Wildlife Restoration via Forest Management in Fire-Suppressed Longleaf Pine Sandhills

by

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Abstract

The once-extensive longleaf pine (*Pinus palustris*) ecosystem of the southeastern United States has been reduced to a fraction of its historic extent. A fire-adapted system, many remaining fragments have been fire-suppressed and invaded by hardwood trees, particularly oaks (*Quercus* spp.). This change in species composition alters the habitat and is to the detriment of wildlife assemblages associated with longleaf pine forests. Fire surrogates and prescribed burning have been suggested as potential management strategies to restore fire-suppressed and hardwood-invaded longleaf pine forests to target conditions; due to the unique effects of fire, it is generally suggested that prescribed burning should follow application of any hardwood removal treatment. To determine whether fire surrogates followed by prescribed burning affected wildlife populations and assemblages, we sampled for birds and reptiles within 20 experimental sites and six reference sites. Experimental sites were initially subjected to either mechanical hardwood removal followed by fire, herbicide application followed by fire, prescribed burning alone, or remained in a fire-suppressed state (i.e., controls). Following initial treatment, all sites experienced over a decade of prescribed burning on an approximately two-year interval. We evaluated the effects of a given treatment by comparison of wildlife populations and assemblages on treatment sites to those on reference sites initially and also after over a decade of prescribed burning. If conditions associated with a given treatment were indistinguishable from those of reference sites, we considered this as evidence that management objectives were met. Over the long-term, application of herbicide followed by prescribed burning was the only method that restored bird assemblages to the reference condition, although species positively associated with longleaf pine in reference condition responded positively to all treatments. Occupancy probabilities for these species on all treatment sites were indistinguishable from those on reference sites by the conclusion of the study. Initially, reptile assemblages within treatment sites treated with prescribed burning alone were most similar to those of reference sites; fire surrogates did not immediately provide an observed benefit. At the conclusion of the study, reptile assemblages at all sites were indistinguishable from those on reference sites except for assemblages on sites treated with herbicide, suggesting herbicide application was relatively ineffective at restoring reptile assemblages. A mark-recapture study of the six-lined racerunner (*Aspidoscelis sexlineatus*) also identified prescribed burning as effective. Initially, abundances on sites treated with prescribed burning alone, as well as on sites treated with mechanical hardwood removal followed by fire, were comparable to abundances within reference sites. Over time, abundances at all sites were comparable to those on reference sites. Overall, effective restoration of wildlife populations and assemblages in fire-suppressed longleaf pine sandhills was achieved and prescribed burning over approximately a decade was generally sufficient to achieve this result. In general, there was little observed benefit or need to employ fire surrogates prior to prescribed burning.

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Chapter 1

General Introduction

Abstract. Within this chapter, I introduce the longleaf pine community and describe important mechanisms that maintain(ed) this system's integrity. I provide a relevant background to succeeding chapters, including the role of disturbance (i.e., fire) in maintaining the longleaf pine community, how fire-suppression has degraded this habitat type, and how restoration efforts have attempted to introduce prescribed burning or other strategies that mimic the effects of fire. I describe the study design of my dissertation and include a conceptual framework describing how I gauged the success of restoration efforts.

Key words: burn, longleaf pine, prescribed fire, restoration.

THE LONGLEAF PINE ECOSYSTEM

The longleaf pine (*Pinus palustris*) historically ranged through the Coastal Plain of the Southeastern United States, from North Carolina south to peninsular Florida and west to eastern Texas (Frost 1993, Ware et al. 1993). The pine forests within this region historically contained a relatively open understory and tree canopy. A fire-maintained system, the forest contains numerous species endemic to the habitat. As a consequence of fire-suppression, conversion to off-site pine plantations, and fragmentation, the extent of longleaf pine ecosystem has been reduced considerably. In the absence of fire, hardwood trees become established and reduce habitat quality for some longleaf pine endemics. To restore hardwood-invaded forests to an open canopy pine forest, managers often remove hardwood trees in concert with introduction of prescribed burning.

THE ROLE OF FIRE IN INFLUENCING COMMUNITY COMPOSITION

In many systems, species have evolved in the presence of natural disturbances such as fire. Consequently, these species may avoid injury or mortality from the disturbance through morphological or behavioral adaptations (Lotan et al. 1985, Russell et al. 1999). In fire-adapted systems, fire may even be required to facilitate successful reproduction and recruitment for some species (Clewell 1989, Brewer and Platt 1994).

Fire fulfills many roles in the systems in which it occurs; for example, Brockway et al. (2005) described the benefits of fire to a fire-adapted system (in this case, the longleaf pine forest) as, "(1) maintaining the physiognomic character of longleaf pine bunchgrass ecosystems by excluding invasive plants that are poorly adapted to fire, (2) preparing a seedbed favorable for the regeneration of longleaf pine seedlings, (3) reducing the density of understory vegetation and thus providing microsites for a variety of herbaceous plants, (4) stimulating increased seed production by native grasses, (5) releasing nutrients immobilized in accumulated phytomass for recycling to the infertile soil and subsequently more rapid uptake by plants, (6) improving forage for grazing, (7) enhancing wildlife habitat, (8) controlling harmful insects and pathogens, and (9) reducing fuel levels and the wildfire hazard."

Lightning strikes are thought to be one of the primary sources of ignition of natural fires (e.g., Rorig and Ferguson 1999); Native Americans also used fire to manage landscapes (Delcourt and Delcourt 1997). The frequency of natural fires is thought to vary depending on the system, for example in subalpine forest fire is infrequent (300-400 years; Romme 1982), as compared to boreal forests (69-132 years; Bergeron et al. 2001), and ponderosa pine forests (1-125 years; Veblen et al. 2000). Longleaf pine forests experience frequent fire relative to these other forest types (2-10 years, Ware 1993). In systems where fire occurs very infrequently, such as the subalpine forest, these events are likely to result in forest destruction leading to succession. In forests where fire frequently occurs, such as longleaf pine forests, less fuel accumulates between fires, thus fire intensity is generally low. In these cases, frequent fires generally do not result in mortality of native species or shifts in community composition.

The intermediate disturbance hypothesis (Connell 1978) suggests diversity will be highest at intermediate levels of disturbance (although empirical evidence does not always support this prediction, e.g., Collins 1992). This high level of diversity is thought to result from a mixture of habitat specialists and generalists persisting in a given area; an intermediate level of disturbance represents a compromise between habitat types thereby making the area suitable for a larger number of species. However, herein we are interested in the response of species assemblages associated with a particular habitat (i.e., those that evolved in the presence of one another, Chapter 2). Therefore, in addition to assemblage-wide analyses, it is also important to evaluate prescribed fire in the context of its effect on assemblages that evolved with its presence (e.g., Steen et al. 2010).

Fire can influence species composition by fulfilling natural history requirements, thereby maintaining species assemblages (Gilliam and Platt 1999). For example, fire facilitates successful reproduction for longleaf pine trees as well as wiregrass (*Aristida sp.*), both characteristic species of longleaf pine forests. Fire exposes soil which is essential for establishment of longleaf pine seedlings (Bruce 1951). In addition, fire removes plant species that are potentially competitors with longleaf pine seedlings (Boyer 1993). In turn, longleaf pine trees are often struck by lightning and serve as an ignition source for fires (Platt et al. 1988). These fires, when they occur during the growing season, stimulate wiregrass to flower and produce viable seed (Mulligan and Kirkman 2002). These complex processes that maintain populations of certain plant species, in addition to the wildlife species that thrive with frequent fire (e.g., Mushinsky 1985, Tucker et al. 2004), suggest a unique ecosystem (i.e., a community). The mechanisms by which wildlife benefit from fire may vary; gopher tortoises (*Gopherus polyphemus*) benefit from forage plants that require open areas created and maintained by fire (Yager et al. 2007) and they, along with other reptiles such as the six-lined racerunners (*Aspidoscelis sexlineatus*), prefer open areas for thermoregulation (Mushinsky 1985).

FIRE SUPPRESSION

Fire frequency in North America generally decreased following Columbian settlement and in particular following the mid-1800's (e.g., Cutter and Guyette 1994). In the southeastern United States, fire suppression was due largely to land use changing to crop farming, pasture, and plantation (Frost 1993, Van Lear et al. 2005) and the perception that fire was inconsistent with preferred land management. One of the consequences of fire suppression was accumulation of coarse woody debris and litter. With this increased fuel load, forests experienced increased potential for catastrophic fires (Varner et al. 2005), which are generally greater in intensity than even fire-adapted species may tolerate.

Another consequence of fire suppression is a change in species composition in response to changes in habitat structure (e.g., Gilliam and Platt 1999). Frequent burning discourages the establishment of species not adapted to persist in the presence of fire. When fire is removed, species richness in an area is likely to increase initially as fire-sensitive species colonize. These colonizing species may eventually out compete the native assemblage, resulting in a decrease in species associated with the ancestral condition. For example, fire maintains the composition and stability of the vegetative community in savannas (Beckage et al. 2009), including longleaf pine forests (Mitchell et al. 2006).

RESTORATION OF FIRE-ADAPTED SYSTEMS

The immediate goal of many restoration efforts in fire-adapted systems is not restoration of native assemblages per se, but reduction of fuel loads and the potential for catastrophic wildfire (Agee and Skinner 2005, Schwilk et al. 2009). Once reduction of excessive fuel loads has been achieved, frequent and relatively low-intensity fires should maintain this reduced fuel level. However, 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.

Reintroduction of natural disturbance regimes is often a goal of restoration efforts, though this strategy alone may underestimate what is necessary to restore a functioning system (e.g., Suding et al. 2004). For example, once hardwoods become established in longleaf pine forests, fire alone may be insufficient to kill mature hardwood trees (Waldrop et al. 1992). Due to concerns associated with fuel loads and inability of fire alone to restore forest structure and function, various fire surrogates have been developed (e.g., Provencher et al. 2001a,b).

Fire surrogates include chemical (i.e., herbicide) application and felling and girdling (i.e., mechanical removal) of oak trees. Various studies have been attempted to determine the effect of fire surrogates on vegetation (Brockway et al. 1998, Provencher et al. 2001a), trees (Provencher et al. 2001b), amphibians and reptiles (Greenberg et al. 1994, Litt et al. 2001), small mammals (Greenberg et al. 2006) and birds (Provencher et al. 2002). However, fire has unique effects on an ecosystem (Brockway et al. 2005). As a consequence, mechanical removal or herbicide application alone is generally considered insufficient to restore fire-adapted systems (Menges and Gordon 2010).

What has emerged from previous studies is that fire surrogates may quickly move a community towards a desired condition or enhance the effects of subsequent burning, but fire is likely necessary to restore and maintain that condition (e.g., Brockway and Outcalt 2000). 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. However, Outcalt and Brockway (2010) documented effective restoration of vegetation communities via this method. To determine the effects of this restoration strategy on wildlife requires large-scale, long-term controlled study (Block et al. 2001).

My research attempted to determine how wildlife assemblages associated with the longleaf pine forest responded to different methods of habitat restoration. My study is a continuation of a project initiated in 1994, in which fire-suppressed longleaf pine forests on Eglin Air Force Base (EAFB) were subjected to different means of hardwood removal (i.e., fire surrogates including herbicide application and mechanical hardwood removal, as well as fire alone). The initial study examined short-term effects of these treatments on forest structure and wildlife relative to control sites and reference sites (e.g., Litt et al. 2001, Provencher et al 2001a, b, 2002, 2003). A randomized-block design was used to assign treatments to sites in this study. After this initial treatment in the mid-1990s, all treatment sites, including controls, received prescribed fire on a two-three year rotation until I collected additional data in 2009-2010. Independent of the study design, several longleaf pine stands that appeared to represent a fire-maintained and natural forest (i.e., a desired future condition) at EAFB were selected as reference sites. As noted in Provencher et al. (2001a), reference sites were, "chosen on the basis of the following criteria, which indicate the original condition of sandhills: an uneven age distribution of *P. palustris*; presence of old-growth *P. palustris*; abundance of largely herbaceous understory species interspersed with bare ground; a sparse midstory; presence of *Picoides borealis* (a characteristic bird species); and a history of frequent growing season fires (Myers 1990)". I gauged restoration success by comparing wildlife assemblages within sites that experienced habitat manipulation to those within reference sites.

STUDY AREA

EAFB consists largely of a forested military reservation (approximately 188,000 ha) located in Santa Rosa, Okaloosa and Walton counties, Florida, United States. Officially established in 1935, a large portion of EAFB's current extent was formed by the addition of the former Choctawhatchee National Forest in 1940. The military mission of EAFB has changed considerably over the last century; today most activity relates to the, "development, testing, procurement and support of air-delivered weapons" (SAIC 2009).

In addition to serving as the site for all things related to any conventional and non-conventional weaponry used by the United States Air Force, EAFB has a land-use history that includes considerable exploitation of the forests now within its confines. For example, longleaf pine trees were harvested in the latter portion of the 19th century; consequently, there is relatively little old-growth forest remaining. However, EAFB still contains the greatest extent of remaining old-growth longleaf pine forest sandhills (SAIC 2009). Many pine trees were tapped for turpentine until the 1930's (SAIC 2009). Until 1989, forest management was typified by fire-suppression, which generally degraded the quality of longleaf pine forests.

The, "primary objective of the Air Force Natural Resources Program is to ensure continued access to land and airspace required to accomplish the Air Force mission while maintaining these resources in a healthy condition" (SAIC 2009). EAFB contains vast extents of natural habitats, the majority of which is longleaf pine sandhills. The current management philosophy of EAFB is based on guidelines outlined within the Eglin Integrated Natural Resources Management Plan (SAIC 2009) and is based on ecosystem management and biodiversity conservation, rather than a focus on timber harvest and silviculture, which typified the management philosophy for much of the 20th century. Management plans are created in consultation with the United States Fish and Wildlife Service and the Florida Fish and Wildlife Conservation Commission, among other organizations, to ensure land use is in compliance with federal law in relation to protected species.

Efforts to reforest areas on EAFB in the middle of the 20th century were typified by establishment of sand pine (*Pinus clausa*) and slash pine (*Pinus elliottii*) plantations. Land managers began to plant longleaf pine seedlings by approximately 1980 (SAIC 2009). Today, forest management activities pertinent to longleaf pine forests include removal of sand pine, conversion of pine plantations to longleaf pine, thinning of forests to recreate uneven-aged stands, and salvage of timber (SAIC 2009). Restoration activities include planting of longleaf pine and herbicide and mechanical removal of undesirable trees. Longleaf pine forests on EAFB are burned frequently as a result of mission (i.e., military) activity as well as a fire program that conducts prescribed burns covering over 28,000 ha each year (SAIC 2009). Prescribed fires are ignited on the ground and through aerial ignition from helicopters. The vast majority of EAFB is burned on a fire-return interval < 10 years (SAIC 2009) with much of the longleaf pine forests burned more frequently.

CONCEPTUAL FRAMEWORK

The goal of ecological restoration is typically to move a degraded site(s), via management, to a state comparable to what existed before degradation (National Research Council 1992). Restoration may be considered as a process (Hobbs and Cramer 2008), referring to management activities changing the conditions on a given site, or a goal, wherein a target state is achieved. Hereafter, I generally use the term restoration when referring to the process, and the term recovery to identify when restoration was effective at replicating the target state. Evaluating whether the goals of restoration have been met requires consideration of appropriate endpoints (Palmer et al. 1997). These endpoints may be characterized by conditions on reference sites, which should serve as a representation of the ancestral condition (White and Walker 1997). If conditions on a restored site become indistinguishable from those on reference sites, it is reasonable to suggest recovery has occurred. If conditions on a previously degraded site are distinct from those at reference sites, by my definition, recovery has not occurred.

Within this dissertation, I evaluate whether management objectives were met based on structural endpoints (Palmer et al. 1997), which include species richness, assemblage composition, or population size. I did not measure functional endpoints, which include the abiotic and biotic processes typical of reference conditions. I have made the assumption that required ecological processes are present if the structural endpoints of a site that experienced restoration are indistinguishable from those at reference sites.

The simplest explanation of how a degraded site becomes comparable to a reference site includes a linear movement to a recovered state (Figures 1, 2). Experimental evidence provides some support for the assumption that structural endpoints can be reached after reintroduction of historic disturbance regimes (Mitsch and Wilson 1996) including those of fire-adapted systems (Copeland et al. 2002). However, ecological restoration may not proceed linearly (Suding et al. 2004, Figure 2) or conform to simple predictions (Hilderbrand et al. 2005). For example, communities may transition to an alternate stable state following habitat degradation (Figure 2). In these cases, restoration may require surpassing ecological thresholds to re-establish ancestral feedback mechanisms (e.g., Martin and Kirkman 2009) before native assemblages may become reestablished.

The restoration methods used in this study (i.e., prescribed burning alone, mechanical hardwood removal, and herbicide application) were all intended to reduce hardwood density. Therefore, in addition to assuming that the different treatment sites were comparable prior to initial treatment (Figure 3), I assume hardwood removal treatments are functionally similar to each other before repeated-prescribed fire was introduced as well as functionally similar to each other after repeated-fire was introduced (Figures 4, 5). In other words, although the hardwood removal treatments may vary in their relative effectiveness (Provencher et al. 2001a,b), I suggest the various treatments are unlikely to send wildlife assemblages on disparate trajectories that would confound interpretation of structural endpoint differences between treatment sites and reference sites (Figure 4). Therefore, if a treatment contains structural endpoints significantly different than those at reference sites, I assume this to mean recovery was not achieved, rather than raise the potential that the treatment is in a transitional or alternative state that requires a longer period of time before creating conditions indistinguishable from reference conditions. To confirm this assumption would require continuous monitoring as community structure changed in response to management.

Although the study design initially included fire-suppressed controls, all control sites were burned periodically following the conclusion of the initial study. Therefore, the long-term study lacks a true control, which limits inferential power. To make inferences regarding whether treatments were effective, I assumed that if control sites were different from references in 1997-1998, they would have been different from references in 2009-2010 (Figure 5). In addition, within each chapter I attempt to demonstrate that if conditions on treatment sites were different from those on references after initial treatment, but were indistinguishable after long-term prescribed burning was applied, it is due to change at treatment sites and not references. I therefore infer that recovery has been achieved if conditions on treatment sites are indistinguishable from conditions on reference sites (Figure 5).

DISSERTATION OUTLINE

Chapter One presents an introduction to the longleaf pine forest community as well as the relevant concepts and assumptions embedded within the succeeding chapters of this dissertation.

Chapter Two is an attempt to philosophically demonstrate that communities are natural entities; thereby establishing that it is appropriate to use communities as targets for restoration. Chapter Three describes how bird assemblages responded to the initial management followed by a decade of prescribed burning. Individual species hypothesized to respond strongly to restoration were selected for population level occupancy modeling. Chapter Four focuses on the response of reptiles to restoration. In addition to determining how the composition of reptile assemblages changed in response to restoration, we were able to link capture rates to specific habitat features to identify potential mechanisms behind this change. This chapter identified *A. sexlineatus* as a species associated with the reference condition of longleaf pine forests. We conducted a mark-recapture study of this species to determine how populations changed after habitat restoration and over time (Chapter Five).

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Figure 1. Restoration scenario wherein reintroduction of a natural disturbance regime restores a degraded site to a previous condition along a linear trajectory. Figure is taken directly from Suding et al. (2004; Figure 2).

Figure 2. Conceptualization of different restoration scenarios potentially leading to ecological recovery. Axis labels in Figures 2-5 are adapted from Bradshaw (1984).

Figure 3. Conceptualization of restoration scenario specific to this dissertation, prior to hardwood removal treatments.

Figure 4. Conceptualization of restoration specific to this dissertation. Green represents fire-suppressed controls. Sites that experienced hardwood removal are not considered recovered.

Figure 5. Conceptualization of restoration specific to this dissertation. After all sites received restoration, they are presumed to have been restored to the reference condition. The study lacks a true control for 2009-2010. The hollow circle represents our expectation regarding the position of a control, should one exist.

Figure 1.

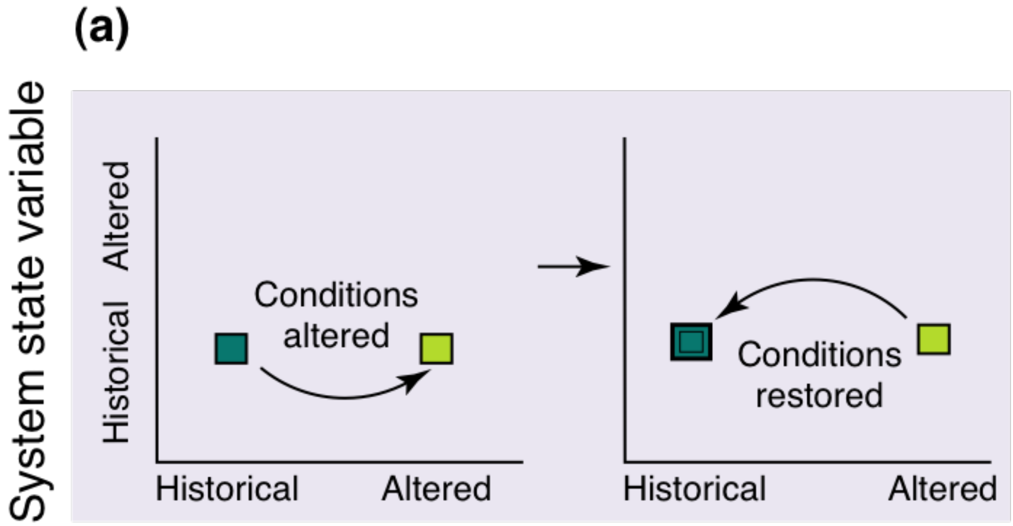
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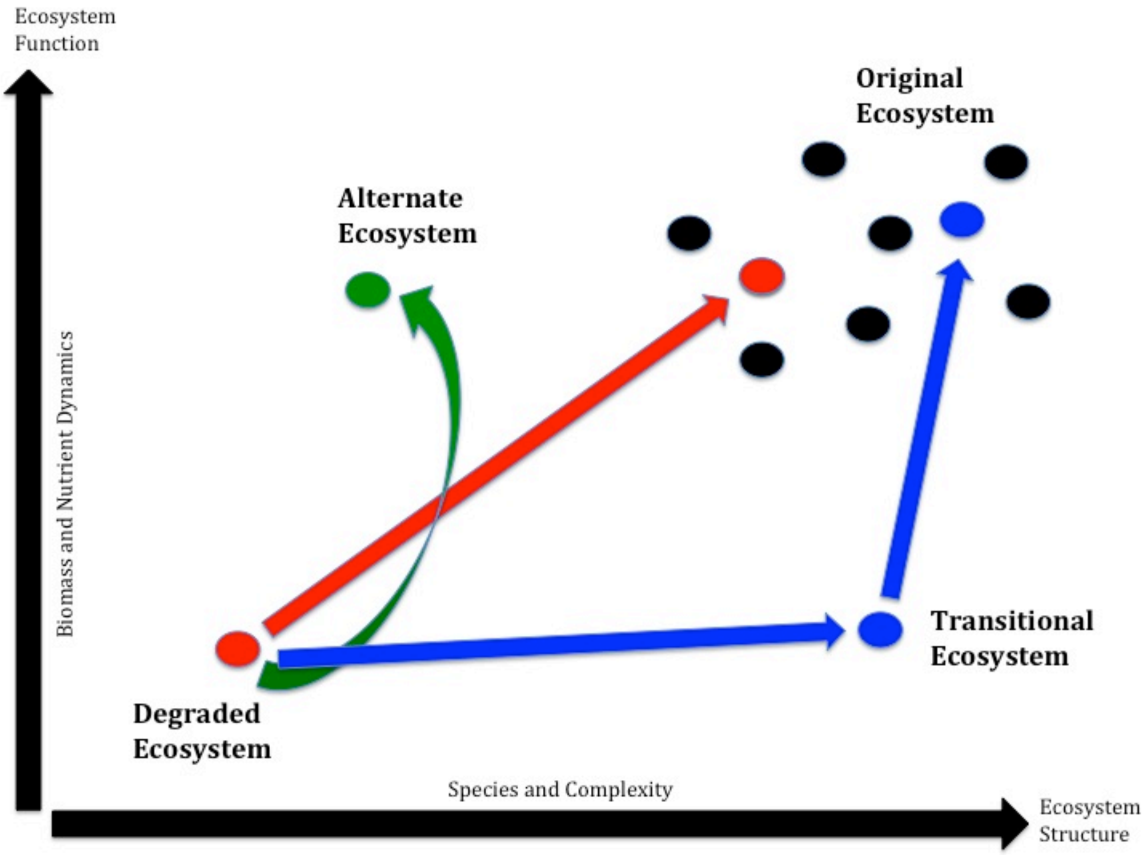
Figure 2.


