

# Ground cover recovery patterns and life-history traits: implications for restoration obstacles and opportunities in a species-rich savanna

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## Summary

**1** We identified species with low re-colonization potential, which could be used as indicators of recovery of species-rich pine savannas, by comparing the ground-cover flora of a 64-year-old slash pine plantation (recovery site) with that of a nearby natural longleaf pine savanna (reference site). We also determined life-history traits that were useful predictors of recolonization potential.

**2** The high floristic overlap in species between reference and recovery sites and similar species richness at scales  $\geq 10 \text{ m}^2$  suggests that substantial vegetation recovery occurred over the 65-year period. However, for areas  $< 10 \text{ m}^2$  the lower species packing in the recovery sites indicates that coexistence of a high number of species at small scales is dependent on local dispersal and establishment, and may take much longer to achieve.

**3** The absence, or near absence, of some species from the recovery site, even after 65 years, suggests that some species may be particularly vulnerable to disturbance and may re-establish infrequently, if ever. Several dispersal distance-restricted species were identified that require active reintroduction. While no particular guild of species was a strong indicator of recovery in this study, we identified a group of species that assess the absence of or the degree of recovery from, prior soil disturbance.

**4** Local dispersal appears to be an important factor structuring species richness patterns in pine savannas. Limitations of dispersal distance in some species, particularly those with gravity and ant-dispersal mechanisms, represent an obstacle to passive restoration that can only be overcome either by introduction of propagules in the restoration process or by allowing for longer periods of recruitment.

**5** This study demonstrates a method for identifying a suite of species that may be unsuccessful at recolonization. The method would be applicable to numerous degraded ecosystems, particularly similar species-rich savannas, grasslands and forests.

*Key-words:* biodiversity, dispersal limitation, indicator species, longleaf pine, myrmecochory, recolonization, reference sites, seed dispersal, species area, species richness

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## Introduction

The life histories of established and colonizing species influence the rate of succession following disturbance of plant communities, especially in understorey and ground cover strata (Brewer 1980; Gross 1987; Kindscher 1994; McLachlan & Bazely 2001). Mechanisms of seed dispersal, flowering phenology, growth form and persistent soil seed banks have been shown to influence post-disturbance changes in species richness in some

forest and prairie communities (Tilman 1997; Eriksson & Jakobsson 1998; McLachlan & Bazely 2001). Thus, elucidating the life-history traits that restrict persistence or species recruitment following soil disturbance is a primary step in developing appropriate restoration strategies, including reintroduction (Pyke & Archer 1991; Pywell *et al.* 2003). Furthermore, the presence of species that are vulnerable to disturbance, or of groups of such species, can be used as an indicator of recovery of restored sites moving towards the composition of less disrupted, high-quality reference sites (Kindscher 1994; Masters 1997; Lindenmayer 1999).

This approach may be useful in understanding the ecology of recovery of species-rich ecosystems, such as the geographically extensive temperate savannas. The natural resources of many of these tree- and grass-dominated communities have been intensively utilized for grazing, livestock production and wood products for many centuries (McPherson 1997; Anderson *et al.* 1999). Particularly during the last century, overhunting and removal of natural herbivores, agriculture, urbanization and fire suppression in natural savannas have resulted in serious degradation or reduction to a small percentage of their former area with negative impacts on biological diversity at regional and continental scales (Archer 1989; Leach & Givnish 1996; McPherson 1997; Scholes & Archer 1997; Anderson *et al.* 1999).

Longleaf pine savannas are an imperilled ecosystem (Noss 1989), in which native ground cover has a key role in ecosystem composition and function. The flora of these fire-maintained communities is characterized by a sparse canopy of *Pinus palustris* Mill., a dominance of perennial grasses and forbs and an exceptionally large number of species compared with other temperate ecosystems (Bridges & Orzell 1989; Peet & Allard 1993). The diverse flora, which has a density of up to 40–50 species m<sup>-2</sup> (Walker & Peet 1988; Kirkman *et al.* 2001), is restricted to the ground layer. This ground layer also serves as fine fuel for the frequent fires needed to maintain longleaf pine savannas. The restoration and long-term persistence of this disturbance-dependent ecosystem therefore necessitates the re-establishment of ground cover structure and composition (Hendricks *et al.* 2002), as well as prescribed burning. While considerable work has been undertaken to document the species richness of such native plant communities of the south-eastern US Coastal Plain (Peet & Allard 1993; Drew *et al.* 1998) and their precipitous decline in area (only 2–5% of its original extent of this ecosystem remains intact and these have numerous rare, endemic species (Noss 1989; Ware *et al.* 1993)), no work has shown the extent to which these communities can recover over time, or the species life-history features, if any, that are consistent with successful re-establishment of individual species.

Many plant species in longleaf pine-wiregrass savannas are long-lived perennials. Although little is known of the levels of seedling recruitment, and evidence regarding persistence of soil seed banks is lacking, it is likely that the processes of species establishment operate over decades to centuries, as in other grassland systems (Franzen & Eriksson 2001; Morgan 2001). For the characteristically fragmented landscapes of the south-east USA today, seed dispersal may be a particularly important influence on patterns of species abundance and distribution in longleaf pine ecosystems at both local and landscape scales (Kiviniemi & Eriksson 1999). Consequently, quantification of the number of species that assemble in an area as time since disturbance increases, i.e. species packing (Kinzig *et al.* 1999), can suggest factors influencing the development and persistence of diversity in this plant community, while revealing plausible timelines for recovery.

Our objective is to determine whether life-history traits are useful predictors of recolonization potential by comparing the ground cover of a recovering site (a 64-year-old slash pine (*Pinus elliottii* Engelm.) plantation) with that of reference sites (nearby natural longleaf pine (*P. palustris* Mill.) savanna) that represent the restoration goal. Slash pine is similar morphologically and ecologically to longleaf pine, but in natural stands, it occurs in more mesic conditions because it is less tolerant of fire during the first several years following establishment (Abrahamson & Hartnett 1990). It has been extensively planted for pulpwood production throughout the former range of longleaf pine and the plantations are usually harvested approximately 20–25 years after planting. Our study site provides a unique setting in which to identify ground-cover species that are most likely to require reintroduction to a restoration site as those that are absent despite 65 years of natural re-establishment processes. Following planting, the 88-ha stand has undergone re-establishment of herbaceous/understorey vegetation within a landscape in which propagules of species found in the fire-maintained longleaf pine savannas are potentially present. This is one of the oldest pine plantations in the southern USA, and its early history predates the invasion of the imported red fire ant, which has decimated much of the native ant fauna (Carroll & Hoffman 1997). Consequently, the site may have partially escaped disruption of natural seed dispersal. The surrounding landscape is one of the few remaining intact areas of longleaf pine forest that once dominated the south-eastern US Coastal Plain and is currently a high restoration priority. Thus, the planted slash pine stand serves as a model to examine the passive recovery of disturbed ground cover over a known period since disturbance.

