FINAL REPORT

Developing and Testing a Robust, Multi-Scale Framework for the Recovery of Longleaf Pine Understory Communities

SERDP Project RC-1695

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14. ABSTRACT

The DoD and DOE are faced with the challenge of implementing the successful recovery of southeastern plant communities in a way that is consistent with continued execution of mission-related activities. Achieving this goal requires (1) quantifying ecological reference models, (2) developing a means to assessing how degraded stands differ from reference stands, (3) determining which recovery strategies will be effective, and (4) devising metrics to quantify recovery progress. To understand recovery of longleaf pine (*Pinus palustris*) stands on Department of Defense (DoD) military installations, this project followed a three-phase process that directly parallels three technical objectives aimed at achieving these four goals. In Phase 1, longleaf pine savanna understory plant communities were assessed using ecological reference models parameterized with available datasets related to historic and contemporary drivers of degradation. In Phase 2, the importance of ecological mechanisms (seed dispersal limitation, plant consumers, plant competition, and microsite availability) were experimentally evaluated for recovery of the savannas identified in Phase 1. In Phase 3, a recovery assessment model was created based on the results of Phases 1 and 2. All three phases were conducted simultaneously at three separate locations: Fort Bragg (DoD) near Fayetteville, North Carolina; Fort Stewart (DoD) near Hinesville, Georgia; and the Department of Energy (DOE) Savannah River Site near Aiken, South Carolina. By combining historical land-use data, contemporary vegetation data, and large-scale field experiments at three separate installations, our findings illustrate that past agricultural land-use leaves persistent legacies of degradation in plant communities, that these legacies may be exacerbated by a lack of frequent fire or dense overstory canopies. We find that readily measured characteristics of plant communities are useful for identifying the degree of degradation in a community as well as for assessing community recovery following management action. We find that recovery is promoted by the addition of seeds of species characteristic of non-degraded sites, as well as by increased frequency of prescribed burns. These findings are summarized in a field-ready document for the SERDP/ESTCP website that should facilitate the implementation of recovery in the field.

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List of Acronyms

AIC: Akaike's information criterion
AICc: Akaike's information criterion, adjusted for small sample size
ANOVA: Analysis of variance
BA: Basal area of overstory trees
CAP: Constrained analysis of principal coordinates
CEC: Cation exchange capacity
CI: Confidence interval
CVS: Carolina Vegetation Survey
DBH: Diameter at breast height
DF: Degrees of freedom
DFA: Discriminate function analysis
DoD: US Department of Defense
DOE: US Department of Energy
ESTCP: Environmental security technology certification program
FTB: Fort Bragg
FTS: Fort Stewart
GA: Georgia, USA
GIS: Geographic Information System
ISA: Indicator species analysis
MANOVA: Multivariate analysis of variance
MAP: Mean annual precipitation
MAT: Mean annual temperature
MN: Minnesota, USA
MPa: Megapascal
NC: North Carolina
OH: Ohio, USA
SE: Standard error
SEM: structural equation model
SERDP: Strategic environmental research and development program
SC: South Carolina, USA
SMHC: Soil moisture-holding capacity
SOM: Soil organic matter
SON: Statement of Need
SRS: Savannah River Site
TER-S: Threatened, endangered, and rare species
UK: United Kingdom
USA: United States of America
USDA: United States Department of Agriculture

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1. ABSTRACT

1.1 Objectives

The objective of this project was to develop and test an ecological assessment framework for recovery of understory plant communities in longleaf pine savannas. Our framework provides a means to determine the degree to which a community is degraded and thus the need for feasibility of recovery, aid in selecting a successful recovery strategy, and assess progress towards recovery via three technical objectives. Our first technical objective was to **assess sites and define recovery goals** by using comprehensive surveys of vegetation in degraded and reference communities at three separate DoD/DOE sites. Our second technical objective was to **use distributed experiments to evaluate the determinants of recovery**. We conducted factorial experiments that manipulated herbivore access, seed addition, and competition across a gradient of common management regimes (e.g., fire frequency, timber density) and common land-use histories (i.e., historical use of land for agriculture vs. land never used for agriculture) to determine how multiple, interacting factors might dictate recovery. Our third technical objective was to **develop the roadmap to recovery**, a model of management recommendations to provide informed guidance to managers for implementing recovery given the unique set of starting conditions at their area.

1.2 Technical Approach

To understand recovery of longleaf pine (*Pinus palustris*) stands on Department of Defense (DoD) military installations, this project followed a three-phase process that directly parallels the three technical objectives. In Phase 1, longleaf pine savanna understory plant communities were assessed using ecological reference models parameterized with available datasets related to historic and contemporary drivers of degradation. In Phase 2 the importance of ecological mechanisms (seed dispersal limitation, plant consumers, plant competition, and microsite availability) were experimentally evaluated for recovery of the savannas identified in Phase 1. In Phase 3, a recovery assessment model was created based on the results of Phases 1 and 2. All three phases were conducted simultaneously at three separate locations: Fort Bragg (DoD) near Fayetteville, North Carolina; Fort Stewart (DoD) near Hinesville, Georgia; and the Department of Energy (DOE) Savannah River Site near Aiken, South Carolina.

1.3 Results

Phase 1—Historical agriculture, low fire frequency, and high tree density all contributed to the degradation of longleaf pine understory plant communities when compared to community-appropriate reference stands. Notable differences occurred among the three geographic locations that depended largely on historical human activities (i.e., intensity of agriculture and related soil compaction), as well as on contemporary management activities (i.e., frequency of prescribed burns and tree density). The seed bank in all geographic locations and especially in post-agricultural sites contained mostly ruderal plant species and, as a result, the seed bank has low potential to assist recovery of plant communities indicative of reference sites. Interactions among local degrading factors (e.g., historical agricultural, fire suppression, high overstory tree density) and edaphic conditions structure longleaf pine understory communities, whereas the role of the surrounding landscape is negligible.

Phase 2—Seed additions promoted the recovery of species that are indicators of reference plant communities, regardless of the initial level of site degradation (i.e., degradation class); however,

degradation class and other restoration techniques interacted to determine how effective seed additions were in recovering understory plants. Reduction of competitors increased the effectiveness of seed additions, but only in degraded sites with few preexisting indicator species. Similarly, removing leaf litter also increased the effectiveness of seed additions, but mainly in fire suppressed sites and sites with high tree density. Fencing to eliminate large mammalian herbivores can also increase the effectiveness of seed additions in some cases, although the effects of fencing are more subtle and variable. Finally, the results from small plots (1 m^2) scale up to larger spatial scales (25 m^2) and, in many cases, recovery effectiveness strengthens at larger spatial scales, suggesting that the results of small experiments can provide valid recovery guidance.

Phase 3—A model of recovery recommendations was developed applicable to a variety of sites throughout southeastern longleaf pine savannas: the *Roadmap to Recovery*. The goal of this latter document is to provide a field-ready means to implement and assess recovery that is easily assessable to land managers. To maximize the utility of the *Roadmap to Recovery*, climatic and biophysical conditions at other DoD/DoE installations in the Southeast were compiled to provide land managers with a means to quantitatively evaluate which of the recovery models is suited to their location.

Overall, the ecological assessment framework developed by this project provides a means to determine the feasibility of recovery, aids in selecting appropriate recovery strategies, and provides a means to assess recovery progress.

1.4 Benefits

The DoD and DOE are faced with the challenge of implementing the successful recovery of southeastern plant communities in a way that is consistent with continued execution of mission-related activities. Achieving this goal requires (1) quantifying ecological reference models, (2) developing a means to assessing how degraded stands differ from reference stands, (3) determining which recovery strategies will be effective, and (4) devising metrics to quantify recovery progress. Through a unique combination of historical land-use data, contemporary vegetation data, and large-scale field experiments at three separate installations, the outcomes of this project provide a means of assessment and recovery of southeastern longleaf pine plant communities.

2. OBJECTIVE

Our objective was to address the SERDP Statement of Need to develop the science to define and support recovery objectives that result in ecologically appropriate, mission supportive, and achievable end states and trajectories for southeastern United States (U.S.) ecological systems at multiple spatial and temporal scales. In particular, we developed an ecological reference model for upland longleaf pine ecological systems using extant references sites, contemporary community data, and statistical models to define recovery objectives. We developed an ecological assessment framework to determine the feasibility of recovery, aid in selection of appropriate recovery strategies, and provide a structure for measuring progress toward recovery in the context of historical land use and environmental conditions including management activities.

Our approach to achieving this goal was to combine historical data, observational studies, large-scale experiments, and landscape-level quantification of connectivity across a range of site conditions. In doing so, we provide a means of assessment as well as practical suggestions for recovery strategies. This approach is unique in that it combines the strong inference of experimental ecology with the large-scale inference normal only available through observation and multi-scale investigations to provide recommendations directly relevant to the large spatial and temporal scales that characterize real-world ecosystem management and recovery. A key component of this project was to use data from our experimental and observational studies to create a "roadmap to recovery," which aims to provide land managers with feasible guidelines to assess site conditions, define and implement recovery strategies, and evaluate the progress of recovery across of range of biophysical conditions.

2.1 TECHNICAL OBJECTIVES

Our project is organized into three discrete technical objectives: First, sites were assessed to determine recovery goals. Second, experiments were conducted across a gradient of management regimes and land-use histories to explore determinants of recovery. Finally, results from the first two objectives were combined to generate recovery guidelines in our roadmap to recovery (Table 2.1).

Table 2.1. List of technical objectives with tasks and subtasks with descriptions.

Section	Technical Objective	Task Description
1		Abstract
2.1		Technical objectives
2.2		Background
2.3		Study site description
3	**1. Assess sites and define recovery goals**	
3.1	Task 1.1	Locate and survey pre-treatment stands at Fort Bragg, Fort Stewart, Savannah River Site
3.2	Task 1.2	Sample pre-treatment seed bank
3.3-3.5	Task 1.3	Compare degraded stands to CVS reference data
4.1	Task 1.4	Select final degraded stands for experiments
4	**2. Use distributed experiments to evaluate the determinants of recovery**	
4.1	Task 2.1	Construct experimental exclosures and implement treatments
4.2-4.3	Task 2.2	Assess post-treatment plant communities
4.4	Task 2.3	Assess soil compaction[a]
4.5	Task 2.4	Compare post-treatment sites to CVS reference data
4.6	Task 2.5	Assess landscape connectivity effects
5	**3. Develop the roadmap to recovery**	
5	Task 3.1	Build predictive recovery model
5	Task 3.2	Create recovery guidelines
	Task 3.3	Prepare publications and reports for SERDP

[a] As documented in our in-progress reviews and quarterly reports, soil compaction replaced our initial task of reassessing the soil seed bank, which did not contain species indicative of high quality sites.

2.1.1. First Technical Objective: Assess sites and define recovery goals

Due to the efforts of the Carolina Vegetation Survey (Peet et al. 1998, see http://cvs.bio.unc.edu/), a tremendous amount of data exists regarding the composition of high-quality longleaf savanna communities. Although these data provide a comparative framework to evaluate degraded communities, no systematic approach to quantify degrading factors and evaluate the potential for recovery has been developed. Based upon earlier recommendations in longleaf communities (Walker and Silletti 2006), our initial framework classifies degraded sites into five categories (Figure 2.1). This initial framework was further honed by field assessment of vegetation along a gradient of degradation to ensure that the number of classes accurately captures relevant ecological variation among and within individual locations. Thus, we explicitly test recovery potential and quantify progress towards recovery across a wide range of initial site conditions.

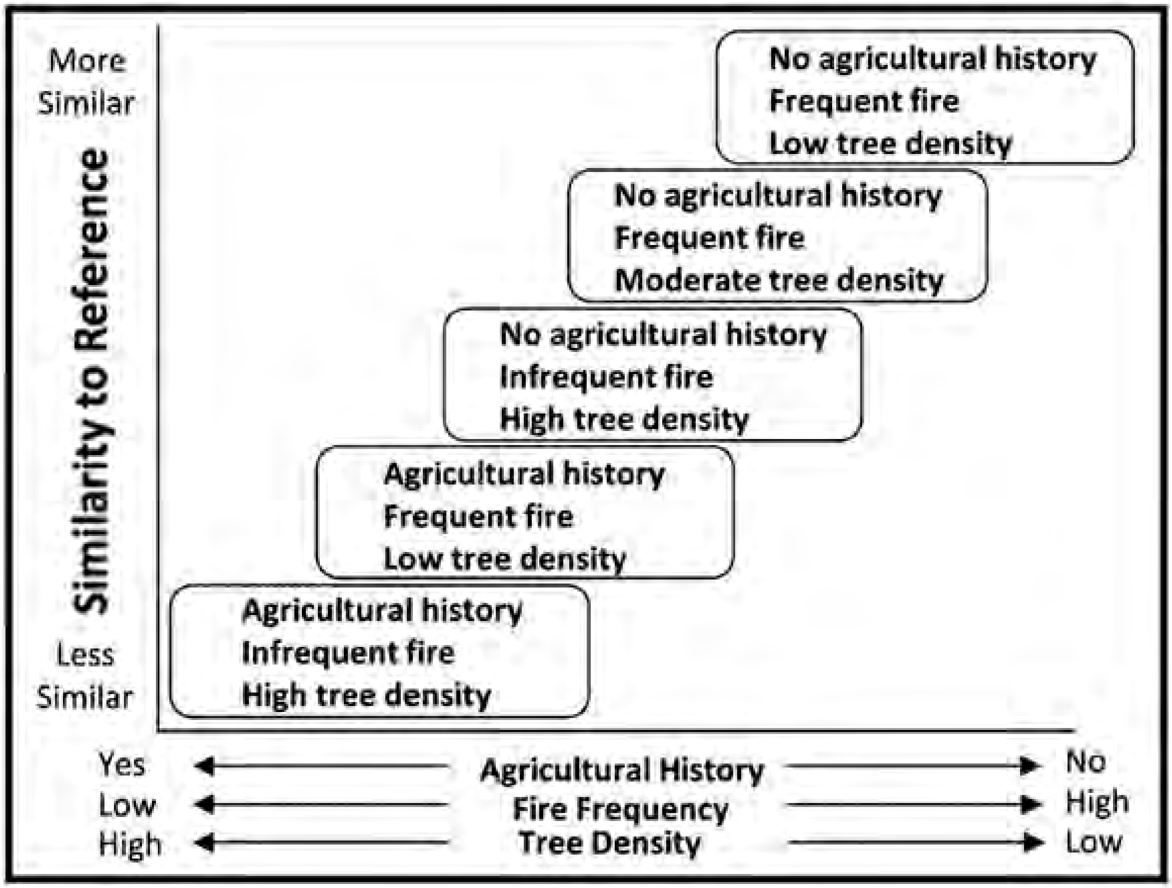

Figure 2.1. Conceptual model of degradation for understory plant communities in longleaf pine savannas. Understory degradation (deviation in community composition from reference site conditions) is predicted to increase with occurrence of agricultural history, increasing overstory density, and declining understory fire frequency. Note: not all combinations of model components are presented in this figure and, while depicted as a linear process in this conceptual diagram, nonlinearities may exist during recovery from degraded states. Model is based on Walker and Silletti (2006).

Defining recovery goals: We develop an *ecological reference model* of longleaf pine savannas as a framework for recovery. In this model, reference stands are defined by the characteristics of communities examined in the Carolina Vegetation Survey. Recovery goals are defined by comparing reference stands with degraded stands based upon common site characteristics of land-use history, fire frequency, tree density, and soil order. Differences in the diversity and composition of plant communities between degraded and reference sites serve as the basis for measuring progress towards recovery.

Site assessment: Our assessment of degraded longleaf pine savanna stands combines several approaches to quantify ecologically relevant community attributes. Rather than focusing solely on the properties of plant communities at small scales, we sample at multiple spatial scales, including the soil seed bank, at sites distributed across different management units, installations, and physiographic regions to quantify the diversity and composition of plant communities at *multiple spatial scales.* This multi-scale approach is increasingly realized to be important for successful management and recovery of longleaf pine communities (Glitzenstein et al. 2001, Van Lear et al. 2005, Hoctor et al. 2006, Brudvig and Damschen 2011), including those associated with DoD installations (Olsen et al. 2007). Our approach includes methods identical to the Carolina Vegetation Survey (Peet et al. 1998, see http://cvs.bio.unc.edu/), making it possible to directly compare characteristics of assessment stands with the characteristics of the most reference communities in the southeast (Fridley et al. 2005). Importantly, our sampling methods are compatible with long-term monitoring protocols recommended for longleaf communities (Jose et al. 2005) and ecological indicators for comparing recovery success and ecosystem health across studies (SER 2005).

2.1.2. Second Technical Objective: Use distributed experiments to evaluate the determinants of recovery

Given the likely multi-scale, interactive nature of the factors that affect savanna communities, an experimental approach is the most effective way to evaluate which factors are important for recovery under specific site conditions. At three separate geographic locations, our project used large-scale experimental manipulations of competition, herbivory, seed supply, and microsite conditions which are potential drivers of degradation or recovery, across a spectrum of longleaf pine site conditions to evaluate the role of these processes in affecting the ecological trajectory of degraded communities. This approach provides a robust test of the determinants of recovery within degraded communities. Moreover, it allows us to determine the site conditions for which recovery is unlikely to be successful, as well as prescribe which processes are likely to underpin effective recovery strategies, as a function of the starting conditions at a site.

2.1.3. Third Technical Objective: Develop the roadmap to recovery

Our research was designed to *use broad-scale experiments to inform large-scale management*, occurring across management units spanning landscapes. The success of our work ultimately hinges on its ability to provide a means for assessing pre-recovery sites conditions, and using this information to provide recommendations that yield recovery across the diversity of degraded site conditions typical of DoD installations. We coupled statistical modeling approaches (structural equation modeling, SEM) with data from large-scale experiments to provide comprehensive guidelines for the recovery of longleaf understory communities. In combination with our ecological assessment framework these guidelines constitute a comprehensive roadmap for assessing recovery potential, implementing recovery strategies, and quantifying progress towards recovery.

2.2 BACKGROUND

2.2.1 Importance of reference models

Human land use is a major force shaping the diversity and distribution of plant communities (Vitousek et al. 1997, Sala et al. 2000, Foster et al. 2003). Human-modified landscapes, however, are often characterized by an array of historical and contemporary disturbances (Foster et al. 2003, Cramer et al. 2008), which together can shape the composition of present-day communities. As such, the potential for legacies of historical land use to interact with contemporary disturbances in structuring plant communities can challenge our understanding of human land-use impacts on plant diversity (Cramer et al. 2008).

Successful, long-term recovery of southeastern plant communities is contingent upon accurate site assessment, clear definition of recovery goals, implementation of recovery strategies, and a means for measuring progress towards recovery objectives (Block et al. 2001, Suding et al. 2004, Jose et al. 2005). All of these components are complicated by ecological processes at multiple spatial and temporal scales and the multiple land-use needs of DoD and DOE; the nature and recovery of plant communities is likely to be affected by land use (e.g., military training, past agricultural history), management (e.g., burn frequency, canopy closure), site characteristics (e.g., soils, aspect, the presence of a seed bank), as well as biotic interactions (e.g., competition with invasive species, effects of herbivory). Importantly, although recovery may be viewed as a stand-level process, there is a growing scientific consensus that recovery efforts must be considered in the context of the landscapes that surround targeted sites (SER 2005, Brudvig 2011). Landscape-scale ecological processes, such as movement of organisms and seeds among stands, are tied to connectivity, which is an important component of the dynamics of diverse native communities and a key contributor to their sustainability in contemporary landscapes, where habitat fragmentation is a leading cause of species endangerment (Dupre and Ehrlen 2002, Lindborg and Eriksson 2004, Piessens et al. 2005, Damschen et al. 2006, 2014, Cousins et al. 2007).

A critical realization is that land use, management, historical legacy, competition, herbivory, and connectivity are likely to interact (e.g., Bakker et al. 1996, Blomqvist et al. 2003, Suding et al. 2004, Lindborg and Eriksson 2004), making it difficult to provide general recommendations for recovery based upon studies of only one or a few of these processes. For example, fire suppression can lead to the loss of herbaceous forbs and grasses in the ground layer, depleting local species in the soil seed bank (Cohen et al. 2004). Without restoring connectivity, these sites may be unlikely to recover even once historical fire regimes are implemented, because of limited seed dispersal. Similarly, overstory reduction and reintroduction of understory fire in longleaf pine savannas stimulates herbaceous plant production, which in turn can increase consumer densities (e.g., deer, quail, turkey; Grelen et al. 1973, Thill et al. 1987, Brockway and Lewis 2003); the increased impacts of these consumers might then thwart recovery of the ground layer. Although the consequences of interactive effects like these are almost certainly important to the community at large, specific impacts are not well understood and most recovery research examines only a few processes (Young et al. 2001, Suding et al. 2004) at relatively small spatial scales (Debinski and Holt 2000), due to the logistical difficulty of implementing large-scale, multi-factor studies. To provide sound recommendations for the management and recovery of plant communities in ways that are consistent with an ecosystem-based management perspective (Christensen et al. 1996) and DoD and DOE needs, we take a large-scale approach to understand how multiple, interacting processes affect the recovery of plant communities.

2.2.2 Importance of longleaf pine habitat

Longleaf pine communities are one of the most diverse ecosystems outside of the tropics and once were the dominant plant community in the southeastern United States, stretching from Virginia to Texas (Frost 1993). Destruction of native longleaf pine savannas over the past four centuries has been driven largely by conversion to agriculture, logging, resin extraction, fire suppression, and introduced consumers (Frost 1993, 2006, Noss et al. 1995). Excluding fire from this ecosystem promotes encroachment by woody plants and results in reduced herbaceous plant diversity (Hiers et al. 2007, Glitzenstein et al. 2012). Collectively, these factors have reduced the current extent of the longleaf pine ecosystem to less than 3% of its historic range, making it one of the most critically endangered ecosystems in North America (Noss et al. 1995, Noss 2013).

We focus on the understory plant communities found within longleaf savannas, areas characterized by relatively open longleaf canopies and a diverse herbaceous understory (Frost 1993, 2006, Brockway et al. 2005, Jose et al. 2005, Peet 2006). Fires every one to six years are critical to maintain open canopies, but fires as frequent as every year or two are sometimes necessary for maintaining these diverse, herbaceous dominated plant communities (Glitzenstein et al. 2012). Frequently burned herbaceous communities contain a rich assemblage of native legumes, sedges, grasses, and composites, including many TER-S plant species (Walker 1993, Sorrie et al. 2006). In addition, frequently burned longleaf pine savanna communities are important habitat for arthropods, herpetofauna, birds, and mammals, including several TER-S vertebrate species, such as the Gopher Tortoise, Red-Cockaded Woodpecker, the Eastern Tiger Salamander, and the Carolina Gopher Frog (Noss et al. 1995, Provencher et al. 2003, Noss 2013).

2.2.3 Relevance to DoD

There are over 15 military installations with longleaf pine savannas, including Camp LeJeune, Fort Benning, Fort Gordon, Fort Stewart, and Fort Jackson (Appendix B). By providing a field-ready method for assessment of recovery potential and by providing a field-tested roadmap to recovery, our findings will help manage longleaf pine savannas within each of these bases as well as inform efforts to form conservation partnerships with surrounding landholders (e.g., Sandhills Conservation Partnership with Fort Bragg Army Base, NC; Gulf Coastal Plain Ecosystem Partnership with Eglin Air Force Base, FL; Onslow Bight Partnership with Camp Lejeune, NC).

Our multi-scale approach, coupled with our multi-base investigation, provides opportunities for synthesis with other projects and gives this project a high degree of transition potential. Our results complement other SERDP-funded research, including work recently completed by Dr. Rebecca Sharitz at Fort Benning (Impacts of Military Training and Land Management on Threatened and Endangered Species in the Southeastern Fall Line Sandhills Communities, SERDP Project SI-1302), and ongoing work to develop methods to convert off-site pine stands at Fort Benning and Camp Lejeune (Managing Declining Pine Stands for the Restoration of Red-Cockaded Woodpecker Habitat, SERDP Project SI-1474). In addition, our work is complementary to research in Northeastern forests, where Dr. Bernd Blossey is examining how multiple biotic and abiotic constraints affect the management of TER-S plants (Identification and Management of Multiple Threats to Rare and Endangered Plant Species, SERDP Project RC-1542).

By combining a large-scale study of landscape connectivity with experimental manipulations, our work will have an additional benefit: in the course of using seed additions and exclosures to untangle the factors that limit recovery, our goal was to increase the quality of existing degraded longleaf plant communities, i.e. **our work yielded actual ecosystem recovery**. Moreover, by facilitating management and recovery of longleaf savannas, our work also increases the quality of habitat for other threatened and endangered species, such as the Red Cockaded Woodpecker, the Gopher Tortoise, and the Carolina Gopher Frog. Similarly, since some longleaf pine savannas harbor many of these TER-S animal species, our results are also applicable to management actions used to preserve these animal species have similarly positive effects on TER-S plant species.

The USDA Forest Service-Savannah River is very interested in utilizing our research findings to guide ongoing and future landscape-level experiments that manipulate fire frequency, tree density, and connectivity layered on an existing land-use history gradient (pers. comm. J. Blake, Assistant Manager of Research). They are currently working with our group to manipulate initial site conditions such as overstory tree density and the use of prescribed fire in a replicated large-scale fashion on sites with and without a past history of agricultural land use, which has been informed by the ecological mechanism experiments from Phase 2 of our study. These ancillary studies are testing whether recovery is achievable if the site conditions (i.e., tree density and fire frequency) are themselves manipulated in addition to the ecological mechanisms manipulated here (i.e., competition, consumers, seed limitation). In other words, these studies are asking what happens if you move from more degraded conditions (i.e., high tree density, low fire frequency) to less degraded conditions (i.e., using thinning to lower tree density, increasing the frequency of prescribed fires) and whether there any interactions with ecological mechanisms (i.e., competition, consumers, seed limitation) when transitions are made from one site condition to another.

2.3 STUDY LOCATION INFORMATION

The geographical extent of longleaf pine savannas encompasses a large portion of the southeast (Frost 1993, 2006) and contains over 20 DoD and DOE facilities, 15 of which are greater than 5000 hectares. Our study was conducted at three of these facilities: Fort Bragg, North Carolina, Fort Stewart, Georgia, and the Savannah River Site, South Carolina (Fig 2.2). The use of these three sites allowed us to evaluate degradation and recovery of stands across a spectrum of site conditions, as well as compare sites that differ in their geographic and edaphic conditions. It is possible to extrapolate our results to diverse longleaf communities because we have comprehensive vegetation, soils, and substrate data for hundreds of sites collected at locations that cover a range of ecological conditions within the longleaf ecosystem. Our selected sites capture diverse local hydrological conditions (our research sites span 4 major soil orders and 31 unique soil subclasses across three states) and vegetation associations (our sites span over 20 of the tertiary vegetation associations in the longleaf vegetation classification created by Peet (2006)). Our three study sites were strategically selected within three of the primary physiographic regions of longleaf savannas (Fig. 2.2): Atlantic Coastal Plain, Fall-line Sandhills, and Southern Coastal Plain. These physiographic regions encompass longleaf communities that stretch from Virginia to Alabama. We selected our sites within these regions to span a wide range of ecological conditions along several primary drivers of degradation identified in our initial reference model (Figure 2.1, see Section 2.1.1 for further details) including variation in historical land use (forested vs. agricultural use), fire frequencies, and timber densities. Our results are intended to transfer to most of the Fall-line and Atlantic and Southern Coastal Plain longleaf associations, with the exception of very wet associations (e.g., pocosins and seeps).

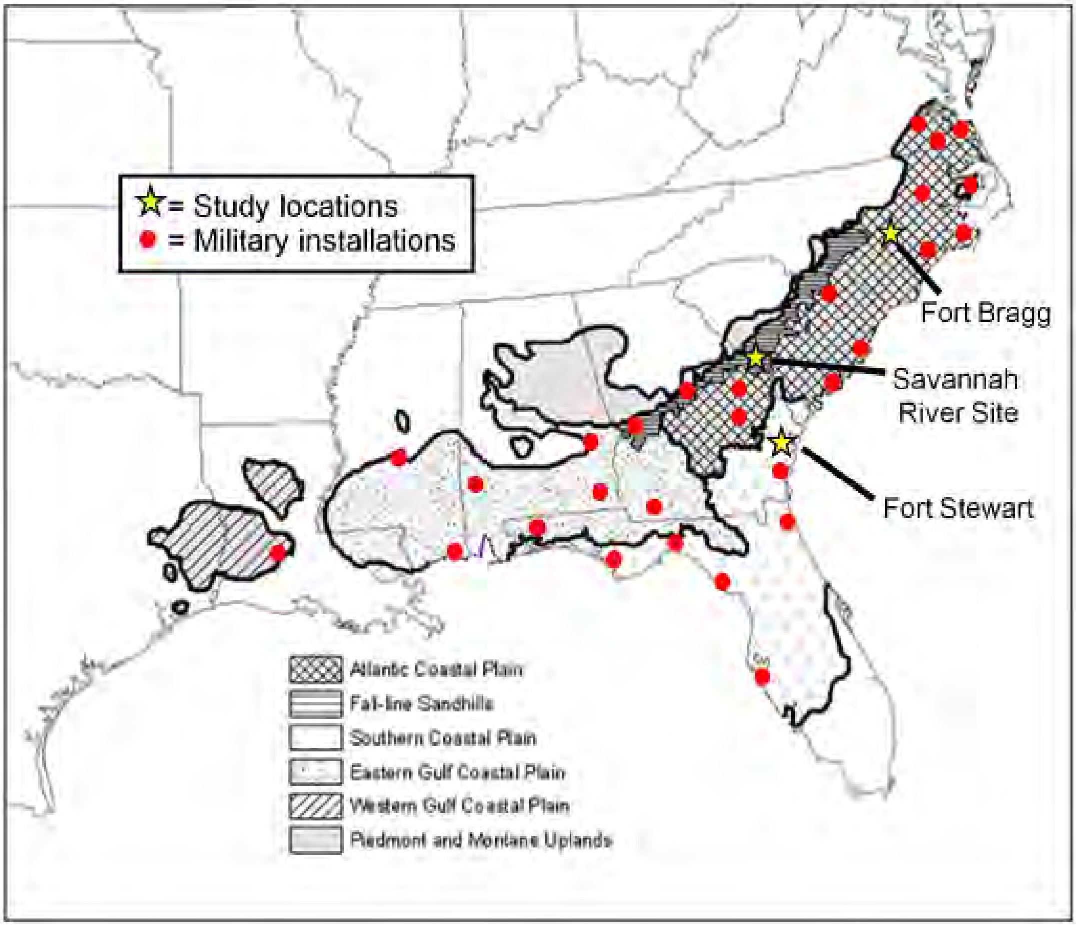

Figure 2.2. Map of military installations in the southeastern USA with longleaf pine habitat (red dots). Focus study sites are shown (stars). Map is from Peet (2006).

Our initial reference model in Figure 2.1 (described further in Section 2.1.1) was based on a conceptual reference model presented in Walker and Silletti (2006). Although this model did not explicitly include different vegetation associations or hydrologic gradients, our extensive field data come from a wide array of sites from several physiographic regions representing several common soil orders (Figure 2.3). We evaluated whether our initial reference model should be modified to include differences in underlying soil conditions, i.e. whether particular associations related to soil order occupy different locations in our overall reference model and (most importantly) if those associations differ in their potential for recovery. All our study sites were located on soils that are primary substrates for longleaf pine communities (Peet 2006), with four soil orders characterizing the majority of our sites (97%): 212 of the 270 sites (78.5%) were located on Ultisols, 38 sites (14.0%) were on Entisols, 13 sites (4.8%) were on Spodosols, and 7 sites (2.6%) were on Inceptisols. In our analyses, we included this soil order information as well as data on soil water holding capacity. These two soil parameters are known to be broadly important in structuring longleaf pine communities (Peet 2006). The inclusion of these soil variables in our models provides an opportunity to evaluate the generality of degrading factors across longleaf pine communities that occur on different substrates, as well as assess the applicability of a regional reference model relative to models for three separate landscapes. Including soil order increased our explanatory power for classifying degraded sites, but only at one location: Fort Stewart, GA (see Section 3.3).

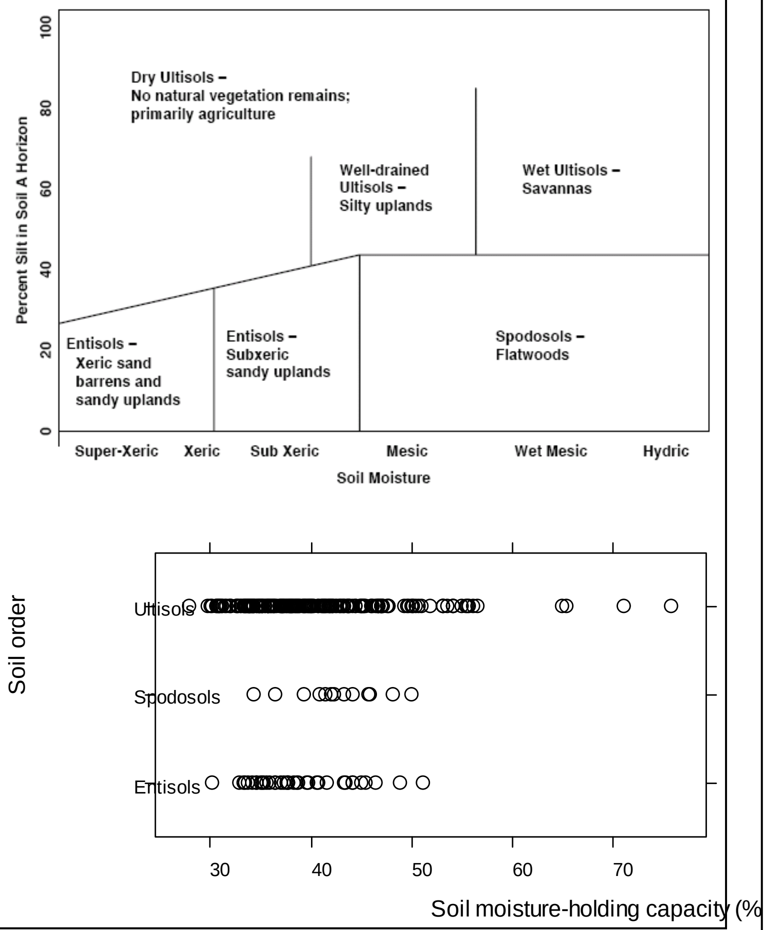

Figure 2.3. Major longleaf pine community types as delineated along a hydrologic gradient characterized by major soil order (from Peet 2006). Lower panel indicates the number of sites where our team has collected intensive vegetation data within these different soil orders (soil moisture-holding capacity illustrates the range of variation in site soil conditions).

2.3.1. Fort Bragg

Fort Bragg Military Reservation (FTB; 73,000 ha, elevation: 43-176 m, mean annual precipitation [MAP]: 1270 mm, mean annual temperature [MAT]: 16°C) contains longleaf pine savanna within the Sandhills region of North Carolina (Sorrie et al. 2006). The sandy, infertile soils of the region largely limited the scale and intensity of agricultural practices in the uplands. Agriculture was abandoned around the time the military reservation was established in 1918, at which point only 7% of the landscape was under cultivation (Aragon 2004). Land abandonment and subsequent reforestation has since yielded post-agricultural sites that have been in forest for nearly a century. Prior to 1989, upland habitat was burned once every 5 years, but since 1990 the prescribed fire program has increased the frequency of burns to a 3-year return interval (Cantrell et al. 1995). Chronically fire-suppressed upland longleaf pine savanna is uncommon at Fort Bragg.

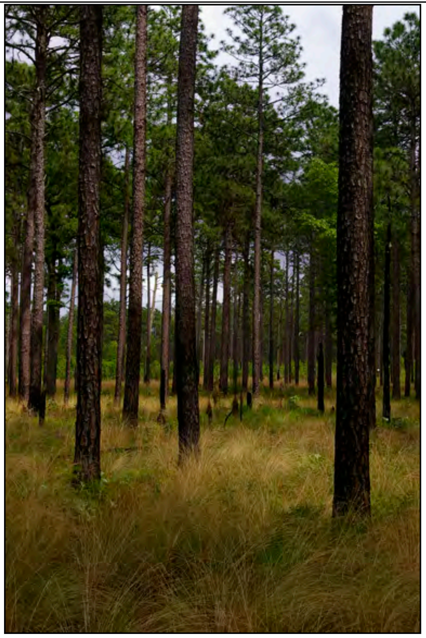

Figure 2.4. Fort Bragg, NC.

2.3.2. Fort Stewart

Fort Stewart Military Reservation (FTS; 114,000 ha, elevation: 2-56 m, MAP: 1220 mm, MAT: 19°C) is located in southeastern Georgia 35 km from the coast, covers of xeric and mesic pine savannas interspersed with mesic and hydric hardwood forests, cypress wetlands, and riparian habitats. Prior to the establishment of the military reservation in 1940, land use included intensive agriculture, livestock grazing, logging, and turpentine extraction (Armstrong 1984). Like SRS, pine stands on former agricultural sites at Ft. Stewart are younger than those at Fort Bragg. Due to frequent accidental fires from military ignitions, historic fire-suppression at Fort Stewart was not nearly as severe as compared to SRS. In recent decades, Fort Stewart managers have used growing season burns, tree thinning, and wiregrass planting to maintain and restore longleaf pine savannas and to improve habitat for the red-cockaded wood pecker and other threatened animals (Mitchell et al. 1995, Stevenson et al. 2003).

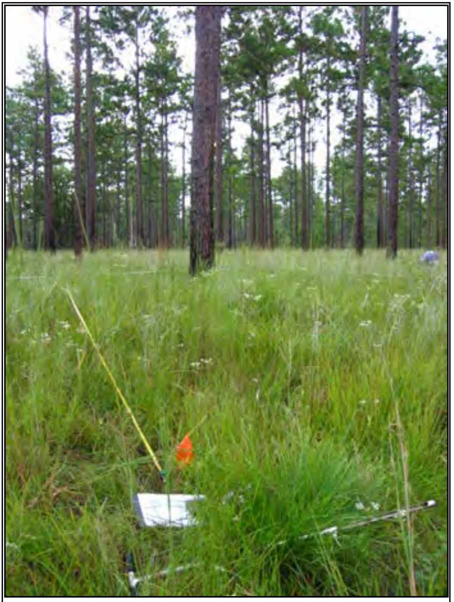

Figure 2.5. Fort Stewart, GA.

2.3.3. Savannah River Site

Figure 2.6. Savannah River Site, SC.

The Savannah River Site (SRS; 77,000 ha, elevation: 20-130 m, MAP: 1225 mm, MAT: 18°C), a National Environmental Research Park in South Carolina, contains longleaf pine savanna within the Atlantic Coastal Plains region (Peet 2006). Although longleaf pine covered nearly 80% of the uplands at SRS prior to European settlement (Frost 2006), the majority of upland habitat was under intensive agricultural production by the time SRS was acquired by the Department of Energy in 1951 (Kilgo and Blake 2005). Following site acquisition, management efforts focused on reforesting abandoned agricultural fields, and much of SRS is now managed for either longleaf pine or loblolly pine timber (Kilgo and Blake 2005). From 1951 until the 1980s, wildfires were suppressed and prescribed fires were rare. For the past ~30 years, SRS has re-introduced prescribed fires to manage habitat for the endangered Red-Cockaded Woodpecker. The total area burned each year has increased from 1980 through 2000, but infrequently or long-unburned areas remain at SRS.

3. DESCRIPTION OF OBSERVATIONAL STUDIES

In the following sections, we first present descriptions of the methods used in the observational portion of our study, and then present the findings from the tasks associated with the observational portion of our study.

3.1 GENERAL DESCRIPTION OF OBSERVATIONAL SET UP (TECHNICAL OBJECTIVE 1)

At each location, we selected a set of study sites that characterized the range in variation of degraded conditions (fire history, overstory density, agricultural history). Sites were each ≥ 1ha, supported overstory longleaf pines, and lacked firebreaks, drainages, or other features causing abrupt transitions in understory vegetation. Sites varied in basal area of overstory trees, recent fire history (1991-2009), and agricultural land-use history (Table 3.1); stand age from the 165 sites with available data was 62±1.2 years (mean±1SE). We classified each site as having a "forest" or "agricultural" land-use history based on its status in historical aerial photographs (Fort Stewart, Savannah River Site) or maps (Fort Bragg) from the year of federal acquisition. We obtained GIS data from prescribed fire managers at each location to reconstruct fire history (prescribed and wild) between 1991 and 2009 for each site. Sites were considered burned in a given year if they occurred within the boundaries of a fire management unit that was burned in that year. We determined overstory basal area for each site during vegetation sampling.

Table 3.1. Attributes across study sites and for each of the three study locations.

Variable	**All Sites**	**Fort Bragg**	**Fort Stewart**	**Savannah River Site**
Number of sites	232	84	68	80
Canopy cover (%)	51.7±2.8	30.8±1.9	62.7±4.8	64.5±3.5
Total basal area (m^2/ha)	18.8±1.0	19.4±1.5	15.8±1.9	20.7±1.8
Pinus basal area (m^2/ha)	17.0±1.0	17.6±1.7	14.2±1.7	18.8±1.6
Non-Pinus basal area (m^2/ha)	1.8±0.4	1.8±0.8	1.7±0.6	1.8±0.8
Years since fire	3.4±0.8	1.0±0.2	2.3±0.7	6.8±2.1
Number of fires (1991-2009)	4.6±0.3	5.8±0.3	5.0±0.6	3.0±0.5
Soil water holding capacity (%)	39.5±0.8	41.2±1.4	40.8±1.6	36.8±1.0
Soil organic matter	1.8±0.1	2.0±0.2	2.0±0.2	1.5±0.1
Species richness/m^2	5.1±0.4	4.7±0.6	6.7±0.8	4.2±0.6
Species evenness/m^2	0.7±0.02	0.6±0.03	0.7±0.02	0.7±0.02
Vegetation cover (%)	23.2±2.3	13.4±2.0	38.3±4.7	20.5±3.0
Bare ground (%)	8.2±1.5	11.4±2.7	10.2±3.2	3.1±1.2
Down woody debris (%)	5.2±0.7	2.1±0.4	5.2±1.2	8.4±1.5
Litter depth (cm)	2.2±0.3	1.0±0.1	2.7±0.4	3.1±0.4
Duff depth (cm)	0.9±0.2	0.2±0.03	0.6±0.2	1.9±0.3

Values exclude data from reference sites and are mean ± 95% confidence interval.

We quantified reference conditions by sampling a set of reference sites at each location (Fort Bragg n=15, Fort Stewart n=14, Savannah River Site n=9). These sites had been previously identified by regional botanical experts at the Carolina Vegetation Survey (CVS) "to document the composition and status of the natural vegetation of the Carolinas" (http://cvs.bio.unc.edu/). Reference sites had no known history of cultivation, were generally well maintained by prescribed fire, and were located within the boundaries of the respective study locations.

All study sites were located on soils that are primary substrates for longleaf pine communities (Peet 2006), with three soil orders characterizing the majority of our sites (97%): 212 of our 270 sites (78.5%) were located on Ultisols, 38 sites (14.0%) were on Entisols, 13 sites (4.8%) were on Spodosols, and 7 sites (2.6%) were on Inceptisols.

3.1.1 Plot design and physical parameters

Between 20 August and 13 November 2009, we surveyed the 270 study sites: 99 at Fort Bragg; 82 at Fort Stewart; 89 at Savannah River Site (Fig. 3.1.1). We used one randomly located and oriented 20×50m plot at each site. This plot design was a modified version of the CVS protocol (Peet et al. 1998), which is broadly employed throughout and beyond our region to characterize forest, savanna, and grassland plant communities. We measured the depth of leaf litter and duff in the center of each subplot. To characterize overstory conditions within each 20×50m plot, we recorded canopy cover with a spherical densiometer held at 1.4m above six points spaced at 10m intervals along the plot center line, and identified and measured the diameter of all trees ≥ 2.5cm diameter at 1.4m, within the plot.

To characterize site-level soil conditions, we collected soil cores (2.5cm diameter by 15cm deep) at 10m intervals along the center line of each 20×50m plot. Soil was composited by site and analyzed by Brookside Laboratories, Inc. (New Knoxville, OH) for soil organic matter content (SOM), which is an indicator of soil degradation in post-agricultural forests (Foster et al. 2003, Flinn and Vellend 2005), and other soil characteristics (Table 3.1). Each composited soil sample was also analyzed for soil water holding capacity following Salter and Williams (1967), because soil moisture availability correlates with longleaf pine understory diversity and productivity (Kirkman et al. 2001). We placed each a subsample of soil from each plot into a 5cm tall by 6.5cm wide soil tin, which had 15 one mm holes drilled in the bottom and was lined with filter paper to prevent soil loss. We then saturated the soil subsamples by placing the tins in a shallow pan with tap water for 24 h, placed them on a wire rack until they stopped dripping (~30 s), collected wet weight, dried the subsamples at 105°C for 72 h, and collected dry weight. Soil water holding capacity was calculated as the proportional difference between wet and dry weight ([wet weight - dry weight] / wet weight), accounting for the weight of the filter paper. We also measured soil hardness by pressing a probe (Dickey-John Soil Compaction Tester, Dickey-John Corp., Minneapolis, MN, USA) into the soil at 10m intervals along the center line of each 20×50m plot. At each position, we recorded the depth (cm) at which 2 MPa was attained. Plant performance can be negatively affected when soil compaction levels approach and exceed 2 MPa (Bassett et al. 2005).

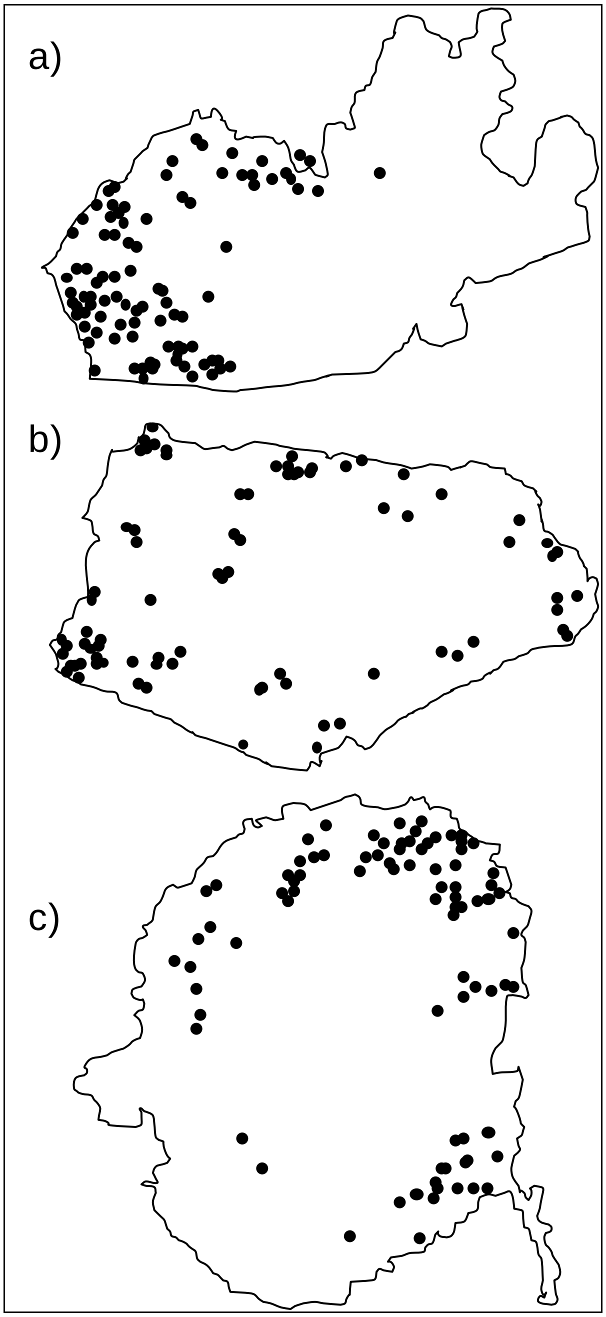

Figure 3.1. Map of the 270 observational sites at the three locations: a) Fort Bragg, b) Fort Stewart, and c) Savannah River Site.

3.1.2 Vegetation sampling

At each study site, we identified and assigned a percent cover value to all understory plant species (herbaceous species and woody species <2.5cm diameter at 1.4m height) rooted within or overhanging each of eight 1×1m subplots located within a 20×20m portion of each plot. Taxonomy follows Radford et al. (1964), except for the genus *Dichanthelium*, which follows Weakley (2008), and the genera *Lyonia* and *Persea*, which follow Wunderlin and Hansen (2003). Within each subplot, we estimated the percent area covered by green vegetation, leaf litter, bare ground, and down woody debris (i.e., fallen logs, sticks, pine cones, and bark on the ground within the plot).

3.1.3 Landscape analyses

We quantified the composition of the landscape that historically surrounded each of our post-agricultural sites to determine the percentage of the contemporary landscape that supports remnant vegetation (i.e., landscape context). We obtained a digitized, georectified, aerial photo or land cover map from the earliest year available following federal acquisition at each study location: a 1919 topographic map for FTB, a 1947 aerial photo for FTS, and a 1951 aerial photo for SRS. In each case, the locations of agricultural fields were either visible (FTS, SRS) or explicitly mapped (FTB). We developed a Geographic Information System (GIS) of historical aerial photos and maps and the GPS coordinates for the center point of each study site. Around each site's midpoint, we used ArcGIS ("ArcGIS Desktop: Release 10." 2011) to draw a buffer with a 150 m radius to serve as the 'landscape' in which we characterize historical land cover. We employed 150 m radius because past work has shown this to be a distance over which connectivity (Damschen et al. 2006, Damschen et al. 2008) and historical landscape composition (Brudvig and Damschen 2011) influence longleaf pine understory richness and composition. We classified the land cover within each 150 m radius landscape as agriculture, remnants (i.e., any natural vegetation, including forests, woodlands, and savannas), water, or missing data. We then calculated the area (m^2) of each land cover type within each buffer using the Field Calculator in ArcMap. In the analyses that follow, 'landscape context' is defined as the percentage of remnant vegetation within 150 m of the center point of each study site: landscape context = remnant area (m^2) / Π * (150 m)^2. To illustrate landscape-scale land-use patterns at our three study locations, we quantified landscape context for additional 147 sites supporting remnant vegetation (FTB, n = 56; FTS, n = 43; SRS, n = 48), and also determined landscape context within a 300 m radius of each site.

3.2 CONTROLS OF SEED BANK DIVERSITY

[This section contains material in preparation: Damschen, E.I., J.L. Orrock, L.A. Brudvig, P.G. Hahn, J.W. Veldman, W.B. Mattingly, and J.L. Walker. 2014. How seed banks vary across a degradation gradient and their recovery potential.]

3.2.1 Introduction

Dormant, viable seeds that are stored in the soil constitute seed banks (Baskin and Baskin 2001a) and are important for contributing to the composition and structure of plant communities in many ecosystems (Thompson and Grime 1979). Soil seed banks may also positively or negatively affect recovery outcomes, with these effects depending on whether or not species found in the seed bank are typical of reference communities (Plue et al. 2008). The evidence for the utility of seed banks contributing to recovery of longleaf pine ecosystems, has been mixed. One study from pine forests in North Carolina that had either been disturbed by intensive forestry practices or not, found some potential for the seed bank to contribute to recovery. While the seed bank contained ruderal species, over half of the species were indicative of undisturbed longleaf pine understories (Cohen et al. 2004). On the other hand, another study from six pine in Georgia concluded that the seed bank has limited potential to contribute to recovery. They found that while native species were present in the seed bank, the vast majority of species and individuals were not indicative of high quality longleaf pine understories and instead were associated with early successional forests and adapted to severe soil disturbance (Andreu et al. 2009). This study included one site with past agricultural land use, which may have dramatic and long-lasting impacts on the seed bank. A study conducted in European forests that were used by Roman for agriculture >1600 ago found a depauperate seed bank relative to sites not used for agricultural (Plue et al. 2008). Given this mixed evidence, more work is needed to understand the composition and diversity of longleaf pine seed banks across the diversity of sites with different environmental conditions, past land uses, and management activities.

Here, we examine the composition of soil seed banks and their potential to contribute to recovery along a gradient of degradation, explicitly accounting for past agricultural land use legacies and current management regimes (e.g., prescribed fire). We quantified the seed bank from 1728 samples spanning 108 sites across three locations (Fort Bragg, NC; Fort Stewart, GA; and Savannah River Site, SC). These sites varied in physiographic region, prescribed fires, and whether they were formerly used for agriculture. We addressed four questions: 1) Is there geographic (among-study location) variation in the abundance and diversity of germinants in the seed bank? 2) How does agricultural land-use history affect the seed bank? 3) How does fire management affect the seed bank? 4) What are the potential for the soil seed bank to contribute to the recovery of the longleaf pine understory plant community across these gradients in geography and disturbance?

