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The effects of fire and fragmentation on occurrence and flowering of a rare perennial plant

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Abstract The pine rocklands of southern Florida are a fire-dependent forest associated with outcroppings of limestone. Pine rockland plants have several adaptations to fire, and for many species burns increase plant growth, flowering, and seedling establishment. The pine rockland forest has been reduced and fragmented in recent decades. Outside of Everglades National Park, only two percent of the original pine rocklands remain, and are in the form of small fragments. Habitat fragmentation may have a negative effect on the biology of plants; we investigated the effects of both fire and fragmentation on *Angadenia berteroi* (A.DC.) Miers, a threatened species of the southern Florida pine rockland. We estimated the density and flowering of *A. berteroi* using adaptive cluster sampling in six study sites with different fire and disturbance histories. *A. berteroi* is more abundant in the largest fragments, and those having experienced fire most recently. However, fragmentation and lack of fire did not appear to have a great impact on flowering or fruit production. Insights from this threatened species may provide impetus not only to conserve, but to properly manage remaining pine rocklands in south Florida.

Keywords *Angadenia berteroi* · Apocynaceae · Adaptive cluster sampling · Reproductive phenology · Pine rocklands

Introduction

The pine rockland forest is unique in the United States and is considered an imperiled habitat (Koptur 2006). Pine rockland forests are a mixture of tropical and temperate taxa (Snyder et al. 1990; US Fish and Wildlife Service 1999) dominated by a single canopy species, *Pinus elliottii*, the slash pine. The subcanopy holds a great variety of shrubs, hardwood trees, and palms, many of which are part of the tropical flora of the West Indies. The herb stratum is diverse, with more than 250 species of ferns, graminoids, and forbs (Snyder et al. 1990; U.S. Fish and Wildlife Service 1999). The high levels of endemism in pine rockland forests may be explained by the presence of limestone outcropping and calcareous, phosphorus-limited soils. The calcium-rich loams and high pH contrast with the acidic quartz sand found in pine forests of northern Florida (O'Brien 1998).

Fire is a vital force, essential to the existence of pine rockland forests. Burns influence vegetation

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structure and species composition. Fires historically occurred in the early wet season (during May and June), with lightning strikes igniting accumulated dry litter, at intervals of 2–10 years (Snyder et al. 1990; U.S. Fish and Wildlife Service 1999). Pinelands in Everglades National Park now are burned mostly by prescribed fires, while fires in the pine rockland fragments are frequently from arson. Within two decades of fire exclusion, pine rockland forest can become closed canopy tropical hardwood forest (known as "hammock"), and the pine trees and diverse herbaceous flora disappear (Snyder et al. 1990).

Pine rockland plants have various adaptations to fire: some herbs and shrubs resprout and grow rapidly after fire, while others respond to burns with improved growth, flowering, seed germination, and establishment of seedlings (Snyder et al. 1990; Spier and Snyder 1998). Some plant species produce more flowers and fruit after fire (Koptur 2006; Liu et al. 2005a; Moreno and Oechel 1991). Although increased reproduction may result from greater light, soil moisture, and nutrient availability after fire (Whelan 1995; Wrobleski and Kauffman 2003), some plants produce flowers in years without fires; this reproduction is also of great importance to plant population viability (Hiers et al. 2000; Wrobleski and Kauffman 2003; Borchert and Tyler 2009).

Plant species are able to exploit the increased resource availability following fire, and the survival of animals (pollinators and herbivores) after fire also affects plant reproduction (Whelan 1995; Liu et al. 2005a). In some native species of the pine rockland forest, fewer flowers have been reported due to increased herbivory after fire (Spier and Snyder 1998; Geiger 2002; Cardel and Koptur 2010).

Landscapes with pine rocklands have undergone dramatic human population growth over the last 100 years, leading to the destruction of most pine rockland habitat. Outside of Everglades National Park, only 2% of the original pine rocklands remain in many small fragments (Snyder et al. 1990; Koptur 2006).

