THE ROLE OF FIRE-RETURN INTERVAL AND SEASON OF BURN IN SNAG DYNAMICS IN A SOUTH FLORIDA SLASH PINE FOREST

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ABSTRACT

Standing dead trees, or snags, are an important habitat element for many animal species. In many ecosystems, fire is a primary driver of snag population dynamics because it can both create and consume snags. The objective of this study was to examine how variation in two key components of the fire regime—fire-return interval and season of burn—affected population dynamics of snags. Using a factorial design, we exposed 1 ha plots, located within larger burn units in a south Florida slash pine (*Pinus elliottii* var. *densa* Little and Dorman) forest, to prescribed fire applied at two intervals (approximately 3-year intervals vs. approximately 6-year intervals) and during two seasons (wet season vs. dry season) over a 12- to 13-year period. We found no consistent effect of fire season or frequency on the density of lightly to moderately decayed or heavily decayed snags, suggesting that variation in these elements of the fire regime at the scale we considered is relatively unimportant in the dynamics of snag populations. However, our confidence in these findings is limited by small sample sizes, potentially confounding effects of unmeasured variation in fire behavior and effects (e.g., intensity, severity, synergy with drought cycles) and wide variation in responses within a treatment level. The generalizing of our findings is also limited by the narrow range of treatment levels considered. Future experiments incorporating a wider range of fire regimes and directly quantifying fire intensity would prove useful in identifying more clearly the role of fire in shaping the dynamics of snag populations.

INTRODUCTION

Standing dead trees, or snags, may proceed through many stages of decay before finally toppling or decaying completely. During some stages of this process, they are a critical component of habitat for numerous species of forest-dwelling wildlife. In pine forests of the southeastern United States, several bat species rely on cavities in snags as roost sites, and many other mammals use cavities as dens (Loeb 1993). Birds as a group are especially reliant on snags: Hamel (1992) estimated that at least 45 species of birds in the southeastern United States required snags to successfully complete some portion of their life history (e. g., nesting, roosting, or foraging). The density or abundance of cavity-nesting birds is often closely correlated with the density of snags (Raphael and White 1984, Zarnowitz and Manuwal 1985, Land *et al.* 1989, Breininger and Smith 1992), and the availability of snags suitable for cavity excavation may directly limit populations in some cases (Brawn and Balda 1988). However, not all snags are equally useful to cavity-nesting birds, with many species showing a distinct preference for excavating nest cavities in snags of a certain decay state (Runde and Capen 1987). Thus, maintaining viable populations of cavity-nesting birds requires maintaining an adequate supply of snags with an appropriate distribution of decay states. In recognition of the importance of snags for cavity-nesting birds and other wildlife, management plans for public lands often identify desired densities of snags for different forest types. Achieving these goals requires that land managers understand the factors that shape snag population dynamics; in particular, managers need to understand the causes of variation in recruitment to the population of standing dead trees, decay rate, and mortality (i.e., falling or decaying to the point that they can no longer be used as nest sites).

Snag populations are affected by a variety of agents, including both those that operate largely independently of human control, such as pathogens or severe weather, and those that can be controlled by managers, such as prescribed fire or timber harvesting. In some ecosystems, however, fire—both wildfire and prescribed fire—is the primary driver of snag population dynamics, because fire can both add snags to the population by killing live trees, and remove them by consuming or toppling existing snags (Morrison and Raphael 1993, Chambers and Mast 2005). Despite the importance of fire, managers still lack much of the basic information needed to use fire as a tool for snag management. The full value of fire as a tool to achieve management targets for snags and snag-dependent wildlife cannot be realized without a better understanding of how snags respond to variation in fire regimes.

The goal of this study was to improve our understanding of the role of fire in the dynamics of snag populations in order to enhance the efficacy of prescribed fire as a tool for managing snags. Our specific objective was to examine how variation in two important components of the fire regime, fire-return interval and the seasons in which fires occur, affect the density of snags at different stages of decay. In addressing this objective, we sought to provide general guidance for land managers on how adjustments to fire-return interval and to the season in which fires are ignited might be used to influence snag densities.