3.2.2 Methods

In July 2010, we collected soil seed bank samples from 16 1×1 m plots from each of the 36 sites at the three study locations described above (see also Section 4.1 on description of experimental plot setup, Fig. 4.1.2, 16 plots × 36 sites × 3 locations = 1728 plots). Sites (Fig. 4.1.1) spanned a gradient of fire frequency and past agricultural land use (historically forested vs. agricultural land-use history). From each side of each 1×1 m plot, we collected 6 soil cores (15 cm deep and 2.5 cm in diameter), for a total of 24 cores per plot (Fig. 4.1.2). The litter layer was brushed away prior to taking each core. This sampling protocol attempts to maximize both the total area sampled, as well as the number of plots sampled, as suggested by Plue et al. (2012), and exceeds both total area and number of plots sampled in other seed bank studies in the longleaf pine ecosystem (e.g., Cohen et al. 2004, Andreu et al. 2009).

The 24 soil cores from each plot were combined and homogenized in paper bags and kept open until the sample was dry. Sample bags were transported in August 2010 to the University of Wisconsin where they were grown out to determine the identity and abundance of germinants (see below). Because the dispersal season for most plants, particularly plants that are indictors of reference longleaf pine savannas, is from September through January, our samples contained seeds dispersed one or more years prior to collection, and that were naturally cold stratified during the 2009-2010 winter.

From 20 January 2011 through 26 May 2011, samples were allowed to germinate within three greenhouses at the University of Wisconsin-Madison, USA. 51 × 26 × 6 cm plastic trays with several small drainage holes were filled approximately 2.5 cm deep with Metro Mix 360 (Sun Gro Horticulture Canada Ltd.) sterile potting medium and separated into three cells using two plastic dividers (n=1728 cells total). Each soil sample was spread across the sterile potting mix in one section of a divided tray, resulting in a sample layer approximately 1.5 - 2.5 cm deep on top of the sterile soil medium. Samples were randomly assigned to tables, trays and cells within the greenhouses. Conditions in the greenhouse where set to mimic the mean monthly average temperatures and daylight of the three study sites (averaged over the three study sites) from April through September. We updated the temperate and daylight schedule every three weeks throughout the experiment (Table 3.2.1).

Table 3.2. Conditions in the greenhouses during the seed bank study.

Week	Day (F)	Night (F)	Lights on	Lights off	Mimics	Sunrise	Sunset	Max	Min	Avg
0	75	68	N/A - natural	N/A - natural	N/A	N/A	N/A	N/A	N/A	N/A
1-3	77	50	7:12 AM	7:46 PM	April means	7:12 AM	7:46 PM	77	50	64
4-6	84	59	6:35 AM	8:10 PM	May means	6:35 AM	8:10 PM	84	59	71
7-9	90	67	6:14 AM	8:32 PM	June means	6:14 AM	8:32 PM	90	67	78
10-12	92	71	6:16 AM	8:42 PM	July means	6:16 AM	8:42 PM	92	71	82
13-15	91	70	6:35 AM	8:27 PM	August means	6:35 AM	8:27 PM	91	70	80
16-end	86	64	6:58 AM	7:51 PM	September means	6:58 AM	7:51 PM	86	64	75

All trays were watered gently with tap water until the soil was saturated starting on 25 January 2011. Watering took place twice per day during the first two days and once per day during the rest of the study. One watering per day was sufficient to keep the soil consistently moist for the duration of the experiment. We fertilized all trays on 21 March 2011, approximately two months after the first watering, for two reasons: 1) some seeds may require fertilization for germination (Baskin and Baskin 2001b), and 2) to assure the survivorship of seedlings growing in trays awaiting identification (see monitoring methods below). Soil was watered to saturation using a solution of 1 teaspoon of Peters 20:10:20 ($N:P_2O_5:K_2O$) fertilizer per gallon of water. Just prior to fertilization, we disturbed each sample once by gently turning over the soil with a clean plastic fork in order to promote the germination of seeds beneath the soil surface, taking care not to combine the soil sample with the underlying sterile potting mix or to disturb already growing seedlings. Our methods were designed to optimize germination and to mimic natural field conditions by providing high light and moisture conditions for seed germination (Thompson and Grime 1979, Gross 1990). Even if germination requirements were not met for all species, our methods were consistent across samples, allowing comparisons among site types (e.g., agricultural history, study location, etc.).

Figure 3.2.1. (top left and right) Sampling the seed bank in the greenhouse. (bottom left). A seed bank sample with color-coded pins to identify unique germinants. (bottom right) Plant specimens being grown out for identification purposes.

Seed bank germination

Seedling monitoring began on 20 January 2011 and continued every two weeks until 26 May 2011. All seedlings were identified to species, counted, and then removed from the trays. If we were unable to identify a seedling, it was counted and marked near the base of the plant with a unique combination of straight colored pins until identification was possible. If an individual began to flower and was still unidentified, it was removed and pressed for later identification. Those seedlings that had not flowered and were still unidentified at the conclusion of the experiment were transplanted to larger pots and allowed to mature until 11 September 2012, when all seedlings were identified or pressed.

Taxonomy follows Radford et al. (1964) except for the genera *Lyonia* and *Persea*, which follow Wunderlin and Hansen (2003), and *Dichanthelium*, which were identified by a regional expert for the genus (R. LeBlond, UNC Herbarium) according to Weakley (2008) or the Flora of North America (2014).

3.2.3 Results

We identified a total of 17,159 germinants across all samples, 89% of which we identified to species (15,321 seedlings). 1,720 individuals (~10% of all 17,159 germinants) were unable to be identified to species (77% of these died before reaching an identifiable stage, 23% of these were unable to be identified for taxonomic reasons). If a germinant died before identification was possible, it was recorded as emerging, but was not included in analyses. Analyses that included or excluded dead individuals were not different in direction or significance.

Pooled across all locations, nearly twice as many germinants recruited from post-agricultural seed banks compared to seed banks from historically forested sites (Figure 3.2.2A). Post-agricultural plots also contained about 50% more species in the seed bank, than plots with no history of agriculture (Figure 3.2.2B). There were no relationships between fire frequency and the number of germinants (Figure 3.2.3A) or the number of species (Figure 3.2.3B) that recruited from the seed bank samples.

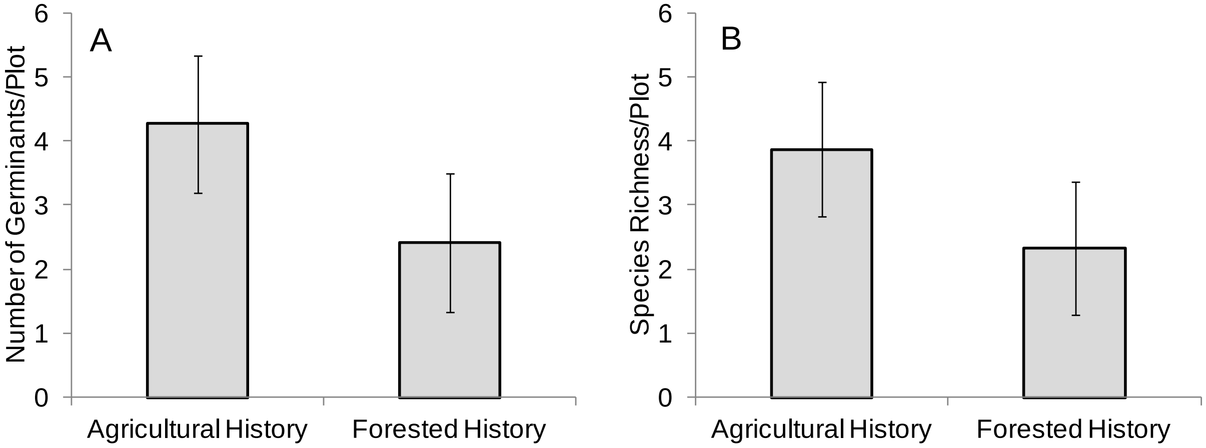

Figure 3.2.2. Seed bank germination in longleaf pine forests with a history a forested history or an agricultural history. A) Total number of germinants recovered from each plot. B) Total number of species recovered from each plot. Data are pooled across the three study locations.

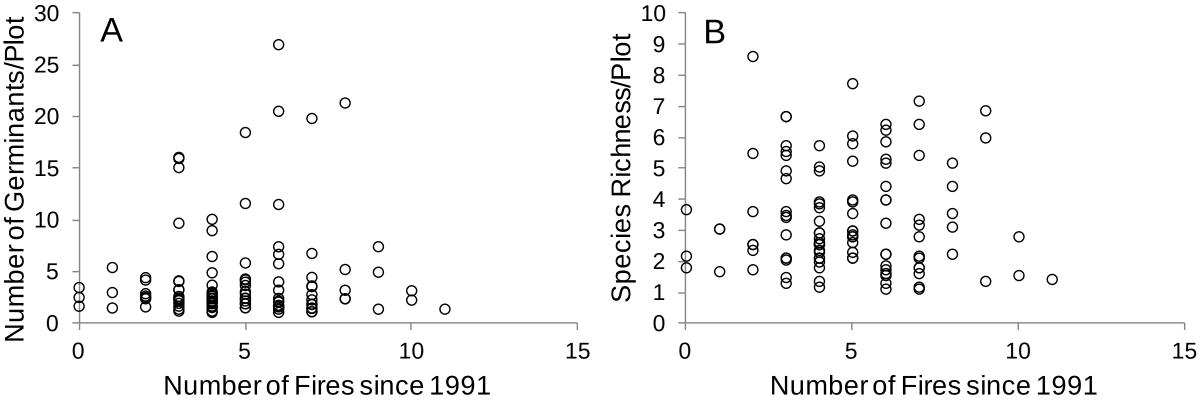

Figure 3.2.3. Relationships between the number of prescribed fires and A) number of germinants and B) number of species recruited from the seed bank samples.

There was considerable geographic variation (i.e., variation among study locations) in both the number of seedlings (Figure 3.2.4A) and the number of species germinating from the seed bank (Figure 3.2.4B). Fort Stewart, GA had over an order magnitude more total germinants and nearly twice as many species compared to either Fort Bragg, NC or the Savannah River Site, SC. Similarly, there were notable geographic differences in the identity of species emerging from the seed banks (Figure 3.2.5). For example, a single species of *Juncus* was the most common species recruited from the seed banks at Fort Bragg and the Savannah River Site, whereas at Fort Stewart, *Polypremum procumbens* was the most common species. On the other hand, *Gnapthalium* spp. were common at all sites. There was only a single species indicative of reference site plant communities that emerged from the soil seed bank, *Rhexia mariana*, which appeared in low abundance at Fort Bragg and Fort Stewart (Fig. 3.2.5).

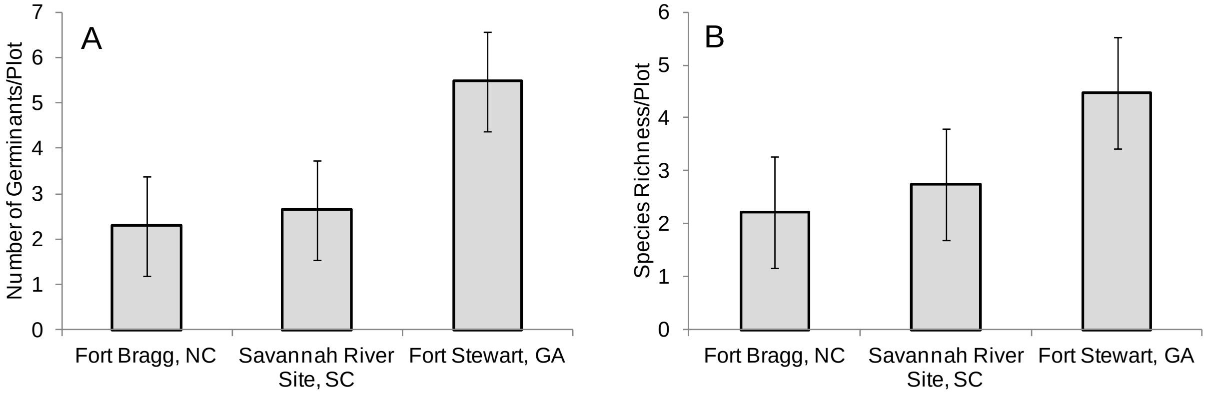

Figure 3.2.4. Geographic variation in the A) number of seedlings germinating per plot from the seed bank and B) number of species germinating per plot.

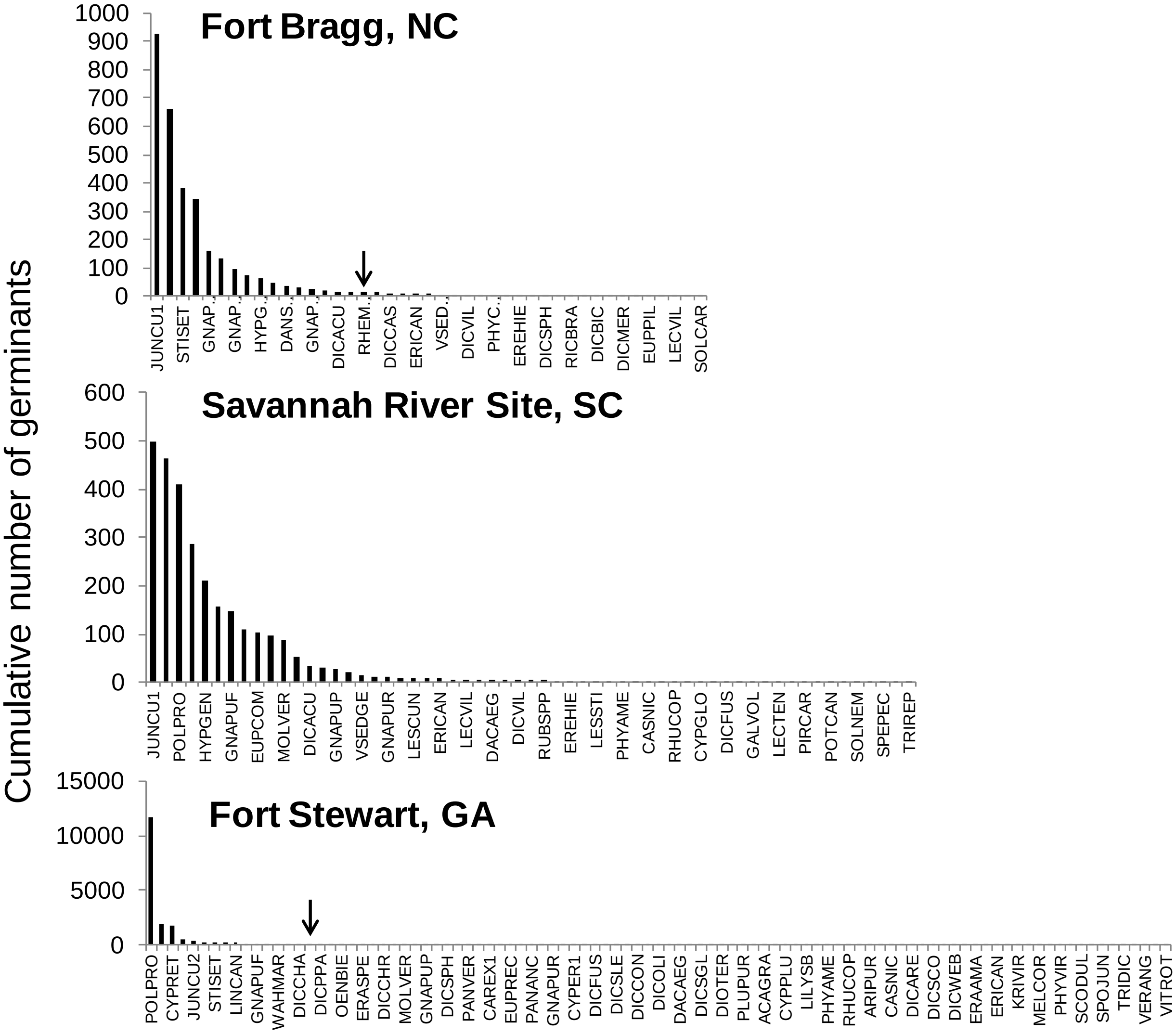

Figure 3.2.5. Cumulative number of seedlings germinating from the seed bank for each of the three locations. Data are sorted by the most common species at each site. The x-axis provides the first three characters for the genus and species. Arrows indicate the presence of the indicator species *Rhexia mariana*, which occurred in low abundance at Fort Bragg and Fort Stewart.

3.2.4 Discussion

We found a greater density of individuals and species in the seed bank of post-agricultural longleaf pine savannas compared to savannas with no agricultural history. However, the seed bank at both remnant and post-agricultural savannas was dominated by ruderal plant species typically found in degraded sites. A site's fire frequency had no effects of either the number of germinants or species in its seed bank. We also found considerable geographic variation in plant recruitment from the soil seed bank, although very few of the species that emerged at any location were plants species typical of reference longleaf pine savanna stands. Thus, it is unlikely that the soil seed bank will contribute to the recovery of longleaf pine understory plant communities at sites undergoing management activities (e.g., overstory tree thinning or prescribed burning). In fact, it is possible that the seed bank may be a source of ruderal species that could inhibit ground-layer recovery at sites undergoing management activities.

Agricultural land use dramatically increased the abundance of individuals in the seed bank, however, it did not impact the number of plant species characteristic of reference sites that emerged. Across sites with and without a history of past agricultural land use, we found only one indicator species (*Rhexia mariana*) indicative of reference longleaf pine understory communities and this species emerged in low abundances. An experimental study examining survival of buried seeds corroborates this finding; plant species that are typical of longleaf pine understories did not form persistent seed banks (Coffey and Kirkman 2006).

We found that fire frequency had little effect on the number of germinants or species emerging from the seed bank. Frequent fires might affect seed banks through a number of means, including direct mortality, modifying germination rates, or by influencing the abundance of savanna versus forest plant species in the community. Temperatures at the soil surface during grassland fires can range from 50-200 °C at the soil surface (Archibold et al. 1998, Wally et al. 2006), which are hot enough to cause mortality of the seeds of some species (Emery et al. 2011, Hahn and Orrock 2014). However, temperatures dramatically decrease at or below the soil surface (Archibold et al. 1998, Wally et al. 2006). In longleaf pine ecosystems, frequent fires promote the diversity and density of understory plants (Hiers et al. 2007, Veldman et al. 2013, 2014), which might result in increased seed deposition and, ultimately, seed bank density or diversity. However, given the low ability of savanna and grassland plant species to form persistent seed banks (Coffey and Kirkman 2005, Benson and Harnett 2006), coupled with the importance of bud banks for post-fire regeneration (Benson and Harnett 2006), the seed bank may contribute little to post-fire regeneration of plant species that are indicators of reference longleaf pine savannas. Rather the bud bank (Benson and Harnett 2006) or post-fire seed inputs (Hiers et al. 2000) may be more important for structuring post-fire plant communities.

We also found significant geographic location with more total germinants and species emerging from the soil seed bank at Fort Stewart, than at either Fort Bragg or the Savannah River Site. One potential explanation is that total species richness and plant cover is highest at Fort Stewart (Brudvig et al. 2014), and thus may have a more dense and diverse seed bank. Alternatively, this may be due to an effect of seed bank species identity. The most common species at Fort Stewart was *Polypremum procumbens*, a ruderal species that was over 10-times more abundant than any other species at that location. This could account for the greater total number of germinants at Fort Stewart, compared to the other two locations.

3.2.5 Conclusions

We conclude that the seed bank in longleaf pine plant communities is unlikely to contribute to the recovery of plant species typically found in undisturbed sites, regardless of the level or type of degradation. Collectively, our work and past work suggests that direct addition of seeds (i.e., propagule additions) is likely necessary for recovery of degraded sites.

3.3 CLASSIFICATION OF SITES VIA ECOLOGICAL REFERENCE MODELS

[This section contains material from Brudvig, L.A., J.L. Orrock, E.I. Damschen, C.D. Collins, P.G. Hahn, W.B. Mattingly, J.W. Veldman, and J.L. Walker. 2014. Land-use history and contemporary management inform an ecological reference model for longleaf pine woodland understory plant communities. *PLoS One* 9: e86604.]

3.3.1 Introduction

Ecological recovery efforts guided by a target range of reference conditions (White and Walker 1997) often fail to achieve these targets (Rey Benayas et al. 2009). In part, this may be because knowledge of reference conditions, while useful, is by itself insufficient for guiding or prioritizing recovery due to variation in degraded states (unrestored conditions that deviate from reference conditions). Human-modified landscapes support a range of degraded states, resulting from land-use legacies and variation in contemporary management (Foster et al. 2003, Hobbs 2007). Thus, an important early step in the recovery of human-modified landscapes is the formalization of ecological reference models, which describe both reference conditions and the spectrum of degraded states that are common for a given ecosystem (Hobbs and Harris 2001, Foster et al. 2003). Reference models have been formulated for many ecosystems (Allen et al. 2002, Asbjornsen and Brudvig 2005, Walker and Silletti 2006); however, these models are frequently qualitative and models of ecosystem degradation have rarely been quantitatively developed or evaluated (Hobbs 2007).

Data-driven ecological reference models that incorporate both the consequences (e.g., altered species compositions) and causes of degradation (e.g., altered disturbance regimes) can promote a better understanding of degraded landscapes, help to prioritize management activities, and contribute toward the goal of tailoring strategies to specific degraded states (Hobbs and Harris 2001, Foster et al. 2003, Hobbs 2007). For example, in fire-maintained ecosystems, qualitative reference models simply predict increasing degradation with fire suppression (Allen et al. 2002, Asbjornsen and Brudvig 2005, Walker and Silletti 2006), but do not detail the nature of this relationship, such as the rate at which degradation increases with fire suppression or whether thresholds exist where degradation increases abruptly with fire suppression. In contrast, a quantitative reference model could describe degradation based on thresholds in fire frequency, allowing for sites to be classified along this axis, and management planning and approaches could be tailed accordingly (Hobbs 2007).

We suggest that a quantitative ecological reference model should have three features to be both ecologically relevant and useful to land managers. First, it would classify sites based on relevant ecological communities, which in many cases will be plants – the basis for many management decisions (Bestelmeyer et al. 2003, Brudvig 2011). Second, suspected drivers of ecosystem degradation would be incorporated into the classification by linking site conditions to factors associated with degradation (Hobbs and Harris 2001, Hobbs 2007). Together, these two steps would describe the range of degraded states and quantify how, in terms of degrading factors, they differ from each other and from reference conditions. Third, to make such a model applicable to management, it would use data routinely available to land managers across sites spanning landscapes; the scale at which recovery planning and most management efforts typically operate (Hobbs and Harris 2001, Hobbs 2007). We define landscape based on Turner

(2001) as “an area that is spatially heterogeneous in at least one factor of interest” – in our case, degradation of sites across a location for which management might be coordinated. In this study, we incorporate these three features to develop a quantitative ecological reference model for longleaf pine (*Pinus palustris*) savannas at three locations (i.e., landscapes) in the southeastern United States.

Fire-maintained longleaf pine savannas support species-diverse understory plant communities that have been widely degraded by human land uses and are an active target for recovery (Walker and Silletti 2006). The starting point for our work is a previously published qualitative reference model (Walker and Silletti 2006), which describes a degradation gradient in longleaf pine understory plant diversity and composition caused by past agricultural land use, altered fire regimes, and silvicultural activities (see also Mitchell 2009). Agricultural legacies can persist for decades following abandonment, leading to reduced understory diversity and modified community composition on post-agricultural sites (Hedman et al. 2000, Brudvig and Damschen 2011, Brudvig et al. 2013). Fire suppression leads to increased tree abundance, canopy cover, and an accumulation of leaf litter and duff (i.e., forest floor), each of which may reduce understory diversity and modify understory community composition (Brockway and Lewis 1997, Harrington and Edwards 1999, Hiers et al. 2007, Kirkman et al. 2013). Historically, lightning and human-ignited surface fires burned longleaf pine savannas as frequently as every 1-6 years, but today fire suppression is widespread and, where fires do occur, they are implemented through prescribed burning (Frost 2006). Overstory trees reduce understory plant diversity through competition with understory plants for light and water (Harrington and Edwards 1999, Harrington et al. 2003); tree density is also altered by silvicultural management, including tree planting and harvesting (Van Lear et al. 2005, Walker and Silletti 2006). Based on these consequences of human land use, we predict longleaf pine understory communities to be most degraded at sites with a history of agriculture, contemporary fire suppression, and a dense overstory (Figure 3.3.1), which are also determinants of degradation in many other ecosystems (Flinn and Vellend 2005, Pyke et al. 2010). Guided by this past work, we focus on fire history, agricultural legacies, and overstory density as likely degrading factors for longleaf pine understory communities; however, we know of no efforts to quantify a reference model based on these factors.

The goals of our study were to quantify and then evaluate a reference model for longleaf pine woodlands, based on a previously described qualitative model (Walker and Silletti 2006) and associated literature (reference above). To achieve these goals, we pursued three specific objectives: 1) classify longleaf pine understory plant communities based on a set of previously identified degrading factors (agricultural history, fire frequency, overstory tree basal area; references above), 2) evaluate the spatial generality of this model by evaluating the roles of degrading factors across sites that vary in soil conditions and by comparing models for three different landscape-scale locations and a region-scale model (three locations combined), and 3) evaluate the resulting regional and location-specific reference models by comparing degraded states to a set of reference sites.

We pursued our first objective through regression tree analysis and data from 232 longleaf pine woodland sites, which were selected to span a range of biophysical conditions across our three study locations in the southeastern U.S. This analysis groups sites with similar plant communities based on data-defined levels and combinations of agricultural history, fire frequency, and overstory tree basal area. We also included soil attributes in this classification because of their importance for determining plant community composition in this system (Peet 2006) and to assist with our second objective. We recognize that additional degrading factors might be identified (e.g., invasive species); however, we selected this set for consideration based on clear linkages with understory degradation (references above), applicability to our study landscapes (e.g., invasive species were in low abundance at all of our study sites), and the likelihood that these data would be easily obtained by land managers, facilitating application of the model to land management and recovery planning. We pursued our second objective in two ways. First, the inclusion of soil variables in our models provides insight into whether degrading factors (e.g., fire frequency) operate generally to determine degraded states, or differently for some types of longleaf pine woodlands vs. others (e.g., those that occur on Entisols vs. Ultisols). Second, by including three locations in our study, we can evaluate the generality of a regional model (spanning all sites) relative to models for three separate landscapes (Table 1). This is important for understanding the degree to which we can generalize our results across a region or to which landscape-to-landscape variation might preclude broad application of the regional model. Finally, to address our third objective, we compared the degraded states resulting from the regional and location-specific models to a set of 38 reference sites based on a suite of biophysical characteristics that are relevant to land management. In doing so, we evaluated whether each model produces a quantifiable gradient in degradation. Given the geographic distribution of our study locations, our results may be most applicable to Atlantic Coast longleaf pine woodlands, but the degrading factors we study – agricultural legacies, altered fire regimes, and altered overstory tree abundance – are broadly relevant across the longleaf pine ecosystem (Walker and Silletti 2006, Mitchell 2009).

3.3.2 Methods

See Section 3.1 for a description of data collection methods. In particular, see Section 3.1.1 for a description of our study sites and our selection process, Section 3.1.2 for details on our vegetation sampling procedure, and Section 3.1.3 for an explanation of our categorization and analysis of the broader landscape context.

Statistical methods

Following data collection (see Section 3.1), we constructed a site-by-species matrix for subsequent plant community analyses, using the mean cover for each species across the eight subplots at each site. To develop ecological reference models, we used multivariate classification and regression tree analysis to classify non-reference sites based on a combination of plant community composition and environmental data (De'ath 2002). This analysis creates a dichotomous tree with splits based on environmental data that minimize compositional dissimilarity within groups of sites (i.e., 'classes'). In our case, we used environmental data that corresponded to the degrading factors in Figure 3.3.1: agricultural history, tree basal area (total basal area, *Pinus* spp. basal area, non-*Pinus* spp. basal area), and fire frequency (number of burns 1991-2009, time since last fire). We investigated *Pinus* and non-*Pinus* overstory separately because these groups respond differently to fire frequency (*Pinus* is more fire tolerant; Glitzenstein et al. 1995, Veldman et al. 2013) and because land managers often remove hardwoods in the course of management activities (Walker and Silletti 2006a, Kirkman et al. 2013). We also included soil order (Entisol, Inceptisol, Spodosol, Ultisol) and soil water holding capacity in the classification, which are two aspects of soils that broadly structure longleaf pine communities (Peet 2006). As we explained above, the inclusion of these soil variables in our models provides an opportunity to evaluate the generality of degrading factors across longleaf pine communities that occur on different substrates. We conducted classifications for all 232 sites together to accomplish our first objective ('All Sites' analysis) and for each of the three locations separately to address our second objective ('Fort Bragg', 'Fort Stewart', and 'Savannah River Site' analyses). To determine the number of final classes generated by each analysis, we conducted 500 cross-validations of the model and selected the most frequently occurring tree size using the 1-SE rule (De'ath and Fabricius 2000). For ease of interpretation, we numbered the resulting classes to align with Figure 3.3.1, so that Class 1 was most degraded. Classes defined by soil attributes do not align with our conceptual framework in Figure 3.3.1 and we do not attempt to attribute degradation to soil conditions; however, we do include soil-defined classes in this alignment based on divergence in biophysical factors from reference conditions (see below).

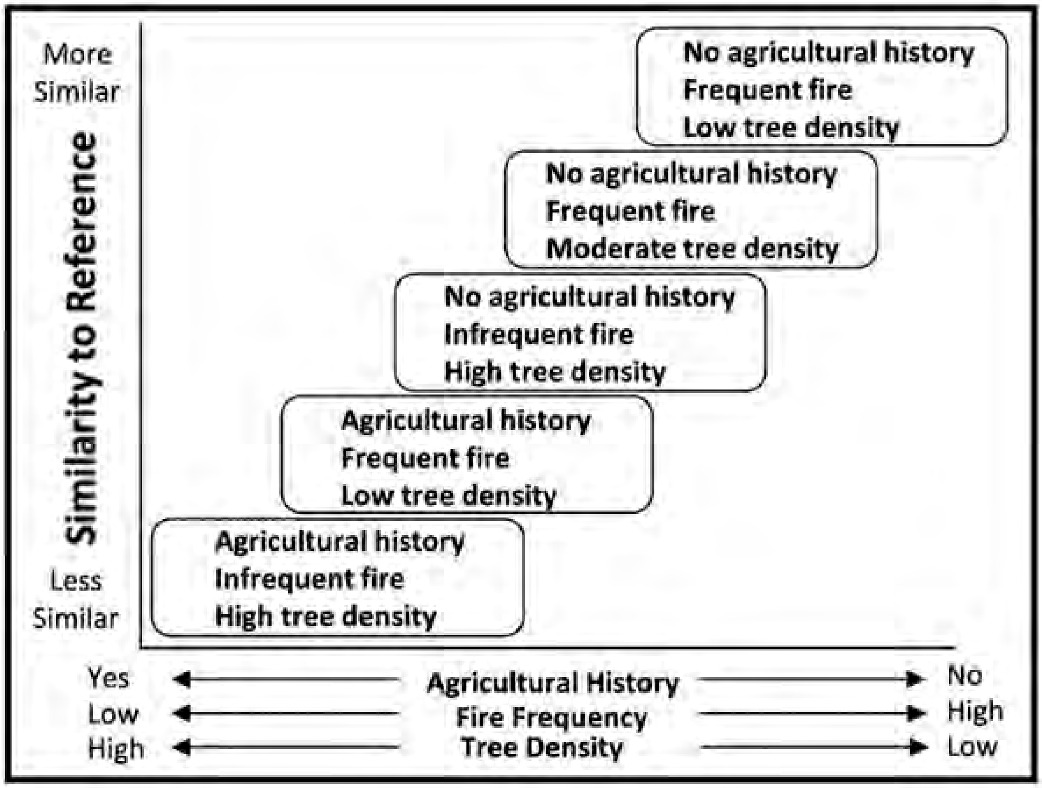

Figure 3.3.1. Conceptual model of degradation for understory plant communities in longleaf pine woodlands. Understory degradation (deviation in community composition from reference site conditions) is predicted to increase with occurrence of agricultural history, increasing overstory density, and declining understory fire frequency. Note: not all combinations of model components are presented in this figure and, while depicted as a linear process in this conceptual diagram, nonlinearities may exist during recovery from degraded states. Model is based on Walker and Silletti (2006).

To accomplish our third objective, we evaluated the ecological relevance of the classes resulting from our classification analyses by comparing biophysical attributes of classes to reference sites.

We calculated means per site (±95% CI) of understory richness and evenness, canopy cover, basal area (total, *Pinus*, non-*Pinus*), years since last fire, number of fires between 1991 and 2009, percent cover of vegetation, bare ground, and down woody debris, litter and duff depth, SOM, and soil water holding capacity. To visualize plant community composition among classes and to compare these classes to reference sites, we used Canonical Analysis of Principal Coordinates (CAP), with Bray-Curtis similarity as the distance measure following square-root transformation of the raw species abundance data (Anderson and Willis 2003). CAP is a constrained ordination analysis that characterizes multivariate differences among groups (i.e., classes, reference sites) (Anderson and Willis 2003). We note that, while many of the attributes we investigated were unrelated to our classification analyses, some attributes were components of the classifications (e.g., community composition). The purpose of these analyses was to quantitatively compare among classes and reference sites, rather than to formally test research hypotheses. To identify species that distinguished classes and reference sites from one another, we used Indicator Species Analysis (ISA) (Dufrêne and Legendre 1997). ISA results are presented in Tables 3.3.3-3.3.7 (located at the end of Section 3.3). We ran separate analyses for each of the four classifications (All Sites, Fort Bragg, Fort Stewart, Savannah River Site). We used PRIMER-E for CAP analyses and calculation of species richness and Pielou’s evenness (Clark and Gorley 2006), SAS for calculation of confidence intervals (Institute 2008), R for multivariate regression trees (R Core Team 2012), and PC-ORD for ISA (McCune and Mefford 2006).

Table 3.3.1. Attributes across study sites and for each of the three study locations.

Variable	**All Sites**	**Fort Bragg**	**Fort Stewart**	**Savannah River Site**
Number of sites	232	84	68	80
Canopy cover (%)	51.7±2.8	30.8±1.9	62.7±4.8	64.5±3.5
Total basal area (m^2/ha)	18.8±1.0	19.4±1.5	15.8±1.9	20.7±1.8
Pinus basal area (m^2/ha)	17.0±1.0	17.6±1.7	14.2±1.7	18.8±1.6
Non-Pinus basal area (m^2/ha)	1.8±0.4	1.8±0.8	1.7±0.6	1.8±0.8
Years since fire	3.4±0.8	1.0±0.2	2.3±0.7	6.8±2.1
Number of fires (1991-2009)	4.6±0.3	5.8±0.3	5.0±0.6	3.0±0.5
Soil water holding capacity (%)	39.5±0.8	41.2±1.4	40.8±1.6	36.8±1.0
Soil organic matter	1.8±0.1	2.0±0.2	2.0±0.2	1.5±0.1
Species richness/m^2	5.1±0.4	4.7±0.6	6.7±0.8	4.2±0.6
Species evenness/m^2	0.7±0.02	0.6±0.03	0.7±0.02	0.7±0.02
Vegetation cover (%)	23.2±2.3	13.4±2.0	38.3±4.7	20.5±3.0
Bare ground (%)	8.2±1.5	11.4±2.7	10.2±3.2	3.1±1.2
Down woody debris (%)	5.2±0.7	2.1±0.4	5.2±1.2	8.4±1.5
Litter depth (cm)	2.2±0.3	1.0±0.1	2.7±0.4	3.1±0.4
Duff depth (cm)	0.9±0.2	0.2±0.03	0.6±0.2	1.9±0.3

Values exclude data from reference sites and are mean ± 95% confidence interval.

Table 3.3.2. Attributes of classes (1-6) for the All Sites classification and reference sites.

Class	**Canopy cover (%)**	**Total basal area (m²/ha)**	**Pinus basal area (m²/ha)**	**Non-Pinus basal area (m²/ha)**	**Years since fire**	**# Fires 1991-2009**	**Soil water holding capacity (%)**
1. Low fire/ Low SM[1]	62.4±4.2	20.3±1.6	18.2±1.6	2.0±0.7	7.6±1.2	2.3±0.4	37.0±1.3
2. Low fire/ High SM	63.0±9.4	18.3±3.5	16.2±3.5	2.2±1.7	3.1±2.6	2.7±0.8	48.9±3.0
3. Ag/High fire	51.8±4.9	20.5±1.8	18.5±1.9	2.0±0.9	1.0±1.3	5.9±0.4	38.9±1.55
4. Forest/High Fire/High BA[2]/Low SM	34.8±6.0	16.2±2.2	14.8±2.6	1.4±1.1	0.8±1.6	6.4±0.5	37.2±1.9
5. Forest/High Fire/High BA/High SM	45.7±7.0	19.6±2.6	18.2±2.6	1.3±1.2	1.0±1.9	6.4±0.6	46.3±2.2
6. Forest/High fire/Low BA	35.1±11.3	7.3±4.2	7.0±4.3	0.4±2.0	1.5±3.1	5.7±1.0	37.9±3.6
Reference	44.4±6.1	15.3±2.4	14.0±2.3	1.3±1.1	1.0±1.7	6.0±0.5	46.6±2.3

Values are mean ± 95% confidence interval.

[1] Soil moisture holding capacity. [2] Basal area

3.3.3 Results

This section describes the site classifications we built in order to generate a recovery plan that addresses the specific qualities of the proposed site. Information on land-use history, historical fire frequency, tree basal area and soil moisture was interpreted using a regression tree analysis, which creates a dichotomous key that groups similar sites together using the site characteristics listed above. Classifications were generated for all three locations combined, as well as for each location separately, resulting in four individual classification models.

The classification of All Sites from the combined three locations resulted in five splits and six classes (Figure 3.3.2). Sites first split according to fire frequency. Infrequently burned sites (≤4 burns since 1991) were further classified based on soil moisture: Class 1 was characterized by infrequent fire and lower soil moisture (<45.08%), whereas Class 2 was characterized by infrequent fire and higher soil moisture (≥45.08%). Frequently burned sites were further classified based on land-use history, with Class 3 characterized by frequent fire and agricultural history. Among sites with forested history, the model made two splits, with the first based on overstory density and the second based on soil moisture. Class 4 was characterized by frequent fire, forested history, high basal area (≥9.965 m²/ha), and lower soil moisture (<42.12%), class 5 by frequent fire, forested history, high basal area, and higher soil moisture (≥42.12%), and class 6 by frequent fire, forested history, and low basal area (<9.965 m²/ha).

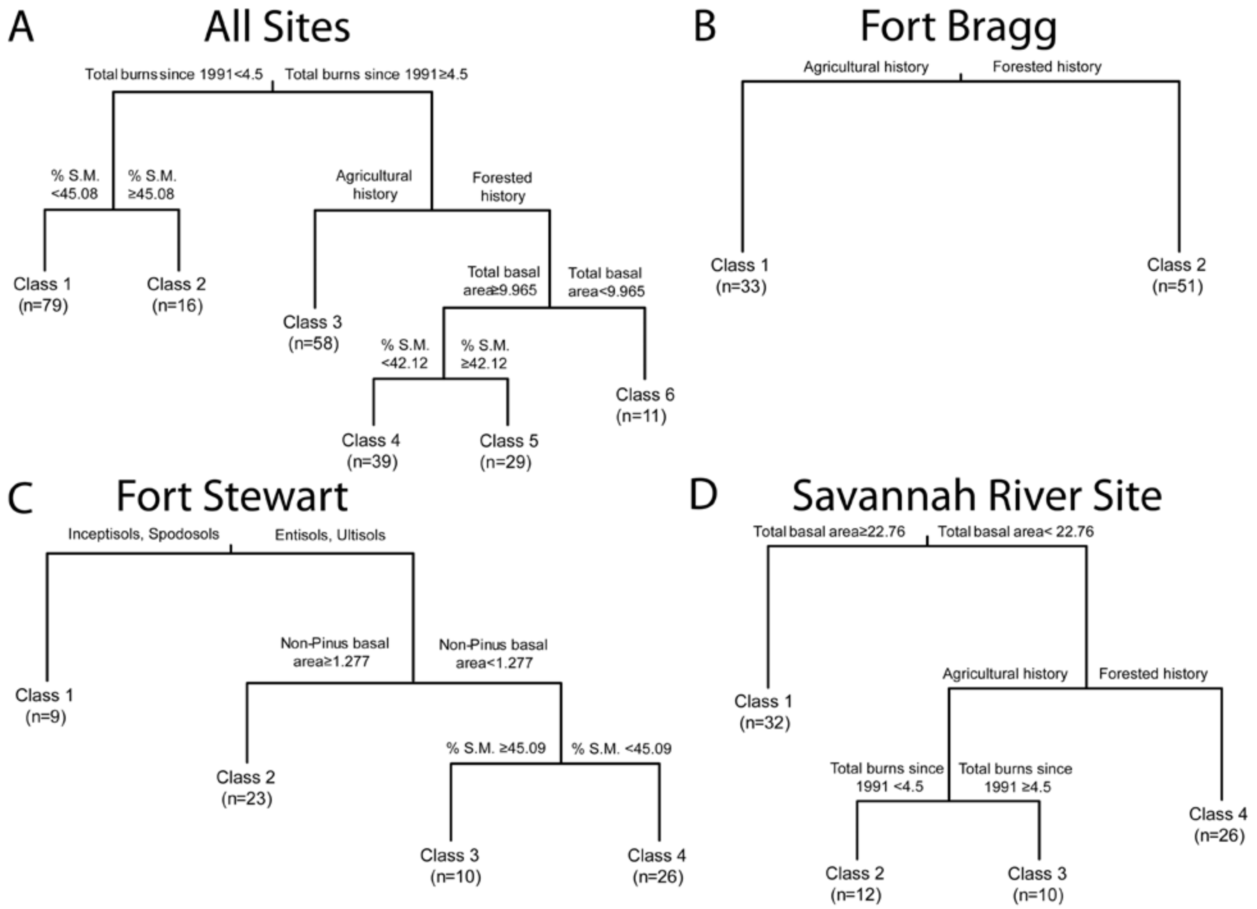

Figure 3.3.2. Results of multivariate classification and regression tree analysis. A) All study sites, B-D) separate study locations. In each analysis, sites are classified based on plant community composition and environmental data and classes are ordered to align with the conceptual model in Figure 3.3.1 (Class 1 = most degraded). Branch length at each split is scaled to the variance explained by the corresponding environmental factor. The number of study sites in each class is presented below each class label.

Location-specific classifications illustrated a number of differences from the All Sites classification, in terms of the identity and ordering of degrading factors, as well as the role of soils (Figure 3.3.3). The Fort Bragg classification contained a single split and two groups defined by agricultural land-use history. The Fort Stewart classification contained three splits and four groups, which illustrated a prominent influence of soils. The first split was between Entisol/Ultisol sites and Inceptisol/Spodosol sites. The only degrading factor in this model, non-*Pinus* basal area, distinguished among sites on Entisol and Ultisol soils (low basal area sites were further split by soil moisture). The Savannah River Site classification contained splits based on all three degrading factors, but with differing order of importance relative to the All Sites classification, as basal area was the most important factor, followed by agricultural land-use history.

The All Sites classification revealed three main delineations in community composition among classes: sites with forested history (Classes 4-6, reference sites), sites with agricultural history or sites with infrequent fire and high soil moisture (Classes 2, 3), and sites with infrequent fire and low soil moisture (Class 1) (Figure 3.3.3). Species richness declined with degradation, whereas species evenness was generally greater at infrequently burned sites (Figure 3.3.3). Among ground cover attributes, vegetation cover was greatest at sites with high soil moisture and at reference sites (Figure 3.3.3), bare ground was greatest at two of the frequently burned classes with forested history, and little difference in down woody debris was apparent (Figure 3.3.3). Forest floor accumulation was related to fire suppression, with greater depths of litter and duff in Classes 1 and 2 (Figure 3.3.3). Soil organic matter was markedly higher on sites with high soil moisture and at reference sites, but not strongly structured by degradation (Figure 3.3.3; Table 3.3.2).

Models resulting from the location-specific classifications produced classes that were compositionally distinct, with the exception of Classes 1 and 2 at Fort Stewart (Figures 3.3.4). Reference sites ranged from compositionally unique at Fort Bragg (Figure 3.3.5) to comparable to less degraded classes on at least one CAP axis at Fort Stewart and Savannah River Site (Figures 3.3.6). Species richness declined with degradation in each location-specific model, whereas many other attributes illustrated location-specific patterns (Figures 3.3.3-3.3.6, Table 3.3.3). Metrics used to classify sites (e.g., years since last fire, basal area; Table 3.3.7) largely mirrored each classification; however, the ways that these variables changed with degradation varied with the different classification rules at each location. Several variables were structured by degradation at one or more sites, including soil organic matter, vegetation cover, and forest floor depth at Savannah River Site, vegetation cover at Fort Bragg, and forest floor depth at Fort Stewart. Other metrics, such as species evenness and soil variables, illustrated location-specific patterns. Lists of indicator species for each class at each location are presented in Tables 3.3.4-3.3.6.

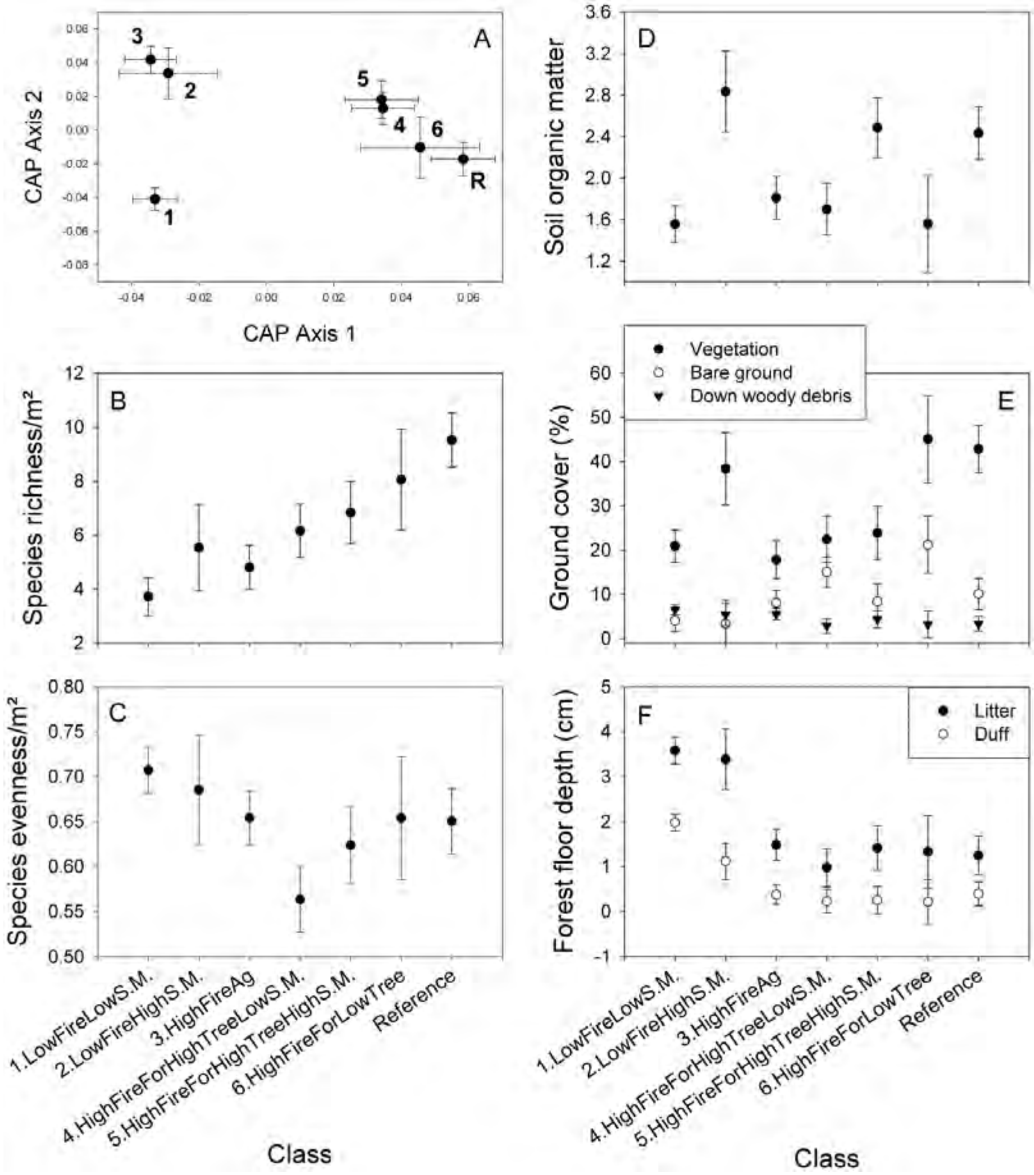

Figure 3.3.3. Comparison of Classes (1-6) from the All Sites classification and regression tree analyses to reference conditions. A) Understory community composition, B) understory species richness, C) understory species evenness, D) soil organic matter content, E) ground cover variables, and F) forest floor depth. All values are means ± 95% confidence intervals.

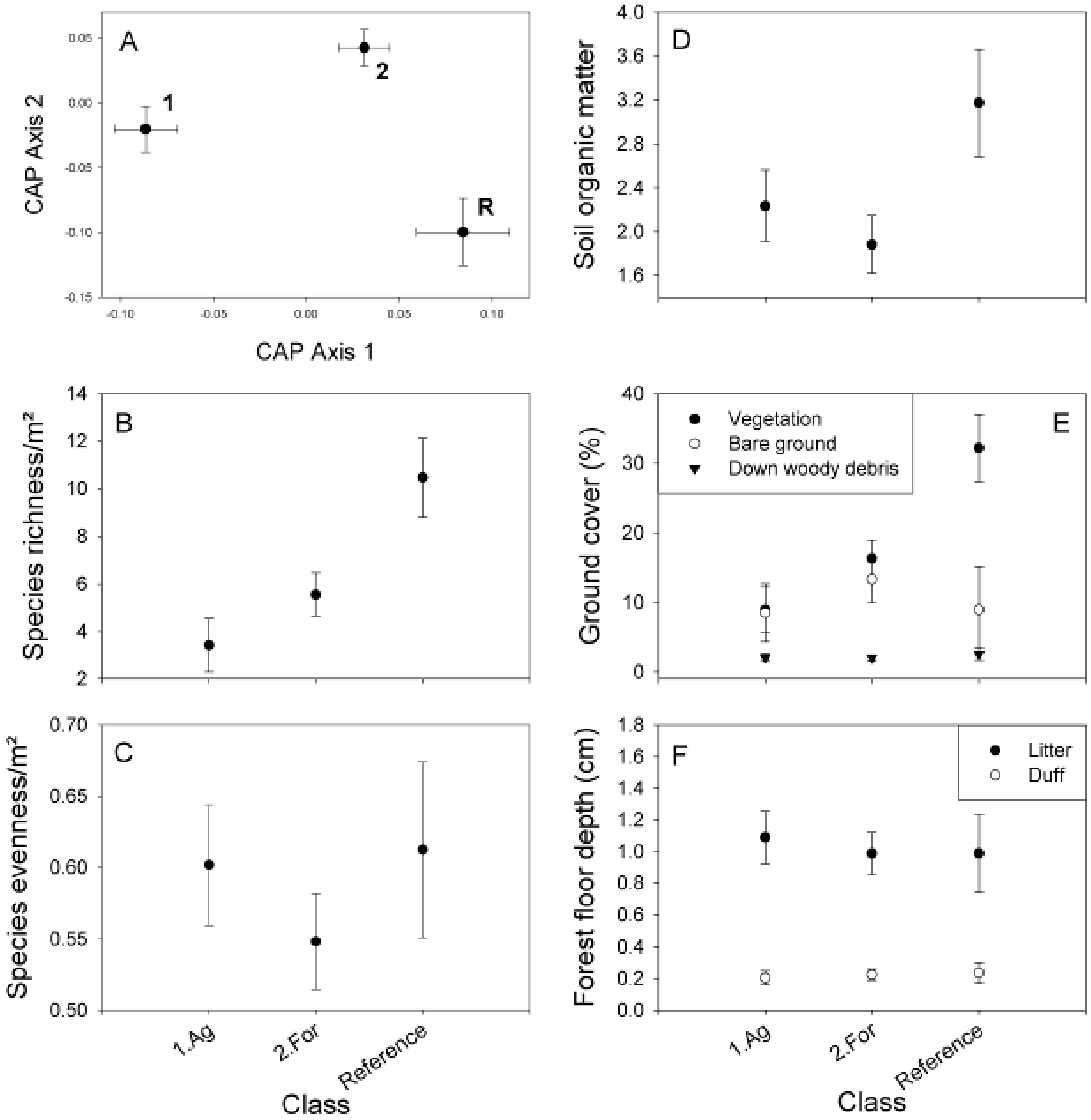

Figure 3.3.4. Comparison of Classes (1–2) from the Fort Bragg classification and regression tree analyses to reference conditions. A) understory community composition, B) understory species richness, C) understory species evenness, D) soil organic matter content, E) ground cover variables, and F) forest floor depth. All values are means ±95% confidence intervals.

