Predicting plant species diversity in a longleaf pine landscape

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Abstract: In this study, we used a hierarchical, multifactor ecological classification system to examine how spatial patterns of biodiversity develop in one of the most species-rich ecosystems in North America, the fire-maintained longleaf pine-wiregrass ecosystem and associated depressional wetlands and riparian forests. Our goal was to determine which landscape features are important controls on species richness, to establish how these constraints are expressed at different levels of organization, and to identify hotspots of biological diversity for a particular locality. We examine the following questions: 1) How is the variance in patterns of plant species richness and diversity partitioned at different scales, or classification units, of the hierarchical ecosystem classification developed for the study area? 2) What are the compositional similarities among ecosystem types? 3) For our study area, what are the sites expected to harbor highest species richness? We used a spatially explicit map of biodiversity to project abundance of species-rich communities in the landscape based on a previously developed ecological classification system for a lower Gulf Coastal Plain landscape. The data indicate that high species richness in this ecosystem was found in sites with frequent fire and high soil moisture. Sites in fire-maintained landscapes with lower frequency of fire were associated with geomorphological characteristics, suggesting a dependence of the diversity-disturbance relationship with soil type. With more frequent fire on some sites, high diversity shifts from canopy component to ground flora, with an overall increase in total species richness. Our approach demonstrates how potential species richness can be identified as a restoration goal and that multiple vegetation endpoints may be appropriate vegetation objectives. We identify basic management needs for the maintenance of biodiversity in this ecosystem that can be derived from an understanding of the combination of factors that most strongly predict diverse plant communities.

Keywords: benchmark site, biodiversity, fire, longleaf pine, reference site, restoration, species richness.

Introduction

Predictive modeling is a relevant tool for management planning and conservation prioritization when it can be applied to a specific locality (Kerr, 1996). A key to predicting sites of high species richness at a scale relevant
for management is to identify environmental correlates and their relationships to landscape hierarchies (Palik et al., 2000). Although an understanding of the basic factors controlling species richness is an obvious need in the development of broad-scale strategic plans, it is through the integration of georeferenced environmental correlates of species richness that extrapolation at a scale useful for management occurs. Based on the environmental parameters associated with high species richness, areas that harbour high numbers of species can be predicted (Dumortier et al., 2002).

Predictions of geographic patterns in plant species diversity require knowledge of multi-scale variation in richness (Wiens, 1989; White & Walker, 1997). Most empirical studies of biodiversity have focused on fine-scale investigations of complex environmental gradients at single sites or limited spatial scales (see review in Huston, 1994) or broad-scale biogeographical studies (Glenn-Lewin, 1977; Currie & Paquin, 1987; Currie, 1991). Few studies have examined scales of environmental variation on plant diversity in a landscape (Heikkinen, 1996; Jobbagy, Paruelo & Leon, 1996; Pollock, Naiman & Hanley, 1998; Hutchinson et al., 1999; Chipman & Johnson, 2002). Landscape models of species diversity-environmental relationships are needed to develop conceptual frameworks for identifying appropriate reference conditions for natural area restoration, and for the management of these ecosystems. This is particularly true in species-rich landscapes, where maintenance of plant species diversity is a primary conservation objective.

In longleaf pine-wiregrass (Pinus palustris - Aristida stricta) landscapes of the southeastern United States, the development of vegetation communities is controlled by a complex interaction of soil characteristics, fire frequency, topographic position, and past land uses. Floristically, high ground cover species richness has been recognized as a prominent feature of longleaf pine-wiregrass savannas regardless of sample scale (Lemon, 1949; Walker & Peet, 1983). This high richness is apparent at the local scales and at landscape scales (Drew, Kirkman & Gholson, 1998; Kirkman et al., 2001). Although these fire-maintained ecosystems were once the dominant plant communities in the southeastern U.S.A., today only a small percentage remains. Thus, there is widespread interest in the conservation and restoration of these species-rich habitats. More broadly, high diversity at large spatial scales results from a landscape mosaic of open-canopied longleaf pine stands occurring across a wide environmental gradient, interspersed with depressional wetlands (Kirkman et al., 2000) and linkages with riparian forests (Goebel et al., 2001).

