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Patterns of frequency in species-rich vegetation in pine savannas: Effects of soil moisture and scale[1]

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Abstract: Our principal objective was to document dominant plant composition and the species frequency pattern in a plant community type, longleaf pine savanna, known for its extraordinary number of vascular plant species. We also tested whether an important habitat factor, soil moisture, affected the resulting patterns, and whether the patterns were scale-dependent. We began with a collection of 120 sample plots (1- × 1-m) in a wet coastal plain savanna. These plots contained 126 plant species. The 3 dominant species by cover were *Rhynchospora gracilenta* (15.37%), *Schizachyrium tenerum* (13.36%), and *Scleria pauciflora* (10.07%). The species frequency distribution was a skewed unimodal pattern with most species occurring infrequently, in less than 10% of the plots. There was no evidence for bimodality. To test whether soil moisture affected species frequency patterns, we sorted the plots into 2 groups: 60 representing wetter conditions and 60 representing drier conditions. Measured by percent cover, the dominants in the wetter plots were *R. gracilenta*, *Dichanthelium scabriusculum*, and *S. pauciflora*, whereas in the drier area they were *S. tenerum*, *Ilex glabra*, and *D. dichotomum*. The species frequency pattern was similar for both wet and dry plots ($\chi^2 = 8.97$, $P > 0.05$). To explore possible effects of sample area on this pattern, we sampled a further 75 plots in a larger tract of similar habitat in De Soto National Forest, using 4 sample areas of 0.1, 1, 10, and 100 m^2. Again, the species frequency distributions all had a skewed unimodal pattern. These patterns are consistent with other studies of savannas but do not appear consistent with the bimodal patterns reported from some grasslands. Further studies of frequency will determine the degree of generality of such patterns and their relationship to mechanistic processes in plant communities.
Keywords: bimodality, longleaf pine savanna, skewed unimodal, species frequency.

Résumé : Notre objectif principal était de documenter la composition végétale dominante et le patron de fréquence des espèces dans un type de communauté végétale, la savane de pin des marais, reconnue pour son nombre extraordinaire d'espèces de plantes vasculaires. Nous avons aussi évalué si un facteur d'habitat important, l'humidité du sol, influençait les patrons obtenus et si ceux-ci étaient dépendants de l'échelle. Nous avons commencé par un échantillonnage de 120 parcelles de 1 × 1 m dans une savane côtière humide. Ces parcelles contenaient 126 espèces de plantes. Les 3 espèces dominantes en couverture étaient *Rhynchospora gracilenta* (15.37 %), *Schizachyrium tenerum* (13.36 %) et *Scleria pauciflora* (10.07 %). La distribution de fréquence des espèces présentait un patron unimodal asymétrique, la plupart des espèces étant rares, présentes dans moins de 10 % des parcelles. Il n'y avait aucune évidence de bimodalité. Afin d'évaluer si l'humidité du sol avait un effet sur les patrons de fréquence des espèces, nous avons divisé les parcelles en deux groupes : 60 représentants des conditions plus humides et 60 autres des conditions plus sèches. En pourcentage de couverture, les espèces dominantes dans les parcelles plus humides étaient *R. gracilenta*, *Dichanthelium scabriusculum* et *S. pauciflora*, alors que dans le secteur plus sec, elles étaient *S. tenerum*, *Ilex glabra* et *D. dichotomum*. Le patron de fréquence des espèces était semblable dans les parcelles humides et sèches ($\chi^2 = 8.97$, $P > 0.05$). Pour explorer les effets possibles de l'aire d'échantillonnage sur ce patron, nous avons utilisé 75 parcelles supplémentaires dans une plus grande étendue d'habitat semblable dans la De Soto National Forest, en utilisant 4 aires d'échantillonnage de 0.1, 1, 10 et 100 m^2. Encore une fois, les distributions de fréquence des espèces présentaient toutes un patron unimodal asymétrique. Ces patrons sont compatibles avec d'autres études sur des savanes, mais ne semblent pas l'être avec les patrons bimodaux rapportés pour quelques prairies. De futures études de fréquence détermineront le degré de généralité de tels patrons et leur rapport aux processus mécanistiques dans les communautés végétales.
Mots-clés : bimodalité, fréquence des espèces, savane de pin des marais, unimodal asymétrique.

