



Land-use history, historical connectivity, and land management interact to determine longleaf pine woodland understory richness and composition

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Restoration and management activities targeted at recovering biodiversity can lead to unexpected results. In part, this is due to a lack of understanding of how site-level characteristics, landscape factors, and land-use history interact with restoration and management practices to determine patterns of diversity. For plants, such factors may be particularly important since plant populations often exhibit lagged responses to habitat loss and degradation. Here, we assess the importance of site-level, landscape, and historical effects for understory plant species richness and composition across a set of 40 longleaf pine *Pinus palustris* woodlands undergoing restoration for the federally endangered red-cockaded woodpecker in the southeastern United States. Land-use history had an overarching effect on richness and composition. Relative to historically forested sites, sites with agricultural histories (i.e. former pastures or cultivated fields) supported lower species richness and an altered species composition due to fewer upland longleaf pine woodland community members. Landscape effects did not influence the total number of species in either historically forested or post-agricultural sites; however, understory species composition was affected by historical connectivity, but only for post-agricultural sites. The influences of management and restoration activities were only apparent once land-use history was accounted for. Prescribed burning and mechanical overstory thinning were key drivers of understory composition and promoted understory richness in post-agricultural sites. In historically forested sites these activities had no impact on richness and only prescribed fire influenced composition. Our findings reveal complex interplays between site-level, landscape, and historical effects, suggest fundamentally different controls over plant communities in longleaf pine woodlands with varying land-use history, and underscore the importance of considering land-use history and landscape effects during restoration.

Three facets of land transformation together represent the greatest threats to the world's biodiversity: habitat destruction, fragmentation, and degradation (Vitousek et al. 1997). How these changes play out across space and time is of key importance; however, in spite of substantial research attention on site-level, landscape, and historical factors in biodiversity research (Fahrig 2003), their interactive contributions are not well understood. Recent studies have begun to reveal how complex interactions between present-day and historic landscape factors determine levels of plant biodiversity, due to temporal lags of habitat loss and fragmentation (Lindborg and Eriksson 2004a, b, Adriaens et al. 2006). What is less well understood is how restoration and management of habitat patches within degraded landscapes interact with landscape and historical effects, such as site-level land-use history and present-day and historical landscape composition (Kuussaari et al. 2009).

The influence of history is of particular relevance for present-day patterns of plant biodiversity for at least two reasons. First, there is a strong role of temporal habitat

continuity, which has been especially well studied for forest plant biodiversity. Ancient forests – those with long temporal continuity – exhibit different composition and, sometimes, diversity, relative to younger forests with a more recent history of agricultural land use (Flinn and Vellend 2005, Hermy and Verheyen 2007). Due to wide-spread dispersal limitations of forest herbs, these effects can be long-lived, persisting for centuries following forest re-establishment from agricultural lands (Hermy and Verheyen 2007, Svenning et al. 2009). Thus, patches of habitat with similar present-day identities (e.g. forest) may differ in species composition due to variation in land-use history. Second, temporal lags can exist between habitat loss and fragmentation and biodiversity declines. Termed “extinction debt” (sensu Tilman et al. 1994), this effect may be particularly prominent for plant biodiversity, due to slow population dynamics of long-lived plant species (Lindborg and Eriksson 2004a, b, Honnay et al. 2005, Helm et al. 2006, Vellend et al. 2006, though see Adriaens et al. 2006, Cousins et al. 2007).

Although habitat degradation is a primary concern in restoration ecology, landscape and historical effects have not been thoroughly investigated in restoration and land management settings. Few restoration studies have considered landscape effects (Bell et al. 1997, Scott et al. 2001), focusing instead almost exclusively on the internal dynamics of patches of habitat undergoing restoration. Although studies of land-use legacies on vegetation and soils suggest the importance of considering history during restoration, direct comparison of restoration on sites with varying land-use histories have been rare to-date. Consideration of agricultural land-use legacies is of particular importance in forested communities throughout much of the eastern United States and portions of Europe, where substantial amounts of agricultural land have been abandoned during the past century (Flinn and Vellend 2005). These second growth forests that are established on old agricultural fields present substantial new opportunities for restoration and land management; however, little is known about if or how restoration approaches and outcomes might differ between forest patches of differing temporal continuity and land-use histories.

Understanding the complex interactions between all three facets of land transformation across local and landscape scales will be critical for restoration planning and assessment (Kuussaari et al. 2009), potentially revealing why some restoration efforts fail and others succeed. Here, we assess the contributions of land-use history, historical and present-day landscape effects (e.g. patch area, connectivity), and site-level factors (Table 1), for understory richness and composition of upland longleaf pine *Pinus palustris* woodland patches undergoing restoration in the southeastern United States. Although all sites are being managed for the same objective – persistence of the federally endangered red-cockaded woodpecker – sites vary in land-use history (forest, pasture, or cultivated field) and historical landscape context, presenting opportunities to assess how restoration outcomes vary with history. Because site-level factors such as land management (e.g. prescribed fire history, overstory tree density) vary across sites, we are able to investigate the relative contributions of landscape factors, history, and site-level factors in a restoration setting. Furthermore, we ask how landscape factors and land-use history modify the outcomes of restoration activities for plant species diversity.

Materials and methods

Study system and sites

We conducted this study within 40 upland longleaf pine woodlands (Peet 2006) being managed for the federally endangered red-cockaded woodpecker at the Savannah River Site (SRS), SC (Fig. 1). SRS – a National Environmental Research Park – is located in the coastal plain of South Carolina, with gently rolling to flat uplands supporting sandy Paleudult soils (80–90% sand; Kolka et al. 2005). Longleaf pine woodlands are characterized by a sparse longleaf pine overstory and a dense, diverse understory layer, with structure and diversity maintained by frequent understory fires (generally <10 yr return interval; Frost 2006, Jose et al. 2006, Peet 2006). At the SRS and elsewhere, red-cockaded woodpeckers function as an umbrella species for conservation of longleaf pine woodlands, as habitat requirements for this species consist of widely spaced, large diameter longleaf pine trees and a sparse or absent mid-story layer (Walters 1991). Prescribed understory fire is central to red-cockaded woodpecker habitat management; however, management may also involve mechanical removal of over- and mid-story trees (Walters 1991), especially at sites where burning is logistically challenging or when tree or mid-story densities are high.

