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Patterns of herbaceous plant diversity in southeastern Louisiana pine savannas

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Abstract
Question: How diverse are Louisiana pine savanna plant communities and how is diversity affected by time since burn and removal of a competitively dominant species?
Location: Lake Ramsay, southeastern Louisiana, USA.
Methods: Species-area curves were constructed from nine nested quadrats in open savanna differing in time since burn (6, 18 and 30 months). Species frequency was determined for 100 1-m^2 quadrats. The dominant grass, *Andropogon virginicus*, was removed with herbicide from moist and dry sites to test for possible effects of competition.
Results: Slopes of log-log species-area relationships were steep (0.195 to 0.379). Time since burn did not affect the richness of herbaceous plants, only woody species. More than half of all species recorded (43/79, 54 %) were infrequent (in < 10 % of quadrats). After two years, there were no differences in species richness and composition for plots with and without *A. virginicus*.
Conclusions: The high species diversity is typical of other savannas across the coastal plain. The large number of infrequent species indicates that the core-satellite pattern of species occurrence found in temperate grasslands does not apply to southern pine savannas. The absence of effects due to removal of a dominant may be due to insufficient observation time, or low competition. Most species have traits, such as diminutive life forms, that suggest they are weak competitors for light in the presence of robust matrix grasses and in the absence of fire. Many species in *Pinus palustris* savannas are likely either fugitive or peripheral species.

Keywords: *Andropogon virginicus*; Competition; Conservation; Disturbance; Diversity; Fugitive species; Longleaf pine; Louisiana; Peripheral species; *Pinus palustris*; Species-area relationship; Species frequency.

Nomenclature: Integrated Taxonomic Information System (http://www.itis.usda.gov/).

Introduction

The available scholarly research on pine savannas largely reflects three research themes. The first theme is a description of pine savanna plant communities, often with use of ordination and classification (e.g. Peet & Allard 1993; Goebel et al. 2001), and we now have a reasonable picture of regional patterns in species distributions along indirect gradients. The second is the effects of natural disturbance from fire (e.g. Platt 1999; Glitzenstein et al. 2003), disturbance being any factor that removes accumulated biomass and litter (Grime 1977). Particular emphasis is often placed upon the responses of *Pinus palustris* (longleaf pine*)* to different fire regimes (Noel et al. 1998; Glitzenstein et al. 2003). The third theme addresses the autecology of individual pine savanna species such as *Drosera capillaris* (Brewer 1998a, 1999a), *Pityopsis graminifolia* (Brewer & Platt 1994; Brewer 1995) and *Sarracenia alata* (Brewer 1999b, 2001). We now, therefore, have (1) a reasonable picture of the gradients in species composition within pine savanna habitats; (2) an understanding that fire regimes must be restored to retain and expand *P. palustris* ecosystems, and (3) a growing body of information on selected pine savanna plants.

Conceptual gaps remain. The first is a lack of detail on the extent of remnant *P. palustris* savannas and forests in some regions. In southeastern Louisiana, in particular, pine savannas remain poorly known in the published literature despite a rich flora (but see Penfound & Watkins 1937; Barker & Williamson 1988). The majority of research on *P. palustris* ecosystems has been done further east, in the Carolinas (e.g. Walker & Peet 1983), Mississippi (e.g. Eleuterius & Jones 1969; Brewer 1998b), Georgia (e.g. Kirkman et al. 1998; Goebel et al. 2001) and Florida (e.g. Glitzenstein et al. 2003).

The second conceptual gap in pine savanna research is a comparative shortage of work on community level models for the maintenance of ecological diversity, perhaps using general conceptual models that seem to work in other herbaceous vegetation types (e.g. Grime 1977, 1980; Huston 1979; Pickett 1980; Grubb 1986; Collins & Glenn 1990; Gaudet & Keddy 1995; Keddy 1990, 2005). It is now clear that most savannas require burning between every one and four years depending upon physiography, soil types, hydrology and exposure, while some questions remain about the appropriate intensity and season for burns. Given that the major fire-related questions are being resolved, we must address the next step: the maintenance of diversity within appropriately burned communities.