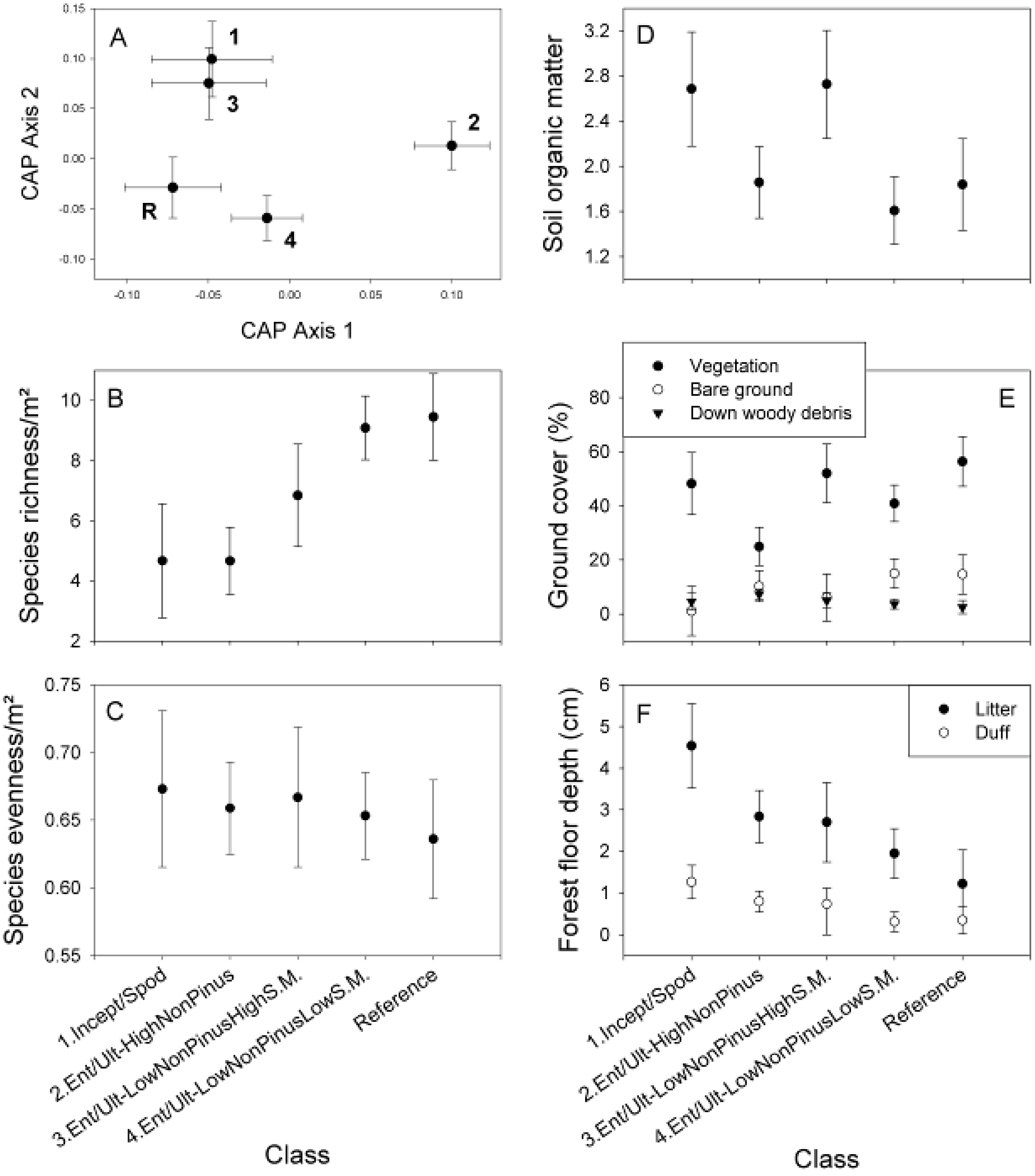

Figure 3.3.5. Comparison of Classes (1–4) from the Fort Stewart classification and regression tree analyses to reference conditions. A) understory community composition, B) understory species richness, C) understory species evenness, D) soil organic matter content, E) ground cover variables, and F) forest floor depth. All values are means ±95% confidence intervals.

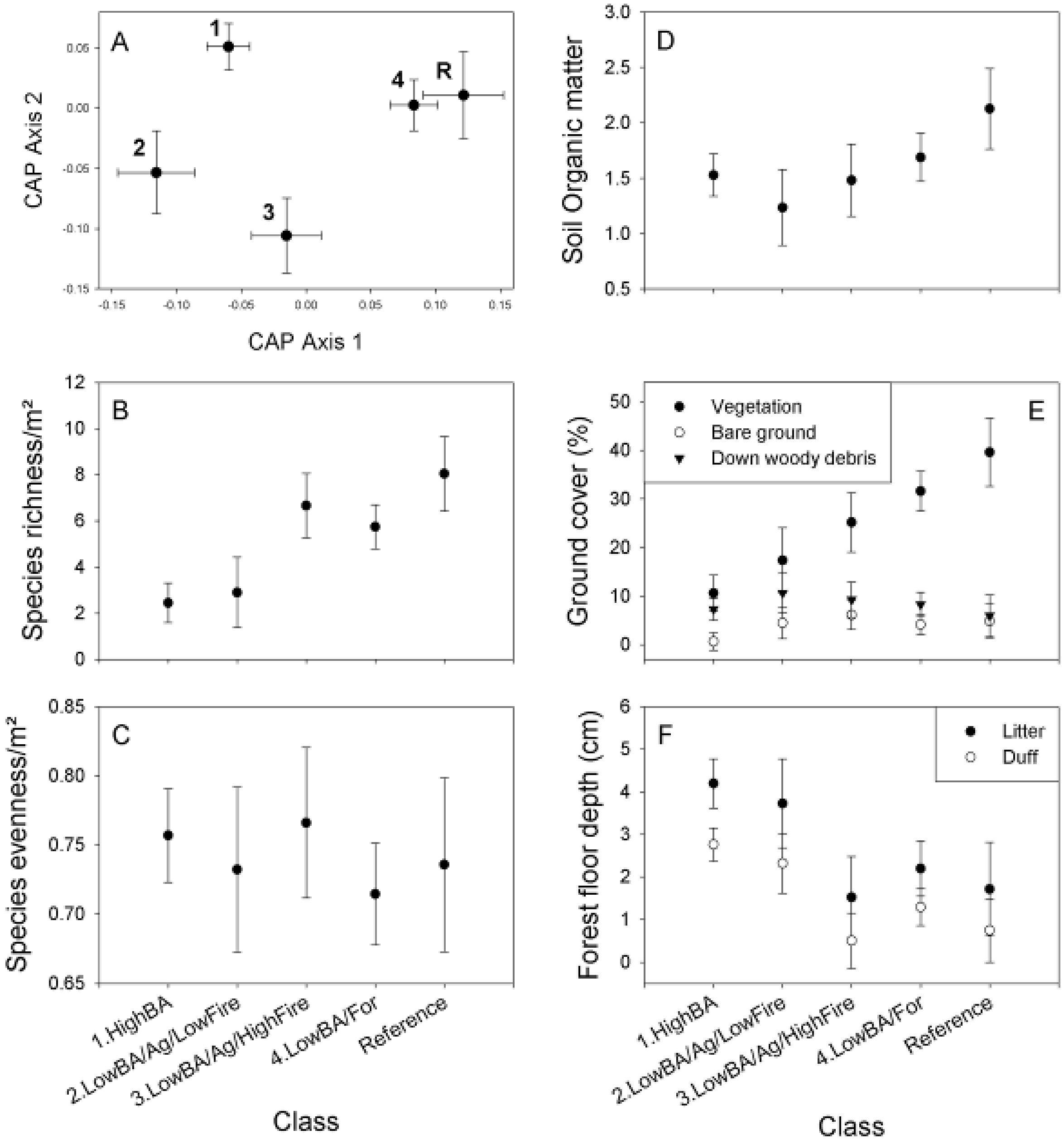

Figure 3.3.6. Comparison of Classes (1–4) from the Savannah River Site classification and regression tree analyses to reference conditions. A) understory community composition, B) understory species richness, C) understory species evenness, D) soil organic matter content, E) ground cover variables, and F) forest floor depth. All values are means ±95% confidence intervals.

3.3.4 Discussion

An ecological reference model for longleaf pine woodlands

Ecological reference models are commonly employed during recovery efforts, but are frequently qualitative, which limits their utility for prioritizing sites for recovery and guiding management efforts on the ground (Hobbs 2007). Using data from 232 sites, we quantified an ecological recovery model for longleaf pine woodland understory plant communities spanning a broad geographic region of the Southeastern United States (Figure 2.2). Three degrading factors – agricultural legacies, recent fire history, and overstory tree density – as well as soil moisture holding capacity, delineated classes of plant communities in this regional model. Location-specific models, however, illustrated substantial variation relative to this regional model and each other (Figure 3.3.2). We suggest that our regional model can help prioritize longleaf pine woodlands for recovery across our study region; however, due to substantial landscape-to-landscape variation, location-specific reference models can help guide localized management decisions.

Our regional model provides general support for the core components of a qualitative model of longleaf pine degradation (Figure 3.3.1); however, by quantifying this conceptual model, we illustrate the relative contributions of degrading factors, as well as threshold values that determine differences between degradation classes. In this regional model, fire frequency was the most important factor (i.e., the first split in the classification), followed by agricultural legacies (Figure 3.3.2). Overstory basal area, while a significant factor in the regional model, was the least important. Based on similarity in community composition to reference sites, Classes 1-3 (infrequently burned and post-agricultural sites) were the most degraded, whereas historically forested sites were less degraded, being both compositionally similar to each other and to reference sites (Figure 3.3.3). Our regional model further quantifies 4 vs. 5 fires since 1991 and ~10m^2/ha as delineations determining degradation related to burning and tree basal area, respectively. These results reinforce the importance of frequent prescribed fires for management of longleaf pine woodlands (Walker and Silletti 2006a, Mitchell 2009), because of its positive influence on understory plant communities (Brockway and Lewis 1997, Brudvig and Damschen 2011a). Our results further highlight the role of agricultural legacies in the degradation of longleaf pine plant communities (Hedman et al. 2000, Brudvig and Damschen 2011a, Brudvig et al. 2013b). The pronounced deviation of fire suppressed and post-agricultural plant communities from reference conditions (Figure 3.3.3) suggests that sites supporting these degraded conditions may require the greatest efforts to restore.

The resulting classes from our regional and location-specific analyses captured relevant gradients of degradation (Figures 3.3.3-3.3.6). As degradation increased, levels of many biotic and abiotic variables became more dissimilar from values at reference sites. This pattern was consistent across the regional and location-specific models for several variables including understory richness, cover, and composition, forest floor accumulation, and tree basal area, whereas other variables including soil organic matter showed a degradation gradient in one or more models. Importantly, a number of these variables were not used in the construction of our ecological reference models (e.g., species diversity metrics, ground cover components, forest floor depth, and soil attributes), yet in many cases these variables corresponded with the degradation gradient.

The explicit consideration of land-use legacies has received increasing attention in conservation (Honnay et al. 2002, Foster et al. 2003, Flinn and Vellend 2005, Lunt and Spooner 2005, Brudvig 2011). Our results illustrate how multiple drivers of ecosystem degradation, including land-use legacies, can be quantitatively incorporated into ecological reference models. This may be of particular importance when legacies interact with contemporary management to influence population viability and community composition. For example, past agricultural activities can mediate the effects of present-day fire management on plant community diversity, such that frequent burning may lead to increased richness, but only in sites with an agricultural land-use history (Brudvig and Damschen 2011). Similarly, past land-use can modify levels and patterns of soil nutrients, with ensuing effects on plant populations (Fraterrigo et al. 2006).

Generality of the ecological reference model

Our location-specific models illustrated notable variation, both relative to each other and to the regional All Sites model (Figure 3.3.2). Only one location-specific model (Savannah River Site) contained all three degrading factors, but with the reverse order of importance compared to the regional model. Conversely, Fort Bragg supported a simple two class model based only on agricultural land-use history, whereas Fort Stewart's model illustrated a prominent role of soils, in addition to hardwood abundance, for structuring understory plant communities (Figure 3.3.2). This variation may reflect differences in underlying environmental factors or differences in land-use and management histories among our three study locations (Table 3.3.1). For example, the presence or absence of fire frequency in location-specific models may be explained in part by variation in prescribed fire management among locations (Table 3.3.1). At Fort Bragg, where fire frequency was not selected as a model component, prescribed fire is highly regimented, resulting in frequent fires and little variation in time since fire among sites (Figure 3.3.2). Conversely, substantial variation in fire frequency exists among sites at the Savannah River Site, where fire frequency was selected as a model component (Figure 3.3.2). Furthermore, our study spanned three physiographic regions of the southeastern U.S. coastal plain (Peet 2006), capturing variation in important ecological factors such as dominant species (Tables 3.3.3-3.3.6) and soil conditions (Table 3.3.1) (Kirkman et al. 2001, Peet 2006). Longleaf pine communities are broadly structured by soils and this influence of soils was most prominent at Fort Stewart – a location that supports longleaf pine woodlands underlain by a variety of soil orders, including Spodosols and Inceptisols, which formed a unique class in the Fort Stewart model. Fort Stewart also illustrated the lone example of how the influence of a degrading factor depended on soil conditions, as non-*Pinus* basal area was important to plant communities on Entisol and Ultisol soils, but not Inceptisol and Spodosol soils. Importantly, at least one hypothesized degrading factors (Figure 3.3.1) was a significant model component at each location, illustrating that they structured understory degradation (i.e., departure from reference conditions) at both regional and landscape scales in this study. The differences in reference model details between our three study locations (Figure 3.3.2) suggests that, while our regional reference model may provide broad-scale insight into patterns of longleaf pine degradation, locations with available resources should consider collecting data to parameterize location-specific reference models.

3.3.5 Conclusions

We suggest that our regional ecological reference model provides a way for managers to broadly infer the degradation status of longleaf pine understory communities in our study region. This model, as well as the location-specific models, employs relatively easily measured data, which serve as proxies for ecological characteristics of interest to land managers (Figure 3.3.3-3.3.7). Agricultural and fire history and, perhaps, overstory basal area, may be available to land managers as GIS data. Thus, our regional and location-specific reference models may be mapped at large spatial scales to assist management and conservation decisions. Longleaf pine understory communities are notable for high levels of species diversity from local (e.g., 1×1m) to regional scales (Peet 2006, Mitchell 2009). Our findings provide guidance over much of this range in scales, spanning sites, landscapes, and portions of a region (the Atlantic Coastal Plain). Future work might explore additional reference models to inform small-scale (e.g., within site) recovery decisions.

Our approach to classifying communities based on degraded conditions should be broadly applicable to other ecosystems around the world modified by human land use and altered fire regimes, including fragmented woodlands in Australia (Lunt and Spooner 2005), fire-suppressed savannas in Brazil (Roitman et al. 2007), and forests in the western United States (Fulé et al. 1997, Allen et al. 2002), among others. During such application, our framework for developing reference models should be modified to include the relevant drivers of degradation for an ecosystem of interest. For example, the presence of invasive species is an important consideration during longleaf pine woodland recovery (Walker and Silletti 2006a) and, while invasive species were not abundant at our study sites, their inclusion as a model variable might be important at other longleaf pine sites or in other ecosystems.

The remaining challenge is to determine how to best restore longleaf pine understory communities once patterns of degradation have been assessed. Our regional and location-specific ecological reference models suggest some strategies for recovery, but these should be interpreted with caution. For example, transitioning sites between Classes 4/5 and 6 in our regional model might simply entail mechanical thinning of overstory trees, a strategy that can increase plant diversity in some contexts (Platt et al. 2009) but has limited effects in others (Provencher et al. 2001, Kirkman et al. 2013). Other transitions might require multiple strategies. For example, reinstating historical fire regimes at post-agricultural sites (e.g., transitioning between Classes 2 and 3 at Savannah River Site) might need to be coupled with introduction of propagules – particularly those of dispersal-limited groups, such as passive and ant dispersed species like *Tephrosia virginiana* and *Aristida stricta*/*beyrichiana* (Kirkman et al. 2004) (Tables 3.3.4-3.3.6). Future experimental work will be necessary to evaluate these hypotheses suggested by our models. Further, reinstating processes may lead to unexpected outcomes for some degraded states. For example, reintroducing fire to long-unburned sites may produce novel fire behavior, leading to unexpected outcomes, such as mortality of longleaf pine overstory trees (Varner et al. 2005). Moreover, while our conceptual reference model (Figure 3.3.1) depicts a simplistic set of linear transitions among degraded states, it remains an open question as to whether a simple linear or a non-linear, such as alternative stable states (Suding et al. 2004) or state and transition model – e.g. (Yates and Hobbs 1997) will be most appropriate during recovery of longleaf pine woodlands. Finally, more work is needed to understand how to best tailor combinations and sequences of recovery strategies (e.g., seed addition, prescribed fire, overstory thinning) to the variety of degraded conditions illustrated by the reference models in our study, for longleaf pine woodlands.

Table 3.3.3. Species with the 10 highest indicator values (from Indicator Species Analysis) for each site class in the All Sites classification. Species identified as indicators of individual site classes ($p<0.05$) are noted by *. P-values are listed for significant indicator species; where not provided p-values were ≥ 0.05. The number of significant indicator species decreased strongly with degradation; Classes 1–6 contained 2, 18, 0, 3, 0, 40 significant indicator species, respectively. Thirteen species were indicative of reference sites.

Class	Species	Indicator value	P
1. Low fire/ Low SM[1]	*Vitis rotundifolia**	23.5	0.006
	*Vaccinium stamineum**	17.0	0.04
	Gelsemium sempervirens	13.0	
	Tragia urens	9.5	
	Smilax glauca	9.3	
	Sassafras albidum	9.0	
	Rhus toxicodendron	7.0	
	Quercus laurifolia	7.2	
	Crataegus flava	7.0	
	Vaccinium arboreum	6.0	
2. Low fire/ High SM	*Vaccinium atrococcum**	36.3	0.0002
	*Quercus nigra**	26.6	0.001
	*Rhexia mariana**	26.2	0.002
	*Gaylussacia frondosa**	21.0	0.003
	*Ilex glabra**	20.9	0.004
	*Lyonia mariana**	20.4	0.003
	Pinus species (excluding *P. palustris*) *	19.2	0.01
	*Lyonia lucida**	15.5	0.005
	*Oldenlandia uniflora**	15.2	0.004
	*Panicum virgatum**	15.0	0.007
3. Ag/High fire	*Vitis rotundifolia*	15.0	
	Dichanthelium species	14.0	
	Diospyros virginiana	10.6	
	Andropogon species	10.0	
	Sassafras albidum	9.7	
	Pinus palustris	9.0	
	Paspalum setaceum	9.1	
	Rubus flagellaris	7.8	
	Eupatorium compositifolium	7.0	
	Prunus serotina	7.3	
4. Forest/High Fire/High BA[2]/Low SM	*Quercus laevis**	40.6	0.0002
	*Cnidoscolus stimulosus**	23.5	0.005
	Gaylussacia dumosa	18.0	
	*Liatris regimontis**	17.5	0.009
	Rhus toxicodendron	12.3	
	Tephrosia virginiana	12.0	
	Aristida stricta	11.0	
	Andropogon species	9.0	
	Silphium compositum	7.6	
	Heterotheca graminifolia	7.0	

Table 3.3.3 (Continued). Species with the 10 highest indicator values (from Indicator Species Analysis) for each site class in the All Sites classification. Species identified as indicators of individual site classes (p<0.05) are noted by *. P-values are listed for significant indicator species; where not provided p-values were ≥0.05. The number of significant indicator species decreased strongly with degradation; Classes 1–6 contained 2, 18, 0, 3, 0, 40 significant indicator species, respectively. Thirteen species were indicative of reference sites.

5. Forest/High Fire/High BA/High SM	_Aristida stricta_	18.0	
	Gaylussacia dumosa	14.0	
	Diospyros virginiana	10.0	
	Andropogon species	9.0	
	Euphorbia curtisii	8.8	
	Quercus laevis	8.0	
	Quercus margaretta	8.5	
	Solidago odora	7.0	
	Eupatorium hyssopifolium	6.7	
	Vaccinium myrsinites	7.0	
6. Forest/High fire/Low BA	_Rhus copallina*_	34.2	0.0006
	Diodia teres*	30.5	0.0004
	Heterotheca graminifolia*	29.1	0.002
	Hypericum gentianoides*	28.4	0.0004
	Lechea villosa*	27.6	0.0002
	Dichanthelium species*	26.7	0.003
	Bonamia patens*	23.8	0.002
	Aristida stricta*	21.3	0.02
	Chamaecrista fasciculata*	21.1	0.004
	Andropogon species*	20.0	
Reference	_Andropogon_ species*	24.1	0.03
	Aristida stricta	21.0	
	Gaylussacia dumosa	21.3	
	Stylosanthes biflora*	20.5	0.01
	Aristida purpurascens*	19.5	0.01
	Aster squarrosus*	16.0	0.01
	Vaccinium crassifolium*	15.8	0.002
	Aster linariifolius*	15.7	0.01
	Heterotheca graminifolia	14.0	
	Tephrosia virginiana	13.9	

Table 3.3.4. Species with the 10 highest indicator values (from Indicator Species Analysis) for each site class in the Fort Bragg classification. Species identified as indicators of individual site classes are noted by *. Indicator species were primarily present at reference sites (n = 59), with 0 and 4 in Classes 1 and 2, respectively.

Class	Species	Indicator value	P
1. Ag	*Pinus palustris*	26.3	
	Dichanthelium species	18.0	
	Danthonia sericea	15.9	
	Vaccinium tenellum	15.0	
	Diospyros virginiana	15.0	
	Sassafras albidum	13.7	
	Quercus laevis	13.0	
	Quercus marilandica	12.0	
	Andropogon species	12.0	
	Pinus species (excluding *P. palustris*)	9.5	
2. Forest	*Quercus laevis**	48.8	0.002
	*Gaylussacia dumosa**	47.3	0.007
	*Rhus toxicodendron**	31.9	0.04
	Aristida stricta	30.0	
	Pinus palustris	23.0	
	Tragia urens	19.7	
	Andropogon species	19.0	
	Cnidoscolus stimulosus	18.3	
	Euphorbia ipecacuanhae	18.2	
	Tephrosia virginiana	18.0	
Reference	*Andropogon* species*	61.8	0.0002
	*Aristida stricta**	56.4	0.0002
	*Chamaecrista nictitans**	44.6	0.0002
	*Eupatorium album**	40.6	0.0002
	*Erigeron canadensis**	40.0	0.0002
	*Vaccinium tenellum**	39.9	0.006
	*Vaccinium crassifolium**	39.9	0.0002
	Dichanthelium species*	38.9	0.01
	*Scleria ciliata**	38.9	0.002
	*Aster squarrosus**	38.1	0.0002

Table 3.3.5. Species with the 10 highest indicator values (from Indicator Species Analysis) for each site class in the Fort Stewart classification. Species identified as indicators of individual site classes are noted by *. 7, 1, 9, and 10 species were significant indicators of classes 1–4, respectively, and 19 species were indicative of reference sites.

Class	Species	Indicator value	P
1. Inceptisols, Spodosols	*Gaylussacia frondosa**	52.0	0.0002
	*Persea palustris**	42.2	0.003
	*Serenoa repens**	27.4	0.03
	*Lyonia ferruginea/fruticosa**	25.5	0.02
	*Lyonia lucida**	24.8	0.01
	*Clethra alnifolia**	24.7	0.01
	*Cyperus globulosus**	19.2	0.02
	*Ilex glabra**	17.0	
	*Vaccinium myrsinites**	15.0	
	*Gaylussacia dumosa**	14.0	
2. Entisols, Ultisols/ High non-*pinus* Basal area	*Vitis rotundifolia**	32.3	0.02
	Gelsemium sempervirens	20.0	
	Cyperus retrorsus	18.5	
	Smilax rotundifolia	15.8	
	Uniola laxa	14.4	
	Callicarpa americana	13.3	
	Carex retroflexa	13.0	
	Chamaecrista fasiculata	12.0	
	Rubus trivialis	11.0	
	Pinus species (excluding *P. palustris*)	11.0	
3. Entisols, Ultisols/ Low non-*pinus* Basal area/ High soil moisture	*Vaccinium atrococcum**	62.6	0.0002
	*Ilex glabra**	38.3	0.002
	*Rhexia mariana**	37.1	0.01
	*Rhexia alifanus**	33.8	0.004
	Vaccinium myrsinites	33.6	
	*Liquidambar styraciflua**	31.6	0.005
	Pinus species (excluding *P. palustris*) *	29.9	0.01
	*Aster paternus**	27.9	0.003
	*Lachnocaulon anceps**	26.5	0.01
	Dichanthelium species	24.0	
4. Entisols, Ultisols/ Low non-*pinus* Basal area / Low soil moisture	*Scleria ciliata**	39.2	0.004
	*Heterotheca graminifolia**	37.5	0.007
	*Diodia teres**	36.2	0.004
	*Pinus palustris**	34.2	0.007
	*Eupatorium compositifolium**	31.4	0.03
	*Rubus trivialis**	30.3	0.02
	Andropogon species	27.0	
	Dichanthelium species	25.0	
	Aristida stricta	25.0	
	*Eupatorium album**	23.9	0.03

Table 3.3.5 (Continued). Species with the 10 highest indicator values (from Indicator Species Analysis) for each site class in the Fort Stewart classification. Species identified as indicators of individual site classes are noted by *. 7, 1, 9, and 10 species were significant indicators of classes 1–4, respectively, and 19 species were indicative of reference sites.

Reference	*Aristida stricta**	46.8	0.0008
	*Quercus pumila**	34.3	0.007
	*Aristida purpurascens**	32.6	0.01
	Heterotheca graminifolia	32.0	
	Andropogon species	31.3	
	Gaylussacia dumosa	27.4	
	*Aster squarrosus**	27.3	0.009
	*Seymeria cassioides**	26.5	0.01
	*Hypericum hypericoides**	24.9	0.03
	*Xyris caroliniana**	24.8	0.008

Table 3.3.6. Species with the 10 highest indicator values (from Indicator Species Analysis) for each site class in the SRS classification. Species identified as indicators of individual site classes are noted by *. There were 0, 3, 14, and 4 significant indicators of classes 1–4, respectively, and 26 species indicative of reference sites.

Class	Species	Indicator value	P
1. High basal area	*Vitis rotundifolia*	17.0	
	Sassafras albidum	12.0	
	Crataegus flava	11.5	
	Vaccinium stamineum	10.0	
	Chimaphila maculata	9.4	
	Lespedeza stuevei	9.4	
	Quercus laurifolia	7.0	
	Diospyros virginiana	6.0	
	Quercus falcata	6.0	
	Carya tomentosa	6.0	
2. Ag/Low fire/Low basal area	*Vitis rotundifolia**	35.2	0.008
	*Gelsemium sempervirens**	32.0	0.02
	*Quercus incana**	23.0	0.05
	Tragia urens	21.3	
	Smilax glauca	19.7	
	Vaccinium stamineum	15.0	
	Rhus toxicodendron	10.0	
	Lupinus diffusus	10.0	
	Aristida tuberculosa	10.0	
	Rubus flagellaris	10.0	
3. Ag/High fire/Low basal area	*Chamaecrista nictitans**	70.7	0.0002
	*Desmodium marilandicum**	51.1	0.0002
	*Prunus serotina**	37.5	0.008
	Dichanthelium species*	35.1	0.03
	*Rubus flagellaris**	33.3	0.007
	*Pinus palustris**	31.7	0.02
	*Erianthus brevibarbis**	29.1	0.002
	*Rhus toxicodendron**	28.8	0.05
	Sassafras albidum	27.0	
	Rhus copallina	24.9	
4. Forest/Low basal area	*Gaylussacia dumosa*	36.0	
	*Quercus laevis**	23.9	0.04
	*Pteridium aquilinum**	23.7	0.03
	Rhus copallina	21.0	
	Vaccinium arboreum	21.0	
	*Vernonia angustifolia**	19.3	0.04
	*Baptisia perfoliata**	19.2	0.03
	Vaccinium stamineum	19.1	
	Quercus stellata	19.0	
	Andropogon species	18.0	
	Dichanthelium species	18.0	
Reference	*Gaylussacia dumosa**	48.0	0.001
	*Tephrosia virginiana**	45.2	0.0004
	Andropogon species*	37.6	0.02
	*Lespedeza repens**	37.1	0.002
	*Dyschoriste oblongifolia**	35.9	0.002
	*Eupatorium album**	34.9	0.002
	*Solidago odora**	32.3	0.02
	*Aster linariifolius**	31.6	0.003
	*Stipa avenacea**	31.6	0.002
	*Aster paternus**	29.4	0.003

Table 3.3.7. Attributes of classes resulting from the location-specific classifications, compared to references sites. Values are mean ±95% confidence interval.

Class	Canopy cover (%)	Total basal area (m^2/ha)	Pinus basal area (m^2/ha)	Non-Pinus basal area (m^2/ha)	Years since fire	# Fires since 1991	Soil water holding capacity (%)
Fort Bragg							
1. Ag	33.9±2.9	21.9±2.3	19.3±2.7	2.6±1.2	1.0±0.4	5.5±0.5	42.4±2.5
2. Forest	28.8±2.4	17.8±1.8	16.5±2.2	1.3±1.0	1.0±0.3	6.0±0.4	40.3±2.0
Reference	34.0±4.1	18.8±2.5	17.7±3.4	1.1±1.8	1.0±0.4	4.9±0.6	55.0±3.7
Fort Stewart							
1. Inceptisols, Spodosols	66.0±12.8	15.9±4.9	14.6±4.7	1.4±1.3	4.0±1.8	4.1±1.7	43.5±3.6
2. Entisols, Ultisols/ High non-Pinus BA[1]	71.3±8.0	18.9±3.1	14.8±2.9	4.1±0.6	3.1±1.0	5.1±1.1	38.5±2.2
3. Entisols, Ultisols/ Low non-Pinus BA/ High SM[2]	60.9±12.1	15.0±4.7	14.8±4.4	0.2±0.9	1.6±1.6	3.9±1.6	49.7±3.4
4. Entisols, Ultisols/ Low non-Pinus BA/ Low SM	54.7±7.5	13.5±2.9	13.2±2.7	0.2±0.6	1.2±1.0	5.6±1.0	38.5±2.1
Reference	25.8±9.5	13.1±3.8	12.5±3.7	0.6±0.5	0.5±1.3	8.0±1.4	42.1±3.5
Savannah River Site							
1. High BA	78.8±3.9	28.3±1.7	24.7±1.7	3.7±1.3	11.5±3	1.8±0.6	36.5±1.4
2. Low BA /Ag/Low fire	53.5±7.0	16.8±2.9	16.6±3.1	0.2±2.4	7.2±5.2	2.1±1.0	36.3±2.6
3. Low BA /Ag/High fire	56.7±6.4	17.0±2.7	17.0±2.9	0.0±2.2	0.9±4.8	5.5±0.9	33.4±2.4
4. Low BA /Forest	54.7±4.3	14.4±1.8	13.4±2	1.0±1.5	3.7±3.3	3.7±0.7	38.8±1.6
Reference	54.5±7.5	13.0±3.1	10.2±3.3	2.8±2.5	1.8±5.8	4.6±1.2	39.7±2.7

3.4 CONTROLS OF LOCAL UNDERSTORY DIVERSITY. I: LANDSCAPE AND LOCAL FACTORS

[This section contains material from a manuscript in preparation: Veldman, J.W., Brudvig, L.A., E.I. Damschen, W.B. Mattingly and J.L. Walker. The influence of landscape context and local factors on the recovery of fire-dependent plant communities on former agriculture lands.]

3.4.1 Introduction

The determinants of plant community composition are often conceptualized as a series of biophysical factors that operate at local or landscape scales. Local factors shape plant communities by influencing competitive interactions, trophic dynamics, recruitment opportunities, and resource availability (Huston 1999). Landscape factors are generally conceptualized in the context of biogeography and influence propagule dispersal and immigration/extinction rates (MacArthur and Wilson 1967). Although both local and landscape factors have been found to be important for local plant community dynamics in a number of systems, the relevance of landscapes in the context of ecosystem recovery is poorly understood (Brudvig 2011).

Most ecological recovery efforts involve the manipulation of local biophysical conditions in hopes that recovery of certain ecosystem attributes such as vegetation structure (e.g., tree density), disturbance regimes (e.g., fire frequency), or competitive interactions (e.g., removal of invasive species) will promote plant community recovery (Brudvig 2011). In severely degraded ecosystems, recovery of local biophysical factors alone may be insufficient to achieve rapid recovery of plant communities, in part because many species of conservation interest are dispersal-limited (Redhead et al. in press, Kirkman et al. 2004). As a result, recovery efforts often require the addition of seeds or transplants of target species. Seeding and transplants can be effective management strategies, but at very large spatial scales the costs and labor associated with propagule additions can become prohibitive (Birch et al. 2010). It is thus important to determine when, and if, remnant plant communities present in the landscape surrounding areas targeted for recovery may contribute to community recovery by serving as propagule sources.

Landscape-scale processes are important to the recovery of forest plant communities on former agricultural land, but little is known about the degree to which landscapes can contribute to the recovery of fire-dependent savanna and grassland plant communities. In secondary forests in the northeastern USA and Europe, proximity to old-growth forest is an important predictor of understory plant dispersal, species richness, and community composition (Jacquemyn et al. 2001, Matlack 2005, Verheyen et al. 2006). Where recovering forests are isolated, or landscapes contain little old-growth forest, plant communities may require at least 200 to 400 yr or longer to recover their pre-agricultural plant diversity and composition (Vellend 2003, Verheyen et al. 2003a, Matlack 2005). Similar patterns, processes, and time-scales may be important to recovering savanna plant communities in post-agricultural landscapes but because forests and savannas are fundamentally different ecosystems, it remains unclear if results from studies of forest plant community recovery can be generalized to savannas. Unlike forest plant species, which are predominantly shade-tolerant, animal-dispersed, and evolved to persist in infrequently disturbed environments, savanna plant species are primarily shade intolerant, wind- or gravity-dispersed, and evolved to survive frequent surface fires (Parr et al. 2014). As a result, savanna plant species may be particularly poor colonizers of former agricultural land and thus landscape context may have relatively little influence on recovery, at least in the short term (Kirkman and Mitchell 2006). Fundamental to this hypothesis is an apparent trade-off between conservative life-history strategies evolved for persistence in fire-frequented environments and sexual reproduction (Lamont et al. 2011). Indeed, recovering savannas and grasslands, degraded by fire-exclusion, plantation forestry, and agriculture appear to be very slow to recover even when remnant plant communities are nearby (Kirkman et al. 2004, Zaloumis and Bond 2011). The question of whether or not landscape context (i.e., the proportion of remnant vegetation in a landscape) is an important predictor of savanna plant community recovery has not been assessed with a highly replicated dataset from a large geographic region.

We assessed the relative contribution of landscape context versus local factors to pine savanna plant community recovery on former agricultural sites at three locations in the southeastern United States. Fire-frequented pine savannas of the longleaf pine ecosystem are characterized by overstories of scattered pine trees and fire-tolerant oaks (Hiers et al. 2014), and species-diverse understory plant communities of grasses, forbs, and shrubs (Walker and Peet 1983). Pine savannas once covered much of the Atlantic and Gulf Coastal Plains, ranging from eastern Texas to Florida and northward to southern Virginia, but are now restricted to ~3% of this area due to the combined effects of agricultural and silvicultural conversion, fire exclusion, timber and resin extraction, and urbanization (Frost 1993). With few remnant savannas remaining, conservation efforts are focused on restoring plant communities that have been degraded by agriculture and fire exclusion. Unfortunately, species-diverse savanna plant communities are typically very slow to recover on former agricultural land (Ostertag and Robertson 2007, Brudvig et al. 2013), even when tree canopy structure and fire regimes have been restored. If we could identify situations in which landscapes are likely to contribute to community recovery, this would help guide management decisions about when plantings (e.g., seeds and/or transplants) are required, versus situations in which prescribed fire and tree thinning alone may be sufficient to meet recovery goals.

To determine if landscape effects are important, we must take into account a host of local biophysical variables that influence plant communities. In particular, we must consider fire frequency, tree basal area, and soil moisture availability, all of which exert strong influences on understory plant communities (Beckage and Stout 2000, Kirkman et al. 2001). Our analyses use AIC model averaging (Grueber et al. 2011), an information theoretic approach that ranks, weights, and averages the contributions of landscape context, local factors, and their interactions in linear models that predict plant community recovery. This statistical approach allows us to assess the relative importance of landscape versus local effects on plant community recovery. By incorporating a variety of plant community metrics, and repeating the analyses at three different study locations in three states, this study provides a broad-scale test of whether landscapes can contribute to plant community recovery on former agricultural land in a fire-dependent savanna ecosystem.

3.4.2 Methods

Data collection

See Section 3.1 for a description of data collection. In particular, see Section 3.1.1 for a description of our study sites and our selection process, Section 3.1.2 for details on our vegetation sampling procedure, and Section 3.1.3 for an explanation of our categorization and analysis of the broader landscape context.

Plant Community Metrics

Using data on species presence/absence for each site, we calculated four plant community metrics to serve as indices of plant community recovery: Number of reference species, Similarity to reference community composition, Species richness, and Proportion of reference species. To determine the number of reference species, we used the Indicator Species Analyses (ISA) of (Brudvig et al. 2014), to establish a list of species with affinities for references sites (see Table 3.3.3), and determined how many of these 'reference species' were present at each site. To determine similarity to reference community composition, we used the site by species presence/absence matrix to calculate the pairwise Jaccard dissimilarity index between each post-agricultural site and each reference site with the *vegan* package in R 2.15.1 (R Development Core Team 2012). We then calculated the mean compositional similarity between each study site and the reference sites as: Similarity to reference = 1 – [mean of pairwise Jaccard dissimilarities between post-agricultural and reference sites]. For species richness, we determined the number of species present at each 1000 m^2 site. We defined proportion of reference species as the [number of reference species]/[total species richness].

Statistical Analyses

To assess the relative contributions of local versus landscape effects on plant community recovery on post-agricultural sites we used AIC model averaging (Grueber et al. 2011) of linear models that relate local and landscape predictor variables to plant community response variables. We conducted separate analyses for each of the four community response variables and conducted separate analyses for each of the three study locations, resulting in 12 distinct analyses. The candidate models included all possible nested combinations of the main effects of fire frequency + basal area + soil moisture + landscape context, and all potential two-way interactions. We conducted the model averaging in R 2.15.1 (R Core Team 2012). First, we defined the candidate models using the *lm* function. We then standardized the dependent and independent variables (Grueber et al. 2011) to a mean of 0 and standard deviation of 0.5 using the *arm* package. We used the *dredge* and *model.avg* functions in the *MuMIn* package to perform the linear regressions for all candidate models, to create a table of the best models, and to average the models with $\Delta AICc \leq 2$ relative to the best model. To visually depict the effects of landscape on select plant community response variables, while accounting for important local effects, we created partial effects plots using the *effects* package.

3.4.3 Results

Landscape patterns

Across locations, post-agricultural sites tend to be surrounded by less remnant habitat compared to sites that were never cultivated, but the magnitude of this pattern varies by study location and spatial scale (Fig. 3.4.1, Table 3.4.1). Most post-agricultural sites at Ft. Bragg are surrounded by remnant pine savannas (mean 85% at 150 m scale), whereas at SRS most post-agricultural sites are surrounded by very little remnant habitat (mean 16 % at 150 m scale). Landscapes surrounding post-agricultural sites at Ft. Stewart range widely in remnant cover (0 to 83% remnant at the 150 m scale), with a mean of 32%.

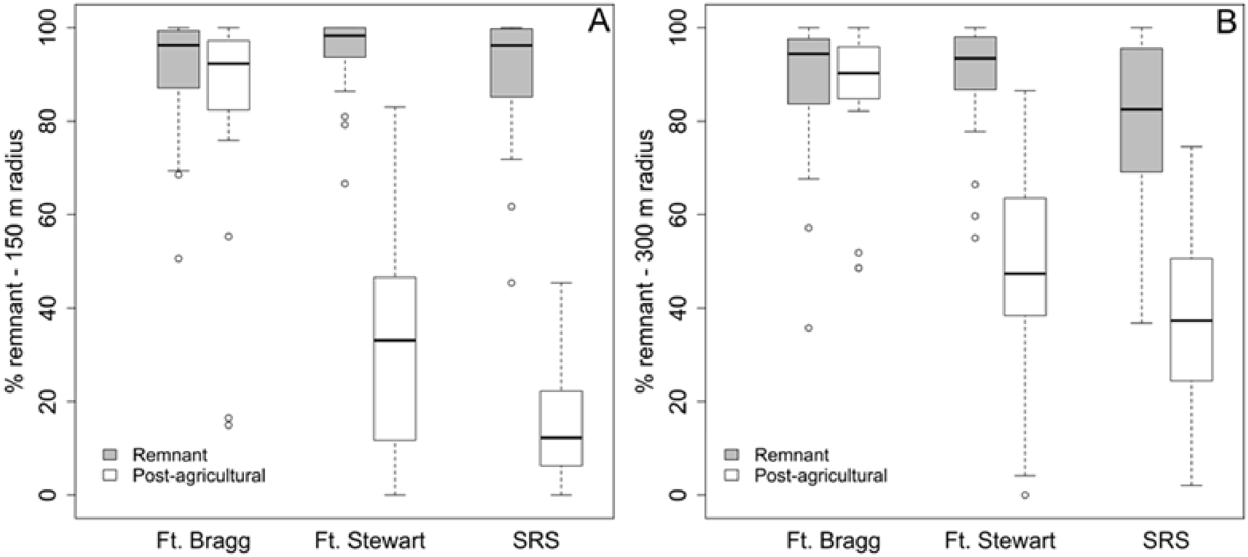

Figure 3.4.1. Quartile boxplots of the percentage of remnant vegetation surrounding present day remnant and post-agricultural study sites (i.e., landscape context) at spatial scales of (A) 150 m radius, the scale analyzed in this study; and, (B) 300 m radius. Note that post-agricultural sites at Ft. Stewart and SRS tend to be surrounded by a low percentage of remnant habitat, whereas most post-agricultural sites at Ft. Bragg are mostly surrounded by remnant vegetation.

Local biophysical variables

Tree basal area is very similar for post-agricultural sites at all three locations (Table 3.4.1). Recent fire frequencies differ between locations. Mean fire frequency is similar for Ft. Bragg and Ft. Stewart (5 burns between 1991-2009), but the range differs: every post-agricultural site at Ft. Bragg burned at least three times whereas some sites at Ft. Stewart only burned once. Post-agricultural sites at SRS burned an average of three times, while some sites never burned (range 0 - 7 burns). Soil moisture holding capacity is similar between locations, though Ft. Bragg has a larger range, including some sites with high moisture availability (maximum of 57% compared 47% and 44% at Ft. Stewart and SRS, respectively; Table 3.4.1).

Table 3.4.1. Summary of plant community, local, and landscape variables used to assess recovery of post-agricultural sites. For comparison, values for reference sites are also shown.

	Fort Bragg						Fort Stewart					
	Post-agricultural			Reference			Post-agricultural			Reference		
	mean	min	max	mean	min	max	mean	min	max	mean	min	max
Community response variables:												
Number of reference species	30	10	55	54	25	76	8	2	21	25	14	42
Similarity to reference composition	0.32	0.17	0.44	0.48	0.39	0.53	0.19	0.10	0.27	0.33	0.26	0.37
Species richness (1000 m^2)	48	21	78	76	35	98	48	25	72	64	36	99
Proportion of reference species (# reference species/species richness)	0.61	0.40	0.79	0.71	0.64	0.78	0.15	0.04	0.33	0.39	0.30	0.44
Landscape predictor variable:												
Percent remnant (150 m radius)	85	15	100	83	51	98	32	0	83	98	90	100
Local predictor variables:												
Tree basal area (m^2/ha)	22.2	7.0	49.1	16.6	11.6	27.2	18.5	2.7	38.6	11.9	3.9	19.8
Fire frequency (number of burns 1991-2009)	5	3	8	4	3	6	5	1	8	9	5	15
Percent soil moisture by weight	43	34	57	48	39	57	39	31	47	42	31	52

Table 3.4.1. (continued)

	SRS					
	Post-agricultural			Reference		
	mean	min	max	mean	min	max
Community response variables:						
Number of reference species	10	3	21	28	18	42
Similarity to reference composition	0.28	0.14	0.37	0.44	0.39	0.48
Species richness (1000 m^2)	47	16	75	71	44	110
Proportion of reference species (# reference species/species richness)	0.21	0.13	0.32	0.39	0.35	0.46
Landscape predictor variable:						
Percent remnant (150 m radius)	16	0	45	84	45	100
Local predictor variables:						
Tree basal area (m^2/ha)	22.2	8.4	41.6	13.0	7.6	19.5
Fire frequency (number of burns 1991-2009)	3	0	7	4	0	6
Percent soil moisture by weight	34	28	44	40	35	47

Plant community metrics

The size of the pool of reference species (based on the indicator species analysis of Brudvig et al. 2014) is different for each location: Ft. Bragg, 119 species; Ft. Stewart, 74 species; and, SRS, 55 species (Table 3.4.1). These differences are reflected in the mean number of reference species present on post-agricultural sites at Ft. Bragg (30), Ft. Stewart (8), and SRS (10). In contrast, the number of references species that never occurred in any post-agricultural site are quite different: Ft. Bragg, 19 of 119 species (16 %); Ft. Stewart, 29 of 74 species (39%); and SRS, 15 of 55 species (27 %). This pattern is reflected in the proportion of reference species (# of reference species / total richness) on post agricultural sites. Mean proportion of reference species were: Ft. Bragg (0.61), Ft. Stewart (0.15), and SRS (0.21). Compositional similarity to reference communities also differs between locations (Table 3.4.1). Because species pools and landscape-scale beta diversity differ among study locations (Mattingly et al. 2015), caution is warranted when comparing plant community metrics between study locations.

Landscape versus local effects on recovery

Linear modeling and AIC model averaging for post-agricultural sites confirms that for most community metrics, local biophysical variables are important predictors of plant community recovery (Table 3.4.2), whereas landscape only influences a small number of community variables at two locations (Ft. Stewart and SRS; Table 3.4.2). At Ft. Bragg, soil moisture holding capacity is the most important predictor of all four plant community metrics (Tables 3.4.3-3.4.10); neither landscape nor fire frequency appear in top models for Ft. Bragg. At Ft. Stewart, landscape appears among top models for number of reference species and proportion of reference species (Tables 3.4.4, 3.4.10), but landscape context is not statistically significant in models that include fire frequency. As a consequence, landscape context is not statistically significant in the model averaging at Ft. Stewart (Tables 3.4.3, 3.4.9). To visualize the potential landscape effect, there is a positive relationship between the amount of remnant habitat in the surrounding landscape and the proportion of reference species, after accounting for the effects of tree basal area, but not fire (Fig. 3.4.2d). Among local factors, fire frequency is consistently important to plant community metrics at Ft. Stewart (Tables 3.4.3 – 3.4.10, Fig. 3.4.2c). Of the three locations, SRS provides the strongest evidence for a landscape effect: landscape context has a positive effect on compositional similarity to reference, even after accounting for the local effects of tree basal area and fire frequency (Fig. 3.4.2f). The landscape does not influence the number of reference species, species richness, or the proportion of reference species (Table 3.4.2). Instead, these community metrics are controlled by fire frequency and tree basal area (Tables 3.4.3, 3.4.4, 3.4.7, 3.4.8, 3.4.9, 3.4.10).

Table 3.4.2. Summary of local and landscape influences by location, response variables, and spatial scale. The words "Local" and "Local + Landscape" indicate whether the top models (ΔAICc < 2) for each combination of study location and community response variable included only local factors (i.e., fire frequency, tree basal area, and/or soil moisture) or if landscape contributed to at least one model (i.e., "Local + Landscape). The numbers listed indicate the relative importance of the main effects of Landscape from the model averaging. A relative importance of 1.00 would indicate a variable contributed to every model with ΔAICc < 2.

Response Variable:	Number of reference species	Similarity to reference	Species richness	Proportion of reference species
Ft. Bragg	Local	Local	Local	Local
Ft. Stewart	Local + Landscape[1] 0.60	Local	Local	Local + Landscape[1] 0.76
SRS	Local	Local + Landscape 0.90	Local	Local[2] + Landscape[2] 0.24

[1] Landscape term was never significant in models that included fire frequency at Ft. Stewart

[2] Neither local or landscape terms were statistically significant predictors of proportion of reference species at SRS.

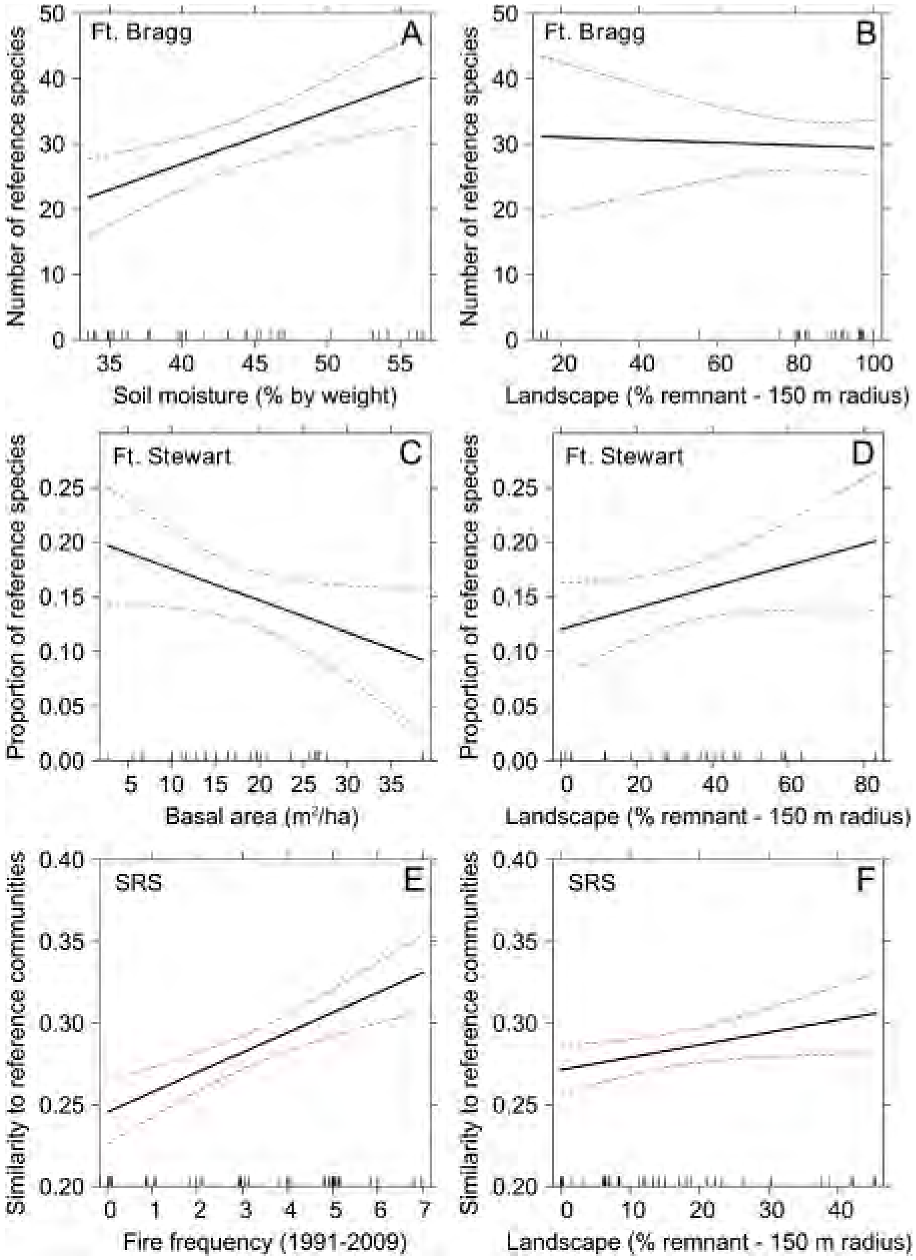

Figure 3.4.2. Partial regression plots depicting the influence of local variables and landscape context on plant community recovery on post-agricultural sites. (A-B) Effects of soil moisture and surrounding landscapes on the number of reference species at Ft. Bragg (n = 29; model: [number of reference species] ~ [soil moisture] + [landscape context]. (C-D) Effect of basal area and landscapes on the proportion of reference species at Ft. Stewart (n = 24; model: [proportion of reference species] ~ [basal area] + [landscape context] + [basal area * landscape]). (E-F) Effect of fire frequency and landscape on compositional similarity to reference plant communities at SRS (n = 41, model: [proportion of reference species] ~ [fire frequency] + [basal area] + [landscape context]). Solid black lines represent the partial effect, accounting for the other model terms. Red dashed lines represent the 95% confidence envelope for the partial effect. The hash marks along the x-axis are the predictor values for each study site.

