

Functional attributes of two subtropical shrubs and implications for the distribution and management of endangered bird habitat

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Abstract

Aims

The fruits of *Erithalis fruticosa* L. and *Lantana involucrata* L. are important in the diet of US federally endangered Kirtland's Warblers (*Setophaga kirtlandii*) wintering in the Bahamas archipelago. These two shrubs occur in tropical and subtropical dry forests, including forests that have been subjected to recent disturbance. Despite their importance to the endangered warbler, the disturbance ecology of these shrubs is poorly understood. We sought to determine, based on functional characteristics of the plants, whether their presence is favored by a particular type or regime of disturbance.

Methods

We used data from field experiments (seed broadcasting and shrub cutting) conducted on the island of Eleuthera, The Bahamas to determine mechanisms of and conditions favoring establishment and persistence ('vital attributes') of *E. fruticosa* and *L. involucrata*, which enabled categorization according to the plant functional types defined by Noble and Slatyer (1980). We then compared hypothesized distributions of these plant functional types among different anthropogenic disturbance regimes to observed distributions of *E. fruticosa* and *L. involucrata* in order to identify disturbance regimes most likely to produce habitat used by Kirtland's Warblers.

Important Findings

E. fruticosa and *L. involucrata* were functionally categorized as widely dispersed but largely shade intolerant species capable of establishing or regenerating individuals after disturbance via both seeds and vegetative mechanisms. Both hypothesized and observed distribution patterns indicated the shrubs were favored by a regime of frequent disturbance producing open canopy and ground layers. Among the anthropogenic disturbances we examined, areas of large-scale land clearing combined with subsequent goat grazing most often supported *E. fruticosa* and *L. involucrata*, while the shrubs were relatively rare in burned areas. Utilizing the plant functional type framework in combination with field data to evaluate predictions of species occurrence among different disturbance regimes provides a strong theoretical basis for conservation strategies. Understanding which disturbance types favor a habitat of concern and the mechanisms by which they do so can aid the prioritization of areas for protection or the design of habitat management protocols.

Keywords: anthropogenic disturbance, black torch, plant functional type, vital attributes, wild sage

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INTRODUCTION

Tropical dry forests and related vegetation types (woodlands, scrub) cover considerable land area and are subject to

intense pressure from human land use. Yet the disturbance dynamics of these communities are not well understood (Chaturvedi *et al.* 2011; Murphy and Lugo 1986). In addition to high plant diversity, tropical dry forest communities

in the Caribbean basin support a diverse fauna, including many Nearctic-Neotropical migratory landbirds (Wunderle and Waide 1993). Among these migrants is the US federally endangered Kirtland's Warbler ('KW', *Setophaga kirtlandii*). One of the rarest migratory songbirds in North America, the KW winters exclusively in the Bahamas archipelago where it feeds on arthropods and fruits of several shrubs, but especially fruits of *Erithalis fruticosa* L. (black torch) and *Lantana involucrata* L. (wild sage) (Sykes and Clench 1998; Wunderle *et al.* 2010). Given the importance of *E. fruticosa* and *L. involucrata* in the winter diet of KWs, there is a need to understand how habitat patches with an abundance of these plants are created or maintained. This understanding will allow prioritization of habitat areas for protection and, if necessary, management action.

E. fruticosa and *L. involucrata* are found in both coastal and inland plant communities throughout the Caribbean (e.g. Coker and Shattuck 1905; Correll 1979; Levins and Heatwole 1973; Moreno-Casasola and Espejel 1986). Although few published studies document the autecology or disturbance responses of either species, *L. involucrata* and *E. fruticosa* have been characterized as species intolerant of competition and shading (Francis 2004). Thus, they may be disturbance dependent. On the island of Eleuthera in The Bahamas, both species were common among the recently (0–25 years) anthropogenically disturbed dry forest habitats favored by KWs (Wunderle *et al.* 2010). However, Byrne (1980) found *E. fruticosa* was most important in older (>25 years), late-successional stands of dry forest on near-by Cat Island.

Because we were interested in identifying disturbance types or regimes that favor the persistence of *E. fruticosa* and *L. involucrata*, we believed it would be useful to characterize the species in terms of their functional types. Plant functional types are expected to provide a general ecological framework for understanding plant community composition in relation to dominant ecosystem processes, including disturbance (Chaturvedi *et al.* 2011). Several procedures have been used to classify species into functional groups (see Gillison 2013; McIntyre *et al.* 1999a and references therein), but many rely on quantitative morphological and physiological data that are not well documented for *E. fruticosa* and *L. involucrata*. Alternatively, the method of Noble and Slatyer (1980) uses combinations of qualitative plant 'vital attributes', defined a priori, to deduce a relatively small number of generalized functional types. Two groups of vital attributes are most important for defining functional type: (i) conditions for establishment and growth and (ii) methods (or mechanisms) of persistence through or arrival after a disturbance (Supplementary Table S1).

These vital attributes are conceptually very similar to the 'phenomenological characteristics' used in the IPCD framework proposed by Pausas and Lavorel (2003; i.e. Individual-persistence, Propagule persistence, Competitive capacity and Dispersal) and are particularly useful for predicting plant community dynamics under varying disturbance regimes (Noble and Gitay 1996). Thus, this functional classification scheme

may be considered a disturbance response trait or strategy-based model (Gillison 2013). In addition to predicting compositional dynamics related to disturbance, a vital attributes-type approach has been used to predict plant composition relative to different land management methods (Tozer *et al.* 2012). While plant functional type approaches may be more often employed to understand or predict community-level differences in response to perturbations or environmental gradients (e.g. Kooyman *et al.* 2010), a trait-based approach can be useful at the species-level, e.g. to aid understanding of differences between fundamental and realized niches (McGill *et al.* 2006).

In this paper, we functionally classify *E. fruticosa* and *L. involucrata* and predict their occurrence relative to disturbance based on multiple steps. First, we use field experiments involving *E. fruticosa* and *L. involucrata* to identify their vital attributes and categorize them according to functional types proposed by Noble and Slatyer (1980). Based on this functional categorization, we then hypothesize whether each species is likely to be present in areas affected by different forms of anthropogenic disturbance common in The Bahamas. Finally, we evaluate our hypotheses by examining actual presence of *E. fruticosa* and *L. involucrata* among plots sampled within these disturbance types.

Although natural disturbances such as hurricanes or lightning-caused fire undoubtedly influenced the historic distribution of KW habitat in The Bahamas, since European settlement at least, vegetation on many islands throughout the archipelago has been extensively disturbed by humans (Byrne 1980; Young 1966). We focus on anthropogenic disturbances in our study for three main reasons. First, spatially explicit information on natural disturbance is less readily available than for anthropogenic disturbance, but human disturbances are likely to also affect areas subjected to natural disturbance. Second, a high proportion of sites where wintering KWs are currently found are in areas disturbed by humans (Lee *et al.* 1997; Wunderle *et al.* 2010), which indicates that anthropogenic disturbance is currently an important driver of habitat availability. Finally, the influence of anthropogenic disturbance on habitat distribution has more direct applicability to management since any potential methods for active habitat management would have to utilize controllable forms of disturbance.

MATERIALS AND METHODS

Study area

Our studies were conducted on the subtropical island of Eleuthera, The Bahamas (25°15'N, 76°20'W). The island's climate is characterized by an annual wet and dry cycle, with most rainfall occurring from May through October (Sealey 2006). The modern undeveloped landscape on Eleuthera is a patchwork of variably aged vegetation primarily as a consequence of shifting agriculture or failed development (Helmer *et al.* 2010). The main vegetation cover is a dry forest type

including both evergreen and deciduous broadleaf trees and shrubs growing on a limestone substrate (Correll 1979; Mooney 1905; Smith and Vankat 1992). The dry forest is locally referred to as 'coppice', which is not a reference to current forestry practices. *Acacia choriophylla* Benth. (cinne-cord), *Bursera simaruba* (L.) Sarg. (gum elemi) and *Coccoloba diversifolia* Jacq. (pigeon plum) are characteristic species of mature coppice stands that also occur with lower stature in younger stands.