In fragmented habitat, the disturbance regime is often altered (Cochrane 2001). Fragmentation results in an increased proportion of "edge" habitat, producing changes in microclimate and community structure at various distances from the edge (Margules and Pressey 2000). Structural changes may lead to increased fuel loading and fire susceptibility (Cochrane and Schulze 1999). Increased leaf litter accumulation (due to fire suppression) affects species richness and diversity (Kirkman et al. 2001), because litter is a physical barrier to plant growth, inhibiting seed germination, and establishment. Litter modifies the forest floor environment, affecting soil moisture and nutrient availability (Hiers et al. 2007). The spatial distribution of fire is highly edge-related, with greater fire frequency in areas nearer to the edge (Cochrane 2001). However, fire suppression in proximity to human settlement has led to reductions in fire frequency and intensity, as well as loss of fire-resilient properties of the vegetation (Dellasala et al. 2004), and reduced sexual reproduction in fire-adapted species (Geiger 2002; Cardel and Koptur 2010). Altered microhabitats resulting from fire suppression can negatively influence flower and fruit production and inhibit seedling establishment (Wendelberger and Maschinski 2009). In some cases, the effect of fire on plant reproduction and growth can be masked by local environmental heterogeneity, changes in weather, and herbivory (Harrod and Halpern 2009).

Habitat fragmentation can affect the reproductive biology of all species (Yates and Ladd 2005), but environmental variation between fire episodes may have greatest effects on the reproductive biology and population dynamics of fire-dependent species, including those endemic to south Florida pine rockland. Plants that rely on insects for pollination are at a disadvantage in fragmented habitats, because size of fragments as well as the distance between fragments may affect the distribution and abundance of insect species (Artz and Waddington 2006).

In this study, we use the pineland golden trumpet, *Angadenia berteroi* (A.DC.) Miers (Apocynaceae), to examine the separate and combined effects of fire and fragmentation on endemic pine rockland plants. *A. berteroi* is a native, perennial sub-shrub listed as threatened by Florida Department of Consumer Services, Division of Plant Industry (FDACS, DPI) (Gann et al. 2002). This wildflower grows in the pine rocklands, rockland hammocks, and marl prairies of Miami-Dade and Monroe Counties (Gann et al. 2002; Wunderlin and Hansen 2003).

The broad distribution of *A. berteroi* in many pine rockland sites makes it an ideal species to study how fire and fragmentation affect flowering of a pollination-dependent native species, and how these two factors affect the population structure and viability of this wildflower. The hypotheses are: (1) fires positively affect the abundance and reproduction of *A. berteroi*; and (2) fragmentation negatively affects the abundance and reproduction of this species. These hypotheses were tested with field observations in areas of different sizes and fire regimes. We quantified the effect of fires on the reproductive phenology of *A. berteroi* in extensive pine rockland habitat in Everglades National Park and in pine rockland fragments under the management of Miami-Dade County.

Materials and methods

Study species

Angadenia berteroi has opposite, coriaceous, entire leaves, with large, showy, yellow flowers. The flowers have no notable fragrance, but offer nectar as a pollinator reward. Within the flower, the five stamens are agglutinated to the stigma (as in other Apocynaceae), and the two carpels of the ovary are fused at the apex. The V-shaped fruit is made up of two terete follicles, up to 5 cm long at maturity (Long and Lakela 1978; Barrios and Koptur 2011).

Study sites

We studied *A. berteroi* and its habitat variables in a total of six pine rockland forest sites scattered along the Miami Rock Ridge (Fig. 1). We selected four fragments of different size based on fire history data from Miami-Dade County: two fragments had high fire frequency (more than five burns since 1987), and two fragments had low fire frequency (fewer than four burns since 1987). We also used two sites from Everglades National Park, with fire return interval of 1–7 years (Sites 5 and 6). All the sites could be called fragments, except the Everglades National Park sites, which are within continuous pine rockland forest (Table 1). Fire history (Table 2) was determined using fire data provided by the Natural Areas Management (2008) and the fire history database from Everglades National Park (Everglades National Park Fire Management Office, personal communication, 2008). At each site, we chose an area to study that was representative of the reported fire history of that site; we did not include very small fires (less than 1% of the total site area) in determining the parameters in Table 2.