Nomenclature: Kartesz, 1994.

Introduction

One of the most fundamental patterns in ecology is the different relative abundances of species in a sample or habitat (Williams, 1964; Pielou, 1975; May, 1981). Most large-scale assemblages have a log normal distribution (May, 1981; 1986), which Preston (1962a,b) called the canonical distribution. However, at much smaller scales, say within single quadrats, relative abundance patterns appear to be best described using negative exponential models (Whittaker, 1965; Wilson *et al.,* 1996). At intermediate scales, say the frequency distributions of species in a set of quadrats, other patterns are possible (Collins & Glenn, 1990; McGeoch & Gaston, 2002). Raunkiaer (1908) proposed, for example, that a J-shaped frequency pattern, the law of frequency, was ubiquitous at this scale.

It is this third category, the frequency of species in sets of quadrats, that we explore in this paper. We address frequency for 3 reasons. First, it is a simple descriptive

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tool that provides one way of summarizing the array of plant populations in a natural community. The focus of our study—pine savanna—contains many rare species, and frequency data are one consistent way of describing the vegetation in such communities. Second, data from other habitats show that in any set of quadrats, a significant proportion of the species are locally uncommon (Collins & Glenn, 1990; McGeoch & Gaston, 2002). That is, a significant proportion of the botanical diversity in any natural area resides in the least common species. Therefore, these patterns are of considerable interest for managing landscapes for conservation (Keddy, 2005). Third, the existing studies of frequency seem to yield conflicting results (McGeoch & Gaston, 2002). Some recent studies have found strongly bimodal patterns (Collins & Glenn, 1990; Partel, Moora & Zobel, 2001), while other studies have found no evidence of bimodality (Penfound & Watkins, 1937; Kirkman *et al.,* 2001).

Our work was therefore directed by 3 questions. (1) What is the frequency pattern? We were particularly intrigued by the possibility of bimodality and its hypothesized relationships to core and satellite models. (2) Whatever the result found, it would be important to know if the pattern was consistent across different sub-habitats. Since it is well known and well documented that soil moisture is a major habitat factor in pine savannas (Peet & Allard, 1993; Kirkman *et al.,* 2001; Christensen, 2000), we chose *a priori* to test whether the shape of the frequency distribution was affected by soil moisture. (3) Once we found that there was no evidence of bimodality, the question arose as to whether this might have been a consequence of our sampling method. We therefore collected data using 4 different quadrat sizes, although this required us to move to a larger patch of the same type of wet savanna habitat. Overall, our view was that whatever pattern emerged, we wished to know whether 2 fairly obvious factors, soil moisture and quadrat size, would shift the shape of the frequency distribution.

Raunkiaer (1934) first drew attention to the possibility of bimodality as a recurring pattern in frequency in 1908, using data compiled from European grasslands, one example being the *Poa nemoralis* grasslands in Allindelille Fredskov, western Denmark. If the frequency distributions were divided into 5 percentage classes (Class A–E), the pattern appeared as a J-shaped curve (bimodal distribution), caused by an increase in Class E after a decreasing trend in the previous classes (McIntosh, 1962). This pattern, which historically precedes the canonical distribution, has been resurrected in recent studies, in part because of the appearance of the core and satellite model (Hanski, 1982), which might provide a theoretical basis for a bimodal pattern (Gotelli & Simberloff, 1987; Collins & Glenn, 1990; Partel, Moora & Zobel, 2001; McGeoch & Gaston, 2002). In this case, communities might consist of 2 kinds of species, core and satellite. Core species are regionally common and usually locally abundant while being well separated in niche space, whereas satellite species are regionally and locally rare and not well separated in niche space (Hanski, 1982; McGeoch & Gaston, 2002).