We focused on these two elements of the fire regime for practical reasons—season of fire and fire-return interval are under the control of land managers, at least in the case of prescribed burns—and for ecological reasons: both play a significant role in shaping the response of living plants to fire (e.g., Abrahamson 1984, Wade and Johansen 1986, Doren *et al.* 1993, Glitzenstein *et al.* 1995, Kaye *et al.* 2001, Menges and Deyrup 2001, Menges *et al.* 2006), although little is known of how either affects snags. All things being equal, longer intervals between fires result in greater fuel loads, which produce more intense fires and higher tree mortality (Byram 1959, Menges

and Deyrup 2001, Sah *et al.* 2006). Longer return intervals might thus result in elevated levels of snag creation, although presumably more intense fires might simultaneously yield higher levels of snag mortality. Season may influence mortality rates of live trees following fire because trees vary in their sensitivity to fire as a function of physiological status (e.g., Wade and Johansen 1986), although mechanisms for such effects remain unknown and empirical support is generally weak (e.g., Glitzenstein *et al.* 1995). Season is more likely to contribute to variation in tree mortality following fire via indirect effects associated with ambient air temperature or fuel moisture; dry-season burns may be more intense because fuel moisture is lower (Byram 1959) and cool-season burns may be less intense because ambient air temperature is lower, requiring more energy for fuels to reach combustion temperature (Rothermel 1972). How any seasonal variation in the risk of mortality among live trees influences snag dynamics depends on whether snags show similar patterns of vulnerability.

METHODS

Study Area

We conducted this experiment in an area of Big Cypress National Preserve, Florida, USA, known as Raccoon Point (25.9° N, 80.9° W) (Figure 1), which contains extensive unlogged stands of south Florida slash pine (*Pinus elliottii* var. *densa* Little and Dorman). The pinelands of Raccoon Point exist as a mosaic of slightly elevated "islands" within a matrix of cypress (*Taxodium ascendens* Brongn.) domes and dwarf cypress prairies. The climate at Raccoon Point is sub-tropical, with a pronounced dry season from November through April, and a wet season from May through October. Dry-season precipitation is associated with passage of cold fronts, whereas wet-season rains are associated with convective thunderstorms or tropical cyclones. Average wet-
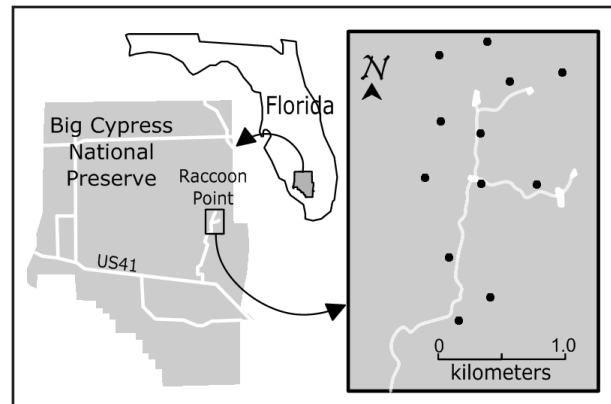

Figure 1. Map showing the location of the study area (Big Cypress National Preserve, Raccoon Point) within the state of Florida, USA, and the arrangement of 1 ha study plots (black dots) within the study area.

season rainfall is 113 cm and average dry-season rainfall is 32 cm, at the Oasis Ranger Station approximately 13 km southwest of Raccoon Point. Average air temperate varies from a low in January of 19 °C to an August high of 29 °C.

Experimental Design and Sampling

We established a single 1 ha plot on 12 different burn units in the pinelands of Raccoon Point. The burn units on which the plots were located ranged in size from 53 ha to 142 ha, with an average area of 84 ha. In each plot we tagged and mapped all living pine trees and snags with diameter at breast height (dbh) >5.0 cm, and assigned each to one of four states: live tree, lightly 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 (*Sitta pusilla* Latham) (G.L. Slater and J.D. Lloyd, Ecostudies Institute, unpublished data), a cavity-nesting bird species that is of management concern and is included on the US Fish and Wildlife Service list of Birds of Conservation Concern (USFWS 2008). Brown-headed nuthatches are weak excavators capable of creating cavities in soft wood only, and so 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.

In an effort to create similar baseline conditions among experimental plots, pre-treatment burns were applied to all study plots during January and February 1990, and again in March and April 1994. Thereafter, each plot was burned 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 to April) or wet (May to October) season. Each of the 12 study plots was 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), yielding a balanced design with three replicates per treatment combination. However, one plot assigned to the wet-season, long-interval treatment had a fire-return interval of only 3.8 years, and so was excluded from the analysis. The final design was thus unbalanced, with a sample size of 3 for all treatments except wet-season, long-interval, which was applied to only 2 plots. We tagged and followed the fate of 4018 trees and snags on the 11 experimental plots.