Our study sites were located within the southern half of Eleuthera (Fig. 1). We determined the vital attributes displayed by *E. fruticosa* and *L. involucreta* based on field experiments conducted at the Leon Levy Native Plant Preserve (LLNPP; 25°11'14"N 76°12'44"W) in Governor's Harbour. The distribution of the two species among anthropogenic disturbance types was determined from plots distributed from Tarpum Bay southward.

Field experiments to identify vital attributes

We conducted two experiments at LLNPP. The first was a seed broadcasting study examining conditions favoring establishment and growth of individuals from seed (vital attribute group 1) as well as the distribution and longevity of seed pools from which *E. fruticosa* and *L. involucreta* might establish following disturbance (i.e. mechanism of persistence; vital attribute group 2). The second study measured the response (mortality, resprouting and time to reproduction) of mature *E. fruticosa* and *L. involucreta* to a hand-cutting treatment approximating the individual biomass loss that would be experienced during land clearing (e.g. small agricultural plots are often cleared by hand and even areas cleared with machinery may have shrub stumps remaining).

Seed broadcasting study

The seeding study was conducted along an infrequently cleared, ~300-m-long dirt access road where *E. fruticosa* and *L. involucreta* occurred in patches. We broadcast seeds of *E. fruticosa* (≈ 1725 seeds/m²) and *L. involucreta* (≈ 4015 seeds/m²) within 60 0.25-m² quadrats per species and compared seedling germination with adjacent (0.25 m separation) unseeded quadrats. Quadrats were located amid sparse to dense vegetation along the road edges to avoid disturbance by occasional vehicle traffic. Seeds were harvested from fruiting shrub populations throughout the study region ~1–4 months prior to broadcasting. Pericarps were removed using a wire mesh colander, providing some seed scarification, and seeds were stored under refrigeration until broadcast. Seeding density for each species was determined, in part, by the amount available for collection but far exceeded estimates of local dispersal based on seasonally matched average fruit densities derived from multi-year, multi-site surveys (Wunderle *et al.*, unpublished data).

We examined new seedling germination following three broadcasting events in two seasons (spring and fall): (i) 30

quadrats per species in April 2010, (ii) 15 quadrats per species in November 2010 and (iii) 15 quadrats per species in April 2011. Quadrats (seeded and unseeded) in the latter two events were cleared of all litter and vegetation within 2 m of the ground prior to broadcasting.

Seedling surveys in all established quadrats were conducted monthly from November through April in 2010–11 and 2011–12. Two additional surveys were conducted in November 2012 and April 2013. New *E. fruticosa* and *L. involucreta* seedlings found at each survey were marked with colored plastic toothpicks, and the approximate height of each seedling present was noted. At each November survey, we visually estimated the percentage of bare ground within the quadrat and the percentage of the quadrat covered by vegetation. In November 2011, we estimated photosynthetic flux density (PPFD) at each quadrat using hemispherical photographs taken near ground level and analyzed using

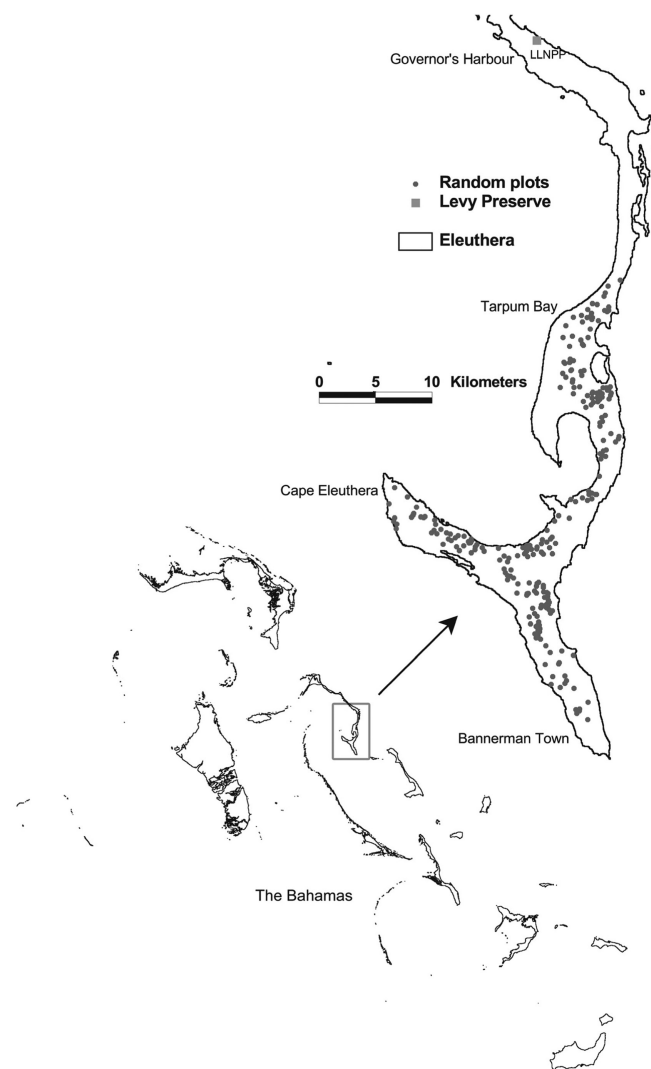


Figure 1: distribution of study sites throughout southern Eleuthera, The Bahamas.

WinSCANOPY Version 2010a (Regent Instruments Inc. Quebec City, Canada). Before calculating PPFD, each photo was adjusted to allow for the greatest contrast between the canopy and the sky before estimating leaf area. The estimate of PPFD provided by WinSCANOPY takes into account the relative spherical area occupied in elevation rings of the hemispherical image, solar declination, atmospheric attenuation and incidence angle. A 365 day growing season was assumed. We used a solar constant of $1370 \text{ J/m}^2\cdot\text{s}^{-1}$ and photosynthetically active radiation represented 0.51 of the solar constant. We also measured, at the time of quadrat establishment, the distance from the quadrat center to the nearest adult *E. fruticosa* and *L. involucrata*.

Analyses examined factors influencing the probability of seedling germination and seedling survival. To examine germination probability, we divided the 3-year study duration into six summer and winter periods (e.g. summer 2010 = May to November 2010; winter 2010–11 = December 2010 to April 2011, etc.) and categorized the presence or absence of any germination within each established quadrat during each period (i.e. 4–6 presence/absence values per quadrat, depending on the date of its establishment). Germination for summer periods was based on the presence of new seedlings at the first fall survey of each field season; germination over winter periods was based on surveys from December through April. We used two-level hierarchical generalized linear models (HGLM; i.e. multilevel logistic regression accounting for surveys nested within quadrats; Raudenbush and Bryk 2002) and data from all quadrats (i.e. all treatments across all broadcasting events) to examine whether the germination probability for a quadrat within a seasonal period (level 1) increased with total precipitation during the period or with a higher light, lower competition environment (increasing bare soil, decreasing plant canopy cover or increasing PPFD). In general, experimentally cleared quadrats had more bare soil and PPFD and less canopy cover than uncleared quadrats. Precipitation was based on rainfall records for Nassau International Airport (www.ncdc.noaa.gov/IPS/mcdw/mcdw.html), 96.6 km west of the study site. After accounting for environment, we evaluated whether variation in germination probability among quadrats (level 2) was influenced by endogenous seed input (indexed by distance to the nearest adult) or exogenous input (seeding) to determine whether seeds of *L. involucrata* and *E. fruticosa* were naturally broadly distributed (or ‘well dispersed’) enough to provide a likely means of post-disturbance recovery in patches where adults were absent. We conducted a separate HGLM analysis, using only seeded quadrats from all broadcasting events, to examine whether any positive effect of seeding declined with time (i.e. seed longevity).