Table 3.4.3. Model averaging for number of reference species on post-agricultural sites. Landscape represents the percent of remnant area within a 150m radius. Candidate models included main effects and all 2-way interactions. Averages are from models within 2 ΔAICc of the top model.

Location	Parameter	Relative Importance	Effect Size	SE	95% CI	95% CI	p>|z|
FTB:	(Intercept)		0.00	0.08	-0.16	0.16	1.000
	Soil moisture	1.00	0.60	0.18	0.24	0.96	0.001
	Basal area	0.41	-0.24	0.18	-0.60	0.12	0.199
FTS:	(Intercept)		0.00	0.08	-0.17	0.17	0.986
	Basal area	1.00	-0.34	0.20	-0.75	0.06	0.105
	Fire frequency	0.67	0.40	0.21	-0.02	0.81	0.068
	Basal area:Fire frequency	0.44	-0.93	0.45	-1.83	-0.03	0.053
	Landscape	0.60	0.33	0.19	-0.05	0.70	0.100
	Basal area:Landscape	0.12	-0.51	0.39	-1.29	0.26	0.214
SRS:	(Intercept)		0.00	0.06	-0.12	0.12	1.000
	Fire frequency	1.00	0.64	0.13	0.38	0.90	0.000
	Basal area	0.43	-0.18	0.13	-0.44	0.08	0.192

Table 3.4.4. Model selection for number of reference species on post-agricultural sites. Landscape represents the percent of remnant area within a 150m radius. Candidate models included main effects and all 2-way interactions.

Location	Top models (ΔAICc < 2):	df	ΔAICc
FTB:			
	Soil moisture	3	0.00
	Soil moisture + Basal area	4	0.75
FTS:			
	Basal area + Fire frequency + Basal area:Fire frequency	5	0
	Basal area + Landscape	4	0.54
	Basal area + Fire frequency + Landscape + Basal area:Fire frequency	6	1.19
	Basal area + Fire frequency	4	1.70
	Basal area + Fire frequency + Landscape + Basal area:Landscape	5	1.76
	Basal area + Fire frequency + Landscape	5	1.98
SRS:			
	Fire frequency	3	0.00
	Fire frequency + Basal area	4	0.55

Table 3.4.5. Model averaging for compositional similarity to reference communities of post-agricultural sites. Landscape represents the percent of remnant area within a 150m radius. Main effects and all possible 2-way interactions were included in candidate models. Averages are from models within ΔAICc < 2 of the top model.

Location	Parameter	Relative Importance	Effect Size	SE	Lower 95% CI	Upper 95% CI	p>|z|
FTB:							
	(Intercept)		0.03	0.10	-0.18	0.23	0.806
	Soil moisture	0.75	0.34	0.19	-0.03	0.72	0.081
	Basal area	0.27	0.12	0.22	-0.31	0.56	0.598
	Basal area:Soil moisture	0.27	-0.82	0.41	-1.64	-0.01	0.054
FTS:							
	(Intercept)		0.00	0.09	-0.18	0.18	0.991
	Fire frequency	1.00	0.50	0.19	0.13	0.88	0.014
	Soil moisture	0.25	-0.20	0.18	-0.57	0.16	0.419
	Basal area	0.62	-0.27	0.20	-0.66	0.12	0.198
	Fire frequency:Basal area	0.19	-0.67	0.47	-1.61	0.27	0.184
SRS:							
	(Intercept)		0.01	0.06	-0.11	0.12	0.911
	Fire frequency	1.00	0.58	0.13	0.32	0.83	0.000
	Landscape	0.90	0.24	0.11	0.02	0.47	0.037
	Basal area	0.83	-0.22	0.13	-0.48	0.03	0.086
	Fire frequency:Landscape	0.17	-0.34	0.27	-0.88	0.20	0.218
	Basal area:Landscape	0.15	0.32	0.26	-0.21	0.84	0.244
	Basal area:Fire frequency	0.15	0.29	0.24	-0.19	0.77	0.246

Table 3.4.6. Model selection for compositional similarity to reference communities on post-agricultural sites. Landscape represents the percent of remnant area within a 150m radius. Main effects and all possible 2-way interactions were included in candidate models.

Location	Top models (ΔAICc < 2):	df	ΔAICc
FTB:			
	Soil moisture	3	0.00
	Soil moisture + Basal area + Basal area:Soil moisture	5	1.15
	(Intercept only)	2	1.33
FTS:			
	Fire frequency + Basal area	4	0.00
	Fire frequency	3	0.25
	Fire frequency + Basal area + Fire frequency:Basal area	5	0.88
	Fire frequency + Basal area + Soil moisture	5	1.59
	Fire frequency + Soil moisture	4	1.94
SRS:			
	Fire frequency + Landscape + Basal area	5	0.00
	Fire frequency + Landscape	4	0.93
	Fire frequency + Landscape + Basal area + Fire frequency:Landscape	6	0.94
	Fire frequency + Landscape + Basal area + Landscape:Basal area	6	1.13
	Fire frequency + Landscape + Basal area + Fire frequency:Basal area	6	1.15
	Fire frequency + Basal area	4	1.85

Table 3.4.7. Model averaging for species richness on post-agricultural sites. Landscape represents the percent of remnant area within a 150m radius. Main effects and all possible 2-way interactions were included in candidate models. Averages are from models within ΔAICc < 2 of the top model.

Location	Parameter	Relative Importance	Effect Size	SE	95% CI	95% CI	p>|z|
FTB:							
	(Intercept)		0.00	0.08	-0.17	0.17	1.000
	Soil moisture	1.00	0.52	0.20	0.11	0.92	0.015
	Basal area	0.63	-0.36	0.19	-0.74	0.02	0.071
FTS:							
	(Intercept)		0.00	0.10	-0.19	0.19	0.995
	Basal area	0.73	-0.37	0.20	-0.77	0.04	0.084
	Fire frequency	0.61	0.35	0.20	-0.05	0.75	0.094
	Basal area:Fire frequency	0.15	-0.62	0.50	-1.61	0.38	0.245
SRS:							
	(Intercept)		0.00	0.10	-0.20	0.20	1.000
	Fire frequency	1.00	0.60	0.11	0.37	0.82	<0.001
	Basal area	1.00	-0.31	0.11	-0.53	-0.08	0.009

Table 3.4.8. Model selection for species richness on post-agricultural sites. Landscape represents the percent of remnant area within a 150m radius. Main effects and all possible 2-way interactions were included in candidate models.

Location	Top models (ΔAICc < 2):	df	ΔAICc
FTB:			
	Soil moisture + Basal area	4	0.00
	Soil moisture	3	1.03
FTS:			
	Basal area + Fire frequency	4	0.00
	Basal area	3	0.41
	Basal area + Fire frequency + Basal area:Fire frequency	5	1.46
	(Intercept only)	2	1.73
	Fire frequency	3	1.76
SRS:			
	Fire frequency + Basal area	4	0.00

Table 3.4.9. Model averaging for proportion of reference species on post-agricultural sites. Landscape represents the percent of remnant area within a 150m radius. Main effects and all possible 2-way interactions were included in candidate models. Averages are from models within ΔAICc < 2 of the top model.

Location	Parameter	Relative Importance	Effect Size	SE	95% CI	95% CI	p>|z|
FTB:							
	(Intercept)		0.02	0.09	-0.15	0.19	0.838
	Soil moisture	1.00	0.48	0.18	0.12	0.85	0.011
	Basal area	0.44	0.29	0.20	-0.11	0.69	0.160
	Basal area:Soil moisture	0.08	-0.59	0.36	-1.31	0.14	0.122
FTS:							
	(Intercept)		0.00	0.09	-0.18	0.17	0.981
	Basal area	0.83	-0.33	0.19	-0.72	0.06	0.105
	Landscape	0.76	0.36	0.18	-0.01	0.73	0.066
	Soil moisture	0.52	-0.31	0.18	-0.67	0.06	0.115
	Basal area:Landscape	0.27	-0.66	0.40	-1.45	0.14	0.119
	Fire frequency	0.15	0.40	0.19	0.02	0.78	0.047
	Basal area:Fire frequency	0.15	-0.95	0.47	-1.89	0.00	0.060
SRS:							
	(Intercept)		0.00	0.08	-0.16	0.16	1.000
	Soil moisture	0.42	-0.24	0.16	-0.55	0.08	0.145
	Landscape	0.24	0.12	0.16	-0.20	0.44	0.476
	Fire frequency	0.16	0.15	0.16	-0.16	0.47	0.343

Table 3.4.10. Model selection for proportion of reference species on post-agricultural sites. Landscape represents the percent of remnant area within a 150m radius. Main effects and all possible 2-way interactions were included in candidate models.

Location	Top models (ΔAICc < 2):	df	ΔAICc
FTB:			
	Soil moisture	3	0.00
	Soil moisture + Basal area	4	1.03
	Soil moisture + Basal area + Soil moisture:Basal area	5	1.03
FTS:			
	Basal area + Landscape + Basal area:Landscape	5	0.00
	Basal area + Landscape + Soil moisture	5	0.11
	Basal area + Landscape	4	0.48
	Basal area + Landscape + Soil moisture + Basal Area:Landscape	6	1.31
	Landscape	3	1.34
	Basal area + Soil Moisture	4	1.47
	Basal area + Soil Moisture + Fire frequency + Basal area:Fire frequency	6	1.50
	Landscape + Soil Moisture	4	1.61
	Basal area + Fire frequency + Basal area:Fire frequency	5	1.90
SRS:			
	(Intercept only)	2	0.00
	Soil moisture	3	0.11
	Fire frequency	3	1.34
	Landscape + Soil Moisture	4	1.80
	Landscape	3	1.92

3.4.4 Discussion

On former agricultural fields in the southeastern United States, proximity to land that was never cultivated has little influence on the recovery of plant species that are indicative of reference conditions, but can contribute to the re-establishment of common understory plant species. Our study, 58-90 years after agriculture was abandoned, shows that remnant habitat within a 150 m radius of recovering agricultural land was not an important predictor of the number of reference species, species richness, or the proportion of reference species. Instead, local factors, including: fire frequency, tree basal area, and soil moisture holding capacity, are the best predictors of these metrics of plant community recovery. Landscape context does appear to be important to the recovery of common plant species: at our most degraded study location, SRS, the similarity between recovering and reference communities is positively related to the proportion of remnant habitat surrounding recovering sites. Our results suggest that landscape context has different influences on common species versus the species most associated with reference plant communities. Our analyses confirm that local biophysical factors (e.g., fire frequency, tree basal area, soil moisture) are always important to plant community recovery.

In a variety of ecosystems, there are substantial time lags (e.g., decades to centuries) between agricultural land abandonment and re-colonization by species of conservation interest. As a result, landscape effects on local plant community recovery may not be detectable over short time periods (e.g., 3-7 yr, Grman et al. 2013) or even after many decades (this study). In temperate forests recovering from agriculture, proximity to old-growth forests has a positive influence on plant re-colonization rates, but plant communities indicative of old growth may require at least 200-350 years to re-assemble (Verheyen et al. 2003, Matlack 2005). In calcareous grasslands in the UK, legacies of past agricultural land use persist for at least 100 years, even in landscapes supporting remnant grasslands (Redhead et al.2014). In subtropical grasslands of southern Africa, ruderal species typical of secondary grasslands are quick to colonize former pine plantations, but species with high affinities for remnant grasslands are absent for at least two decades and probably much longer (Zaloumis and Bond 2011). In pine savannas of the southeastern USA, plant communities on post-agricultural land are missing remnant species for many decades to a century, even when in close proximity to remnant savannas (Appendix 1, Kirkman et al. 2004, Ostertag and Robertson 2006, Brudvig et al. 2013, 2014). Our present work confirms that landscapes surrounding recovering pine savannas contribute propagules of common species, but that many reference species remain absent for at least 58-90 years. Of reference species in this study: 40 of 119 (34%), 47 of 74 (64%), and 31 of 55 (56%) occurred at <10% of post-agricultural sites at Ft. Bragg, Ft. Stewart, and SRS, respectively. Our results confirm that for a large number of species at each study location, efforts to restore plant communities on time-scales less than several decades will require seeding or transplants (Walker and Silletti 2006), but that for a substantial subset of species, recovery can be achieved through unassisted dispersal and establishment from seed sources in surrounding landscapes.

For passive recovery of common species or seeding of reference species to be successful, local conditions must be considered. In our analyses, low tree basal area and high fire frequency were important to all metrics of plant community recovery at Ft. Stewart and SRS. At Ft. Bragg, where sites are burned every 3 years and little variation in fire frequency exists, soil moisture and basal area emerge as the best predictors of plant community recovery. Of these local factors, soil moisture is not easily changed through management, but tree thinning and prescribed fire are common methods for promoting recovery (e.g., Provencher et al. 2001, Harrington 2011). Note that mechanical (e.g., chainsaws or bulldozers) or chemical (e.g., herbicide) control of tree basal area should not target pyrophytic savanna oaks (e.g., *Quercus laevis*), which are a natural part of the longleaf pine ecosystem, are uncommon on recovering agricultural land, and provide food and habitat for longleaf fauna (Hiers et al. 2014).

It is perhaps not surprising that the importance of landscape context in a disturbance-dependent ecosystem, like the savannas in this study, appears to be relatively small compared to local factors that are known to influence seed establishment and survival. Frequent fires improve establishment opportunities by stimulating flowering, consuming leaf litter and duff, exposing mineral soil, and top-killing dominant competitors (e.g., Myers and Harms 2009, Lamont and Downes 2011). Soil moisture availability is also critical to seed germination and seedling survival (Iacona et al. 2010). As such, landscape contributions to local plant communities should only matter when local conditions are suitable for seedling establishment and growth. The candidate models in our analyses include such local-by-landscape interactions, but they are not predictive of local plant community recovery. This may be due to co-linearity between our landscape and fire frequency variables, which might occur if prescribed burning activities are targeted toward portions of a landscape harboring more remnant habitat. For example at Ft. Stewart, the landscape term appears in top models predicting the proportion of reference species, but never in the same models as fire frequency (Table 3.4.10). Weak correlations between land-use history and fire frequency do exist in this dataset (Veldman et al. 2014) suggesting that experimental methods, rather than observational data, are ultimately needed to solidify our understanding of the relationships between land-use history, landscape context, prescribed fire management, and local community recovery. Nonetheless, the absence of a clear role of landscapes in predicting plant community recovery in our models confirms that pine savanna recovery will often need to involve seeding and/or transplants (e.g., Walker and Silletti 2006). The weak role of landscapes in this study suggests that compared to forest ecosystems (e.g., Verheyen et al. 2003, Matlack 2005), recovery of fire-dependent savanna plant communities may depend far more on local conditions rather than landscape context, consistent with the hypotheses that many fire-adapted savanna understory species are poor colonizers (Kirkman et al. 2004, Zaloumis and Bond 2011). Another plausible explanation for the limited role of landscapes in this study, is that widespread plant community degradation, due to historic fire suppression and cattle grazing, may limit the ability of landscapes to contribute propagules for local plant community recovery (Hoctor et al. 2006).

3.4.5 Conclusion

This study sought to determine if the landscapes surrounding recovery sites should be considered as a potential source of plant propagules when land managers plan plant community recovery efforts in a fire-dependent ecosystem. Our method for quantifying landscape context (i.e., the amount of remnant habitat within 150 m of a site) relied on historic maps and aerial photos. This information is qualitatively similar to the sorts of remotely sensed information that is often used when prioritizing recovery activities across large spatial scales, like the federal government installations in this study, and may be used to determine the pool of species that will need to be reintroduced during recovery efforts. On post-agricultural sites in close proximity to savanna remnants, only species that are very poor colonizers will need to be introduced. In contrast, recovery of sites in landscapes with very little remnant habitat may require a much larger pool of species to be introduced. Regardless of landscape context, frequent prescribed fire and wildfire are essential to restoring and maintaining longleaf pine plant communities at both local and landscape scales.

3.5 CONTROLS OF LOCAL UNDERSTORY DIVERSITY. II: LOCAL FACTORS

[This section contains material from Veldman, J.W., L.A. Brudvig, E.I. Damschen, J.L. Orrock, W.B. Mattingly, and J.L. Walker. 2014. Fire frequency, agricultural history, and the multivariate control of pine savanna understory plant diversity. *Journal of Vegetation Science* 25:1438-1449.]

3.5.1 Introduction

Altered fire regimes and agricultural conversion are two pervasive forms of human-induced environmental change (Foster et al. 2003). Agriculture can impose dramatic and persistent changes to ecosystems, including losses to biodiversity (Flinn and Vellend 2005). When plant communities are eliminated by intensive agriculture, it can take centuries or longer for locally extinct species to recolonize (Turner et al. 1997, Verheyen et al. 2003). The mechanisms by which past agricultural land use continues to influence contemporary species diversity are not fully understood, but are likely to involve multiple biophysical factors (e.g. altered soils and vegetation structure, or dispersal limitation) that determine plant community diversity and composition (Flinn and Vellend 2005, Verheyen et al. 2006, Cramer et al. 2008). The lasting effects of agriculture are particularly pronounced in understory plant communities of woodlands, savannas, and grasslands (e.g. Ostertag and Robertson 2006) where plant species have evolved life-history strategies to survive periodic natural disturbances, including frequent surface fires (Kirkman et al. 2004, Zaloumis and Bond 2011).

Altered fire regimes, including changes in frequency, intensity, or seasonality of fires, pose a global threat to biodiversity that often coincide with agricultural land uses. Human colonization and land clearing along agricultural frontiers are initially associated with increased fire frequencies that are catastrophic for forest ecosystems composed of fire-intolerant species (e.g. Nepstad et al. 2001). In contrast, agricultural expansion in fire-dependent ecosystems can incentivize fire exclusion (e.g. Frost 1993). Biodiversity losses from fire exclusion are particularly severe in ecosystems where frequent fires are required to limit tree abundance, prevent forest succession, and promote understory plant diversity (Rogers et al. 2008, Noss 2013). Recognition of the complex relationships between understory plants, trees, fire, and resource gradients that are characteristic of savannas (e.g. Hoffmann et al. 2012) calls for a multivariate approach to studying plant diversity in these systems (Weiher 2003, Veldman et al. 2013).

Distinct from treeless grasslands and closed-canopy forests, a defining characteristic of savanna ecosystems is the coexistence of scattered trees and understory plants. Fire and the availability of limiting resources (e.g. precipitation, soil nutrients) are key determinants of vegetation structure (i.e. tree and understory abundance) and savanna distributions from local to continental scales. In “mesic savannas” (*sensu* Lehmann et al. 2011), where resources are sufficient to support forest development, frequent fires are required to limit tree abundances that can otherwise constrain fine fuel production by the understory and reduce ecosystem flammability (Hoffman et al. 2012). In addition to fueling fires, savanna understory plant communities often support species-rich assemblages of graminoids, forbs, and shrubs of high conservation value (Ratter 1997, Sankaran 2008, Bond and Parr 2010). As such, we should expect the determinants of savanna vegetation structure to be integral to understanding relationships between fire, land use, and understory plant diversity (Fig. 3.5.1).

In many ecological systems, including savannas, it can be challenging to understand the controls over species diversity because of complex relationships that exist among organisms and their environments. Contributing to this complexity is the potential for indirect effects (i.e. relationships that are influenced by one or more intermediaries; Grace 2006). Indirect effects are widespread in natural systems, and studies of the roles of indirect effects have informed our thinking about food webs (e.g. Estes et al. 2011), species diversity (e.g. Harrison et al. 2008), and vegetation structure (e.g. Van Langevelde et al. 2003). Because of the prevalence of indirect effects, analyses of simple bivariate relationships are often insufficient for understanding ecological systems and their biological diversity (Grace et al. 2012). Indeed, analytical frameworks such as structural equation modeling (SEM) that incorporate direct and indirect relationships among multiple biotic and abiotic factors are proving useful for understanding species diversity in a variety of systems (e.g. Weiher 2003, Grace et al. 2011, Stomp et al. 2011).

In this study, we use SEM to determine how fire frequency and agricultural land-use history influence local-scale understory plant species richness in pine savannas of the southeastern USA. Specifically, we investigate how six factors (fire frequency, agricultural history, resource availability, tree abundance, understory plant abundance, and the O horizon) directly and indirectly influence species richness. We begin by developing a multivariate conceptual model, based on previous work in pine savannas and current theory regarding savanna vegetation globally, of how these factors affect each other and influence understory species richness (Fig. 3.5.1). We then assess these hypothesized relationships using a large-scale vegetation dataset from 256 sites at three locations that span broad environmental gradients (Table 3.5.1), including gradients in prescribed fire frequency (from frequently-burned to fire-excluded from 1991 to 2009). We include sites on former agricultural land (fields abandoned for 60-90 yr) as well as remnant savannas with no evidence of past cultivation. This is the first broad-scale investigation of how fire and agricultural legacies directly and indirectly (through influences on additional factors) control savanna plant diversity in a model study system. Our results provide a conceptual framework that may be tested in other mesic savannas around the world, and provide insight into the future of other fire-dependent ecosystems that are currently experiencing widespread agricultural conversion and fire exclusion.

3.5.2 Methods

Study system

We carried out this study in savannas and woodlands (hereafter “savannas”, (Glitzenstein et al. 1995, Ratnam et al. 2011) within the longleaf pine (*Pinus palustris*) ecosystem of the southeastern USA. This ecosystem is characterized by scattered pine trees and species-diverse understory plant communities (Peet 2006). Frequently-burned pine savannas with high moisture availability are among the most species-rich ecosystems in North America, supporting up to 35 species m^{-2} (Walker and Peet 1984). Like many of the world’s savannas (Bond and Parr 2010), this high understory plant diversity includes not just grasses (i.e. Poaceae) but a mixture of graminoid, forb, and shrub species. Savannas have probably existed in parts of the southeastern

USA throughout the past 2.6 million years resulting in many endemic fire-adapted species (see discussion by Noss 2013 and references therein).

Pine savannas are a model ecosystem for studying mesic savannas in fragmented agricultural landscapes. We specify "mesic" because the subtropical climate, mild seasonality, and ample precipitation of the region can support either savannas of C_4 graminoids or forests of fire-intolerant tree species, depending on the fire regime (Heyward 1938, Beckage and Stout 2000). Pine savannas once covered much of the southeastern USA but have been reduced to ~3% of their original area due to the combined effects of fire suppression, logging, resin extraction, agricultural and silvicultural conversion, and urbanization (Frost 1993). Given this regional land-use history, studies of the ecology, conservation and recovery of pine savannas may offer insight into the future of other mesic savannas that are currently undergoing rapid agricultural conversion (e.g. Ratter 1997, Klink and Machado 2005).

Table 3.5.1. Summary of observed variables included in the structural equation model.

Variables (units)	**Mean**	**Median**	**Range**
Understory plant species richness (species.m^{-2})	5.6	4.9	0.1 - 17.9
Fire frequency (number of fires 1991-2009)	4.7	5	0 - 17
Litter depth (cm)	2.2	1.5	0.1 – 7.7
Duff depth (cm)	0.9	0.3	0 – 5.2
Total understory cover (total %)	64	54	1 - 225
Tree basal area (m^2.ha^{-1})	18	17	2.7 – 49
Tree canopy cover (%)	56	56	30 - 78
Soil moisture holding capacity (% by mass)	40	39	28 - 57
Soil organic matter (% by mass)	1.9	1.6	0.7 – 5.6
Cation exchange capacity (mEq.$100g^{-1}$)	2.2	2	0.4 – 6.9
Agricultural history	97 post-agricultural, 159 remnant sites		

Meta-model development

An important part of SEM is meta-model development, the *a priori* conceptual framework that provides the basis for the statistical model (Grace et al. 2010). We based our SEM on a meta-model that depicts hypothesized relationships among factors that are thought to influence species richness in savannas (Appendix S1), with a specific emphasis on fire frequency and agricultural land-use history (Figure 3.5.2). We began with a simple framework derived from current ecological theory of savanna vegetation structure, in which tree abundance and understory abundance are a function of fire frequency and resource availability. Similar frameworks have proven to be relevant at both global (Staver et al. 2011) and local scales (Hoffmann et al. 2012), and thus provide a starting point to link fire frequency and agricultural land-use history to patterns of species richness via effects on vegetation structure. We incorporated agricultural history into the model based largely on mechanisms documented in forest ecosystems, because agricultural history has rarely been considered in studies of savanna plant diversity. We also included the O horizon (litter and duff depth), a factor that is often neglected in plant community studies (Fridley et al. 2012), but that can be important in fire-dependant ecosystems, particularly in the context of fire exclusion (Varner et al. 2005, Hiers et al. 2007). Below, we briefly describe the theoretical basis for each of the hypothesized paths in the meta-model. Hypotheses H_{1-16} correspond to the path numbers in Figure 3.5.1.

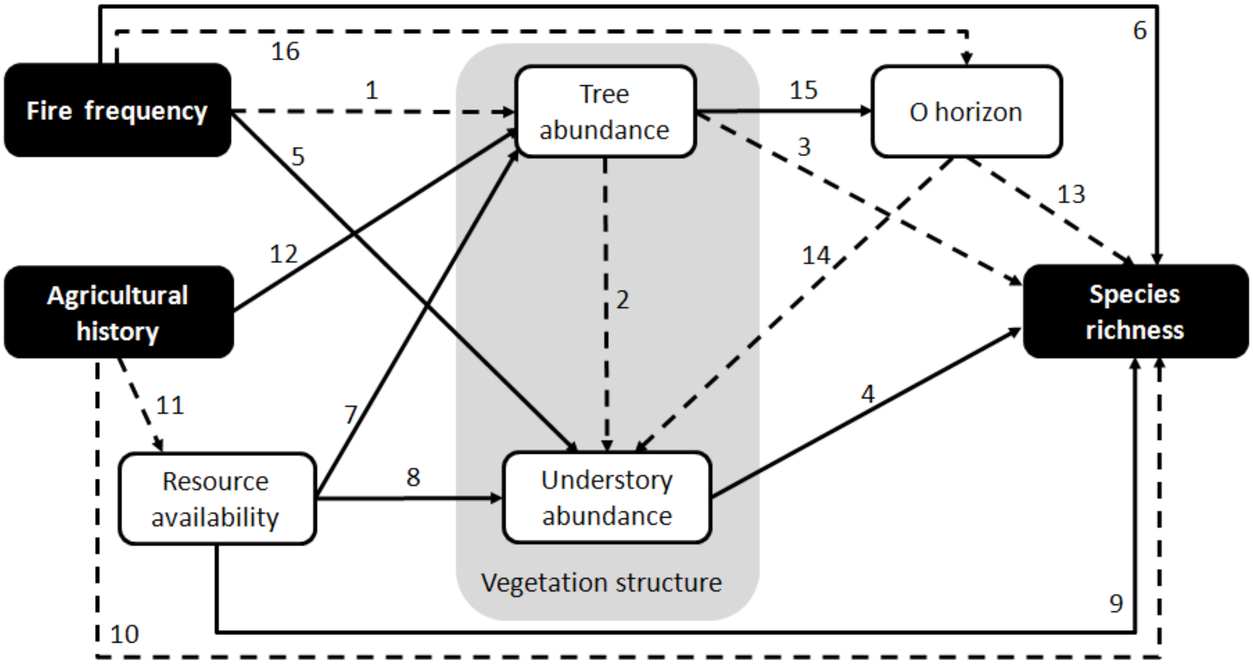

Figure 3.5.1. The meta-model that guided the structural equation modeling. Rounded boxes represent system components (i.e. measurable variables, conceptual factors, and theoretical constructs). Arrows indicate the hypothesized direction of influence, with positive and negative relationships represented by solid and dashed lines, respectively. Black shading denotes the components of primary interest whose relationships are thought to be mediated by other system components (in white). Path numbers correspond to the hypotheses in Appendix S1. In this framework, fire frequency and agricultural history are hypothesized to effect species richness by influencing vegetation structure (i.e. the balance between tree and understory plant abundance; gray shading) and through alternative pathways that involve resource availability, the O horizon, and direct (unmediated) effects.

H_1: *Fire limits tree abundance.* In a variety of systems, fire imposes a critical demographic bottleneck on trees (e.g. (Fenshm 1990). In pine savannas, fire topkills fire-sensitive tree species (Beckage and Stout 2000), limits the recruitment of fire-tolerant trees into large size classes (Glitzenstein et al. 1995), and causes crown scorch that reduces tree growth and canopy cover (Hoffmann et al. 2009).

H_2: *High tree abundance reduces understory plant abundance.* The negative effect of trees on understory productivity is well established for savannas (e.g. Scholes and Archer 1997) and has been experimentally demonstrated in pine savannas of the southeastern USA (Grelen et al. 1973, Harrington 2011).

H_3: *High tree abundance reduces understory species richness.* High tree abundance is associated with reduced understory species richness in a variety of systems (e.g. (Peterson and Reich 2001, Rogers et al. 2008, Grace et al. 2011, Ratajczak et al. 2012), and has been experimentally demonstrated in pine savannas of the southeastern USA (Platt et al. 2009, Harrington 2011).

H_4: *Understory abundance has a positive effect on species richness.* Understory abundance should be positively linked to species richness if "abundance" (total cover) acts in a similar manner as "number of individuals", which is probabilistically linked to the number of species present in a given area (Weiher 2003, Grace et al. 2011).

H_5: *Fire promotes understory plant abundance.* Frequent fires are associated with high understory productivity in savannas (Scholes and Archer 1997), including pine savannas (Walker and Peet 1984, Kirkman et al. 2004). Increased understory abundance may result from fire-stimulated clonal growth of forbs (Brewer and Platt 1994) and resprouting in shrubs (Drewa et al. 2002).

H_6: *Fire promotes richness through other processes (modeled as direct effects).* Potential mechanisms include: fire-stimulated reproduction and fire-mediated competitive interactions within the understory (Brewer and Platt 1994, Brewer et al. 2008, Myers and Harms 2009).

H_7: *Resource availability increases tree abundances.* The availability of limiting resources influences tree growth and survival by determining how quickly trees can recover from topkill and reach fire-tolerant sizes (Hoffmann et al. 2012). In the southeastern USA, soil moisture, texture, and cation exchange capacity influence tree species distributions and abundances (Heyward 1938, Monk 1968, Goebel et al. 2001). In particular, moisture availability interacts with fire to determine tree abundances and distributions (Grady and Hoffmann 2012). Additionally, fertilization experiments show that the growth of pines and broadleaf trees can increase in response to additions of Ca, N, and P (Haywood 2010, Hu et al. 2012).

H_8: *Resource availability increases understory abundance.* In frequently-burnt pine savannas, water availability is a strong predictor of understory productivity (Kirkman et al. 2001).

H_9: *Resource availability directly promotes richness.* Nutrient and moisture stress can exclude species from plant communities on low resource sites (Grime 1977).

H_{10}: *Agriculture has a direct negative effect on species richness.* In a variety of ecosystems (e.g. Verheyen et al. 2003, Flinn and Vellend 2005), including pine savannas (Hedman et al. 2000, Kirkman et al. 2004, Ostertag and Robertson 2006), agriculture directly eliminates species-diverse plant communities and it can take long periods of time for locally extinct species to recolonize.

H_{11}: *Agricultural history reduces resource availability.* Agricultural history is associated with reduced soil organic matter and plant available water in both temperate forest ecosystems (Flinn and Marks 2007) and pine savannas (Brudvig et al. 2013).

H_{12}: *Agricultural history leads to high tree abundance.* In pine savannas, abandoned agricultural fields are often colonized by (or planted with) high densities of pines and/or mesic forest trees (Heyward 1938), which can inhibit understory plants (Harrington 2011, Veldman et al. 2013).

H_{13}: *A deep O horizon reduces understory species richness.* The accumulation of litter and duff can act as a physical barrier to herbaceous plant establishment, growth, and light acquisition (Facelli 1991), and in pine savannas can lead to the exclusion of some understory plant species (Hiers et al. 2007).

H_{14}: *The O horizon limits understory plant abundance.* In pine savannas, litter accumulation is associated with fire suppression and reduced cover of understory grasses and forbs (Heyward 1938, Brockway and Lewis 1997, Hiers et al. 2007).

H_{15}: *Tree abundance contributes to O horizon development.* Trees produce litter that contributes to the depth of the O horizon (Hiers et al. 2007).

H_{16}: *Frequent fires prevent O horizon development.* By consuming litter and duff, fire limits the O horizon independent of the effects of fire on tree abundance (Hiers et al. 2007).

Field sampling

See Section 3.1 for a description of data collected. In particular, see Section 3.1.1 for a description of our study sites and our selection process, Section 3.1.2 for details on our vegetation sampling procedure, and Section 3.1.3 for an explanation of our categorization and analysis of the historical landscape context.

Statistical Analysis

Following data collection (Section 3.1), we used the meta-model as a guide (Figure 3.5.1) to develop a structural equation model comprised of 11 observed variables (Table 3.5.1) and four latent variables (resource availability, tree abundance, understory abundance, and O horizon).

Latent variables represent theoretical constructs that are not directly measured, but are inferred from measured (observed) variables. In our model, we specified the latent variables as combinations of one, two, or three indicator variables. We inferred: 1) resource availability from soil moisture holding capacity, SOM, and CEC (interrelated variables that are indicators of water, nitrogen, and cation availability, respectively); 2) tree abundance from basal area and canopy cover; 3) understory abundance from total percent plant cover; and, 4) the O horizon from litter and duff depth. Before fitting the model, we inspected univariate distributions and bivariate relationships in the data (Grace 2006). It is common in SEM to explore relationships between key model variables (e.g., Harrison et al. 2006); we performed select regressions using the lm function in R 2.15.1 (R Core Team 2012). To meet assumptions of linearity and to correct skew, we applied a $\log_{10}$ transformation to species richness and SOM. We fit the model in IBM SPPS Amos 20.0 (Amos Development Corporation, Meadville, Pennsylvania, USA). To improve overall fit, we modeled several correlations that are due to unknown causes (Grace 2006; Table 3.5.2). To achieve an analysis that encompassed a wide range of conditions and that spanned regional gradients in edaphic factors that influence plant species richness, we combined data from all three study locations (Veldman et al. 2013).

3.5.3 Results

In bivariate analyses, fire frequency is positively correlated with species richness (Figure 3.5.2a), and agricultural land-use history is associated with decreased richness (Figure 3.5.2b). In a multiple regression, the main effects of these two factors combine to explain 31% of variance in species richness ($R^2 = 0.31$, $F = 56.0$, $df = 2$ and 253, $P < 0.001$); additional factors are likely to be involved. Indeed, species richness is correlated with multiple variables related to resource availability (Figure 3.5.3a), tree abundance (Figure 3.5.3b), understory abundance (Figure 3.5.3c), and the O horizon (Figure 3.5.3d). We use SEM to disentangle these interrelated variables (Figure 3.5.4; Table 3.5.3).

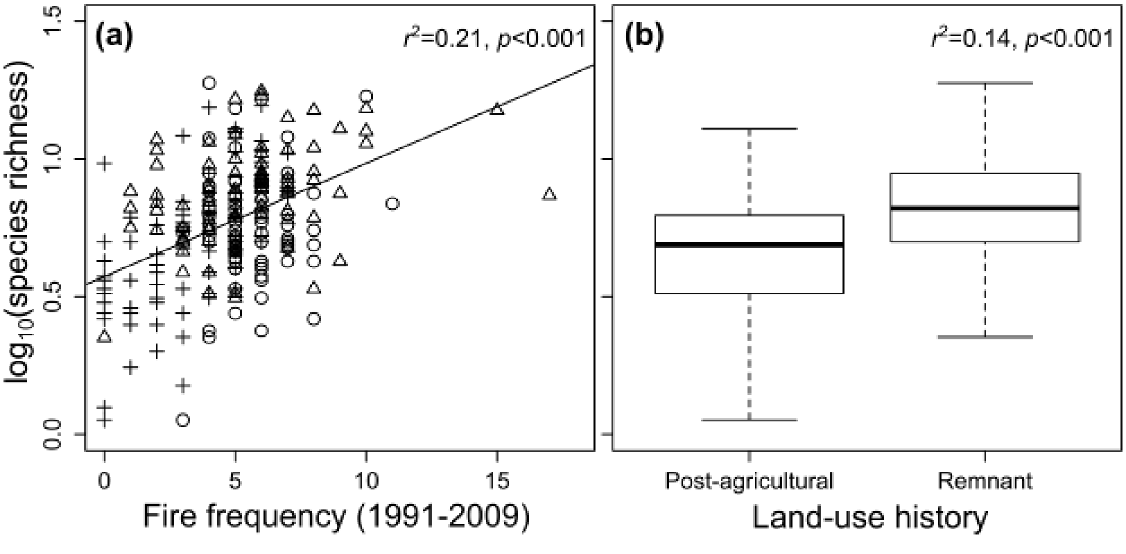

Figure 3.5.2. Species richness in relation to (a) fire frequency and (b) agricultural land-use history. Symbols correspond to study locations: Fort Bragg, ○; Fort Stewart, Δ; and Savannah River Site, +. The boxplots display quartiles.

The SEM provides a good fit to the data ($\chi^2 = 18.7$, $df = 23$, $p = 0.72$; saturated model ΔAIC = 17.3), and explains 65% of the variance in understory species richness ($R^2 = 0.65$; Figure 3.5.4). The model is a good predictor of the O horizon ($R^2 = 0.55$), and explains a significant fraction of the variance in tree abundance ($R^2 = 0.20$) and understory abundance ($R^2 = 0.21$). The model explains relatively little variation in resource availability ($R^2 = 0.07$). All modeled factors (i.e. fire frequency, agricultural history, resource availability, tree abundance, understory abundance and O horizon) contribute directly or indirectly to understory plant species richness (Table 3.5.2, Table 3.5.3, Figure 3.5.4). Thirteen of 16 hypothesized paths are statistically significant ($p<0.05$; Table 2), though the strength these relationships ranges widely (Figure 3.5.4, Table 3.5.3).

The SEM shows that bivariate patterns of species richness in relation to fire frequency and agricultural history can be largely explained through indirect effects. For fire frequency, 70% of the total positive effect on species richness is through reductions in the O horizon, and 30% through reductions in tree abundance (Table 3.5.5). There is no significant direct effect of fire frequency on species richness or understory abundance. Instead, fire frequency limits trees, which increases understory cover and species richness (Figure 3.5.4). Fire influences richness independent of vegetation structure (i.e. tree and understory abundance) by limiting the development of the O horizon, a factor with strong negative effects on richness (Table 3.5.3, Figure 3.5.4). For agricultural history, 51% of the total negative effect on species richness is explained through increased tree abundance, 10% through decreased resource availability, and 38% through direct negative effects (Table 3.5.3, Figure 3.5.4).

In addition to fire frequency and agricultural history, the model reveals the influences of other biophysical factors on species richness. The relationship between resource availability and species richness is complex, with both strongly positive effects and indirect negative effects due to increases in tree abundance (Table 3.5.3, Figure 3.5.4); when these contrasting effects are combined, the total effect of resource availability on richness is weakly positive (Table 3.5.3). Understory abundance, which is completely controlled by resource availability and tree abundance, is a strong predictor of species richness (Table 3.5.3, Figure 3.5.4). The O horizon, which was controlled by fire frequency and tree abundance, has a strong direct negative effect on richness (Table 3.5.3, Figure 3.5.4). Contrary to our hypotheses, there are no direct effects of fire frequency on understory abundance or richness, and no direct effect of the O horizon on understory abundance (Table 3.5.2, Figure 3.5.4).

Table 3.5.2. Summary of modeled correlations.

Correlated Variables			Coefficient	*S.E.*	*P*	Correlation
Fire frequency	↔	Agricultural history	-0.137	0.075	0.068	-0.115
(error) Soil moisture holding capacity	↔	(error) Duff depth	-0.809	0.231	< 0.001	-0.452
(error) Soil moisture holding capacity	↔	(error) Litter depth	-0.747	0.364	0.040	-0.229
(error) Soil moisture holding capacity	↔	(error) Tree canopy cover	8.263	2.370	< 0.001	0.369
(error) Cation exchange capacity	↔	(error) Duff depth	-0.078	0.042	0.068	-0.158
(error) Cation exchange capacity	↔	(error) Tree basal area	-1.025	0.358	0.004	-0.418
(error) Soil organic matter	↔	(error) Tree canopy cover	0.145	0.060	0.015	0.275
(error) Tree canopy cover	↔	(error) Litter Depth	1.635	0.411	< 0.001	0.320
(error) Litter depth	↔	(error) Understory abundance	6.316	2.726	0.021	0.188

Table 3.5.3. Unstandardized path coefficients for hypothesized causal relationships.

Response	Predictor	Coefficient	*S.E.*	*P*	95% C.I.	Hypothesis number
$\log_{10}$ (species richness)	Fire frequency	0.004	0.005	n.s.	-0.006 to 0.014	6
	Agricultural history	-0.051	0.020	0.010	-0.090 to -0.012	10
	Resource availability	0.008	0.002	<0.001	0.004 to 0.012	9
	Tree abundance	-0.005	0.002	0.002	-0.009 to -0.001	3
	Understory abundance	0.002	0.000	<0.001	0.002 to 0.002	4
	O horizon	-0.074	0.014	<0.001	-0.10 to -0.047	13
Understory abundance	Fire frequency	2.3	1.5	n.s.	-0.61 to 5.3	5
	Resource availability	1.3	0.57	0.025	0.16 to 2.4	8
	Tree abundance	-2.5	0.5	<0.001	-3.4 to -1.6	2
	O horizon	2.4	4.3	n.s.	-6.1 to 10.9	14
Tree Abundance	Fire frequency	-0.67	0.18	<0.001	-1.0 to -0.32	1
	Agricultural history	5.3	1.0	<0.001	3.4 to 7.2	12
	Resource availability	0.39	0.11	<0.001	0.18 to 0.61	7
Resource availability	Agricultural history	-2.6	0.7	<0.001	-4.0 to -1.3	11
O horizon	Fire frequency	-0.27	0.02	<0.001	-0.31 to -0.23	16
	Tree abundance	0.031	0.007	<0.001	0.017 to 0.045	15

Abbreviations: S.E., standard error; C.I., confidence interval; n.s., not significant.

Table 3.5.4. Direct, indirect, and total standardized effects on species richness.

Predictor	Pathway	Standardized effect
Fire frequency	direct	n.s.
	indirect through tree abundance	0.10
	indirect through understory abundance	n.s.
	indirect through O horizon	0.22
	total	0.32
Agricultural history	direct	-0.11
	indirect through tree abundance	-0.15
	indirect through resource availability	-0.03
	total	-0.30
Resource availability	direct	0.17
	indirect through tree abundance	-0.11
	indirect through abundance	0.06
	total	0.12
Tree Density	direct	-0.18
	indirect through understory abundance	-0.19
	indirect through O horizon	-0.08
	total	-0.44
Understory abundance	direct	0.44
O horizon	direct	-0.34
	indirect through understory abundance	n.s.

n.s., not significant

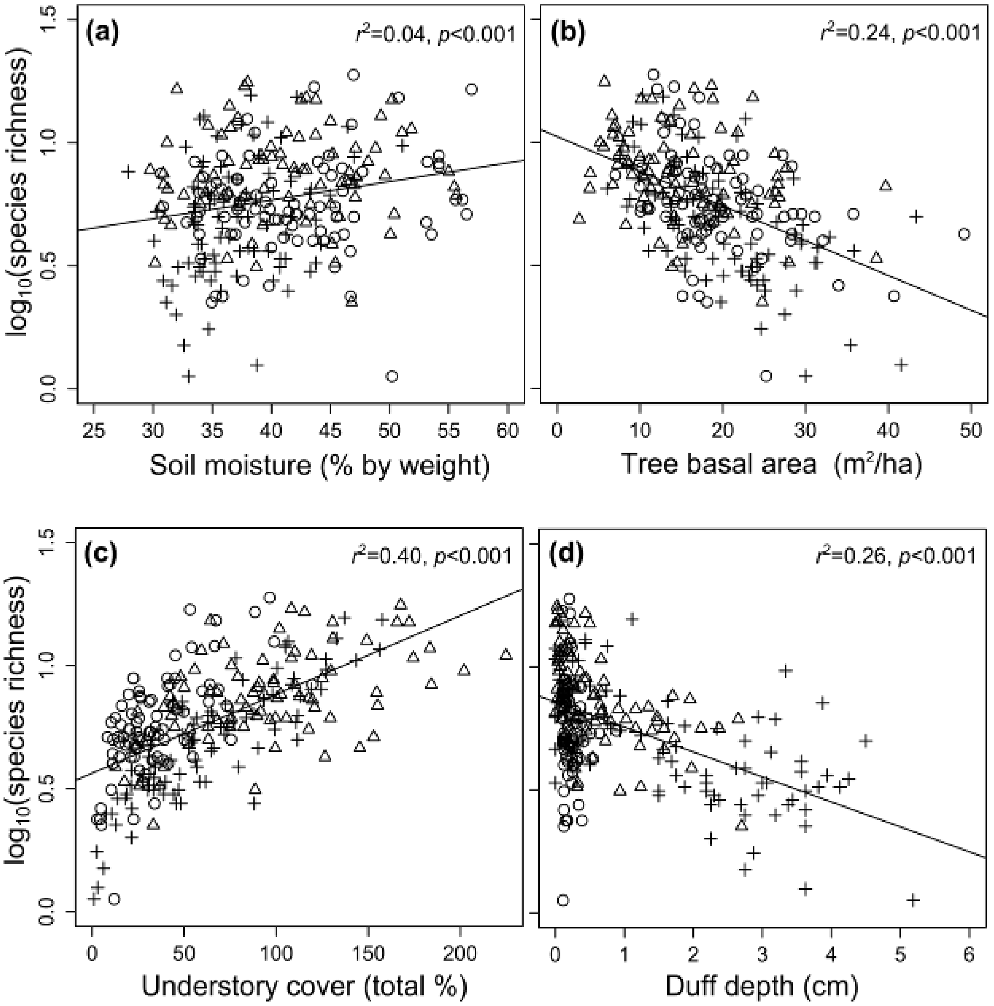

Figure 3.5.3. Bivariate scatter plots of species richness and select measured variables. In the SEM, (a) soil moisture holding capacity, (b) tree basal area, (c) understory plant cover, and (d) duff depth contribute to the latent variables: resource availability, tree abundance, understory abundance, and O horizon, respectively. Symbols correspond to study locations: Fort Bragg, ○; Fort Stewart, Δ; and Savannah River Site, +.

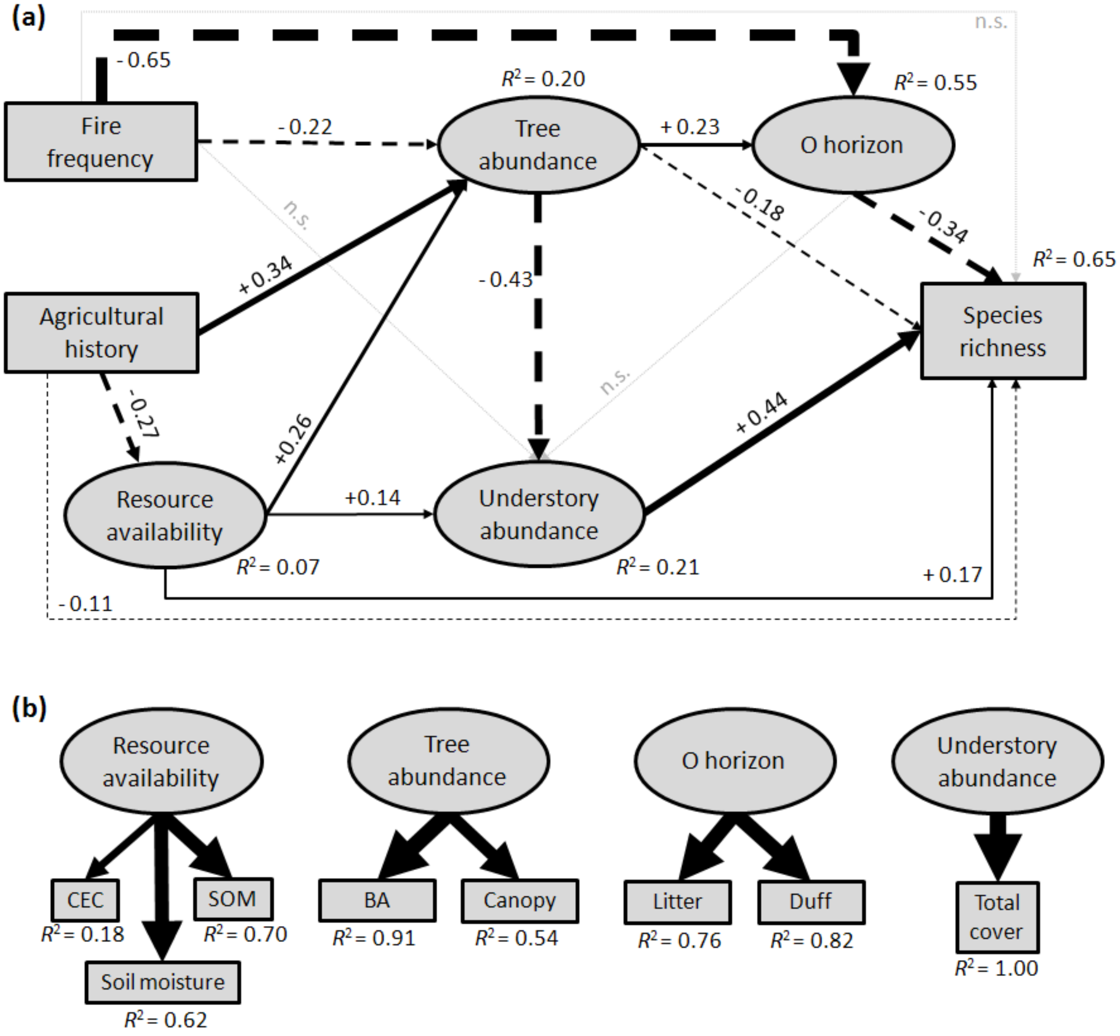

Figure 3.5.4. Results of the structural equation modeling: (a) path diagram of relationships among the main variables of interest, and (b) the structure of the latent variables. Rectangles represent observed (measured) variables; ovals represent latent (unmeasured) variables that are inferred from observed variables. Arrows indicate the hypothesized direction of influence, with positive and negative relationships indicated by solid and dashed lines, respectively. The thickness of each significant ($P < 0.05$) path is scaled to the strength of the correlation (i.e. the standardized effect); thin gray arrows indicate modeled (hypothesized) paths that were not significant. Abbreviations: CEC, cation exchange capacity; SOM, soil organic matter; BA, tree basal area; Canopy, tree canopy cover; n.s., not significant.

