

EFFECTS OF HURRICANE KATRINA AND SALVAGE LOGGING ON BACHMAN'S SPARROW

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Abstract. In the southeastern U. S., longleaf pine savannas, important habitat for grassland birds, are subject to hurricanes and subsequent management. The intensity of tropical storms is predicted to increase with climate change, heightening the importance of understanding the effects of storm disturbance and salvage logging on species of concern such as Bachman's Sparrow (*Peucaea aestivalis*), a pine-savanna specialist. To determine how Bachman's Sparrow occupancy varies with the age and salvage history of pine stands, and to identify the vegetation and post-hurricane habitat features influencing stand occupancy, we surveyed Bachman's Sparrows in Mississippi savannas affected by Hurricane Katrina. Our point counts and vegetation surveys covered 89 stands over two breeding seasons, beginning one year after salvaging. Bachman's Sparrow occupancy was best predicted by increasing graminoid cover and density, with evidence of a quadratic effect reversing the relationship at high levels, decreasing tree density, also with a quadratic effect, decreasing shrub cover and density, and increasing abundance of downed tree crowns and upturned root balls. Occupancy was higher in mature stands, regardless of salvage, and in stands of seedlings and saplings, but lower in middle-aged stands. Our results suggest that disturbance from Katrina may have benefited Bachman's Sparrows by thinning trees, creating perches in the form of downed tree crowns, from which males sing, and creating refugia from predators in upturned root balls. Three years after the disturbance, salvage logging appeared to have no effect on occupancy, but such logging could be detrimental if it alters ground-layer vegetation severely.

Key words: *Peucaea aestivalis*, *Bachman's Sparrow*, *Hurricane Katrina*, *longleaf pine*, *salvage logging*, *tropical storms*.

Efectos del Huracán Katrina y de la Subsiguiente Extracción de Madera sobre *Aimophila aestivalis*

Resumen. En el sureste de los Estados Unidos, las sabanas con pinos de hoja larga, un ambiente importante para las aves de pastizal, están sujetas a huracanes y al manejo subsiguiente. Se predice que la intensidad de las tormentas tropicales aumentará con el cambio climático, lo que incrementa la importancia de entender los efectos de los disturbios causados por las tormentas y de la extracción de madera de los árboles caídos sobre las especies de interés para la conservación. Una de estas especies es *Aimophila aestivalis*, un ave especialista de sabanas con pinos. Para determinar cómo varía la ocupación de sitios por parte de *A. aestivalis* con respecto a la edad y a la historia de extracción de árboles caídos de rodales de pinos, y para identificar las características de la vegetación y del ambiente luego de los huracanes que influyen en la ocupación de los rodales, hicimos censos de esta especie en sabanas de Mississippi que fueron afectadas por el huracán Katrina. Nuestros puntos de conteo y censos de vegetación cubrieron 89 rodales a lo largo de dos épocas de cría, comenzando un año después de la extracción de madera. La ocupación por parte de *A. aestivalis* se predijo mejor por un incremento en la cobertura y la densidad de gramínoideas (con evidencia de un efecto cuadrático que invirtió la relación a niveles altos), por una disminución en la densidad de árboles (también con efecto cuadrático), por una disminución en la cobertura y densidad de arbustos, y por un incremento en la abundancia de copas de árboles caídas y de raíces levantadas y volteadas. La ocupación fue mayor en rodales maduros (independientemente de la extracción de madera subsiguiente) y en rodales de plántulas y renovales, y menor en rodales de edad intermedia. Nuestros resultados sugieren que el disturbio causado por Katrina podría haber beneficiado a *A. aestivalis* al reducir la densidad de árboles, al crear perchas en forma de copas de árboles caídas que los machos usan para cantar y al crear refugios ante depredadores en cúmulos de raíces levantadas. Tres años después del disturbio, la extracción de madera subsiguiente al huracán pareció no tener efecto sobre la ocupación, pero dicha extracción podría tener efectos negativos si alterara de forma severa la vegetación del nivel del suelo.

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INTRODUCTION

Bachman's Sparrow (*Peucaea aestivalis*) is a species of concern that occurs only in pine savannas and early-successional habitats in the southeastern U. S. It is considered a watch-list species by Partners in Flight and is classified as "near threatened" on the 2009 Red List of the International Union for Conservation of Nature (BirdLife International 2009). This ground-dwelling sparrow prefers the dense herbaceous layer of well-managed pine savannas and recent clearcuts (Plentovich et al. 1998, Tucker et al. 2004). It uses early-successional and mature pine stands and tends to avoid denser middle-aged stands (Dunning and Watts 1990, Tucker et al. 1998, Stober and Krementz 2006). Bachman's Sparrow avoids areas of high density of trees (Hardin et al. 1982, Haggerty 1998, 2000) possibly because canopy closure reduces the cover, density, and species richness of the herbaceous layer (Harrington and Edwards 1999, McGuire et al. 2001, Platt et al. 2006).

Much of Bachman's Sparrow's remaining habitat is subject to multiple disturbances. Timber harvesting and prescribed fire are common management practices in many longleaf pine (*Pinus palustris*) savannas. Prescribed fire, which has taken the place of naturally occurring fires, is a necessary disturbance that helps maintain the pine-savanna ecosystem through its effects on vegetation structure, thus improving Bachman's Sparrow habitat (Tucker et al. 2004, Conner et al. 2005, Cox and Jones 2009). Disturbance by tropical storms also affects coastal pine savannas but on a temporal scale different from fire. Decades generally elapse between hurricanes, compared to a historical average of about 4 years between fires (Platt and Rathbun 1993, Gilliam et al. 2006). Recent studies have shown that hurricanes play an important role in maintaining coastal pine-savanna ecosystems, particularly by mediating patch dynamics of trees (Platt and Rathbun 1993, Palik and Pederson 1996, Gilliam et al. 2006). Hurricanes can alter the spatial and temporal distribution of trees by creating gaps, which become prime recruitment zones for longleaf pines (Platt et al. 1988, Platt and Rathbun 1993). Subsequent changes in sunlight availability affect herbaceous plants directly, in turn affecting grassland birds. Additionally, hurricanes interact with fire by increasing fuel load from downed trees and pine needles (Platt et al. 2002).

Effects of fire on Bachman's Sparrow habitat are well documented, but consequences of hurricane disturbance and subsequent salvage logging are not well understood. In the only study considering hurricane damage directly, Dunning and Watts (1991) found that Bachman's Sparrow occupancy of clearcut savannas in South Carolina increased after Hurricane Hugo. At their site, damage to mature stands from salvage logging made previously used stands unsuitable.