Natural fire-return intervals in the slash pine forests of south Florida remain a subject of debate, although Wade *et al.* (1980) suggested that most of these forests had burned, on average, every 3 to 6 years historically, and

most agree that slash pine forests probably burned at least twice per decade (e.g., Snyder *et al.* 1990). Thus, our treatment bracketed the approximate range of fire-return intervals deemed likely for this system. The times of year at which we applied fire mimicked the historically natural timing of most fires (the wet season) and the traditional timing of most prescribed burns (the dry season). Most lightning-started fires ignite in July, but the area burned by lightning fires peaks in May, at the transition from dry to wet seasons, presumably because lightning is relatively common yet fuels remain dry (Gunderson and Snyder 1994). Historically, most prescribed fires in this ecosystem were set during the dry season, often between November and March, following the passage of a cold front; wet-season fires were avoided "because of possibility of disturbance to animal reproduction" (Taylor 1981: 17). More recently, prescribed fires have been started at the transition between dry and wet seasons to replicate the putatively natural fire regime.

Plots assigned to receive the dry-season, short-interval treatment had an average fire-return interval of 3.3 years (range: 1.9 to 3.9 years), and each plot was burned four times over the course of the study (excluding the two initial burns in 1990 and 1994 that covered every plot in the study area; Table 1). The average date on which a plot in this treatment was burned was 4 February, and actual burn dates ranged from 1 January to 11 March. Plots receiving the dry-season, long-interval treatment had an average return interval of 6.2 years (range: 5.9 to 7.0 years), and each plot was burned twice between the initial and final observations. These plots had an average burn date of 9 February and a range of burn dates from 7 January to 13 March. The wet-season, short-interval treatment had an average fire-return interval of 3.2 years (range: 2.9 to 3.8 years), and all but one plot were burned four times over the course of the study. A single plot in this treatment was only burned three

Table 1. Summary of schedule of prescribed burns for 11 experimental plots used to examine the effect of fire-return interval (short, 3 years; or long, 6 years) and season of burn on density of snags of south Florida slash pine (*Pinus elliottii* var. *densa*).

Burn season	Target return interval (yr)	Replicate	Burn date			
			First	**Second**	**Third**	**Fourth**
Dry	6	1	13 Mar 1998	20 Jan 2004	--	--
Dry	6	2	25 Feb 1999	23 Feb 2006	--	--
Dry	6	3	4 Feb 1997	7 Jan 2003	--	--
Wet	6	1	2 Jun 1996	4 Jun 2003	--	--
Wet	6	2	28 May 1997	5 Jul 2004	--	--
Dry	3	1	11 Mar 1998	31 Jan 2001	20 Jan 2004	1 Feb 2007
Dry	3	2	12 Feb 1997	16 Feb 2000	28 Jan 2003	3 Mar 2006
Dry	3	3	17 Feb 1999	7 Jan 2003	21 Dec 2004	--
Wet	3	1	1 Jun 1996	30 Mar 2000	21 May 2003	14 Jul 2006
Wet	3	2	4 May 2000	22 May 2003	14 Jul 2006	--
Wet	3	3	26 May 1997	4 May 2000	22 May 2003	14 Jul 2006

times between the first and last observations. Plots in this treatment were burned on average on 29 May, with a range of burn dates from 30 March to 14 July. The fire on 30 March was an outlier, actually occurring at the end of the dry season; all of the remaining 10 prescribed burns applied in this treatment occurred in May, June, or July. We retained the plot with the single, out-of-season burn because the other three burns that this plot received occurred during the appropriate season and interval, and thus we believed that the response on this plot was reflective of its assigned treatment combination. The wet-season, long-interval treatment had an average fire-return interval of 7.1 years (range: 7.0 to 7.1 years), and each plot was burned twice. The average burn date was 9 June. Actual burn dates for plots in this treatment ranged from 28 May to 5 July.

We recorded the initial density of trees and snags immediately before the first treatment burn was applied (Table 1). Pre-treatment sampling occurred from April 1995 to May 1996; variation in when initial treatments were applied was due to constraints associated with weather conditions during the burn window and the logistical limitations of arranging personnel and equipment necessary to conduct the prescribed burns. The final state of each tree and snag was recorded 12 to 13 years later, in January 2008.

Statistical Analyses

We evaluated the effects of the treatments on snag populations in two ways. First, we estimated 12- to 13-year transition probabilities among states by dividing the number of marked individuals undertaking each transition by the number of marked individuals in the original state at the first sampling period. Our sampling protocol allowed only a snapshot at two points in time, and the condition of trees and snags that had fallen during the study was not always noted, requiring us to make assumptions about the course of events that occurred between sampling. Trees alive at the initial sampling period and toppled at the final sampling period were assumed to have moved directly to the toppled state. We made this as-

