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Predicting plant species diversity in a longleaf pine landscape[1]

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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 harbour 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.

Résumé : Nous avons utilisé un système de classification écologique hiérarchique à facteurs multiples pour vérifier comment se dégagent les patrons spatiaux de biodiversité dans un écosystème nord-américain particulièrement riche en espèces. Nous nous sommes donc concentrés sur les forêts claires de pins des marais et d'aristides assujetties à un cycle de feux ainsi qu'aux milieux humides associés que l'on trouve dans les dépressions et aux forêts riveraines avoisinantes. Nous voulions cerner quelles sont les caractéristiques du paysage qui influencent la richesse en espèces, déterminer comment ces caractéristiques s'expriment à différents niveaux d'organisation et identifier les points chauds de diversité biologique au sein d'une région. Dans cette étude, nous avons tenté de répondre aux questions suivantes : 1) Comment la variance des patrons de richesse en espèces et de diversité se partage-t-elle selon différentes échelles ou selon les diverses unités de classement définies par la classification hiérarchique? 2) Quelles sont les similitudes dans la composition des différents types d'écosystèmes? 3) Dans notre aire d'étude, quels sont les sites susceptibles d'avoir une richesse en espèces particulièrement élevée? Nous avons utilisé une carte de biodiversité pour extrapoler dans le paysage l'abondance des communautés riches en espèces, cette abondance étant basée sur un système antérieur de classification écologique développé pour un paysage des plaines côtières du golfe. Selon les données, dans cet écosystème, les sites riches en espèces sont ceux où les feux sont fréquents et où l'humidité du sol est élevée. Les sites qui se trouvent dans les paysages assujettis à des feux moins fréquents sont associés à certaines caractéristiques géomorphologiques, ce qui suggère l'existence d'une dépendance entre la relation diversité-perturbation et le type de sol. Dans les sites où les feux sont particulièrement fréquents, la diversité la plus élevée se trouve non plus dans la voûte forestière, mais plutôt au niveau du sol. On y observe également, de façon globale, un plus grand nombre d'espèces. Notre approche montre que la détermination de la richesse potentielle en espèces d'un site peut servir à définir des objectifs de restauration. Dans ce travail, nous identifions les mesures d'aménagement minimales qui devraient être appliquées pour maintenir la biodiversité d'un écosystème grâce à la compréhension d'une combinaison de facteurs qui sont particulièrement utiles pour prédire la diversité des communautés végétales en présence.
Mots-clés : biodiversité, feu, pins des marais, restauration, richesse en espèces, site de référence.

Nomenclature: Wunderlin, 1998.

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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-km^2 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 $\times$ 10^6 y BP) and Cenozoic Eras (present to 65 $\times$ 10^6 y BP) (Keys *et al.*,1995). Most upland soils are paleudults and hapludults, with some localized quartzipsamments.

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 hammocks, 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-m^2 circular plots, each with two nested 0.5-m^2 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-m^2 circular plot and four nested 0.5-m^2 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 (> 2.5 cm DBH) was recorded by species in 2.5-cm-diameter classes in each 800-m^2 fluvial and upland plot and in each 500-m^2 wetland plot. The ground cover (woody and herbaceous species < 30 cm tall) coverage was recorded by visual estimation in each of the 0.5-m^2 quadrats using the following six coverage classes: < 1%, 1-5%, 6-15%, 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-m^2 subplots); and 2) species richness, diversity, and evenness in overstory stratum (data from 500- or 800-m^2 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.

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

* Denotes an ecosystem not sampled.

We compared mean species richness, diversity, and evenness 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 × 100 and the diversity variable × 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 m^2) 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