Our long-term objective is to understand patterns and mechanisms of plant diversity in wet *P. palustris* savannas and herbaceous plant communities in general. This requires basic knowledge of the regional flora and vegetation in southeastern Louisiana. The first goal of this paper is to present an overview of *P. palustris* savannas of southeastern Louisiana, their conservation status, and data on rare plants found therein. These savannas are nationally significant as they represent the westernmost part of the Southeastern Conifer Forest Ecoregion (according to World Wildlife Fund), and the westernmost part of the East Gulf Coastal Plain Ecoregion (according to The Nature Conservancy).

Second, we present our ongoing research investigating the patterns of plant diversity in *P. palustris* savannas and the possible controls on species richness, specifically (1) patterns in species-area relationships; (2) patterns in relative frequency; (3) the competitive effects of a dominant grass on the remaining flora.

Remnant *P. palustris* savannas in southeastern Louisiana

The *P. palustris* uplands and flatwood savannas in southeastern Louisiana (Fig. 1) represent the westernmost extension of the once essentially contiguous *Pinus palustris* system of the East Gulf Coastal Plain, the coastal plain being a North American region of high biological diversity (White et al. 1998; Stein et al. 2000). The East Gulf Coastal Plain has a long history of resource exploitation, leaving few examples of *P. palustris* forest and wet savanna (Williams 1989; White 1998; Platt 1999). In eastern Louisiana, *P. palustris* savannas occur on Pleistocene terrace deposits to the north and east of the Mississippi River alluvial plain, deposits subsequently buried by loess along a gradient of declining depth from west to east (Spearing 1995). To the west of the Mississippi River, there are other areas of *P. palustris* savanna, although the species composition is different (Allen et al. 1988; Harcombe et al. 1993; Keith & Carrie 2002).

The topography is flat in the southern half of these Pleistocene terraces, with the water table close to the surface. Examples of remnant flatwood *P. palustris* savannas are protected and being restored in St. Tammany Parish (Fig. 1, Table 1). The topography becomes more rolling to the north, and *P. palustris* communities become drier. Several upland *P. palustris* forests are protected in Tangipahoa and Washington parishes. Further west, *P. palustris* still dominates the other parishes (St. Helena, Livingston, East Feliciana,

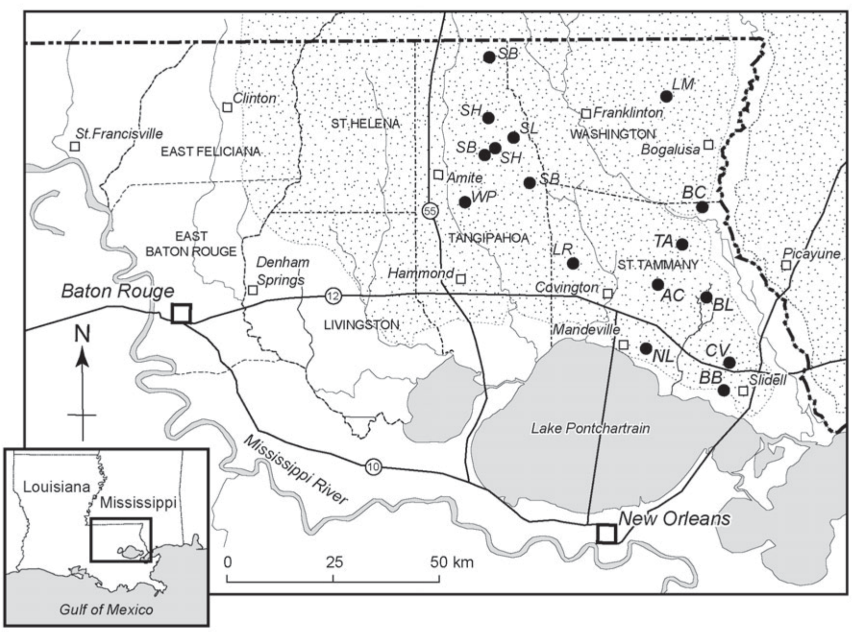

Fig. 1. Locations of protected longleaf *P. palustris* savannas and forests in the Florida parishes of southeastern Louisiana. The stippled area is the Pleistocene uplands east of the Mississippi River dominated by *Pinus palustris*. Refer to Table 1 for site details.

Table 1. Remnant *P. palustris* areas in the Florida parishes of Louisiana owned or overseen by government agencies or private non-profit groups. The area column includes relatively high-quality *P. palustris* habitat or areas under active restoration management. A few sites that are publicly owned with potential for restoration are included in italics. Part A includes only savannas and flatwoods, while part B includes upland *Pinus palustris* forests.