We address the following questions. (i) How do species–area relationships differ between sites with different disturbance histories, i.e. recovery and reference sites? (ii) Are dispersal distance-limited traits, specific growth form or flowering phenologies associated with species' capacity to recolonize following disturbance? (iii) Within a growth form guild, which species are conservative indicators of relatively undisturbed systems?

## Methods

### STUDY SITES

The recovery and reference study sites were located on Ichauway, an 11 600-ha privately owned reserve of the J.W. Jones Ecological Research Center, in the Coastal Plain of south-western Georgia (Baker County). The recovery site, an 88-ha slash pine plantation established in 1939, is in the initial stages of conversion to a diverse longleaf pine forest. The earliest available aerial photography (1938, black and white, USDA 371–21) indicates that this site was in cultivation prior to tree planting. This evidence is substantiated by the absence of *Aristida beyrichiana* Trin. & Rupert., or *A. stricta* Michx. (the

two species may not be taxonomically distinct (Kesler *et al.* 2003)), perennial grasses, commonly known as wiregrass, which decline with fire exclusion and excessive soil disturbance (Myers 1990). With the exception of periodic canopy thinning, the vegetation represents a 65-year-old successional stage since tree planting in an agricultural field. Based on aerial photographic interpretations, this stand of timber has been thinned twice since planting, between 1953 and 1957 (1953, black and white, USDA 2M-108; 1957 black and white, USDA 5T-18), and between 1962 and 1968 (1962 black and white, IDD-122, ASCS 3–63 DC; 1968 black and white IKK-147, ASCS 1–69 DC). At the time of this study, the stand had a widely spaced canopy with an average basal area of 16 m<sup>2</sup> ha<sup>-1</sup> and tree density of 123 stems ha<sup>-1</sup>. The pine plantation had been prescription-burned irregularly at approximately 5–8-year intervals (L. Neel, personal communication) and, as a result of infrequent fire, the stand has a mid-storey composed of hardwood species such as *Quercus nigra* L., *Q. virginiana* Mill., *Sassafras albidum* (Nutt.) Nees. and *Diospyros virginiana* L. Ground cover includes numerous grass and forb species.

Twelve reference sites of frequently burned (return interval of 2–4 years) longleaf pine-wiregrass vegetation were selected from a group of sites identified by a site classification of Ichauway based on landscape position, soil type and vegetation (Goebel *et al.* 2001). Vegetation of the reference sites has been managed with this fire frequency for over seven decades to promote bobwhite quail habitat, and for a long period prior to European settlement was presumably burned with a similar frequency, with human- or lightning-ignited fires (Ware *et al.* 1993). The sites are characterized by the widely spaced, single dominant overstorey species, *Pinus palustris*. A mid-storey is generally absent, with the exception of patches of young longleaf pines. Dense ground cover at these sites is dominated by the perennial grass, *Aristida stricta*, with numerous other perennial grasses and forbs as interstitial species (Goebel *et al.* 2001).

#### STUDY DESIGN, VEGETATION SAMPLING AND SPECIES CHARACTERIZATIONS

This study was designed as a component of a long-term restoration project with the goal of converting the slash

pine plantation to a multi-aged longleaf pine forest with a diverse ground cover, sustainable with prescribed fire (Kirkman & Mitchell 2002). Prior to restoration canopy thinning in 1999, and planting of longleaf pine seedlings, we randomly located 60 plots (20 × 20 m) in the slash pine forest (recovery site). Similar plots for vegetation sampling were established at 12 reference locations.

We sampled vegetation in each 20 × 20 m plot using a nested sampling design (adapted from Peet *et al.* 1998) to obtain species area curves and vegetation abundance measures. Each plot consisted of four 10 × 10 m modules. Within each module, vegetation was sampled in nested units of area 0.1 m<sup>2</sup>, 1 m<sup>2</sup> and 10 m<sup>2</sup>. We repeated this nested approach twice within each module, with the sample initiation point located in two different corners of the plot (eight corners sampled per plot). All species present in each module were recorded. We sampled vegetation of the recovery plots in summer 1998 following a dormant season burn that year. Vegetation of three reference plots had been sampled in summer 1993 and the remainder was sampled in summer 1998. Even though some of the reference sites were sampled in different years, these data are valid for comparison of species richness per unit area, and frequency of occurrence of species, with that of the recovery sites because the species-rich flora is composed primarily of perennial species (Drew *et al.* 1998), with little year-to-year turnover (Kirkman *et al.* 2001). We have measured this plant community in multiple seasons and multiple years, finding close congruity in species composition (Kirkman *et al.* 2001).

Species nomenclature was based on Wunderlin (1998) with the exception of *Chamaecrista deeringiana* Small & Pennell, which is recognized at the specific level by Isley (1990). A few species were combined for analyses due to difficulties in consistently identifying vegetative individuals (Table 1). To characterize species life-history traits, we assigned a guild designation and dispersal distance category to each species. The classification of life-form guilds was modified from one developed for tallgrass prairie (Kindscher 1994), whose structure and function is similar to that of the longleaf pine ecosystem (Kirkman *et al.* 2001). These guilds included C<sub>3</sub> photosynthetic pathway grasses, C<sub>4</sub> photosynthetic pathway grasses, spring/summer perennial forbs, fall perennial forbs, legumes, woody species, ferns and annuals.