A number of site-level factors, some related to land management, are thought to be important for understory dynamics in longleaf pine woodlands. Available soil moisture is a primary limiting resource in this system and soil water holding capacity is positively correlated with understory species diversity (Kirkman et al. 2001, 2004b). Understory fire is frequently manipulated through prescribed burning and is a key disturbance that promotes understory diversity by removing forest floor accumulation and by decreasing the density of competing mid-story hardwood species (Brockway and Lewis 1997, Hiers et al. 2007). Overstory tree density is manipulated by management through prescribed fire and mechanical thinning and is negatively correlated with levels of understory diversity (Harrington and Edwards 1999). Legacies of intensive (i.e. tillage) agriculture play a prominent role in determining understory composition in longleaf pine woodlands; however, the effect of historic agricultural land use on understory diversity is less well understood (Hedman et al.

Table 1. Description of longleaf pine woodlands with forest (n = 18), pasture (n = 10), or cultivated field (n = 12) land-use history. Values are mean/standard error.

	Land-use history		
	Forest	Pasture	Cultivated field
Historical connectivity (m ²) ¹	60 182.8/2511.9	8875.3/3370.0	5909.5/3076.4
Soil moisture holding capacity (%) ²	23.5/0.7	24.6/0.9	21.6/0.8
Present-day patch size (ha)	20.9/3.9	13.5/5.2	24.4/4.7
Canopy cover (%)	41.7/2.7	53.2/3.7	53.9/3.3
Overstory basal area (m ² ha ⁻¹)	10.3/0.4	13.5/1.8	14.7/1.7
Shrub density (stems ha ⁻¹)	318.9/74.4	430.0/99.9	335.0/91.1
Litter depth (cm)	2.6/0.5	3.8/0.7	4.6/0.6
No. fires since 1970 ³	4.3/0.4	3.5/0.5	4.2/0.5

¹ Forested area within 150 m of the sampling point.

² ((wet weight-dry weight)/dry weight) × 100.

³ Record keeping commenced in 1970.

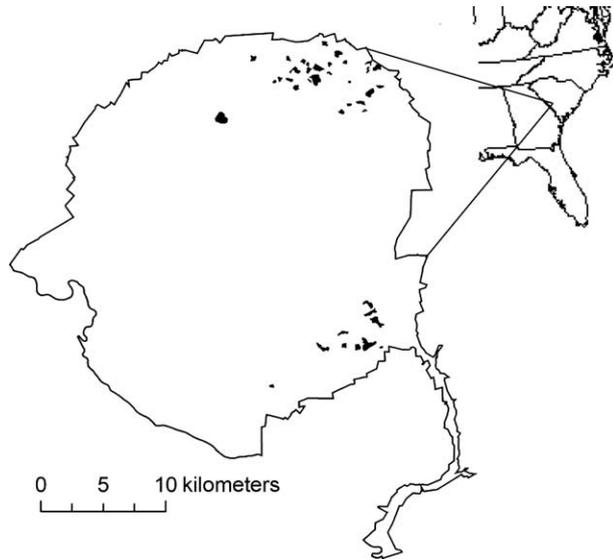


Figure 1. Distribution of 40 longleaf pine woodlands managed for the red-cockaded woodpecker at the Savannah River Site (SRS), SC, and location of SRS within the southeastern United States.

2000, Walker and Silletti 2006). Also not well understood are legacies of less intensive agricultural land-use (e.g. pasturing), with some evidence suggesting little effect on understory composition (Brockway and Lewis 1997). At the SRS, >50% of the uplands were in intensive agriculture at the time of land acquisition in 1951 (White 2005). Former agricultural lands have since been afforested and longleaf pine woodlands managed for red-cockaded woodpeckers support both agricultural and forested land-use histories (Johnston 2005) (Fig. 2).

Data collection

We conducted vegetation surveys in the 40 longleaf pine woodland sites between 1 September and 15 October 2007, using a modified version of the protocol developed by Peet et al. (1998). At the geometric center of each site, we established a randomly oriented 20×50 m plot, which contained a set of nested square plots (Fig. 2). Site boundaries were delineated by red-cockaded woodpecker management and related to landscape features (e.g. drainages and roads that function as fire breaks during burning management), as well as stand age and tree density (Johnston 2005). In each of four 10×10 m compartments, we established nested square plots in two of the corners, with dimensions 0.1×0.1 m, 0.32×0.32 m, 1×1 m, and 3.16×3.16 m. We recorded all vascular plant species rooted in this set of plots, the 10×10 m compartments, and the full 20×50 m plot, with which we quantified species richness across six orders of magnitude of sampling area: 0.01 – 1000 m^2 . Evaluating species richness at different spatial scales may be important because of scale-dependent effects of factors such as landscape context (Öster et al. 2007). Nomenclature follows Radford et al. (1964), except the genera *Dichanthelium*, and *Digitaria*, which follow Weakley (2008).

