Ecological Applications, 23(1), 2013, pp. 148–158

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

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Abstract. Measuring the effects of ecological restoration on wildlife assemblages requires study on broad temporal and spatial scales. Longleaf pine (*Pinus palustris*) forests are imperiled due to fire suppression and subsequent invasion by hardwood trees. We employed a landscape-scale, randomized-block design to identify how reptile assemblages initially responded to restoration treatments including removal of hardwood trees via mechanical methods (felling and girdling), application of herbicides, or prescribed burning alone. Then, we examined reptile assemblages after all sites experienced more than a decade of prescribed burning at two- to thee-year return intervals. Data were collected concurrently at reference sites chosen to represent target conditions for restoration. Reptile assemblages changed most rapidly in response to prescribed burning, but reptile assemblages at all sites, including reference sites, were generally indistinguishable by the end of the study. Thus, we suggest that prescribed burning in longleaf pine forests over long time periods is an effective strategy for restoring reptile assemblages to the reference condition. Application of herbicides or mechanical removal of hardwood trees provided no apparent benefit to reptiles beyond what was achieved by prescribed fire alone.

Key words: Aspidoscelis sexlineata; *Eglin Air Force Base, Florida, USA; longleaf pine; nonmetric multidimensional scaling;* Pinus palustris; *prescribed fire; squamates;* Tantilla coronata.

Introduction

Forest management and ecological restoration of vegetation communities can have diverse and wide-ranging effects on associated wildlife populations and assemblages (Russell et al. 2004, Van Lear et al. 2005). The magnitude of these effects is not often quantified, perhaps due to the considerable challenges associated with accurately characterizing population demography and change over time (e.g., Block et al. 2001, Gardner et al. 2007). For example, although it is likely important to study wildlife response to management over a long temporal scale (Zedler and Callaway 1999, Cunningham et al. 2007), most investigations typically last only a few years (e.g., Bennett and Adams 2004, Greenberg and Waldrop 2008, Kilpatrick et al. 2010, Steen et al. 2010*a*). Similarly, experimental studies allow for strong inference regarding the effects of ecological restoration on wildlife assemblages (Block et al. 2001), but it is often difficult to apply an experimental design on a relatively large scale (i.e., the landscape) and maintain managed disturbance regimes (e.g., fire or timber activity) without affecting planned treatments or replicates.

Fire plays an important role in maintaining the structure and function of multiple ecosystems (Nowacki and Abrams 2008, Pausas and Keeley 2009). The fire-adapted longleaf pine (*Pinus palustris*) ecosystem of the southeastern United States was once extensive (Landers et al. 1995) but is now highly imperiled (Noss 1988). Longleaf pine forests not lost to human development or land-use conversion may become degraded due to fire suppression (Noss 1989). Hardwood trees (e.g., oaks, *Quercus* spp.) often eventually dominate forests in which fire has been excluded, altering forest structure, composition, and forest fuels (Mitchell et al. 2006, Hiers et al. 2007).

Restoration of longleaf pine forests typically includes reintroduction of frequent fire (Brockway et al. 2005). However, public acceptance of prescribed fire is mixed (e.g., Shindler and Toman 2003, Brunson and Evans 2005), and reintroducing fire to a long-unburned area may have unintended consequences, such as excessive mortality of native species (e.g., Varner et al. 2005). As a result, it is occasionally necessary to reduce fuel loads via means other than fire. In addition, fire alone may be

Manuscript received 3 February 2012; revised 5 June 2012; accepted 13 June 2012. Corresponding Editor (ad hoc): D. B. Tinker.

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ineffective at restoring the functions of highly degraded ecosystems (Brockway et al. 2005). Consequently, fire surrogates have been developed, including herbicides and mechanical removal of hardwood trees, to facilitate reaching restoration goals. Attempts have been undertaken to determine the relative effectiveness of these surrogates at reducing fuel loads (McIver et al. 2009) as well as at restoring the vegetation to the ancestral condition (Brockway et al. 1998). However, the effects of fire surrogates on wildlife populations are rarely documented (Russell et al. 1999), particularly following the initial impact of the surrogate, as the habitat moves along a trajectory toward reference condition.

Herbicides and mechanical means of hardwood removal are unlikely to replicate the ecological effects of frequent, prescribed burning in longleaf pine forests (Menges and Gordon 2010); however, they may be useful tools in restoring conditions necessary to reintroduce fire into these forests (Provencher et al. 2001*a*, Brockway et al. 2005). It is generally suggested that these fire surrogates may quickly alter forest structure toward a desired condition, and that this change can be maintained or enhanced through subsequent applications of prescribed fire (Brockway et al. 2005, Outcalt and Brockway 2010). Although short-term effects of fire surrogates on wildlife in the longleaf pine ecosystems have been described, the long-term legacy of these surrogates and their effects on wildlife remain elusive. However, application of fire over long time periods may be necessary to move the ecosystem to a condition comparable to that which was assumed to occur prior to European settlement (Waldrop et al. 1992).

