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# Response of early-successional Bahamian dry forest habitat to goat grazing and implications for Kirtland's warbler (*Setophaga kirtlandii*) wintering ground management

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**Abstract.—Limited financial resources coupled with competing social demands may require novel approaches for biodiversity conservation. Within the Bahamas archipelago, subtropical dry forest ("coppice") provides habitat for many resident and migratory bird species including the U.S. federally endangered Kirtland's warbler (*Setophaga kirtlandii*). On the islands, this migratory bird relies heavily on fruits of shrubs in early-successional coppice. Evidence indicates shrub species of particular importance in the bird's diet may not be generally widespread, while attempts to actively manage for these plant species could be cost-prohibitive or counterproductive to other conservation concerns. Because these shrubs and Kirtland's warblers have been frequently found on goat farms we investigated whether periodic goat grazing might be a practical tool for maintaining suitable coppice habitat in other semi-natural areas where late-successional coppice is unsupportable (e.g. utility rights-of-way) and whether it promotes increased abundance of important fruiting shrubs. In experiments conducted in young coppice within a pipeline corridor, we found little evidence that grazing would increase abundance of these shrubs, but our grazed coppice plots returned quickly to their pre-grazing state and exhibited few subsequent structural or compositional differences from ungrazed coppice plots. Thus, if appropriately applied and managed, goat grazing may serve as an economically viable tool for biodiversity preservation because (1) suitability as habitat for Kirtland's warblers and many other birds returns quickly after a short-term grazing treatment and (2) periodic, short-term grazing will forestall succession toward a vegetation type less appropriate for these birds or for certain types of human land use.**

**Keywords.— Bahamian coppice; endangered species conservation; *Erithalis fruticosa*; habitat management; *Lantana involucrata*; subtropical dry forest**

## Introduction

Conserving critical habitat for rare species often involves socio-economic challenges. For migratory species, these can be magnified by disparities between the breeding and wintering grounds in availability of resources for and societal attitudes toward conservation. Yet, effective conservation may require active management in both environments because wintering ground conditions can affect migrant fitness (Marra et al. 1998; Reudink et al. 2009). Where resources are scarce, unconventional management techniques deserve consideration if they show an ability to satisfy both conservation goals and socio-economic needs.

The Kirtland's warbler (*Setophaga kirtlandii*), one of North America's rarest Nearctic-Neotropical migratory songbirds, has been the focus of a largely successful recovery effort, but one occurring almost entirely on its Michigan breeding grounds (Mayfield 1992). Late winter drought on the warbler's wintering grounds, almost exclusively in the Bahamas archipelago, is negatively related to Kirtland's warbler annual survival and breeding ground reproductive success (Rockwell et al. 2016; Rockwell et al. 2012). This likely arises from a drought-induced decline in the warbler's winter food supply and, subsequently, its pre-migration body condition (Wunderle et al. 2014). Ensuring availability of habitat with critical late winter food resources should strengthen conservation efforts for this endangered bird and benefit other species that share the warbler's winter habitat.

In The Bahamas, Kirtland's warblers have primarily been found in early-successional (3-28 yr) tropical dry forest locally known as

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[#] Current address: American Bird Conservancy, P.O. Box 249, The Plains, VA 20198 "coppice" (Jones et al. 2013; Wunderle et al. 2010). Early-successional Bahamian coppice is also utilized by a number of other migratory and permanent resident birds (Currie et al. 2005a; Currie et al. 2005b). Though coppice, in general, is the dominant vegetation on many Bahamian islands, its physical structure and local composition vary with topography and disturbance history (Byrne 1980; Correll 1979). The coppice where Kirtland's warblers are found is characterized by short-statured (~2 m) shrubs or trees, a high density of foliage and small stems between 0.5-1.0 m from the ground, and the presence of fruiting *Lantana involucrata* (wild sage), *Erithalis fruticosa* (black torch), or *Chiococca alba* (West Indian snowberry) (Sykes and Clench 1998; Wunderle et al. 2010; Wunderle et al. 2014). In contrast to most dry forest species (Murphy and Lugo 1986), *E. fruticosa* and *L. involucrata* are year-round fruiters that provide an important food resource for frugivores in late winter (Wunderle et al. 2014). Kirtland's warblers have also been observed among stands of *Pinus caribaea* var. *bahamensis* (Caribbean pine) (Haney et al. 1998), but coppice with *E. fruticosa* and *L. involucrata* is often interspersed with pines and may be an important factor determining the bird's presence (Lee et al. 1997).

The most intensive published studies of wintering Kirtland's warblers have been conducted on the island of Eluethera, where most Kirtland's warbler-occupied coppice was recently disturbed by humans (Wunderle et al. 2010). Although anthropogenic disturbance is extensive across many Bahamian islands (Byrne 1980; Helmer et al. 2010; Young 1966), only a low proportion of anthropogenically disturbed areas on Eleuthera have been found to support the fruiting shrubs important in the Kirtland's warbler's diet (Fleming et al. 2015). Because fruiting of these shrubs is highly variable over space and time (Wunderle et al. 2014), the distribution of critical late-winter food sources may be even more limited. This warrants consideration of strategies for protecting habitat with these shrubs, but protected land is scarce in The Bahamas. In addition, application of periodic disturbance to maintain early-successional habitat may be inappropriate for broader conservation goals in protected areas or cost-prohibitive for conservation organizations.

These challenges encouraged our investigation of a novel strategy, in terms of both technique and location, to manage habitat for Kirtland's warblers and co-occurring species – i.e. using controlled goat grazing/browsing (hereafter, grazing) within semi-natural coppice on lands currently used primarily for human benefit. We hypothesized that controlled goat grazing might be a feasible tool for maintaining coppice in a state suitable for Kirtland's warblers based on: (1) personal observations of numerous Kirtland's warblers and an abundance of *L. involucrata* and *E. fruticosa* on Eleuthera goat farms; and (2) analyses indicating occurrence of *E. fruticosa* and *L. involucrata* was disproportionately high (Fleming et al. 2015) and the persistence time of *L. involucrata* was long (Larkin et al. 2012) in goat grazed areas. Yet we were unaware of any studies indicating a mechanism for the association between goat grazing and the fruiting shrubs favored by Kirtland's warblers. We were also motivated by the potential socio-economic benefits that might be derived from using goats in habitat management (Hart 2001). Successful incorporation of goats could potentially improve the cost-effectiveness of large-scale habitat management efforts while also improving availability of a popular, but currently limited, food commodity in The Bahamas.

Because we would not advocate conversion of mature coppice to create habitat for Kirtland's warblers, we were particularly interested in investigating whether goat grazing could be effectively used to maintain critical habitat in human-utilized tracts of semi-natural coppice requiring periodic clearing, such as utility rights-of-way (ROWs). ROWs cover extensive land area and require vegetation maintenance to enable access and reduce risk of damage to utility infrastructure. In other regions, researchers have found positive associations between managed ROW vegetation and various taxa including butterflies (Lensu et al. 2011), land snails (Nekola 2012), and especially birds (see Lanham and Whitehead 2011 for review). If (a) goat grazing in early-successional Bahamian coppice maintains or favors development of Kirtland's warbler habitat and (b) a grazing regime can be developed that cost-effectively achieves utility management needs and goat-production needs, then conservation and socio-economic goals may be simultaneously aided.

As a first step in evaluating the potential for using goats in Kirtland's warbler winter habitat management, we conducted two small-scale grazing experiments within early-successional coppice to address four main questions concerning both a mechanistic link between grazing and the occurrence of Kitland's warbler habitat as well as some practical information needed for the design of a grazing-based management program:

1. Compared to ungrazed stands, how and for how long does a single goat grazing treatment alter vegetation structure, and do these effects vary with different grazing intensities?

For habitat management on utilized lands not dedicated to livestock production, a periodic grazing regime (repeated treatments separated by some interval) would likely be most appropriate, and reduction of vegetation below some minimally suitable level for habitat may be necessary during the grazing period to achieve other goals. It is important to know how long an interval is needed after an individual grazing treatment to allow the vegetation structure to return to a minimum level of suitability for the conservation target. We expected recovery interval length would vary positively with grazing intensity.

2. Do the forage preferences of goats produce differences in the compositional structure of grazed versus ungrazed stands?

Consumer selectivity can affect vegetation structure and composition (Coblentz 1978; El Aich and Waterhouse 1999). Low palatability of *L. involucrata* has been suggested to contribute to its relative abundance in goat-grazed areas (Byrne 1980; Larkin et al. 2012). However, we have found that goats exhibit a greater preference for both *L. involucrata* and *E. fruticosa* relative to many co-occurring coppice plants (Fleming et al. 2016). Nonetheless, goat grazing may still favor *E. fruticosa* and *L. involucrata* if, for example, the two shrubs are able to recover grazing-related canopy losses more quickly than competitors.

3. Does grazing improve seedling recruitment of *E. fruticosa* or *L. involucrata*?

Another mechanism by which grazing could promote an abundance of *E. fruticosa* or *L. involucrata* is through seedling recruitment. *L. involucrata* has been found to have higher germination and seedling survival in high light conditions (Fleming et al. 2015) and may recruit a high number of seedlings in the post-grazing environment that could eventually contribute to increasing dominance of the shrub through time.

4. How does goat grazing affect the primary fruit resources utilized by Kirtland's warblers?

Because our focus on *E. fruticosa* and *L. involucrata* was motivated by the importance of their fruit for birds, we wanted to know how an individual grazing treatment influenced subsequent fruit abundance. We expected grazing would cause a short-term reduction in fruit compared to ungrazed plots, with duration of the reduction increasing with grazing intensity.

## Materials and Methods

### *Study Site*

We conducted our grazing studies in southwestern Eleuthera, The Bahamas (24°49'N, 76°19'W), where coppice (subtropical dry forest) is composed of both evergreen and deciduous broadleaf trees and shrubs growing on a limestone substrate (Correll 1979; Mooney 1905; Smith and Vankat 1992). Our study plots were located within the pipeline network of a fresh-water well field on the grounds of Cape Eleuthera Resort. The well field was chosen for its accessibility and similarity to other utility ROWs on the island (e.g., power-line ROWs). Vegetation within an approximately 7-10 m wide corridor around the water pipes was heavily thinned ~4 yr prior to our study, but was probably infrequently disturbed during the prior 10-20 yr since resort operations were minimal due to multiple changes in ownership. The cleared corridors were dominated by shrubs or trees with a typical height ~2 m, had an understory of grasses, and high cover of mostly herbaceous vines. The regenerating vegetation resembled other areas where Kirtland's warblers had been found on Eluethera and was considered at least minimally suitable as habitat. Older forest (>25yr) surrounded the corridors, with a large expanse separating the well field from current resort development.

Eleuthera's climate is characterized by an annual wet and dry cycle. Most rainfall occurs during the Atlantic hurricane season (June through October). Two hurricanes passed over Eleuthera during our study (August 2011 and October 2012). Given the sheltered locations of our plots and the low stature of vegetation, the main visible effects of these storms on the plants were partial leaf loss or burn due to wind and salt spray.