Map code	Site name	Parish	Ownership	Area (ha)	Comments
A. Flatwoods and Savannas					
TA	Talisheek Flatwoods	St. Tammany	TNC[1]	1190	22 rare plant species,1 known only from here in LA. Includes a high-quality *Pinus elliottii-Taxodium ascendens* forest. Active restoration management since 1998.
BL	Bayou Lacombe Mitigation Bank	St. Tammany	Private	790	Active restoration management since 1999.
LR	Lake Ramsay Savanna	St. Tammany	LDWF[2] & TNC	530	27 rare plant species, 3 known only from here in LA. Best remnant *P. palustris* flatwood savanna in region.TNC portion is a *P. palustris* flat-wood wetland mitigation bank. Active restoration management since 1993.
CV	Camp Villere	St. Tammany	LANG[3]	400	Active fire management since 1996.
AC	Abita Creek Flatwoods	St. Tammany	TNC	340	27 rare plant species. Includes a high quality hillside seepage bog. Active restoration management since 1998.
BB	Big Branch National Wildlife Refuge	St. Tammany	USFWS[4]	100	Only public land in the Florida Parishes supporting Red-cockaded Woodpecker. Includes 'marsh-fringing' variant of *P. palustris* flatwoods. Active restoration management since 1995.
NL	North Lake Nature Center	St. Tammany	LDHH[5]	80	Active restoration management since 1996.
B. Upland *Pinus palustris* woodlands					
SH	Sandy Hollow Wild-life Management Area	Tangipahoa	LDWF	1130	Supports a full topographic gradient of communities. The largest known state population of globally-imperiled orchid *Pteroglossaspis ecristata*. Large *Gopherus polyphemus* population Active restoration management since 1986.
SB	*School Board Lands* (3 tracts)	Tangipahoa	Parish School Board	400 400	Most not being actively managed for restoration.
WP	Camp Whispering Pines	Tangipahoa	Girl Scouts	120	Research area for Dr. W. Platt since 1995. Active restoration management since 1995.
SL	*State lands longleaf*	Tangipahoa	Louisiana Office of State Lands		120 Not being actively managed for restoration.
BC	Bogue Chitto National Wildlife Refuge	St. Tammany	USFWS	110[1]	Small *Gopherus polyphemus* population. Active restoration management since 1990.
LM	Lee Memorial Research Forest	Washington	Louisiana State University	24	Active fire management since 1970s. Very diverse native ground cover community.

[1]The Nature Conservancy; [2]Louisiana Department of Wildlife and Fisheries; [3] Louisiana Army National Guard; [4] United States Fish and Wildlife Service; [5] Louisiana Department of Health and Hospitals.

East Baton Rouge) and additional field work is needed to locate other remnants, particularly those that may occur on private land. Even if other high quality remnants can no longer be found, it is likely that many relatively large areas of degraded *P. palustris* forest could be restored by appropriate forestry methods including prescribed fire. The map therefore should be regarded only as a starting point, not an end point, for future exploration, conservation and restoration.

Lake Ramsay savanna

The Lake Ramsay savanna is among the highest-quality *Pinus palustris* flatwoods found in southeastern

Louisiana. It consists of ca. 530 ha of adjoining lands owned by the Louisiana Department of Wildlife and Fisheries and The Nature Conservancy. The main vegetation types are wet *Pinus palustris* flatwood savannas and mesic *Pinus palustris* flatwoods that have developed on acidic very fine sandy loams and silt loams. These habitats at Lake Ramsay are aggressively managed with a regime of prescribed burns on a 1 to 3 year rotation, applied mainly in the growing season.

Fig. 2 shows four main vegetation types in the Lake Ramsay Conservation Area, the source of our descriptive data. Five distinctive vegetation types actually occur, but two of these, wet *Pinus palustris* flatwood savannas and mesic *Pinus palustris* flatwoods, are combined as one on the map, since they intergrade locally depending upon local elevation and consequent hydrology. The location of our nine species-area plots and the site for collecting frequency data are noted in Fig. 2.

Pinus palustris flatwood savannas

These are floristically rich, herb-dominated wetlands with scattered *P. palustris*. They historically dominated the outer Gulf coastal plain flatwoods regions of southeast and southwest Louisiana, as well as occurring from eastern Texas to western Virginia. Wet savannas occur on hydric soils in an interdigitated mosaic with low, broad ridges (see following type) having higher densities of *P. palustris* . The water table fluctuates: in late fall/winter/early spring there is saturation and shallow flooding whereas in midsummer soils are often dry.