Longleaf pine forests contain a high diversity of vertebrate animals (Means 2006). Many reptiles occur largely in longleaf pine forests, to the extent that several are considered specialists of this ecosystem (Guyer and Bailey 1993, Means 2006). Because small reptiles may be abundant in high-quality habitats, they comprise a considerable component of the vertebrate biomass (e.g., Bullock and Evans 1990). Consequently, this group may be useful for monitoring the effects of forest management on wildlife (e.g., Greenberg et al. 1994, Todd and Andrews 2008). Although restoration of natural disturbance regimes in frequently burned ecosystems is thought to benefit highly associated species (e.g., Greenberg et al. 1994, Litt et al. 2001), it is difficult to predict how assemblages may respond because the mechanisms driving changes may be complicated (Lindenmayer et al. 2008); in addition, even species highly associated with the longleaf pine forest may select other habitats (Steen et al. 2012*b*).

Within this study, we used a landscape-scale, randomized-block design to apply prescribed fire and fire surrogates (herbicide and mechanical hardwood removal) to fire-suppressed longleaf pine sandhills. We then used ordination techniques and similarity indices to examine how reptile assemblages varied among sites immediately after treatment and again to explore legacy effects on wildlife after application of frequent prescribed burning over a 15-year period. Then, we used indicator species analysis to identify the species driving these changes and canonical correspondence analysis to identify potential habitat features influencing the changes we observed. Finally, we evaluated whether restoration goals were met by comparison of assemblages on treatment sites to those on reference sites, which were in a condition that we considered a target of restoration efforts.

Materials and Methods

Study site

This study took place on fire-suppressed longleaf pine sandhills on Eglin Air Force Base, Okaloosa and Santa Rosa Counties, Florida, USA (see Fig. 1 in Steen et al. 2013). A randomized block design was used to assign hardwood removal method treatments to 16 sites (a subsample of the sites used in a concurrent study evaluating bird response to hardwood removal; Steen et al. 2013); each site was 81 ha in size and arranged in four blocks (Litt et al. 2001, Provencher et al. 2001*a*). With the exception of six sites that experienced a single burn between 1977 and 1989, all treatment sites had not been burned since at least 1973 (when record-keeping began; B. Williams, *personal communication*); because the natural fire frequency in this system is every 1–10 years (Myers 1990), we considered them all fire-suppressed. Hardwood removal treatments included (1) prescribed burning (burn), (2) herbicide application (herbicide), or (3) felling-girdling (mechanical). Control sites were also represented within each block; these sites experienced no treatment in 1995. Independent from the randomized-block design, we included four 81-ha reference sites. Reference site selection is described in Provencher et al. (2001*a*). Briefly, reference sites had been burned at frequent intervals over the long term due to ordnance fires and contained flora and wildlife assemblages we considered representative of a longleaf pine forest.

Treatment application

Initial hardwood removal treatments occurred in 1995. Burn-only treatments were applied in April–June. 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 and mechanical hardwood removal was conducted between June and November. In 1997, after application of herbicide and mechanical removal of hardwoods, herbicide and mechanical sites received a prescribed burn (Provencher et al. 2001*a*, *b*). After treatment application, all sites received comparable management, which included prescribed fire on a two- to three-year rotation but no additional targeted removal of hardwoods or application of herbicide. After 1999, sites that were formerly fire-suppressed control sites began to receive prescribed fire on the same rotation as treatment sites. For clarity, we continue to refer to these sites as controls. One reference site received herbicide application in 2006; thus, we excluded data collected from this site during 2009–2010.

Reptile trapping

To capture squamates, drift fence arrays (Campbell and Christman 1982) were placed at the center of each of 16 treatment sites and four reference sites. Hereafter, all captured squamates and turtles are collectively referred to as reptiles. Fences were made of aluminum flashing and 16 19-L pitfalls were placed along the fences of each array (30 m total of flashing per array). In the initial study, arrays were sampled from May to August 1997 and from April to August 1998 (Litt 1999, Litt et al. 2001; hereafter, early posttreatment); arrays were removed in 1998. In the second phase of the study, we reinstalled arrays in the same location at each site and reptiles were trapped from May to September 2009 and May to August 2010 (hereafter, late posttreatment). Late posttreatment, we added box traps to the center of the arrays as part of a separate study and slightly modified the array design (Burgdorf et al. 2005, Steen et al. 2010*b*), but used the same length of drift fence and the same number of pitfall traps per array as in the original study.