Ecosystem
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Biomass and Nutrient Dynamics
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Ecosystem
Species and Complexity
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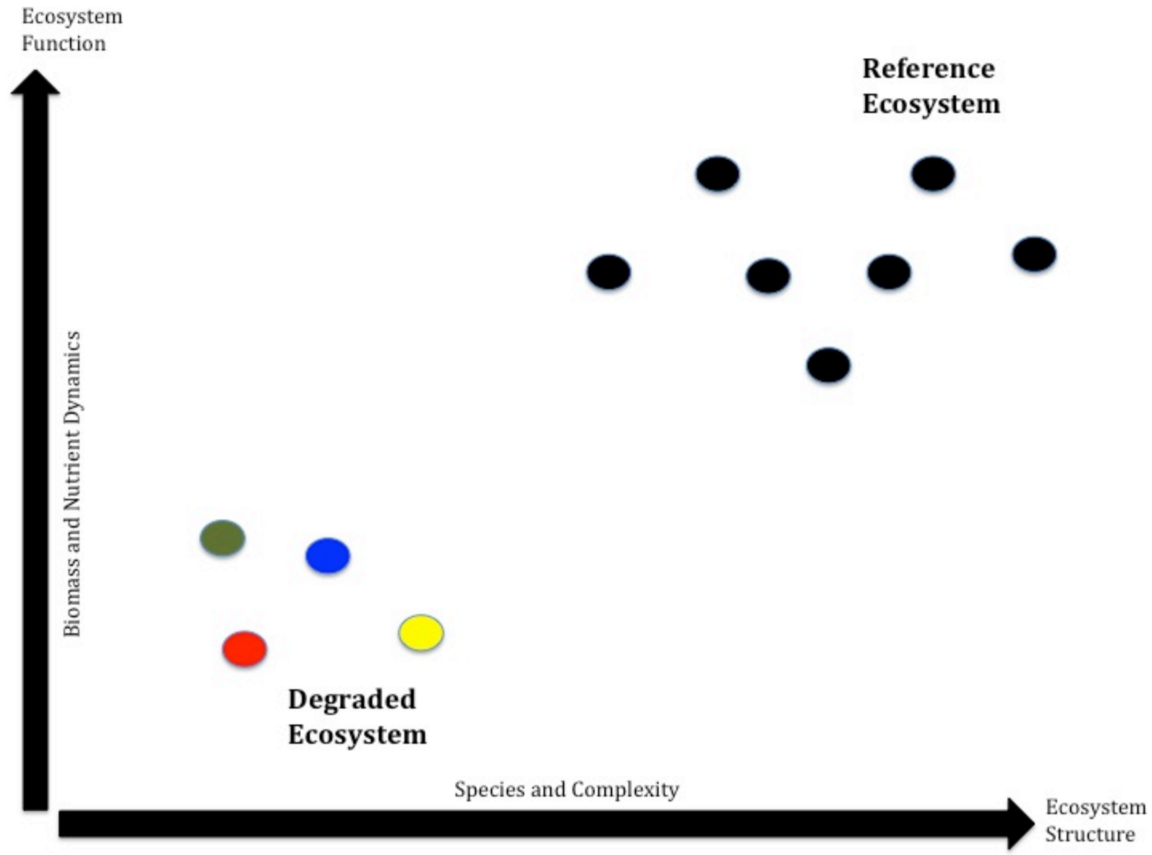
Structure

Figure 3.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Species and Complexity
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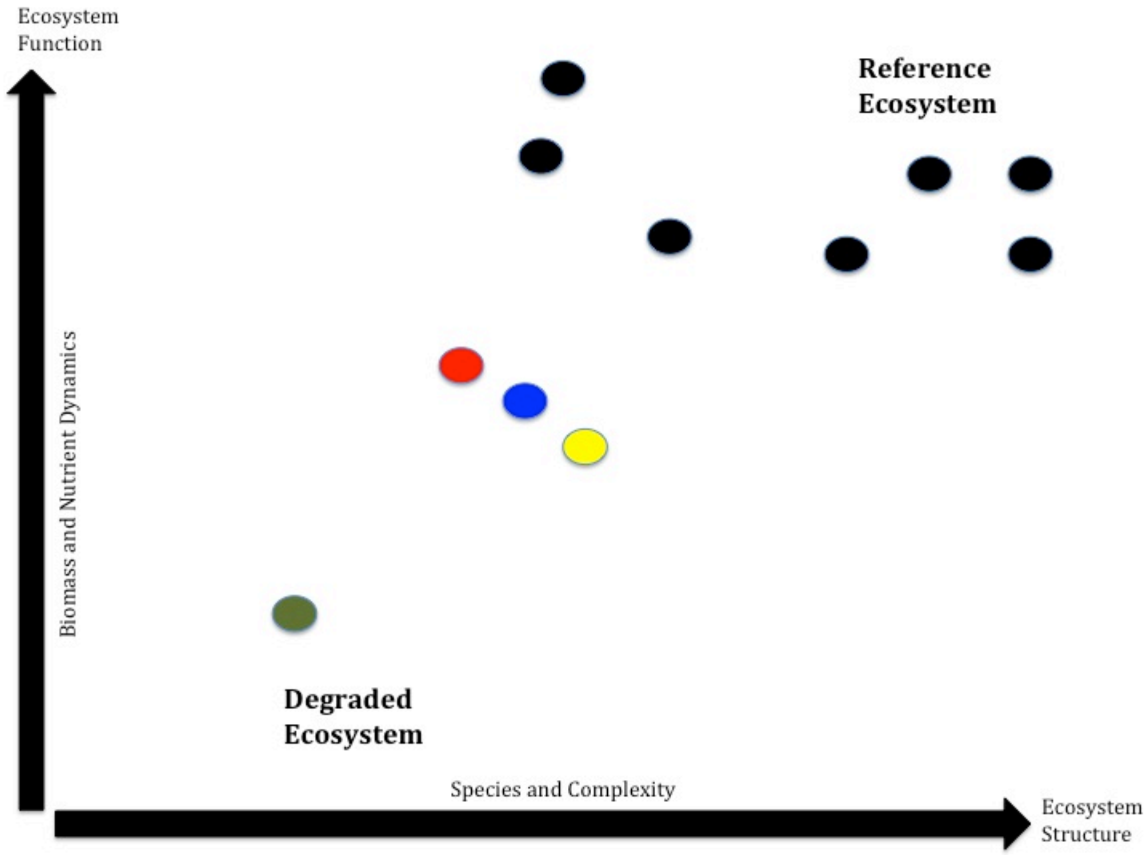
Figure 4.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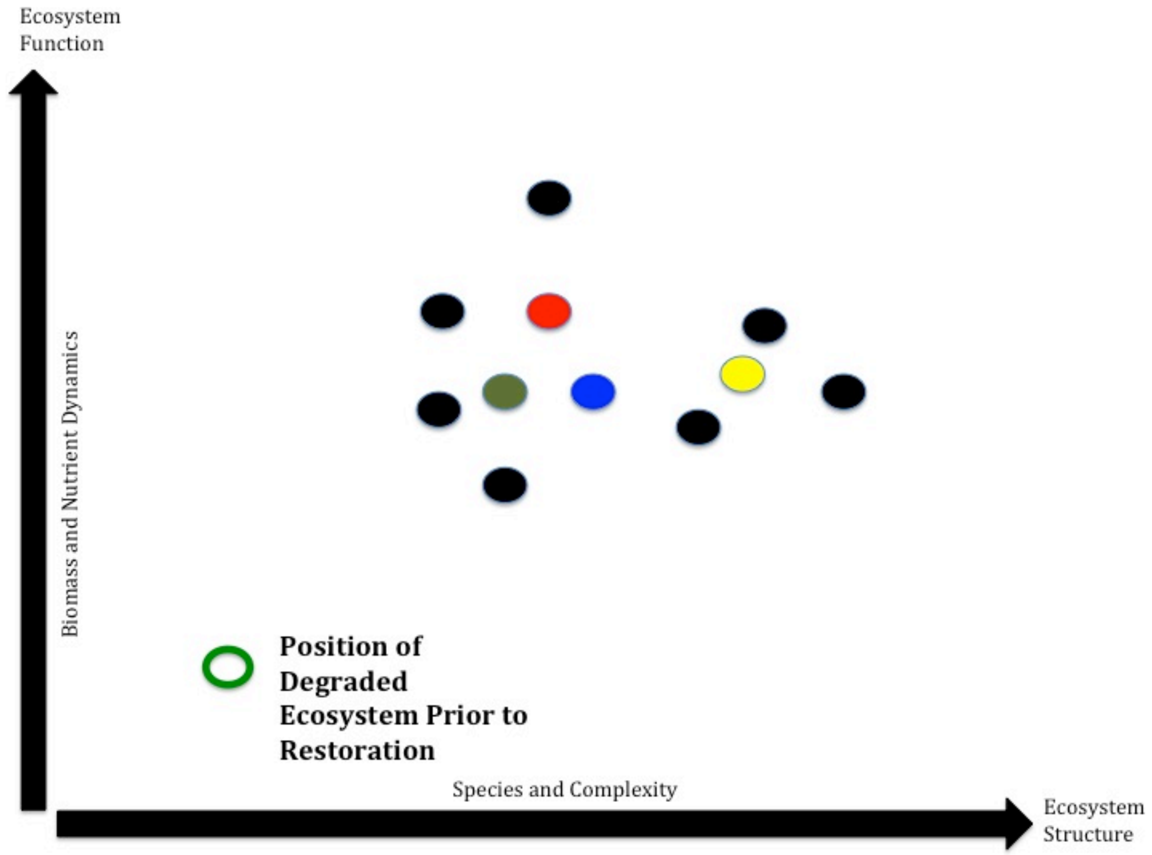
Ecosystem Function
Biomass and Nutrient Dynamics
Position of Degraded Ecosystem Prior to Restoration
Species and Complexity
Ecosystem Structure

Chapter 2

Conceptualizing Communities as Individuals with Implications for Conservation and Restoration Ecology

Abstract. Recent work has suggested that conservation efforts such as restoration ecology and invasive species eradication are largely value-driven pursuits, as opposed to science-driven. Additionally, changes to global climate are forcing ecologists to consider if and how collections of species will migrate, and whether or not we should be assisting such movements. Within this chapter, I propose a philosophical framework for addressing these issues by identifying an ecological community as a natural entity (i.e., an individual). Essential to making this conceptualization (termed the Evolutionary Community Concept, ECC) applied is identification of a unique collection of species that interact and have co-evolved in a given geographic area. I first establish that communities should be considered entities by examining them in light of the various qualities other entities, such as taxonomic species and areas of endemism, have been shown to possess. I then map out the implications of ECC for a number of global conservation issues. Specifically, this framework allows us to establish a biological and science-driven rationale for restoring ecosystems to reference conditions and removal of exotic species, and the ECC has implications for how we view shifts in species assemblages due to climate change. In addition, conceptualizing a community as an individual advances our understanding of various ecological concepts, such as resilience.

Key words: individual, class, community, exotic, invasive species, restoration

INTRODUCTION

Ecological restoration is the, "…process of repairing damage caused by humans to the diversity and dynamics of indigenous ecosystems" (Jackson et al. 1995). Although the field of restoration ecology is based on scientific principles, restoration goals may be influenced, for example, by ethics, morals, or aesthetics (Higgs 1997). Without establishing a given indigenous ecosystem as a natural ecological entity (i.e., an individual), there is no basis for demonstrating whether restoration efforts are driven by goals that reflect the evolutionary history of the system being repaired. In other words, if the target condition of a given restoration ecology effort is an artificial construct (i.e., a class), managing a damaged ecosystem so that it moves towards this condition may result in a reconstructed system with missing parts or a failed reconstruction altogether.

Restoration efforts often focus on species assemblages within a given area, and these assemblages are often considered communities. However, communities have been suggested to have no, "…intrinsic evolutionary or ecological purpose…" and therefore it is not valid to, "…invoke any ecological (or evolutionary) rational to establish particular restoration goals" (Davis and Slobodkin 2004). The logical consequence of this philosophy is to conclude that attempting to restore communities is a value-driven pursuit based on our judgments and independent of natural laws (Choi 2007). Some have contested this point, suggesting restoration ecology is not solely value-driven (Winterhalder et al. 2004); however, to convincingly demonstrate that the goals of restoration ecology are based on natural laws requires establishing that restoration targets are natural entities.

Herein, I argue that an ecological community can be conceptualized as a unique assemblage of species that occurs in a given geographic area and is connected by interspecific and abiotic interactions. Just as a species consists of multiple parts (i.e., organisms), a community may be made up of multiple parts, (e.g., forest patches, isolated wetlands). Given this conceptualization, which I term the Evolutionary Community Concept (ECC) we may establish boundaries around communities and describe how they fulfill the criteria of natural ecological entities that exist independent of anthropogenic naming conventions. This exercise is analogous to the well-tread discussion regarding whether species are individuals or classes (below) but the topic has not been explored in-depth in relation to ecological communities.

Designating a community as a natural entity is a philosophical exercise and operational difficulties are omnipresent when applying philosophical notions to biological entities (Frost and Hillis 1990); however, it is important not to confuse community conceptualization with community delineation (as for species, de Queiroz 2007). Based on the ECC, it is difficult to determine the spatial boundaries between communities. In addition, one consequence of conceptualizing a species as an individual is that some organisms do not qualify as a species (e.g., an individual incapable of breeding cannot be a member of any species under the Biological Species Concept; Baum 1998). Similarly, some species assemblages do not qualify as a community at certain scales. In any case, it is unlikely that any one conceptualization will provide a completely satisfying answer on how to best conceptualize a community, as evidenced by the plethora of concepts used to define a species. However, a philosophical discussion of the topic may help ensure our classification system is an accurate representation of natural processes and that research questions and conservation and restoration goals are properly formulated. As mentioned by Ghiselin (2002) in reference to species, appreciating that they are individuals,

"…can help us to clarify the roles of history on the one hand and the laws of nature on the other in evolutionary biology."

The ECC can be applied to extant assemblages. For example, longleaf pine (*Pinus palustris*) forests once dominated the coastal plain of the southeastern United States. Typified by a relatively open canopy, sandy soils, and frequent fire, there are many species that evolved within this forest system. The environmental conditions of the region allowed for a unique species assemblage to persist. Comparisons of species lists from a random sampling of comparable-sized areas across the planet will find interacting species such as longleaf pine trees, red-cockaded woodpeckers (*Picoides borealis*) gopher tortoise (*Gopherus polyphemus*) among others, occurring in sympatry more often than expected by chance. Population fluctuations in one species are likely to influence the other species in the assemblage. Under the ECC, this assemblage can be recognized as a community (i.e., the longleaf pine community).

WHAT IS A COMMUNITY?

Although the concept of a community is frequently invoked, there has been little examination into how to differentiate among communities or identify them as ecological entities. Consequently, some have suggested they are of little importance (Ricklefs 2008). Perhaps this argument can be attributed to the complexity of these systems, which tends to preclude development of general laws (Lawton 1999). However, despite their complexity, the relevance of the concept of communities to current ecological and conservation-oriented problems seems to necessitate their investigation and inclusion in the ecological sciences (Simberloff 2004). To enhance the context of community-oriented studies, it seems obligatory to establish whether communities are arbitrary designations (i.e., classes) or entities with diagnostic properties (i.e., individuals).

Progress in science may be hampered when multiple definitions are allowed to proliferate (McCoy and Shrader-Frechette 1992, Mikkelson 1997). However, there are numerous definitions for ecological communities. For example, definitions include those that stress dominant species (e.g., Ricklefs 1990), interactions (e.g., Wilbur 1972, Holt 1977), or statistical properties (Field et al. 1982, Clarke 1993). Some researchers have presented more refined definitions (e.g., Looijen and Andel 1999) to enhance precision for addressing ecological questions, while others have argued that a very general definition for what constitutes a community will suffice for most studies (Fauth et al. 1996, McGill 2010). However, common definitions of communities struggle to capture their unique nature. Dominant species or interactions, for two examples, may be considered components of an ecological community, and multiple communities may even share such components. Therefore, current definitions suggest communities are classes.

The inconsistencies among current community definitions may be attributed to an ecological dichotomy described by Losos (1996), in discussing proximate and ultimate approaches to community ecology. Proximate approaches concern themselves with, "the processes occurring within communities and the effect those processes have on community structure" (Losos 1996). However, the species present in a given area are not solely influenced by current forces and may be a function of the evolution of a particular lineage in a given area (Helmus et al. 2007, Cavender-Bares et al. 2009). Ultimate approaches to community ecology, which acknowledge that evolutionary lineages are likely to be spatially constrained, come closer to helping us conceptualize communities as something more than just a collection of arbitrary species. Such an approach is defined by Losos as, "involv[ing] study of *why* communities have particular organization and *why* differences exist between communities [emphasis mine]."

WHAT IS AN INDIVIDUAL?

Conceptualizing units in biology as individuals or classes has been discussed in depth regarding species (e.g., Ghiselin 1987), and more recently regarding areas of endemism (Crother and Murray 2011). Therefore, I do not delve deeply into a review of these concepts. In short, individuals are ecological entities that exist because of their evolutionary history whereas classes are actually groups of entities. Classes may not represent natural kinds; therefore their use may be limited when attempting to understand evolutionary relationships (Ghiselin 2002). Individuals, in this context, are entities with a definite location in space and exist for a finite period of time. Individuals can be single things (e.g., Luke Skywalker) or can be composed of multiple parts (e.g., Auburn University faculty or *Panthera tigris*). In contrast, classes are abstract constructs that cannot be attributed to a discrete time or place, and they have members that are assigned to the class on the basis of defining properties. For example, “university faculty” is a class to which any number of people may belong if they meet the criterion of being academic staff at a university, and the concept itself is not rooted to any particular place or time. Species in the class sense refers to all groups of organisms that meet some criteria (e.g., Biological Species Concept) to warrant designation as such, and it would be reasonable to talk about a kind of species. Species in the individual sense is a particular thing (e.g., *Panthera tigris*), and it would not make sense to discuss a kind of *Panthera tigris*. As noted by Crother and Murray (2011) in relation to areas of endemism, designating communities as natural entities requires accepting species as individuals; the reader is referred elsewhere to make this case (Hennig 1966, Ghiselin 1974, 1981, 1987, Hull 1976, Wiley 1980, Bernier 1984, Holsinger 1984, Kitcher 1984, Mishler and Brandon 1987, Ereshefsky 1992, Frost and Kluge 1994, Baum 1998, de Queiroz, 1999, Coleman and Wiley 2001, Mayden 2002, Brogaard 2004, Rieppel 2007, Reydon 2009).

For something to be an individual, several criteria must be met: 1) it must have temporal and spatial boundaries, 2) definitions must be crafted ostensively, 3) there must be cohesiveness in response to change, and 4) there can be no instances of this entity; it must represent a unique entity (e.g., Ghiselin 1974, Hull 1976, Frost and Hillis 1994, Crother and Murray 2011). Therefore, if a community is an individual, it must be discovered through some process of identifying its boundary, inferring its origin, and determining its ultimate demise. As mentioned earlier, I suggest that within a given geographical area, there is likely a species assemblage comprised of species that are unlikely to occur together elsewhere. Essentially, this group of species can be considered as an area of endemism (Crother and Murray 2011). I believe the rationale used to identify areas of endemism as individuals is relevant here but it is important to add that communities differ because the structure and composition of communities are influenced by interspecific, as well as abiotic, interactions (Fontaine et al. 2011). I argue that this group of coevolved and interacting species, which is unique to a given area, is a community, and under this conceptualization, we can consider communities as individuals.

A FRAMEWORK FOR IDENTIFYING COMMUNITIES AS INDIVIDUALS

BOUNDARIES

Eldredge (1985 p. 162) states that, "some ecologists…take strong issue with the suggestion that communities can be construed as individuals. The problem seems to come from the apparent lack of definitive boundedness to such entities". It is difficult to delineate a discrete boundary surrounding an assemblage in a finite space without identifying arbitrary thresholds for particular variables, such as the density of a given species or interaction levels between two or more species. This is analogous to a population of one species with varying genotypes, i.e., to what degree do two groups have to differ in their genetic make-up before they are considered separate species? To have any application, thresholds delineating communities should have biological and evolutionary relevance. Although some may argue for a specific threshold beyond which individuals are considered separate entities (e.g., Highton 1989), these thresholds can be considered arbitrary (Frost and Hillis 1990). It is most consistent with some conceptualizations (e.g., the Phylogenetic Species Concept; Cracraft 1983, 1987) to suggest any evidence of a unique evolutionary lineage is sufficient to identify something as an individual (e.g., Young and Crother 2001).

Biogeographical patterns in species richness and assemblage composition may help demonstrate that spatial boundaries exist around a unique assemblage of species. For example, an area's biological uniqueness may be inferred after using null models to demonstrate that observed patterns differ from random expectations (e.g., the mid-domain effect, Colwell and Lees 2002). It is necessary to have some *a priori* designation of the spatial boundaries of areas so that patterns of species richness may be compared for these analyses; areas may be defined by a grid system (e.g., Hawkins and Diniz-Filho 2002), political boundaries (e.g., Means and Simberloff 1987), or elevation (e.g., McCain 2004).

Species richness alone tells us little about assemblage composition, which may allow us to distinguish between areas with similar species richness patterns. If a group of species occurs in sympatry more frequently than expected (e.g., as defined by null models, Gotelli 2000), this suggests the area is subject to ecological or evolutionary forces resulting in a particular species assemblage. If these same species occur together more frequently in a given geographical area than they do in other geographic areas, these areas may be considered discrete. In addition to co-occurrence analyses, parsimony analysis of endemicity (Morrone 1994) is a method of identifying areas with unique species compositions.

Defining boundaries prior to analysis does not allow us to identify the scale of forces influencing patterns of species composition. Therefore, demonstrating that patterns of species richness or composition are not random does not inform us regarding the spatial extent of the area influenced by the same biogeographical processes. However, if given areas possess unique patterns of species richness or different species compositions, there must be a spatial boundary beyond which these features are no longer unique. These boundaries exist, but we are limited in our ability to delineate them. This is not necessarily a weakness of the ECC outlined here; boundaries may be fuzzy when characterizing something as an individual (e.g., Ghiselin 2002, Crother and Murray 2011). In fact, it is likely folly to assume precisely delineated boundaries accurately represent a natural entity; allowing a certain degree of boundary fuzziness when delineating boundaries is not a concession to our limitations at identifying their extent but rather a more accurate characterization of the entity in question (Baum 1998).

Ecotones are generally considered, “transitional areas between adjacent ecological systems” (Risser 1995) and may possess attributes of two or more systems. Some areas that could be defined as ecotones, such as the intertidal zone of the Pacific Northwest, United States, are probably better considered as an independent community under the ECC, as they contain a characteristic set of species that are highly adapted to the system. However, ecotones should be conceptualized at multiple scales (Gosz 1993), therefore it may also make sense to consider some ecotones as the fuzzy boundaries between communities (e.g., riparian areas), and others as simply a function of species-specific attributes (e.g., microhabitat transition zones between patches colonized by allelopathic plants). Because ecotones could either be considered communities, the fuzzy boundary between communities at a larger scale, or as resulting from a process occurring within a community, my concept subsumes that of the ecotone.

At some point in time, due to shifting patterns in species composition (e.g., due to extirpation or stochasticity), co-occurrence patterns may cease to be different from nearby geographic areas. Species diagnostic to a community would at that point stop interacting, or the nature of the interactions could shift outside the bounds of the distribution by which they were previously characterized. Conversely, at some point in time, random species assemblages in a given area can become non-random and different from other areas. Species within such areas would likely begin interacting and shaping the evolutionary trajectories of one another. So, while it is operationally difficult to pinpoint precise beginnings or ends, it is theoretically plausible that one could assign temporal boundaries to a unique group of species within a spatial area.

Changes in species assemblages leading to such boundaries may be attributed to several causes. Over ecological time-scales, the habitats in a given area may change due to anthropogenic climate change or succession (Gleason 1926). Direct anthropogenic disturbances may also influence a species assemblage. For example, due to habitat loss and land conversion, the longleaf pine forests, and associated species, of the southeastern United States have been reduced to a fraction of their historic extent. Over geologic time, climate patterns or geomorphology will become unsuitable for species within a given area. Species will either adapt or become extirpated. Biogeography, and its influence on evolutionary lineages (Wiley 1988) must also be considered when conceptualizing temporal community boundaries. Individual phylogenies of species are influenced by vicariance and dispersal events, and these individual phylogenies may ultimately influence community assembly (Webb et al. 2002; Figure 1). It is also the case that such biogeographic events may act directly on the incipient community, rather than being propagated through species. For example, the creation of a river, or separation of tectonic plates could split a community, a divergence of ecological significance. Similarly, the removal of geographic barriers will allow two communities to converge.

It follows from the ECC that a given area will possess multiple communities over geological time as changing climates alter habitat suitability for a given suite of species. Since species and interactions will be replaced over time, succession will also result in multiple communities. Thus, a community can transition into another community (i.e., a branching event is not required to result in new communities). As an analogy, if a species changes considerably over geologic time it is logical to consider the oldest organism as one species and the youngest as another (Simpson 1961) and acknowledge that the initial species went extinct at some point in time (Hull 1976).

Although we argue that communities may eventually transition into different individuals (Figure 2), the scale of relevance to most ecological studies suggests communities can change to some degree through time yet retain their identity. Allowing for a certain degree of change is not necessarily a problem. For example, it is generally accepted that each organism is an individual. Over the course of an organism's life, it may undergo relatively drastic changes, such as in the case of a tadpole developing into a frog or a caterpillar into a butterfly. Although the organism changes, its essence, perhaps best conceived as its genotype, remains the same (Hull 1976). Each organism came into existence some short yet fuzzy amount of time before it was born, or hatched, and each organism ceases to exist some fuzzy yet short amount of time after it dies, as it is broken down and the parts are assimilated into other organisms. Similarly, unique assemblages of co-evolved and interacting species may change, for example as when populations of competitors, or of predator and prey, fluctuate in abundance. Fluctuations in the frequency of natural disturbance may also occur. Although it is most philosophically straightforward to consider a community a new individual as soon as it changes at all, if organisms and species can change and stay the same individual, why cannot communities? So long as the unique coevolved assemblage of species and their associated interactions are extant and functional, a community remains the same individual.