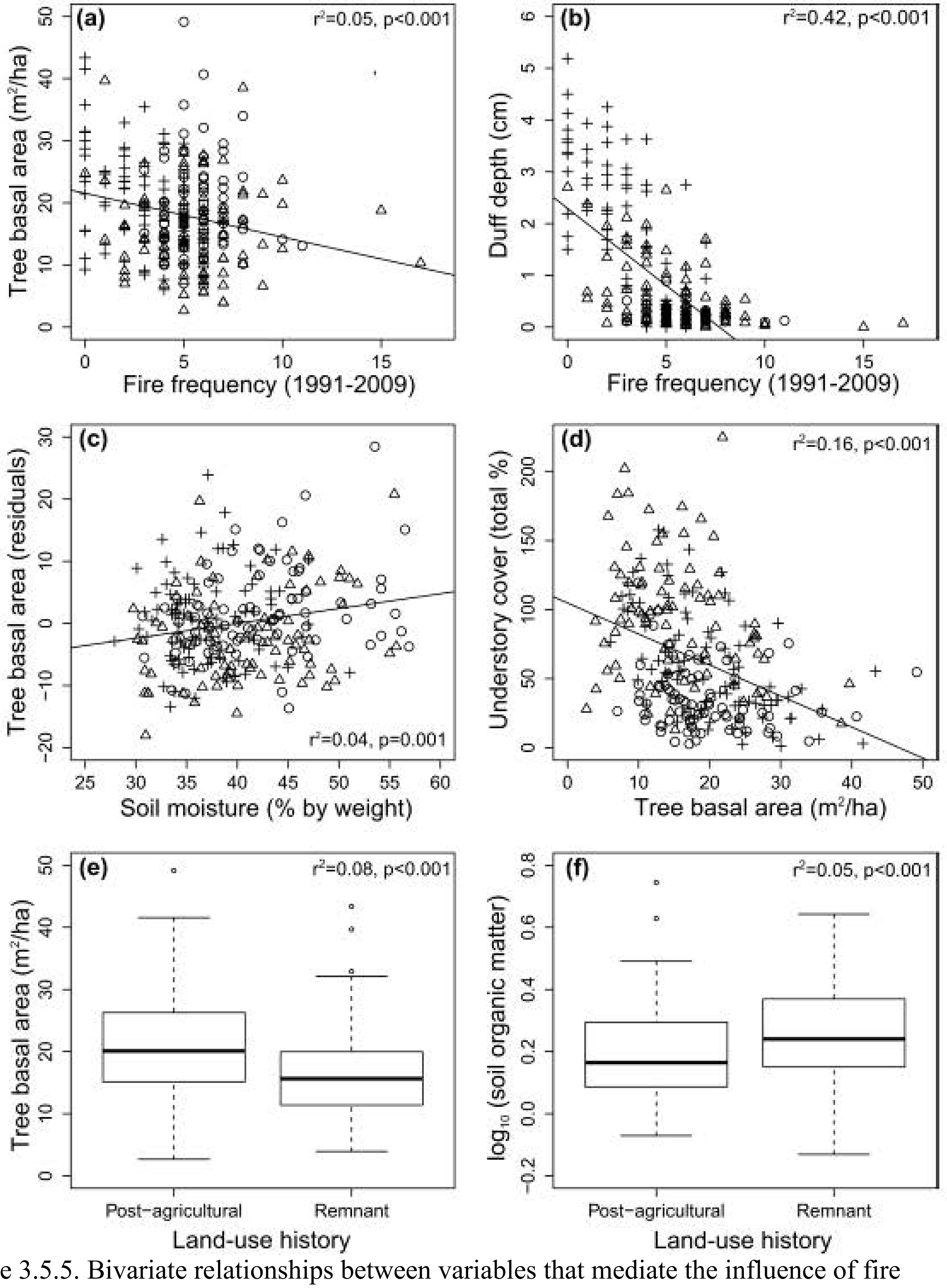

Figure 3.5.5. Bivariate relationships between variables that mediate the influence of fire frequency and agricultural history on species richness. Note that in (c) tree basal area is plotted as residuals from a linear model accounting for the main effects of fire and agricultural history. Symbols correspond to study locations: Fort Bragg, ○; Fort Stewart, Δ; and Savannah River Site, +.

3.5.4 Discussion

In pine savannas of the southeastern United States, fire exclusion and agricultural land-use history are associated with decreased understory plant species richness (Figure 3.3.1) (Walker and Silletti 2006). Our results provide mechanistic insight into these relationships by modeling direct and indirect effects among multiple factors that are thought to broadly influence plant diversity in savanna ecosystems, including: resource availability, tree abundance, understory abundance, and the O horizon. Our study presents the first model of its kind for savannas anywhere in the world. The SEM analytical framework enables us to explore the controls over savanna understory plant diversity in a way that would be difficult or impossible with other statistical approaches or manipulative experiments (Grace 2006). Our model incorporates indirect effects, includes many interrelated variables, uses data that covered wide biophysical gradients and a large geographic region, and includes information on site history that is not available for most study systems. The similarities between the fitted model and the *a priori* meta-model suggest that in combination, decades of fire research in pine savannas, ecological theory on grass-tree coexistence, and previous studies of agricultural legacies in a variety of systems have given us a good understanding of the factors that control understory plant species richness. Nonetheless, some unexpected results did emerge. We find no direct effect of fire frequency on either species richness or understory abundance; all positive effects of fire on the understory are mediated by tree abundance and the O horizon.

A history of agriculture is an important determinant of plant community composition and diversity in many ecosystems (e.g. Flinn and Vellend 2005), including pine savannas (Hedman et al. 2000, Kirkman et al. 2004). Our results suggest that post-agricultural sites have reduced species richness compared to savanna remnants for three reasons. First, intensive agriculture appears to constrain richness by depleting soil resource availability (Figure 3.5.4) (Flinn and Marks 2007). But because a reduction in resources can also constrain tree abundance, the overall effect of agricultural history on richness mediated by resource availability is modest (10% of the total effect, Table 3.5.3; see discussion on resource availability below). The consequences of altered biophysical conditions (e.g. reduced soil organic matter) on post-agricultural land can be quite different in savannas, where diversity is heavily influenced by tree-understory interactions, compared to grasslands and forests (e.g. Baer et al. 2003, Plue et al. 2008). Second, agricultural history reduces richness by increasing tree abundance. We suspect that this effect represents the legacy of post-agricultural tree community succession and historic fire exclusion (before 1991) not captured in our fire data. In the initial years following abandonment, old fields may have been less likely to burn compared to savanna remnants and thus developed dense stands including fire-intolerant tree species (Heyward 1938, Frost 1993) that inhibit the spread of fire (Kane et al. 2008, Kreye et al. 2013). Additionally, if old fields were preferentially managed for timber, fire suppression would have been incentivized (Frost 1993), resulting in high tree abundances and low species richness on post-agricultural sites. Such a relationship between historic land use and fire frequency may still be evident in contemporary prescribed fire management; we model a weak, marginally significant correlation between contemporary fire frequency and agricultural history (Table 3.5.2). The SEM accounts for this correlation, but the relationship needs further investigation. Finally, there is a direct negative effect of agricultural history on richness. Statistically, this direct effect represents covariance not explained through other model variables and, as such, does not reveal a specific mechanism. Nonetheless, we suspect that this direct negative effect represents a combination of dispersal limitation and successional time, influenced by the degree of spatial isolation of post-agricultural sites from savanna remnants (Kirkman et al. 2004, Brudvig and Damschen 2011). This hypothesis would be consistent with Verheyen and others (2003) who conclude that forest colonization by understory herbs is strongly influenced by distance from seed sources and forest age, with effects on plant communities persisting for at least 195 to 350 years after agricultural abandonment. For long-lived fire-adapted savanna grasses, forbs, and shrubs that are poor colonizers (Kirkman et al. 2004) and do not form persistent seed banks (Cohen et al. 2004), savanna plant community recovery following agricultural abandonment is slow in the absence of intensive management efforts (e.g. seeding or seedling transplants; Aschenbach et al. (2010).

Fire frequency is positively associated with species richness in many fire-dependent plant communities, including our study system (Fig. 3.5.2a). However, we found no evidence for a direct relationship between species richness and fire. Instead, our results suggest that frequent fires indirectly promote plant diversity by preventing trees from reaching sufficient abundance to limit understory plant cover and species richness (Fig. 3.5.3) (Peterson and Reich 2007). As such, fire may be viewed as a factor that limits the growth of dominant competitors (e.g. forest trees, Hoffmann et al. (2009) and in doing so, favors fire-adapted understory plants (Cavender-Bares and Reich 2012). There are a number of hypothesized mechanisms by which fire may directly promote richness (e.g. through reduced competition among understory plants; Myers and Harms 2009), but such effects were not detected in our model. If a direct effect of fire on the understory exists, it may be more important to community composition than to richness, or may be more related to other aspects of fire regimes such as season of burn or variation in fire-return interval (e.g. Brewer et al. 2008).

In addition to limiting tree abundance, fire also indirectly promotes richness by reducing the O horizon. O horizon development, caused by fire exclusion and high tree abundance, is thought to be a primary factor limiting understory plant communities in our study system (Hiers et al. 2007), but the effects of the O horizon has not previously been examined at a regional scale or in concert with other factors in our model. For example, our model, which separates understory cover and species richness, suggests that the O horizon is a strong filter on communities, directly limiting the number of species without influencing understory abundance; previous studies had not made this distinction (e.g. Hiers et al. 2007). The linkages between fire exclusion, increased abundance of fire-intolerant trees, and decreased plant diversity are well documented for many open-canopied ecosystems (Ratajczak et al. 2012), but the potential role of the O horizon is often neglected (Fridley et al. 2012). Fire-intolerant, mesophyllic, forest trees appear to be particularly important contributors to the O horizon because they produce low-flammability leaf litter that can impede the spread of fire (Kane et al. 2008). To keep our model tractable, we do not distinguish between tree functional groups that are thought to differ in the strength of their negative relationships with understory plants (Veldman et al. 2013). More work is needed to fully understand the relationships between tree community composition, litter characteristics, ecosystem flammability, and understory plant diversity (Parr et al. 2012, Trauernicht et al. 2012, Veldman et al. 2013, Kreye et al. 2013).

Vegetation structure figures prominently in ecological theory of grass-tree coexistence, vegetation-fire feedbacks, and savanna-forest distributions (Hoffmann et al. 2012, Murphy and

Bowman 2012). In our model, we depict vegetation structure as two separate factors: tree abundance and understory abundance. Numerous studies have concluded that tree abundance controls savanna understory species richness (e.g. Beckage and Stout 2000), but typically without considering the role of understory abundance. Our results suggest that both tree abundance and understory abundance are important determinants of understory species richness (Weiher 2003, Grace et al. 2011) that mediate the effects of fire frequency, agricultural history and resource availability. We expected to see direct positive effects of fire frequency on understory abundance (Figure 3.5.1); instead, all effects of fire on understory abundance are mediated by tree abundance (Figure 3.5.4). In our model, which is static and hierarchical (i.e. lacking looping paths and feedbacks), trees exert a negative effect on understory abundance. We should expect that in a dynamic model that incorporates vegetation-fire feedbacks, understory plant abundance would have a negative influence on tree abundance by increasing fuel loads and fire intensity (e.g. Beckage et al. 2009). Although such feedbacks are potentially important, our model confirms that a focus on tree abundance, a dominant paradigm in savanna ecology (e.g. Sankaran et al. 2005), can be both predictive and ecologically meaningful for understanding other important parameters of savanna ecosystems (e.g. understory abundance, species richness, O horizon development). Given the dynamic nature of savanna ecosystems, our approach is just one of many ways to look at causal relationships among multiple variables that influence plant diversity.

As hypothesized, understory abundance is a strong predictor of species richness (Table 3.5.3; Figure 3.5.4) and a critical factor that links fire frequency, agricultural history, soil resources, and tree abundance with species richness. The concept of a causal relationship between plant diversity and measures of abundance, biomass, or productivity, has existed for several decades (Grime 1973). Although once assumed to be unimodal, bivariate productivity-diversity relationships in grasslands without trees may assume many different forms, including positive linear (Adler et al. 2011). When considering productivity-diversity relationships in savannas, it is important to note that biomass is not limited to understory plants, but is partitioned between overstory trees and understory plants (House et al. 2003); where tree biomass is high (as in fire-excluded savannas), understory cover and diversity decline (Veldman et al. 2013). Biomass also accumulates in the O horizon and is thus another carbon pool that should be factored into studies of these relationships (Fridley et al. 2012).

Resource availability plays a complex role in the regulation of understory species richness, involving relationships that are obscured in bivariate analyses. In the sandy soils of the southeastern USA, small differences in organic content and moisture holding capacity (which is related to SOM, silt, and clay content; Salter and Williams 1967) are thought to influence understory productivity and diversity (Kirkman et al. 2004) as well as tree distributions (Goebel et al. 2001). In our model the total effect of resource availability on species richness is weakly positive, but the role of resource availability is complicated because it includes both positive and negative effects (Table 3.5.3). Favorable resource conditions promote species richness directly and indirectly though understory abundance, but these positive effects are offset by the contribution of soil resources to trees, which compete with understory plants and contribute to O horizon development. These results are consistent with a wider body of literature on the interactions of resource availability, tree growth, grass abundance, and fire in savannas: on high resource sites, frequent fires are required to limit trees, prevent closed-canopy forest development, and maintain a grassy understory (Lehmann et al. 2011, Hoffmann et al. 2012, Murphy and Bowman 2012). Our study suggests how these same factors are causally linked to understory plant diversity and are influenced by agricultural land-use history.

3.5.5 Conclusion

This study demonstrates that multiple factors influence local-scale plant species richness in pine savannas and details specific indirect effects of fire frequency and agricultural land-use history on plant diversity. Understory abundance is a strong predictor of species richness; the factors that influence the balance between understory abundance and tree abundance are important determinants of plant diversity in this system. Fire influences this balance by limiting trees, whereas a history of agriculture increases tree abundance. We also identified ways that fire frequency and agricultural history influence species richness independent of vegetation structure. These include inhibition of the O horizon by frequent fires, reduced resource availability in post-agricultural soils, and persistent direct negative effects of agriculture on richness. By bringing together biophysical variables that had not previously been incorporated in a single model, this study improves our understanding of how multiple factors (which are often examined independently) may limit the recovery of species-diverse savanna plant communities in post-agricultural landscapes worldwide. Given the many obstacles to recovery, conservation efforts should prioritize the protection of savannas that have never been cultivated and maintain historic fire regimes through prescribed fire and wildfire. Where recovery efforts are undertaken, manipulation of several ecosystem attributes (i.e. fire regimes, soils, tree abundances, O horizon depth, and propagule dispersal) may be necessary to facilitate the recovery of understory plant diversity.

4. DESCRIPTION OF EXPERIMENTAL STUDIES

4.0 BACKGROUND

Land managers often seek to replicate reference conditions associated with an intact ecosystem when attempting to promote the recovery of degraded ecosystems. However, the causes and severity of environmental degradation vary substantially, potentially complicating the use of reference conditions alone to guide management practices. For instance, heavily degraded ecosystems may not be as responsive to certain management techniques as less degraded ecosystems (i.e., hysteresis; Suding et al. 2004, Cramer et al. 2008). The potential to mitigate degradation during recovery requires identifying the multiple, potentially interacting factors causing ecosystem degradation and then evaluating the effectiveness of various management techniques along a gradient of degradation (Brudvig 2011). Furthermore, because human activities are continuously affecting ecological communities, including reference communities, management goals need to consider contemporary examples of reference communities, rather than only historical examples (Hobbs 2007, Kirkman et al. 2013).

Our work builds off a previously published reference model for longleaf pine savanna which describes a degradation gradient in longleaf pine understory plant diversity and composition caused by past agricultural land use, altered fire regimes, and silvicultural activities (Walker and Silletti 2006, Mitchell 2009). Agricultural legacies can persist for decades in longleaf pine ecosystems following agricultural abandonment, leading to reduced understory diversity and modified community composition (Hedman et al. 2000, Brudvig and Damschen 2011, Brudvig et al. 2013). Fire suppression leads to increased tree abundance, canopy cover and accumulation of leaf litter, which may all contribute to declines in understory diversity (Glitzenstein et al. 1995, 2003, 2012, Hiers et al. 2007, Brudvig et al. 2013, Veldman et al. 2014). Overstory trees may also directly reduce understory plant diversity by competing for light and water (Harrington and Edwards 1999, Harrington et al. 2003, Harrington 2011). Our ecological reference model provides a strong empirical foundation that allows us to predict that the most heavily degraded longleaf stands will be those with a history of agriculture, fire suppression, a dense overstory, or some combination of those degrading factors (Brudvig et al. 2014, Section 3.3). However, in order to leverage this knowledge to guide management efforts, we also need to experimentally test how variation in these degrading factors may affect the ecological processes underpinning the outcomes of various management efforts.

4.1 GENERAL METHODS FOR EXPERIMENTAL SET UP (TECHNICAL OBJECTIVE 2)

4.1.1 Selection of stands based on the ecological reference models

We selected stands for inclusion in subsequent experiments (i.e. Technical Objective 2) by using our ecological reference model based on Brudvig et al. (2014, see also Section 3.3). We first used the ecological reference model classification scheme from Section 3.3 to assign each experimental site a degradation class. Because we used fewer sites in the experimental phase of this project, we could not fully replicate all degradation classes from the original ecological reference models. The ‘All locations’ reference model resulted in three of the six original classes, with Class 1 representing fire suppressed sites (<4.5 burns between 1991 and 2009), Class 3 representing frequently burned sites (>4.5 burns between 1991 and 2009) with an agricultural history, and Class 4-6 representing frequently burned sites with a forested history, pooled across variation in basal area and soil moisture. Class 2 had too few sites to include in this analysis. Thus, our revised ecological reference model for 'All locations' focuses on variation in agricultural history and fire frequency, pooled across edaphic and tree density gradients. We were able to fully replicate the original Fort Bragg reference model of two classes, with Class 1 representing sites with an agricultural history and Class 2 representing sites with a forested history. Of the four original degradation classes for the reference model of Fort Stewart, our experimental sites captured three of these classes, with Class 1 representing sites on Inceptisols or Spodosols, Class 2 representing sites on Entisols or Ultisols and high non-*Pinus* basal area (>1.28 m^2/ha), and Class 3-4 representing sites on Entisols or Ultisols with low non-*Pinus* basal area (<1.28 m^2/ha). Class 3-4 was pooled across a gradient of soil moistures. Our experimental sites fully encompassed the original reference model at the Savannah River Site, with Class 1 representing high total basal area sites (>22.8 m^2/ha), Class 2 representing sites with low basal area (<22.8 m^2/ha), a history of agriculture, and low fire frequency (<4.5 burns since 1991), Class 3 representing sites with low basal area, a history of agricultural, and frequent fires (>4.5 burns since 1991), and Class 4 representing sites with low basal area, and a forested history. To ensure that we captured a substantial range of variation in overstory tree density and the time since a site last burned (Harrington and Edwards 1999, Harrington et al. 2003, Kirkman et al. 2004), stands were also selected to maximize the variation in these continuous characteristics. These selection criteria resulted in a total of 108 experimental stands, 36 at each location, sampled across our three study locations (Fig. 4.1.1).

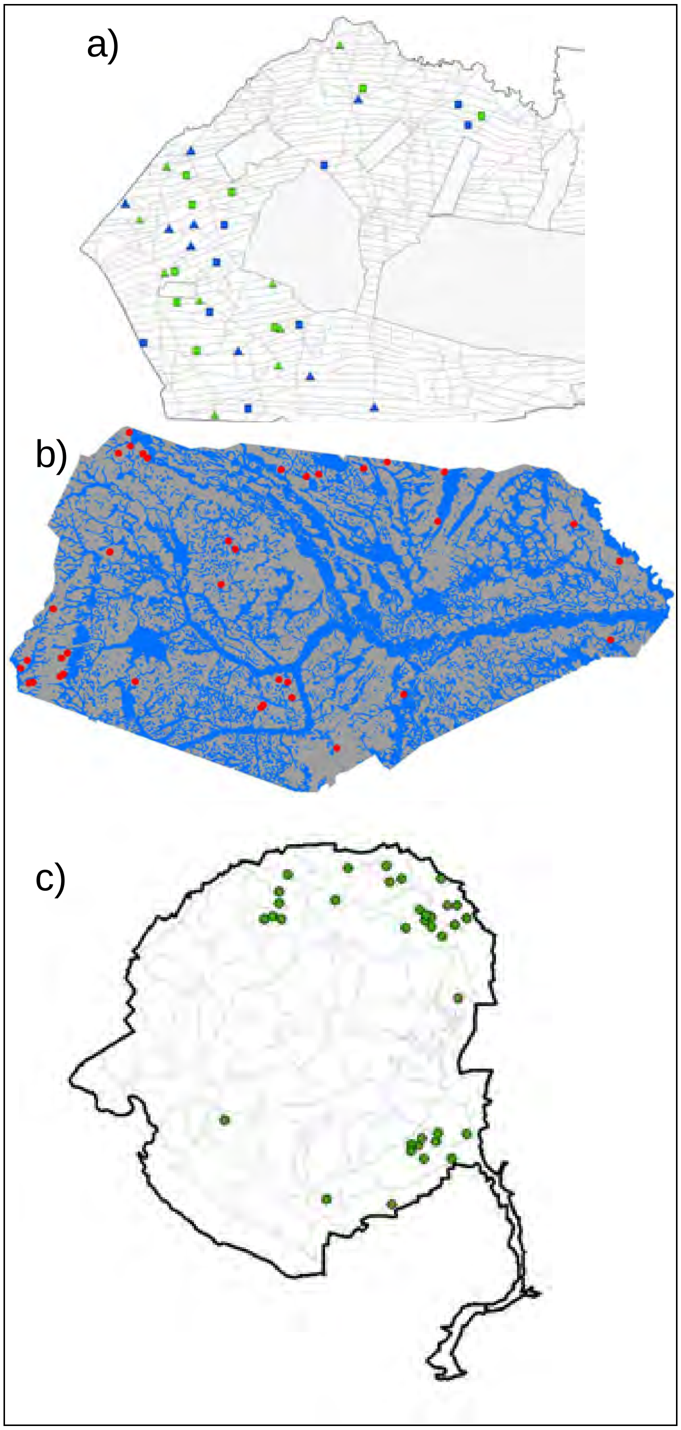

Figure 4.1.1. Maps of the 36 experimental sites within each of the three geographic locations: a) Fort Bragg, NC, b) Fort Stewart, GA, and c) Savannah River Site, SC. Sites within locations are separated by >250 m.

4.1.2 Plot design and treatments

At each of the 108 sites, we established eight 7×7m plots, in which we factorially manipulated consumer access, competitor presence, and dispersal limitation, resulting in eight treatment combinations per site. The consumer access treatment focused on excluding large vertebrate consumers (e.g., deer, feral pigs) and was applied by fencing half of the 7×7m plots using a ~2.4m tall fence. The base was constructed out of woven wire mesh (1.2m height, mesh 61×20cm), with a top layer of chicken wire (1.2m height). Fences were erected between December 2010 and March 2011. Competitor presence was manipulated by applying a broad spectrum herbicide (OneStep, active ingredients: Imazapyr, 8.36% and Glyphosate, 22.13%) at a rate of 1 gallon per acre to half of the 7×7m plots in August, 2010. The dispersal limitation treatment was applied by adding seeds of 21 plant species that are indicators of reference, upland longleaf pine savannas (Table 4.1.1) to the center 5×5m of each plot. Seeds were collected on-site at each location between November 2010 and February 2011 and added to half of the plots in March, 2011 after all other manipulations were completed.

Table 4.1.1. Species and number of seeds added to the experimental plots at each of the three locations.

Family	**Species (FTS)**	**Species (SRS)**	**Species (FTB)**	**Live seeds added m^{-2}**
Poaceae	*Aristida stricta*	*Aristida beyrichiana*	*Aristida stricta*	63
Poaceae	*Sorgastrum secundum*	*Sorgastrum secundum*	*Sorgastrum nutans*	72
Poaceae	*Aristida purpurescens*	*Aristida purpurescens*	*Aristida purpurescens*	53
Poaceae	*Sporobolus junceus*	*Sporobolus junceus*	*Sporobolus junceus*	6
Poaceae	*Anthenantia villosa*	*Anthenantia villosa*	*Anthenantia villosa*	36
Fabaceae	*Tephrosia virginiana*	*Tephrosia virginiana*	*Tephrosia virginiana*	14
Fabaceae	*Baptisia perfoliata*	*Baptisia perfoliata*	*Baptisia cinerea*	3
Fabaceae	*Lespedeza hirta*	*Lespedeza hirta*	*Lespedeza hirta*	79
Asteraceae	*Vernonia angustifolia*	*Vernonia angustifolia*	*Vernonia angustifolia*	60
Asteraceae	*Eupatorium album*	*Eupatorium album*	*Eupatorium album*	88
Asteraceae	*Eupatorium rotundifolium*	*Eupatorium rotundifolium*	*Eupatorium rotundifolium*	178
Asteraceae	*Aster tortifolius*	*Aster tortifolius*	*Aster tortifolius*	10
Asteraceae	*Solidago odora*	*Solidago odora*	*Solidago odora*	253
Asteraceae	*Silphium compositum*	*Silphium compositum*	*Silphium compositum*	17
Asteraceae	*Coreopsis major*	*Coreopsis major*	*Coreopsis major*	11
Asteraceae	*Liatris secunda*	*Liatris secunda*	*Liatris squarrosa*	17
Asteraceae	*Heterotheca graminifolia*	*Heterotheca graminifolia*	*Heterotheca graminifolia*	71
Asteraceae	*Aster linariifolius*	*Aster linariifolius*	*Aster linariifolius*	18
Ericaceae	*Gaylussacia dumosa*	*Gaylussacia dumosa*	*Gaylussacia dumosa*	7
Scrophulariaceae	*Aureolaria pectinata*	*Aureolaria pectinata*	*Aureolaria pectinata*	142
Melastomataceae	*Rhexia mariana*	*Rhexia mariana*	*Rhexia mariana*	221

We also conducted a litter manipulation in a 1.2×1.2m sub-plot within each plot. All leaf litter, duff, and other plant debris (e.g., pine cones, branches) was removed in February, 2011 to expose bare mineral soil, although care was taken not to disturb mineral soil. Vegetation stems (<10 diameter) were also clipped at the soil surface and removed from these plots. See Figure 4.1.2 for an overview of the plot layout.

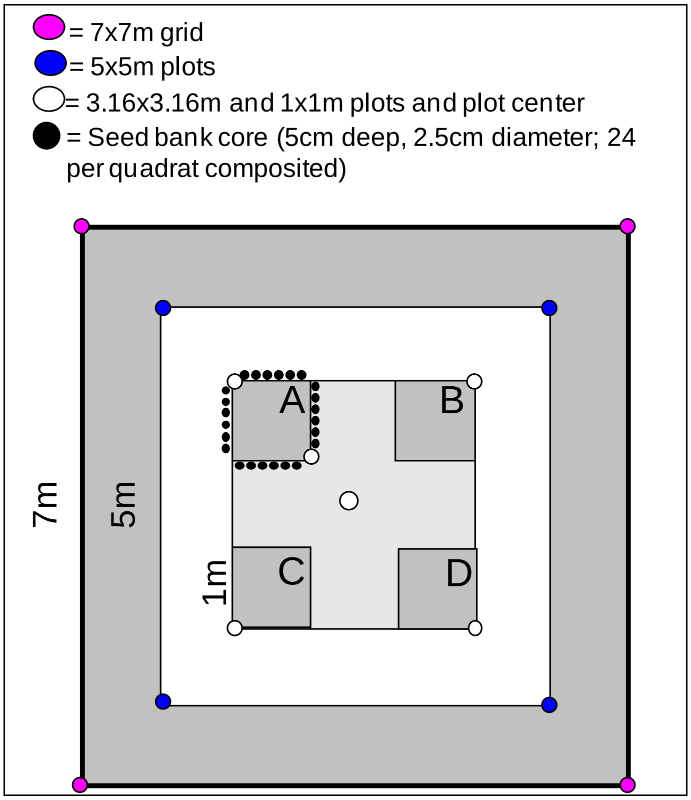

Figure 4.1.2. Generlized experimental plot layout. Fencing was applied at the 7×7m scale. Seed additions and herbicide were applied at the 5×5m scale. A) 1×1m plot that was the focal vegatation sampling plot. Litter removal was conduct in a 1.2×1.2m area catercorner to a randomly selected plot B,C, or D. Eight of these plots were installed at each of the 108 experimental sites.

Prior to initiating the experiment, we conducted apparent seed viability assays by squeezing and sectioning a subset of seeds with forceps to determine the proportion of seeds with intact embryos. Results of these viability assays were used to inform the experimental seeding rate. To confirm viability, we subsequently conducted a germination trial on all of the collected seed species. We attempted to germinate 750 seeds from each species from each site for a period of two weeks to determine viability rates. Seeds were grown in petri dishes with 25 seeds from a single species and site per dish. Blotter paper was placed at the bottom of each dish, and watered as needed throughout the course of the germination trial. All dishes were placed in a growth chamber, which was set to mimic climate norms in South Carolina for May (29.5 °C during the 13.5 hour day, with nighttime temperatures of 14.2 °C). When present, fungal growth was treated with a 5% bleach solution applied directly to the affected area. Throughout the two week trial, seeds were checked daily for germination. After a seed germinated, it was removed from the petri dish. At the end of the trial, we calculated the proportion of viable seeds of each species and for each site (Figure 4.1.3). Germination trials began on 11 July 2011 and were conducted in three randomized blocks of two-week periods.

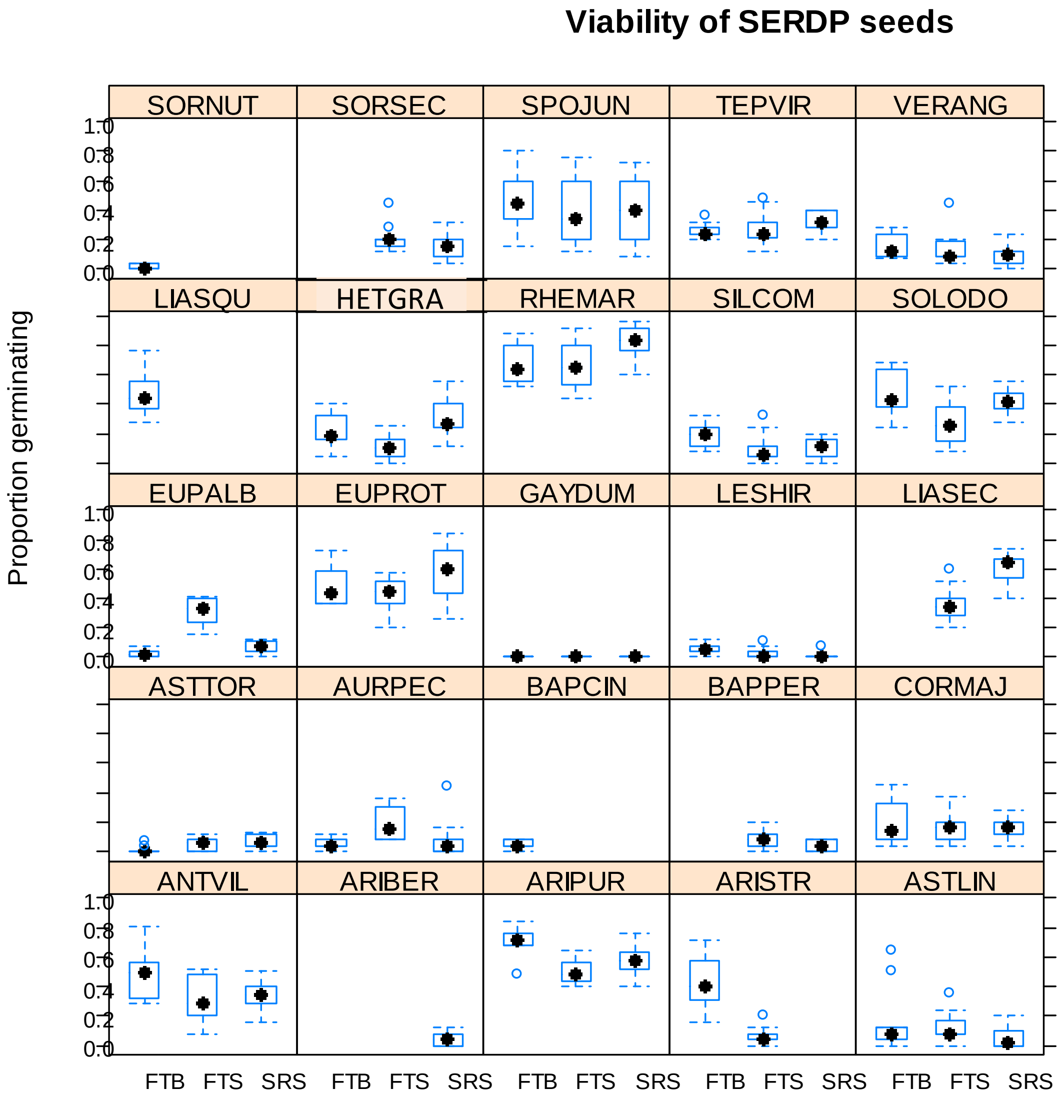

Figure 4.1.3. Summary of viability of seeds collected for SERDP experiments (from the same batches used in seed additions). Viability based on germination trials conducted on moist filter paper in a climate chamber. Species codes are the first three letters from the genus and species. Dots represent means and the whiskers represent quantiles.

4.1.3 Vegetation sampling

In each 7×7m plot, we recorded the species and diameter at breast height (DBH) of each tree (wood stems >2.5cm DBH and >1m tall) with trunks at least partly within the plot. DBH was recorded at 1.37m off the ground. In the 5×5m center of each plot, we recorded the richness of all indicator species added as seed. In the 3.16×3.16m center of each plot (Figure 4.1.2), we recorded the species richness of all plants (woody and herbaceous) rooted within or overhanging the plot, including the richness of all indicator species added as seed. We also visually estimated the percent cover of the foliage of all shrub species (< 1m tall) overhanging the plot. Woody stems >1m tall and woody vines were not included in this estimate.

In a 1×1m quadrat located in the corner of the 3.16×3.16m plot, and within a 1×1m quadrat in the litter removal plot (Figure 4.1.2), we recorded richness of all plant species and visually estimated the percent cover of all herbs and woody plant species up to shrub class. We included all overhanging foliage, whether or not the plant was rooted in the plot. For plants greater than 1m in height, we estimated the coverage both below and above 1m. All plant species were recorded individually, regardless of whether they were overhanging other vegetation, so the total vegetation cover of a plot could exceed 100%. Included in these measurements was the richness and cover of indicator species added as seed. Taxonomy follows Radford et al. (1964), except for the genus *Dichanthelium*, which follows Weakley (2008), and the genera *Lyonia* and *Persea*, which follow Wunderlin and Hansen (2003).

All vegetation data were collected in mid-June. We collected pre-treatment data in 2010 prior to implementation of the experiments, as well as for the three years following experiments (2011-2013). Cover of indicator species that were used for seed additions was monitored during the vegetation surveys in 2011-2013.

4.1.4 Additional environmental data collection

In each 1×1m quadrat, we also measured percent cover of green vegetation, leaf litter, woody debris (bark, pine cones, tree branches, etc.), tree trunks, bare mineral soil, and non-vascular plants. These categories summed to 100%. Depth of the leaf litter and duff layers was also measured in each corner of the 1×1m vegetation quadrat and 1.2×1.2 litter removal plot. We collected all vegetation cover estimates and environmental data annually in June between 2010 and 2013. Tree DBH was recorded in 2010, 2011, and 2013.

We estimated canopy closure using hemispherical images. A camera equipped with a 180° fish-eye lens was positioned on a tripod ~1m above ground-level in the center of each 7×7m plot. Photos were taken during the growing season (July-August) at dusk, dawn, or on overcast days. We then digitized the images using a threshold that converted all pixels that were canopy to black and all pixels that were sky to white using HemiView Software v2.1 (Delta-T Devices, Cambridge, UK). Canopy closure was calculated as the proportion of canopy (dark) pixels in each image. Photos were taken in 2010, 2011, and 2013.

To characterize site-level soil conditions, we collected soil cores (2.5cm diameter by 15cm deep) at eight locations surrounding the 3.16×3.16m plot. Litter and duff were scraped away to expose mineral soil before the samples were taken. Samples were composited by plot, allowed to air dry, and then homogenized. We also analyzed soil samples for nutrients (Brookside Laboratories, Inc., New Knoxville, OH) and water holding capacity as the proportionate difference between saturated wet weight and oven-dried weight, following the method of (Salter and Williams 1967), as described in section 3.1.1 and by Brudvig and Damschen (2011). Soil moisture availability correlates with longleaf pine understory diversity and productivity (Kirkman et al. 2001).

4.1.5 Characterization of reference communities

To understand recovery potential for degraded stands with varying site conditions, we quantified reference plant community composition for longleaf pine savanna communities by sampling previously identified CVS plots that are as close to historical conditions as possible. These sites provide a key comparison group in our ecological reference model (i.e. the upper right-hand group in Figure 3.3.1). The CVS plots include many stands from undegraded longleaf pine savannas across the southeastern United States (pers. comm. Tom Wentworth). Reference stands were selected to encompass the range of geographic and hydrological variation represented by our three study locations. At each CVS plot present at each of our study locations, we collected vegetation, substrate, and landscape data in the same manner used for all degraded stands in our study.

We employed several approaches to understand the differences and similarities between understory communities at degraded and reference stands. In general, there are two basic approaches to classifying degraded vegetation communities to facilitate subsequent comparison: 1) use multivariate methods to create groups of plant communities that are similar to each other, using only data from the plant communities themselves (i.e. cluster analysis of vegetation data), and; 2) use characteristics known to be important in affecting plant communities (e.g. an ecological reference model) to create a priori groups, then examine differences in vegetation communities among those groups.

Both of these approaches have advantages and disadvantages. For vegetation communities affected by strong gradients and where ecological reference models include these gradients, both approaches should yield complementary results: groups created by cluster analysis should be consistent with groups that would be defined a priori using the reference model. In the analysis of our data, we performed both approaches and found strong agreement: vegetation classes constructed using our a priori reference model were highly consistent with vegetation classes constructed using cluster analysis of the vegetation data. Groups created using cluster analysis and their key features (e.g. species richness and evenness) were presented at our 2010 IPR. In this report, we focus on comparisons that utilize our ecological reference model as the basis for creating classes for comparison (Figure 3.3.1). The similarity between our a priori groups and significant differences among vegetation communities suggests that our reference model is highly effective for assessing the degree of degradation in vegetation communities.

We base our primary comparisons among reference groups and degraded stands by using our ecological reference model to place stands into five a priori groups (Fig 3.3.1). Starting with the least degraded habitats, these groups are: reference stands (never used for historical agriculture), forested stands (degraded stands never used for historical agriculture) with a high fire frequency (fire occurs at least once every 4 years), forested stands (degraded stands never used for historical agriculture) with a low fire frequency (fire occurs at most once every 5 years), degraded stands that were historically used for agriculture (but have been in timber production via natural recruitment and/or active planting for at least 50 years) with a high fire frequency (fire occurs at least once every 4 years), and degraded stands that were historically used for agriculture with a low fire frequency (fire occurs at least once every 5 or more years). Our fire frequency cutoffs were chosen based on literature for longleaf burn-return intervals that suggests that 2-4 year burn return intervals are thought to reflect the historical burn regime (Walker and Peet 1983, Mehlman 1992, Glitzenstein et al. 1995, Glitzenstein et al. 2001, Kirkman et al. 2004, Frost 2006).

To compare degraded and reference stands among these categories, we use univariate statistics (i.e. standard general linear models) to determine differences in species richness and evenness among stands. Prior to initiating analyses of plant species richness, we evaluated the degree to which estimators of richness (e.g. Chao's estimator) were correlated with observed species richness, as this was a suggestion made by Science Advisory Board Panel member Dr. Rosenzweig. In addition to Chao's estimator (one of the recommendations of Dr. Rosenzweig), we also evaluated the first- and second-order jackknife estimators (Figure 4.1.4). These three estimators are among the most commonly used for vegetation data and, most importantly, are also the estimators found to have the most desirable properties of precision and lack of bias (Walther and Moore 2005).

In addition to univariate metrics of plant community composition, we evaluated multivariate composition of plant communities along our reference model by using Canonical Analysis of Principal Coordinates (CAP) analyses (Anderson and Willis 2003). This approach is similar in principle to discriminant function analysis (DFA) in that it seeks to

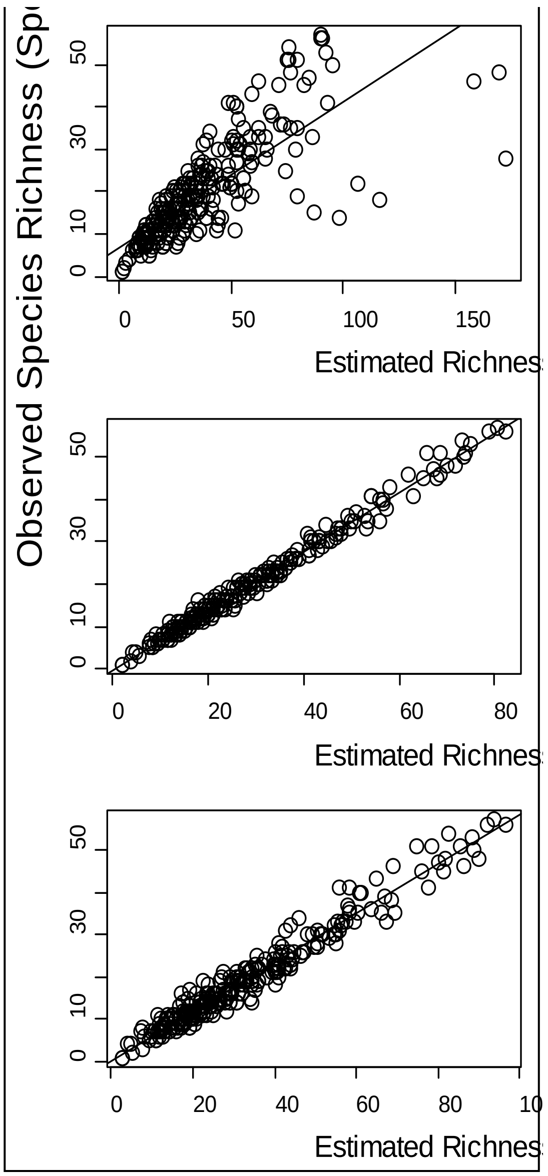

Figure 4.1.4. The relationship between observed species richness and three incidence-based estimators of species richness.

determine which variables in a multivariate dataset are most useful for discriminating membership in a priori groups. The difference between classic DFA and CAP is that DFA implicitly uses Mahalanobis distance to quantify similarity and dissimilarity (Anderson and Willis 2003), which may not be the most appropriate distance metric for ecological data. CAP can use a wide range of similarity and dissimilarity measures (Anderson and Willis 2003). In our analysis, we follow the general recommendation of Anderson and Willis (2003), and utilize Bray-Curtis similarity as the distance metric.

4.2 IMPACTS OF EXPERIMENTAL TREATMENTS ON LOCAL DIVERSITY. I: LOCAL FILTERS

[This section contains material in preparation: Orrock, J. L. J. A. Brudvig, E. I. Damschen, W. B. Mattingly, J. W. Veldman, and J.L. Walker. 2014. Experimental evidence that dispersal limitation drives large-scale, long-term legacies of past agricultural land-use on plant communities.]

4.2.1 Introduction

More than 200 million hectares of agricultural land has been abandoned in North America over the last century (Ramankutty and Foley 1999), creating potential new habitat for native species of conservation interest (Cramer et al. 2008). However, the legacies of historic agriculture generally result in altered soil properties and plant community composition characterized by a lack of native, remnant plant species (Flinn and Vellend 2005, Cramer et al. 2008). Results from surveys of reestablished plant communities suggest that dispersal limitation drives patterns of reestablishment in recovering forests (Matlack 1994, Flinn and Vellend 2005, Vellend et al. 2007, Brudvig and Damschen 2011). However, many species that are indicators of reference habitat fail to recolonize post-agricultural sites, even when in close proximity to remnant seed sources (Kirkman et al. 2004, Grman et al. 2013, Brudvig et al. 2013, 2014, Section 3.3-3.5), suggesting that filters to establishment of these species exist in post-agricultural sites. A recent meta-analysis of recruitment in post-agricultural forests in Europe and North America supports a strong role of establishment limitation, coupled with a weaker role of dispersal limitation, in structuring post-agricultural plant communities (Baeten et al. *in press*). While some sowing experiments find similar recruitment rates between remnant and post-agricultural forests (Jackson et al. 2013), many experiments find that recruitment is more limited in post-agricultural forests compared to remnant forests (Verheyen and Hermy 2004, Flinn 2007, Baeten et al. 2009, Mattingly and Orrock 2013). These experimental results also suggest a stronger filter at the establishment stage, likely in addition to dispersal limitation. However, the mechanisms driving differences in recruitment have not been thoroughly examined.

Lower seedling recruitment in post-agricultural forests could be related to altered soil properties or limitation of suitable microsites (Verheyen et al. 2003, Flinn 2007, Cramer et al. 2008). Early establishment of ruderal plants in post-agricultural sites may limit subsequent establishment by remnant species via priority effects or competition (Egler 1954, Baeten et al. 2010), which could potentially interact with other factors (Myers and Harms 2009, 2011) to further reduce establishment. Moreover, because land-use history can also affect herbivore taxa and herbivory rates (Hahn and Orrock 2015a, Hahn and Orrock 2015b), land-use history may indirectly affect seedling establishing by altering the abundance of consumers. Furthermore, agricultural abandonment often occurs in conjunction with other management activities, such as altered fire regimes (Thébault et al. 2014), which could potentially affect recruitment via reduced light availability following woody plant encroachment (Briggs et al. 2005, Ratajczak et al. 2012, Glitzenstein et al. 2012). Understanding how seedling establishment differs in response to these multiple, interacting factors will help to guide recovery processes in post-agricultural landscapes.

In this section, we examine the role of degradation class, herbicide, fencing, seed additions, and litter removal on total species richness and richness of indicator species in 1m^2 plots.

4.2.2 Methods

See section 4.1 for a description of the stand selection protocol (Section 4.1.1), experimental design (Section 4.1.2), and data collection (Section 4.1.3). This section uses vegetation data collected in 2013, three years after the experiments were implemented.

Statistical Analysis

To analyze the effects of our experimental treatments on longleaf pine understory communities, we used generalized linear mixed models with a Poisson distribution to account for the discrete (count) nature of the species richness data. We focused on two response variables in 1m^2 plots: 1) total species richness and 2) richness of indicator species added as seed. Both response variables were measured in 2013, three years after the treatments were implemented. We conducted 5-way factorial analyses of variance with degradation class, seed addition, herbicide application, fencing, litter removal, and all possible interactions as fixed-effect predictor variables. To account for the nestedness in our experimental design, we treated each site (i.e. degradation class) as the whole plot, the experimental manipulations as the split-plot treatments (i.e. seed additions, herbicide, and fencing), and litter removal as the split-split-plot. We conducted analyses for all three locations combined (‘All Locations’ analysis) and separately for each individual location.

4.2.3 Results

All locations models

For species richness at ‘All locations’, the 5-way interaction among degradation class, seed additions, herbicide, fencing, and litter removal was significant ($F = 4.14$, $P = 0.016$, Table 4.2.1). The herbicide application had consistent negative effects on species richness across all degradation classes. In the fire suppressed sites (Class 1), seed additions resulted in the greatest increases in species richness when the herbicide application, fencing, and litter removal treatments were also applied (Figure 4.2.1A). In sites with an agricultural history (Class 3) the seed additions were less effective, with negligible increases in species richness across all other experimental treatments (Figure 4.2.1B). The sites with a forested history (Class 4-6) had the highest overall species richness, compared to the other degradation classes, and also responded positively to the seed additions across most other experimental treatments (Figure 4.2.1C).

For richness of indicator species at ‘All locations’, two-way interactions between degradation class and herbicide ($F = 34.78$, $P < 0.001$), between herbicide and seed additions ($F = 7.20$, $P = 0.008$), and between litter removal and seed addition ($F = 10.34$, $P = 0.001$), were significant (Table 4.2.1). The herbicide treatment had a strong negative effect on indicator species richness in sites with a forested history (Class 4-6), a weak negative effect on indicator species richness in fire suppressed sites (Class 1), and no effect in sites with an agricultural history (Class 3). The positive effect of seed additions in fire suppressed sites (Class 1) was greatest when herbicide or litter removal were also applied, but because of the presence of preexisting indicator species in non-herbicide plots, the seed additions resulted in similar levels of indicator species richness across most experimental treatments (Figure 4.2.1D). The exception was in the herbicide and no-litter removal treatments, which had the fewest indicator species present. The low presence of preexisting indicator species in sites with an agricultural history (Class 3) resulted in seed additions having fairly consistent, positive contributions to indicator species richness across most treatments, but especially in treatments with litter removal (Figure 4.2.1D). Sites with a forested history had the highest overall levels of indicator species richness and seed additions increased this even further (Figure 4.2.1E).

Table 4.2.1. All location results of species richness in 1x1m plots in 2013. Significant effects (*P* < 0.05) are in bold.

			Total richness		Indicator richness	
Effect	**Num DF**	**Den DF**	***F***	***P***	***F***	***P***
Class	2	105	1.60	0.208	**8.28**	**0.0005**
Herbicide	1	735	**463.89**	**<.0001**	**72.44**	**<.0001**
Class × Herbicide	2	735	**4.22**	**0.015**	**34.78**	**<.0001**
Fence	1	735	1.84	0.175	0.37	0.5426
Class × Fence	2	735	**3.34**	**0.036**	0.76	0.4685
Herbicide × Fence	1	735	0.17	0.684	0.65	0.4217
Class × Herbicide × Fence	2	735	0.25	0.776	0.84	0.4342
SeedAddition	1	735	**24.05**	**<.0001**	**108.64**	**<.0001**
Class × SeedAddition	2	735	0.39	0.679	0.38	0.6823
Herbicide × SeedAddition	1	735	**5.41**	**0.020**	**7.2**	**0.0075**
Class × Herbic × SeedAdd	2	735	0.23	0.797	0.05	0.9558
Fence × SeedAddition	1	735	1.51	0.220	0.07	0.7948
Class × Fence SeedAdd	2	735	1.52	0.220	1.04	0.3530
Herbic × Fence × SeedAdd	1	735	1.03	0.311	0.78	0.3779
Class × Herbic × Fence × Seed	2	735	0.63	0.533	0.75	0.4746
Litter removal	1	840	**52.63**	**<.0001**	**16.87**	**<.0001**
Litter × Class	2	840	1.82	0.163	0.84	0.4329
Litter × Herbicide	1	840	**20.54**	**<.0001**	1.52	0.2174
Litter × Class × Herbic	2	840	2.39	0.092	0.66	0.5191
Litter × Fence	1	840	1.40	0.238	0.26	0.6124
Litter × Class × Fence	2	840	0.03	0.969	0.5	0.6048
Litter × Herbicide × Fence	1	840	0.20	0.656	0.26	0.6072
Litter × Class × Herbic × Fence	2	840	0.79	0.453	0.23	0.7924
Litter × SeedAddition	1	840	1.66	0.198	**10.34**	**0.0014**
Litter × Class × SeedAd	2	840	0.89	0.410	0.68	0.5051
Litter × Herbic × SeedAd	1	840	0.25	0.617	1.74	0.1877
Litter × Class × Herb × SeedAd	2	840	1.97	0.140	1.25	0.2882
Litter × Fence × SeedAdd	1	840	0.05	0.829	0.09	0.7656
Litter × Class × Fenc × SeedA	2	840	0.66	0.516	0.4	0.6721
Litter × Herb × Fenc × SeedA	1	840	0.72	0.398	0.27	0.6055
Litter × Class × Herb × Fen × Seed	2	840	**4.14**	**0.016**	0.39	0.6755

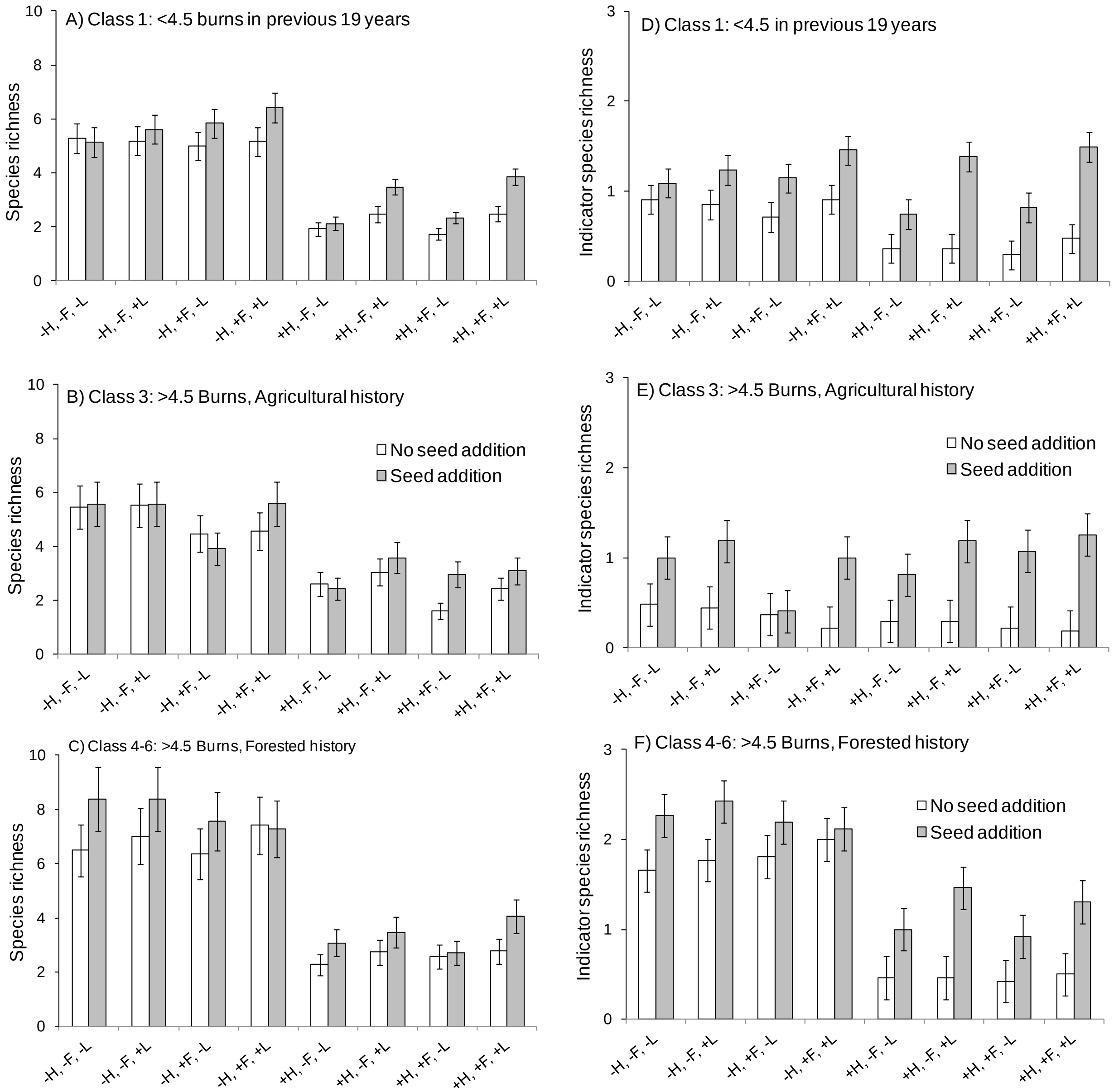

Figure 4.2.1. (A-C) total species richness and (D-F) richness of indicator species from all three study locations in 1x1m plots by degradation class. H = herbicide application; F = fencing, L = litter removal.