sumption because most of the downed trees appeared to have been tipped up or broken by wind while still alive, although we cannot rule out the possibility that the trees died and then toppled. We further assumed that snags in decay state 1 at the initial sampling period and down at the final sampling period had moved directly between these states. We made this assumption because snags in decay state 2 tended to persist for much longer than the interval between sampling periods, making it unlikely that a snag in decay state 1 proceeded through decay state 2 and fell prior to the final sampling period. We estimated confidence intervals around average transition probabilities using a Monte Carlo routine. We created 10 000 vectors, each equal in length to the number of experimental plots, by sampling with replacement from the observed transition probabilities, and then calculated the average value for each vector. We used the 2.5th and 97.5th percentiles of the resulting distribution to define the approximate 95 % confidence interval around the average transition probability. We compared selected transition probabilities (the probability that a tree became a snag, the probability that a snag in decay state 1 decayed further or toppled, and the probability that snag in decay state 2 toppled) among treatments using a generalized linear model (assuming normally distributed errors, assessed using residual plots) with the main effects of season and interval and a term for the interaction between main effects. Finally, we calculated the approximate lifespan of snags in both decay states as the negative inverse of the natural log of annual survival rate. Annual survival rate was calculated by annualizing the calculated probability that a snag undertook no transition during the study.

For the second analysis, we used generalized linear models to evaluate treatment effects on snag density by comparing post-treatment densities (those measured in 2008) among treatments. Predictor variables were season of burn (dry or wet), length of interval (short or long), and the initial density of snags on each plot. We used a model-selection approach to identify which of the predictor variables were related to variation in post-treatment snag densities. We considered six different models: a null model in which snag density was constant; a model in which post-treatment density depended only on pre-treatment density; a model including pre-treatment snag density and season of burn; a model including pre-treatment snag density and length of return interval; a model including pre-treatment snag density and the additive effect of return interval and season of burn; and finally, a model including pre-treatment snag density and the additive and interactive effects of season of burn and return interval. We ranked models according to the small-sample version of Akaike's Information Criteria (AIC_c) and their Akaike weight (Burnham and Anderson 2002). We interpreted the strength of the relationship between snag density and each predictor variable by calculating model-averaged regression coefficients (Burnham and Anderson 2002); predictors with model-averaged coefficients indistinguishable from zero (based on the unconditional 95 % confidence interval) were considered unimportant in explaining variation in snag density. In calculating average regression coefficients, we assigned a value of 0 to coefficients of parameters not included in a model. These analyses were conducted separately for snags in decay state 1 and snags in decay state 2.

Because our response variable was in the form of a count (number of snags per 1 ha plot), we considered both a Poisson and negative-binomial error structure. To choose between the possible error structures, we fit the most complex model (pre-treatment snag density + interval + season + interval*season) using each error structure and then compared the relative degree of fit using a likelihood-ratio test. We used the negative-binomial model, which requires estimating an additional parameter, only if the negative log-likelihood was significantly ($\alpha = 0.05$) reduced in the negative-binomial model.

All analyses were conducted in R (R Development Core Team 2011, Vienna, Austria).

RESULTS

The average number of new snags created per plot during the course of the experiment was 25.6, but the mean value was highly influenced by a single plot (burned during the dry season on a long interval) on which 131 (127 in state 1, and 4 in state 2) new snags were created. The mean number of new snags created on all other plots was 16.0. The median number of new snags created on all plots was 15. The median number of snags that toppled or completely decayed was 12. The median net change in the number of lightly to moderately decayed snags was +8, and the median net change in the number of heavily decayed snags was −3.5.

The probability that a tree became a snag during the course of the experiment was relatively low (Table 2) and did not vary among treatments (all $P > 0.58$). Across all plots, the average probability that a tree alive at the initial sampling period ended the experiment as a snag was 0.10 (95 % CI = 0.06 − 0.15). Experiment-long mortality rates (the summed probability of decaying further or toppling) of snags in decay state 1 were high (average across all plots = 0.83, 95 % CI = 0.68 − 1.0), but did not vary across treatments (all $P > 0.27$). Snags in decay state 1 were more likely to have fallen down by the final sampling period than to have transitioned to a heavily decayed snag (Table 2), but we found no evidence that either transition probability varied as a function of fire regime (all $P > 0.17$). Mortality rates of snags in decay state 2 were much lower (20 %) (Table 2), and did not exhibit any relationship with treatment (all $P > 0.10$). The annual probability of survival for a snag in decay state 1 (i.e., the probability that a snag remained in state 1) was approximately 0.84, implying an average lifespan of 5 to 6 years. The annual probability of survival for a snag in decay state 2 was 0.98, implying an average lifespan of approximately 58 years.

