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RESEARCH ARTICLE

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Fire History and the Structure of Pine-rockland Bird Assemblages

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ABSTRACT: Managers of natural areas often employ controlled disturbances as a tool to manage plant and animal populations. This approach assumes that disturbances are responsible for the structure of biological communities and that appropriate application of the disturbance will ensure the persistence of native plants and animals. If species in a community do not respond predictably to variation in disturbance regime, then management strategies based on emulating disturbance may fail to ensure the persistence of all species. In this study, we examined the efficacy of using prescribed fire as a tool for managing populations of breeding and wintering birds in the pine rocklands of southern Florida. We found that variation in fire history had little effect on vegetation structure and no effect on bird abundance. Instead, vegetation structure was more closely associated with water-table elevation and soil type, whereas most of the observed variation in the structure of bird assemblages appeared to be a function of degree of urbanization in the landscape. That the structure and composition of bird assemblages was independent of variation in fire history suggests that manipulating the fire regime, at least within the range of variability observed in this study, is unlikely to prove effective as a means to manage bird populations. In general, our results argue for caution in assuming that a single process can be used to control the structure of biological communities, especially in systems where landscapes have been substantially altered by human activity.

Index terms: Florida, hydrology, pine rocklands, prescribed fire, slash pine

INTRODUCTION

Many of the concepts central to conservation biology have received relatively little empirical evaluation (e.g., Simberloff 2001), yet they form the basis for managing most populations of plants and animals (Schulte et al. 2006). For example, the concept of coarse filters (Noss 1987; Hunter et al. 1988; Hunter 2005) argues that populations of most species in a community can be controlled by manipulating key structuring processes, especially disturbances that shape the abundance and distribution of important habitat elements. This approach is commonly applied in a variety of ecosystems to manage plant and animal populations (Leopold et al. 1963; Hunter 1993; Haufler et al. 1996; Long and Smith 2000). Coarse-filter management strategies that focus on restoring normative disturbance regimes assume that the abundance of each species in a community is a predictable function of the intensity and frequency of the disturbance. Maintaining a characteristic community structure requires only that disturbance is applied at an intensity and frequency that approximates the historic range of variability. Intuitively appealing, coarse-filter management strategies allow managers to address the needs of multiple species with a single action and do not require a detailed understanding of the habitat requirements of each species in a community.

The use of disturbances as a coarse filter is not without its critics, however; concerns include whether scientists and managers have sufficient knowledge of how natural disturbances act to adequately replicate them (Landres et al. 1999) or whether we can identify which disturbances to manipulate or replicate (Simberloff 2001). As such, it remains unclear under what set of conditions a process-oriented, coarse-filter approach to conservation will reliably ensure the persistence of the majority of species in a community. Additional case studies that evaluate the efficacy of this approach are sorely needed (Bestelmeyer et al. 2003; Hunter 2005).

In this paper, we present the results of a case study in which we examined how one taxonomic group responded to the application of a coarse-filter management strategy. In particular, we examined how breeding- and wintering-bird assemblages responded to variation in prescribed-fire regimes in the pine-rockland ecosystem of south Florida. Pine rocklands are fire-dependent, found only on limestone outcrops in south Florida, the Bahamas, and Cuba. In the absence of fire, hardwoods come to dominate the canopy, inhibiting growth and reproduction of pines, and eventually the pine rockland is replaced by a dry, broad-leafed tropical forest. In the presence of natural fire regimes, pine rocklands are characterized by relatively open-canopied stands of south Florida slash pine (*Pinus elliottii* var. *densa* Little and Dorman) rising above understories of grasses, hardwood shrubs, and palms (*Serenoa repens* Bartram, *Sabal palmetto* (Walter) Lodd. ex Schult. & Schult. f., and *Coccothrinax argentata* (Jacq.) L.H. Bailey). Most (> 90%) of the area in south Florida once covered by pine rocklands, known as the Miami Rock Ridge, has been replaced by agricultural fields and residential or commercial developments (USFWS 1999).

Accepting that fire is necessary in checking successional pathways that lead inevitably to the replacement of pine rocklands by broad-leafed forests, a critical and outstanding question remains: within the range of fire-return intervals that prevent succession to hardwood hammocks, does variation in fire regime explain extant variation in the composition and structure of plant and animal assemblages at different sites within the pine rocklands? In other words, is any fire regime that prevents the encroachment of hardwoods adequate in promoting the mix of plants and animals characteristic of pine rocklands, or is some level of fine-tuning required? The primary management objective in pine rocklands has been to restore putatively natural fire regimes (Maguire 1995; USFWS 1999), the assumption being that doing so will create and maintain the environmental conditions necessary to support the characteristic assemblage of plants and animals. However, this assumption has rarely been tested. As a coarse filter, fire at any reasonable interval may be adequate in maintaining forests of slash pine. Within the broad range of fire-return intervals that prevent encroachment of hardwoods, however, sites burned at different intervals may support very different assemblages of plants and animals. If so, this information is of great importance in fine-tuning fire as a coarse filter. Alternatively, variation in biological assemblages among different sites within the pine rocklands may be driven by factors other than fires – hydrology, for example. In this case, at shorter temporal scales, fire does not act as a coarse filter; and managers looking to effect change in the numbers of a species would need to manipulate variables other than fire.

In this study, we tested a corollary of the coarse-filter approach, namely that variation in the fire regime should produce variation in vegetation structure, which should in turn produce variation in bird species composition and abundance of birds. If bird assemblages in pine rocklands do not predictably vary as a function of variation in the fire regime, then fire, at least within the range of variation observed, does not act as a coarse filter for birds in this system and alternative management strategies may be needed to maintain or restore bird populations in the pine rocklands. We tested these predictions by examining the relationship between fire history (the number of fires and length of the fire-free period), vegetation structure, and bird abundance at 156 locations in south Florida, while at the same time controlling for a suite of potentially confounding variables that might mask the effect of fire history.

We focused on birds because they have been particularly vulnerable to the degradation and destruction of the pine rocklands and, as such, are of concern to land managers. Seven species of breeding birds have been extirpated from the pine rocklands since the middle of the last century: wild turkey (*Meleagris gallopavo* Linneaus), summer tanager (*Piranga rubra* Linneaus), brown-headed nuthatch (*Sitta pusilla* Latham), Eastern bluebird (*Sialia sialis* Linneaus), red-cockaded woodpecker (*Picoides borealis* Vieillot), Southeastern American kestrel (*Falco sparverius paulus* Linneaus), and hairy woodpecker (*Picoides villosus* Linneaus). Three species, including wild turkey, brown-headed nuthatch, and Eastern bluebird, have been reintroduced to Everglades National Park, although the long-term viability of these populations is uncertain (Lloyd et al. 2009).

METHODS

Study area

We conducted this study at Long Pine Key, located within Everglades National Park, and in a series of small pine-rockland preserves in the greater Miami metropolitan area that were managed by Miami-Dade County (Figure 1). Long Pine Key is the largest remaining patch of pine rockland in North America (USFWS 1999), and includes approximately 4600 ha of pine rockland. The climate within the study area is subtropical, with a pronounced dry season from November to April and a wet season from May to October. About 75% of rainfall occurs during the wet season, with most of the wet-season rains falling during convective storms early in the season or during tropical cyclones in the late wet-season; July and August are relatively dry (Snyder et al. 1990). Annual temperature variation is relatively modest, with an average July temperature of 29 °C and an average January temperature of 19 °C.