### *Study plots*

Ten pairs of plots (N = 20) were established at ten sites throughout an approximately 60 ha area. Plot pairing within sites ensured grazed and ungrazed plots, as groups, encompassed similar environmental variation, but each plot generally served as its own control in quantitative analyses of change through time. Study plots were 6 m * 17 m (102 m$^2$). The plot dimensions were primarily determined by the size of the cleared corridor, attempts to keep the plot pairs in reasonably homogenous vegetation, and the cost and size of electric fencing (see below).

Plots were largely dominated by *Acacia choriophylla* (cinnecord), *Bourreria ovata* (strong-back), and *Trema lamarckianum* (pain-in-the-back), but *L. involucrata* and *E. fruticosa* occurred on all plots in varying abundances. The latter two species are typically low statured (< 2 m, though larger shrubs may be encountered) and relatively shade intolerant species that establish or regenerate after disturbance via both seeds and vegetative mechanisms (Fleming et al. 2015). Flowering, fruiting, and seedling recruitment can occur any time of year when conditions are favorable, but annual peaks are likely to be associated with the timing and amount of summer rain (Fleming et al. 2015; Francis 2004).

### *Grazing Treatments*

We conducted two grazing trials differing in stocking density and grazing intensity to evaluate how moderate versus heavy grazing affected habitat characteristics. The heavy treatment exceeded the grazing intensity that would typically be found on a well-managed goat farm. The moderate treatment may also have been relatively intense. However, we imposed such intensities assuming periodic application of grazing to non-farm land might require moderate to heavy thinning of vegetation.

Due to logistical and funding constraints, grazing trials were conducted in consecutive years. The first trial (Trial 1; moderate grazing) occurred during late winter/early spring (February-April) of 2011 and involved confinement of three female goats within study plots for ~13 days per plot (i.e., 39 goat-days). The second trial (Trial 2; heavy grazing) occurred during late winter/early spring of 2012, and nine female goats were confined within plots for ~6.5 days per plot (58.5 goat-days). Ten plots (five plot pairs) were used in each trial. One plot from each pair was randomly selected for grazing, the other was ungrazed. Portable electric fencing was used to confine goats within the plots during daylight hours.

### *Vegetation Measures*

Vegetation was measured prior to and following the goat grazing treatments at approximately 6 mo intervals coinciding with the beginning (~November) and end (~April) of the winter dry season. We sampled through 2 yr post-moderate grazing (Trial 1) and 1.5 yr post-heavy grazing (Trial 2). Plant species were identified following the nomenclature of Correll and Correll (1996).

To assess grazing-related changes in general vegetation structure (Question 1), we measured (see Appendix 1 for details): (1) ground surface litter cover and depth; (2) the percentage of the plot with any live vegetation cover ("total plant cover"); and (3) aboveground plant biomass (dry g.m$^{-2}$) estimated from visual obstruction (Fleming et al. 2014). We examined litter cover and depth because Kirtland's warblers forage for arthropods in litter (Wunderle et al. 2014), and because ground shading by litter has a negative influence on *L. involucrata* seedling germination (Fleming et al. 2015). Biomass and total plant cover also indicate relative ground shading by plant canopies as well as structural characteristics relevant to Kirtland's warblers. For example, higher biomass plots in our study system typically have a greater density of small foliage bearing stems than plots with lower biomass (Fleming et al. 2014). However, while biomass captures elements of local vegetation density, cover incorporates spatial distribution properties not captured by biomass. We also examined vegetation cover within two vertical height strata (0.0-0.5 m and 0.5- 1.0 m), but these variables showed qualitatively similar responses to cover of grasses and total plant cover, respectively, and are not presented here.

To assess whether goats' forage preferences influenced compositional change (Question 2) we measured (a) percent cover of five "forage preference groups" and (b) individual canopy volumes of five species of preferred shrubs (see Appendix 1). Relative preference among species was determined from quantitative analysis of dietary choices made by goats prior to depletion of preferred resources (Fleming et al. 2016). Goat forage preference groups included: (1) grasses (a less-preferred group); (2) "less-preferred shrubs" (combined cover of *Bourreria ovata*, *Nectandra coriacea*, *Psychotria ligustrifolia*, and *Trema lamarckianum*); (3) "Kirtland's warbler shrubs" (combined cover of *E. fruticosa*, *L. involucrata*, *Chiococca. alba, and C. parvifolia*; a preferred group); (4) "other preferred shrubs" (combined cover of shrubs for which goats showed a relative preference similar to Kirtland's warbler shrubs: *Acacia choriophylla*, *Pithecellobium keyense*, *Reynosia septentrionalis*, and *Thrinax morrisii*); and (5) vines (mostly preferred species, especially *Passiflora* spp. and *Jacquemontia havenensis*).

Canopy volume of individual *E. fruticosa* and *L. involucrata* shrubs was measured pre- and post-treatment on both grazed and ungrazed plots. Volume of individual *A. choriophylla*, *P. keyense*, and *R. septentrionalis* shrubs ("preferred competitors") was measured on grazed plots only. Preferred competitors were measured post-treatment only in Trial 1 and both pre- and post-treatment in Trial 2. Only browsed shrubs of the preferred competitors were measured to compare their relative re-growth rates with browsed *E. fruticosa* and *L. involucrata*. Pre-treatment volume of preferred competitors was not measured in Trial 1 since we did not know which species would be browsed by goats.

At each survey, the numbers of flowers and fruits (including unripe, ripe, and dead) on each marked shrub were counted (Question 4). The numbers of newly emerged (since the prior survey) *E. fruticosa* and *L. involucrata* seedlings were also counted in 0.25 m$^2$ quadrats used for biomass estimation, and the percentage of the quadrat showing bare soil was visually estimated (Question 3).

### *Analytical Methods*

Analyses examined whether (a) patterns of vegetation change through time within grazed plots differed, on average, from those within ungrazed plots; and (b) vegetation characters differed between grazed and ungrazed plots, as groups, at particular time points. Separate analyses were performed within each grazing trial because our statistical power was likely too low to detect complex interactions among treatment, trial, and time. Also, to avoid complex patterns that might interact with treatment, grazing effects (except on fruit and seedlings) were typically examined over three time periods in separate analyses. First, we tested comparability of pre-grazing vegetation between grazed and ungrazed plots (univariate *t*-tests). Second, we assessed treatment impact among grazed plots within trials by examining whether vegetation measures immediately post-treatment or at 6 mo post-treatment differed from those prior to grazing (repeated-measures ANOVA followed by paired samples *t*-tests, or 3-level hierarchical linear models (HLM) sensu Raudenbush and Bryk (2002); see Appendix 1 for additional detail). Finally, we examined differences in vegetation between treatments (grazed or ungrazed) and within plots through time from 6 mo to 1.5 or 2 yr (depending on trial) post-treatment (repeated-measures ANOVA followed by paired and independent samples *t*-tests or 3-level HLM; see Appendix 1).

When analyzing changes in the log volume of individual shrubs over the three periods described above, we included an effect of season (wet *v*. dry) and examined: (a) volume of *E. fruticosa* and *L. involucrata* (separately) through time and differences between treatment groups, and (b) how volume changes in browsed *E. fruticosa* or *L. involucrata* (separately) compared to volume changes of browsed *A. choriophylla*, *P. keyense*, and *R. septentrionalis* (3-level HLM; see Appendix 1).

Within each grazing trial, seedlings of *E. fruticosa* and *L. involucrata* were combined for analysis (“Kirtland’s warbler shrub seedlings”). We used linear regression to evaluate whether the total number of Kirtland’s warbler shrub seedlings observed across all quadrats within a plot by 18 mo depended on percent cover of bare soil or aboveground plant biomass within quadrats (averaged over surveys and plots) or differed between grazed and ungrazed plots.

When analyzing grazing effects on Kirtland’s warbler shrub fruit production, we considered *E. fruticosa* and *L. involucrata* shrubs with flowers or fruits at a survey as “fruiting” and combined flower and fruit counts to yield an index of fruit production not limited to the specific survey timing (i.e., assumed some flowers eventually became fruit). Because the presence and abundance of fruit on any individual shrub in a patch is naturally highly variable in our system, we examined several aspects of fruit production. First, we examined whether the proportion of *E. fruticosa* or *L. involucrata* shrubs producing any fruit at all within the entire post-treatment period differed between browsed and unbrowsed shrubs (i.e., post-treatment fruit presence, ignoring timing and abundance; Yates corrected chi-square tests). Second, among those shrubs in each trial that fruited at least once, we evaluated (Mann-Whitney *U* tests) whether fruiting shrubs on grazed *v*. ungrazed plots in each trial differed in the typical number of post-treatment surveys where fruiting was observed (i.e., fruiting frequency) or in how soon after treatment (in months) they were typically first observed fruiting (i.e., latency). Finally, we examined whether the abundance of fruit produced (i.e. the index of fruit production) by individual *E. fruticosa* and *L. involucrata* shrubs, across occasions during which they fruited (i.e., surveys with zero-values excluded), showed any linear trend through time or relationship to treatment. For the latter two analyses, species were combined due to generally low numbers of fruiting shrubs. For fruit abundance analyses, we used the log of the combined number of flowers and fruits counted within a survey on a fruiting shrub, and we included effects for season and individual canopy volume (3-Level HLM; see Appendix 1).

## Results

We found no pre-treatment differences between grazed and ungrazed plots in our vegetation measures. Many characteristics varied through time on all plots, often showing dry season declines and wet season increases. Post-treatment differences between grazed and ungrazed plots are described below in the context of our four main questions.

### *Question 1: Grazing Effects on General Vegetation Characters*

Percent litter cover increased with time among all plots but was not substantially affected by grazing (Appendix 2, Table S1). Mean litter depth (Appendix 2, Table S1) was lower (~0.5 cm) on heavily grazed compared to ungrazed plots at 6 mo post-treatment ($t_8 = 3.3$, $P = 0.011$), but not beyond (Fig. 1).

