

Project title: Effects of fuel treatments and wildfire on the avifauna of the pine rockland ecosystem in southern Florida.

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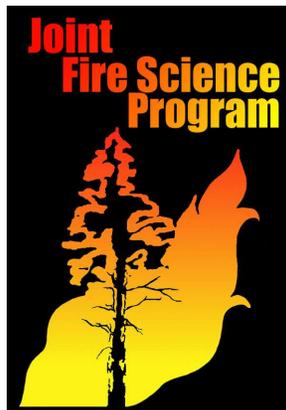
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I. Abstract

The response of plants and animals in the pine forests of southern Florida to variation in fire and hydrological regimes remains inadequately described, hindering the ability of resource managers to manipulate fire and water to achieve desired ecological outcomes. In this study, we took advantage of natural variation in two measures of fire history (the number of days since last fire and the number of times an area had been burned during the previous ten years) and one measure of hydrology (water table elevation) to explore how plants, breeding birds, and wintering birds in slash-pine (*Pinus elliottii* var. *densa*) forests responded to variation in fire and water levels.

At the largest spatial scale, considering samples taken from 441 points located across the range of slash pine in south Florida, variation in the structure and composition of the plant (72% of the explained variation) and both bird assemblages (73% and 80% of the explained variation in the breeding- and wintering-bird assemblages, respectively) is driven primarily by variation in water-table elevation, with the remainder explained by fire history. The relative importance of hydrology was also apparent when examining variation in plant and bird assemblages at a smaller spatial scale. Within study sites, local variation in water-table elevation drove variation in structure and composition of vegetation at 5 of 7 sites, of breeding-bird assemblages at 4 of 7 sites, and of wintering birds at 7 of 7 sites. However, the responses of individual components of vegetation and individual bird species at this smaller scale were not always concordant with patterns observed at the larger spatial scale. Indeed, the effects of variation in water-table elevation that emerged at the smaller scale often ran counter to the effects described at the larger scale. The within-site effects of fire, although generally less important than those associated with variation in water level, were more consistent with patterns described at the larger scale. At both scales of observation, areas burned more recently and frequently tended to contain short, sparse understories and had more standing dead trees, an important component of habitat for several bird species. As expected within a fire-dependent ecosystem, no bird species were associated with fire-suppressed conditions, although most species were able to tolerate fire-return intervals as long as 5 years without any significant effect on abundance.

II. Background and purpose

The south Florida slash pine (*Pinus elliottii* var. *densa*) ecosystem – herein defined to include both the pine rocklands of the Miami Rock Ridge and Tamiami limestone and the more widespread transitional pine flatwoods further to the west – once covered most of the upland area of south Florida. Beginning in the early 20th century, however, large areas of slash pine were cleared for residential, commercial, and agricultural development, and by some estimates the areal extent of this ecosystem is now < 10% of what it once was (Noss and Scott 1997). This ecosystem also supports a large number of endemic and rare plants and animals, and thus management of remaining slash pine is of critical importance to the conservation of biological diversity in southern Florida (USFWS 1999).

Variation in the structure and composition of the slash-pine ecosystem of south Florida is thought to be controlled primarily by fire and, to a lesser extent, by hydrology (Robertson 1953, Alexander 1967, Wade et al. 1980, Gunderson 1994, Platt 1999, Duever 2005). Historic fire-return intervals remain the subject of debate, although consensus estimates suggest that slash-pine forests probably burned, on average, at least twice a decade (Wade et al. 1980, Snyder et al. 1990). As fire-return intervals increase, the density and size of understory shrubs increases, eliminating the open conditions that characterize the ecosystem and reducing the diversity of herbaceous plants, many of which are intolerant of shade (Snyder et al. 1990, Carlson et al. 1993, Platt 1999, Liu et al. 2005). In extreme cases of fire suppression (fire-return intervals >20 years), slash pine is successional to hardwoods (Robertson 1953, Alexander 1967). Because of the difficulty in managing natural fires in this highly fragmented ecosystem, which is embedded within a largely urban matrix, prescribed fire is the primary tool used to restore and maintain the south Florida slash pine ecosystem and its component plants and animals.

Despite its importance as a management tool, questions remain surrounding the ecological effects of prescribed fire in this ecosystem. Most notably, there is relatively little quantitative information describing the response of plants and animals to variation in fire-return interval. This hinders the ability of resource managers to use fire to achieve desired ecological outcomes. In this study, we addressed this information gap by examining the influence of fire history (measured as the time since last fire and the number of times an area had burned during the past 10 years) on present-day variation in vegetation structure and bird abundance at sample points located across the range of south Florida slash pine. In addition, because variation in hydrological conditions can influence the behavior and ecological effects of fire (Lockwood et al. 2003, Slocum et al. 2003), we also examined the relative importance of variation in water-table elevation. Understanding the influence of hydrology on plants and animals in this ecosystem is important as large-scale efforts to restore normative hydrological processes (i.e., the Comprehensive Everglades Restoration Program) begin to impact this system. Finally, we took advantage of experimental fires conducted at a long-term research site on one portion of the study area to examine in detail how variation in the season and frequency of fire affected the demography of standing dead pine trees or snags, which are an important component of habitat for many bird species. The results of this study will help refine fire-management plans for south Florida slash pine forests, identify ecological targets for monitoring and management, and improve our ability

to predict how this ecosystem may change as a result of efforts to restore normative hydrological processes in the greater Everglades.

III. Study description and location

Objective 1) Determine the large-scale patterns of relationship between fire management, hydrology, and abundance and distribution of breeding and wintering landbirds and their habitats.

Bird Survey Stations

During the period from November 2005 – January 2006, we established a network of avian monitoring stations on federal and state lands. Survey stations were established at seven sites dominated by south Florida slash pine. Sites varied in stand age, elevation, fire history, and understory vegetation associations (Fig. 1, Table 1). In Long Pine Key, Everglades National Park (ENP) and Raccoon Point, Big Cypress National Preserve (BCNP) bird survey stations were previously established as part of a long-term monitoring effort of reintroduced cavity-nesting species (G.L. Slater, Ecostudies Institute, unpublished report). One-hundred four and 95 stations were established in Long Pine Key and Raccoon Point, respectively, under the criteria that stations were ≥ 350 m apart and were surrounded by at least 100 m of contiguous pine forest. We used these same criteria to identify survey stations in each of the five remaining sites. To obtain station locations prior to field visits, we first created maps of each site using ArcGIS (ESRI, Redland, CA) and satellite imagery obtained through the South Florida Natural Resource Center's (SFNRC) GIS library and from other agency partners.

Next, we gathered vegetation cover layers for each site to identify all pine-forest patches, and merged annual fire-history layers from each site to determine the time since each patch was burned. Using ArcGIS and our site maps with vegetation and fire history, we overlaid a 50m grid and selected points to serve as survey stations in a stratified random fashion, with strata based on time since an area last burned.

In the field, using the criteria identified above, we determined whether the station could be established at the pre-determined location or whether it needed to be removed from the list. In total, we established 238 points in addition to the 199 established in Long Pine Key and Raccoon Point, for a total of 441 (Table 1).

Bird Surveys

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. Surveys were conducted between sunrise and 10:00 as long as weather conditions remained suitable (i.e., light winds and light or no precipitation).

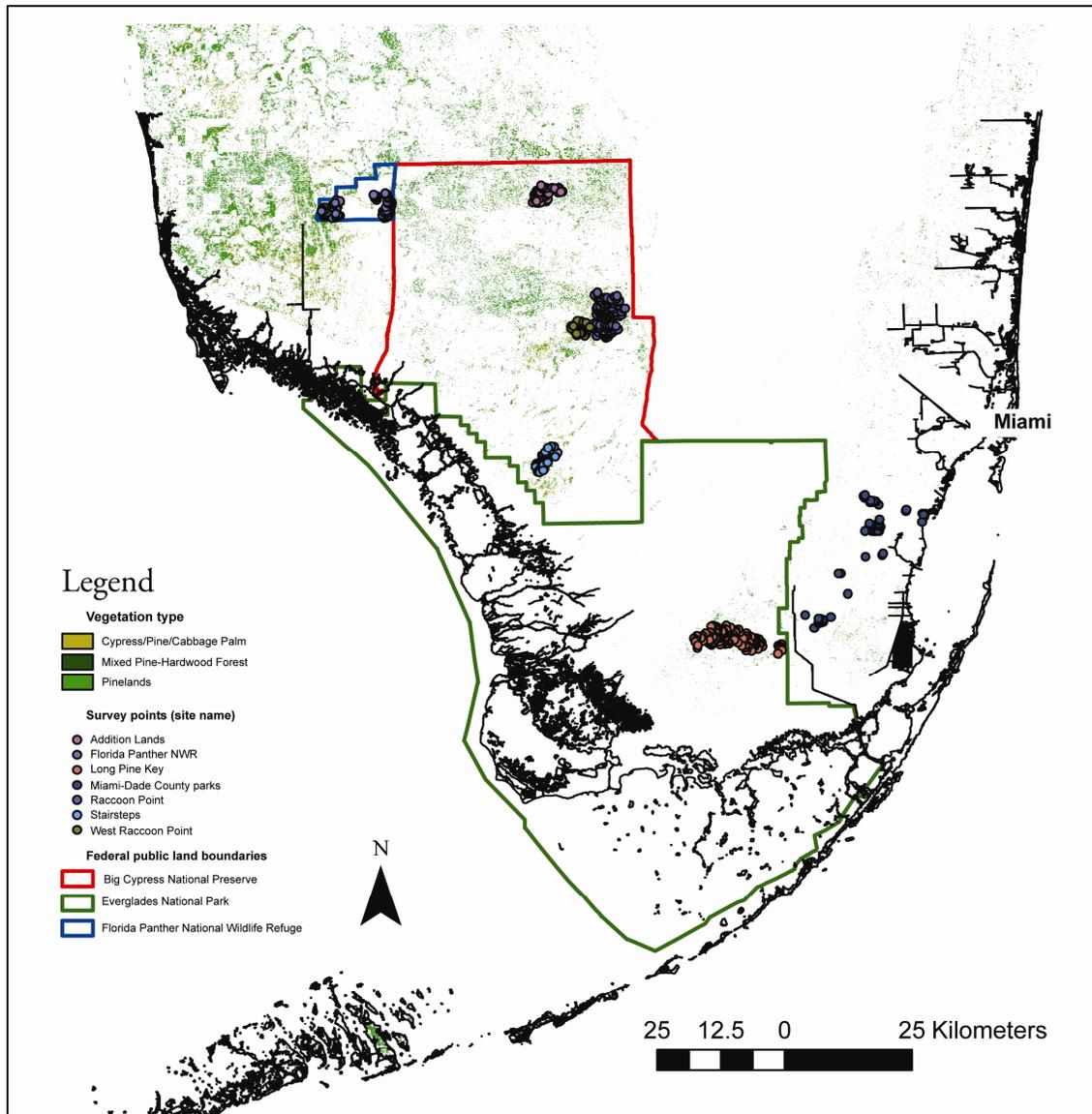


Figure 1. Map of south Florida, USA, showing the 441 points in south Florida slash pine (*Pinus elliotii* var. *densa*) at which bird abundance and vegetation structure were sampled during 2005-2008.