We used Cox regression to evaluate seedling survival, assuming mortality occurred midway between the last two surveys for seedlings that died. We examined whether the relative risk of mortality was influenced by precipitation within the first 2 months surrounding (the month of and the

month following) germination or the environment (percent bare soil averaged over the study, average percent canopy cover and PPFD). The variables were entered into the model in the order presented, based on theoretical prioritization, and were retained or rejected based on likelihood ratio tests.

Shrub cutting study

This study was conducted on an open-canopied plateau adjacent to an old rock quarry and examined how season and frequency of disturbance influenced mortality, regrowth and fruit production of *E. fruticosa* and *L. involucrata*. A total of 120 adults of each species were cut to a height between 0.2 and 0.5 m, resulting in a loss of 35–99% of pre-treatment canopy volume (median loss = 99%). Shrubs were selected using a random starting point at one end of the plateau and nearest neighbor criteria moving toward the opposing end. The nearest neighbor approach was employed to aid relocation and reduce shading effects from surrounding shrubs. Sixty shrubs, per species, were first cut in April 2010 (spring), and an additional 60 per species were cut in November 2010 (fall). In April and November 2011, half of the shrubs were cut again to near-first-cut size (30 per species, selecting every other shrub in numerical order).

Because our design did not eliminate differences in shading among shrubs, we subjectively categorized each shrub, after cutting, as ‘shaded’ (mostly to fully) or ‘unshaded’ (none to part). Live canopy volume was measured immediately pre- and post-cutting and on a monthly basis from November through April 2010–11 and 2011–12. Two additional measurements were made in November 2012 and April 2013. Volume was calculated from canopy height and two perpendicular width measurements using the equation for an ellipsoid. At each survey, the numbers of flowers and fruits on each shrub were counted.

We used logistic regression, within species, to investigate whether shading, season of treatment or number of cuts influenced probability of mortality. Variables were entered in the order presented and evaluated using likelihood ratio tests. Among surviving shrubs, we used separate two-level hierarchical linear models (i.e. multilevel linear regression accounting for surveys nested within shrubs; Raudenbush and Bryk 2002) to examine whether: (i) canopy volume regrowth during the first year (one cut only) was related to pre-treatment size or differed between the two species or the two seasons of treatment and (ii) regrowth during the second through third experimental years differed between species, seasons or number of cuts after accounting for any influence of pre-treatment size (where treatment here = recut or not). We used logistic and linear regression, respectively, to examine whether the probability of flowering or fruiting within a year or the total abundance of fruits and flowers (combined) produced during winter months of that year (among reproductive shrubs only) was dependent on post-treatment shrub volume (averaged over winter surveys), species, season of treatment or number of cuts.

Plant functional types and presence within disturbance types

Based on combination of the vital attributes (conditions for establishment and mechanisms of persistence) indicated by our experiments, we identified a subset of the plant functional types proposed by Noble and Slatyer (1980) most likely to apply to *E. fruticosa* and *L. involucrata*. We then hypothesized patterns of presence for these functional types among four classes of anthropogenic disturbance: (i) large-scale clearing (often by bulldozing) for agriculture or unsuccessful development, followed by abandonment; (ii) small-scale clearing and burning for temporary agricultural use; (iii) escaped fire (wildfire) and (iv) clearing followed by repeated goat grazing.

Our hypothesized patterns of presence were compared to observed patterns among 246 circular 12.6-m² (4 m diameter) plots randomly distributed throughout southern Eleuthera. Plot locations were stratified by the four disturbance classes and approximate time since disturbance (ranging from ~1 to 28 years since disturbance among most types) using remote sensing maps developed from a time series of cloud-cleared Landsat and Advance Land Imager satellite image mosaics covering the period from 1984 to 2005 (Helmer *et al.* 2010). The geographic coordinates for the centroid of a randomly chosen map pixel within in each disturbance stratum served as the plot center. All plots were contained entirely within patches of natural to semi-natural (e.g. mixed with agricultural species) coppice vegetation (or with the potential to succeed to coppice) affected by the same disturbance. At each plot, all plant species with canopy occurring within the plot boundary were recorded. We used chi-square contingency tables with Fisher's Exact Test (due to sparse data in some cells) to examine whether the presence of *E. fruticosa* or *L. involucrata* across plots was independent of disturbance type.

RESULTS

We present our results in four main parts following the order in which the steps of our overall study were taken: (i) experimental results, (ii) identification of applicable vital attributes, (iii) determination of plant functional types and hypothetical distributions among disturbances and (iv) comparison of hypothesized and observed distributions. Latter parts necessarily require some discussion and interpretation of the results preceding them.

Field experiments

Conditions for establishment

Seedling germination throughout our 3-year seed broadcasting study was sparse, especially for *E. fruticosa*. Germination of 564 *L. involucrata* seedlings was recorded across 41% of the 240 established quadrats, compared to a total of only 48 *E. fruticosa* seedlings across 10% of all quadrats. Consequently, with the exception of survival analyses, statistical modeling was limited to *L. involucrata*, but summary statistics are reported for *E. fruticosa*. Seedlings of *E. fruticosa* and *L. involucrata* germinated in

both summer and winter, indicating no strict seasonal limitation on recruitment. The seasonal period with the highest proportional quadrat occurrence of *L. involucrata* germination was winter of 2010–11 (21% of all quadrats with one or more seedlings; range over all periods = 2–21%) followed by summer of 2011 (19% of quadrats)—periods that immediately followed quadrat clearing and seed broadcasting. Proportional quadrat occurrence of *E. fruticosa* germination was typically around 2% within seasonal periods (range = 1–5%).

Both *E. fruticosa* and *L. involucrata* germinated under a broad range of ground (0–92% bare soil) and canopy cover (0–98%), but average values were similar between species where germination was observed (*E. fruticosa*: 37.1 ± 25.3% bare soil and 45.3 ± 26.2% canopy; *L. involucrata*: 37.9 ± 24.7% bare soil and 44.8 ± 26.2% canopy). Analyses indicated the probability of *L. involucrata* germination was favored under higher light and lower competition environments, increasing with percent bare soil (Table 1, all quadrats, γ_{10}) and decreasing with higher plant canopy cover (Table 1, all quadrats, γ_{20} ; Fig. 2a).

Seedling survival was generally low and aboveground growth was slow. Among seedlings germinating prior to the final survey, 15% of *L. involucrata* survived to the final survey, 79% of which germinated ~17 months prior (summer of 2011); 22% of *E. fruticosa* survived also with an average survival time of ~17 months. Cox regression indicated increasing precipitation within the 2 months surrounding germination substantially reduced mortality risk relative to baseline rates (Table 2), though the increased mortality risk appeared concentrated at the lowest levels of precipitation for *E. fruticosa* (<25 mm; Fig. 3a) while persisting through somewhat higher precipitation levels for *L. involucrata* (up to ~50 mm; Fig. 3b). Higher light levels also contributed to lower mortality risk for *L. involucrata* seedlings (Table 2), as indicated by an approximate doubling in risk over canopy cover values between 60 and 100% and decreasing risk with increased PPFD (Fig. 3c and d). Cover and PPFD did not significantly influence mortality risk of *E. fruticosa*. Among the final surviving seedlings 1 year or more in age, 49% of *L. involucrata* and 71% of *E. fruticosa* were still ≤5 cm in height. No seedlings reached reproductive maturity.