Grazing reduced the local density of vegetation (Biomass, Table S1) more than its spatial extent (Total plant cover, Table S1), but effects were short-lived (Fig. 1). Relative to pre-grazing, plant biomass was immediately reduced by an average ~52% on moderately grazed plots (paired $t_4 = 8.5$, $P = 0.001$) and 82% on heavily grazed plots ($t_4 = 5.5$, $P = 0.005$). Total plant cover was reduced by 29% relative to pre-grazing values on moderately grazed (or 25 percentage points; $t_4 = 17.4$, $P < 0.001$) and by 43% on heavily grazed plots (37 percentage points; $t_4 = 27.8$, $P < 0.001$). By 6 mo post-treatment and beyond, neither biomass nor total cover differed significantly between grazed and ungrazed plots from either Trial. However, the seasonal variation in total cover within moderately grazed plots was larger than

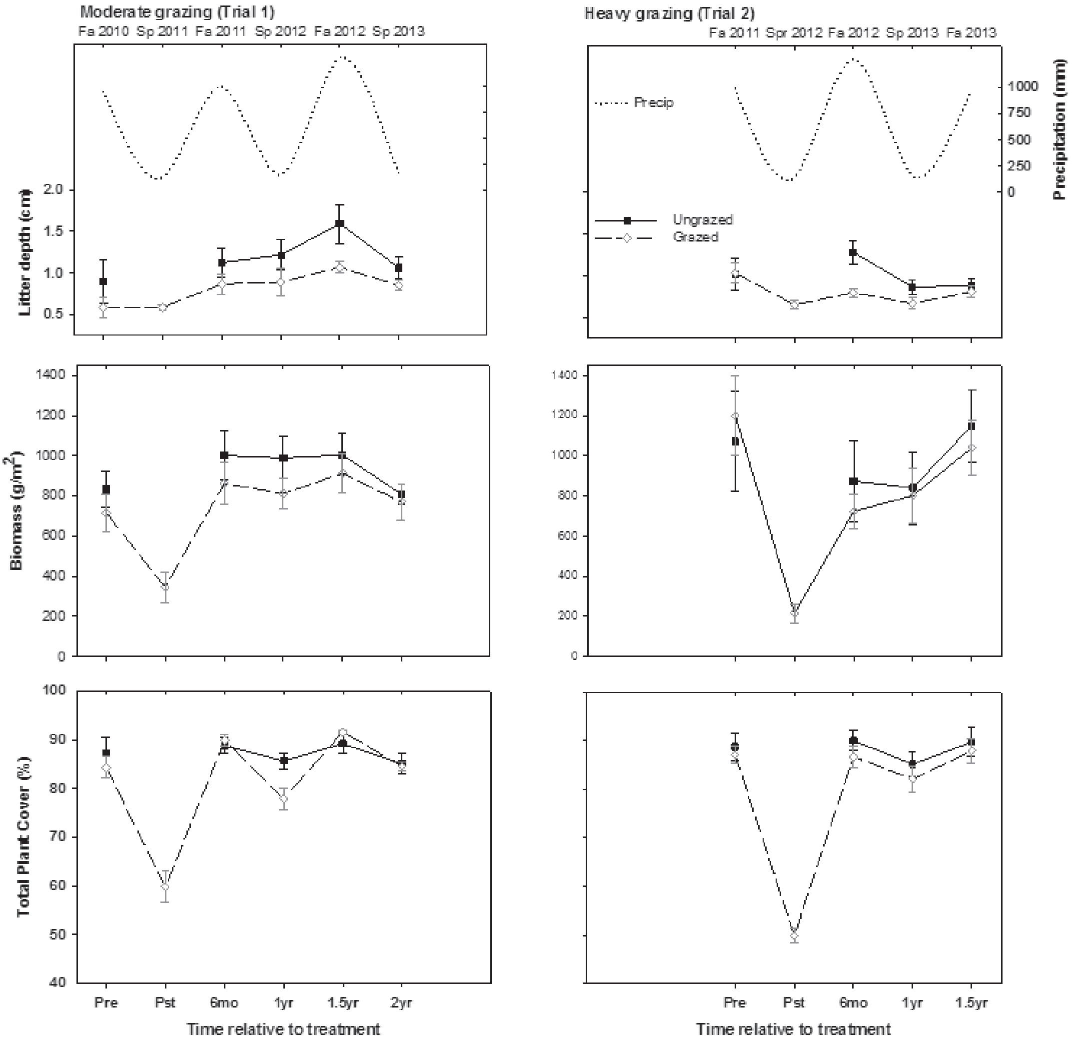

FIG. 1. Changes in vegetation characteristics through time on goat-grazed and ungrazed plots in coppice vegetation on Eleuthera, The Bahamas. Symbols are means within treatment groups; vertical bars are one standard error. Total precipitation recorded at Nassau International Airport during the 6 mo preceding each survey is shown in the top panels to highlight vegetation change between the wet vs. dry season. The timing (Fall or Spring and calendar year) of each survey is also shown at the top.

within ungrazed plots. Moderately grazed plots showed an average 12-percentage point decline in cover between the first post-treatment wet and dry seasons ($t_4$ = 7.5, $P$ = 0.002) followed by a 14-point increase in the second wet season ($t_4$ = 5.5, $P$ = 0.005) compared to much smaller fluctuations on ungrazed plots (Fig. 1).

### *Question 2: Effects of Grazing on Goat Forage Preference Groups*

*Cover of less- and more-preferred groups.*— In general, percent cover of all goat forage preference groups was reduced relative to pre-treatment levels immediately following grazing (Appendix 2,Table S2). Significant reduction of less-preferred forage resulted from continued goat confinement after preferred forage was exhausted, which forced consumption of less-preferred plants. Nonetheless, relative to cover on ungrazed plots, few forage groups showed reductions lasting beyond a few months.

Percent cover of less-preferred grasses and shrubs were significantly lower immediately following both moderate and heavy grazing (*Grasses*: Trial 1, 54% reduction over pre-grazing cover, paired $t_4$ = 4.7, $P$ = 0.009; Trial 2, 99% reduction, $t_4$ = 8.5, $P$ = 0.001; *Shrubs*: Trial 1, 29% reduction, $t_4$ = 3.8, $P$ = 0.019; Trial 2, 39% reduction, $t_4$ = 4.7, $P$ = 0.009). By 6 mo, only less-preferred shrub cover on heavily grazed was still lower than pre-treatment values ($t_4$ = 5.0, $P$ = 0.007), but there was little significant difference between grazed and ungrazed plots in the cover of those shrubs or grasses (Fig. 2). However, the seasonal fluctuation of grass cover on grazed *v*. ungrazed plots qualitatively mirrored the differences observed for total plant cover, while less-preferred shrub cover showed a slightly stronger decline through time on ungrazed plots from Trial 1.

Percent cover of goat-preferred Kirtland's warbler shrubs was qualitatively lower but not significantly reduced immediately post-grazing (Fig. 3) likely due to relatively low change in the total cover of *E. fruticosa*. However, the percentage of that cover comprised of foliage (*v*. woody stems or intra-canopy gaps) declined by 0-50% under moderate grazing and by 75-100% under heavy grazing. Cover of Kirtland's warbler shrubs on heavily grazed plots only was significantly lower compared to ungrazed plots when averaged over 6 mo to 1.5 yr post-treatment (main effect of treatment, Appendix 2,Table S2), but the effect was primarily driven by differences occurring within the first year (Fig. 3).

Cover of other goat-preferred shrubs showed significant immediate reduction following moderate (55% reduction over pre-grazing, $t_4$ = 5.0, $P$ = 0.008) and heavy (60% decline, $t_4$ = 4.7, $P$ = 0.010) grazing, but did not differ from ungrazed plots by 6 mo post-treatment or beyond (Fig. 3). Across post-treatment surveys, percent cover of vines (goat-preferred) on grazed plots was generally lower than on ungrazed plots (Fig. 3; treatment main effect, Appendix 2, Table S2), though the difference between heavily grazed and ungrazed plots diminished by 1.5 yr (time*treatment interaction).

*Canopy volume of goat-preferred shrubs.*— Relative to their pre-grazing values, canopy volumes among all marked shrubs were immediately reduced by grazing (Fig. 4; see values associated with parameter $\pi_1$ in Appendix 2, Table S3 A, B, & C). By 6 mo post-treatment, there was 5% (Trial 1) and 0% (Trial 2) mortality among *E. fruticosa* on moderately and heavily grazed plots, respectively, compared to 30% and 40% mortality among *A. choriophylla* shrubs. There was no mortality among the other species within the first 6 mo. Among the survivors, *L. involucrata* on moderately and heavily grazed plots and *E. fruticosa* on moderately grazed plots recovered to near-pre-treatment levels by 6 mo, but canopy volumes of *E. fruticosa* and all three preferred competitors on heavily grazed plots were still lower than their pre-treatment values (Fig. 4; see values associated with parameter $\pi_2$ in Table S3).

From 6 mo through 1.5 or 2 yr following treatment, *E. fruticosa* shrubs on moderately grazed plots had slower growth rates compared to *E. fruticosa* on ungrazed plots, but *E. fruticosa* and *L. involucrata* on heavily grazed plots had higher growth rates than on ungrazed

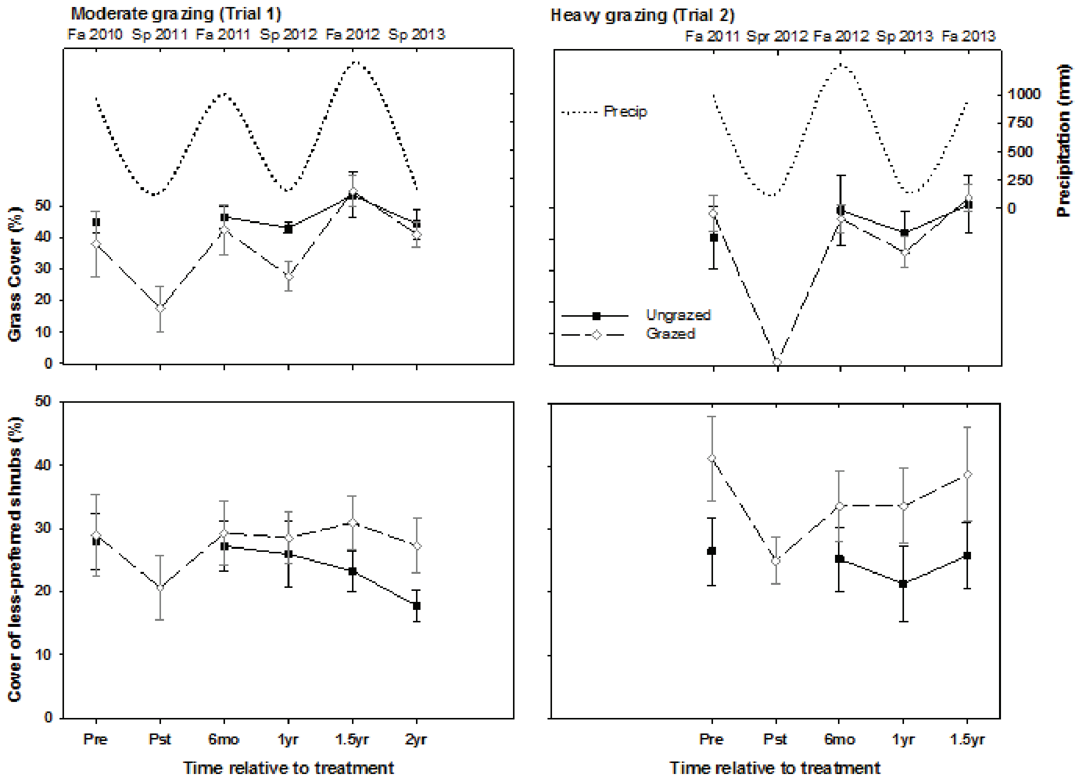

FIG. 2. Changes in percent cover of grasses (a less preferred forage group; top panels) and less preferred shrubs (bottom panels) on goat-grazed and ungrazed coppice plots on Eleuthera, The Bahamas. Less-preferred shrubs include *Bourreria ovata, Nectandra coriacea, Psychotria ligustrifolia, and Trema lamarckianum*. Symbols are means within treatment groups; vertical bars are one standard error. Total precipitation recorded at Nassau International Airport during the 6 mo preceding each survey is shown in the top panels to highlight vegetation change between the wet vs. dry season. The timing (Fall or Spring and calendar year) of each survey is also shown at the top.

plots (see values associated with parameter $\gamma_{101}$ in Appendix 2, Table S4 A and B). In all cases, there was no significant difference between browsed and unbrowsed average shrub volumes by 18 mo (1.5 yrs) post-treatment (Fig. 4; see values associated with parameter $\gamma_{001}$ in Table S4 A and B).