All reptiles were individually marked early posttreatment but due to low recapture rates of most species (e.g., eastern fence lizard, *Sceloporus undulatus*, 7.4%; broad-headed skink, *Plestiodon laticeps*, 6%; little brown skink, *Scincella lateralis*, 0%) and low recapture rates for these animals in general (e.g., Todd and Andrews 2008), we only individually marked six-lined racerunners (*Aspidoscelis sexlineata*) late posttreatment (Steen 2011). We suggest data used in our analyses (i.e., the number of captures, irrespective of recapture status) are comparable to those used in other comparisons of capture rates (e.g., McCoy and Mushinsky 1999, Matthews et al. 2010). In addition, analysis of individual-level data of *Aspidoscelis sexlineata* returned results consistent with capture-level data (Steen et al., *in press*). We did not convert overall captures to captures per trap night because trapping effort was standardized across all treatments within each study period (e.g., Litt 1999, Steen 2011). We excluded box trap captures from the analysis because this method was not used in the initial study.

Vegetation data

Vegetation data were collected in 1994, 1998, 2009 (reference sites only), and 2010 (treatment sites only). The original subplots in the sampling design were arranged in four transects with either a 10-m "clumped" or 50-m "spaced" separation. Late posttreatment, we chose to revisit only the 16 clumped subplots. For one burn site late posttreatment, we substituted four clumped subplots within a transect with spaced subplots randomly chosen from the remaining transects because it was clear that the clumped subplots were in a riparian fire shadow and had not burned in decades. Midpoints of vegetation cover classes (1–5%, 5–25%, 25–50%, 50–75%, 75–95%, 95–100%) for three ground cover vegetation categories (i.e., grass, woody litter, fine litter) were used to calculate mean percent cover for each site.

Midstory trees were distinguished from overstory trees based on their diameter at breast height (dbh). A pine tree was considered overstory if it had dbh $\geq$4 inches (10.16 cm). An oak tree was considered overstory if it had dbh $\geq$6.3 inches (16 cm). We calculated the mean basal area (square meters per hectare) of midstory and overstory trees for each site.

Reptile assemblage similarity

We calculated the Morisita-Horn similarity index for all reptiles at each site with Estimate S software version 8.2 (Colwell 2009). We selected this particular similarity index because it is statistically robust and relatively insensitive to low species richness and sample sizes (Magurran 2004). We first derived similarity values between reference sites early posttreatment and again late posttreatment. Each site within a study period was then compared to the mean similarity index of reference sites for that study period. In other words, we determined whether hardwood removal sites differed from reference sites more than reference sites, on average, differed from each other.

We used a before–after control–impact study design (Stewart-Oaten et al. 1986) to compare reptile similarity with separate least squares means analyses of variance. Because we lacked pretreatment data, the impact we are evaluating with this analysis is long-term prescribed burning, not the effects of the initial treatments on a fire-suppressed condition. We compared similarity on fire-suppressed controls and burn, mechanical, and herbicide treatments to similarity on reference sites early posttreatment. We also compared similarity on treatments early posttreatment to similarity on treatments late posttreatment to determine if reptile assemblages differed following a decade of prescribed burning. Finally, we compared similarity on all treatment sites to that of reference sites late posttreatment. Our alpha level for all analyses was 0.10.

Nonmetric multidimensional scaling

We conducted a single nonmetric multidimensional scaling ordination, based on Bray-Curtis (Sorenson) distances, such that each site appeared in the ordination twice, once based on early posttreatment data and again based on late posttreatment data. We used a multi-response permutation procedure (MRPP; Mielke and Berry 2001) to determine whether a particular treatment (or reference site) was distinct from the other treatments within a given time period. Statistical significance was determined with Monte Carlo simulations. Analysis was implemented with PC-ORD version 4.25 (McCune and Mefford 1999).

Table 1. Tree basal area (mean with SE in parentheses) within treatment and reference sites, Santa Rosa and Okaloosa Counties, Eglin Air Force Base, Florida.

	Basal area (m^2/ha)		
Site, treatment	Pretreatment	Early posttreatment	Late posttreatment
Pinus palustris midstory			
Burn	0.13 (0.05)	0.05 (0.02)	0.05 (0.02)
Control	0.10 (0.02)	0.07 (0.01)	0.01 (0.01)
Herbicide	0.09 (0.02)	0.04 (0.01)	0.28 (0.10)
Mechanical	0.10 (0.02)	0.03 (0.01)	0.07 (0.02)
Reference	0.03 (0.01)	0.02 (0.01)	0.13 (0.06)
Pinus palustris overstory			
Burn	12.78 (1.85)	12.01 (1.72)	12.93 (1.66)
Control	7.88 (0.93)	8.71 (0.93)	10.09 (0.40)
Herbicide	11.84 (2.35)	12.01 (2.41)	11.36 (1.50)
Mechanical	12.15 (2.43)	11.14 (3.16)	11.79 (2.18)
Reference	16.15 (2.34)	16.65 (2.69)	18.12 (4.74)
Quercus sp. midstory			
Burn	0.79 (0.16)	0.22 (0.11)	0.56 (0.21)
Control	1.07 (0.13)	1.23 (0.19)	0.72 (0.24)
Herbicide	0.56 (0.14)	0.02 (0.01)	0.14 (0.04)
Mechanical	0.87 (0.08)	0.09 (0.07)	1.59 (0.33)
Reference	0.11 (0.03)	0.17 (0.13)	0.11 (0.11)
Quercus sp. overstory			
Burn	10.08 (2.45)	5.41 (2.79)	5.22 (1.65)
Control	10.10 (1.34)	9.36 (1.97)	3.76 (1.19)
Herbicide	9.08 (1.27)	0.40 (0.15)	0.04 (0.02)
Mechanical	11.74 (1.73)	2.18 (1.22)	7.82 (6.78)
Reference	4.93 (1.93)	2.93 (0.33)	0.93 (0.64)