Table 1. Location and description of study areas.**Administrative Unit: Everglades National Park**

Long Pine Key, ENP. 104 survey points. This 8,100 ha upland site lies at the southwest tip of the Miami Rock Ridge and contains ~4,600 ha of pine forest. Within the relatively continuous pine forest, embedded habitats include *Muhlenbergia* prairie, hardwood hammocks, and cypress forest. The pine forest is mostly even-aged, a result of extensive logging in the 1940's. After a decade of fire suppression, the fire management program in the mid-1990s began implementing prescribed burns at the peak of the natural fire ignition season (May- July) to reduce fuel loads and restore natural vegetation communities. Recent fire management applies prescribed fire on a 3-year average fire interval during the natural fire ignition season. Access to this site is through fire roads within the area.

Administrative Unit: Big Cypress National Preserve

Raccoon Point, BCNP. 95 survey points. Raccoon Point contains approximately 9,000 ha of virgin, old-growth pine forest within a cypress mosaic. Raccoon Point has a shallow sandy substrate underlain by limestone bedrock, making it transitional between the pine rocklands further south and the pine flatwoods to the north. For the last decade, this area has been the site of an experimental fire study directed by Dr. Jim Snyder. As is typical for hydric pinelands, the herbaceous and grass components are well developed, while the shrub layer contains a small to moderate amount of hardwoods and saw palmetto. Access to this site is by a gravel road created for oil-extraction activities.

West Raccoon Point, BCNP. 40 survey points. West Raccoon Point lies 5 km west of Raccoon Point separated by large cypress strands. Forest structure and understory composition is similar to Raccoon Point, but the area is slightly lower in elevation than Raccoon Point and has not received prescribed fire as frequently as Raccoon Point. Access to this site is by off-road buggy trails.

Addition Land, BCNP. 42 points. The Addition Land site is approximately 30 km north of Raccoon Point and contains ~30,000 ha of pine forest. This pine forest/dry prairie mosaic floods infrequently because of its higher elevation. The Addition Land was acquired by BCNP in 1996. Its management history included logging, grazing, and frequent burning during the non-growing season, which has resulted in a mature, even-aged forest, a low density of trees and snags, and an overdeveloped shrub layer of palmetto and hardwoods. The area has been subject to several recent wildfires.

Stairsteps, BCNP. 42 points. Stairsteps lies at the northwestern extent of the pine rocklands and contains ~25,000 ha of pine forest. This site was logged in the mid 1900's, resulting in largely second growth stands of pines. Pines are interspersed with wet prairies and small hardwood hammocks. This site has the lowest elevation of all the sites and has a mostly herbaceous understory. Prescribed fire was applied to this area in 2001.

Administrative Unit: Florida Panther National Wildlife Refuge

Florida Panther National Wildlife Refuge. 66 points (only 60 sampled for wintering birds). This site occurs within the Big Cypress Basin, west of Big Cypress National Preserve, and contains ~2,300 ha of pine forest. The refuge is separated into 52 management compartments, originally outlined by old roads and vegetation features. Compartments are burned on a 4-year rotation primarily during the non-growing season (January-February). Cabbage palm dominates the shrub layer, and its abundance may be a consequence of reduced hydrological flow through the refuge. Mechanical thinning was applied to 500 ha in 2005.

Administrative Unit: Miami-Dade County Parks and Recreation Department

Miami-Dade County Parks and Recreation. 52 points. This county agency is responsible for the management of more than 50 environmentally sensitive and natural areas in Miami-Dade County. These sites are relatively small, highly fragmented, and lie in a mostly urban matrix. Less than 2% of Miami-Dade County's original pine rocklands remain. Fire management is difficult due to restrictions related to smoke, citizen acceptance, and availability of personnel to conduct fuel treatments. Wildfire is the primary fuel management technique within these lands, and most sites have high fuel loads as a result of long-term fire suppression.

Vegetation sampling

We sampled vegetation at each survey station 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.

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. At the survey point and at each of the three sampling plots centered 40 m from the survey point we determined percent ground cover (<1.5 m) and shrub cover (between 1.5 and 8 m) for understory habitat components (e.g., herbs and graminoids, hardwood species, and palms) within a 5-m-radius circular plot. Finally, we visually estimated the tallest and average heights of pines, hardwoods, and palms within the shrub layer (<8 meters) along each of the spoke transects.

Estimating fire history

Using annual fire history layers from each organizational unit, we determined the time since each survey point was burned and the total number of times it had been burned in the last 10 years. Time since last fire ranged from 3 days to > 10 years, and the number of burns in the past 10 years ranged from 0 to 9.

Estimating 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/dbhydroplsql/show_dbkey_info.main_menu). We then averaged the daily data to estimate the average water stage for each sampling period (defined by the non-breeding [15 Dec – 15 Feb] and breeding [15 Apr – 1 Jun] seasons). Average stage elevations were then kriged 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 bird-survey station had data from both models (i.e., models overlapped at that point), then we used the average of the 2 models. We then subtracted the elevation ASL at each survey point from the estimated stage height to calculate water-table elevation.

Based on a random-effects analysis, most (50%) of the variation in our estimates of water-table elevation was due to differences between sampling periods – that is, differences between the wet and dry seasons. Within a season, however, variation was attributable to differences among sites (22%) and among points within sites (27%). Less than 1% of the variation was due to annual variation in water-table elevation. Thus, our measure of water-table elevation served as a measure of average differences among survey points and study sites, essentially allowing us insight into how plants and birds respond along a gradient from relatively dry to relatively wet locations.

Statistical analyses

We began by screening out vegetation variables that we suspected were of little biological significance using two criteria: variables included in the analysis had to have a median value >0 and had to have a non-zero value on >70% of the points. After screening, we retained 22 vegetation variables for inclusion in subsequent analyses (Table 2). We used multivariate multiple regression to examine whether vegetation structure at each survey point exhibited a statistically significant relationship with the independent (i.e.,

Table 2. Twenty-two measures of vegetation structure used in multivariate analyses.

Percent bare ground
Percent ground cover: herbaceous ¹
Percent ground cover: hardwoods
Percent ground cover: palms
Percent ground cover: total
Percent shrub cover: hardwoods ²
Percent shrub cover: palms ³
Percent shrub cover: total
Average height of understory palms
Average height of understory pines
Maximum height of understory palms
Maximum height of understory hardwoods
Maximum total height of the understory
Number of small pine trees (<10.5 cm diameter at breast height [DBH])
Number medium pine trees (10.5 – 18.5 cm DBH)
Number of large pine trees (>18.5 cm DBH)
Total basal area of pine trees
Number of small snags
Number of medium snags
Number of large pine snags
Total number of pine snags
Total basal area of pine snags

¹ Ground cover was defined as the amount of ground surface overlain by vegetation <1.5 m tall

² Shrub cover was defined as the amount of ground surface overlain by vegetation between 1.5 m and 8 m tall

³ Palms lumped to include saw palmetto (*Serona repens*) and cabbage palm (*Sabal palmetto*).

predictor) variables describing fire history and hydrological conditions, while controlling for the random effect of site. However, we expected that these data were unlikely to meet the assumptions of a traditional multiple regression, in particular that the errors were normally distributed (because, e.g., of the abundance of zeros in the data set). Thus we used permutation tests (Anderson 2001, McArdle and Anderson 2001) to calculate the probability of obtaining a squared partial correlation coefficient greater than that observed, given a distribution of possible squared partial correlation coefficients created by permutation. No exact permutation test for a partial regression is possible (Anderson and Robinson 2001), and so we used an approximate test (Freedman and Lane 1983) in which residuals, rather than observations, are exchanged during permutation.

Complicating the interpretation of these tests was the autocorrelation introduced by sampling vegetation at the same survey point in multiple years. Treating measurements from the same point in multiple years would artificially inflate the sample size and potentially increase the risk of committing a Type I error. To address this problem, we restricted permutations such that the residuals associated with a location sampled in multiple years were permuted as a unit, rather than individually (Anderson and ter Braak 2002). As a consequence, the tests were based on 441 permutable units (the number of points in the study), as opposed to the total number of observations taken during the

course of the study (1,516). The multivariate multiple regression was implemented in DISTLM (Anderson 2004). Data were transformed to $x = \ln(x+1)$ prior to analysis to account for the different scales (i.e., integer or percentage) on which dependent (i.e., response) variables were measured. We used Euclidean distances in the analysis, and did not standardize any of the dependent variables prior to analysis (in preliminary analyses we explored standardization and different distance measures, but found no appreciable effect on the outcome of any analysis).

We then used partial canonical analysis of principal coordinates (CAP; Anderson and Willis 2003, Legendre 2008), controlling for the effect of site, to visualize the multivariate patterns suggested by the results of the multivariate multiple regression analysis. We conducted this analysis using the *capscale* function in R (R Development Core Team 2008). As with the multivariate multiple regression, we transformed data to $x = \ln(x+1)$, did not standardize values of dependent variables, and used Euclidean distances. To evaluate the contribution of each measured vegetation variable to the multivariate pattern identified in the CAP, we calculated product-moment correlation coefficients between the CAP score for each point on each axis and the ln-transformed value of each vegetation variable at that point. We only considered correlation coefficients ≥ 0.20 ; values less than this were assumed to reflect biologically insignificant relationships. We also conducted these ordinations on a site-by-site basis to examine the extent to which patterns observed at the largest spatial scale – the entire study area – were concordant with patterns of variation observed within individual study sites.

We estimated density and abundance of birds using distance sampling as implemented by Program Distance (Thomas *et al.* 2006). 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 because the detection functions for these encounters were almost certainly different from detection functions generated from encounters with birds that were singing or calling. We could not conduct separate analyses for males and females as most of the detections were not identifiable to sex, either because both sexes share a vocal array (e.g., Northern Cardinal (*Cardinalis cardinalis*) or because the individual was detected via a vocalization used by both sexes.

Following Buckland *et al.* (2001), we modeled detection functions using one of three key functions (uniform, half normal, and hazard rate). In addition, we examined whether changing the shape of each key function via a series expansion term (cosine, simple polynomial, or hermite polynomial) improved the ability of the model to describe the detection function. We evaluated the strength of support for each model using Akaike's Information Criteria, as adjusted for small sample size (AIC_c) and normalized Akaike weights (w_i). 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. We used the estimated probability of detection from the best model to adjust the counts at each survey point, using only detections from within a 50-m radius of the point. We limited detections to this area so that our estimates of bird density covered approximately the same area as our measures of vegetation structure. We examined relationships between density of birds at each point and fire history and hydrology using

Multivariate multiple regression and CAP, as described for the analysis of variation in vegetation structure. Bird densities were not transformed prior to analysis.