We collected a set of site-level variables at each longleaf pine woodland site during vegetation surveys (except

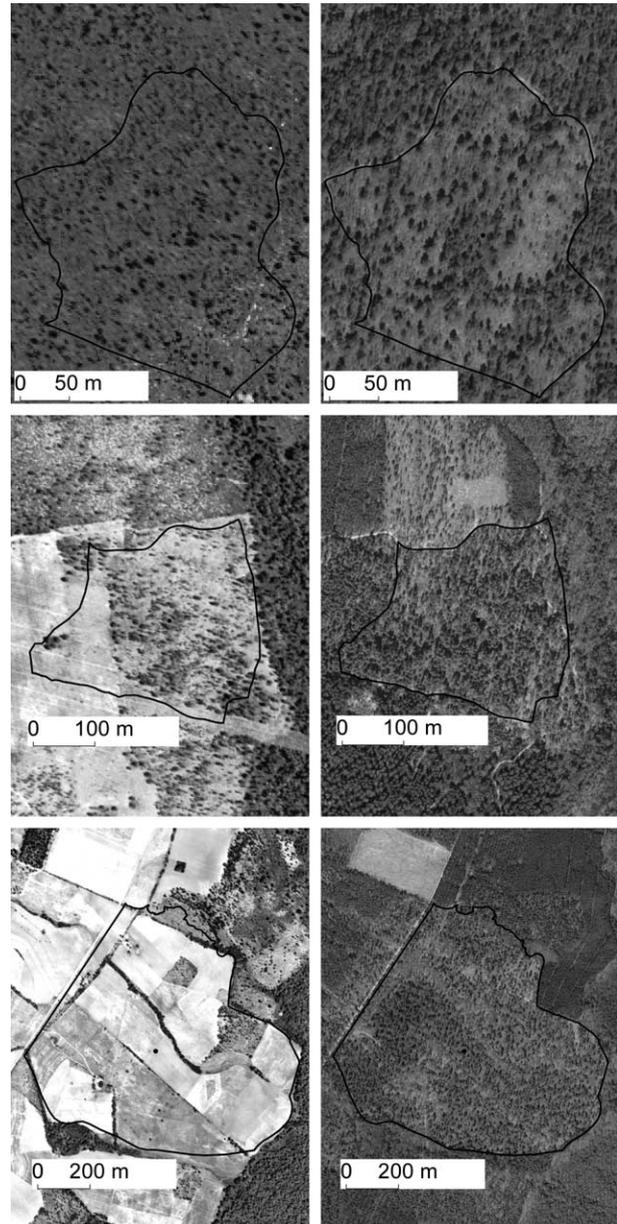


Figure 2. Aerial photos of longleaf pine woodlands with forest (top panels), pasture (middle panels) and cultivated field land-use history (bottom panels). Left panels are aerial photographs taken in 1951, when the Savannah River Site was obtained. Right panels are aerial photographs taken in 2007, when this study was conducted.

soil moisture holding capacity; see below) (Table 1). We quantified overstory basal area ha^{-1} (Avery and Burkhart 2002) by recording diameter at 1.37 m for all woody stems >5 cm diameter, rooted within each 20×50 m plot. We quantified mid-story stem density/ha by recording the number of woody stems >1.5 m tall and <5 cm diameter at 1.37 m, rooted within each 20×50 m plot. We quantified canopy cover at 10 m intervals along the mid-line of the 20×50 m plot (six measurements per site) using a spherical densiometer held at 1.37 m height. All densiometer measurements were conducted by a single

observer (Brudvig). We quantified the depth of the litter layer in the center of each 1 × 1 m plot (eight measurements per site). We calculated soil water holding capacity following the method of Salter and Williams (1967). We focused on this soil attribute because soil moisture is the primary limiting soil resource in longleaf pine woodlands (Kirkman et al. 2001, 2004b). In April 2009 we collected soil samples from each site, using a composite of 12 subsamples (collected every 10 m along the mid-line of the 20 × 50 m plot and three samples along the long side of each plot boundary, taken at 10, 20, and 30 m from the plot corner), each of which was composed of eight 2.5 cm diameter × 20 cm deep soil cores. Following collection, we refrigerated soils until analysis (< 1 month). Analysis for soil water holding capacity involved placing a subsample of the soil from each site in a 5 cm tall by 6.5 cm wide soil tin, which had 15 one mm wide holes drilled in the bottom and was lined with filter paper to prevent soil loss. We then placed tins in shallow pans of tap water for 24 h, removed saturated tins and placed them on wire racks until they stopped dripping (~ 30 s), collected wet weight, dried the samples at 105°C for 72 h, and collected dry weight. We calculated soil water holding capacity as the proportional difference between wet and dry weight [(wet weight-dry weight)/dry weight], accounting for the weight of the tin and filter paper.

To determine historical and landscape-level variables for each site, we created a Geographic Information System (GIS) containing historical and present day high resolution (≤ 2 m) digitized aerial photographs of the SRS, from the year of site acquisition (1951) and the year of field data collection (2007), sampling plot boundaries, management boundaries for each longleaf pine woodland in this study, and annual prescribed and wildfire records beginning in 1970. From this GIS, we determined historical land use of each sampling plot (forest, pasture, cultivated field), historical connectivity of each sampling plot (area of forest within 150 m of the sampling plot), present day patch area (area of the patch managed for the red-cockaded woodpecker), and two metrics of fire history for each sampling plot (number of burns in the past decade, number of burns on record [since 1970]). We determined historic land use by visually inspecting the 1951 aerial for tree and understory density. Forests contained a continuous tree layer, pastures a scattered tree layer, and arable fields no trees and no understory vegetation (the later clearly visible due to the light color of bare sandy soil in our system) (Fig. 2). We calculated two metrics for fire history because, although fire history is an important explanatory variable of species richness in longleaf pine woodlands

(Brockway and Lewis 1997, Kirkman et al. 2004b), we did not know over which time scales this would operate at our sites. Our connectivity metric, though potentially conservative if connectivity extends past 150 m, is based on a distance for which connectivity is known to impact richness of this flora (Damschen et al. 2006). We did not calculate historic patch size because our sites varied in land-use history and it was unclear how to define patch size for sites that were historically non-forested (Fig. 2). We did not calculate present-day connectivity because, in this system, both patches and matrix are now forested and can support many of the species we recorded in our surveys (Fig. 2). Thus, standard definitions of connectivity, which define habitat as either suitable or non-suitable (Calabrese and Fagan 2004), may not be appropriate.