Notes: One reference site was not included in late posttreatment summaries.

Because we lacked pretreatment data, we assumed that control sites early posttreatment were representative of the pretreatment condition at all treatment sites prior to hardwood removal. If the MRPP indicated no significant difference between a treatment and reference sites, we interpreted this to mean that the treatment resulted in conditions indistinguishable from those of reference sites. If the MRPP revealed a significant difference between conditions on treatment and reference sites, we considered the treatment as ineffective for restoration of reptile assemblages.

Indicator species analysis

We identified indicator reptile species by quantifying the relative exclusivity and abundance of each species to a particular treatment (Dufrêne and Legendre 1997). We compared a treatment (or reference) only to other treatments within a study period. Statistical significance was determined with 1000 Monte Carlo simulations. Analysis was completed with PC-ORD version 4.25 (McCune and Mefford 1999).

Canonical correspondence analysis

To identify habitat features within our sites that may have influenced reptile abundances, we conducted a separate canonical correspondence analysis (CCA; ter Braak 1986) for each study period with species captured at least 10 times. CCA is a form of multivariate regression useful for identifying relationships between abundance data and environmental variables (Palmer 1993). Within a CCA, a least squares regression of site scores (dependent variable, derived from weighted species abundance data) against environmental variables (independent variable) is conducted. In this manner, each site receives a score based on the regression equation (LC scores; Palmer 1993). An advantage of this technique is that it is unaffected by correlated environmental variables or skewed distributions (Palmer 1993) and may identify relationships other than those that are unimodal (ter Braak and Verdonschot 1995). The analysis allows production of a biplot that graphs sites and species in ordination space according to their association with environmental variables. Important environmental variables may be graphed onto the biplot as vectors, the length of which represents their relative importance (Methratta and Link 2006).

Environmental data included in the CCA included vegetative categories of grass, woody litter, fine litter, oak midstory, pine midstory, and oak overstory. Count data were square-root transformed and environmental variables were log-transformed prior to analysis (Palmer 1993). Statistical significance was determined via Monte Carlo simulations of eigenvalues and species–environment correlations. Analysis was completed with PC-ORD version 4.25 (McCune and Mefford 1999).

Results

Vegetation data

Mean oak basal area decreased initially at the three hardwood removal treatments (Table 1). Burn, control,

