that exclusion of invasive species may enhance the regeneration of native vegetation, promote the establishment of native species, and decrease surface soil compaction (Carrion et al. 2011, Glen et al. 2013, Howald et al. 2007), but other studies have shown that unwanted secondary outcomes of exclusion can also include increased growth of other invasive species, declines in native populations, failure of native species or ecosystems to recover, and environmental changes which can delay the return to baseline conditions (Cabin et al. 2002a, Campbell et al. 2005, Zavaleta et al. 2001). In the case of Mona Island forests, even when we detected positive responses in the relative changes of plant abundance and species richness for woody and non-woody species related to ungulate exclusion, the magnitude and significance of those responses varied greatly between these functional groups and were not necessarily consistent over time. While we have detected significant changes in relative abundance and species richness for woody and non-woody species inside and outside fenced plots, these changes do not appear to follow linear successional pathways. For our study site, 2 different but not mutually exclusive hypotheses may help us to explain these differences. First, insufficient time may have elapsed for significant ecological changes to have occurred (or been detected). Second, it is also possible that ecological factors interacting with ungulate disturbance may be preventing regeneration at some sites despite the removal. Indeed, a previous study conducted on Mona Island suggested that synergistic effects between herbivore–plant interactions and hurricane-induced changes in tree-community composition and structure could be the factors preventing Mona Island forests from reaching historical tree-community conditions that prevailed before the introduction of ungulates (Rojas-Sandoval et al. 2014).

Long-term monitoring studies like the one presented here suggest that a number of factors may influence plant-community responses to ungulate exclusion to

the extent that these responses may not be apparent for many years. Based on the combined results of this study, we propose that further studies on the effects of ungulate exclusion on the regeneration of depression forests on Mona Island need to be complemented with monitoring of plant densities, distributions, population dynamics, and soil seed banks, as well as experimental studies to provide practical suggestions for enhancing the recovery of this Caribbean dry forest type.

Acknowledgments

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Appendix 1. List of all plant species found within fenced and unfenced plots across 4 depression-forest sites on Mona Island over 10 y of understory vegetation monitoring. Classification based on data from USDA-NRCS Plant Database (2014). [F] indicates species only found in fenced plots. Species with asterisk (*) have been listed as invasive in the Puerto Rican Archipelago (Rojas-Sandoval and Acevedo-Rodríguez 2014).

Species	Family	Life form	Growth type	Origin
Achyranthes aspera L.	Amaranthaceae	Herb	Perennial	Alien
Amaranthus dubius Mart. ex Thell.	Amaranthaceae	Herb	Annual	Native
Amyris elemifera L.	Rutaceae	Tree	Perennial	Native
Antirhea acutata (DC.) Urb.	Rubiaceae	Shrub	Perennial	Native
Ayenia insulicola Cristobal	Malvaceae	Herb	Perennial	Native
Bastardia bivalvis (Cav.) Kunth	Malvaceae	Herb	Perennial	Native
Bastardia viscosa (L.) Kunth	Malvaceae	Herb	Perennial	Native
Boerhavia diffusa L.	Nyctaginaceae	Herb	Annual	Native
Bourreria succulenta Jacq.	Boraginaceae	Tree	Perennial	Native
Bucida buceras L.	Combretaceae	Tree	Perennial	Native
Bursera simaruba (L.) Sarg.	Burseraceae	Tree	Perennial	Native
Callisia repens (Jacq.) L.	Commelinaceae	Herb	Perennial	Native
Calyptranthes pallens Griseb.	Myrtaceae	Shrub	Perennial	Native
Canella winterana (L.) Gaertn.	Canellaceae	Tree	Perennial	Native
Capparis cynophallophora L.	Capparaceae	Tree	Perennial	Native
Capparis flexuosa L.	Capparaceae	Vine	Perennial	Native
Centrosema virginianum (L.) Benth.	Fabaceae	Vine	Perennial	Native
Chamaecrista lineata (Sw.) Greene	Fabaceae	Herb	Perennial	Native
Chamaecrista nictitans (L.) Moench	Fabaceae	Herb	Perennial	Native
Chamaesyce cowellii Millsp. ex Britton	Euphorbiaceae	Herb	Perennial	Native
Chamaesyce turnipii (Boiss.) Millsp.	Euphorbiaceae	Succulent	Perennial	Native
Cissus trifoliata L.	Vitaceae	Vine	Perennial	Native
Coccoloba microstachya Willd.	Polygonaceae	Tree	Perennial	Native
Commelina diffusa Burm. f.	Commelinaceae	Herb	Annual	Native
Commelina elegans Kunth	Commelinaceae	Herb	Perennial	Native
Comocladia dodonaea (L.) Urb.	Anacardiaceae	Shrub	Perennial	Native
Consolea moniliformis (L.) Britton	Cactaceae	Cacti	Perennial	Native
Consolea rubescens (Salm-Dyck ex DC.) Lem.	Cactaceae	Cacti	Perennial	Native
Corchorus hirsutus L.	Malvaceae	Shrub	Perennial	Native
Croton betulinus Vahl	Euphorbiaceae	Shrub	Perennial	Native
Croton discolor Willd.	Euphorbiaceae	Shrub	Perennial	Native
Croton humilis L.	Euphorbiaceae	Shrub	Perennial	Native
Croton lucidus L.	Euphorbiaceae	Shrub	Perennial	Native
Cyperus filiformis Sw.	Cyperaceae	Grass	Perennial	Native
Cyperus nanus Willd.	Cyperaceae	Grass	Perennial	Native
Desmanthus virgatus (L.) Willd.	Fabaceae	Herb	Perennial	Native
Desmodium incanum DC.	Fabaceae	Herb	Perennial	Native
Desmodium triflorum (L.) DC.	Fabaceae	Herb	Perennial	Native
Digitaria horizontalis Willd.	Poaceae	Grass	Annual	Alien
Domingoa haematochila[F] (Rchb. f.) Carabia	Orchidaceae	Succulent	Perennial	Native
Eragrostis ciliaris (L.) R. Br.	Poaceae	Grass	Annual	Alien
Erithalis fruticosa L.	Rubiaceae	Shrub	Perennial	Native
Erythroxylum areolatum L.	Erythroxilaceae	Tree	Perennial	Native
Eugenia axillaris (Sw.) Willd.	Myrtaceae	Shrub	Perennial	Native
Eugenia foetida Pers.	Myrtaceae	Shrub	Perennial	Native
Eugenia monticola (Sw.) DC.	Myrtaceae	Shrub	Perennial	Native