Mesic Pinus palustris flatwoods

This upland community is intermixed with the preceding wetland community, occurring on non-hydric soils of low, broad ridges. It is drier yet greatly dominated (at least historically) by *P. palustris*. As in the wet savannas, frequent fire is the major factor controlling species occurrence and community structure – without frequent fire, shrubs and eventually trees, especially hardwoods, would gain dominance and eliminate *P. palustris* and most of the herbaceous flora. Historically, these habitats probably burned every 2 to 4 years, mainly from lightning strikes in late spring and early summer. The soils are normally mesic but may be saturated in winter or dry in summer.

Mixed hardwood-Pinus taeda forests

These forests are common state-wide, but at Lake Ramsay are restricted to stream valleys, probably due to the higher soil moisture and relative protection from fire. While *Pinus taeda* (loblolly pine) can be dominant, it is usually mixed with many kinds of oaks including *Quercus nigra, Q. alba, Q. falcata, Q. stellata, Q. laurifolia* and *Q. michauxii*. Other trees include *Fagus grandifolia*, *Magnolia grandiflora*, *Liquidambar styraciflua*, *Nyssa sylvatica* and *Acer rubrum*.

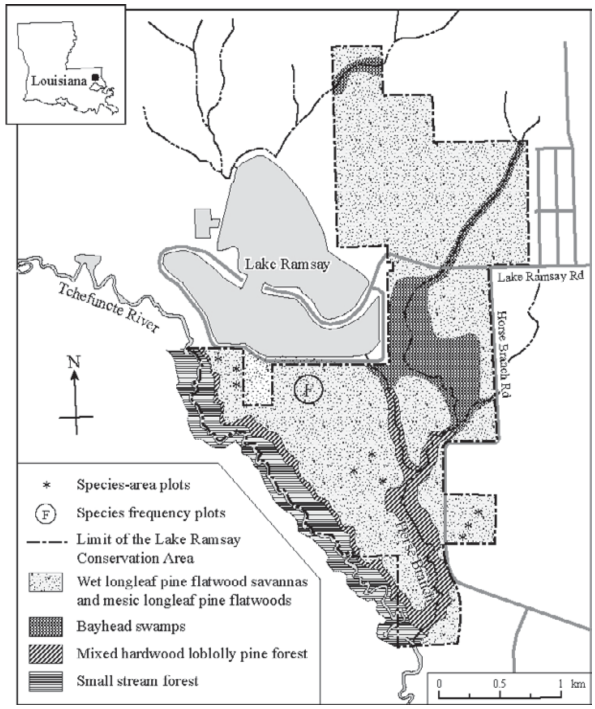

Fig. 2. The Lake Ramsay study area and its vegetation types, showing areas sampled for the species-area and species frequency analyses.

Bayhead swamps

These forested wetlands develop in broad, shallow drains or relatively deep depressions amidst pine flatwoods. They are seasonally to semi-permanently

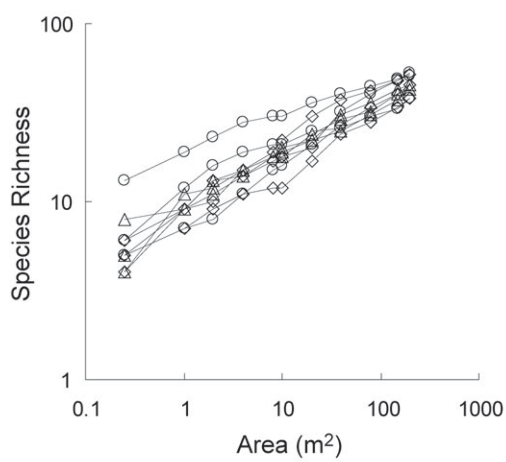

Fig. 3. Species-area relationship for individual nested plots in the Lake Ramsay savanna.

saturated or flooded, and vary locally in size from ca. 1 ha to > 40 ha. The overstorey is typically a closed canopy dominated by *Magnolia virginiana*, *Nyssa biflora* and *Q. laurifolia*. *Taxodium ascendens* also may be found as scattered individuals.

