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Disturbance Type and Plant Successional Communities in Bahamian Dry Forests

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ABSTRACT

Different disturbances in similar habitats can produce unique successional assemblages of plants. We collected plant species composition and cover data to investigate the effects of three common types of disturbances—fire, anthropogenic clearing ('cleared'), and clearing followed by goat grazing ('cleared-and-grazed')—on early-successional coppice (dry forest) community structure and development on Eleuthera, Bahamas. For each disturbance type, both the ground layer (< 0.5 m height) and shrub layer (> 0.5 m height) were sampled in eight patches (> 1 ha) of varying age (1–28 yr) since large-scale mature coppice disturbance. Overall, plant communities differed among disturbance types; several common species had significantly higher cover in the shrub layer of fire patches, and cleared-and-grazed patches exhibited higher woody ground cover. Total percent cover in the shrub layer increased in a similar linear fashion along the investigated chronosequence of each disturbance type; however, cover of the common tree species, *Bursera simaruba*, increased at a notably slower rate in cleared-and-grazed patches. The pattern of increase and subsequent decrease in cover of *Lantana* spp. and *Zanthoxylum fagara* in the shrub layer was characterized by longer persistence and higher covers, respectively, in cleared-and-grazed patches, which also exhibited low peak cover and fast decline of nonwoody ground cover. Our results suggest that goats may accelerate some aspects of succession (*e.g.*, quickly removing nonwoody ground cover) and retard other aspects (*e.g.*, inhibiting growth of tree species and maintaining early-successional shrubs in the shrub layer). These effects may lead to different successional trajectories, and have important conservation implications.

Key words: Bahamas; coppice; dry evergreen forest; fire; goat grazing; Kirtland's Warbler; succession.

Different disturbances in similar habitats can produce unique successional assemblages of plants. This may be explained by the different selective filters that various disturbances impart on the plants that are directly affected. For example, anthropogenic clearing and fire, two large-scale disturbances within tropical forests, would be expected to result in different plant communities and successional trajectories through time. Clearing for agriculture and pasture, which is often followed quickly by abandonment, is arguably the most common large-scale disturbance in Neotropical forests (Chazdon *et al.* 2007) and involves the near complete removal of vegetation. Regeneration of tropical and subtropical plant communities following abandonment depends on root resprouting abilities, release from soil seed banks, and immigration. Fire tends to be a disturbance of low intensity in tropical and subtropical systems (compared with its effects elsewhere; Giglio *et al.* 2006); though prospects of its increasing frequency due to deforestation, fragmentation, and climate change (Cochrane *et al.* 1999; Cochrane 2001, 2003) make it a disturbance of high concern. Regeneration of tropical and subtropical plant communities following fire will depend on fire tolerance and resprouting abilities of plants directly affected by fire, plants escaping the potentially patchy nature of fire in such systems (see Kellman & Tackaberry 1993), local seed inputs, and immigration via wind and animal seed dispersal. A general increase in species diversity over time has been documented in some instances following clearing (Chazdon *et al.* 2007), and fire (Uhl *et al.* 1981), though the composition of early-successional plant communities in such settings should differ.

Managed grazing of anthropogenically cleared lands can also affect successional trajectories and resultant plant communities in tropical and subtropical forest systems. After an initial clearing event, grazers reduce recovery of species-richness and diversity of natural vegetation in tropical dry forest (Stern *et al.* 2002). Grazers also affect structural attributes of early-successional plant communities by increasing numbers of small stems and preventing the growth and development of larger stems (Stern *et al.* 2002); both of these effects can be interpreted as retarding forest succession. When grasses and nonwoody vegetation dominate cleared landscapes, however, grazers at low stocking densities can accelerate

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the establishment and cover of woody/shrubby vegetation (Posada *et al.* 2000). Because land use history, including grazing, is a major driver of developing plant communities in tropical forests (see Aide *et al.* 1996), inclusion of data on the effects that grazers may have on vegetation dynamics following an initial clearing, rather than solely after the removal of grazing, is necessary to strengthen our understanding of succession in these systems.

In this study, we collected plant species composition data to investigate the effects of three different types of disturbances—fire, clearing (*i.e.*, bulldozing), and clearing followed by goat grazing—on the vegetation composition and structure of resultant early-successional coppice (also known as 'dry evergreen forest'; see Smith & Vankat 1992) communities (> 1 ha) on Eleuthera, the Bahamas. Coppice, a term used to describe dry broadleaf (as opposed to pine) forested communities with low to high canopy height (2–12 m) throughout the Bahamian archipelago (see Smith & Vankat 1992), is found at various stages of development on Bahamian islands, and makes up a substantial portion of the vegetation on large islands and cays of the archipelago's central and southern portions (Correll & Correll 1982). Fire and clearing via bulldozing are common in the Bahamas (see Smith & Vankat 1992), and goat farming is practiced on a number of the Commonwealth's islands. Although information on contemporary rates of such disturbances in the Bahamas is lacking, it has been argued that anthropogenic disturbance has led to the loss of coppice plant species (Correll & Correll 1982), and that disturbance-related pressures on coppice communities will invariably increase in the future, with the potential for further loss of plant species, even at local (within island) scales (Smith & Vankat 1992). Identifying different vegetation patterns in coppice habitats recently impacted by different disturbances may assist conservation efforts aimed at maintaining the diversity of the plant community. In addition, early-successional coppice habitats have been identified as important to resident and Neotropical migratory birds (Currie *et al.* 2005), including the Kirtland's Warbler, which winters in early-successional habitats exclusively in the Bahamian archipelago and consumes fruits of early-successional coppice species (Wunderle *et al.* 2010). Therefore, identifying which disturbance types best promote desired habitats may be beneficial to bird conservation.