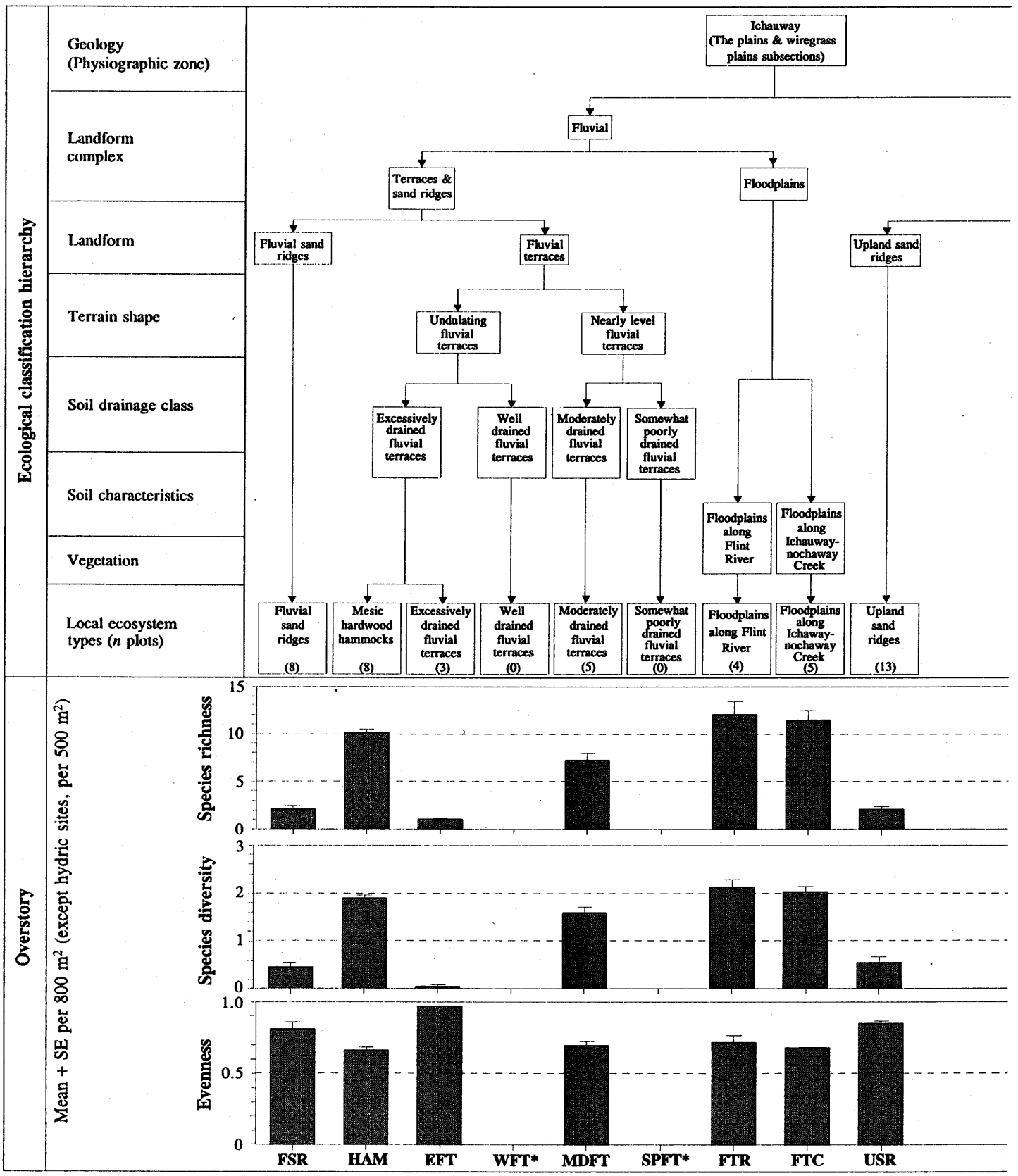
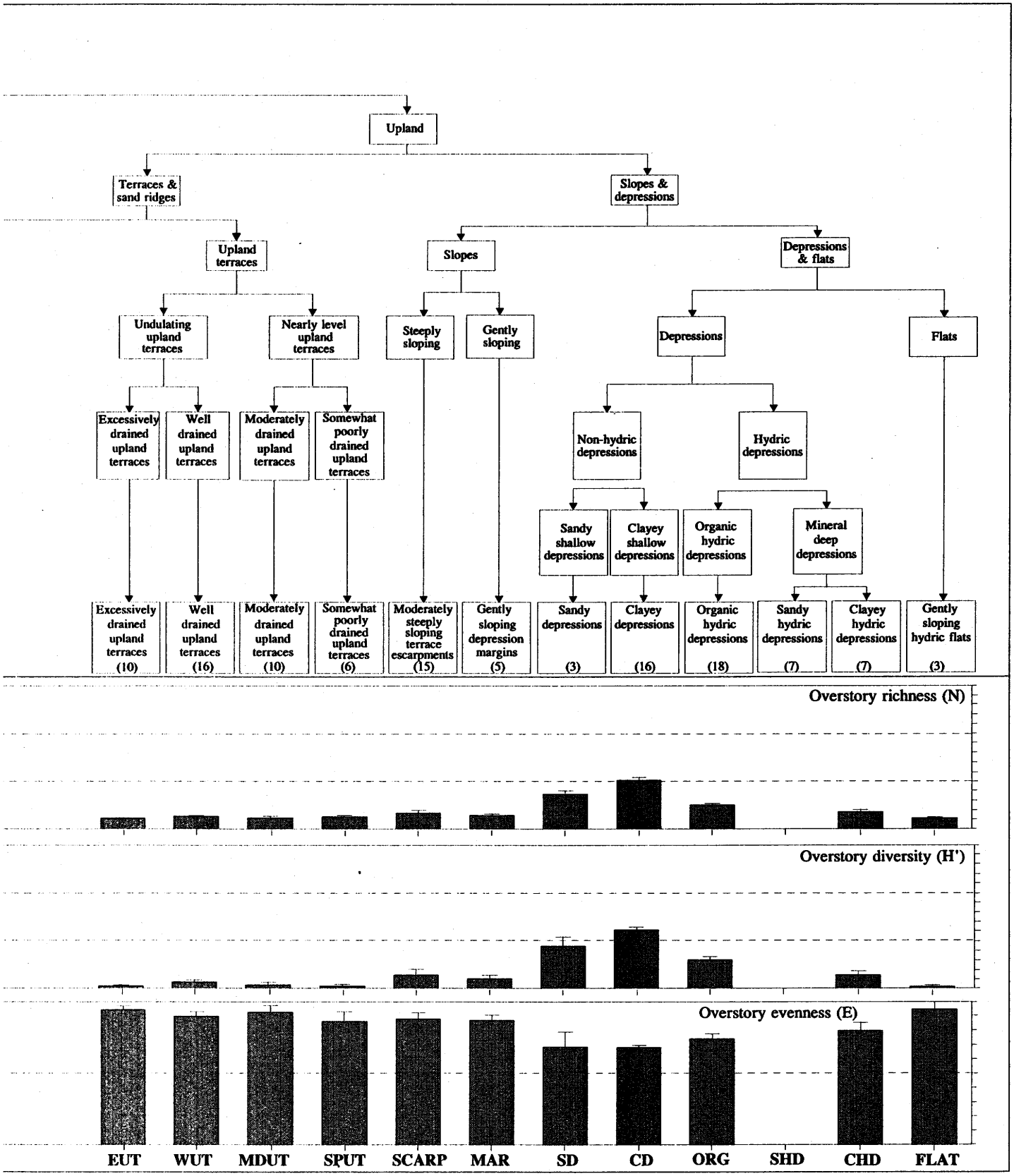