Objective 2) Investigate the role of fire in snag dynamics.

Study area and field methods

We conducted this experiment in Raccoon Point, BCNP, which contains the most extensive unlogged stands of south Florida slash pine in the region (see Table 1). In 1993, we established 12 1-ha plots in the pinelands of Raccoon Point and in each plot we tagged and mapped all trees with diameter at breast height (dbh) > 5.0 cm and assigned each to one of four states: live, low-to-moderately decayed snag (decay state 1; ranged from newly created snags with tight bark and intact branches to moderately decayed snags with some or no bark remaining, branches mostly absent, and sapwood intact to sloughing), heavily decayed snag (decay state 2; only heartwood remaining), and down (any tree or snag completely consumed by fire, completely uprooted or broken at a height of < 1.5 m, or decayed to a height of < 1.5 m or DBH < 5.0 cm). We chose to categorize the continuous process of decay in this fashion because these categories generally reflect the suitability of a snag for Brown-headed Nuthatches and Eastern Bluebirds (G.L. Slater and J. D. Lloyd, unpublished data), both of which are species of management concern. Brown-headed Nuthatches are weak excavators, capable of creating cavities in soft wood, but Eastern Bluebirds are secondary cavity nesters and rely exclusively on cavities excavated by other species. Both species rarely use cavities in live trees or in snags in decay state 2, presumably due to the hardness of the heartwood of south Florida slash pine. Indeed, 91% (n = 409) of nests of both species that we monitored from 1998-2005 were found in snags in decay state 1 (Ecological Institute, unpubl. data). Given that many of the cavities used by these two species were likely excavated by other species (e.g., Red-bellied Woodpeckers (*Melanerpes carolinus*) or Downy Woodpeckers (*Picoides pubescens*), we assume that other cavity-nesting birds show similar preferences.

The initial state of each tree or snag was recorded between July 1993 and October 1994. The final state of each tree was recorded 15 years later in January 2008. All plots were subject to baseline prescribed fires conducted during January-February 1990 and March-April 1994. Thereafter, between 1996 and 2006, each plot was treated with experimental burns on a short interval (target interval was 3 years between successive fires) or a long interval (target interval was 6 years between successive fires), with fires conducted during the dry (November – April) or wet season (May – October). Plots were randomly assigned to one of the four treatment combinations (dry season, long interval; dry season, short interval; wet season, short interval; and wet season, long interval). Each treatment combination was applied to three study plots. We used bark char height (height of the blackened trunk) as an index of fire intensity (e.g., Waldrop and Van Lear 1984). Bark char height was measured one month after the first experimental fire in all plots, and one month after the second experimental fire in four of the plots that received the short-interval treatment.

Statistical analyses

We examined treatment effects on transition probabilities – as measured by the state of each marked tree or snag at the first (1993/1994) and final (2008) sampling periods - by fitting baseline category, multinomial logit models using the *multinom* function in R (Venables and Ripley 2002). We evaluated a set of five candidate models in this analysis (Table 3).

Table 3. Candidate set of multinomial logit models used to examine the effects of season of burn (dry or wet season) and fire-return interval (short or long) on the dynamics of snags in a south Florida slash pine forest in Big Cypress National Preserve, Florida.

Model name	Model structure ^a
Null model	Initial state + observation days + DBH
Season	Initial state + observation days + DBH + season
Interval	Initial state + observation days + DBH + interval
Season + interval	Initial state + observation days + DBH + season + interval
Season*interval	Initial state + observation days + DBH + season + interval + season*interval

The response variable for the analysis was the state of the tree or snag at the final observation. Every model in the candidate set included a term for the initial state of the tree or snag because the initial state determined which states were possible at the final observation (e.g., a snag in decay state 2 at the initial observation could end the experiment in only one of two possible states (decay state 2 or down), whereas a tree that was alive at the initial observation had four possible endpoints: still alive, decay state 1, decay state 2, or down). Every model also included a term for the number of days that a tree was under observation, which accounted for any differences in transition probability arising from variation in the date of the initial observation, and a term for DBH, which can have an important effect on the persistence of snags (Morrison and Raphael 1993). We examined the effects of our treatments by including dummy variables for season of burn and fire-return interval in some of the models. We evaluated the degree of support for each model using Akaike’s Information Criteria (AIC) and Akaike weights (w), which reflect the relative likelihood that a given model is the best model in the set of candidate models. Akaike weights were calculated as

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^R \exp\left(-\frac{1}{2}\Delta_r\right)}$$

where Δ_i is the difference in the AIC value between model i and the model with the minimum AIC.

We used the coefficients from the best-fitting model to evaluate the strength and direction of treatment effects on transition probabilities. We also calculated the percentage change in the odds of a transition occurring as a function of a change in the value of our predictor variables by subtracting 1 from the odds ratio (calculated as the exponent of the coefficient of the predictor variable) and multiplying the value by 100. We did not interpret odds ratios for predictor variables where 95% confidence limits overlapped one. However, interpretation of the coefficients in a multinomial logit model is non-intuitive, as they represent the relative log-odds of membership in a particular decay state as opposed to the baseline category, which in this case was a live tree. As such, much of our interpretation is based on the fitted values for transition probabilities as generated from the best-supported model (Fox and Anderson 2006), which we believe provide a more readily interpretable presentation of the results. When comparing transition probabilities among different treatment groups, we considered non-overlapping 95% confidence intervals as evidence of statistically significant differences. We also calculated average lifespan of snags as

$$l = \frac{-1}{\ln(S)},$$

where (S) was the annualized probability that a snag in either decay state remained in that decay state, as calculated from the estimated probability from the best model that a snag that began the study in either decay state remained in that same state until the end of the study.

To further ease in the interpretation of our results, we also used the fitted transition probabilities from the best-supported model to project changes in the population of snags at Raccoon Point under each of the treatment combinations. The purpose of these simulations was not to predict future changes in the population of snags, but rather to translate the matrix of predicted transition probabilities into a more intuitive quantity (density of trees and snags). We used 50 15-year time steps, which appeared sufficient to illustrate the consequences of variation in transition probabilities among treatments (i.e., an approximate asymptote was reached by 50 time steps). Starting vectors were equal to the average density of individuals in each state at the final observation. Changes in the density of snags and trees between time steps were based on transition probabilities randomly drawn from a beta distribution centered on the estimated mean for each transition and with the estimated variance for each transition (means and variances were estimated from the best-supported model in the candidate set). We chose to use the beta distribution as it is considered the most reasonable choice for simulating matrix elements, such as the transition probabilities reported here, that are limited to values between 0 and 1 (Morris and Doak 2002). For example, the number of stage 1 snags at time $t+1$ was projected as

$$N_{1(t+1)} = N_{0(t)} (P_{0,1}) + N_{1(t)} (P_{1,1})$$

where

$N_{0(t)}$ = number of live trees at time t ,

$P_{0,1}$ = probability that a live tree enters decay state 1 between time t and $t+1$,

$N_{1(t)}$ = number of snags in decay state 1 at time t , and

$P_{1,1}$ = probability that a tree in decay state 1 remains in decay state 1 from time t to $t+1$.

The fifty-step projection for each treatment combination was repeated 1,000 times. We estimated the mean projected number of snags in each decay state at each time step from the 1,000 simulated projections, and used the 2.5 and 97.5 percentiles from the simulations to define the 95% confidence limits around each mean.

IV. Key findings

Objective 1) Determine the large-scale patterns of relationship between fire management, hydrology, and abundance and distribution of breeding and wintering landbirds and their habitats.

Key finding 1) Variation in hydrology was the primary driver of large-scale variation in vegetation structure and the distribution and abundance of breeding and wintering birds across the range of south Florida slash pine. Fire history was of secondary importance.

Water-table elevation, the number of days since last fire, and the number of times a sample plot had burned explained a significant ($P < 0.001$) amount of variation in both vegetation structure and abundance of breeding birds. Only water-table elevation explained a significant amount of variation in the density of birds during the winter; neither of the axes related to the two fire variables explained a significant amount of variation ($P > 0.3$). Despite the statistically significant relationship between our predictor and response variables, the vast majority of variation in the structure of vegetation and the distribution and abundance of birds was not accounted for by either hydrology or fire history (for plants, 6.8% of the total variation was explained by the predictor variables; for breeding birds, 4.8%; and for wintering birds, only 0.5%). Of the variation explained by the predictor variables, water-table elevation accounted for the majority: 72% of the explained variation in vegetation structure, 73% of the explained variation in breeding-bird densities, and 77% of the explained variation in densities of wintering birds.

Across all sample points, hardwood ground and shrub cover, the maximum height of understory hardwoods, the number of small and medium pines and pine snags, the total number of snags, and the height of understory pines all declined as water-table elevation increased (Fig. 2). The average height of understory palms, the maximum height of understory palms, palm shrub cover, the number of large pine trees, and total basal area of pine trees all increased as sites grew wetter (Fig. 2). Points burned more recently and frequently were characterized by less grass cover, less ground and shrub cover by hardwoods, shorter understory hardwoods, less total shrub cover, shorter understory pines, fewer small and medium pines, and more pine snags of all size classes (Fig. 2).

Breeding birds associated with wetter sites included Blue-gray Gnatcatcher (*Polioptila caerulea*; BGGN), Brown-headed Nuthatch (*Sitta pusilla*; BHNU), Carolina Wren (*Thryothorus ludovicianus*; CARW), Common Yellowthroat (*Geothlypis trichas*; COYE), Downy Woodpecker (DOWO), Eastern Bluebird (EABL; *Sialia sialis*; EABL), Great-crested Flycatcher (*Myiarchus crinitus*; GCFL), Pine Warbler (*Dendroica pinus*; PIWA), Red-bellied Woodpecker (RBWO); Tufted Titmouse (*Baeolophus bicolor*; TUTI), and White-eyed Vireo (*Vireo griseus*; WEVI) (Fig. 3). Only two species were more common on dry sites: Blue Jay (*Cyanocitta cristata*; BLJA) and Northern Mockingbird (*Mimus polyglottos*; NOMO) (Fig. 3). Downy Woodpecker, Great-crested Flycatcher, Northern Cardinal, Pine Warbler and Red-bellied Woodpecker were also associated with more recently or frequently burned points; no species was associated with fire-suppressed conditions (Fig. 3).

Wintering birds showed weaker associations in general with all of the independent variables. Three species – American Robin (*Turdus migratorius*; AMRO), Pine Warbler, and Yellow-rumped Warbler (*Dendroica coronata*; YRWA) – were associated with wetter sites; none were associated with lower water-table elevations (Fig. 4). Densities of wintering birds were not associated with any particular fire history (Fig. 4).

The relatively poor performance of the models summarized in Figures 2, 3, and 4 suggests the importance of biotic interactions, other past and ongoing sources of disturbance, and biogeographical considerations in understanding the present appearance of the pine ecosystems of southern Florida, at least when viewed at large spatial scales.