We test several hypotheses regarding the general and temporal effects of fire, clearing, and clearing with subsequent managed goat grazing on several plant community metrics in a chronosequence context. Although the mechanisms underlying vegetation dynamics cannot be identified in chronosequence studies (see Chazdon *et al.* 2007), these studies provide a means of identifying general patterns of successional vegetation dynamics following disturbance and can help generate hypotheses of underlying mechanisms, which could later be tested using long-term permanent plots (see Bakker *et al.* 1996). In addition, metrics related to 'cover', which is of interest in our study, have shown consistent linear patterns in successional chronosequences and long-term permanent-plot studies (Chazdon *et al.* 2007). We predicted that there would be general differences in coppice plant communities as a function of disturbance type due to species-specific responses to different disturbances. We also predicted there to be temporal differences in (A) subsets of species or species groups and (B) total cover (%) of vegetation as a function of disturbance type. Specifically, here, we were concerned with recovery of primary tree species such as *Bursera simaruba* (L.) Sarg. (Burseraceae) and *Coccoloba diversifolia* Jacq. (Polygonaceae) following different disturbances. We also expected species with mechanical defenses or low palatability to goats (*i.e.*, less preferred browse; see Relva & Veblen 1998), such as *Zanthoxylum fagara* (L.) Sarg. (Rutaceae) and *Lantana* spp. (Verbenaceae), to perform better in cleared-and-grazed patches. We intend our findings to contribute to a better conceptual understanding of three common disturbances in terms of their successional outcomes.

METHODS

STUDY SITE.—Fieldwork for the study was conducted on the southern end of Eleuthera, the Bahamas (Fig. S1). Eleuthera (26° 06′ N, 76°08′ W) is a low elevation (63 m maximum elevation) island located in the middle of the Bahamian Archipelago and has a climate consisting of an annual wet and dry season, with most of its mean annual rainfall (1090 mm/yr) occurring from May through October (Campbell 1978, Sealey 2006). Vegetation on the island is dominated by coppice scrub. Coppice plant communities include primarily evergreen and semi-deciduous broadleaf trees and shrubs, which form thick brush or dense vegetation on poorly developed soils on limestone substrate (Correll 1979, Byrne 1980, Sealey 2006). The most common plant families include Leguminosae, Gramineae, Asteraceae, Euphorbiaceae, and Cyperaceae (Vincent & Kwit 2007).

Early-successional habitat patches (> 1 ha) matching descriptions of having been (1) cleared for agriculture or intended development (hereafter, 'cleared' patches); (2) cleared and subsequently subjected to managed grazing by goats (hereafter, 'cleared-and-grazed' patches); and (3) created exclusively by fire (hereafter, 'fire' patches), were initially identified using remote sensing-based maps of forest disturbance type and age since large-scale disturbance in mature coppice (Helmer *et al.* 2010). The maps came from simultaneously classifying forest disturbance type and age with a time series of cloud-cleared image mosaics extending from 1984 to 2005. The image mosaic for each time step was composed of the clear parts of Landsat and Advance Land Imager data and was created with regression tree normalization. Vegetations resulting from the various disturbance types and the various years of disturbance have unique spectral signatures over time, making their distinction possible when the image bands from all dates in a time series are used when developing maps from the satellite imagery. Vegetation recovering from disturbance in 1 yr, for example, has a different spectral-temporal signature from vegetation disturbed during some other year, with spectral indices indicative of green vegetation and canopy structure dropping sharply at time of disturbance and gradually increasing afterwards. Time since disturbance, therefore, is detectable and defined in this manner. In addition, the different disturbance types differ spectrally, both initially and in the pattern of spectral changes over time. Return to pre-disturbance spectral signatures, for example, takes ~ 8 yr for escaped fire but up to 14 yr for land cleared by bulldozing at our study site. Validation of disturbance types with mature coppice disturbance occurring from 1996 onward was accomplished by field verification; for disturbances before 1996, disturbance type was validated with visual interpretation of single image dates. Other chronosequence studies in tropical forests have also used time series of aerial photos or satellite images in choosing sites (*e.g.*, Aide *et al.* 1996, Ruiz *et al.* 2005), and in our case, the resultant maps have been useful in other studies on southern Eleuthera (Wunderle *et al.* 2010). Cleared patches were typically bulldozed and subsequently abandoned or left alone. Patches of coppice on Eleuthera are cleared for two reasons: (1) proof of land utilization (*e.g.*, clearing to exhibit, at a minimum, intention of agriculture, especially on community-held land) and (2) development, the latter of which often does not materialize. Cleared-and-grazed patches were typically bulldozed and subsequently grazed intermittently by goats for up to several years. Fire patches were the result of escaped fires of natural or anthropogenic origin. Large-scale 'gaps' during the timeframe of interest were not created by tropical cyclones, although Hurricane Floyd, which impacted Eleuthera in September 1999, may have contributed to increased fuels, and thus improved fire spread, as well as the ability to detect burned areas remotely (Helmer *et al.* 2010). A total of eight patches of each type of disturbance were selected in a stratified random fashion. Sampled patches ranged in size and age from 1 to 23 ha and 1 to 28 yr since onset of disturbance (Table 1), and were not subject to subsequent large-scale disturbances.

