

Influence of Fire and Water Regimes on Pineland Bird Assemblages

John D. Lloyd^{1,3}

¹Ecostudies Institute
PO Box 106
South Strafford, VT 05070

Gary L. Slater²

²Ecostudies Institute
PO Box 703
Mount Vernon, WA 98273

³ Corresponding author:
jlloyd@ecoinst.org; 971-645-5463

ABSTRACT: At the broadest spatial scales, the distribution of south Florida slash pine (*Pinus elliottii* var. *densa* Little and Dorman) is limited by variation in fire and hydrological regimes, occurring only in relatively dry areas and succeeding to hardwood hammocks when fire is absent. These same forces also appear important in driving smaller-scale variation in the structure and composition of slash-pine forests. Important gaps remain, however, in our understanding of how plants and animals in slash-pine ecosystems respond to variation in fire and hydrological regimes. We addressed this issue for one taxon – landbirds – by estimating density at 285 locations in southwest Florida that differed in fire history and water-table elevation. Bird densities during the breeding season and during the winter did not vary appreciably as a function of either fire history or water-table elevation, and neither did vegetation structure at our survey locations. Birds and plants in this fire-climax forest are both resilient and resistant to changes brought about by frequent, low-intensity fire, and we suspect that significant effects of variation in fire history are only observable under extreme conditions (e.g., complete fire suppression) outside of the range of variation that we sampled. Water-table elevation had a stronger, albeit still small, effect on bird densities and vegetation structure, but the effects were difficult to generalize. Sampling across a broader range of hydrological conditions may yield valuable insight into the structure of pineland bird assemblages, especially given the likelihood that ecosystem restoration efforts in south Florida will produce substantial changes in water-table elevation.

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

INTRODUCTION

Understanding the forces that shape the structure and composition of biological communities is critical to the effective management of natural areas. For example, the recognition of fire as a process critical to the persistence of south Florida slash pine (*Pinus elliottii* var. *densa* Little and Dorman) forests (Egler 1952; Robertson 1953; Wade et al. 1980) led eventually to the adoption of prescribed burning as the primary tool for the management and restoration of these forests (e.g., Burch 2004). A substantial body of literature has accumulated regarding the ecological effects of fire in forests of south Florida slash pine, which include both the pine flatwoods (*sensu*, USFWS 1999) and the pine rocklands (*sensu*, Snyder et al. 1990), and the management implications of these effects, yet some gaps remain. In particular, little is known of how variation in fire regimes – including fire-return intervals and the season in which fires occur – affects wildlife populations (Main and Richardson 2002). However, this information is of critical importance to the design and implementation of effective, scientifically defensible restoration and management plans for pine forests in south Florida (USFWS 1999; USDO 2005).

We examined how landbirds responded to variation in fire history across the pine flatwoods of southwest Florida, with the

goal of generating a better understanding of the role fire plays in structuring landbird assemblages in this forest type. We examined responses during both the breeding season and during the winter, when the pine flatwoods play host to a very different assemblage of birds dominated by short-distance migrants arriving from breeding areas to the north. We focused on landbirds because they are often targets for management yet their response to fire in pine flatwoods is poorly studied. Indeed, responses to fire have been examined for only two species, northern bobwhite (*Colinus virginianus* Linnaeus) and wild turkey (*Meleagris gallopavo* Linnaeus) (Stoddard 1963; Moore 1972).

Our specific objectives were twofold: first, to describe variation in the density of breeding and wintering birds as a function of fire history, while controlling for differences in hydrology, which may influence the ecological effects of fire (Lockwood et al. 2003; Slocum et al. 2003); and second, to describe variation in vegetation structure among survey points so as to identify potential mechanisms by which changes in fire history or hydrology influenced bird populations. In doing so, we assumed that any relationship between landbird density and either fire regime or hydrology would be mediated primarily by changes in the structure and composition of the plant community, because physiognomic and floristic changes might result in changes

to the availability of nest sites, of foraging habitat, and of food itself.

METHODS

Study Area

We conducted this study within the hydric and mesic pine flatwoods of Big Cypress National Preserve (BCNP) and Florida Panther National Wildlife Refuge (FPNWR), southwestern Florida (cover types based on the Cooperative Land Cover Map, version 1.1, available online at <http://www.fnai.org/LandCover.cfm>; these categories cross-walk as wet flatwoods and mesic flatwoods, respectively, in FNAI [2010]) (Figure 1). Within BCNP, points were located in four distinct areas: (1) Raccoon Point, (2) West Raccoon Point, (3) Addition Lands, and (4) Stairsteps (Figure 1). The climate within the study area is subtropical, with a pronounced dry season from October to May and a wet season from June to September. About 75% of rainfall occurs during the wet season, with most of the wet-season rains falling during convective storms in the early 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. During the course of this study, parts of the study area were affected by Hurricanes Wilma (2005), Katrina (2005), and Ernesto (2006), and Tropical Storm Fay (2008). Some significant wind damage was associated with Hurricane Wilma; heavy rainfall was the primary impact of the other tropical cyclones.

Historic fire intervals have not been as thoroughly examined in the pine flatwoods of southwestern Florida as in the pine rocklands, but the two forest types likely had very similar natural fire regimes. For the pine rocklands, natural fire-return intervals are thought to average from 3-7 years, and it is likely that this approximates the fire-return interval for the pine flatwoods as well (Wade et al. 1980; Snyder 1986; Snyder et al. 1990; Liu et al. 2005; Sah et al. 2006). The wet season was likely when most fires occurred, with a peak in area burned reached in June, when lightning