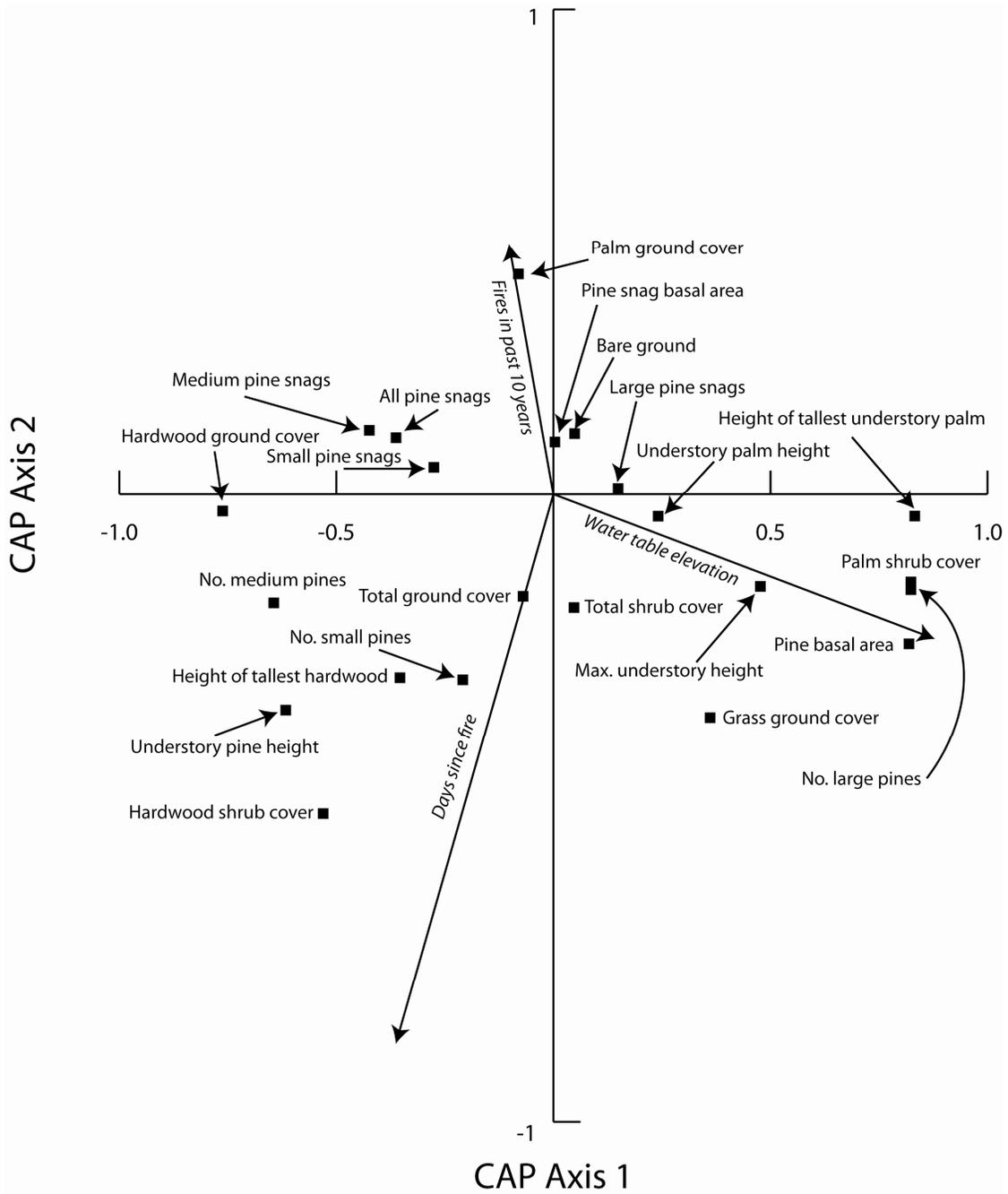


Figure 2. Results of a partial canonical analysis of principal coordinates (CAP) conducted on vegetation variables measured in slash-pine (*Pinus elliottii* var. *densa*) forests across southern Florida, 2005-2008. CAP axis 1 is positively correlated with water-table elevation ($r = 0.50$), and CAP axis 2 is negatively correlated with the time since last fire ($r = -0.34$) and positively correlated with the number of times a point burned ($r = 0.20$). The position of each vegetation variable indicates the strength and sign of its association with the independent variables.

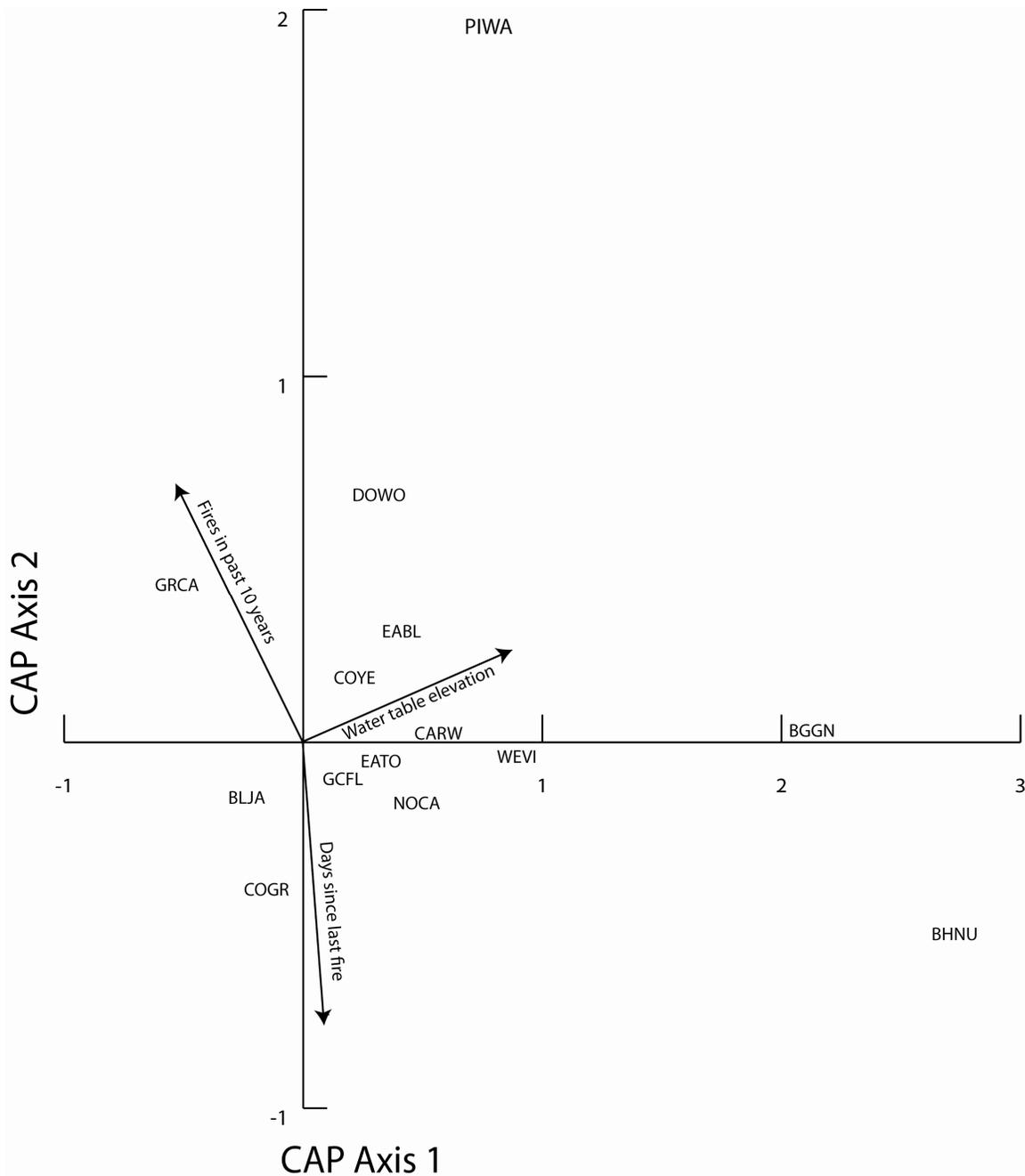


Figure 3. Results of a partial canonical analysis of principal coordinates (CAP) conducted on breeding-bird densities estimated in slash-pine (*Pinus elliottii* var. *densa*) forests across southern Florida, 2005-2008. CAP axis 1 is positively correlated with water-table elevation ($r = 0.40$), and CAP axis 2 is negatively correlated the time since last fire ($r = -0.15$) and positively correlated with the number of times a point burned ($r = 0.22$). The position of each bird species code indicates the strength and sign of its association with the independent variables.

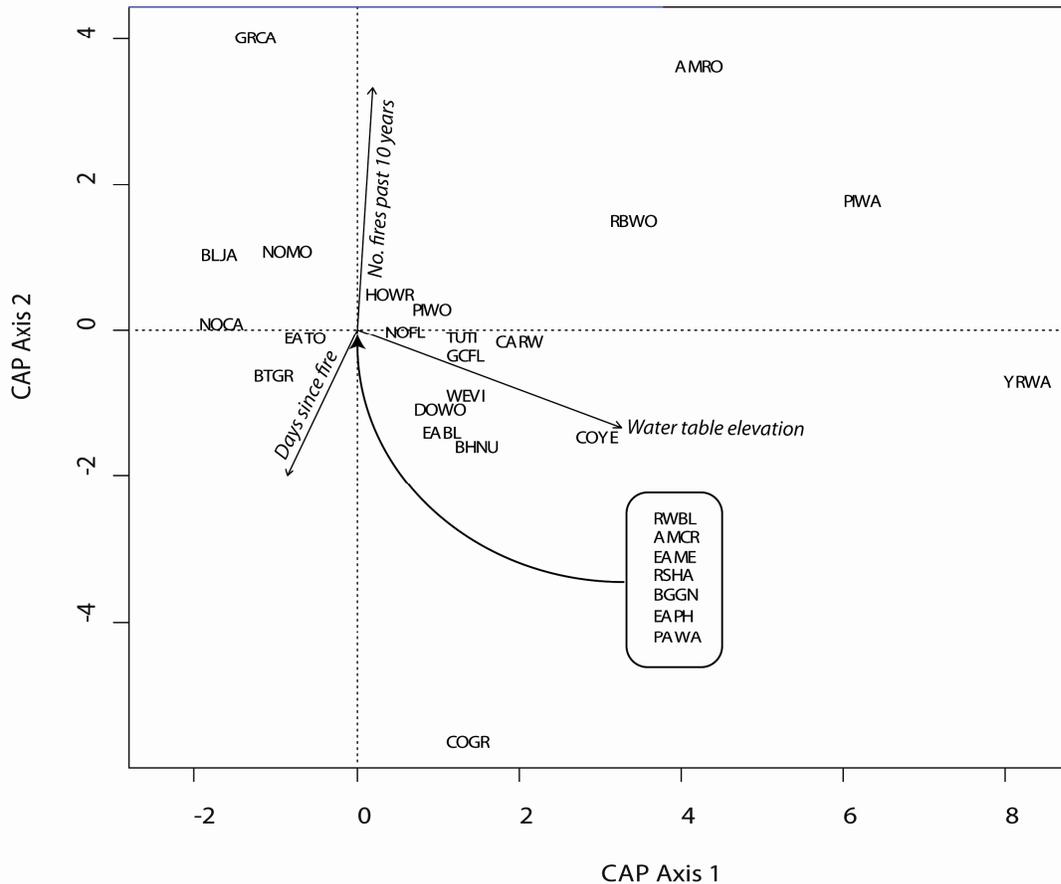


Figure 4. Results of a partial canonical analysis of principal coordinates (CAP) conducted on nonbreeding-bird densities estimated in slash-pine (*Pinus elliottii* var. *densa*) forests across southern Florida, 2005-2008. CAP axis 1 is positively correlated with water-table elevation ($r = 0.11$). CAP axis 2 was non-significantly related to time since last fire ($r = -0.05$) and the number of times a point burned ($r = 0.09$). The position of each bird species code indicates the strength and sign of its association with the independent variables. Species clustered near the origin show no relation to any of the independent variables.