TABLE 1. *General information on 24 study sites (*i.e.*, patch) sampled for species composition data on Eleuthera, the Bahamas. Each patch has been disturbed by clearing (*i.e.*, bulldozing), clearing followed by subsequent goat grazing, or fire.*

Patch	Disturbance	Elevation (m)	Size (ha)	Patch age (yr)	Line intercept length (m)
1	Cleared	2.4	1	2	50
2	Cleared	4.5	2.61	6	100
3	Cleared	1.72	1.35	7.5	50
4	Cleared	1.32	1	4	50
5	Cleared	5.38	2.79	10	100
6	Cleared	9.28	4.23	10	100
7	Cleared	4.02	6.6	7.5	150
8	Cleared	3.1	4	21	100
9	Cleared-and-grazed	−0.06	7.29	10	150
10	Cleared-and-grazed	1.14	5	10	100
11	Cleared-and-grazed	3.98	16.83	2	150
12	Cleared-and-grazed	0.08	1	6	50
13	Cleared-and-grazed	0.1	5.5	4	100
14	Cleared-and-grazed	1.86	1	1	50
15	Cleared-and-grazed	4.42	1	28	50
16	Cleared-and-grazed	0.96	5	15	90
17	Fire	3.6	3.4	5	50
18	Fire	2.3	5	5	100
19	Fire	5.9	2.97	6.5	100
20	Fire	4.6	600	8.5	150
21	Fire	4.2	4.5	10	100
22	Fire	8.4	13.84	23	100
23	Fire	5.3	5	5	90
24	Fire	13.4	6	7	100

VEGETATION SAMPLING.—The line-intercept method (Canfield 1941) was used to sample vegetation in each patch. Vegetation was sampled in May and June of 2008 and 2009, periods that encompassed the beginning of the rainy season in the Bahamian archipelago. A total of 50–150 m was sampled in each patch depending on the size of the patch; patches <2 ha had 50 m sampled, patches between 2 and 6 ha had 100 m sampled, and patches > 6 ha had 150 m sampled. Both the ground layer (< 0.5 m height) and the shrub/tree layer (> 0.5 m height; hereafter 'shrub layer') were sampled simultaneously along the same line. When possible, one line, originating > 10 m from a patch edge at a random location along the patch perimeter and proceeding in a random direction toward the patch center, was used for vegetation sampling. Because of certain barriers such as thick brush and karst sinkholes, one continuous line was not always used to sample each patch, and sometimes several lines were needed to sample a patch. All shrubs, trees, and herbs (excluding vines) intersecting the line at a height > 0.5 m (hereafter, 'shrub layer') were identified to species or genus, and horizontal linear measurements (cm) of plant intercepts along the course of the transect were recorded. The sampling regime used sufficiently captured the α richness of each patch; this was determined by producing sample-based rarefaction curves for each patch (using EstimateS software; Colwell 2006) by splitting the 'transect' (line intercept) into 10 m segments and counting the number of 'hits' for each species along the 10-m segment. In all cases, the 95% confidence interval of the sample-based rarefaction estimate at the end of the line intercept overlapped with the 95% confidence interval of the Chao 2 species-richness estimator for the sampled patch. Vegetation < 0.5 m height (hereafter, the 'ground layer') was categorized as woody or nonwoody (*i.e.*, no species-level data were collected for the ground layer) due to lack of floral structures necessary to distinguish among species (especially nonwoody species) at the time of sampling, and linear measurements of these two categories were taken in the same manner as described for species in the shrub layer. Linear measures were converted to percent cover and relative cover (*i.e.*, percent of total plant cover) in each patch. Measures of cover reflected the canopy 'influence' and hence may have included minute breaks in cover (see Bonham 1989). Nomenclature of plant species followed Correll and Correll (1982), and voucher specimens were collected and deposited in the Bahamas National Herbarium in the Nassau Botanical Garden.