We have been examining variation in community composition and structure along with patterns of diversity and richness across environmental and disturbance gradients in a longleaf pine-dominated landscape (Kirkman et al., 2001). We use the term landscape as a mosaic of heterogeneous landforms, vegetation types, and land uses (Urban, O’Neill & Shugart, 1987; Noss, 1990). As part of this work, we developed a multifactor ecological classification model for upland, riparian, and wetland systems (Kirkman et al., 2000; Goebel et al., 2001). Multifactor ecological classification systems (ECS) provide an organizing framework for examining biodiversity at multiple scales. These systems delineate landscape segments based on nested, hierarchically arrayed physiographic, geomorphic, edaphic, and vegetative characteristics (Lapin & Barnes, 1995; Pregitzer, Goebel & Wigley, 2000). Multiple and hierarchical factors (e.g., climate, geology, plants, animals, and time) that mediate the development of ecosystems are expressed in the spatial arrangement of geologic parent materials, surficial topography, landforms, soil morphology, natural disturbances, and the composition and relative abundance of plant and animal species (Barnes et al., 1982; Host et al., 1989; Host & Pregitzer, 1992; Hutchinson et al., 1999).

Our goal is to determine which landscape features are important controls on species richness, to establish how these constraints are expressed at different levels of organization, and to identify hotspots of biological diversity for a particular locality. In this study, we examine the following questions: 1) How is the variance in patterns of plant species richness and diversity partitioned at different scales, or classification units, of the hierarchical ecosystem classification developed for the study area? 2) What are the compositional similarities among ecosystem types? 3) For our study area, what are the sites expected to harbour highest species richness? Finally, to predict species richness based on gradients of historical fire frequency and soil moisture, we incorporate fire history information into our general model as an additional predictive variable.

**Methods**

**Study site**

The study site is located at Ichauway, a 115-km² ecological reserve in the Coastal Plain of southwestern Georgia, U.S.A. The climate of this region is characterized as humid subtropical (Christensen, 1981), with an average annual precipitation of 131 cm, evenly distributed throughout the year. Mean daily temperatures range from 21 °C to 34 °C in summer and from 5 °C to 17 °C in winter (National Climate Data Center, Asheville, North Carolina). Ichauway is located within the Dougherty Plain physiographic region in the Gulf Coastal Plain Province of Walker and Coleman (1987) or the Lower Coastal Plain and Flatwoods (LCPF) section (Plains and Wiregrass Plains subsections) of McNab and Avers (1994). The LCPF Province is a karst landscape, characterized by flat, weakly dissected alluvial deposits over Ocala Limestone (Hodler & Schretter, 1986). Parent materials are marine and continental sand and clay deposits formed during the Mesozoic (65 to 225 × 10⁶ y BP) and Cenozoic Eras (present to 65 × 10⁶ y BP) (Keys et al., 1995). Most upland soils are paleudults and hapludults, with some localized zipsoltsamsments.

Ichauway has one of the largest contiguous tracts of second-growth longleaf pine-wiregrass woodlands in the Southeast. Over the past several decades, Ichauway has been managed with low intensity, dormant-season prescribed fires with a return interval of 1-3 y. Frequent fire has resulted in floristically diverse savanna-like forests in...
the uplands (Wells & Shunk, 1931; Wahlenberg, 1946; Walker & Peet, 1983). The flora of Ichauway is extremely diverse, with over 1,000 vascular plants documented (Drew, Kirkman & Gholson, 1998). In contrast to the regional landscape, many of the embedded wetlands at Ichauway are relatively undisturbed by agricultural practices, recent timber harvest, or altered hydrology, and as such, provide a unique setting to describe patterns. Wetland vegetation types include grass-sedge marshes, cypress savannas, and cypress-gum swamps (Kirkman et al., 2000). Two major streams dissect the karst topography: the Flint River, a stream originating in the Piedmont of northern Georgia, and Ichawaynochaway Creek, a Coastal Plain stream with headwaters originating in a large wetland complex. Along the riparian corridors, southern mixed hardwood forests, locally known as hameocks, are the dominant vegetation type (Quarterman & Keever, 1962; Myers, 1990).

