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Bird assemblage response to restoration of fire-suppressed longleaf pine sandhills

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Abstract. The ecological restoration of fire-suppressed habitats may require a multifaceted approach. Removal of hardwood trees together with reintroduction of fire has been suggested as a method of restoring fire-suppressed longleaf pine (*Pinus palustris*) forests; however, this strategy, although widespread, has not been evaluated on large spatial and temporal scales. We used a landscape-scale experimental design to examine how bird assemblages in fire-suppressed longleaf pine sandhills responded to fire alone or fire following mechanical removal or herbicide application to reduce hardwood levels. Individual treatments were compared to fire-suppressed controls and reference sites. After initial treatment, all sites were managed with prescribed fire, on an approximately two- to three-year interval, for over a decade. Nonmetric multidimensional scaling ordinations suggested that avian assemblages on sites that experienced any form of hardwood removal differed from assemblages on both fire-suppressed sites and reference sites 3–4 years after treatment (i.e., early posttreatment). After >10 years of prescribed burning on all sites (i.e., late posttreatment), only assemblages at sites treated with herbicide were indistinguishable from assemblages at reference sites. By the end of the study, individual species that were once indicators of reference sites no longer contributed to making reference sites unique. Occupancy modeling of these indicator species also demonstrated increasing similarity across treatments over time. Overall, although we documented long-term and variable assemblage-level change, our results indicate occupancy for birds considered longleaf pine specialists was similar at treatment and reference sites after over a decade of prescribed burning, regardless of initial method of hardwood removal. In other words, based on the response of species highly associated with the habitat, we found no justification for the added cost and effort of fire surrogates; fire alone was sufficient to restore these species.

Key words: Eglin Air Force Base, Florida, USA; longleaf pine; nonmetric multidimensional scaling; occupancy modeling; Picoides borealis; Pinus palustris; *prescribed fire; Red-cockaded Woodpecker.*

INTRODUCTION

Reintroduction of natural disturbance regimes is often essential to restoration efforts in fire-maintained habitats (Mitchell et al. 2006), though this strategy may underestimate what is necessary to restore a functioning system (Suding et al. 2004). Due to concerns associated with fuel loads and inability of fire alone to restore ecological structure and function, various fire surrogates have been evaluated (Provencher et al. 2001*a*, *b*). However, fire surrogates are generally considered insufficient to restore fire-adapted systems (Menges and Gordon 2010); fire is thought to be necessary for ecological function and to maintain a desired condition (e.g., Brockway and Outcalt 2000, Brockway et al. 2005). Therefore, some have recommended a restoration strategy that includes fire surrogates initially, followed by reintroduction of frequent fire for long-term management (Menges and Gordon 2010). There have been limited opportunities to quantify the effects of this strategy, as it requires long-term monitoring.

Longleaf pine (*Pinus palustris*) forests once ranged throughout the southeastern United States but have declined considerably due to land use conversion and suppression of frequent fire (Ware et al. 1993). The disruption of the frequent fire regime (fire every 1–10 years; Myers 1990) allows hardwood trees (e.g., oak, *Quercus* spp.) to become established in the midstory (Mitchell et al. 2006). These trees and their litter alter forest composition, generally degrading the habitat for longleaf pine associates (Means 2006, Hiers et al. 2007).

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Restoration is a management objective for many longleaf pine forests and is generally attempted by removing hardwood trees and reintroducing fire (Brockway et al. 2005). Several methods of hardwood removal are commonly used, including mechanical removal (i.e., felling and girdling), application of herbicides, fire, or a combination of these methods. These restoration strategies are typically evaluated by measuring vegetation response (e.g., Provencher et al. 2001*a*, *b*). Fauna are generally assumed to respond to changes in the habitat (i.e., passive restoration; Scott et al. 2001).

The initial effects of habitat restoration on wildlife may become less pronounced over time (e.g., Hanowski et al. 2007) but it is generally thought that periodic burning is sufficient to maintain the initial response of longleaf pine forests to hardwood removal. For example, mechanical removal of hardwood trees coupled with reintroduction of fire is beneficial for bird species associated with pine–grassland ecosystems, and this management is likely sufficient to maintain their populations (Cram et al. 2002, Provencher et al. 2002*b*). However, fire may need to be applied repeatedly over long time periods to achieve effective restoration of southern pine forests (Waldrop et al. 1992). Therefore, long-term studies are essential to accurately characterize wildlife response to restoration activities (Zedler and Callaway 1999, George and Zack 2001), including change in abundance (Purcell et al. 2005).

Birds play vital roles in forests as predators, prey, consumers, and seed dispersers (Means 2006). This faunal group may be sensitive to landscape-scale habitat change (e.g., McGarigal and McComb 1995, Drapeau et al. 2000, Lindenmayer et al. 2002); it is therefore important to understand how birds respond to forest management and restoration. Assemblage-level study may identify general trends in how wildlife responds to habitat change (Luck and Daily 2003, Bennett et al. 2004). Measures of assemblage structure, however, may obscure species-specific and population-level trends (Maas et al. 2009). Empirical justification should be provided when species are selected for monitoring the response of ecological restoration on wildlife (Block et al. 2001).

Although it is essential to characterize the effects of forest management on long temporal scales, most studies of the subject last only a few years (Sallabanks et al. 2000, Bennett and Adams 2004). In addition, most studies do not include experimental replication at the landscape scale (Bennett and Adams 2004); however, experiments allow for strong inference regarding how wildlife responds to ecological restoration (Marzluff et al. 2000, Block et al. 2001). To determine how birds respond to forest restoration of fire-suppressed longleaf pine sandhills over long time scales, we used a randomized-block experimental design at the landscape scale to investigate bird assemblage-level response after hardwood removal and again after all sites received prescribed fire for over 10 years. We used this assemblage-level analysis to empirically inform selection of species closely associated with reference sites, which represented our target for restoration efforts, and examined changes in occupancy for these species over time. If avian assemblages and occupancy probabilities on sites that experienced hardwood removal and/or prescribed burning were indistinguishable from those on reference sites, we assumed management objectives were met.

MATERIALS AND METHODS

Study site and experimental design

This study took place on Eglin Air Force Base, Okaloosa, Santa Rosa, and Walton Counties, Florida, USA (Fig. 1). We focused our study on fire-suppressed longleaf pine sandhills. The study was based on a randomized-block design to assign hardwood removal treatments to 24 sites, each 81 ha in size and assigned to one of six blocks (Rodgers and Provencher 1999, Provencher et al. 2001*a*, *b*). Methods of hardwood removal (i.e., treatments) applied in 1995 included (1) burning (burn), (2) herbicide application (herbicide), or (3) felling-girdling (mechanical). Each block also contained a fire-suppressed control, which received no treatment. Six reference sites (also 81 ha in size but independent from the randomized-block design) were also designated; reference sites had been subjected to a fire frequency over a long time span similar to the natural disturbance regime and were selected as a representation of the ancestral condition and a target of restoration efforts (White and Walker 1997). More details regarding reference site selection can be found in Provencher et al. (2001*a*). Most of the treatment sites had no records of having been burned since 1973, when record keeping began (B. Williams, *personal communication*). Ten sites experienced burns of varying extent from unknown causes between 1977 and 1989.