Mechanisms for persistence: seeds

Pre-existing *L. involucrata* was more widely distributed along our experimental site than *E. fruticosa*. For both species, the distance from the center of a quadrat to a pre-existing adult ranged from 0 m to well over 10 m, but 50% of all quadrats were <1 m from an adult *L. involucrata* shrub (median distance = 0.9 m), while the median distance to an adult *E. fruticosa* (7.4 m) was much greater. The distribution of adults could have reflected the distribution of suitable patches for species establishment, regardless of propagule availability, and HGLM analysis with all quadrats indicated the probability of *L. involucrata* germination decreased as distance to the nearest adult increased (Table 1, all quadrats, γ_{01}). However, availability of additional suitable patches for both *L. involucrata* and *E. fruticosa* was supported by germination of seedlings in

Table 1: results from two-level HGLM predicting the log odds of *Lantana involucreta* seedling germination within 0.25-m² quadrats over a 3-year study period at the LLNPP, Eleuthera, The Bahamas

All quadrats				
Fixed effects	Coefficient	SE	df	P
Model for average log odds of seedling germination: $\beta_{00} = \gamma_{00} + \gamma_{01} + \gamma_{02}$				
Log odds with average bare soil, cover, distance to adult and no seeding; γ_{00}	-2.988	0.180	236	<0.001
Incremental change in log odds with change in distance to adult, γ_{01}	-0.286	0.090	236	0.002
Difference in log odds for seeded quadrat, γ_{02}	0.625	0.294	236	0.035
Model for change in log odds of germination with change in bare soil: $\beta_{10} = \gamma_{10}$				
Incremental change in log odds with change in % bare soil, γ_{10}	0.023	0.007	1255	0.001
Model for change in log odds of germination with change in canopy cover: $\beta_{20} = \gamma_{20}$				
Incremental change in log odds with change in % cover, γ_{20}	-0.023	0.007	1255	0.001
Random effects	Variance	df	χ^2	P
Variation within shrubs (dispersion)	0.478			
Variation among shrubs	2.291	236	768.56	<0.001
<i>L. involucreta</i> -seeded quadrats				
Fixed effects	Coefficient	SE	df	P
Model for average log odds of seedling germination: $\beta_{00} = \gamma_{00} + \gamma_{01}$				
Log odds at 6 months post-treatment with average cover and PPFDF; γ_{00}	-1.437	0.321	57	<0.001
Incremental change in log odds with change in PPFDF, γ_{01}	0.074	0.033	57	0.028
Model for change in log odds of germination with change in canopy cover: $\beta_{10} = \gamma_{10}$				
Incremental change in log odds with change in % cover, γ_{10}	-0.024	0.010	308	0.017
Model for change in log odds of germination with time since treatment: $\beta_{20} = \gamma_{20}$				
Incremental change in log odds per month, γ_{20}	-0.079	0.020	308	<0.001
Random effects	Variance	df	χ^2	P
Variation within shrubs (dispersion)	0.539			
Variation among shrubs	2.355	57	187.35	<0.001

An analysis utilizing 239 seeded or unseeded quadrats (i.e. all quadrats), each surveyed for germination within four to six periods ($N = 1260$), focused on assessing the effect of seed addition after accounting for influential environmental factors. An analysis utilizing a subset of 59 *L. involucreta*-seeded quadrats, surveyed over the same periods ($N = 312$), focused on assessing whether the effect of seed addition decreased with time. Coefficients for fixed effects are used to estimate the log odds of germination (y) at time t for quadrat i according to the level 1 model: $y_{it} = \beta_{0i} + \beta_{1i}X_{1it} + \dots + \beta_{mi}X_{mit}$, where β_n may be further defined by a level 2 sub-model incorporating variables differing among quadrats (e.g. $\beta_{0j} = \gamma_{00} + \gamma_{01}$).

quadrats far (>10 m) from adults. In addition, after controlling for adult proximity, *L. involucreta*-seeded quadrats were 1.9 times more likely to have seedlings germinate than unseeded quadrats indicating endogenously dispersed seeds were more limited than suitable germination sites (Table 1, all quadrats, γ_{02} ; Fig. 2a). The occurrence of *E. fruticosa* seedlings qualitatively mirrored *L. involucreta*, most commonly appearing close to adults (quadrats with seedlings had a median distance of 2.8 m from an adult) but also appearing more commonly in *E. fruticosa*-seeded quadrats (17% of seeded quadrats with germination) than unseeded quadrats (8% with germination). Although neither species appeared to have exceptionally well-dispersed seeds across a local scale, *L. involucreta* may have had a greater local dispersal range than *E. fruticosa*. The

maximum distance of an unseeded quadrat from an adult in which an *E. fruticosa* seedling was observed was 7.5 m compared to >10 m for *L. involucreta*.

Analyses also indicated that dispersed seeds may be relatively short-lived. Among quadrats seeded with *L. involucreta* (i.e. where age of the majority of seed was known), the probability of *L. involucreta* seedling germination decreased with time since seeding after accounting for influential environmental conditions (Table 1, *L. involucreta*-seeded quadrats, γ_{20}). By 18 months post-seeding, the estimated probability of *L. involucreta* seedlings germinating in seeded quadrats was less than half that at 6 months (Fig. 2b), and 88% of all *L. involucreta* seedlings germinating in seeded quadrats did so within 18 months (77% within 1 year). Among *E. fruticosa*

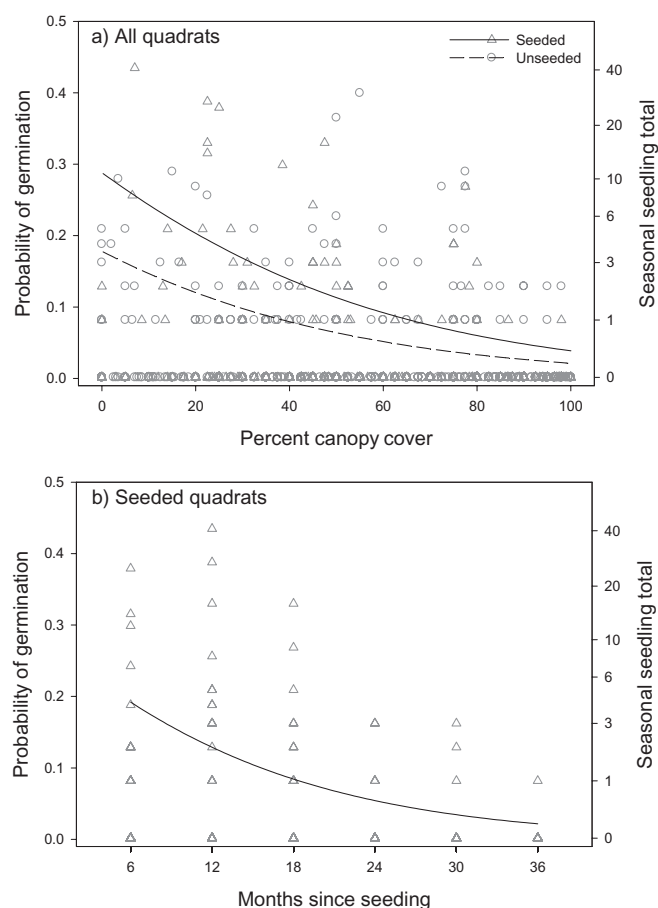


Figure 2: probability of any and actual abundance of *Lantana involucrata* seedling germination within individual 0.25-m² quadrats during six seasonal periods over 3 years. Lines and the left vertical axis show the predicted probability of germination based on hierarchical generalized linear modeling (Table 1); symbols and the right vertical axis show observed germination totals for quadrats within seasonal periods. The top graph (a) shows germination in all established quadrats as a function of visually estimated plant canopy cover. Predicted probability curves assume constant, average values for bare soil and distance to the nearest adult. The bottom graph (b) shows germination as a function of months since seeding within experimentally seeded quadrats only. Predicted probability curves assume constant, average values for canopy cover and PPF.

seedlings germinating in quadrats seeded with *E. fruticosa*, 59% did so within 1 year and 94% did so within 18 months of the seeding treatment.