FIGURE 1. Hierarchical structure and comparisons of overstory flora among ecosystem types. Species richness, N = number of species; Shannon diversity number of species. * indicates no data.



index, $H' = \sum_{i=1}^{S} p_i \ln p_i$, where S = species of a group and p_i = proportional abundance of each species; Sheldon evenness index, $E = e^{H'}/S$, where S = the total

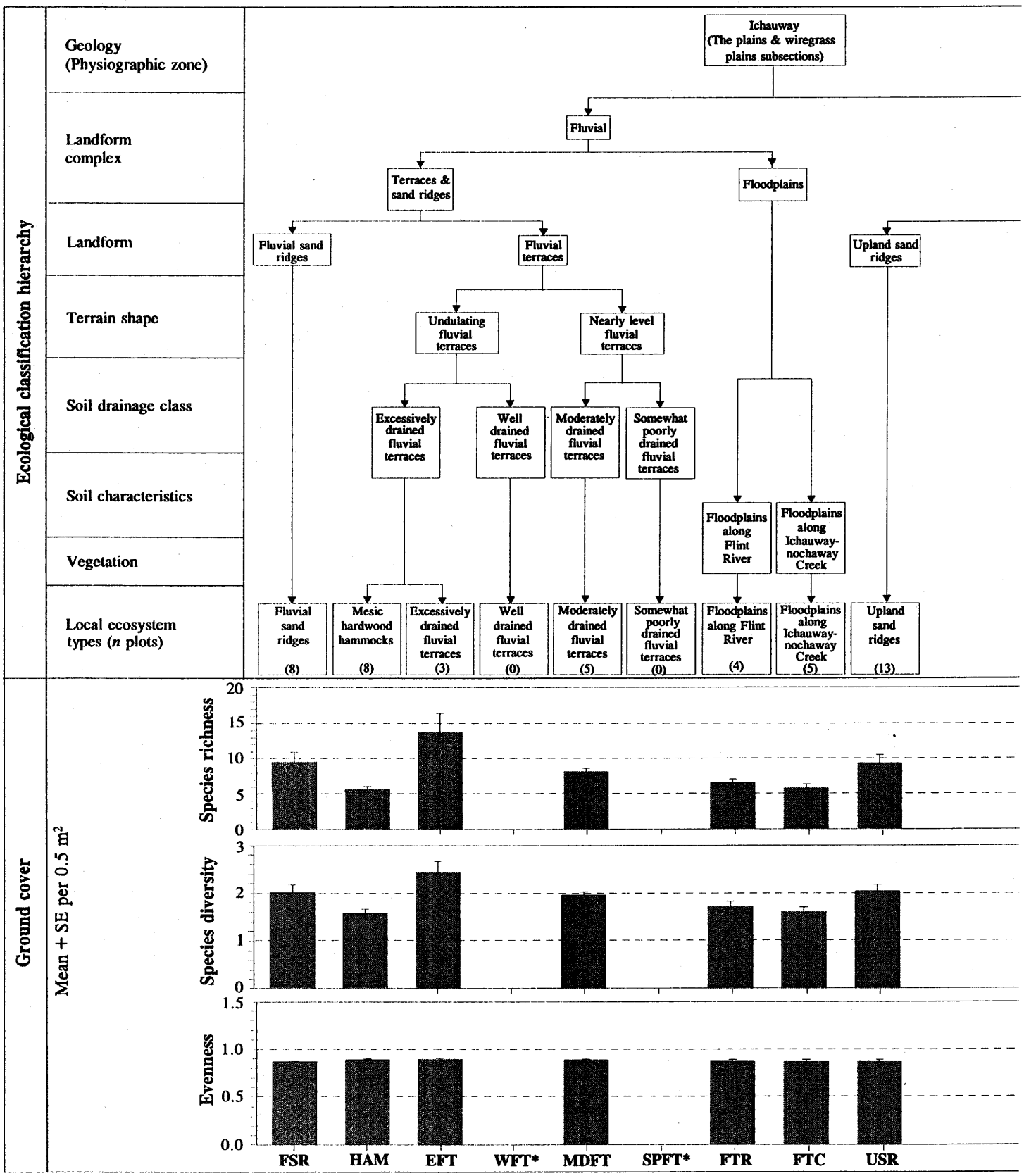
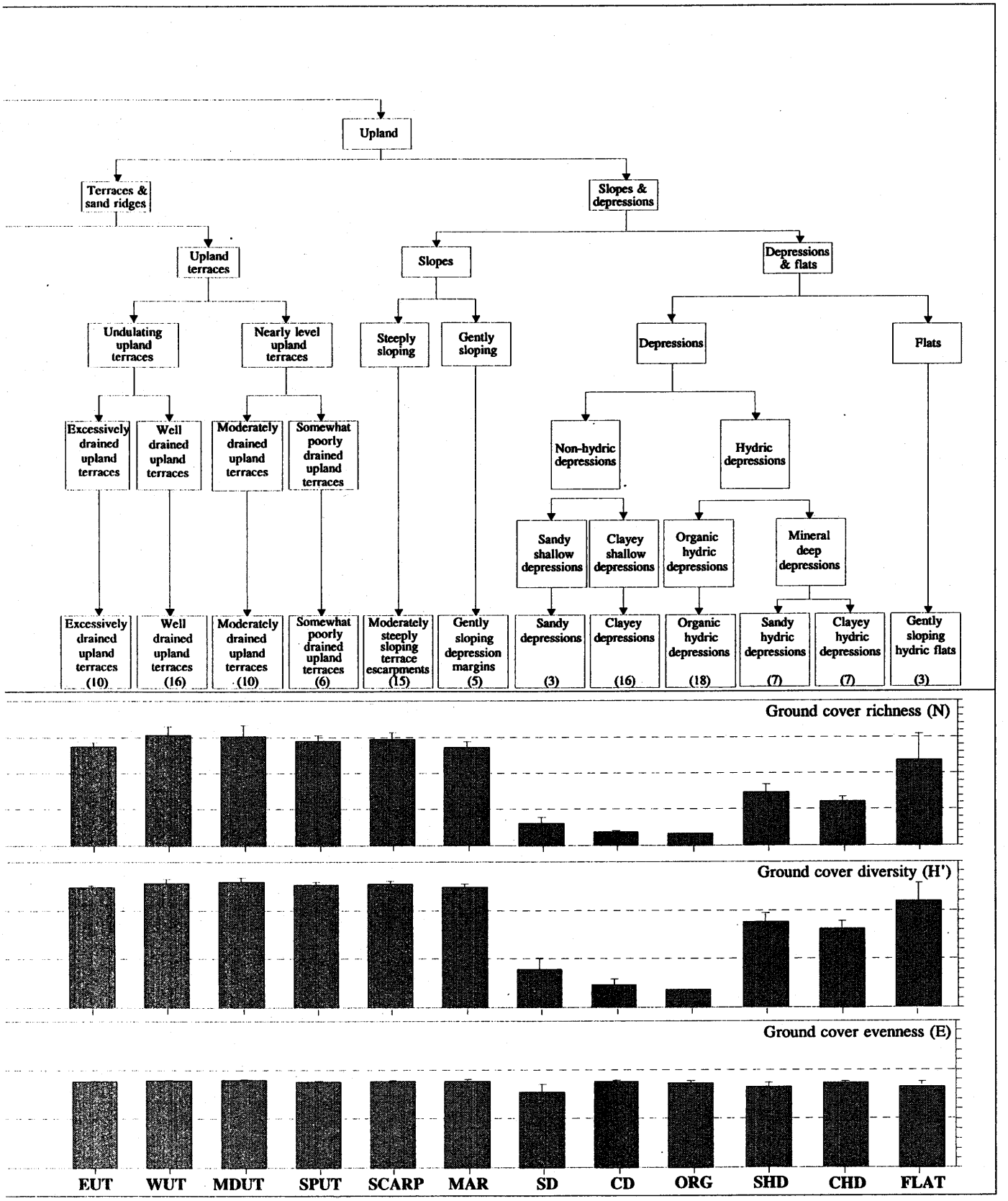