After accounting for seasonal fluctuations, which were less pronounced for *A. choriophylla* and *P. keyense* on moderately grazed plots (Fig. 4; see values associated with parameter $ß_{22}$ in Appendix 2, Table S5), all five goat-preferred shrub species had similar rates of canopy growth through time, except for slower growth of *R. septentrionalis* compared to *E. fruticosa* on heavily grazed plots (Fig. 4; see values associated with parameter $ß_{11}$ in Table S5). By 18 mo (1.5 yrs) post-treatment, browsed *A. choriophylla* and *P. keyense* had larger volumes than browsed *E. fruticosa* but were not substantially different from browsed *L. involucrata* (Fig. 4; see values associated with parameter $ß_{02}$ in Table S5 A & B), which was larger than *R. septentrionalis* on moderately grazed plots by 18 mo (Fig. 4; see values associated with parameter $ß_{01}$ in Table S5B).

### *Question 3: Grazing effects on Kirtland's warbler Shrub Seedling Recruitment*

We found little support for any effect of goat grazing on the total number of Kirtland's warbler shrub seedlings that emerged between 6 and 18 mo post-treatment, but seedling emergence was generally sparse (a total of 28 *E. fruticosa* and

28 *L. involucrata* seedlings in Trial 1 and 61 *E. fruticosa* and 74 *L. involucrata* seedlings in Trial 2) Typically only one seedling-occupied quadrat per plot with a median 1.5 seedlings was observed per survey, though most new seedlings were observed during fall surveys, especially the fall 2013 survey of Trial 2 plots. Among Trial 2 plots only, we did find the total number of observed seedlings decreased as average quadrat biomass across the plot increased (linear regression, $\beta_{\text{biomass}}$ = -0.104, $P$ = 0.021, $R^2$ = 0.51).

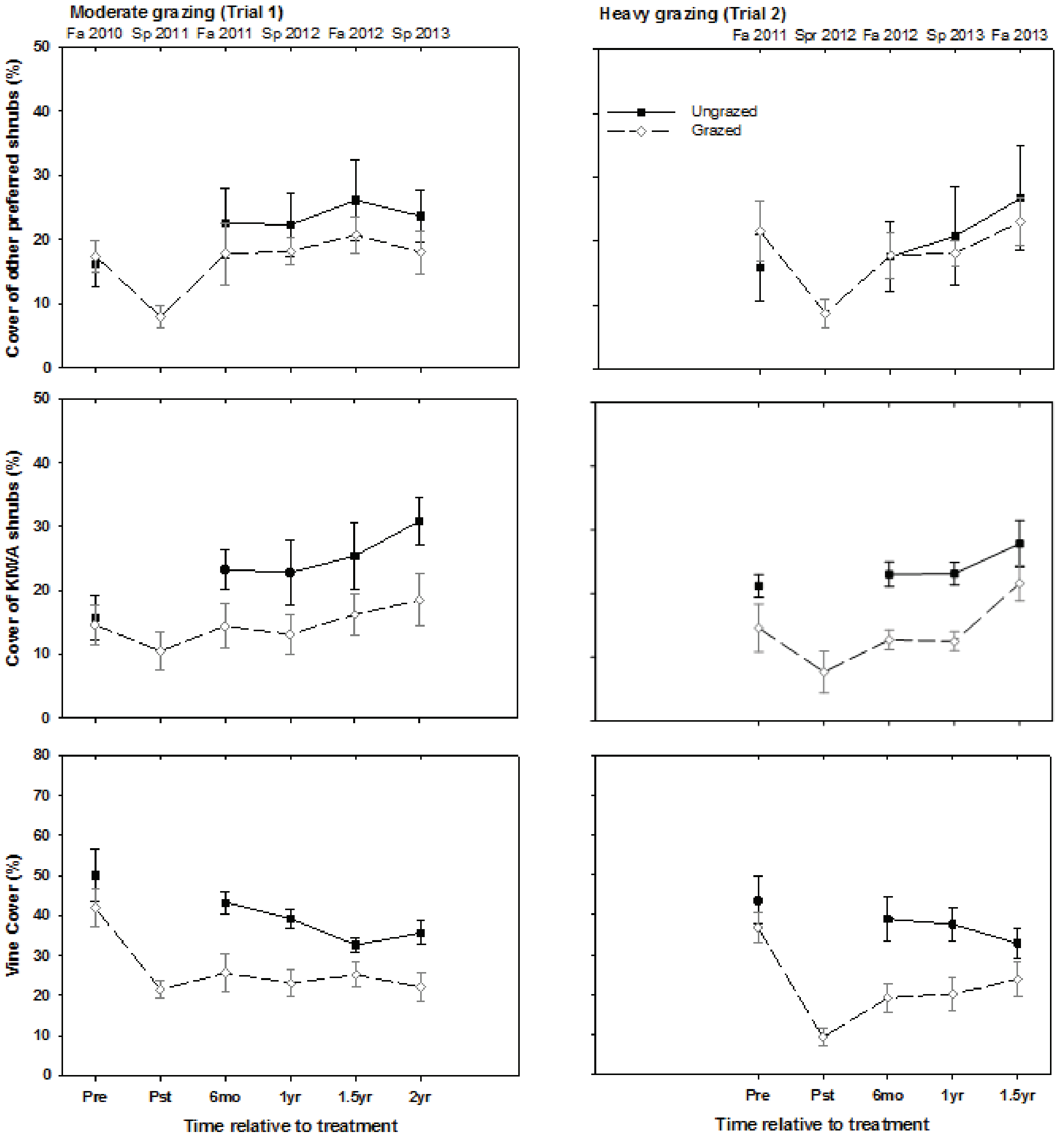

FIG. 3. Changes in percent cover of more preferred forage groups on goat-grazed and ungrazed coppice plots on Eleuthera, The Bahamas. Symbols are means within treatment groups; vertical bars are one standard error. The timing (Fall or Spring and calendar year) of each survey is also shown at the top. "Other preferred shrubs" (top panels) include *Acacia choriophylla, Pithecellobium keyense, Reynosia septentrionalis, and Thrinax morrisii*; "Kirtland's warbler (KIWA) shrubs" (middle panels) include *Erithalis fruticosa*, *Lantana involucrata*, and *Chiococca* spp.

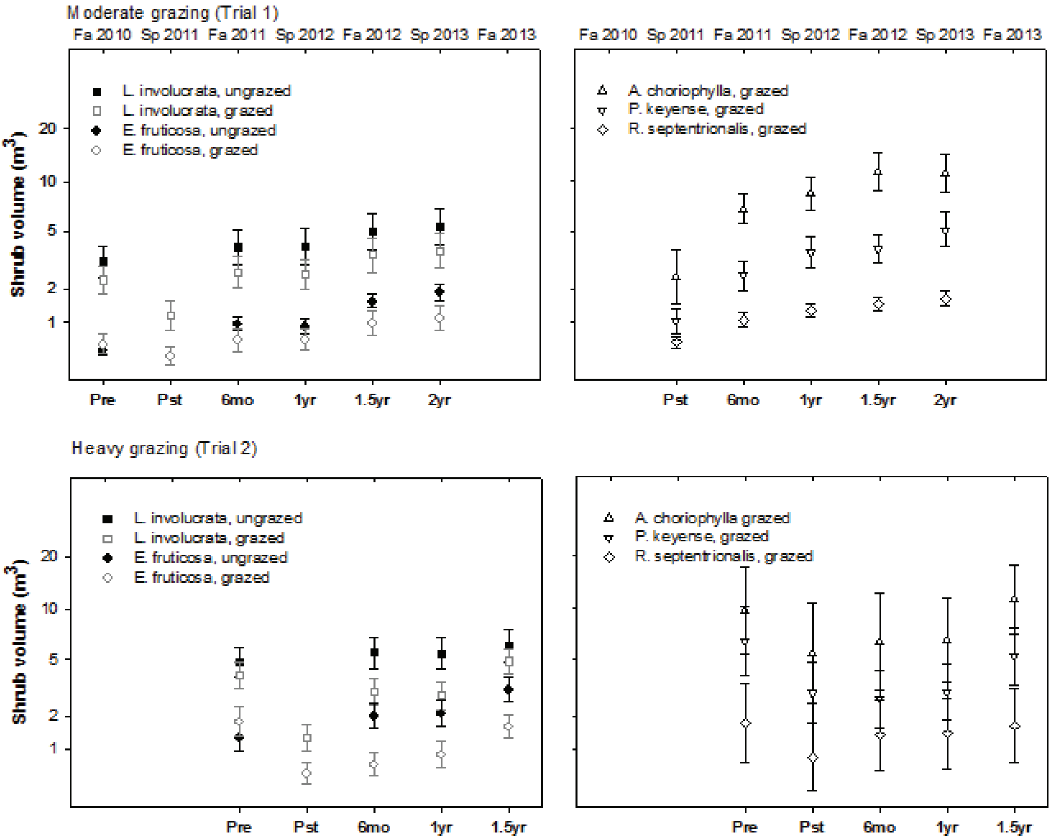

FIG. 4. Changes in shrub volume through time. Left panels show changes for *Erithalis fruticosa* and *Lantana involucrata* on goat-grazed and ungrazed coppice plots on Eleuthera, The Bahamas. Right panels show changes for *Acacia choriophylla, Pithecellobium keyense,* and *Reynosia septentrionalis* on grazed plots only. Symbols are means of log volume within species and treatment groups; vertical bars are one standard error. Labeling of the y-axis reflects volume in its arithmetic scale ($m^3$), but compression of the axis reflects the log-scaling used in analyses. The timing (Fall or Spring and calendar year) of each survey is also shown at the top.

### *Question 4: Grazing Effects on Kirtland's warbler Shrub Fruit Production*

We found lower than expected proportions (16% and 20%, respectively) of moderately and heavily browsed *E. fruticosa* shrubs fruited at least once during the post-treatment period compared to unbrowsed (60% per Trial) *E. fruticosa* shrubs (Trial 1, $\chi^2$ = 6.3, $P$ = 0.012; Trial 2, $\chi^2$ = 5.1, $P$ = 0.024). The proportion of *L. involucrata* shrubs fruiting at least once ranged from 65% - 85% with no significant difference in proportions between treatments.