**Ecological site classification**

In prior work, we developed a hierarchical classification of Ichauway reference ecosystems through several integrated steps. The steps included reconnaissance to develop an initial classification, plot sampling (soils, physiography, and vegetation), multivariate analysis, and refinement of the classification (Kirkman et al., 2000; Palik et al., 2000; Goebel et al., 2001). An assumption of our approach is that minimally disturbed ecosystems are the basis for the reference classification. Although the current plant communities of these ecosystems may not be wholly representative of pre-European-settlement conditions, they represent the best examples of the longleaf pine landscape available regionally (Palik et al., 2000).

To develop the classification, overstory and ground cover vegetation were sampled in a total of 104 minimally disturbed stands. In each stand, fluvial and upland sample plots consisted of four 800-m² circular plots, each with two nested 0.5-m² quadrats centred at 5 m and 10 m from the plot centre at an azimuth of 0°. Because the size of wetland ecosystems varied considerably, wetland (hydric depressions) sample plots included a single 500-m² circular plot and four nested 0.5-m² quadrats placed 5 m from the plot centre in each cardinal direction (N, E, S, and W).

Physiography, soils, and vegetation were determined in each plot. Physiographic measurements included landform class, topographic relief class, and slope percent. Landform classes included sand ridges, terraces (both marine and alluvial in origin), floodplains, hillslopes, depression margins, and shallow, non-wetland depressions. Topographic relief classes included steeply sloping (> 8%), undulating (> 3-8%), or nearly level (1-3%). Basins of wetlands were surveyed, and volume development, total area, and elevation above sea level were determined. A bucket auger was used to sample soil to a depth of 3.4 m (or to a restrictive layer) at the centre plot of each sample area. A complete soil description was made following Soil Conservation Service procedures (Soil Survey Division Staff, 1993), and bulk soil samples were collected from each horizon for the entire profile. Sand (> 0.1 mm), silt (0.1-0.001 mm), and clay (< 0.001 mm) fractions were determined after air drying using the pipette method.

The diameter at breast height (DBH, 1.4 m) of all living overstory trees (≥ 5 cm DBH) was recorded by species in 2.5-cm-diameter classes in each 800-m² fluvial and upland plot and in each 500-m² wetland plot. The ground cover (woody and herbaceous species < 30 cm tall) coverage was recorded by visual estimation in each of the 0.5-m² quadrats using the following six coverage classes: 0%, 1%, 1-5%, 5-15%, 16-30%, 31-60%, and 61-100%. Few, if any, plants fell into a category of > 30 cm tall with a diameter ≤ 2.5 cm DBH, and therefore this stratum was not analyzed for this study.

Our approach was iterative, including reconnaissance, plot sampling, and multivariate analysis. Specifically, principal components analysis (PCA) was used to summarize variation in the physiographic and soil variables among the sample areas and identify outliers or sample areas that occurred in transitional zones between ecosystem types. The ecosystem classification incorporated factors of landform, soil texture, and vegetative cover associated into ecological species groups identified by Two Way Indicator Species Analysis (TWINSPAN). Canonical correspondence analysis, which measures the degree of distinctness among ecosystems using different combinations of physiographic, soil, and vegetation datasets, was used to verify the classification (see Kirkman et al., 2000 and Goebel et al., 2001 for details of the analyses and classification procedures). The final iteration included 21 ecosystem types (Table I).

We identified 17 non-wetland ecosystem types and four wetland (hydric) types. For two rarely occurring ecosystem types of fluvial terraces (somewhat poorly drained and well drained fluvial terraces), vegetation data were not obtained (Table I), and thus these ecosystem types are excluded from the analysis presented in this paper. The multifactor classification has a hierarchical structure consisting of six levels (Table I). The first level of the hierarchy differentiates major physiographic zones (fluvial versus upland) (Figures 1 and 2). The next two levels separate landscape units by landform complexes and landforms (10s-100s ha). The fourth level differentiates terrain shapes (e.g., undulating versus flat). The fifth level separates units by several soil characteristics that reflect moisture regime. The final two levels identify ecosystems based on overstory and ground cover plant communities.