AN OSTENSIVE DEFINITION

As noted above, certain species will co-occur together within a given area more often than expected by chance and more often than they co-occur together elsewhere. These species are often considered specialists of a given habitat with limited geographic distributions. Indicator species analysis (Dufrêne and Legendre 1997) may be a useful means of identifying characteristic species of a given area. We can point to these species and therefore diagnose communities based on their presence. For example, at the scale of a forest stand, the presence of longleaf pine, gopher tortoises, red-cockaded woodpeckers, and wiregrass in a given area is sufficient to identify that this area is unique to the Coastal Plain of the Southeastern United States. In sum, we can define communities by identifying characteristic species, i.e., identify communities ostensively.

We must revisit the issue of scale. If our area of interest was the planet Earth and we wished to compare the species assemblage of planet Earth to neighboring planets, then every species is an indicator of Earth. As the focal scale decreases, widespread species will begin to stop playing a role in what makes a given area unique (Figure 2). For example, the gopher tortoise is an indicator of planet Earth, the continent of North America, the Coastal Plain of southeastern United States, and the longleaf pine forest, but not the pitcher plant bogs that may occur within longleaf pine forests. Beyond the scale of the longleaf pine forest, the gopher tortoise is not useful for differentiating between areas. Thus, again, the relevant scale is reliant on the decision of the researcher.

This matter of scale may shed some light on controversial subjects in ecology. Neutral theory (Hubbell 2001) suggests communities may be comprised of assemblages of organisms arising from forces independent of species interactions. Similarly, Gleason (1927) argued that the structure of a particular assemblage is due largely to pioneering species; these species become established due to their dispersal abilities, rather than because they belonged to any discrete entity. These ideas, at least on small temporal and spatial scales, appear to run counter to some of community ecology’s most basic underpinnings (Chase and Leibold 2003). Examining an assemblage at an inappropriate scale may encourage misleading interpretation. Continuing our longleaf pine forest example, quantifying species composition within forest stands of a few hectares each may reveal that the species within each stand appear random. However, at a larger scale, the species characteristic of longleaf pine forests are different than those that appear in a ponderosa pine, *Pinus ponderosa*, forest, or in the Sonoran desert. At this scale, species assemblages are not random, they are distinct.

One may argue that the unique species assemblage of a given community could be relocated to another location and thereby create another part of that community. Similarly, one may suggest a community can be restored following habitat conversion that resulted in a change to a new community. However, it is important to consider the evolutionary origin of the species in a given assemblage as well the interactions between the species. Once an evolutionary lineage diverges into separate lineages, the parts of the different lineages can never again be the same. They have experienced different evolutionary histories. As an analogy, an organism cannot die and then arise as the same organism again. A species cannot become extinct and then be resurrected through an independent evolutionary lineage (Hull 1976). You cannot take the components of a community (i.e., the unique assemblage) into an environment with similar abiotic conditions and recreate that community without breaking spatial and temporal boundaries; therefore, the relocated assemblage would be an independent and new community.

COMMUNITIES ARE COHESIVE

Communities are comprised of species. Thus, the issue is how to conceptualize a group of species responding to change as a cohesive unit. This topic was recently discussed in reference to areas of endemism (Crother and Murray 2011). The unique species assemblage of a given area (see *An Ostensive Definition*) likely engages in important interspecific interactions that sustain the identity of a particular community. These interactions may promote co-evolution and community structure and dynamics (Johnson and Stinchcombe 2007).

For example, within the community associated with pine forests in the Coastal Plain of the southeastern United States, longleaf pine trees are conduits for lightning strikes that ignite a highly flammable understory (Platt et al. 1988). The resulting ground fires are necessary for reproduction of other species (e.g., wiregrass, Mulligan and Kirkman 2002) and maintain habitat suitable for others (e.g., gopher tortoises, Yager et al. 2007). Gopher tortoises, through the process of burrow creation, provide structure important to other species (e.g., Jackson and Milstrey 1989, Kinlaw and Grasmueck, in press). The establishment of one or more of these species facilitated the persistence of additional species. In addition, a change, such as gradual climate change that alters the abiotic conditions in a given area, will likely reduce habitat suitability for one or more species. Due to the influence of interspecific interactions, many species within the unique assemblage are likely to respond; this response may be manifested in changes in abundance. Thus, species within a geographic area may respond cohesively to change and therefore fulfill this criterion to be considered an individual.

THERE ARE NO INSTANCES

If we recognize a community as an individual, for example, the longleaf pine forest community (which consists of multiple parts), there cannot be another longleaf pine forest community. I have discussed how communities may be spatially and temporally bounded, based on patterns of co-occurrence of characteristic species. I have identified how these communities may be defined by the presence of a unique assemblage of species and how these species respond cohesively to change. It is difficult to conceive of how there may be multiple instances of a community that fulfill these criteria. If a community is bounded by specific limits (e.g., climatic, physiological) and those limits help characterize a community, along with a suite of specialist species that provides the ostensive definition, another independent community cannot share the same limits and same species composition. This delineation is no different from saying that independent evolutionary trajectories delineate between species.

Certain situations are problematic for this conceptualization, such as new islands. A new island is subject to the climatic influences of that particular region. Abiotic factors interact with early colonizers to facilitate the persistence of these pioneering species. At this point communities are best characterized in the proximate sense (Losos 1996), since they are a function of a species' ability to colonize an area, rather than a function of the myriad of interactions that constitute community ecology. It could be unlikely, at the earliest stages, to have species present that had developed important interspecific relationships, unless they emigrated from habitats where they previously co-occurred. Very quickly, however, biotic factors will play important roles in influencing which species persist. At this point, the species composition and abundance in the area are a function of its unique adaptive and evolutionary past and they can qualify as a community under the ECC.

Since the species that colonize islands originated elsewhere, there are unlikely to be endemic species on very young islands. Nevertheless, there is likely to be a unique assemblage comprised of species that are good dispersers, and a unique suite of species may be sufficient to allow us to consider an assemblage an individual (Crother and Murray 2011). However, if this unique suite of species appeared on multiple new islands due to their dispersal capabilities and perhaps not initially influenced by interspecific interactions, it does not qualify as a single community under my conceptualization.

APPLICATIONS OF THE EVOLUTIONARY COMMUNITY CONCEPT

EXOTIC SPECIES

Perhaps the most relevant application of the ECC concerns exotic species (i.e., a species living outside its native range, Hunter 1996). Some species become invasive by influencing the unique species assemblage of a given area (e.g., Fritts and Rodda 1998); invasive species management is often driven by a desire to rid a particular area of species deemed damaging to the native species or communities (e.g., brown tree snakes, *Boiga irregularis*, in Guam) but this type of management has been criticized as potentially xenophobic or based primarily on ethics (e.g., Brown and Sax 2005). This criticism is likely encouraged by the fact that identification of communities has heretofore been subjective (Simberloff et al. 2003) and did not sufficiently differentiate between species considered native versus those that are considered introduced (e.g., Fauth et al. 1996). However, if communities are spatially and temporally bounded and consist of a unique assemblage of species and their associated interactions, then exotic species threaten their continuity.

Because humans influence the planet on a scale larger than any other single species (Vitousek et al. 1997), it is reasonable to categorize human activity as distinct from other biotic processes. Species physically moved by humans or whose movements were facilitated through infrastructure, such as imported decorative plants, invertebrates within ballast water, or escaped pets, are not components of native communities. The proximate cause of invasion by many species is clearly direct human intervention and their presence in an area is not due to the community's unique evolutionary lineage. Since exotic species may result in the functional extirpation of a native species, as well as the functional extinction of interactions between native species (e.g., Ricciardi and Simberloff 2009), they may result in the demise of the original community. Consequently, under the ECC, efforts to eradicate exotic species are justified while assisted migration efforts (McLachlan et al. 2009) are not.

On the other hand, human activities may drastically alter native assemblages, for example by reducing densities of dominant predators (e.g., Friedlander and DeMartini 2002), and also by changing abiotic parameters, such as in the case of global climate change (e.g., Walther et al. 2002). In these circumstances, a species may colonize an area because it represents suitable habitat when it previously did not. Examples include coyotes colonizing the eastern coast of the United States to fill the niche of extirpated wolf populations or birds shifting ranges in concordance with climate changes (Tingley et al. 2009). In these cases, the species have not invaded an area because humans physically aided their dispersal, rather they are using their own dispersal capabilities to respond to changes in the habitat. In these circumstances, eradication campaigns are not an effective management tool as the area in question has become an extension of their native range.

Many exotic species either do not become established or establish populations without noticeably influencing native species (Williamson et al. 1986, Manchester and Bullock 2000), some have argued that the presence of exotic species in a given area may even have conservation benefits (Schlapefer et al. 2011). For example, exotic species may fill the role of extinct organisms. In this case, although co-evolution was not a factor in an exotic species' role within a community, its role is indistinguishable from those that arise from co-evolutionary processes. If we regard the interspecific interactions a species partakes in as the defining component of its identity, we may recognize these exotic species as components of communities. However, if we regard identity as a function of unique evolutionary trajectories and spatio-temporal boundaries, as outlined in this essay, then exotic species can never be components of communities. This dichotomy has important implications for the debate regarding whether restoration of ecological processes may be more important than the species used to restore them (e.g., Pleistocene re-wilding of North America; Donlan 2005).

CLIMATE CHANGE

I lay out an argument here that a subset of species within an area comprise a unique assemblage, are strongly interacting, and are consistently present within a given community type and not elsewhere. Once we can identify a community as an individual, it is these species that help us differentiate between communities. The ECC has immediate implications for how to view changing global dynamics. For example, climate change is expected to lead to range shifts among individual species (Parmesan and Yohe 2003), which may in turn lead to community disassembly (Thuiller 2004). If one views communities simply as the groups of species residing within a given area, the effects of climate change may be mitigated by complex landscapes, which will likely continue to harbor a diversity of species (Anderson and Ferree 2010). However, if we recognize the importance and unique nature of interspecific interactions, we may be less optimistic regarding how communities will fare in response to anthropogenic-driven climate change, as interacting species may have varying abilities to adapt and persist (e.g., Parmesan 2006).

REFERENCE CONDITIONS

Many restoration efforts are gauged by comparison to reference communities. However, current definitions for communities characterized by dominant species, interactions, or statistical properties are often inconsistent with the goals of restoration ecology. In the United States, for example, restoration ecology is often primarily concerned with returning degraded communities into a condition consistent with the species composition and abundance that may be expected prior to settlement of this area by Europeans. It is thought that these assemblages, which will always include some degree of natural variation (White and Walker 1997), likely best represent the ancestral condition. The ECC, which posits these communities are individuals due to unique species assemblages, evolutionary histories, and interspecific interactions, offers a scientific rationale for this approach.

Disruption of natural disturbance regimes within a given community may encourage the proliferation of a species present at low levels. Although these species are not exotic, they may disrupt the continuity of a community. For example, fire-suppression of longleaf pine forests allows oak trees to increase in abundance, resulting in a change in the habitat structure and a reduction in habitat quality for other species (Mitchell et al. 2006). This change may eventually result in a transition to a new community. Therefore, efforts to restore natural disturbance regimes and manage species to levels that best typify a community are warranted, as they will maintain a community that exists due to natural processes.

Restoration ecologists often strive to replicate the species composition and abundance derived from a unique evolutionary history and use dominant species, interactions, or statistical properties as secondary metrics to evaluate success. For example, much has been discussed regarding the relative merits of focusing on one species for conservation efforts versus a suite of species (e.g., Lambeck 1997, 2002; Lindenmayer et al. 2002) or rather, perhaps most comprehensive, on a community level (Simberloff 2004). However, the ultimate goal is always the same, i.e., to restore, or at least conserve in some form, the group of species in a given area that best represents what was found in the area due to evolutionary processes.

I have argued here that the evolutionary origin of a community is an important component of its identity because this origin facilitates interspecific interactions between species unlikely to co-occur together elsewhere. In addition, individuals have temporal boundaries. Following this logic, once a given community has transitioned into another community (for example, through habitat degradation and/or disruption of normal disturbance regimes), it is philosophically impossible to change this community such that it becomes a part of the original community (Figure 1). Operationally though, it is possible to create a community that is functionally and structurally identical to the target community.

COMMUNITY RESILIENCE

Resilience refers to the time required for a system to return to its equilibrium following disturbance (Pimm 1984). Unless we allow a community to experience some change while remaining the same individual, the concept of ecological resilience is difficult to appreciate. Specifically, if we define communities based solely on their structure and/or function, as is accomplished by most current definitions, then a community often cannot be resilient, because once its structure and/or function changes it is no longer a member of the same class.

For example, if we define a longleaf pine community as any *P. palustris* dominated-forest that is burned at least once every two years (by designating definable properties, we establish the longleaf pine community as a class), then the forest no longer is a longleaf pine community once two years has passed without a fire. Although a forest that has been fire-suppressed for a few years will likely appear somewhat different than a forest that was burned more frequently, this is due primarily to fluctuations in the densities of species that were always present; I suggest its essence remains the same. Even after a *P. palustris* dominated forest is fire-suppressed (i.e., disturbed) for decades, restoration of fire alone is sufficient to alter the structural components of the forest (e.g., vegetation, bird and reptile populations) such that they are indistinguishable from forests that have been burned regularly (Outcalt and Brockway 2010, Chapters 3, 4, 5). Over this time period, it makes more sense to conceive of a longleaf pine community as an individual changing over time and in response to disturbance than it does to conceive of a forest switching classes depending on the structural and functional components of a given definition. However, once the unique species assemblage begins to change through extirpation and colonization, the original community has ceased to exist and can never return to an equilibrium.

CONCLUSION

I have made a case that communities may fulfill the criteria necessary to be considered individuals. Furthermore, I have described how communities may fulfill these criteria due to their unique evolutionary history. In doing so, I have built upon the work of Losos (1996), who identified a dichotomy in how communities are conceptualized and my conceptualization complements work emphasizing the importance of historical influences in current community structure (e.g., Losos 1996, Ricklefs 2008, Cavender-Bares et al. 2009). If the components of a community result from historical forces, it is likely most appropriate to consider these forces when conceptualizing what a community is. Restoration ecology goals and ecological questions should be focused on the unique species assemblage of a given area as well as the associated interactions. I argue that these components help conceptualize a community, a commonly invoked entity.

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Figure 1. New communities can arise from a variety of different processes. Transitions (represented here as fuzzy bars in the absence of discrete geologic events) may occur simply because communities change constantly over time (A). Whether such change (X to Z) is of relevance depends on the scale researchers designated as important. In (B) community W transitions into two communities (X and Y) following biogeographic divergence (e.g., the division of a community following a shifting river channel). If a biogeographic convergence event merged communities X and Y, they would form a new community Z. These changes are likely of ecological relevance. In (C) community X transitions to a new state as a result of either a natural transition (e.g., succession) or some anthropogenic disturbance. Transitions may also occur as a result of repairing community degradation (fuzzy gray bar in D). It is philosophically impossible to manage a community that has changed to a new community such that it once again becomes a part of the original community (see text under “An Ostensive Definition). However, it is possible to recreate the structure and function of the original community (represented by X_1). In all of the above scenarios, the scale of relevance to the researcher may allow for a community to experience some degree of change over time while remaining the same individual.

Figure 2. The number of species in a given area is a subset of the species that occur in a larger area. Therefore, for example, only a subset of all the species that make a large assemblage (D) unique will be unique to a smaller community (A). Conversely, many species within a small assemblage (A) will not be unique to this habitat type but will be unique to a larger assemblage (B). The nested nature of species assemblages across spatial scales suggests the researcher is responsible for designating the relevant scale when identifying the unique species assemblage of a given area.

Figure 1.

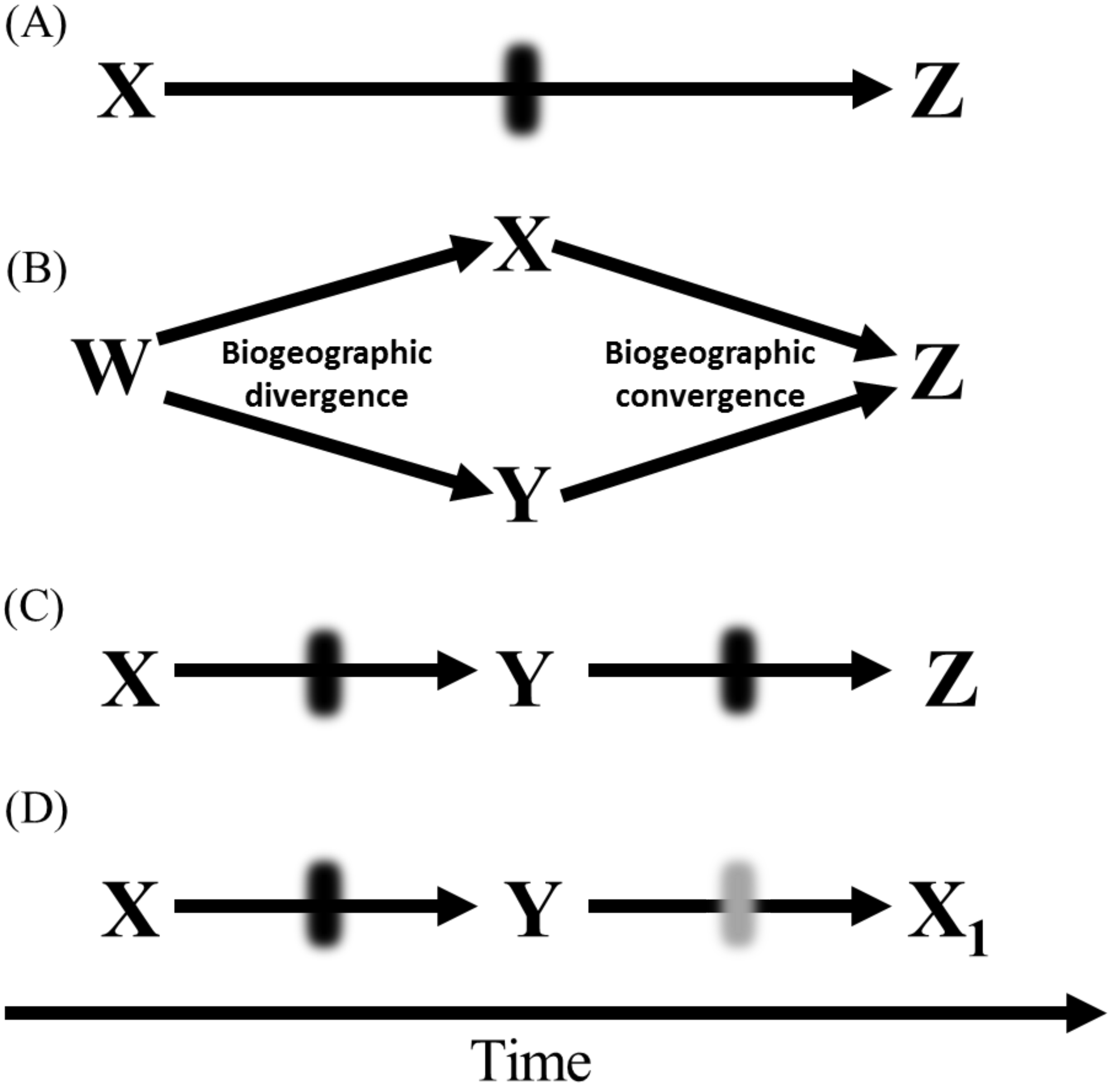
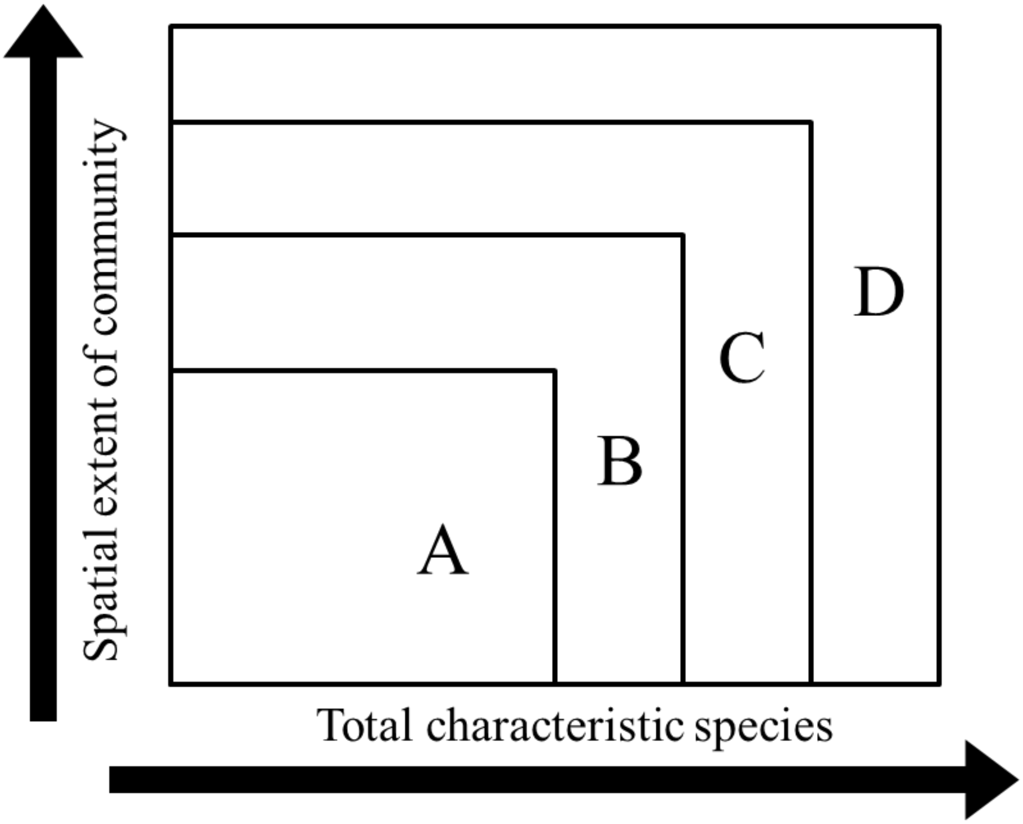

(A)
X
Z
(B)
X
W
Biogeographic divergence
Biogeographic convergence
Z
Y
(C)
X
Y
Z
(D)
X
Y
X1
Time

Figure 2.


Spatial extent of community
A
B
C
D
Total characteristic species

Chapter 3

Restoration of Avian Populations and Assemblages: Long-term Effects of Fire Surrogates and Prescribed Burning

Abstract. 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, wildlife response to this restoration method is not well documented. We examined how bird populations and assemblages in fire-suppressed longleaf pine-sandhills responded to mechanical removal or herbicide application or fire alone to reduce hardwood levels. Individual treatments were compared to untreated controls and reference sites. After initial treatment, all sites were managed with prescribed fire, on an approximately two-year interval, for over a decade. Non-metric dimensional 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 in the 3-4 years after treatment. After >10 years of prescribed burning on all sites, only assemblages at sites treated with herbicide were indistinguishable from assemblages at reference sites. Species indicative of reference sites became evenly distributed among all treatments by the end of the study. Occupancy modeling of individual species highly associated with reference sites also demonstrated increasing homogeneity 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.

Key words: longleaf pine, non-metric dimensional scaling, occupancy modeling, prescribed fire, red-cockaded woodpecker.

INTRODUCTION

The longleaf pine (*Pinus palustris*) forest once ranged throughout the southeastern United States but has declined considerably due to land use conversion and suppression of frequent fire (Ware et al. 1993). In the absence of a natural fire regime (fire every 1-10 years, Myers 1990), hardwood trees (e.g., Oak, *Quercus* spp.) become established in the midstory (Mitchell et al. 2006). These trees alter forest composition, generally degrading the habitat for longleaf pine associates (Means 2006).

Restoration is a management objective for many longleaf-pine forests (Brockway et al. 2005) and is generally attempted by removing hardwood trees and reintroducing fire. 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. 2001a,b), and fauna are generally assumed to respond to changes in the habitat (i.e., become passively restored, Scott et al. 2001).

The initial effects of 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 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 manage their populations (Cram et al. 2002, Provencher et al. 2002b). 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, 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). However, measures of assemblage structure may obscure species-specific and population-level trends (Maas et al. 2009). To determine how avian populations and assemblages respond to forest restoration of fire-suppressed longleaf pine sandhills over long time scales, we investigated assemblage-level response in breeding birds after hardwood removal and again after all sites received prescribed fire for over ten years. We used this analysis to inform selection of species closely associated with reference sites and examined changes in occupancy for these species over time. If avian populations and assemblages on treatment sites were indistinguishable from those on reference sites, we assumed management objectives were met.

METHODS

Study Site and Experimental Design

This study took place on Eglin Air Force Base, Okaloosa, Santa Rosa, and Walton Counties, Florida, U.S. We focused our study on fire-suppressed longleaf-pine sandhills. Most of the treatment sites had no records of having been burned since 1973, when record keeping began (B. Williams, Jackson Guard, pers. comm.). Ten sites experienced burns of varying extent from unknown causes between 1977 and 1989. The study was based on a randomized block design to assign hardwood removal treatments to 24 sites, each 81 ha in area and assigned to six blocks (Provencher et al. 2001). Methods of hardwood removal applied in 1995 included burning (Burn), herbicide application (Herbicide), or felling-girdling (Mechanical). There was also a control, which received no treatment. Six reference sites (also 81 ha in size) were also designated. These 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. (2001a).

The burn treatment was applied between April-June 1995, herbicide (ULW, hexazinone, 1.68 kg of active ingredient/ha, 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. (2001a,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 have approached the analysis in the context of 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. Reference sites were still considered representative of the desired condition. For clarity, we refer to treatments according to naming conventions designated during the initial phase of the project.