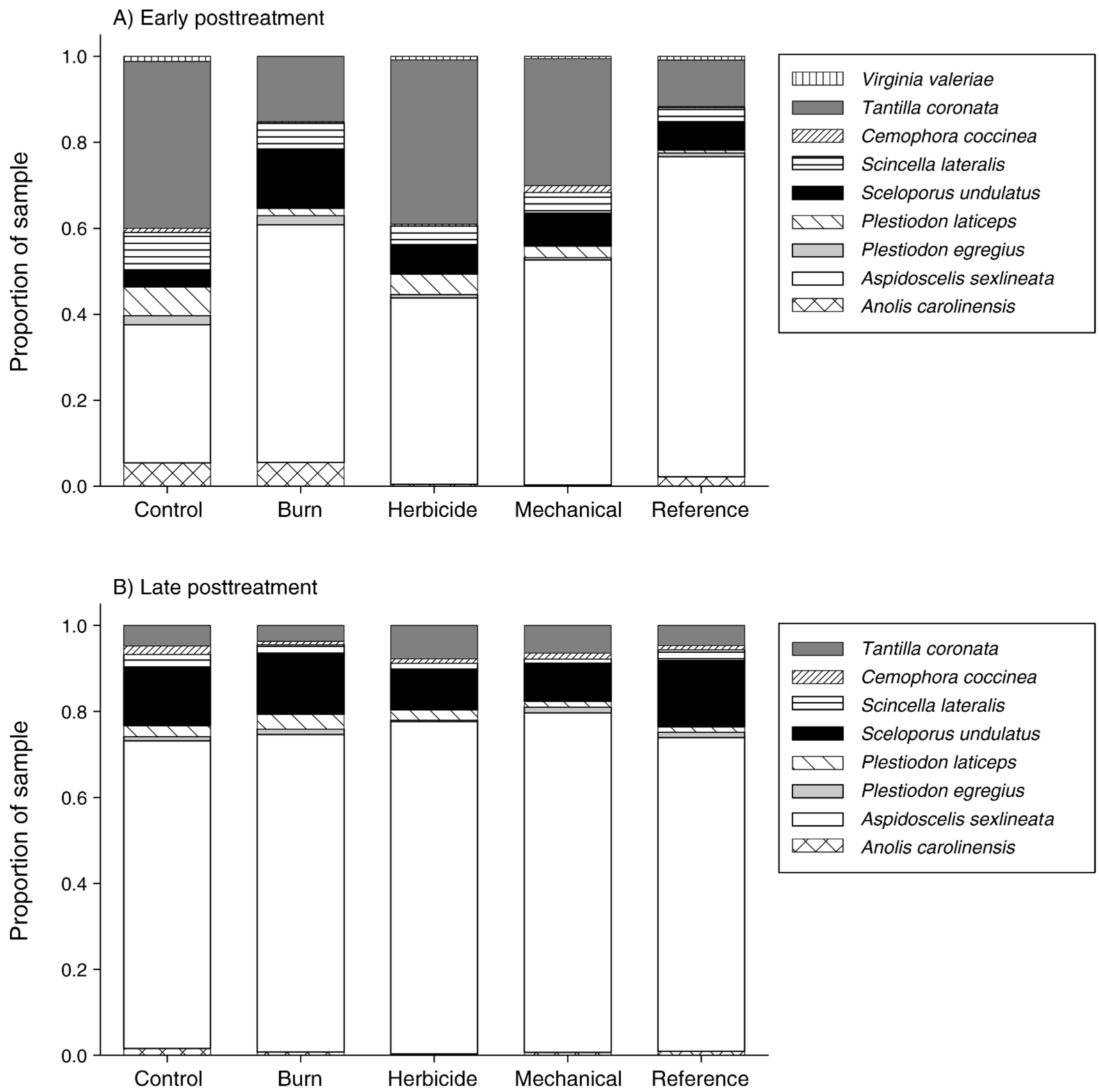

FIG. 1. (A) Relative proportion of reptile species on fire-suppressed longleaf pine (*Pinus palustris*) sandhills captured in treatment and reference sites on Eglin Air Force Base, Florida, USA, early posttreatment. Species captured ≤ 5 times are not included in the figure. (B) Relative proportion of species captured in treatment and reference sites on Eglin Air Force Base, late posttreatment. Species captured ≤ 5 times are not included in the figure.

and herbicide treatment sites had lower oak overstory basal area late posttreatment than early posttreatment, while oak basal area increased at mechanical sites. Oak midstory decreased at control and herbicide sites between the early posttreatment period and the late posttreatment period, while it increased at burn and mechanical sites.

Reptile assemblage similarity

We recorded 1775 captures of 16 reptile species early posttreatment and 1648 captures of 19 reptile species late posttreatment. Similarity (Morisita-Horn index) changed over time and differed between the hardwood removal treatments ($F_{4,1} = 2.20$, $P = 0.093$). Specifically, during the early posttreatment period, reference sites were more similar to each other than they were to herbicide ($P = 0.05$) and control sites ($P = 0.0006$). These trends are likely influenced heavily by two species; the relative proportion of *A. sexlineata* was low in control and herbicide sites, while the relative proportion of southeastern crowned snakes (*Tantilla coronata*) was higher in these sites (Fig. 1A).

Late posttreatment, similarity did not differ among treatments (Fig. 1B); similarity changed significantly at control ($P = 0.0006$) and herbicide ($P = 0.06$) sites between the two study periods. Cumulatively, this suggests that burn and mechanical treatments were effective at replicating the target condition shortly after treatment application (i.e., early posttreatment). Between this time period and late posttreatment, the reptile