FIGURE 2. Hierarchical structure and comparisons of ground cover flora among ecosystem types. See legend of Figure 1 for explanation of indices.


Upland
Terraces & sand ridges
Slopes & depressions
Upland terraces
Slopes
Depressions & flats
Undulating upland terraces
Nearly level upland terraces
Steeply sloping
Gently sloping
Depressions
Flats
Excessively drained upland terraces
Well drained upland terraces
Moderately drained upland terraces
Somewhat poorly drained upland terraces
Non-hydric depressions
Hydric depressions
Sandy shallow depressions
Clayey shallow depressions
Organic hydric depressions
Mineral deep depressions
Excessively drained upland terraces (10)
Well drained upland terraces (16)
Moderately drained upland terraces (10)
Somewhat poorly drained upland terraces (6)
Moderately steeply sloping terrace escarpments (15)
Gently sloping depression margins (5)
Sandy depressions (3)
Clayey depressions (16)
Organic hydric depressions (18)
Sandy hydric depressions (7)
Clayey hydric depressions (7)
Gently sloping hydric flats (3)
Ground cover richness (N)
Ground cover diversity (H')
Ground cover evenness (E)
EUT
WUT
MDUT
SPUT
SCARP
MAR
SD
CD
ORG
SHD
CHD
FLAT

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.