Streamside forests

This type of forest typically occurs along annual floodplains of small to intermediate-sized perennial streams throughout the state. The species composition varies with geology, soil and flooding regimes. Here, along the Tchefuncte River, this forest includes the species listed above in the mixed hardwood-*Pinus taeda* forest, as well as widespread species of East Gulf Coastal Plain floodplains including *Taxodium distichum*, *Platanus occidentalis* and *Pinus glabra*.

The herbaceous ground cover communities of the savannas and flatwoods at Lake Ramsay are among the best remaining in southeastern Louisiana, rich in *Poaceae*, *Cyperaceae*, *Orchidaceae* and *Asteraceae*. Carnivorous plant species present include *Sarracenia alata*, *S. psittacina*, *Pinguicula lutea*, *Drosera brevifolia*, *D. capillaris* and *Utricularia subulata*. Over 200 native plant species have been recorded in the open savannas (L. Smith unpubl.).

The Louisiana Natural Heritage Program of the Louisiana Department of Wildlife and Fisheries tracked 28 rare plant species which are currently known from the area (Table 2). Most are exclusively associated with regularly burned wet *Pinus palustris* flatwood savannas and mesic *Pinus palustris* flatwoods. The greatest numbers of rare species occur, respectively, in the *Cyperaceae* (five species), *Orchidaceae* (four species) and *Scrophulariaceae* (three species). This diversity of rare plant species exceeds all other comparably-sized conservation areas in the state, regardless of habitat type. The only other conservation areas in Louisiana that rival the study area in this regard are two other *P. palustris* savanna conservation areas in southeastern Louisiana owned by The Nature Conservancy (Abita Creek Preserve and Talisheek Preserve).

The rarest species at the global scale are *Ruellia noctiflora*, *Calopogon multiflorus* and *Cirsium lecontei*, all considered imperiled throughout their range. The population of *R. noctiflora* at the Lake Ramsay Conservation Area appears to be the largest known in the state. *Calopogon multiflorus* is known in Louisiana only from this location. Following closely behind in global rarity are *Agalinis aphylla*, *A. filicauli*, *A. linifolia*, *Platanthera integra*, *Polygala hookeri* and *Xyris stricta*, all considered rare globally. Four of the species (*C. multiflorus, Carex turgescens, P. hookeri, A. aphylla*) are believed to be protected in Louisiana only at the Lake Ramsay Conservation Area.

Results of ongoing research

Species-area patterns

To describe diversity patterns, we collected data from nine sets of nested plots in the Lake Ramsay savanna (Fig. 2) in autumn 2000, using $n = 3$ replicates in each of three patches representing 6, 18, and 30 months elapsed since fire. Each set of plots had eleven nested circular quadrats from 0.25 to 200 m^2 in area. In this small area (only 1800 m^2 in total) we identified 139 species of plants representing 72 genera in 34 families. The most frequent genera encountered were *Dichanthelium* and *Rhynchospora*. The dominant species according to mean percent cover were all grasses, *Andropogon virginicus* (19%), *Dichanthelium dichotomum* (17%) and *Ctenium aromaticum* (10%).

On a log-log scale, species richness increases with area in an approximately linear fashion (Fig. 3). If linear regressions are applied to log-log transformed data, strong linear relationships are observed, with individual slopes ranging from 0.195 to 0.379 ($r^2 > 0.90$), although

Table 2. Rare plant species recorded from longleaf pine savannas of Lake Ramsay Conservation Area[1]. S= subnational scale, G = global scale, conservation status from 1 (critically imperiled) to 5 (demonstrably secure), double level rank indicates range of uncertainty in status.

Scientific name	Status
Agalinis aphylla[2]	S1G3G4
Agalinis filicaulis	S1G3G4
Agalinis linifolia	S1G3G4
Asclepias michauxii	S2G4G5
Calopogon multiflorus[2]	S1G2G3
Calopogon pallidus	S2G4G5
Carex turgescens[2]	S1S2G4G5
Cirsium lecontei	S2G2G3
Cleistes bifaria	S1G4
Ilex amelanchier	S2G4
Ilex myrtifolia	S2G5?
Lachnanthes caroliniana	S2S3G4
Lobelia amoena var. *glandulifera*	S1G4?
Lophiola aurea	S2S3G4
Panicum tenerum	S2S3G4
Pinguicula lutea	S2G4G5
Platanthera integra	S2G3G4
Polygala hookeri[2]	S1G3
Rhynchospora chapmanii	S2G4
Rhynchospora compressa	S1S2G4
Rhynchospora debilis	S1G4?
Ruellia noctiflora	S1G2
Sarracenia psittacina	S3G4
Scleria hirtella	S2G4G5
Tofieldia racemosa	S2S3G5
Xyris stricta	S1G3G4
Zigadenus leimanthoides	S1G4Q