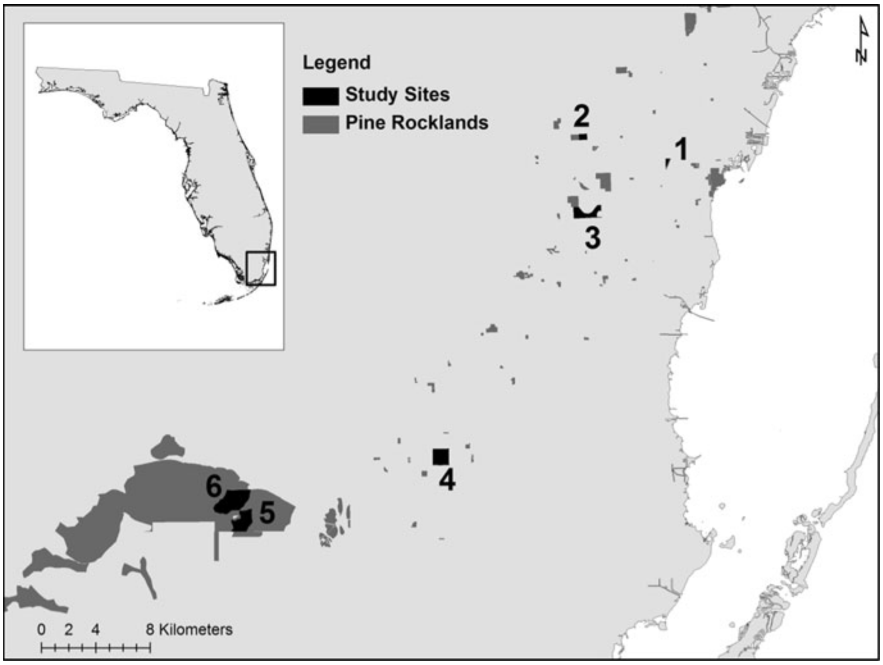

Fig. 1 Map of the pine rockland habitat in southern Florida 2007. Study sites shown, as described in Table 1

Table 1 Pine rockland study sites in Miami-Dade County, Florida, used for *A. berteroi* study

Site name	Site no.	Area (km^2)	UTM coordinates	
			Easting	Northing
Rockdale Preserve	1	0.11	566214	2835342
Nixon Smiley Park	2	0.51	560127	2837016
Larry & Penny Thompson Park	3	1.09	559449	2831668
Navy Wells Preserve	4	1.43	549776	2813432
Everglades I1	5	1.76	535196	2808244
Everglades G	6	3.22	534659	2809774

Site names, number designation, area, and UTM coordinates (UTM Zone 17R, WGS 1984)

Table 2 Fire regime at each fragment and fire unit in Everglades National Park

Site	Fires since 1987	Years since last fire (2009)	Total area that was burned in the last fire (km^2)	Fire frequency	Fragment/ continuous
1	1	8	0.01	Low	Small fragment
2	3	9	0.47	Low	Small fragment
3	38	2	0.32	High	Large fragment
4	10	1	0.30	High	Large fragment
5	8	3	1.69	High	Continuous
6	6	5	2.67	High	Continuous

Data (all columns except the last two) provided by the Natural Areas Management (2008) and the fire history database from Everglades National Park (ENP F.M.O., personal communication, 2008). Designations in last two columns made by authors

Abundance of pineland golden trumpet

To quantify the density of *A. berteroi* at each site, we used Adaptive Cluster Sampling (ACS; Thompson 1990, Philippi 2005). This sampling design is the most efficient method to estimate densities of low-abundance and rare species occurring as clustered individuals (Thompson 1990; Thompson and Seber 1996). A 40 × 50 m area was selected at each site, representative of the fire history of each fragment, avoiding edges; within that area 40–44 random quadrats (1 × 1 m) were selected, without replacement. We implemented the ACS method as follows: If *A. berteroi* was present in the quadrat, the quadrats neighboring the randomly chosen quadrat were added to the study. If a neighboring quadrat contained *A. berteroi*, it was incorporated into the network, and its neighbors were sampled. The criterion for sampling the adjacent quadrats was the presence of *A. berteroi*; consequently, we sampled quadrats until each network was enclosed by empty quadrats not containing *A. berteroi*. A neighborhood is defined as the four quadrats adjacent to the initial randomly sampled quadrat; a network is either an initial sampled quadrat with *A. berteroi* present plus all the neighboring quadrats with it present, or an initial random quadrat without *A. berteroi* (Thompson 1990; Philippi 2005). Therefore, we studied 40–44 random quadrats at each site plus all quadrats neighboring those that included *A. berteroi*.

We recorded the number of individuals of *A. berteroi* in each quadrat. Each separate aerial stem was considered a separate individual, although we observed this species can have rhizomes that may connect one “individual” with another. We may, therefore, have overestimated the number of individuals, since individual stems may have been ramets of the same genet. The Horvitz–Thompson and Hansen–Hurwitz estimators of the population means in ACS allow unbiased estimation of the population means with unequal inclusion probabilities (Thompson 1990; Thompson and Seber 1994; Philippi 2005).