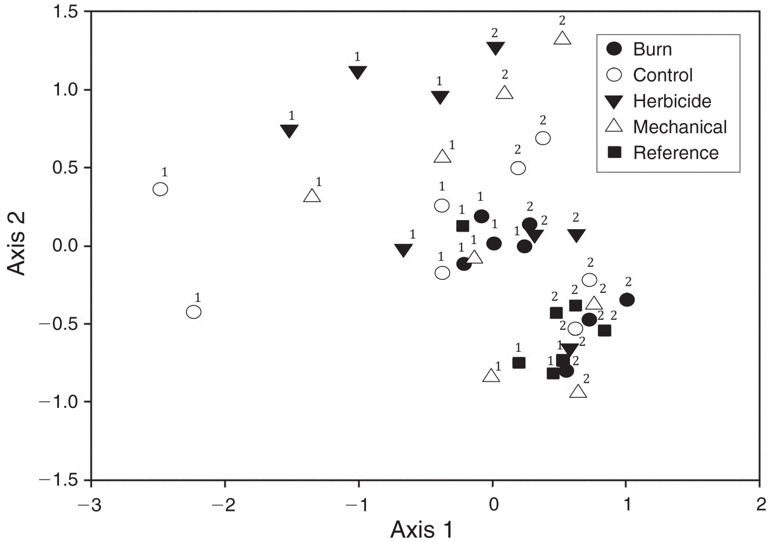

FIG. 2. Nonmetric multidimensional scaling of treatment and reference sites for early and late posttreatment, Eglin Air Force Base, Santa Rosa and Okaloosa Counties, Florida. Key: 1, early posttreatment; 2, late posttreatment.

assemblages at control and herbicide sites changed significantly to become indistinguishable from those on reference sites.

Nonmetric multidimensional scaling

A two-dimensional solution best fit the data, with a final stress of 9.3 and instability of 0.00009 after 55 iterations. The stress was less than expected by chance ($P = 0.03$; Fig. 2). Early posttreatment, control, mechanical, and herbicide sites were indistinguishable, based on the MRPP (Table 2). Reference sites were distinct from all treatments, as were burn sites. This suggests that mechanical and herbicide treatments did not alter the reptile assemblages such that they were different from assemblages at sites that experienced no hardwood removal. Reptile assemblages at burn sites likely represented an intermediate condition, different from those of control sites but still distinguishable from those of reference sites. Late posttreatment, reptile assemblages at herbicide sites were distinct from those of references; otherwise there were no differences (Table 2).

Indicator species analysis

Three species were significantly associated with a particular treatment early posttreatment (Table 3). *Aspidoscelis sexlineata* was positively associated with reference sites, ring-necked snake (*Diadophis punctatus*) was positively associated with control sites, and *S. undulatus* was positively associated with burn sites. No significant indicator species were identified in any of the treatments late posttreatment, indicating a relatively uniform distribution of species across treatments.

Canonical correspondence analysis

For the early posttreatment data, 35.5% of the species distribution variance was explained by the first two axes (Fig. 3). Eigenvalues for axis 1 and 2 were significant ($P = 0.03$ and 0.09, respectively). Important habitat variables explaining variation on axis 1 included Fine

TABLE 2. Results (P values) associated with multi-response permutation procedure on pairwise comparisons of reptile assemblages on treatment and reference sites (early and late posttreatment).

Site, treatment	Burn	Control	Mechanical	Herbicide	Reference
Early posttreatment					
Burn		**0.01**	**0.008**	**0.01**	**0.034**
Control			0.46	0.24	**0.02**
Mechanical				0.3	**0.09**
Herbicide					**0.02**
Late posttreatment					
Burn		0.44	0.47	0.69	0.77
Control			0.53	0.77	0.19
Mechanical				0.9	0.19
Herbicide					**0.08**

Notes: Boldface indicates a significant difference between groups ($\alpha = 0.10$).

TABLE 3. Percentage indicator values for reptile species significantly associated with a particular treatment on Eglin Air Force Base, early posttreatment.

Species	Burn	Control	Mechanical	Herbicide	Reference	*P*
Aspidoscelis sexlineata	21	11	21	11	**36**	0.007
Diadophis punctatus	0	**75**	0	0	0	0.025
Sceloporus undulatus	**36**	9	21	12	22	0.015

Notes: 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. Boldface indicates a significant association with a particular treatment ($P < 0.05$).

Litter (intraset correlation of –0.78). Species with CCA scores >0.5 from 0 on this axis included scarlet snake (*Cemophora coccinea*; –0.53), and smooth earth snake (*Virginia valeriae*; –0.51). Important variables explaining variation on axis 2 included oak midstory (intraset correlation of 0.67) and oak overstory (intraset correlation of 0.86). Species with scores >0.5 from 0 on axis 2 included green anole (*Anolis carolinensis*; 0.55) and *C. coccinea* (–0.53). Eigenvalues for the late posttreatment data were not significantly different than expected by chance, suggesting variables did not explain variance in reptile abundance.

Discussion

We demonstrate that, over the short term, application of prescribed fire resulted in increased similarity of reptile assemblages on treatment sites to that of reference sites, corroborating the findings of Litt et al. (2001). Over the long term, repeated use of prescribed fire was effective at restoring assemblages at all treatment sites, such that they became indistinguishable from those at reference sites. Thus, we conclude that reintroduction of a natural disturbance regime (i.e., burning on a two- to three-year return interval) is a sufficient method of restoring reptile assemblages in fire-suppressed longleaf pine forests (see Plate 1). As noted in reference to bird assemblages (Steen et al. 2013), it is possible that reptiles are responding to a change in vegetation structure or in response to changes in insect populations due to prescribed fire (Provencher et al. 2002*a*), but the role of forest floor development (litter and duff) may also be influential (Hiers et al. 2007).