[1] In addition, *Chasmanthium ornithorhynchum*, birdbill spike-grass, S2G4, occurs in the bayhead swamp;
[2] Currently known to be protected/conserved in Louisiana only at the Lake Ramsay Conservation Area.

the species-area slope did not change with time since burn (P = 0.101). The number of herbaceous species remained constant over the three burn treatments at around 35 species in 100 m^2, whereas the number of woody species doubled from 8 to 16 after 30 months without fire, as woody plants returned (Roth 2003).

Species frequency patterns

The high slopes found in the species-area analyses indicate that the species composition in these savannas is variable – most quadrats contain species not found in nearby quadrats. To quantify this heterogeneity, we next explored patterns of relative frequency, the distribution of these species across a set of quadrats. We collected percent cover data for each species in 50 1 m × 1 m quadrats from a wet savanna and another set of 50 quadrats from drier savanna.

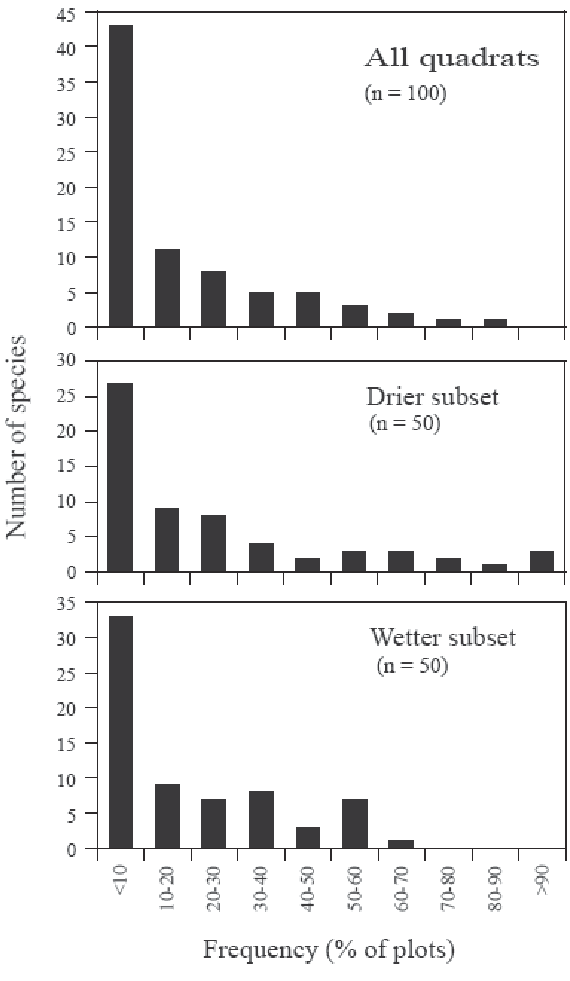

Fig. 4. The relative frequency of plant species in wet *Pinus palustris* flatwoods for drier sites (n = 50 1 m × 1 m quadrats), adjoining wetter sites (n = 50 1 m × 1 m quadrats), and the two combined. In each case, a majority of the plant species occurred in less than 10% of the quadrats sampled.

Dominants differed from those areas sampled for the species-area study. In the drier subset *Scleria ciliata, Ctenium aromaticum*, *Dichanthelium leucothrix* and *Muhlenbergia capillaris* were the most frequent, while in the wetter subset of quadrats, the four dominants were *Scleria ciliata*, *Rhynchospora pusilla*, *R. plumosa* and *Lobelia floridana*.

When the subsets of quadrats were combined (n = 100), more than half of all species (43/79 = 54%) occurred in less than ten percent of the quadrats (Fig. 4). When the data set is subdivided, this preponderance of infrequent species is still evident in both sites, although it is greater in the wetter site (33/68 = 48%) than in the drier site (27/62 = 43%). Further, in the wetter site, the distribution appears truncated on the right, no species occurring in more than 70 % of the quadrats.