In order to better understand such patterns, we need examples from a variety of habitats and a variety of scales. Since habitats with very large numbers of species are of interest from the point of view of both theory and conservation, we selected a habitat known to have many plant species in relatively small areas, a habitat with plants that are rare locally and regionally, and a habitat with a large number of plant functional types (including graminoids, carnivorous plants, legumes, vines, evergreen shrubs, and rosette plants). We documented the overall pattern of frequency in a set of 120 plots. We next tested if this pattern changed with soil moisture. Finally, we tested whether it was affected by quadrat size.

Methods

Habitat type

The Atlantic and Gulf Coastal Plain area of North America has remarkable plant diversity, particularly in pine savannas (White, Wilds & Thunhorst, 1998; Platt, 1999; Stein, Kutner & Adams, 2000; Estill & Cruzan, 2001). These pine savannas are naturally occurring fire-prone, nutrient-poor ecosystems (Platt, 1999; Glitzenstein, Platt & Streng, 1995; Glitzenstein, Streng & Wade, 2003) that once covered over 228 500 km^2 across the southeastern coastal plain of the United States (Frost, 1993). Natural fire frequency is at least once per decade (Platt, 1999), although managers often burn at shorter intervals of 1 to 3 y (Walker & Peet, 1983; Kirkman *et al.,* 2001; Glitzenstein, Streng & Wade, 2003). Within Louisiana these pine savannas are officially classified as "Eastern Longleaf Pine Savannah," one of 37 Louisiana Terrestrial Habitats designated by Lester *et al.* (2005)

Patterns in the Lake Ramsay savanna

We began our work at the Lake Ramsay Conservation Area near Covington, Louisiana (30° 32' N, 90° 07' W), which is jointly owned by The Nature Conservancy and the Louisiana Department of Wildlife and Fisheries. The area contains clearings of open wet savanna further described in Keddy *et al.* (2006) and Lester *et al.* (2005). The landscape is gently sloped (≤ 2%), with scattered depressions. The climate is humid subtropical; rainfall in 2004 in the Covington area was 169.67 cm. Mean daily temperatures were 11 °C in January and 27.4 °C in July (NOAA, 2004). Soils are classified mainly as Myatt-Stough-Prentiss series, which are poorly drained to moderately well drained soils (USDA, 1990). Prescribed burning occurs, usually in the spring, every 2–4 y depending on moisture conditions and fuel accumulation.

In April 2004, 40 plots (1-m^2) were established at 3 different sites, each site consisting of a wet (20 plots) and a dry (20 plots) sub-area (a map is given in Clark, 2005, Figure 5). Each of the 120 plots was visited twice, in spring (May) and in autumn (September/October), to identify the species present. Voucher specimens have been placed in the Southeastern Louisiana University herbarium and the Louisiana State University herbarium. A chi square test (Siegel & Castellan, 1988) was used to test for a difference in species frequency distribution between the wet and dry sub-areas.

The selection of sampling areas to represent the 2 classes of soil moisture (wet, dry) was initially based upon field observations of soil moisture and standing water after heavy rain. Soil moisture was further documented by measurement approximately every 2 weeks (from April to December) using a TH_2O Theta soil moisture meter (Dynamax Inc., Houston, Texas). Soil moisture was not measured during or immediately following rain. According to Dynamax, accuracy is 5% when using the generalized organic soil calibration.

To further document the general study area, aggregate soil samples were collected from each of the 6 sample areas. Each aggregate sample contained cores from 5 plots taken with an open-faced 1.8-cm-diameter push tube to a 25-cm maximum depth. The samples were stored in a plastic bag overnight and taken to the Louisiana State University Ag Center's Soil Testing and Plant Analysis Lab in Baton Rouge for basic nutrient analysis (Ca, Mg, Na, P, K, and pH).