Habitat structure and fragmentation

We measured several habitat variables for the first 30 of the 40–44 random quadrats that were the initial quadrats of the networks: litter depth, canopy closure, and sub-canopy closure. These are different measurements of habitat structure and physical indicators of time since the last fire. All estimates were obtained by taking the average of the values obtained for the four corners of every quadrat. We measured litter depth with a rigid wire and a rule scale to the nearest 0.5 cm. To estimate canopy closure, we counted how many squares of a forestry densiometer were occupied by canopy image, in each of the four corners of the quadrat at a height of 1.30 m, looking from the corner to the center of the quadrat. The same was done to estimate subcanopy closure, but at a height of only 0.5 m.

Fragment size was determined using geographic information system (GIS) data provided by the Fire History database from Everglades National Park and The GIS data generated by Florida Natural Areas Inventory (Public Lands-June 2008 shape files) for the Miami-Dade County fragments. The UTM coordinates were taken at the center point of the 40 × 50 m plot at each site (Table 1).

Fire regime

Fire history data for each site were available from two different sources: Everglades National Park and Miami-Dade County. We utilized information about fires since 1987 (Table 2), but since the fire data for only the Everglades sites were geographically detailed, we used the fragment overall fire frequency and "years-since-last-fire" for each site as an indicator of the fire history at each site (Table 2).

Habitat effects on the reproduction of *Angadenia berteroi*

We systematically selected 15–17 circular plots (1-m radius) that containing *A. berteroi*; at each site, these circular plots were in the same part of the site that included the 40 × 50 m plots, and located in a circular array around the center of the area. Flowering phenology was monitored every 2–4 weeks, from the first days of the flowering period to fruit maturity. Data were recorded for a period of 4 months (April through July, 2009) in all sites. The total number of aerial stems that produced flowers and fruits were recorded for each plot. In addition, for each stem we recorded the number of open flowers, number of flower buds, number of inflorescences, and the number of fruits. The percentage of plants that flowered was estimated by counting all stems with inflorescences in the sample plots and dividing by the total number stems in each plot, averaging for each site. The flowering period, flowering peaks, and the maximum number of fruits per site are illustrated as means for each site.

Statistical analysis

To obtain accurate and unbiased estimates of population densities of *A. berteroi* (means and standard deviations at each site), we used the Horvitz–Thompson and Hansen–Hurwitz estimators (Philippi 2005). We calculated these estimators using the algorithm implemented in the macro available as an on-line supplement of Philippi (2005), Ecological Archives E086-058-S1, for SAS 9.1 (SAS 2003). Student's *t* tests were performed by hand calculator with the mean and the standard deviation for both estimates obtained from the macro. We used the Bonferroni method to control type I error for all pairwise comparisons.

At the quadrat level, we used the first 30 random quadrats at each site for which we had data for number of individuals (of any height, from mature plants to seedlings with one or two pairs of leaves) and the measured site parameters. Since the data satisfied the assumptions, analysis of variance (ANOVA) was used to test for differences among sites for the site variable parameters. Bonferroni comparison tests were used post hoc to elucidate differences among sites. We performed correlation analyses, using Spearman's rank correlation analysis to investigate the relationship between population abundance and the mean of the site parameters.

The proportions of plants at each site with flowers during the flowering peak, and fruits, were analyzed with χ^2 to assess the differences in flower and fruit production among sites. We used the Bonferroni method to control type I error for all pairwise comparisons. Statistical analyses were performed using SPSS 17 (SPSS 2009).

Results

Abundance of *A. berteroi*

The Horvitz–Thompson and Hansen–Hurwitz estimates of the population means for each site revealed

Table 3 Hansen–Hurwitz and Horvitz–Thompson estimates for *Angadenia berteroi* population abundance at the study sites listed in Table 1

Site	Networks	Hansen–Hurwitz estimator			Horvitz–Thompson estimator		
		Total	Mean	SD	Total	Mean	SD
Site 1	44	227.27	0.11^{a}	0.06	228.76	0.11^{a}	0.06
Site 2	43	304.11	0.15^{b}	0.07	313.60	0.16^{b}	0.07
Site 3	41	663.43	0.33^{c}	0.11	725.71	0.36^{c}	0.11
Site 4	44	363.64	0.18^{b}	0.09	370.61	0.19^{b}	0.09
Site 5	42	624.56	0.31^{c}	0.11	738.77	0.37^{c}	0.11
Site 6	40	1353.84	0.68^{d}	0.17	1406.07	0.70^{d}	0.17

Numbers are for total number of individuals and mean number of individuals per network. Superscript letters indicate significant differences with Student's *t* test analysis at the 0.05 significance level

significant differences in plant abundance among sites (Table 3). Abundance of *A. berteroi* was the highest in Site 6, while Sites 3 and 5 did not differ significantly, as well as Sites 2 and 4. Site 1, a smaller fragment with low fire frequency and 8 years since the last fire, had the lowest abundance of *A. berteroi* plants (Table 3).