Tree Basal Area

We calculated basal area density 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 individual 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 subsites, summed, and divided by total sampled area to generate basal area density.. 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

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 (see figure in Provencher et al. 2002b). All samples were collected between approximately 0545 h and 1000 h. The order of sites sampled within a given morning was varied to reduce bias associated with time; however, we were unable to sample sites in random order because of occasional restrictions on access to sites because of military training activities. Four treatment sites or 2-4 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 approximately 450 m long.

1994 Sampling (Pre-Treatment)

All sites were visited four times between 4 May and 18 July 1994, prior to hardwood removal treatments (Provencher et al. 2002b). Each time a treatment site was visited, two observers conducted eight minute point counts approximately 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

All sites were visited six times each between 1 May and 30 June in 1998 and again in 1999 (12 total samples). In contrast to pre-treatment 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 approximately 22 minutes. With the addition of the eight-minute point count, each observer sampled birds for approximately 30 minutes per site (Provencher et al. 2002b).

2009-2010 Sampling

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

We treated each point count as an independent sample for the pre-treatment 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 from consideration to make data from these years comparable to that of the other study periods. We created a presence/absence matrix where if a species was detected within a sample it was given a score of “1”, whereas species not detected in a given sample were assigned a score of “0”. Therefore, a species could have scored a maximum of 16 detections in a given site for the pre-treatment study period, eight for 1998-1999 and seven for 2009-2010.

We used non-metric dimensional scaling (NMDS), which is a nonparametric ordination (Clarke 1993) useful for graphically demonstrating differences in assemblages based on species identity and an index of abundance (e.g., Kennedy et al. 2010). We conducted two NMDS ordinations with Bray-Curtis (Sorenson) distances. The first ordination included pre-treatment and 1998-1999 data. The second ordination included the 1998-1999 and 2009-2010 data. As some sites were not sampled in every time period, we conducted separate ordinations to facilitate comparisons. 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). Ordination graphs were prepared with SigmaPlot (Systat software, San Jose, CA) and Microsoft PowerPoint 2008.

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, artificial cavities were installed in pine trees between the 1998-1999 and 2009-2010 study periods (K. Gault, pers. comm. Jackson Guard). Therefore, we cannot interpret any change in their status as an indicator species after 1999 as due to the restoration methods used in this study. Red-headed woodpeckers 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 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, above) of reference conditions in 1994. 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 1994, eight point counts were conducted in each reference site per visit; we randomly removed four point counts. Since four point counts were conducted during each visit in 1994 (and only two for the following study periods), we removed point counts conducted in the middle of the transect (half of all point counts in 1994) from analysis. In 2009, four point counts were conducted in each reference site; we randomly selected two of these for analysis. We again removed the first two samples of 1998-1999. We pooled data such that each time a site was visited, one sample was generated. As a result, we generated four samples for the pre-treatment data, eight samples for the 1998-1999 sampling period, and seven samples for the 2009 and 2010 sampling period.

To model occupancy, we used the multi-season model (MacKenzie et al. 2003) in Program PRESENCE (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 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 pre-treatment data (1994), immediate post-treatment (1997-1998) and long-term post-treatment (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) regarding how bird populations 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). 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 post-treatment data (1998-1999) 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 oaks in Mechanical sites increased after initial treatment to levels higher than observed in pre-treatment conditions. In Control sites, oak basal area decreased over time. Longleaf pine basal area was similar among treatments over time, but basal area in treatment sites had not approached that of reference sites by the end of the study.

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; $P = 0.03$; Figure 1). 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 separated from Reference sites on Axis 2. All sites that experienced some form of hardwood removal in 1995 moved considerably along Axis 1 and approached references sites along Axis 2 (Figure 1).

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; Figure 2). Control sites moved considerably along Axis 2. These sites displayed the greatest degree of change from 1998-1999 to 2009-2010, which was not unexpected since the management regime they received during this time shifted more drastically than other treatment sites (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 were significantly different from treatment sites in 1994, whereas no differences were detected among treatments (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 for Herbicide sites, and Herbicide sites were different from Controls and Mechanical sites (Table 3).

Identification of Indicator Species

Eight species were positively associated with reference sites in 1994; eight species were also positively associated with Mechanical sites three years post-treatment (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.

Occupancy Modeling

For occupancy modeling, we selected six species that were positively associated with reference sites in 1994: American kestrel (*Falco sparverius*), Bachman's sparrow (*Peucacea aestivalis*), blue grosbeak (*Passerina caerulea*), brown-headed nuthatch (*Sitta pusilla*), northern bobwhite (*Colinus virginianus*) and red-headed woodpecker (*Melanerpes erythroceophalus*, Table 5). Goodness of fit-tests for the 1998-1999 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, but these values were similar after hardwood removal (Table 6). Northern bobwhite occupancy remained relatively high throughout the duration of the study.

Estimated occupancy probabilities for Bachman's sparrow, brown-headed nuthatch, red-headed woodpecker, and blue grosbeak exhibited similar patterns through time (Figures 3-6). 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 the 2-3 years following hardwood removal and in general, occupancy probabilities for these species in Mechanical and Herbicide sites were similar to those of reference sites. By the end of the study 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 small temporal and spatial scales (Bennett and Adams 2004). Our study, which incorporates a landscape-scale experimental design and spans more than a decade, revealed that hardwood reduction in a longleaf pine forest may benefit avian assemblages and, specifically, populations of species positively associated with sites in reference condition.

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 would appear to 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 species positively associated with longleaf pine in reference sites suggested any of the methods of hardwood removal used in this study (including burning alone) together with long-term prescribed burning was likely sufficient to recover populations of these species.

Hardwood removal together with reintroduction of fire within fire-suppressed longleaf pine sandhills is likely to benefit avian species associated with the reference habitat. However, complete eradication of hardwood trees may be to the detriment of even longleaf pine specialists (Perkins et al. 2008). 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 the concept (Guénette and Villard 2005).

Ordination and Indicator Species

Eight species were significant indicators of reference sites during the pre-treatment 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; 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). Although we expected all treatments to have had similar bird assemblages prior to hardwood removal in 1995, 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 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.

Three years after treatment application, there was a clear distinction between avian assemblages on sites that experienced hardwood removal and assemblages on Control sites. This suggests all three methods of hardwood removal were effective at altering the bird assemblage from those that inhabit fire-suppressed sandhills, corroborating earlier analyses (Provencher et al. 2002b). However, bird assemblages at reference sites 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 clustered together in 1998-1999, they were not distinct from other sites. However, eight bird species were positively associated with Mechanical sites, in contrast to only one species in Controls and two in reference sites (Table 4). With the exception of blue grosbeak, a species of open woodlands, these species are not those that we would expect to necessarily use either pine or hardwood-dominated forests more than any other species. We suggest the trends we identified are temporary and result from disturbance unique to felling and girdling trees (i.e., mechanical removal).

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). We view the bird assemblages at these sites as transitional. Since bird assemblages at these sites resembled those of reference sites by the end of the study, we suggest occupancy declined for the majority of species identified as indicator species in Mechanical sites in 1998-1999 while longleaf pine specialists remained. By 2009-2010, bird assemblages more closely resembled that of reference sites. However, additional monitoring of these sites would have been necessary to confirm this hypothesis.

Mechanical removal of trees was initially as effective at reducing oak overstory density as application of herbicides (Table 2 and Provencher et al. 2001b). Both methods are thought to quickly advance restoration, as compared to fire alone (Menges and Gordon 2010). However, 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. 2001b). Although we did not find evidence to suggest birds positively associated with Mechanical sites were exclusive to these areas, our analysis corroborates work suggesting these sites have relatively high avian species richness (Provencher et al. 2003). Provencher et al. (2002b) suggested that although mechanical hardwood removal (and also herbicide application) may benefit bird assemblages in the short-term, additional management, such as prescribed fire, is necessary to maintain these trends.

There were eight species associated with reference sites in the initial survey, but only two (red-cockaded woodpeckers and red headed woodpeckers) were positively associated with these sites three years later. Fifteen years into the study, none of the original indicator species were still associated with reference sites (although Mississippi kites, which previously had revealed 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.

Population Level Effects of Restoration

Prior to hardwood removal, there were several species with relatively high occupancy probabilities only in reference sites. By the end of the study, occupancy probabilities for these species had generally increased and become relatively uniform across all sites. This suggests that, for birds positively associated with longleaf pine forests in reference condition, burning alone over a long period of time 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.

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. (2002b) 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.

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 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 pre-treatment fire-suppressed longleaf-pine sandhills, the species was present in all treatment sites even prior to hardwood removal.

Blue grosbeak was an indicator of reference sites in the initial phase of the study, which is consistent with its known habitat preferences (Engstrom et al. 1984), but this species exhibited trends inconsistent with those of other bird species for which we modeled occupancy. Although occupancy probability for blue grosbeak at treatment sites generally increased over time, probabilities at treatment sites were distinguishable from those of reference sites. However, our ability to model occupancy for this species was limited because it was detected at nearly every site.

Synthesis

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 to restoration on the population and assemblage level in birds. 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.

Application of herbicide likely prohibited resprouting of oaks for a longer period of time than mechanical removal (Table 2), allowing for the bird assemblage to gradually transition to one comparable to that of reference sites. 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). 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 which include hexazinone application.

If the goal is to restore avian assemblages to a condition representative of those 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 Per Anglestam 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. 2002b) would be an appropriate approach.

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Figure 1. Non-metric dimensional scaling ordination of bird assemblages observed on fire-suppressed longleaf pine sandhills on Eglin Air Force Base, 1994 and 1998-1999; 1 = 1994, 2 = 1998-1999.

Figure 2. Non-metric dimensional scaling ordination of bird assemblages observed on longleaf pine sandhills following hardwood removal on Eglin Air Force Base, 1998-1999 and 2009-2010; 1 = 1998-1999, 2 = 2009-2010.

Figure 3: Relationship between probability of occupancy and year of study for Bachman's sparrow pre-treatment (1994; A), and three years (1998-1999; B) and fourteen years (2009-2010, C) following hardwood removal on fire-suppressed longleaf pine sandhills, Eglin Air Force Base, Florida. Lack of numerical convergence and an inability to compute variance-covariance matrix suggest standard errors should be interpreted with caution.

Figure 4: Relationship between probability of occupancy and year of study for brown-headed nuthatch pre-treatment (1994; A), and three years (1998-1999; B) and fourteen years (2009-2010, C) 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 B and C.

Figure 5: Relationship between probability of occupancy and year of study for red-headed woodpecker pre-treatment (1994; A), and three years (1998-1999; B) and fourteen years (2009-2010, C) following hardwood removal on fire-suppressed longleaf pine sandhills, Eglin Air Force Base, Florida.

Figure 6: Relationship between probability of occupancy and year of study for blue grosbeak pre-treatment (1994; A), and three years (1998-1999; B) and fourteen years (2009-2010, C)

following hardwood removal on fire-suppressed longleaf pine sandhills, Eglin Air Force Base, Florida.

Table 1. Models used to evaluate occupancy probabilities for select bird species detected from 1994-2010 to determine how their populations responded to hardwood removal on fire-suppressed longleaf pine sandhills.

Treatment Occupancy Models	Hypotheses
Ψ(PRD), γ (PRD),p(x)*	Occupancy and colonization varied by primary sampling period
Ψ(TRT + PRD), γ (TRT + PRD), p(x)	Occupancy and colonization varied by primary sampling period and treatment type
Ψ(TRT + PRD), ε (TRT + PRD), p(x)	Occupancy and extinction varied 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 Models	
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

Table 2. Oak and longleaf pine basal area in treatment and reference sites before and after oak removal. All units are m^2/ha (standard error).

	1994	1998-1999	2009-2010
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)

Table 3. P-values associated with multi-response permutation procedure on pairwise comparisons of treatment and reference sites (1994, 1998-1999, and 2009-2010). Bold indicates a significant difference between groups.

1994

	Burn	Control	Mechanical	Herbicide	Reference
Burn		0.55	0.94	0.85	**0.0006**
Control			0.86	0.21	**0.0006**
Mechanical				0.81	**0.0007**
Herbicide					**0.002**

1998-1999

	Burn	Control	Mechanical	Herbicide	Reference
Burn		**0.01**	0.10	0.25	**0.003**
Control			**0.0009**	**0.001**	**0.0005**
Mechanical				0.16	**0.0006**
Herbicide					**0.04**

2009-2010

	Burn	Control	Mechanical	Herbicide	Reference
Burn		0.36	0.54	0.05	**0.04**
Control			0.93	**0.02**	**0.01**
Mechanical				**0.01**	**0.01**
Herbicide					0.58

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

		Percent Indicator Value					
Treatment of Maximum Association	Species	Burn	Control	Mechanical	Herbicide	Reference	P-value
1994							
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
1998-1999							
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
2009-2010							
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

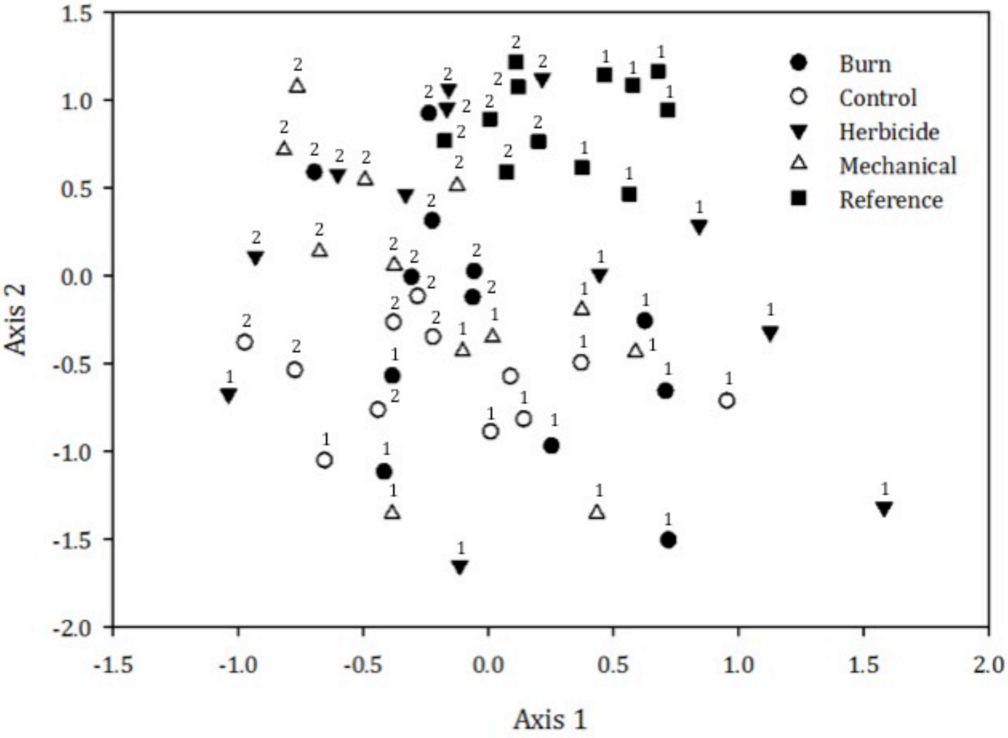
Table 5. Top models explaining occupancy patterns of select bird species within fire-suppressed longleaf pine sandhills undergoing hardwood removal, 1994-2010.

Species	Site	Model	AIC	ΔAIC	Weight	Likelihood	Par.	-2*Loglike
American Kestrel								
	TRT	ψ(PRD),γ(PRD),p(TRT)	255.79	0	0.94	1.00	9	237.79
	REF	ψ(.),γ(.),p(SURV)	103.08	0	0.90	1.00	21	61.08
Blue Grosbeak								
	TRT	ψ,γ(TRT + PRD),ε(TRT + PRD),p(TRT + PRD)	468.64	0	0.46	1.0	17	434.64
		ψ(PRD),γ(PRD),p(TRT + PRD)	469.15	0.51	0.36	0.77	11	447.15
	REF	ψ(.),γ(.),p(SURV)	120.59	0	0.88	1.0	21	78.59
Bachman's Sparrow								
	TRT	ψ,γ(TRT + PRD),ε(TRT + PRD),p(TRT + SURV)	339.23	0	0.97	1.00	33	273.23
	REF	ψ(.),γ(.),p(SURV)	119.01	0	0.70	1.00	21	77.01
		ψ(PRD),γ(PRD),p(SURV)	120.68	1.67	0.30	0.43	24	72.68

Brown-headed Nuthatch								
	TRT	ψ,γ(TRT + PRD),ε(TRT + PRD),p(TRT + SURV)	294.13	0	0.79	1.00	33	228.13
	REF	ψ(.),γ(.),p(.)	111.22	0	0.91	1.00	3	105.22
Northern Bobwhite								
	TRT	ψ(PRD),γ(PRD),p(TRT + PRD)	544.44	0	0.97	1.00	11	522.44
	REF	ψ(.),γ(.),p(.)	134.42	0	0.99	1.00	3	128.42
Red-headed Woodpecker								
	TRT	ψ,γ(TRT),ε(TRT + PRD),p(TRT + PRD)	410.66	0	0.54	1.00	16	378.66
	TRT	ψ,γ(TRT + PRD),ε(TRT + PRD),p(TRT + PRD)	410.98	0.32	0.46	0.85	17	376.98
	REF	ψ(.),γ(.),p(.)	121.8	0	0.98	1.00	3	115.8

Table 6: Probability of occupancy (and standard errors) for American kestrel and northern bobwhite observed on longleaf pine sandhills on Eglin Air Force Base, 1994-2010.

	1994	1998-1999	2009-2010
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)



