Predictors of Species Richness in Northwest Florida Longleaf Pine Sandhills

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Abstract: *Soil characteristics, disturbance histories, and species richness among distinct groups of plants and animals may be useful predictors of important conservation areas when data are limited. We used multivariate analysis of covariance to test the hypothesis that the species richness of plants, arthropods, herpetofauna, and breeding birds are correlated and increase with soil fertility (silt and clay content in sandy soils), soil variability, and hardwood midstory reduction in subxeric, nutrient-poor longleaf pine sandhills at Eglin Air Force Base in northwest Florida. During 1994–1995 and 1998–1999, we sampled 30 81-ha plots with varying fire-exclusion histories and at two spatial scales of resolution (10 × 40 m and 81 ha). The relationship between the number of plant species and percent silt and clay and its coefficient of variation was significant and positive at the plot level (81 ha) but not at the subplot level (10 × 40 m). Herpetofaunal species richness was the only faunal variable that increased with silt and clay content, but the coefficient of variation did not. Multivariate effects of hardwood reduction were significant in 1998–1999 but not in 1994–1995, which suggests that the reintroduction of fire increased species richness across taxa. Univariate effects of hardwood reduction were marginally significant for plant species richness at the subplot level and not significant for herpetofaunal species richness at either scale. Plant and arthropod species richness were not correlated. Herpetofaunal species richness was not correlated with that of other taxa (plant and animal). The species richness of plants and arthropods were each significantly positively correlated with the richness of breeding bird species at the subplot level during 1994–1995, whereas only arthropod species richness was positively correlated with bird species richness at the plot level in either year. Our results suggest that the restoration of fire regime may be the most effective tool with which to increase diversity in pyrogenic areas considered for conservation protection.*

Key Words: biodiversity, disturbance, Eglin Air Force Base, fire, hardwood reduction, longleaf pine, soil fertility, species richness

Predictores de Riqueza de Especies en Colinas de Pinos del Noroeste de Florida

Resumen: *Las características del suelo, la historia de perturbaciones y la riqueza de especies en grupos distintos de plantas y animales pueden ser predictores útiles de áreas de conservación importantes cuando los datos son limitados. Utilizamos un análisis multivariado de covarianza para probar la hipótesis de que la riqueza de plantas, artrópodos, herpetofauna y aves reproductoras están correlacionadas e incrementan con la fertilidad del suelo (contenido de limo y arcilla en suelos arenosos), la variabilidad del suelo y la disminución de madera dura en las colinas de pinos pobres en nutrientes en la Base Eglin de la Fuerza Aérea en el noroeste de Florida. Durante 1994/1995 y 1998/1999, muestreamos 30 parcelas de 81 ha con variadas historias de exclusión de fuego y con resolución a dos escalas espaciales (10 × 40 m y 81 ha). La relación entre el número de especies de plantas y el porcentaje de limo y arcilla y su coeficiente de variación fue significativa y positiva a nivel de parcela (81 ha) pero no a nivel de sub-parcela (10 × 40 m). La riqueza de especies herpetofaunísticas fue la única variable de fauna que incrementó con el contenido de limo y arcilla. Sin embargo, el coeficiente de variación no aumentó. Los efectos multivariados de la disminución de madera*

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dura fueron significativos en 1998/1999, pero no en 1994/1995, lo que sugiere que la reintroducción de fuego incrementó la riqueza de especies en los taxones revisados. Los efectos univariados de la disminución de madera dura fueron marginalmente significativos para la riqueza de especies de plantas al nivel de sub-parcela y no significativos para la riqueza de especies de herpetofauna a ninguna de las escalas. Las riquezas de especies de plantas y artrópodos no estuvieron correlacionadas. La riqueza de especies de herpetofauna no se correlacionó con otros taxones (plantas y animales). La riqueza de especies de plantas y artrópodos estuvo correlacionada positiva y significativamente en cada caso con la riqueza de especies de aves reproductoras al nivel de sub-parcela durante 1994/1995, mientras que sólo la riqueza de especies de artrópodos se correlacionó positivamente con la riqueza de especies de aves al nivel de parcela en todos los años. Nuestros resultados sugieren que la restauración de regímenes de fuego puede ser la herramienta más eficaz de incrementar la diversidad en áreas pirogénicas consideradas para la conservación.

Palabras Clave: Base Eglin de la Fuerza Aérea, biodiversidad, fertilidad del suelo, fuego, perturbación, pino, reducción de maderas duras, riqueza de especies

Introduction

Identifying priority areas for protection has become increasingly important as an ever-growing number of threatened areas tax the limited resources of public and private conservation organizations (Huston 1994; The Nature Conservancy 2000). Frequently, selection criteria for conservation have been based on rare and endemic plant species because these taxa are more easily identified or data already exist. Data are often not available for many sites, however, or sites lack data on single species or groups of species, especially for less-frequently studied groups of taxa (e.g., arthropods). Even in the absence of data, conservation plans must be developed. Therefore, methods are needed to identify areas of more concentrated species diversity. Methods that identify tentative correlates of species diversity, where we do not have data, are desirable.

Several hypotheses regarding global patterns of species diversity have been proposed (reviewed in Rosenzweig & Abramsky 1993; Huston 1994). Conservation organizations and state- or locally funded programs, however, are more likely to be interested in patterns and mechanisms that are regional and local because funding often follows ecophysiographic or political boundaries. One hypothesis that applies at many scales suggests that plant species diversity will peak at intermediate levels of soil fertility (Rosenzweig & Abramsky 1993; Huston 1994). At low levels of soil fertility, few species are capable of survival, but the number of species increases rapidly under improved soil conditions. At some intermediate, but still low level of soil productivity, competitive exclusion becomes increasingly important and species diversity progressively decreases as conditions for growth improve. At any level of productivity, species diversity is further increased by intermediate frequencies of disturbance and geomorphological heterogeneity. Herbivores and carnivores are also thought to have a similar unimodal relationship with soil fertility, with the position of the mode varying depending on the way the group utilizes resources (Huston 1994).