Analyses

We first determined how patterns of understory species richness, across all 40 sites, were correlated with site-level, landscape, and historical factors with stepwise linear regression models (PROC REG, SAS 2003). We conducted separate models for three sampling scales (1, 100, 1000 m²), averaging values for 1 and 100 m² plots, which were replicated four and eight times, respectively, at each site, to arrive at one species richness value for each sampling scale at each site. We performed no transformations for any of our analyses, as richness values were normally distributed within sampling scales. We chose these three sampling scales because of the possibility that site-level and landscape factors might influence richness differently at local (1 m²), intermediate (100 m²), and large (1000 m²) sampling scales (Öster et al. 2007). In each regression model, we included the following predictor variables for each site: soil moisture holding capacity, canopy cover, mid-story density, litter depth, number of burns on record (since 1970), present-day site area, historical land use, and historical connectivity (Table 1). We did not include overstory density or overstory basal area, to avoid multicollinearity problems with overstory canopy cover, which was a better predictor of understory richness across scales in univariate regression. For the same reasons, we did not include number of burns in the previous decade, in favor of number of burns on record, in our models. We retained variables with $p < 0.1$ for partial r^2 in the final models.

Based on these initial regressions, it was clear that land-use history was the predominant driver of species richness (see Results and Table 2). To explore the role of land-use history on species richness in more detail, we conducted two

Table 2. Results of stepwise linear regression for species richness sampled at 1, 100, and 1000 m² in longleaf pine woodlands managed for red-cockaded woodpeckers at the Savannah River Site, SC.

	DF	Model F/p	Model r^2	Factor	Parameter estimate ± SE	Partial r^2 /F/p
1 m ² species richness	1,38	12.8/0.001	0.25	Intercept	3.9 ± 1.1	F = 12.2, p = 0.001
				Forested in 1951	3.5 ± 0.9	0.25/12.8/0.001
100 m ² species richness	1,38	11.7/0.001	0.24	Intercept	23.7 ± 4.0	F = 35.0, p < 0.0001
				Forested in 1951	11.9 ± 3.4	0.24/11.7/0.001
1000 m ² species richness	1,38	13.8/0.0007	0.27	Intercept	63.6 ± 3.7	F = 294.6, p < 0.0001
				Forested in 1951	20.5 ± 5.5	0.27/13.8/0.0007

additional sets of analyses. First, to test for differences in species richness between the three land-use history types, we used one-way ANOVA (PROC GLM, SAS 2003) with land-use history type (forest, pasture, cultivated field) as the independent variable and species richness as the dependent variable. We ran separate ANOVA's for each of the six sampling scales (0.01–1000 m²), again averaging values for plots replicated within sites (0.01–100 m² sampling scales) to arrive at one species richness value per sampling scale for each site. Second, to understand whether site-level and landscape factors have differential effects on patterns of species richness, depending on land-use history, we repeated the above multiple linear regression analyses for the historic forest (n = 18) and post-agricultural (i.e. pasture and cultivated field; n = 22) sites separately. Grouping sites as historic forest and post-agricultural was based on the initial multiple linear regression and ANOVA results (see Results, Table 2, Fig. 3).

We next determined how plant community composition was influenced by site-level, landscape, and historical factors with nonmetric multidimensional scaling (NMS) in PC-ORD (McCune and Mefford 1999). We ordinated the 40 longleaf pine woodland sites based on species presence/absence data from the 1000 m² plots, for the 168 plant species with >3 occurrences (McCune and Grace 2002). We used Sørensen distances with a random starting configuration on 40 runs with real data, each with 400 iterations, a stability criterion of 0.00001, and selected the number of dimensions in the final solution based on further dimensions reducing stress by <5 (McCune and Grace 2002). We then correlated the resulting axis scores with the following second matrix variables: soil moisture holding capacity, canopy cover, mid-story density, litter depth, number of burns on record (since 1970), present-day site area, historical land use, and historical connectivity. We considered second matrix variables significantly correlated with axes based on a critical Pearson's *r* value of 0.31 (*p* < 0.05, DF = 38).

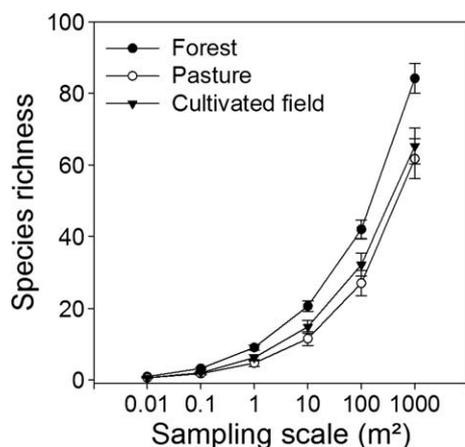


Figure 3. Species richness across six orders of magnitude of sampling scale from longleaf pine woodlands with forest, cultivated field, and pasture land-use history. Woodlands with forested land-use history have significantly greater species richness at every sampling scale, relative to woodlands with cultivated field or pasture land-use history, whereas woodlands with cultivated field and pasture land-use history do not differ at any scale.