**Table 1** List of species combined at time of data collection due to identification constraints of vegetative plant material

Taxon used in analyses	Taxa included
<i>Ambrosia artemisiifolia</i>	<i>A. psilostachya</i> DC., <i>A. artemisiifolia</i> L.
<i>Andropogon virginicus</i>	All species of <i>Andropogon</i> , <i>Schizachyrium scoparium</i> (Michx.) Nash
<i>Anthraenantia villosa</i>	<i>A. villosa</i> (Michx.) Beauv., <i>A. rufa</i> (Ell.) Shult.
<i>Chrysopsis mariana</i>	<i>C. gossypina</i> (Michx.) Ell., <i>C. mariana</i> (Michx.) Ell.
<i>Galium pilosum</i>	<i>G. pilosum</i> Ait., <i>G. hispidulum</i> Michx.
<i>Gymnopogon ambiguus</i>	<i>G. ambiguus</i> (Michx.) BSP., <i>G. brevifolius</i> Trin.
<i>Pityopsis graminifolia</i>	<i>P. graminifolia</i> (Michx.) Nutt., <i>P. adenolepis</i> (Fern.) Semple
<i>Stylisma humistrata</i>	<i>S. humistrata</i> (Walt.) Chapman, <i>S. patens</i> (Desr.) Myint
<i>Vaccinium myrsinites</i>	<i>V. myrsinites</i> Lam., <i>V. darrowii</i> Camp

Guild designation was determined from floristic manuals and lists of  $C_3$  and  $C_4$  species (Downton 1975; Raghavendra & Das 1978; Hakansson 1995). Dispersal distances have been demonstrated to differ with dispersal agents; seeds with structures that facilitate wind or vertebrate dispersal have the greatest dispersal distances, whereas explosively dispersed, gravity-dispersed or ant-dispersed seed have the shortest (Stamp & Lucas 1990; Willson 1993). We assumed that plants with fleshy fruits are vertebrate-consumed, seeds with protrusions for adherence are carried externally by vertebrates, seeds with adaptations (such as plumose pappus bristles) permitting seeds to be airborne are wind-dispersed, seeds with elaiosomes are ant-dispersed, ballistically dehiscing fruits are explosive, and all others are gravity-dispersed. Such a classification of species by their major dispersal agent is an over-simplification because many species may have multiple dispersal agents. Because seeds of several species with ballistically dehiscing fruits are frequently ant-dispersed, we combined this category prior to data analyses. The dispersal agents were then classed as either restricted in distance (gravity, ant), or unrestricted (wind, vertebrate-carried and vertebrate-consumed), following McLachlan & Bazely (2001).

#### DATA ANALYSES

Species richness was determined as the number of species occurring in each of the nested levels within each module and summed cumulatively for the total vegetation sampling plot. Values for the nested units of area  $< 100 \text{ m}^2$  were obtained as a mean of values from the two corners of each module. Values for area units  $\geq 100 \text{ m}^2$  were obtained by cumulative addition of species in each module. This process was computed iteratively for each possible starting module and then averaged to obtain the mean species richness for each area within a plot. Differences in mean species richness between reference plots and recovery plots were examined using a one-way analysis of variance for each unit of area.

We used multidimensional scaling (MDS) to present differences between reference and recovery sites with respect to overall species composition. For these analyses, we used the Jaccard Index and the city-block distance as measures of plot distance for presence/absence of species and frequency of each species, respectively. An interval-level analysis (SAS PROC MDS LEVEL = INTERVAL, SAS version 9.0, SAS Institute, Cary, NC, USA) was performed to preserve the original index or species frequencies in the analyses that allowed for later correlation analyses. We then superimposed a minimum spanning tree (Gower & Ross 1969), which was computed using all three dimensions obtained from the resulting analyses on the two-dimensional MDS plots. The minimum spanning tree connects nearest-neighbour plots as determined by MDS, enabling the presentation of high-dimensional information in two dimensions. We computed the correlation between presence-absence of species, or frequency, with each of the MDS solution

dimensions (axes). We represented these correlations as vectors in a graph to show dominant species associated with each dimension and to aid with the interpretation of the scaling results.

To examine the relationship between capacity to recolonize and dispersal mechanism, we developed a randomization test procedure (Good 1994). We based the test on the idea that if a dispersal mechanism is unrelated to site, then assignment of each species to a site based upon its greater relative frequency should result in the same proportion of species with a particular dispersal mechanism (i.e. dispersal mechanism would be unrelated to the assignment). Thus, a preponderance of species with a particular dispersal mechanism assigned to either of the sites (recovery vs. reference) suggests that the dispersal mechanism is associated with that site, and therefore reflects its capacity to recolonize a disturbed site, even though the overall frequency differences for some of the species may be quite small. Those species that had a higher occurrence in the reference site than in the recovery site were considered to have a low capacity to recolonize, or were 'vulnerable to disturbance'. Those exhibiting equal or greater occurrence in the recovery site were considered 'resilient to disturbance' (*sensu* McLachlan & Bazely 2001).

We first estimated species relative frequency of occurrence as the proportion of  $1\text{-m}^2$  nested subplots in which a species occurred for the reference plots ( $n = 96$ ) and recovery plots ( $n = 480$ ), and assigned species to site based on where they had greater relative frequency. Species that occurred less than twice on both sites were excluded from this analysis. We then used a likelihood ratio chi-square test statistic computed from the  $2 \times 2$  contingency table of dispersal mechanism vs. vulnerability-resilience class. The Monte Carlo randomization test procedure was used to calculate a  $P$ -value associated with the test statistic, to control for the fact that the species abundances are likely to be correlated (sampled together on the same plots). To simulate the null hypothesis of no vulnerability-resilience effect, plots were randomly re-assigned between reference and recovery sites, maintaining the original sample sizes, and then vulnerability-resilience was re-computed for each species using the new site assignments. This randomization process was performed 9999 times for each specific dispersal category (five categories of dispersal agents) plus the distance-restricted dispersal category (ant and gravity vs. others combined). The test statistic was computed for the original data plus the 9999 randomized data sets. The original test statistic was then ranked among the 10 000 total values (9999 + original) to obtain the  $P$ -value of the test statistic (Good 1994). If the site on which a plot was sampled has nothing to do with the dispersal characteristic, then the test statistic would be similar to those for which the site labels are simply randomized. If dispersal differs, then the test statistic should be an extreme value when ranked with the randomized data. Statistical significance was determined at  $P = 0.05$ . We examined the relationship



between life-form guild categories and vulnerability-resilience to disturbance with the same Monte Carlo test procedure. Analyses were performed using SAS (SAS version 9.0, SAS Institute) software.

To depict relative vulnerability to disturbance, we calculated a vulnerability score for each species similar to that developed by McLachlan & Bazely (2001). We defined vulnerability score as the proportional frequency of occurrence in reference sites divided by the proportional frequency of occurrence in recovery sites; the higher the ranking of this score for a species, the more vulnerable it was to disturbance.