Soil fertility, disturbance frequency, and soil heterogeneity may not be sufficient, however, to indicate areas of relatively high biological diversity. Several authors (Kremen 1992; Prendergast et al. 1993; Kerr 1997; Panzer & Schwartz 1998) have proposed that the diversity of well-studied taxa be used as surrogates for the diversity of data-poor groups. They found a relationship between high species richness or diversity of one taxa with that of another (e.g., flowering plants and butterflies), but not every pair-wise relationship was significant. These investigators worked with different taxonomic groups at several spatial scales (from local to continental) and used various analyses; therefore, general patterns have yet to emerge. For instance, we might expect a positive correlation between plant and arthropod diversity based on the coevolution of vascular plants and insects (Wilson 1992), but the relationship may not be that simple (e.g., Kremen 1992; Panzer & Schwartz 1998).

We investigated the relationships among soil fertility, fire-exclusion history, and plant and animal species richness within longleaf pine (*Pinus palustris*) sandhills at Eglin Air Force Base (Eglin), located in the western panhandle of Florida. This area was especially suited for examining the topic of species diversity because it is within one of the top six biodiversity hotspots identified in the United States (Stein et al. 2000).

Study Area

Eglin Air Force Base is described in detail by Rodgers and Provencher (1999) and by Provencher et al. (2001*a*). The base encompasses 187,555 ha in the southern portions of Walton, Okaloosa, and Santa Rosa counties east of Pensacola. At least 74% of Eglin is sandhills dominated by longleaf pine, most of which was fire-excluded (managed to prevent fire) for at least 5 decades before 1990.

The sandy soils of Eglin sandhills (Overing et al. 1995) are on the low end of the soil fertility continuum, where species richness is expected to increase with greater soil fertility. The soils are mainly composed of sands 2–10 m deep in the Lakeland series (Overing et al. 1995). This series is a thermic, coated Typic Quartzipsamments that is rapidly permeable, strongly acidic, and located on nearly level to steep slopes. Silt content varies from 4% to 8% (Overing et al. 1995). Patches of soil richer in silt of the Troup series are occasionally found within the Lakeland soil matrix. Eglin sandhills (1- to 5-year fire-free interval) contained 179–273 ppm (95% confidence interval, $n = 6$) total Kjeldahl nitrogen, 1.26–1.44 ppm of phosphorus, and <0.9% organic matter (Rodgers & Provencher 1999; Provencher, L., A. R. Lih, K. E. M. Galley, D. R. Gordon, G. W. Tanner, L. A. Brennan, N. M. Gobris, S. J. McAdoo, J. P. McAdoo, and B. J. Herring. 2001. Restoration of fire-suppressed longleaf pine sandhills at Eglin Air Force Base, Niceville, Florida. Science Division, The Nature Conservancy, Gainesville, Florida). Greater silt and clay increases soil water retention and, in turn, soil fertility. Changes in silt content of as little as 4% can alter plant community composition and vegetation structure (Harcombe et al. 1993). Variation in silt and clay across the larger landscape provided the opportunity to test the hypothesis within a single community type.

Eglin Air Force Base is also ideal for this study because of the variation in fire frequency. Frequent fire (i.e., low-intensity, growing season, lightning-induced wildfires occurring every 1–5 years, depending on soil moisture) was the dominant historical process shaping longleaf pine sandhills (Robbins & Myers 1992). However, Eglin's sandhills were fragmented by roads and logging and were fire-excluded for decades. Thus, we were able to observe the interaction between soil characteristics and the reestablishment of disturbance in a forest that lacked fire over a long period.

Methods

Study Plots

We examined 30, 81-ha plots to determine the relationships among the species richness of various taxa and soil fertility. All plots were from deep sandy soil (i.e., sandhills). Twenty-four of these plots had been identified previously for an experiment comparing experimental hardwood midstory reduction, whereas the remaining 6 plots were from fire-maintained, nonexperimental reference plots that approximated the old-growth condition (Provencher et al. 2001*a*). For the purpose of analysis, however, we ignored the spatial structure of the experimental design and focused on the fire-exclusion history of all 30 plots.

Conforming to a randomized complete block design (Steel & Torrie 1980), we established 24 81-ha plots in six blocks of four fire-excluded plots across a west-east transect on Eglin (map in Rodgers & Provencher 1999). Sites were selected if they contained a high density of relatively large-diameter hardwood trees (95% confidence interval for oak density was 11–13 stems/100 m^2; $n = 24$), if they had been fire-excluded for several decades, and if they were adjacent to three other such areas to form an experimental block. The closest sampling areas between any 2, 81-ha plots, however, were at least 1 km apart. Plots had a relatively sparse herbaceous understory and a thick litter of hardwood leaves interspersed with bare ground. Analysis of the earliest aerial photography revealed that all blocks, except one, had not burned since the 1940s. Each plot within an experimental block was randomly assigned without replacement to either a control (no treatment), or to one of three hardwood-reduction treatments applied during the spring and early summer of 1995 (Table 1): (1) growing season burn in May and June, (2) herbicide (granular hexazinone applied at a rate of 1.68 kg of active ingredient/ha), and (3) oak (*Quercus* spp.) and sand pine (*Pinus clausa*) felling or girdling by chainsaw (slash not removed). Herbicide and felling/girdling plots were burned for fuel reduction from early March to late April 1997, a standard fire-management practice in the southeastern United States. Each plot contained 32, 10 × 40 m subplots located within a 20-ha section (layout in Rodgers & Provencher 1999). Any sampling unit within a subplot was referred to as a sub-subplot.

Table 1. Number of experimental blocks and reference plots per taxa and per year.