**Data analyses**

From the prior ecological site classification (ESC) plant composition dataset (104 stands), we calculated two sets of diversity statistics: 1) species richness (number of species), Shannon’s index of diversity (Ludwig & Reynolds, 1988), and Sheldon’s index of evenness (Sheldon, 1969 in Ludwig & Reynolds, 1988) in herbaceous ground cover (data from 0.5-m² subplots); and 2) species richness, diversity, and evenness in overstory stratum (data from 500- or 800-m² plots). Sheldon’s index refers to how the species abundances are distributed among the species and is not strongly sensitive to the most minor species (see equation in Figure 1 legend). Shannon’s index (see equation in Figure 1 legend) incorporates both species richness and evenness into a single value and, as such, describes heterogeneity (Peet, 1974).
TABLE I. Ecosystem types of Ichauway, Baker County, Georgia.

<table>
<thead>
<tr>
<th>Ecosystem type name</th>
<th>Landform complex</th>
<th>Terrain shape</th>
<th>Soil drainage class</th>
<th>Overstory species group</th>
<th>Ground cover species group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Somewhat poorly drained</td>
<td>fluvial</td>
<td>terrace</td>
<td>sand to sandy loam over</td>
<td>longleaf pine-lobolly</td>
<td>-</td>
</tr>
<tr>
<td>fluvial terraces (SPFT)*</td>
<td></td>
<td></td>
<td>sandy clay loam to clay</td>
<td>pine-water oak</td>
<td>Vaccinium-Ruellia</td>
</tr>
<tr>
<td>Moderately drained</td>
<td>fluvial</td>
<td>terrace</td>
<td>sandy clay loam over sand</td>
<td>longleaf pine-lobolly</td>
<td>-</td>
</tr>
<tr>
<td>fluvial terraces (MDFT)</td>
<td></td>
<td></td>
<td>loamy sand over sandy</td>
<td>pine-water oak</td>
<td></td>
</tr>
<tr>
<td>Well drained fluvial</td>
<td>fluvial</td>
<td>terrace</td>
<td>loamy sand over sandy</td>
<td>longleaf pine</td>
<td>Aristida-Andropogon</td>
</tr>
<tr>
<td>terraces (WFT)*</td>
<td></td>
<td></td>
<td>loam to sandy clay loam</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Excessively drained</td>
<td>fluvial</td>
<td>terrace</td>
<td>sand and loamy sand</td>
<td>longleaf pine</td>
<td>Aristida-Andropogon</td>
</tr>
<tr>
<td>fluvial terraces (EFT)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mesic hardwood</td>
<td>fluvial</td>
<td>terrace</td>
<td>sand</td>
<td>laural oak-pignut hickory</td>
<td>Parthenocissus-Bignonia</td>
</tr>
<tr>
<td>hammocks (HAM)</td>
<td></td>
<td></td>
<td></td>
<td>southern magnolia</td>
<td></td>
</tr>
<tr>
<td>Fluvial sand ridges (FSR)</td>
<td>fluvial</td>
<td>sand ridge</td>
<td>sand</td>
<td>longleaf pine-turkey</td>
<td>Aristida-Andropogon</td>
</tr>
<tr>
<td>Floodplains along the Flint River (FTR)</td>
<td>fluvial</td>
<td>floodplain</td>
<td>sandy clay loam over</td>
<td>live oak-sweetgum</td>
<td>Parthenocissus-Bignonia</td>
</tr>
<tr>
<td>Floodplains along the Ichauway Creek (FTC)</td>
<td>fluvial</td>
<td>floodplain</td>
<td>sandy loam over sandy</td>
<td>live oak-sweetgum</td>
<td>Parthenocissus-Bignonia</td>
</tr>
<tr>
<td>Somewhat poorly drained</td>
<td>upland</td>
<td>terrace</td>
<td>sandy loam over sandy</td>
<td>longleaf pine</td>
<td>Aristida-Dyschoriste</td>
</tr>
<tr>
<td>upland terraces (SPUT)</td>
<td></td>
<td></td>
<td>clay loam to clay</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Moderately drained</td>
<td>upland</td>
<td>terrace</td>
<td>loamy sand over sandy</td>
<td>longleaf pine</td>
<td>Aristida-Dyschoriste</td>
</tr>