Mechanisms for persistence: resprouting

Overall, 36% of *L. involucrata* and 21% of *E. fruticosa* died within 2 years of a cutting treatment (91% of all mortalities occurred within 12 months), while the remaining shrubs produced new branches from remaining stem bases. However, the probability of mortality was 18 (*L. involucrata*) to 48 (*E. fruticosa*) times greater for shaded vs. unshaded shrubs and 2.5 (*L. involucrata*) to 38.5 (*E. fruticosa*) times greater for shrubs cut in fall vs. spring (Table 3). Only mortality of *E. fruticosa*

was related to repeated disturbance, but shrubs were much less likely to die after a second cutting compared to the first (Table 3). This was likely associated with the severity of the proximal disturbance and the typical growth habit of *E. fruticosa*. Median percent canopy reduction was generally lower and median post-cut canopy volume was higher among twice-cut than once-cut shrubs, and *E. fruticosa* often had decumbent branches close to the ground remaining after cutting.

After the first cutting treatment, resprouting shrubs attained a median 11% of their pre-treatment volume by 12 months (range ≤ 1 –258%; both species combined). Growth rates through the first year were higher for: (i) *L. involucrata* compared to *E. fruticosa* (Table 4, first experimental year, γ_{11}); (ii) shrubs cut in the spring vs. fall (Table 4, first experimental year, γ_{12}) and (iii) shrubs that were larger pre-treatment (Table 4, first experimental year, γ_{13}). Among all resprouting shrubs (species combined), 26% produced flowers or fruit within the first year following cutting. Both the probability of any flower or fruit production during the first year and the abundance of flowers and fruit produced through the first winter increased with average canopy volume through that period (log odds of production = $-2.95 + 5.88 \times$ average volume, $P < 0.001$; log abundance = $1.53 + 2.10 \times$ average log volume, $P < 0.001$), but neither differed significantly between species or shrubs cut in different seasons after accounting for volume differences.

During the second through third experimental years, after half of all shrubs were cut a second time, growth rates were still positively related to pre-treatment shrub volume (Table 4, second through third experimental years, γ_{13}). However, *E. fruticosa* showed a higher average growth rate than *L. involucrata* (Table 4, second through third experimental years, γ_{11}) and resprouting twice-cut shrubs grew at ~ 1.4 times the rate of once-cut shrubs (Table 4, second through third experimental years, γ_{12}). By 12 months post-treatment, twice-cut *E. fruticosa* shrubs regained a median 145% (range = 9–398%) and twice-cut *L. involucrata* 64% (range = 1–267%) of their pre-second-cut volume. Average growth rates for once-cut shrubs were qualitatively lower than in the first experimental year. The percentage of all resprouting shrubs flowering or fruiting in the second experimental year (27%) was similar to the first year and included both once- and twice-cut shrubs (40 and 14%, respectively, within treatment). The probability of reproduction was again positively related to canopy volume (logistic regression: $\beta_{\text{volume}} = 2.9$, $P < 0.001$), but *L. involucrata* was seven times more likely than *E. fruticosa* to produce any flowers or fruit during that year ($\beta_{\text{species}} = 2.0$, $P < 0.001$). This could indicate *L. involucrata* is a more reliable reproducer, even under adverse conditions, which could partly explain the better seed dispersal of *L. involucrata* relative to *E. fruticosa* noted previously.

Identification of vital attributes

Improved seedling germination and survival in higher light environments suggested *L. involucrata* as a shade intolerant species with respect to establishment (I vital attribute;

Table 2: results from Cox proportional hazards regression (survival analysis) examining factors influencing the relative mortality risk (the log hazard ratio) of *Erithalis fruticosa* and *Lantana involucrata* seedlings

Species	Cox and Snell R^2	Effects	Coefficient	SE ^a	P
<i>E. fruticosa</i>	0.19	Instantaneous rate of change in log hazard ratio with mean log precipitation in first 2 months	-0.305	0.148	0.026
		Acceleration in rate of change in log hazard ratio with changes in log precipitation	0.217	0.105	0.016
<i>L. involucrata</i>	0.22	Incremental change in log hazard ratio with log precipitation in first 2 months	-0.486	0.043	0.001
		Instantaneous rate of change in log hazard ratio with mean canopy cover	0.004	0.002	0.081
		Acceleration in rate of change in log hazard ratio with changes in canopy cover	0.0003	0.0001	0.007
		Incremental change in log hazard ratio with change in PPFD	-0.012	0.005	0.018

Precipitation was quantified as the total millimeters recorded at the Nassau airport during the month of plus the month after germination and was log transformed. Based on residuals analysis and theoretical considerations, precipitation and percent canopy cover were represented in one or both models by polynomials (e.g. cover and cover²) to capture nonlinear relationships with the log hazard ratio described by an instantaneous rate of change at the mean of the variable and an acceleration (or deceleration) parameter.

^aSEs and *P* values are based on 1000 bootstrap samples.

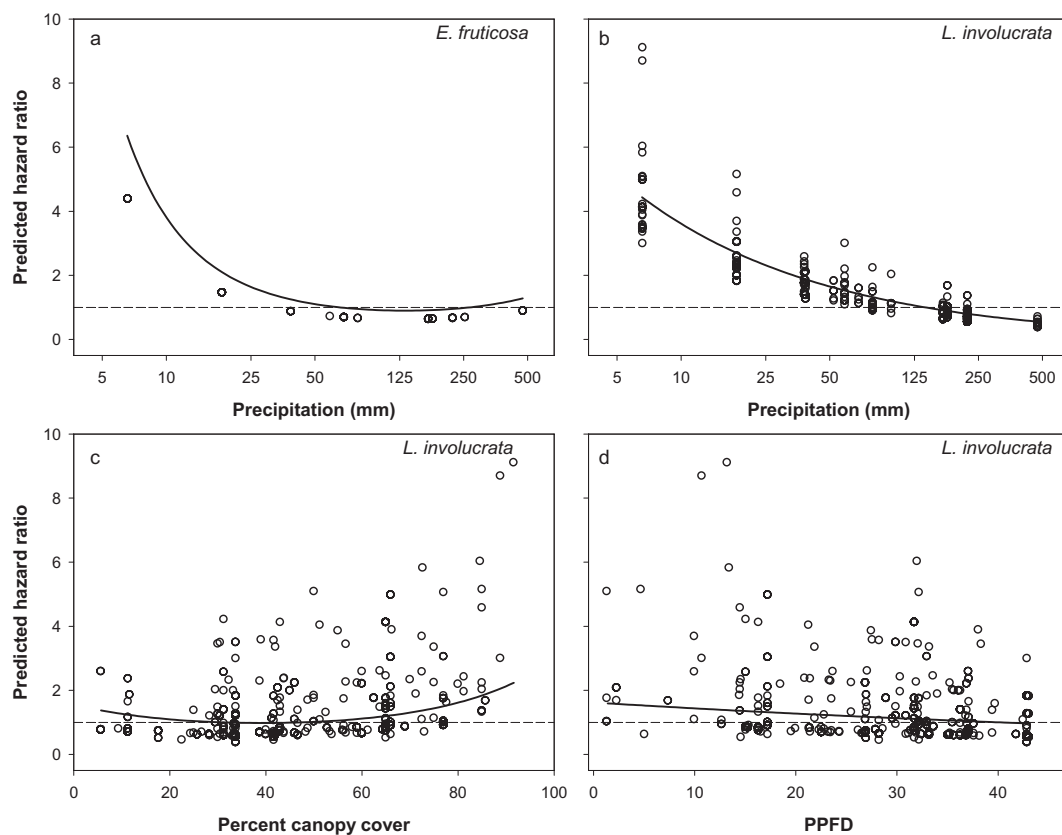


Figure 3: mortality risk functions for *Erithalis fruticosa* (a) and *Lantana involucrata* (b–d) seedlings based on Cox regression (Table 2). The dashed horizontal indicates the baseline mortality risk (hazard ratio = 1). Solid line curves show model-predicted change in the risk of mortality relative to baseline (the hazard ratio) with changes in precipitation during the first 2 months after germination (a and b), canopy cover (c) or PPFD (d) while holding all other influential variables constant at their means. Symbols show predicted hazard ratios for individual seedlings based on their observed values for all influential variables.