Plot type	*Pretreatment 1994–1995*	*Post-treatment 1998–1999*
All taxa except herpetofauna		
control	6	6
spring burning	6	6
herbicide	6	6
felling/girdling	6	6
subtotal	24	24
reference	6	6
total	30	30
Herpetofauna		
control	4	4
spring burning	4	4
herbicide	4	4
felling/girdling	4	4
subtotal	16	16
reference	4	4
total	20	20

In addition to the 24 experimental plots, six 81-ha plots with a 1- to 5-year fire-free interval and dominated by longleaf pine (hereafter, reference plots) were established to provide objective goals for the restoration of fire-excluded plots (Table 1; for descriptions see Rodgers & Provencher 1999; Provencher et al. 2000). Each reference plot contained the same subplot sampling design as the experimental plots. Historical photography and accounts we collected suggest that references plots were fire-excluded from the 1930s to the 1960s. Reference plots burned before and during the study. Some plots experienced two to three patchy fires between 1994 and 1999.

Sampling Timeline

We sampled breeding-bird detection rates prior to treatment from 4 May to 30 June 1994. Within a season of bird sampling, plots were visited three or four times. We only show the data based on the first three visits because few birds and no additional species were detected during the fourth visit. Pretreatment vegetation and herb-layer arthropod sampling were conducted from 15 July until early December 1994. Pretreatment sampling for herb-layer arthropods was conducted from 1 April until 15 June 1995. Following sampling, hardwood-reduction treatments were applied in the spring and early summer of 1995.

With some minor exceptions, post-treatment sampling periods approximately matched pretreatment dates. The last year of sampling was 1998–1999. We collected soil for texture analysis during the spring and summer of 1997. Fall arthropod sampling was conducted from 15 July to early October after 1994. Herpetofauna were sampled from 1997 to 1998 (Litt 1999); thus, only post-treatment data were available.

Soil Texture Analyses

Soil texture analysis was conducted on random subsamples of 8 of the 32, 10 × 40 m subplots from each 81-ha plot. Subsampling was necessary to reduce our workload and because soils were expected to be fairly homogeneous over distances of <150 m. For each subsampling area, two soil cores (30 cm deep) were extracted from opposite ends of each subplot. The two samples were analyzed separately and results were averaged. Roots, detritus, and organic particulates were manually removed from each sample. We used a rolling pin to disaggregate soil particles (Folk 1980).

We performed particle size analysis on each prepared sample by partitioning each sample into its respective silt-clay and sand-size fractions and measuring each fraction separately to obtain total textural class ratios (Miller & Donahue 1990). We analyzed the silt-clay fraction of each sample using the pipette extraction method (Miller & Donahue 1990). We separated sand and silt-clay fractions by wet-sieving the sample through a 0.063-mm mesh screen with a 50-M solution of sodium hexametaphosphate ($Na_6(PO_3)_6$), a dispersing agent. The silt-clay fraction was collected and brought to 1 L with $Na_6(PO_3)_6$ in a graduated cylinder. Following Stokes Law, different volumes of the silt-clay solution were extracted at specified time intervals after thorough mixing. We dried and then weighed silt and clay extracts. To determine grain sizes, the sand portion of each sample was wet-sieved through a mesh screen column of six size classes (4.0, 2.0, 0.5, 0.25, 0.125, and 0.063 mm). Each size class was dried and weighed as a ratio to total sample weight.

For the purpose of this study, we used the percent total silt and clay as a surrogate measure of soil fertility because silt and clay hold far more soil moisture than the dominant sand matrix. Soil moisture limits plant growth in deep, rapidly permeable sands (Harcombe et al. 1993; Huston 1994). Differences in silt content as little as 4% can change soil type from Lakeland (<8% silt content) to Troup (≥8%) series in sandhills. In addition to silt and clay content, we used the coefficient of variation to calculate the spatial variation of this variable within a plot. We included soil variation because plant species richness should increase in patchy soils (Palmer & White 1994).

Groundcover Species

We determined groundcover species richness by counting all plant species present in each 10 × 40 m subplot (Provencher et al. 2000, 2001*a*). Although a species-area relationship has not been systematically investigated for Eglin, our work has shown a near doubling of plant species across three spatial scales: 1 m^2, 400 m^2, and the plot level (i.e., all unique species from all 32, 400 m^2 subplots per plot). Because 1 m^2 was too small and not responsive to treatment effects, we retained the 400-m^2 subplot and plot scales for analysis. Nomenclature followed that of Clewell (1985).

Herb-Layer Arthropods

Methods for sampling herb-layer arthropods are presented by Provencher et al. (2002*a*). We collected arthropods with a sweep net and then we sampled the same area with a modified insect vacuum (Rincon-Vitova Insectaries Inc., Ventura, California). In 1994 we collected from four 0.5 × 2 m areas per subplot. After 1994 we collected from one 0.5 × 8 m subplot. The area sampled matched that of quantitative vegetation sampling (Provencher et al. 2001*a*). We determined herb-layer arthropod richness by identifying specimens to species or morphospecies. Because we could not identify most immature individuals, the number of species present among all species we could identify in each sampling season (>300) was our estimate for species richness.

Herpetofauna

Herpetofaunal sampling was a subset of the overall project that could not be feasibly conducted in all plots (Litt 1999; Litt et al. 2001). Four experimental blocks and four reference plots situated west of Highway 85 and in proximity of one another were retained. One inverted T-shaped trapping array was placed at the center of 16 of the restoration plots, with the direction randomly determined. Each array had eight pieces of drift fence (four per arm of the T), constructed with galvanized steel flashing and 16 19-L pitfall traps (two traps per fence). This totaled 320 traps in 20 plots. We trapped from April until

August 1998. Animals were marked and recaptures noted to eliminate double counting (Litt 1999).