Among the individual browsed *E. fruticosa* and *L. involucrata* shrubs that fruited at least once (species combined), we found no differences from unbrowsed shrubs in fruiting frequency (Trial 1 mode = 4 surveys; Trial 2 mode = 1 survey). Modal fruiting latency for both browsed and unbrowsed shrubs producing any fruit was 6 mo post-treatment in both Trials. We also found no systematic differences between treatments in the fruit abundance index for fruiting shrubs. Among browsed and unbrowsed shrubs from the heavy grazing trial, fruit production increased with canopy volume (see values associated with parameter $\gamma_{100}$ in Appendix 2, Table S6 Trial 2), decreased in the dry season (Fig. 5; see values associated with parameter $\gamma_{200}$, in Table S6, Trial 2), and increased over time (Fig. 5; see values associated with parameter $\gamma_{300}$ in Table S6, Trial 2). By contrast, fruit production showed a

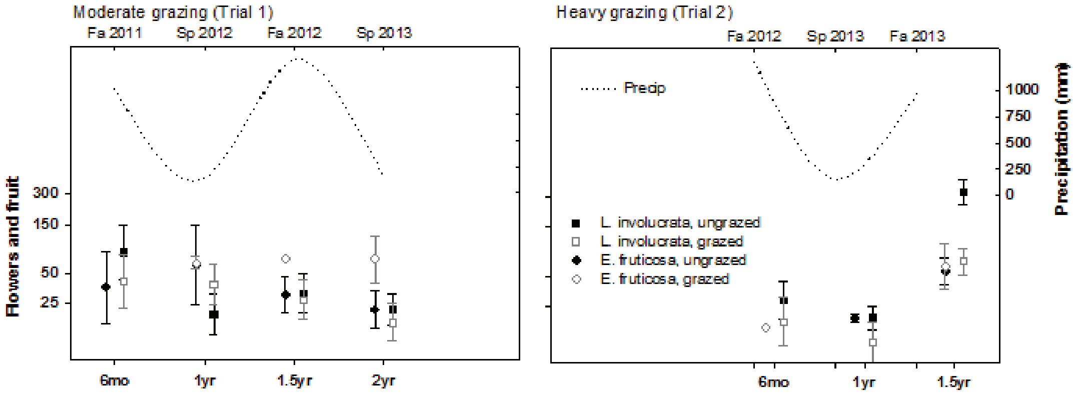

FIG. 5. Total numbers of flowers and fruits (combined as a fruit index) counted on individual fruiting *E. fruticosa* or *L. involucrata* shrubs from 6 mo through 1.5 or 2 yr post-treatment on grazed and ungrazed plots coppice plots on Eleuthera, The Bahamas. Analyses were done using combined numbers for *E. fruticosa* and *L. involucrata*, but separate abundances are shown here for qualitative comparison. Symbols are means of log abundance within species and treatment groups; vertical bars are one standard error. Labeling of the y-axis reflects volume in its arithmetic scale ($m^3$), but compression of the axis reflects the log-scaling used in analyses. Total precipitation recorded at Nassau International Airport during the 6 mo preceding each survey is shown in the top panels to highlight differences between the wet vs. dry season. The timing (Fall or Spring and calendar year) of each survey is also shown at the top.

small decrease through time among shrubs from the moderate grazing Trial (Fig. 5; see values associated with parameter $\gamma_{300}$ in Table S6, Trial 1), and we detected no substantial influence of canopy volume or season.

## DISCUSSION

Since our goat-grazed coppice showed rapid recovery toward its pre-grazing structure, which was minimally suitable for wintering Kirtland's warblers, our study suggests some feasibility for using periodic grazing to maintain their winter habitat. Our study was conducted in a pipeline corridor, but the results are applicable to other areas since the vegetation community was similar to that found elsewhere under equivalent disturbance and edaphic conditions. Yet, even in semi-natural areas, the use of goats for habitat management may be met by some skepticism given the negative impacts feral animals have had on many islands (Chynoweth et al. 2013; Coblentz 1978). However, controlled use of livestock is being successfully incorporated into land management efforts (Foderaro 2012; Mancilla-Leyton et al. 2013; Ruiz-Mirazo et al. 2011). Still, effective development of goat-based management is limited by poor availability of information in the scientific literature (Hart 2001).

We examined (a) how quickly suitable habitat structure returned following a single grazing treatment; (b) possible compositional change due to selective pressures; and (c) effects on critical food resources following grazing. We found vegetation structure (plant biomass, cover, and shrub volume) returned to near pre-treatment levels by 6 mo post-grazing and showed few significant differences from ungrazed coppice. This illustrates young coppice vegetation is quite resilient to anthropogenic and repetitive disturbance. Our goat grazing treatments occurred about 4 yr after mechanical clearing and in even closer proximity to two hurricanes. In some vegetation communities, the cumulative effects of repeated disturbances over short intervals can lead to dramatic and long-lasting changes in community structure and composition (e.g., Zedler et al. 1983).

Resilience of Bahamian coppice, in general, is likely derived from a collection of factors including vigorous resprouting of shrubs and trees (Lugo et al. 2006; Van Bloem et al. 2006). Resilience to short disturbance intervals may arise from the selective pressure of frequent tropical storms. Because the immediate effects of goat-grazing on woody plants mirror the defoliation and stem damage commonly occurring during hurricanes (Brokaw and Walker 1991; Lugo 2008), the rapid recovery of vegetation structure is not too surprising.

However, in contrast to hurricanes, goat grazing should be a more selective disturbance (e.g., Hadar et al. 1999) because goat forage preferences should result in disproportionate reduction of the most preferred plants. Although our goat confinement resulted in high selection of non-preferred forage, preferred shrub cover was reduced by 1.4-1.9 times the amount seen for less-preferred shrubs in our trials. The lack of strong differences between treatments in the cover of these groups 1.5 yr subsequent to grazing suggests our single treatments did not give less-preferred shrubs an obvious advantage in terms of their local abundance. Nonetheless, it is possible an advantage could emerge if the grazing treatment, *v.* some less selective disturbance, was repeated in a short time frame. Repeated goat grazing could also shift the balance among preferred shrub species due to differential mortality. *A. choriophylla* shrubs were most susceptible to death because goats stripped most available bark from these shrubs. Even among survivors, frequent goat browsing could reduce the production of new stems and substantially minimize the species in a stand (Larkin et al. 2012; Rojas-Sandoval et al. 2014).

Some herbaceous forage did show disproportionate responses to our single grazing treatments that could affect successional processes (e.g. Paul and Yavitt 2011). We have observed some vines in our system forming dense masses covering the canopy of low-stature shrubs or causing bending and breaking of small-diameter shrub stems. Reduced vine cover subsequent to grazing may allow smaller-stemmed shrubs, such as *L. involucrata*, to compete more effectively with larger species.

Grasses also appeared disproportionately affected by moderate grazing only, though the complex nature of the response suggests the possible combined influence of grazing and drought stress. Compared to other growth forms, grasses on moderately grazed plots showed the largest wet-dry seasonal swings in cover. Based on data from Nassau International Airport (~100 km west, available through the NOAA National Climatic Data Center), annual rainfall totals during the post-treatment years of our study were in the lowest 25% of historical values since 1978-1979. However, summer rainfall totals immediately following the moderate grazing treatment were 25% lower than summer rainfall following the heavy grazing treatment (see Figure 2: Fa 2011 *v.* Fa 2012). Despite evidence of wet season compensatory growth, it may have been more difficult for grasses stressed by grazing and more extreme summer drought to maintain foliage through the subsequent dry season (Barker et al. 1985; Ferraro and Oesterheld 2002). Such circumstances could influence post-grazing succession if other plants were able to take advantage of the decreased competition by, for example, increasing seedling recruitment.

We expected *E. fruticosa* and *L. involucrata* might benefit from the decreased competition because their seedlings may germinate at any time of year and are favored under high light conditions. However, prevailing drought conditions throughout our study probably contributed to generally low levels of fruit and, hence, seed production both on and around (i.e., dispersal sources) study plots, as well as to low germination rates. Similarly, the hurricanes occurring after each grazing treatment could have reduced fruit production and seedling recruitment on both grazed and ungrazed plots (Rathcke 2001; van Lent et al. 2014). Nonetheless, drought and storm effects being equal across treatments, we would have expected the added stress of grazing to show greater influence on fruiting. This mostly did not appear to be the case, except for a generally lower proportion of fruiting goat-browsed *E. fruticosa* shrubs.

### *Management implications*

Although goat grazing could prove to be an economically viable bird habitat management tool in the Bahamas, important caveats must be considered. First, we re-emphasize possible advocacy of such action only where it is impractical to allow natural succession toward older forest but where a low-stature, semi-natural plant assemblage is acceptable. We focused on utility ROWs due to the large area they cover and in light of the substantial spatially variability of late winter fruit resources. If extensive tracts of utilized land can be managed to support a vegetation community including fruit plants important to Kirtland's warblers and other frugivorous birds, it increases the probability there will be areas with available food resources prior to spring migration.

We also reiterate that our study is a first step toward the development of goat-based habitat management and strongly recommend evaluating the socio-economic feasibility of using goats to manage utility ROWs. The age of coppice in our study was at the low end of that used by Kirtland's warblers observed on Eleuthera by Wunderle et al (2010), and greater development of vegetation (e.g., 10 – 15 yr) may generally be desirable. It must be determined what maximum level of vegetation growth would be acceptable to utility companies gaining increased land-clearing capabilities and whether this is likely to yield suitable bird habitat. Then, research can focus on development of a grazing regime (stocking rates, grazing duration, season, etc.) that is economically and operationally feasible for goat producers while maintaining the desired vegetation and critical food resources for wildlife.

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## APPENDIX 1. ADDITIONAL METHODOLOGICAL DETAILS

### *Vegetation Measurement*

Litter cover, total plant cover, and percent cover of forage preference groups were estimated on a percentage scale using a point-intercept sampling method. Seventy sample points were regularly distributed at 0.5 m intervals along two intersecting transects (35 points per transect) running between opposing corners of the plot. Cover was calculated as the number of points where litter or vegetation (including leaves, stems, and small gaps within shrub canopies) were present divided by the total number of points sampled and multiplied by 100.

Aboveground plant biomass (average dry weight as g.m-2) was estimated using a visual obstruction technique (Fleming et al. 2014) within eight systematically spaced (to guarantee good coverage and aid relocation), individually marked 0.25 m2 quadrats per plot.

Canopy volume of individual shrubs was calculated as the volume of an ellipsoid using vertical canopy height and two perpendicular, horizontal width measurements. On all plots four shrubs, each, of *Erithalis fruticosa* and *Lantana involucrata* were measured; two shrubs, each of *Acacia choriophylla*, *Pithecellobium keyense*, *Reynosia septentrionalis* were measured, except for two plots where *R. septentrionalis* did not occur.

### *Analytical Methods*

Differences in litter depth, biomass, and vegetation cover (Questions 1 and 2, in part) on grazed plots only from pre-grazing through 6 months post-grazing were examined using the univariate approach to repeated-measures ANOVA (rmANOVA), which assumes sphericity in the covariance matrix (homogeneity of variance in differences between repeated measures). To correct for violations of sphericity, we used Greenhouse-Geisser adjusted degrees of freedom to assess F-ratios associated with within-subjects effects (e.g. time). Where omnibus analyses indicated a significant main effect of time, we used paired samples t-tests with a Bonferroni-corrected per-comparison $\alpha = 0.025$ to specifically test differences between pre-grazing vegetation and the two post-grazing surveys. Differences in those same variables between treatments (grazed or ungrazed) and within plots through time from 6 months to 1.5 or 2 years post-treatment were also examined using rmANOVA. In cases involving a significant time*treatment interaction, we followed with two "families" of simple comparisons conducted (1) within and (2) between treatment groups. Each simple comparison family included three specific comparisons with a per-comparison $\alpha = 0.017$. Within treatment we used paired samples t-tests to examine differences for: (1) 6 months *v*. 1 year post-treatment; (2) 6 months *v*. 1.5 years post-treatment, and (3) 1 *v*. 1.5 years post-treatment. Between treatment groups, we used independent samples t-tests to examine differences at 6 months, 1 year, and 1.5 years post-grazing.