We suggest that additional research on effects of hurricane and salvage logging on Bachman's Sparrow could be important for two reasons. First, almost the entire distribution of Bachman's Sparrow is within the Gulf and Atlantic

coastal plains, areas vulnerable to hurricanes. Second, the intensity of tropical storms is predicted to increase with global climate change and increased sea-surface temperatures (Emanuel 2005, Webster et al. 2005, Bender et al. 2010), probably increasing the role of storms in pine-savanna-ecosystem processes (Gilliam and Platt 2006, Gilliam et al. 2006). Understanding the effects of natural disturbances and post-disturbance management on species of concern is crucial if we are to manage ecological systems successfully in a changing climate (Lindenmayer and Noss 2006).

We surveyed Bachman's Sparrow occupancy in salvage-logged and unsalvaged pine stands affected by Hurricane Katrina in De Soto National Forest in coastal Mississippi. Our objectives were to (1) determine how Bachman's Sparrow occupancy varies with stand ages and salvage history several years after the hurricane and (2) identify the vegetation and post-hurricane habitat features that influence stand occupancy.

METHODS

STUDY AREA

De Soto National Forest (DSNF), located 12–90 km from the coast of the Gulf of Mexico, includes >100 000 ha of longleaf and slash pine (*Pinus elliottii*) stands interspersed with pitcher plant bogs, baygalls, and hardwood forests (Windham 2005). The pine stands in DSNF vary in age and fire history; they are both harvested and subjected to prescribed burning regularly, resulting in a mosaic of stands of different ages and different times since last fire. Stands, delineated by the U. S. Forest Service (USFS), are units of land consisting of similar-aged trees of the same species and subject to the same fire regime. Stands used in our study ranged from approximately 2 ha (the majority of sites) to just over 10 ha.

On 29 August 2005, Hurricane Katrina passed over southern Mississippi with winds exceeding 230 km hr⁻¹ (Meeker et al. 2005). It affected almost all mature pine stands in DSNF, resulting in downed, snapped, bent, and root-sprung trees (Meeker et al. 2005). The following winter, the forest was open to wide-scale salvage logging to reduce the risk of tree-pest outbreak, to clear clogged fire breaks, and to reduce risks to human safety. The majority of salvaging consisted of removal of downed, twisted, bent, or root-sprung pine trees. Damaged trees were cut between the base of the bole and the crown. Boles were then removed from stands, mainly by log skidders, leaving behind root balls and tree crowns. The number of trees removed depended on the number of trees damaged. After the salvage, some stands showed remnants of logging trails, but there were generally few signs of major soil disturbances. Salvaging was carried out by multiple private companies over a 6-month period beginning in the fall following Hurricane Katrina. Records of exact salvaging methods and the amount of timber removed from specific stands are not available (D. L. Tyron, USFS biologist, pers. comm.). No salvaging was allowed in wet or mesic savannas or bogs.

We focused on five conditions of forest stands distinguished by age class and post-hurricane salvage status, with age and salvage information provided by USFS records. We defined three age classes, seedling/sapling, pole, and mature, further distinguishing pole and mature stands as either salvage-logged or unsalvaged (no seedling/sapling stands were salvage-logged). Seedling/sapling stands were stands of longleaf pine <20 years old. Pole stands consisted of tall, thin, densely growing pines that, in our study sites, ranged from 22 to 44 years old. These stands were characterized by high mean canopy closure (~50%) and high basal area of trees (>300 m² ha⁻¹) in comparison to other stand types (~20–40% canopy closure; basal area 50–170 m² ha⁻¹). Because of the limited availability of light in pole stands, the herbaceous layer was often sparse, particularly >2 growing seasons since fire. Mature stands in our study were >70 years old. These stands were the most affected by the hurricane because the open canopies were more vulnerable to wind damage (Windham 2005). Some mature stands had a continuous herbaceous layer, but many had a patchy layer because of encroaching shrubs.

We established a total of 89 sites (Table 1). Although our main interest was in examining the effects of hurricane disturbance and salvage logging, past research has indicated a strong effect of fire on habitat quality for Bachman's Sparrows, so we stratified our sampling to include the range of fire histories available at DSNF. Fire histories varied by site, ranging from 1 to >5 years since fire. We categorized sites burned 3–5 years previously as >2 years because encroachment of the woody understory and decline of herbaceous plants were generally similar 3–5 years after fire and differed from vegetation in sites burned 1 or 2 years previously (M. E. Brooks, pers. obs.). The number of sites per stand-condition and fire-history combination was roughly proportional to the availability of these types across the forest during the years of our sampling, as determined through our personal observations and USFS records. Stands with some combinations of stand condition and fire history were not available at DSNF.

TABLE 1. Number of study sites subject to each fire history and stand condition.

	Growing seasons since fire			2007	2009	Total
	1	2	>2			
Stand condition						
Seedling/sapling	0	2	20	12	10	22
Salvaged pole	0	2	3	4	1	5
Unsalvaged pole	2	4	9	11	4	15
Salvaged mature	2	1	14	12	5	17
Unsalvaged mature	3	9	18	12	18	30
2007	0	5	46	51		
2009	7	13	18		38	
Total	7	18	64			89

BACHMAN'S SPARROW SAMPLING

We surveyed for Bachman's Sparrow occupancy with fixed-radius (100 m) 10-min point counts from late April through late June 2007 and 2009. We could not sample in 2008 because of logistical constraints. Point-count locations varied by stand age, salvage history, and time since fire. We repeated point counts two or three times in 2007 and three times in 2009. We counted from 15 min after sunrise until 09:30 or earlier if temperatures exceeded 26 °C. Counts were rotated among four observers, two in 2007 and two others in 2009. We did not count in severe wind or rain.

We surveyed 51 stands in 2007 and 38 different stands in 2009 (Table 1). We sampled different sites in 2009 for several reasons. First, no sites sampled in 2007 had been burned in <2 years because the prescribed-fire program had been disrupted by Hurricane Katrina and subsequent salvaging. These recently burned stands typically form a significant proportion of DSNF, so we needed to sample them in 2009. Second, by 2009 some 2007 sites were approaching 7 years since fire, making them unsuitable for Bachman's Sparrows because they were dominated by shrubs and lacked an herbaceous component (Gobris 1992, Haggerty 2000). Third, we selected our stands to include the major combinations of fire, salvage, and stand age that were available at DSNF 2–4 years after the hurricane. These conditions would be expected after storms in other managed pine forests.