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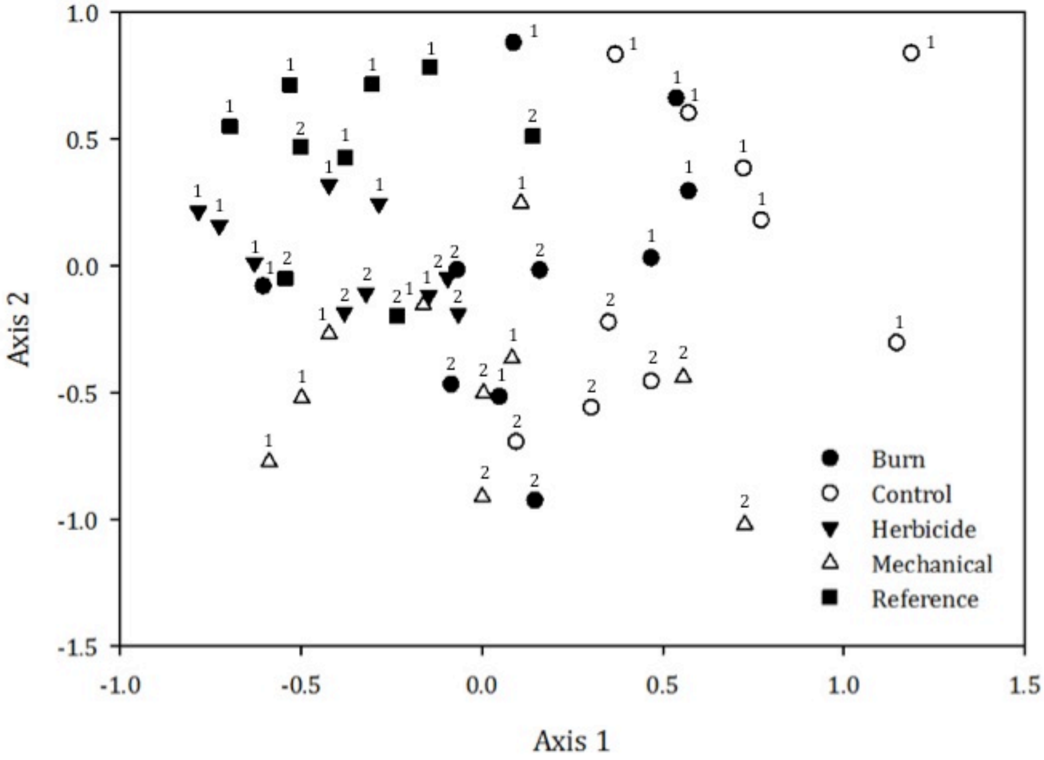
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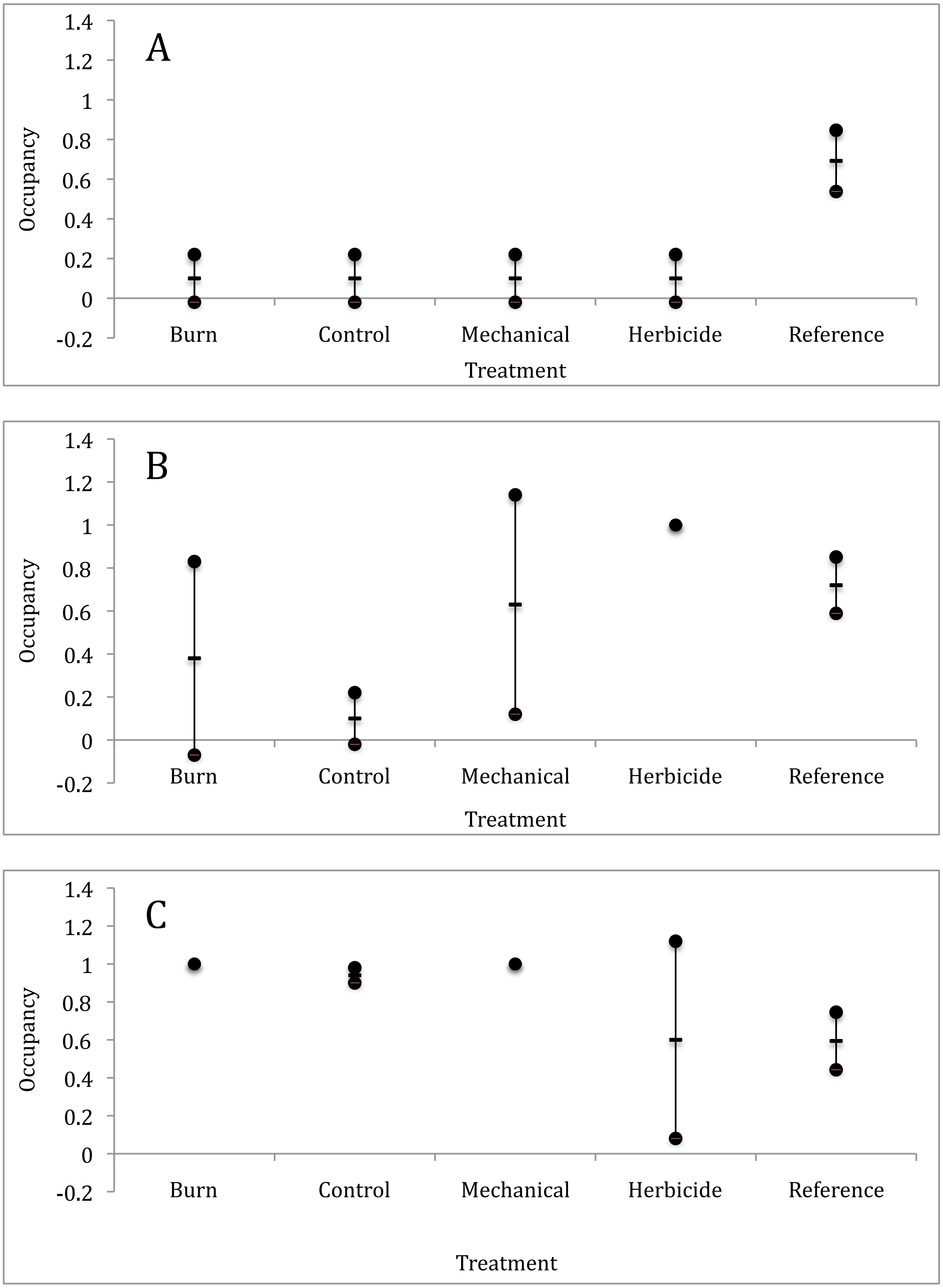
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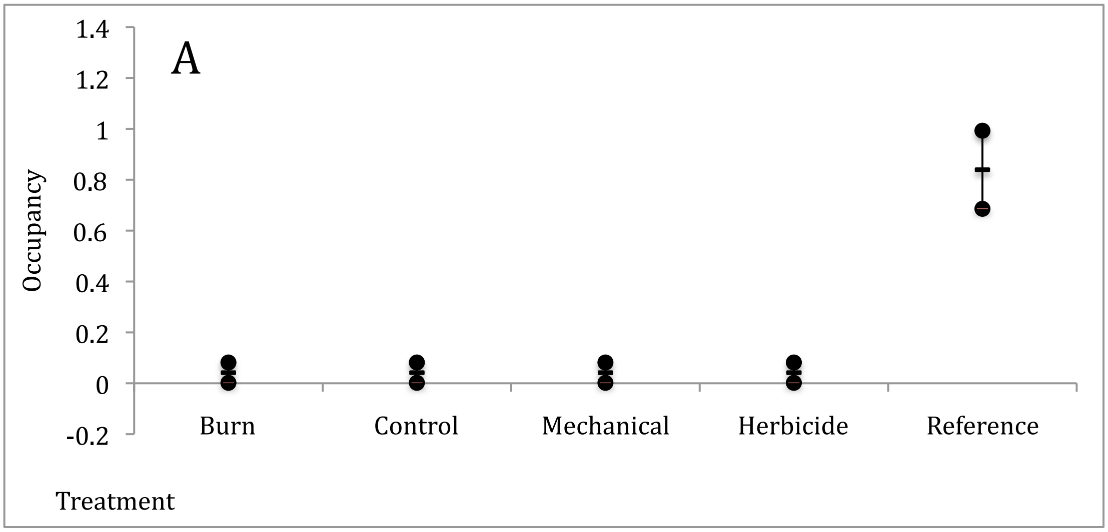
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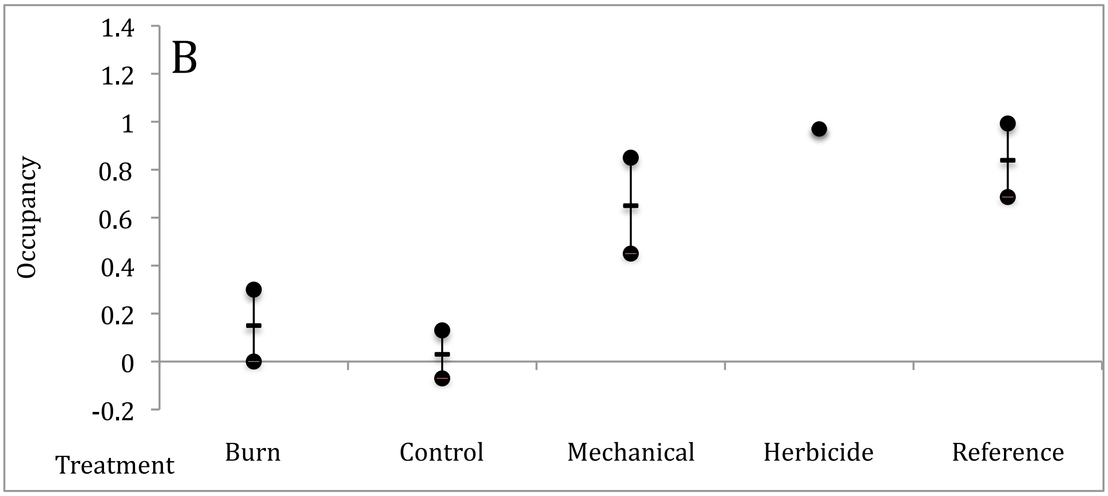
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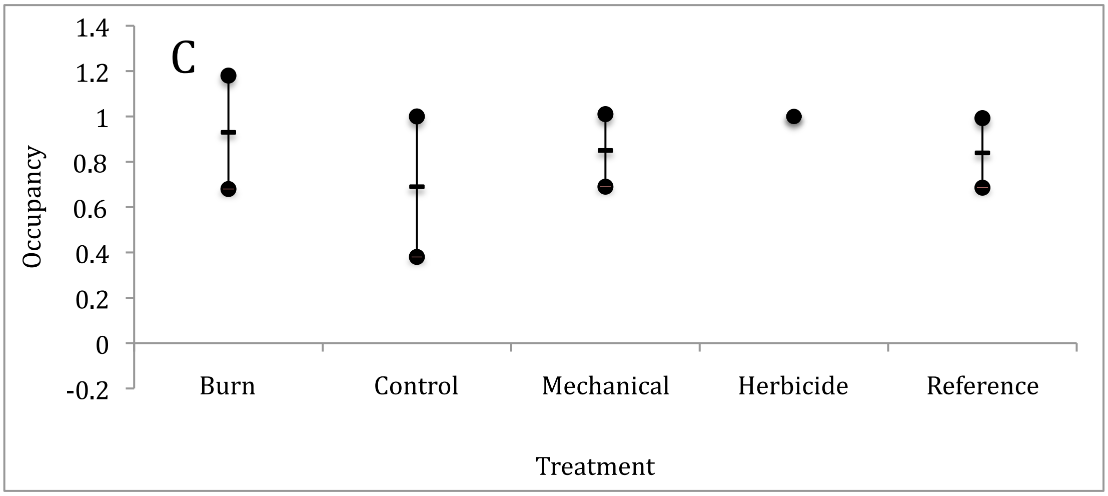
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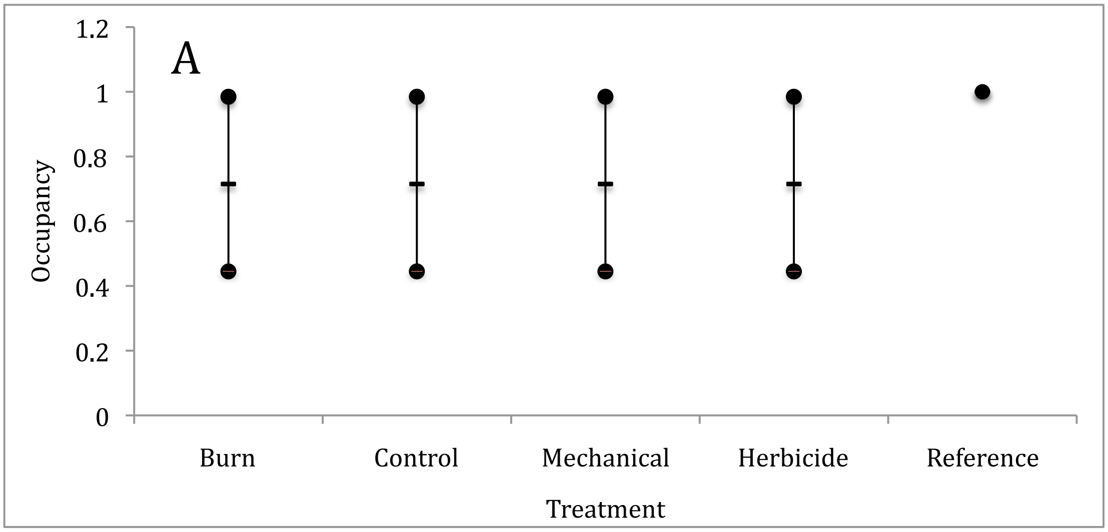
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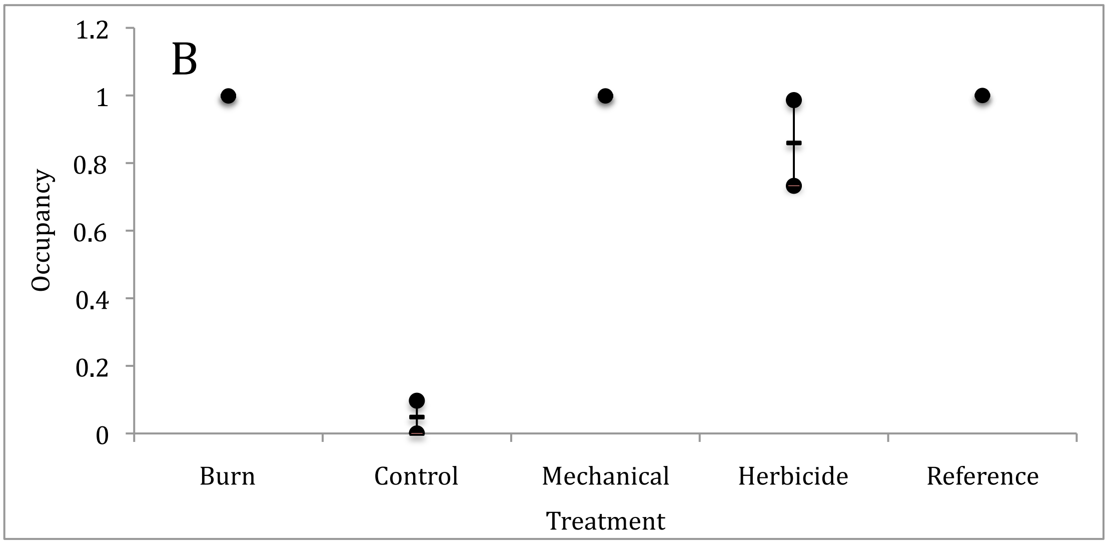
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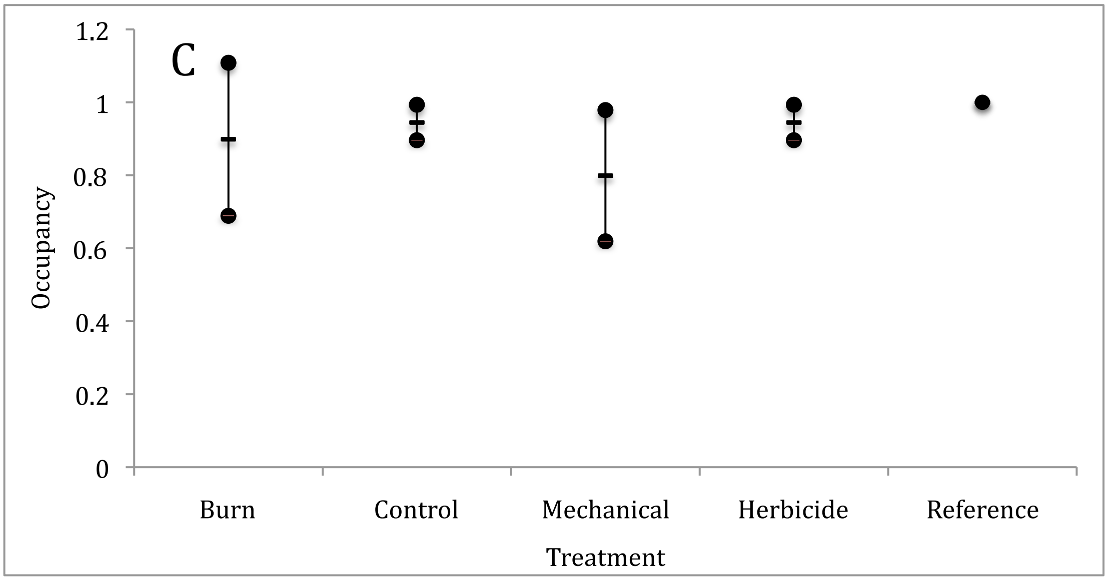
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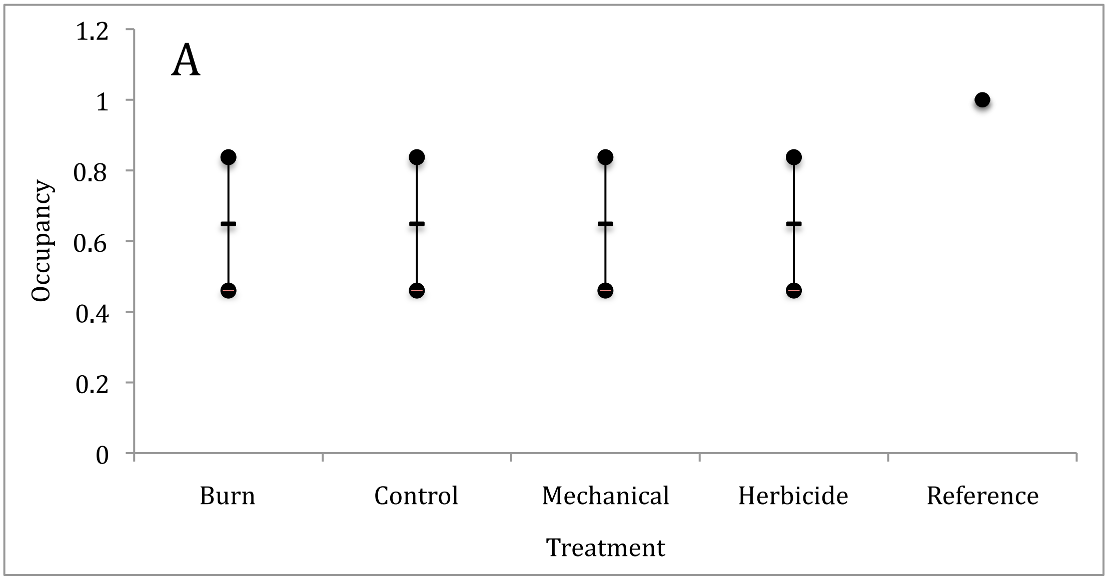
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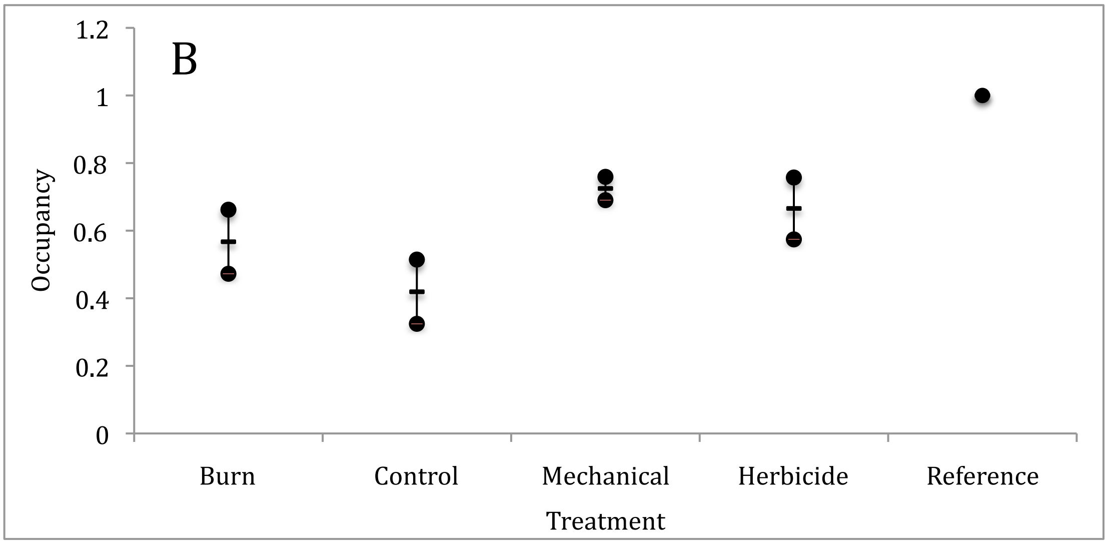
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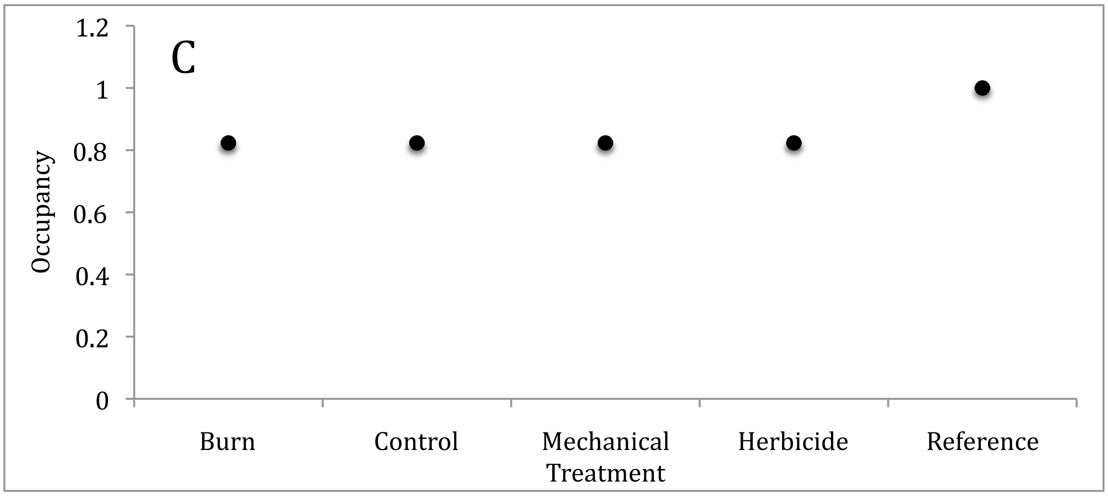
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Chapter 4

Restoration of Reptile Assemblages: Long-term Effects of Fire Surrogates and Prescribed Burning

Abstract. Attempts to restore fire-suppressed and hardwood-invaded longleaf pine forests are common but the long-term effects on wildlife are rarely measured. We employed a landscape-scale, randomized-block design to identify how reptile assemblages initially responded to restoration treatments including removal of hardwood trees via felling and girdling, herbicide application, or prescribed burning alone. Then, we examined reptile assemblages after all sites experienced more than a decade of prescribed burning at 2-3 year return intervals. Data were collected concurrently at reference sites chosen to represent target conditions for restoration. Reptiles responded to the greatest extent, initially, to prescribed burning but reptile assemblages at all sites, including reference sites, were generally indistinguishable by the end of the study. Thus, we suggest prescribed burning in longleaf pine forests over long time-periods is an effective strategy for restoring reptile assemblages to the reference condition.

Key Words: Aspidoscelis sexlineatus, longleaf pine, non-metric dimensional scaling, prescribed fire, squamates, Tantilla coronata.

INTRODUCTION

The longleaf pine ecosystem of the southeastern United States was once extensive (Landers et al. 1995) but is now highly imperiled (Noss 1988). A fire-adapted habitat, 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 and composition (Mitchell et al. 2006).

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). In addition, fire alone may be 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. 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 less well known (Russell et al. 1999).

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); although they may be useful tools in restoring conditions necessary to reintroduce fire into these forests (Provencher et al. 2001a, Brockway et al. 2005). It is generally suggested that these fire surrogates may quickly alter a forest towards 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). However, it may be necessary to apply fire over long time-periods to move the habitat to a condition comparable to that which was observed prior to European settlement (Waldrop et al. 1992).

Longleaf pine forests contain a rich diversity of vertebrate animals (Means 2006) and forest management may have considerable effects on associated wildlife (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 relevant parameters (e.g., Block et al. 2001, Gardner et al. 2007). For example, although it is likely necessary to study wildlife response to management on 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. 2009, Steen et al. 2010).

Small reptiles may be abundant in suitable habitats, comprising a considerable component of the vertebrate biomass (e.g., Bullock and Evans 1990). Many reptiles occur largely in longleaf pine forests, to the extent that several are considered specialists of this habitat (Guyer and Bailey 1993, Means 2006). Consequently, this group may be particularly sensitive to forest management (e.g., Greenberg et al. 1994, Todd and Andrews 2008) but it is difficult to predict how they may respond (Lindenmayer et al. 2008). Within this study, we used ordination techniques and similarity and diversity indices to examine how reptile assemblages varied among fire-suppressed longleaf pine sandhills treated with prescribed fire and fire surrogates (herbicide and mechanical hardwood removal) and how repeated prescribed burning affected these initial patterns.

METHODS

Study Site

This study took place on Eglin Air Force Base, Okaloosa and Santa Rosa Counties, Florida, U.S. We focused our study on fire-suppressed longleaf-pine sandhills. A randomized block design was used to assign hardwood removal method treatments to 16 sites, each 81 ha in area and arranged in four blocks (Litt et al. 2001, Provencher et al. 2001a). Six of these sites had experienced a single burn between 1977 and 1989; since this burn frequency is less than the natural fire frequency (i.e., every 1-10 years, Myers 1990), we treat them all as fire-suppressed. All other treatment sites had not been burned since at least 1973 (when record-keeping began, B. Williams, Jackson Guard, pers. comm.). Methods of hardwood removal included burning (Burn), herbicide application (Herbicide), or felling-girdling (Mechanical) and Controls, which experienced no treatment in 1995 (below). Four 81 ha reference sites were also designated. Reference site selection is described in Provencher et al. (2001a); sites were selected as representations of the ancestral condition and a target condition of restoration efforts (White and Walker 1997).

Treatment Application

Initial hardwood removal treatments occurred in 1995. Burn treatments were applied in April-June. Herbicide, (ULW, hexazinone, 1.68 kg of active ingredient/ha, Gonzalez 1985) was applied in early May and mechanical hardwood removal was conducted between June and November. Herbicide and Mechanical sites were subjected to a prescribed burn in 1997. More details on treatments are available in Provencher et al. (2001b). After treatment application, all sites received comparable management, which included prescribed fire on a 2-3 year rotation but no additional targeted removal of hardwoods or application of herbicide. One reference site received herbicide application between 1997-2009; thus, we excluded data collected from this site during 2009-2010.

Reptile Trapping

Drift fence arrays (Campbell and Christman 1982) were placed at the center of each of 16 treatment sites and four reference sites to capture representatives of Squamata and Testudines, hereafter, reptiles. Fences were made of aluminum flashing and sixteen 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-August 1997 and from April-August 1998 (Litt 1999, Litt et al. 2001); 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-September 2009 and May-August 2010. For 2009 and 2010, we added box traps to the center of the arrays as part of a separate study (Burgdorf et al. 2005, Steen et al. 2010), but used the same number and position of pitfall traps per array as in the original study.

All reptiles were individually marked in 1997-1998 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 *A. sexlineatus* in 2009-2010. 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). 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). We excluded box trap captures from the analysis since this method was not used in the initial study.

Vegetation Data

Vegetation data were collected in 1994, 1998, 2009 (treatment sites only) and 2010 (reference sites only). To quantify groundcover vegetation and tree density, we collected data within 16 subplots at Step 10 in each site (see study design in Provencher et al. 2001a,b). In 1994-1998, it was necessary to use data from Step 50 within one Burn site. Vegetation cover classes (1-5%, 5-25%, 25-50%, 50-75%, 75-95%, 95-100%) for four ground cover vegetation categories (i.e., Grass, Woody Litter, Fine Litter) were converted to midpoints to create 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 was ≥ 4 inches (10.16 cm) dbh. An oak tree was considered overstory if it was ≥ 6.3 inches (16 cm) dbh. We calculated the mean basal area (m^2/ha) of midstory and overstory trees for each site.

Reptile Diversity

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 in 1997-1998 and again for 2009-2010. Each site within a study period was then compared to the mean reference similarity index for that study period. We calculated the Shannon index (Magurran

2004) to quantify diversity for each site in both study periods. This index is commonly used to describe reptile diversity (e.g., Greenberg et al. 1994, Michael et al. 2008).

We used a before-after control-impact study design (Stewart-Oaten et al. 1986) to compare reptile similarity and diversity with separate least squares means analyses of variance. We compared similarity and diversity on fire-suppressed Controls and Burn, Mechanical, and Herbicide treatments to similarity and diversity on reference sites in 1997-1998. We also compared similarity and diversity on treatments in 1997-1998 to similarity and diversity on treatments in 2009-2010 to determine if reptile assemblages differed following a decade of prescribed burning. Finally, we compared similarity and diversity on all treatment sites to that of reference sites in 2009-2010. Our alpha level for all analyses was 0.10.

Non-metric Dimensional Scaling

We conducted a single non-metric dimensional scaling ordination, based on Bray-Curtis (Sorenson) distances, such that each site appeared in the ordination twice, once based on the 1997-1998 data and again based on 2009-2010 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 v. 4.25 (McCune and Mefford 1999). Ordination graphs were prepared with SigmaPlot (Systat software, San Jose, CA) and Microsoft PowerPoint 2008.

We assumed that control sites in 1997-1998 were representative of the pre-treatment 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.

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 v. 4.25 (McCune and Mefford 1999).

Canonical Correspondence Analysis

To determine if reptile abundance was significantly associated with treatment type or reference sites while accounting for variation in habitat characteristics, we conducted separate canonical correspondence analysis (CCA, ter Braak 1986) for each study period with species captured at least ten 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 is conducted of site scores (dependent variable, derived from weighted species abundance data) against environmental variables (independent variable). In this manner, each site receives a site 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 v. 4.25 (McCune and Mefford 1999).

RESULTS

Vegetation Data

Oak density decreased initially at the three hardwood removal treatments (Table 1). Burn, Control, and Herbicide treatment sites had lower in oak overstory basal area in 2009-2010, while oak basal area increased at Mechanical sites between 1997-1998 and 2009-2010. Oak midstory decreased at Control and Herbicide sites between 1997-1998 and 2009-2010 while it increased at Burn and Mechanical sites.

Reptile Diversity

We recorded 1775 captures of 16 reptile species in 1997-1998 and 1648 captures of 19 reptile species in 2009-2010 (Table 2). Similarity (Morisita-Horn index) interacted significantly between treatment and time ($F_{4,1} = 2.20$, $P = 0.093$). In 1997-1998, similarity indices at Reference sites were different than Herbicide ($P = 0.05$) and Control sites ($P = 0.0006$). These trends are likely influenced heavily by two species; the relative proportion of *A. sexlineatus* and southeastern crowned snakes, *Tantilla coronata*, was lower and higher, respectively, in Control and Herbicide sites (Figure 1).

In 2009-2010, similarity did not differ between treatments (Figure 2), similarity changed significantly at Controls ($P = 0.0006$) and Herbicide ($P = 0.06$) sites between 1997-1998 and 2009-2010. Cumulatively, this suggests that Burn and Mechanical treatments were effective at replicating the ancestral condition shortly after treatment application (i.e., by 1997-1998). Between this time period and 2009-2010, the reptile assemblages at Control and Herbicide sites changed significantly to become indistinguishable from those on reference sites. We documented no significant changes in Shannon's diversity index ($F_{4,1} = 0.52$, $P = 0.72$).

Non-metric Dimensional Scaling

A two-dimensional solution was the best fit for the data, with a final stress of 9.3 and an instability of 0.00009 after 55 iterations. The stress was less than expected by chance ($P = 0.03$; Figure 3). For 1997-1998, the MRPP indicated that Controls, Mechanical, and Herbicide sites were indistinguishable (Table 3). 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 on Control sites but still distinguishable to those of Reference sites. Reptile assemblages at Herbicide sites were distinct from those of references in 2009-2010; otherwise there were no differences (Table 3).

Indicator Species Analysis

Three species were significantly associated with a particular treatment in 1997-1998 (Table 4). *Aspidoscelis sexlineatus* was positively associated with reference sites, ring-necked snake, *Diadophis punctatus*, was positively associated with Control sites, and eastern fence lizard, *S. undulatus*, was positively associated with Burn sites. No significant indicator species were identified in any of the treatments in 2009-2010, indicating a relatively uniform distribution of species across treatments.

Canonical Correspondence Analysis

For the 1997-1998 data, 35.5% of the species distribution variance was explained by the first two axes (Figure 4). 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 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 2009-2010 data were not significantly different than expected by chance, suggesting axes were not effective at explaining species distribution variances.