Supplementary Table S1). Similar germination patterns indicated this might also be true of *E. fruticosa*, though our survival models possibly signaled a higher shade and even drought tolerance (T vital attribute) among *E. fruticosa* seedlings compared to *L. involucrata*.

With respect to persistence, the appearance of relatively short-lived seeds indicated existence of a soil seed bank after local extinction of adults (S and G vital attributes) was unlikely. So, recolonization of disturbed sites after local adult extinction would have to rely on broadly dispersed

Table 3: results from logistic regression examining factors influencing the log odds of mortality among hand-cut *Erithalis fruticosa* and *Lantana involucrata*

Species	Nagelkerke R^2	Effects	Coefficient	SE ^a	P
<i>E. fruticosa</i>	0.712	Increase in log odds of mortality ratio with shading	3.874	8.474	0.001
		Increase in log odds of mortality ratio with fall cut	3.65	14.208	0.013
		Decrease in log odds of mortality ratio second cut	-4.768	10.861	0.001
		Constant	-3.993	14.245	0.015
<i>L. involucrata</i>	0.318	Increase in log odds of mortality ratio with shading	2.904	3.914	0.001
		Increase in log odds of mortality ratio with fall cut	0.911	0.464	0.034
		Constant	-1.559	0.353	0.001

^aSEs and P values are based on 1000 bootstrap samples.

seed. Our field studies indicated some limitation to local (within-site) dispersal and seed availability, but the seeds of both species may be dispersed over larger areas (between sites) by frugivorous birds (Bancroft and Bowman 1994; Wunderle *et al.* 2010) or even ocean currents (Negron-Ortiz and Watson 2002). Long-distance seed dispersal combined with year-round fruit production (Francis 2004) and a lack of seasonal restriction on germination indicated post-disturbance establishment from seed as a mechanism potentially available at any time appropriate conditions are created (D vital attribute), though initial recruitment may not be abundant. However, the lower germination rate and more limited dispersal range we observed for *E. fruticosa* compared to *L. involucrata* suggested that germinable seed of *E. fruticosa* might not be so effectively dispersed (sensu Schupp *et al.* 2010) to make recovery from seed very likely where adults were absent pre-disturbance—i.e. the C vital attribute could apply to *E. fruticosa*.

Following our cutting disturbances, resprouting shrubs displayed a period of relatively rapid canopy recovery in the first post-disturbance year and some larger shrubs produced flowers or fruit. Reproduction within the first post-disturbance year suggested that some plants of both species can effectively persist through a disturbance as mature individuals while others plants revert to or remain as juveniles. This pattern was indicative of the U vital attribute, which dominates even where the C attribute is exhibited (Noble and Slatyer 1980), or the Δ vital attribute when combined with the D vital attribute (well-dispersed seeds).

Plant functional types and disturbance hypotheses

Combination of the identified vital attributes suggested *L. involucrata* was best functionally classified as Δ I (Supplementary Table S2). The best functional classification for *E. fruticosa* was less clear. The Δ I classification also appeared applicable to *E. fruticosa*, but the evidence (albeit weak) for poorer seed dispersal could justify classification of *E. fruticosa* as UI. Potential shade tolerance of *E. fruticosa* seedlings also suggested the possible classifications of Δ T or

UT, which are functionally equivalent because both combinations result in species with mature individuals capable of persisting through disturbance and producing seeds capable of transitioning to maturity in the absence of disturbance (Noble and Slatyer 1980).

Despite uncertainty about which classification best applied to *E. fruticosa*, we expected the three possible functional types should show different patterns of occurrence among the disturbances we evaluated on Eleuthera (Supplementary Table S2). These patterns arise from restrictions associated with the vital attributes combined with the frequency and severity (or subsequent level of shading) expected for each disturbance type (Fig. 4). For example, clearing followed by repeated grazing is a frequent disturbance regime most often found on well-established farms. Our conversations with local farmers indicate both the clearing and grazing occur in repeated cycles, maintaining open (low shade) conditions over a long period. As such, it should favor intolerant species types, especially those capable of resprouting following repeated disturbance (Δ I and UI), as well as tolerant species that are resilient to frequent disturbance (Δ T/UT; Fig. 4).

Clearing for small-scale agriculture accompanied by burning also involves two closely spaced disturbances, but in contrast to clearing and grazing, the disturbance combination is not likely to occur repeatedly on the same site (infrequent disturbance). The clearing is typically accomplished by hand and often leaves behind large stumps and downed plant material that may be incompletely consumed by a small, controlled and probably low-intensity fire (Giglio *et al.* 2006), resulting in subsequent shading at ground level. The planting of relatively fast-growing crops (e.g. tomatoes, peppers, squashes) also increases shading in the short term. Although our experiments do not provide any direct evidence for the persistence of *E. fruticosa* or *L. involucrata* through fire, it has been reported that coppice shrubs, generally, can resprout after the low-intensity fires common in Bahamian pinelands (e.g. Lee *et al.* 1997). We have casually observed post-fire resprouting of *L. involucrata* and suspect both species could resprout after a low-intensity, small-scale agriculture burn. However, the

Table 4: results from two-level hierarchical linear models for log volume (m^3) of individual, hand-cut black torch and wild sage shrubs within the first experimental year ($n = 94$ and 91 shrubs, respectively, with less than or equal to seven post-treatment measurements) or within the second through third experimental years ($n = 93$ and 76 shrubs, respectively, with ≤ 11 measurements)

First experimental year				
Fixed effects	Coefficient	SE	df	P value
Model for average immediate post-treatment volume: $\beta_{00} = \gamma_{00} + \gamma_{01} + \gamma_{02}$				
Log volume for black torch with average pre-treatment log volume, γ_{00}	0.111	0.016	182	<0.001
Difference in log volume for wild sage with average pre-treatment log volume, γ_{01}	-0.059	0.019	182	0.002
Incremental change log volume with change in pre-treatment log volume, γ_{02}	0.050	0.014	182	0.001
Model for monthly change in log volume (slope): $\beta_{10} = \gamma_{10} + \gamma_{11} + \gamma_{12} + \gamma_{13}$				
Slope for black torch cut in spring, γ_{10}	0.022	0.002	181	<0.001
Difference in slope for wild sage, γ_{11}	0.011	0.003	181	<0.001
Difference in slope for shrub cut in fall, γ_{12}	-0.008	0.003	181	0.007
Change in slope with change in pre-treatment log volume, γ_{13}	0.017	0.002	181	<0.001
Random effects	Variance	χ^2	df	P value
Variation within shrubs through time (r)				
Proportion of within-shrub variance explained by months since treatment	0.009			
	67.2			
Variation among shrubs in immediate post-treatment volume (u_0)				
Proportion of variance explained by species and pre-treatment volume	0.012	640.59	182	<0.001
		10.7		
Variation among shrubs in monthly change (u_1)				
Proportion of variance explained by species, season and pre-treatment volume	0.0003	698.85	181	<0.001
	50.0			
Second through third experimental years				
Fixed effects	Coefficient	SE	df	P value
Model for average immediate post-treatment volume: $\beta_{00} = \gamma_{00} + \gamma_{01} + \gamma_{02} + \gamma_{03}$				
Log volume for black torch cut once in spring, γ_{00}	0.431	0.052	165	<0.001
Difference in log volume for wild sage, γ_{01}	0.171	0.045	165	<0.001
Difference in log volume for shrub cut in fall, γ_{02}	-0.169	0.033	165	<0.001
Difference in log volume for shrub cut twice, γ_{03}	-0.307	0.043	165	<0.001
Model for monthly change in log volume (slope): $\beta_{10} = \gamma_{10} + \gamma_{11} + \gamma_{12} + \gamma_{13}$				
Slope for black torch cut once, γ_{10}	0.014	0.001	165	<0.001
Difference in slope for wild sage, γ_{11}	-0.019	0.002	165	<0.001
Difference in slope for shrub cut twice, γ_{12}	0.006	0.002	165	0.002
Change in slope with change in pre-treatment log volume, γ_{13}	0.034	0.005	165	<0.001
Random effects	Variance	χ^2	df	P value
Variation within shrubs through time (r)				
Proportion of within-shrub variance explained by months since treatment	0.007			
	65.0			
Variation among shrubs in immediate post-treatment volume (u_0)				
Proportion of variance explained by species and pre-treatment volume	0.081	5197.21	165	<0.001
	32.6			
Variation among shrubs in monthly change (u_1)				
Proportion of variance explained by species, season and pre-treatment volume	0.0002	1476.88	165	<0.001
	15.0			