ANALYSES: PLANT COMMUNITIES AND SPECIES AS A FUNCTION OF DISTURBANCE.—Nonmetric multidimensional scaling (NMDS) was used to construct ordinations depicting distances among sampled patches as a function of species percent covers (shrub layer), which were transformed (Wisconsin standardization) to reduce undue emphasis on the most common species and to adjust for differences in total vegetation cover among sites. More specifically, each species entry (*i.e.*, each value in a column in a site x species matrix) was divided by its own maximum value. For each site (*i.e.*, each row in the site x species matrix), the resultant species entries were divided by their resultant total for that site. The Bray–Curtis distance measure was used because it is known to be consistently interpretable across very long gradients (McCune & Grace 2002). This approach allowed the visualization of general differences in plant community composition, in the shrub layer, among the three disturbance types (see McCune & Grace 2002). The fewest number of axes that would adequately represent the data in the NMDS ordination was determined by using stress values (McCune & Grace 2002). Stress values showed that two dimensions was the lowest number of axes that would adequately represent our shrub layer data in the NMDS plots (one axis ~ 30, two axes ~ 15.56, three axes ~ 10.22, four axes ~ 7.19, five axes ~ 5.55). Adding a third dimension did not provide additional insight and did not substantially alter NMDS plots. All NMDS analyses included multiple random initializations to help reduce the possibility that the numerical optimization procedures were not trapped far from global optima. In addition, the Bray–Curtis distances were utilized in a permutational multivariate analysis of variance (MANOVA) (Excoffier *et al.* 1992, McArdle & Anderson 2001). In general, this method partitions multivariate variation among independent variables, and here tests for differences in plant communities (based on species and their associated covers in each patch) as a function of disturbance type. All multivariate analyses were accomplished using the vegan package (Oksanen *et al.* 2010) in the R language and environment (R Development Core Team 2010).

To compare percent cover of individual species in the shrub layer among the three different patch types, single-factor analysis of variance (ANOVA) was conducted on all species found in more than 50 percent of the patches (*i.e.*, >12 patches). Tukey's pairwise comparisons were calculated for species with P-values that were statistically significant ($P<0.05$). Shapiro–Wilks test of Normality and Levene's test of homogeneity were used to test for normality and homogeneity of variance, respectively.

Tests for differences in α diversity among different disturbance types were accomplished by ANOVA. We calculated Shannon–Weiner diversity indices (H') for each patch using the following equation:

$$H' = \sum_{i=1}^{S} p_i \ln p_i,$$

where s is species-richness, and p_i is the relative cover of the ith species (*e.g.*, Whittaker 1960, Bazzaz 1975, Ikeda 2003).

ANALYSES: CHRONOSEQUENCE TRENDS.—Successional trends among the three disturbances were investigated for the following variables obtained in each patch's shrub layer: total plant cover, cover of the two primary tree species, and cover of two species of ephemeral and unpalatable shrub species (*i.e.*, species which contain significant secondary compounds or mechanical defenses). Total plant cover was calculated as the sum of percent covers of all species sampled in a patch. Primary tree species with sufficient cover data to address separately included *B. simaruba* and *C. diversifolia*. Ephemeral and unpalatable shrub species with sufficient cover data included *Lantana* spp. (summed covers of *Lantana bahamensis* Britt. (Verbenaceae), *Lantana involucrata* L., and *Lantana demutata* Millsp., all of which are native to the study area), which is known to contain secondary compounds harmful to ruminant grazers (Sharma *et al.* 2007), and *Z. fagara*, which is the most abundant thorny shrub in our study system.

For total plant cover and primary tree species cover through time (years since large-scale mature coppice disturbance; hereafter, 'age'), our goal was to test whether the linear rate of increase (*i.e.*, slope) in percent cover differed among disturbance categories. A no-intercept analysis of covariance (ANCOVA) approach was used for total plant cover and for *B. simaruba* cover. For *C. diversifolia*, we used a full ANCOVA (intercept included) approach due to the presence of significant intercept and intercept adjustment terms, and the simultaneous alteration of the inference regarding the slope adjustment term. In each case, an F-test for the inclusion of a slope adjustment term was used to test for different linear chronosequence patterns among the three disturbance types (MIXED procedure, SAS Institute Inc. 2008).

For ephemeral and nonpalatable species in the shrub layer, as well as for woody and nonwoody cover in the ground layer, a nonlinear approach was used to test for different patterns of cover increase and subsequent decline among the different disturbance types. More specifically, full and reduced Ricker models of the general form

$$y = axe^{-ba},$$

where y is the percent cover, x is the age, and a and b are maximum-likelihood-estimated parameters, were used. Full models contained separate parameter estimates for a and b for each disturbance, and an F-test was used to test whether these parameters differed among the different disturbances. When this occurred, we interpreted this as evidence for different successional trajectories. This nonlinear modeling approach is practical here, where ephemeral and nonpalatable species 'enter' the patches after clearing, generally increase in cover, and then decline to zero (or near zero) by the end of the chronosequence. In addition, the Ricker model can be used to estimate the peak of percent cover and the time (yr) at which this occurs. These analyses were performed using the NLIN procedure and the SSReductionTest macro in SAS (SAS Institute Inc. 2008).