The number of snags in decay state 1 present at the initial sampling period varied substantially among plots (range: 2 to 27 snags ha^{-1}) but did not vary systematically among plots assigned to the different treatments (all $P > 0.30$). In the analysis of density changes among snags in decay state 1, the best model was the global model, fit using a Poisson error structure (Table 3). Model-averaged regression coefficients indicated positive effects of pre-treatment snag density (b = 0.12, 95 % CI = 0.09 − 0.15), greater densities in plots burned at 3- vs. 6-year

Table 2. Probabilities (95 % confidence intervals beneath in parentheses) that trees and snags in a slash pine (*Pinus elliottii* var. *densa*) forest in south Florida sampled in 1995 or 1996 remained in that state or undertook a transition by the time they were resampled in 2008. Probabilities were averaged across fire treatments (3-year vs. 6-year fire-return interval; wet-season burning vs. dry-season burning). Numbers of trees in each state shown in parentheses (number of trees at the final sampling period does not include recruitment since the initial sampling period).

Initial state	State at final sampling period			
	Tree **(*n* = 2193)**	**Decay stage 1** **(*n* = 290)**	**Decay stage 2** **(*n* = 670)**	**Down**
Tree (*n* = 2716)	0.82 (0.76 − 0.87)	0.09 (0.05 − 0.14)	0.01 (0.01 − 0.02)	0.08 (0.06 − 0.12)
Decay stage 1 (*n* = 99)		0.16 (0.08 − 0.27)	0.37 (0.21 − 0.54)	0.46 (0.34 − 0.59)
Decay stage 2 (*n* = 708)			0.80 (0.75 − 0.85)	0.20 (0.15 − 0.25)

Table 3. Variation in density of lightly to moderately decayed snags in a slash pine (*Pinus elliottii* var. *densa*) forest in south Florida after experimental burning was best explained by the effect of pre-treatment snag density (baseline) and the additive and interactive effects of season of burn (season) and fire-return interval (interval).

Model	ΔAIC_c [a]	Akaike weight[b]
Baseline + season + interval + season*interval	0	0.99
Baseline + season	9.6	0.01
Baseline + season + interval	10.8	0
Baseline	52.7	0
Baseline + interval	56.0	0
Null	290.0	0

[a] ΔAIC_c is the difference between each model's AIC_c score and the score for the best model; models with lower AIC_c scores are better supported by the data.
[b] Akaike weight provides an estimate of the likelihood that each model is the best model in the candidate set.

intervals ($b = 1.01$, 95 % CI = 0.39 – 1.63; for the purposes of interpreting b, 6-year intervals are the baseline category), a negative effect of the interaction between interval and season of burn ($b = -1.79$, 95 % CI = $-2.84 – -0.74$), and no independent effect of season ($b = -0.04$, 95 % CI = $-0.79 – 0.71$). After adjusting for pre-treatment densities of snags, predicted post-treatment densities of snags in decay state 1 were greatest in plots burned during the dry season and on a short interval, lowest in plots burned during the dry season and on a long interval, and intermediate in both of the wet-season treatments (Figure 2). However, the global model fit the data poorly in a chi-square test of the residual deviance (residual deviance = 30.2, df = 6; $P = 0.01$). The cause of the poor fit was the outlier discussed earlier, at which 127 new snags in decay state 1 were present at the final sampling period in 2008 (Figure 3). Not only did this point contribute to the lack of fit, but it also exerted substantial influence over the results of the analysis, as measured by Cook's distance: Cook's distance for the outlying plot was 44.2; all of the other points had influence values of <1.

With the outlying plot removed, the global model with a negative-binomial error structure was preferred over the global model fit with a Poisson error structure (likelihood-ratio test χ^2
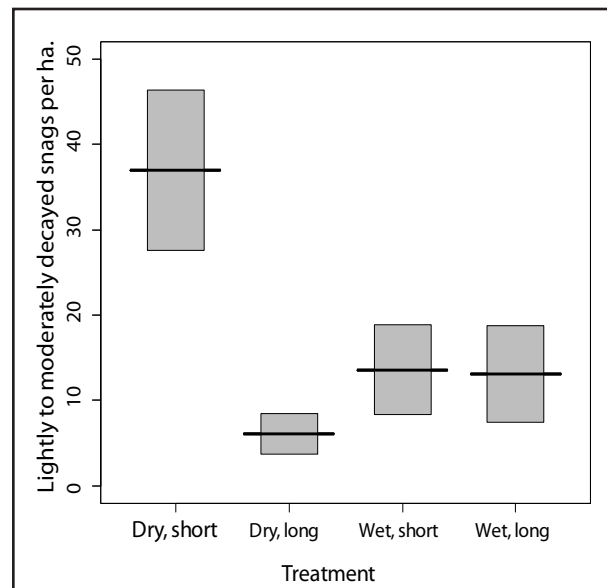

Figure 2. With an outlier included, predicted density of lightly to moderately decayed snags of south Florida slash pine (*Pinus elliottii* var. *densa*) was greatest in plots burned during the dry season at shorter intervals (3 years), lowest in plots burned in the dry season at longer intervals (6 years), and intermediate in both wet-season burns. Predicted mean values (solid black line) and 95 % confidence intervals (gray box) were generated by weighted averaging across all models in the candidate set.