Based on the importance of historical factors for plant community composition (see Results), we ran two follow-up analyses. First, we ran follow-up NMS analyses to control for land-use history (i.e. separate analyses for historic forest and post-agricultural sites), with all other analysis attributes the same as in the original NMS. Critical Pearson's *r* values for correlation with second matrix variables were 0.44 for historical forest sites (*p* < 0.05; *n* = 18) and 0.4 for post-agricultural sites (*p* < 0.05; *n* = 22). Second, we used Indicator Species Analysis (ISA) in PC-ORD (McCune and Mefford 1999) to describe species affinities for sites with forest, pasture, and cultivated field land-use history. As with the NMS analysis, we ran ISA using species presence/absence data from the forty 1000 m² plots, first removing species with <4 occurrences (168 total plant species). We considered species significant indicators of a given land-use history at *p* < 0.05 for 1000 Monte Carlo permutations.

Finally, we recognize the potential for non-random land-use history in our study. We do note, however, that all of our sites were on relatively level uplands and supported sandy Paleudult soils, suggesting that non-random land-use history, if present in our system, might be less problematic than in systems with wider variation in topography or soil productivity.

Results

Based on our first multiple linear regression analyses, land-use history was the predominant (and only significant) driver of species richness (Table 2). Whether or not a sampling point was forested in 1951 accounted for 24–27% of the variation in species richness across local, intermediate, and large sampling scales, with historically forested sites (n = 18) supporting 24–41% greater species richness than post-agricultural sites (pasture or cultivated field; n = 22) across sampling scales (0.01–1000 m²; minimum *t* = 2.4, *p* = 0.02) (Fig. 3). Secondary ANOVA analyses revealed that within post-agricultural sites, the type of land use did not alter species richness: sites historically supporting pasture (n = 10) or cultivated fields (n = 12) did not differ in species richness at any sampling scale (maximum *t* = 1.3, *p* > 0.2).

Secondary multiple linear regression analyses indicated differential influences of site-level factors on species richness for historically forested vs post-agricultural sites. For historically forested sites, species richness was not significantly correlated with any of the predictor variables (Table 3), whereas for post-agricultural sites, species richness was positively correlated with the number of burns on record (since 1970) and negatively correlated with canopy cover (Table 3, Fig. 4, 5). Although burning history and canopy cover were significant predictors of richness at all sampling scales in post-agricultural sites, burning history was most strongly correlated with richness at small sampling scales (*r*² = 0.37), canopy cover was most strongly correlated at large samplings scales (*r*² = 0.22), and the two variables were roughly equivalent predictors of richness at intermediate sampling scales (*r*² = 0.22–0.24) (Fig. 4, 5).

The NMS of all sites resulted in a three dimensional solution with a stress value of 14.7 (stress below 20 is

Table 3. Results of stepwise linear regression for species richness sampled at 1, 100, and 1000 m² in longleaf pine woodlands with agricultural land-use history, presently managed for red-cockaded woodpeckers at the Savannah River Site, SC. Equivalent models for historically forested sites did not contain significant predictor variables at any scale.

	Land-use history	DF	Model F/p	Model r ²	Factor	Parameter estimate ± SE	Partial r ² /F/p
1 m ² species richness	Agricultural	2,19	9.3/0.002	0.50	Intercept	7.1 ± 2.6	F = 7.6, p = 0.01
					Burns since 1970	0.9 ± 0.05	0.37/11.8/0.003
					Canopy cover	-0.1 ± 0.2	0.12/4.6/0.04
100 m ² species richness	Agricultural	2,19	8.08/0.003	0.46	Intercept	46.1 ± 9.2	F = 25.3, p < 0.0001
					Burns since 1970	2.5 ± 0.9	0.24/8.5/0.009
					Canopy cover	-0.5 ± 0.2	0.22/5.6/0.03
1000 m ² species richness	Agricultural	2,19	5.4/0.01	0.36	Intercept	87.6 ± 13.4	F = 43.0, p < 0.0001
					Canopy cover	-0.6 ± 0.2	0.22/5.5/0.03
					Burns since 1970	2.6 ± 1.3	0.14/4.3/0.05

considered adequate; McCune and Grace 2002). Axis 1 accounted for 35% of the variation in species composition and was positively associated with historical connectivity and negatively correlated with litter depth, canopy cover, and historical land use (coding for land use: forest = 0,

pasture = 1, cultivated field = 2) (Fig. 6). Axis 2 accounted for 34% of the variation in species composition and was positively associated with historical land use and negatively associated with historical connectivity (Fig. 6). Axis 3 accounted for 15% of the variation in species composition

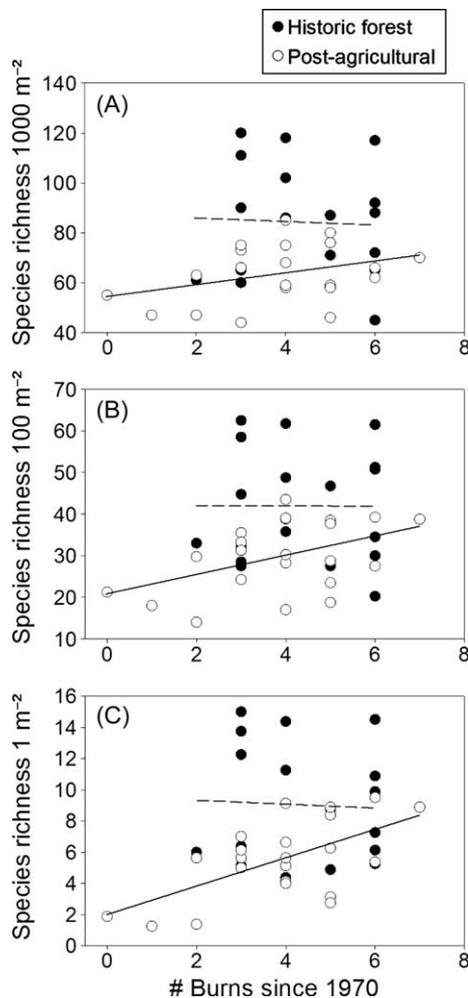


Figure 4. Correlations between number of understory fires since 1970 and species richness at small (1 m²), intermediate (100 m²) and large (1000 m²) sampling scales. This relationship increases in strength from large (r² = 0.14) to small scales (r² = 0.37) in post-agricultural sites, whereas no relationship exists in historically forested sites.