<tr>
<td>upland terraces (MDUT)</td>
<td></td>
<td></td>
<td>loamy sand over clay</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Well drained upland</td>
<td>upland</td>
<td>terrace</td>
<td>loamy sand over sandy</td>
<td>longleaf pine</td>
<td>Aristida-Dyschoriste</td>
</tr>
<tr>
<td>terraces (WUT)</td>
<td></td>
<td></td>
<td>loam to sandy clay loam</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Excessively drained</td>
<td>upland</td>
<td>terrace</td>
<td>loamy sand to sandy loam</td>
<td>longleaf pine</td>
<td>Aristida-Dyschoriste</td>
</tr>
<tr>
<td>upland terraces (EUT)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upland sand ridges (USR)</td>
<td>upland</td>
<td>sand ridge</td>
<td>sand</td>
<td>longleaf pine-turkey</td>
<td>Aristida-Dyschoriste</td>
</tr>
<tr>
<td>Depression margins (MAR)</td>
<td>upland</td>
<td>slope</td>
<td>loamy sand over sandy</td>
<td>longleaf pine-slash post oak</td>
<td>Aristida-Dyschoriste</td>
</tr>
<tr>
<td>Terrace escarpments (SCARP)</td>
<td>fluvial</td>
<td>slope</td>
<td>loamy sand over sandy</td>
<td>longleaf pine-sand post oak</td>
<td>Aristida-Andropogon</td>
</tr>
<tr>
<td>Clayey depressions (CD)</td>
<td>upland</td>
<td>depression</td>
<td>sand to sandy loam over</td>
<td>live oak-water oak</td>
<td>Quercus-Campsis</td>
</tr>
<tr>
<td>Sandy depressions (SD)</td>
<td>upland</td>
<td>depression</td>
<td>sandy clay loam to clay</td>
<td>swamp laurel oak</td>
<td></td>
</tr>
<tr>
<td>Organic hydric depressions (ORG)</td>
<td>upland</td>
<td>depression</td>
<td>organics over clay</td>
<td>pond cypress-blackgum</td>
<td>Nyssa-Taxodium</td>
</tr>
<tr>
<td>Clayey hydric depressions (CHD)</td>
<td>upland</td>
<td>depression</td>
<td>loamy sand over sandy</td>
<td>pond cypress</td>
<td>Panicum-Andropogon</td>
</tr>
<tr>
<td>Sandy hydric depressions (SHD)</td>
<td>upland</td>
<td>depression</td>
<td>loamy sand over sandy</td>
<td>none</td>
<td>Ppanicum-Leersia</td>
</tr>
<tr>
<td>Hydric flats (FLAT)</td>
<td>upland</td>
<td>flat</td>
<td>loamy sand over sandy</td>
<td>slash pine</td>
<td>Sporobolus-Pityopsis</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>clay loam to clay</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Denotes an ecosystem not sampled.

We compared mean species richness, diversity, and even-ness among ecosystem types. To examine how total variation in each of the vegetation parameters is distributed among hierarchical levels (Pagel & Harvey, 1988), we estimated the variance components for each variable using the SAS PROC MIXED nested variance components model with REMYL (Version 9.0, SAS Institute Inc., Cary, North Carolina, U.S.A.). (For purposes of reporting, we re-scaled the evenness variable x 100 and the diversity variable x 10.)

Mean species richness (ground layer only) per ecosystem type was used to develop a spatially explicit biodiversity map derived from a potential ecosystem type map for the study area (Palik et al., 2000). Four categories of species richness (0-3 species, >3-9 species, >9-15 species, >15 species per 0.5 m²) were utilized to develop the map based on plot-richness frequency distributions. The category breaks of species richness were obtained through Jenk's Optimization, a default algorithm that minimizes the sum of the variance within each of the classes (ArcView GIS 3.2, Environmental Systems Research Institute, Redlands, California, U.S.A.), and then rounded to the nearest integer.