DISCUSSION

We demonstrate that application of prescribed fire resulted in increased similarity of reptile assemblages on treatment sites to assemblages on reference sites in the short-term, corroborating Litt et al. (2001). In the long-term, repeated use of prescribed fire was effective at altering assemblages at all treatment sites such that they became indistinguishable from those on references sites. Thus, we conclude that long-term prescribed burning is an effective method of restoring reptile assemblages in fire-suppressed longleaf pine forests.

Based on similarity indices, reptile assemblages at sites treated with prescribed fire alone, as well as those treated with mechanical hardwood removal, were indistinguishable from assemblages on reference sites in 1997-1998 while assemblages on Control sites and sites treated with herbicide were not. Non-metric dimensional scaling for the same time period suggested Burn sites contained reptile assemblages different from those at other treatment sites but also distinguishable from those on reference sites. The NMDS also suggested that assemblages on Mechanical sites were indistinguishable from those on Control and Herbicide sites. Both analyses were consistent in identifying assemblages on Control and Herbicide sites as having significantly different assemblages from those at reference sites in 1997-1998, corroborating previous analyses (Litt et al. 2001). Litt et al. (2001) suggested that some species benefit from habitat heterogeneity, which may be relatively low in both Herbicide and Control sites. Herbicide sites experienced a reduction in ground cover vegetation following herbicide application and a reduction in woody debris due to 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 treatments, our results were generally consistent in suggesting reptile assemblages at all treatments were indistinguishable from those at reference sites by 2009-2010 (with the exception of the NMDS distinguishing assemblages on Herbicide sites from those on reference sites). Since 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. 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).

Based on the results of the NMDS ordination, reptile assemblages at sites treated with herbicide and over a decade of prescribed burning were distinct from those at reference sites. Therefore, it appears that this treatment was relatively ineffective at restoring reptile assemblages. Herbicide application was highly effective at reducing of oak overstory density, to the point that density levels were lower than at reference sites. Hardwood trees are important to certain wildlife species associated with the longleaf pine ecosystem (Perkins et al. 2008), thus, it is possible that the low hardwood densities at Herbicide sites was detrimental to reptiles. Although the limited research examining wildlife response to hexazinone and related products suggest it is generally safe (Berrill et al. 1994, Michael et al. 1999, but see Wan et al. 1988), it is also possible that this herbicide had a long-lasting and negative effect on reptiles either directly or on their prey.

Although some species likely benefited from hardwood removal, particularly *A. sexlineatus*, we suggest the assemblage level change we documented is due largely to the decline of hardwood-associated species. For example, *D. punctatus*, although observed only rarely, was an indicator of Controls in 1997-1998 but was not detected in 2009-2010 despite increased trapping effort. *Diadophis punctatus* prefers areas with abundant undisturbed litter and detritus (Perison et al. 1997), as does *Scincella lateralis* (Conant and Collins 1998), which also declined in observed numbers between the two study periods. Both species are likely to avoid frequently burned landscapes (Wilgers and Horne 2006).

Canonical correspondence analysis identified potential mechanisms behind the assemblage-level change. Fine litter, oak midstory, and oak overstory were important variables in explaining species distribution patterns in 1997-1998 (Figure 4). Since Control sites had relatively high levels of Fine Litter and Oak Midstory (Figure 4), these variables are likely important to several species which declined in relative proportion between the two study periods.

The CCA suggested that *Virginia valeriae* and *Cemophora coccinea* were positively associated with fine litter cover. *Cemophora coccinea* also had a negative relationship with oak tree 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* (Table 2, Figures 1 and 2), 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. Our results from natural longleaf pine stands appear to corroborate this finding.

Anolis carolinensis was also observed less frequently in the second study period. In 1997-1998, this species was positively associated with midstory oak trees, which likely offer suitable perching habitat for this arboreal species (Irschick et al. 2005). Since 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 terrestrial traps.

Aspidoscelis sexlineatus in fire-suppressed habitats benefit from restoration including hardwood removal and reintroduction of fire (Mushinsky 1985, Perry et al. 2009). We documented considerable shifts in the relative proportion of this species between the two study periods (Figures 1 and 2). Initially, *A. sexlineatus* capture rates on all treatment sites differed from those on reference sites (Tables 2 and 4). However, the relative proportion of *A. sexlineatus* at all sites was similar after repeated prescribed fire over the long-term. Thus, frequent fire is likely to benefit this species (Mushinsky 1985) as it does for other reptile species highly associated with the longleaf pine ecosystem (e.g., Yager et al. 2007). It is important to note that several reptile species associated with the longleaf pine ecosystem, such as gopher tortoise, *Gopherus polyphemus*, indigo snake, *Drymarchon corais*, eastern diamond-backed rattlesnake, *Crotalus adamanteus*, southern hognosed 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. It is unknown whether the trends we documented are applicable to this group.

Evaluating reptile assemblage response to forest restoration based solely on the first few years following treatment may be an inappropriate time scale for reptiles. The potential importance of time since treatment is demonstrated by contrasting reptile assemblages at Burn sites with those at Herbicide and Mechanical sites. All three treatments received fire before reptile sampling was initiated in 1998; however, Burn sites received fire in 1995 while Mechanical and Herbicide sites were burned early in 1997. The disparate reptile assemblages observed among the treatment sites suggests time since burn may influence the reptile assemblage.

Due to patterns of change in vegetation, even this study may not have been conducted on a time scale necessary to detect long-term trends in reptile assemblage response to the treatments and subsequent reintroduction of frequent fire. For example, sites that experienced mechanical removal of hardwood trees initially experienced a considerable decline in oak density (Table 1); however, by 2009-2010, oaks had rebounded to the extent that their overstory density approached levels observed at Controls in 1997-1998. This pattern is likely due to increased resprouting following mechanical removal (Provencher et al. 2001b). Continued monitoring of these sites may document a gradual increase in oak density and a transition of the reptile assemblage towards one more associated with hardwood-dominated habitats.

It is important to consider how heterogeneity in detection probability influences capture rates when making inferences about relative abundances (Mazerolle et al. 2007). In fact, it is likely more appropriate to assume detection probabilities are unequal when comparing populations (MacKenzie and Kendall 2002). 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 et al. 2011, Chapter 5). Most species within this study were detected infrequently and in low numbers.

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 habitats. Since our study design did not include long-term monitoring of sites treated only with mechanical removal of hardwood trees or herbicides, we are unable to determine if continued disturbance of this type would have had the same effects as frequent fire. In any case, given the uncertainty regarding long-term trends in oak density at Mechanical sites and the differences in reptile assemblages between Herbicide and reference sites, reintroduction of frequent fire is the only management strategy we can recommend without caveat for effective restoration of small reptile assemblages. Opportunely for land managers, prescribed burning is the most inexpensive hardwood removal treatment evaluated in this study (Provencher et al. 2002).

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Figure 1. Relative proportion of species captured in treatment and reference sites on Eglin Air Force Base, 1997-1998. Species captured ≤ 5 times are not included in graph. Species codes are provided in Table 2.

Figure 2. Relative proportion of species captured in treatment and reference sites on Eglin Air Force Base, 2009-2010. Species captured ≤ 5 times are not included in graph. Species codes are provided in Table 2.

Figure 3. Non-metric dimensional scaling of treatment and reference sites for 1997-1998 and 2009-2010, Eglin Air Force Base, Santa Rosa and Okaloosa Counties, Florida. 1 = 1997-1998, 2 = 2009-2010.

Figure 4: Canonical correspondence biplot for reptiles captured in 1997-1998, Eglin Air Force Base, Santa Rosa and Okaloosa Counties, Florida. B = Burn, C = Control, H = Herbicide, M = Mechanical and R = Reference.

Table 1. Tree density within hardwood-removal sites and reference sites, Santa Rosa and Okaloosa Counties, Eglin Air Force Base, Florida. One reference site was not included in 2009-2010 summaries. All units are m^2/ha (standard error).

	1994	1998-1999	2009-2010
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)

Table 2. Total captures of reptiles by treatment and reference sites on Eglin Air Force Base, 1997-1998 and 2009-2010. Trapping effort within a year increased in 2009-2010 and one reference site was excluded from study (see Methods).

	Control	Burn	Herbicide	Mechanical	Reference	Total
Anolis carolinensis (ACAR)						
1997-1998	18	20	1	1	10	50
2009-2010	5	3	1	2	3	14
Aspidoscelis sexlineatus (ASEX)						
1997-1998	106	200	101	197	338	942
2009-2010	224	297	228	233	232	1214
Cemophora coccinea (CCOC)						
1997-1998	3	1	1	6	1	12
2009-2010	6	3	3	4	3	19
Coluber constrictor						
1997-1998	0	1	3	1	0	5
2009-2010	0	0	1	1	3	5
Coluber flagellum						
1997-1998	0	0	0	0	0	0
2009-2010	1	0	1	2	0	4
Diadophis punctatus						

1997-1998	3	0	0	0	0	3
2009-2010	0	0	0	0	0	0
Gopherus polyphemus						
1997-1998	0	0	0	0	0	0
2009-2010	0	0	0	0	1	1
Heterodon platyrhinos						
1997-1998	0	0	0	0	0	0
2009-2010	1	0	0	0	1	2
Lampropeltis elapsoides						
1997-1998	0	0	1	1	0	2
2009-2010	1	0	0	0	0	1
Micrurus fulvius						
1997-1998	0	0	1	0	0	1
2009-2010	0	0	0	0	0	0
Nerodia fasciata						
1997-1998	0	1	1	0	1	3
2009-2010	0	0	0	1	0	1
Plestiodon egregius (PEGR)						
1997-1998	7	8	2	2	4	23
2009-2010	3	5	1	4	4	17
Plestiodon laticeps						

(PLAT)						
1997-1998	22	6	11	10	3	52
2009-2010	8	14	7	4	4	37
Regina rigida						
1997-1998	0	0	0	0	0	0
2009-2010	0	1	0	0	0	1
Sceloporus undulatus (SUND)						
1997-1998	13	50	16	29	30	138
2009-2010	42	56	28	26	49	201
Scincella lateralis (SLAT)						
1997-1998	29	22	10	18	15	94
2009-2010	10	9	4	3	8	34
Sistrurus miliarius						
1997-1998	2	1	0	1	0	4
2009-2010	2	0	1	1	1	5
Storeria occipitomaculata						
1997-1998	1	0	0	1	0	2
2009-2010	1	0	0	0	0	1
Tantilla coronata (TCOR)						

1997-1998	128	55	89	111	49	432
2009-2010	15	15	23	19	15	87
Terrapene carolina						
1997-1998	0	0	0	0	0	0
2009-2010	0	0	1	1	0	2
Virginia valeriae (VVAL)						
1997-1998	4	0	2	2	4	12
2009-2010	0	1	1	0	0	2

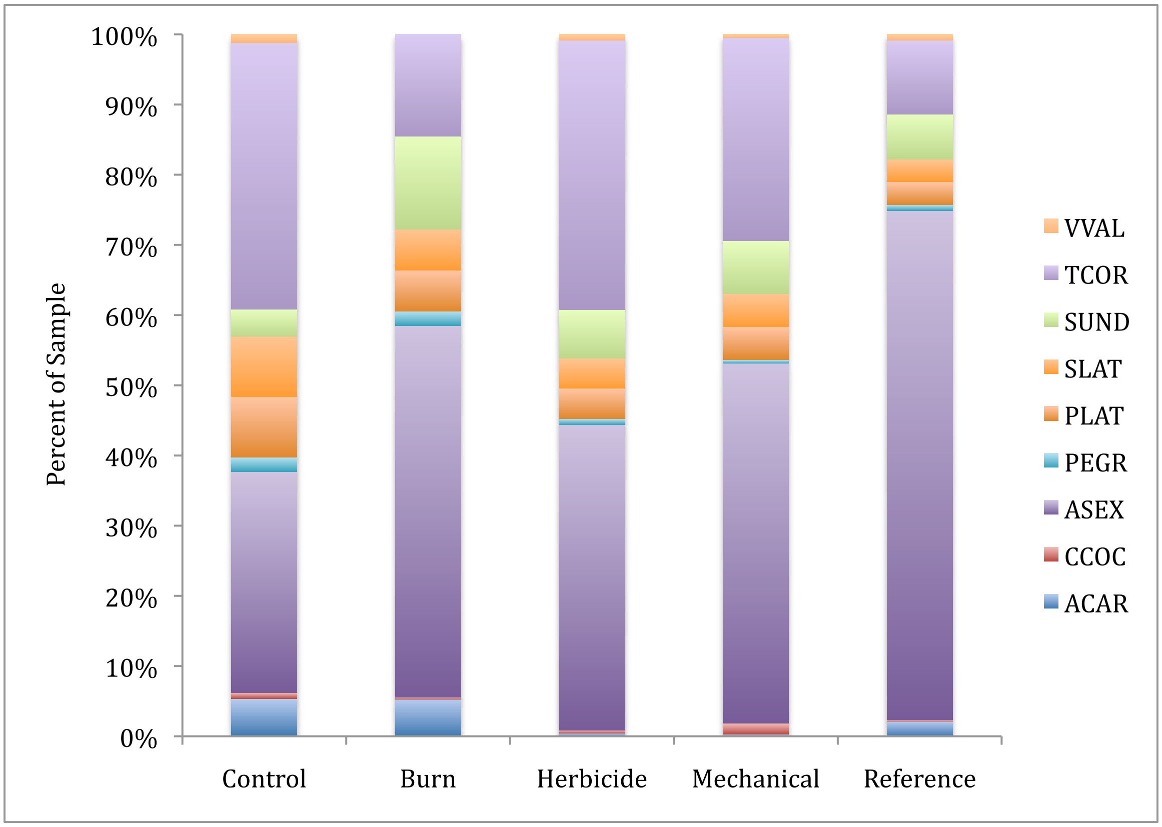
Table 3. P-values associated with multi-response permutation procedure on pairwise comparisons of treatment and reference sites (1997-1998 and 2009-2010). Bold indicates a significant difference between groups (α = 0.10)

	Burn	Control	Mechanical	Herbicide	Reference
1997-1998					
Burn	X	**0.01**	**0.008**	**0.01**	**0.034**
Control	X	X	0.46	0.24	**0.02**
Mechanical	X	X	X	0.3	**0.09**
Herbicide	X	X	X	X	**0.02**
2009-2010					
Burn	X	0.44	0.47	0.69	0.77
Control	X	X	0.53	0.77	0.19
Mechanical	X	X	X	0.9	0.19
Herbicide	X	X	X	X	**0.08**

Table 4: Percent indicator values for reptile species significantly associated with a particular treatment on Eglin Air Force Base, 1997-1998. Bold indicates a significant association with a particular treatment.

	Burn	Control	Mechanical	Herbicide	Reference	P-value
Aspidoscelis sexlineatus	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

Figure 1.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PLAT
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CCOC
ACAR

Figure 2.

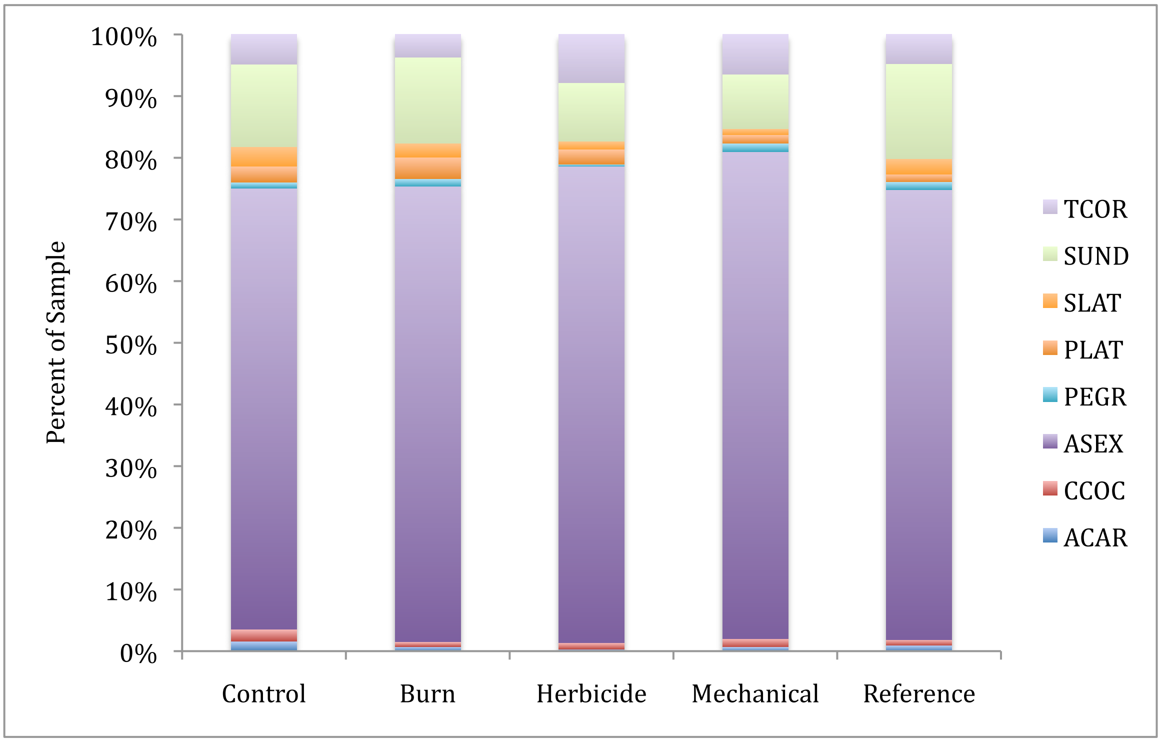
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Figure 3.

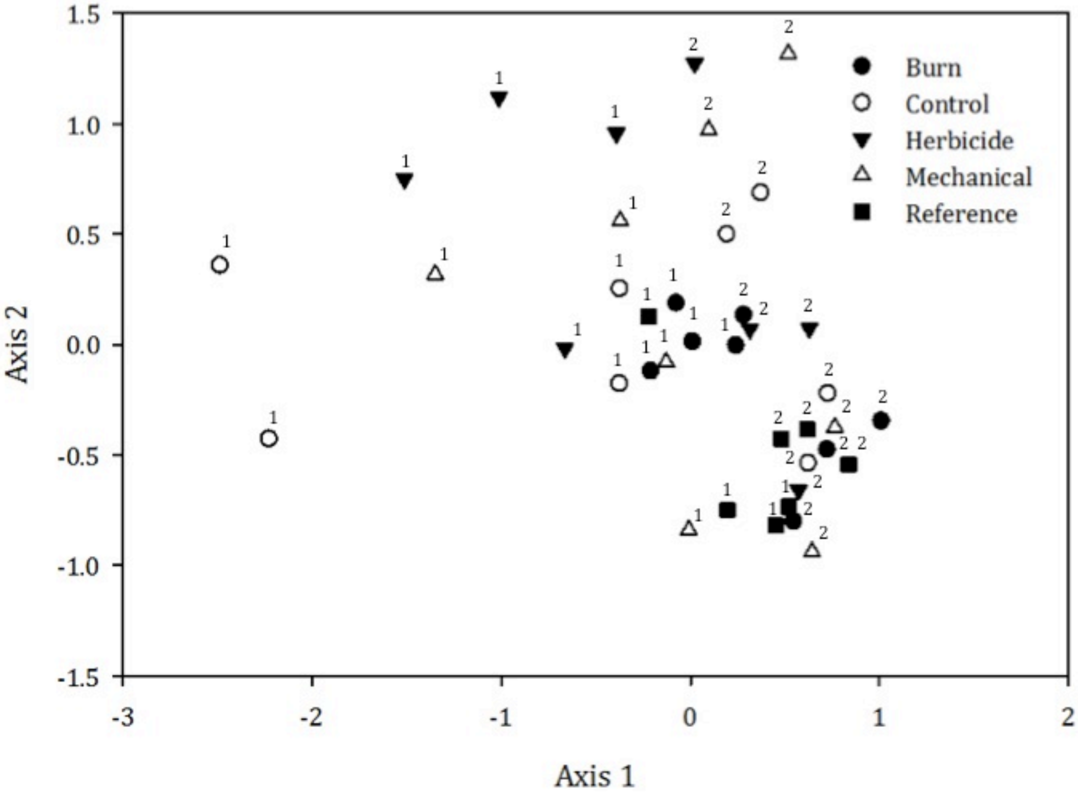

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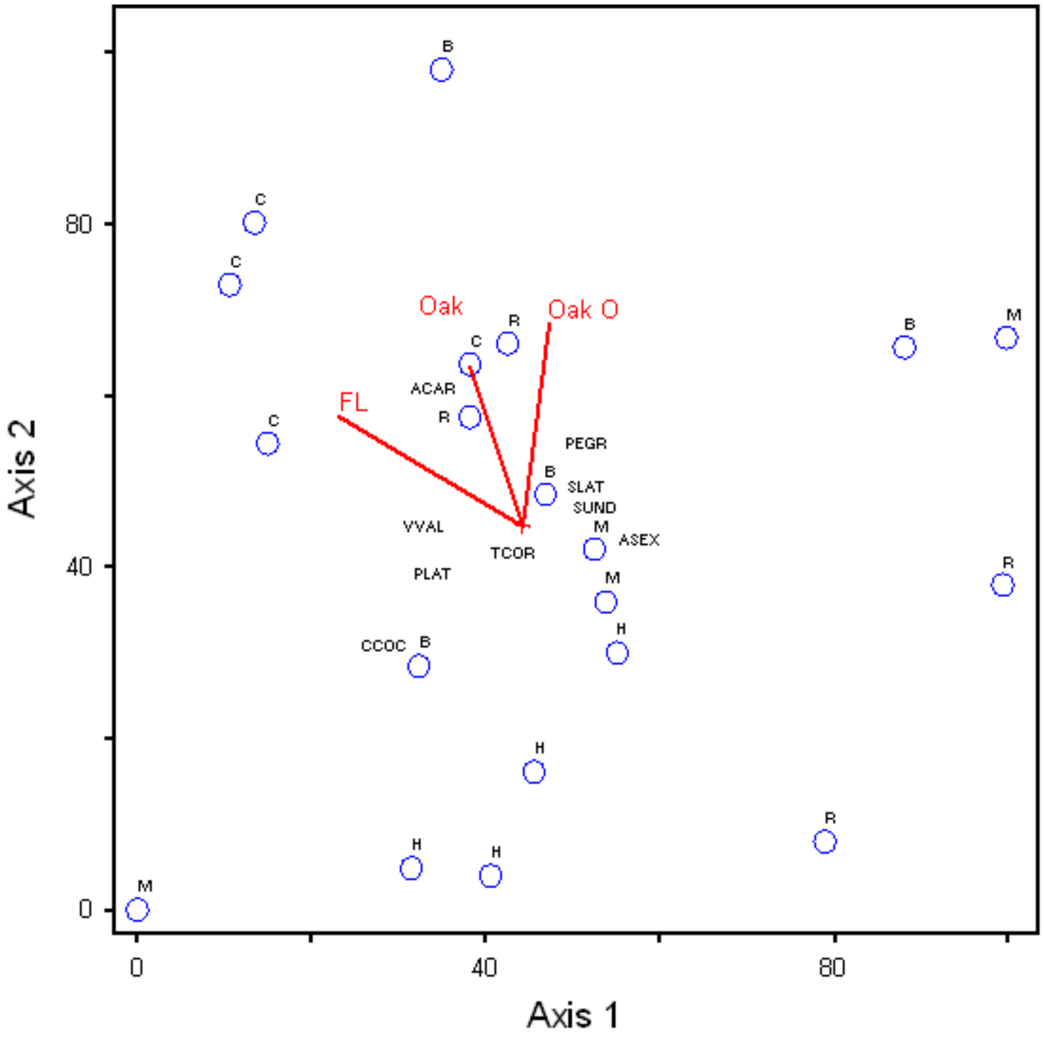
Figure 4.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Chapter 5

Six-lined Racerunner, *Aspidoscelis sexlineatus*, Population Size and Survivorship: Long-term Effects of Fire Surrogates and Prescribed Burning

Abstract. Fire surrogates and prescribed burning are management tools for the restoration of fire-suppressed and hardwood-invaded longleaf pine forests. To evaluate how populations of a common squamate, the six-lined racerunner, *Aspidoscelis sexlineatus*, responded to forest restoration, we conducted a mark-recapture study of populations in formerly fire-suppressed longleaf pine forests exposed to prescribed fire or fire surrogates (i.e., mechanical or herbicide-facilitated hardwood removal) as well as in untreated control sites and reference sites. After initial treatment, all sites were exposed to over a decade of prescribed burning with an average interval of approximately two years. Our population analysis (POPAN) produced counter-intuitive results, which we attribute to uncertainty resulting from low sample sizes and detection probabilities. However, the mean number of marked adults and juveniles at sites treated with prescribed burning and sites treated with mechanical removal of hardwoods was comparable to the mean number of marked adults and juveniles at reference sites over relatively short-time scales. Over the long-term, mean numbers of marked individuals observed at all treatments was not different from the mean number of marked individuals observed at reference sites. We conclude that prescribed burning over long time scales is an effective approach for restoring *A. sexlineatus* populations in fire-suppressed longleaf pine sandhills.

Key Words: Before-After-Control-Impact, Longleaf Pine, Mark-recapture, *Pinus palustris*, POPAN, Prescribed Fire, Reptile, Survival

INTRODUCTION

Longleaf pine forests, which once spanned throughout the coastal plain of the southeastern United States (Ware 1993), contain diverse vertebrate assemblages (Means 2006). These forests historically had a sparse canopy of pines with a diverse herbaceous understory maintained by frequent wildfires that occurred every 1-10 years (Myers 1990). However, due to fire suppression, hardwood trees have become established in the midstory of many former longleaf pine-grassland habitats. This has functioned to reduce habitat quality for many species associated with the ancestral condition (Mitchell et al. 2006).