VEGETATION SAMPLING

We sampled vegetation density and cover at all count points in 2007 and 2009. In each stand with a count point, we sampled vegetation in three circles of radius 1.3 m, one centered on the point and two in random directions 50 m from the point. In each vegetation circle, we visually estimated cover of graminoids, forbs, vines, and coarse woody debris to the nearest 5%. Cover of shrubs <0.5 m and >0.5 m in height was estimated separately. We measured density of graminoids, forbs, and woody plants by the pole method (Wiens 1974). For this method, we recorded the number of contacts by each life form in decimeter increments on a pole 2 m tall and 3 cm in diameter, repeating this procedure nine times in each vegetation circle. From these measurements we estimated horizontal density (total contacts <10 cm) and vertical density (total contacts on the entire pole; Wiens and Rotenberry 1981) for each life form. At each location where vegetation density was measured, we measured canopy closure with a spherical densiometer (Lemmon 1956). We used a 10-factor prism (Avery 1967) and Biltmore stick to measure the basal area of trees (Jackson 1911) in each vegetation circle. In 2009 only, we recorded the numbers of crowns of downed pine trees and of root balls of upturned pine trees in each vegetation circle. We added downed crowns to our protocol after noticing that Bachman's Sparrows made extensive use of them for singing perches. We added root balls on the basis of winter observation

of flushed Bachman's Sparrows flying toward upturned root balls, where they presumably took cover in tunnels beneath the root balls (Dean and Vickery 2003, Brooks 2010). All vegetation measurements were averaged across each stand with a count point.

STATISTICAL ANALYSES

We grouped the bird and vegetation data into two sets, one with all data from both years combined (the "two-year" set), omitting root-ball and tree-crown counts ($n = 89$ stands), the other (the "second-year" set) with just the second-year data, including root-ball and tree-crown counts ($n = 38$ stands). The sample unit for all analyses was the stand, consisting of one count point and three vegetation-sampling plots.

We used principal components analyses (PCA) to reduce vegetation variables into fewer, orthogonal components. We used PCA because the number of raw vegetation variables measured was too many for the size of our sample of stands, because of multicollinearity, and because all variables might be important predictors of occupancy and deserved inclusion in candidate models. For the PCA of the correlation matrix, we used PROC FACTOR in SAS 9.2 with a varimax rotation. We retained all principal components (PCs) with eigenvalues >1.0 (McGarigal et al. 2000). We analyzed the two-year and second-year datasets separately because of their different sample sizes. For the second-year dataset, we did not include tree crowns and root balls in the PCA.

We modeled occupancy of Bachman's Sparrows with PRESENCE 2.1 (Hines 2006), which allows for simultaneous modeling of detection (p) and occupancy (ψ) parameters and specification of covariates for each. We modeled the two datasets separately because they contained different variables of interest. Modeling of the two-year dataset was used to compare occupancy estimates among stand conditions and to determine what vegetation was important; the second-year dataset was used to model occupancy in relation to vegetation, root balls, and downed tree crowns resulting from the hurricane. Observer, temperature, and month were used as potential detection covariates for both datasets. We included four vegetation PCs as occupancy covariates in all models and also included tree-crown and root-ball abundances as occupancy covariates in models for the second-year dataset. We specified an intercept [$p(\cdot)$ and $\psi(\cdot)$] in all detection and occupancy models. We tested for an effect of year in the modeling of the two-year data because of possible differences in occupancy or vegetation 1 and 3 years after the hurricane.

We did not include time since fire as a categorical variable in the models because we considered this effect to be more appropriately represented by the vegetation conditions we measured directly. The effects of fire on Bachman's Sparrows are well documented; our intent was to examine how the combination of hurricane disturbance and salvage logging affected habitat quality for birds across a range of stand ages and fire

histories. Fire benefits birds by maintaining the density of ground-layer vegetation optimal for foraging and breeding, thus increasing the birds' local population density (Gobris 1992, Haggerty 1998, Tucker et al. 1998, 2004, 2006, Conner et al. 2005). Measuring vegetation directly is a better way to assess these effects as they relate to birds (Tucker et al. 2004); a simple variable such as time since fire does not capture the variation in stands' response to fire. Hurricane disturbance likely affects the results of fire, as by increasing fuel loads (e.g., Platt et al. 2002). Moreover, inclusion of time since fire initially overparameterized the models, but results from models without time since fire were biologically interpretable (see Results).

For each dataset, our first step in modeling occupancy was to fit the global model containing all covariates for occupancy and detection and to estimate overdispersion (\hat{c}) via the bootstrap method (MacKenzie et al. 2006). All global models had $\hat{c} < 1$, so we set $\hat{c} = 1$ for each analysis (Burnham and Anderson 2002).

We used a complementary log-log link function for the second-year dataset because the small sample size and data structure initially caused inflated parameter estimates when we attempted to use a logit link (Nemes et al. 2009). Complementary log-log models are appropriate when binary outcomes are skewed. Unlike logit models, the probability curve is asymmetrical around $P = 0.5$ (Nandram 1989). The link function and basic model is

$$\log[-\log(1 - P_i)] = \beta_0 + \beta_1(x_i),$$

thus the back-transformed parameter estimates ($1 - \exp^{-\exp(\beta_i)}$) for independent variables are not odds ratios but probabilities, making the original transformed parameter estimates easier to interpret.

We used a two-step process to model detection and occupancy with an information-theoretic approach for model selection. First, we carried out model selection on detection covariates only while maintaining a null model for occupancy. Next, we carried out model selection on occupancy covariates while maintaining the best detection model (Bailey et al. 2004, MacKenzie 2006). We selected candidate models on the basis of combinations of vegetation PCs and hurricane-damage variables that were biologically meaningful in the context of both our observations in the field and other studies of Bachman's Sparrow. For example, many studies stress the importance of herbaceous vegetation, but Wan A. Kadir (1987), Gobris (1992), and Dunning (1993) speculated that the birds may prefer cespitose ground cover over uniform ground cover. This, along with the known effects of fire suppression on Bachman's Sparrow and vegetation, led us to include a quadratic effect of graminoid structure (see Results). From our observations of the sparrows' use of root balls and downed tree crowns, we hypothesized that these variables could be important in predicting occupancy and included them in most

second-year models. We used AIC_c as our information criterion, estimating parameters and variables' relative importance by averaging models with $\Delta AIC_c < 2.0$ (Burnham and Anderson 2002). All reported means and parameter estimates are \pm standard error.