Historically, fire-return intervals in the pine rocklands are thought to have averaged between three and seven years (Wade et al. 1980; Snyder 1986; Snyder et al. 1990; Liu et al. 2005; Sah et al. 2006). Most fires probably occurred during the wet season, with the greatest acreage burning in June, when lightning is common but fuel moisture remains low (Taylor 1981). Ignitions by humans have greatly extended the fire season; most human-caused fires in south Florida occur during the dry season, although, as with natural fires, the largest fires occur at the transition from dry to wet season (Gunderson 1994; Gunderson and Snyder 1994).

Establishing survey points

We collected data at 104 points in Long Pine Key and 52 points in pine-rockland preserves managed by Miami-Dade County (Figure 1). We established points at Long Pine Key in 2005 and in Miami-Dade County parks in 2006. For Long Pine Key, we placed survey points at randomly chosen locations, with the restriction that survey points were ≥ 350 m apart and were surrounded by ≥ 100 m of contiguous pine forest. We had fewer potential sites to choose from in the Miami-Dade County park system, so our selection of survey locations was essentially systematic: we established points in any patch of pine rockland as long as they met the criteria identified for points in Long Pine Key. The 52 points surveyed in Miami-Dade County parks were located in 17 different sites; however, three sites (Linda and Penny Thompson, Martinez Site, and

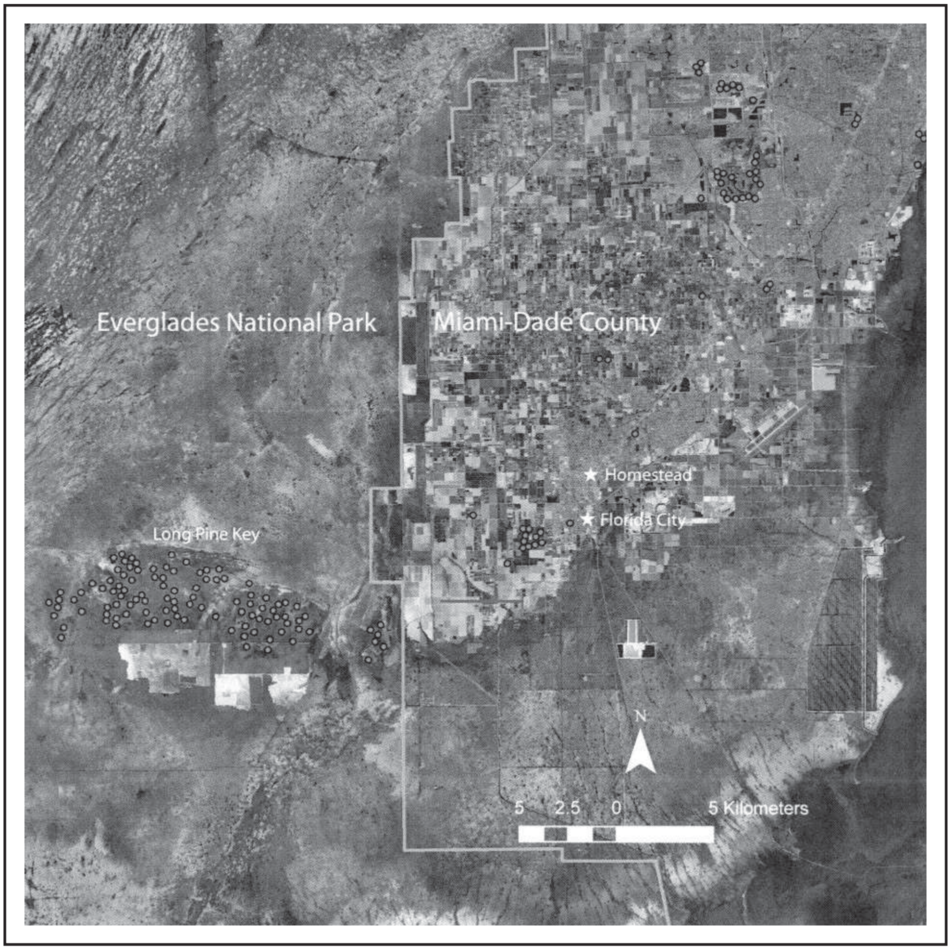

Figure 1. Map of the study area, showing the 104 points in Long Pine Key, Everglades National Park, and 52 points in Miami-Dade County, Florida, at which bird and plant surveys were conducted from 2005-2008. All points were located within pine rocklands.

Miami Metrozoo) were adjacent, forming a single large patch of pine forest. Thus, we sampled 14 unique patches of pine rockland, each containing from 1 – 17 survey points. We treated each point as a replicate in our analyses because fire histories varied substantially, even among adjacent points within a site.

Quantifying vegetation structure

We quantified vegetation structure because it is assumed to be the causal link through which fire affects bird populations. We sampled vegetation at each survey point annually between 1 December and 1 March. We determined the number and diameter of living and dead pine trees ≥ 8.0 cm diameter at breast height (dbh) in an 11.3-m-radius circular plot centered on each survey point and at three additional sampling plots centered 40 m from the survey point at bearings of 0, 120, and 240. We also used dbh to group living trees into three categories for the purposes of analysis: small (≤ 10.5 cm dbh), medium (10.6 – 18.5 cm dbh), and large (> 18.5 cm dbh). We used measurements of dbh to derive estimates of basal area, where basal area was equal to the cross-sectional area of trees and snags (πr^2; where r = dbh/2). At the survey point and at each of the three sampling plots centered 40 m from the survey point, we visually estimated the percent cover by plants at ground level (< 1.5 m) and at the shrub level (between 1.5 and 8 m) in a 5-m-radius circular plot. We estimated percent cover for three major understory habitat components at both the ground and shrub levels: grasses, palms, and hardwood shrubs. Finally, we used a marked pole to estimate average height of palms and the maximum heights of pines, hardwoods, and palms within the shrub level.

Estimating bird abundance

We conducted avian surveys during the non-breeding (15 Dec – 15 Feb) and breeding (15 Apr – 1 Jun) seasons. Each station was visited once per season. Each survey consisted of a seven-minute count, during which observers recorded the radial distance from the sampling station to all birds detected within 50 m of the point. Surveys were conducted between sunrise and 10:00 AM. We estimated density and abundance (number of birds per 50-m-radius sampling plot) using distance sampling as implemented by Program Distance (Thomas et al. 2009). Distance sampling is one of several methods that adjusts counts of birds to address imperfect detectability.

Quantifying fire regime

We quantified fire history with two variables: the number of days since each survey point had burned and the total number of times each point had burned within the 10 years prior to the survey. We obtained fire history data from each organizational unit (Miami-Dade County and Everglades National Park). For many of the points, data did not extend beyond 10 years prior to the survey, and so the maximum number of days since last fire was artificially truncated at 3650.

Potentially confounding variables

In a review of the literature concerning pine rocklands, we identified two other factors that might influence vegetation structure, and therefore bird assemblages, and which might mask the effects of variation in fire: (1) hydrology (Olmsted et al. 1983; also see Duever 2005 for an example from the ecologically similar pine flatwoods) and (2) soil type (Robertson 1953; Possley et al. 2008). In addition, we suspected that vegetation structure and bird assemblages in patches of pine rockland might be strongly influenced by conditions outside of the patch, especially within the network of small reserves in Miami-Dade County.