Interest in restoring ecological communities has increased as natural habitats are lost outright (Hobbs and Harris 2001) or degraded by disruption of natural disturbance regimes (e.g., Nowacki and Abrams 2008). Restoration methods for fire-suppressed longleaf pine forests include direct removal of hardwoods via mechanical means or application of herbicides. However, due to the unique effects of fire, burning is likely an essential component of any successful longleaf pine forest restoration effort; if mechanical removal or herbicides are employed, they should be used together with eventual reintroduction of fire (Brockway et al. 2005).

The short and long-term effects of these different measures on the structure of longleaf pine forests can be readily apparent; however, the effects of habitat change on wildlife are not well known (e.g., Gardner et al. 2007). Previous research has suggested application of herbicides or mechanical hardwood removal, which some consider to be fire surrogates, may have varied short-term effects on wildlife assemblages (e.g., Litt et al. 2001) but long-term use of prescribed burning may be necessary to replicate reference conditions (Chapters 3, 4), as has been demonstrated among vegetation communities (Outcalt and Brockway 2010).

Response of reptiles to habitat management and restoration is generally studied at the assemblage level (Greenberg et al. 1994, 2008, Russell et al. 2002, Renken et al. 2004, Leynaud and Bucher 2005, Matthews 2010), including within longleaf pine forests (e.g., Litt 2001, Smith and Rissler 2010, Chapter 4). However, without careful attention to what constitutes a target assemblage, general trends may be obscured because reptiles are a diverse group (Barrett and Guyer 2009) and habitat associations of individual species may differ (Steen et al. 2010a). In addition, similarity is generally quantified by comparison of raw counts as an approximation of abundance, overlooking variation in detection probabilities (MacKenzie et al. 2006, Mazerolle et al. 2007). Consequently, assemblage-level study may obscure trends among species highly sensitive to forest management (e.g., Maas et al. 2009, Chapter 3).

Small squamates are abundant in longleaf pine forests and play important roles in the ecosystem (Means 2006); in addition, they may respond to habitat restoration in relatively short time scales (e.g., Trainor and Woinarski 1994, Bateman et al. 2008, Lettink et al. 2010). Therefore, focus on a squamate may be a useful proxy for wildlife community response to restoration. Six-lined racerunners, *Aspidoscelis sexlineatus*, are widely distributed across North America (Fitch 1958, Hardy 1962), but prefer open and xeric habitats, particularly longleaf pine forests, within the southeastern United States (Guyer and Bailey 1993). *Aspidoscelis sexlineatus* has been found to respond positively to frequent burning (Mushinsky 1985, Chapter 4). Therefore, *A. sexlineatus* may be an appropriate focal species for monitoring the success of restoration efforts in longleaf pine forests (Block et al. 2001).

Due to long generation times or delayed responses to vegetation changes, long-term studies may be necessary to characterize wildlife response to habitat change (Congdon et al. 1993, Brooks et al. 1999, Helm et al. 2006). In addition, immediate response to restoration may not be reflective of long-term patterns (Chapters 3, 4). Within this study, we used a randomized block design and quantified *A. sexlineatus* population sizes, while accounting for variation in capture probability, to determine how the species responded to ecological restoration over a 15-year period. Since accurate abundance estimates may be difficult to generate for squamates that have low detection probabilities (Steen 2010, Steen et al. 2011), we also compared the mean number of marked adults and the mean number of marked juveniles within each treatment to reference sites. If the structural endpoints we measured here (i.e., population estimates, number of marked adults and juveniles) were indistinguishable between treatment and reference sites, we infer management objectives were met; otherwise, we suggest a treatment was ineffective.

METHODS

Study Site

This study took place in fire-suppressed longleaf pine sandhills on Eglin Air Force Base, Santa Rosa and Okaloosa Counties, Florida, U.S. A randomized block design was used to assign hardwood removal method treatments to 24 81-ha sites (six blocks, Provencher et al. 2001). With the exception of six sites that experienced a single burn between 1977 and 1989, all sites had been fire-suppressed since at least 1973 (when records began). Methods of hardwood removal included burning (Burn), herbicide application (Herbicide), or felling-girdling (Mechanical) and a control, which experienced no hardwood removal. Six 81 ha reference sites were also designated. Provencher et al. (2001a) describe criteria for selection of reference sites; they were selected as representative of a natural longleaf pine forest, based on forest structure, disturbance regime, and the presence of characteristic wildlife, and were the target condition of restoration efforts.

Treatment Application

Hardwood removal occurred in 1995. Burn sites were burned April-June. Herbicide was applied in early May, and mechanical hardwood removal was conducted between June and November. Herbicide and Mechanical sites were subjected to a prescribed burn in 1997. After treatment application, all sites received comparable management, which included prescribed fire on an approximately 2-year rotation but no additional mechanical hardwood removal or application of herbicides.

Vegetation Data Collection

Vegetation data were collected in treatment sites and reference sites in 1998. Data for treatment sites were collected again in 2009 and reference sites were resampled in 2010. Sampling for vegetation occurred along transects in each site (as described in Provencher et al. 2001a, b). Vegetation was characterized by cover classes (1-5%, 5-25%, 25-50%, 50-75%, 75-95%, 95-100%) and converted to midpoints. These midpoints were used to generate mean percent cover for all sites. Oak midstory (trees < 16 cm, diameter at breast height) basal area (m^2/ha) for each site was also collected.

Aspidoscelis sexlineatus *Trapping*

Drift fence arrays (Campbell and Christman 1982) were placed in four treatment blocks (one drift fence in each of 16 treatment sites) and four reference sites. However, one reference site was treated with herbicide following the initial sampling, which fell outside of the study design, thus it was excluded from analysis. Traps were placed at the center of each site. *Aspidoscelis sexlineatus* were trapped in drift fence and pitfall arrays as described in Litt (1999) in 1997 and 1998 (Litt et al. 2001). Each array contained 30 m of 50 cm tall-galvanized steel flashing and 16 19-L pitfall traps. Arrays were placed in the same locations and lizards trapped from May-September 2009 and May-August 2010. In 2009 and 2010, we added box traps (Burgdorf et al. 2005, Steen et al. 2010b) at the center of arrays but used the same number of pitfall traps per array.

Aspidoscelis sexlineatus ≤ 500 mm snout-vent length were considered juveniles (slightly smaller than the size of reproductively active females, as reported for Arkansas animals, Trauth 1983). All other lizards were characterized as male or female based on a single secondary sexual characteristic, i.e., blue coloration on males (Conant and Collins 1998). Lizards were individually marked by toe clip and released (those that escaped before receiving a mark were not included in analysis). Clipping toes may influence recapture probability or survivorship of some vertebrates (Murray and Fuller 2000), and can interfere with normal behavior of climbing lizards (e.g., Bloch and Irschick 2004). However, toe-clipping did not affect running speed of a ground-dwelling skink (Borges-Landáez and Shine 2003) or of *A. sexlineatus* elsewhere (Dodd 1993). Therefore, we assumed this method of marking did not influence the parameters of interest within this study.

Analysis

We used the R 2.9.1 (R Development Core Team 2009) package RMark 1.9.6 (Laake and Rexstand 2008) to build POPAN models (Schwarz and Arnason 1996) in Program MARK 6.0 (White and Burnham 1999) to estimate monthly apparent survival (*phi*), capture probability (*p*), probability of entry into the population (*pent*) and population size (*N*) separately for 1997-1998 and 2009-2010. The POPAN model assumes a superpopulation from which trapped individuals are sampled, which may be appropriate when not all individuals are available for capture during every survey (Williams et al. 2011). POPAN is modified from the Jolly-Seber model (Pollock et al. 1990, Schwarz and Arnason 1996). Jolly-Seber models are commonly used in wildlife population analyses and the POPAN parameterization may be well-suited for lizards (e.g., Wiederhecker et al. 2003, Gracceva et al. 2008). Only a subset of traps were open in May 1997, and since POPAN models cannot handle unequal sampling effort among sites, we removed May 1997 from consideration in analysis.

We included grass/sedge and bare ground coverages as covariates when building models. Both of these vegetative characteristics may represent important structural features for *A. sexlineatus* (e.g., Mushinsky 1985, Litt et al. 2001, Lindenmayer et al. 2008). We also included midstory oak total basal area in the models because reduction of this component of the habitat was the objective of the experimental treatments. Although additional vegetation data were collected, previous analyses did not identify a correlation between *A. sexlineatus* capture rates and vegetative characteristics (Chapter 4), so they were excluded from model building.

Although we considered *phi* and *N* parameters of primary interest, accurate estimates of *phi* and *N* depend on appropriate specification of *p* and *pent*. Therefore, we developed an *a priori* set of models to explore the best means of modeling *p* and *pent*. For both *p* and *pent*, we considered the potential influence of the habitat variables described above (bare ground, grass/sedge, and midstory oak), treatment, and sex/age. For *phi*, the candidate model set considered models including treatment and sex/age effects. We specified *N* only as varying by site. We calculated the standard error of *N* by summing variances from gross initial population estimates (the population of animal present during the first trapping session), adding these values to overall net superpopulation estimates, and converting to standard errors for each *N* estimate.

We used a sequential framework to generate estimates for *p* and *pent* and ranked models with Akaike's Information Criteria corrected for small sample size (AICc, Burnham and Anderson 2002). When generating models for *p* or *pent*, other parameters were held constant in their most-parameterized iteration in the candidate model set. The best models estimating *p* and *pent* were then used in the model set to estimate *phi* (Tables 1 and 2). Within any model set, models that failed to estimate multiple parameters (likely due largely to overparameterization) were excluded from the set. We considered *phi* estimates as significantly different if 95% confidence intervals did not overlap. We attempted to assess fit using the goodness of fit tests in U-CARE 2.3.1 (Choquet et al. 2009), but lacked sufficient data to estimate $\hat{c}$ (variance inflation factor, a term which indicates overdispersion). As a result, we instead investigated the robustness of the model sets by manipulating $\hat{c}$ from 1.0 (no dispersion) to 3.0 (extreme dispersion; Devries et al. 2003).

We used a before-after control-impact study design and analysis of variance (Stewart-Oaten et al. 1986) to compare the 1) gross population size, 2) number of marked adults and 3) number of marked juveniles between treatments and over time with SAS 9.2 (SAS Institute, Inc. Cary, NC). Comparisons of *a priori* interest were whether population sizes and number of marked adults and juveniles within treatment sites were indistinguishable from those of reference sites for both study periods and whether these parameters within treatments changed over time. We set our alpha level to 0.05.

We assumed that *A. sexlineatus* population sizes and survivorship at treatment sites prior to hardwood removal in 1995 were comparable to those we observed on control sites in 1997-1998. We considered *A. sexlineatus* populations to be restored if population size estimates or the number of marked adults and juveniles at a given treatment did not differ from those on reference sites.

RESULTS

We had 712 captures of 584 individual *A. sexlineatus* in 1997-1998 and 1075 captures of 846 individuals in 2009-2010. Among individuals captured in 1997-1998, the proportion of females ranged from 0.25 in Control sites and 0.44 in Burn sites and the proportion of juveniles ranged from 0.15 in Control sites and 0.29 in Burn sites (Table 3). The proportion of female lizards captured in 2009-2010 ranged from 0.45 in Control sites to 0.54 in Burn sites. and the proportion of juveniles ranged from 0.15 in Herbicide sites to 0.26 in Mechanical sites (Table 3).

The model that best explained variation in capture probability (*p*) for the 1997-1998 period was one that allowed this variable to vary by bare ground. For the 2009-2010 period, the best supported specification of *p* allowed *p* to vary by grass/sedge, bare ground, and oak midstory (Tables 1 and 2). Estimated capture probability was 0.14 (standard error = 0.02) in 1997-1998 and 0.21 (standard error 0.02) in 2009-2010. The best model explaining variation in probability of entry into the population (*pent*) for the 1997-1998 period allowed this variable to vary by sex and age and treatment. For the 2009-2010 period, the best supported specification of *pent* allowed *pent* to vary by sex and age of the individual animal (Tables 1 and 2). The best models explaining survivorship for both study periods allowed this parameter to vary by treatment and sex (Tables 1 and 2).

The best-supported model (*phi*(sex/age+treatment)) in these sets was unchanged for $\hat{c}$ values up to 1.5 for the 2009-2010 data set and up to 1.25 for the 1997-1998 data set. However, this model remained within 4 AICc units of the adjusted best-supported model (*phi*(sex/age)) until $\hat{c}$ values of 3.0 for the 2009-2010 set, and of 2.75 for the 1997-1998 set. This indicates some sensitivity to changes in $\hat{c}$, although without an estimate of the actual $\hat{c}$ value for these sets, we are unable to say the degree to which (if any) overdispersion actually occurred.

With regard to gross population estimates, there was no significant interaction between treatment and time ($F_{4,1} = 0.76$, $P = 0.56$). Mean population size at reference sites (76.89) was significantly smaller than Burn sites (167.63, $P = 0.04$). No differences were detected between reference sites and Control (102.01, $P = 0.56$), Herbicide (116.67, $P = 0.36$), or Mechanical (122.62, $P = 0.29$) sites in 1997-1998 (Figure 1). In 2009-2010, mean population size at reference sites (132.38) was not significantly different from Burn (132.88, $P = 0.99$), Control (94.66, $P = 0.38$), Herbicide (77.23, $P = 0.21$) or Mechanical sites (122.95, $P = 0.65$; Figure 1). We did not observe significant differences in survivorship between treatments or age/sex classes (Table 4).

There was no significant interaction between treatment and time ($F_{4,1}$ = 1.45, P = 0.24) for the number of marked adults. In 1997-1998, the mean number of marked adults on reference sites (38) was not significantly different than on Burn (23.25, P = 0.06) or Mechanical (23.75, P = 0.06) but larger than on Control (13, P = 0.002) and Herbicide (13.75, P = 0.003). In 2009-2010, the number of marked adults on reference sites (37) did not differ from those on Burn (39.25, P = 0.76), Control (29.75, P = 0.34), Herbicide (32.5, P = 0.55) or Mechanical sites (27.75, P = 0.22; Figure 2).

With regards to the number of marked juveniles, there was no significant interaction between treatment and time ($F_{4,1}$ = 0.89, P = 0.49). In 1997-1998, the mean number of marked juveniles on reference sites (10.33) was not significantly different than on Burn (9.5, P = 0.80) or Mechanical (5, P = 0.12) but higher than on Control (2.25, P = 0.02) and Herbicide (3.5, P = 0.046). In 2009-2010, the mean number of marked juveniles on references (10) was not significantly different than Burn (7.25, P = 0.41), Control (5.75, P = 0.21), Herbicide (5.75, P = 0.21), or Mechanical (10, P = 1.0; Figure 3).

In summary, long-term prescribed burning did not interact with a specific hardwood removal treatment to result in different gross population estimates or in the number of marked adults or juveniles, rather, burning affected *A. sexlineatus* similarly for all treatments. In 1997-1998, the mean gross population size at Burn sites was larger than at reference sites. In 2009-2010, the mean gross population size at all treatments was comparable to that of reference sites. The mean number of marked adults and juveniles at Burn and Mechanical sites was indistinguishable from that of reference sites in 1997-1998 and all treatments were indistinguishable from references in 2009-2010.

The long-term effects of hardwood removal on vegetation structure varied by treatment (Table 5). Oak densities decreased in all treatment sites following initial treatment and remained relatively high in Controls. However, all treatments experienced gradual increases in midstory oak density, a trend most pronounced in Mechanical sites.

DISCUSSION

Aspidoscelis sexlineatus is an indicator of longleaf pine forests in reference condition (Chapter 4) and this species may play an important role in the ecosystem. Our results suggest effective restoration of *A. sexlineatus* populations may be achieved following restoration of fire-suppressed longleaf pine sandhills. Our findings based on relatively traditional measures of abundance (i.e., the number of marked adults and juveniles) suggest prescribed burning resulted in effective restoration of *A. sexlineatus* populations on relatively short-time scales (as did mechanical removal of hardwoods followed by prescribed fire). Over the long-term, prescribed burning in all treatments resulted in numbers of animals comparable to the number of animals observed on reference sites. In this sense, our findings corroborate multi-taxa, assemblage-level analyses on the same study site indicating prescribed burning is an effective, and perhaps necessary, method of restoring fire-suppressed longleaf pine sandhills for wildlife (Chapters 3, 4). These findings also corroborate studies conducted elsewhere on the species' response to habitat restoration (e.g., Mushinsky 1985, Greenberg et al. 1994). Although all treatments eventually resulted in numbers of *A. sexlineatus* indistinguishable from reference conditions, plots treated with prescribed burning alone and those treated with mechanical removal of hardwoods quickly achieved this result (≤ 4 years). Due to the added cost of mechanical hardwood removal, we recommend reintroducing prescribed burning to fire-suppressed longleaf pine sandhills to restore *A. sexlineatus* populations, as has been recommended elsewhere for the entire reptile assemblage (Chapter 4).

Abundance values alone may not be appropriate as comprehensive indices of how populations respond to habitat change (e.g., Todd and Rothermel 2006). For example, in many cases the number of individuals required to constitute a minimum viable population is unknown and abundance values may not reflect the effective population size; this limits the use of these values when quantifying wildlife response to habitat restoration (Smallwood 2001). Density also cannot be assumed to be positively related to habitat quality; measurement of population dynamics is likely more informative (Van Horne 1983). However, although we do not know the number of individuals required to represent a minimum viable population in *A. sexlineatus*, we assume the number of individuals observed at reference sites are representative of an ideal or target condition.

Previous research identifying changes in *A. sexlineatus* abundance in relation to prescribed fire frequency suggested that increases in abundance were attributable primarily to immigration (Mushinsky 1985). Our study sites were relatively large (81-ha) and our traps were located in the center of each site, suggesting immigration is unlikely to be the primary mechanism resulting in the trends we observed. Given that we observed as many juveniles in Burn and Mechanical plots as we did in reference sites in 1997-1998, we suggest that relatively high numbers of *A. sexlineatus* caught in these areas is due largely to either higher rates of successful reproduction or increased fecundity. *Aspidoscelis sexlineatus* mature relatively quickly (i.e., ~ one year of age; Clark 1976); therefore an increase in the number of successful reproductive events may quickly increase the number of sexually mature adults.

Similarities and differences in our gross population estimates of *A. sexlineatus* among sites are difficult to interpret. In 1997-1998, we did not detect a difference in gross population size and survivorship between Controls, which had been fire-suppressed for decades, and reference sites, which were fire-maintained and represented the ancestral condition. Thus, we are unable to make inferences regarding how gross population estimates of *A. sexlineatus* changed in response to forest management; our results suggest fire-suppression of longleaf pine forests is not to the detriment of *A. sexlineatus* populations.

Our gross population estimates of *A. sexlineatus* herein differed from estimates presented in most previous squamate studies in that ours were derived from a relatively rigorous mark-recapture analysis that incorporated heterogeneity in detection probability. Integration of detection probability may elucidate biological patterns that were not otherwise apparent (MacKenzie et al. 2006; Mazerolle et al. 2007) and it is possible that *A. sexlineatus* are more resilient to fire-suppression than previously indicated. In general, squamates are thought to maintain relatively stable populations over time (Schoener 1985), and our population estimates are consistent with this trend. However, mark-recapture analyses may fare poorly at estimating population parameters when capture probabilities are < 0.30 (White et al. 1982), and we estimated capture probabilities of 0.14 in 1997-1998 and 0.21 in 2009-2010. In addition, we recorded a relatively small number of individuals (Table 6), and this may increase bias and uncertainty of estimates derived from mark-recapture studies.

As a result of small population sizes and low capture probabilities for *A. sexlineatus*, model-based estimators may be a poor method for estimating population size (Menkens and Anderson 1988). For example, although only one animal was captured in one of our Control sites in 1997-1998, likely indicating a relatively poor-quality habitat, we estimated there were nearly

58 individuals present in the population (Table 6). Thus, we conclude that although it is important in principle to incorporate heterogeneity in detection probabilities when quantifying abundances, low detection probabilities confound a researcher's ability to derive reasonable estimates, as has been observed among other terrestrial squamates (i.e., snakes, Steen 2010, Steen et al. 2011). Future efforts to derive estimates of squamate population size based on mark-recapture techniques should include multiple trapping arrays within a site to achieve capture probabilities high enough to facilitate associated analyses.

Habitat restoration may not be sufficient to recover a population that is already in decline (Schrott et al. 2005). Presumably *A. sexlineatus* populations can persist at relatively low levels even in poor-quality habitats, such as those that typify fire-suppressed longleaf pine sandhills (i.e., our control sites in 1997-1998). We therefore suggest the species is unlikely to be extirpated in longleaf pine sandhills following invasion of hardwood trees. We are unable to determine if the populations we sampled were supplemented by emigration following treatment and by extension, whether it is necessary to consider the landscape matrix and neighboring population densities in future restoration efforts; however, this is an important consideration in determining how populations of small squamates respond to habitat restoration (Mushinsky 1985).

Mushinsky (1985) described increased abundance of *A. sexlineatus* in frequently-burned habitats and Greenberg et al. (1994) noted a higher abundance of the species in habitats that were disturbed in a manner that mimicked some effects of fire, as compared to mature pine forests that were infrequently burned. On our study site, the species was previously identified as an important driver of assemblage-level change on multiple time-scales in response to prescribed fire (Litt et al. 2001, Chapter 4) and an indicator of longleaf pine forests in reference condition (Chapter 4). Herein, our data suggest *A. sexlineatus* populations may become indistinguishable from those of sites in reference condition through application of prescribed burning. Thus, we conclude prescribed burning is an effective strategy for restoration of *A. sexlineatus* populations in fire-suppressed longleaf pine sandhills.

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Figure 1. Mean population sizes (gross population and standard errors) of *Aspidoscelis sexlineatus* in longleaf pine sandhills subjected to various hardwood removal strategies on Eglin Air Force Base in 1997-1998 (A) and 2009-2010 (B).

Figure 2. Mean number of marked adults (and standard errors) of *Aspidoscelis sexlineatus* in longleaf pine sandhills subjected to various hardwood removal strategies on Eglin Air Force Base in 1997-1998 (A) and 2009-2010 (B).

Figure 3. Mean number of marked juveniles (and standard errors) of *Aspidoscelis sexlineatus* in longleaf pine sandhills subjected to various hardwood removal strategies on Eglin Air Force Base in 1997-1998 (A) and 2009-2010 (B).

Table 1: Model comparison table for POPAN capture-mark-recapture analysis assessing effects on capture probability (*p*), entry probability (*pent*) and apparent survival (*phi*) on *Aspidoscelis sexlineatus* populations in longleaf pine sandhills subjected to various hardwood removal strategies on Eglin Air Force Base between 1997-1998. Table includes number of parameters (K), model weights (relative likelihood of models in the set), and difference in Akaike's information criterion corrected for small sample size (ΔAIC_c).

Model no.	Model	K	ΔAIC_c	Model weight
	Effects on *p*a			
1	*p*(bare ground)	37	0.00	0.46
2	*p*(grass sedge)	37	1.19	0.25
3	*p*(sex/age)	39	2.66	0.12
4	*p*(constant)	36	3.37	0.09
5	*p*(oak midstory)	37	4.00	0.06
6	*p*(sex/age + treatment)	43	7.60	0.01
7	*p*(treatment)	40	9.64	0.00
	Effects on *pent*b			
1	*pent*(sex/age + treatment)	43	0.00	1.00
2	*pent*(constant)	36	12.67	0.00
3	*pent*(treatment)	40	13.85	0.00
4	*pent*(grass sedge)	37	14.87	0.00
5	*pent*(oak midstory)	37	14.87	0.00
6	*pent*(bare ground)	37	14.95	0.00

7	*pent*(grass sedge + bare ground + oak midstory)	39	19.47	0.00
	Effects on *phi*[c]			
1	*phi*(sex/age + treatment)	37	0.00	0.86
2	*phi*(sex/age)	33	3.61	0.14
3	*phi*(treatment)	34	26.64	0.00
4	*phi*(constant)	30	34.01	0.00

[a] Additional parameters modeled as *phi*(sex/age + treatment)*pent*(sex/age + treatment)*N*(site)

[b] Additional parameters modeled as *phi*(sex/age + treatment)*p*(sex/age + treatment)*N*(~site)

[c] Additional parameters modeled as *p*(bare ground)*pent*(~sex/age + treatment)*N*(~site)

Table 2: Model comparison table for POPAN capture-mark-recapture analysis assessing effects on capture probability (*p*), entry probability (*pent*) and apparent survival (*phi*) on *Aspidoscelis sexlineatus* populations in longleaf pine sandhills subjected to various hardwood removal strategies on Eglin Air Force Base between 2009-2010. Table includes number of parameters (K), model weights (relative likelihood of models in the set), and difference in Akaike's information criterion corrected for small sample size (ΔAIC_c).