Population mean estimates indicated that *A. berteroi* is more abundant in larger forest fragments with less time since the last fire (with the exception of Site 4). Overall, it appears that fragmentation plays a role in the density of *A. berteroi*.

Both canopy cover (at 1.3 m above ground) and subcanopy cover (0.5 m above ground) differed significantly among sites ($F_{5,173} = 61.98$, $P < 0.0001$, $F_{5,173} = 91.17$, $P < 0.0001$, respectively, Fig. 2a, b). Sites 1 and 2 (with historically low fire frequency) represent the sites with highest canopy cover and subcanopy cover. Although significantly different from the other sites, they did not differ significantly from each other in terms of subcanopy cover. Sites 3 and 5 had the lowest canopy cover and subcanopy cover, differing from the other sites with the exception of Site 6 in the case of subcanopy cover (subcanopy cover mean = 20.47, SE = 2.50). When we compared the mean of subcanopy cover, Site 4 was intermediate (Canopy cover mean = 39.07, SE = 3.6, subcanopy cover mean = 38.03, SE = 3.6) (Fig. 2). Litter depth differed significantly among sites ($F_{5,173} = 40.48$, $P < 0.0001$, Fig. 2). Sites 1 and 2 did not differ significantly from each other, and had the greatest litter depth. Site 5 had the lowest litter depth (mean = 0.11 cm, SE = 0.03), but did not differ significantly from Sites 3 and 4. Site 6 (mean = 3.19 cm, SE = 0.52) did not differ significantly from Sites 3 and 4, but was significantly different from Site 5 (Fig. 2). In addition, canopy and subcanopy cover were positively correlated with litter depth ($r = 0.69$, $P < 0.0001$, and $r = 0.68$, $P < 0.0001$, respectively). Canopy cover, subcanopy cover, and litter depth are negatively associated with population abundance of pineland golden trumpet. Sites 1 and 2, with highest canopy and subcanopy cover and litter depth (Fig. 2), were the fragment sites with the lowest overall fire frequency (Table 2); these sites also displayed the lowest density of *Angadenia berteroi.*

The site parameters we measured exhibited a strong correlation with the abundance of *A. berteroi* (Spearman ρ, Table 4), being significant in all cases, except litter depth, one of the estimates for fragmentation, and one of the estimates for percent cover at 1.3 m. Canopy cover and litter depth, both indicators of time since fire, were negatively correlated with *A. berteroi* abundance. The other variables (area of the fragment, fragmentation) showed a positive correlation with A. *berteroi* abundance (Table 4).

Habitat effects on reproduction of pineland golden trumpet

Flowering began at the end of the dry season, in early April, and continued into the early wet season, until late June, for four of the sites (Fig. 3). In Sites 1 and 4, the flowering period continued until at least mid July. The flowering peak occurred in early May at most of the sites. Fruit production began in early May, and lasted through July, when the majority of