When analyzing changes in the log volume of individual shrubs (Question 2, in part), we used 3-level hierarchical linear models (HLM, sensu Raudenbush and Bryk (2002); a.k.a. multilevel or mixed models) to account for correlations among measures clustered within shrubs and plots by including random effects (variance associated with shrubs within plots and variance associated with plots) along with fixed effects of explanatory variables (e.g., treatment). Though ultimately defined by a single regression equation including both main and interaction effects, the HLM model may be more readily conceived as a multilevel analysis where, in our case, multiple measures of individual shrubs within plots were modeled at Level 1 as a function of time or season (wet *v*. dry), with variable inclusion based on likelihood ratio tests. At Level 2, differences in average volume among shrubs within plots or in the effect of time, etc., were modeled as a function of species, where applicable (i.e., *E. fruticosa v. A. choriophylla*, *P. keyense*, and *R. septentrionalis*). At Level 3 differences among plots in average volume or changes through time were modeled as a function of treatment (grazed or ungrazed), where applicable. When examining volume changes of browsed shrubs from pre-grazing through 6 months post-grazing, time was represented by two variables contrasting pre-grazing volume with volume (1) immediately post-grazing and (2) at 6 months post-grazing. When examining volume of browsed and unbrowsed shrubs from 6 months through 1.5 or 2 years post-treatment, time was represented by the approximate number of months since the grazing treatment occurred and was scaled so that the intercept of the HLM regression represented average log volume at 18 months (1.5 years) post-treatment. In analyses comparing *E. fruticosa* or *L. involucrata* to the three competitors, species effects were represented by two dummy coded variables representing the difference between *E. fruticosa* or *L. involucrata* and (1) *R. septentrionalis* or (2) *A. choriophylla* and *P. keyense*, which were found to be very similar in volume and growth rates in preliminary analyses.

When analyzing the fruit abundance index among individual *E. fruticosa* and *L. involucrata* shrubs (combined) from 6 months through 1.5 or 2 years post-treatment, we again used 3-level HLM analyses within each trial. At Level 1 we examined whether the fruit index among fruiting shrubs was related to season (wet *v.* dry) or log shrub volume. After accounting for any effects of season or volume, we examined whether the index of fruit produced by individual shrubs, across occasions during which they fruited, showed any linear trend through time since treatment. Time was included at Level 1 and scaled so that the intercept of the HLM regression represented the average fruit index at 18 months post-treatment. At Level 3 we examined whether fruit production was related to treatment (grazed or ungrazed).

## APPENDIX 2. STATISTICAL TABLES

TABLE S1. Results from repeated measures ANOVA examining differences in vegetation characteristics through time within plots or between grazed and ungrazed plots in coppice vegetation on Eleuthera, The Bahamas. Separate analyses were performed for two time periods: pre-grazing through 6 mo post-grazing and 6 mo through 1.5 (Trial 2) or 2 yr (Trial 1) post-grazing. Trial 1 involved a moderate goat grazing treatment; Trial 2 involved heavy goat grazing. Significant effects are highlighted with **bold-face** *P* values.

| | | | **Trial 1** | | | **Trial 2** | | |
|---|---|---|---|---|---|---|---|---|
| Vegetation character | Period | Effect | *F* | *df* | *P* | *F* | *df* | *P* |
| Litter Cover | Pre - 6 mo (Grazed only) | time | 4.5 | 1.7, 6.9 | 0.059 | 0.8 | 1.2, 4.9 | 0.444 |
| | 6 mo - 1.5 or 2 yr | time | 5.1 | 2.4, 18.9 | **0.014** | 4.8 | 1.2, 9.8 | **0.049** |
| | | time*treatment | 1.7 | 2.4, 18.9 | 0.202 | 0.3 | 1.2, 9.8 | 0.642 |
| | | treatment | 1.2 | 1.0, 8.0 | 0.312 | 0.3 | 1.0, 8.0 | 0.605 |
| Mean litter depth | Pre - 6 mo (Grazed only) | time | 3.1 | 1.7, 6.9 | 0.112 | 8.2 | 1.3, 5.2 | **0.030** |
| | 6 mo - 1.5 or 2 yr | time | 6.9 | 2.4, 19.5 | **0.004** | 7.7 | 1.6, 13.1 | **0.008** |
| | | time*treatment | 1.1 | 2.4, 19.5 | 0.346 | 4.4 | 1.6, 13.1 | **0.041** |
| | | treatment | 3.1 | 1.0, 8.0 | 0.115 | 5.0 | 1.0, 8.0 | 0.056 |
| Biomass | Pre - 6 mo (Grazed only) | time | 26.4 | 1.2, 4.8 | **0.004** | 28.0 | 1.0, 4.1 | **0.006** |
| | 6 mo - 1.5 or 2 yr | time | 8.3 | 2.0, 15.9 | **0.003** | 21.9 | 2.0, 15.7 | **<0.001** |
| | | time*treatment | 1.4 | 2.0, 15.9 | 0.281 | 0.6 | 2.0, 15.7 | 0.539 |
| | | treatment | 0.8 | 1.0, 8.0 | 0.404 | 0.2 | 1.0, 8.0 | 0.656 |
| Total plant cover | Pre - 6 mo (Grazed only) | time | 75.8 | 1.2, 5.0 | **<0.001** | 417.2 | 1.6, 6.4 | **<0.001** |
| | 6 mo - 1.5 or 2 yr | time | 21.3 | 1.5, 12.3 | **<0.001** | 23.3 | 1.7, 13.4 | **<0.001** |
| | | time*treatment | 6.8 | 1.5, 12.3 | **0.014** | 0.4 | 1.7, 13.4 | 0.630 |
| | | treatment | 0.5 | 1.0, 8.0 | 0.501 | 0.6 | 1.0, 8.0 | 0.449 |

TABLE S2. Results from repeated measures ANOVA examining differences in cover of goat forage preference groups through time within plots or between grazed and ungrazed plots in coppice vegetation on Eleuthera, The Bahamas. Separate analyses were performed for two time periods: pre-grazing through 6 mo post-grazing and 6 mo through 1.5 (Trial 2) or 2 yr (Trial 1) post-grazing. Trial 1 involved a moderate goat grazing treatment; Trial 2 involved heavy goat grazing. “Other preferred shrubs” included *Acacia choriophylla*, *Pithecellobium keyense*, *Reynosia septentrionalis*; “Kirtland’s warbler shrubs” included *Lantana involucrata*, *Erithalis fruticosa*, and *Chiococca* spp. Significant effects are highlighted with **bold-face** *P* values.

| | | | **Trial 1** | | | **Trial 2** | | |
|---|---|---|---|---|---|---|---|---|
| Response | Period | Effect | *F* | *df* | *P* | *F* | *df* | *P* |
| Grass Cover (less preferred) | Pre - 6 mo (Grazed only) | time | 14.4 | 1.8, 7.3 | **0.003** | 48.3 | 1.8, 7.0 | **<0.001** |
| | 6 mo - 1.5 or 2 yr | time | 11.7 | 2.5, 19.7 | **<0.001** | 9.6 | 1.6, 12.9 | **0.004** |
| | | time*treatment | 2.5 | 2.5, 19.7 | 0.100 | 0.9 | 1.6, 12.9 | 0.405 |
| | | treatment | 0.7 | 1.0, 8.0 | 0.414 | 0.1 | 1.0, 8.0 | 0.823 |
| Less-preferred shrub cover | Pre - 6 mo (Grazed only) | time | 5.4 | 1.6, 6.5 | **0.046** | 17.9 | 1.3, 5.1 | **0.007** |
| | 6 mo - 1.5 or 2 yr | time | 6.6 | 2.4, 19.1 | **0.005** | 1.9 | 1.4, 11.3 | 0.203 |
| | | time*treatment | 3.5 | 2.4, 19.1 | **0.046** | 0.5 | 1.4, 11.3 | 0.570 |
| | | treatment | 0.9 | 1.0, 8.0 | 0.361 | 2.0 | 1.0, 8.0 | 0.196 |
| Other preferred shrub cover | Pre - 6 mo (Grazed only) | time | 7.0 | 1.5, 5.9 | **0.033** | 14.5 | 1.8, 7.4 | **0.003** |
| | 6 mo - 1.5 or 2 yr | time | 1.8 | 2.1, 16.6 | 0.191 | 9.6 | 1.9, 15.4 | **0.002** |
| | | time*treatment | 0.1 | 2.1, 16.6 | 0.920 | 0.7 | 1.9, 15.4 | 0.514 |
| | | treatment | 0.7 | 1.0, 8.0 | 0.425 | 0.1 | 1.0, 8.0 | 0.795 |
| Kirtland’s warbler shrub cover (preferred) | Pre - 6 mo (Grazed only) | time | 2.7 | 1.6, 6.7 | 0.139 | 1.7 | 1.1, 4.3 | 0.258 |
| | 6 mo - 1.5 or 2 yr | time | 5.2 | 2.4, 19.2 | **0.012** | 9.1 | 1.6, 12.7 | **0.005** |
| | | time*treatment | 0.4 | 2.4, 19.2 | 0.727 | 0.9 | 1.6, 12.7 | 0.416 |
| | | treatment | 3.9 | 1.0, 8.0 | 0.085 | 13.2 | 1.0, 8.0 | **0.007** |
| Vine Cover (preferred) | Pre - 6 mo (Grazed only) | time | 9.4 | 1.5, 5.9 | **0.017** | 17.4 | 1.7, 6.6 | **0.003** |
| | 6 mo - 1.5 or 2 yr | time | 2.6 | 1.8, 14.4 | 0.113 | 0.1 | 1.4, 10.9 | 0.912 |
| | | time*treatment | 1.9 | 1.8, 14.4 | 0.190 | 5.2 | 1.4, 10.9 | **0.035** |
| | | treatment | 15.1 | 1.0, 8.0 | **0.005** | 7.0 | 1.0, 8.0 | **0.030** |

TABLE S3. Results from 3-level hierarchical linear models for log volume of individual *Erithalis fruticosa* (A), *Lantana involucrata* (B), or *Acacia choriophylla*, *Pithecellobium keyense*, and *Reynosia septentrionalis* (C) shrubs for the time period covering pre-grazing through 6 mo post-treatment. Individual shrubs were sampled repeatedly through time within coppice plots on Eleuthera, The Bahamas. Coefficients for fixed effects of variables (e.g., time) are used to estimate log volume (y) for a shrub *i* in plot *j* at time *t* according to the model: $y_{tij} = \pi_{0ij} + \pi_{1ij}X_{tij\ldots} + \pi_{nij}Z_{tij}$, where $\pi_n$ may be further defined by a sub-model incorporating variables differing among shrubs within plots (e.g., $\pi_{0ij}$ = ß$_{00j}$ + ß$_{01j}$) or among plots (e.g., ß$_{00j} = \gamma_{000} + \gamma_{001}$). Proportional variance explained (under Random Effects) is derived from reduction in the estimated variance at a particular level following the addition of variables at that level and holding all else constant. Only fixed effects associated with a significant reduction in model deviance (likelihood ratio test, $P < 0.05$) were retained, but the significance (*P*) of effects based on univariate *t*-tests is also shown. Note that more than one variable may be used to capture a single effect (e.g., time contrasts).