As a measure of hydrological conditions, we focused on water-table elevation because it likely has direct effects on vegetation in the pinelands (Olmsted et al. 1983; Ish-Shalom et al. 1992; Ewe et al. 1999) and because it is correlated with hydroperiod, which may influence the intensity and frequency of fire (Lockwood et al. 2003; Slocum et al. 2003). To estimate water-table elevation, we downloaded daily stage data from the South Florida Water Management District for all stations within 25 km of a survey point. We then averaged the daily data to estimate the average water stage for the spring sampling period (15 Apr – 1 Jun) in each year of the study. We chose to use average water-table elevation during April – June as our sole measure of hydrological conditions because water-table elevations at a point were closely correlated between the winter and spring sampling periods ($r^2 = 0.85$, 95% CI = 0.76 – 0.94) but were more variable among points during the spring sampling period (winter CV = 1.6%, spring CV = 3.6%) and, thus, perhaps more useful as a predictor variable. We kriged average stage elevations using Universal Kriging (spherical model with anisotropy), and extracted the value for each survey point. We calculated the elevation above sea level using the United States Geological Survey's High Accuracy Elevation Data model and the Southwest Florida Feasibility Study elevation model. If a point had data from both models (i.e., models overlapped at that point), we used the average of the two models. We then subtracted the elevation above sea level at each survey point from the estimated stage height to calculate water-table elevation.

Previous authors (Robertson 1955; Olmstead et al. 1983; Snyder et al. 1990; Possley et al. 2008) have noted small-scale variation in the structure and composition of pine rocklands and have attributed this variation to differences in soil types. Areas furthest north along the Miami Rock Ridge (the "northern Biscayne" region of Snyder et al. (1990)) occur on the Opalocka-Rock outcrop complex (Noble et al. 1996), which consists of up to 15 cm of sand above limestone bedrock. Further south (the "Redlands" region of Snyder et al. (1990)), pine rocklands occur on the Cardsound-Rock outcrop complex, a shallow (10 cm) layer of silty loam above limestone bedrock (Noble et al. 1996). Long Pine Key, furthest south along the Miami Rock Ridge, is not included in existing soil surveys but, in general, soils are almost non-existent and bare limestone is the dominant substrate. We identified the soil type at all of the points within the Miami-Dade County park network using soil survey maps (Noble et al. 1996).

We assumed that the composition of the surrounding landscape might influence bird abundance and vegetation structure, and so we estimated the percent of agricultural land and the percent of urban land (the two primary cover types outside of Everglades National Park) within a 500-m radius around each point in the Miami-Dade county parks. All points in Long Pine Key were surrounded by a mix of pineland and open glades. We used the 2004 Florida Land Cover Database (available at http://www.fgdl.org/) to determine land cover.

Statistical analyses

Survey points were sampled each year from 2005 (Long Pine Key) or 2006 (Miami-Dade County) to 2008, but we decided that measures of bird abundance taken at the same point in different years were not independent of one another, even if the values for the predictor variables changed from one year to the next. For example, birds may show no short-term response even to significant habitat changes simply because of fidelity to a particular site (Wiens and Rotenberry 1985). Thus, we chose to analyze only a random subset of the data collected, drawing at random data from one of the three (Miami-Dade County) or four (Long Pine Key) years of data collected at each point. Therefore, the total sample size in our analyses was N=156.

We analyzed data from Long Pine Key and Miami-Dade County parks separately. We did so out of concern that differences in fire regime were confounded by gross differences in soil type, hydrology, and landscape composition. Long Pine Key is a single, large patch of pine forest surrounded by a largely natural environment that has been protected since the 1940s. Pineland preserves in Miami-Dade County are much smaller (the largest patch is < 5% of the size of Long Pine Key) and are surrounded by urban or agricultural land; in most cases, the pineland preserves are the only natural plant communities on the landscape. In addition, most of the fires that affected the pine-rockland preserves in Miami-Dade County were unplanned wildfires, whereas nearly all of the fires at Long Pine Key were prescribed. We also expected that the structure of plant and bird assemblages in the two areas would differ for purely historical reasons. Nearly every pine tree in Miami-Dade County parks died following Hurricane Andrew in 1992, either due to direct mortality from wind damage or indirect mortality caused by a combination of drought, hurricane damage, and infestation by *Ips* beetles; Long Pine Key was affected to a much lesser degree (USFWS 1999). Thus, we decided that analyzing the two areas separately would better allow us to isolate the effects of variation in fire history.

We used a constrained ordination technique, canonical analysis of principal coordinates (CAP; Anderson and Willis 2003), to examine whether variation in vegetation structure and bird abundance was associated with variation in fire history. We controlled for potentially confounding effects of hydrology by including water-table elevation as a predictor; for the analyses of points in Miami-Dade County parks, we also included soil type and surrounding land cover. We did not include soils or land cover as covariates in our analysis of points at Long Pine Key because neither varied among points within that site. We conducted the analysis using the capscale function in the R package vegan (Oksanen et al. 2009). The statistical significance of the canonical axes was calculated using the permutation tests implemented in capscale (Oksanen et al. 2009).

We identified the measures of vegetation structure or bird species that were responsible for any patterns revealed by the CAP by examining correlations between canonical axes and measures of vegetation structure and bird abundance (Jongman et al. 1995; Anderson and Willis 2003). We conducted follow-up, univariate analyses on vegetation variables or bird species that showed a strong (i.e., |r|> 0.20) correlation with at least one canonical axis. To do so, we used generalized linear models (GLM) with the response variable being bird abundance or vegetation structure and the predictors being water-table elevation, number of days since fire, and number of fires in the past 10 years (and, for points in Miami-Dade County parks, soil type, percent agricultural land within 500 m, and percent urban land within 500 m). We did not attempt to simplify these models, instead including all predictor variables. For count data, we assumed a Poisson distribution with a log link function. For other data (e.g., percent cover or height), we assumed a normal distribution of errors, but examined quantile-quantile plots and plots of fitted values versus residuals to determine the validity of this assumption. In cases where the assumption of normally distributed errors appeared invalid, we found that log-transforming the response variable addressed problems both of normality of errors and constancy of variance. All analyses were conducted using R version 2.9.1 (R Development Core Team 2009).

RESULTS

Descriptive statistics: fire regime, hydrology, and surrounding land use

Points in Long Pine Key had burned more frequently and more recently than points located in pine-rockland preserves managed by Miami-Dade County (Figure 2). Variation in fire frequency among points within the two areas was relatively small. At Long Pine Key, 50% of the points had burned between 3 and 5 times in the preceding 10 years, 25% had been burned between 6 and 9 times, and 25% had burned once or twice. In the Miami-Dade County parks, 50% of the points had been burned once or twice, 25% had never burned, and 25% had been burned between 3 and 5 times. Average water-table elevation at survey points in Long Pine Key was higher than that in Miami-Dade County parks during both April – June and December – February (Figure 2). The only significant correlations among fire and hydrology variables were