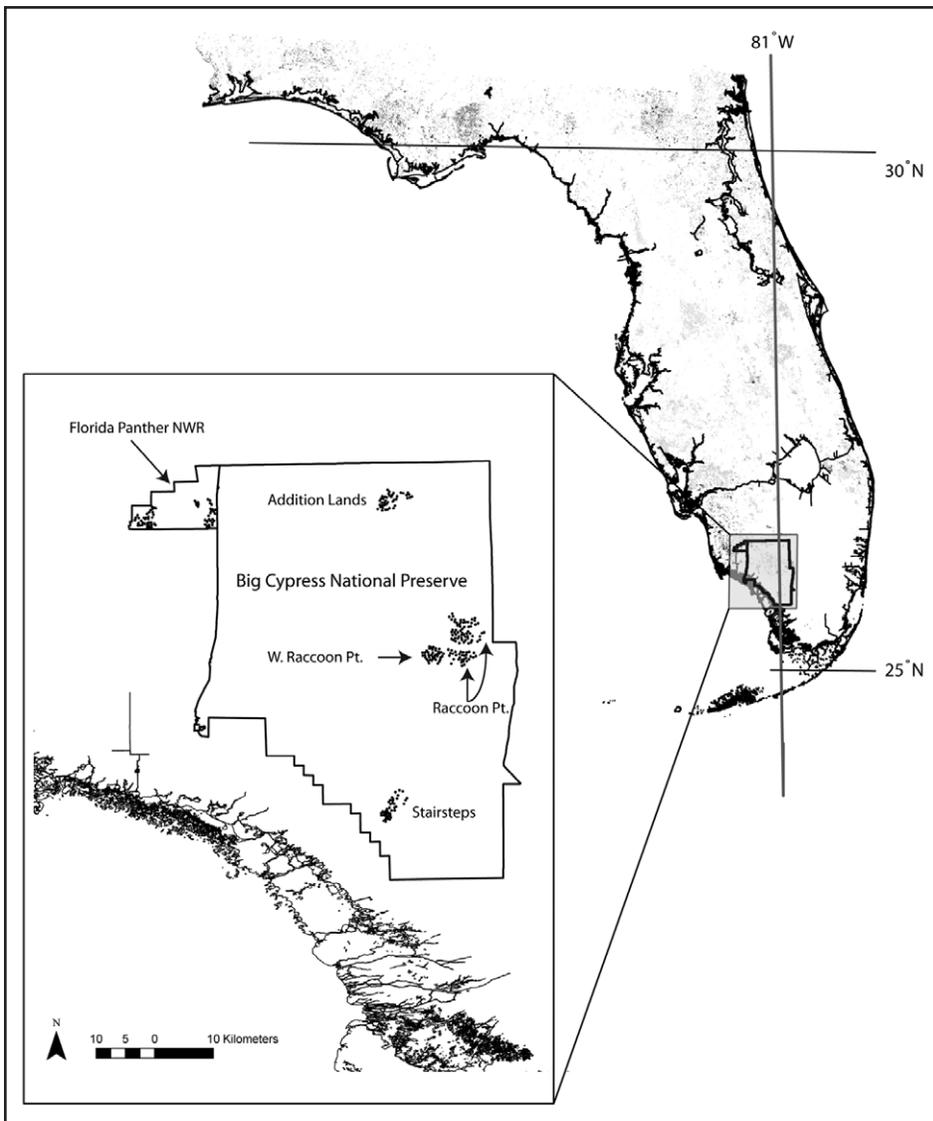


Figure 1. Map of the study area. Shaded areas show the extent of hydric and mesic pine flatwoods. Points on the inset map are locations where bird abundance and vegetation structure was sampled between 2005 and 2008 (Raccoon Point) or 2006 and 2008 (all other locations).

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).

Sampling Methods

Establishing Survey Points

We derived measures of fire history and hydrology and surveyed birds and

vegetation structure at 285 points: 95 in Raccoon Point, 66 in FPNWR, 42 in both Stairsteps and Addition Lands, and 40 in West Raccoon Point. We established and began surveying points in Raccoon Point in 2005; all other points were established and surveyed beginning in 2006. We conducted surveys each year until 2008, resulting in four years of data from Raccoon Point and three years of data from points at all other sites. To identify the location of points, we first created maps of the study area using ArcGIS (ESRI, Redland, Calif.) and aerial imagery (digital orthographic quarter quads). Next, we added vegetation cover layers for each site to identify all pine-

forest patches. We overlaid a 50-m grid onto the resultant site maps, and randomly selected points from the grid intersections to serve as survey points. We applied two constraints to the randomization process: survey points were ≥ 350 m apart and were surrounded by at least 100 m of contiguous pine forest. Actual conditions at each point were verified by a field visit prior to any sampling, and we eliminated points that did not meet our criteria.

Quantifying Fire History and Hydrology

Using annual fire-history layers obtained from the agencies responsible for the management of the lands on which we worked, we determined the number of days since each survey point was burned and the total number of times it had been burned in the 10 years prior to the survey. We considered any survey point within 100 m of the mapped boundaries of a fire to have been burned by that fire. Although the number of fires and the time since fire were closely correlated ($r = -0.71$), we chose to include both in our models because we suspected that neither variable alone would adequately describe conditions at each point. For example, a point burned twice in the past decade, and most recently within the last year, would likely have different vegetation structure than a point burned twice in the last decade but which had not been burned for eight years. For many of the points, data did not extend beyond 10 years prior to the survey, and so to avoid creating artificial differences among sites based on differences in record-keeping, we artificially truncated the maximum number of days since last fire at 3650. Only 42 points had been unburned this long, so we doubt that our truncation had any effect on our results. 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 for all stations within 25 km of a survey point (data are from the South Florida Water

Management District, available online at http://my.sfwmd.gov/dbhydroprosql/show_dbkey_info.main_menu). We then averaged the daily data to estimate the average water stage at each point during the early dry season (1 Dec – 15 Feb), when we conducted winter bird surveys, and during the late dry season and early wet season (15 Apr – 1 Jun), when we conducted breeding-bird surveys. We kriged average stage elevations using Universal Kriging (spherical model with anisotropy), and the value for each bird-survey station was extracted. We calculated the elevation above sea level (ASL) using the ATLSS elevation model (NGVD M) and the Southwest Florida Feasibility Study elevation model (NAVD FT). 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 ASL at each survey point from the estimated stage height to calculate water-table elevation.

Quantifying Vegetation Structure

We sampled vegetation at each survey point annually between 1 December and 1 March, unless vegetation changed due to fire between the non-breeding and breeding-season bird surveys. In those instances, we resampled vegetation at the survey point during the breeding season (15 April – 1 June). Vegetation sampling was based on a “spoke and wheel” structure. We determined the number and diameter of living and dead trees (by species) around the survey point in a 11.3-m radius circular plot and at three additional sampling plots centered 40 m from the survey station at bearings of 0, 120, and 240. We split living trees into three categories: (1) small (< 8 cm dbh), (2) medium (8.1 – 15 cm dbh), and (3) large (> 15 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 $r = \text{dbh}/2$). 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 (1.5 – 8 m). Finally, we visually estimated the maximum height of understory vegetation along each of the

spoke transects.

Estimating Bird Density

We conducted avian surveys during the non-breeding (15 Dec – 15 Feb) and breeding (15 Apr – 1 Jun) seasons. Each point 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. Surveys were conducted between sunrise and 10:00 a.m. as long as weather conditions remained suitable (i.e., light winds and light or no precipitation).

We estimated density of birds (individuals per ha) using multiple-covariate distance sampling (Marques et al. 2007), as implemented by Program Distance (Thomas et al. 2009). Distance sampling is one of several methods that can be used to adjust counts of birds to address imperfect detectability. For these analyses, we excluded all individuals detected visually during counts because the detection functions for these encounters were almost certainly different from detection functions generated from encounters with birds that were singing or calling. The consequence of excluding visual detections was likely minimal, as 96% of detections were aural. We did not estimate density for species with fewer than 70 detections, as this is considered the minimum sample size required to generate reliable estimates from distance sampling (Buckland et al. 2001).

Because we were primarily concerned with potential confounding of abundance effects and detectability effects, we focused our covariate models on the predictor variables of main interest in this study: the number of days since fire, the number of times an area had burned in the past 10 years, and average water-table elevation. We chose not to include other covariates that may have affected detectability, such as time of day that the survey was conducted or the identity of the observer, because these factors were distributed at random with regards to fire history and water-table elevation. Thus, although their exclusion may affect the precision of our estimates, leaving them out of the detectability analysis is unlikely

to bias our findings. For example, whereas a negative correlation between detectability and days since fire, if uncorrected, might lead to a biased estimate of the effect of fire on bird density, a negative correlation between survey date and detectability would have no bearing on our conclusions about the effects of fire on bird density because survey dates were distributed at random with regards to the number of days since fire. Furthermore, from a practical standpoint, we found that models with > 3 covariates rarely converged.

We evaluated all possible combinations of the three covariates, although we found that some combinations rarely converged. We checked for convergence by comparing the log-likelihood of the covariate model with the log-likelihood of the model containing only the key function and series adjustment; if convergence was reached, the multiple-covariate model should always have a log-likelihood as great as the model containing no covariates. We evaluated the strength of support for each model using Akaike's Information Criteria (AIC), as adjusted for small sample size (AIC_c), and normalized Akaike weights (w_i) (Burnham and Anderson 2002). We always used the best model for inference, even when AIC_c and w_i indicated model-selection uncertainty, as we found that the estimates of density produced by distance sampling were robust to variation in the specified detection function, and model-averaged values were always identical, or nearly so, to those obtained from the best model.