Fort Bragg

For species richness at Fort Bragg, the main effect of degradation class ($F = 9.85$, $P = 0.004$), the main effect of seed addition ($F = 14.45$, $P < 0.001$), and the interaction between litter removal and herbicide ($F = 6.00$, $P = 0.015$) were significant (Table 4.2.2). Seed additions increased species richness by nearly 1 species per m^2 across all treatments (Figure 4.2.2). The negative effect of herbicide was less severe in the litter removal plots (Figure 4.2.2).

The richness of indicator species at Fort Bragg was affected by the main effect of seed addition ($F = 36.33$, $P <0.001$), the main effect of litter removal ($F = 4.13$, $P = 0.04$), the interaction between degradation class and herbicide ($F = 92.67$, $P < 0.001$), and the interaction between degradation class and fencing ($F = 7.63$, $P = 0.006$, Table 4.2.2). Seed additions increased the richness of indicator species by about 0.5 species, pooled across all other treatments. Litter removal slightly increased the richness of indicator species. Herbicide application had a much stronger negative effect on species richness in historically forested sites (decrease of about 2 species) compared to sites historically in agriculture (decrease of about 0.5 species). Fencing had a slightly negative effect on indicator species richness in sites with a history of agricultural land use and a slightly positive effect on indicator species richness in historically forested sites (Figure 4.2.2).

Table 4.2.2. FTB results for species richness in 1x1m plots in 2013. Significant effects ($P <$ 0.05) are in bold.

			Total richness		**Indicator richness**	
Effect	**Num DF**	**Den DF**	***F***	***P***	***F***	***P***
Class	1	34	**9.85**	**0.0035**	**58.33**	**<.0001**
Herbicide	1	238	**313.3**	**<.0001**	**188.47**	**<.0001**
Class × Herbicide	1	238	2.69	0.1020	**92.67**	**<.0001**
Fence	1	238	0.42	0.5200	1.37	0.2424
Class × Fence	1	238	2.25	0.1350	**7.63**	**0.0062**
Herbicide × Fence	1	238	0.45	0.5018	0.70	0.4034
Class × Herbicide × Fence	1	238	0.17	0.6785	0.34	0.5585
SeedAddition	1	238	**14.45**	**0.0002**	**36.33**	**<.0001**
Class × SeedAddition	1	238	0.20	0.6520	1.58	0.2105
Herbicide × SeedAddition	1	238	0.22	0.6371	0.11	0.7380
Class × Herbic × SeedAdd	1	238	0.14	0.7097	0.01	0.9334
Fence × SeedAddition	1	238	1.90	0.1694	0.03	0.8672
Class × Fence SeedAdd	1	238	0.07	0.7932	0.06	0.8019
Herbic × Fence × SeedAdd	1	238	1.36	0.2444	2.80	0.0954
Class × Herbic × Fence × Seed	1	238	1.65	0.2002	2.53	0.1131
Litter removal	1	272	**10.36**	**0.0014**	**4.13**	**0.0432**
Litter × Class	1	272	0.44	0.5092	3.03	0.0827
Litter × Herbicide	1	272	**6.00**	**0.0150**	0.01	0.9230
Litter × Class × Herbic	1	272	0.00	0.9757	0.34	0.5621
Litter × Fence	1	272	2.20	0.1395	2.71	0.1012
Litter × Class × Fence	1	272	1.44	0.2317	0.00	1.0000
Litter × Herbicide × Fence	1	272	0.64	0.4241	2.71	0.1012
Litter × Class × Herbic × Fence	1	272	1.60	0.2075	0.04	0.8467
Litter × SeedAddition	1	272	0.05	0.8278	0.01	0.9230
Litter × Class × SeedAd	1	272	0.50	0.4814	0.15	0.6991
Litter × Herbic × SeedAd	1	272	0.01	0.9137	0.01	0.9230
Litter × Class × Herb × SeedAd	1	272	0.01	0.9210	3.03	0.0827
Litter × Fence × SeedAdd	1	272	0.06	0.8074	0.46	0.4988
Litter × Class × Fenc × SeedA	1	272	1.77	0.1850	1.35	0.2467
Litter × Herb × Fenc × SeedA	1	272	0.03	0.8695	0.01	0.9230
Litter × Class × Herb × Fen × Seed	1	272	0.03	0.8534	1.35	0.2467

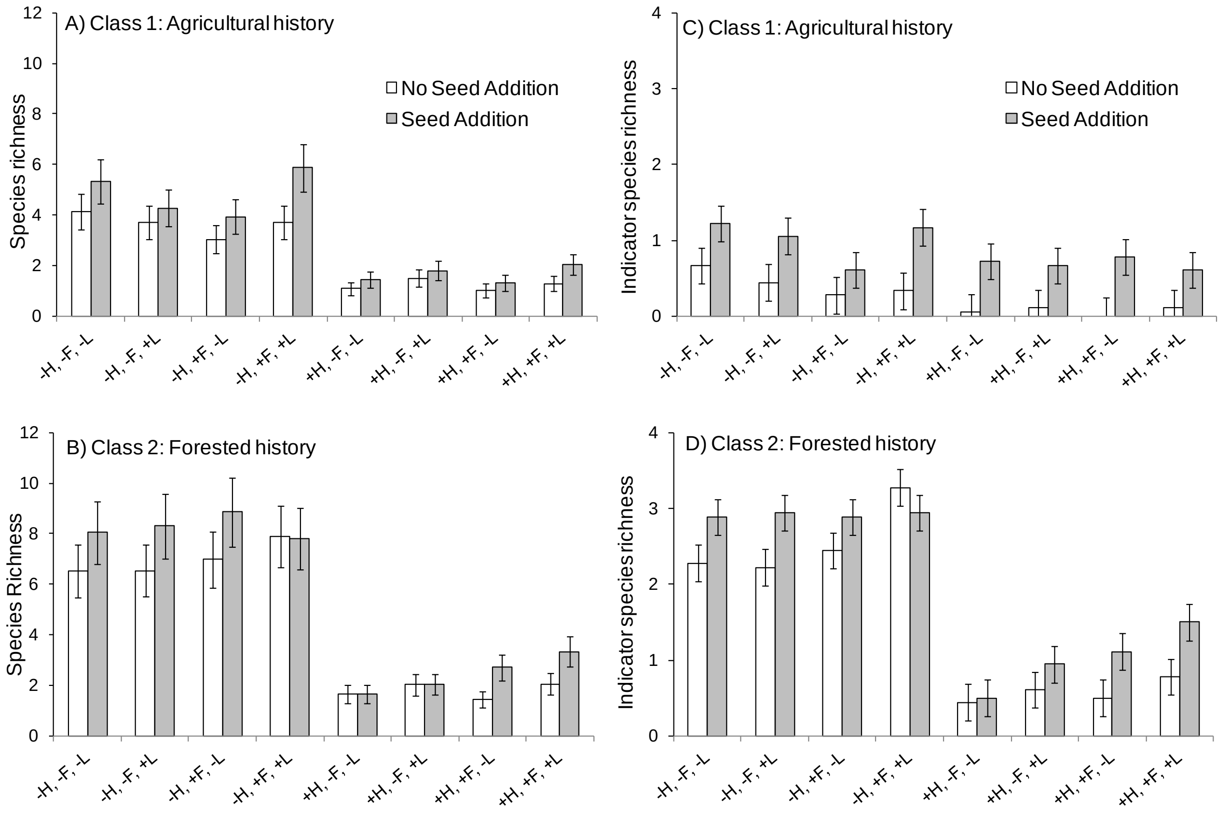

Figure 4.2.2. (A-B) Total species richness and (C-D) richness of indicator species from Fort Bragg, NC in 1x1m plots by degradation class. H = herbicide application; F = fencing, L = litter removal.

Fort Stewart

For species richness at Fort Stewart, the interaction between degradation class and herbicide (F = 24.79, $P < 0.001$), the interaction between seed addition and herbicide (F = 5.96, $P = 0.015$), and the interaction between litter removal and herbicide (F = 11.70, $P < 0.001$) were significant (Table 4.2.3). Herbicide reduced species richness by about four species m^{-2} in both class 1 and 3, but the effect of herbicide was much smaller in class 2 (Figure 4.2.3). Seed addition increased species richness by about one species per m^2 pooled across all other treatments, but the effect of seed addition was only significant when herbicide was applied (Figure 4.2.3). Finally, the negative effect of herbicide on species richness was reduced when litter was also removed (Figure 4.2.3).

The richness of indicator species at Fort Stewart was affected by the interaction between degradation class and herbicide (F = 11.51, $P < 0.001$) and the interaction between litter removal and seed additions (F = 5.25, $P = 0.022$, Table 4.2.3). The negative effect of herbicide on the richness of indicator species was largest in the least degraded sites (Class 3-4) and had no detectable effects in the more degraded sites (Class 1 and 2). The seed addition increased richness of indicator species, but only when litter was also removed (Figure 4.2.3).

Table 4.2.3. FTS results for species richness in 1x1m plots in 2013. Significant effects (*P* < 0.05) are in bold.

			Total richness		**Indicator richness**	
Effect	**Num DF**	**Den DF**	***F***	***P***	***F***	***P***
Class	2	33	**7.27**	**0.0024**	**1.93**	**0.1612**
Herbicide	1	231	**174.10**	**<.0001**	**5.54**	**0.0194**
Class × Herbicide	2	231	**24.79**	**<.0001**	**11.51**	**<.0001**
Fence	1	231	0.34	0.5625	0.06	0.8040
Class × Fence	2	231	1.60	0.2037	1.88	0.1554
Herbicide × Fence	1	231	2.32	0.1289	0.74	0.3893
Class × Herbicide × Fence	2	231	0.81	0.4483	0.49	0.6104
SeedAddition	1	231	**4.02**	**0.0461**	**17.36**	**<.0001**
Class × SeedAddition	2	231	1.10	0.3349	0.85	0.4279
Herbicide × SeedAddition	1	231	**5.96**	**0.0154**	3.34	0.0690
Class × Herbic × SeedAdd	2	231	0.84	0.4339	0.85	0.4279
Fence × SeedAddition	1	231	0.00	0.9745	1.14	0.2871
Class × Fence SeedAdd	2	231	0.80	0.4510	2.75	0.0659
Herbic × Fence × SeedAdd	1	231	0.86	0.3534	0.74	0.3893
Class × Herbic × Fence × Seed	2	231	1.75	0.1760	0.99	0.3720
Litter removal	1	264	**14.17**	**0.0002**	**6.56**	**0.0110**
Litter × Class	2	264	1.75	0.1752	0.37	0.6918
Litter × Herbicide	1	264	**11.70**	**0.0007**	0.89	0.3464
Litter × Class × Herbic	2	264	0.67	0.5121	0.32	0.7264
Litter × Fence	1	264	2.24	0.1356	1.12	0.2907
Litter × Class × Fence	2	264	0.73	0.4835	0.01	0.9899
Litter × Herbicide × Fence	1	264	0.01	0.9334	0.62	0.4307
Litter × Class × Herbic × Fence	2	264	0.01	0.9940	1.25	0.2883
Litter × SeedAddition	1	264	2.01	0.1574	**5.25**	**0.0228**
Litter × Class × SeedAd	2	264	0.68	0.5056	0.08	0.9274
Litter × Herbic × SeedAd	1	264	0.69	0.4057	0.96	0.3271
Litter × Class × Herb × SeedAd	2	264	0.49	0.6128	0.35	0.7032
Litter × Fence × SeedAdd	1	264	1.20	0.2742	0.11	0.7437
Litter × Class × Fenc × SeedA	2	264	0.44	0.6421	0.22	0.8009
Litter × Herb × Fenc × SeedA	1	264	0.11	0.7460	0.23	0.6307
Litter × Class × Herb × Fen × Seed	2	264	2.22	0.1106	0.94	0.3921

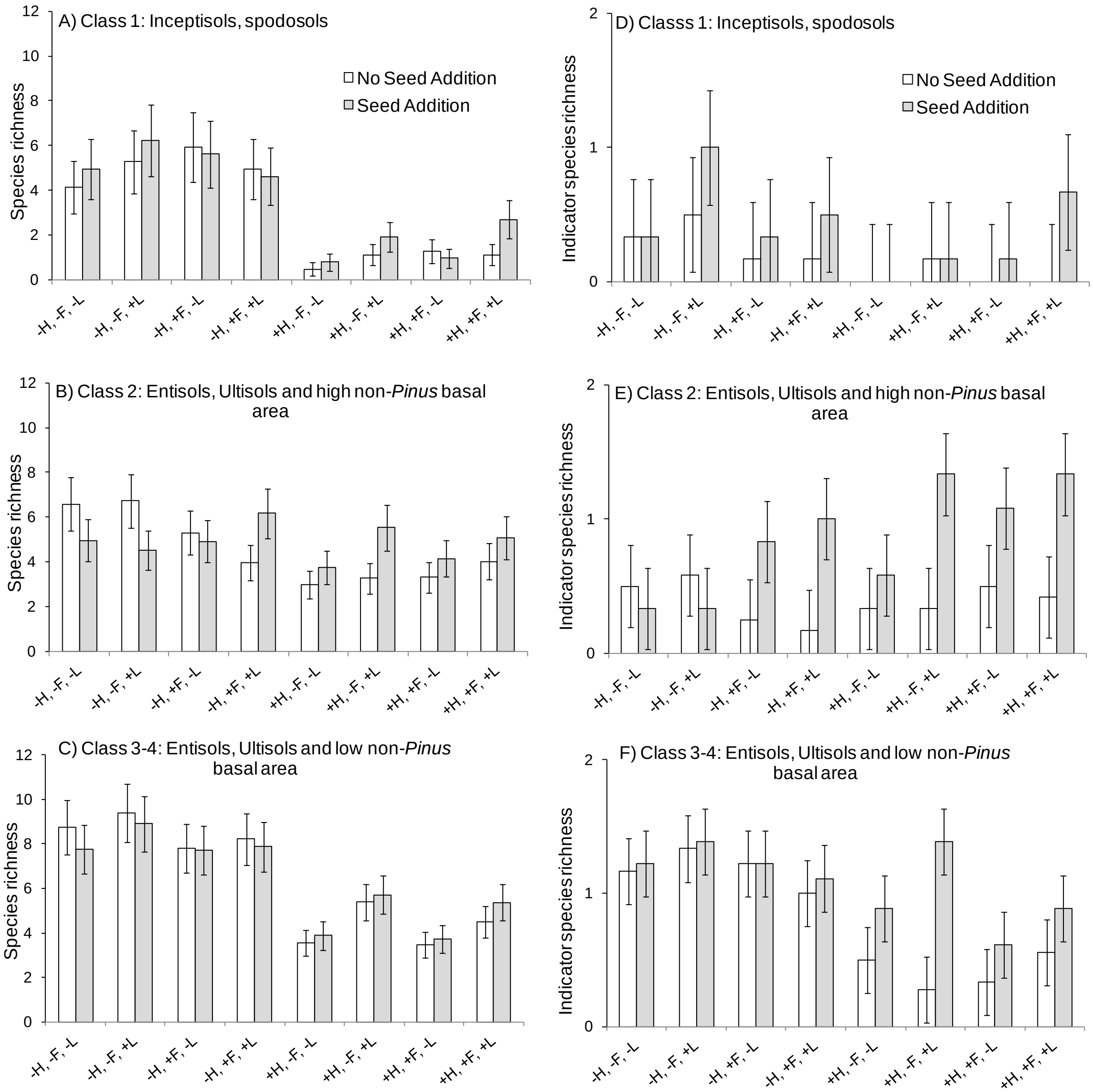

Figure 4.2.3. (A-C) Total species richness and (D-F) richness of indicator species from Fort Stewart, GA in 1x1m plots by degradation class. H = herbicide application; F = fencing, L = litter removal.

Savannah River Site

For species richness at the Savannah River Site, the main effect of seed addition ($F = 19.95$, $P < 0.001$), the two-way interaction between litter removal and herbicide ($F = 8.10$, $P = 0.005$), and the three-way interaction among degradation class, herbicide, and fencing ($F = 3.05$, $P = 0.029$) were significant (Table 4.2.4). Seed additions increased species richness by about one species per m^2, pooled across all other treatments (Figure 4.2.4). The negative effect of herbicide was slightly reduced when litter was also removed (Figure 4.2.4). The low preexisting richness in the most degraded sites (Class 1) resulted in herbicide having only a slight negative effect on richness in this class; the negative effect of herbicide was stronger in less degraded classes (Class 2-4). The non-fenced, non-herbicided plots in Class 3 had nearly double the richness of other treatments, potentially driving the significant three-way interactions (Figure 4.2.4).

The richness of indicator species at the Savannah River Site was affected by the two-way interaction between litter removal and seed addition ($F = 15.93$, $P < 0.001$) and the four-way interaction between degradation class, herbicide, fencing and seed additions ($F = 2.88$, $P = 0.037$, Table 4.3.4). Seed additions increased the richness of indicator species in both litter treatments, although this effect was larger in the litter removal treatment (Figure 4.2.4). The seed additions had more consistent effects of increasing the richness of indicator species in the least degraded sites (Class 3-4), but seed additions under certain combinations in the more degraded classes (Class 1-2) also experienced increases of up to three additional indicator species, especially when litter was also removed (Figure 4.2.4).

Table 4.2.4. SRS results for species richness in 1x1m plots in 2013. Significant effects ($P <$ 0.05) are in bold.

Effect	**Num DF**	**Den DF**	**Total richness**		**Indicator richness**	
			F	***P***	***F***	***P***
Class	3	32	**3.85**	**0.0185**	**3.00**	**0.0451**
Herbicide	1	224	**91.94**	**<.0001**	1.15	0.2841
Class × Herbicide	3	224	1.06	0.3669	**2.67**	**0.0482**
Fence	1	224	**4.26**	**0.0403**	1.78	0.1830
Class × Fence	3	224	1.56	0.2010	1.04	0.3742
Herbicide × Fence	1	224	0.95	0.3317	0.15	0.6948
Class × Herbicide × Fence	3	224	**3.05**	**0.0293**	1.05	0.3734
SeedAddition	1	224	**19.95**	**<.0001**	**89.38**	**<.0001**
Class × SeedAddition	3	224	0.29	0.8327	0.09	0.9662
Herbicide × SeedAddition	1	224	**6.16**	**0.0138**	**8.45**	**0.0040**
Class × Herbic × SeedAdd	3	224	0.46	0.7134	0.20	0.8936
Fence × SeedAddition	1	224	1.86	0.1735	0.20	0.6566
Class × Fence SeedAdd	3	224	2.12	0.0991	2.01	0.1141
Herbic × Fence × SeedAdd	1	224	2.53	0.1133	0.94	0.3336
Class × Herbic × Fence × Seed	3	224	1.49	0.2173	**2.88**	**0.0369**
Litter removal	1	256	**32.39**	**<.0001**	**13.78**	**0.0003**
Litter × Class	3	256	2.50	0.0601	1.04	0.3765
Litter × Herbicide	1	256	**8.10**	**0.0048**	1.44	0.2312
Litter × Class × Herbic	3	256	1.36	0.2554	0.46	0.7090
Litter × Fence	1	256	3.64	0.0576	0.28	0.5964
Litter × Class × Fence	3	256	1.03	0.3815	0.11	0.9560
Litter × Herbicide × Fence	1	256	0.05	0.8220	0.00	0.9778
Litter × Class × Herbic × Fence	3	256	0.55	0.6453	0.45	0.7177
Litter × SeedAddition	1	256	2.49	0.1158	**15.93**	**<.0001**
Litter × Class × SeedAd	3	256	0.25	0.8610	0.64	0.5907
Litter × Herbic × SeedAd	1	256	0.13	0.7148	1.31	0.2536
Litter × Class × Herb × SeedAd	3	256	0.53	0.6647	0.56	0.6406
Litter × Fence × SeedAdd	1	256	2.03	0.1559	0.01	0.9333
Litter × Class × Fenc × SeedA	3	256	1.66	0.1753	0.96	0.4109
Litter × Herb × Fenc × SeedA	1	256	1.38	0.2406	0.06	0.8019
Litter × Class × Herb × Fen × Seed	3	256	2.06	0.1059	0.30	0.8253

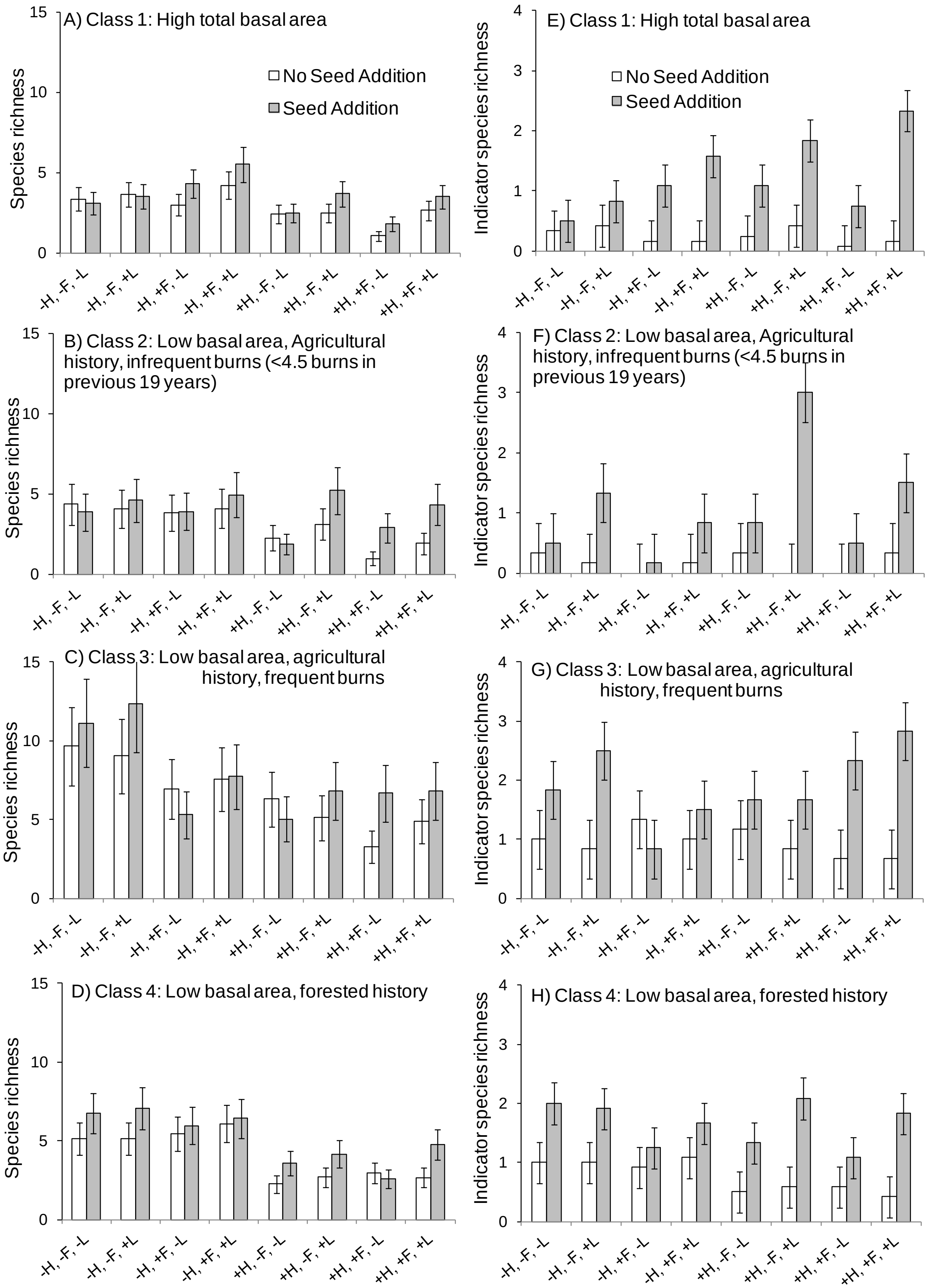

Figure 4.2.4. (A-D) Total species richness and (E-H) richness of indicator species at the Savannah River Site, SC in 1x1m plots by degradation class. H = herbicide application; F = fencing, L = litter removal.

4.2.4 Discussion

We found evidence of seed limitation in all sites regardless of degradation status, as seed addition increased species richness across all site types. Seed limitation has been previously reported to interact with other ecological filters in longleaf pine savannas with low levels of preexisting degradation (Myers and Harms 2011). However, our study highlights that the degree to which other ecological factors filter seedling establishment depends on the extant plant community, disturbance regimes, or interactions between overstory and understory plants. Priority effects were an important factor filtering seedling establishment in sites recovering from historic agriculture, which were dominated by early successional ruderal plant species. In these sites, reducing competition via herbicide application increased establishment of supplemental seeds. In sites with greater mid- and overstory plants, leaf litter inputs from these woody plants were an important filter, as we found that removing leaf litter to increase microsite availability resulted in greater seedling establishment. The effects of herbivores on the plant community and seedling establishment were more variable. It is possible that large vertebrate animals are not important consumers of herbaceous plant seedlings under some circumstances in this system, or that these effects take more time to consistently manifest. Our work extends previous work that has shown that resource availability, competitors, and disturbance by fire are important filters of seedling establishment in longleaf pine ecosystems (Myers and Harms 2009, 2011, Iacona et al. 2010) by showing that ecological filters depend on initial levels of degradation.

Our results have five main implications for the use of ecological reference models as a framework for conserving and restoring species richness in longleaf pine understory plant communities. First, our results show clear benefits of seed addition towards restoring diversity in longleaf pine understories, as seed additions had consistent positive effects on both total species richness and the richness of indicator species. Second, our results emphasize the importance of sites without a history of agriculture towards conserving plant species richness and also potentially as efficient targets for future recovery, as sites with no history of agriculture were also the sites that responded most positively to seed addition. Third, in sites with few preexisting plant species that are indicative of reference longleaf pine stands, herbicide application may be beneficial for reducing competition from the standing community of woody shrubs, woody vines, and herbaceous ruderal plants. In contrast, herbicide is never beneficial in sites with a forested history that have a high level of preexisting indicator species, and may also reduce similarity to reference in any site where it is applied (see Section 4.5). Although fire history is explicitly incorporated into our ecological reference models, we note that in some cases prescribed fires may be a more natural approach than herbicide to reduce competition from the standing plant community (Varner et al. 2005, Pyke et al. 2010). Fourth, leaf litter removal also had consistent positive effects on the recovery of indicator species added as seed, particularly in fire-suppressed sites. Finally, the effects of fencing to exclude large mammalian herbivores (deer and hogs) are more subtle and variable, but often resulted in the greatest levels of total species richness and richness of indicator species richness when applied concurrently with the other treatments (seed additions, herbicide, and litter removal). Overall, the results of our experiments provide valuable insight into the contingencies of ecosystem recovery, with direct applications for using ecological reference models as a framework towards the recovery of degraded longleaf pine savannas.

Studies spanning numerous ecosystems, from grasslands to forest understories, suggest that most plant communities are seed limited and therefore species richness can be increased through seed additions (Clark et al. 2007). This has strong relevance for management practices, where seed limitation may be alleviated through seed additions (Walker and Silletti 2006, Grman et al. 2013). Our work supports past findings of seed limitation, but also illustrates how the degree of seed limitation can be modulated by site characteristics including those affected by human land use, as well as other ecological factors. For instance, although we found that seed additions resulted in significant increases in both total species richness and the richness of indicator species, at some geographic locations these increases were generally greater in less degraded sites and, usually, those without a history of agriculture. This finding suggests that seed addition in the most degraded sites (i.e., fire suppressed sites and/or with a history of agriculture) are less effective as a management tool, than they are in less degraded sites. As a consequence, when management resources are limited, prioritizing seed addition for promoting the recovery of less degraded sites should be most cost effective. While this approach (i.e., increasing the quality of less-degraded sites while not increasing the quality of more-degraded sites) may be most cost-effective, it is important to note that the successful establishment of just a few indicator species may yield large dividends in more-degraded sites over long timescales for two reasons. First, because indicator species are often wholly absent from more-degraded sites (Brudvig et al. 2013, 2014) and our results clearly demonstrate strong seed limitation, it is likely that a few established indicator species in more-degraded habitats could serve as important drivers of recruitment and spread in degraded sites. Second, because landscapes are likely dominated by more-degraded sites compared to less-degraded sites, focusing efforts on more-degraded sites would be a means to elevate diversity and promote recovery at landscape scales.

For the most degraded sites, applying multiple management strategies may increase the success of seed additions. For instance, herbicide had consistent negative effects on species richness in our study, but did increase the effectiveness of the seed addition treatment. Therefore, if the management goal is to promote the abundance of indicator species, and since pre-existing abundances of indicator species are low in the most degraded class, herbicide applications could actually increase the effectiveness of seed additions in the most degraded sites. However, we caution that herbicide application reduced total species richness in all sites, regardless of degradation, so herbicide should only be used as a management tool in the most degraded sites. Similarly, raking litter can have positive, negative, or no effect on species richness, depending on the preexisting plant community (Kelly et al. 2000, 2002). In our study, litter removal consistently increased the effectiveness of the seed addition treatment and thus a reduction to the litter layer should be combined with seed additions when resources allow, especially in degraded sites where there are low levels of preexisting indicator species. Leaf litter layers can also be reduced by prescribed fires (Hiers et al. 2007). However, our results also illustrate that manual leaf litter removal can serve as an alternative to prescribed fires to reduced litter depth and promote establishment of seeded plant species. This alternative may be particularly useful in cases where burning may not be possible (e.g. near roads, buildings, and infrastructure) or for smaller-scale recovery efforts where implementing large burns would be prohibitive in terms of crew costs and time constraints. Importantly, we note that our manual litter removal was only conducted once, so it is not possible to generalize our results to systems where litter removal occurs frequently, such as locations where pine straw is commonly collected for sale as commercial mulch.

We found fairly consistent effects of seed additions, litter removal, and herbicide among our all three study locations. Thus, our results appear to be general at least to upland longleaf pine savannas along the Atlantic coastal plain, especially for sites degraded by reduced fire frequency and historical agriculture, as these degrading factors were used to classify our sites at in the 'All locations' groups and two individual study locations. A potential exception to this classification scheme was Fort Stewart, where differences among sites were driven primarily by edaphic factors and management-related activities (i.e., tree density; Section 3.3).

4.2.5 Conclusions

Seed additions were effective at increasing both total species richness and the richness of indicator species at all three of our study sites. The effect of seed addition was greatest in the least degraded sites, highlighting the conservation value and recovery potential of less degraded longleaf pine savannas. Applying multiple management techniques, such as litter removal and removal of competing vegetation, should increase the effectiveness of seed additions in longleaf pine savannas heavily degraded by fire suppression and historic agriculture. Where accumulated litter and the abundance of woody plants can be reduced with frequent prescribed fire, herbicides should be unnecessary. Further, since herbicides can drastically reduce native plant species richness in high quality and moderately degraded sites, their use should be limited only to cases of extreme fire suppression, where competing vegetation severely limits the establishment of savanna herbs and forbs, and prescribed fire cannot be employed.

4.3 IMPACTS OF EXPERIMENTAL TREATMENTS ON LOCAL DIVERSITY. II: SPATIAL SCALE

[This section contains material in preparation: Orrock, J. L., L. A. Brudvig, E. I. Damschen, W. B. Mattingly, J. W. Veldman, and J. L. Walker. 2014. Geographically distributed factorial experiments reveal the scale-dependent signature of competition, herbivory, and dispersal in plant communities.]

4.3.1 Introduction

Most experiments that test the role of seed additions on plant species richness are conducted at small spatial scales, most typically in $1m^2$ plots (Clark et al. 2007). Seed additions are a common management tool; however, most projects aimed at promoting the recovery of understory vegetation are carried out at much larger spatial scales (Bestelmeyer et al. 2003, Brudvig 2011). Understanding how the effects of seed additions promote the recovery of understory vegetation requires knowledge of how seed addition effects scale spatially. Furthermore, few studies have evaluated the combined effects of several, simultaneous management techniques under varying levels of degradation and at multiple spatial scales. In this section we evaluate the roles of three experimental treatments – seed additions, herbicide, and fencing to exclude consumers – on the richness of species that are indicators of high-quality, reference longleaf pine savannas in sites with varying preexisting levels of degradation and at three spatial scales: $1m^2$, $10m^2$, and $25m^2$.

4.3.2 Methods

See section 4.1 for a description of the stand selection protocol (Section 4.1.1), experimental design (Section 4.1.2), and data collection (Section 4.1.3). This section uses vegetation data collected in 2013, three years after the experiments were implemented.

Data analysis

See section 4.1.1 for a description of the degradation classes resulting from our ecological reference model (Section 3.3) for the experimental sites. In this section we use species richness of indicator species added as seed measured at the $1m^2$, $10m^2$, and $25m^2$ scales. We conducted four-way analyses of variance with degradation class, seed addition, herbicide, fencing and all interactions as the predictor variables. The litter removal treatment was not included in these analyses because this treatment was only applied at the $1\text{-}m^2$ scale. To account for the nestedness of our experimental design, we treated degradation class as the whole-plot, with all other factors as split-plots. We conducted separate analyses for each of the three scales, as well as for the 'All location' analysis and each individual study site.

4.3.3 Results

Indicator species richness at 'All locations' was affected by the main effect of degradation class, the main effect of herbicide, and the main effect of seed additions at all three spatial scales (Table 4.3.1). At the $1m^2$ and $10m^2$ scale, the interaction between degradation class and herbicide was also significant (Table 4.3.1). The interaction between degradation class and seed addition was significant only at the 10m^2 scale (Table 4.3.1). The interaction between seed addition and herbicide was significant at the 10m^2 and the 25m^2 scales (Table 4.3.1). At the 1m^2 and 10m^2 scales, herbicide had slight negative effects on indicator species richness, particularity in the least degraded sites (Class 4-6), which have the highest level of preexisting indicator species (Figure 4.3.1A-F). Seed additions fully compensated for the negative effects of herbicide on species richness at the two larger spatial scales, especially in the most degraded sites (Figure 4.3.1). However, despite the positive effects of the experimental treatments, the richness of indicator species in the sites that were fire suppressed (Class 1) or had an agricultural history (Class 3) never reached levels found in historically forested sites (Class 3-6) (Figure 4.3.1).

Table 4.3.1. Results from the ‘All location’ analysis of indicator species richness at 1m^2, 10m^2, and 25m^2 spatial scales. Significant terms ($P < 0.05$) are bolded.

			1x1m		3.16x3.16m		5x5m	
Effect	Num DF	Den DF	*F*	*P*	*F*	*P*	*F*	*P*
Class	2	105	**8.18**	**0.0005**	**7.83**	**0.0007**	**4.16**	**0.0182**
Herbicide	1	735	**72.49**	**<.0001**	**68.13**	**<.0001**	**10.86**	**0.0010**
Class × Herbicide	2	735	**29.91**	**<.0001**	**5.49**	**0.0043**	0.08	0.9275
Fence	1	735	0.82	0.3654	1.67	0.1966	0.27	0.6024
Class × Fence	2	735	0.28	0.7578	0.49	0.611	0.08	0.9210
Herbicide × Fence	1	735	1.18	0.2780	1.38	0.2401	0.39	0.5303
Class × Herbicide × Fence	2	735	1.3	0.2729	0.02	0.9844	0.06	0.9426
SeedAddition	1	735	**50.13**	**<.0001**	**179.2**	**<.0001**	**18.76**	**<.0001**
Class × SeedAddition	2	735	0.45	0.6404	**3.76**	**0.0236**	1.41	0.2451
Herbicide × SeedAddition	1	735	2.18	0.1406	**39.82**	**<.0001**	**7.58**	**0.0061**
Class × Herbic × SeedAdd	2	735	0.66	0.5148	0.31	0.7301	0.59	0.5553
Fence × SeedAddition	1	735	0.00	0.9821	0.07	0.7875	0.07	0.7870
Class × Fence × SeedAdd	2	735	0.79	0.4539	1.26	0.2837	0.13	0.8806
Herbic × Fence × SeedAdd	1	735	1.34	0.2473	0.55	0.4604	0.09	0.7602
Class × Herbic × Fence × Seed	2	735	1.20	0.3007	1.29	0.2747	0.10	0.9067

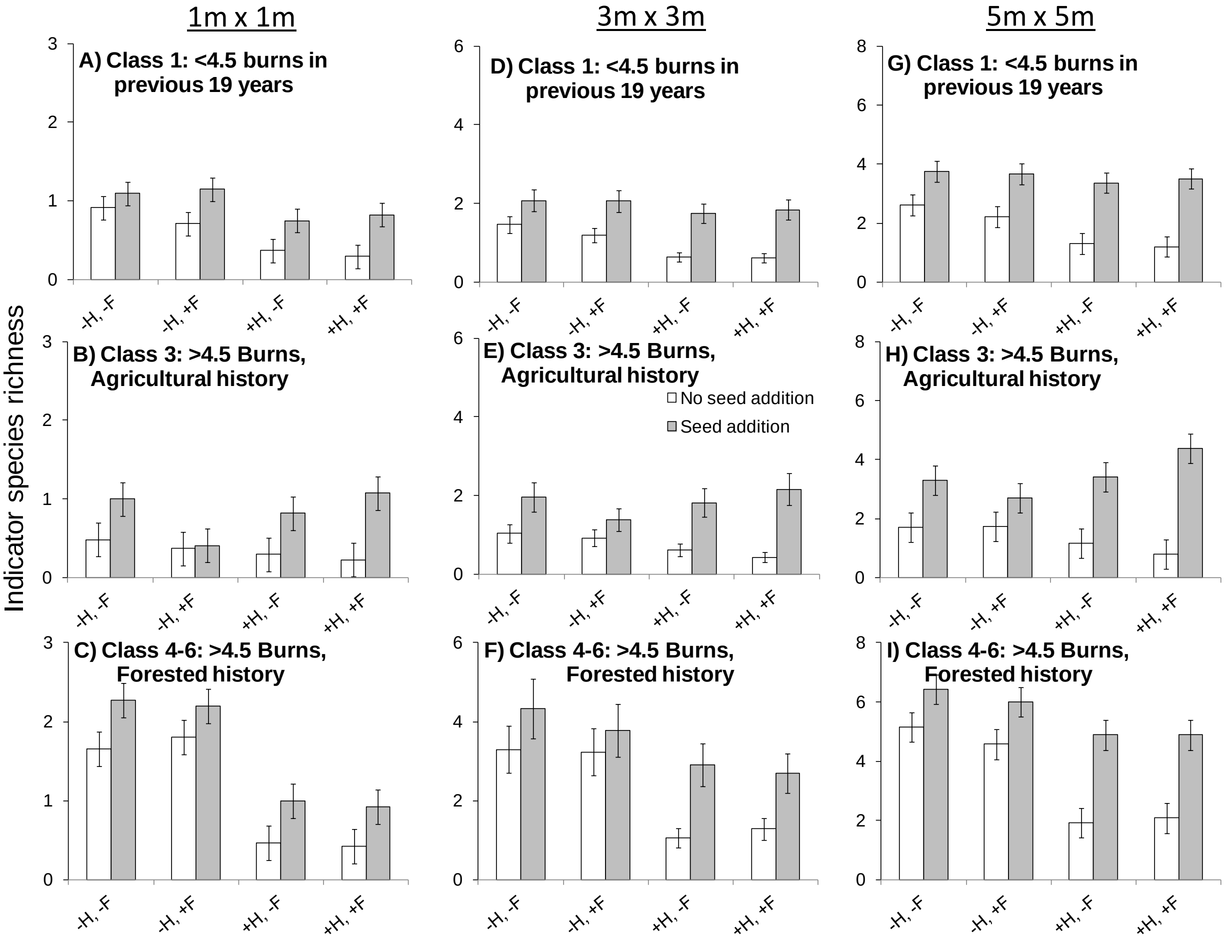

Figure 4.3.1. Richness of indicator species added as seed from all three study locations in 1x1m, 3x3m, and 5x5m plots by degradation class. Note that the y-axis changes at each spatial scale. H = herbicide; F = Fencing.

Indicator species richness at Fort Bragg was affected by the main effects of degradation class, herbicide, and seed additions, as well as the interaction between degradation class and seed addition, at all three spatial scales (Table 4.3.2). At the 1m^2 scale, the interaction between degradation class and herbicide was also significant (Table 4.3.2). The interaction between degradation class, herbicide, and seed addition was also significant at the 10m^2 and 25m^2 scale (Table 4.3.2). Herbicide negatively affected indicator species richness, particularity in sites with a forested history (Class 2), which have the highest level of preexisting indicator species (Figure 4.3.2). Seed additions increased indicator species richness and more than compensated for the negative effects of herbicide, especially in the degraded sites with an agricultural history (Figure 4.3.2). However, despite the positive effects of the experimental treatments, the richness of indicator species in the sites with an agricultural history never reached levels found in historically forested sites (Figure 4.3.2).

Table 4.3.2. Results from FTB of indicator species richness at $1m^2$, $10m^2$, and $25m^2$ spatial scales. Significant terms ($P < 0.05$) are bolded.

			1 m^2		10 m^2		25 m^2	
Effect	Num DF	Den DF	*F*	*P*	*F*	*P*	*F*	*P*
Class	1	34	**45.23**	**<.0001**	**28.92**	**<.0001**	**22.02**	**<.0001**
Herbicide	1	238	**127.13**	**<.0001**	**94.56**	**<.0001**	**112.88**	**<.0001**
Class × Herbicide	1	238	**68.37**	**<.0001**	0.00	0.9446	0.04	0.8496
Fence	1	238	0.04	0.8377	0.04	0.8395	1.78	0.1830
Class × Fence	1	238	5.09	0.0250	0.61	0.4348	3.33	0.0695
Herbicide × Fence	1	238	3.40	0.0663	1.10	0.2954	0.00	0.9518
Class × Herbicide × Fence	1	238	0.38	0.5391	0.48	0.4897	0.20	0.6556
SeedAddition	1	238	**24.88**	**<.0001**	**56.07**	**<.0001**	**77.32**	**<.0001**
Class × SeedAddition	1	238	0.57	0.453	**12.38**	**0.0005**	**17.54**	**<.0001**
Herbicide × SeedAddition	1	238	0.04	0.8377	**11.58**	**0.0008**	**10.7**	**0.0012**
Class × Herbic × SeedAdd	1	238	1.35	0.2465	1.82	0.1789	3.41	0.066
Fence × SeedAddition	1	238	0.12	0.7329	0.17	0.6779	2.92	0.0889
Class × Fence × SeedAdd	1	238	0.38	0.5391	**4.70**	**0.0312**	0.03	0.8607
Herbic × Fence × SeedAdd	1	238	1.69	0.1954	0.09	0.761	2.91	0.0892
Class × Herbic × Fence × Seed	1	238	0.23	0.6328	2.47	0.1172	0.32	0.5716

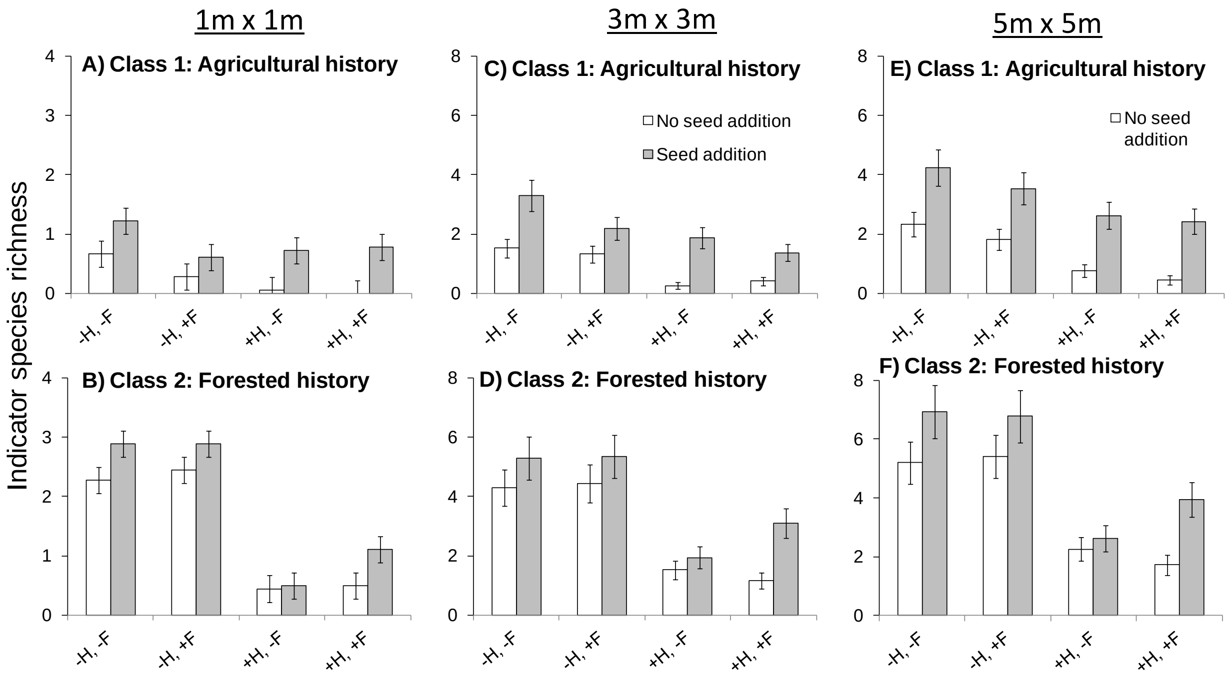

Figure 4.3.2. Richness of indicator species added as seed from Fort Bragg, NC in 1x1m, 3x3m, and 5x5m plots by degradation class. Note that the y-axis changes at each spatial scale. H = herbicide; F = Fencing.

Indicator species richness at Fort Stewart was affected by the main effect of seed additions as well as the interaction between degradation class and herbicide at all three spatial scales (Table 4.3.3). At the 1m^2, the interaction between degradation class and herbicide was also significant (Table 4.3.2). The two-way interaction between degradation class and herbicide, and the interaction between degradation class and seed addition, as well as the three-way interactions between degradation class, seed addition, and fencing were also significant at the 10m^2 and 25m^2 scale (Table 4.3.3). Herbicide negatively affected indicator species richness only in the least degraded sites (Class 3-4), which have the highest level of preexisting indicator species (Figure 4.3.3). Seed additions increased indicator species richness and at least compensated for the negative effects of herbicide (Figure 4.3.2). The combination of seed addition and fencing further increased the levels of indicator species richness, but only in the sites with high non-*Pinus* basal area (Figure 4.3.3). In many cases, experimental treatments in the high non-*Pinus* basal area sites (Class 2) were able to match or exceed levels of indicator species richness in low non-*Pinus* sites (Class 3-4; the least degraded classes).

Table 4.3.3. Results from FTS of indicator species richness at 1m^2, 10m^2, and 25m^2 spatial scales. Significant terms ($P < 0.05$) are bolded.

			1 m^2		10 m^2		25 m^2	
Effect	Num DF	Den DF	*F*	*P*	*F*	*P*	*F*	*P*
Class	2	33	2.06	0.1439	2.91	0.0683	3.22	0.0527
Herbicide	1	231	**7.25**	**0.0076**	**5.01**	**0.0261**	1.49	0.2232
Class × Herbicide	2	231	**8.95**	**0.0002**	**7.85**	**0.0005**	**5.89**	**0.0032**
Fence	1	231	0.24	0.6267	0.12	0.7341	0.04	0.8355
Class × Fence	2	231	1.61	0.2024	1.81	0.1657	1.61	0.2025
Herbicide × Fence	1	231	0.05	0.8177	2.17	0.1419	2.04	0.1543
Class × Herbicide × Fence	2	231	0.93	0.3965	0.15	0.8606	0.93	0.3966
SeedAddition	1	231	**4.53**	**0.0344**	**27.8**	**<.0001**	**61.99**	**<.0001**
Class × SeedAddition	2	231	0.50	0.6101	**4.25**	**0.0154**	**9.69**	**<.0001**
Herbicide × SeedAddition	1	231	0.90	0.3439	**5.4**	**0.021**	**11.77**	**0.0007**
Class × Herbic × SeedAdd	2	231	0.22	0.8023	0.15	0.8606	0.79	0.4563
Fence × SeedAddition	1	231	1.33	0.2499	0.43	0.5151	0.74	0.3921
Class × Fence × SeedAdd	2	231	1.46	0.2335	**5.15**	**0.0065**	**2.84**	**0.0604**
Herbic × Fence × SeedAdd	1	231	0.19	0.6634	0.01	0.9323	0.01	0.9173
Class × Herbic × Fence × SeedAdd	2	231	0.15	0.8624	0.02	0.9781	0.03	0.9707

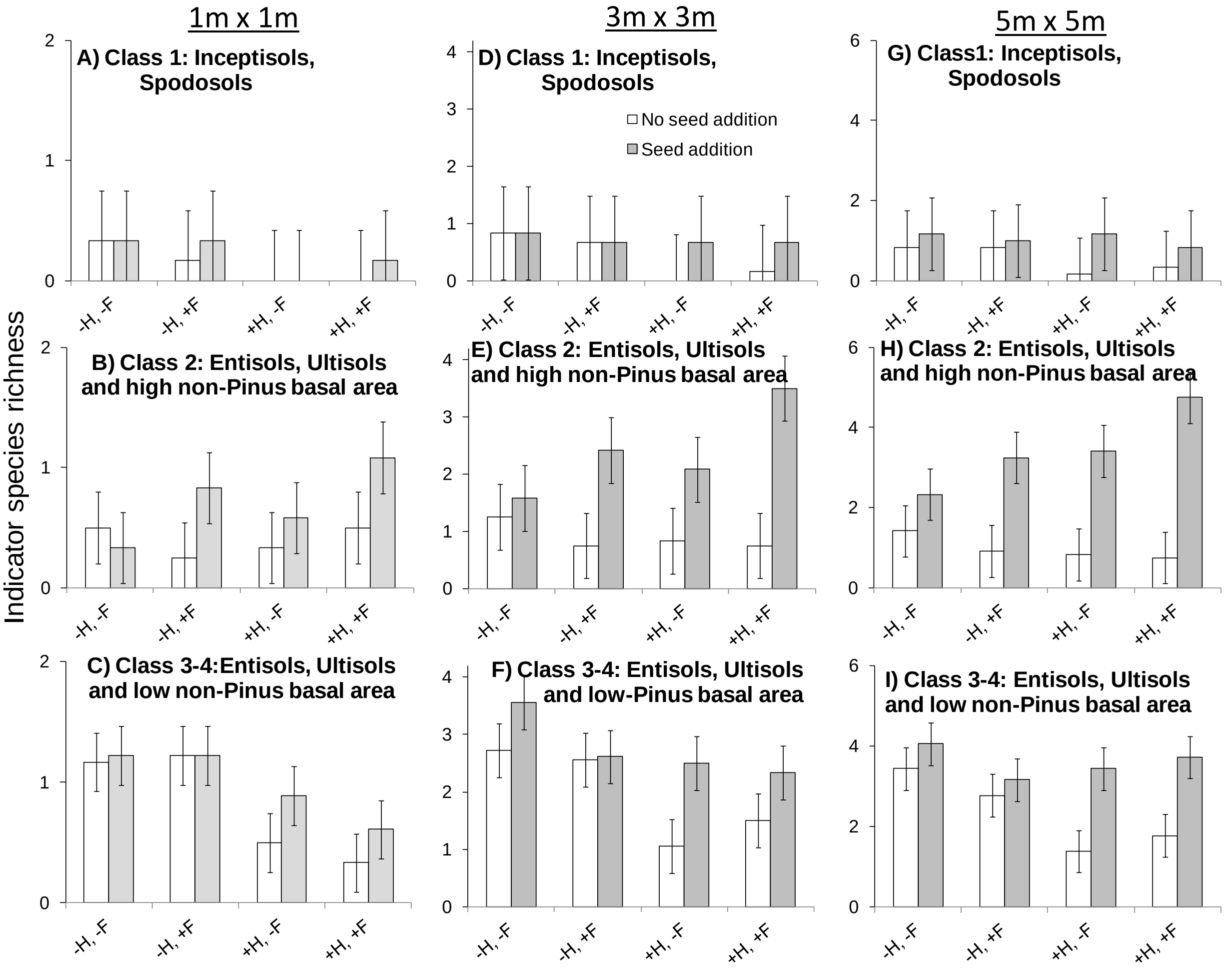

Figure 4.3.3. Richness of indicator species added as seed from Fort Stewart, GA in 1x1m, 3x3m, and 5x5m plots by degradation class. Note that the y-axis changes at each spatial scale. H = herbicide; F = Fencing.