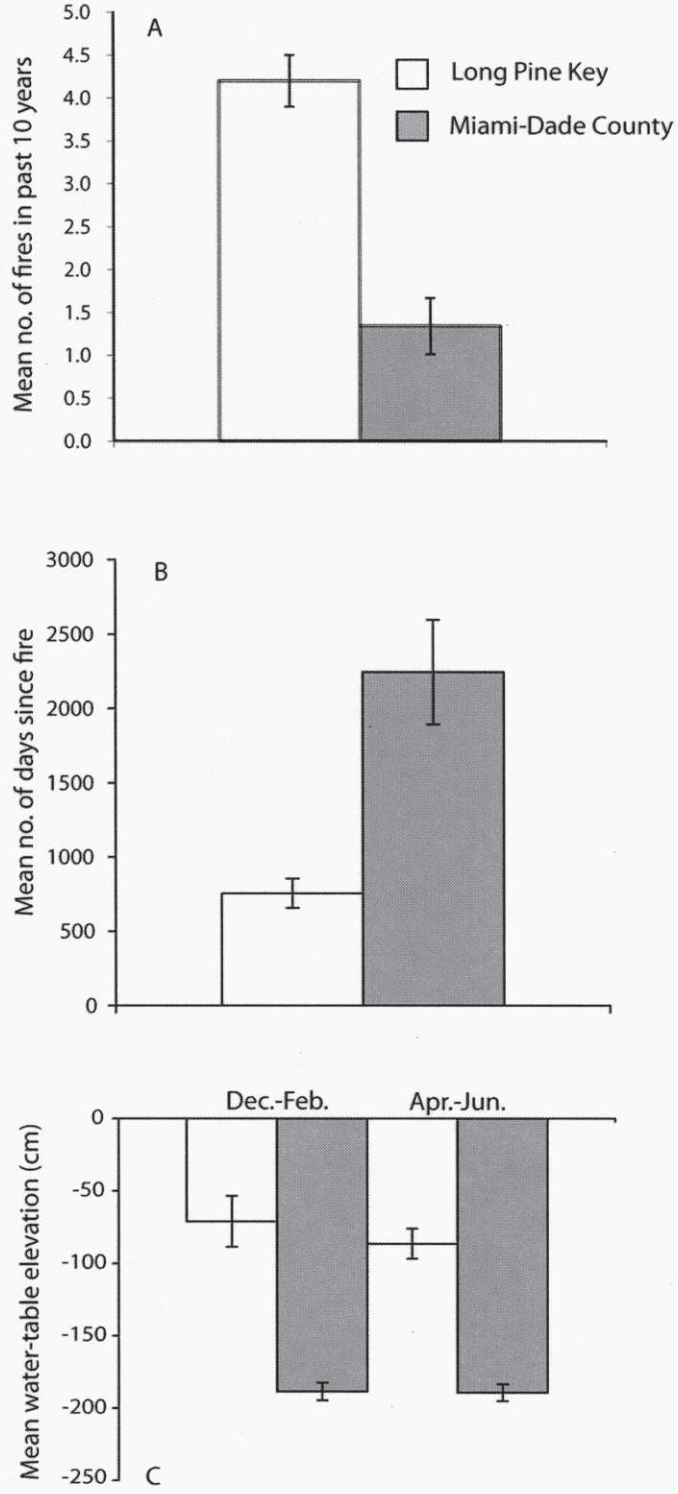

Figure 2. (A) Average number of fires in the 10 years preceding the date on which a bird or plant survey was conducted at locations in Long Pine Key, Everglades National Park (white bar), or Miami-Dade County, Florida (gray bar); (B) Average number of days between the date a point was surveyed and the last time it was burned; and (C) water-table elevation in Long Pine Key, Everglades National Park (white bars) or Miami-Dade County, Florida (gray bars), during breeding-season (April – June) and winter (December – February) surveys for birds. Error bars are 95% confidence intervals.

between the number of fires in the past 10 years and the number of days since last fire (Long Pine Key: *r* = -0.47 [95% CI = -0.61 – -0.31]; Miami-Dade County: *r* = -0.74 [95% CI = -0.85 – -0.59], respectively).

Most of the land within 500 m of survey points in Miami-Dade parks was classified as urban (mean = 61.6%, range = 3.7% – 96.5%), with agriculture accounting for the majority of the remainder (mean = 10.8%, range = 0.0% – 58.8%). The ratio of agricultural land to urban land increased from the northeast portion of the study area, closer to the Miami city center, to the southwest, which has relatively little commercial or residential development. As a result, soil type and landscape were confounded: points in landscapes dominated by agriculture occurred on the Cardsound soil type, whereas points in urban landscapes occurred on the Opalocka soil type (Figure 3a). Points on the Opalocka soils also tended to have lower water tables, with the surface of the water table found on average 199.0 cm below ground surface (Figure 3b). Fire histories were similar across soil types (days since fire: Opalocka = 2278; Cardsound = 2173; number of fires in past 10 years: Opalocka = 1.4; Cardsound = 1.3).

Breeding birds: Long Pine Key versus Miami-Dade County parks

Breeding-bird assemblages of the two areas were readily distinguishable from one another (Table 1; see table for scientific names). Indeed, although Northern Cardinal was the most abundant breeding species in both areas, little overlap existed in species composition (Table 1). Species characteristic of intact pinelands, such as Pine Warbler or Downy Woodpecker, were absent outside of Long Pine Key, and were replaced in the parks of Miami-Dade County by a suite of generalist, human-commensal species such as Common Grackles, Blue Jays, and Northern Mockingbirds (Table 1).

Breeding birds: effects of fire, hydrology, soil, and landscape conditions

Constrained ordination revealed only weak effects of the predictor variables on breeding-bird assemblages in both Long Pine Key and Miami-Dade County parks. At Long Pine Key, fire history and water-table elevation explained a small (3.8%) and insignificant (all P > 0.10) amount of variation in bird abundance. In the pineland preserves of Miami-Dade County, fire history, soil type, hydrology, and landscape conditions were not significant predictors of variation in the structure and composition of the breeding-bird assemblages (percent of variation explained = 11.6%, P = 0.43).