Statistical Analyses

All analyses were conducted using R version 2.9.2 (R Development Core Team 2009). We used canonical correspondence analysis (CCA; Jongman et al. 1995), as implemented by the R package *vegan* (Oksanen et al. 2009), to examine the influence of water-table elevation, number of days since fire, and number of fires on bird density and vegetation structure. We log-transformed vegetation data prior to analysis to reduce differences among variables caused by measurements taken at different scales (e.g., measurements of height vs. measurements of percent cover). For the analyses of bird assemblages, we

used the estimated density of each species at each point, as corrected by the detectability estimate from the best-supported model in Program Distance. We standardized vegetation data using the Wisconsin standardization and used Bray-Curtis distances as our measure of dissimilarity (Bray and Curtis 1957). We standardized bird data using a chi-square standardization (Legendre and Gallagher 2001), and used Euclidean distances to estimate dissimilarity in bird assemblages among survey points. We assessed the significance of the resulting ordination in two ways. First, we examined the ordination eigenvalues; ter Braak and Verdonschot (1995) suggest as a rule of thumb that reliable ordination results require eigenvalues > 0.3, and Jongman et al. (1995) suggest eigenvalues > 0.5 indicate a useful ordination result. Second, we used permutation tests to examine whether the correlation between the predictor variables and bird abundance or vegetation structure described by the ordination was greater than expected by chance alone. We used $\alpha = 0.05$ as the critical value for assessing significance of the permutation tests. To interpret the results of the ordination, we fit a vector representing each of the predictor variables onto

the ordination results using least-squares regression as implemented by the *envfit* function of *vegan* (Oksanen et al. 2009). These vectors allowed us to examine the influence of each of the predictor variables on variation in vegetation structure and bird assemblages. The significance of fitted vectors was assessed using permutation tests, again as implemented by the *envfit* function of *vegan* (Oksanen et al. 2009).

RESULTS

Fire history and hydrology

The survey points were burned by 67 different fires over the 13-year period that we considered (beginning in 1995, 10 years prior to our first survey, and ending in 2008) (Figure 2). Area burned by individual fires ranged from nearly 15,000 ha to < 1 ha. Fires – mostly prescribed burns – were most frequent in the mid-dry season (January and February), but the area burned by fires was greatest during May, at the transition between dry and wet-seasons (Figure 2). Thus, the fire regime during our study period was similar to that reported for other areas of south Florida (e.g., Gunderson and Snyder 1994). Ten-year fire frequency was

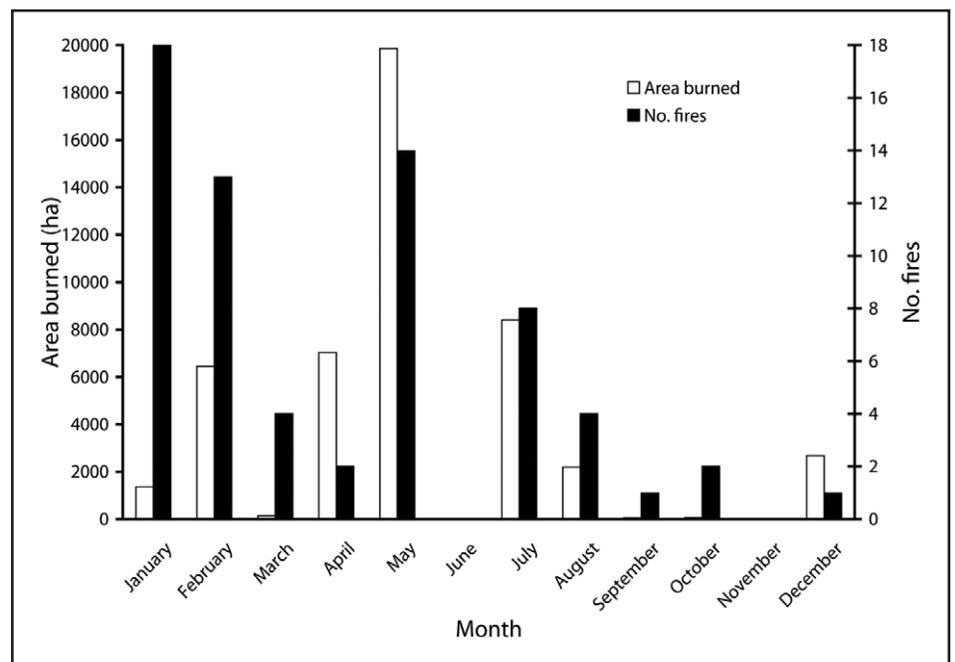


Figure 2. Total area burned of all fires that affected points within the study area (clear bars), by month in which the fire began, and total number of fires that affected points within the study area (black bars), by month in which the fire began.

relatively invariant within and among sites (Figure 3a). Raccoon Point had the most variation in fire frequency, and contained points that had burned more frequently than at any other site; Stairsteps and Addition Lands were the least variable sites and had been burned the fewest number of times. The number of days since the last fire was more variable (Figure 3b). Most points at Raccoon Point, W. Raccoon Point, and FPNWR had burned within three years of the survey date, whereas most of the points at the infrequently burned Addition Lands and Stairsteps sites had gone more than five years without fire. Timing of fires varied substantially among sites. Raccoon Point and FPNWR, which had the most active fire-management programs, had more fires than other sites and tended to have fires occur throughout the year. Raccoon Point had fires in all months

except April and November, with peaks in January, March, July, and December. Florida Panther National Wildlife Refuge had burns in all months except August to November, with peaks in January and April. West Raccoon Point had fires only during the dry season from October to January, whereas Stairsteps only had fires in April and May. Addition Lands had fires only during May, July, and December.

Water-table elevations at the end of the dry season were lowest at FPNWR, intermediate at the Addition Lands, and relatively high at the remaining sites (Figure 4a). Water-table elevations at the beginning of the dry season were higher and differed little among sites (Figure 4b). Water-table elevations during the two periods were positively correlated ($r = 0.58$, 95% CI = 0.54 – 0.62).

Vegetation Structure

Vegetation structure was relatively similar along gradients of water-table elevation (Table 1) and fire history (Table 2). In general, ground cover tended to increase with water-table elevation, whereas shrub cover decreased (Table 1). The density of pines of all sizes tended to decrease with increasing water-table elevation, but the effect size was quite small (Table 1). In contrast, pine snags were slightly more common at wet sites, as was the average basal area of pine snags (Table 1). Ground and shrub cover was greater at points burned less frequently and less recently (Table 2). The number of large pines tended to be greater at sites burned more recently and more frequently, whereas the number of small and medium pines showed the opposite pattern (Table 2).

The results of the CCA also suggested weak effects of fire and water regime on vegetation structure: the canonical axes explained 2.3% of the variation in vegetation structure, and the sum of the first four eigenvalues was 0.007, well below the level that generally indicates a reliable ordination result (0.3 – 0.5; ter Braak and Verdonschot [1995] and Jongman et al. [1995]). However, despite explaining relatively little overall variation in vegetation structure, the ordination explained more variation than expected by chance alone ($P < 0.005$). Variation in ordination scores was associated with the number of fires in the preceding 10 years ($r^2 = 0.03$, $P < 0.001$), the average water-table elevation during the late dry-season and early wet-season ($r^2 = 0.02$, $P < 0.001$), and the number of days since fire ($r^2 = 0.02$, $P = 0.02$). Average water-table elevation during the early dry-season was not a significant predictor of variation in vegetation structure ($r^2 = 0$, $P = 0.3$).