With regard to the effectiveness of fire surrogates in early posttreatment analyses, we found consistent differences in reptile assemblages between control and herbicide sites vs. those on reference sites, again corroborating previous analyses (Litt et al. 2001). Litt et al. (2001) suggested that some species benefit from habitat heterogeneity, which is present in burned and mechanical sites but may be relatively low in both control and herbicide sites. Herbicide sites experienced a reduction in ground cover vegetation following herbicide application and a reduction in woody debris due to

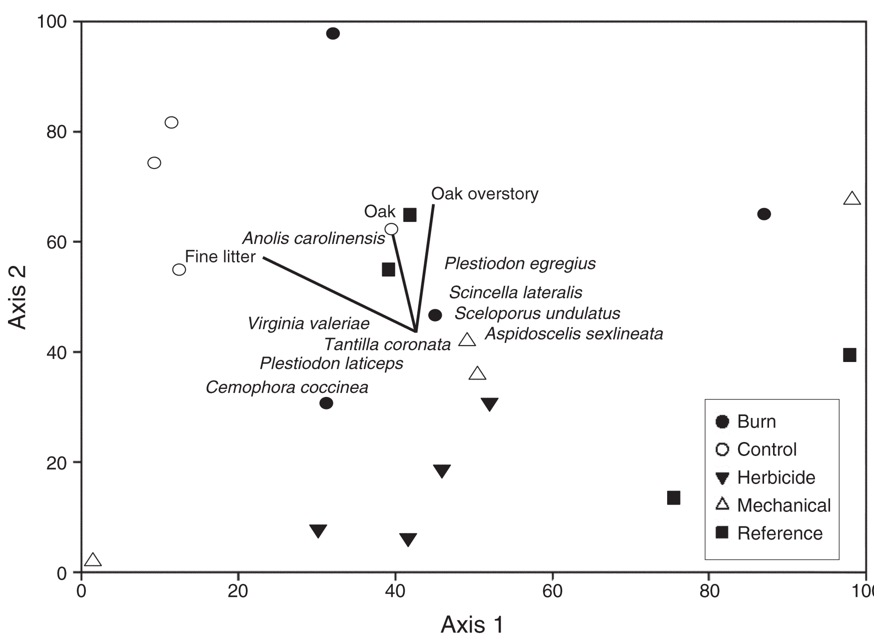

FIG. 3. Canonical correspondence biplot for reptiles captured early posttreatment, Eglin Air Force Base, Santa Rosa and Okaloosa Counties, Florida.

Plate 1. A site that experienced only fire (prescribed burning) over the course of this study, photographed late posttreatment. Photo credit: D. A. Steen.

prescribed burns, whereas control sites contained a high percentage of litter and woody debris (Litt et al. 2001).

Regardless of the initial relative effectiveness of the three hardwood removal treatments, our results were generally consistent in suggesting that reptile assemblages at all treatment sites were indistinguishable from those at reference sites late posttreatment (with the exception of the NMDS distinguishing assemblages on herbicide sites from those on reference sites). Because reptile assemblages responded quickly following the prescribed burn treatment and assemblages at all sites eventually became indistinguishable from those of reference sites, we see no long-term benefit to mechanical or herbicide removal of hardwoods over the use of fire alone. Prescribed fire alone was sufficient to recover reptile assemblages of the longleaf pine ecosystem over the long term, as has been observed among vegetation communities in longleaf pine forests elsewhere (Outcalt and Brockway 2010).

Our findings are not without caveats. Despite the 15-year time frame, our study may not have been conducted on a time scale sufficient to detect long-term trends in the response of reptile assemblages to the treatments and subsequent reintroduction of frequent fire. For example, mechanical sites initially experienced a considerable decline in oak density (Table 1); however, by the late posttreatment study period, oaks had rebounded to the extent that their overstory density approached levels observed at controls early posttreatment as coppice sprouting of mechanically removed hardwoods reached the midstory (Provencher et al. 2001*b*). Continued monitoring of these sites may document a gradual increase in oak density and a transition of the reptile assemblage toward one more associated with hardwood-dominated habitats. This would require us to reevaluate whether prescribed fire alone is sufficient to move a site toward the reference condition. Additionally, considering how heterogeneity in detection probability influences capture rates is important when making inferences about relative abundance of animals (Mazerolle et al. 2007). Although there are methods to integrate variation in detection probability to generate estimates of relative abundance (e.g., Royle and Nichols 2003), they may not be effective at small sample sizes or low detection rates (Steen 2010, Steen et al. 2012*a*). Most species within this study were detected infrequently and in low numbers; thus, we were unable to account for variability of detection.

Our results highlight the potential importance of time since treatment in recovery of reptile assemblages. For example, all three treatments received fire before reptile sampling was initiated in 1998; however, burn treatments received fire in 1995 whereas mechanical and herbicide sites were burned early in 1997. The disparate reptile assemblages initially observed among the treatment sites suggests time since burn may be influential.