Competition as a possible mechanism

To test for a competitive effect of grasses on species composition and diversity, we created a series of experimental plots in savannas at nearby Camp Whispering Pines (Fig. 1, Table 1) when the area was still smoldering from a recent burn (Roth 2003). Two sets of 20 quadrats (1 m × 1 m) were arranged in a 4 plot × 5 plot rectangle, one set in a moist site, and the other in a dry site. Dominant species at both sites were *Andropogon virginicus* and *Dichanthelium* spp. In half the plots at each site, selected at random, we applied a glyphosate herbicide to individual shoots of *A. virginicus*, and re-applied it periodically throughout the experiment to ensure that *A. virginicus* did not re-establish. Species presence and percent cover were recorded in each plot for two years.

Using repeated measures analyses, we found no difference in species richness between the removal and the control plots at either site over two growing seasons (Roth 2003). Mean total plant cover was slightly lower in the removal plots than in the control plots over the course of the study (mean cover: 56.9% and 69.7%, respectively), but this simply reflected the continued removal of shoots of *A. virginicus* as they appeared. Using Mantel tests, we could not detect significant differences in species composition between control and treatment quadrats in the dry site ($0.11 < P < 0.50$) nor in the moist sites ($0.06 < P < 0.43$). One might wonder if differences could be found at the level of functional groups rather than species, but after sorting species into 13 functional groups, we again found no differences between treatments and control using Mantel tests.

Discussion

Patterns of plant diversity

Plant species composition and richness were within the range of other studies of pine savannas (e.g. Walker & Peet 1983; Kirkman et al. 2001; Glitzenstein et al. 2003), all of which report extremely high diversity, up to 40 species in a square meter (exceeding all other values yet reported for the western Hemisphere) and up to 140 species in 1000 m^2 (the highest values recorded in the temperate Western Hemisphere, Peet & Allard 1993). The steep slopes found in our sites at Lake Ramsay are therefore noteworthy in the context of herbaceous vegetation, but not unlike other *Pinus palustris* savannas on the coastal plain. It is further evidence of the botanical value of the Lake Ramsay savanna and the richness of savannas in southeastern Louisiana.

Most of the plant diversity consisted of species that were relatively uncommon at the local scale, that is, found in less than 1/10th of the quadrats sampled. Similar frequency patterns have been reported from restored savannas in Georgia (Kirkman et al. 2001), and in virgin *P. palustris* forests in southeastern Louisiana (Penfound & Watkins 1937). We were particularly interested in assessing the possible occurrence of a bimodal frequency distribution in the relative frequency of species. This pattern has been reported from other herbaceous plant communities (Raunkiaer 1934; Collins & Glenn 1990; Pärtel et al. 2001), and interpreted as evidence for core and satellite species (*sensu* Hanski 1982; Collins & Glenn 1990; Pärtel et al. 2001). There is no evidence of such a pattern in pine savannas, whether wet, moist, or dry.

As with most savannas, grasses were a common group in the study areas. Examples included *Andropogon virginicus, Panicum dichotomum, Ctenium aromaticum, Dichanthelium acuminatum* and *Muhlenbergia capillaris*. Sedges such as *Scleria ciliata*, *Rhynchospora pusilla*, *R. plumosa* and *R. oligantha* co-dominated in wetter sites. Studies in other habitats indicate that grasses could control the diversity of other herbaceous plant species (e.g. Goldsmith 1973a; Grime 1980; Gurevitch & Unnasch 1989; Carson & Pickett 1990; Jutila & Grace 2002). The results of our two-year removal experiment were, however, inconclusive. This is a short time for competitive effects to exert an influence on long-lived perennials. Only more, and longer, field experiments will settle this question.

Many of the 28 regionally rare species have traits that suggest they are relatively weak competitors. *Pinguicula lutea* and *Chaptalia tomentosa* are rosette species, and these genera are weak competitors in many other vegetation types including cliffs (Goldsmith 1973 a, b, 1978), grasslands (Grime 1980; Keddy et al. 2002) and shorelines (Wilson & Keddy 1986; Moore et al. 1989). *Polygala hookeri* and the three *Agalinis* species are annual plants, and annuals typify fugitive species that depend upon the formation of gaps (e.g. Grime 1977; Platt & Weiss 1977; Pickett 1980). In the case of fire-sustained communities, such gaps are likely created by varying intensities of fire. *Agalinis aphylla, Calopogon multiflorus, C. pallidus* and *Cleistes bifaria* have relatively small leaves, consistent with species that have minimal competitive effect upon neighbours (Wilson & Keddy 1986; Gaudet & Keddy 1995). Other savanna plants including *Drosera capillaris* (Brewer 1998a, 1999a) and *Sarracenia alata* (Brewer 1999b) have regeneration stimulated by removal of grasses and litter.