The gradient associated with water-table elevation during the late dry-season and early wet-season was almost parallel with the gradient of the number of days since fire, and thus, from the standpoint of vegetation structure, points that had been burned relatively infrequently were similar to points that were relatively dry (Figure 5). The number of pine snags and

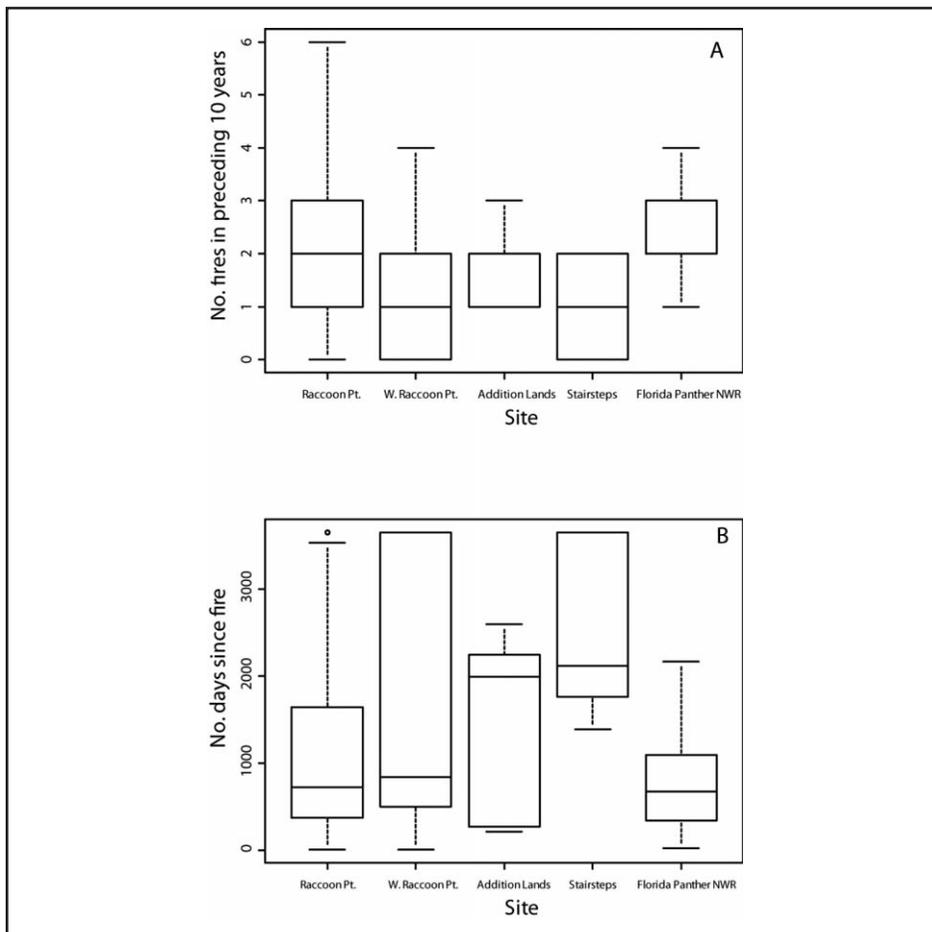


Figure 3. Boxplots summarizing two measures of fire history at each site included in the study (A: Number of fires in the 10 years preceding each survey of birds and vegetation; B: Number of days preceding each survey of birds and vegetation since a point burned).

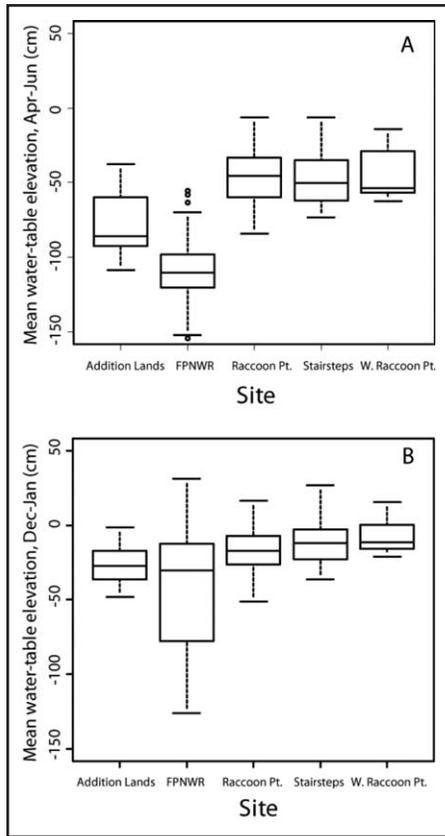


Figure 4. Boxplots summarizing water-table elevations at the end of the dry season (A) and at the beginning of the dry season (B) at each site included in the study.

the basal area of pine snags were greater at wet sites with greater fire activity, but otherwise no strong relationships were apparent (Figure 5). Shrub cover exhibited a weak, positive relationship with the length of time since the last fire, and the density of large pine trees and the basal area of pine trees tended to be greater at relatively dry points that had not been burned frequently or recently. None of the remaining measures of vegetation structure showed any obvious pattern of covariation with the predictor variables.

Bird Density

Breeding Birds

The breeding-bird assemblage was dominated numerically by northern cardinals (Table 3; see table for scientific names). Also occurring at relatively high densities were white-eyed vireos, pine warblers, brown-headed nuthatches, and common

Table 1. Average value (1 standard deviation in parentheses) for measures of vegetation structure recorded on 0.04 ha plots in south Florida slash pine (*Pinus elliottii* var. *densa*) flatwoods during 2005-2008 as a function of average water-table elevation. Vegetation data were collected at 4, 0.04 ha plots centered on each of 285 bird-survey points in southwestern Florida in Big Cypress National Preserve and Florida Panther National Wildlife Refuge. Daily estimates of water-table elevation at each bird-survey point during two periods (December to February and April to June) were averaged and used to define the driest 25% of points, the intermediate 50% of points, and the wettest 25% of points.

Vegetation variable	Relative water-table elevation		
	Wettest	Intermediate	Driest
No. small pines	0.8 (1.7)	1.3 (2.2)	1.9 (2.5)
No. medium pines	2.4 (2.7)	3.1 (3.3)	3.7 (3.7)
No. large pines	4.0 (1.1)	4.0 (1.1)	4.3 (1.0)
Basal area (cm ²), pine trees	29.4 (13.5)	32.7 (13.7)	32.8 (15.8)
No. pine snags	1.8 (2.1)	1.7 (1.4)	1.2 (1.0)
Basal area (cm ²), pine snags	6.5 (8.8)	4.8 (5.3)	3.0 (3.1)
Percent ground cover	40.1 (15.5)	43.8 (18.9)	35.8 (15.6)
Percent shrub cover	5.0 (5.5)	5.9 (6.3)	10.4 (9.0)
Max. height of understory (m)	4.0 (1.1)	4.0 (1.1)	4.3 (1.0)

yellowthroats. A second group of birds existed at moderate densities, including Carolina wrens, eastern towhees, red-bel-

lied woodpeckers, blue-gray gnatcatchers, and great crested flycatchers. The remaining species were far less abundant (Table

Table 2. Average value (1 standard deviation in parentheses) for measures of vegetation structure recorded on 0.04 ha plots in south Florida slash pine (*Pinus elliottii* var. *densa*) flatwoods during 2005-2008 as a function of the frequency and recency of fire. Vegetation data were collected at 4, 0.04 ha plots centered on each of 285 bird-survey points in southwestern Florida in Big Cypress National Preserve and Florida Panther National Wildlife Refuge. Bird-survey points that were in the lowest quartile for the number of days since fire and the highest quartile for the number of fires in the past 10 years were defined as having high levels of fire activity, points in the middle 50% of values for both the number of days since fire and the number of fires in the past 10 years were defined as having intermediate levels of fire activity, and points in the highest quartile for the number of days since fire and the lowest quartile for the number of fires in the past 10 years were defined as having low levels of fire activity.