The burn treatment was applied between April and June 1995; herbicide (hexazinone [ULW], 1.68 kg of active ingredient/ha; E. I. du Pont de Nemours, Wilmington, Delaware, USA; Gonzalez 1985) was applied in early May 1995; and mechanical removal was conducted between June and November of 1995. Herbicide and mechanical sites were subjected to a prescribed burn in 1997. More details on the treatments are available in Provencher et al. (2001*a*, *b*).

After 1999, all sites received comparable management, which included prescribed fire on a 2–3 year rotation, but no additional hardwood removal or herbicide application. Because prescribed fire was applied to all sites following the initial experimental treatments, we approached the analysis in two phases. The first phase employed a randomized-block design with multiple treatments plus reference sites. After 1999, all treatment sites, including those that were originally considered controls (i.e., fire-suppressed longleaf pine sandhills) were subjected to prescribed burning but no additional forest management.

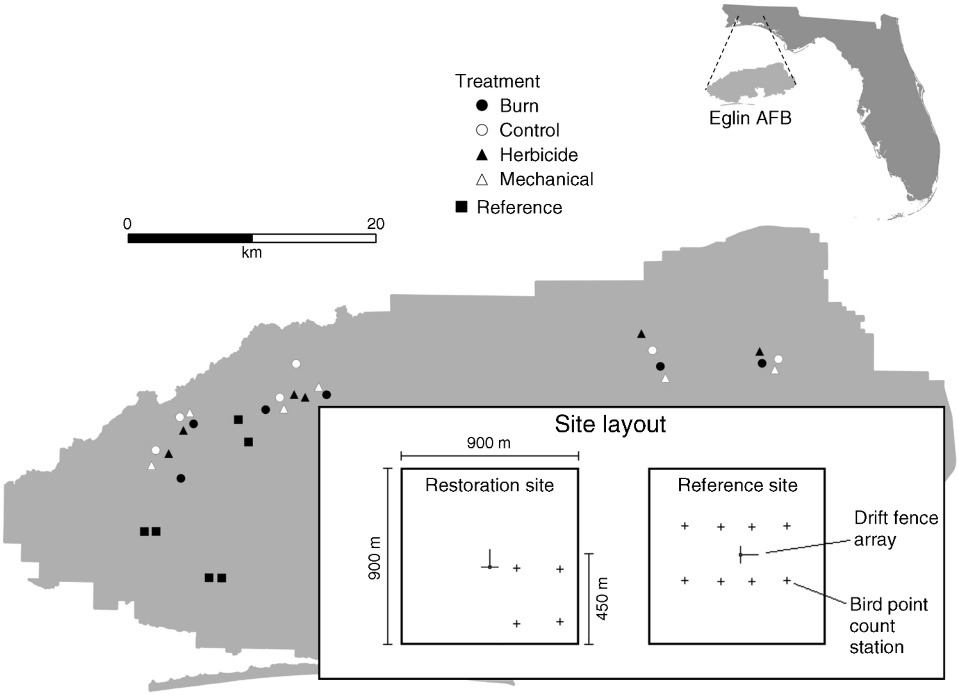

FIG. 1. Map of the study site, including geographic location of Eglin Air Force Base, Florida, USA, distribution of treatment and reference sites, and layout of sampling design.

Tree basal area

We calculated basal area per hectare for longleaf pine and all oak (*Quercus* spp.) trees for each site using data collected in 1995, 1998, and 2009–2010. We considered individual pine trees ≥4 cm diameter at breast height (dbh) as a component of the overstory and those <4 cm dbh as components of the midstory. We considered an oak tree a component of the overstory if it was ≥6.3 cm dbh and a component of the midstory if it was less. Data on individual trees were collected in subplots (see study design in Provencher et al. 2002*b*), summed, and divided by total sampled area to generate basal area per hectare. In generating mean values for 2009–2010, we excluded one block and a single reference site that experienced additional management activities outside of this study.

Avian sampling

Avian sampling included combinations of point counts and transects; specific methodology varied over the course of the study (see sections immediately below for methodology specific to each sampling period). To maximize the likelihood of independence, all avian sampling in treatment sites occurred in the corners furthest from other treatment sites. Sampling within reference sites occurred within the center of the site (Fig. 1). All samples were collected between ~05:45 and 10:00 hours. We rotated the order of sites sampled within a given morning to reduce bias associated with time; however, we were unable to sample sites in random order because of occasional restrictions on access to sites due to military training activities. Four treatment sites or two to four reference sites were sampled in a morning unless access was restricted due to military training. Two observers visited a site during each sampling occasion and walked along parallel transects 250 m apart from each other and ~450 m long (Fig. 1). We recorded all birds estimated to be within the study site; we excluded birds that appeared to be only flying over the site. In the pretreatment and early posttreatment study periods, the two observers took measures to remove any duplicate observations of the same individual bird (Provencher et al. 2002*b*); this was not completed in the late posttreatment period. This discrepancy was of no consequence to our results because of our focus on species-level data. Similarly, potential differences in observer skill are of little concern herein because of our emphasis on species-level data as well as our pooling of all observations within each sample during the early and posttreatment study periods.

1994 sampling (pretreatment)

All sites were visited four times between 4 May and 18 July 1994, prior to hardwood removal treatments (Provencher et al. 2002*b*). Each time a treatment site was visited, two observers conducted eight-minute point counts ~200 m apart along the transects (four total point counts each visit) and recorded all detected birds. Effort was doubled on reference sites, which resulted in eight point counts on four transects per site.

1998–1999 sampling (early posttreatment)

All sites were visited six times each between 1 May and 30 June in 1998 and again in 1999 (12 total samples). Similar to the pretreatment data collection, two observers sampled for birds simultaneously along parallel transects. However, in contrast to pretreatment data collection, each observer conducted only one point count per visit (the point was at either the beginning or end of a transect, varying by visit). In addition, observers walked an entire transect (450 m) and recorded all birds detected. Walking a transect took ~22 minutes. With the addition of the eight-minute point count, each observer sampled birds for ~30 minutes per site (Provencher et al. 2002*b*).

2009–2010 sampling (late posttreatment)

We attempted to sample four blocks and three reference sites four times each between 27 May and 13 July of 2009. Exceptions include one mechanical site that was sampled only three times, a reference site that received a single visit, and a reference site that was sampled twice. Five blocks and five reference sites were sampled three times each between 11 May and 18 June of 2010. Four transects were walked in reference sites in 2009, otherwise sampling methods replicated those used in 1998–1999.