Birds

From 1994 (pretreatment) to 1999, we sampled breeding birds with standard point-count methodology (Blondel et al. 1981; Ralph et al. 1993; Provencher et al. 2002*b*). In each hardwood-reduction plot, two observers conducted 8-minute point counts from four permanent stations erected on two alternating transects about 200 m apart. On reference plots, we conducted point counts from eight stations along four transects about 200 m apart. Detections were truncated after 200 m, and birds that were detected by two observers at the same time were not double counted (Provencher et al. 2002*b*). We standardized the sampling effort by retaining the two most interior stations separated by at least 200 m in all plots. Therefore, breeding birds were never detected from adjacent 81-ha plots. Birds flying over plots were recorded only if there was evidence that they were foraging over the plot or had been perched in the plot prior to taking flight. All bird-detection data were collected within the first 3 hours after sunrise.

Data Analysis

We limited our analyses to the pretreatment and fourth-year post-treatment data for two reasons. The first 3 years after treatment corresponded to transient effects for hardwood-reduction methods applied during the springs of 1995 and 1997. We also documented delayed mortality of hardwoods in spring burn plots until 1997 (Provencher et al. 2001*b*). Thus, 1994–1995 and 1998–1999 represent years with some semblance of constancy but with contrasting disturbance (fire-exclusion) histories. The analysis of the data from all years showed remarkable consistency of soil-vegetation relationships among years for species richness despite transient hardwood-reduction effects; thus, no new information was gained from their inclusion.

We tabulated the total number of species found from all seasons sampled per year. This calculation was performed at two spatial scales for both plants and arthropods: (1) subplot level (10 × 40 m, the scale at which the data were collected, averaged over all subplots and (2) plot level (81 ha), the number of unique species detected over the entire plot. Spatial scale was included because species richness, especially that of plants, varies with area and scale (Palmer & White 1994).

We performed multivariate analysis of covariance (MANCOVA) in which the hardwood-reduction condition (the four hardwood-reduction methods and the reference condition) was the categorical variable and other variables were covariates to determine the effect of both soil variables and hardwood reduction on the species richness of plant and animal taxa (dependent variables). Statistical models were built trophically. For instance, plant species richness was explained only by the percentage of silt and clay, its coefficient of variation (plot level only), and hardwood-reduction method, whereas bird, plant, and arthropod species richness were simultaneously explained by total silt and clay, its coefficient of variation, and hardwood-reduction effects. We performed analyses at the appropriate scale: for example, arthropod species richness at the subplot level was explained by plant species richness at the subplot level and total silt and clay. The relationships among the species richness of tested taxa were obtained from the partial correlation.

The MANCOVA was not an accurate representation of the layout of plots because reference plots were not part of the experimental design and we omitted the block effect in the model (normally, the experimental plots would conform to a randomized complete block design, which is a two-way analysis of variance). We verified that soil variables accounted for a large fraction of the spatial variation caused by the position of experimental blocks and reference plots.

We transformed data when variances proved sufficiently heterogeneous among hardwood-reduction treatments and based on the residuals from the covariate analysis. We applied the following transformations for plant species richness to stabilize variances among hardwood-reduction effects: $\log_{10}(x)$ in 1994 and $\sqrt{x}$ in 1998 were used at the plot level and $\log_{10}(x)$ in 1998 at the subplot level. For arthropod species richness, transformation was not required at the plot level, but $\sqrt{x}$ was needed at the subplot level during both years. Herpetofaunal species richness required $\log_{10}(x)$ to stabilize variances at both the plot and subplot levels. No data transformation was necessary to meet the assumptions of the tests for avian species richness.

We used the sequential Bonferroni technique (Rice 1989) to correct threshold significance values in the overall model (not regression coefficients) because regressions were repeated over several years with species richness data that were most likely autocorrelated. Thus, for each variable measured for 2 years, the first and second significance thresholds were, respectively, 0.025 and 0.05 (Rice 1989).

Results

Plant Species Richness

Silt and clay content varied between 3.7% and 10%. Average silt and clay content was approximately 6.3% in reference plots, whereas it varied between 4.6% and 5.1% for all other plots (Fig. 1). The highest average coefficient of variation for silt and clay content was observed in felling/girdling plots (25%), followed by spring burn plots (21%), whereas herbicide plots showed the smallest value (14%) (Fig. 1).

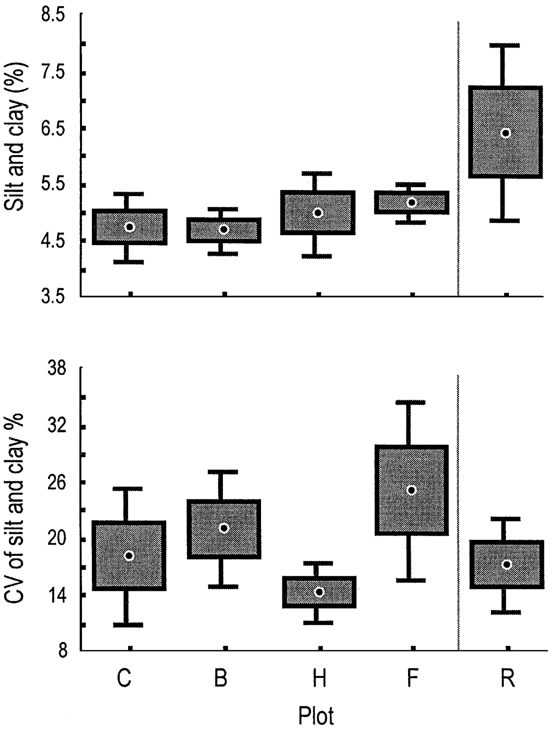

Figure 1. Percent silt and clay and its coefficient of variation among hardwood-reduction and reference plots at Eglin Air Force Base during 1997. Center of each box is the mean, upper and lower edges of box are the mean ± 1 SE, and error bars represent the 95% confidence interval. The vertical line between plots F and R separates experimental from nonexperimental parts of the design. Plots: C, control; B, burn; H, herbicide; F, felling/girdling; and R, reference. There were six replicates per plot type.