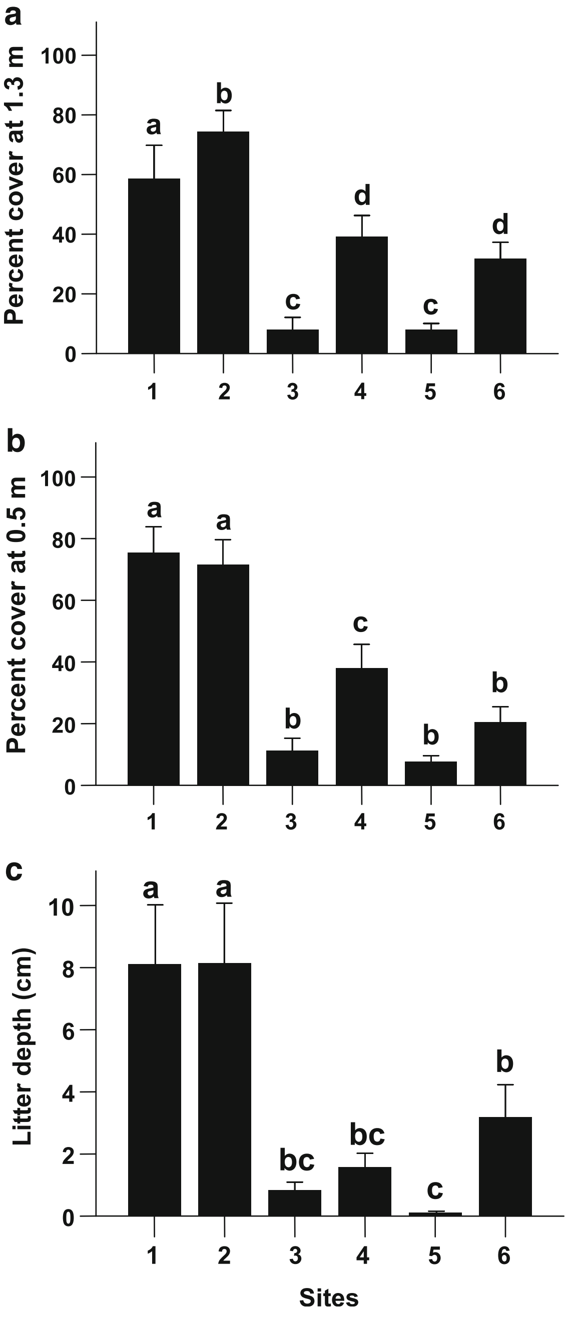

Fig. 2 Environmental variables (mean ± 1 SE) measured for sites described in Table 1. **a** Percent cover of vegetation was determined by spherical densiometer at 1.3 m aboveground (canopy); **b** percent cover at 0.5 m (subcanopy); **c** Litter depth ($n = 30$). Sites with the *same letter* do not differ significantly with Bonferroni post hoc test analysis from each other ($P < 0.05$). Environmental variables were collected from a total of four pine rockland forest sites in Miami-Dade County (Sites 1 and 2 are small fragments, Site 3 and 4 are large fragments) and two burn units in Everglades National Park (Sites 5 and 6)

fruits had matured. Peak fruiting occurred in early June, about 4 weeks after the flowering peak.

The total number of plants that produced flowers during the flowering peak differed significantly among the six sites ($X^2_{5,n=470} = 58.31$, $P < 0.0001$). Post hoc tests showed Sites 3 and 6 (with very few flowers) differed significantly from Sites 1, 4, and 5 (Fig. 4a). Sites 4 and 5 had much higher proportions of plants with flowers (51.6 and 32.7% respectively). Sites 1 and 2 did not differ significantly from each other, intermediate between the other two groups. Sites 1, 4, and 5 did not significantly differ from each other (Fig. 4a). The maximum fruit set differed significantly among the six sites ($X^2_{5,\mathrm{n}=472} = 22.489$, $P > 0.0001$, Fig. 4b). Sites 1, 4, and 5 did not significantly differ from each other. Site 1 had the highest number of fruits produced, while Site 6 had the lowest (Fig. 4b). The higher flowering rates reported at Site 4 and Site 5, with low litter depth and canopy cover (Fig. 2), may indicate that less time since fire has a positive effect on flowering. The results also indicate the positive relationship between light availability and flower production: more than 50% of the plots that produced flowers in the majority of the sites were found in open areas (edge or low canopy plots, Table 5).

Discussion

Effects of fire and fragmentation were found only on the abundance of pineland golden trumpet. Our results showed that adaptive cluster sampling was efficient in determining the abundance of this species, because *A. berteroi* populations were composed normally of a few clusters of plants. The dispersal and establishment of seeds close to parent plants may explain this clumped distribution. In addition, *A. berteroi* exhibits clonal growth. Vegetative reproduction has been described in other Apocynaceae (Johnson et al. 1998) with shoots connected underground via rhizomes.

The Horvitz–Thompson and Hansen–Hurwitz estimates of the population means indicated that *A. berteroi* is more abundant in larger natural habitat sites with greater fire activity (as indicated by litter depth and canopy cover, and records of fire frequency). Fragment size appears to be associated with plant density, as continuous habitats like the sites located in

Table 4 Spearman's rho correlation between site parameters and the estimators of the population abundance means ($n = 6$)

Spearman's ρ correlation	Percent cover at 1.30 m	Percent cover at 0.5 m	Litter depth	Area	Fragmentation
Hansen–Hurwitz estimates	−0.771*	−0.771*	−0.543	0.829*	0.621
Horvitz–Thompson estimates	−0.714	−0.829*	−0.600	0.943*	0.828*