RESULTS

General findings.—A total of 74 species in the shrub layer ($>$ 0.5 m) were identified (Table S1). Both fire and cleared patches had a mean species-richness of 23 species, while cleared-and-grazed patches had a mean species-richness of 19 species. Of the 74 species, most were woody, and 18 species were found in at least 50 percent of the patches (*i.e.*, ≥ 12 patches). These species included *Acacia choriophylla* Benth. (Leguminosae), *Bourreria ovata* Miers (Boraginaceae), *Bumelia salicifolia* (L.) Sw. (Sapotaceae), *B. simaruba*, *Chiococca alba* (L.) Hitchc. (Rubiaceae), *C. diversifolia*, *Erithalis fruiticosa* L. (Rubiaceae), *Eugenia axillaris* (Sw.) Willd. (Myrtaceae), *Guapira discolor* (Spreng.) Little (Nyctaginaceae), *Guapira obtusata* (Jacq.) Little (Nyctaginaceae), *Lantana* spp. *Leucaena leucocephala* (Lam.) de Wit (Leguminosae), *Metopium toxiferum* (L.) Krug & Urb. (Anacardiaceae), *Pithecellobium keyense* Britt. (Leguminosae), *Psychotria ligustrifolia* (Northrop) Millsp. (Rubiaceae), *Randia aculeata* L. (Rubiaceae), *Tabebuia bahamensis* (Northrop) Britt. (Bignoniaceae), *and Z. fagara.*

Six of the 18 species found in the shrub layer in more than 50 percent of the patches had significantly different mean percent cover among patches with differing disturbances. Three of these species, *A. choriophylla* ($F_{2,\ 21} = 6.99$, $P < 0.01$), *B. simaruba* ($F_{2,\ 21} = 8.06$, $P < 0.001$), and *C. diversifolia* ($F_{2,\ 21} = 6.12$, $P < 0.01$), contributed, on average, a substantial portion of the total cover in patches (mean percent covers of 6.9, 7.8, and 11.1, respectively, across all patches). For these species, higher cover (at least twice as much) was found in fire patches than in cleared and cleared-and-grazed patches (Fig. S2). The other three species, *B. salicifolia* ($F_{2,\ 21} = 4.07$, $P < 0.05$), *E. axillaris* ($F_{2,\ 21} = 9.91$, $P < 0.001$), and *P. ligustrifolia* ($F_{2,\ 21} = 5.28$, $P < 0.05$), though exhibiting significant differences in cover among patches with different disturbance types, contributed on average $<$ 5 percent cover within patches.

Shrub layer vegetation (based on species composition and their percent cover) differed as a function of disturbance type. Our NMDS ordination showed separation in shrub layer communities, particularly between fire patches vs. cleared and cleared-and-grazed patches (Fig. 1). Permutational MANOVA indicated that disturbance type explained approximately 23 percent of the among-patch variation in plant community composition ($F_{2,\ 21} = 3.12$, $P < 0.001$), and pairwise comparisons indicated unique plant communities for each disturbance ($P < 0.05$ for each pairwise comparison).

Shannon–Weiner α diversity indices differed significantly among the three disturbance types ($F_{2,\ 21} = 5.10$, $P < 0.05$; Fig. S3). Cleared-and-grazed patches had a lower mean Shannon–Weiner diversity index ($H' = 1.91$) compared with cleared ($H' = 2.33$) and fire patches ($H' = 2.40$).

Chronosequence trends.—Total percent cover in the shrub layer linearly increased across the investigated chronosequence (Fig. 2A). The rate of increase, which was positive and differed significantly from zero ($F_{1,\ 21} = 78.54$, $P < 0.001$), was similar across all disturbance types ($F_{2,\ 21} = 2.48$, $P = 0.11$).

For *C. diversifolia*, fire patches had the highest initial *C. diversifolia* cover at time zero (Fig. 2B). The test for the inclusion of separate slope parameters for each disturbance was not significant for *C. diversifolia* ($F_{2,\ 18} = 1.32$, $P = 0.29$), suggesting increase in percent cover through the chronosequence for *C. diversifolia* occurs at the same rate among the three disturbance types (Fig. 2B).

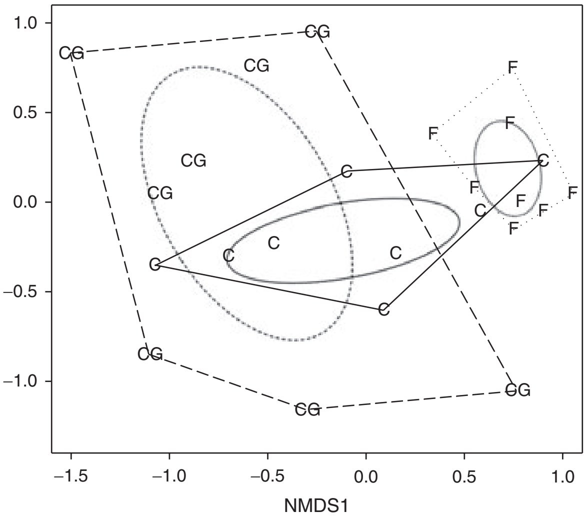

FIGURE 1. Ordination derived from nonmetric multidimensional scaling comparing percent cover of shrub layer (>0.5 m) species in early-successional coppice patches on Eleuthera, the Bahamas. Plots (patches) are labeled by their disturbance, which include cleared (C), cleared-and-grazed (CG), and fire (F). Polygons represent range of data and ellipses represent 95% confidence intervals drawn around the data centroids.

Increase in percent cover through the chronosequence for *B. simaruba* was affected by disturbance type ($F_{2,\ 21} = 18.52$, $P < 0.0001$; Fig. 2C). Percent cover increased quickest in fire plots, followed by cleared and cleared-and-grazed, respectively. *Bursera simaruba* had a negligible increase in cover in cleared-and-grazed plots across our chronosequence (Fig. 2C).