RESULTS

We detected Bachman's Sparrows at 27 of 89 sites. During 2007, birds were detected at eight of 51 sites; during 2009, birds were detected at 19 of 39 sites. Occupancy estimates from the 2-year dataset, corrected for detection and occupancy covariates, were highest for salvaged mature stands, unsalvaged mature stands, and seedling/sapling stands (Fig. 1). Estimates for salvaged and unsalvaged pole stands were lower. Occupancy estimates corrected for detection and occupancy covariates were higher than naïve estimates. Naïve estimates of proportions of stands occupied were 0.23 for seedling/sapling, 0.20 for salvaged pole, zero for unsalvaged pole, 0.47 for salvaged mature, and 0.43 for unsalvaged pole. The mean model-produced estimate of occupancy for seedling/sapling stands (0.56 ± 0.07) was twice as large as the naïve proportional estimate (0.23; see below); for all other stand types differences in these estimates were < 0.11 . At only the sites occupied by Bachman's Sparrow, naïve estimates of densities averaged across the three samples at each site ranged from 0.33 to 2.33 ha^{-1} . Occupancy estimates averaged by year since fire, corrected for detection and occupancy covariates, ranged from 0.40 to 0.55, with the highest estimate for 2 years since fire.

VEGETATION

For each of the two datasets, we retained four principal components with eigenvalues > 1 describing vegetation density and cover. The retained PCs from the 2-year dataset combined to include 73% of the original variance. These four PCs represented (1) increasing graminoid cover, vertical and horizontal density, decreasing basal area of trees, and canopy closure

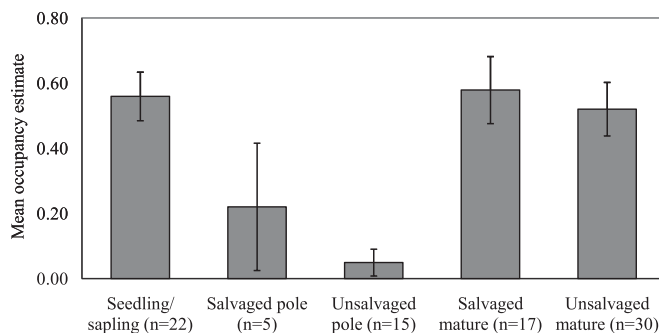


FIGURE 1. Mean (\pm SE) estimates of Bachman's Sparrow occupancy by stand condition. Estimates are from the 2-year dataset and were calculated from the model-averaged occupancy estimates of the two best models with $\Delta AIC_c < 2$.

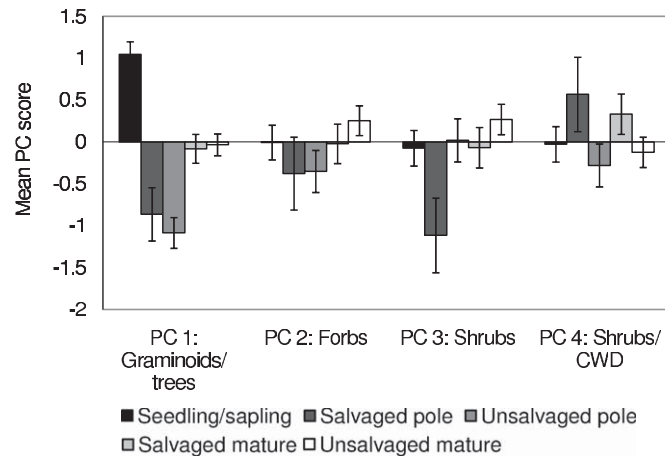


FIGURE 2. Mean (\pm SE) principal component scores by stand condition for the 2-year dataset ($n = 89$). The first PC is positively correlated with graminoid structure and negatively correlated with tree density. The other PCs are positively correlated with the variables with which they are most correlated (see Table 2). CWD is coarse woody debris.

("graminoids/trees"), (2) increasing forb cover, vertical density, and horizontal density ("forbs"), (3) increasing shrub cover below and above 0.5 m and woody vertical density ("shrubs"), (4) and increasing coarse woody debris and woody horizontal density ("CWD/shrubs"; Appendix 1). The retained PCs from the second-year data explained 77% of the original variance. These PCs represented (1) the same graminoid and tree-density variables and loading directions as the 2-year PCA ("graminoids/trees"), (2) increasing forb cover, vertical density and horizontal density, decreasing shrub cover below 0.5 m, and woody vertical density ("forbs/shrubs"), (3) increasing shrub cover above 0.5 m and woody horizontal density ("shrubs"), (4) and increasing coarse woody debris ("CWD"; Appendix 2). Mean PC scores varied widely by stand condition (Fig. 2).

OCCUPANCY MODELING

Occupancy modeling with the 2-year dataset revealed that specific structural characteristics of vegetation best predicted stand occupancy. The best detection model contained the observer covariate; thus certain observers detected Bachman's Sparrows at higher rates, so we included the observer covariate in all candidate models except the main null model. Out of 12 candidate models, two had a $\Delta AIC_c < 2$ (Table 2). The model averaged from these two included the PC representing increasing graminoid structure and decreasing tree density, the quadratic effect of this PC, and the PC representing shrub structure. Thus, an increase in graminoid structure and a decrease in tree density correspond with an increase in occupancy estimates to a point, but there is a threshold beyond which occupancy estimates begin to decrease (Table 3). The averaged model explained 30% of the variation.

TABLE 2. Candidate models of Bachman's Sparrow occupancy based on the 2-year dataset. Vegetation variables are principal components (see Appendix 1). All models contain intercepts for detection and occupancy and the variable observer as a detection covariate, except the model Null (no observer covariate), which does not contain any covariates for detection or occupancy. The differences in AIC_c from the best model (ΔAIC_c), number of parameters (K), and Akaike weights (w_i) are shown for each model. CWD is coarse woody debris.

Model	ΔAIC_c^a	w_i	K
Graminoids/trees + (graminoids/trees) ²	0.00	0.43	5
Graminoids/trees + (graminoids/trees) ² + shrubs	1.60	0.19	6
Graminoids/trees + (graminoids/trees) ² + shrubs/CWD	2.12	0.15	6
Graminoids/trees + (graminoids/trees) ² + year	2.80	0.11	7
Graminoids/trees + (graminoids/trees) ² + shrubs/CWD + shrubs	3.80	0.06	7
Graminoids/trees + (graminoids/trees) ² + shrubs + year	5.09	0.03	8
Graminoids/trees	6.24	0.02	4
Null (with observer covariate)	19.14	0.00	3
Shrubs	19.33	0.00	4
Shrubs/CWD	21.23	0.00	4
Year	22.49	0.00	5
Forbs	28.79	0.00	2
Null (no detection covariates)	32.60	0.00	4

^a Values of AIC_c for the best models in order of increasing ΔAIC_c were 187.85 and 189.45.