Vegetation variable	Relative levels of fire activity		
	High	Intermediate	Low
No. small pines	0.9 (1.7)	1.1 (1.8)	1.8 (2.7)
No. medium pines	2.8 (3.0)	3.2 (3.4)	3.3 (3.3)
No. large pines	5.3 (2.8)	4.5 (2.6)	4.0 (2.3)
Basal area (cm ²), pine trees	35.3 (15.0)	31.6 (14.7)	29.4 (12.6)
No. pine snags	1.7 (1.9)	1.6 (1.5)	1.6 (1.3)
Basal area (cm ²), pine snags	4.4 (5.3)	5.0 (6.4)	4.7 (6.4)
Percent ground cover	37.3 (15.7)	41.2 (16.5)	43.4 (19.7)
Percent shrub cover	5.3 (5.6)	7.2 (7.7)	7.5 (7.6)
Max. height of understory (m)	4.1 (1.1)	4.1 (1.1)	4.0 (1.1)

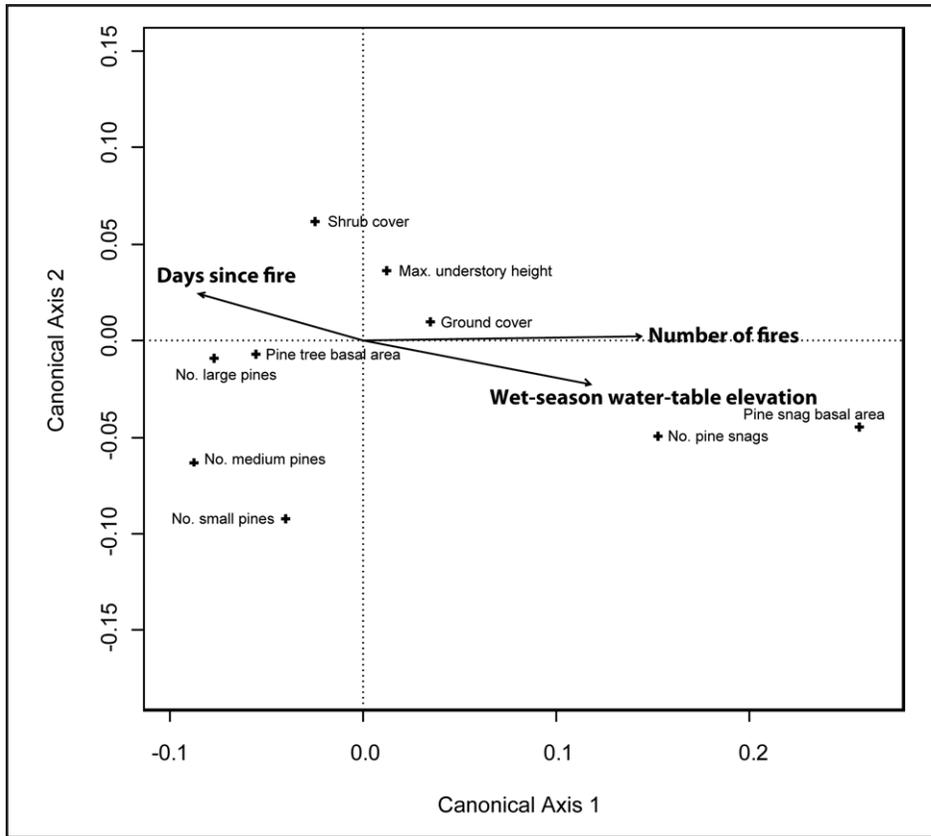


Figure 5. Results of a canonical correspondence analysis of vegetation structure at 285 points in hydric and mesic slash-pine flatwoods in south Florida. Arrows represent the strength (longer lines were more closely correlated with variation in ordination scores) and direction of maximum change in the value of the predictor variables. Measures of vegetation structure on the right side of the diagram were greater at points that had relatively high water-table elevation in April through June and that had been burned frequently and recently; measures on the left side were greater at relatively dry points that had not been burned recently and that had experienced few fires in the past 10 years.

3). We detected an additional 41 species during the breeding season (including nocturnal species, wading birds, diurnal raptors, ducks, and migrants en route to northern breeding areas), but at numbers too low to allow for robust estimates of density or to include in our analyses.

Canonical correspondence analysis suggested weak, albeit significant, relationships between the density of breeding birds and variation in fire and water regimes. The first two eigenvalues of the CCA were 0.03 and 0.02, far below the 0.3 – 0.5 suggested to indicate a reliable ordination (Jongman et al. 1995; ter Braak and Verdonschot 1995). Indeed, the linear combinations selected by the ordination explained only about 3% of the total variation in bird density. Nonetheless, the ordination explained more variation than could be explained by chance alone ($P = 0.005$).

Of the variation explained by the ordination, most was attributable to wet-season ($r^2 = 0.14$, $P < 0.001$) and dry-season ($r^2 = 0.09$, $P < 0.001$) water-table elevations, with lesser amounts of variation explained by the number of fires at a point ($r^2 = 0.07$, $P < 0.001$) and the number of days since fire at a point ($r^2 = 0.06$, $P < 0.001$). The direction of the gradients explained by the number of fires and the number of days since fire were almost opposite (Figure 6), as expected, given the strong negative correlation between these two variables. In contrast, water-table elevations during the different seasons tended to exert similar effects on bird assemblages, a reflection of the positive relationship between dry- and wet-season water-table elevations at points (Figure 6).

One group of birds – eastern towhees, northern flicker, and red-winged blackbird

– was associated with points that had been unburned for longer periods of time (Figure 6). Eastern bluebirds and common yellowthroats tended to prefer relatively wet points, whereas tufted titmice and downy woodpeckers were more abundant at relatively dry points (Figure 6). The remaining species were distributed primarily along the second canonical axis (from blue-gray gnatcatcher to common grackle), which was not closely correlated with any of the predictor variables (Figure 6).

Non-breeding Birds

Density of birds during the winter (5.3 individuals ha^{-1} , 95% CI = 5.1 – 5.6) was nearly twice as great as during the breeding season (2.7 individuals ha^{-1} , 95% CI = 2.6 – 2.8), reflecting the addition of large numbers of migrants, especially yellow-rumped warblers, to the resident bird assemblage (Table 4; see table for scientific names). Yellow-rumped warblers were numerically dominant during the winter, and their presence alone accounted for most of the post-breeding-season increase in density (Table 4). Other common wintering species were pine warblers and common yellowthroats, both of which are resident species likely supplemented during the winter by migrants from northern populations, and gray catbirds (Table 4). Palm warblers, house wrens, and American robins were all relatively abundant migrants that did not breed in the study area. Density estimates for most of the resident species were similar in the breeding and non-breeding seasons; however, density estimates for northern cardinals, Carolina wrens, white-eyed vireos, great crested flycatchers, and eastern towhees were lower during the winter. Whether densities were indeed lower, for example because of seasonal movements out of the pine flatwoods, or whether winter estimates were biased low, for example due to a reduced availability for detection caused by the cessation of singing, is unknown.