Variable	Species richness (N)				Shannon diversity index (H′)				Sheldon evenness index (E)			
Variance component	Variance estimate	% total	Numerator df	Error df	Variance estimate	% total	Numerator df	Error df	Variance estimate	% total	Numerator df	Error df
A. GROUND COVER FLORA												
Landform complex	0.9407	3.6	1	5.08	0	0	1	5.05	0	0	1	5.06
Landform within landform complex	7.8116	29.9	5	4.36	11.3950	22.9	5	4.78	2.6364	10.9	5	5.30
Terrain shape within landform	4.4074	16.9	4	8.70	10.0059	20.1	4	8.21	0	0	4	9.69
Ecotype within terrain shape	5.1204	19.6	8	111	18.7389	37.7	8	111	1.5444	6.4	8	111
Stand	7.8232	30.0	111		9.5895	19.3	111		19.9200	82.7	111	
Total	26.1033	100.0			49.7293	100.0			24.1008	100.0		
B. OVERSTORY FLORA												
Landform complex	11.8367	51.55	1	4.83	40.4105	49.19	1	4.97	45.7993	20.02	1	5.40
Landform within landform complex	5.1047	22.23	5	8.72	11.2083	13.64	5	5.20	0	0	5	4.36
Terrain shape within landform	0	0	4	5.03	0	0	4	7.10	30.5232	13.53	4	7.94
Ecotype within terrain shape	5.0597	22.04	5	87	25.6090	31.17	7	105	35.9562	15.72	7	105
Stand	0.9593	4.18	87		4.9200	6.00	105		116.4700	50.92	105	
Total	22.9604	100.00			82.1478	100.00			228.7487			

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 (Glitzenstein, 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