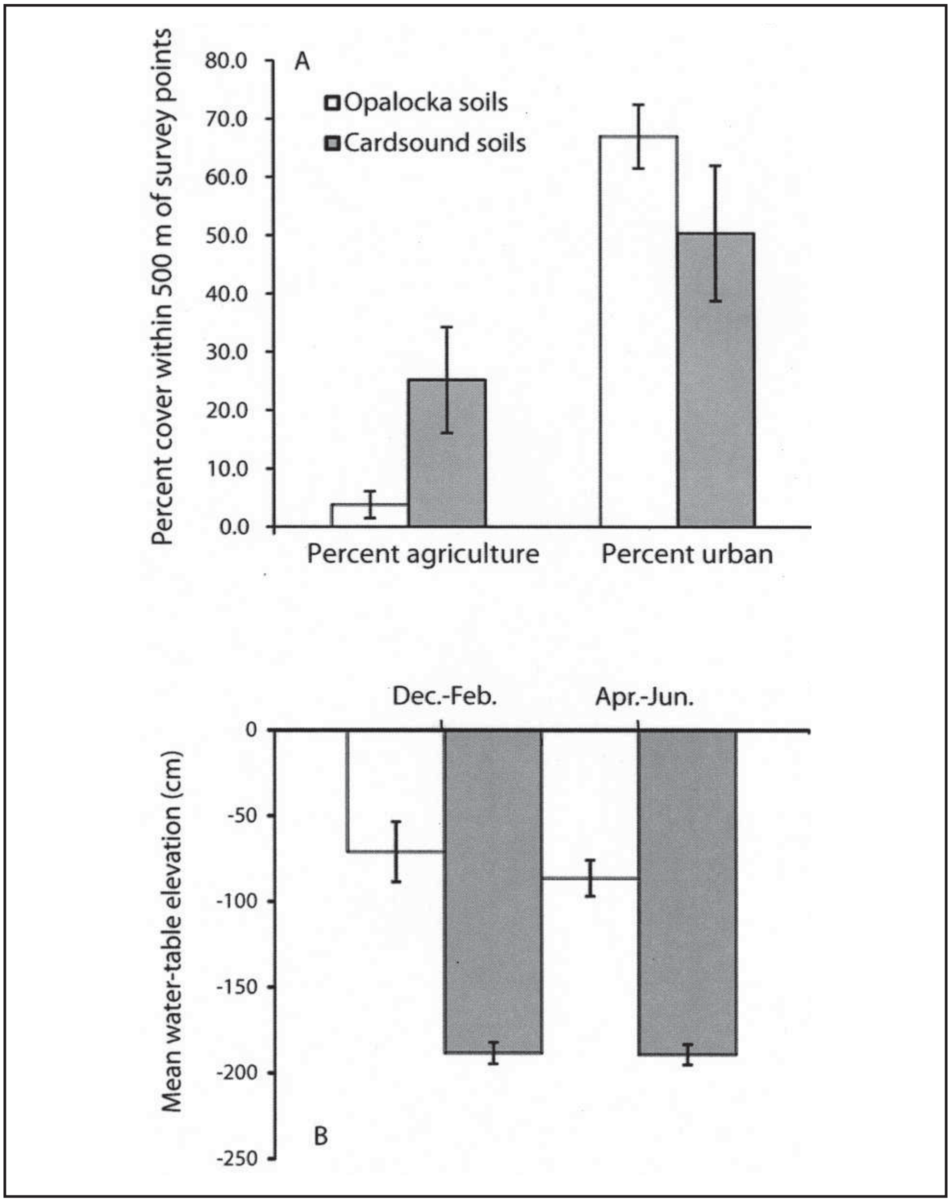

Figure 3. (A) Percent agriculture and percent urban land within 500 m of survey points (N=52) on the two main soil types underlying pine-rockland preserves in Miami-Dade County and (B) water-table elevation on these same soil types during breeding-season (April – June) and winter (December – February) surveys for birds. Error bars are 95% confidence intervals.

Non-breeding birds: Long Pine Key versus Miami-Dade County parks

Bird assemblages present during the non-breeding season at Long Pine Key and in Miami-Dade County parks were, as during the breeding season, readily distinguishable (Table 2; see table for scientific names). The estimated total density of birds both at Long Pine Key and in Miami-Dade County parks rose appreciably during the winter, from a breeding-season average of 2.7 individuals ha^{-1} (95% CI = 2.3 – 3.1)

Table 1. Estimated density (95% confidence interval) of breeding birds (number of individuals ha-1) in pine rocklands at Long Pine Key, Everglades National Park, Florida, and in parks managed by Miami-Dade County, Florida.

Variable	Density (individuals ha^{-1}) Long Pine Key	 Miami-Dade County
Northern Cardinal (*Cardinalis cardinalis* Linneaus)	0.57 (0.51 – 0.65)	0.75 (0.50 – 1.11)
Red-bellied Woodpecker (*Melanerpes carolinus* Linnaeus)	0.24 (0.16 – 0.37)	0.16 (0.06 – 0.38)
Pine Warbler (*Dendroica pinus* Wilson)	0.21 (0.13 – 0.34)	0
Eastern Towhee (*Pipilo erythrophthalmus* Linnaeus)	0.21 (0.14 – 0.33)	0.14 (0.06 – 0.34)
Great-crested Flycatcher (*Myiarchus crinitus* Linnaeus)	0.19 (0.11 – 0.30)	0.03 (0.01 – 0.08)
White-eyed Vireo (*Vireo griseus* Boddaert)	0.18 (0.11 – 0.29)	0
Downy Woodpecker (*Picoides pubescens* Linneaus)	0.09 (0.05 – 0.17)	0
Brown-headed Nuthatch (*Sitta pusilla* Latham)	0.08 (0.04 – 0.18)	0
Northern Flicker (*Colaptes auratus* Linnaeus)	0.05 (0.04 – 0.07)	0.03 (0.01 – 0.06)
Carolina Wren (*Thryothorus ludovicianus* Latham)	0.04 (0.03 – 0.06)	0
Mourning Dove (*Zenaida macroura* Linnaeus)	0.03 (0.02 – 0.04)	0.04 (0.02 – 0.08)
Blue Jay (*Cyanocitta cristata* Linneaus)	0.02 (0.01 – 0.03)	0.20 (0.15 – 0.27)
European Starling (*Sturnus vulgaris* Linneaus)	0.02 (0.01 – 0.04)	0.08 (0.05 – 0.14)
Common Grackle (*Quisculus quiscula* Linneaus)	0.01 (0.01 – 0.03)	0.38 (0.23 – 0.61)
Northern Mockingbird (*Mimus polyglottus* Linneaus)	0.01 (0.01 – 0.03)	0.30 (0.16 – 0.59)
Boat-tailed Grackle (*Quiscalus major* Vieillot)	0	0.05 (0.03 – 0.09)
Eurasian Collared Dove (*Streptopelia decaocto* Frivaldszky)	0	0.03 (0.01 – 0.06)

and 3.3 individuals ha^{-1} (95% CI = 2.8 – 3.9), respectively, to an average of 6.0 individuals ha^{-1} (95% CI = 5.5 – 6.5) and 6.4 individuals ha^{-1} (4.9 – 8.2), respectively. At both sites, winter brought the arrival of large numbers of migrant warblers, especially Yellow-rumped Warbler and Palm Warbler, but also increased numbers of Pine Warblers. In fact, Pine Warblers were abundant during winter in Miami-Dade County parks, despite their near-absence from these same points during the breeding season. White-eyed Vireos and Boat-tailed Grackles were also more common during winter than during the breeding season in Miami-Dade County parks. Other short-distance migrants that wintered in relatively large numbers in pinelands in both areas included Gray Catbird, Common Yellowthroat, Blue-gray Gnatcatcher, House Wren, and American Robin. American Robins were far more common in winter in Long Pine Key than in Miami-Dade County parks (Table 2).

Non-breeding birds: effects of fire, hydrology, soil, and landscape conditions

Structure and composition of non-breeding bird assemblages in Long Pine Key were unrelated to fire history or hydrology (r^2 = 3.1%, P = 0.32). Likewise, soil type, fire history, hydrology, and landscape conditions were not significant predictors of bird assemblages in Miami-Dade County parks during winter (percent of variation explained = 13.8%, P = 0.6).

Vegetation structure: Long Pine Key versus Miami-Dade County parks

Long Pine Key contained more large pine trees and fewer small pine trees than did the pineland preserves of Miami-Dade County (Table 3). Ground cover by hardwoods and grasses tended to be somewhat greater in Long Pine Key; ground cover by palms was greater in Miami-Dade County parks (Table 3). Shrub cover by palms was also greater in the Miami-Dade County parks, as was the average and maximum height of understory palms (Table 3).

Vegetation structure: effects of fire, hydrology, soil, and landscape conditions

Long Pine Key

In a constrained ordination, the number of days since fire, average water-table elevation, and the number of fires in the past 10 years explained a significant (P < 0.005) albeit small (8.5%) percentage of the observed variation in vegetation structure. When tested sequentially, only the first canonical axis accounted for a significant amount of variation in vegetation structure (P < 0.005), explaining 4.4% of the total variation in vegetation structure, and accounting for 83.1% of the explained variation. This axis was negatively correlated with the number of days since fire (r = -0.36) and water-table elevation (r = -0.35) and positively correlated with the number of fires at a point over a trailing

Table 2. Estimated density (95% confidence interval) of birds (number of individuals ha-1) wintering in pine rocklands at Long Pine Key, Everglades National Park, Florida, and in parks managed by Miami-Dade County, Florida.