Certain species and species groups exhibited an initial increase in shrub layer cover, followed by a decline through the chronosequence. This general nonlinear pattern differed among patches with different disturbance types for *Lantana* spp. ($F_{4,\ 18} = 6.38$, $P < 0.01$) and Z. *fagara* ($F_{4,\ 18} = 6.91$, $P < 0.01$). *Lantana* spp. cover increased rapidly in cleared patches early in the chronosequence reaching peak estimated cover (~ 30%) 3 yr after clearing, followed by a sharp decline through the chronosequence (Fig. 3A). Although *Lantana* spp. cover was not estimated to be as high in cleared-and-grazed patches compared with cleared patches initially after disturbance, the Ricker model depicted *Lantana* spp. being maintained longer through the chronosequence in clear-and-grazed patches compared with cleared patches (Fig. 3A). *Zanthoxylum fagara* exhibited highest estimated cover in cleared-and-grazed patches reaching peak cover (~ 25%) 7 yr following disturbance, and then subsequently declined. *Zanthoxylum fagara* was estimated to increase in fire and cleared patches reaching 10 percent cover $>$ 20 yr after disturbance (Fig. 3B).

In the ground layer, the cover of woody and nonwoody species exhibited an initial increase, followed by a decline through

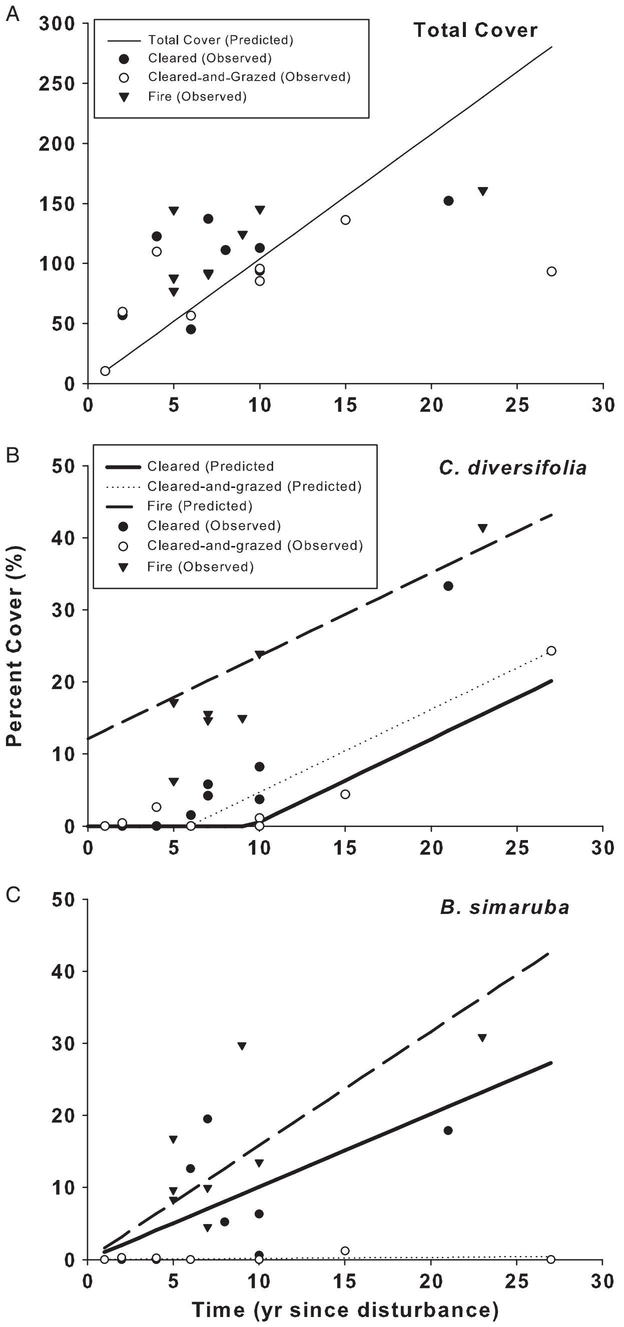

FIGURE 2. Analysis of covariance-based estimates (predicted) and observed values of (A) total percent cover summed across all species; (B) *Coccoloba diversifolia*; and (C) *Bursera simaruba* in cleared, cleared-and-grazed, and fire patches. Plots depict where differences among disturbance types were detected. *Note*: Linear regression line for *B. simaruba* in cleared-and-grazed patches hugs the *x*-axis.