## Results

Differences in mean species richness between recovering and reference ground-cover vegetation were scale-dependent (Fig. 1). For larger sample areas ( $\geq 10 \text{ m}^2$ ), differences in the number of species occurring between recovery sites and reference sites were not significant ( $F < 3.39$ ,  $P > 0.05$ ), but for smaller areas, recovery sites were much less species rich ( $0.1 \text{ m}^2$ ,  $F = 34.9$ ,  $P < 0.0001$ ;  $1.0 \text{ m}^2$ ,  $F = 21.67$ ,  $P < 0.0001$ ). A total of 218 species were recorded, of which 185 occurred in recovery sites and 134 in reference sites. Most of the species that were unique to the recovery sites ( $n = 73$ ) were woody species although the other species included weedy annual forbs and C3 grasses.

Species composition was also strongly affected by disturbance history, both for presence/absence of species and species abundance patterns (frequency). MDS analysis represented the plots well in three-dimensional space (MDS badness of fit = 0.05). Plots from recovery and reference sites are well separated from each other in MDS ordination space, indicating greater dissimilarity in composition between the site types than between plots within either recovery or reference sites (Fig. 2).

Of the species sampled, 88 were classified as vulnerable to disturbance and 130 were classed as resilient based on proportional frequencies in reference vs. recovery sites (Fig. 3). Nearly half of the species (46%) were characterized by gravity dispersal. Of the gravity-dispersed species, approximately equal numbers of species occurred more frequently in reference as did in recovery sites (Fig. 4). Less than 20% of the species were represented by each of the other dispersal agents (wind = 17%, animal consumed = 17%, animal carried = 11%, ant = 8%). Of the species that were unique to reference sites, 80% were in the restricted-distance dispersal group (Fig. 4, Table 2). In contrast, 60% of the species more common to, or restricted to, recovery sites, were in the non-restricted-distance dispersal group (wind, vertebrate-carried or vertebrate-consumed) (Fig. 4).

Both the vulnerability and resilience classes of species were significantly associated with particular dispersal agents. A positive association was found between species vulnerable to disturbance and both types of distance-restricted dispersal agents (ant- and gravity-dispersed combined,  $\chi^2 = 18.05$ ,  $P < 0.01$ ) and individually for both dispersal mechanisms (ant-dispersed,  $\chi^2 = 5.53$ ,  $P < 0.05$ ; gravity-dispersed,  $\chi^2 = 8.7$ ,  $P < 0.05$ ). In contrast, animal-consumed and animal-carried seed dispersal were significantly associated with resilience ( $\chi^2 = 9.25$ ,  $P < 0.05$ ;  $\chi^2 = 10.9$ ,  $P < 0.01$ ). The proportion of wind-dispersed species was not related to the vulnerability-resilience class of the species ( $\chi^2 = 0.01$ ,  $P > 0.05$ ).

The resilient class of species was only significantly associated with woody species ( $\chi^2 = 11.43$ ,  $P < 0.05$ ;  $\chi^2 < 5$ ,  $P > 0.05$  for all other life-forms). The assemblage of highly vulnerable species (i.e. those unique to reference sites) included all life-form types except annuals, and was equally represented by species with summer and fall phenologies (Table 1).