| ***A) Erithalis fruticosa*** | **Trial 1** | | | | **Trial 2** | | | |
|---|---|---|---|---|---|---|---|---|
| **Fixed Effects** | **Coeffi-cient** | ***SE*** | ***df*** | ***P*** | **Coeffi-cient** | ***SE*** | ***df*** | ***P*** |
| *Model for initial (pre-grazing) volume:* $\pi_0$ = ß$_{00} = \gamma_{000}$ | | | | | | | | |
| Average log volume, $\gamma_{000}$ | 0.433 | 0.121 | 4 | 0.035 | 1.037 | 0.151 | 4 | <0.001 |
| *Model for immediate post- v. pre-grazing:* $\pi_1$ = ß$_{10} = \gamma_{100}$ | | | | | | | | |
| Average difference in log volume (pre- post), $\gamma_{100}$ | -0.142 | 0.049 | 54 | 0.006 | -0.622 | 0.073 | 57 | <0.001 |
| *Model for 6 mo post- v. pre-grazing:* $\pi_2$ = ß$_{20} = \gamma_{200}$ | | | | | | | | |
| Average difference in log volume (pre- 6 mo), $\gamma_{200}$ | 0.048 | 0.049 | 54 | 0.336 | -0.519 | 0.073 | 57 | <0.001 |
| **Random Effects** | **Variance** | ***χ2*** | ***df*** | ***P*** | **Variance** | ***χ2*** | ***df*** | ***P*** |
| Final variation among time points within shrubs | 0.023 | | | | 0.053 | | | |
| *Proportion of initial within-shrub variance explained by time contrasts* | *67.9* | | | | *29.6* | | | |
| Final variation among shrubs within plots | 0.254 | 554.01 | 14 | <0.001 | 0.373 | 333.30 | 15 | <0.001 |
| Final variation among plots | 0.00002 | 2.61 | 4 | >0.500 | 0.007 | 5.36 | 4 | 0.251 |

TABLE S3. (Continued)

| ***B) Lantana involucrata*** | **Trial 1** | | | | **Trial 2** | | | |
|---|---|---|---|---|---|---|---|---|
| **Fixed Effects** | **Coeffi-cient** | ***SE*** | ***df*** | ***P*** | **Coeffi-cient** | ***SE*** | ***df*** | ***P*** |
| *Model for initial (pre-grazing) volume:* $\pi_0 = ß_{00} = \gamma_{000}$ | | | | | | | | |
| Average log volume, $\gamma_{000}$ | 1.206 | 0.214 | 4 | 0.001 | 1.580 | 0.152 | 4 | <0.001 |
| *Model for immediate post- v. pre-grazing:* $\pi_1 = ß_{10} = \gamma_{100}$ | | | | | | | | |
| Average difference in log volume (pre- post), $\gamma_{100}$ | -0.432 | 0.091 | 57 | <0.001 | -0.724 | 0.143 | 54 | <0.001 |
| *Model for 6 mo post- v. pre-grazing:* $\pi_2 = ß_{20} = \gamma_{200}$ | | | | | | | | |
| Average difference in log volume (pre- 6 mo), $\gamma_{200}$ | 0.092 | 0.091 | 57 | 0.314 | -0.206 | 0.143 | 54 | 0.154 |
| **Random Effects** | **Variance** | ***χ2*** | ***df*** | ***P*** | **Variance** | ***χ2*** | ***df*** | ***P*** |
| Final variation among time points within shrubs | 0.082 | | | | 0.193 | | | |
| *Proportion of initial within-shrub variance explained by time contrasts* | *48.76* | | | | *41.85* | | | |
| Final variation among shrubs within plots | 0.430 | 250.59 | 15 | <0.001 | 0.234 | 65.02 | 14 | <0.001 |
| Final variation among plots | 0.102 | 9.45 | 4 | 0.050 | 0.003 | 5.11 | 4 | 0.275 |

TABLE S3. (Continued)

| ***C) A. choriophylla, P. keyense, & R. septentrionalis*** | **Trial 2** | | | |
|---|---|---|---|---|
| **Fixed Effects** | **Coefficient** | ***SE*** | ***df*** | ***P*** |
| *Model for initial (pre-grazing) volume:* $\pi_0$ = ß$_{00}$ = $\gamma_{000}$ | | | | |
| Average log volume, $\gamma_{000}$ | 1.836 | 0.265 | 4 | <0.001 |
| *Model for immediate post- v. pre-grazing:* $\pi_1$ = ß$_{10}$ = $\gamma_{100}$ | | | | |
| Average difference in log volume (pre- post), $\gamma_{100}$ | -0.539 | 0.092 | 63 | <0.001 |
| *Model for 6 mo post- v. pre-grazing:* $\pi_2$ = ß$_{20}$ = $\gamma_{200}$ | | | | |
| Average difference in log volume (pre- 6 mo), $\gamma_{200}$ | -0.484 | 0.092 | 63 | <0.001 |
| **Random Effects** | **Variance** | ***χ2*** | ***df*** | ***P*** |
| Final variation among time points within shrubs | 0.094 | | | |
| *Proportion of initial within-shrub variance explained by time contrasts* | *48.39* | | | |
| Final variation among shrubs within plots | 1.451 | 910.21 | 17 | <0.001 |
| Final variation among plots | 0.000 | 2.79 | 4 | >.500 |

TABLE S4. Results from 3-level hierarchical linear models for log volume of individual *Erithalis fruticosa* (A), *Lantana involucrata* (B) shrubs in Bahamian coppice for the time period covering 6 through 18 (Trial 2, heavy goat grazing) or 24 mo (Trial 1, moderate goat grazing) post-treatment. Coefficients for fixed effects of variables are used to estimate log volume (y) for a shrub *i* in plot *j* at time *t* according to the model: $y_{tij} = \pi_{0ij} + \pi_{1ij}X_{tij\ldots} + \pi_{nij}Z_{tij}$, where $\pi_n$ may be further defined by a sub-model incorporating variables differing among shrubs within plots (e.g., $\pi_{0ij} = ß_{00j} + ß_{01j}$) or among plots (e.g., $ß_{00j} = \gamma_{000} + \gamma_{001}$). Proportional variance explained (under Random Effects) is derived from reduction in the estimated variance at a particular level following the addition of variables at that level and holding all else constant. Only fixed effects associated with a significant reduction in model deviance (likelihood ratio test, $P < 0.05$) were retained, but the significance (*P*) of effects based on univariate *t*-tests is also shown.

| ***A) Erithalis fruticosa*** | **Trial 1** | | | | **Trial 2** | | | |
|---|---|---|---|---|---|---|---|---|
| **Fixed Effects** | **Coefficient** | ***SE*** | ***df*** | ***P*** | **Coefficient** | ***SE*** | ***df*** | ***P*** |
| *Model for volume at 18 mo post-grazing:* $\pi_0 = \gamma_{000} + \gamma_{001}$ | | | | | | | | |
| Average log volume, $\gamma_{000}$ | 0.975 | 0.111 | 8 | <0.001 | 1.427 | 0.161 | 8 | <0.001 |
| Difference in average volume on grazed plots $\gamma_{001}$ | -0.273 | 0.157 | 8 | 0.120 | -0.447 | 0.227 | 8 | 0.085 |
| *Model for volume at* **t** *months post-grazing:* $\pi_1 = \gamma_{100} + \gamma_{101}$ | | | | | | | | |
| Average change in log volume per month, $\gamma_{100}$ | 0.027 | 0.002 | 149 | <0.001 | 0.027 | 0.004 | 115 | <0.001 |
| Difference in average change on grazed plots $\gamma_{101}$ | -0.008 | 0.003 | 149 | 0.009 | 0.011 | 0.005 | 115 | 0.030 |
| *Model for seasonal difference in volume:* $\pi_2 = \gamma_{200}$ | | | | | | | | |
| Average decrease in log volume in dry *v.* wet season, $\gamma_{200}$ | -0.089 | 0.022 | 149 | <0.001 | -0.118 | 0.026 | 115 | <0.001 |
| **Random Effects** | **Variance** | ***χ2*** | ***df*** | ***P*** | **Variance** | ***χ2*** | ***df*** | ***P*** |
| Final variation among time points within shrubs | 0.015 | | | | 0.018 | | | |
| *Proportion of initial within-shrub variance explained by time & season (where applicable)* | *63.45* | | | | *69.79* | | | |
| Final variation among shrubs within plots | 0.236 | 2103.65 | 29 | <0.001 | 0.365 | 1878.46 | 30 | <0.001 |
| Final variation among plots | 0.00004 | 6.99 | 8 | >0.500 | 0.034 | 13.71 | 8 | 0.089 |
| *Proportion of initial among-plot variance explained by treatment* | *42.86* | | | | *65.60* | | | |

TABLE S4. (Continued)

| ***B) Lantana involucrata*** | **Trial 1** | | | | **Trial 2** | | | |
|---|---|---|---|---|---|---|---|---|
| **Fixed Effects** | **Coefficient** | ***SE*** | ***df*** | ***P*** | **Coefficient** | ***SE*** | ***df*** | ***P*** |
| *Model for volume at 18 mo post-grazing:* $\pi_0 = \gamma_{000} + \gamma_{001}$ | | | | | | | | |
| Average log volume, $\gamma_{000}$ | 1.667 | 0.222 | 9 | <0.001 | 1.989 | 0.169 | 8 | <0.001 |
| Difference in average volume on grazed plots $\gamma_{001}$ | | | | | -0.253 | 0.245 | 8 | 0.332 |
| *Model for volume at* **t** *months post-grazing:* $\pi_1 = \gamma_{100} + \gamma_{101}$ | | | | | | | | |
| Average change in log volume per month, $\gamma_{100}$ | 0.019 | 0.003 | 157 | <0.001 | 0.007 | 0.007 | 109 | 0.330 |
| Difference in average change on grazed plots $\gamma_{101}$ | | | | | 0.023 | 0.011 | 109 | 0.033 |
| *Model for seasonal difference in volume:* $\pi_2 = \gamma_{200}$ | | | | | | | | |
| Average decrease in log volume in dry v. wet season, $\gamma_{200}$ | -0.092 | 0.037 | 157 | 0.015 | -0.139 | 0.056 | 109 | 0.015 |
| **Random Effects** | **Variance** | ***χ2*** | ***df*** | ***P*** | **Variance** | ***χ2*** | ***df*** | ***P*** |
| Final variation among time points within shrubs (e) | 0.045 | | | | 0.080 | | | |
| *Proportion of initial within-shrub variance explained by time & season (where applicable)* | *28.66* | | | | *17.47* | | | |
| Final variation among shrubs within plots ($r_0$) | 0.412 | 1140.25 | 30 | <0.001 | 0.498 | 576.74 | 28 | <0.001 |
| Final variation among plots ($u_{00}$) | 0.380 | 45.96 | 9 | <0.001 | 0.0005 | 8.58 | 8 | 0.379 |
| *Proportion of initial among-plot variance explained by treatment* | | | | | *96.50* | | | |