	Density (individuals ha^{-1})	
Variable	Long Pine Key	Miami-Dade County
Yellow-rumped Warbler (*Dendroica coronata* Linnaeus)	3.04 (2.89 – 3.20)	2.26 (2.14 – 2.38)
Gray Catbird (*Dumetella carolinensis* Linnaeus)	1.07 (1.00 – 1.14)	0.74 (0.69 – 0.79)
Pine Warbler (*Dendroica pinus* Wilson)	0.74 (0.67 – 0.81)	0.28 (0.25 – 0.31)
Common Yellowthroat (*Geothlypis trichas* Linnaeus)	0.66 (0.62 – 0.69)	0.03 (0.03 – 0.04)
House Wren (*Troglodytes aedon* Vieillot)	0.42 0.39 – 0.46)	0.17 (0.16 – 0.19)
Palm Warbler (*Dendroica palmarum* Gmelin)	0.26 (0.23 – 0.30)	0.34 (0.30 – 0.39)
Blue-gray Gnatcatcher (*Polioptila caerulea* Linnaeus)	0.25 (0.24 – 0.28)	0.45 (0.41 – 0.48)
American Robin (*Turdus migratorius* Linnaeus)	0.21 (0.18 – 0.25)	0.02 (0.01 – 0.03)
Red-bellied Woodpecker (*Melanerpes carolinus* Linnaeus)	0.20 (0.19 – 0.22)	0.09 (0.09 – 0.10)
Northern Cardinal (*Cardinalis cardinalis* Linnaeus)	0.17 (0.15 – 0.19)	0.48 (0.42 – 0.55)
Eastern Towhee (*Pipilo erythrophthalmus* Linnaeus)	0.11 (0.09 – 0.12)	0.05 (0.05 – 0.06)
Downy Woodpecker (*Picoides pubescens* Linnaeus)	0.10 (0.09 – 0.11)	0
Northern Mockingbird (*Mimus polyglottus* Linneaus)	0.09 (0.08 – 0.11)	0.19 (0.17 – 0.22)
Eastern Phoebe (*Sayornis phoebe* Latham)	0.08 (0.07 – 0.10)	0.08 (0.07 – 0.09)
White-eyed Vireo (*Vireo griseus* Boddaert)	0.08 (0.06 – 0.10)	0.04 (0.03 – 0.05)
Northern Flicker (*Colaptes auratus* Linnaeus)	0.06 (0.05 – 0.07)	0.04 (0.03 – 0.04)
Carolina Wren (*Thryothorus ludovicianus* Latham)	0.04 (0.03 – 0.05)	0
Blue Jay (*Cyanocitta cristata* Linneaus)	0.02 (0.02 – 0.03)	0.12 (0.11 – 0.13)
Boat-tailed Grackle (*Quiscalus major* Vieillot)	0	0.26 (0.20 – 0.34)
European Starling (*Sturnus vulgaris* Linneaus)	0	0.08 (0.06 – 0.11)
Eurasian Collared Dove (*Streptopelia decaocto* Frivaldszky)	0	0.03 (0.02 – 0.06)

10-year window (r = 0.28). Points with positive scores along the first axis had been burned more frequently and more recently and tended to be drier (Figure 4).

Ordination results suggested that the height of most understory components – young pines, palms, and hardwood shrubs – increased as water-table elevation rose and as the time since last fire increased (Figure 4). In contrast, drier sites, and those burned more recently and frequently, had a greater number of large pine trees, more pine snags, and increased cover at the ground level by hardwoods and palms (Figure 4).

Of the six variables strongly correlated (|r|> 0.20) with the first canonical axis, all showed significant relationships with at least one of the predictor variables in follow-up, univariate analyses. One variable was related to fire history only. Percent ground cover by palms was negatively related to the number of days since last fire (P = 0.04), but was unrelated to water-table elevation (P = 0.54) or the number of fires in the past 10 years (P = 0.74). Model-estimated ground cover by palms ranged from 3.5% at sites that had gone without fire for 2030 days, the maximum observed, to 8.1% at sites burned 146 days prior to sampling. Despite the statistical significance of the relationship, the absolute effect size – a change of < 5% cover – is of questionable biological significance.

Four variables showed significant relationships with water-table elevation only. First, the basal area of pine snags was negatively related to water-table elevation (P = 0.02), but showed no association with either the number of fires in a trailing 10-year window (P = 0.29) or the number of days since last fire (P = 0.09). Based on predictions from the generalized linear model, basal area of pine snags varied from 0.3 m^2 ha^{-1} on the wettest sites to 1.3 m^2 ha^{-1} on the driest sites, or approximately a 330% difference. Second, the density of large pine trees around a survey point was also negatively related to water-table elevation (P = 0.02) and unrelated to the other predictors (days since fire: P = 0.28; number of fires: P = 0.11). The density of large pine trees was estimated to range from 43 ha^{-1} at the wettest sites to 100 ha^{-1} at the driest sites, a difference of approximately 135%. Third, height of the tallest palm was positively related to water-table elevation (P = 0.004), but the effect size was relatively small: maximum height at the driest site was estimated at 1.3 m; at the wettest site, 2.0 m. Neither the number of days since fire (P = 0.92) nor the number of fires in the past 10 years (P = 0.43) was related to variation in the maximum height of palms. Finally, the density of pine snags was

Table 3. Average values (95% confidence interval) for measures of vegetation structure in pine rocklands at Long Pine Key, Everglades National Park, Florida, and in parks managed by Miami-Dade County, Florida.

Variable	Long Pine Key	Miami-Dade County
Small pines ha^{-1}	20.0 (15.2 – 24.8)	65.0 (44.6 – 85.4)
Medium pines ha^{-1}	113.8 (97.4 – 130.1)	131.8 (100.2 – 163.3)
Large pines ha^{-1}	80.3 (70.2 – 90.3)	24.0 (11.8 – 36.2)
Pine snags ha^{-1}	46.3 (37.1 – 55.3)	56.5 (44.3 – 68.7)
Pine snag basal area (m^2 ha^{-1})	0.8 (0.6 – 0.9)	0.9 (0.7 – 1.2)
Ground cover (%)	47.1 (43.7 – 50.5)	34.0 (30.3 – 37.8)
Grass cover (%)	16.9 (15.0 – 18.8)	12.5 (10.3 – 14.7)
Hardwood ground cover (%)	11.3 (9.8 – 12.8)	7.5 (5.7 – 9.4)
Palm ground cover (%)	6.4 (5.4 – 7.4)	11.4 (9.6 – 13.2)
Shrub cover (%)	5.8 (5.0 – 6.6)	8.6 (5.9 – 11.4)
Hardwood shrub cover (%)	2.9 (2.2 – 3.5)	2.9 (1.6 – 4.2)
Palm shrub cover (%)	0.5 (0.4 – 0.6)	2.4 (1.4 – 3.5)
Average palm height (m)	0.9 (0.8 – 1.0)	1.2 (1.1 – 1.3)
Height of tallest understory pine (m)	4.7 (4.1 – 5.3)	6.6 (6.0 – 7.2)
Height of tallest hardwood (m)	3.1 (2.9 – 3.3)	3.1 (2.6 – 3.5)
Height of tallest palm (m)	1.6 (1.5 – 1.7)	2.4 (2.2 – 2.7)

negatively related to water-table elevation (P = 0.003) and showed a weakly negative relationship with the number of days since fire (P = 0.06; *b* = -0.001, 95% CI = -0.002 – 0). We found no relationship between snag density and the number of fires at a point (P = 0.15). Estimated number of pine snags ranged from 13 ha^{-1} – 85 ha^{-1} at the wettest and driest sites, respectively, a 580% difference.

One vegetation variable was related to both fire history and hydrology. The maximum height of understory pines was positively related to the number of days since fire (P = 0.01) and water-table elevation (P = 0.04). Estimated effect sizes were similar for both water-table elevation (driest to wettest: 3.4 m – 6.4 m) and days since fire (fewest to most: 3.7 m – 6.9 m), each yielding estimated changes in understory pine height of approximately 86% and 88%, respectively, across the range of observed values. Understory pine height was unrelated to the number of fires at a point in the past 10 years (P = 0.82).