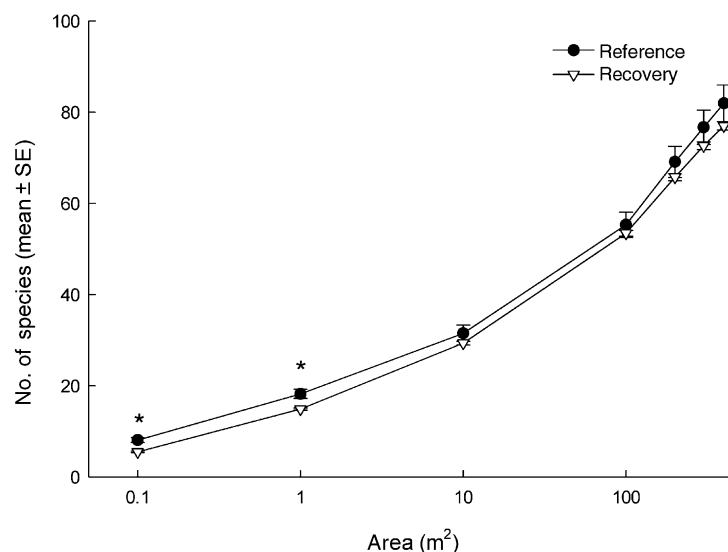
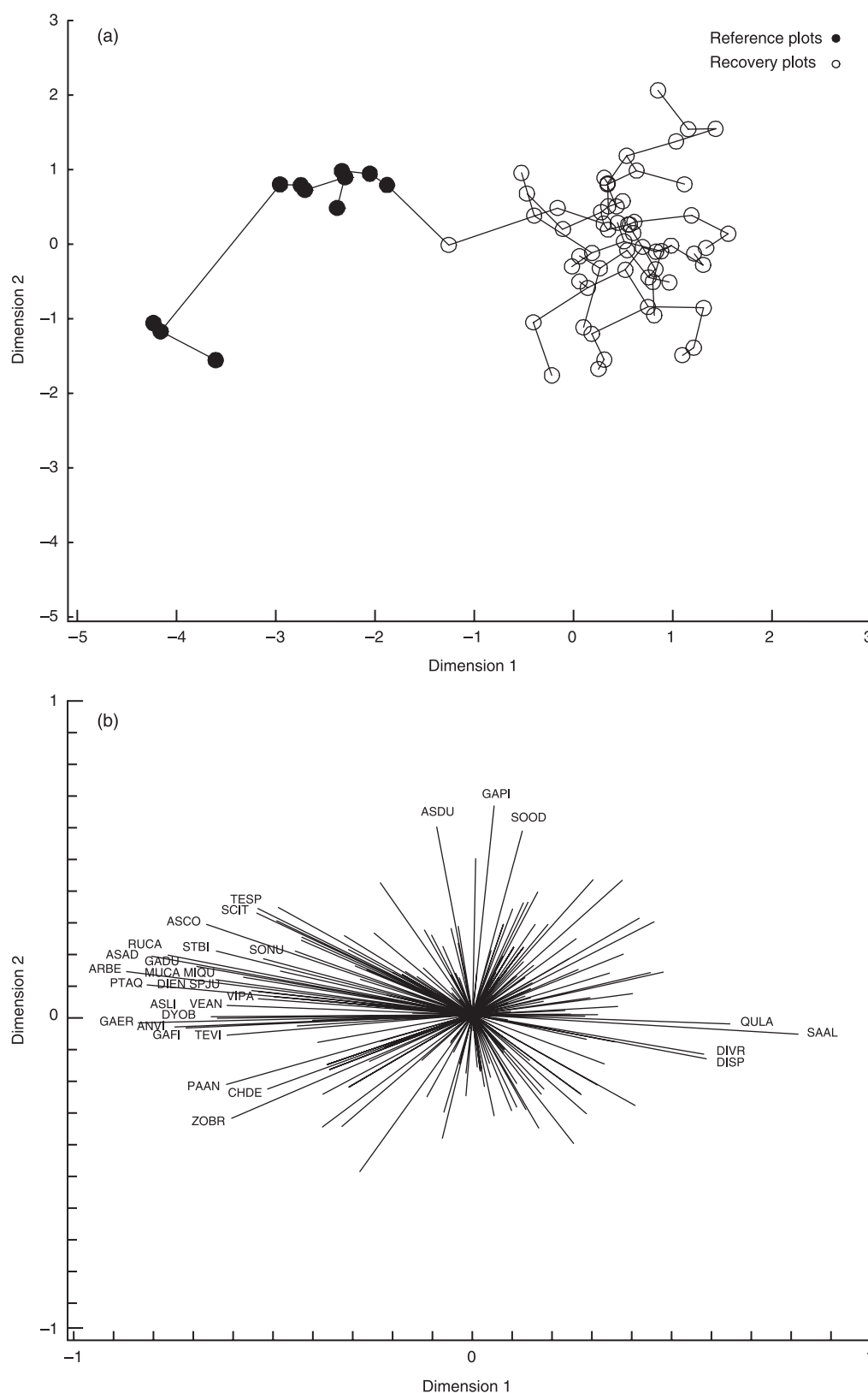
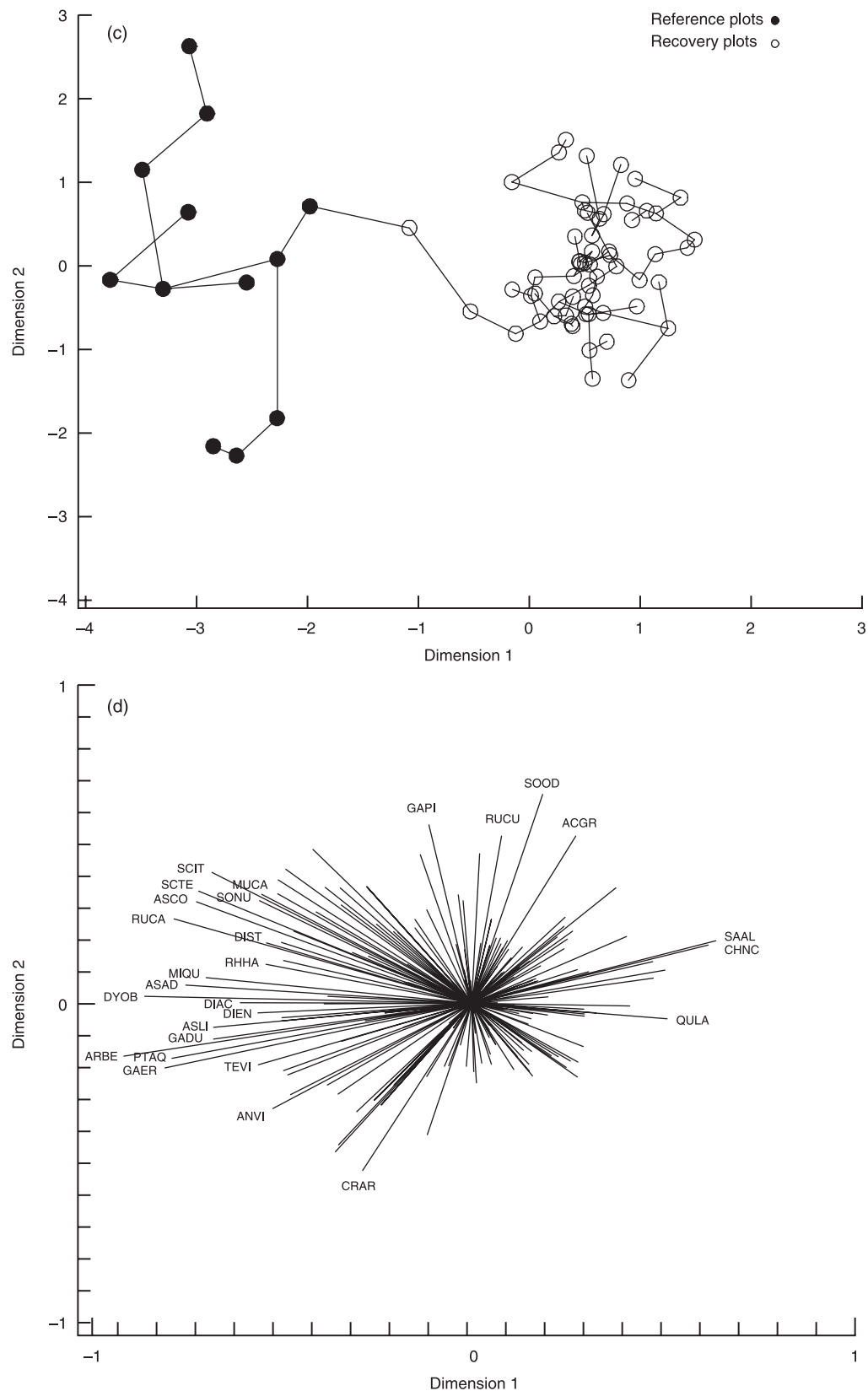


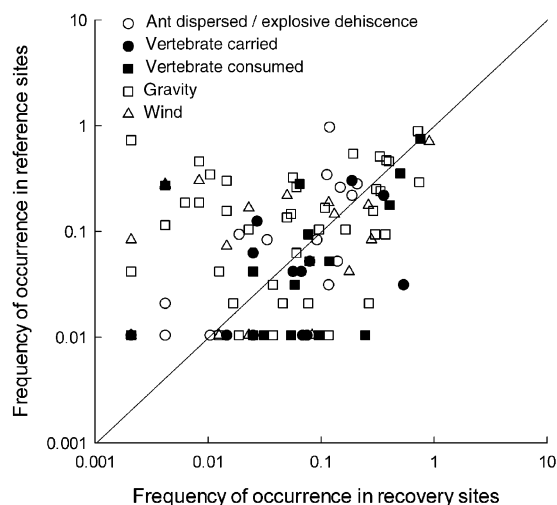
Fig. 1 The relationship between species richness and sampling area. Data points with \* indicate a significant difference (at  $P = 0.05$ ) in species richness between reference and recovery plots.