TABLE S5. Results from 3-level hierarchical linear models comparing post-goat browsing volume changes in *Erithalis fruticosa* (A) or *Lantana involucrata* (B) to volume changes of *Acacia choriophylla*, *Pithecellobium keyense*, and *Reynosia septentrionalis* in Bahamian coppice from 6 through 18 (Trial 2, heavy goat grazing) or 24 mo (Trial 1, moderate goat grazing) post-treatment. Coefficients for fixed effects of variables are used to estimate log volume (y) for a shrub *i* in plot *j* at time *t* according to the model: $y_{tij} = \pi_{0ij} + \pi_{1ij}X_{tij\ldots} + \pi_{nij}Z_{tij}$, where $\pi_n$ may be further defined by a sub-model incorporating variables differing among shrubs within plots (e.g., $\pi_{0ij} = \beta_{00j} + \beta_{01j}$) or among plots (e.g., $\beta_{00j} = \gamma_{000} + \gamma_{001}$). Proportional variance explained (under Random Effects) is derived from reduction in the estimated variance at a particular level following the addition of variables at that level and holding all else constant. Only fixed effects associated with a significant reduction in model deviance (likelihood ratio test, $P < 0.05$) were retained, but the significance (*P*) of effects based on univariate *t*-tests is also shown.

| ***A) Grazed E. fruticosa vs. R. septentrionalis, A. choriophylla & P. keyense*** | **Trial 1** | | | | **Trial 2** | | | |
|---|---|---|---|---|---|---|---|---|
| **Fixed Effects** | **Coefficient** | ***SE*** | ***df*** | ***P*** | **Coefficient** | ***SE*** | ***df*** | ***P*** |
| *Model for volume at 18 mo post-grazing:* $\pi_0 = \beta_{00} + \beta_{01} + \beta_{02}$ | | | | | | | | |
| Average log volume of *E. fruticosa*, $\beta_{00}$ | 0.700 | 0.131 | 4 | 0.002 | 0.904 | 0.183 | 4 | 0.005 |
| Difference in volume of *R.septentrionalis*, $\beta_{01}$ | 0.203 | 0.224 | 43 | 0.370 | 0.078 | 0.401 | 42 | 0.847 |
| Difference in volume of *A. choriophylla* and *P. keyense*, $\beta_{02}$ | 1.232 | 0.191 | 43 | <0.001 | 1.171 | 0.285 | 42 | <0.001 |
| *Model for volume at* **t** *months post-grazing:* $\pi_1 = \beta_{10} + \beta_{11} + \beta_{12}$ | | | | | | | | |
| Average change in *E. fruticosa* log volume per month, $\beta_{10}$ | 0.019 | 0.003 | 175 | <0.001 | 0.038 | 0.005 | 120 | <0.001 |
| Difference in change for *R. septentrionalis*, $\beta_{11}$ | -0.005 | 0.005 | 175 | 0.276 | -0.028 | 0.009 | 120 | 0.004 |
| Difference in change for *A. choriophylla* and *P. keyense*, $\beta_{12}$ | 0.007 | 0.004 | 175 | 0.070 | 0.005 | 0.007 | 120 | 0.497 |
| *Model for seasonal difference in volume:* $\pi_2 = \beta_{20} + \beta_{21} + \beta_{22}$ | | | | | | | | |
| Average decrease in *E. fruticosa* log volume in dry *v*. wet season, $\beta_{20}$ | -0.086 | 0.036 | 175 | 0.016 | -0.113 | 0.047 | 120 | 0.019 |
| Difference for *R. septentrionalis*, $\beta_{21}$ | 0.086 | 0.061 | 175 | 0.155 | 0.073 | 0.098 | 120 | 0.461 |
| Difference for *A. choriophylla* and *P. keyense*, $\beta_{22}$ | 0.113 | 0.052 | 175 | 0.030 | -0.081 | 0.071 | 120 | 0.254 |
| **Random Effects** | **Variance** | ***χ2*** | ***df*** | ***P*** | **Variance** | ***χ2*** | ***df*** | ***P*** |
| Final variation among time points within shrubs) | 0.019 | | | | 0.030 | | | |
| *Proportion of initial within-shrub variance explained by time & season* | *52.39* | | | | *59.97* | | | |
| Final variation among shrubs within plots | 0.314 | 2837.49 | 39 | <0.001 | 0.733 | 3181.86 | 38 | <0.001 |
| *Proportion of initial among-shrub variance explained by species contrasts* | *51.41* | | | | *26.23* | | | |
| Final variation among plots | 0.00002 | 3.25 | 4 | >0.500 | 0.0001 | 2.178 | 4 | >0.500 |

TABLE S5. (Continued)

| ***B) Grazed L. involucrata vs. R. septentrionalis, A. choriophylla & P. keyense*** | **Trial 1** | | | | **Trial 2** | | | |
|---|---|---|---|---|---|---|---|---|
| **Fixed Effects** | **Coefficient** | ***SE*** | ***df*** | ***P*** | **Coefficient** | ***SE*** | ***df*** | ***P*** |
| *Model for volume at 18 mo post-grazing:* $\pi_0 = ß_{00} + ß_{01} + ß_{02}$ | | | | | | | | |
| Average log volume of *L. involucrata*, $ß_{00}$ | 1.526 | 0.164 | 4 | <0.001 | 1.767 | 0.216 | 4 | <0.001 |
| Difference in volume of *R. septentrionalis*, $ß_{01}$ | -0.623 | 0.261 | 44 | 0.021 | -0.785 | 0.432 | 37 | 0.077 |
| Difference in volume of *A. choriophylla* and *P. keyense*, $ß_{02}$ | 0.424 | 0.222 | 44 | 0.063 | 0.307 | 0.315 | 37 | 0.336 |
| *Model for volume at t months post-grazing:* $\pi_1 = ß_{10} + ß_{11} + ß_{12}$ | | | | | | | | |
| Average change in *L. involucrata* log volume per month, $ß_{10}$ | 0.021 | 0.003 | 179 | <0.001 | 0.031 | 0.006 | 111 | <0.001 |
| Difference in change for *R. septentrionalis*, $ß_{11}$ | -0.006 | 0.006 | 179 | 0.285 | -0.021 | 0.011 | 111 | 0.069 |
| Difference in change for *A. choriophylla* and *P. keyense*, $ß_{12}$ | 0.006 | 0.005 | 179 | 0.246 | 0.012 | 0.008 | 111 | 0.144 |
| *Model for seasonal difference in volume:* $\pi_2 = ß_{20} + ß_{21} + ß_{22}$ | | | | | | | | |
| Average decrease in *L. involucrata* log volume in dry *v.* wet season, $ß_{20}$ | -0.109 | 0.045 | 179 | 0.016 | -0.233 | 0.059 | 111 | <0.001 |
| Difference for *R. septentrionalis*, $ß_{21}$ | 0.109 | 0.078 | 179 | 0.162 | 0.193 | 0.118 | 111 | 0.105 |
| Difference for *A. choriophylla* and *P. keyense*, $ß_{22}$ | 0.136 | 0.066 | 179 | 0.041 | 0.039 | 0.086 | 111 | 0.651 |
| **Random Effects** | **Variance** | ***χ2*** | ***df*** | ***P*** | **Variance** | ***χ2*** | ***df*** | ***P*** |
| Final variation among time points within shrubs (e) | 0.032 | | | | 0.042 | | | |
| *Proportion of initial within-shrub variance explained by time & season* | *41.21* | | | | *51.14* | | | |
| Final variation among shrubs within plots ($r_0$) | 0.429 | 2271.47 | 40 | <0.001 | 0.799 | 2103.14 | 33 | <0.001 |
| *Proportion of initial among-shrub variance explained by species contrasts* | *26.91* | | | | *8.63* | | | |
| Final variation among plots ($u_{00}$) | 0.022 | 7.45 | 4 | 0.113 | 0.0002 | 3.96 | 4 | >0.500 |

TABLE S6. Results from 3-level hierarchical linear models for the index of fruit production (log fruit and flower total) by individual *Erithalis fruticosa* and *Lantana involucrata* shrubs (combined) on grazed and ungrazed Bahamian coppice plots from 6 through 24 mo post-treatment. Only shrubs observed fruiting at a given survey are included in analyses. Coefficients for fixed effects of variables are used to estimate the fruit index (y) for fruiting shrub *i* in plot *j* at time *t* according to the model: $y_{tij} = \pi_{0ij} + \pi_{1ij}X_{tij\ldots} + \pi_{nij}Z_{tij}$, where $\pi_n$ may be further defined by a sub-model incorporating variables differing among shrubs within plots (e.g., $\pi_{0ij} = \beta_{00j} + \beta_{01j}$) or among plots (e.g., $\beta_{00j} = \gamma_{000} + \gamma_{001}$). Proportional variance explained (under Random Effects) is derived from reduction in the estimated variance at a particular level following the addition of variables at that level and holding all else constant. Only fixed effects associated with a significant reduction in model deviance (likelihood ratio test, $P < 0.05$) were retained, but the significance (*P*-value) of effects based on univariate *t*-tests is also shown.

| | **Trial 1** | | | | **Trial 2** | | | |
|---|---|---|---|---|---|---|---|---|
| **Fixed Effects** | **Coefficient** | ***SE*** | ***df*** | ***P*** | **Coefficient** | ***SE*** | ***df*** | ***P*** |
| *Model for fruit index at 18 mo post-grazing:* $\pi_0 = \gamma_{000}$ | | | | | | | | |
| Average log fruit abundance with average canopy volume, $\gamma_{000}$ | 3.253 | 0.199 | 9 | <0.001 | 4.731 | 0.211 | 9 | <0.001 |
| *Model for fruit index with changes in canopy volume:* $\pi_1 = \gamma_{100}$ | | | | | | | | |
| Change in log fruit abundance per unit change in log volume, $\gamma_{100}$ | | | | | 0.872 | 0.194 | 88 | <0.001 |
| *Model for seasonal difference in fruit index:* $\pi_2 = \gamma_{200}$ | | | | | | | | |
| Average decrease in log fruit abundance in dry *v.* wet season, $\gamma_{200}$ | | | | | -1.183 | 0.271 | 88 | <0.001 |
| *Model for fruit index at* **t** *months post-grazing:* $\pi_1 = \gamma_{300}$ | | | | | | | | |
| Average change in log fruit abundance per month, $\gamma_{300}$ | -0.047 | 0.017 | 117 | 0.007 | 0.141 | 0.023 | 88 | <0.001 |
| **Random Effects** | **Variance** | ***χ2*** | ***df*** | ***P*** | **Variance** | ***χ2*** | ***df*** | ***P*** |
| Final variation among time points within shrubs | 1.489 | | | | 1.152 | | | |
| *Proportion of initial within-shrub variance explained by volume, season, and time (where applicable)* | *8.98* | | | | *48.85* | | | |
| Final variation among shrubs within plots | 0.723 | 76.25 | 35 | <0.001 | 0.083 | 38.93 | 37 | 0.383 |
| Final variation among plots | 0.068 | 12.83 | 9 | 0.17 | 0.169 | 21.45 | 9 | 0.011 |