Species	Family	Life form	Growth type	Origin
Eugenia rhombea (Berg) Krug & Urb.	Myrtaceae	Shrub	Perennial	Native
Eupatorium corymbosum Aubl.	Asteraceae	Shrub	Perennial	Native
Euphorbia petiolaris Sims.	Euphorbiaceae	Shrub	Perennial	Native
Ficus citrifolia Mill.	Moraceae	Tree	Perennial	Native
Galactia dubia DC.	Fabaceae	Vine	Perennial	Native
Guaiacum sanctum L.	Zygophyllaceae	Tree	Perennial	Native
Gymnanthes lucida Sw.	Euphorbiaceae	Shrub	Perennial	Native
Harrisia portoricensis[F] Britton.	Cactaceae	Cacti	Perennial	Native
Helicteres jamaicensis Jacq.	Malvaceae	Shrub	Perennial	Native
Heliotropium angiospermum Murray	Boraginaceae	Herb	Annual	Native
Heliotropium microphyllum Sw. ex Wikstr.	Boraginaceae	Shrub	Perennial	Native
Hypelate trifoliata Sw.	Sapindaceae	Shrub	Perennial	Native
Ipomoea triloba[F] L.	Convolvulaceae	Vine	Perennial	Native
Jatropha multifida L.	Euphorbiaceae	Shrub	Perennial	Alien
Krugiodendron ferreum (Vahl) Urb.	Rhamnaceae	Tree	Perennial	Native
Lantana camara L.	Verbenaceae	Shrub	Perennial	Native
Malachra alceifolia Jacq.	Malvaceae	Herb	Annual	Native
Malpighia emarginata DC.	Malphigiaceae	Herb	Annual	Native
Melochia tomentosa L.	Malvaceae	Shrub	Perennial	Native
Metastelma lineare Bello	Apocynaceae	Shrub	Perennial	Native
Metopium toxiferum (L.) Krug & Urb.	Anacardiaceae	Tree	Perennial	Native
Mirabilis jalapa L.	Nyctaginaceae	Herb	Perennial	Alien
Myrcianthes fragrans (Sw.) McVaugh	Myrtaceae	Tree	Perennial	Native
Nicotiana tabacum L.	Solanaceae	Herb	Annual	Alien
Ocimum tenuiflorum L.	Lamiaceae	Herb	Perennial	Alien
Oeceoclades maculata[*] (Lindl.) Lindl.	Orchidaceae	Succulent	Perennial	Alien
Opuntia repens Bello	Cactaceae	Cacti	Perennial	Native
Megathyrsus maximus[*] (Jacq.) B.K. Simon & S.W.L. Jacobs	Poaceae	Grass	Perennial	Alien
Paspalum blodgetti Chapm.	Poaceae	Grass	Perennial	Native
Paspalum caespitosum Flueggé	Poaceae	Grass	Perennial	Native
Paspalum laxum Lam.	Poaceae	Grass	Perennial	Native
Passiflora suberosa L.	Passifloraceae	Vine	Perennial	Native
Pectis linifolia L.	Asteraceae	Herb	Annual	Native
Pentalinon luteum (L.) B.F. Hansen & Wunderlin	Apocynaceae	Shrub	Perennial	Native
Phyllanthus epiphyllanthus L.	Euphorbiaceae	Shrub	Perennial	Native
Phyllanthus niruri L.	Euphorbiaceae	Herb	Annual	Native
Pilea herniarioides (Sw.) Lindl.	Urticaceae	Herb	Perennial	Native
Pilea margarettiae Britton	Urticaceae	Herb	Perennial	Native
Pilea microphylla (L.) Liebm.	Urticaceae	Herb	Annual	Native
Pilosocereus royenii (L.) Byles & Rowley	Cactaceae	Cacti	Perennial	Native
Pisonia albida (Heimerl) Britton ex Standl.	Nyctaginaceae	Tree	Perennial	Native
Pithecellobium unguis-cati (L.) Benth.	Fabaceae	Tree	Perennial	Native
Portulaca pilosa L.	Portulacaceae	Herb	Annual	Native
Portulaca rubricaulis Kunth	Portulacaceae	Succulent	Annual	Native
Prestonia agglutinata (Jacq.) Woodson	Apocynaceae	Vine	Perennial	Native
Prosopis juliflora[*] (Sw.) DC.	Fabaceae	Herb	Perennial	Alien
Psychilis monensis Sauleda	Orchidaceae	Succulent	Perennial	Native
Psychotria nutans Sw.	Rubiaceae	Shrub	Perennial	Native
Randia aculeata L.	Rubiaceae	Shrub	Perennial	Native
Randia portoricensis (Urb.) Britton & Standl.	Rubiaceae	Shrub	Perennial	Native
Rauvolfia viridis Roem. & Schult.	Apocynaceae	Shrub	Perennial	Native