* $P < 0.05$

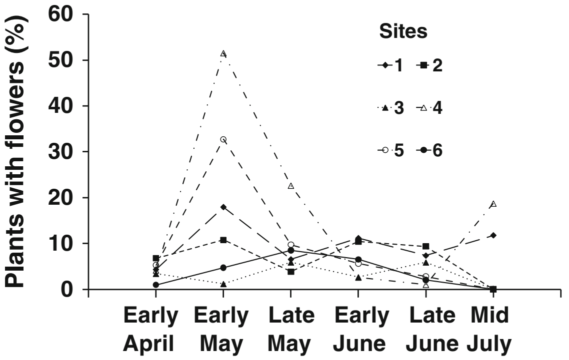

Fig. 3 Flowering phenology of *Angadenia berteroi* at sites described in Table 1. **a** Percentage of plants that produced flowers during the study period (April–July 2009). Flowering phenology data were collected from Sites 1, 2 (small fragments); Sites 3, 4 (large fragments) from pine rockland forest sites in Miami-Dade County; and Sites 5 and 6, two burn units in Everglades National Park

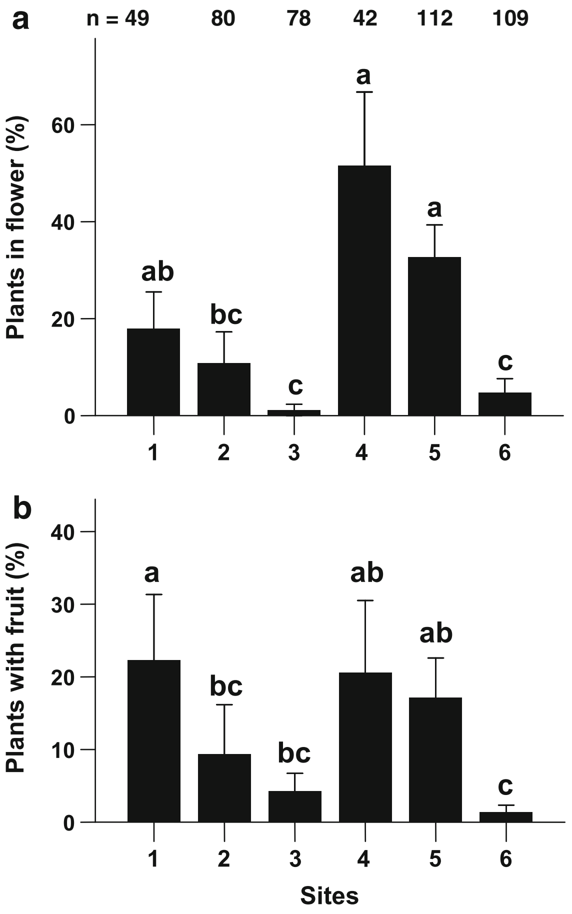

Fig. 4 Mean maximum percentage of plants (mean ± 1 SE) flowering and fruiting at the sites described in Table 1. **a** Flowering. **b** Fruiting. Sites with the same letter do not differ significantly from each other with χ^2 analysis ($P < 0.05$). Sites as in Figs. 1 and 2

Everglades National Park displayed the highest density of this species, followed by the larger fragments, with the exception of Site 4. These results are in contrast to the conclusions of O'Brien (1998), where fragment area did not affect abundance of *Galactia* species. The lower density of *A. berteroi* in Site 4 may also be explained by the high herbivory rate at the site; in summer 2008, 65% of marked plants were lost to herbivores. *Syntomeida epilais* (the oleander moth) is the primary herbivore of *A. berteroi*, with caterpillars often consuming all the foliage and flowers of stems they encounter. Once a plant was devoured, we were unlikely to detect that individual.

Our results also show that sites with higher abundance of *A. berteroi* are those with less time since the last fire; site parameters, such as litter depth and canopy closure, are negatively correlated with the abundance of *A. berteroi*. With fire exclusion, pine rockland can become closed canopy tropical hardwood forest (Snyder et al. 1990); increased canopy reduces light availability and contributes to litter development (Hiers et al. 2007). Increased litter depth and light reduction due to fire suppression create conditions where adult plants in the subcanopy are outcompeted and seedling establishment is inhibited (Hiers et al. 2007; Wendelberger and Maschinski 2009). The lower density of *A. berteroi* at Sites 1 and 2, with the lowest fire activity, suggests that fire plays a role in the density of this species. In the Florida Keys, time since the last fire was negatively

Table 5 Number of plots with *A. berteroi* plants that produced flowers during the flowering peak

Site	Number of plots monitored	Total plots with flowers	Plots that were in a open area that produced flowers	Percent of plots that produced flowers that were in a open area
1	17	7	4	57
2	16	4	2	50
3	17	1	1	100
4	16	10	8	80
5	15	13	11	85
6	15	3	0	0

The percent of these plots that were in an open area was estimated by plots that produced flowers that were in an open area over the total number of plots that produced flowers per site

correlated with population growth rates, and density, of *Chamaecrista keyensis* in pine rockland fragments that were more than 15 years postburn (Liu et al. 2005b).