Ordination

Because the number of sites sampled changed over time and to better visualize the change in bird assemblages within treatments, we first conducted multivariate analyses. We treated each point count as an independent sample for the pretreatment data, such that four samples were created per visit. When necessary, we randomly removed from consideration half of the point counts conducted on reference sites to make sampling effort comparable to that of treatment sites. For both study periods following hardwood removal treatments, we pooled detections from both observers collected within a transect and point count, such that each time a site was visited one sample was created. We removed the first two samples in each of 1998–1999 (early posttreatment) from consideration to make data from these years comparable to that of the other study periods. We created a presence/absence matrix where a species was given a score of "1" if detected within a sample and a score of "0" if not detected. Therefore, a species could have scored a maximum of 16 detections in a given site for the pretreatment study period, eight for early posttreatment, and seven for late posttreatment.

We used nonmetric multidimensional scaling (NMDS), a nonparametric ordination (Clarke 1993), to graphically demonstrate differences in assemblages based on species identity and the number of times a species was detected (e.g., Kennedy et al. 2010). As some sites were not sampled in every time period and we were interested in how sites moved over time, we conducted two separate NMDS ordinations with Bray-Curtis (Sorenson) distances. The first ordination included pretreatment and early posttreatment data. The second ordination included the early posttreatment and late posttreatment data. Statistical significance was determined by comparing observed stress to that obtained by Monte Carlo simulations. We used a multi-response permutation procedure (MRPP; Mielke and Berry 2001) to test the hypothesis that avian assemblages did not differ between treatments and reference sites. For each ordination, we removed species detected in only one sample to reduce the impact of rare and rarely detected species. Although rare species may be important to include in some analyses (e.g., Cao et al. 1998), removing rare species is a common strategy within NMDS (e.g., Kreutzweiser et al. 2005). We also did not include two aquatic species, the Great Blue Heron (*Ardea herodias*) and Common Loon (*Gavia immer*). Ordinations and MRPP were completed using PC-ORD 4.0 (McCune and Mefford 1999).

If the MRPP indicated no significant difference between a given treatment and reference sites in either of the study periods following hardwood removal, we considered this evidence that the treatment was effective at restoring the avian assemblage. Treatment sites significantly different than reference sites were suggested to be ineffective at restoring the avian assemblage.

Indicator species analysis

We identified indicator species for the different treatments and reference sites using methods described by Dufrêne and Legendre (1997). This analysis considered the number of detections and exclusivity of each species to sites within a treatment. Indicator species were assigned a value of 0–100. A 100 would indicate a species was observed in all sites of a given treatment and no other sites (Dufrêne and Legendre 1997). We used the matrices described in the ordination section to identify indicator species. Statistical significance was determined with 1000 Monte Carlo simulations. Indicator species analyses were completed within PC-ORD 4.0 (McCune and Mefford 1999).

As part of Eglin Air Force Base's recovery plan for Red-cockaded Woodpeckers (*Picoides borealis*), artificial cavities were installed in pine trees between the early and late posttreatment study periods (K. Gault, *personal communication*). Therefore, we cannot interpret any change in their status as an indicator species between these study periods as due to the restoration methods used in this study. Red-headed Woodpeckers (*Melanerpes erythrocephalus*) are kleptoparasites of Red-cockaded Woodpecker cavities (USFWS 2003) and may also have benefitted from installation of artificial cavities; however, this benefit was likely relatively small, compared with that of Red-cockaded Woodpeckers; hence, we interpret change in parameters associated with this species as relevant to hardwood removal treatments.

Occupancy modeling

The species we selected for occupancy modeling included those identified as indicators (as determined with indicator species analysis) of pretreatment reference conditions. Of these species, we excluded Red-cockaded Woodpeckers and Blue Jays (*Cyanocitta cristata*). We excluded Red-cockaded Woodpeckers due to the additional management this species received and excluded Blue Jays due to their generalist habitat use and widespread distribution.

To standardize the methodology across study periods, we used only point count data and made each visit (i.e., sampling occasion) equivalent to the sum of the detections from two point counts. In the pretreatment study period, eight point counts were conducted in each reference site per visit; we randomly removed four point counts. Because four point counts were conducted in treatment sites during each visit pretreatment (and only two for the following study periods), we removed point counts conducted in the middle of the transect (one-half of all point counts pretreatment) from analysis. In the first year of the late posttreatment study period, four point counts were conducted in each reference site; we randomly selected two of these for analysis. We again removed the first two surveys in both years sampled early posttreatment. We pooled data such that each time a site was visited, one sample was generated. As a result, we generated four samples for the pretreatment data, eight samples for the early posttreatment sampling period, and seven samples for the late posttreatment sampling period. We then constructed a separate site × sample (i.e., survey) matrix for each indicator species chosen for analysis; a "1" was used to indicate whether a species was detected in a given sample and a "0" if it was not.

We used the multi-season model (MacKenzie et al. 2003) in Program PRESENCE to model occupancy (Hines 2010). In contrast to the single season model (MacKenzie et al. 2002), the multi-season model allows for changes in occupancy within a site. This is accomplished by distinguishing between primary sampling periods, between which occupancy may change, and secondary sampling periods, in which the population is considered closed to immigration, emigration, or extinction. We defined the pretreatment data (1994), early posttreatment (1998–1999), and late posttreatment (2009–2010) as our three primary sampling periods. Each visit within a primary sampling period was considered a secondary sampling period.

We modeled occupancy in treatment and reference sites separately for each species. Our interest was in detecting changes in species occupancy; therefore, we considered detection probability a nuisance parameter. We first modeled detection probability for each species and used the combination of covariates that best predicted detection probability, based on Akaike's Information Criteria (AIC), in successive occupancy models. Models used to evaluate detection probability in treatment sites included (1) constant detectability over all three study periods, (2) varying detectability by treatment type, (3) varying detectability by treatment type and each secondary sample, and (4) varying detectability by treatment type and primary sampling period. Models used to evaluate detection probability in reference sites included (1) constant detectability over all three study periods, (2) varying detectability by secondary sampling period, and (3) varying detectability by primary sampling period.

We evaluated five occupancy models for each species in treatment sites; these models represented several hypotheses (Table 1) for how birds may respond to hardwood removal. We evaluated two occupancy models for each species in reference sites and used the combination of covariates producing the best estimate of detection probability for each species to model this parameter within occupancy models for that species. Models were ranked using AIC and we considered models with ΔAIC values <2 as important (Burnham and Anderson 2002). We did not correct AIC for small sample size ($\mathrm{AIC_c}$) or for overdispersion (QAIC) because of problems obtaining numerical convergence. When more than one model had ΔAIC values <2, we used model averaging to estimate occupancy probability. No formal method exists for determining goodness of fit for multi-season models. Therefore we used the single-season model (MacKenzie et al. 2002) for the early posttreatment data with occupancy (Ψ) as a function of treatment type and detection probability varying by survey and treatment type to account for unmeasured heterogeneity (e.g., Adams et al. 2011). We conducted this analysis for data associated with treatment sites only.