Key finding 2) Variation in hydrology was the primary driver of within-site variation in vegetation structure and the distribution and abundance of breeding and wintering birds. Fire history was of secondary importance.

Variation in water-table elevation was more strongly associated with among-point, within-site variation in vegetation structure at 5 of 7 study sites than either of the fire variables. The number of days since last fire was the strongest predictor of vegetation structure at the other two study sites (Addition Land and Miami-Dade County parks). Variation in breeding-bird density was most strongly related to variation in water-table elevation at 4 of 7 sites, with breeding-bird density responding to the number of days since fire at a single site (Addition Land) and to the number of fires at two sites (Miami-Dade

County parks and Raccoon Point). Water-table elevation was always the strongest predictor of bird densities during the non-breeding season.

Key finding 3) The effects of hydrology on plants were strongly scale dependent, and effects described at large spatial scales were not always concordant with effects described at smaller scales. The effects of hydrology on birds tended to be more consistent among scales.

Some of the large-scale associations between water-table elevation and birds and plants reflect differences among study sites, and these relationships were often not apparent when examined within study sites. For example, at the largest scale, hardwood ground and shrub cover was negatively associated with water-table elevation; that is, hardwood shrubs were denser and more abundant at wetter sites. This is concordant with existing understanding of the role of hydrology in shaping the structure and composition of south Florida slash pine forests: sites with shallower water tables have fewer hardwood shrubs and grassier understories than drier sites, presumably because an elevated water table reduces the ability of hardwoods to establish and grow (e.g., Duever 2005). However, within each of the seven sites we studied, the opposite was true: hardwood ground and shrub cover was greater at points with higher water tables. This may reflect the inability of prescribed fires to carry across wetter portions of a site, resulting in longer fire-return intervals for these points and decreased mortality of hardwoods.

The relationship between water-table elevation and breeding bird densities tended to be more consistent across spatial scales. For example, Pine Warbler, Red-bellied Woodpecker, and Common Yellowthroat were all positively associated with water-table elevation at the largest spatial scale and were also positively associated with water-table elevation within each of the study sites.

Relationships between bird densities during the winter and water-table elevation differed between scales, which is not unexpected given the weak association between non-breeding birds and any of the measured environmental variables. For example, Yellow-rumped Warbler, which was strongly and positively associated with water-table elevation at the largest scale, was more abundant at dry points at 4 out of 6 study sites (and showed no relationship with water-table elevation at the remaining site).

Key finding 4) In contrast to hydrology, the effects of fire history on plants were consistent between scales, but the effects of fire history on bird densities were variable between scales.

Recent and frequent fires produced a similar vegetation structure regardless of the scale of observation: more bare ground, less shrub cover, shorter understories, and fewer overstory pine trees. The effects of fire on breeding birds were less consistent. Pine Warblers were strongly and positively associated with fire across all study sites, but within 4 of the study sites their abundance increased as the number of burns decreased and the time since last fire increased. At two sites they showed the expected positive relationship with fire, and at the remaining site abundance of Pine Warblers was not associated with variation in fire history.

Key finding 5) Breeding birds tolerated fire-return intervals of as long 5 years without significant changes in density. For some species, density declined when fire-return intervals exceeded 5 years.

For the five species (Northern Cardinal, Pine Warbler, Red-bellied Woodpecker, Downy Woodpecker, Great-crested Flycatcher) that showed a positive association with fire across all study sites, all showed a similar pattern of abundance in relation to the time since last fire, wherein abundance remained constant for up to 5 years after fire, then declined sharply from 5-7 years post-fire, and finally leveled out at > 7 years post-fire (e.g., Figs. 5 and 6). Three of these species are cavity nesters – Downy Woodpecker, Red-bellied Woodpecker, and Great-crested Flycatcher – and their increased abundance at shorter fire-return intervals may be due to the increase in number of snags associated with recent fires.

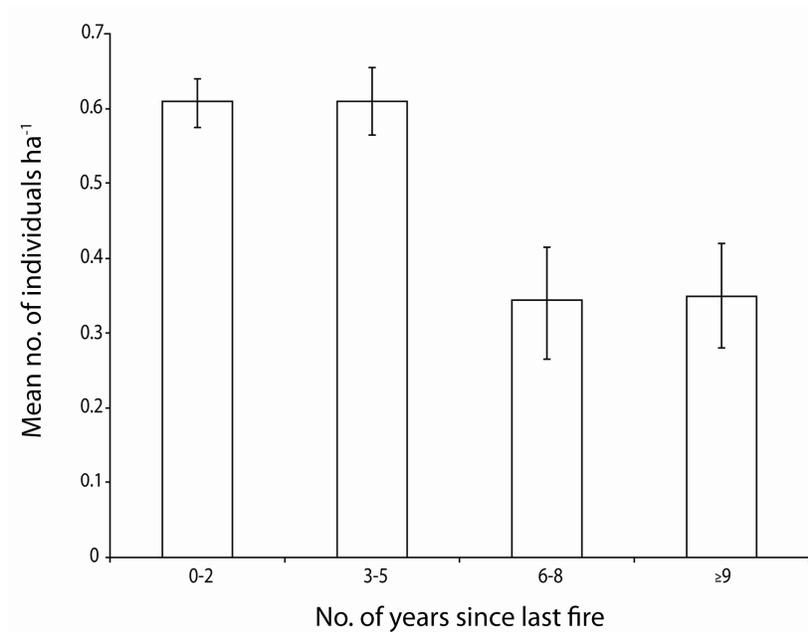


Figure 5. Abundance of Pine Warblers (*Dendroica pinus*) breeding in slash-pine (*Pinus elliottii* var. *densa*) forests of south Florida during 2005-2008 as a function of time since last fire.

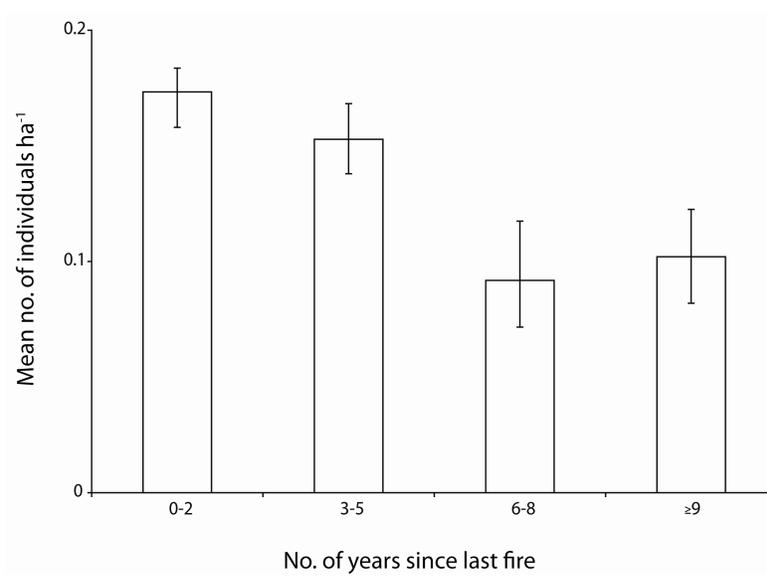


Figure 6. Abundance of Great-crested Flycatchers (*Myiarchus crinitus*) breeding in slash-pine (*Pinus elliottii* var. *densa*) forests of south Florida during 2005-2008 as a function of time since last fire.

Objective 2) Investigate the role of fire in snag dynamics.

Key finding 1) Dry-season burns were more intense than wet-season burns and resulted in a higher probability of snag creation than wet-season burns.

Fire intensity, as measured by the average height of bark char one-month postfire, was much greater for dry-season burns (4.4 m, 95% CI = 2.9 – 6.0) than for wet-season burns (2.7, 95% CI = 1.7 – 3.7). Increased fire intensity during dry-season burns may have led to increased mortality of pine trees, resulting in an increase in the probability of snag creation. The estimated probability that a live tree became a snag over the course of the study was significantly greater for plots burned during the dry season (Fig. 7).