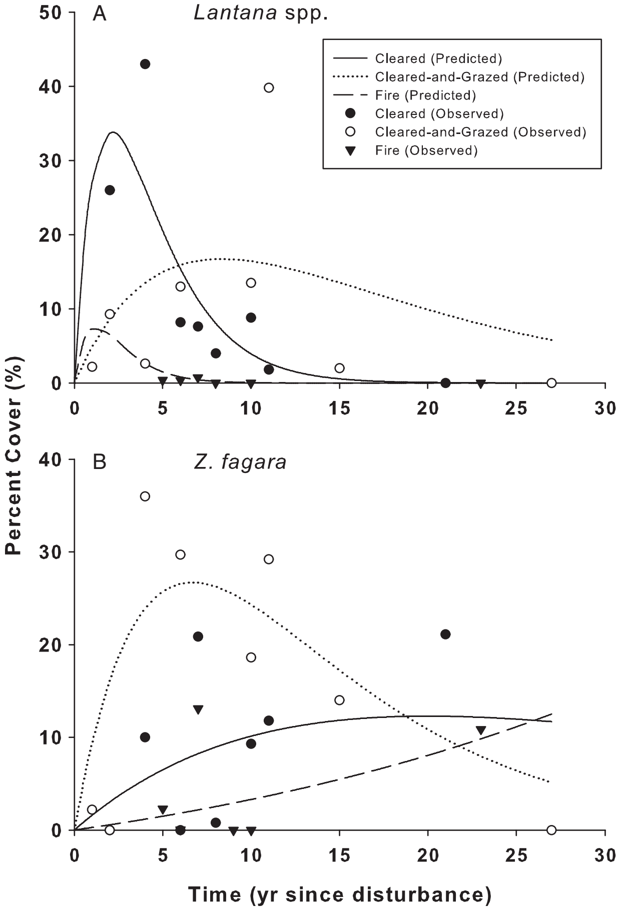

FIGURE 3. Ricker model-based estimates (predicted) and observed values of percent cover of (A) *Lantana* spp. and (B) *Zanthoxylum fagara* in cleared, cleared-and-grazed, and fire patches.

the chronosequence. For nonwoody species collectively in the ground layer, the nonlinear pattern differed among patches with different disturbances ($F_{4,\ 18} = 5.44$, $P < 0.01$). Nonwoody species had higher estimated cover in the cleared patches early in the chronosequence compared with those exhibited in cleared-and-grazed and fire patches (Fig. 4A). For woody species collectively in the ground layer, this nonlinear pattern did not differ among patches of different disturbance types (Fig. 4B; $F_{4,\ 18} = 2.69$, $P = 0.06$).

DISCUSSION

Our results indicate significant differences in early-successional coppice plant communities as a function of disturbance type. Our NMDS ordination, as well as results from permutational MANOVA, demonstrated that shrub layer plant communities in patches disturbed by fire were notably different compared with patches affected by clearing and clearing followed by goat grazing. This is partly due to the significantly greater cover of three tree species in fire patches including *B. simaruba*, *C. diversifolia*, and *A. choriophylla*. Although the proportion of land affected in patches differing in their disturbance is similar, intensity of fires in fire patches was not determined from the remote sensing maps. Fire severity differed within and among some patches of burned forest (Helmer *et al.* 2010), and in some places fires may have been lower intensity ground cover fires, which would not

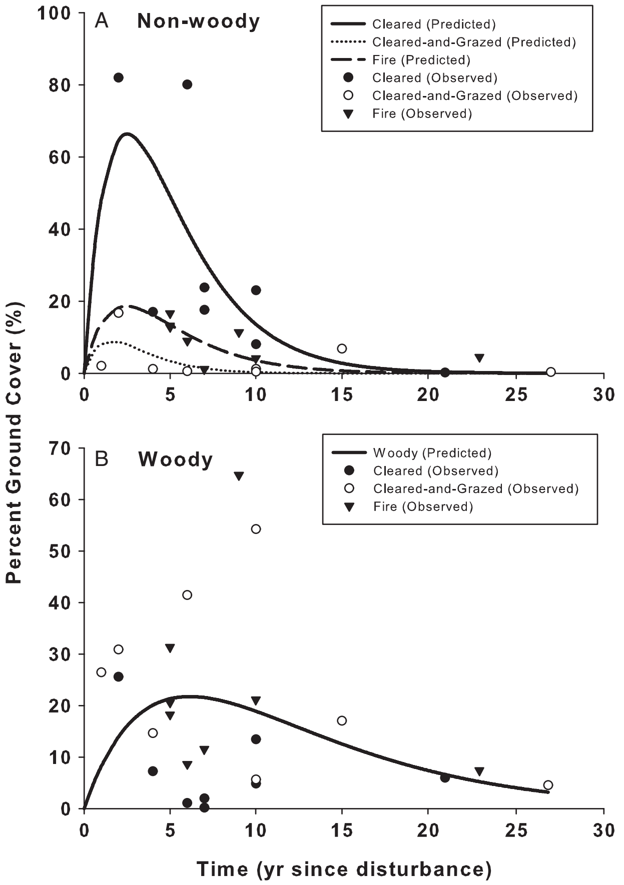

FIGURE 4. Ricker model-based estimates (predicted) and observed values of percent: (A) nonwoody and (B) woody ground cover in cleared, cleared-and-grazed, and fire patches. Plots depict where differences among disturbance types were detected.

affect larger trees such as *B. simaruba*, *C. diversifolia*, and *A. choriophylla*. Evidence from the full ANCOVA model for *C. diversifolia* would suggest this to be the case, because fire patches were predicted to have a significantly higher cover at time zero compared with cleared and cleared-and-grazed patches (Fig. 2B). Given that fire is usually of low intensity in tropical systems (compared with those experienced by temperate systems; Giglio *et al.* 2006), patches affected by fire may have been subjected to a lower intensity disturbance than those that were cleared. It is well-known that fire is needed to maintain open Caribbean pine (*Pinus caribaea* var. *bahamensis* [Griseb.] W.H. Barrett and Golfari [Pinaceae]) forest in the Bahamas (see Campbell 1978); however, broadleaf coppice is not considered fire dependent (see Currie *et al.* 2005), and fire is typically assumed to be detrimental to coppice (Campbell 1978). Our results indicate that coppice patches impacted by fire structurally recover at rates similar to those patches affected by clearing and clearing and goat grazing; though species composition and cover, irrespective of time since disturbance, appears to differ in the fire patches.