Effects of sampling scale in the National Forest

In order to explore the possibility that quadrat size might have affected our results, we needed a much larger tract of the same habitat type subjected to a similar management regime of recurring fire. Larger areas of wet savanna representing Eastern Longleaf Pine Savannah (Lester *et al.,* 2005) occur in De Soto National Forest in southern Mississippi. Our study site there (known as Buttercup Flats, from the yellow flowers of *Sarracenia*) is burned by the US Forest Service every other year. We sampled in approximately 1 km^2 of savanna dominated by species of *Rhynchospora* interspersed among drier areas dominated by the grass *Schizachyrium tenerum*.

Seventy-five plots were chosen randomly across the site with the restriction that all plots were to have less than 25% cover by shrubs and trees. At each of the 75 locations, we demarcated 4 circular subplots with areas of 0.1, 1, 10, and 100 m^2 and recorded all species present in each. Voucher specimens were deposited in the herbaria of Southeastern Louisiana University, Louisiana State University, and the University of Southern Mississippi. Identification advice was provided by Glen Montz. Nomenclature follows Kartesz (1994).

To test for differences among frequency distributions at 4 scales, we used Kolmogorov–Smirnov two-sample tests (Sokal & Rohlf, 1995). The null hypothesis was that each pair of samples was distributed identically. Our data comprised 4 frequency distributions, so all possible pairwise comparisons were made with a Bonferroni adjustment. With an experiment-wise error rate of 0.01, the critical probability for individual tests is $\alpha' = \alpha/k = 0.01/6 = 0.00167$, where k is the number of comparisons.

Results

Frequency patterns at Lake Ramsay

The study plots contained 126 taxa, of which 30 species had percent cover greater than 1% (Table I). The 3 dominants (by percent cover) in the wet areas were *Rhynchospora gracilenta*, *Dichanthelium scabriusculum*, and *Scleria pauciflora*, while in the dry area they were *Schizachyrium tenerum*, *Ilex glabra*, and *Dichanthelium dichotomum*.

Overall, 2 species, *Rhexia alifanus* (110 plots) and *Eupatorium leucolepis* (109 plots), occurred most frequently. The next most frequent were *Drosera brevifolia* and *Dichanthelium dichotomum*, occurring in 108 and 103 plots, respectively.

There was no evidence of bimodality (Figure 1). Most of the flora was composed of infrequent species, with 81 out of the 126 taxa occurring in fewer than 10% of the plots.

Effects of soil moisture upon frequency patterns

Soil moisture content changed with time, being lowest in late September and early October and higher in the winter (Figure 2). On 11 out of 14 sampling days, there was a sig-

TABLE I. The 30 most abundant species at Lake Ramsay according to mean percent cover (means include zero values; $n = 120$ plots).

Species	Mean cover (%)	Life form
Rhynchospora gracilenta	15.37	Sedge
Schizachyrium tenerum	13.36	Grass
Scleria pauciflora	10.07	Sedge
Ilex glabra	8.69	Evergreen shrub
Dichanthelium dichotomum	8.28	Grass
Scleria lithosperma	7.70	Sedge
Dichanthelium leucothrix	6.86	Grass
Rhynchospora pusilla	6.56	Sedge
Dichanthelium scabriusculum	6.33	Grass
Muhlenbergia capillaris	5.69	Grass
Andropogon virginicus	5.33	Grass
Rhynchospora chapmanii	4.28	Sedge
Myrica cerifera	3.75	Deciduous shrub
Rhexia alifanus	3.62	Erect herb
Andropogon mohrii	3.56	Grass
Eriocaulon decangulare	3.54	Rosette herb
Eupatorium leucolepis	3.51	Erect herb
Ctenium aromaticum	2.77	Grass
Panicum anceps	2.24	Grass
Rhynchospora plumosa	2.13	Sedge
Schizachyrium scoparium	2.01	Grass
Polygala ramosa	1.93	Erect herb
Lobelia brevifolia	1.78	Erect herb
Drosera brevifolia	1.69	Rosette herb
Panicum hians	1.57	Grass
Dichanthelium strigosum	1.43	Grass
Dichanthelium ovale	1.42	Grass
Aristida purpurascens	1.40	Grass
Rhynchospora caudica	1.18	Sedge
Nyssa sylvatica	1.08	Deciduous tree