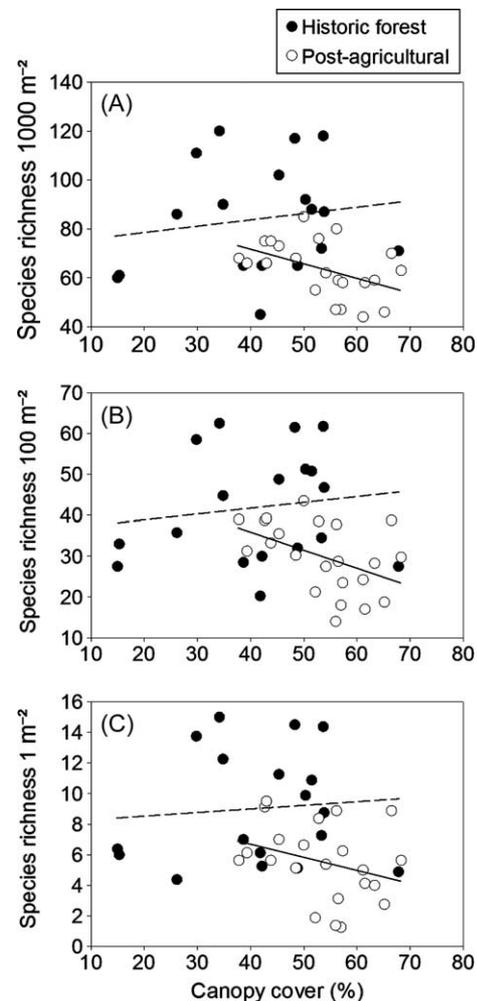


Figure 5. Correlations between canopy cover and species richness at small (1 m²), intermediate (100 m²) and large (1000 m²) sampling scales. This relationship increases in strength from small (r² = 0.12) to large scales (r² = 0.22) in post-agricultural sites, whereas no relationship exists in historically forested sites.

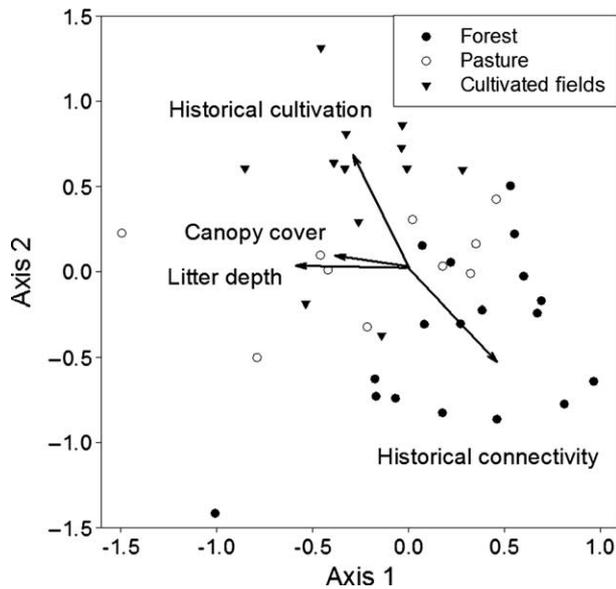


Figure 6. NMS of understory species recorded in 40 longleaf pine woodlands with varying land-use history (forest, pasture, cultivated field). Axis 1 ($r^2=0.35$) is correlated with canopy cover, litter depth, prescribed fire history, and historical connectivity. Axis 2 ($r^2=0.42$) is correlated with historical connectivity and land-use history.

and was positively correlated with historical connectivity and the total number of burns since 1970 and negatively correlated with historical land use.

Follow-up NMS analyses controlling for land-use history resulted in three dimensional solutions for both historically forested and post-agricultural sites, with stress values of 8.1 and 12.9, respectively. For historically forested sites, axis 1 and 3 accounted for 29 and 9% of the variation in species composition, respectively, but neither axis significantly correlated with any second matrix variables. Axis 2 accounted for 55% of the variation in species composition and was negatively correlated with litter depth and the number of burns since 1970. For post-agricultural sites, axis 1 accounted for 15% of the variation in species composition and was negatively correlated with soil moisture holding capacity. Axis 2 accounted for 40% of the variation in species composition and was positively correlated with historical land use and the number of burns since 1970 and negatively correlated with soil moisture holding capacity and litter depth. Axis 3 accounted for 29% of the variation in species composition and was positively correlated with historical connectivity and negatively correlated with litter depth.

ISA revealed that 42/168 understory species were indicative of sites with forest, pasture, or cultivated field land-use history (Table 4). Of these, 28 were indicators of historical forests, 11 of historical cultivated fields, and 3 of historical pastures.

Discussion

Land-use history had an overarching effect on both plant species richness and composition during management of

longleaf pine woodlands for the federally endangered red-cockaded woodpecker. Effects of land-use history on richness were scale independent, as historically forested sites contained higher species richness across all spatial scales (0.01–1000 m²). Conversely, sites with post-agricultural histories (pasture vs cultivated fields), that had been reforested for similar time periods (~50–60 yr), did not differ in species richness at any scale, suggesting that temporal forest continuity is critically important in this system. We found varying influences of landscape effects. Historical connectivity altered plant community composition, but not richness, and we found no effects of present-day patch size on richness or composition.