Although some species likely benefited from hardwood removal, particularly *A. sexlineata* (Steen et al., *in press*), we suggest that the assemblage-level change we documented was due largely to the decline of hardwood-associated species. For example, *D. punctatus*, although observed only rarely, was an indicator of control sites early posttreatment but was not detected late posttreatment despite increased trapping effort. *Diadophis punctatus* prefers areas with abundant undisturbed litter and detritus (Perison et al. 1997), as does *S. lateralis* (Conant and Collins 1998), which also declined in number between the two study periods. Both species are likely to avoid frequently burned landscapes (Wilgers and Horne 2006).

Virginia valeriae and *C. coccinea* were positively associated with fine litter cover. *Cemophora coccinea* also had a negative relationship with oak density, suggesting this snake prefers relatively open canopy habitat with abundant fine litter. Both fine litter cover and oak density were positively associated with control sites and are likely to be altered considerably following hardwood removal and reintroduction of fire. We also observed a decline in the relative number of captures of *T. coronata* (Fig. 1A, B), another species that may select landscapes based on microhabitat features (Semlitsch et al. 1981). Cumulatively, our data suggest that small snakes decline in abundance at fire-suppressed sites following hardwood removal and reintroduction of frequent fire. Todd and Andrews (2008) observed that declines among this poorly known group of snakes occur in response to timber harvest in pine plantations and suggested that the declines were due largely to reduction in canopy cover and litter density. Similarly, management of canopy cover was sufficient to restore reptile assemblages elsewhere (Pike et al. 2011). Our results from natural longleaf pine stands appear to corroborate studies emphasizing the importance of these habitat features.

Anolis carolinensis was also observed less frequently late posttreatment. Early posttreatment, this species was positively associated with midstory oaks, which likely offer suitable perches for this arboreal species (Irschick et al. 2005). Because frequent burning reduces midstory oak density, *A. carolinensis* populations may decline following a reduction in this habitat feature. On the other hand, the species may shift habitat use to larger and taller oaks in the absence of midstory oaks, making them less susceptible to capture in drift fence arrays.

Aspidoscelis sexlineata benefits from hardwood removal and reintroduction of fire in fire-suppressed ecosystems (Mushinsky 1985, Perry et al. 2009). As expected, we documented shifts in the relative proportion of this species between the two study periods (Fig. 1A, B), when all sites were subjected to frequent prescribed fire. Thus, we suspect that frequent fire is likely to benefit other reptile species highly associated with the longleaf pine ecosystem (e.g., Yager et al. 2007). However, several reptile species associated with the longleaf pine ecosystem, such as gopher tortoise (*Gopherus polyphemus*), indigo snake (*Drymarchon couperi*), eastern diamond-backed rattlesnake (*Crotalus adamanteus*), southern hog-nosed snake (*Heterodon simus*), pinesnake (*Pituophis melanoleucus*), and mimic glass lizard (*Ophisaurus mimicus*; Guyer and Bailey 1993, Means 2006) were either undetected or captured only rarely given our sampling methodology; as such, we know little about whether the trends we documented are applicable to this group.

Greenberg et al. (1994) suggested that disturbance in general, rather than a specific forest-restoration treatment, may be important in maintaining reptile communities associated with frequently burned ecosystems. Our study design did not include long-term monitoring of sites treated only with mechanical removal of hardwood trees or herbicides; therefore we are unable to determine if continued disturbance of either type would have had the same effects as frequent fire. Previous data have suggested that felling/girdling or application of herbicides may be effective when attempting to quickly advance the midstory of a fire-suppressed longleaf pine forest to a reference condition; however, this strategy may overlook vital components of comprehensive ecological restoration (i.e., vegetation and insects; Provencher et al. 2001*b*). Because we observed no unique benefits to application of herbicides or mechanical removal of hardwoods and these management techniques require more time and effort than burning alone (Provencher et al. 2002*b*), we recommend prescribed burning for effective restoration of small reptile assemblages in fire-suppressed longleaf pine sandhills.

Acknowledgments

Funding was provided by the Strategic Environmental Research and Development Program (SERDP) Project Number SI-1696. Portions of the project were funded through the Gopher Tortoise Council's J. Larry Landers Student Research Award. B. Williams (Eglin) provided logistic help. A. Barnett provided assistance with data management. J. Grand, C. Anderson, and N. Chadwick provided input on earlier drafts. O. Sylvester provided helpful discussion on statistical analyses and reviewed an earlier draft of the manuscript. D. Simpson, M. Baragona, M. Cent, and M. Betzhold provided assistance in the field. Numerous volunteers assisted with trap installation. E. P. Cox (Jones Center) and Auburn University librarians provided assistance obtaining references.

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