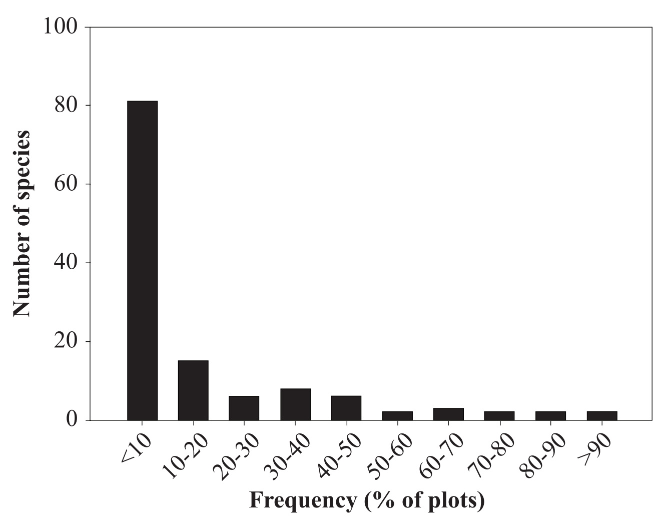

FIGURE 1. Plant frequency in the Lake Ramsay savanna ($n = 120$ plots, Total no. species = 126).

nificant difference in soil moisture between the wet ($n = 60$) and dry ($n = 60$) plots using a Bonferroni adjusted P-value ($P = 0.00357$). On 3 occasions (16 May, 14 June, 4 October 2004) there were no significant differences in moisture between wet and dry plots. Mean nutrient measurements were Ca: 127.82, Mg: 34.50, P: 4.97, K: 14.65, and Na: 30.11 mg·L^{-1} for $n = 6$ samples. Although these sample sizes were insufficient for significance tests, the wet and dry habitats had identical pH (4.8), while the wet habitats appeared to have higher nutrient levels over all, particularly for Ca (dry: 104.67; wet: 150.97 mg·L^{-1}).

The species frequency pattern was similar in both dry and wet areas, with over half the species (58 and 54, respectively) found in 10% or fewer of the plots (Figure 3). The wet areas had a slightly higher number of species than dry areas (110 in wet *versus* 101 in dry). There was no significant difference between the 2 frequency distributions ($\chi^2 = 8.97$, $P > 0.05$).

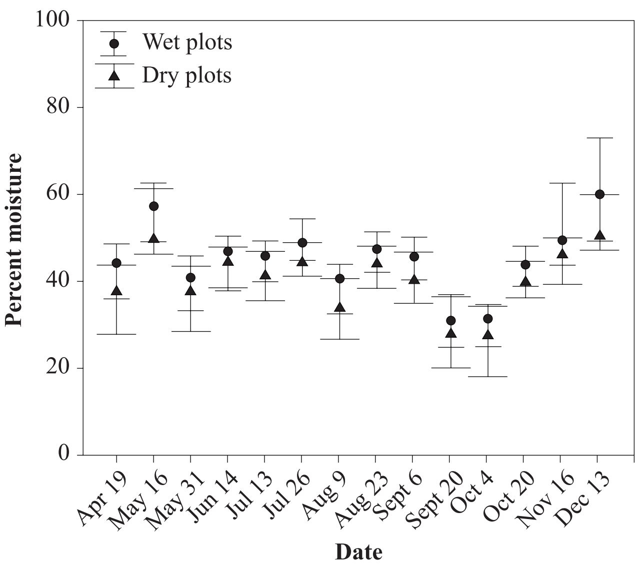

FIGURE 2. Soil moisture in 120 plots as a function of time during the study. Points are medians and whiskers represent the 10th and 90th percentiles. On 11 out of 14 sampling days, there was a significant difference in soil moisture between the *a priori* categories of wet ($n = 60$) and dry ($n = 60$) plots using a Bonferroni adjusted P-value ($P = 0.00357$).