**Fig. 2** Multi-dimensional scaling (MDS) results for presence-absence and frequency of occurrence data. (a) MDS based on the Jaccard index of species presence-absence indicating reference and recovery sites with superimposed minimum spanning tree computed from the three-dimensional solution. (b) Vectors indicating the correlations between presence-absence of each species with axes from the MDS solution in (a). Species labeled are highly correlated with axes 1 or 2 or both ( $r > 0.5$ ). (c) MDS based on the city-block distance of frequency of occurrence of species indicating reference and recovery sites with superimposed minimum spanning tree computed from the three-dimensional solution. (d) Vectors indicating the correlations between presence-absence of each species with axes from the MDS solution in (c). Species labelled are highly correlated with axes 1 or 2 or both ( $r > 0.5$ ). Species codes: ACGR – *Acalypha gracilens*, ANVI – *Anthraenantia villosa*, ARBE – *Aristida beyrichiana*, ASAD – *Aster adnatus*, ASCO – *Aster concolor*, ASDU – *Aster dumosus*, ASLI – *Aster linariifolius*, CHDE – *Chamaecrista deeringiana*,



CHNC – *Chamaecrista nictitans*, CRAR – *Croton argyranthemus*, DIAC – *Dichanthelium aciculare*, DIEN – *Dichanthelium ensifolium* var. *unciphellum*, DISP – *Dichanthelium sphaerocarpon*, DIVR – *Diospyros virginiana*, DYOB – *Dyschoriste oblongifolia*, GADU – *Gaylussacia dumosa*, GAER – *Galactia erecta*, GAFI – *Gaura filipes*, GAPI – *Galium pilosum*, MIQU – *Mimosa quadrivalvis*, MUCA – *Muhlenbergia capillaris*, PTAQ – *Pteridium aquilinum*, QULA – *Quercus laurifolia*, RHHA – *Rhynchospora harveyi*, RUCA – *Ruellia caroliniensis*, RUCU – *Rubus cuneifolius*, SAAL – *Sassafras albidum*, SCIT – *Scutellaria integrifolia*, SCTE – *Schizachyrium tenerum*, SONU – *Sorghastrum nutans*, SOOD – *Solidago odora*, SPJU – *Sporobolus junceus*, STBI – *Stylosanthes biflora*, TESP – *Tephrosia spicata*, TEVI – *Tephrosia virginiana*, VEAN – *Vernonia angustifolia*, VIPA – *Viola palmata*, ZOBR – *Zornia bracteata*.



**Fig. 3** Proportional frequency of occurrence of species in reference and recovery sites. The diagonal line marks the null hypothesis that a species' proportional frequency is the same in the two sites. Species above the line are more frequently associated with reference sites (= vulnerable to disturbance); species below the line are more frequently associated with recovery sites (= resilient to disturbance). Data are plotted in log–log space.

## Discussion

Our findings regarding the presence, absence and abundances of various plant species answer several questions about post-disturbance processes and recovery in this vegetation type. Importantly, the floristic overlap between reference and recovery sites, and similar species richness at scales  $\geq 10 \text{ m}^2$  suggest that substantial vegetation recovery has occurred over the 65-year period. However, for areas  $< 10 \text{ m}^2$ , the notably lower species packing in the recovery site indicates that coexistence of a high number of species at small scales probably takes longer to achieve. Moreover, the absence, or near absence, of some species from the disturbed site even after 65 years, suggests that they may be particularly vulnerable to disturbance and may re-establish infrequently, if ever. Our finding of a positive association between vulnerability and ant and gravity dispersal is consistent with other patterns of recovery and dispersal limitations (McLachlan & Bazely 2001). Our results identify several dispersal-restricted species across a range of guild types and taxonomic families that are important candidates for active reintroduction in longleaf pine ecosystem recovery sites.

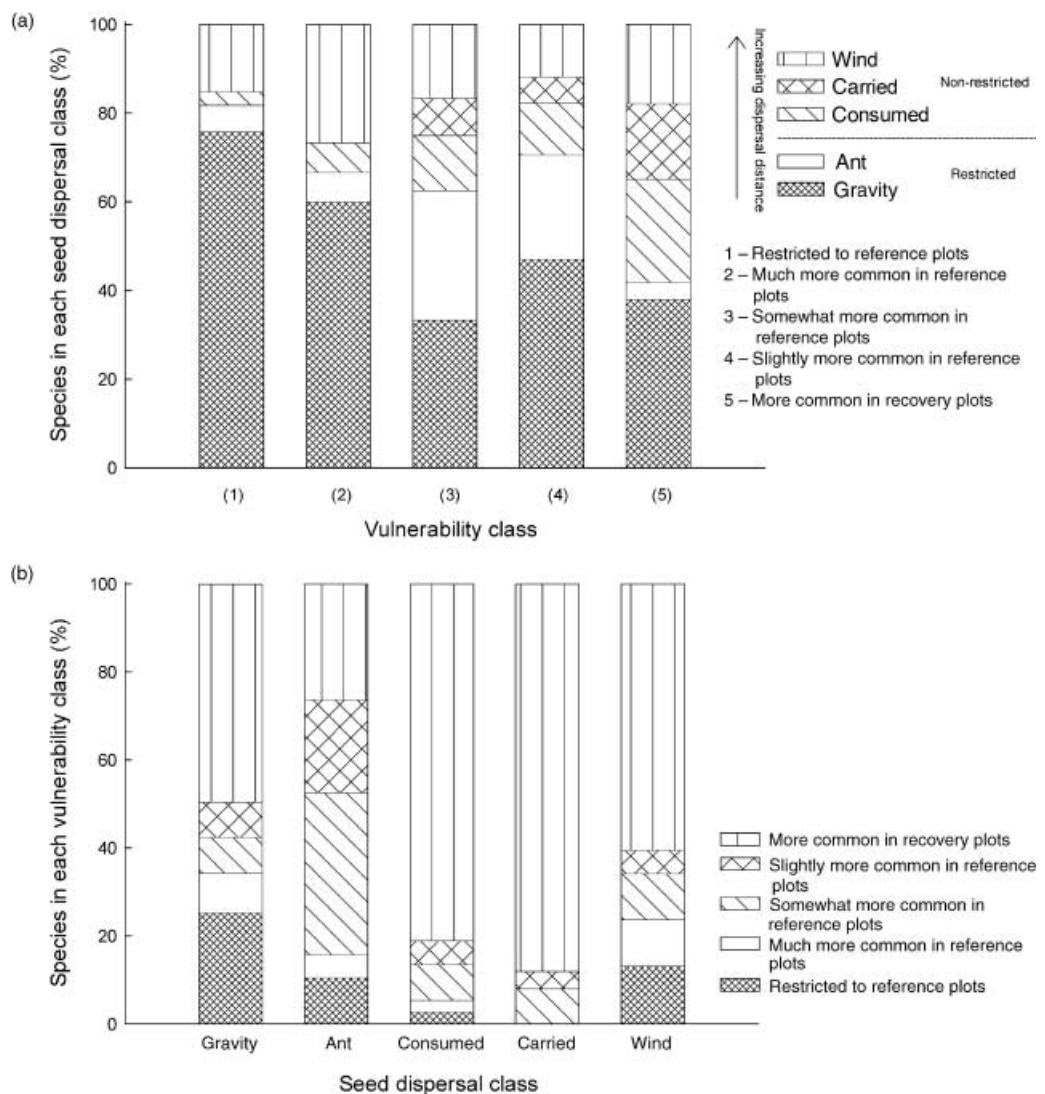
The list of species with low recolonization potential provides a tool for assessing high-quality ground-cover conditions that are associated with minimally disturbed ecosystems. While a particular guild of species did not emerge as a strong indicator group, our results suggest a group of species that could furnish a metric for assessing the absence of prior soil disturbance or the degree of recovery that a restored system has attained. Such a technique, known as floristic quality assessment (FQA), has been applied in prairie habitats (Swink & Wilhelm