RESULTS

Tree basal area

Oak basal area generally decreased following treatment (Table 2). However, midstory oak basal area in mechanical sites increased after 1997–1998 to levels higher than observed in pretreatment conditions, as hardwood coppiced sprouts reached midstory stature. In control sites, oak basal area decreased over time. Longleaf pine basal area was similar among treatments over time, but never equaled that of reference sites.

Ordination

A two-dimensional solution was the best fit for the 1994 and 1998–1999 data with a final stress of 17.91 and an instability of 0.0005 after 200 iterations (stress was less than expected by chance; $P = 0.03$; Fig. 2). Reference sites, located within the middle of axis 1 in 1994, moved slightly along this axis between 1994 and 1998–1999. With one exception, control sites also moved slightly along axis 1 between 1994 and 1998–1999 but were always separated from reference sites on axis 2. All sites that experienced some form of hardwood removal in

TABLE 1. Models used to evaluate occupancy probabilities for selected bird species detected from 1994 to 2010 to determine how they responded to hardwood removal on fire-suppressed longleaf pine sandhills in Eglin Air Force Base, Florida, USA.

Models	Hypotheses
Treatment occupancy	
Ψ(PRD), γ(PRD), $p(x)$	occupancy and colonization vary by primary sampling period
Ψ(TRT + PRD), γ(TRT + PRD), $p(x)$	occupancy and colonization vary by primary sampling period and treatment type
Ψ(TRT + PRD), ε(TRT + PRD), $p(x)$	occupancy and extinction vary by primary sampling period and treatment type
Ψ, γ(TRT + PRD), ε(TRT + PRD), $p(x)$	colonization and extinction rates vary by primary sampling period and treatment type and are based on initial occupancy
Ψ, γ(TRT), ε(TRT + PRD), $p(x)$	colonization varies by treatment type and extinction rates vary by primary sampling period and treatment type, both are based on initial occupancy
Reference occupancy	
Ψ(.), γ(.), $p(x)$	occupancy and colonization rates are constant
Ψ(PRD), γ(PRD), $p(x)$	occupancy and colonization rates vary by primary sampling period

Notes: An "x" denotes the covariates best explaining detection probability, which varied by species (Table 5). Abbreviations are: PRD, primary sampling period; TRT, treatment.

1995 moved considerably along axis 1 and approached references sites along axis 2 (Fig. 2).

A three-dimensional solution was the best fit for the 1998–1999 and 2009–2010 data with a final stress of 11.29 and an instability of 0.004 after 200 iterations (stress was less than expected by chance; $P = 0.03$; Fig. 3). Control sites moved considerably along axis 2. These sites displayed the greatest degree of change between 1998–1999 to 2009–2010, which was expected because the fire treatment they received was being initiated during this time while the other treatment sites were well into their restoration trajectories (i.e., they had not received a hardwood-removal treatment or prescribed burning by 1998–1999). There was considerable variation in the spatial arrangement of burn, mechanical, and herbicide sites but they appeared to be generally converging to the center of axis 1 and the bottom of axis 2.

Reference sites differed from treatment sites in 1994, whereas treatments were similar (Table 3). Following hardwood removal, control and reference sites were distinct from each other and all other treatment sites. In 2009–2010, reference sites were distinct from all treatments except herbicide sites, and herbicide sites differed from controls and mechanical sites (Table 3).

Identification of indicator species and occupancy modeling

Eight species were positively associated with reference sites in 1994; eight species were also positively associated with mechanical sites early posttreatment (Table 4). All other treatments had fewer, or no, indicator species (Table 4). Only two species were associated with the same treatment for both study periods following hardwood removal.

For occupancy modeling, we selected six species that were positively associated with reference sites pretreatment: American Kestrel (*Falco sparverius*), Bachman's Sparrow (*Peucaea aestivalis*), Blue Grosbeak (*Passerina caerulea*), Brown-headed Nuthatch (*Sitta pusilla*), Northern Bobwhite (*Colinus virginianus*), and Red-headed Woodpecker (Table 5). Goodness-of-fit tests for early posttreatment data did not provide evidence for any unexplained heterogeneity.

Occupancy of American Kestrel and Northern Bobwhite in treatment sites was best explained by models that allowed occupancy to vary by primary sampling period. American Kestrel occupancy was considerably lower in treatment sites than in references pretreatment, but these values were similar after hardwood removal (Table 6). Northern Bobwhite occupancy remained relatively high throughout the duration of the study.

TABLE 2. Oak and longleaf pine basal area in treatment and reference sites before and after oak removal.

	Basal area (m^2/ha)		
Site, treatment	Pretreatment	Early posttreatment	Late posttreatment
Pinus palustris midstory			
Burn	0.10 (0.04)	0.04 (0.02)	0.04 (0.01)
Control	0.08 (0.01)	0.07 (0.01)	0.02 (0.01)
Herbicide	0.06 (0.02)	0.04 (0.01)	0.29 (0.08)
Mechanical	0.09 (0.02)	0.04 (0.01)	0.08 (0.02)
Reference	0.04 (0.02)	0.03 (0.02)	0.13 (0.05)
Pinus palustris overstory			
Burn	10.20 (2.06)	9.50 (1.94)	11.22 (2.14)
Control	7.19 (0.78)	7.63 (0.90)	8.86 (1.26)
Herbicide	9.39 (2.22)	9.56 (2.22)	10.18 (1.65)
Mechanical	10.00 (2.06)	9.64 (2.25)	11.25 (1.77)
Reference	17.62 (1.91)	17.92 (1.97)	18.71 (2.64)
Quercus spp. midstory			
Burn	1.53 (0.65)	0.43 (0.16)	0.81 (0.30)
Control	1.08 (0.09)	1.13 (0.13)	0.66 (0.20)
Herbicide	0.76 (0.19)	0.04 (0.01)	0.15 (0.03)
Mechanical	0.92 (0.18)	0.08 (0.05)	1.58 (0.26)
Reference	0.09 (0.03)	0.12 (0.09)	0.08 (0.07)
Quercus spp. overstory			
Burn	14.26 (3.40)	8.18 (2.52)	7.09 (2.26)
Control	11.54 (1.27)	10.53 (1.55)	5.08 (1.61)
Herbicide	13.54 (2.97)	2.73 (0.13)	0.11 (0.07)
Mechanical	13.04 (2.12)	4.50 (2.52)	6.42 (5.43)
Reference	4.88 (1.30)	2.73 (0.25)	1.42 (0.82)

Note: Values are means with SE in parentheses.