At the plot level, all analyses of covariance (only one dependent variable) were significant (Table 2). The effects on plant species richness of silt and clay content and its coefficient of variation were positive and significant in both years. The hardwood-reduction effect on plant species richness, however, was only significant for 1998. At the subplot level, the overall model achieved marginal significance only in 1998 ($p = 0.0355 > \alpha = 0.025$; Table 2). Plant species richness was not explained by silt and clay content at the subplot level, whereas the hardwood-reduction effect was marginally significant for 1998 ($p = 0.0513$) at this scale. There was a strong effect of hardwood-reduction methods (Fig. 2). Only plot-level results are shown because they were highly correlated with subplot-level results.

Arthropod Species Richness

The overall univariate model for arthropod species richness was only significant during 1998–1999 at either the plot level (Table 3) or the subplot level (Table 3). The univariate hardwood-reduction effect, but not the soil variables, was associated with this effect. The multivariate hardwood-reduction effect (plant and arthropod species richness were the dependent variables) was significant at the plot and subplot levels (Table 3) during 1998–1999. The partial correlation between arthropod and plant species richness was not significant at any scale or for any year. Hence, plant species richness was not a good predictor of arthropod species richness. Fuel reduction methods, which all involved fire, increased arthropod species richness (Fig. 2). No pattern was evident in 1994–1995; however, arthropod species richness during 1998–1999 decreased in the following plot order: reference, felling/girdling, herbicide, spring burn, and control plots.

Herpetofauna Species Richness

The overall univariate models for herpetofaunal species richness were not significant at either scale, but the multivariate hardwood-reduction effect on plant, arthropod, and herpetofaunal species richness was significant (Table 4). There was a positive and significant contribution of silt and clay content. The partial correlations between the three dependent variables were not significant. Although the reversal of hardwood encroachment showed a trend of decreased herpetofaunal

Table 2. Effects of silt and clay content, its coefficient of variation (CV) (plot level only), and hardwood-reduction methods on plant species richness at the plot level (81 ha) and subplot level (10 × 40 m) as measured by analysis of covariance.

Scale and year	Hardwood-reduction effect[a] (p)	Silt and clay B[c]	Silt and clay p	Silt and clay CV[b] B[c]	Silt and clay CV[b] p	Model R^2	Model p
Plot 1994	0.9945	0.505	0.005	0.044	0.004	0.486	0.011
Plot 1998	0.0315	4.780	0.009	0.592	<0.001	0.652	<0.001
Subplot 1994	0.9601	0.261	0.1327			0.159	0.4942
Subplot 1998	0.0513	0.146	0.201			0.375	0.035

[a] *Hardwood-reduction methods for experimental plots were one spring burn in 1995, herbicide application in 1995 followed by one early spring burn in 1997, and chainsaw felling/girdling during 1995 followed by one early spring burn in 1997; in reference plots the method was frequent fire. There were six replicates of hardwood-reduction methods at both scales.*