Indicator species richness at the Savannah River Site was affected by the main effects of degradation class and seed additions at all three spatial scales (Table 4.3.4). The two-way interaction between degradation class and seed addition, and the interaction between herbicide and seed addition were also significant at the 10m^2 scale (Table 4.3.4). The four-way interaction between degradation class, herbicide, seed addition, and fencing was also significant at the 25m^2 scale. The seed additions were more effective in sites that were burned frequently (Class 3-4) and also when herbicide was applied (Figure 4.3.4). At the 25m^2 scale, the seed additions were consistently effective in the sites with high total basal area (Class 1, Figure 4.3.4I). In fire-suppressed sites with an agricultural history and low basal area (Class 2), seed additions increased richness of indicator species when herbicide was also applied (Figure 4.3.4J). In post-agricultural sites with low basal area and frequent fire (Class 3), the combination of seed additions with herbicide and fencing produced the highest levels of indicator species richness (Figure 4.3.4K). In historically forested sites, seed additions only increased the richness of indicator species when herbicide was also applied (Figure 4.3.4L). In most cases, experimental treatments in high basal area sites (Class 1) and frequently burned post-agricultural sites (Class 3), but not in infrequently burned post-agricultural sites (Class 2), were able to match levels of indicator species richness found in frequently burned post-agricultural sites (Class 4, the least degraded class) (Figure 4.3.4).

Table 4.3.4. Results from SRS of indicator species richness at 1m^2, 10m^2, and 25m^2 spatial scales. Significant terms ($P < 0.05$) are bolded.

			1 m^2		10 m^2		25 m^2	
Effect	Num DF	Den DF	*F*	*P*	*F*	*P*	*F*	*P*
Class	3	32	**4.64**	**0.0083**	**5.85**	**0.0027**	**5.53**	**0.0035**
Herbicide	1	224	0.00	0.9634	0.21	0.6492	**4.49**	**0.0353**
Class × Herbicide	3	224	1.89	0.1315	0.44	0.7256	1.41	0.2401
Fence	1	224	2.58	0.1097	2.71	0.1008	0.54	0.462
Class × Fence	3	224	0.42	0.741	1.00	0.392	**3.28**	**0.0218**
Herbicide × Fence	1	224	0.10	0.7484	0.00	0.9827	0.48	0.4904
Class × Herbicide × Fence	3	224	0.98	0.4011	0.64	0.5875	0.57	0.6339
SeedAddition	1	224	**25.02**	**<.0001**	**69.05**	**<.0001**	**116.11**	**<.0001**
Class × SeedAddition	3	224	0.41	0.745	**3.30**	**0.0213**	0.89	0.4491
Herbicide × SeedAddition	1	224	2.58	0.1097	**11.88**	**0.0007**	**32.08**	**<.0001**
Class × Herbic × SeedAdd	3	224	0.70	0.5544	0.15	0.9287	2.30	0.0779
Fence × SeedAddition	1	224	0.10	0.7484	0.84	0.36	0.00	0.9633
Class × Fence SeedAdd	3	224	0.77	0.5115	0.55	0.6489	0.87	0.4578
Herbic × Fence × SeedAdd	1	224	1.11	0.2924	0.24	0.6265	0.54	0.462
Class × Herbic × Fence × Seed	3	224	2.38	0.0703	1.37	0.2528	**4.71**	**0.0033**

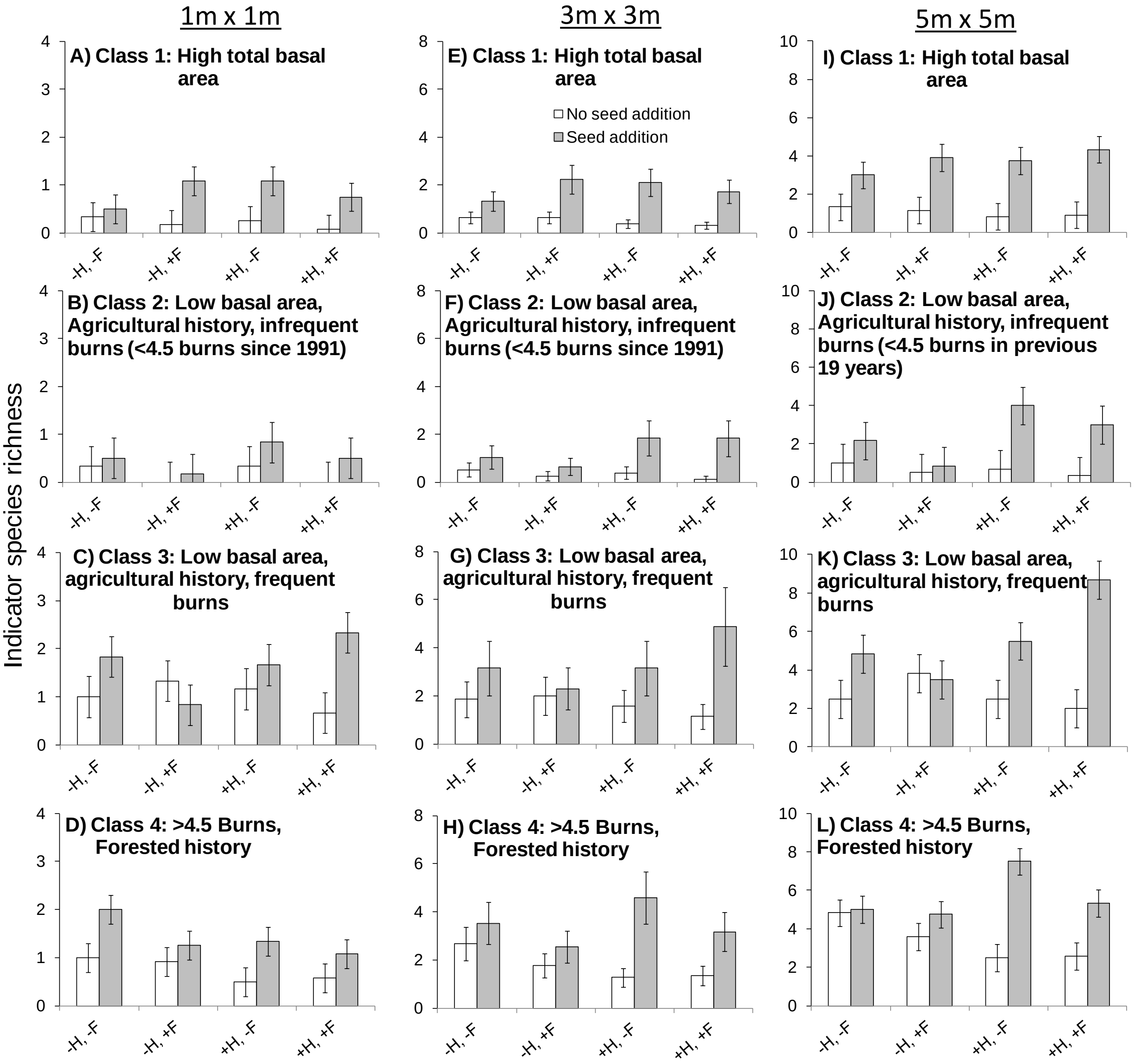

Figure 4.3.4. Richness of indicator species added as seed from the Savannah River Site, SC in 1x1m, 3x3m, and 5x5m plots by degradation class. Note that the y-axis changes at each spatial scale. H = herbicide; F = Fencing.

4.3.4 Discussion

Degradation can yield changes in species richness that are often apparent at smaller spatial scales (e.g. 1-10m^2; Kirkman et al. 2007, Brudvig and Damschen 2011). The results from our large-scale surveys confirm this pattern and indicate that degradation can also yield differences in richness and community composition that are evident at larger scales (i.e. 1000m^2; Section 3.3, Brudvig et al. 2014, Mattingly et al. 2015). The results of our experiments demonstrate that the effects of our treatments at the 1m^2 scale were generally consistent with findings at the two larger spatial scales. Moreover, the positive effect of the experimental treatments (e.g. seed additions and in some cases seed additions combined with removal of competing vegetation via herbicide) often increased at larger spatial scales. In the context of sites with an agricultural history (which are often the most degraded; Section 3.3), we expect that our results will translate to larger spatial scales (e.g. 1000m^2) because the large change in richness caused by our experimental treatments consists of species that are rarely found in post-agricultural habitats regardless of the scale of observation (Section 3.3). Moreover, our previous results suggest that removal of leaf litter can increase establishment of plants added as seed, particularly in fire suppressed sites or sites with high litter input (Section 4.2). We expect that the results of litter removal would also scale up to larger spatial scales and prescribed fires may be a feasible means to achieve both reductions of competitors and leaf litter reductions at large spatial scales (i.e., >1 ha). Given that large-scale seed collection is feasible in some areas (Walker and Silletti 2006), our findings suggest that seed additions at large scales (i.e. greater than the 25m^2 in our experimental plots) would be a promising method for promoting large-scale recovery, especially if seeds of indicator species were the primary focus of seed collections.

This study also reinforces the results presented in Section 4.2.2 above, supporting the consistent positive effects of seed additions and also the positive combined effects of herbicide and seed additions in the most degraded sites (i.e., sites with low preexisting levels of indicator species). These effects were also fairly consistent across the ‘All locations’ analysis and at each individual location, with a few caveats. At Fort Bragg, recovery of the degraded post-agricultural sites was never able to reach the levels of indicator species richness in the historically forested sites. This is perhaps do to the high floristic quality (i.e., total richness or richness of indicator species) in the historically forested sites at Fort Bragg (Section 3.3), which experienced relatively low levels of historical degradation (Aragon 2004) compared to our other two study locations (Section 3.1). Our finding that indicator richness in sites degraded by fire suppression and historic agriculture in the ‘All locations’ analysis also never reached levels found in the control plots of historically forested sites suggests fundamental recovery challenges in post-agricultural sites, likely at the seedling establishment stage. Lower seedling establishment in post-agricultural sites could be related to soil compaction or other soil properties (Mattingly and Orrock 2013, see also Section 4.4) that are altered by historic agriculture (Section 3.3). However, at the Savannah River Site, sites with combinations of low basal area and frequent fires coupled with local management activities (seed additions, herbicide, and fencing) did reach levels of indicator species richness found in historically forested sites with high fire frequency, even in plots that also received additional experimental treatments.

4.3.5 Conclusions

Seed additions contributed to the recovery of all longleaf pine savannas regardless of preexisting degradation status, but degraded sites may gain additional benefit by also removing existing vegetation prior to seeding. Furthermore, the positive effects of seed addition and in some cases combined with removal of competing vegetation via herbicide (or other means) that we documented at small spatial scales (1m^2) were generally consistent and often increased at larger spatial scales (10-25m^2). However, to reach levels of indicator species richness found in the least degraded sites, local management activities may need to be coupled with site-level management activities such as canopy thinning and maintaining frequent fires. Overall, the use of ecological reference models are valuable for predicting recovery at any given site based on its preexisting level of degradation and likely scale up to the spatial scales that management activities usually occur.

4.4 EFFECTS OF SOIL COMPACTION ON LOCAL DIVERSITY

[This section contains material in preparation: Mattingly, W.B., A. Alstad, L.A. Brudvig, E.I. Damschen, P.G. Hahn, J.L. Orrock, J.W. Veldman, and J.L. Walker. 2014. Soil legacy effects of agricultural land use reduce longleaf pine understory plant diversity.]

4.4.1 Introduction

The legacy of agricultural land use can shape many contemporary ecological patterns and processes (Foster et al. 2003, Flinn and Vellend 2005, Cramer et al. 2008). For example, post-agricultural lands often exhibit substantial reductions in plant diversity and abundance (Flinn and Vellend 2005, Hermy and Verheyen 2007), altered soil microbial communities and nutrient availability (Baer et al. 2003, Fraterrigo et al. 2005, 2006, Kulmatiski and Beard 2008) and lasting changes in soil properties, including reductions in organic matter and water-holding capacity (Knops and Tilman 2000, Foster et al. 2003, McLauchlan 2006).

The lasting effects of agricultural land use on plant communities are thought to be driven primarily by soil properties (Dupouey et al. 2002, Foster et al. 2003, Fraterrigo et al. 2006, Dambrine et al. 2007). Soil compaction is considered the most serious environmental degradation resulting from conventional agriculture (McGarry 2001). Agricultural practices compact soil though use of heavy machinery, short crop rotations and heavy grazing (Hamza and Anderson 2005). Soil compaction alters the structure of the soil by decreasing void space between particles and increasing soil density (Defossez and Richard 2002). These structural changes may in turn affect the plant community by interfering with soil processes such as water infiltration (Lipiec et al. 2006) and nutrient mineralization (Hamza and Anderson 2005). To date, however, much of what we know about the impacts of soil compaction on plants and plant communities comes from research on crop plants. Therefore, understanding the effects of soil compaction on non-agricultural plant communities is critically important, especially in order to enhance outcomes of management efforts on formerly cultivated lands.

In this section we examined the relationship between agricultural land-use history, soil compaction and understory plant abundance and diversity. Specifically, we ask: (1) whether post-agricultural longleaf pine savannas exhibit reduced soil quality (in terms of reduced soil organic matter and moisture holding capacity and increased soil compaction), relative to savannas lacking agricultural disturbances, and (2) whether areas with highly compacted soils are characterized by lower plant cover and richness, and if these relationships differ between historically cultivated and forested savannas at our three study locations. Relationships between soil organic matter or water holding capacity and plant cover/richness are presented in Section 3.5, so we focus on the effects of soil compaction in this section.

4.4.2 Methods

Study system and site selection

See section 3.1 for a description of the three study locations. For the selection of remnant and post-agricultural sites used in this section, we restricted our selection to those sites with soil types belonging to the Ultisol soil order, a common soil order throughout much of the southeastern United States (Wyatt 1995). We standardized our selection of study sites based on soil order because soil quality may influence the magnitude of compaction effects on plant community structure (McLauchlan 2006). Finally, we used annual fire records to confirm that our final selection of study sites spanned a broad range of fire-return intervals. Over the past several decades, managers at each study location have used prescribed fires to restore and maintain upland longleaf pine savannas. Because fire management is not uniform across the landscape, each location contains fire-suppressed sites interspersed among more frequently burned areas. Using these selection criteria, 90 sites in total were selected across the study region (Fort Bragg: 18 remnant vs. 18 post-agricultural sites; SRS: 12 remnant vs. 15 post-agricultural sites; and Fort Stewart: 11 remnant vs. 16 post-agricultural sites).

Data collection

See Section 3.1.2 for a description of vegetation surveys in the observational sites. Following vegetation surveys, we quantified soil compaction and measured three additional environmental variables that are known to be important determinants of understory plant diversity in this study system: soil organic matter (OM), overstory canopy cover, and prescribed fire frequency (Kirkman et al. 2001; Walker and Silletti 2006). For each location, replicate sites spanned broad environmental gradients with respect to these variables (Table 3.1), and thus we included these variables as covariates in our analyses to better evaluate relationships between soil compaction and understory plant diversity. For each 10-m^2 plot, soil compaction was quantified by taking the mean of four measurements from a cone penetrometer (Dickey-John Corporation, Auburn, IL, USA) positioned at the midpoint along each side of the plot. Here, we measured the soil depth at which 2 MPa was attained, a level of soil compaction beyond which plant performance is generally constrained (Bassett et al. 2005). Soil OM was quantified for each 10-m^2 plot, wherein 8 soil cores (each 2.5 cm in diameter and 15 cm in depth) were collected along the perimeter of the plot, homogenized, and processed by determining the loss of mass on ignition at 360° C (Brookside Laboratories, Inc., New Knoxville, OH, USA). Canopy cover was quantified through the analysis of hemispherical images (Hemiview Version 2.1, Dynamax Inc., Houston, TX, USA) taken at a 1-m height above the center of each 10-m^2 plot, following standard methods. Finally, for each site, fire frequency was determined as the number of fires occurring between 1991 and 2009. As with the understory plant variables, all plot-level environmental measurements were averaged to derive the site-level measures used in our analyses.

Data analysis

Objective 1: examining variation in soil compaction between land-use history at the three study locations

We used linear models to evaluate relationships between historical land-use status, soil properties, and understory plant species richness (SAS Version 9.1, SAS Institute Inc., Cary, NC, USA). To test hypothesis 1, we used a multivariate analysis of variance to evaluate the effects of historical land-use status (i.e. remnant vs. post-agricultural) and study location on soil organic matter, moisture holding capacity, and compaction. Soil variables were highly correlated (App 1), necessitating this multivariate approach to evaluating the effects of historical land-use status on soil properties. For this model, land-use status and study location were treated as fixed effects, and we present Wilks' lambda as the test statistic for multivariate analysis (Scheiner 2001). Subsequent univariate analyses were then used to assess land-use effects on each of the three soil properties per study location.

Objective 2: examining relationships between soil compaction and vegetation cover and species richness at three locations.

We used analysis of covariance to examine the response of vegetation characteristics (cover or richness) to soil compaction (continuous variable), land-use history (categorical variable), and their interaction. A significant soil compaction by land-use history interaction would indicate that the relationship between soil compaction and vegetation characteristics differs between land-use history categories. We present the results from the observational sites only (see Section 3.1).

4.4.3 Results

Objective 1

Soil organic matter, moisture holding capacity, and compaction differed substantially among study locations and between remnant and post-agricultural sites and the strength of the land-use effect on each of these soil properties differed among study locations (location × land use interactions: Table 4.4.1). Specifically, agricultural land-use legacies were associated with reduced soil organic matter and moisture holding capacity at SRS and Fort Stewart and with increased soil compaction at Fort Bragg and SRS (Figure 4.3.1).

Table 4.4.1. Results of a MANOVA and subsequent univariate analyses of the effects of study location and land-use history on three soil properties: soil organic matter (SOM), soil moisture holding capacity (SMHC), and soil compaction.

	Location			Land-use history			Location × land use		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Multivariate effects									
Wilks' lambda	6,480	15.3	**<0.001**	3,240	18.2	**<0.001**	6,480	9.0	**<0.001**
Univariate effects									
SOM	2,242	6.6	**0.002**	1,242	9.5	**0.002**	2,242	8.7	**<0.001**
SMHC	2,242	14.5	**<0.001**	1,242	13.9	**<0.001**	2,242	9.2	**<0.001**
Compaction	2,242	40.8	**<0.001**	1,242	28.1	**<0.001**	2,242	13.9	**<0.001**

At Fort Bragg, soil organic matter was positively correlated with moisture holding capacity (r = 0.64, $P < 0.001$), but neither of these soil properties differed between remnant and post-agricultural sites (Figure 4.4.1a,b). Conversely, soil compaction was greater among sites with a history of agriculture, relative to remnant sites (Figure 4.3.1c). For example, 66% of post-agricultural sites exhibited compaction levels exceeding 2 MPa within the upper 15 cm of the soil profile, whereas this level of compaction was observed at 36% of remnant sites. At Fort Bragg, soil compaction was not correlated with soil organic matter ($r = -0.15$, $P = 0.17$) or moisture holding capacity ($r = 0.10$, $P = 0.34$).

At SRS, soil moisture holding capacity was positively correlated with soil organic matter ($r = 0.53$, $P < 0.001$) and compaction ($r = 0.33$, $P = 0.003$), but there was no correlation between organic matter and compaction at this study location ($r = 0.03$, $P = 0.80$). Post-agricultural sites exhibited reduced soil organic matter and moisture holding capacity, relative to sites lacking a history of agriculture (Figure 4.4.1a,b). Further, as observed at Fort Bragg, post-agricultural sites were more compacted than remnant sites at SRS (Figure 4.4.1c). At this study location, 27% of post-agricultural sites exhibited compaction levels exceeding 2 MPa within the upper 15 cm of the soil profile. In comparison, 7% of the remnant sites at SRS exhibited this level of compaction.

At Fort Stewart, soil organic matter was positively correlated with moisture holding capacity ($r = 0.68$, $P < 0.001$). Further, both of these soil properties differed between the two land-use categories, whereby post-agricultural sites exhibited reduced levels of soil organic matter and moisture holding capacity relative to remnant sites (Figure 4.4.1a,b). Conversely, land-use history did not affect soil compaction at this study location (Figure 1c). Compaction levels exceeding 2 MPa within the upper 15 cm of the soil profile were observed at 37% and 31% of post-agricultural and remnant sites, respectively. As with Fort Bragg, soil compaction was neither correlated with soil organic matter ($r = -0.14$, $P = 0.21$) nor moisture holding capacity ($r = -0.19$, $P = 0.08$) at Fort Stewart.

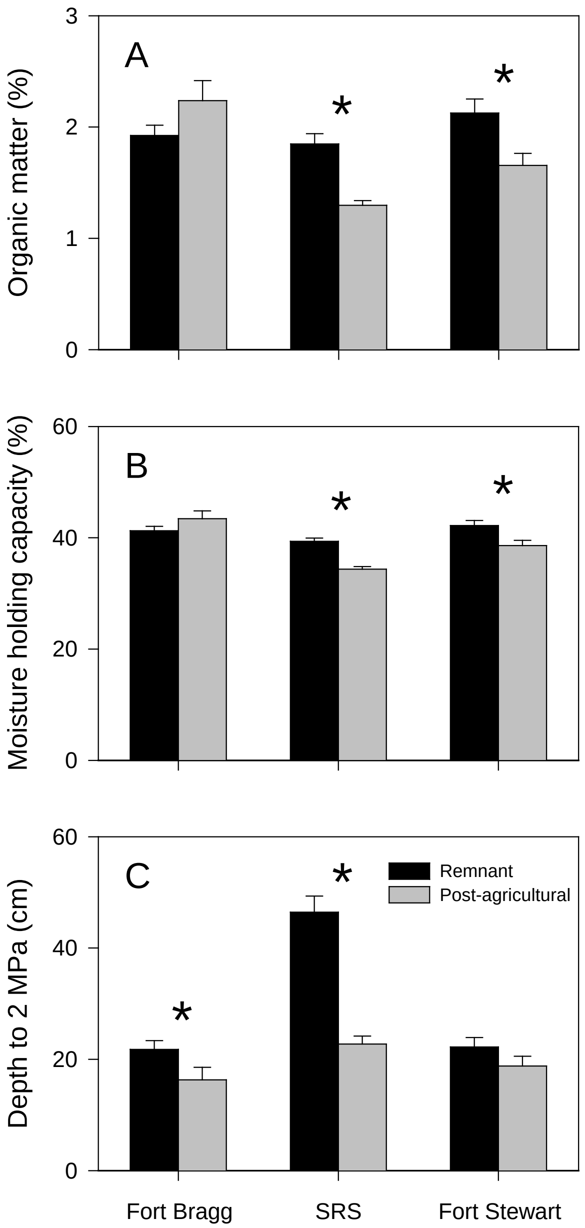

Figure 4.4.1. The effects of land-use history on soil organic matter (A), soil moisture holding capacity (B), and soil compaction (C) at each of the three study locations. Data represent mean values ± one standard error. Asterisks denote significant differences in mean soil property values between remnant and post-agricultural sites per study location.

Objective 2

At Fort Bragg, both vegetation cover and plant species richness differed with land-use history and soil compaction negatively correlated with vegetation cover but did not correlate with plant species richness (Figure 4.4.2). The interaction between land-use history and soil compaction was not significant for either vegetation cover or richness (Table 4.4.2).

Table 4.4.2. ANOVA table showing the results of the effect of soil compaction and land-use history on vegetation cover and plant species richness. Soil compaction was measured as the depth to 2 MPa using a push probe.

	Vegetation cover			**Plant species richness**		
Variable	**df**	***F***	***P***	**df**	***F***	***P***
FTB						
Depth to 2 Mpa	1	5.11	0.026	1	0.01	0.912
Land-use history	1	16.63	0.000	1	12.04	0.001
Depth × Land-use	1	0.07	0.796	1	2.45	0.121
Residuals	94			94		
FTS						
Depth to 2 Mpa	1	0.04	0.834	1	1.03	0.313
Land-use history	1	12.65	0.001	1	3.86	0.053
Depth × Land-use	1	0.23	0.634	1	0.04	0.848
Residuals	77			77		
SRS						
Depth to 2 Mpa	1	4.50	0.038	1	0.87	0.355
Land-use history	1	13.72	0.000	1	8.82	0.004
Depth × Land-use	1	0.31	0.579	1	0.08	0.784
Residuals	65			65		

At Fort Stewart, land-use history affected both vegetation cover and plant species richness but soil compaction and the interaction between land-use history and soil compaction did not (Table 4.4.2).

At the Savannah River Site, both vegetation cover and plant species richness differed with land-use history and soil compaction negatively correlated with vegetation cover but showed no correlation with plant species richness (Figure 4.4.2). The interaction between land-use history and soil compaction was not significant for either vegetation cover or richness (Table 4.4.2).

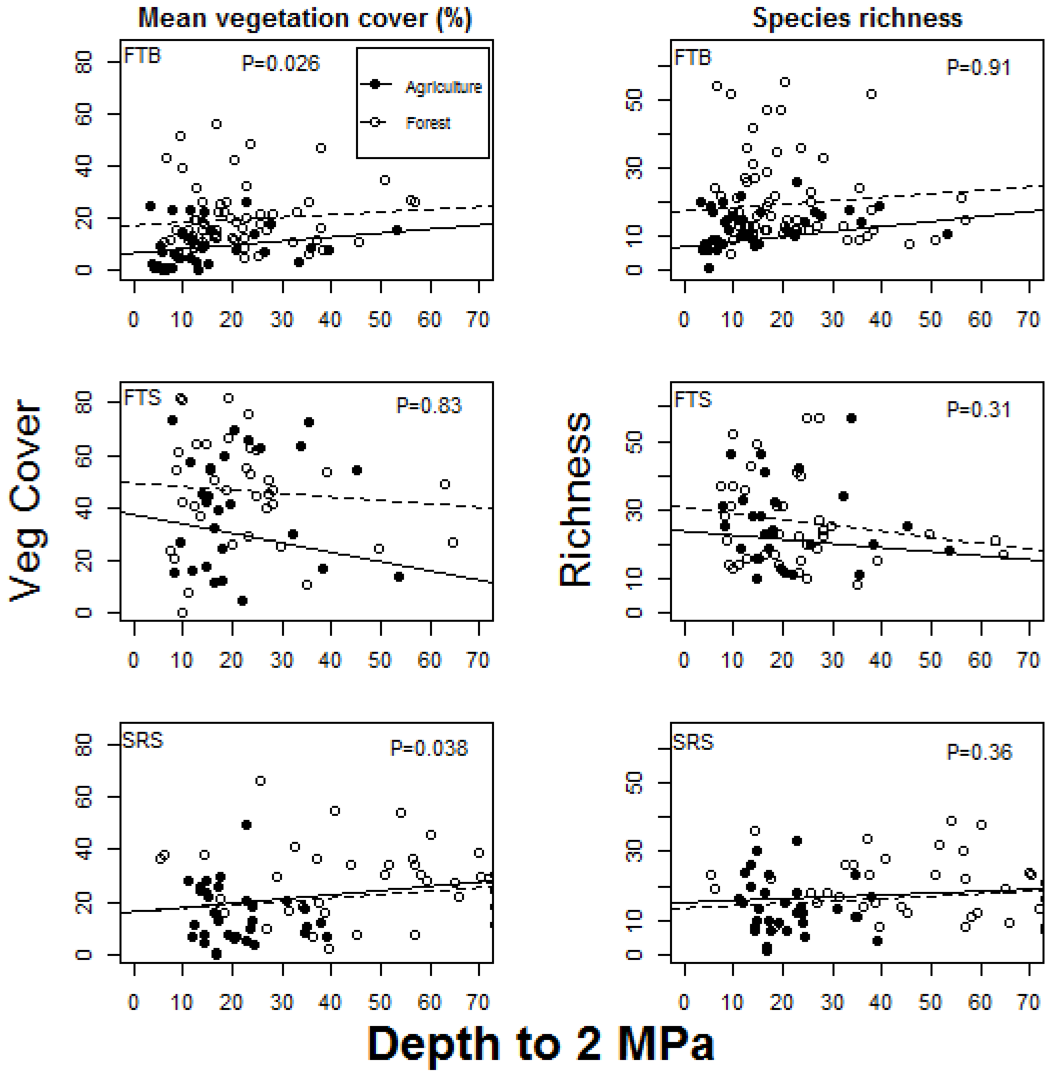

Figure 4.4.2. Effects of soil compaction on vegetation cover (left column) and plant species richness (right column) in sites with a history of agriculture (Agriculture) or a forested history (Forest). Soil compaction was measured as the depth to 2 MPa using a push probe, where higher values indicate less compacted soils. Lines are fit through data for each land-use history type. P-values are for the effect of soil compaction on the vegetation characteristic, pooled across land-use histories.

4.4.4 Discussion

Agricultural land-use legacy effects on soil quality

We found significant changes in two or three ecologically relevant soil properties measured in post-agricultural longleaf pine savannas at all three of our study locations. Generalizing across our three locations, we found decreased organic matter, moisture holding capacity, and increased compaction in soils with a history of agriculture (Figure 4.3.1). This finding, that historical agriculture can create persistent changes in soil properties, agrees with other research in grasslands and pine forests (Foster et al. 2003, McLauchlan 2006, Maloney et al. 2008, Brudvig et al. 2013). Alterations to soil properties have been shown to have important and long-lasting impacts on nutrient cycling, plant growth, and soil biota (Fraterrigo et al. 2005, Postma-Blaauw et al. 2010), and thus are important to consider in management and conservation contexts aimed at promoting the recovery of plant diversity (Foster et al. 2003).

We also found substantial variation in the response of soil properties among our three locations, which may be understood in context of the intensity and time since abandonment of historical agriculture. After initial destruction of soil carbon pools by cultivation, organic carbon tends to accumulate following the abandonment of agricultural fields, although the carbon pool can take up to centuries to fully recover (Richter et al. 1999, Knops and Tilman 2000, Maloney et al. 2008). The low intensity of historical agriculture (Aragon 2004) and nearly a century since agricultural abandonment at Fort Bragg appears to have allowed soil organic matter and water holding capacity to recover. However, a legacy on soil compaction still exists at FTB. In contrast, we detected significant reductions in soil organic matter and moisture holding capacity at both FTS and SRS, perhaps due to the more recent abandonment of agriculture at these two sites (~70 and 60 years, respectively). Soil compaction was also greater in post-agricultural sites compared to remnant sites, but only at SRS. The dominant soil order at SRS is Ultisols, whereas a variety of soil orders are at FTS, including Ultisols, Entisols, Inceptisols, and Spodosols. Different soil orders may be more or less susceptible to compaction (McLauchlan 2006), which could potentially account for the lack of soil compaction we found in post-agricultural sites at FTS. Nevertheless, our results highlight long-lasting agricultural legacy effects on soil properties, which might alter plant community composition through a variety of mechanisms.

Plant-soil relationships in understory communities

Previous studies in the longleaf ecosystem have documented negative impacts of agricultural land use on native understory plant communities (Brudvig and Damschen 2011, Veldman et al. 2014), but have not converged on a mechanistic understanding of these impacts. Our results reveal that one key mechanism may be the significant and long-lasting effects of historic agriculture on soil compaction, as we found significant reductions in plant cover at FTB and SRS related to soil compaction. Soil compaction levels as low as 0.6 MPa can restrict plant establishment and growth, although this varies among species and has largely been tested with crop species (Bassett et al. 2005). In a separate study at Fort Bragg, we found that establishment of two species of *Lespedeza* was greater in remnant longleaf forests, with no history of agriculture compared to post-agricultural forests and establishment success negatively correlated with high levels of soil compaction (Mattingly and Orrock 2013). However, we caution that the effects of soil compaction on plant cover do not appear to be universal, as we found no effect of soil compaction on plant cover at FTS or on plant richness at any of our three locations.

In addition to the effects of soil compaction, we also found significant differences in SOM and SMHC between land-use histories, which might also affect plant cover and richness (see Section 3.6). Since there can be strong correlations among soil compaction, soil organic matter, and moisture holding capacity, it is difficult to disentangle the relative roles of different soil properties in driving plant community dynamics. However, our results show that legacies of historic agriculture have persistent effects on soil properties that can manifest themselves as altered metrics of plant community structure.

Implications for recovery and conservation

Recovery of longleaf habitat on post-agricultural sites may be hampered by altered soil properties. Typical management techniques in this system include sowing seeds of native species and reinstating disturbance via prescribed fire. However, seedling establishment is known to be lower on sites with a history of agriculture than they are on remnant sites (Mattingly and Orrock 2013, Hahn and Orrock in review), and work in other systems has shown that prescribed fire alone may not restore plant community composition or soil structure (Motzkin et al. 1996, Stephenson 1999). The degree to which altered soils prevent management efforts from producing a plant community similar to reference or a historic condition remains to be seen. If effects are large, successful recovery on post-agricultural sites may require treatments that mitigate soil compaction and approximate historic soil conditions before plant propagules are added or fire is reinstated. To date, few recovery studies have explored possible treatments for mitigating agricultural soil compaction or nutrient imbalance. Exceptions include Kay (1988), who reported mixed success with a revegetation project in California desert after soil compaction was reduced by using a chisel to rip the soil to a depth of 25cm, and Blumenthal et al. (2003), who found that soil carbon amendments increased recovery in a Minnesota tallgrass prairie. Studies from agricultural systems recommend reducing the negative effects of soil compaction by planting species with taproots or by using deep cultivation methods (Hamza and Anderson 2005). Nevertheless, our results suggest that future research should examine the potential for various soil management practices to increase the effectiveness of more common management techniques, such as prescribed fire and propagule introduction. Such work will also better inform the degree to which altered soil properties represent a recovery-impeding legacy of historical agriculture.

4.5 EFFECTS OF EXPERIMENTAL TREATMENTS ON SIMILARITY TO REFERENCE SITES

[This section contains material in preparation: Orrock, J. L., L. A. Brudvig, E. I. Damschen, W. B. Mattingly, J. W. Veldman, and J. L. Walker. 2014. Geographically distributed factorial experiments reveal the scale-dependent signature of competition, herbivory, and dispersal in plant communities.]

4.5.1 Introduction

In this section, we evaluate how sites with varying levels of initial degradation respond to different experimental treatments aimed at recovering understory vegetation by comparing experimental plots to reference sites. We selected longleaf pine stands with different levels of degradation based on our previous ecological reference model (Section 3.3). The major degrading factors were fire suppression, high tree basal area, and historical agricultural land use. These three factors are key drivers of degradation across our study locations and throughout the longleaf pine ecosystem (Brudvig et al. 2014). Within these stands we conducted a factorial manipulation of processes that may limit the recovery of understory vegetation including seed limitation, competition with pre-existing understory plants, herbivory, and forest floor accumulation. We then compared these experimental plots to the reference stands in order to understand how these ecological processes limit the similarity of plant community composition to that of reference sites and in which ways these limitations may differ among sites that vary in their initial levels of degradation.

4.5.2 Methods

See section 4.1 for a description of the stand selection protocol (Section 4.1.1), experimental design (Section 4.1.2), data collection (Section 4.1.3), and classification of reference stands (4.1.5). This section uses vegetation data collected in 2013, three years after the experiments were implemented.

Statistical Analysis

We report the results from all three locations combined (“All Locations” analysis) and for each individual location. We used the ecological reference model classification scheme from Section 3.3 to assign each experimental site a degradation class. Because we used fewer sites in the experimental phase of this project, we could not fully replicate all degradation classes from the original classification scheme. See Section 4.1.1 for a description of the reference model for the experimental sites.

To analyze the effects of our experimental treatments on similarity to reference site understory community composition, we used linear mixed models with the similarity between experimental plot and reference site community composition as the response. We first calculated the pair-wise Jaccard dissimilarity index for each experimental plot compared to each of eight plots in the reference sites within each location. We used data from 15 reference sites at Fort Bragg, 8 at Fort Stewart, and 10 at the Savannah River Site (see also Section 3.4). We then averaged values for each plot to get a mean dissimilarity for each experimental plot to all reference plots within a location. Similarity was then calculated as 1-mean Jaccard dissimilarity (see also Section 3.4). Reference sites were identified by regional experts and were part of the Carolina Vegetation Survey (see also Section 3.3 and Section 4.1.5 for more details). We conducted 5-way factorial analyses of variance with degradation class, seed addition, herbicide application, fencing, litter removal, and all possible interactions as fixed-effect predictor variables. To account for the nestedness in our experimental design, we treated each site (i.e. degradation class) as the whole plot, the experimental manipulations as the split-plot treatments (i.e. seed additions, herbicide, and fencing), and litter removal as the split-split-plot.

4.5.3 Results

Similarity to reference stands in the 'All locations' analysis was affected by the 5-way interaction among degradation class, seed addition, herbicide, fencing, and litter removal (F = 3.83, P = 0.02, Table 4.5.1). Overall, the sites with a forested history were most similar to the reference sites (Figure 4.5.1). Herbicide application reduced similarity to reference stands in fire suppressed sites (Class 1) and sites with a forested history (Class 4-6), but had no effect in sites with an agricultural history (Class 3). The effect of seed addition was variable, but generally weak in all degradation classes and when combined with other management strategies (Figure 4.5.1).

Table 4.5.1. All location results of similarity to reference measured in 1m^2 plots in 2013.

Effect	Num DF	Den DF	*F*	*P*
Class	2	105	17.07	<.0001
Herbicide	1	735	454.58	<.0001
Class × Herbicide	2	735	44.92	<.0001
Fence	1	735	1.46	0.2271
Class × Fence	2	735	1.22	0.2946
Herbicide × Fence	1	735	0.00	0.9778
Class × Herbicide × Fence	2	735	0.02	0.9816
SeedAddition	1	735	0.00	0.9705
Class × SeedAddition	2	735	0.29	0.7519
Herbicide × SeedAddition	1	735	0.08	0.7765
Class × Herbic × SeedAdd	2	735	1.32	0.2670
Fence × SeedAddition	1	735	0.41	0.5208
Class × Fence × SeedAdd	2	735	0.03	0.9684
Herbic × Fence × SeedAdd	1	735	1.23	0.2687
Class × Herbic × Fence × Seed	2	735	0.01	0.9854
Litter removal	1	835	32.77	<.0001
Litter × Class	2	835	0.01	0.9864
Litter × Herbicide	1	835	11.13	0.0009
Litter × Class × Herbic	2	835	3.00	0.0505
Litter × Fence	1	835	1.34	0.2472
Litter × Class × Fence	2	835	0.91	0.4022
Litter × Herbicide × Fence	1	835	3.12	0.0776
Litter × Class × Herbic × Fence	2	835	1.53	0.2164
Litter × SeedAddition	1	835	0.04	0.8477
Litter × Class × SeedAdd	2	835	1.40	0.2480
Litter × Herbic × SeedAdd	1	835	2.67	0.1023
Litter × Class × Herb × SeedAdd	2	835	1.68	0.1878
Litter × Fence × SeedAdd	1	835	4.15	0.0420
Litter × Class × Fence × SeedAdd	2	835	0.33	0.7190
Litter × Herb × Fence × SeedAdd	1	835	0.97	0.3257
Litter × Class × Herb × Fen × SeedAdd	2	835	3.83	0.0222

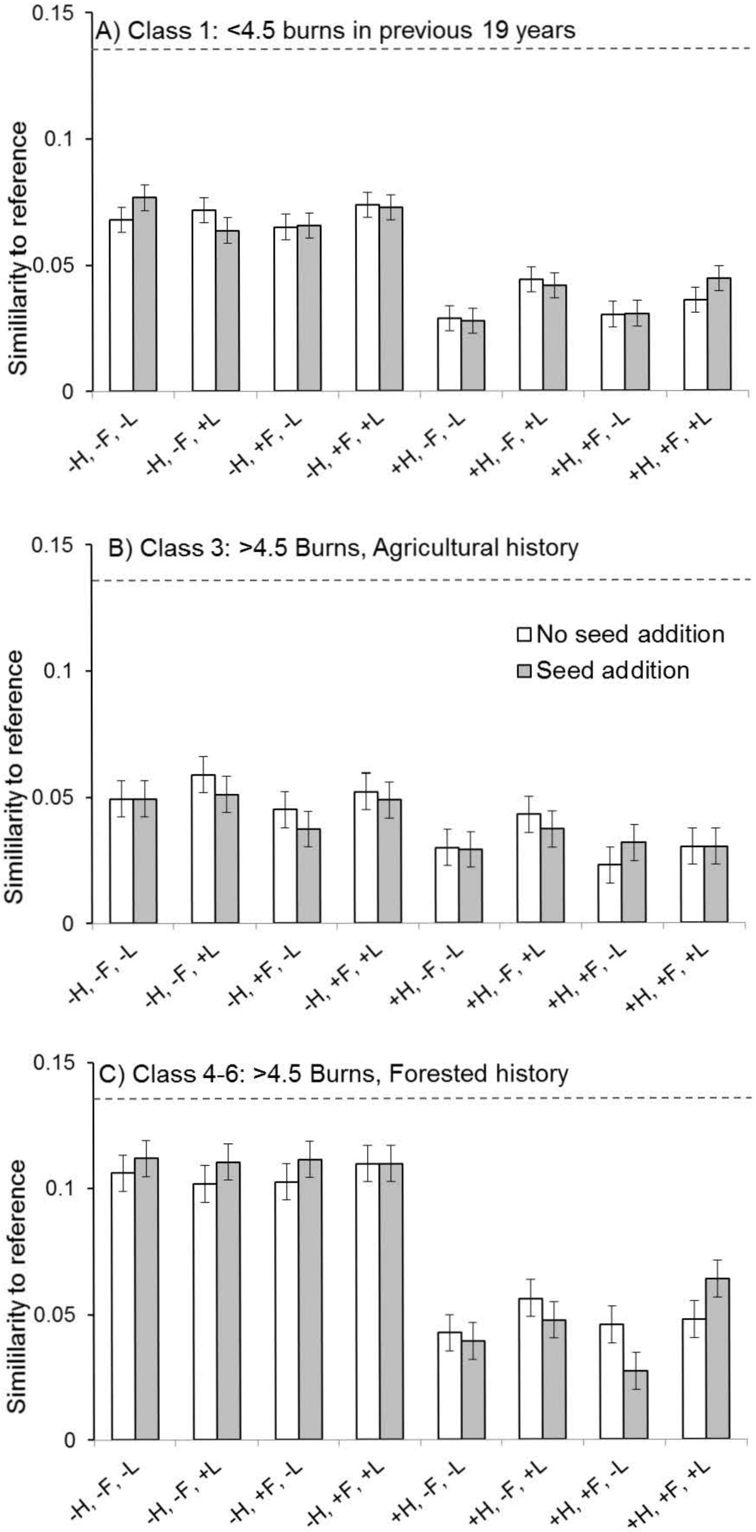

Figure 4.5.1. Similarity of plant communities in 1x1m plots compared to the reference longleaf pine savannas using the Jaccard similarity index by degradation class. H = herbicide application; F = fencing, L = litter removal. Dashed lines indicate the mean similarity value among reference stands.

Similarity to reference stands at Fort Bragg was affected by the three-way interactions among degradation class, herbicide, and litter removal (*F* = 4.01, *P* = 0.046) and among herbicide, fencing, and litter removal (*F* = 4.07, *P* = 0.044). There was also a marginally significant two-way interaction between degradation class and seed addition (*F* = 3.55, *P* = 0.061, Table 4.5.2). Herbicide application reduced similarity to reference stands across all degradation classes, although this effect was largest in sites with a forested history and lowest in sites with an agricultural history (Figure 4.5.2). Litter removal and fencing had variable effects on similarity to reference stands and no clear patterns emerged. In some treatment combinations, seed additions increased similarity to reference conditions, although these increases were small (Figure 4.5.2).

Table 4.5.2. Fort Bragg, NC results of similarity to reference measured in 1m^2 plots in 2013.

Effect	**Num DF**	**Den DF**	***F***	***P***
Class	1	34	70.00	<.0001
Herbicide	1	238	442.00	<.0001
Class × Herbicide	1	238	90.27	<.0001
Fence	1	238	2.12	0.1472
Class × Fence	1	238	1.14	0.2858
Herbicide × Fence	1	238	1.76	0.1856
Class × Herbicide × Fence	1	238	0.21	0.6435
SeedAddition	1	238	0.35	0.5572
Class × SeedAddition	1	238	3.55	0.0606
Herbicide × SeedAddition	1	238	0.16	0.6866
Class × Herbic × SeedAdd	1	238	0.03	0.8732
Fence × SeedAddition	1	238	1.02	0.3135
Class × Fence × SeedAdd	1	238	1.54	0.2165
Herbic × Fence × SeedAdd	1	238	0.68	0.4113
Class × Herbic × Fence × Seed	1	238	0.04	0.8505
Litter removal	1	271	16.51	<.0001
Litter × Class	1	271	0.32	0.5721
Litter × Herbicide	1	271	1.06	0.3042
Litter × Class × Herbic	1	271	4.01	0.0463
Litter × Fence	1	271	1.51	0.2206
Litter × Class × Fence	1	271	1.25	0.2651
Litter × Herbicide × Fence	1	271	4.07	0.0447
Litter × Class × Herbic × Fence	1	271	0.05	0.8234
Litter × SeedAddition	1	271	0.42	0.5156
Litter × Class × SeedAdd	1	271	0.02	0.8984
Litter × Herbic × SeedAdd	1	271	0.07	0.7923
Litter × Class × Herb × SeedAdd	1	271	0.06	0.8120
Litter × Fence × SeedAdd	1	271	1.70	0.1930
Litter × Class × Fence × SeedAdd	1	271	0.35	0.5562
Litter × Herb × Fence × SeedAdd	1	271	0.24	0.6242
Litter × Class × Herb × Fence × SeedAdd	1	271	1.63	0.2033

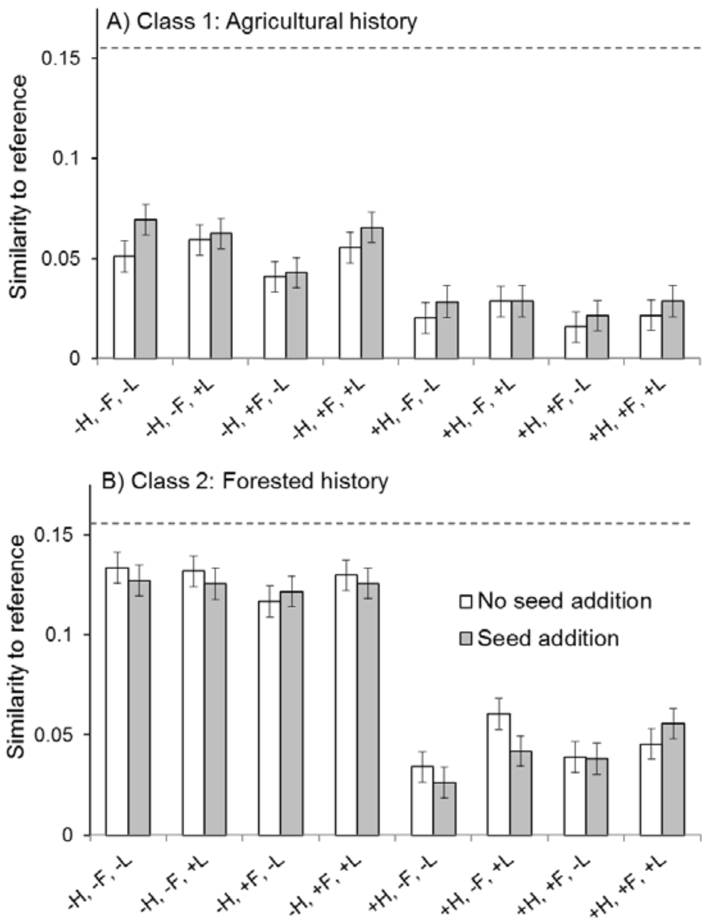

Figure 4.5.2. Similarity of plant communities at Fort Bragg, NC in 1x1m plots compared to the reference longleaf pine savannas using the Jaccard similarity index by degradation class. H = herbicide application; F = fencing, L = litter removal. Dashed lines indicate mean similarity among reference stands.

Similarity to reference stands at Fort Stewart was affected by the three-way interactions among degradation class, fencing and litter removal ($F = 3.47$, $P = 0.033$) and among seed addition, herbicide, and litter removal ($F = 4.63$, $P = 0.032$, Table 4.5.3). Herbicide applications reduced similarity reference on Inceptisol or Spodosol sites (Class 1) and on Entisol or Ultisol sites with low non-*Pinus* basal area (Class 3), but no effect on Entisol or Ultisol sites with high non-*Pinus* basal area (Class 2). Seed additions slightly increased similarity to reference stands in Inceptisol/Spodosol sites, especially in sites that also received herbicide and litter removal. However, seed additions did not compensate for the negative effect of herbicide (Figure 4.5.3).

Table 4.5.3. Fort Stewart, GA results of similarity to reference measured in $1m^2$ plots in 2013.