Although alteration of the fire regime in fragmented landscapes affects plant abundance and seedling germination, the introduction of exotic species could also have adverse effects on the presence of rare native plants (Yates and Ladd 2005). O'Brien (1998) found that density of native species was negatively correlated with density of exotic species such as Brazilian pepper (*Schinus terebinthifolius*). Possley et al. (2008) also reported that in a survey of pine rockland fragments, Navy Wells (Site 4 in this study) was the area with the highest mean cover of non-native plant species in the Redland region; the negative impact of non-native species could also explain the unexpectedly low density of *A. berteroi* at that site. Although we do not have data to examine the correlation between non-native species and the abundance of *A. berteroi*, the high incidence of non-native species reported in remaining pine rockland fragments, plus our field observations, suggest that introduction of exotics negatively affects *A. berteroi*.

In this study, we could not perform a more robust correlation between site parameters and the abundance of this native species, as the ACS design is not compatible with the available statistical programs (Philippi, personal communication). Even though our total sample size ($n = 6$) was relatively small, a positive correlation was found for *A. berteroi* abundance with fragment area, and a negative correlation with canopy closure and litter depth. Our data suggest that lack of fire and habitat fragmentation negatively influence the abundance of this native species.

Angadenia berteroi has a short, well-defined flowering period that was synchronous in all sites studied. Well-defined flowering periods have been reported for several species in the Apocynaceae (Torres and Galetto 1999; Krings 2006; Sloan et al. 2007; DiTommaso et al. 2009). Snyder et al. (1990) also reported similar phenological synchrony for several herbaceous species native to the pine rocklands. Surprisingly, flower production does not show a correlation with fire, nor does fragmentation influence fruit set of *A. berteroi*. These results concur with those of Yates and Ladd (2005) who found that reproduction biology of a rare Myrtaceae shrub was not affected by fragmentation.

However, our results suggest that fire could stimulate flowering and fruit production, as shown by the higher flowering rates observed at Sites 4 and 5. Flowering appears to be stimulated by increased light availability as the result of recent fires (Harrod and Halpern 2009), or due to site heterogeneity in unburned areas: we observed greater flowering in plots that were in edge or low cover areas in the majority of the sites. Yates and Ladd (2005) also observed increased reproduction and germination on roadsides and disturbed areas with little plant cover. Other studies have shown that fire stimulates flowering in pine rockland plants (Snyder et al. 1990; Spier and Snyder 1998; Liu et al. 2005b; Cardel and Koptur 2010), but for some species in other fire-dependent ecosystems, reproduction is not strictly fire-dependent (Wrobleski and Kauffman 2003; Hiers et al. 2000; Borchert and Tyler 2009), and reproduction in years without fire plays an important role in maintenance of the species in the ecosystem (Hiers et al. 2000).

The effects of fire can also be overridden by local environmental heterogeneity, herbivory, or other factors (Harrod and Halpern 2009). We found that Site 3 had few flowers during the flowering peak. This may be attributable to heavy flower damage by oleander moth caterpillars, as well as by beetles (Coleoptera) and orthopteran nymphs. We observed active herbivores and herbivory on plants in at least 25% of the plots in Site 3. Low flower production due to herbivory, and herbivory on flowers has been reported for several native species of the pine rockland forest (Spier and Snyder 1998; Cardel and Koptur 2010). Fire may stimulate flowering, making the plants more visible to herbivores, with the consequence of reduced numbers of flowers and fruits.

Angadenia berteroi is a threatened species of the pine rockland forest. Pine rockland habitat has been drastically reduced and fragmented in recent decades. Altered fire regimes in proximity to human settlement have led to reductions in fire frequency, and loss of fire resilient properties of the habitat. These changes result in increased fuel loading and fire susceptibility. Conservation efforts should be directed to the remaining forest fragments and concentrated on the restoration of the natural ecosystem processes with the implementation of prescribed fire at natural intervals and exotic plant control.

The aim of this study, to test the common assumption that fire and fragmentation influence both abundance and flowering of the native species of the pine rockland ecosystem, was met with mixed results. Fragment size and time since last fire both correlated with the abundance of *A. berteroi*. On the other hand, fragmentation did not have a great impact on reproduction of this native species, and while the effect of fire was not clearly established, the association of fire and factors that favored reproduction suggests that fire may favor reproduction. Other factors, such as herbivory, exotic invasion, soil composition, and local habitat characteristics, warrant further study, as they all may also have substantial effects on the abundance and reproduction of this native species.

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