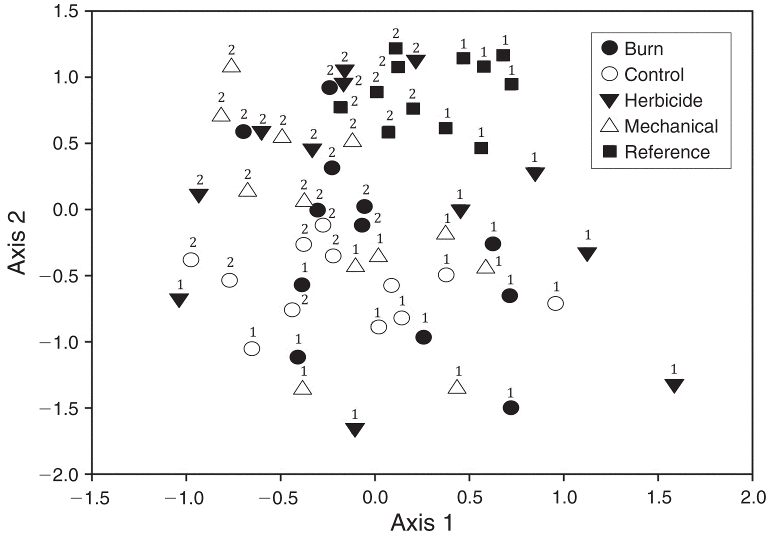

FIG. 2. Nonmetric multidimensional scaling ordination of bird assemblages observed on fire-suppressed longleaf pine sandhills on Eglin Air Force Base, pretreatment (1) and early posttreatment (2).

Estimated occupancy probabilities for Bachman's Sparrow, Brown-headed Nuthatch, Red-headed Woodpecker, and Blue Grosbeak exhibited similar patterns through time (Figs. 4–7). The most important models for each species included treatment as a covariate (Table 5). Occupancy probabilities for all four species were lower in treatment sites than in reference sites prior to hardwood removal. In general, occupancy probabilities for these species in mechanical and herbicide sites became similar to those in reference sites early posttreatment. By late posttreatment, however, occupancy probabilities in all treatment sites were similar to those in reference sites for all four species.

DISCUSSION

Controlled experiments are the most effective means of determining how wildlife assemblages respond to ecological restoration (Block et al. 2001). Yet, it is difficult to experimentally apply treatments at a scale applicable to many wildlife species due to their long lives and spatial ecology. For the few controlled studies that exist, most take place over relatively limited temporal and spatial scales (Bennett and Adams 2004). Our study, which incorporates a landscape-scale experimental design and spans more than 15 years, revealed that hardwood reduction in a longleaf pine forest may benefit avian assemblages and, specifically, species positively associated with sites in reference condition.

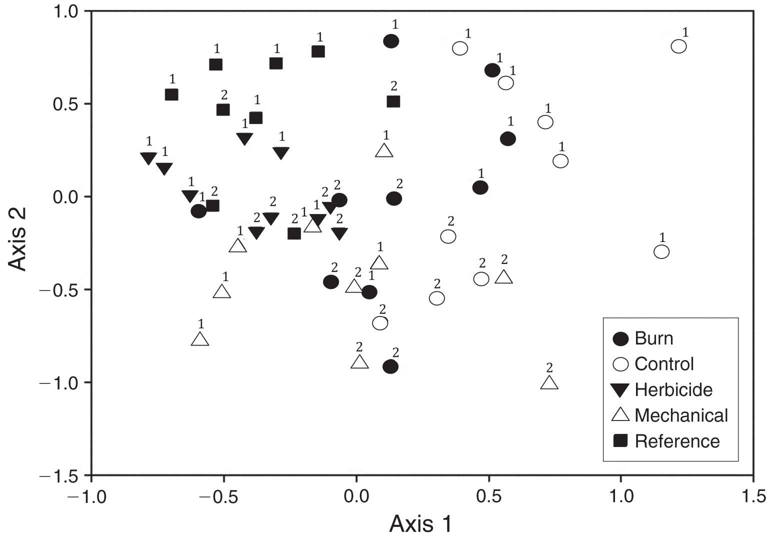

FIG. 3. Nonmetric dimensional scaling ordination of bird assemblages observed on longleaf pine sandhills following hardwood removal on Eglin Air Force Base, early posttreatment (1) and late posttreatment (2). Axes 1 and 2 of the 3-D solution are presented.

TABLE 3. *P* values associated with multi-response permutation procedure on pairwise comparisons of avian assemblages on treatment and reference sites.

Period and treatment	Burn	Control	Mechanical	Herbicide	Reference
Pretreatment					
Burn		0.55	0.94	0.85	**0.0006**
Control			0.86	0.21	**0.0006**
Mechanical				0.81	**0.0007**
Herbicide					**0.002**
Early posttreatment					
Burn		**0.01**	0.10	0.25	**0.003**
Control			**0.0009**	**0.001**	**0.0005**
Mechanical				0.16	**0.0006**
Herbicide					**0.04**
Late posttreatment					
Burn		0.36	0.54	0.05	**0.04**
Control			0.93	**0.02**	**0.01**
Mechanical				**0.01**	**0.01**
Herbicide					0.58

Note: Boldface indicates a significant difference ($P < 0.05$) between groups.

Our results are consistent with Maas et al. (2009), in that assemblage level diversity may be a poor proxy for an individual species' response to habitat change. Trends documented herein suggest that application of herbicide followed by frequent prescribed burns was the most effective method for increasing the similarity of avian assemblages to those observed at reference sites. However, in-depth consideration of only those species positively associated with longleaf pine in reference sites suggested all methods of hardwood removal used in this

TABLE 4. Bird species identified as having a significant association with treatment or reference sites for all three study periods at Eglin Air Force Base, Florida.

Treatment of maximum association	Species	Percentage indicator value†					*P*
		Burn	Control	Mechanical	Herbicide	Reference	
Pretreatment							
Reference	American Kestrel	18	0	0	0	54	0.006
	Bachman's Sparrow	0	0	1	4	60	0.002
	Brown-headed Nuthatch	0	2	0	0	60	0.009
	Blue Grosbeak	2	8	11	5	51	0.003
	Blue Jay	14	23	17	17	29	0.007
	Northern Bobwhite	9	10	8	13	50	0.001
	Red-cockaded Woodpecker	7	1	3	4	60	0.001
	Red Headed Woodpecker	0	1	1	4	81	0.001
Control	Downy Woodpecker	6	43	16	3	2	0.016
	Northern Cardinal	19	35	23	10	2	0.047
	Pileated Woodpecker	17	34	8	17	4	0.048
Early posttreatment							
Control	Eastern Titmouse	22	31	16	18	11	0.001
Mechanical	Blue Grosbeak	15	2	37	23	14	0.036
	Brown Thrasher	8	11	42	12	5	0.004
	Carolina Wren	19	20	36	12	1	0.043
	Chimney Swift	3	9	38	12	3	0.04
	Eastern Bluebird	6	1	41	35	5	0.023
	Eastern Towhee	13	6	48	5	0	0.008
	Indigo Bunting	6	0	50	2	0	0.01
	Summer Tanager	5	5	41	17	2	0.027
Reference	Red-cockaded Woodpecker	12	0	10	22	39	0.007
	Red Headed Woodpecker	24	0	20	16	37	0.004
Late posttreatment							
Control	Eastern Titmouse	24	35	27	10	3	0.001
Mechanical	Eastern Towhee	27	28	37	2	3	0.018
Herbicide	Brown-headed Nuthatch	20	9	12	30	23	0.02
Reference	Mississippi Kite	0	0	0	0	67	0.022

† As described by Dufrêne and Legendre (1997), species are assigned indicator values of 0–100. A value of 100 would indicate a species was observed in all sites of a given treatment and no other sites.