The results regarding goat grazing on plant species diversity in early-successional coppice communities on Eleuthera may, at first glance, seem to corroborate with other studies highlighting the ill effects of introduced grazers in island ecosystems (Coblentz 1978, Schofield 1989, Desender *et al.* 1999). We posit, though, that the difference among the α diversity indices may not be substantial, and moreover, that the compositional and structural diversity exhibited by cleared-and-grazed patches across the landscape (*i.e.*, β diversity) may have been greatest in those patches (Fig. 1). In addition, it is worth noting that the managed grazing in our study area on Eleuthera is far different from the feral goat grazing in many tropical and subtropical island systems, where spatial and population controls are lacking or insufficient.

Our results shed new light on the effects of managed grazing on plant succession in dry tropical and subtropical forest settings. More specifically, our results suggest that grazing by goats in coppice communities could accelerate or retard succession. Managed goat grazing may accelerate succession in the ground layer by quickly removing nonwoody ground cover and allowing the brief formation of a more notable woody community therein. In contrast, by slowing growth or establishment of common coppice trees such as *B. simaruba* in the shrub layer, goats may also be inhibiting or retarding canopy development. It has been demonstrated that like other ungulates, goats selectively feed on vegetation and can subsequently alter vegetation composition (Lepš *et al.* 1995). Studies have documented alteration of woody species composition due to preferential feeding by goats (Riggs & Urness 1989). Lepš *et al.* (1995) cites four other effects of grazers on vegetation including trampling, creation of gaps, increase of nutrients via excretion of wastes, and increase of nutrient availability due to turnover of nutrients. The exact mechanisms by which goats may alter species composition in forested habitats in subtropical regions are in need of further research.

In addition to slowing cover of common coppice trees, goats may allow a subset of early-successional shrub species to remain in early-successional systems for longer periods of time. Early-successional species such as *Lantana* spp. were found in higher cover in older goat-grazed patches compared with cleared patches of similar age, which suggest that *Lantana* spp. are maintained longer in goat-grazed patches. The overall effects of grazing, particularly at early stages following initial clearing, may allow for a preponderance of shrub species (relative to that of tree species), perhaps physiognomically similar to those that typified nearby Andros Island 3200–1500 year before present (Kjellmark 1996). Other studies have shown that grazing maintains early-successional plant species. In patches intermittently grazed by cattle in Costa Rica, early-successional species such as *Tabebuia rosea*, *Cassia pallida*, and *Piscidia carthagenesis* were found to be some of the most abundant species (Stern *et al.* 2002). Because of secondary compounds contained in many *Lantana* spp., herbivory by livestock such as goats may be deterred, favoring the growth of *Lantana* spp. (Sharma *et al.* 2007). This may benefit species such as the Kirtland's Warbler (*Dendroica kirtlandii*) which feeds on *L. involucrata* fruits during the winter (Wunderle *et al.* 2010).

Other studies in the Caribbean have highlighted the resistance and resiliency of coppice-like systems to large-scale disturbances. Low plant species turnover following hurricanes has been noted on the Bahamian islands of Andros, Exuma Cays (Morrison 2003), and Exuma (Morrison & Spiller 2008). Although turnover was not directly measured in our study, many of the same plant species were found in patches regardless of the disturbance type or time since disturbance. In addition, basal area recovery was quick and notable (~1/3 pre-disturbance levels attained in ~1 yr) in cleared Jamaican dry forest (McLaren & McDonald 2003). Although we lacked pre-disturbance data, total cover in the shrub layer increased at similar rates in patches regardless of the disturbance type. Our study provided baseline data relating to three common disturbances in coppice communities; however, the effects of only one type of disturbance per patch on succession in coppice communities were tested. Future research should include work on smaller disturbances, as well as the interactions of these and other disturbances on successional trajectories in subtropical and tropical dry forest systems.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Species identified in the shrub layer in coppice patches on Eleuthera, the Bahamas, affected by different disturbances including clearing, clearing and subsequent goat grazing (i.e., cleared-and-grazed), and fire.*

FIGURE S1. Location of Eleuthera within the Commonwealth of the Bahamas.

FIGURE S2. Mean percent cover of *A. choriophylla*, *B. simaruba*, and *C. diversifolia* in early-successional coppice patches on Eleuthera, the Bahamas.

FIGURE S3. Mean Shannon–Weiner diversity indices of cleared, cleared-and-grazed, and fire patches on Eleuthera, the Bahamas.

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