An empirically derived graphic depicting the interactions of soil moisture and fire regime on species richness was created with a three-dimensional smoothing function (Jandel, 1995). Ranked soil moisture categories were based on soil texture characteristics from the ESC (ranked...
Figure 1. Hierarchical structure and comparisons of overstory flora among ecosystem types. Species richness, N = number of species; Shannon diversity number of species. * indicates no data.
Index, $H' = \frac{1}{S} \sum p_i \ln p_i$, where $S$ = species of a group and $p_i$ = proportional abundance of each species; Shannon evenness index, $E = e^{H'/S}$, where $S$ = the total
Figure 2. Hierarchical structure and comparisons of ground cover flora among ecosystem types. See legend of Figure 1 for explanation of indices.
in ascending order: excessively drained, somewhat excessively drained, well drained, moderately well drained, somewhat poorly drained, poorly drained, and very poorly drained). Relative fire return intervals were based on a priori observations and estimates in the literature for the various ecosystem types in the study area (Lemon, 1949; Walker & Peet, 1983; Myers, 1985; Abrahamson & Hartnett, 1990; Ewel, 1990; Myers, 1990; Platt & Schwartz, 1990; Rebertus, Williamson & Platt, 1993; Ware, Frost & Doerr, 1993). Fire return intervals were assigned to one of the following class variables: < 3 y, 3-10 y, 11-20 y, > 20 y.

Results

A total of 350 species were sampled in the overstory and ground cover strata. As a group, the fluvial ecosystem types had the greatest number of taxa in the overstory (66) and the ground cover (298) because both longleaf pine ecosystems and mesic hardwood hammocks develop on this landform (Table I); this combination inflates numbers of species because these ecosystem types do not share many species.

The hierarchical partitioning of variance in richness, evenness, and diversity of the ground cover suggests that the total variance was more uniformly distributed for richness and diversity than for evenness (Table II). For ground cover species richness, approximately 30% of the total variance in species richness was attributable to landform. However, a similar percentage of variance occurred at the stand level, indicating substantial variance in stand richness that is independent of differences in landform. For evenness, differences among the stands accounted for over 80% of the total variation. A different pattern of variance partitioning occurred for the overstory flora variables. For species richness and diversity, nearly 75% of the total variance was attributable to differences in landform complex or landforms (Table II), suggesting that species richness and diversity of the overstory flora is more strongly driven by landform than that of ground cover flora. However, for these measures, noteworthy variance independent of landform also occurred at the ecosystem level. Most of the variance in overstory evenness values was attributable to differences in hierarchical levels independent of landform and was due primarily to differences at the stand level.

Greatest overstory richness in the landscape was associated with floodplains (mean ± SE: 12.0 ± 1.4 species·800 m−2). Striking differences in mean species richness of the canopy occurred on similar soil types of excessively drained fluvial terraces (Figure 1), with the development of longleaf pine-wiregrass (2.1 ± 0.38 species·800 m−2) versus hardwood hammock vegetation (10.1 ± 0.4 species·800 m−2). This difference in vegetation composition most likely reflects differences in a disturbance factor, such as fire. In hardwood dominated sites, many species co-dominate in the canopy; thus, diversity is higher with higher richness and evenness.

For ground cover, evenness was high regardless of ecosystem type, reflecting the lack of dominance by any single ground cover species. Therefore, the diversity index of ground cover was largely determined by species richness. A pattern of decreasing ground cover richness occurred with increasing overstory richness at the ecosystem type level (Figures 1 and 2). Within the fluvial landform complex, terraces and sand ridges had greater ground cover richness than the floodplains, due to the existence of a well-developed herbaceous ground flora in the longleaf pine woodlands of some ecosystem types. However, if mesic hardwood forests (hammocks) developed on the fluvial terraces (HAM), ground cover richness was reduced as overstory richness increased (Figures 1 and 2).