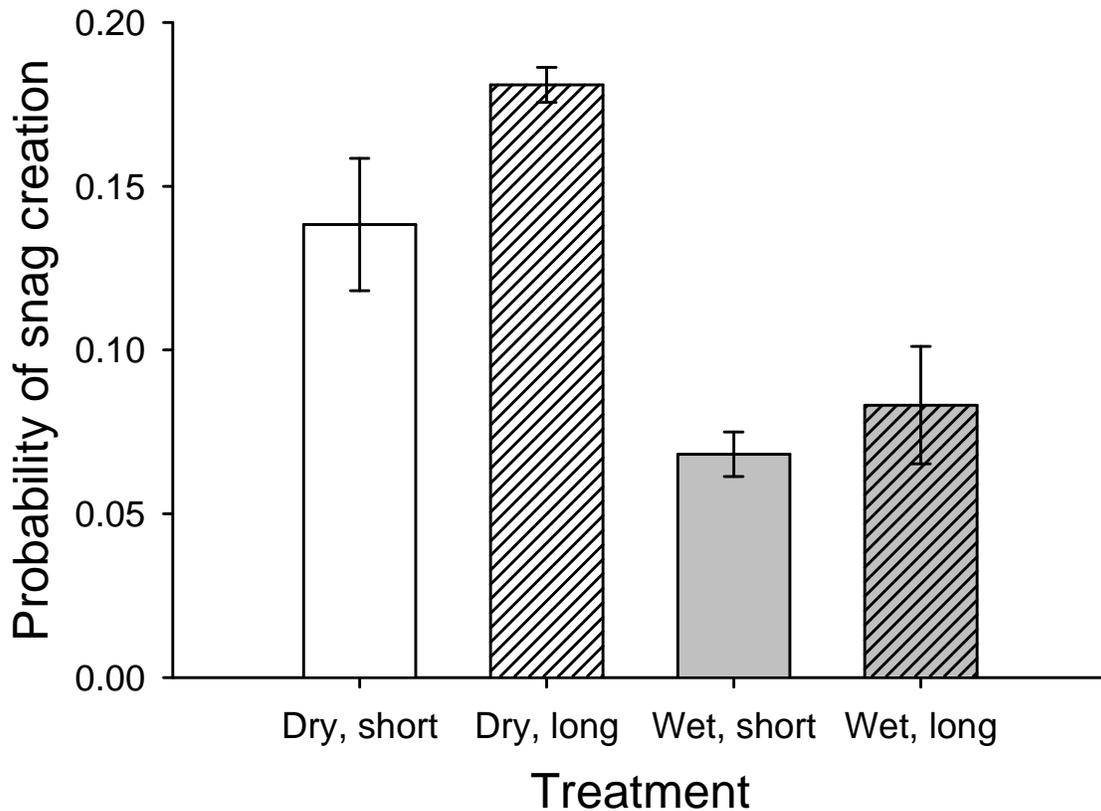


Figure 7. Predicted probability (\pm 95% confidence interval) that a live south Florida slash pine (*Pinus elliottii* var. *densa*) tree in Big Cypress National Preserve, Florida became a snag between 1993 and 2008 as a function of experimental treatment. Treatments included burning during the dry season and with a short (c.a. 3 years) fire-return interval (dry, short), during the dry season and with a long (c.a. 6 years) fire-return interval (dry, long), during the wet season and with a short fire-return interval (wet, short), and during the wet season and with a long fire-return interval (wet, long). Predictions were generated from the best-supported multinomial logit model.

Key finding 2) Burns conducted at longer intervals increased the probability of snag creation. We found that live trees on plots burned on a longer interval had a significantly greater probability of becoming a snag (Fig. 7). Return interval had a smaller effect on snag creation than did season of burn (Key Finding #1).

Key finding 3) The probability of mortality of existing snags (snag loss) was greater with wet-season burns.

The mortality rate for snags – that is, the probability that a snag was consumed, fell over, or decayed completely – was significantly lower on plots that were burned during the dry season (Fig. 8). Given the general correlation between fire intensity and the rate of spread, wet-season burns likely moved more slowly, with lower flame heights, and thus may have concentrated heat transfer around the base of trees and snags, which may explain why wet-season burns killed fewer live pine trees. At the same time, by focusing heat transfer at the base of existing snags, wet-season burns may have been more likely to consume sapwood at the base of low-to-moderately decayed snags, weakening structural support and increasing the probability that these snags fell during the course of the study.

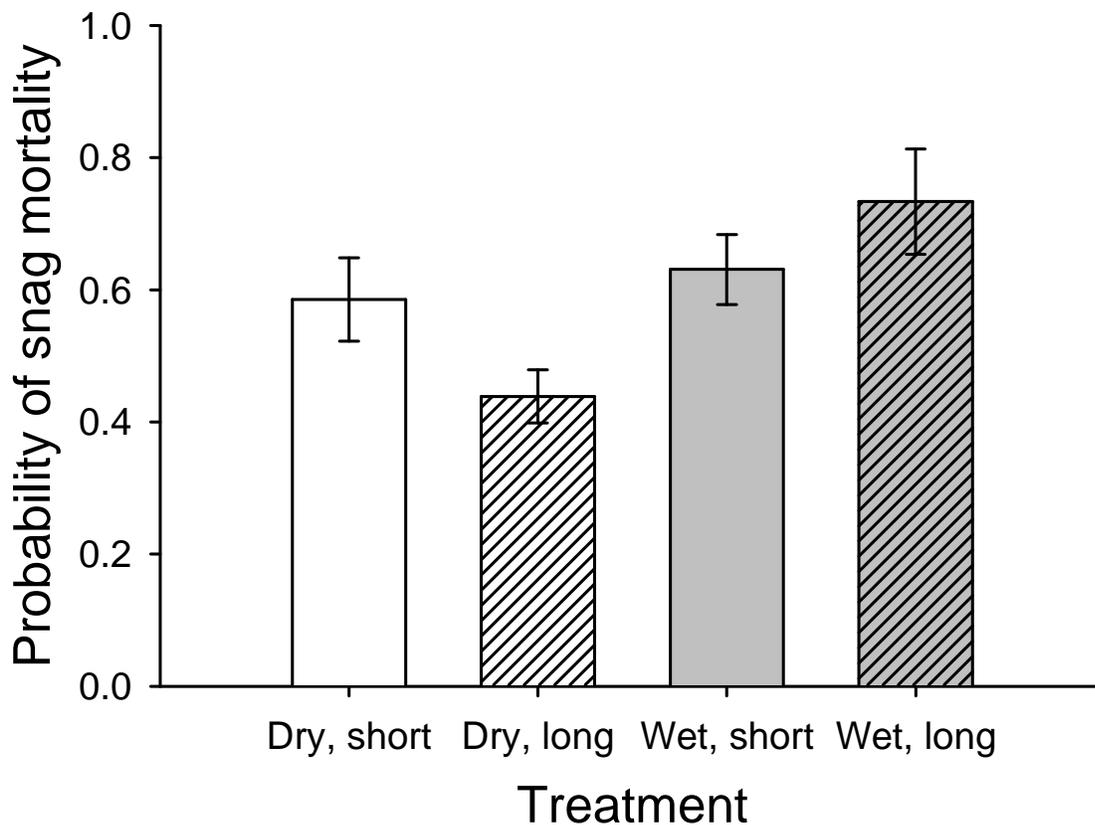


Figure 8. Predicted probability (\pm 95% confidence interval) that a south Florida slash pine (*Pinus elliottii* var. *densa*) snag in Big Cypress National Preserve, Florida fell down or decayed or was consumed by fire to a height of < 1.5 m or a dbh of < 5.0 cm between 1993 and 2008 as a function of experimental treatment. Treatments included burning during the dry season and with a short (c.a. 3 years) fire-return interval (dry, short), during the dry season and with a long (c.a. 6 years) fire-return interval (dry, long), during the wet season and with a short fire-return interval (wet, short), and during the wet season and with a long fire-return interval (wet, long). Predictions were generated from the best-supported multinomial logit model.

Key finding 4) Burning in the dry season and with longer return intervals is predicted to yield greater densities of snags.

Live pines were more likely to become lightly to moderately decayed snags, and snags in this state were more likely to remain in this state, on plots burned during the dry season and on a longer interval, which resulted in a substantially greater projected density of lightly to moderately decayed snags than in other treatments (Fig. 9). In general, these lightly to moderately decayed snags are more valuable to cavity-nesting birds than other decay classes. Dry-season burns were also projected to result in a greater density of heavily decayed snags than wet-season burns, apparently because of an increase in transition probabilities to this state from live trees and low-to-moderately decayed snags (Fig. 10).

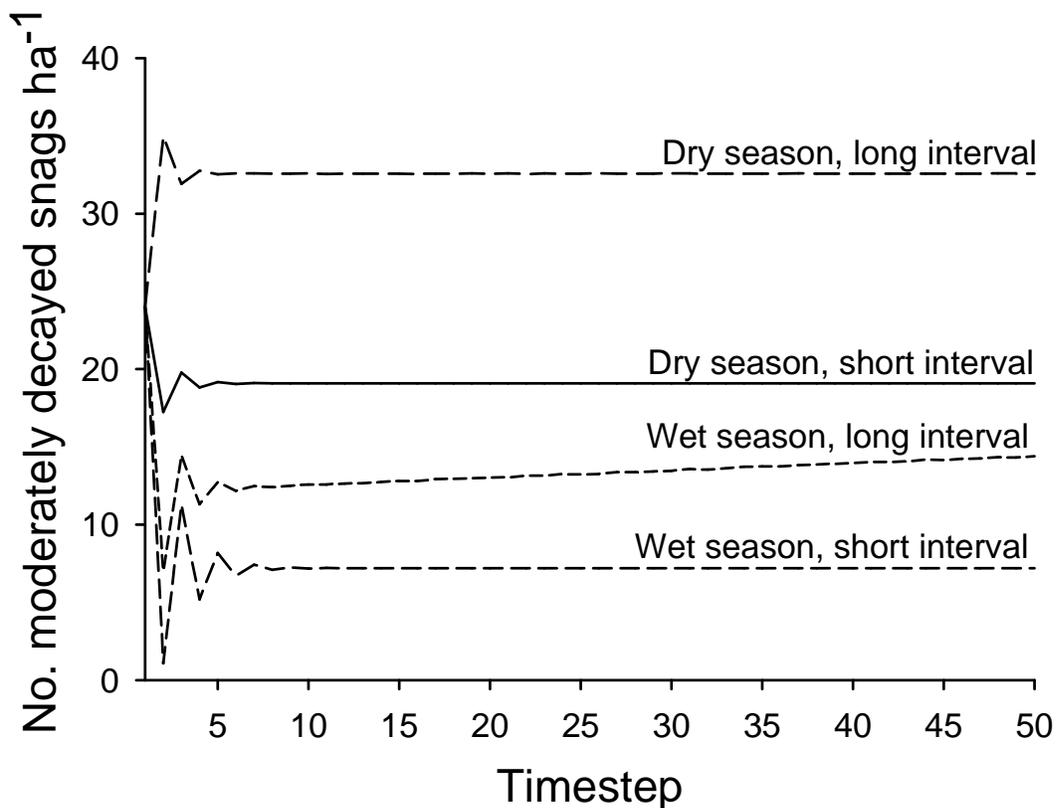


Figure 9. Projected density of low-to-moderately decayed south Florida slash pine (*Pinus elliottii* var. *densa*) snags in Big Cypress National Preserve, Florida as a function of experimental treatment. Treatments included burning during the dry season and with a short (c.a. 3 years) fire-return interval (dry, short), during the dry season and with a long (c.a. 6 years) fire-return interval (dry, long), during the wet season and with a short fire-return interval (wet, short), and during the wet season and with a long fire-return interval (wet, long). Projections were based on beta-distributed random numbers with a mean and variance equal to those predicted from the best-supported multinomial logit model, fit to data on the fate of marked trees and snags between 1993 and 2008. Densities at each 15-year timestep were calculated as the average from 10,000 simulations; 95% confidence intervals were estimated but were too narrow to be represented on the y-axis.