Occupancy modeling of the second-year dataset yielded results similar to those of the 2-year dataset, except the best models ($\Delta AIC_c < 2$) did not include the shrub PC but did include tree crowns and root balls. In the second year, no covariates for detection were better than the null model, so all candidate occupancy models contained only an intercept for the detection model. Out of 14 candidate models, four had $\Delta AIC_c < 2$ (Table 4). The averaged model from the best four included the PC for increasing graminoid structure and decreasing tree density, the quadratic effect of this PC—again

TABLE 3. Model-averaged parameter estimates for the best ($\Delta AIC_c < 2$) models of Bachman's Sparrow occupancy based on the 2-year dataset (Table 2). Relative importance ranges from 0 to 1 and is the contribution of each variable to an averaged model as determined from the number of models in which the variable occurs and the model weights.

Effect	Odds ratio	OR 95% CI	Relative importance
p (observer)	1.880	0.982 3.598	1
ψ (graminoids/tree density)	13.061	8.306 17.816	1
ψ (graminoids/tree density) ²	0.202	-3.346 3.749	1
ψ (shrubs)	0.877	-1.512 3.266	0.31

TABLE 4. Candidate models of Bachman's Sparrow occupancy based on the second-year dataset. The vegetation variables are principal components (see Appendix 2) except for roots and crowns, which are abundances. All models contain intercepts for detection and occupancy; there are no detection covariates in any model except the global model, which contains all detection and occupancy covariates. The differences in AIC_c (ΔAIC_c), number of parameters (K), and Akaike weights (w_i) are shown for each model.

Model	ΔAIC_c^a	w_i	K
Graminoids/trees + (graminoids/trees) ² + crowns	0.00	0.22	5
Graminoids/trees + (graminoids/trees) ² + roots	0.27	0.19	5
Graminoids/trees + (graminoids/trees) ² + roots + crowns	0.66	0.16	3
Graminoids/trees + (graminoids/trees) ² + crowns + shrubs	1.03	0.13	6
Graminoids/trees + (graminoids/trees) ² + roots + crowns	2.05	0.08	4
Graminoids/trees + (graminoids/trees) ² + crowns + shrubs	2.12	0.08	6
Roots+crowns	2.15	0.08	4
Graminoids/trees + (graminoids/trees) ² + shrubs	2.91	0.05	5
Graminoids/trees	5.80	0.01	3
Crowns	9.10	0.00	3
Null	12.62	0.00	2
Shrubs	14.57	0.00	3
Forbs/shrubs	14.85	0.00	3

^a Values of AIC_c for the best models in order of increasing ΔAIC_c were 113.84, 114.11, 114.50, and 114.87.

showing occupancy estimates increasing in response to the lower end of these PC values and decreasing in response to the higher end of these values—tree-crown abundance and root-ball abundance (Table 5). The composite model explained 27% of the variance.

DISCUSSION

Salvage logging did not appear to affect Bachman's Sparrow occupancy during the 3 years after Katrina. Estimates of occupancy of mature stands were similar regardless of salvage history. These results contrast with those of Dunning and Watts (1991), who observed that salvage logging made mature

TABLE 5. Model-averaged parameter estimates for the best ($\Delta AIC_c < 2$) models of Bachman's Sparrow occupancy based on the second-year dataset.

Effect	Estimate	95% CI	Relative importance
ψ (graminoids/tree density)	1.379	-0.713 3.470	0.77
ψ (graminoids/tree density) ²	-1.499	-3.725 0.726	0.77
ψ (roots)	1.072	-0.293 2.437	0.69
ψ (crowns)	0.443	-0.339 1.225	0.50

stands inhospitable to Bachman's Sparrows by destroying the herbaceous layer. In DSNF, salvage logging did not appear to have lasting effects on the herbaceous layer. Although numerous timber companies salvaged, their operations were closely monitored by the Forest Service. Our results cannot be used as the basis for universal inferences about the effects of salvage logging because results will vary regionally with disturbance type, weather, geography, and, most importantly, oversight of management. Our results do show, however, that salvage logging does not necessarily have a negative effect on Bachman's Sparrows.

Our estimates of Bachman's Sparrow occupancy were higher in seedling/sapling and mature stands, paralleling the results of numerous other studies. Higher tree densities and canopy closure limit the availability of light to the understory and thus the growth of herbaceous plants (Harrington and Edwards 1999, McGuire et al. 2001, Platt et al. 2006). In DSNF, most pole stands have very high tree densities, contain an understory and midstory dominated by *Ilex* spp., and lack a well-developed herbaceous component. High tree densities can also lead to increased establishment of these shrubs, further limiting growth of herbaceous plants (Hinman et al. 2008). These patterns reflect Bachman's Sparrow's preference for a well-developed herbaceous layer and lower densities of trees.

Many salvaged stands were burned between salvaging and sampling, and these fires likely improved conditions for Bachman's Sparrows through effects on herbaceous vegetation. Areas not burned in >2 years would be less suitable regardless of salvage history because of changes in vegetation structure associated with fire suppression. Graminoid structure and tree density had the strongest influence on Bachman's Sparrow occupancy. These results confirm those of other studies, but in our models the quadratic effect better represents the birds' vegetation preferences, particularly in relation to fire. Bachman's Sparrows prefer a well-developed herbaceous layer, but too much herbaceous cover has a negative effect on them (Haggerty 1986, Harrington and Edwards 1999, Cox and Jones 2009), especially as herbaceous material accumulates in the absence of fire (Fuller 2004). This upper threshold for graminoid structure suggests that Bachman's Sparrows prefer patchy herbaceous cover, possibly because too much herbaceous cover can hamper birds' ability to capture prey (Wan A. Kadir 1987, Gobris 1992, Haggerty 1998). This may be the case in DSNF, where herbaceous cover in most of the stands Bachman's Sparrows occupied was patchy. The birds did not occur in habitats with more continuous herbaceous cover, such as bogs (Brooks 2010). Tree density also showed a quadratic effect, indicating that Bachman's Sparrows may prefer intermediate tree density even though they sometimes occur in early-successional treeless areas. Several authors have suggested that the species' use of early-successional stands results from limited availability of mature stands relative to the local population size rather than habitat preference per se (Dunning and Watts 1991, Gobris 1992).