= 6.3, $P = 0.01$). An examination of fitted values versus deviance residuals and observed values revealed no obvious deviations from
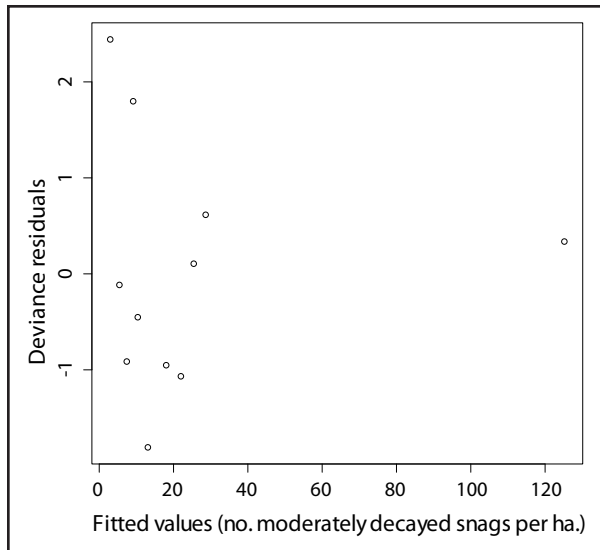
Figure 3. Fit of models predicting the relationship between the density of lightly to moderately decayed snags of south Florida slash pine (*Pinus elliottii* var. *densa*) and fire-return interval and season of burn was poor due to the influence of a single plot—burned during the dry season and at long intervals—on which 127 snags were created.

model assumptions. The global negative-binomial model also appeared to fit well (fitted versus observed values: $r^2 = 0.64$, $P = 0.006$). Assuming a negative-binomial error structure, substantial changes were produced in the relative support for candidate models (Poisson models run on the reduced data set produced results similar to those reported for the models run on the complete data set), and models containing treatment effects received little support (Table 4). Indeed, the model with the most support was the null model of constant density. None of the model-averaged regression coefficients were distinguishable from zero (pre-treatment snag density: $b = 0.0$, 95% CI = $-0.09 - 0.09$; interval, $b = 0.01$, 95% CI = $-0.92 - 0.95$; season, $b = 0.01$, 95% CI = $-1.0 - 1.02$; season*interval, $b = 0.0$, 95% CI = $-1.53 - 1.53$). Model-averaged predictions of densities of snags in decay state 1 were similar among all treatments when the outlying plot was removed (Figure 4). Under the null model, the predicted post-treatment density of lightly to moderately decayed snags was 15.9 (95% CI = $10.6 - 23.8$), more than double the initial observed density of snags in decay state 1 (6.3 snags ha^{-1}, 95% CI = $3.9 - 9.6$).

Density of heavily decayed snags, those in decay state 2, varied widely among plots at the initial sampling period (range: 17 to 103 snags ha^{-1}), but did not vary systematically among plots assigned to different treatments (all $P > 0.41$). For snags in decay state 2, the global model with Poisson errors fit the data as well as the more complex negative-binomial model ($\chi^2 = 0.0$, $P = 1.0$). In addition, the global model with Poisson errors provided a reason-

Table 4. With an outlying point removed, variation in density of lightly to moderately decayed snags in a slash pine *(Pinus elliottii* var. *densa)* forest in south Florida after experimental burning was unrelated to season of burn (season) or fire-return interval (interval), and was best explained by a null model or a model including only the density of snags prior to treatment.

Model	Δ AIC$_c$ [a]	Akaike weight [b]
Null	0	0.86
Baseline	4.3	0.10
Baseline + interval	7.6	0.02
Baseline + season	8.1	0.01
Baseline + interval + season	15.7	0
Baseline + interval + season + interval*season	24.3	0