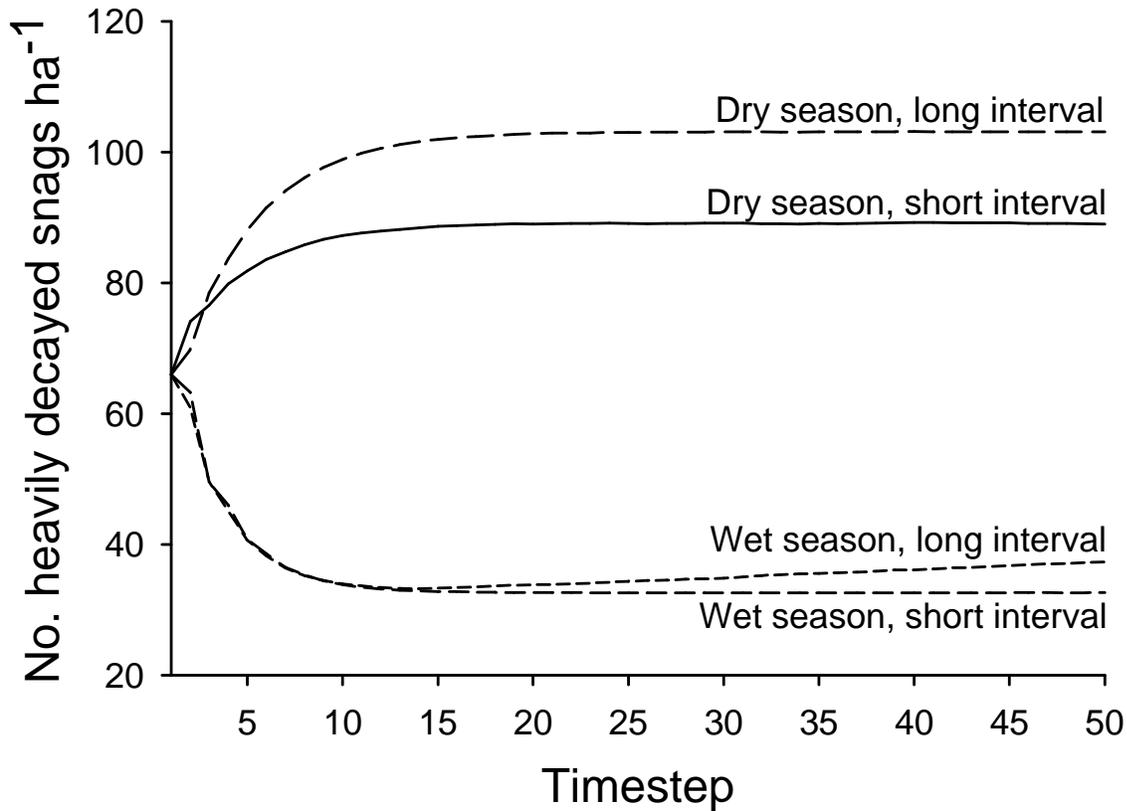


Figure 10. Projected density of heavily decayed south Florida slash pine (*Pinus elliottii densa*) snags in Big Cypress National Preserve, Florida as a function of experimental treatment. Treatments included burning during the dry season and with a short (c.a. 3 years) fire-return interval (dry, short), during the dry season and with a long (c.a. 6 years) fire-return interval (dry, long), during the wet season and with a short fire-return interval (wet, short), and during the wet season and with a long fire-return interval (wet, long). Projections were based on beta-distributed random numbers with a mean and variance equal to those predicted from the best-supported multinomial logit model, fit to data on the fate of marked trees and snags between 1993 and 2008. Densities at each 15-year timestep were calculated as the average from 10,000 simulations; 95% confidence intervals were estimated but were too narrow to be represented on the y-axis.

V. Management implications

Management implication 1) Hydrological restoration in the greater Everglades that results in widespread changes to water-table elevation will effect change in the structure and composition of plant and animal communities even in the pine-dominated uplands.

Annual cycles of flooding and drought play a key role in structuring biological communities in the greater Everglades. As such, “getting the water right” is viewed as the critical element in the restoration of the greater Everglades. Wetland communities are expected to respond strongly to the restoration of a more natural hydropattern, but relatively little is known of how hydrological restoration will affect upland communities. Our results suggest that changes in water-table elevation have the potential to produce large and direct changes in the physiognomy of slash-pine forests and in the structure and composition of the bird assemblages inhabiting these forests. Changes in the structure of the plant community brought about by changes in water-table elevation will likely produce changes in the composition and accumulation rate of fuels, which may produce changes in fire behavior. Changes in fire behavior may in turn produce further changes in the structure of the plant community. Our understanding of how fire shapes the slash-pine forests – including the results presented here - has developed during a period when water-table elevations have been unnaturally low, and as a consequence fire-management plans may require substantial revision as hydrological restoration proceeds.

Management implication 2) Fire-return intervals of up to 5 years are appropriate for maintaining populations of most breeding birds

All of the breeding birds that exhibited a strong relationship with fire history had a similar pattern of abundance, wherein abundance dropped sharply when fire-return intervals extended beyond 5 years. This suggests a general adaptation among breeding birds in this ecosystem to fires that occur, on average, approximately 2 times per decade. No species was positively associated with fire-suppressed conditions; however, data from our experimental study of fire effects on snag populations (Objective 2) suggest that snag densities may decline under short (i.e., 3 years) fire-return intervals and thus species that require snags for nesting may benefit from occasional fire-free periods that last 6-7 years. Incorporating variable fire-return intervals into fire-management planning may be a useful approach for creating conditions suitable to a variety of bird species.

Management implication 3) Density of snags – a key element of habitat for several bird species of concern – can be increased by applying fire at longer intervals and by burning at the transition between dry-season and wet-season.

Prescribed burns could be an effective tool for increasing the density of snags, provided that the fire is sufficiently intense to induce mortality among live trees and moving rapidly enough to limit the consumption of sapwood on existing snags. Prescribed burns conducted early in the wet season might be useful for increasing snag densities as long as fuel and weather conditions are suitable to support a relatively intense fire. As the wet season progresses, and fuel moistures increase, prescribed burns will likely have an

increasingly detrimental effect on snag density because fewer snags will be created and more will be consumed. Longer fire-return intervals might also help optimize the balance between snag creation and snag consumption during a fire, and lengthening this interval on occasion to > 5 years may be beneficial. Doing so would increase the density of low-to-moderately decayed snags, which, in slash-pine forests, afford suitable nest sites for a variety of cavity-nesting birds, including species of management concern such as Eastern Bluebirds, Brown-headed Nuthatches, and Hairy Woodpeckers.

VI. Relationship to other recent findings and ongoing work on this topic

Objective 1) Determine the large-scale patterns of relationship between fire management, hydrology, and abundance and distribution of breeding and wintering landbirds and their habitats.

There has been relatively little study of the role that hydrology plays in shaping the composition of slash-pine forests. However, hydrology is an important determinant of species composition and physiognomy in other southeastern pine ecosystems (Peet and Allard 1993, Allen et al. 2006), and Duever (2005) argued that hydroperiod and water-table elevation played a major role in shaping the composition of slash-pine forests in BCNP. Fire has received more attention as a key ecosystem process, and the seminal work of Robertson (1953) and Alexander (1967) established the controlling role of fire in preventing the succession of slash pine to hardwood hammock. More recently, Slocum et al. (2003) found that higher-elevation locations in the pine rocklands at Long Pine Key tended to experience more intense and uniform fires than did relatively low-elevation locations in the same area. This pattern may have arisen due to an interaction with hydrology, whereby fuel moistures were greater at the wetter, lower-elevation sites. Although he presented no data in support of his contention, Loveless (1959) made a similar argument, suggesting that the effects of fire were strongly influenced by water levels.

Almost nothing is known of the response of birds in slash-pine forests to variation in hydrology. Working in a longleaf-pine forest, Allen et al. (2006) found substantial variation in the structure and composition of a breeding-bird community along moisture gradients, although the gradient in that study encompassed non-pine plant communities (e.g., pocosins). The few studies that have examined the effect of fire on birds in slash-pine forests have not found any strong relationship between bird abundance and fire history (Emlen 1970, Johnson and Landers 1982), although both studies examined a limited range of fire-return intervals (the maximum time since fire was 5 years). Given our results, which indicate that most species tolerate fire-return intervals of up to 5 years with no appreciable effect on abundance, studies examining the importance of fire may need to include a wider range of fire histories.

Objective 2) Investigate the role of fire in snag dynamics.

Elevated rates of snag creation observed in the dry-season treatments were due in large part to increased mortality of live trees. Whether this pattern was actually a result of season of burn is unclear, however. The average height of charred bark, a good indicator of fire intensity (e.g., Wade and Johansen 1986, Williams et al. 1998), tended to be greater during dry-season burns: fire intensities during the dry season were medium (91 – 235

BTU sec⁻¹ ft⁻¹) and were low (1 – 90 BTU sec⁻¹ ft⁻¹) to medium during the wet season (using the scale in Byram 1959). Fire intensity, in turn, is often a good predictor of mortality of pine trees following fire (Glitzenstein et al. 1995, Menges and Deyrup 2001, Snyder et al. 2005). Although several *a priori* reasons exist to expect that season of burn may affect the ecological outcome of fire (see review of hypotheses in Glitzenstein et al. 1995), in this case season is confounded with variation in fire intensity and in general there is scant evidence for consistent seasonal patterns in the vulnerability of south Florida slash pine and related species to fire, in part because fire intensity does not vary consistently with season of burn (see, e.g., Snyder 1986, Glitzenstein et al. 1995, Menges and Deyrup 2001, Snyder et al. 2005). Although higher rates of tree mortality – presumably a consequence of more intense fires – were the primary reason that the dry-season burns were projected to yield higher densities of snags, dry-season burns also had lower rates of snag mortality, particularly for low-to-moderately decayed snags. Again, this was likely a consequence of differences in the behavior of fires initiated in different seasons. Given the general correlation between fire intensity and the rate of spread (Rothermel 1972), wet-season burns likely moved more slowly, with lower flame heights, and thus may have concentrated heat transfer around the base of trees and snags (Wade and Johansen 1986). Snyder (1986) reported a similar phenomenon, in which a wet-season prescribed burn in the pine rocklands of Everglades National Park produced much hotter median ground-level temperatures (316°C v. 232°C) than a faster and more intense dry-season burn conducted on a nearby study plot. Wade and Johansen (1986) argued that most fire-related mortality in southern pines with dbh > 5.0 cm is due to crown damage, rather than cambial damage on the tree bole or root damage, which may explain why wet-season burns killed fewer live pine trees. At the same time, by focusing heat transfer at the base of existing snags, wet-season burns may have been more likely to consume sapwood at the base of low-to-moderately decayed snags, weakening structural support and increasing the probability that these snags fell during the course of the study. Snags of south Florida slash pine that had lost all sapwood from ground level to approximately 1 m above ground level were frequently observed (J. D. Lloyd and G. L. Slater, personal observation), and may reflect the action of slow-moving, low-intensity ground fires that may be typical of wet-season burns.