The results of the CCA suggested weak effects of the predictor variables on bird abundance during the winter: the ordination, although explaining significantly more variation than expected by chance

Table 3. Average density (no. individuals ha⁻¹; total detections in parentheses), and 95% CI of density estimate, of breeding landbirds in south Florida slash pine (*Pinus elliottii* var. *densa*) flatwoods during 2005-2008. Density estimates were generated using distance sampling and were based on data collected from April – June at 285 survey locations in Big Cypress National Preserve and Florida Panther National Wildlife Refuge. An additional 41 species not listed here had fewer than 75 detections each over the course of the study and were not included in this analysis.

Species	Density (total detections)	95% CI
Northern Cardinal (<i>Cardinalis cardinalis</i> Linnaeus)	0.45 (1135)	0.41 – 0.49
White-eyed Vireo (<i>Vireo griseus</i> Boddaert)	0.33 (770)	0.32 – 0.34
Pine Warbler (<i>Dendroica pinus</i> Wilson)	0.32 (1206)	0.30 – 0.34
Brown-headed Nuthatch (<i>Sitta pusilla</i> Latham)	0.31 (529)	0.28 – 0.35
Common Yellowthroat (<i>Geothlypis trichas</i> Linnaeus)	0.30 (788)	0.26 – 0.34
Carolina Wren (<i>Thryothorus ludovicianus</i> Latham)	0.24 (1129)	0.22 – 0.28
Eastern Towhee (<i>Pipilo erythrophthalmus</i> Linnaeus)	0.24 (308)	0.22 – 0.26
Red-bellied Woodpecker (<i>Melanerpes carolinus</i> Linnaeus)	0.23 (1806)	0.22 – 0.25
Blue-gray Gnatcatcher (<i>Poliophtila caerulea</i> Linnaeus)	0.23 (351)	0.20 – 0.26
Great Crested Flycatcher (<i>Myiarchus crinitus</i> Linnaeus)	0.18 (1356)	0.17 – 0.19
Downy Woodpecker (<i>Picoides pubescens</i> Linnaeus)	0.09 (360)	0.08 – 0.10
Common Grackle (<i>Quiscalus quiscula</i> Linnaeus)	0.07 (348)	0.05 – 0.09
Eastern Bluebird (<i>Sialia sialis</i> Linnaeus)	0.05 (306)	0.04 – 0.06
Northern Flicker (<i>Colaptes auratus</i> Linnaeus)	0.04 (321)	0.03 – 0.05
Red-winged Blackbird (<i>Agelaius phoeniceus</i> Linnaeus)	0.04 (270)	0.02 – 0.06
Mourning Dove (<i>Zenaida macroura</i> Linnaeus)	0.02 (161)	0.01 – 0.03
Tufted Titmouse (<i>Baeolophus bicolor</i> Linnaeus)	0.02 (367)	0.01 – 0.03

($P < 0.005$), explained only 3.4% of the total variation in bird abundance. The sum of the eigenvalues for the canonical axes was 0.07. All of the predictor variables explained significant amounts of variation in ordination scores (all $P < 0.001$). Water-table elevation during the late dry-season and early wet-season showed the strongest correlation with ordination scores ($r^2 = 0.13$), followed closely by water-table elevation during the early dry-season ($r^2 = 0.10$). Both measures of fire history showed relatively weak correlations with ordination scores (days since fire, $r^2 = 0.04$; number of fires, $r^2 = 0.02$).

As with the other ordinations, the two measures of fire history formed essentially a single gradient; species on the upper left side of the ordination diagram reached greater densities at points that had been unburned for relatively long periods and that had been burned relatively infrequently, whereas species on the lower right were more abundant at sites with a more

active fire history (Figure 7). The moisture gradient defined by the vector associated with water-table elevation during the early dry-season was nearly parallel to the fire gradient, suggesting a resemblance, in terms of the bird assemblage, between wetter points and points experiencing relatively infrequent fire (Figure 7).

The ordination results suggest no strong relationships between bird abundance and fire history, with the possible exception of common yellowthroat, which increased in abundance as the time since fire increased. A large group of species was associated with wetter points, either as measured during the early dry-season (northern flicker and common yellowthroat) or the late dry-season and early wet-season (eastern towhee, eastern bluebird, brown-headed nuthatch, palm warbler, and common grackle). Only two species, gray catbird and American robin, were more abundant at relatively dry points.

DISCUSSION

Extant variation in vegetation structure and the structure of breeding and non-breeding bird assemblages in mesic and hydric flatwoods of south Florida slash pine was significantly, albeit weakly, related to variation in fire history and water-table elevation. In general, plants and birds responded more strongly to variation in water-table elevation than in fire history. However, for both plants and birds, more than 95% of the variation among points was unrelated to our measures of fire history or hydrology.

The relationships that we documented between vegetation structure, fire history, and hydrology were concordant with current understanding of how water and fire shape the structure of pine flatwoods. Fire exerts a strongly negative, but very temporary, effect on aboveground biomass of shrubs ((Robertson 1953; Wade et al. 1980; Taylor and Herndon 1981; Hofstet-

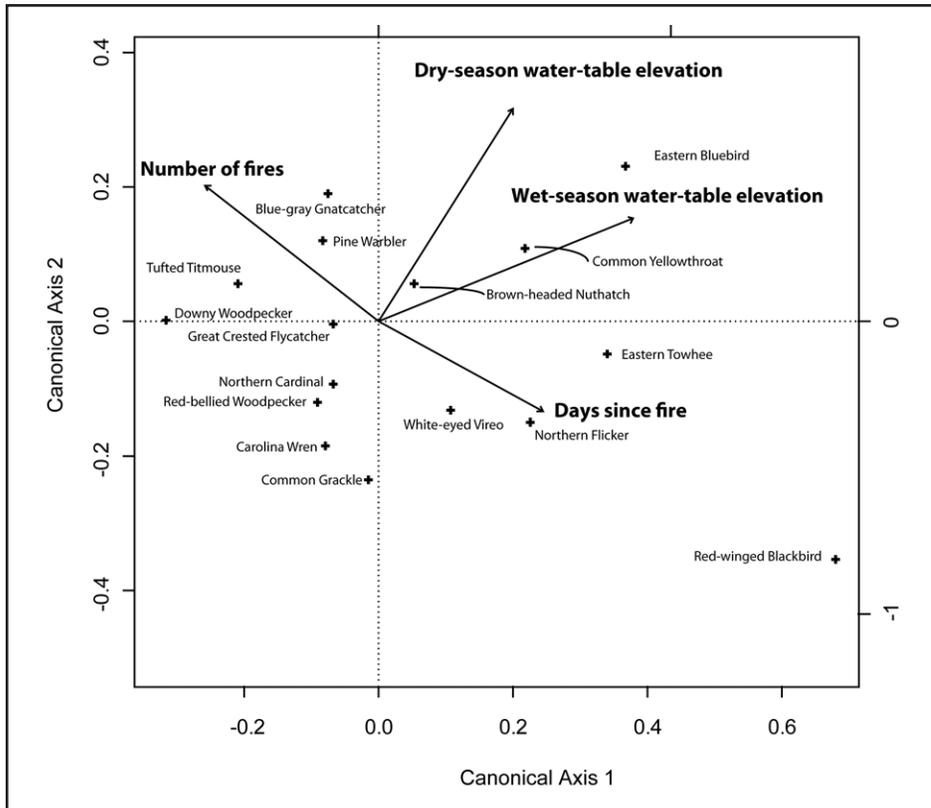


Figure 6. Results of a canonical correspondence analysis of breeding-bird density at 285 points in hydric and mesic slash-pine flatwoods in south Florida. Arrows represent the strength (longer lines were more closely correlated with variation in ordination scores) and direction of maximum change in the value of the predictor variables. The position of each species indicates the relative position of sample points (for clarity, position of each point is not shown in the ordination diagram) where the species was most abundant.