Stand-occupancy estimates increased with abundance of downed tree crowns, perhaps because birds were attracted to them as song perches. In DSNF, we frequently observed Bachman's Sparrows singing from horizontal branches in downed pine tree crowns. Meanley (1959), Dunning and Watts (1990), and Gobris (1992) suggested the importance of song-perch structures to Bachman's Sparrow, but their observations were all post hoc. Bachman's Sparrows do sing from branches in the canopy (Brooks 1938, Wan A. Kadir 1987), but prefer perches within 2–3 m of the ground (Meanley 1959). Pine savannas often lack midstory vegetation, and strong, low, horizontal perches may be an important component of Bachman's Sparrow habitat (Haggerty 2000) and a critical difference between seemingly similar, well-managed habitat. The crowns of downed trees, which may remain for years, depending on fire frequency and intensity, could provide Bachman's Sparrow its principal song perches in storm-affected pine savannas. Trees damaged by tropical storms could be beneficial to Bachman's Sparrow if downed crowns are allowed to remain after post-disturbance management. Furthermore, routine timber harvesting and site preparation could be used to increase the availability of song perches (Meanley 1959, 1988, Gobris 1992, Dunning and Watts 1990), but more research is needed to quantify and validate the importance of perches further.

Uprturned root balls from trees blown over by Hurricane Katrina increased Bachman's Sparrow occupancy, possibly by providing refugia from predators in the form of tunnels or holes. Dean and Vickery (2003) documented flushed Bachman's Sparrows escaping into burrows in dry prairies in Florida. We observed similar behavior in DSNF during flush-net surveys for grassland birds in winter. Flushed birds routinely flew to upturned root balls and disappeared, presumably taking refuge in or under the root ball. Indeed, one of our technicians witnessed a flushed Bachman's Sparrow run into an opening under a root ball. Bowers and Dunning (1985) described similar use of tunnels by Cassin's Sparrow (*Peucaea cassinii*) in Arizona. Dean and Vickery (2003) speculated that Bachman's Sparrow's use of tunnels may be limited to treeless habitats, with trees probably the preferred refugia from predators in wooded habitats. Our observations suggest otherwise, but we lack data on the species' actual use of and preference for root balls. Although upturned root balls increased occupancy estimates, further research documenting the use of tunnels and selection of escape refugia is crucial to validating our interpretation.

The observer was an important detection covariate in the 2-year dataset. With four different observers over the course of the study, their ability to detect Bachman's Sparrow was likely to vary. A further explanation is that in the first year of the study the sparrows occupied a lower proportion of the sites. These sites were sampled by two observers, while the second-year sites were sampled by two different observers. The observer effect could reflect this difference in occupancy between the sites sampled the first year and the different sites sampled the second year, as well as variation by observer.

A year effect included as a covariate in some models was not important, which leads us to think that observer bias alone had some effect beyond potential effects of yearly differences in observers and sites.

The higher proportion of sites with >2 years since fire in 2007 is the most plausible explanation for this difference in occupancy between the years, rather than changes in Bachman's Sparrow abundance at a larger scale (or strong differences among observers). In 2007, these unburned sites suffered from greater shrub encroachment and had either almost no herbaceous layer or a multiyear accumulation of herbaceous litter that may have made the normally patchy ground cover too thick for the birds' foraging (Gobris 1992, Haggerty 1998). In contrast, in 2009, we surveyed more stands that had been burned following the resumption of normal management of DSNF with prescribed fire.

As infrequent but large-scale disturbances, hurricanes are seldom studied despite their important role in coastal longleaf pine savannas. Our results suggest that damage to trees from Hurricane Katrina may have benefited Bachman's Sparrow habitat in DSNF in three ways: by increasing song perches, by increasing escape refugia in root balls, and by thinning canopy trees. We quantify the effects of song perches and root balls for the first time. The thinning effect largely conforms to expectations from previous studies, even if thinning as a direct result of hurricanes has never been examined. Hurricanes thin trees and create patches in which trees can regenerate, helping create the uneven-aged stands characteristic of old-growth pine savannas. Tree mortality increases light penetration to the herbaceous layer, increasing plant diversity and biomass.

Fire and hurricanes both determine the physiognomic structure of pine savannas, and restoration efforts and management focused on pine-savanna species, including Bachman's Sparrow, should attempt to mimic both types of disturbances (Gilliam et al. 2006). For example, harvesting trees of uneven ages, the creation of patches, leaving downed trees, and fires during the growing season all help recreate disturbance-mediated dynamics of the pine savanna. To improve habitat for Bachman's Sparrow, we recommend tree thinning, along with prescribed fire, in high-density stands. Management that results in patchy distributions of uneven-aged trees will generate pine savanna that more closely resembles old growth, and this physiognomy best encourages natural regeneration of pines and a healthy herbaceous layer (Platt and Rathbun 1993, Gilliam et al. 2006). In many longleaf pine savannas prescribed fire is applied as a tool for restoration and management, but tree thinning mimicking natural disturbance is a method less commonly applied and should be considered when both pine-savanna restoration and timber harvesting are goals (Palik et al. 2002), although more research in this area is needed.

After a hurricane, salvage logging should be allowed on a region-specific, case-by-case basis. In many habitats, salvage logging can modify the landscape in ways that reduce the

important ecological value of the disturbance (Lindenmayer et al. 2004, Foster and Orwig 2006). For example, in western North America, removing burned snags affects the American Three-toed Woodpecker (*Picoides dorsalis*) negatively (Hutto and Gallo 2006). In wet pine savannas, soil disturbance may be one of the more damaging results of logging, and severe disturbance could negate any beneficial effects of opening the canopy. Weather, safety, threats of pest outbreak and catastrophic fire, and the economic effects of saturating the timber market are all important factors that must be considered before salvaging. Any salvaging should be closely monitored by agencies that have wildlife conservation at interest. The pre-salvage ecological-impact assessments required on federal lands and the monitoring of the salvage by DSNF personnel serve as good beginning models for forest managers (Gainey 2005, Gainey and James 2005). If over the next century global climate change causes an increase in the intensity of tropical storms, then the ecological effects of these storms and forest management after them will require continued study. In a given region, hurricanes are infrequent, but each storm brings enormous, albeit ephemeral, potential for research—these opportunities should not be missed.