Coefficients for fixed effects of variables are used to estimate log volume (y) at post-treatment month t for shrub i according to the level 1 model: $y_{it} = \beta_{0i} + \beta_{1i}X_{1it} + \dots + \beta_{ni}X_{nit}$, where β_n may be further defined by a level 2 sub-model incorporating variables differing among shrubs (e.g. $\beta_{0j} = \gamma_{00} + \gamma_{01}$). 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.

infrequent nature of this disturbance type could result in local extinction of mature individuals and the subsequent shading could prevent seedling germination of intolerant species.

Consequently, we expect only shade-tolerant species ($\Delta T/UT$) to persist through small-scale agricultural clearing and burning (Fig. 4; Supplementary Table S2).

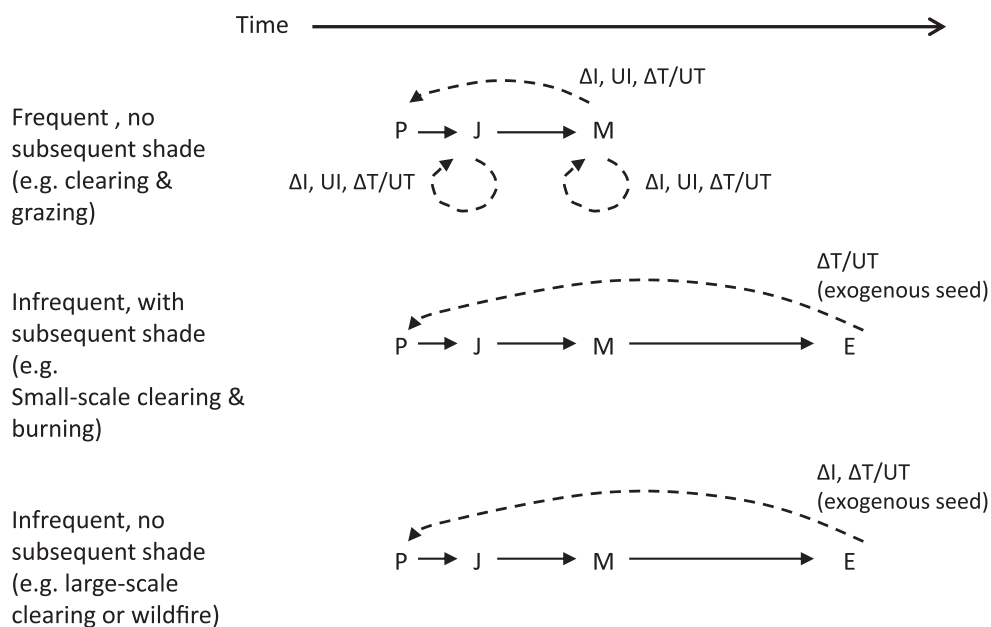


Figure 4: theoretical depiction of processes giving rise to hypothesized pattern of presence of three plant functional types (Supplementary Table S2 for descriptions) among different disturbance regimes. Solid arrows represent life-stage transitions occurring for all functional types during disturbance free intervals. Dashed arrows are transitions occurring after disturbance for only the functional types listed adjacent. In this model a frequent disturbance occurs while juvenile (J) or mature (M) individuals are extant on site. An infrequent disturbance occurs after mature individuals and the short-lived propagules (P) they produce are locally extinct (E) so that recolonization must occur from seed dispersed into the site from exogenous sources.

While also infrequent, large-scale clearing followed by abandonment is typically achieved with heavy machinery, producing open conditions in the aftermath that may not be as rapidly reduced in the absence of agricultural crops. Similarly, uncontrolled wildfires are larger (Helmer *et al.* 2010) and likely to be more severe than small agricultural fires, leaving behind patches with very open conditions (G. Fleming, personal observation). However, the infrequent nature of both disturbance types could lead to local extinction or high fire severity could lead to high shrub mortality. The combination of open conditions following infrequent disturbance would favor intolerant species and those with widely dispersed seeds (ΔI , $\Delta T/UT$; Fig. 4; Supplementary Table S2). Intolerant species with short-lived, poorly dispersed seeds (UI) are not expected in a high proportion of such sites due to the relatively high probability of local extinction and low probability of recolonization by exogenous seed.

Observed vs. hypothesized presence within disturbance types

Among our 246 randomly located plots, *E. fruticosa* was present on only 9.3% and *L. involucrata* on 6.5% of plots, with the two species occurring together on only 2% of plots. Both species were present in all but the small-scale agriculture disturbance category, which (ignoring proportions) fit the pattern of presence expected for the ΔI plant functional

type (Table 5). However, presence of both *E. fruticosa* and *L. involucrata* was disproportionately favored on cleared and grazed plots (Table 5)—a pattern not entirely inconsistent with predictions for the UI functional type (Supplementary Table S2).

DISCUSSION

Our field experiments suggested both *E. fruticosa* and *L. involucrata* are largely shade intolerant species that can establish or regenerate individuals after disturbance via both seeds and vegetative mechanisms. From this functional classification, we derived expected patterns of species presence among different disturbances that closely matched the patterns we observed among a large number of sites across southern Eleuthera. Employing this deductive process provides us with a strong theoretical and mechanistic framework, we can use to predict where desirable habitat that includes these species might occur or to design strategies for habitat management.

Despite the close match between observed and expected patterns of presence, there is still some uncertainty in our functional classification for *E. fruticosa*. A few ambiguities are almost certain to arise when trying to fit individual species into broadly defined functional categories. In this case, incomplete knowledge of the extent of effective long-distance seed dispersal for *E. fruticosa* was a contributing factor combined

Table 5: percentage of study plots ($N = 246$) within four disturbance types on southern Eleuthera where *Erithalis fruticosa* or *Lantana involucrata* was present

Species	Disturbance type			
	Clearing and grazing ($n = 50$)	Large-scale clearing ($n = 86$)	Small-scale clearing w/ burning ($n = 34$)	Wildfire ($n = 76$)
<i>E. fruticosa</i>	26.0 (3.9)	7.0 (-0.7)	0.0 (-1.8)	5.3 (-1.2)
<i>L. involucrata</i>	20.0 (3.7)	4.7 (-0.7)	0.0 (-1.5)	2.6 (-1.3)

Chi-square contingency tests indicated *E. fruticosa* ($\chi^2 = 17.8$, $P < 0.001$) and *L. involucrata* ($\chi^2 = 14.8$, $P < 0.001$) occurrence were not simply proportional to sample sizes within disturbance types (null hypothesis). Numbers in parentheses are the standardized residuals showing the relative magnitude of the discrepancy between observed occurrence within disturbance types and null hypothesis expectations.

with its disproportionate occurrence primarily in the high frequency disturbance regime, which somewhat resembles the expected pattern for the UI type as well as for the Δ I type. The difference between the two functional types in our hypothesized model is that presence among the less frequent forms of disturbance is expected relatively more often for Δ I species than for UI species. But we do not expect Δ I species to be found in less frequently disturbed areas as often as in frequently disturbed areas. Among Δ I species, seed dispersal over large areas provides the potential for re-establishment from seed at any time following disturbance, but there is no guarantee seed will be available within a given disturbed patch. Instead, long-distance colonization of 'new' (or extinction) sites should be less frequent than regeneration at sites with extant populations. Thus, colonization of infrequently disturbed patches by seed should be relatively rare for both Δ I and UI types, but more rare for UI species. The ability to reliably distinguish between these two patterns of rarity in our system may require a larger sample than found in our study, but the practical impact of the ambiguity is limited when applying our results to habitat management concerns since a more frequent disturbance regime is most favorable to both functional types.