[a] ΔAIC$_c$ is the difference between each model's AIC$_c$ score and the score for the best model; models with lower AIC$_c$ scores are better supported by the data.
[b] Akaike weight provides an estimate of the likelihood that each model is the best model in the candidate set.
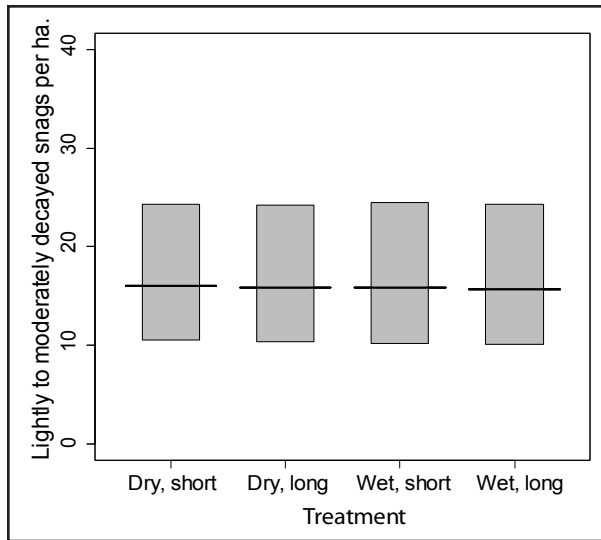
Figure 4. With an outlier excluded, predicted density of lightly to moderately decayed snags of south Florida slash pine (*Pinus elliottii* var. *densa*) was unrelated to fire-return interval or season of burn. Predicted mean values (solid black line) and 95 % confidence intervals (gray box) were generated by weighted averaging across all models in the candidate set.

able fit to the complete data set, including the plot removed from the analysis of snags in decay state 1 (residual deviance = 8.8, df = 6, *P* = 0.19). The model containing an effect of pre-treatment snag density received the most support from the data (Table 5), but other plau-

sible models included those with effects of fire-return interval and season of burn. Model-averaged coefficients for all variables except pre-treatment snag density were indistinguishable from zero (interval, *b* = −0.07, 95 % CI = −0.26 – 0.12; season, *b* = −0.01, 95 % CI = −0.21 – 0.19; interval*season, *b* = 0.0, 95 % CI = −0.46 – 0.46); pre-treatment snag density had a small but consistently positive effect on post-treatment snag density (*b* = 0.019, 95 % CI = 0.015 – 0.023). This result is expected: plots with relatively more snags at the beginning of the experiment should, all things being equal, also contain relatively more snags at the end of the experiment. Model-averaged predictions (Figure 5) also suggested a weak effect of interval—plots burned on a longer rotation time had more snags in decay state 2 at the end of the experiment, but 95 % confidence intervals were broadly overlapping for all treatments—and no effect of season.

DISCUSSION

Resource managers and scientists alike have adopted season of burn and fire-return interval as useful surrogates for the suite of factors that actually shape the ecological effects of fire that we wish to understand, predict, and control. In our experiment, we found that nei-

Table 5. Variation in density of heavily decayed snags in a slash pine (*Pinus elliottii* var. *densa*) forest in south Florida after experimental burning was best explained by the effect of pre-treatment snag density (baseline), fire-return interval (interval), and, to a lesser extent, season of burn (season). Evidence in support of additive or interactive effects among predictors was weak.

Model	Δ AIC$_c$[a]	Akaike weight[b]
Baseline	0	0.43
Baseline + interval	0.1	0.42
Baseline + season	2.7	0.11
Baseline + interval + season	5.0	0.04
Baseline + interval + season + interval*season	12.2	0
Null	232.5	0

[a] ΔAIC$_c$ is the difference between each model's AIC$_c$ score and the score for the best model; models with lower AIC$_c$ scores are better supported by the data.
[b] Akaike weight provides an estimate of the likelihood that each model is the best model in the candidate set.
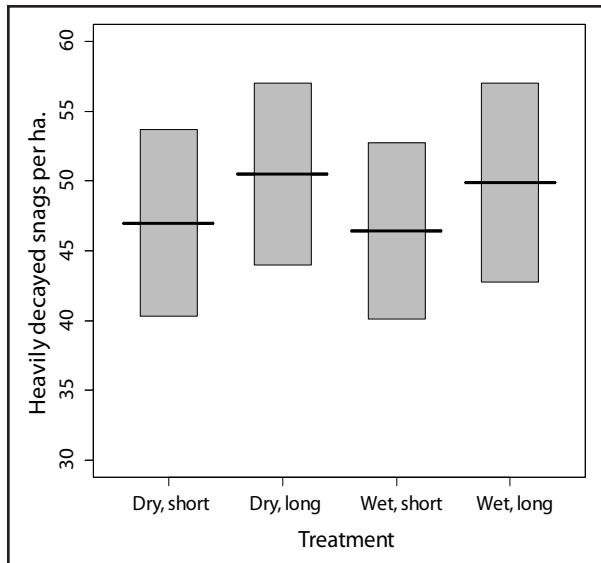
Figure 5. Predicted density of heavily decayed snags of south Florida slash pine (*Pinus elliottii* var. *densa*) was greater in plots burned at longer intervals (6 years) than in plots burned at shorter intervals (3 years), irrespective of the season of burn. Predicted mean values (solid black line) and 95 % confidence intervals (gray box) were generated by weighted averaging across all models in the candidate set.