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LITERATURE CITED

- AVERY, T. E. 1967. Forest measurements. McGraw-Hill, New York.
- BAILEY, L. L., T. R. SIMONS, AND K. H. POLLOCK. 2004. Estimating site occupancy and species detection probability parameters for terrestrial salamanders. *Ecological Applications* 14:692–702.
- BENDER, M. A., T. R. KNUTSON, R. E. TULEYA, J. J. SIRUTIS, G. A. VECCHI, S. T. GARNER, AND I. M. HELD. 2010. Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. *Science* 327:454–458.
- BIRDLIFE INTERNATIONAL [ONLINE]. 2009. Species factsheet: *Aimophila aestivalis*. <<http://www.birdlife.org>> (12 March 2010).
- BROOKS, M. 1938. Bachman's Sparrow in the north-central portion of its range. *Wilson Bulletin* 50:86–109.
- BROOKS, M. E. 2010. Status of wintering grassland birds in a post-hurricane, salvage-logged forest. M.Sc. thesis, Louisiana State University, Baton Rouge, LA.
- BOWERS, R. K., AND J. B. DUNNING. 1985. Predator avoidance through burrow use by Cassin's and Black-throated Sparrows. *Western Birds* 16:51.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

- CONNER, R. N., C. E. SHACKELFORD, R. R. SCHAEFER, AND D. SAENZ. 2005. The effects of fire suppression on Bachman's Sparrows in upland pine forest of eastern Texas. *Bulletin of the Texas Ornithological Society* 38:6–11.
- COX, J. A., AND C. D. JONES. 2009. Influence of prescribed fire on winter abundance of Bachman's Sparrow. *Wilson Journal of Ornithology* 121:359–365.
- DEAN, T. E., AND P. D. VICKERY. 2003. Bachman's Sparrows use burrows and palmetto clumps as escape refugia from predators. *Journal of Field Ornithology* 74:26–30.
- DUNNING, J. B. 1993. Bachman's Sparrow (*Aimophila aestivalis*), no. 38. In A. Poole and F. Gill [EDS.], *The Birds of North America*. Academy of Natural Sciences, Philadelphia.
- DUNNING, J. B., AND B. D. WATTS. 1990. Regional differences in habitat occupancy by Bachman's Sparrows. *Auk* 107:463–472.
- DUNNING, J. B., AND B. D. WATTS. 1991. Habitat occupancy by Bachman's Sparrow in the Francis Marion National Forest before and after Hurricane Hugo. *Auk* 108:723–725.
- EMANUEL, K. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. *Nature* 436:686–688.
- FOSTER, D. R., AND D. A. ORWIG. 2006. Preemptive and salvage harvesting of New England forests: when doing nothing is a viable alternative. *Conservation Biology* 20:959–970.
- FULLER, G. T. 2004. Diet of Henslow's Sparrows (*Ammodramus henslowii*) wintering in pine savannas of coastal Mississippi. M.Sc. thesis, Georgia Southern University, Statesboro, GA.
- GAINEY, J. 2005. Hurricane Katrina restoration: wildlife and PETS resources reports. USDA Forest Service, Region 8, Jackson, MS.
- GAINEY, J., AND C. JAMES. 2005. Biological evaluation (FSM 2672.4) for Hurricane Katrina tree removal and hazardous fuels treatment on the De Soto National Forest. USDA Forest Service, Region 8, Jackson, MS.
- GILLIAM, F. S., AND W. J. PLATT. 2006. Conservation and restoration of the *Pinus palustris* ecosystem. *Applied Vegetation Science* 9:7–10.
- GILLIAM, F. S., W. J. PLATT, AND R. K. PEET. 2006. Natural disturbances and the physiognomy of pine savannas: a phenomenological model. *Applied Vegetation Science* 9:83–96.
- GOBRIS, N. M. 1992. Habitat occupancy during the breeding season by Bachman's Sparrow. M.Sc. thesis, University of Georgia, Athens, GA.
- HARDIN, K. I., T. S. BASKETT, AND K. E. EVANS. 1982. Habitat of Bachman's Sparrows breeding on Missouri glades. *Wilson Bulletin* 94:208–212.
- HAGGERTY, T. M. 1986. Reproductive ecology of Bachman's Sparrow (*Aimophila aestivalis*) in central Arkansas. Ph.D. Dissertation, University of Arkansas, Fayetteville, AK.
- HAGGERTY, T. M. 1998. Vegetation structure of Bachman's Sparrow breeding habitat and its relationship to home range. *Journal of Field Ornithology* 69:45–50.
- HAGGERTY, T. M. 2000. A geographic study of the vegetation structure of Bachman's Sparrow (*Aimophila aestivalis*) breeding habitat. *Journal of Alabama Academy of Science* 71:120–129.
- HARRINGTON, T. B., AND M. B. EDWARDS. 1999. Understory vegetation, resource availability, and litterfall responses to pine thinning and woody vegetation control in longleaf pine plantations. *Canadian Journal of Forestry Research* 29:1055–1064.
- HINES, J. 2006. PRESENCE 2.1 Software to estimate patch occupancy and related parameters. USGS Patuxent Wildlife Research Center, Laurel, MD.
- HINMAN, S., J. S. BREWER, AND S. W. ASHLEY. 2008. Shrub seedling establishment is limited by dispersal, slow growth, and fire in two wet pine savannas in Mississippi. *Natural Areas Journal* 28:37–43.
- HUTTO, R. L., AND S. M. GALLO. 2006. The effects of postfire salvage logging on cavity-nesting birds. *Condor* 108:817–831.
- JACKSON, A. G. 1911. The Biltmore stick and its use on national forests. *Journal of Forestry* 9:406–411.
- LEMMON, P. E. 1956. Spherical densiometer for estimating forest overstory density. *Forest Science* 2:314–320.
- LINDENMAYER, D. B., D. R. FOSTER, J. F. FRANKLIN, M. L. HUNTER, R. F. NOSS, F. A. SCHMIEGELOW, AND D. PERRY. 2004. Salvage harvesting policies after natural disturbance. *Science* 303:1303–1303.
- LINDENMAYER, D. B., AND R. F. NOSS. 2006. Salvage logging, ecosystem processes, and biodiversity conservation. *Conservation Biology* 20:949–958.
- MACKENZIE, D. I. 2006. Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. *Journal of Wildlife Management* 70:367–374.
- MACKENZIE, D. I., J. D. NICHOLS, J. A. ROYLE, K. H. POLLOCK, L. L. BAILEY, AND J. E. HINES. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier/Academic Press, Burlington, MA.
- MCGARIGAL, K., S. CUSHMAN, AND S. STAFFORD. 2000. Multivariate statistics for wildlife and ecology research. Springer, New York.
- MCGUIRE, J. P., R. J. MITCHELL, E. B. MOSER, S. D. PECOT, D. H. GJERSTAD, AND C. W. HEDMAN. 2001. Gaps in a gappy forest: plant resources, longleaf pine regeneration, and understory response to tree removal in longleaf pine savannas. *Canadian Journal of Forest Research* 31:765–778.
- MEANLEY, B. 1959. Notes on Bachman's Sparrow in central Louisiana. *Auk* 76:232–234.
- MEANLEY, B. 1988. Notes on Bachman's Sparrow in the Croatan National Forest. *Chat* 52:2–3.
- MEEKER, J. R., T. J. HALEY, S. D. PETTY, AND J. W. WINDHAM. 2005. Forest health evaluation of Hurricane Katrina damage on the De Soto National Forest. USDA Forest Service, Alexandria Field Office Report 2006-02-02.
- NANDRAM, B. 1989. Discrimination between the complementary log-log and logistic model for ordinal data. *Communications in Statistics—Theory and Methods* 18:2155–2164.
- NEMES, S., J. M. JONASSON, A. GENELL, AND G. STEINECK. 2009. Bias in odds ratios by logistic regression modelling and sample size. *BMC Medical Research Methodology* 9:1–5.
- PALIK, B. J., AND N. PEDERSON. 1996. Overstory mortality and canopy disturbances in longleaf pine ecosystems. *Canadian Journal of Forest Research* 26:2035–2047.
- PALIK, B. J., R. J. MITCHELL, AND J. K. HIERS. 2002. Modeling silviculture after natural disturbance to sustain biodiversity in the longleaf pine (*Pinus palustris*) ecosystem: balancing complexity and implementation. *Forest Ecology and Management* 155:347–356.
- PLATT, W. J., B. BECKAGE, R. F. DOREN, AND H. H. SLATER. 2002. Interactions of large-scale disturbances: prior fire regimes and hurricane mortality of savanna pines. *Ecology* 83:1566–1572.
- PLATT, W. J., S. M. CARR, M. REILLY, AND J. FAHR. 2006. Pine savanna overstorey influences on ground-cover biodiversity. *Applied Vegetation Science* 9:37–50.
- PLATT, W. J., G. W. EVANS, AND S. L. RATHBUN. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). *American Naturalist* 131:491–525.
- PLATT, W. J., AND S. L. RATHBUN. 1993. Populations dynamics of an old growth population of longleaf pine (*Pinus palustris*), p. 200–226. In S. M. Hermann [ED.], *The longleaf pine ecosystem: ecology, restoration and management*. Proceedings 18th Tall Timbers Fire Ecology Conference.
- PLENTOVICH, S., J. W. TUCKER, N. R. HOLLER, AND G. E. HILL. 1998. Enhancing Bachman's Sparrow habitat via management of