TABLE 5. Top models explaining occupancy patterns of select bird species within fire-suppressed longleaf pine sandhills undergoing hardwood removal, 1994–2010.

Species and site	Model	AIC	ΔAIC	w_i	L	np	−2LL
American Kestrel							
TRT	$\psi(\mathrm{PRD}), \gamma(\mathrm{PRD}), p(\mathrm{TRT})$	255.79	0	0.94	1.00	9	237.79
REF	$\psi(.), \gamma(.), p(\mathrm{SURV})$	103.08	0	0.90	1.00	21	61.08
Blue Grosbeak							
TRT	$\psi, \gamma(\mathrm{TRT} + \mathrm{PRD}), \varepsilon(\mathrm{TRT} + \mathrm{PRD}), p(\mathrm{TRT} + \mathrm{PRD})$	468.64	0	0.46	1.0	17	434.64
	$\psi(\mathrm{PRD}), \gamma(\mathrm{PRD}), p(\mathrm{TRT} + \mathrm{PRD})$	469.15	0.51	0.36	0.77	11	447.15
REF	$\psi(.), \gamma(.), p(\mathrm{SURV})$	120.59	0	0.88	1.0	21	78.59
Bachman's Sparrow							
TRT	$\psi, \gamma(\mathrm{TRT} + \mathrm{PRD}), \varepsilon(\mathrm{TRT} + \mathrm{PRD}), p(\mathrm{TRT} + \mathrm{SURV})$	339.23	0	0.97	1.00	33	273.23
REF	$\psi(.), \gamma(.), p(\mathrm{SURV})$	119.01	0	0.70	1.00	21	77.01
	$\psi(\mathrm{PRD}), \gamma(\mathrm{PRD}), p(\mathrm{SURV})$	120.68	1.67	0.30	0.43	24	72.68
Brown-headed Nuthatch							
TRT	$\psi, \gamma(\mathrm{TRT} + \mathrm{PRD}), \varepsilon(\mathrm{TRT} + \mathrm{PRD}), p(\mathrm{TRT} + \mathrm{SURV})$	294.13	0	0.79	1.00	33	228.13
REF	$\psi(.), \gamma(.), p(.)$	111.22	0	0.91	1.00	3	105.22
Northern Bobwhite							
TRT	$\psi(\mathrm{PRD}), \gamma(\mathrm{PRD}), p(\mathrm{TRT} + \mathrm{PRD})$	544.44	0	0.97	1.00	11	522.44
REF	$\psi(.), \gamma(.), p(.)$	134.42	0	0.99	1.00	3	128.42
Red-headed Woodpecker							
TRT	$\psi, \gamma(\mathrm{TRT}), \varepsilon(\mathrm{TRT} + \mathrm{PRD}), p(\mathrm{TRT} + \mathrm{PRD})$	410.66	0	0.54	1.00	16	378.66
TRT	$\psi, \gamma(\mathrm{TRT} + \mathrm{PRD}), \varepsilon(\mathrm{TRT} + \mathrm{PRD}), p(\mathrm{TRT} + \mathrm{PRD})$	410.98	0.32	0.46	0.85	17	376.98
REF	$\psi(.), \gamma(.), p(.)$	121.8	0	0.98	1.00	3	115.8

Note: Abbreviations are: w_i, weight; L, likelihood; np, number of parameters; −2LL, −2Loglike; PRD, primary sampling period; SURV, secondary sampling period; TRT, treatment.

study (including burning alone) together with long-term prescribed burning were sufficient to recover populations of these longleaf-associated species.

These findings suggest that reintroduction of fire or hardwood removal together with fire is sufficient to restore avian species associated with the reference longleaf pine habitat. However, complete eradication of hardwood trees may be to the detriment of even longleaf pine specialists (Perkins et al. 2008, Steen et al. 2012). We did not identify thresholds of hardwood density required to sustain the species we identified as indicators of reference conditions, though it may be worthwhile to explore this concept (Guénette and Villard 2005).

Ordination and indicator species

Eight species were significant indicators of reference sites during the pretreatment period (Table 4), including four species identified elsewhere as longleaf pine specialists: Red-cockaded Woodpecker, Bachman's Sparrow, Brown-headed Nuthatch, and Northern Bobwhite (Engstrom 1993, Means 2006), and three species that prefer open woodlands (American Kestrel, Red-headed Woodpecker, and Blue Grosbeak; Engstrom et al. 1984, Ingold 1993, Smallwood and Bird 2002). Interestingly, Blue Jays were also significantly associated with reference sites; this is counterintuitive due to their general use of many habitats and penchant for oak trees (Tarvin and Woolfenden 1999). Examination of percentage indicator values suggest that although Blue Jays were significantly associated with reference sites, they were relatively evenly distributed across all treatments (Table 4). Although we expected all treatments to have had similar bird assemblages during the pretreatment period, three species (Downy Woodpecker, *Picoides pubescens*; Northern Cardinal, *Cardinalis cardinalis*; and Pileated Woodpecker, *Dryocopus pileatus*) were significantly associated with sites that would eventually become control sites (Table 4). However, given that these three species were not positively associated with

TABLE 6. Probability of occupancy (mean with SE in parentheses) for American Kestrel and Northern Bobwhite observed on longleaf pine sandhills on Eglin Air Force Base, 1994–2010.