Model no.	Model	K	ΔAIC_c	Model weight
	Effects on *p*a			
1	*p*(grass sedge + bare ground + oak midstory)	39	0.00	0.95
2	*p*(grass sedge)	37	6.13	0.04
3	*p*(sex/age)	39	15.47	0.00
4	*p*(sex/age + treatment)	43	16.99	0.00
5	*p*(oak midstory)	37	32.43	0.00
6	*p*(treatment)	40	34.17	0.00
7	*p*(bare_ground)	37	45.67	0.00
8	*p*(constant)	36	46.11	0.00
	Effects on *pent*b			
1	*pent*(sex/age)	39	0.00	0.9040
2	*pent*(constant)	36	6.64	0.0327
3	*pent*(sex/age + treatment)	43	7.18	0.0249
4	*pent*(bare ground)	37	8.81	0.0110

5	*pent*(grass sedge)	37	8.81	0.0110
6	*pent*(oak midstory)	37	8.81	0.0110
7	*pent*(treatment)	40	10.83	0.0040
8	*pent*(grass sedge + bare ground + oak midstory)	39	13.18	0.0012
	Effects on *phi*[c]			
1	*phi*(sex/age + treatment)	35	0.00	0.90
2	*phi*(sex/age)	31	4.36	0.10
3	*phi*(treatment)	32	33.90	0.00
4	*phi*(constant)	28	45.68	0.00

a Additional parameters modeled as *phi*(sex/age + treatment)*pent*(sex/age + treatment)*N*(site)

b Additional parameters modeled as *phi*(sex/age + treatment)*p*(sex/age + treatment)*N*(~site)

c Additional parameters modeled as *p*(grass sedge + bare ground + oak midstory) *pent*(sex/age)*N*(site)

Table 3. Sex ratios and age classes of *Aspidoscelis sexlineatus* populations in longleaf pine sandhills subjected to three hardwood removal treatments on Eglin Air Force Base. Individuals that escaped without receiving a mark are not included.

	Burn	Control	Herbicide	Mechanical	Reference
1997-1998					
Female	41	13	20	30	38
Male	52	39	35	65	76
% Female	0.44	0.25	0.36	0.32	0.33
Juvenile	38	9	14	20	31
% Juvenile	0.29	0.15	0.20	0.17	0.21
2009-2010					
Female	85	54	64	58	51
Male	72	65	66	53	60
% Female	0.54	0.45	0.49	0.52	0.46
% Juvenile	0.16	0.16	0.15	0.26	0.21

Table 4: Survivorship estimates (*phi*, and standard errors) and 95% confidence intervals for *Aspidoscelis sexlineatus* populations in longleaf pine sandhills subjected to various hardwood removal treatments on Eglin Air Force Base.

	1997-1998			2009-2010		
	phi	LCL	UCL	*phi*	LCL	UCL
Female						
Burn	0.77 (0.05)	0.67	0.86	0.81 (0.03)	0.73	0.87
Control	0.92 (0.03)	0.83	0.97	0.84 (0.04)	0.76	0.90
Herbicide	0.83 (0.05)	0.70	0.91	0.93 (0.03)	0.86	0.97
Mechanical	0.91 (0.04)	0.79	0.97	0.81 (0.04)	0.72	0.87
Reference	0.87 (0.05)	0.76	0.94	0.86 (0.04)	0.75	0.92
Male						
Burn	0.86 (0.03)	0.80	0.91	0.82 (0.04)	0.74	0.88
Control	0.96 (0.02)	0.91	0.98	0.85 (0.03)	0.77	0.90
Herbicide	0.90 (0.03)	0.82	0.95	0.93 (0.02)	0.87	0.97
Mechanical	0.95 (0.02)	0.89	0.98	0.82 (0.04)	0.74	0.88
Reference	0.93 (0.02)	0.87	0.96	0.87 (0.04)	0.77	0.93
Juvenile						
Burn	0.73 (0.07)	0.58	0.84	0.65 (0.07)	0.50	0.78
Control	0.90 (0.05)	0.77	0.96	0.70 (0.07)	0.54	0.82
Herbicide	0.79 (0.08)	0.60	0.91	0.85 (0.05)	0.72	0.93
Mechanical	0.89 (0.06)	0.72	0.96	0.65 (0.07)	0.52	0.77
Reference	0.85 (0.06)	0.68	0.93	0.73 (0.09)	0.53	0.87

Table 5. Tree density within hardwood removal sites, Santa Rosa and Okaloosa Counties, Eglin Air Force Base, Florida. One reference site was not included in 2009-2010 summaries. All units are m^2/ha (standard error).

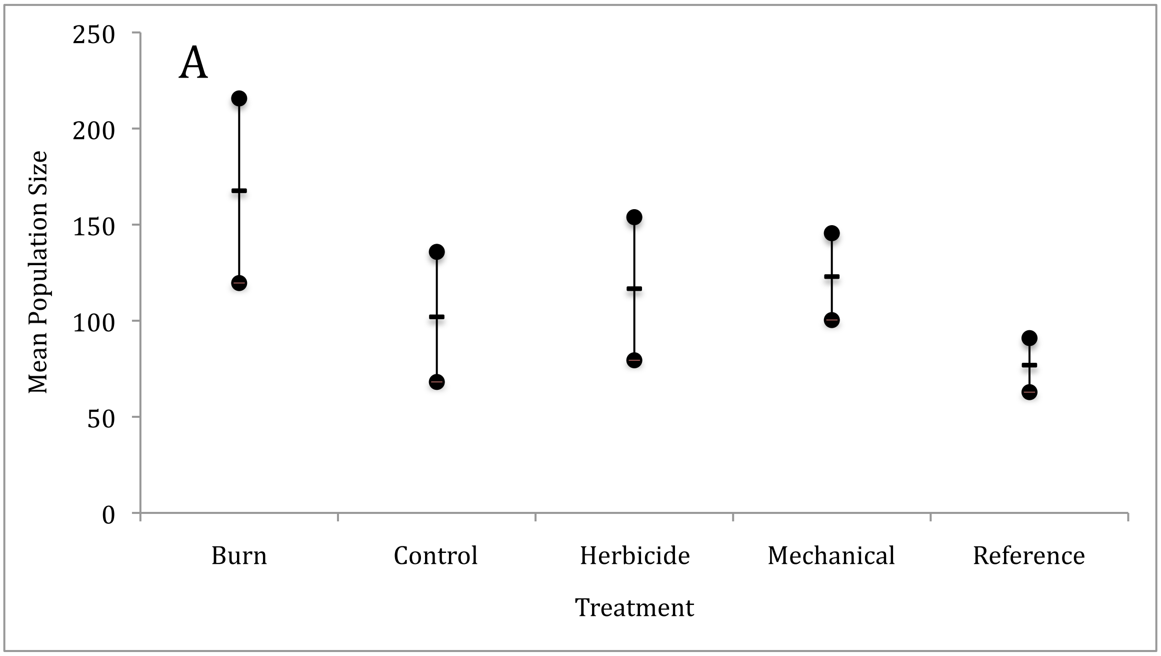
	1994	1998-1999	2009-2010
Pinus palustris midstory			
Burn	0.13 (0.05)	0.05 (0.02)	0.05 (0.02)
Control	0.1 (0.02)	0.07 (0.01)	0.01 (0.01)
Herbicide	0.09 (0.02)	0.04 (0.01)	0.28 (0.10)
Mechanical	0.10 (0.02)	0.03 (0.01)	0.07 (0.02)
Reference	0.03 (0.01)	0.02 (0.01)	0.13 (0.06)
Pinus palustris overstory			
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 spp. 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 spp. 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)

Table 6. The number of *Aspidoscelis sexlineatus* marked within each hardwood removal and reference site, Santa Rosa and Okaloosa Counties, Eglin Air Force Base, Florida and corresponding gross population estimates (and standard errors) and 95% confidence intervals.

		1997-1998				2009-2010			
Site	Treatment	Marked Individuals	Population Estimate	95% LCL	95% UCL	Marked Individuals	Population Estimate	95% LCL	95% UCL
1ANE	Herbicide	26	215.22 (17.07)	181.77	248.67	49	98.95 (6.43)	86.35	111.56
1ANW	Control	23	199.17 (14.68)	170.39	227.94	33	77.56 (6.44)	64.94	90.18
1ASE	Burn	38	182.21 (15.28)	152.27	212.16	29	99.03 (10.63)	78.20	119.85
1ASW	Mechanical	13	129.08 (12.04)	105.48	152.67	20	61.82 (6.98)	48.14	75.50
1CE	Reference	48	71.35 (6.02)	59.55	83.15	44	119.56 (12.82)	94.43	144.68
1CW	Reference	67	55.84 (5.28)	45.49	66.20	51	149.43 (17.22)	115.68	183.18
2ANE	Mechanical	29	77.81 (7.37)	63.37	92.25	23	64.58 (6.75)	51.34	77.82
2ANW	Control	11	97.54 (12.00)	74.02	121.06	19	51.51 (6.14)	39.48	63.54
2ASE	Burn	33	42.97 (5.93)	31.33	54.60	45	113.53 (9.29)	95.32	131.73
2ASW	Herbicide	12	45.56 (5.76)	34.28	56.84	30	59.92 (4.35)	51.40	68.44

3ANE	Herbicide	13	75.47 (8.41)	58.98	91.96	39	80.53 (5.71)	69.34	91.72
3ANW	Control	26	53.81 (6.85)	40.39	67.24	48	150.03 (14.55)	121.51	178.55
3ASE	Mechanical	47	101.97 (8.76)	84.80	119.14	62	193.36 (17.74)	158.58	228.13
3ASW	Burn	34	168.64 (12.81)	143.55	193.74	56	164.45 (14.30)	136.42	192.48
3CN	Reference	30	103.48 (10.11)	83.65	123.30	46	128.14 (14.04)	100.62	155.66
4ANE	Mechanical	26	182.96 (15.04)	153.48	212.44	46	130.74 (11.76)	107.68	153.79
4ANW	Control	1	57.51 (11.49)	34.99	80.04	42	99.53 (7.86)	84.13	114.92
4ASE	Burn	26	276.71 (21.64)	234.29	319.13	56	154.52 (12.89)	129.25	179.79
4ASW	Herbicide	18	130.44 (11.57)	107.75	153.12	35	69.75 (5.18)	59.60	79.89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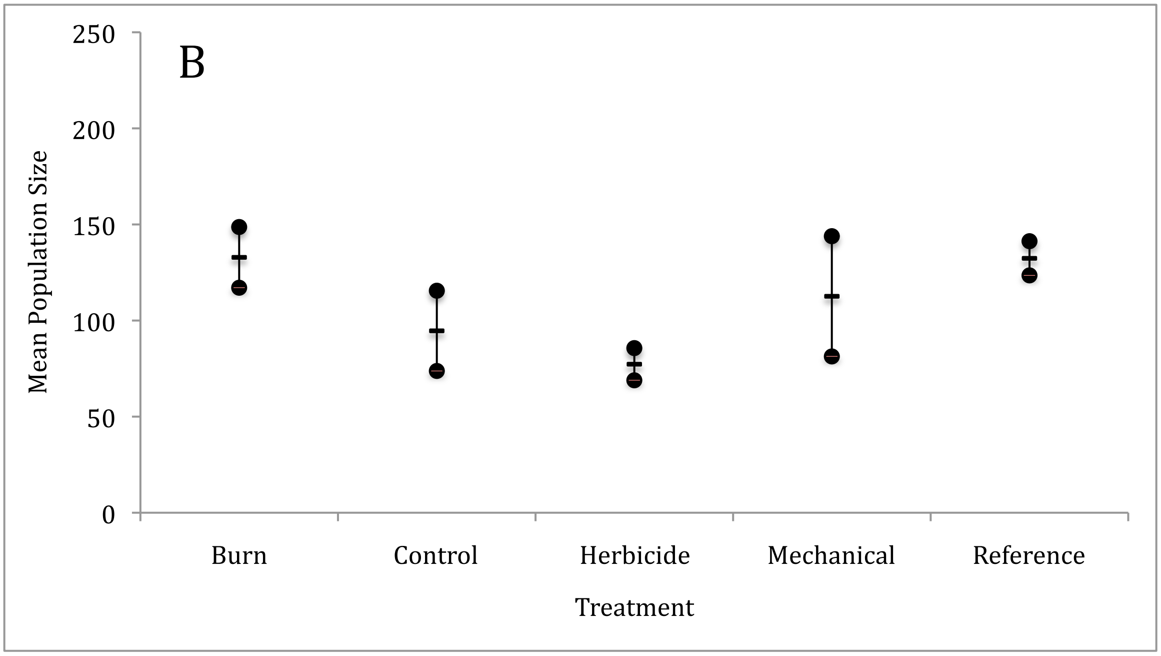
150
100
50
0
Burn
Control
Herbicide
Mechanical
Reference
Treatment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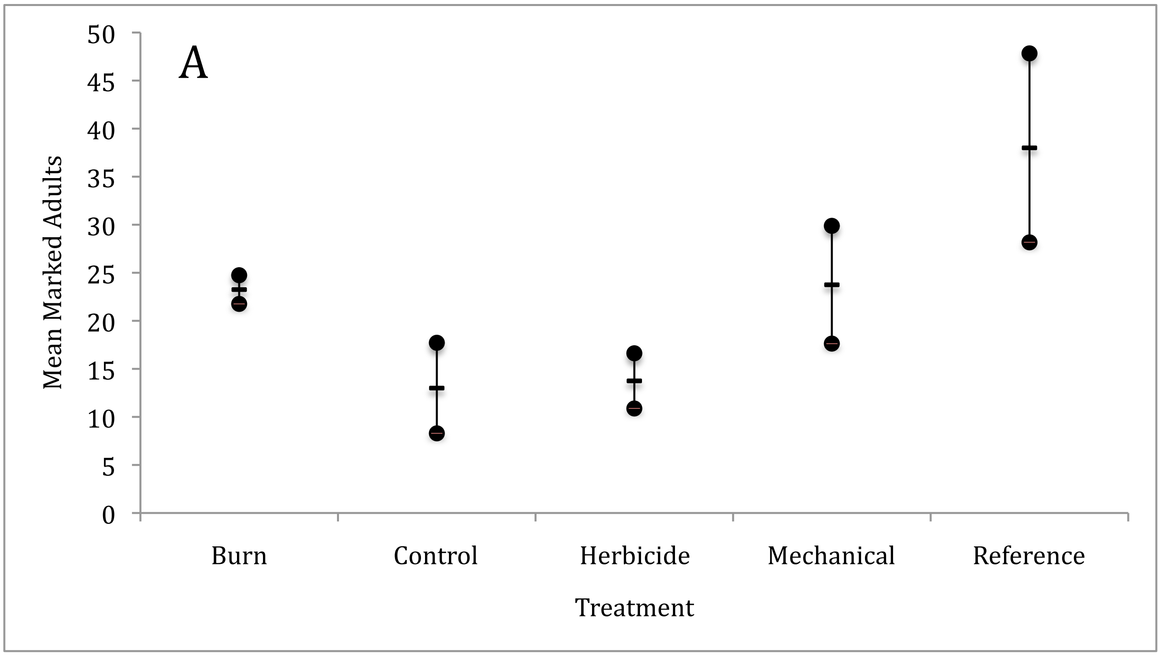
Burn
Control
Herbicide
Mechanical
Reference
Treatment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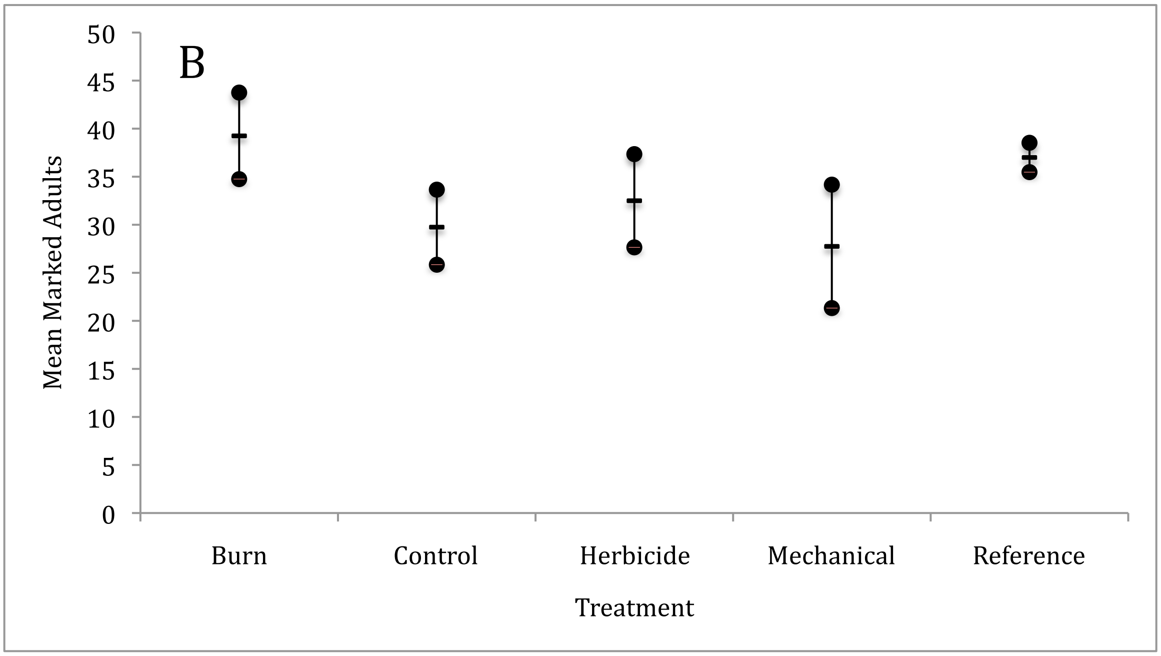
Reference
Treatment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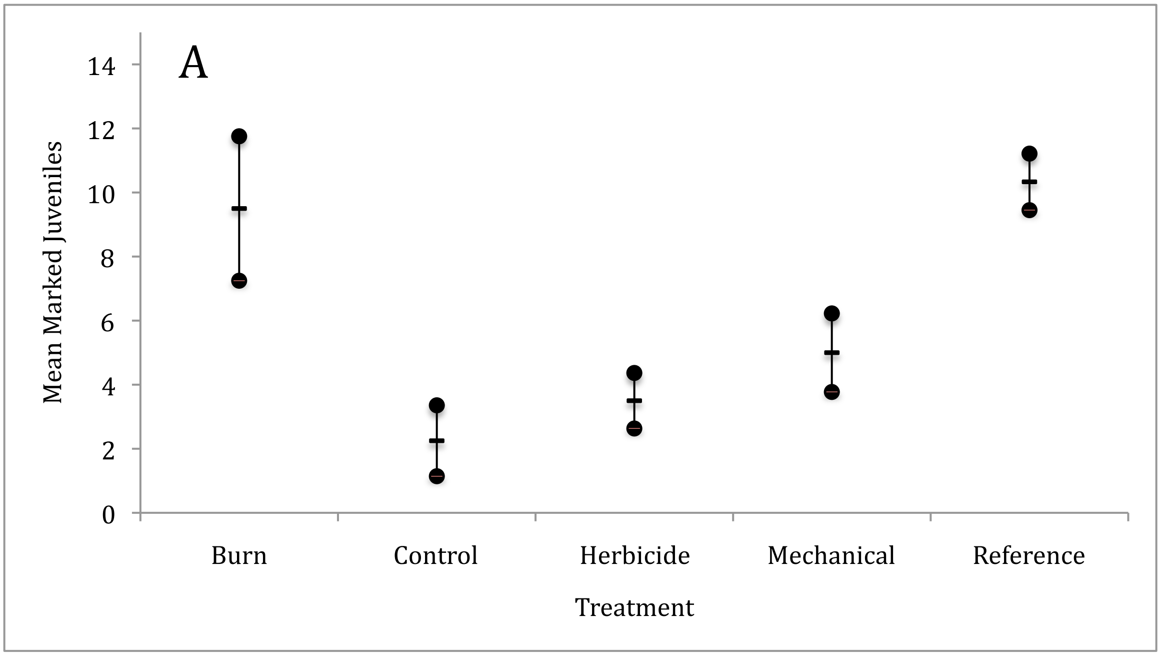
Control
Herbicide
Mechanical
Reference
Treatment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8
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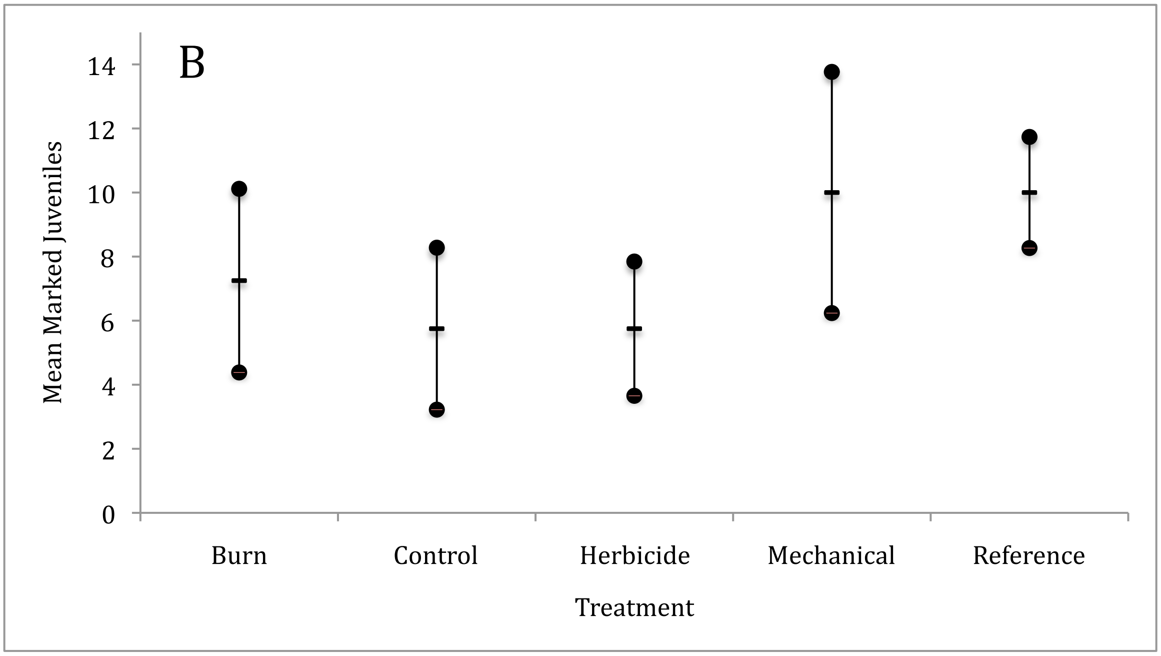
12
14
Burn
Control
Herbicide
Mechanical
Reference
Treatment


B
Mean Marked Juveniles
0
2
4
6
8
10
12
14
Burn
Control
Herbicide
Mechanical
Reference
Treatment

Appendix I: Species included in non-metric dimensional scaling ordinations (Chapter 3).

Species Code	Species	Species Code	Species
AMCR	American Crow	GCFL	Great Crested Flycatcher
AMKE	American Kestrel	GHOW	Great Horned Owl
BACS	Bachman's Sparrow	HAWO	Hairy Woodpecker
BARS	Barn Swallow	INBU	Indigo Bunting
BGGN	Blue-gray Gnatcatcher	LOSH	Loggerhead Shrike
BHNU	Brown-headed Nuthatch	MIKI	Mississippi Kite
BLGR	Blue Grosbeak	MODO	Mourning Dove
BLJA	Blue Jay	NOBO	Northern Bobwhite
BRTH	Brown Thrasher	NOCA	Northern Cardinal
BWHA	Broad-winged Hawk	NOMO	Northern Mockingbird
CACH	Carolina Chickadee	OROR	Orchard Oriole
CARW	Carolina Wren	PIWA	Pine Warbler
CEDW	Cedar Waxwing	PIWO	Pileated Woodpecker
CHSW	Chimney Swift	PUMA	Purple Martin
COGD	Common Ground Dove	RBWO	Red-bellied Woodpecker
COGR	Common Grackle	RCWO	Red-cockaded woodpecker
CONI	Common Nighthawk	REVI	Red-eyed Vireo
COYE	Common Yellowthroat	RHWO	Red-headed Woodpecker
CWWI	Chuck-will's Widow	RSHA	Red-shouldered Hawk
DOWO	Downy Woodpecker	RTHA	Red-tailed Hawk
EABL	Eastern Bluebird	SUTA	Summer Tanager

EAKI	Eastern Kingbird	TUVU	Turkey Vulture
EAME	Eastern Meadowlark	WEVI	White-eyed Vireo
EASO	Eastern Screech-owl	WITU	Wild Turkey
EATO	Eastern Towhee	WOTH	Wood Thrush
ETTI	Eastern Titmouse	YBCU	Yellow-billed Cuckoo
FICR	Fish Crow	YSFL	Yellow-shafted Flicker

Appendix II. UTM coordinates for center of sites sampled in 2009-2010. Reference site 3CS was not included in analyses pertaining to the time period following 1998-1999 and including 2009-2010.

Block	Treatment	X	Y
2CE	Reference	-86.7828	30.4711
2CW	Reference	-86.7944	30.4713
1CE	Reference	-86.8433	30.5084
1CW	Reference	-86.854	30.5083
1	Burn	-86.8202	30.5506
1	Mechanical	-86.8476	30.5601
1	Herbicide	-86.8325	30.5705
1	Control	-86.8429	30.5734
2	Herbicide	-86.8178	30.5893
2	Burn	-86.8084	30.5941
2	Control	-86.8208	30.5994
2	Mechanical	-86.8118	30.603
3CN	Reference	-86.7672	30.5976
3CS	Reference	-86.7577	30.5796
3	Burn	-86.742	30.6049
3	Mechanical	-86.7259	30.6062
3	Control	-86.7287	30.6149
3	Herbicide	-86.7167	30.618
4	Control	-86.7136	30.6408

4	Mechanical	-86.6935	30.6236
4	Herbicide	-86.7047	30.6158
4	Burn	-86.686	30.6171
6	Herbicide	-86.2869	30.6504
6	Burn	-86.2844	30.6411
6	Control	-86.2707	30.6445