- Red-cockaded Woodpeckers. *Journal of Wildlife Management* 62:347–354.
- STOBER, J. M., AND D. G. KREMENTZ. 2006. Variation in Bachman's Sparrow (*Aimophila aestivalis*) home-range size at the Savannah River Site, South Carolina. *Wilson Journal of Ornithology* 118:138–144.
- TUCKER, J. W., G. E. HILL, AND N. R. HOLLER. 1998. Managing mid-rotation pine plantations to enhance Bachman's Sparrow habitat. *Wildlife Society Bulletin* 26:342–348.
- TUCKER, J. W., W. D. ROBINSON, AND J. B. GRAND. 2004. Influence of fire on Bachman's Sparrow, an endemic North American songbird. *Journal of Wildlife Management* 68:1114–1123.
- TUCKER, J. W., W. D. ROBINSON, AND J. B. GRAND. 2006. Breeding productivity of Bachman's Sparrows in fire-managed longleaf pine forests. *Wilson Journal of Ornithology* 118:131–137.
- WAN A. KADIR, W. R. 1987. Vegetational characteristics of early successional sites utilized for breeding by the Bachman's Sparrow (*Aimophila aestivalis*) in eastern Texas. M.Sc. thesis, Stephan F. Austin University, Nacogdoches, TX.
- WEBSTER, P. J., G. J. HOLLAND, J. A. CURRY, AND H. R. CHANG. 2005. Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science* 309:1844–1846.
- WIENS, J. A. 1974. Habitat heterogeneity and avian community structure in North American grasslands. *American Midland Naturalist* 91:195–213.
- WIENS, J. A., AND J. T. ROTENBERRY. 1981. Habitat associations and community structure of birds in shrubsteppe environments. *Ecological Monographs* 51:21–41.
- WINDHAM, J. W. 2005. Forest vegetation analysis: Hurricane Katrina damaged tree removal and hazardous fuels treatment. USDA Forest Service, Region 8, Jackson, MS.

APPENDIX 1. Correlations of raw vegetation variables and principal components for the 2-year dataset ($n = 89$). Highest correlations of a variable within each component are in bold. A qualitative description of each component is in parentheses. CWD is coarse woody debris.

Variable	PC 1 (graminoids/trees)	PC 2 (forbs)	PC 3 (shrubs)	PC 4 (shrubs/CWD)
Graminoid vertical density	0.94	0.10	−0.15	−0.08
Graminoid horizontal density	0.93	0.06	−0.17	−0.11
Graminoid cover	0.84	0.35	−0.12	−0.18
Tree basal area	− 0.82	−0.17	−0.07	−0.14
Canopy closure	− 0.86	−0.16	−0.04	−0.18
Forb vertical density	0.21	0.83	−0.15	0.04
Forb horizontal density	0.09	0.78	−0.10	−0.20
Forb cover	0.30	0.76	−0.06	0.10
Shrub cover <0.5 m	−0.06	−0.32	0.76	−0.15
Woody vertical density	0.05	−0.33	0.73	0.15
Shrub cover >0.5 m	−0.11	0.14	0.59	0.05
Coarse woody debris	0.22	−0.17	−0.15	0.75
Woody horizontal density	−0.26	0.12	0.26	0.72
Proportion s^2 explained	0.38	0.16	0.10	0.09

APPENDIX 2. Correlations of raw vegetation variables and principal components for the second survey year only ($n = 38$). Highest correlations of a variable within each component are in bold. A qualitative description of each component is in parentheses. CWD is coarse woody debris.

Variable	PC 1 (graminoids/trees)	PC 2 (forbs/shrubs)	PC 3 (shrubs)	PC 4 (CWD)
Graminoid vertical density	0.90	0.06	−0.15	0.26
Graminoid horizontal density	0.89	0.00	−0.16	0.30
Graminoid cover	0.81	0.39	−0.18	0.02
Tree basal area	− 0.83	−0.02	−0.14	0.14
Canopy closure	− 0.87	−0.17	−0.01	−0.12
Forb vertical density	0.00	0.91	−0.13	−0.07
Forb cover	0.03	0.87	−0.10	0.00
Forb horizontal density	0.12	0.73	0.15	−0.18
Shrub cover <0.5 m	−0.39	− 0.58	−0.52	−0.05
Woody vertical density	−0.38	− 0.65	−0.26	−0.20
Shrub cover >0.5 m	−0.08	0.03	0.77	0.24
Woody horizontal density	−0.26	−0.07	0.69	−0.45
Coarse woody debris	0.19	−0.13	0.11	0.89
Proportion s^2 explained	0.38	0.20	0.11	0.08