Longer fire-return intervals generally result in increased fuel loads, more intense fires, and higher mortality of live trees (Sackett 1975, Platt et al. 1991, Outcalt and Wade 2004). To the contrary, we found no evidence of consistent variation in fire intensity among plots burned at different intervals, which may explain why the effect of fire-return interval on rates of snag creation and mortality was somewhat muted relative to the effect of season of burn. In general, shorter return intervals increased the mortality rate of live trees, but more of these trees had fallen down by the end of the study than on plots burned at longer intervals. This pattern could have arisen either because short-return intervals increased the probability of live trees transitioning directly to the down category or because short-return intervals hastened the process of decay (i.e., trees that were alive at the beginning of the study were killed by fire and transitioned through one or both decay states to the down category prior to the final sampling period). Given that fire intensity did not vary with return interval (at least for the first two intervals), we have no reason to believe that live trees were more likely to be consumed or toppled by fire on plots with shorter return intervals. Rather, we believe that the latter scenario is more likely, and that short-return intervals simply hastened the transition from live tree to snag to downed

wood. Indeed, the estimated lifespan of snags in decay state 1 was somewhat lower on plots burned at shorter intervals. Holden et al. (2006) reported similar findings for snags of ponderosa pine (*Pinus ponderosa*), in that snag density in areas burned multiple times was significantly lower than snag density in areas that had only been burned once. They attributed this result to the gradual consumption of wood at the base of snags during successive fires, which reduced structural support for the snag and led to increased fall rates.

Our results suggest that prescribed burns could be an effective tool for increasing the density of snags, provided that the fire is sufficiently intense to induce mortality among live trees and moving rapidly enough to limit the consumption of sapwood on existing snags. In this study, these conditions occurred during burns conducted during the dry season and on plots with longer fire-return intervals. Other studies have found the opposite (e.g., Glitzenstein et al. 1995, Snyder et al. 2005), and thus we believe that our results reflect less on the role of season of burn than they do on the role of fire intensity, which may not vary predictably among seasons. For example, Snyder (1986) found that prescribed burns conducted during the wet and dry seasons had similar characteristics (in terms of fuel consumption, rate of spread, and intensity) when fuel moisture was similar, but that the characteristics of dry- and wet-season burns diverged strongly when conducted with different fuel moisture levels. Indeed, any effort to increase the density of snags should be incorporated into the overall goals of a fire management plan, most of which now seek to replicate natural fire regimes (e.g., Slocum et al. 2003). In southern Florida, lightning-started fires are most frequent in July, although the area burned by lightning-started fires peaks in May during the transition between dry and wet seasons when lightning strikes are frequent and fuels remain dry (Komarek 1964, Doren et al. 1993, Gunderson and Snyder 1994). Thus, whereas prescribed burns used to be most common from October – March (Snyder 1991, Gunderson and Snyder 1994), they tend now to be initiated during the early wet season (Slocum et al. 2003). Prescribed burns conducted early in the wet season might be useful for increasing snag densities as long as fuel and weather conditions are suitable to support a relatively intense fire. As the wet season progresses, and fuel moistures increase, prescribed burns will likely have an increasingly detrimental effect on snag density because fewer snags will be created and more will be consumed.

Longer fire-return intervals might also help optimize the balance between snag creation and snag consumption during a fire. All things being equal, longer fire-return intervals should allow for the build-up of greater fuel loads, which in turn should promote more intense fires (Rothermel 1972, Sackett 1975). The historic fire-return interval in the slash pine forests of southern Florida is thought to have ranged from as short as 2-3 years to as long as 10 or 15 years, although general agreement exists that, on average, most areas would have burned at least every 5 years (Snyder et al. 1990, USFWS 1999, Slocum et al. 2003). After many years of fire suppression, followed by infrequent fires that were often set outside of the historic fire season, prescribed fire regimes now generally attempt to mimic the putative natural pattern of fire and tend to use short fire-return intervals; for example, the pine rocklands of Everglades National Park have been burned on a 2-3 year rotation (Slocum et al. 2003). In situations where snags suitable for use by cavity-nesting birds are limiting, which McComb et al. (1986) argue is generally the case for all of Florida's slash pine forests, lengthening this interval in some areas, perhaps to 4 – 6 years, may be

beneficial. Doing so would increase the density of low-to-moderately decayed snags, which, in slash pine forests, afford suitable nest sites for a variety of cavity-nesting birds, including species of management concern such as Eastern Bluebirds, Brown-headed Nuthatches, and Hairy Woodpeckers. Other considerations may preclude burning large blocks of slash pine forest at longer intervals, but a similar effect might be achieved by relying on ignition methods that promote patchy fires (e.g., single-source ignition methods) and result in a mosaic of return intervals with at least some patches remaining unburned for longer periods.

VII. Future work needed

1) Predictive models of the response of pineland birds to the changes in hydrology (e.g., water-table elevation)

We have described a pattern in which variation in water-table elevation is the primary correlate of large-scale (i.e., region-wide) variation in vegetation structure and in the distribution and abundance of breeding and wintering birds. However, our analysis is purely exploratory, and confirmatory research, utilizing a study design explicitly targeted at revealing the effects of variation in water-table elevation and other hydrological variables (i.e., hydroperiod) is needed. Future work on this question should take advantage of naturally occurring gradients, at a variety of spatial scales, to test hypotheses about the influence of water-table elevation on birds and plants. This work should also recognize that large-scale gradients in water-table elevation are confounded with many other factors (soil type, biogeographical history, climate) and that small-scale gradients may be confounded with variation in fire history.

2) Predictive models of the response of fuels to changes in hydrology (e.g., water-table elevation)

By using ordination analyses that identify orthogonal (i.e., uncorrelated) axes of variation, we have identified how hydrology and fire can shape the structure and composition of the South Florida slash-pine ecosystem independent of one another. In reality, however, hydrology and fire interact with one another to shape biological communities. We have identified spatial variation in vegetation structure that is correlated with spatial variation in water-table elevation, and it is reasonable to assume that temporal variation in water-table elevation and hydroperiod, as will accompany restoration of normative hydrological processes, will produce similar changes within a location. These changes in vegetation structure will likely produce changes in the composition of fuels and in the rate at which they accumulate, both of which may influence fire behavior. These changes could be modulated by accompanying changes in fire-management plans (e.g., increase rate of fuel accumulation might mandate a shortened fire-return interval), but refining these plans will require a better understanding of how changes in water-table elevation will change patterns of fuel accumulation. Again, these future studies might take advantage of existing gradients in water-table elevation as means for predicting how conditions at a particular location may change over time. Future studies addressing these questions should identify relevant response variables with the input of fire managers.

3) Identification of ecological targets for monitoring the response of the south Florida slash pine ecosystem to changes in water-table elevation and other hydrological factors (e.g., hydroperiod)

Predictive models can be a useful tool in evaluating management alternatives, but should always be verified with monitoring data. Understanding the response of the South Florida slash-pine ecosystem to hydrological restoration of the greater Everglades will require long-term monitoring, but the best targets for such monitoring remain unidentified. Based on our results, measures such as the relative understory dominance by hardwoods and palms, the height of the understory, growth rate of slash pine, basal area of slash pine, size-class distribution of slash pine, and density of pine snags might all be useful in assessing the effects of hydrological restoration on this ecosystem. However, confirmatory studies – such as those that might also address needs 1 and 2 – would be useful in identifying the most sensitive and biologically significant targets for long-term monitoring.

4) Identification of ecological targets for monitoring the response of slash-pine ecosystem to variation in fire regime

Although the effects of fire on plants and animals in the South Florida slash-pine ecosystem are better understood than are the effects of hydrology, long-term ecological monitoring is needed for continued refinement of the scientific basis underlying existing fire-management plans. In addition to monitoring fuels, the efficacy of fire-management plans might be enhanced by identifying targets for monitoring that relate directly to ecological goals for slash-pine forests. In some cases, these may overlap with targets for fuels monitoring. Based on our results, many of the same response variables that might be measured for monitoring the effects of changes in water-table elevation (see need 3) could also be used to monitor the long-term effects of variation in fire regime.

5) Research into the factors that drive snag recruitment and mortality.

Snags are both an important fuel source and an important ecological attribute. They are an essential component of habitat for cavity-nesting birds, many of which are considered to be species of high importance by land managers. Our research highlights the relationship between fire and snag dynamics, but more detailed monitoring is needed to improve our understanding of the links between prescribed fire, fire intensity, fuel moisture, and hydrology with snag recruitment and mortality. In addition, this information needs to be assessed with the knowledge that many remaining pine forests in south Florida are small and fragmented, and thus attempts to mimic the full variation of naturally occurring fires through prescribed fire may prove difficult.

6) Research into factors that drive variation in the distribution and abundance of cavity-nesting birds.

The extirpation of as many as five cavity-nesting birds in sites throughout the south Florida slash pine ecosystem indicates the sensitivity of this avian group to management actions, particularly fire. Snag abundance is an important factor in regulating populations of this group and the long-term viability of existing and reintroduced populations will rely

on effective management strategies (i.e., prescribed fire) that maintain snags. Understanding how the distribution and abundance of cavity-nesters varies with respect to snag abundance and other factors will provide critical information to guide fire management, including the development of ecological targets for cavity-nesting birds.

7) Research into factors that drive variation in the distribution and abundance of wintering birds

The slash-pine forests of south Florida are an important wintering ground for a variety of species, including Yellow-rumped Warbler and Palm Warbler, yet little is known of the habitat requirements of species wintering there. Evaluating the effects of management actions (most importantly, efforts at restoring natural hydrological and fire regimes) on wintering birds is difficult absent a better understanding of the factors that shape their distribution and abundance. Given the importance of fruit in the diet of many wintering birds (e.g. Eastern Bluebird, Yellow-rumped Warbler, and American Robin), future studies might profitably examine the relationship between bird abundance and fruiting shrubs, and whether variation in fire regime has any effect on the availability of fruit.

IX. Status of deliverables

Deliverable	Description	Date delivered
1st Annual Progress Report	Summarization of winter bird surveys; compilation of snag data.	Completed
2nd Annual Progress Report	Summarization of first year of data collection; preliminary results of fire, fuel, bird models.	Completed
3rd Annual Progress Report	Summarization of second year of data collection; preliminary results of snag models.	Completed
Final Report	Report will include executive summary, introduction of topic, description of methods, work results (including all models, figures, graphs, and tables), discussions, and conclusions.	Completed
Peer-reviewed article	Snag dynamics in the pine rocklands: the role of fuel treatments.	In revision; Canadian Journal of Forest Research
Peer-reviewed article	The ecological effect of fire management: large-scale patterns between breeding and wintering birds and wildland fuels in south Florida	In preparation
Peer-reviewed article	Effects of fuel treatment on the biological condition of pine rocklands as represented by bird communities	In preparation
State of the Science Symposium	Symposium to disseminate results of this study, present ongoing work by other researchers and managers working in the pine rockland ecosystem, develop a biennial action plan, and encourage inter-agency communication and collaboration	In preparation; Pine Rockland Conference February 2010

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