A mechanistic hypothesis: fugitive and peripheral species

Our working hypothesis is that the majority of the plant diversity is comprised of species that must escape competition from canopy-forming grasses. There may be at least two rather different means of doing so: fugitive and peripheral.

Fugitive species

One might speculate that many of the less frequent species are fugitive species (Horn & MacArthur 1972), interstitial species (Grubb 1986), or ruderal species (Grime 1977) that colonize small patches that arise among the grasses, or larger patches that arise when the grasses are burned. The fugitive concept is well-illustrated by the species that occupy small badger mounds in prairies (Platt & Weiss 1977), but it can be extended to the much larger gaps created by storms, drought, fire and or flooding, where buried seed banks often play a major role in recolonization (Pickett & White 1979; Leck et al. 1989). Thus, species can disperse in space or in time. Those that disperse in time usually occur as reserves of buried propagules, dispersing forward in time until a new disturbance temporarily removes the dominant species and allows regeneration. Seed banks are important in many kinds of herbaceous vegetation, but their densities in wetlands are enormous (van der Valk & Davis 1978; Leck et al. 1989; Keddy 2000). Further, many familiar coastal plain genera such as *Drosera*, *Eriocaulon*, *Juncus*, *Panicum, Rhexia*, and *Xyris* have significant seed banks further north (e.g. Keddy & Reznicek 1982; McCarthy 1987; Schneider 1994) but research has only just begun to examine seed bank dynamics in *Pinus palustris* systems of the southeast. Sutter & Kral (1994) report these genera, as well as *Rhynchospora*, from seed banks in pond cypress savannas; Jutila & Grace (2002) showed that experimentally created gaps stimulate germination of plants in coastal prairies. Overall, one might turn the logic around and suggest that if large seed banks of certain species were detected, that would suggest that natural disturbance plays an important role in their persistence.

Peripheral species

One could also hypothesize that the infrequent and rare species may occupy sites with extreme conditions, such as dry patches or wet depressions, that better competitors are unable to tolerate. In the broadest context, we could even think of such sites as taking the concept of gaps to its logical extreme – rock outcrops, or wet depressions, might be gaps with negligible rates of creation, but very long persistence. These habitats may produce such extreme constraints that those species capable of dominating the more desirable adjoining sites simply cannot survive. Depressions near our study plots at the Lake Ramsay savanna had few plants, and seemed to offer refuges for *Lachnanthes caroliniana* and *Xyris laxifolia*. Species restricted to extreme sites are termed 'peripheral species' (Keddy 1990; Wisheu & Keddy 1992) rather than 'fugitive species', placing more emphasis upon persistence of stress tolerance (*sensu* Grime 1977) than recurring colonization.

Conclusions

Remnants of *P. palustris* flatwood savannas and upland *Pinus palustris* forests still occur in southeastern Louisiana. Small areas are protected and under active restoration. Field work is still needed, particularly on private land, and in the west of the region of Fig. 1. Large areas could be restored with appropriate management. Lake Ramsay is the best example of *P. palustris* flatwood savanna in Louisiana. It is particularly species rich, and has been the principal study site for our research on controls of herbaceous plant diversity in savannas.

The factors that maintain plant diversity in pine savannas are poorly understood. We know that shading from woody plants can eliminate the local herbaceous flora in these savannas. Once a regular fire regime eliminates most woody plants, the interactions among herbaceous species should become more important. The importance of grasses in controlling plant diversity is well-documented in other habitats, and while we strongly suspect the same to be the case in *P. palustris* savannas, this is yet to be substantiated by research. There are at least two hypothetical routes for escaping this hypothesized competition: the fugitive and the peripheral strategies, but their relative importance has not yet been evaluated. From the scientific perspective, future field experiments and studies of life history traits will be necessary to evaluate the mechanisms maintaining plant diversity. From the management perspective, the continued acquisition of land and re-establishment of natural fire regimes remains a high priority.

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