ter 1984; Snyder 1986); that most shrubs typically regain pre-burn stem densities within one to three years following fire likely explains the fairly weak, negative relationship that we found when examining shrub cover across a chronosequence of fires. The increased density of pine snags and greater basal area of pine snags at relatively wet points and at points that had been burned more often may reflect both fire-induced mortality of pine trees and mortality associated with the stress of living in water-logged soils (Hofstetter 1984; O'Hare and Dalrymple 2006).

Relationships between breeding-bird abundance and our predictor variables were weak, but three relationships stand out. First, both eastern bluebirds and common yellowthroats reached greater densities at relatively wet points. Common yellowthroats prefer wet areas throughout their range (Guzy and Ritchison 1999), and we

suspect that the association between eastern bluebirds and water-table elevation reflects their preference for nesting at the ecotone between pinelands and adjacent vegetation types. The pineland ecotone tends to have more snags, which offer nest sites for the cavity-nesting eastern bluebird, and tends to be relatively open, offering ample foraging habitat (Gowaty and Plissner 1998). The ecotone also tends to be lower in elevation, and thus has a water table lying closer to the ground surface. Second, three species were associated with points that had gone longer without fire: eastern towhee, northern flicker, and red-winged blackbird. Red-winged blackbirds commonly breed in areas with standing water (Yasukawa and Searcy 1995) that are unlikely to burn, which likely drives the apparent positive relationship with time since fire. Eastern towhees breed in areas with abundant shrub cover (Greenlaw 1996), which, in our study, tended to occur in areas that had

been unburned for longer periods of time. Why the density of northern flickers would increase with time since fire is unclear, given this species' habit of foraging on the ground in relatively open areas (Wiebe and Moore 2008).

Finally, both tufted titmice and downy woodpeckers showed a weak negative relationship with water-table elevation. The nature of this relationship is uncertain, but may be related to foraging habits. Both species forage for insects on various parts of pine trees (Grubb and Pravasudov 1994; Jackson and Ouellet 2002), and the density of pine trees tended to be greater at relatively dry points. However, other species that forage on pine trees (e.g., pine warbler and brown-headed nuthatch) did not show a similar relationship with water-table elevation.

Bird assemblages during the winter were also weakly related to our predictor variables, but, as during the breeding season, tended to be driven more by water-table elevation than fire history. A large group of species (common yellowthroat, northern flicker, eastern towhee, eastern bluebird, brown-headed nuthatch, palm warbler, and common grackle) was associated with higher water tables, and only two, American robin and gray catbird, were more abundant at relatively dry points. Common yellowthroats and eastern bluebirds were also associated with wetter points during the breeding season, suggesting a general preference for the conditions associated with a higher water table, but we are uncertain why the remaining species tended to distribute themselves along a moisture gradient. One possible explanation is that the species associated with drier points rely more on fruits produced by hardwood shrubs (Cimprich and Moore 1995; Sallabanks and James 1999), which tended to cover a greater area at relatively dry points. However, some of the species associated with relatively wet points also consume large quantities of fruit during the winter (e.g., eastern bluebird).

We suspect that our failure to find strong, consistent associations between the structure of bird and plant assemblages and fire

Table 4. Average density (no. individuals ha⁻¹; total detections in parentheses), and 95% CI of density estimate, of non-breeding landbirds in south Florida slash pine (*Pinus elliottii* var *densa*) flatwoods during 2005-2008. Density estimates were generated using distance sampling and were based on data collected from December – February at 285 survey locations in Big Cypress National Preserve and Florida Panther National Wildlife Refuge. An additional 41 species not listed here had fewer than 75 detections each over the course of the study and were not included in this analysis.

Species	Density (total detections)	95% CI
Yellow-rumped Warbler (<i>Dendroica coronata</i> Linnaeus)	3.19 (1554)	2.93 – 3.47
Pine Warbler (<i>Dendroica pinus</i> Wilson)	0.95 (946)	0.84 – 1.09
Gray Catbird (<i>Dumetella carolinensis</i> Linnaeus)	0.67 (583)	0.58 – 0.78
Common Yellowthroat (<i>Geothlypis trichas</i> Linnaeus)	0.63 (688)	0.56 – 0.71
Red-bellied Woodpecker (<i>Melanerpes carolinus</i> Linnaeus)	0.24 (871)	0.21 – 0.26
Brown-headed Nuthatch (<i>Sitta pusilla</i> Latham)	0.24 (367)	0.20 – 0.28
Palm Warbler (<i>Dendroica palmarum</i> Gmelin)	0.24 (170)	0.19 – 0.30
Northern Cardinal (<i>Cardinalis cardinalis</i> Linnaeus)	0.21 (374)	0.17 – 0.27
House Wren (<i>Troglodytes aedon</i> Vieillot)	0.21 (263)	0.18 – 0.25
Blue-gray Gnatcatcher (<i>Poliophtila caerulea</i> Linnaeus)	0.21 (243)	0.21 – 0.28
American Robin (<i>Turdus migratorius</i> Linnaeus)	0.20 (333)	0.17 – 0.24
Downy Woodpecker (<i>Picoides pubescens</i> Linnaeus)	0.14 (375)	0.12 – 0.16
Carolina Wren (<i>Thryothorus ludovicianus</i> Latham)	0.11 (525)	0.10 – 0.12
Eastern Bluebird (<i>Sialia sialis</i> Linnaeus)	0.08 (302)	0.07 – 0.10
White-eyed Vireo (<i>Vireo griseus</i> Boddaert)	0.08 (163)	0.06 – 0.10
Common Grackle (<i>Quiscalus quiscula</i> Linnaeus)	0.06 (114)	0.05 – 0.09
Northern Flicker (<i>Colaptes auratus</i> Linnaeus)	0.05 (292)	0.05 – 0.06
Great Crested Flycatcher (<i>Myiarchus crinitus</i> Linnaeus)	0.04 (222)	0.03 – 0.06
Eastern Towhee (<i>Pipilo erythrophthalmus</i> Linnaeus)	0.04 (137)	0.03 – 0.05
Tufted Titmouse (<i>Baeolophus bicolor</i> Linnaeus)	0.03 (157)	0.02 – 0.05

regimes reflects the tendency of organisms in this ecosystem to resist changes imposed by fire or to recover from them rapidly. The effects of most fires on understory and midstory plants in slash-pine forests are ephemeral, with pre-burn conditions generally regained within a few years following fire (Taylor and Herndon 1981; Snyder 1986). More significant effects, including mortality of overstory pines, appear to arise only in unusually intense fires, for example as occur when fire is reintroduced after long periods of fire suppression (Doren et al. 1993; Menges and Deyrup 2001). The resiliency and resistance of plants in slash-pine forests to fire, therefore, will tend to obscure any relationship between fire history and vegetation structure, except at the extremes; that is, significant effects of fire – or the lack thereof – may only be observed im-

mediately after fire or following long periods of fire suppression (e.g., Alexander 1967; Loope and Dunevitz 1981). Birds, in turn, appear insensitive to the frequent, minor, and largely ephemeral disturbances that characterize the pine flatwoods of south Florida (Emlen 1970; Hofstetter 1984). Given how rapidly plants recover following fire, and given that birds benefit from developing a familiarity with particular breeding or wintering locations (Hinde 1956; Greenwood and Harvey 1982; Pärt 1991), individuals may have little incentive to abandon areas affected by fire.