Species	Family	Life form	Growth type	Origin
Reynosia uncinata Urb.	Rhamnaceae	Shrub	Perennial	Native
Rhynchosia minima (L.) DC.	Fabaceae	Vine	Perennial	Native
Rhynchosia reticulata (Sw.) DC.	Fabaceae	Herb	Perennial	Native
Rivina humilis L.	Phytolacaceae	Herb	Perennial	Native
Salvia serotina L.	Lamiaceae	Herb	Perennial	Native
Samyda dodecandra Jacq.	Salicaceae	Shrub	Perennial	Native
Schaefferia frutescens Jacq.	Celastraceae	Shrub	Perennial	Native
Setaria pradana (Léon ex Hitchc.) Léon	Poaceae	Grass	Perennial	Native
Setaria setosa (Sw.) P. Beauv.	Poaceae	Grass	Perennial	Native
Setaria utowanaea (Scribn. ex Millsp.) Pilg.	Poaceae	Grass	Perennial	Native
Sida abutifolia Mill.	Malvaceae	Herb	Annual	Native
Sida glabra Mill.	Malvaceae	Herb	Perennial	Native
Sidastrum multiflorum (Jacq.) Fryxell	Malvaceae	Shrub	Perennial	Native
Sideroxylon obovatum Lam.	Sapotaceae	Shrub	Perennial	Native
Sideroxylon salicifolium (L.) Lam.	Sapotaceae	Shrub	Perennial	Native
Spermacoce confusa Rendle	Rubiaceae	Herb	Annual	Native
Cereus hildmannianus K. Schum.	Cactaceae	Cacti	Perennial	Alien
Stigmaphyllon emarginatum (Cav.) A. Juss.	Malphigiaceae	Vine	Perennial	Native
Synedrella nodiflora (L.) Gaertn.	Asteraceae	Herb	Annual	Native
Tephrosia cinerea (L.) Pers.	Fabaceae	Herb	Perennial	Native
Teramnus labialis (L. f.) Spreng.	Fabaceae	Herb	Perennial	Native
Tillandsia recurvata L.	Bromeliaceae	Succulent	Perennial	Native
Tillandsia utriculata L.	Bromeliaceae	Succulent	Perennial	Native
Trichostigma octandrum (L.) H. Walt.	Phytolacaceae	Shrub	Perennial	Native