The spatial distribution of species richness can be illustrated using a reference ground cover richness map predicted by correlations of physiography, soils, and plant communities obtained through the site classification (Figure 3). The matrix of the landscape (greater than 65 percent of the 11,400-ha site) falls into the highest potential richness category (> 15 ground cover species·0.5 m−2). The role of landform is particularly emphasized by the development of hardwood forests along riparian corridors that are relatively species-poor in ground cover. Alternatively, throughout the landscape, species richness in depressions varies from extremely low to extremely high and may be related to other features such as hydrologic conditions of these wetland and upland sites or to fire regimes.

Figure 4 (derived from mean species richness, estimated fire frequency score, and soil moisture gradient) indicates the role of fire and its interaction with soil moisture. The highest species richness is found in mesic communities where fire frequency is greatest. The importance of fire is illustrated by the fact that species richness can drastically differ on similar landforms and soil conditions depending on fire regime. The apparent role of disturbance thus may explain the degree of variance in richness that was shown to be independent of landform. Nevertheless, these patterns do suggest how landform may influence natural disturbance regimes or, in the current landscape, limit the potential for prescribed fire. For example, less frequent fire may be associated with riparian corridors as a result of floodplain conditions or with extremely xeric conditions in which low productivity results in low fuel loadings. The abrupt trough associated with poorly drained soils (Figure 4) reflects the near absence of ground cover species in clayey depressions that seldom burn and are dominated by a canopy of live oak. A hump-shape species richness curve may be associated with disturbance frequency in poorly drained soils. This pattern is likely a function of the absence of sites representing the combination of very high fire frequency and the wettest depressional sites.

Discussion

This study demonstrates the interacting influences of soil, topography, and disturbance with plant diversity relationships. Landscape configuration not only influences community structure through soil moisture controls on vegetative composition and fuel production, but it also may modify the development of fire regimes. This complexity has implications for interpretation of ecosystem development pathways and patterns of species richness. For example, plant communities of the longleaf pine ecosystem may shift types and diversity patterns with the
TABLE II. Variance components at hierarchical levels of classification for species richness, diversity, and evenness.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Species richness (N)</th>
<th>Shannon diversity index (H')</th>
<th>Sheldon evenness index (E)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Variance estimate</td>
<td>% total</td>
<td>Numerator df</td>
</tr>
<tr>
<td>A. Ground cover flora</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Landform complex</td>
<td>0.9407</td>
<td>3.6</td>
<td>1</td>
</tr>
<tr>
<td>Landform within landform</td>
<td>7.8116</td>
<td>29.9</td>
<td>5</td>
</tr>
<tr>
<td>Terrain shape within landform</td>
<td>4.4074</td>
<td>16.9</td>
<td>4</td>
</tr>
<tr>
<td>Ecotype within terrain shape</td>
<td>5.1204</td>
<td>19.6</td>
<td>8</td>
</tr>
<tr>
<td>Stand</td>
<td>7.8232</td>
<td>30.0</td>
<td>111</td>
</tr>
<tr>
<td>Total</td>
<td>26.1033</td>
<td>100.0</td>
<td></td>
</tr>
<tr>
<td>B. Overstory flora</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Landform complex</td>
<td>11.8367</td>
<td>51.55</td>
<td>1</td>
</tr>
<tr>
<td>Landform within landform</td>
<td>5.1047</td>
<td>22.23</td>
<td>5</td>
</tr>
<tr>
<td>Terrain shape within landform</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Ecotype within terrain shape</td>
<td>5.0597</td>
<td>22.04</td>
<td>5</td>
</tr>
<tr>
<td>Stand</td>
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<td>4.18</td>
<td>87</td>
</tr>
<tr>
<td>Total</td>
<td>22.9604</td>
<td>100.00</td>
<td></td>
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</tbody>
</table>

removal or addition of fire. On lower slopes of riparian corridors, frequency of fire may be suppressed by the duration of soil saturation or proximity to natural fire barriers (i.e., adjacent streams or less fire-prone vegetation). Alternatively, because the origin of natural fire in these landscapes was primarily in surrounding upland longleaf pine stands, fire could be carried downslope into riparian hardwood forests under dry fuel and low humidity conditions (Komarek, 1974), and a very different plant community could develop. Along a gradient of increasing fire frequency, high diversity would shift from canopy component to the ground flora, with an overall increase in total species richness. Similarly, the ground cover richness in depressional wetlands is related to fire frequency, which may be driven by hydrologic regime, but it is also dependent on the use of prescribed fire in the immediate area or surrounding upland (Kirkman et al., 2000).