[b] *There is no variation in silt and clay at the subplot level.*

[c] *Regression coefficient, n = 30 plots.*

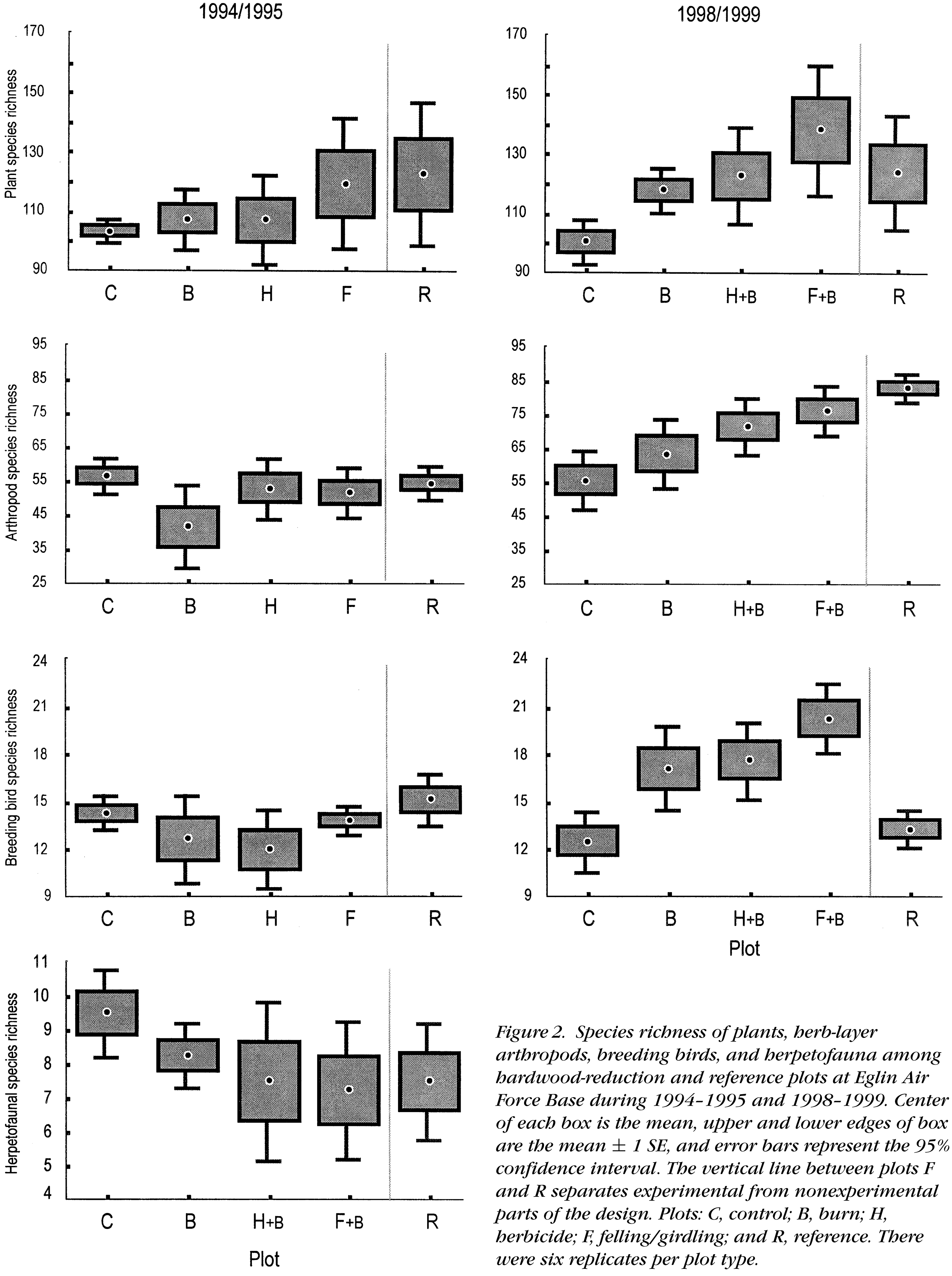

Figure 2. Species richness of plants, herb-layer arthropods, breeding birds, and herpetofauna among hardwood-reduction and reference plots at Eglin Air Force Base during 1994–1995 and 1998–1999. Center of each box is the mean, upper and lower edges of box are the mean ± 1 SE, and error bars represent the 95% confidence interval. The vertical line between plots F and R separates experimental from nonexperimental parts of the design. Plots: C, control; B, burn; H, herbicide; F, felling/girdling; and R, reference. There were six replicates per plot type.

Table 3. Effects of silt and clay content, its coefficient of variation (CV) (plot level only), and fire-exclusion history on plant species richness and on herb-layer arthropod species richness at the plot level (81 ha) and subplot level (10 × 40 m) as measured by multivariate analysis of covariance.

Scale and year	*Univariate hardwood-reduction effect*[a] (p)	*Silt and clay*		*Silt and clay CV*[b]		*Model*		*Plants*		*Multivariate hardwood reduction effect*	
		B[c]	p	B[c]	p	R^2	p	r[d]	p	λ[e]	p
Plot 1994–1995	0.0735	26.573	0.306	4.462	0.050	0.367	0.078	0.061	0.775	0.694	0.381
Plot 1998–1999	0.0026	−9.135	0.734	2.502	0.280	0.558	0.002	0.022	0.919	0.347	0.002
Subplot 1994–1995	0.1740	−0.623	0.421			0.237	0.241	0.240	0.248	0.741	0.503
Subplot 1998–1999	0.0054	−0.110	0.664			0.477	0.006	0.164	0.432	0.433	0.009

[a] *Hardwood-reduction methods for experimental plots were one spring burn in 1995, herbicide application in 1995 followed by one early spring burn in 1997, and chainsaw felling/girdling during 1995 followed by one early spring burn in 1997; in reference plots the method was frequent fire. There were six replicates of hardwood-reduction methods at both scales.*

[b] *There is no variation in silt and clay at the subplot level.*

[c] *Regression coefficient.*

[d] *Partial correlation coefficient between dependent variables.*

[e] *Wilk's lambda,* n = *30 plots.*

species richness (Fig. 2), the large variability prevented significance.

Bird Species Richness

Silt and clay content had no significant role in any of the univariate models for bird species richness (Table 5). For 1994–1995, the overall univariate model was not significant in 1994 because the hardwood-reduction effect was not significant. For 1998–1999, however, the univariate hardwood-reduction effect and the overall model were significant at both spatial scales. The multivariate hardwood-reduction effect (Wilk's λ for multiple dependent variables) was only significant during 1998–1999. The partial correlation between dependent variables varied with scale and year. During 1994–1995, bird species richness was significantly correlated with arthropod but not plant species richness at the plot level, but the species richness of plants and arthropods were each significantly correlated with bird species richness at the subplot level. For 1998–1999, only arthropod species richness at the plot level was significantly correlated with bird species richness (the correlation was marginal [$p = 0.0591$, Table 5] at the subplot level). The significant partial correlation between bird and arthropod species richness was somewhat surprising given that the former was low in reference plots but at its maximum for arthropods in those plots (Fig. 2). Plant and bird species richness had more in common visually (Fig. 2), although not statistically, because the relationship was calculated on the residuals after other sources of variability were removed.

Discussion

Soil Effects

We suggest that Eglin sandhills fall on the left side of a right-skewed, unimodal curve of species richness (Rosenzweig & Abramsky 1993; Huston 1994) that varies

Table 4. Effects of silt and clay content, its coefficient of variation (CV) (plot level only), and fire-exclusion history on plant species richness, herb-layer arthropod species richness, and herpetofauna species richness at the plot level (81 ha) and subplot level (10 × 40 m) as measured by multivariate analysis of covariance.

Scale and year	*Univariate hardwood-reduction effect*[a] (p)	*Silt and clay*		*Silt and clay CV*[b]		*Model*		*Plants*		*Arthropods*		*Multivariate hardwood reduction effect*	
		B[c]	p	B	p	R^2	p	r[d]	p	r[d]	p	λ[e]	p
Plot 1998	0. 073	1.694	0.012	0.039	0.183	0.533	0.080	0.406	0.150	0.066	0.823	0.109	0.005
Subplot 1998	0. 073	1.694	0.012			0.533	0.080	0.040	0.892	0.104	0.722	0.134	0.007

[a] *Hardwood-reduction methods for experimental plots were one spring burn in 1995, herbicide application in 1995 followed by one early spring burn in 1997 and chainsaw felling/girdling during 1995 followed by one early spring burn in 1997; in reference plots the method was frequent fire. There were four replicates of hardwood-reduction methods at both scales.*

[b] *There is no variation in silt and clay at the subplot level.*

[c] *Regression coefficient.*

[d] *Partial correlation coefficient between dependent variables.*

[e] *Wilk's lambda,* n = *20 plots.*

Table 5. Effects of silt and clay content, its coefficient of variation (CV) (plot level only), and fire-exclusion history on plant species richness, herb-layer arthropod species richness, and on breeding bird species richness at the plot (81 ha) and subplot (10 × 40 m) levels as measured by multivariate analysis of covariance.