Bird species	Pretreatment	Early posttreatment	Late posttreatment
American Kestrel			
Treatment	0.18 (0.12)	0.85 (0.13)	0.7 (0.17)
Reference	0.83 (0.12)	0.83 (0.12)	0.83 (0.12)
Northern Bobwhite			
Treatment	0.99 (0.12)	0.97 (0.0)	1.0 (0.0)
Reference	1.0 (0.001)	1.0 (0.001)	1.0 (0.001)

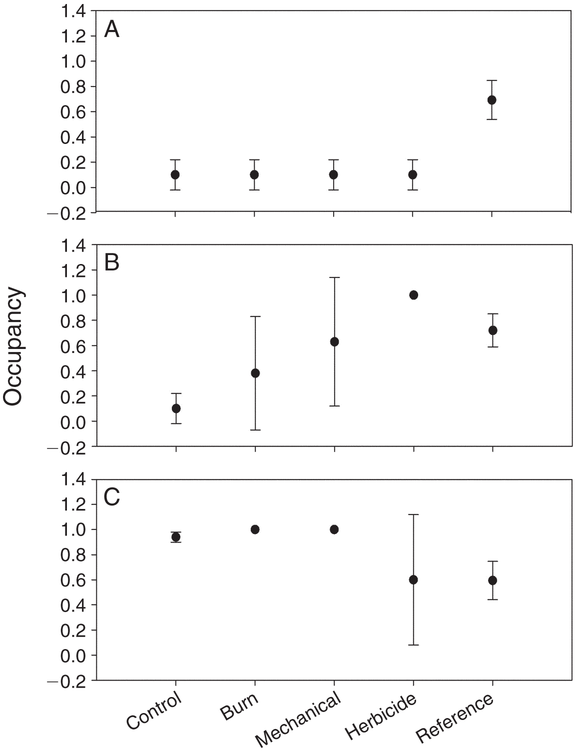

FIG. 4. Relationship between probability of occupancy (and standard errors) and year of study for Bachman's Sparrow (A) pretreatment, (B) early posttreatment, and (C) late posttreatment following hardwood removal on fire-suppressed longleaf pine sandhills, Eglin Air Force Base, Florida. Lack of numerical convergence and an inability to compute the variance–covariance matrix suggest that standard errors should be interpreted with caution.

control sites after hardwood removal, we assume this association did not confound our interpretations. The multi-response permutation procedure provided support for this assumption and suggested that all treatments were comparable to each other and distinct from reference sites prior to hardwood removal.

Early posttreatment, there was a clear distinction between avian assemblages on sites that experienced hardwood removal and assemblages on control sites. Thus, all three methods of hardwood removal were effective at altering the bird assemblage from those that inhabit fire-suppressed sandhills in the short term, corroborating earlier analyses (Provencher et al. 2002*b*). Bird assemblages at reference sites, however, were also distinct from those on hardwood removal sites, suggesting that hardwood removal was insufficient to restore the avian assemblage to the reference condition.

Although mechanical sites (early posttreatment) clustered together in our ordination, they were not distinct from other treatments. However, eight bird species were positively associated with mechanical sites during this time period, in contrast to only one species associated with controls and two in reference sites (Table 4). Although birds positively associated with mechanical sites were not exclusive to these areas, our analysis corroborates work suggesting these sites have relatively high avian species richness (Provencher et al. 2003). We suggest the trends we identified were temporary and resulted from disturbance unique to felling and girdling trees (i.e., mechanical removal). Specifically, the species positively associated with mechanical sites may be responding to short-term changes in insect communities brought on by killing adult oak trees and leaving the slash (e.g., Aulén 1991). Visual examination of the data reveals that the relative number of detections of species designated as indicators of mechanical sites declined in these sites following 1998–1999; by 2009–2010, these birds were detected in similar numbers across all treatments.

There were eight species associated with reference sites pretreatment, but only two (Red-cockaded Woodpeckers and Red-headed Woodpeckers) were positively associated with these sites early posttreatment. By the late posttreatment period, none of the original indicator species were still associated with reference sites (although Mississippi Kites, which previously had revealed

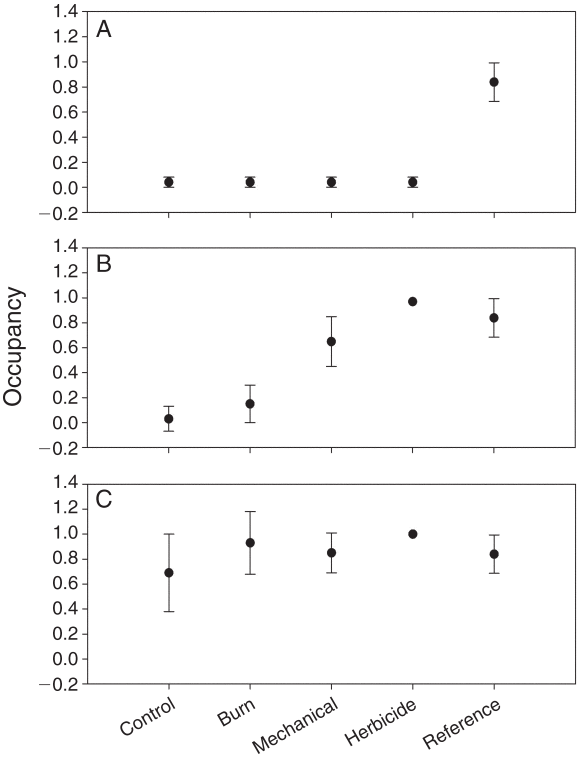

FIG. 5. Relationship between probability of occupancy (and standard errors) and year of study for Brown-headed Nuthatch (A) pretreatment, (B) early posttreatment, and (C) late posttreatment following hardwood removal on fire-suppressed longleaf pine sandhills, Eglin Air Force Base, Florida. Program PRESENCE was unable to produce standard errors surrounding occupancy at herbicide sites in panels (B) and (C).

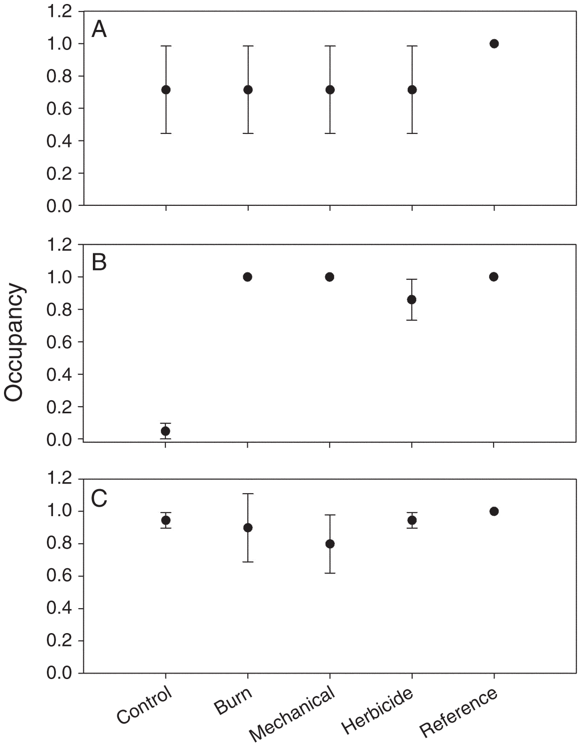

FIG. 6. Relationship between probability of occupancy (and standard errors) and year of study for Red-headed Woodpecker (A) pretreatment, (B) early posttreatment, and (C) late posttreatment following hardwood removal on fire-suppressed longleaf pine sandhills, Eglin Air Force Base, Florida.

no relationship, were; Table 4). This suggests hardwood removal in treatment sites increased the similarity of bird assemblages on treatment sites to those of reference sites over the long term, to the extent that they were indistinguishable by the conclusion of the study. The association between Mississippi Kites and reference sites is attributed to a 2009 nest on one reference site; they were not detected elsewhere.