Effect	**Num DF**	**Den DF**	***F***	***P***
Class	2	33	7.17	0.0026
Herbicide	1	231	176.62	<.0001
Class × Herbicide	2	231	35.00	<.0001
Fence	1	231	2.00	0.1590
Class × Fence	2	231	0.79	0.4564
Herbicide × Fence	1	231	0.03	0.8591
Class × Herbicide × Fence	2	231	0.02	0.9845
SeedAddition	1	231	0.00	0.9994
Class × SeedAddition	2	231	2.97	0.0531
Herbicide × SeedAddition	1	231	0.21	0.6485
Class × Herbic × SeedAdd	2	231	0.65	0.5256
Fence × SeedAddition	1	231	0.39	0.5347
Class × Fence × SeedAdd	2	231	0.37	0.6882
Herbic × Fence × SeedAdd	1	231	0.38	0.5375
Class × Herbic × Fence × Seed	2	231	0.28	0.7538
Litter removal	1	262	7.12	0.0081
Litter × Class	2	262	0.48	0.6185
Litter × Herbicide	1	262	7.15	0.0080
Litter × Class × Herbic	2	262	0.68	0.5062
Litter × Fence	1	262	1.21	0.2723
Litter × Class × Fence	2	262	3.47	0.0325
Litter × Herbicide × Fence	1	262	0.00	0.9570
Litter × Class × Herbic × Fence	2	262	0.75	0.4718
Litter × SeedAddition	1	262	0.06	0.8068
Litter × Class × SeedAdd	2	262	0.97	0.3808
Litter × Herbic × SeedAdd	1	262	4.63	0.0323
Litter × Class × Herb × SeedAdd	2	262	1.00	0.3690
Litter × Fence × SeedAdd	1	262	2.51	0.1142
Litter × Class × Fence × SeedAdd	2	262	0.92	0.3985
Litter × Herb × Fence × SeedAdd	1	262	2.09	0.1499
Litter × Class × Herb × Fence × SeedAdd	2	262	0.09	0.9149

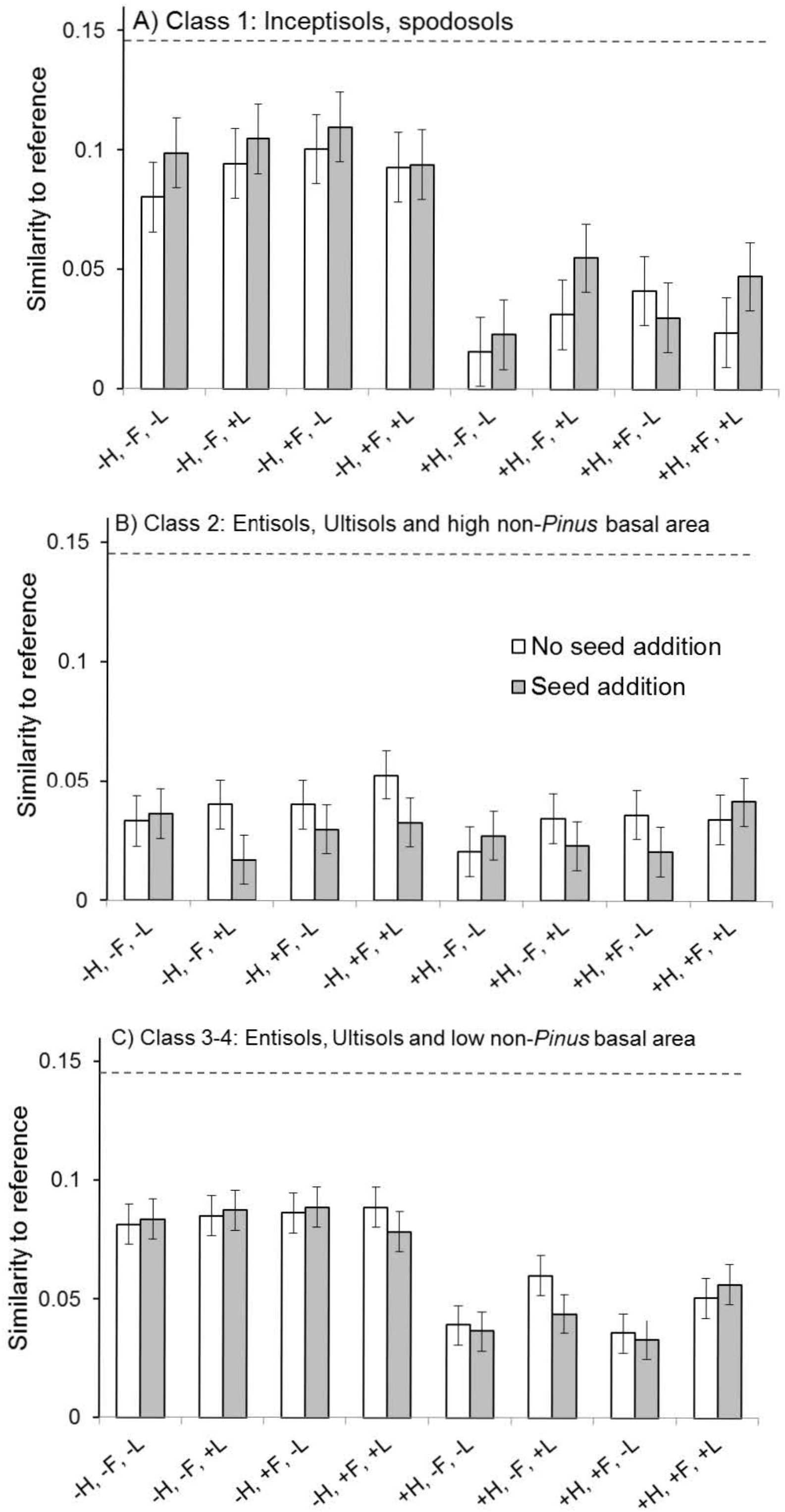

Figure 4.5.3. Similarity of plant communities at Fort Stewart, GA in 1x1m plots compared to the reference longleaf pine savannas using the Jaccard similarity index by degradation class. H = herbicide application; F = fencing, L = litter removal. Dashed lines indicate mean similarity value among reference stands.

Similarity to reference stands at the Savannah River Site was affected by the 5-way interaction among degradation class, seed addition, herbicide, fencing, and litter removal (*F* = 3.63, *P* = 0.014, Table 4.5.4). Herbicide only negatively affected similarity to reference stands in the historically forested sites (Class 4). The effects of seed additions, herbicide, and fencing were variable and generally small (Figure 4.5.4).

Table 4.5.4. Savannah River Site, SC results of similarity to reference measured in 1m^2 plots in 2013.

Effect	**Num DF**	**Den DF**	***F***	***P***
Class	3	32	6.15	0.0020
Herbicide	1	224	48.56	<.0001
Class × Herbicide	3	224	3.30	0.0212
Fence	1	224	3.56	0.0605
Class × Fence	3	224	1.27	0.2854
Herbicide × Fence	1	224	0.86	0.3539
Class × Herbicide × Fence	3	224	1.02	0.3852
SeedAddition	1	224	0.05	0.8155
Class × SeedAddition	3	224	0.76	0.5201
Herbicide × SeedAddition	1	224	0.21	0.6460
Class × Herbic × SeedAdd	3	224	1.14	0.3332
Fence × SeedAddition	1	224	0.64	0.4243
Class × Fence × SeedAdd	3	224	0.12	0.9458
Herbic × Fence × SeedAdd	1	224	0.11	0.7355
Class × Herbic × Fence × Seed	3	224	0.18	0.9089
Litter removal	1	254	11.27	0.0009
Litter × Class	3	254	0.50	0.6819
Litter × Herbicide	1	254	5.38	0.0212
Litter × Class × Herbic	3	254	0.14	0.9348
Litter × Fence	1	254	0.91	0.3418
Litter × Class × Fence	3	254	1.36	0.2545
Litter × Herbicide × Fence	1	254	4.97	0.0267
Litter × Class × Herbic × Fence	3	254	0.96	0.4117
Litter × SeedAddition	1	254	0.58	0.4464
Litter × Class × SeedAdd	3	254	0.53	0.6588
Litter × Herbic × SeedAdd	1	254	1.59	0.2086
Litter × Class × Herb × SeedAdd	3	254	0.92	0.4300
Litter × Fence × SeedAdd	1	254	0.56	0.4555
Litter × Class × Fence × SeedAdd	3	254	0.30	0.8239
Litter × Herb × Fence × SeedAdd	1	254	5.38	0.0212
Litter × Class × Herb × Fence × SeedAdd	3	254	3.63	0.0136

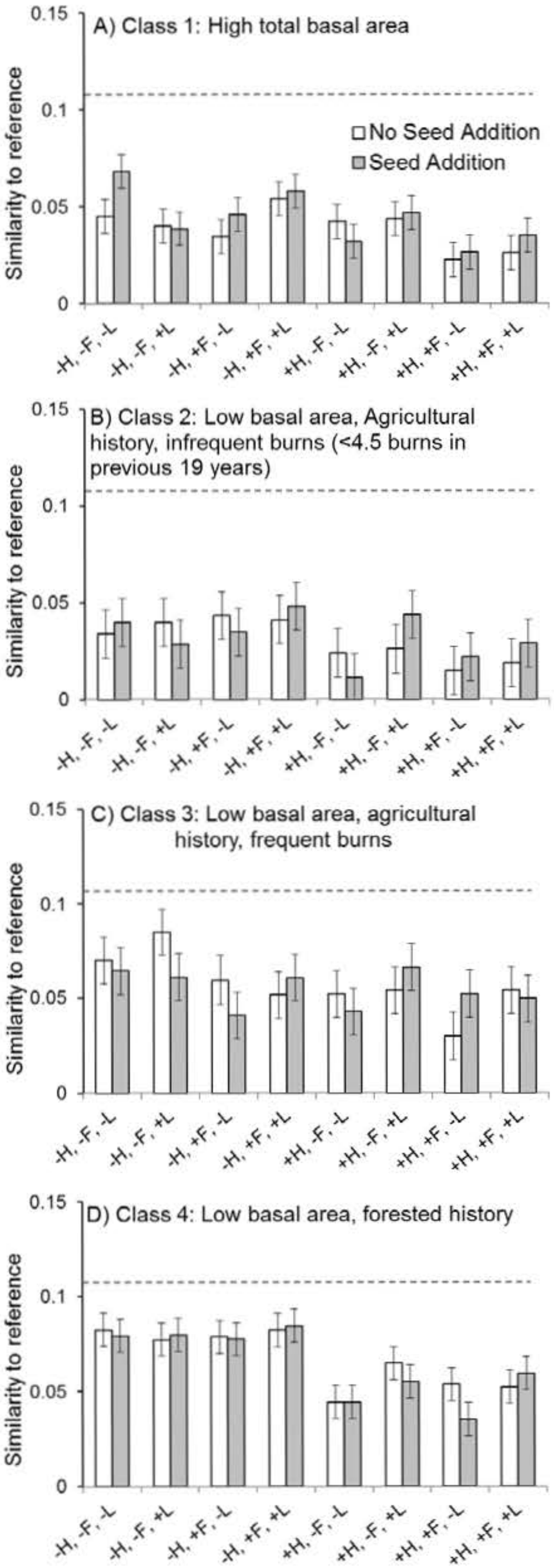

Figure 4.5.4. Similarity of plant communities at the Savannah River Site, SC in 1x1m plots compared to the reference longleaf pine savannas using the Jaccard similarity index by

degradation class. H = herbicide application; F = fencing, L = litter removal. Dashed lines indicate mean similarity value among reference stands.

4.5.4 Discussion

Although trends of seed addition increasing the similarity to reference were found in some cases, there were no clear, over-arching patterns that emerged from this study with regards of our experimental treatments shifting plant communities towards the reference state. The exception is the clear negative effect of herbicide on similarity to reference plant communities in most classes and at all locations. Based on our results, the deleterious effects of broad-spectrum herbicide application on indicator species associated with recovery are greater than the benefits of using herbicide to eliminate undesired, often ruderal, species. When possible, other methods for the control of ruderal species (e.g., prescribed fire) are preferable based upon our data if similarity to reference is the primary metric being used to assess plant community recovery.

The lack of a consistent trend in similarity to reference is an interesting finding: given that some treatments (e.g., seed addition) consistently increased species richness and the presence of indicator species (Sections 4.2-4.3), a logical expectation is that the significant effects of experimental treatments would translate into increased similarity to reference communities for some treatments. Yet, we found little evidence that seed addition – either alone or in combination with other treatments – increased the similarity of degraded sites' community composition to that of reference sites. This result is not due to failed establishment of sown species, as we found significant and biologically relevant increases in the richness of indicator species from our seed additions (e.g., increases of >3 indicator species that more than doubled the richness of indicator species richness per 25m^2 in some treatments; section 4.2-4.3).

We suspect that our results are not the reflection of the experimental treatments to promote recovery. Rather, we suspect that our similarity results largely reflect the high degree of spatial variation in community composition among the sites we sampled for this work. Specifically, we expect that the high levels of diversity possible and the large regional species pools may generate considerable spatial variation in plant community composition both within a site and between sites. This is exemplified by the variation in community composition between our reference sites alone, where the mean compositional similarity value was only 0.09. This low similarity does not arise because reference sites do not share a large number of species. If this were the case, our indicator species analysis would not have been so significant (Section 3.3). Rather, we suspect that a primary factor contributing to low similarity is that there is substantial species turnover in space (i.e., spatial beta diversity) within and between sites. The effect of spatial turnover on similarity values would be to yield low similarity values when plot sizes are small, when sites are heterogeneous, or both. Spatial variation within sites would be further amplified by variation between sites, which is expected to be high given that the relatively limited subset of species at a site is derived from a very large regional species pool (i.e., typically >200 species per location).

Given this potential for variation, it seems reasonable that low levels of similarity would be observed across all degradation classes we studied (i.e., most classes were less than 15% similar to reference communities). Because this pattern is evident across our very large geographical extent (i.e. South Carolina, North Carolina, and Georgia) and across an experiment conducted at 108 separate sites, our work suggests that the high levels of species turnover and large species pool characteristic of understory plant communities in longleaf ecosystems make it unlikely that any site will exhibit very high levels of similarity to reference, unless very large plots are used to quantify community composition. Mean compositional similarity values among our reference plots was only 0.09. Values of similarity metrics (e.g., Sorensen dissimilarity) from other studies in longleaf pine savannas are generally lower than 0.5 (Mattingly et al. 2015, Grman et al. in press, Section 3.4). These other studies support our general conclusion that the large species pools and significant spatial turnover of species (even if those species are indicator species) may limit the utility of similarity metrics as an indicator of recovery in longleaf ecosystems.

While similarity to reference remains an important metric, our findings illustrate that assessment of degradation and recovery success should not be based on similarity to reference alone, because it may not be reasonable to expect any site (even if not degraded) to be highly similar to a reference site. Rather, managers should also consider species richness and the presence of indicator species (Brudvig et al. 2014) in assessment of recovery. For example, although experimental treatments had relatively modest effects on compositional similarity to reference sites, the experimental treatments (especially seed addition) consistently led to increased species richness and presence of indicator species.

Prompted by our findings regarding similarity to reference, we conducted additional analyses to determine whether species richness at small scales was reliably correlated with similarity to reference communities. Across the 108 sites used for our experiments, we find that there is a strong, significant relationship between richness and similarity (Figure 4.5.5). This result suggests that richness is indicative of similarity to reference. Because it is more rapidly quantified than similarity and because the two are significantly correlated, we suggest that richness, not similarity, will be a more efficient means for managers to assess recovery of degraded communities.

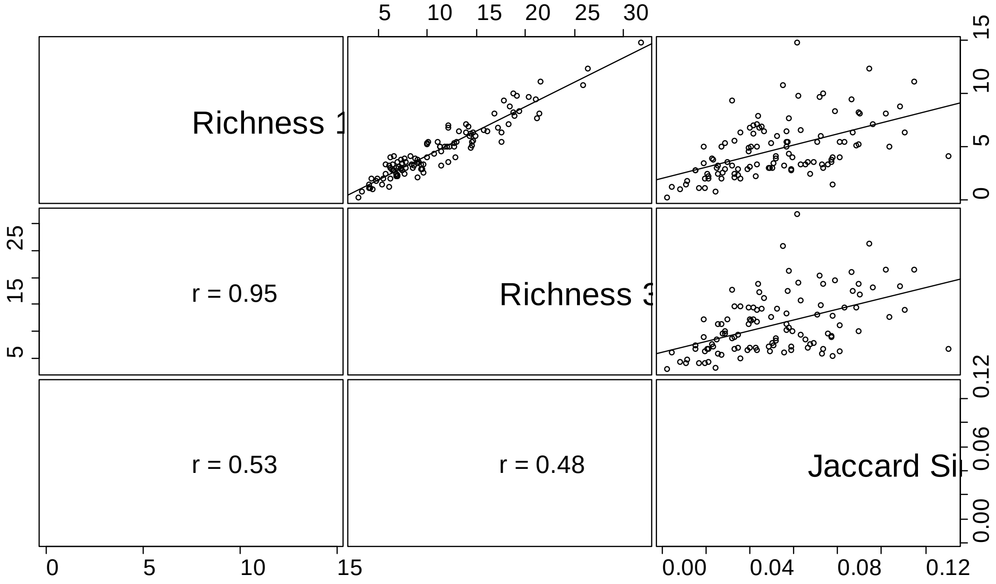

Figure 4.5.5. Relationship between similarity to reference longleaf pine stands and species richness in 1x1m and 3x3m plots, measured using the Jaccard similarity index. Similarity to reference in 2013 was averaged across all 8 treatment combinations at each site to derive a mean value of similarity for each of the 108 sites (36 sites at FTB, 36 sites at SRS, 36 sites at FTS). Pearson correlation coefficients are presented in the lower portion of the matrix; all correlations are highly significant ($p<0.001$).

Second, these results suggest that similarity is likely to be most meaningful if quantified at very large scales (i.e., scales large enough such that spatial variation in species composition is greatly reduced). In practice, this may be difficult or impractical to achieve, because the scale of spatial variation itself is affected by the type of degradation and may vary among geographic locations. For example, at two of our three study locations, we have found that spatial turnover is lower in sites with a history of agricultural land use (i.e., plant communities are more homogeneous in space; Mattingly et al. 2015). As a result, we recommend that managers focus on species richness and the richness of indicator species in assessing degradation and recovery. Additional analyses of the 270 sites in our observational study (Section 3) suggest that small-scale samples of richness (e.g., 1 x 1 m plots) are reliable indicators of richness at the scale of an entire sampling site (i.e., 100 x 100 m); see Figure 4.5.6. These findings suggest that managers can use relatively quick small-scale surveys without loss of generality when assessing recovery and prioritizing management plans.

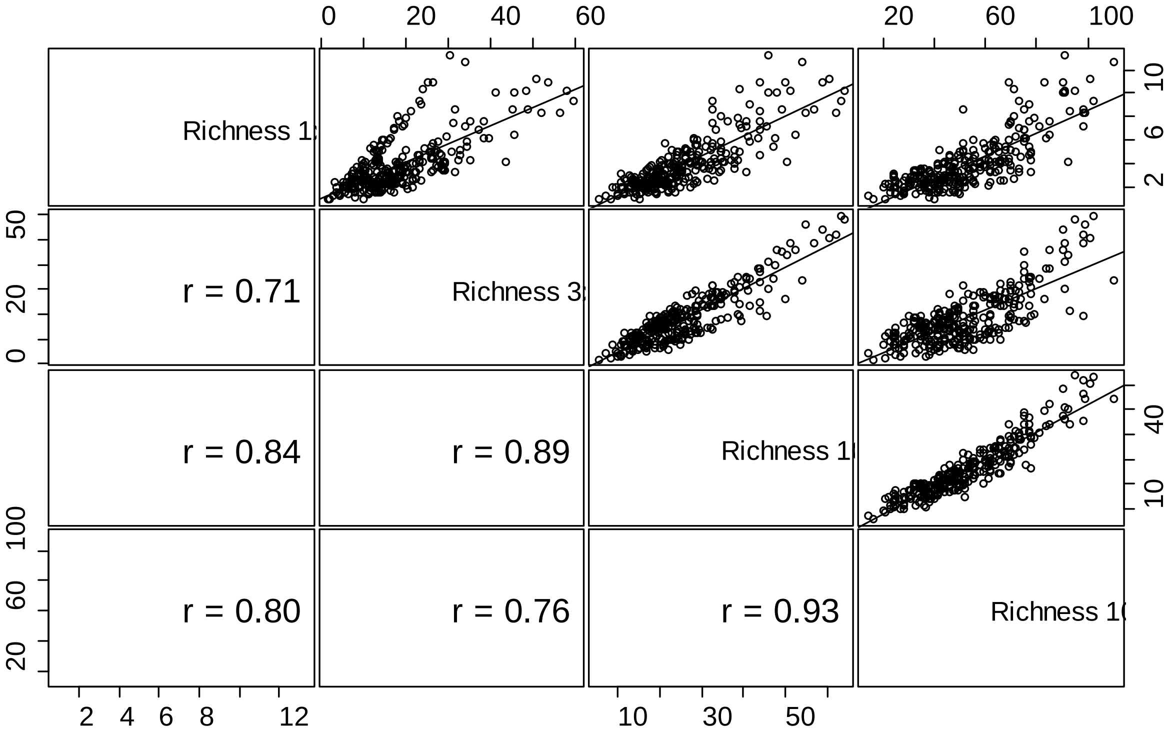

Figure 4.5.6. Relationships between species richness quantified at different spatial scales. Data were collected from the 270 sites where observational data were taken; these sites are described in Section 3 (99 sites at FTB, 89 sites at SRS, 82 sites at FTS). A mean value of richness at each scale was derived for each site. Pearson correlation coefficients are presented in the lower portion of the matrix; all correlations are highly significant ($p<0.001$).

4.6 ASSESS LANDSCAPE CONNECTIVITY EFFECTS

Based on our finding that historical landscape connectivity had a small effect on plant community composition in our observational data (Section 3.4), we did not evaluate landscape connectivity in the analysis of our experimental data.

5. CONCLUSIONS AND IMPLICATIONS FOR FUTURE RESEARCH / IMPLEMENTATION

5.1 SYNTHESIS

The longleaf pine ecosystem in the southeastern United Stated is a highly diverse but critically endangered ecosystem. Our goal was to develop and test an ecological assessment framework for recovery of the understory plant communities in longleaf pine savannas. Our framework was intended to achieve several objectives: provide a means to determine the degree to which a community is degraded and thus the need for feasibility of recovery, aid in selecting a successful recovery strategy, and assess progress towards recovery via three technical objectives.

In phase 1, we addressed our first technical objective, which was to **assess sites and define recovery goals** by using comprehensive surveys of vegetation in degraded and reference communities at three separate DoD/DOE sites. We developed an ecological reference model based upon three factors that degrade longleaf pine understory plant communities: historical agricultural land use, low frequency of prescribed burns, and a high density of trees in the overstory. The utility of this reference model was evaluated by using comprehensive plant community data, soil data, and seed-bank samples collected from 232 sites at three locations (Fort Bragg and Fort Stewart (DoD); Savannah River Site (DOE)). The 232 sites we sampled were explicitly chosen to span a gradient from highly degraded to minimally degraded (i.e., reference sites that are thought to have little or no degradation). Multivariate classification and regression trees applied to plant community data found that the components of degradation in our ecological reference model were predictably related with significant variation in community degradation. Importantly, our comprehensive dataset allowed the creation of a unique model for each study location (i.e., Fort Bragg, Fort Stewart, and SRS) that could be compared with a model that used all locations (Brudvig et al. 2014). We found that historical agricultural land use, low fire frequency, and high tree density all contributed to the degradation of the plant community when compared to reference stands. The effect of past agricultural land use on plant communities seemed related to altered soil properties and increased soil compaction, likely direct consequences of past tillage and fertilizer application. In addition to these general patterns, we also found notable differences among our three geographic regions that might have depended on variation in historical human activities (i.e., intensity of agriculture and other activities), contemporary management activities (i.e., frequency of prescribed burns), and/or local soil attributes. The seed bank in all geographic locations, and especially in post-agricultural sites, contained mostly weedy plant species, and thus the seed bank has low restoration potential. We also found that interactions among local degrading factors and edaphic factors structure longleaf pine understory communities, whereas the role of the surrounding landscape is negligible.

In phase 2, we addressed our second technical objective, to **use distributed experiments to evaluate the determinants of recovery**. We experimentally evaluated the determinants of recovery by manipulating four ecological factors that could potentially limit the recovery of the plant community in each of the degradation classes: seed additions to overcome seed limitation, herbicide to reduce competition, fencing to exclude herbivores, and litter removal to enhance microsite conditions. We found that seed additions promoted the recovery of species that are indicators of reference plant communities, regardless of the initial degradation class. However, degradation class and other experimental treatments interacted to determine how effective seed additions were in facilitating the recovery of understory plant communities. Reduction of competitors increased the effectiveness of seed additions, but only in degraded sites with few preexisting indicator species. The effect of herbivore exclusion was often smaller than the effect of seed addition or herbicide application; herbivore exclusion was also typically most effective and apparent when herbivores were excluded from sites where seeds were also added. Similarly, removing leaf litter also increased the effectiveness of seed additions, but mainly in fire suppressed sites and sites with high tree density. We found the results from small plots ($1m^2$) scale up and in many cases become greater at larger spatial scales ($25m^2$), suggesting that the results of small experiments likely provide valid recovery guidance. Moreover, we also found strong relationships between species richness in small plots ($1m^2$) and species richness in much larger plots (e.g., $10m^2$, $100m^2$, and $10{,}000m^2$), further reinforcing that small-scale assessment of richness may be a reasonable surrogate for richness at larger scales.

In phase 3, we synthesized the results of phases 1 and 2 to address our third technical objective, to **develop the roadmap to recovery**, which represents a model of data-driven recovery recommendations applicable to a variety of sites throughout southeastern longleaf pine locations: The Roadmap to Recovery (a User Guide that can be found on the Tools and Training page of the SERDP/ESTCP website) provides a field-ready document that managers can use to assess the degradation of their site using either 1) knowledge of site characteristics (e.g. burn frequency, presence of past agricultural land use), or 2) the presence of particular indicator species. To maximize transferability, we compiled and analyzed climatic conditions at other DoD/DOE installations in the southeast to provide managers with a means to quantitatively predict which of our four recovery models is likely to be most useful at their location.

5.2 EXISTING KNOWLEDGE GAPS RESOLVED

Our research has resolved several important knowledge gaps. Although longleaf pine understory plant communities are affected by a complex set of factors related to management (e.g., fire frequency, canopy tree density), past land use, and ecological constraints (e.g., soil type, connectivity), it has been unclear how all of these factors may act, alone or in concert, to affect plant community composition. Using structural equation modelling (Veldman et al. 2013, Veldman et al. 2014) and multivariate classification and regression trees (Brudvig et al. 2014), our work has provided the first comprehensive examination of all of these factors. Second, most studies focus only on a few scales of analysis or on a single metric (e.g., species richness). Our study has taken a multi-scale approach to evaluate how past land use and contemporary management affect species richness, beta diversity (species turnover), and community similarity (Brudvig et al. 2014, Mattingly et al. 2015). Our experimental evaluation of the factors that limit plant establishment has provided the first large-scale experimental comparison of the relative importance of dispersal limitation, herbivores, and competition in affecting the establishment of plant populations and the structure of plant communities. We have also resolved important questions for that were gaps in our applied knowledge. For example, our work now provides managers with a means to effectively characterize habitats along degradation gradients. Moreover, because we simultaneously evaluated several gradients, our work can help managers prioritize which factor of degradation is more important for their goals. For example, due to finite resources, a manager may need to decide whether to focus recovery efforts on sites that are fire-suppressed or sites that are on areas once used for agriculture. Our research can be used to help the manager understand the relative benefits of prioritizing the different types of sites. Moreover, once the manager has decided which sites to prioritize for recovery, our experimental studies provide a means to help the manager select the optimal recovery approach for the sites they seek to recover.

5.3 SUMMARY OF RECOMMENDATIONS FOR IMPLEMENTING RECOVERY

The primary drivers of degraded in southeastern longleaf pine savannas that emerge from our work are legacies of historic agriculture, fire suppression, and dense overstory tree canopies. Our work confirms the utility of using seed additions to restore understory plant communities in longleaf pine savannas of the southeastern USA degraded by these three factors and also highlights that initial levels of degradation can affect the outcome of restoration involving seed addition and manipulation of other processes, such as the removal of competing vegetation or leaf litter. Simultaneously employing multiple restoration techniques may maximize the benefits of seed additions depending on initial site conditions. For example, in highly degraded sites that contain few plant species that are indicators of high-quality reference plant communities, eliminating weedy competitors via herbicide or other methods applied prior to seeding can increase the number of indicator species that establish from seed. Again, because of their strong potential for eliminating desirable species as well as undesirable species, we emphasize that herbicide applications should be used with caution and only at highly degraded sites. Similarly, in fire-suppressed sites or savannas with a dense overstory canopy, manually removing leaf litter prior to seed additions can increase the effectiveness of seed additions. Litter removal may be a viable option to maintain herbaceous understory plant community when frequent prescribed fires are not feasible, but more work is necessary to directly compare the effects of litter removal and prescribed burning on understory plant communities and other ecosystem attributes. Fencing to eliminate large mammalian herbivores can also increase the effectiveness of seed additions in some cases, although the effects of fencing are more subtle and variable. Because our study did not manipulate the duration of fence installation, we cannot directly inform the optimal number of years that fences should be deployed if they are to be used. However, we note that many of the perennial grass species in longleaf understory plant communities are likely to be able to tolerate herbivory once established. As such, much as protection from herbivores for the first year of growth may be a critical for plants to reach a size refuge, just as early herbivory is important for shaping the recovery of perennial bunchgrasses in California grasslands (Orrock et al. 2009). However, given their variable effects, the material and labor costs necessary to construct herbivore exclosures may make them prohibitively expensive for large-scale recovery efforts. Although not evaluated in our study, species that are highly susceptible to herbivory when seedlings might be best grown in a greenhouse and then planted into the field once plants had grown to appreciable size, as this would likely reduce exposure of seedlings to herbivores at a life stage when herbivores might place constraints on seedling establishment. In addition to these local recovery-promoting treatments, site-level management activities should include overstory tree thinning, when appropriate, and frequent prescribed fires (e.g., 1-2 fires every four years), as these were the classes that responded most positively to our treatments.

5.4 REMAINING RESEARCH QUESTIONS

Although it represents the largest observational and experimental study of its kind, our study was inherently limited to only three DoD/DOE installations, and we focused primarily on upland longleaf pine habitats. While our results will logically be most applicable to those areas and habitats, the generally consistent role of past agriculture, contemporary burn regime, soil compaction, and seed addition that we found at all three of the study locations suggests that our results should be generally transferable to other DoD/DOE locations in the southeast. We believe that an important and interesting future direction will be to understand how the legacies of past land use affects other ecological processes in longleaf understory communities. For example, we have found that past land use dramatically reduces plant diversity, leads to the maintained absence of indicator species, and changes the physical composition and compaction of the soil. These effects of past land use also lead to changes in arthropod communities and rates of herbivory. Given the importance of plants and arthropods to other species of DoD concern (e.g. red-cockaded woodpeckers), understanding the potentially far-reaching ecological consequences of past agricultural land use may be an important future direction.

5.5 POTENTIAL FOR DIRECT IMPLEMENTATION BY DoD AND OTHERS

Our results have a high degree of potential for direct implementation by DoD as well as any other group interested in assessing degradation of longleaf pine understory plant communities and promoting recovery. Our results provide an ecological reference model that can be used to predict degradation using two complementary methods, so managers can select the method that best suits their needs: 1) sites can be placed into degradation classes using readily available data regarding site condition (e.g., fire frequency, canopy density), 2) sites can be placed into degradation classes using field surveys that assess the presence of class-specific indicator species, or both. Our experimental results provide recommendations that can be implemented to maximize recovery given a particular starting condition. In particular, our results highlight the utility of approaches that managers are already familiar with implementing, e.g., prescribed burning is a tool that DoD managers commonly use to promote recovery, and our results provide a means to prioritize burning efforts to maximize recovery. Similarly, our results suggest that seed additions are a particularly useful means of promoting recovery, and the implementation of this approach by managers is likely facilitated by the existence of mechanized seed-collection and seed-sowing machines that make it possible to treat relatively large areas. Finally, using the presence of indicator species, managers can assess whether their efforts are resulting in the desired recovery. To further increase the potential for the implementation of our work by DoD and others, we have also produced a stand-alone field-ready guide (the Roadmap to Recovery) which will be made available via the SERDP/ESTCP website. This guide is intended to give managers the tools they need to classify degradation, inform recovery actions that will be most effective, and quantify recovery.

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APPENDICES

APPENDIX A: SUPPORTING DATA

A1. List of additional military installations with longleaf habitat

Branch	Name	Code	STATE	Area_ha	lat	long	MAT	MAP	Elevation (m)	Dominant soil order	Physiographic region
Army DOD	Fort McClellan	FM	AL	10599	33.701	-85.746	17.1	1266	279	Ultisols	Piedmont and Montane Uplands
Army DOD	Fort Rucker	FR	AL	22211	31.343	-85.715	18.9	1347	107	Ultisols	Eastern Gulf Coastal Plain
Army DOD	Fort Benning	FBN	AL-GA	73440	32.357	-84.970	18	1188	94	Ultisols	Fall-line Sandhills
Air Force DOD	Avon Park	AP	FL	43286	27.640	-81.347	22.7	1292	20	Spodosols, Entisols, Ultisols	Southern Coastal Plain
Navy DOD	Cecil Field	CF	FL	7248	30.218	-81.874	20.7	1318	21	Spodosols, Entosols	Southern Coastal Plain
Air Force DOD	Eglin Air Force Base	EAB	FL	183350	30.463	-86.518	18.8	1808	4	Entilsols, Ultisols	Southern Coastal Plain
Army DOD	Fort Gordon	FG	GA	22528	33.414	-82.146	17.8	1110	137	Ultisols	Atlantic Coastal Plain
Army DOD	Fort Stewart	FS	GA	113115	31.880	-81.608	19	1220	18	Spodosols, Ultisols	Southern Coastal Plain
Army DOD	Fort Polk	FPK	LA	76767	31.086	-93.057	19.6	1547	90	Alfisols, Ultisols	Western Gulf Coastal Plain
Marine Corps DOD	Camp Lejeune	CL	NC	29728	34.642	-77.285	16.7	1378	11	Spodosols, Entisols, Ultisols	Atlantic Coastal Plain
Air Force DOD	Dare County Range	DCR	NC	11540	35.753	-75.857	17.1	1273	1	Histosols, Ultisols	Atlantic Coastal Plain
Army DOD	Fort Bragg	FBG	NC	57286	35.148	-79.038	16	1270	83	Ultisols	Atlantic Coastal Plain
Army DOD	Fort Jackson	FJ	SC	20006	34.058	-80.831	19.5	1180	113	Entilsols, Ultisols	Fall-line Sandhills
DOE	Savannah River Site	SRS	SC	86300	33.364	-81.683	18	1225	119	Ultisols	Fall-line Sandhills
Army DOD	Fort Pickett	FPT	VA	18561	37.047	-77.936	13.8	1172	115	Ultisols	Atlantic Coastal Plain

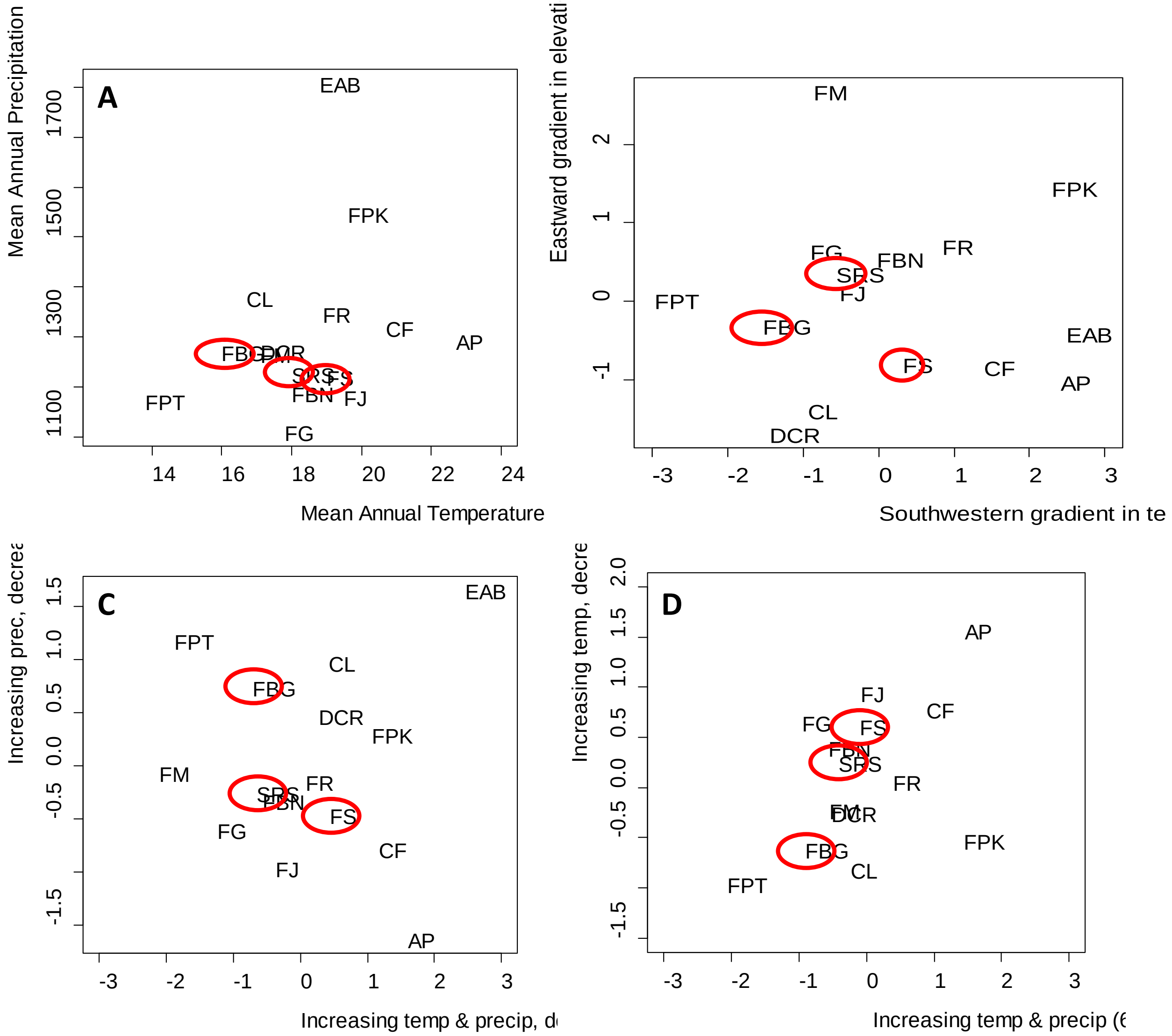

Figure A1. Graph of military bases greater than 5000 ha with longleaf habitat. A) biplot of mean annual precipitation by mean annual temperature. Principal component ordinations based on B) latitude, longitude, mean annual temperature, mean annual precipitation, and elevation; C) mean annual temperature, mean annual precipitation, and elevation, and D) mean annual temperature and mean annual precipitation. Codes are listed in the table above in Appendix B. Focal locations are circled in red.

A2. People trained

To date, this project has employed and trained 6 postdoctoral researchers, 35 research technicians, and 4 graduate students, 23 of whom are women or underrepresented groups in science. Many of these researchers have initiated independent research projects, participated in publishing scientific manuscripts, and obtained competitive positions following their work on our project.

Key to symbols used in lists below:

# indicates undergraduates who have made presentations at university or national scientific meetings
* indicates author on scientific papers
† indicates undergraduates who subsequently entered graduate school or are in the process of applying to graduate school

Undergraduate students

1. Nichole Boyea #
2. Laura Brusson
3. Bliss Capener
4. Ben Gottsacker†
5. Gavin Jones †
6. Emily Lannoye
7. Ivan Mei
8. Lindsey Meyer†
9. Nick Mills#
10. Abby Mitchell
11. Jeff Nahn
12. Lauren Schwinghammer#
13. John Stuhler #†
14. Natasha Thompson
15. Ross VanderCreek

Postgraduate M.S. research technicians:

1. Danielle Racke †
2. Nick Reif *†

Postgraduate B.S. research technicians:

1. Jordan Kremer
2. Anthony Lucia
3. Nicholas Mills
4. John Mordasky
5. Kira Santulli
6. Julia Sosin
7. Stephanie Koontz
8. Amanda Powell †
9. Chelsea Blake †

10. Diana Guzmán # †
11. Marilena Nuñez †
12. Bonnie Cooper
13. Timothy Thomas
14. Beth Stevenson
15. Rod Grills †
16. Emily Meineke †
17. Lauren Bizzari * †
18. Rick Ranalli †

Graduate students

1. Amy Alstad
2. Phil Hahn*
3. Maria Melnechuk
4. John Stuhler

Postdoctoral researchers:

1. Dirk Baker; now a research scientist for Campbell Scientific, Logan, UT
2. Susan Carr; now an ecologist for the U.S. Department of Agriculture Natural Resources Conservation Service (NRCS), Gainesville, FL
3. Cory Christopher*; now Graduate Program Manager at Cincinnati Zoo and Botanical Garden, Cincinnati, OH
4. Cathy Collins*; now an Assistant Professor at Colby College, Waterville, ME
5. Brett Mattingly*; now an Assistant Professor at Eastern Connecticut State University, Willmantic, CT
6. Joseph Veldman*; now a Postdoctoral research associate at Iowa State University, Ames, IA

APPENDIX B. LIST OF SCIENTIFIC/TECHNICAL PUBLICATIONS

B1. Articles in peer-reviewed journals

Manuscripts in print, accepted, or submitted for publication

Bizzari, L.E., C.D. Collins, L.A. Brudvig, E.I. Damschen. In press. Historical agriculture and fire frequency alter soil properties in longleaf pine woodlands. Forest Ecology and Management.

Brudvig, L.A., J.L. Orrock, E.I. Damschen, C.D. Collins, P.G. Hahn, W.B. Mattingly, J.W. Veldman, and J.L. Walker. 2014. Land-use history and contemporary management inform an ecological reference model for longleaf pine woodland understory plant communities. PLoS One 9: e86604.

Hahn, P. G. and J. L. Orrock. 2014. Effects of temperature on seed viability of six Ozark glade herb species and eastern redcedar (*Juniperus virginiana*). American Midland Naturalist 171: 147-152.

Hahn, P.G. and J.L. Orrock. 2015. Land-use legacies and present fire regimes interact to mediate herbivory by altering the neighboring plant community. Oikos 124:497-506.

Hahn, P.G. and J.L. Orrock. 2015. Land-use history alters contemporary insect herbivore assemblages and decouples plant-herbivore relationships. Journal of Animal Ecology 84:745-754.

Hahn, P.G. and J.L. Orrock. In press. Spatial arrangement of canopy structure and land-use history alter herbivory in a landscape experiment. Ecosphere.

Hahn, P.G. and J.L. Orrock. In review. Establishment of multiple plant species is contingent upon land-use history, overstory tree thinning, and consumers. Global Change Biology.

Mattingly, W. B. and J. L. Orrock. 2013. Historic land use influences contemporary establishment of invasive plant species. Oecologia 172:1147-1157.

Mattingly, W.B., J. L. Orrock, and N. T. Reif. 2012. Dendroecological analysis reveals long-term, positive effects of an introduced understory plant on canopy tree growth. Biological Invasions 14:2639-2646.

Mattingly, W.B., J.L Orrock, C.D. Collins, L.A. Brudvig, E.I. Damschen, J.W. Veldman, and J.L. Walker. 2015. Historical agriculture alters the effects of fire on understory plant beta diversity. Oecologia 177:507-518.

Veldman, J. W., W. B. Mattingly, and L. A. Brudvig. 2013. Understory plant communities and the functional distinction between savanna trees, forest trees, and pines. Ecology 94:424-434.

Veldman, J.W., L.A. Brudvig, E.I. Damschen, J.L. Orrock, W.B. Mattingly, and J.L. Walker. 2014. Fire frequency, agricultural history, and the multivariate control of pine savanna understory plant diversity. Journal of Vegetation Science 25:1438-1449.

Manuscripts in preparation for publication

Damschen, E.I., J.L. Orrock, L.A. Brudvig, P.G. Hahn, J.W. Veldman, W.B. Mattingly, and J.L. Walker. How seed banks vary across a degradation gradient and their restoration potential. In preparation.

Hahn, P.G. and J.L. Orrock. Habitat type and herbivory alter demography of four herbaceous plant species. In preparation.

Hahn, P.G. and J.L. Orrock. Disentangling the roles of neighboring plant density and frequency in providing associational defense against herbivory within different habitats. In preparation.

Mattingly, W. B. and N. A. Mills. Soil legacies limit legume performance in post-agricultural woodlands. In preparation.

Mattingly, W. B., Alstad, A., Brudvig, L. A., Damschen, E. I., Hahn, P. G., Orrock, J. L., Veldman, J. W., and J. L. Walker. Soil legacy effects of agricultural land use reduce longleaf pine understory plant diversity. In preparation.

Orrock, J. L. J. A. Brudvig, E. I. Damschen, W. B. Mattingly, J. W. Veldman, and J.L. Walker. Experimental evidence that dispersal limitation drives large-scale, long-term legacies of past agricultural land-use on plant communities. In preparation.

Orrock, J. L., L. A. Brudvig, E. I. Damschen, W. B. Mattingly, J. W. Veldman, and J. L. Walker. Geographically distributed factorial experiments reveal the scale-dependent signature of competition, herbivory, and dispersal in plant communities. In preparation.

Stuhler, J.D. and J.L. Orrock. Legacies of past agricultural land use interact with contemporary fire regimes to affect patterns of rodent and arthropod seed predation. In preparation.

Stuhler, J.D. and J.L. Orrock. Historic agriculture and contemporary canopy cover affect ant mound distribution and abundance. In preparation.

Stuhler, J.D. and J.L. Orrock. Accelerated germination of two perennial species at high, relative to low, conspecific densities. In preparation.

Veldman, J.W., Brudvig, L.A., E.I. Damschen, W.B. Mattingly and J.L. Walker. The influence of landscape context and local factors on the recovery of fire-dependent plant communities on former agriculture lands. In preparation.

Theses

Hahn, P.G. 2015 Land-use history and fire management drive context-dependent plant-herbivore interactions. PhD Dissertation. University of Wisconsin-Madison, WI.

Stuhler, J.D. 2015. The influence of anthropogenic legacies on contemporary consumer abundance and plant-granivore interactions. M.S. Thesis. University of Wisconsin-Madison, WI.

Media coverage

Coverage of Hahn and Orrock paper in press at Journal of Animal Ecology:

- Science Daily. Grasshoppers signal slow recover of post-agricultural woodlands, study finds. http://www.sciencedaily.com/releases/2014/11/141124160456.htm
- WORT, Community Radio, Madison, WI. Interview on "8 O'Clock Buzz" with Phil Hahn.

Yale Environment 360. Military bases provide unlikely refuge for south's longleaf pine. http://e360.yale.edu/mobile/feature.msp?id=2463

B2. Technical reports

Orrock, J. L., E. I. Damschen, L. A. Brudvig, and J. L. Walker. (2015). Roadmap to recovery: a data-driven framework for implementing management techniques and assessing recovery of understory plant communities in longleaf pine ecosystems [www page]. URL http://______

B3. Conference or symposium proceedings scientifically recognized and referenced

None

B4. Conference or symposium abstracts

Scientific meetings

Brudvig, L. A., W. B. Mattingly, J. L. Orrock, E. I. Damschen, J. W. Veldman, J. L. Walker. 2011. Land use history alters soil compaction and affects the plant community: implications for diversity in longleaf pine ecosystems. SERDP/ESTCP Partners Symposium, Washington, D.C.

Brudvig, L. A., J. Orrock, E. I. Damschen, J. Walker, W. B. Mattingly, C. Collins, and M. Melnechuk. 2010. A classification framework for assessing degradation and recovery potential of understory plant communities in longleaf pine forests on DOD/DOE lands. SERDP/ESTCP Partners Symposium, Washington, D.C.

Damschen, E. I., J. L. Orrock, L. A. Brudvig, P. G. Hahn, J. W. Veldman, W. B. Mattingly, J. L. Walker. 2013. How seed banks vary across a degradation gradient and their restoration potential. Society for Ecological Restoration Meeting, Madison, WI.

Guzman-Colon, D. K., N. T. Reif, W. B. Mattingly, and J. L. Orrock. 2012. Historic land use affects ground-dwelling ant community structure in longleaf pine savannas. Ecological Society of America Meeting, Portland, OR.

Hahn, P. G. and J. L. Orrock. 2011. Anthropogenic legacies mediate contemporary plant-herbivore interactions. Ecological Society of America Meeting, Austin TX

Hahn, P.G. and J. L. Orrock. 2012. Agricultural land use history and fire suppression strengthen herbivore impacts. Ecological Society of America Meeting, Portland, OR.

Hahn, P.G. and J.L. Orrock. 2013. Habitat quality and herbivory interact to have species-specific effects on plant growth. Ecological Society of America Annual Meeting, Minneapolis, MN.

Hahn, P.G. and J.L. Orrock. 2014. Are associational effects driven by insect herbivore abundance or foraging behavior? A test of foraging decisions by grasshoppers (Order: Orthoptera). 62nd Entomological Society of America Annual Meeting.

Mattingly, W. B., C. Collins, L. Brudvig, C. Christopher, E. Damschen, J. Orrock, and J. Walker. 2010. Geographic variation in patterns of alpha and beta diversity along a degradation gradient in longleaf pine savannas. Ecological Society of America Meeting, Pittsburgh, PA.

Melnechuk, M. E., C. Christopher, L. Brudvig, C. Collins, E. Damschen, W. B. Mattingly, J. Orrock, and J. Walker. 2010. Changes in reference stands over time and implications for restoration. Ecological Society of America Meeting, Pittsburgh, PA

Mills, N. A. and W. B. Mattingly. 2013. Agricultural land-use legacies shape plant-soil interactions in present-day landscapes. Northeast Undergraduate Research and Development Symposium, University of New England, Biddeford, ME.

Mills, N. A. and W. B. Mattingly. 2013. Agricultural land-use legacies shape plant-soil interactions in present-day landscapes. Arts and Sciences Research Conference and Exhibition, Eastern Connecticut State University, Willimantic, CT.

Stuhler, J. D. and J. L. Orrock. 2013. Fire and land use interact to affect patterns of rodent granivory. American Society of Mammalogists meeting, Philadelphia, PA.

Stuhler, J.D., J.L. Orrock, J.A. Ledvina, and L.A. Brudvig. Historic agricultural land-use legacies affect the contemporary abundance of small mammals. Ecological Society of America 99th Annual Meeting, Sacramento, CA. Presented August 12, 2014.

Veldman, J.W. Ecology and conservation of species-diverse savanna plant communities. University of San Francisco, Department of Biology (13 February 2013).

Veldman, J.W., L.A. Brudvig, E.I. Damschen, J.L. Orrock, W.B. Mattingly, and J.L. Walker. 2013. Prescribed fire, land-use history, and connectivity in the restoration of species-

diverse, subtropical pine savannas. Society for Ecological Restoration Meeting, Madison, WI.

Veldman, J. W., L. A. Brudvig, and W. B. Mattingly. 2012. Differing effects of savanna trees and forest trees on savanna understory plant diversity. Ecological Society of America Meeting, Portland, OR.

Invited presentations and seminars

Mattingly, W. B. Conservation and restoration of a biodiversity hotspot: longleaf pine savannas. Department of Biology, Eastern Michigan University, Ypsilanti, MI. January 23, 2012.

Mattingly, W. B. Conservation and restoration of a biodiversity hotspot: longleaf pine savannas. Department of Biology, Eastern Connecticut State University, Willimantic, CT. February 1, 2012.

Mattingly, W. B. Conservation and restoration of a biodiversity hotspot: longleaf pine savannas. Department of Biology, Buffalo State College, Buffalo, NY. February 24, 2012.

Orrock, J.L. 2009. Spatial variation in consumer pressure and the invasion, restoration, and conservation of plant communities. University of Missouri, Columbia (hosted by UM graduate student conservation group).

Orrock, J.L. 2010. Large-scale consequences of plant-consumer interactions: landscape-level experiments of the factors that limit plant establishment. University of Wisconsin, Madison.

Orrock, J.L. 2011. Stochastic and deterministic perspectives on large-scale patterns in predation, disease, and communities. Michigan State University.

Veldman, J.W. 2012. Grasses, trees, and fire in human-modified landscapes. Michigan State University, Department of Plant Biology.

Veldman, J.W. 2013. Grasses, trees, and fire in human-modified landscapes. University of San Francisco, Department of Biology.

Veldman, J.W. 2014. Grasses, trees, and fire in human-modified landscapes. North Central College, Department of Biology.

Veldman, J.W. 2014. Grasses, trees, and fire in human-modified landscapes. Iowa State University, Dept. of Ecology, Evolution, and Organismal Biology.

Veldman, J.W., L. A. Brudvig, E.I. Damschen, J.L. Orrock, W.B. Mattingly, and J.L. Walker. 2014. Approaches and constraints to restoring high conservation value longleaf pine plant communities. Symposium: *Developing the Linkage Between Ecological Restoration and Conservation Biology*; organized by James Hallett. *In:* The 2nd North America Congress for Conservation Biology. Missoula, Montana, USA.

Veldman, J.W., L. A. Brudvig, E.I. Damschen, J.L. Orrock, W.B. Mattingly, and J.L. Walker. 2013. Prescribed fire, land-use history, and connectivity in the restoration of species-diverse, subtropical pine savannas. Symposium: *Restoration of tropical and subtropical grassland ecosystems*; organized by Elise Buisson (University of Avignon). *In*: The 5th World Conference on Ecological Restoration. Madison, Wisconsin, USA.

B5. Text books or book chapters

None