The influence of land management activities on plant species richness varied with land-use history. Richness at post-agricultural sites was correlated with fire management and canopy cover, whereas we found no relationships between any of our measured variables and richness at any scale in historically forested sites. From the simplified perspective of species richness, these results are encouraging for post-agricultural sites. Although these sites lack the species richness of historically forested sites, restoration by burning and canopy cover reduction might help to minimize this discrepancy. Management activities appear effective for post-agricultural sites, as burning and mechanical thinning are the two most commonly employed restoration techniques for longleaf pine woodlands at SRS (Johnston 2005). Furthermore, management of post-agricultural sites altered richness differently at small vs large spatial scales, presenting interesting hypotheses for future work. In particular, at local scales, richness increased most strongly with rates of burning, suggesting that factors such as understory competition or litter accumulation might drive diversity at small scales (Hiers et al. 2007). At large scales, richness declined most strongly with canopy cover, suggesting that competition by overstory trees and the spatial distribution of gaps might drive diversity at larger scales (Harrington and Edwards 1999). At the same time, the absence of significant predictor variables for richness in sites with forested land-use history suggests that very different mechanisms maintain species richness in sites with forested vs agricultural histories. Relative to post-agricultural sites, understories in historically forested sites may be more resilient to degradation resulting from high tree densities and fire suppression; however, we do not argue that historically forested sites will persist indefinitely without management. Although sites varied in fire frequency, the number of burns ranged from 2–6 burns over the last 37 yr. In the complete absence of fire, even the highest quality remnant sites have been shown to degrade over time (Jose et al. 2006).

We believe that reduced canopy cover, a significant predictor of richness in post-agricultural sites, is the result of mechanical mid- and overstory thinning, not burning activities. Had burning impacted canopy cover through mid- and overstory mortality, we would expect a negative relationship between burning and canopy cover (i.e. declining canopy cover with increasing burn frequency) and we found no evidence for this relationship (Fig. 7). Interestingly, however, we saw different relationships between burning and canopy cover for historically forested (positive relationship) vs post-agricultural (no relationship)

Table 4. Species identified by ISA as significant indicators of longleaf pine woodlands with forest, pasture, or cultivated field land-use histories. Species are organized alphabetically by the land-use history for which they were a significant indicator (noted by bold font). Species identified as upland longleaf pine woodland community members by Kilgo and Blake (2005) are noted by *.

Species	Family	Historical land use (% of sites occupied)		
		Forest	Pasture	Cultivated field
<i>Agalinis fasciculata</i> *	Scrophulariaceae	39	0	0
<i>Aristida lanosa</i> *	Poaceae	67	30	8
<i>Aster concolor</i> *	Asteraceae	44	0	0
<i>Aster linariifolius</i> *	Asteraceae	67	0	0
<i>Carphephorus bellidifolius</i> *	Asteraceae	50	0	0
<i>Ceanothus americanus</i> *	Rhamnaceae	33	0	0
<i>Cnidocolus stimulosus</i> *	Euphorbiaceae	50	10	0
<i>Coreopsis major</i> *	Asteraceae	72	10	0
<i>Dyschoriste oblongifolia</i> *	Acanthaceae	78	0	0
<i>Eriogonum tomentosum</i> *	Polygonaceae	83	0	0
<i>Eupatorium album</i> *	Asteraceae	39	0	0
<i>Euphorbia corollata</i> *	Euphorbiaceae	39	0	17
<i>Euphorbia ipecacuanhae</i> *	Euphorbiaceae	61	30	8
<i>Gaylussacia dumosa</i> *	Ericaceae	94	0	8
<i>Hypericum gentianoides</i> *	Hypericaceae	89	30	58
<i>Liatris secunda</i> *	Asteraceae	89	40	8
<i>Pteridium aquilinum</i> *	Pteridaceae	50	10	0
<i>Quercus laevis</i> *	Fagaceae	89	40	33
<i>Quercus margaretta</i> *	Fagaceae	44	10	8
<i>Salvia azurea</i> *	Lamiaceae	28	0	0
<i>Silphium compositum</i> var. <i>compositum</i> *	Asteraceae	72	10	0
<i>Sorghastrum secundum</i> *	Poaceae	22	0	0
<i>Sporobolus junceus</i> *	Poaceae	39	0	0
<i>Stipa avenacea</i> *	Poaceae	33	0	8
<i>Tephrosia virginiana</i> *	Poaceae	72	0	8
<i>Vaccinium arboretum</i> *	Ericaceae	100	80	42
<i>Vernonia angustifolia</i> *	Asteraceae	94	20	8
<i>Viola pedata</i> *	Violaceae	33	0	0
<i>Lespedeza stuevei</i>	Fabaceae	28	90	58
<i>Petalostemum pinnatum</i> *	Fabaceae	22	50	0
<i>Quercus nigra</i>	Fagaceae	50	100	92
<i>Celtis occidentalis</i> var. <i>georgiana</i>	Ulmaceae	11	10	42
<i>Centrosema virginianum</i> *	Fabaceae	28	50	75
<i>Cornus florida</i>	Cornaceae	6	0	42
<i>Desmodium lineatum</i> *	Fabaceae	6	0	50
<i>Desmodium marilandicum</i> *	Fabaceae	56	30	80
<i>Desmodium strictum</i> *	Fabaceae	67	70	100
<i>Dichanthelium commutatum</i>	Poaceae	28	70	83
<i>Digitaria cognate</i>	Poaceae	28	0	85
<i>Helianthemum rosmarinifolium</i> *	Cistaceae	11	50	75
<i>Lechea villosa</i> *	Cistaceae	33	30	83
<i>Lespedeza cuneata</i>	Fabaceae	6	10	42