Water-table elevation, like fire, plays an important role in determining the distribution and structure of pine flatwoods (e.g., Duever 2005; McKee and Shoulders 1970; Olmsted et al. 1983; O'Hare and Dalrymple 2006) and, at least in other ecosystems,

can profoundly affect the structure of bird assemblages (e.g., Wakeley and Roberts 1996; Wakeley et al. 2007; Hoover 2009). In this study, water-table elevation explained more variation in vegetation structure and the structure and composition of bird assemblages than did fire history, but the effects were nonetheless exceedingly small. It is likely that the lack of any clear, consistent effect of water-table elevation was a consequence of incorporating a relatively narrow range of variation. Our survey points were restricted to the interior of patches of pine flatwoods, and thus we excluded ecotonal areas where water-table elevations tend to be higher (e.g., along the wet prairie/pine flatwood ecotone). Had we sampled points with a broader range of water-table elevations, we almost certainly would have detected stronger effects on vegetation structure

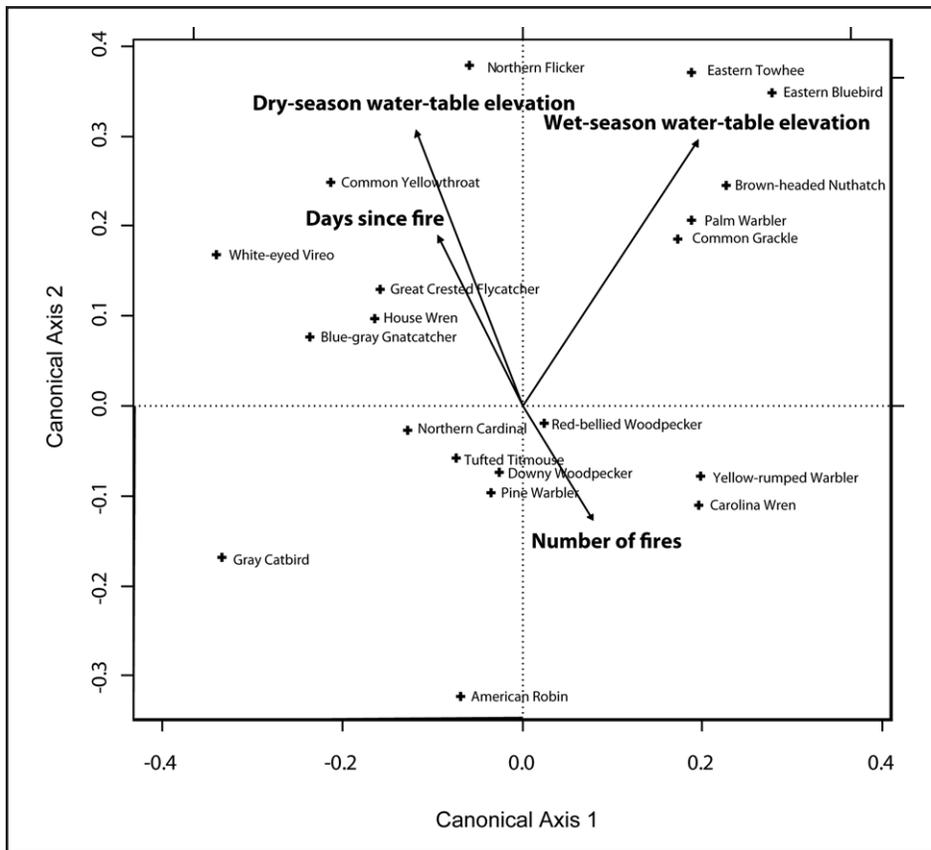


Figure 7. Results of a canonical correspondence analysis of wintering-bird density at 285 points in hydric and mesic slash-pine flatwoods in south Florida. Arrows represent the strength (longer lines were more closely correlated with variation in ordination scores) and direction of maximum change in the value of the predictor variables. The position of each species indicates the relative position of sample points (for clarity, position of each point is not shown in the ordination diagram) where the species was most abundant.

and, presumably, bird abundance.

In sum, we found that variation in fire history and water-table elevation explained < 5% of the extant variation in vegetation structure and composition and structure of bird assemblages during the breeding season and the winter. We do not interpret this as strong evidence, however, that fire and hydrology are unimportant; rather, we believe that the effects of variation in fire or water regimes may only be apparent under more extreme conditions. Frequent fire is thought to be a hallmark of Florida's pine flatwoods, and, accordingly, the organisms that inhabit this ecosystem appear both resilient and resistant to changes brought about by frequent, low-intensity fire. In this study, most of the points that we sampled shared a similar fire history – a consequence of the active fire-management programs now in place across most of the public land

in south Florida. Detecting strong effects of fire history on plants or birds would likely require sampling points across a much broader gradient, including points recently burned and points at which fire had been suppressed. Given that prescribed burning is widespread in the pine flatwoods, locating areas where fire has been excluded for long periods is difficult and would likely require a coordinated approach between researchers and fire managers. Detecting effects of water-table elevation on plants and birds may be more straightforward, as a broader gradient of conditions could be incorporated into future research simply by ensuring that samples are taken from both the edge and interior of pine flatwoods.

CONCLUSION

Component organisms of this ecosystem are highly tolerant of periodic, low-inten-

sity fire. Current fire regimes as applied by most land-management agencies in south Florida, thus, are suitable for maintaining the pineland bird assemblages that we observed and for maintaining vegetation structure in a relatively stable, intermediate stage of succession. Water-table elevation, although not often under direct control of land managers in this ecosystem, may be a more important target for future research. Our results suggested that variation in water-table elevation can drive changes in bird populations and vegetation structure, although the changes we observed were small. Changes in water-table elevations that will accompany ecosystem restoration efforts in south Florida, however, may be large enough to produce substantial direct and indirect effects on plants and wildlife, even in upland environments like the pine flatwoods. Our results provide little guidance, but do suggest that future studies that incorporate a broader range of water-table elevations may yield results useful in refining current land-management plans.

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John Lloyd is Senior Research Ecologist at Ecostudies Institute. Research interests include quantitative natural history and the role of biotic and abiotic factors in determining patterns of distribution and abundance of birds. Current research examines the distribution, abundance, and habitat requirements of mangrove land birds in south Florida and the natural history of mangrove cuckoos.

Gary Slater is Research Director at Ecostudies Institute. Research includes studies of habitat use by wintering shore-

birds and the use of alternative farming practices to create wildlife habitat. *Current conservation activities include reintroduction of Western bluebirds to San Juan Island, Washington State.*

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