Effects of restoration on occupancy probability

Prior to hardwood removal, there were several species with relatively high occupancy probabilities only in reference sites. Late posttreatment, occupancy probabilities for these species had generally increased and become relatively uniform across all sites. These results indicate that, for birds positively associated with longleaf pine forests in reference condition, burning alone, on a two- to three-year return interval over ~15 years, is sufficient to increase occupancy probability on previously fire-suppressed sites to levels typical of reference sites. Mechanical removal of hardwood trees or herbicide application accelerated the observed response. This finding was further supported by the long-term change in occupancy probability at control sites, which received prescribed fire after the first phase of the study, thus representing a delayed fire-only treatment.

American Kestrel, Blue Grosbeak, Red-headed Woodpecker, Bachman's Sparrow, and Brown-headed Nuthatch responded positively to hardwood removal. For the latter three species, occupancy probabilities were similar to those of reference sites immediately following treatments at the mechanical and herbicide sites, which may have influenced the interpretation by Provencher et al. (2002*b*) that these treatments are relatively effective. Red-headed Woodpecker and Blue Grosbeak had relatively high occupancy probabilities prior to treatment, which is likely a function of low detection probabilities. These species were detected infrequently within several different treatments, and it is difficult to confirm that a species is absent if it has a low detection probability. Low sample sizes limited our ability to estimate occupancy. This is reflected in the lack of standard errors around some occupancy estimates (e.g., Fig. 7). Therefore, we suggest our results related to occupancy probabilities are useful for examination of general trends but not necessarily for specific comparisons between treatments.

Northern Bobwhite, although detected more often in reference sites prior to treatment (Table 4), were likely present in all sites in every study period (Table 6). This

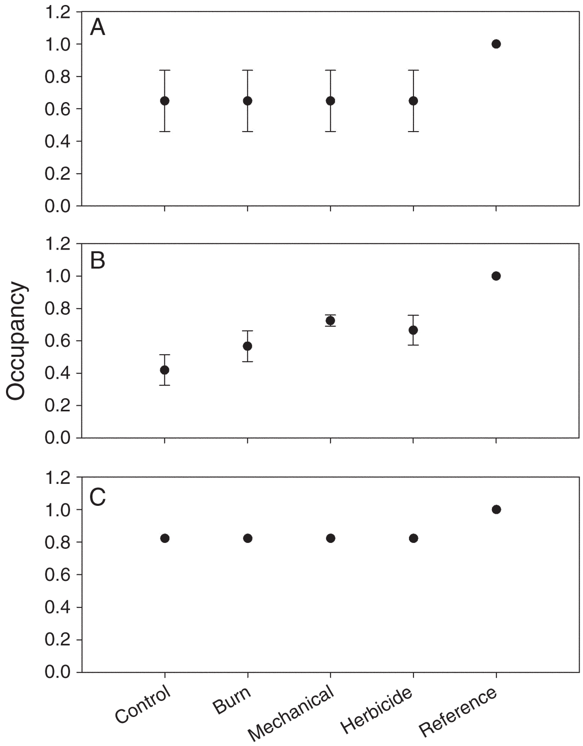

FIG. 7. Relationship between probability of occupancy (and standard errors) and year of study for Blue Grosbeak (A) pretreatment, (B) early posttreatment, and (C) late posttreatment following hardwood removal on fire-suppressed longleaf pine sandhills, Eglin Air Force Base, Florida.

species is of conservation concern and population declines have been attributed to habitat degradation and fire suppression (Brennan 1991). Our results suggest that, although Northern Bobwhite abundance may be greater in reference sites than in pretreatment fire-suppressed longleaf pine sandhills, the species was present in all treatment sites even prior to hardwood removal.

Synthesis and management implications

Avian assemblages at formerly fire-suppressed longleaf pine sandhills became indistinguishable from those on reference sites only after application of herbicide followed by over a decade of prescribed burning. However, for species highly associated with the ancestral condition of this habitat, occupancy probabilities on treatment sites generally became comparable to those on reference sites over the long term, regardless of initial method of hardwood removal. Overall, our study demonstrated different temporal and treatment responses by birds to restoration. These shifts may be ongoing, for example, midstory oak density at burn and mechanical sites appear to be increasing relative to levels immediately after treatment (Table 1). If oak density continues to increase, we might expect to observe declines in the occupancy probability of longleaf pine specialists.

Mechanical removal of trees was initially as effective at reducing oak overstory density as application of herbicides (Table 2 and Provencher et al. 2001*b*). Both methods are thought to quickly advance restoration of pine trees, as compared to fire alone (Provencher et al. 2001*b*, Menges and Gordon 2010), but these strategies may not be as effective for restoration of other groups (e.g., vegetation and insects; Provencher et al. 2001*b*). In addition, although herbicide application prohibits resprouting of oaks (Brockway et al. 1998), mechanical removal may actually encourage oak resprouting, at least in the absence of prescribed fire (Provencher et al. 2001*b*). In this study, application of herbicide likely prohibited resprouting of oaks for a longer period of time than mechanical removal (Table 2), which allowed herbicide sites to maintain a vegetation structure most similar to reference sites. This similarity in vegetation structure over a long time period may have allowed the bird assemblage to gradually transition to one most comparable to that of reference sites. In any case, it is likely that avian assemblages became more similar to reference sites over time at all sites due to a gradual change in vegetation structure resulting from hardwood removal and prescribed burning as well as from prescribed burning stimulating an increased productivity of herbivorous insects (Provencher et al. 2002*a*), which serve as prey for many of our study species.

Although herbicide application appeared to be the most effective long-term strategy for moving avian assemblages toward that of reference sites, further research is warranted. For example, the active ingredient of the herbicide in this study, hexazinone, can reach surrounding bodies of water (Neary et al. 1983); hexazinone is generally considered safe for wildlife (Michael et al. 1999) but limited research has been conducted pertaining to some groups (Berrill et al. 1994, Bridges and Semlitsch 2000). In addition, application of herbicides was relatively ineffective at restoring reptile assemblages at the same site (Steen et al. 2013). Given the diversity and rarity of some wildlife species in longleaf pine ecosystems (Means 2006) and on Eglin Air Force Base in particular (e.g., Enge 2005), we suggest caution when developing management plans that include hexazinone application.

If the goal is to use avian assemblages as a measure of ecological restoration on fire-maintained longleaf pine forests, our data suggest that application of herbicides followed by long-term prescribed burning is an effective approach. However, it may be more appropriate to focus restoration goals on a suite of indicator species associated with the longleaf pine ecosystem (Lambeck 1997, 2002, Roberge and Angelstam 2004); these are the species likely to be of conservation concern due to the global imperilment of this habitat type. In this case, reintroduction of burning alone over the long term (a relatively inexpensive method; Provencher et al. 2002*b*) would be an appropriate approach.

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