Because the relationship between plant functional traits and disturbance may be context specific, it is notable that using vital attributes for our species enabled predictions of occurrence among disturbance regimes separate from those under which the attributes presumably evolved (Hadar et al. 1999; McIntyre et al. 1999b). Identification of general traits mediating plant responses to a variety of disturbance types provides a valuable tool in light of the new disturbances or altered regimes that often accompany expanding human populations. In our case, the vital attributes exhibited by *E. fruticosa* and *L. involucrata* were likely shaped under a regime of frequent tropical storm and hurricane disturbance, which may have been an important factor in KW habitat production before human settlement (Wunderle et al. 2007).

Lugo et al. (2006) describe hurricanes as one of three main forces (including seasonal drought and humans) shaping dry forest vegetation of the Antillean subregion. Throughout the Caribbean, though, strong storm winds in the coastal zones

where *E. fruticosa* and *L. involucrata* frequently occur can cause substantial physical damage to trees and shrubs, reducing the size of larger competitors. Wind- and wave-driven salt spray can also cause substantial canopy and shade reduction (Brokaw and Walker 1991; Smith and Vankat 1992). Low-lying islands, such as those of the Bahamas archipelago (i.e. 80% of land area <1.5 m above sea level), are especially vulnerable to storm surges that can flood extensive areas (Sealey 2006) and eliminate soil and leaf litter (Schoener et al. 2001). All these effects create openings for recruitment and growth of shade intolerant species such as *E. fruticosa* and *L. involucrata*. Because strong storms can occur annually, advantages may also be realized by species that (i) regenerate and reproduce quickly following an initial disturbance and (ii) store enough resources during long disturbance intervals to allow repeat recovery during short disturbance intervals. Our field experiments indicate *E. fruticosa* and *L. involucrata* exhibit both strategies, especially since slow growth of seedlings and resprouting shrub canopies (after initial rapid recovery) may be indicative of high resource allocation to belowground structures.

Very high winds can occur at any time, but the strongest tropical storms in the Caribbean typically occur during the summer Atlantic hurricane season (June to November), which is also the season of highest rainfall in the Bahamas. On Eleuthera, we have observed that many fields are cleared for agriculture in the month or two prior to this period. Our shrub cutting study showed *E. fruticosa* and *L. involucrata* canopy recovery was more rapid following disturbances occurring in spring, just prior to the onset of the summer rainy period, likely because rainfall is very important to the recovery process regardless of the source of disturbance. Summer rains would likely also improve survival of any seedlings germinating in storm- or clearing-related openings.

If storms are a driving force behind occurrence of *E. fruticosa* in coastal zones, it could explain the discrepancy between Byrne's (1980) characterization of the plant as late successional and our categorization as an intolerant species favored by frequent disturbance (i.e. early successional). Byrne was primarily concerned with successional patterns following agricultural abandonment and, as such, might not have

considered storm-affected areas as recently disturbed or early successional.

Due to highly variable species composition within and among tropical dry forest types, [Quesada et al. \(2009\)](#) argued a greater focus on functional traits would bring a better general understanding of dry forest succession. Within many tropical dry forests, the resprouting abilities and zoochory (bird dispersal) noted for *E. fruticosa* and *L. involucreta* are characteristic of a large proportion of species ([Murphy and Lugo 1986](#)). Thus, shade intolerance and other traits contributing to seed dispersal, such as year-round flowering and seedling recruitment, are probably more important to the occurrence of the two species in early-successional stands. For example, in wet tropical forest, [Kang and Bawa \(2003\)](#) found that, compared to late-successional species, early-successional species exhibited more continuous (year-round) flowering. [Murphy and Lugo \(1986\)](#) estimated ~25% of dry forest species exhibit continuous flowering, but within older (>35 years) dry forests in the Virgin Islands, the majority of species observed by [Ray and Brown \(1994\)](#) exhibited a bimodal distribution of flower production and synchronous germination.

Implications for habitat management

The very low occurrence of *E. fruticosa* and *L. involucreta* across our randomly located study plots could, in part, be a consequence of our relatively small plot size. The species might have appeared more frequently had plots been larger, but we doubt the difference would have been substantial. Our qualitative observations indicated species composition within our small plots was very representative of the surrounding areas within the same disturbance patch. This suggests preferred KW winter habitat is not widespread on Eleuthera. Yet, Eleuthera is probably not a sub-optimal site for regional generalization because, to date, the highest published number of wintering KWs has been observed there [i.e. compare numbers reviewed in [Haney et al. \(1998\)](#) to those given in [Wunderle et al. \(2010\)](#)]. Potential rarity of the habitat coupled with substantial temporal and spatial variability in the winter fruit resources consumed by warblers ([Wunderle et al. 2014](#)) warrants consideration of specific habitat protection or management measures.

Management will require strategic but relatively frequent application of disturbance aimed at maintaining the open conditions required by intolerant plant functional types. Determining the appropriate frequency will require determination of certain critical events, or life-stage parameters, considered by [Noble and Slatyer \(1980\)](#) as part of a third group of vital attributes that influence changes in species composition through succession: (i) age of reproductive maturity for individuals recruited from seed and (ii) the lifespan of the adult population. It would also be useful to understand how fecundity changes with the age of adults. In addition, more work is required to determine what forms of disturbance are likely to be most successful. Despite the occurrence of natural, lightning-ignited fires prior to human settlement and

their importance in maintaining stands of Caribbean pine in the Bahamas ([O'Brien et al. 2008](#)), our data suggest fire may be poorly suited for managing coppice habitat for KWs. Fire is largely a human-driven phenomenon in the present-day Caribbean ([Murphy and Lugo 1986](#)), and its increased frequency since human settlement may have allowed the expansion of pinelands at the expense of coppice on some Bahamian islands ([Franklin and Steadman 2013](#)). Nonetheless, *L. involucreta*, *E. fruticosa* and KWs are found in Bahamian pinelands where frequent, low-intensity fires maintain an open pine canopy ([Correll 1979](#); [Eshbaugh and Wilson 1990](#); [Lee et al. 1997](#); [Little et al. 1977](#)). Future studies should evaluate the response of these plants to fires varying in intensity and frequency within stands of both pine and coppice.

Alternatively, well-managed application of goat grazing/browsing may be particularly well suited for management needs. This suggestion is likely to be met by some skepticism given the negative impacts feral goats have had on islands world-wide ([Chynoweth et al. 2013](#); [Coblentz 1978](#)). Yet, goats and other livestock are being successfully incorporated into various land management efforts ([Fernandez-Lugo et al. 2013](#); [Mancilla-Leyton et al. 2013](#); [Ruiz-Mirazo et al. 2011](#)), and our data show a controlled grazing regime favors the occurrence of quality KW habitat. In fact, some of the highest densities of KWs on Eleuthera have been found in active, goat-grazed pastures where their primary fruit resources were exceptionally abundant ([Wunderle et al. 2010](#) and unpublished data). Nonetheless, further research would be needed to determine an intensity and frequency of browsing that would maximize winter fruit production and best maintain the vegetation in a suitable state for KWs and associated species. If the regime can be effectively implemented in areas where existence of mature coppice is highly undesirable or impractical but where low-stature, early-successional coppice is tolerable (e.g. corridors serving as utility rights-of-way), it may yield both conservation benefits and socioeconomic benefits for local farmers and domestic food production.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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