Miami-Dade County parks

The predictor variables explained 25.1% of the variation in vegetation structure as described by the constrained ordination (P = 0.005). Most (57.4%) of the variation explained by the ordination was due to the first canonical axis and indeed, when tested sequentially, only the first canonical axis accounted for a significant amount of variation in vegetation structure (P = 0.005; all other axes, P > 0.15). Site scores along the first canonical axis were most closely correlated with variation in soil type (*r* = 0.72), percent agriculture (*r* = -0.60), and percent urban land (*r* = 0.50), indicating that points on the Opalocka soil type, which also tended to be in more urban settings, differed in vegetation structure from points on the Card Sound soil type, which tended to be found in patches in agricultural landscapes (Figure 5). The number of days since fire (*r* = -0.25), water-table elevation (*r* = -0.19), and the number of fires in the past 10 years (*r* = 0.13) were relatively unimportant in explaining variation in vegetation structure.

Ordination results indicated differences in vegetation structure between pineland preserves located in urban landscapes, which tended to occur on Opalocka soils, and pineland preserves in agricultural landscapes, which tended to occur on Card Sound soils (Figure 5). By every measure – height, ground cover, and shrub cover – hardwoods were a more important component of pineland preserves on Card Sound soils than of pinelands on the Opalocka soils (Figure 5). In contrast, palms formed a more important component of the understory of pine rocklands on the Opalocka soils (Figure 5).

Univariate analyses on variables strongly correlated with the first CAP axis suggested that only two measures of vegetation structure were related to fire history: (1) height of the tallest hardwood and (2) height of the tallest understory palm. Both increased as the number of days since last fire increased (hardwoods: P < 0.001; palms: P = 0.04). Estimated effect sizes were greater for hardwoods than for palms. At points burned most recently (three days since fire), the tallest hardwood was predicted to be 1.7 m (95% CI = 0.9 – 2.6); at points unburned for at least 10 years, the predicted height was 3.9 m (95% CI = 3.2 – 4.6). Over the same range of fire-free periods, the predicted height of the tallest understory palm ranged from 1.9 m (95% CI = 1.4 – 2.4) to 2.7 m (95% CI = 2.3 – 3.1).

These same variables were also affected by soil type, with effect sizes approximately equal to those predicted for the number of days since fire. The height of the tallest understory hardwood was significantly greater on Card Sound soils (P < 0.001), with predicted values on Card Sound soils (4.5 m, 95% CI = 3.7 m – 5.3 m) nearly twice as great as those on Opalocka soils (2.4 m, 95% CI = 1.9 m – 2.9 m). The height of the tallest understory palm was significantly greater (P = 0.006) on the Opalocka soil type, although the effect size was small (Opalocka soils, tallest understory palm = 2.7 m, 95% CI = 2.4 m – 3.0 m; Card Sound soils, tallest understory palm = 1.8 m, 95% CI = 1.4 m – 2.2 m).

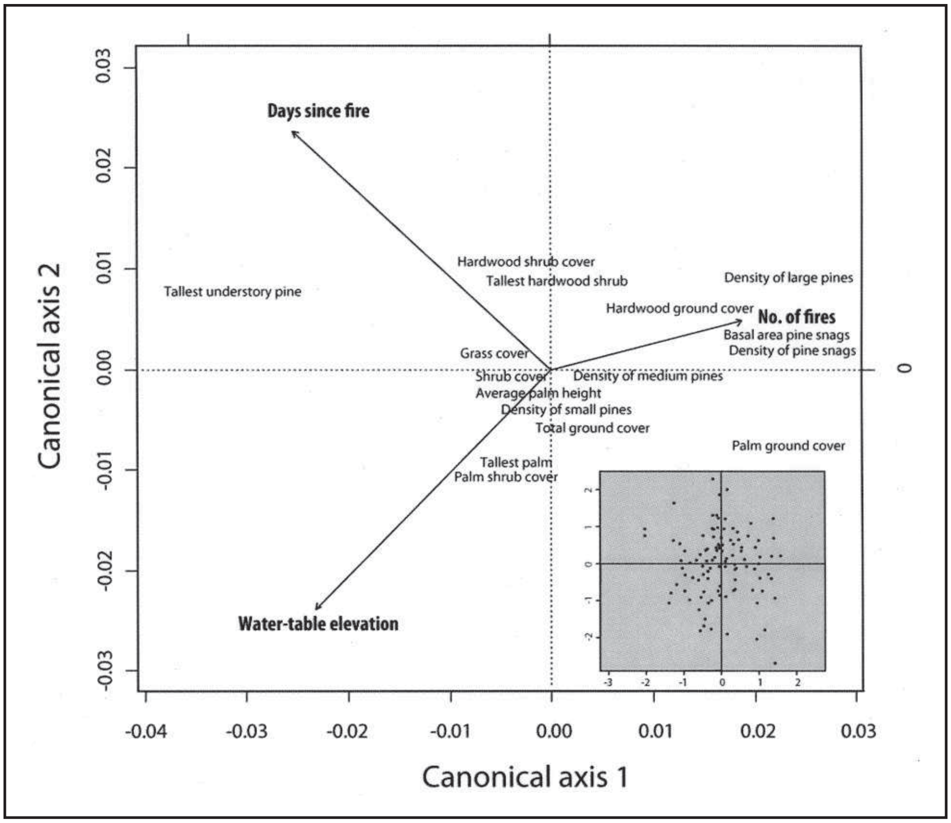

Figure 4. Results of a canonical analysis of principal coordinates of vegetation structure at points in pine rocklands within Long Pine Key, Everglades National Park. Arrows represent the strength of correlation between predictor variables and ordination scores; variables with longer arrows explained more variation in ordination scores. Orientation of the arrows indicates the direction of maximum change in the value of the predictor variables. The position of each labeled variable indicates the relative position of survey points where that variable reached its greatest value. Variables close to an arrow were more closely correlated with variation in that predictor. Variables positioned close to the origin were poorly explained by the ordination. The highlighted inset figure shows the actual position of survey points in the ordination. The lack of strong pattern in the position of points reflects the poor explanatory power of the ordination.

Soil type also exerted significant influence on three other measures of vegetation structure. Hardwood shrub cover was significantly greater at sites on the Cardsound soil type (P = 0.02). Predicted cover by hardwood shrubs at sites on Cardsound soils was 5.5% (95% CI = 3.1% – 7.9%) but only 1.6% (95% CI = 0.1% – 3.1%) on Opalocka soils. Hardwood ground cover was also significantly greater (P = 0.01) on Cardsound soils (11.4%, 95% CI = 9.0% – 13.8%) than on Opalocka soils (5.6%, 95% CI = 3.4% – 7.8%). The percent of the ground covered by palms was significantly greater on the Opalocka soils ($P < 0.001$) and the predicted effect size was much larger (Opalocka soils, percent ground covered by palms = 14.2%, 95% CI = 12.0% – 16.4%; Cardsound soils, percent ground covered by palms = 5.8%, 95% CI = 2.4% – 9.2%).

DISCUSSION

Prescribed fire is the primary tool used to manage biological communities in the pine-rockland ecosystem. The assumption underlying this approach is that fire is the key structuring process in pine rocklands (Robertson 1953; Alexander 1967), creating the physical conditions required by the characteristic groups of species occupying pine rocklands. This assumption is based largely on the observation that periodic fire resets successional pathways that appear to lead inevitably to replacement of pine rocklands by broad-leafed forest. Given this, we predicted that vegetation structure and the composition and structure of bird assemblages would vary among areas differing in fire history. Contrary to expectation, neither vegetation structure nor bird assemblages were closely associated with variation in fire history. Instead, we found that vegetation structure responded more strongly to relative water-table elevation (Long Pine Key) and soil type (Miami-Dade County parks) and that the composition and structure of bird assemblages at our survey points was not associated with any of our predictor variables.