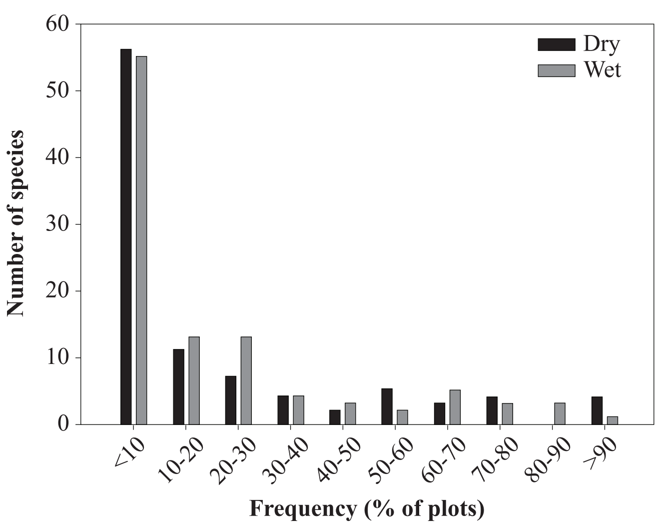

FIGURE 3. Plant frequency patterns sorted by soil moisture ($n = 60$ in each moisture class, total no. species = 110 in wet areas and 101 in dry areas). There was no significant difference in frequency distribution between dry and wet areas ($\chi^2 = 8.97$, $P > 0.05$).

EFFECTS OF SAMPLING SCALE

Overall, 250 species were encountered in the largest-scale plots. Table II shows the 10 species with highest cover at each scale. The frequency of the most frequent species increased with scale, with *Drosera rotundifolia* found in 37% of the smallest plots, *Andropogon mohrii* found in 57% and 74% of the 2 intermediate-sized plots, and *Ilex glabra*

TABLE II. The 10 most abundant species at each sample scale at Buttercup Flats in De Soto National Forest. Mean cover includes zero values; $n = 75$ for each plot size. Grass stage and saplings of *Pinus palustris* are excluded from the table.

Plot size	Rank	Species	Mean cover (%)	Life form
0.1 m^2	1	*Schizachyrium tenerum*	4.74	Grass
	2	*Rhynchospora plumosa*	3.95	Sedge
	3	*Rhynchospora chapmanii*	3.25	Sedge
	4	*Rhynchospora gracilenta*	2.50	Sedge
	5	*Eriocaulon decangulare*	2.13	Erect herb
	6	*Andropogon mohrii*	1.70	Grass
	7	*Zigadenus glaberrimus*	1.65	Erect herb
	8	*Muhlenbergia expansa*	1.45	Grass
	9	*Ctenium aromaticum*	1.11	Grass
	10	*Aristida purpurascens* var. *purpurascens*	1.11	Grass
1 m^2	1	*Schizachyrium tenerum*	6.61	Grass
	2	*Rhynchospora plumosa*	4.02	Sedge
	3	*Rhynchospora chapmanii*	3.35	Sedge
	4	*Muhlenbergia expansa*	2.57	Grass
	5	*Rhynchospora gracilenta*	2.50	Sedge
	6	*Aristida purpurascens* var. *purpurascens*	2.05	Grass
	7	*Eriocaulon decangulare*	1.92	Erect herb
	8	*Aristida purpurascens* var. *virgata*	1.66	Grass
	9	*Zigadenus glaberrimus*	1.56	Erect herb
	10	*Ctenium aromaticum*	1.48	Grass
10 m^2	1	*Schizachyrium tenerum*	7.37	Grass
	2	*Rhynchospora plumosa*	3.23	Sedge
	3	*Rhynchospora chapmanii*	2.88	Sedge
	4	*Aristida purpurascens* var. *purpurascens*	2.45	Grass
	5	*Rhynchospora gracilenta*	2.44	Sedge
	6	*Muhlenbergia expansa*	2.38	Grass
	7	*Aristida purpurascens* var. *virgata*	2.27	Grass
	8	*Eriocaulon decangulare*	2.12	Erect herb
	9	*Ilex glabra*	2.01	Shrub
	10	*Zigadenus glaberrimus*	1.72	Erect herb
100 m^2	1	*Schizachyrium tenerum*	7.28	Grass
	2	*Ilex glabra*	3.01	Shrub
	3	*Rhynchospora plumosa*	2.67	Sedge
	4	*Aristida purpurascens* var. *purpurascens*	2.58	Grass
	5	*Muhlenbergia expansa*	2.33	Grass
	6	*Sarracenia alata*	1.97	Erect herb
	7	*Aristida purpurascens* var. *virgata*	1.97	Grass
	8	*Rhynchospora gracilenta*	1.93	Sedge
	9	*Rhynchospora chapmanii*	1.92	Sedge
	10	*Zigadenus glaberrimus*	1.86	Erect herb