ther the length of time between prescribed burns nor the season in which fires were ignited had consistent effects on rates of survival or recruitment, and snag densities at the conclusion of the experiment were similar, irrespective of differences in these fire regime factors. However, the generality of our results is limited because seasonality and return interval are not themselves apt to directly influence snags; rather, they may predict the intensity of a fire, which is often the causal mechanism underlying the ecological effects of fire (e.g., Glitzenstein *et al.* 1995, Menges and Deyrup 2001, Keeley 2009). For example, mortality in south Florida slash pine is a function largely of fire intensity (Menges and Deyrup 2001); therefore, intense fires should lead to higher rates of snag creation. In south Florida, fire intensity is often greater during the dry season (Slocum *et al.* 2003) and following longer fire-free periods (Glitzenstein *et al.* 1995, Menges and

Deyrup 2001, Snyder *et al.* 2005). These generalizations are imperfect, however, because fire intensity can be influenced by myriad other factors, such as means of ignition or ambient weather conditions (Byram 1959, Wade and Johansen 1986), and so the lack of significant treatment effects in our experiment may simply reflect a disconnect between our treatment levels and fire intensity. We did not measure fire intensity and so cannot be certain that our treatments were different in a manner that was relevant to snag dynamics. Using indirect measures to predict the ecological effects of fire is unlikely to lead to strong inference, and future studies would benefit by measuring, and manipulating where possible, putatively causative agents.

The lack of significant treatment effects may also reflect the importance of unmeasured variables, including water-table depth. In most years, the water table at our study area is only slightly below ground level during the latter parts of the wet season and the early parts of the dry season. A wet-season burn during a normal year or a wet year might produce very little root damage—a potentially important mechanism underlying tree mortality following fire (Swezy and Agee 1991)—on account of the wet soils, whereas a wet-season burn in a very dry year might produce substantial root damage and, consequently, elevated rates of tree mortality and increased rates of snag creation. Any effect of water-table depth would tend to increase variance within a treatment, potentially obscuring the effect of our treatments. The study area was subject to at least three periods of drought, including the notably dry period of 1998 to 2002. Burns conducted during this period ($n = 9$) may have produced unusually high rates of tree mortality. We were unable to isolate potential effects of annual variation in water-table depth because our sampling was limited to two time periods, but we note that future efforts to address the relationship between fire and snags in south Florida would benefit from explicitly considering

the potentially confounding effects of water-table depth.

Our ability to draw inference about the role of fire in shaping snag population dynamics is also limited by the narrow range of treatment levels that we considered. The timing and return intervals of fires applied in our experiment mimicked the range considered normal in south Florida slash pine, and so do not allow us to draw conclusions about the role of rare, extreme events. For example, an unusually long fire-free period coupled with drought could produce heavy loads of very dry fuels that would result in especially intense fires and perhaps a large pulse of new snags. In some systems, large and infrequent disturbances play a key role in structuring biotic assemblages (e.g., Dale *et al.* 1998), and it may be that fire is only episodically important in the dynamics of snag populations in south Florida slash pine forests. Although we did apply a randomized, experimental approach to our question, confidence in our results is weakened by the small sample sizes at each of our treatment levels. For example, results of our analysis of snags in decay state 1 were not at all robust to the choice of a model and we suspect that this is due to the small sample of plots and the inherent variability among them. Snag population dynamics probably include substantial stochastic elements, and this noisiness, coupled with the limits of our study design, restricts our ability both to generalize our findings more broadly and to state with confidence that we have identified robust, causal relationships.

At least two important questions remain regarding the role of prescribed fire in managing snags in south Florida slash pine forests, and should be the target of future research. First, the influence of fire intensity on snag recruitment and mortality rates should be examined directly to rule out the possibility that our treatment levels masked a real effect of variation in fire intensity. Potentially confounding variables such as water-table depth should be addressed as well. Ideally, these studies should incorporate a wider range of variation in fire conditions and larger sample sizes than our study did. Second, the absolute importance of fire in creating snags is unclear. We did not include unburned controls and our data collection did not allow us to isolate the causes of tree mortality, so we have no way of knowing whether fire is more or less important than other agents, such as insects or severe storms. Tropical cyclones can create large numbers of snags (e.g., Hurricane Andrew; Platt *et al.* 2000) but occur relatively infrequently. Insects can be a significant cause of mortality, but appear to exert their strongest effect in concert with other stressors, such as drought, fire, or hurricanes (USFWS 1999, Menges and Deyrup 2001, Platt *et al.* 2002). Continued long-term monitoring of marked populations of trees and snags would allow for a more complete understanding of the factors governing snag population dynamics.

ACKNOWLEDGMENTS

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