Our results suggest that the vegetation of the pine rocklands is so resilient and resistant to fire that variation in fire history, at least within the range we observed, has relatively little effect on vegetation structure. After a quick recovery following fire, most of the spatial variation in vegetation structure appears to be a function of persistent differences among sites in relative water-table elevation and soil type (see also Robertson 1955; Taylor and Herndon 1981; Olmsted et al. 1983; Possley et al. 2008; Slapcinsky et al. 2010). Fire history may be the primary source of variation in vegetation structure only when sites representing the tails of the distribution of fire histories are well represented in the sample. In studies such as ours, where variation in fire history was relatively small, the effects of fire will appear small or non-existent.

The rapid recovery of vegetation likely minimized any change in habitat availability for birds, such that bird assemblages showed little response to variation in fire history. Other studies in southeastern pine forests have yielded similar findings (Emlen 1970; Lloyd and Slater 2011). Indeed, organisms in ecosystems where fire is frequent, such as the pine rocklands, are apt to be highly tolerant of fire and may show no response to fire history except under extreme conditions (Parr and Andersen 2006). The only clear pattern of variation for birds was the distinction between assemblages found at points in the Miami-Dade County parks, which were small and embedded within highly modified landscapes, and points in Long Pine Key, which were surrounded by mostly intact pine forest and glades. Breeding-bird assemblages in Miami-Dade County parks were dominated by human-commensal species such as Common Grackle, Northern Mockingbird,

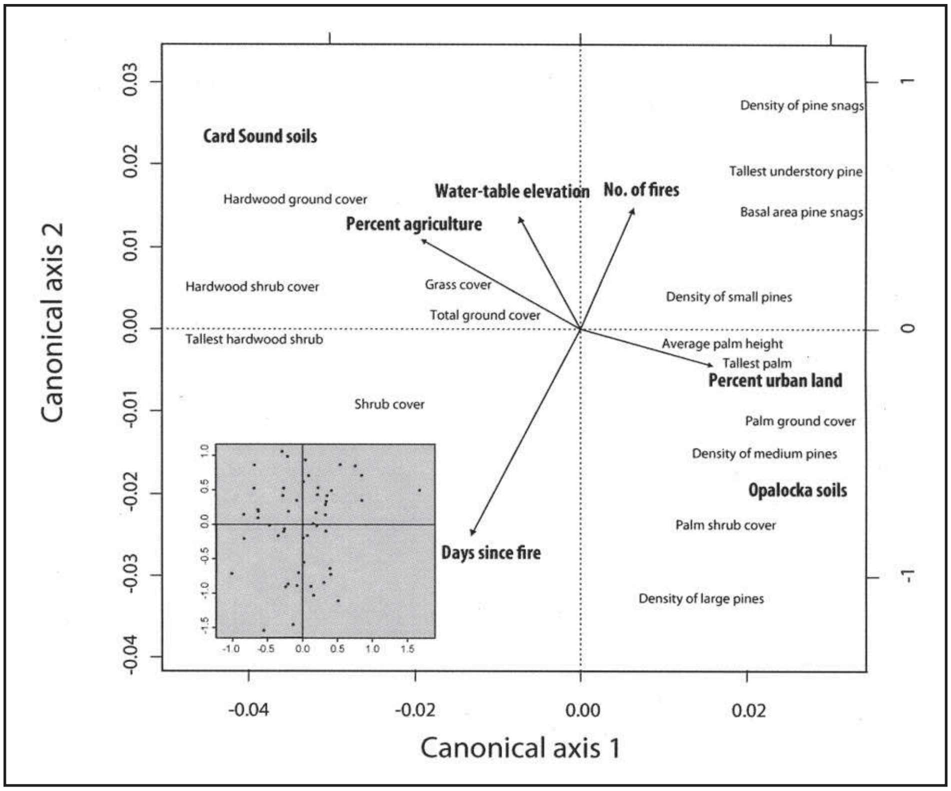

Figure 5. Results of a canonical analysis of principal coordinates of vegetation structure at points in pine-rockland preserves in Miami-Dade County, Florida. Arrows represent the strength of correlation between predictor variables and ordination scores; variables with longer arrows explained more variation in ordination scores. Orientation of the arrows indicates the direction of maximum change in the value of the predictor variables. The position of each labeled variable indicates the relative position of survey points where that variable reached its greatest value. Variables close to an arrow were more closely correlated with variation in that predictor. Variables positioned close to the origin were poorly explained by the ordination. The highlighted inset figure shows the actual position of survey points in the ordination. The lack of strong pattern in the position of points reflects the poor explanatory power of the ordination.

and Blue Jay, and lacked characteristic pineland species such as Pine Warbler and Downy Woodpecker (See Table 1 for scientific names). The composition of bird assemblages in the two areas converged in the winter with the arrival of migrants such as Yellow-rumped Warbler, Gray Catbird, and Palm Warbler (See Table 2 for scientific names), which were abundant in both Long Pine Key and the pineland parks of Miami-Dade County.

The management implications are twofold. First, birds of the pine rocklands appeared relatively insensitive to fine-scale variation in fire regime, which suggests that they should tolerate fire-management plans developed for other pine-rockland organisms, such as the many endemic plants that inhabit this ecosystem and that seem to have more narrowly defined requirements (Snyder et al. 1990; USFWS 1999). As long as fire is applied frequently enough to prevent hardwood encroachment, birds appear tolerant of a range of fire-return intervals. At the same time, our results suggest that fire, at least as it was prescribed during this study, is unlikely to prove useful in effecting change in bird populations. However, the range of fire histories that we observed within our study sites was relatively small, and thus we had no way to evaluate the importance of extreme conditions, such as might occur following a long fire-free interval and an unusually severe fire. In some systems, large and infrequent disturbances play a key role in structuring biotic assemblages (e.g., Dale et al. 1998). Frequent, low-intensity fires may be the rule for pine rocklands, but large and intense fires may have swept through the entire Everglades region on occasion (e.g., Davis 1943:253), and we cannot rule out the possibility that some birds may show strong positive or negative responses to these unusual occurrences.

Second, the substantial differences in the bird assemblages present at Long Pine Key and the Miami-Dade parks highlighted the limits of the coarse-filter approach to biodiversity conservation. Restoring a key ecosystem process – fire – to the pineland preserves in Miami-Dade County will not, in all likelihood, produce breeding-bird assemblages that mimic those found in the largely intact pine rocklands at Long Pine Key. Many exotic plants that have invaded remnant pine rocklands in Miami-Dade County are tolerant of fire (e.g., Doren and Whiteaker 1990) and can greatly affect the composition of bird assemblages (Curnutt 1989). Furthermore, the suitability of many of these small patches as habitat for breeding birds may be driven largely by factors unaffected by fire. For example, surrounding land uses likely encourage high densities of predators, such as feral or free-ranging cats (*Felis catus* Linnaeus), and also subsidize exotic bird species that compete with native species (e.g., Ingold 1989). Some patches may simply be too small to attract individuals or support breeding territories. Our results suggest that the greatest value of the pineland preserves from the standpoint of bird conservation is the habitat that they provide for wintering species, which appear more flexible in their willingness to use small patches of pineland within the Miami-Dade County network of parks. In sum, although other examples exist of capturing ecosystem processes for use as coarse filters, and although fire is clearly an important filter in this system at relatively long temporal scales (e.g., ≥ 10 years), variation in fire-return intervals at shorter time scales was of little consequence for breeding and wintering birds. Our study highlights several limits of the coarse-filter approach, in particular the substantial constraints imposed by realities such as small patch sizes, baseline conditions that have been substantially altered by the presence of non-native species, and the overriding importance of the condition of the surrounding landscape.

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