found in 86% of the largest plots. *Schizachyrium tenerum* was most dominant as measured by the sum of the percent cover values across all plots, for all plot sizes, with mean percent cover between 4.74% and 7.37% (24.05% and 32.73% excluding values of zero). The majority of the 10 most dominant plants, in terms of sum of the cover values, were grasses and sedges (of the genus *Rhynchospora*) for all plot sizes. Most plant species were found in less than 10% of the plots at all plot sizes, with 79% of the 124 species found at 0.1 m^2, 54% of the 184 species at 1 m^2, 69% of the 216 species at 10 m^2, and 62% of the 250 species at 100 m^2.

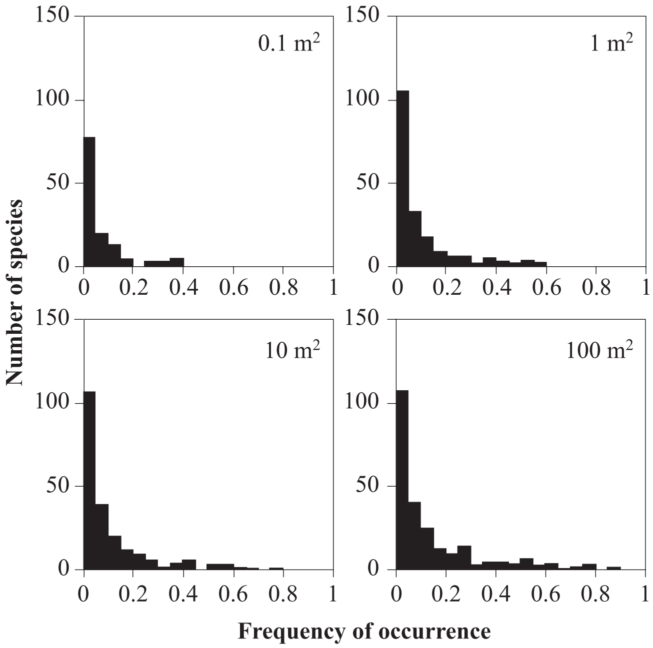

FIGURE 4. Plant frequency at 4 sample scales in De Soto National Forest (*n* = 75 plots, total no. species = 250 species in the largest plots). No significant differences were found among scales (Kolmogorov–Smirnov 2-sample tests, D calculated < than D critical for all pairs of comparisons).

Figure 4 shows that there was no evidence of bimodality at any scale. With regard to possible scale effects, the largest pairwise calculated D value was 0.19, and for all comparisons, D calculated was less than D critical. Therefore, we accept the null hypothesis that the frequency distributions are not significantly different among scales.

Discussion

The species frequency distributions all had a skewed unimodal pattern, with most species occurring infrequently, in less than 10% of the plots. This type of frequency distribution is similar to that observed in other savannas (Table III). Penfound and Watkins (1937) found this pattern in 3 virgin longleaf areas, 1 second growth, and 1 cutover longleaf savanna studied in the Florida Parishes of southeastern Louisiana. In these systems the most frequent species found were *Andropogon virginicus, Aristida virgata,* and *Schizachyrium scoparium* (= *A. scoparius*). In longleaf pine savannas of southwestern Georgia, where up to 70 species were found in a single 3-m^2 plot, *Aristida beyrichiana* was the most abundant species (Kirkman *et al.,* 2001).