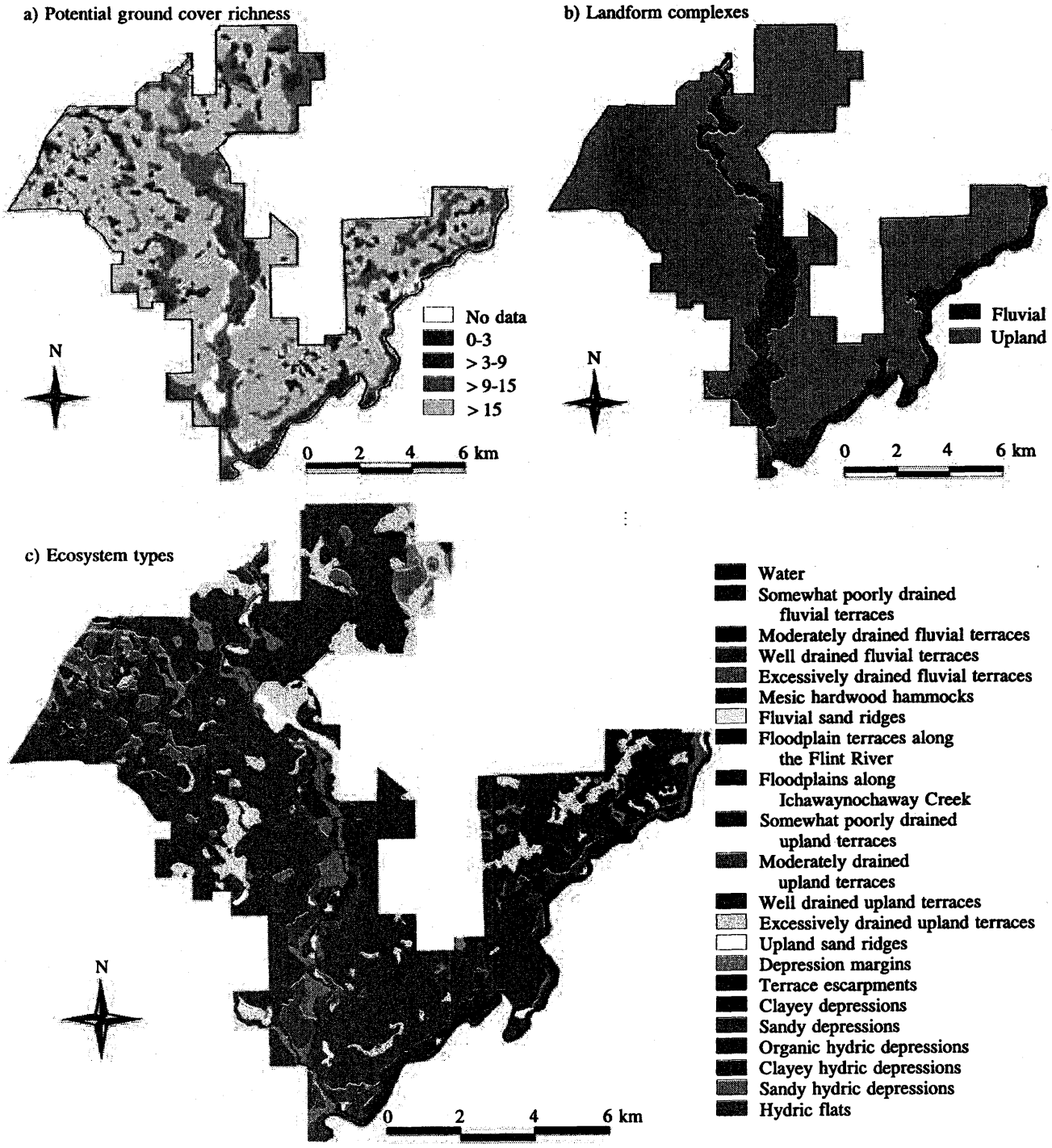


FIGURE 3. a) Potential mean ground cover plant species richness (0.5 m^{-2}) of Ichauway based on ecosystem classification. b) Landforms of Ichauway. c) Ecosystem types of Ichauway based on ecosystem classification.

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

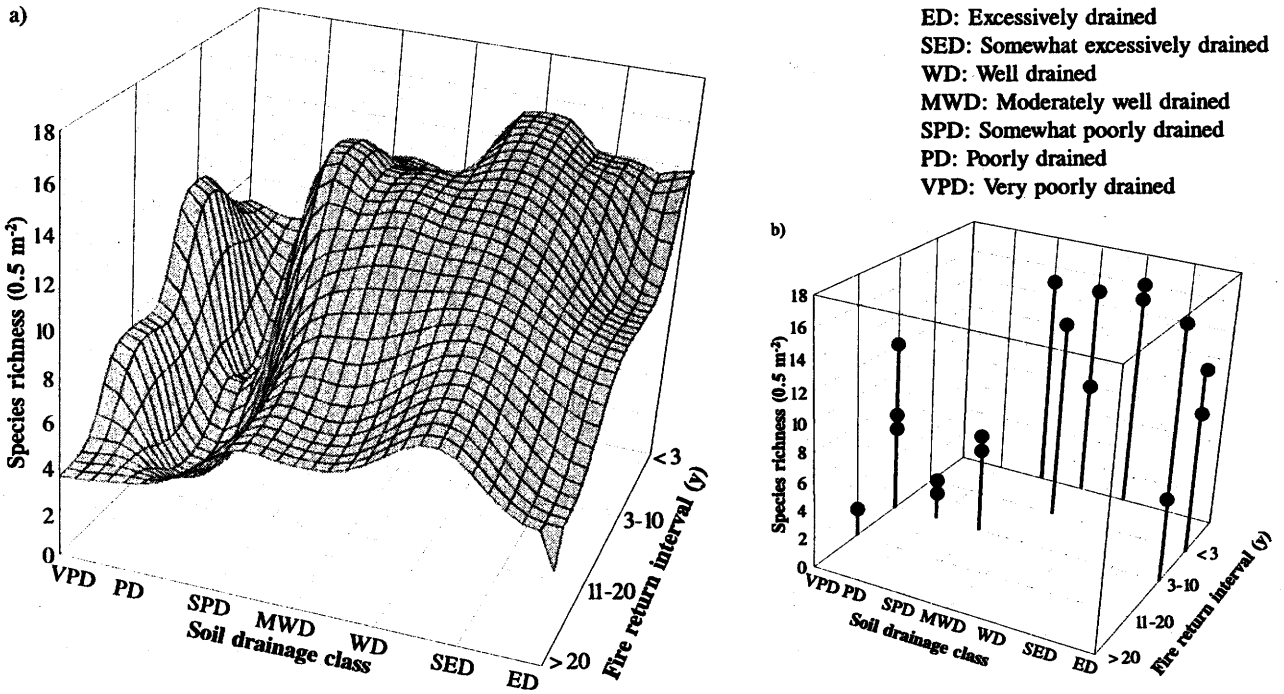


FIGURE 4. Three-dimensional graphic representation for species richness from ecosystem classification data (mean ground cover species richness [0.5 m^{-2}] and soil moisture conditions) and estimated fire return interval. a) Smoothed surface. b) Data points.

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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