1994; Masters 1997) and could be a useful model for site assessments in longleaf pine as more data emerge to corroborate the conservatism of individual species across multiple sites. Our findings were markedly consistent with other studies of reference/non-reference site observations in longleaf pine stands. Hedman *et al.* (2000) identified eight indicator species of reference longleaf pine sites in south-western Georgia using similar ordination procedures. Of these species, six (*Dyschoriste oblongifolia* (Michx.) Kuntze, *Aristida beyrichiana* = *A. stricta* in Hedman *et al.* (2002), *Pteridium aquilinum* (L.) Kuhn, *Aster adnatus* Nutt., *Ruellia carolinensis* (Walt ex. Gmel.) Steud. and *Tephrosia virginiana* (L.) Pers.) were among our list of vulnerable species. Because we did not distinguish *Schizachyrium scoparium* (Michx.) Nash separately from *Andropogon virginicus* L. in our study, we were unable to compare their results for *S. scoparium* with our data. However, we found their eighth species, *Solidago odora* Ait., more frequently in the recovery sites than in the reference sites. Smith (2000) also found greater abundance of the six consistent species in natural vs. planted longleaf stands in South Carolina and several other species had similar affinities to those in our study. These included *Dichanthelium ensifolium* var. *unciphyllum* (Trin.) B. F. Hansen & Wunderlin (= *D. tenue* in Smith 2000), *Viola palmata* L. (= *V. septemloba*), *Strophostyles umbellata* (Muhl. ex Willd.) Britt, *Gaylussacia dumosa* (Andrz.) T. & G., *Mimosa quadrivalvis* (Torrey & Gray) Barneby (= *Schrankia microphylla*), and *Dicanthelium aciculare* (Desv. Ex Poir.) Gould & C. A. Clark. Studies of indicators of anthropogenic disturbance in longleaf pine stands on a military base in Georgia suggest that ground-cover species can serve as surrogate measures of disturbance (Dale *et al.* 2002). Even though the reference sites of Dale *et al.* (2002) did not have a wiregrass-dominated ground cover, 4 of the 11 species they observed as indicative of relatively undisturbed sites were also found to be associated with reference conditions in our study (i.e. *Aster concolor*, *Pteridium aquilinum*, *Ruellia carolinensis* and *Strophostyles umbellata*).

Several myrmecochorous (ant-dispersed) species were found to be extremely vulnerable to disturbance, particularly *Viola palmata*, *Dyschoriste oblongifolia*, *Croton argyranthemus* Michx. and *Ruellia carolinensis*. Gravity- and ant-dispersal mechanisms may represent a significant impediment to restoration potential that may be overcome either by introduction of propagules during the restoration process or by allowing longer for recruitment. The role of native ant dispersal in this system, as well as the increasing impact of the imported fire ant (*Solenopsis invicta*) (Carroll & Hoffman 1997) on the recruitment process, needs further investigation.

The species-area relationships we observed, coupled with the fact that gravity- and ant-dispersed species were considerably less represented in sites recovering after disturbance, are consistent with current knowledge of processes that govern species richness and composition in this fire-maintained ecosystem. The coexistence of many species in the longleaf pine-wiregrass system is





**Fig. 4** Vulnerability-resilience groups and distance-restricted and non-distance restricted seed dispersal mechanisms. Vulnerability groups are defined in Table 1 by vulnerability ratios (Vratio). Group 1, Vratio = 8; group 2, Vratio = 16; group 3,  $16 < \text{Vratio} = 5$ ; group 4,  $5 < \text{Vratio} = 2$ ; group 5,  $\text{Vratio} < 2$ . (a) Percentage of total species in each dispersal type by classes of vulnerability. (b) Percentage of total species in each vulnerability class by dispersal type.

due to a combination of the frequent removal of woody vegetation with fire, the perennial life histories of the ground cover flora, and the non-rhizomatous characteristic of the dominant wiregrass (Kirkman *et al.* 2001). In relatively undisturbed ground-cover sites subjected to frequent fire, soil moisture appears to be an important factor regulating the number of species present across the xeric-mesic landscape. In contrast to many temperate grasslands (Abrams & Hulbert 1987; Gibson & Hulbert 1987; Franzen & Eriksson 2001), there is little/no evidence for competitive exclusion as a factor regulating species richness in the ground cover of longleaf pine-wiregrass forests (Kirkman *et al.* 2001). Water limitation may inhibit seedling establishment so that vegetation is likely to facilitate survival by moderation of microclimate (DeSteven 1991). Once established, however, individuals of many perennials may persist for several to many years. Provided this is the case, long adult life spans decrease the probability of population decline over

a series of low-recruitment periods (Warner & Chesson 1985).