The skewed unimodal distribution contrasts with the bimodal pattern reported in tall grass prairie (Gotelli & Simberloff, 1987; Collins & Glenn, 1990). Partel, Moora, and Zobel (2001) also obtained a bimodal distribution studying species frequency in alvar grasslands of Estonia.

The lack of a bimodal distribution in our data indicates that there is no evidence for core or satellite species in longleaf pine savannas. The reason for the differences among tall grass prairies, alvars, and longleaf pine savannas is unclear. Three hypotheses might be entertained. (1) Perhaps pine savannas are more heterogeneous with respect to environmental factors, or the plant species are more specialized

TABLE III. Summary of some studies of species frequency distributions.

Study	Location and vegetation type	Number of plots Plot size·No. areas^{-1}	Species	Characteristic species	Number of frequency categories	Pattern
Penfound & Watkins (1937)	SE Louisiana pineland communities	250 1-m^2·7 areas^{-1}	168	*Andropogon virginicus* *Aristida virgata* *Andropogon scoparius*	6	Unimodal
Gotelli & Simberloff (1987)	NE Kansas tallgrass prairie	15–119 10-m^2·7 areas^{-1}	170	*Andropogon gerardii* *Ambrosia psilostachya* *Aster ericoides*	8	Bimodal
Collins & Glenn (1990)	NE Kansas tallgrass prairie	20 10-m^2·18 sites^{-1}	144	*Andropogon gerardii* *Schizachyrium scoparium* *Poa pratensis*	10	Bimodal
	SW Oklahoma prairie	100 0.5-m^2·7 sites^{-1}	122	*Andropogon gerardii* *Schizachyrium scoparium* *Ambrosia psilostachya*	10	Bimodal
Kirkman *et al.* (2001)	SW Georgia longleaf pine savanna	90 1- × 3-m·1 area^{-1}	203	*Aristida beyrichiana*	Continuous	Unimodal
Partel, Moora & Zobel (2001)	Estonia alvar grasslands	15 1-m^2·16 stands^{-1}	122	*Pimpinella saxifraga* *Centaurea jacea*	16	Bimodal
Clark (2005)	SE Louisiana longleaf pine savanna	120 1-m^2·3 sites^{-1}	126	*Rhynchospora gracilenta* *Schizachyrium tenerum* *Scleria pauciflora*	10	Unimodal

upon microhabitats, in which case a few common species cannot occur across most sites. (2) Perhaps recurring disturbance from fire, flooding, and drought prevent a few potentially dominant competitors from excluding neighbours and occupying most quadrats. (3) Perhaps sampling across a broader number of sites (looking among rather than within specific sites) would have found such a pattern.

There are 4 areas of research that would improve our understanding of frequency patterns in plant communities and their potential utility in plant conservation. The first addresses the nature of the patterns. (1) We need more examples of frequency distributions in order to provide a comparative database representing a broad array of herbaceous plant communities, with, if appropriate, tests to determine the influence of local factors such as soil moisture, soil fertility, or sampling scale. (2) We need predictive models for frequency patterns with different numbers of species and with different scales of sampling. (3) We need experiments that explore the mechanisms that control the frequency of species at each scale. In the case of herbaceous communities, it seems in general that disturbances such as fire and grazing have important effects on composition (Grubb, 1977; Grime, 1979; Grace, 1999; Keddy, 2001), but how this extends to frequency patterns is poorly understood. (4) We can test whether certain life history traits determine frequency (Rabinowitz & Rapp, 1981; Kunin & Gaston 1997; Eriksson & Jakobsson, 1998). Although 100 y have elapsed since Raunkiaer's work, the general patterns of relative frequency remain unclear and deserve continued attention.

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