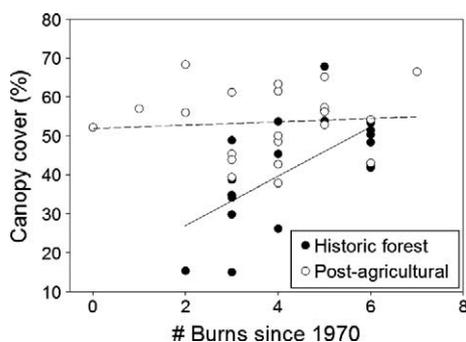


Figure 7. Correlation between number of understory fires since 1970 and overstory canopy cover for longleaf pine woodlands with forested vs agricultural land-use history. A significant positive relationship exists for historically forested sites ($r^2 = 0.41$), whereas no relationship exists for post-agricultural sites ($r^2 < 0.01$).

sites. The two site types did not differ in number of burns ($p = 0.35$); however, post-agricultural sites had greater canopy cover ($p < 0.01$) (Table 1). The reason for this difference may lie in how overstory regeneration occurs. Post-agricultural sites have primarily been regenerated artificially (White 2005) resulting in dense pine plantations, necessitating mechanical overstory thinning during restoration for red-cockaded woodpeckers (Johnston 2005). Conversely, in historically forested sites, which regenerated naturally, a history of directed management where burning activities have been focused on stands with higher tree density and canopy cover, perhaps in an attempt to reduce woody stems, might explain the positive relationship between overstory cover and fire history.

Our compositional results also showed history and management-related site-level conditions to be major drivers of understory plant communities at our sites. These findings were generally in-line with our richness results,

with composition determined by overstory density (NMS axis 1: canopy cover and, as a consequence, litter depth; Hiers et al. 2007), history (NMS axis 2: land-use history, historical connectivity), and fire management (NMS axis 3: total number of fires on record) (Fig. 6). Axis 1 and 3 further underscore the importance of overstory thinning and prescribed fire for longleaf pine woodland understory biodiversity. Qualitatively, this ordination showed a distinction between sites with forest vs cultivated field land-use history, with historical pasture sites of intermediate composition. Although the influence of historical connectivity on present-day plant community composition, across our full set of 40 sites, is intriguing and in-line with some past findings (Lindborg and Eriksson 2004a, b, Adriaens et al. 2006), we believe that correlations between historical land-use and historical connectivity may be driving this result. Historically forested plots were 6–9 times better connected to forest in the past, than were historical pastures or cultivated fields ($F_{2,37} = 122.3$, $p < 0.0001$). Thus, support for historical connectivity altering understory composition must be interpreted cautiously and there is a clear need for future research to determine the independent influences of land-use history and historical landscape effects. To our knowledge, such an analysis has yet to be conducted in longleaf pine woodlands or elsewhere. We provide some insight on this front with our follow-up NMS analyses that controlled for land-use history, which showed understory composition at post-agricultural sites to be related to historical connectivity with forests. This suggests that historically better connected old fields and pastures experienced elevated colonization rates by forest species during succession to forest (relative to poorly connected sites), a phenomenon reported elsewhere (Vellend 2003), with clear relevance for recovery of longleaf pine woodlands in afforested landscapes.

Our findings suggest the need for longleaf pine woodland management strategies to account for land-use history. We suggest two general strategies for management. First, whenever possible, new management initiatives for red-cockaded woodpeckers should focus on sites with forested histories. As an umbrella management approach, protection of these sites will pay the largest dividends for preserving plant diversity. Second, although management by prescribed fire and tree thinning has promoted plant species richness in post-agricultural sites, these sites – especially those with histories of cultivation – differ in species composition from historically forested sites. Investigating our ISA results, 28/28 indicators of historical forests, 6/11 indicators of historic cultivated fields, and 1/3 indicator of historic pastures were upland longleaf pine woodland community members – species considered representative of fire maintained upland longleaf pine woodlands at SRS (Kilgo and Blake 2005). This suggests that agricultural land-use legacies act as a strong filter for longleaf woodland plant communities. Although land management can act upon the resulting plant communities, by increasing richness, dispersal limitations may inhibit the recovery of this flora (Kirkman et al. 2004a), suggesting that reintroductions by seed may be an important restoration strategy. Although managers might consider proximity to ancient forest sites during this process, it will be important to determine for which subset of the longleaf pine flora such

sites will act as seed sources and for which species dispersal limitations will preclude recolonization (Kirkman et al. 2004a, Damschen et al. 2008).

We recommend additional future work on two fronts. First, a better understanding of connectivity in this and other systems is warranted. Most commonly used connectivity metrics rely on a dichotomization of focal patch and matrix habitat (Calabrese and Fagan 2004). Such a view of the world might be appropriate in some instances – island systems or when inhospitable agriculture separates patches of habitat, for example (Freckleton and Watkinson 2002). However, in many systems, such as our longleaf pine woodland/pine plantation system, matrix habitat is variably hospitable to community members. Second, experiments in longleaf pine woodlands are needed to assess whether the factors we identified are cause-and-effect controls over species richness. Longleaf pine woodlands have among the most diverse plant communities of any system outside of the tropics, but are highly fragmented and often degraded and in need of restoration (Jose et al. 2006). Thus, a better understanding of the mechanistic drivers of plant biodiversity, especially in how they relate to land-use history and restoration, would be useful and afforded by an experimental approach.

We believe that studies, like this one, comparing the relative influences of landscape, historical, and site-level factors have much to offer both basic and applied ecology. Basic studies of how historical and present-day habitat loss and fragmentation influence patterns of biodiversity (e.g. extinction debt studies) have rarely considered present-day land management activities. Conversely, restoration ecology studies have rarely considered how landscape or historical factors modify restoration outcomes. Here, we show clear interaction between history and restoration and suggest that similar interactions may be at play in the many other fragmented landscapes being managed or restored. As noted by Kuussaari et al. (2009), consideration of recent landscape modification during restoration and management activities is of particular importance due to lagged population responses and ensuing extinction debt dynamics. We underscore the importance of considering such historical legacy effects during restoration and show how patterns of understory biodiversity were dictated by management only once history is accounted for.

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