	Univariate hardwood-reduction	*Silt and clay*		*Silt and clay* CV[b]		*Model*		*Plants*		*Arthropods*		*Multivariate hardwood-reduction effect*	
Scale and year	*effect*[a] (p)	B[c]	p	B[c]	p	R^2	p	r[d]	p	r[d]	p	λ[e]	p
Plot 1994	0.302	2.342	0.712	0.793	0.150	0.282	0.221	0.126	0.556	0.647	0.001	0.516	0.232
Plot 1999	0.001	−2.568	0.720	0.631	0.304	0.611	0.001	0.242	0.253	0.534	0.007	0.167	<0.001
Subplot 1994	0.263	0.405	0.949			0.212	0.299	0.578	0.002	0.564	0.003	0.604	0.440
Subplot 1998	<0.001	−4.109	0.559			0.592	<0.001	0.360	0.077	0.382	0.059	0.237	0.001

[a] *Hardwood-reduction methods for experimental plots were one spring burn in 1995, herbicide application in 1995 followed by one early spring burn in 1997, and chainsaw felling/girdling during 1995 followed by one early spring burn in 1997; in reference plots the method was frequent fire. There were six replicates of hardwood-reduction methods at both scales.*

[b] *There is no variation in silt and clay at the subplot level.*

[c] *Regression coefficient.*

[d] *Partial correlation coefficient between dependent variables.*

[e] *Wilk's lambda,* n = *30 plots.*

with soil fertility. The species richness of most taxa, therefore, should increase rapidly with greater soil fertility (Huston 1994). As predicted, plant species richness increased with greater silt and clay content and its spatial variability, but only at the plot level. This effect of spatial scale is straightforward. In subplots, the number of plant species was less variable, although the identity of the species may change from subplot to subplot even with increasing soil moisture. At the plot level, increased silt and clay content and their variability allowed new species to grow, as we expected for the richer soils of reference and felling/girdling plots. Thus, pockets of more mesic soil will contain a sufficient number of new plant species to affect the total count of unique species in the plot (Palmer & White 1994).

Longleaf pine savannas achieve high species richness at small spatial scales of 1 m^2, and the addition of new species levels off rapidly for progressively larger scales (Walker & Peet 1983; Peet et al. 1998). In contrast, our results showed a large increase in species richness with greater spatial area. This difference was probably due to the more homogenous and continuous topography of Eglin compared with the systems studied by others, where hydrologic gradients occur over short distances (e.g., Green Swamp, North Carolina, Walker & Peet 1983; Peet & Allard 1993). The coefficient of variation for soil heterogeneity was <30% at Eglin, which indicates uniform soils. This result also supports our observation that few and small patches of more mesic soil accounted for the greater plant species richness at the plot than at the subplot scale.

We did not expect to find a direct relationship between silt and clay content and animal species richness, but we thought there might be indirect relationships, based on food resources or habitat association with soil fertility. Theoretically, greater soil fertility increases the chance for greater plant species richness, which can cause vegetation structure to become more heterogeneous (e.g., shrubs and trees are more likely to grow on more mesic soils) (Gibson 1992; Harcombe et al. 1993; Huston 1994). We observed that areas of higher silt and clay content supported more and larger shrubs and trees, but the structural effect was most noticeable in fire-excluded forests because fire reduces the woody vegetation in the under- and midstory. Vegetation structural heterogeneity increases the diversity of invertebrates (Murdoch et al. 1972), lizards (Pianka 1967), and birds (MacArthur 1964). We found that soil fertility explained, albeit weakly, the species richness of herpetofauna but not that of arthropods and birds.

Disturbance Effects and Taxa

Our results suggest that the relationships among plant, arthropod, and bird species richness were mainly due to hardwood-reduction treatments, which all included fire at some point. Several studies have reported increased plant species richness following fire (Lewis & Harshbarger 1976; Walker & Peet 1983; White et al. 1991; Mehlman 1992; Herring & Judd 1995). White et al. (1991) experimentally determined that fire of any frequency and seasonality increased the richness of herbaceous species (grasses, legumes, and other forbs) compared with no fire in a 43-year experiment in the Santee Fire plots of the Francis Marion National Forest, South Carolina, (U.S.A.). Mehlman (1992) found that species richness is high and relatively uniform under several fire regimes of moderate to high frequency in northern Florida longleaf pine communities, whereas low fire frequencies result in distinctly lower richness. In tallgrass prairies, however, Collins et al. (1995) detected a decline in plant species richness with fire of any frequency and the highest species richness at an intermediate time interval since last disturbance.

Based on a study from northwest Florida pinelands, Streng et al. (1993) hypothesized that changes in groundcover plant density and species richness are most constrained by the rarity of seedling establishment in a forest floor dominated by long-lived perennial plants. They suggest that plant responses to fire regimes should be observed over an extended period of time because long-lived plants that prevent seedling establishment through competition usually survive fire. In our experiment, herbicides killed some perennial plants during 1995 (Provencher et al. 2001*a*), and hot fires in herbicide and felling/girdling plots, fueled by large amounts of heavy, dead fuels, potentially thinned perennials and exposed bare ground to a greater extent than accomplished in spring burn plots. A greater abundance of bare ground would promote additional seedling establishment and an increase in species richness. (The greater spatial variability of silt and clay content in felling/girdling plots contributed to their high plant species richness, the highest observed.) It is possible that repeated, hot burns could have produced comparable results. Based on Streng et al.'s (1993) hypothesis, we also predicted that less intense fires in reference plots would result in little change over time, as was observed from 1994 to 1998.