While fire frequency (natural as well as human-ignited fires) may be linked to landscape features, it appears that frequently recurring fire is a primary determinant of high species richness at the landscape level. Although species richness is often postulated as a peaked function of disturbance (Huston, 1994), the interpretation of our findings in view of such widely held ecological concepts is ambiguous for many reasons (Mackey & Currie, 2000; 2001). In particular, the definition of an intermediate level of disturbance for a particular locality is elusive because the axes of theoretical models are not parameterized. For example, the low-intensity fires characteristic of the fire regime of the longleaf pine ecosystem could be considered an intermediate level of disturbance relative to the degree of biomass removal that occurs in stand-replacing fires of other conifer forests (Franklin et al., 2002). Alternatively, within the range of potential fire frequencies for the longleaf pine ecosystem, a return interval of 1 or 2 y might be considered to be an extreme level of disturbance frequency, because more frequent fires are not even possible due to lack of fuel accumulation (Glitenstein, Platt & Streng, 1995). Regardless of these conceptual enigmas, fire disturbance is an important factor affecting species diversity in this landscape because of its role in decreasing hardwoods that otherwise competitively exclude herbaceous species.

As a tool for targeting hot spots of diversity, the ESC can be part of a larger predictive model that includes biotic indicators of land use. It may be possible to use information about the life history of indicator species to link their occurrence with landscape-scale variables such as land use and fire history (Caro & O’Doherty, 1999; MacNally & Fleishman, 2002). For example, abundant wiregrass in the ground cover of longleaf pine stands is recognized as an indicator of a history of frequent fire and absence of agricultural soil cultivation, as well as high species richness (Noss, 1989; Hedman, Grace & King, 2000). The presence of this species can be combined with maps of potential species richness in longleaf pine ecosystems to further discern species-rich sites in a particular locality. Future predictive models of species richness combining environmental factors and biotic indicators may be hindered by some past land use activities in the longleaf pine ecosystem. Prior disturbances such as grazing probably could reduce species richness without negatively affecting wiregrass, if the site was frequently burned. As additional biotic indicators of such past legacies become evident, these can be used to extract those sites with the greatest probability of exceptionally high numbers of species versus those in need of species reintroductions.

In a broader conservation management context of the longleaf pine-wiregrass ecosystem, the importance of fire frequency in maintaining high species richness is often overlooked in management planning (Hiers, Wyatt & Mitchell, 2000). Even though prescribed fire is widely accepted as critical to the maintenance of biodiversity of
the longleaf pine-wiregrass ecosystem (Wells & Shunk, 1931; Lemon, 1949), emerging management philosophies not addressed in this study (such as rigid application of a particular season of fire) may, in fact, jeopardize the opportunities for application of frequent fire to a particular site. We recommend that conservation efforts should focus more concertedly on fire frequency (and less on season of fire) as a priority management tool.

While this study addresses questions about disturbance-diversity relationships in a particular ecosystem of considerable conservation concern in the southeastern U.S.A., the methodological framework is applicable to other ecosystems with high biological diversity. For sites where most or all native vegetation has been eliminated, determining appropriate reference conditions to use as a restoration guide can be problematic without adequate
knowledge of potential communities associated with different soil types and their spatial context (Fulé, Covington & Moore, 1997; White & Walker, 1997; Palik et al., 2000). Our approach illustrates how potential species richness can be identified as a restoration goal and demonstrates that multiple vegetation endpoints may be appropriate vegetation objectives. It also suggests how sites that are the most likely to support especially high species abundances can be identified and selected for restoration priority.

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Literature cited