Plots with the most frequent or recent and hottest fires harbored the greatest number of arthropod species. These fires promote a greater availability of palatable resprouts of herbaceous and woody species for up to 3 years (Vallentine 1989) and thus potentially support a greater variety and population growth of herbivorous arthropods (Owensby et al. 1970; Nagel 1973; Dunwiddie 1991; Stein et al. 1992). In addition, fire stimulates flowering in many species (Platt et al. 1988*a*), which could attract pollinators. Predatory arthropods would be drawn to both the increased abundance and variety of herbivores, pollinators, and other predators.

The more recent and hotter fires, the fewer the number of herpetofaunal species, although differences were not significant (four instead of six replicates were used for the herpetofauna; Litt et al. 2001). Control plots harbored both open- and closed-forest species because these plots were both relatively open (average canopy cover of 48%), with abundant sunlight reaching the forest floor, and the groundcover sustained the highest leaf litter, which benefits some species (Litt et al. 2001). Thus, the reduction of midstory vegetation may have decreased the number of substrates required by salamander and frog species because these were not found in reference plots.

Species richness of breeding birds was highest in plots where both hardwood resprouts and herbaceous vegetation were abundant as a result of burning and felling/girdling operations (Provencher et al. 2001*a*, 2001*b*). This treatment, therefore, provides for a canopy, a growing hardwood midstory, and an abundant herbaceous cover that satisfied the requirements of many species of birds (Provencher et al. 2002*b*). It is a classic finding of avian ecology that increased structural complexity is associated with greater species diversity (MacArthur 1964; Huston 1994). The spring burn plots also supported a combination of these features, but the intermediate level of hardwood encroachment after a single spring burn (Provencher et al. 2001*b*) caused reduced rates of detection of some breeding birds preferring open forests (e.g., Bachman's Sparrow [*Aimophila aestivalis*]) (Provencher et al. 2002*b*). The negative influence of hardwoods was stronger in fire-excluded control plots, where even fewer open-forest species were detected (e.g., American Kestrel [*Falco sparverius*], Red-cockaded Woodpecker [*Picoides borealis*], and Red-headed Woodpecker [*Melanerpes erythrocephalus*]).

Burned herbicide plots had the second-highest species richness of breeding birds. These plots contained few live hardwoods but the highest density of dead standing hardwoods, even after fuel-reduction burns (Provencher et al. 2002*b*). The unusually abundant and tall growth of bluestem grasses (*Andropogon virginicus* [L.], *Schizachyrium scoparium* [Michx.] Nash., *A. gyrans* Ashe) combined with a number of hardwood snags may have attracted open-forest and grassland species (e.g., Loggerhead Shrike [*Lanius ludovicianus*]), especially species such as woodpeckers that forage on and nest in decaying, standing hardwoods.

In frequently burned reference plots, species richness was barely greater than in control plots. These plots had a monospecific open canopy of longleaf pines and a herbaceous groundcover in which tall bluestems were not as predominant as in burned herbicide plots. The midstory was generally lacking. It is possible that the frequent fires may be a constraint on species of birds not adapted to this pyrogenic habitat.

Relevance to Conservation

On Eglin's 187,555 ha, land managers plan fire-management, silvicultural, and military operations partially according to their effects on the ecological condition of different areas. As in the selection of areas for conservation protection by public agencies and private organizations, Eglin managers choose areas where they want to minimize human impacts and maintain a close approximation of a "natural" fire regime. Often, the ecological condition of an area is based on the presence of rare, threatened, and endangered species and communities. Both Red-cockaded Woodpecker clusters and longleaf pine old-growth sandhills feature prominently in these management considerations.

If stewardship of the land, however, implies conservation of biodiversity in addition to legal requirements associated with endangered species, then it is worthwhile to include species richness from various taxa when delineating areas of high ecological value. Although the composition of plant, herpetofaunal, and bird communities could be relatively rapidly assessed in sandhills, this is not the case for herb-layer arthropods (not to mention forest-floor, soil, and canopy arthropods), which are studied less. Arthropods represent >50% of all known species worldwide (Wilson 1992), of which 4000–5000 are estimated to occur in longleaf pine sandhills (Folkerts et al. 1993). Therefore, it is important to find correlates of arthropod species richness in the absence of data or pending the completion of ecological inventories.

Silt and clay content and its variability predicted areas of higher plant species richness (and somewhat higher herpetofauna richness) but did not predict areas of high species richness for herb-layer arthropods or breeding birds. Panzer and Schwartz (1998) also found no relationship between plant species richness and common or rare insect species richness, although native plant species richness explained 28–49% of the variance in “conservative” (strongly habitat-dependent) insect species richness. In our study, regardless of fire exclusion, arthropod species richness was the best correlate of bird species richness, which suggests that bird species richness could be used to predict areas rich in herb-layer arthropods. The relationship was not as good for reference plots, however, most of which were the old-growth areas already identified for protection on Eglin.

Fuel reduction was the best predictor of average herb-layer arthropod and plant species richness, and, as Provencher et al. (2001*a*) have shown for the whole post-treatment period, fire alone was the main reason for this result. In other words, the maintenance and restoration of the dominant ecological process, namely fire, was the best predictor of higher diversity for taxa that are difficult to study. Fire does not act alone. On the Florida gulf coast, frequent tropical storms and hurricanes can change fuel loads and create future fire hotspots favorable to certain species and longleaf pine regeneration (Platt et al. 1988*b*). Provencher et al. (2001*c*) showed that storm events reinforce the effects of fire in sandhills. Although our results may be more representative of pyrogenic forests than other systems, this was an encouraging conclusion because managers whose lands have been identified for their significant potential for high biodiversity or for the uniqueness of and threat to their communities can further restore diversity with prescribed burning. Taxa not favored by hardwood reduction were common and will likely persist in temporary fire shadows at the landscape scale.

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