Recruitment in this system is probably explained by stochasticity in recruitment success, as suggested for other grassland ecosystems (van der Maarel & Sykes 1993; Franzen & Eriksson 2001), where an occasional recruitment event can sustain population size over long periods (Warner & Chesson 1985). Accordingly, in the longleaf pine-wiregrass ecosystem, site moisture conditions suitable for establishment (as opposed to space limitations) and the available seed pools are feasible factors limiting recruitment (Zobel 1992, 1997; Franzen & Eriksson 2001). Seed pool composition, in turn, is controlled by dispersal distances, seed production rates, fragmentation of the surrounding landscape, and seed longevity in the soil (Gross 1987; Eriksson & Ehrlén 1992). The importance of recruitment in the restoration process will also depend on the soil disturbance history as well as fire frequency in the recovery period.

**Table 2** Frequency of occurrence, relative vulnerability to disturbance and life-history traits of species. Species presented had frequency > 0.02 in reference sites and a vulnerability ratio ≥ 2.5

Species by vulnerability ranking	Family	Common name	Occurrence of species (mean freq of nested plots)		Vulnerability ratio (Vratio) (Frf/Frc)	Dispersal type	Guild type
			Reference sites (Frf)	Recovery sites (Frc)			
Species restricted to reference sites							
<i>Tephrosia virginiana</i>	Fabaceae	Goat’s rue	0.20	0	∞	Gravity	Legume
<i>Anthaenantia villosa</i>	Poaceae	Silky scale	0.17	0	∞	Gravity	C4 grasss
<i>Gaura filipes</i>	Onagraceae	Slenderstalk bee blossom	0.14	0	∞	Gravity	Summer forb
<i>Dichanthelium ensifolium</i> var. <i>unciphyllum</i>	Poaceae	Witchgrass	0.13	0	∞	Gravity	C3 grass
<i>Panicum anceps</i>	Poaceae	Beaked panicum	0.11	0	∞	Gravity	C4 grass
<i>Rhynchospora harveyi</i>	Cyperaceae	Harvey’s beaksedge	0.10	0	∞	Gravity	C3 grass
<i>Dichanthelium strigosum</i>	Poaceae	Roughhair witchgrass	0.08	0	∞	Gravity	C3 grass
<i>Rudbeckia hirta</i>	Asteraceae	Black-eyed susan	0.08	0	∞	Gravity	Fall forb
<i>Zornia bracteata</i>	Fabaceae	Viperina	0.08	0	∞	Gravity	Legume
<i>Panicum virgatum</i>	Poaceae	Switch grass	0.06	0	∞	Gravity	C4 grass
<i>Pinus palustris</i>	Pinaceae	Longleaf pine	0.06	0	∞	Wind	Woody
<i>Viola palmata</i>	Violaceae	Blue violet	0.05	0	∞	Ant &/or explosive	Summer forb
<i>Helianthus radula</i>	Asteraceae	Rayless sunflower	0.04	0	∞	Gravity	Fall forb
<i>Dichanthelium commutatum</i>	Poaceae	Variable witchgrass	0.03	0	∞	Gravity	C3 grass
<i>Strophostyles umbellata</i>	Fabaceae	Sand beans	0.03	0	∞	Gravity	Legume
Species much more common in reference sites							
<i>Aristida beyrichiana</i>	Poaceae	Three-awn wiregrass	0.73	< 0.01	350.0	Gravity	C4 grass
<i>Aster adnatus</i>	Asteraceae	Scale leaf aster	0.28	< 0.01	67.5	Wind	Fall forb
<i>Aster concolor</i>	Asteraceae	Eastern silver aster	0.27	< 0.01	65.0	Wind	Fall forb
<i>Gaylussacia dumosa</i>	Ericaceae	Dwarf huckleberry	0.27	< 0.01	65.0	Consumed	Woody
<i>Schizachyrium tenerum</i>	Poaceae	Slender bluestem	0.46	< 0.01	55.0	Gravity	C4 grass
<i>Aster linariifolius</i>	Asteraceae	Stiff-leaved aster	0.08	< 0.01	40.0	Wind	Fall forb
<i>Pteridium aquilinum</i>	Pteridaceae	Bracken fern	0.30	< 0.01	36.3	Wind	Fern
<i>Galactia erecta</i>	Fabaceae	Erect milkpea	0.34	0.01	33.0	Gravity	Legume
<i>Scutellaria integrifolia</i>	Lamiaceae	Skullcap	0.19	< 0.01	30.0	Gravity	Summer forb
<i>Ruellia caroliniensis</i>	Acanthaceae	Wild petunia	0.11	< 0.01	27.5	Ant &/or explosive	Summer forb
<i>Sporobolus junceus</i>	Poaceae	Dropseed	0.11	< 0.01	27.5	Gravity	C4 grass
<i>Sorghastrum nutans</i>	Poaceae	Yellow indiangrass	0.19	< 0.01	22.5	Gravity	C4 grass
<i>Mimosa quadrivalvis</i>	Fabaceae	Sensitive briar	0.30	0.01	20.7	Gravity	Legume
<i>Sorghastrum secundum</i>	Poaceae	Lop-sided indiangrass	0.04	< 0.01	20.0	Gravity	C4 grass
<i>Muhlenbergia capillaris</i>	Poaceae	Muhly grass	0.15	0.01	10.7	Gravity	C4 grass

Table 2 continued

Species by vulnerability ranking	Family	Common name	Occurrence of species (mean freq of nested plots)		Vulnerability ratio (Vratio) (Frf/Frc)	Dispersal type	Guild type
			Reference sites (Frf)	Recovery sites (Frc)			
Species more common in reference sites							
<i>Dyschoriste oblongifolia</i>	Acanthaceae	Twin flower	0.97	0.12	8.1	Ant &/or explosive	Summer forb
<i>Elephantopus elatus</i>	Asteraceae	Elephant's foot	0.17	0.02	7.3	Wind	Fall forb
<i>Stylosanthes biflora</i>	Fabaceae	Pencil flower	0.32	0.06	5.7	Gravity	Legume
<i>Croton argyranthemus</i>	Euphorbiaceae	Silver croton	0.09	0.02	5.0	Ant &/or explosive	Summer forb
<i>Chrysopsis mariana</i>	Asteraceae	Golden aster	0.07	0.01	5.0	Wind	Fall forb
<i>Lespedeza repens</i>	Fabaceae	Creeping lespedeza	0.13	0.03	4.6	Carried	Legume
<i>Tephrosia spicata</i>	Fabaceae	Hoary pea	0.10	0.02	4.5	Gravity	Legume
<i>Vernonia angustifolia</i>	Asteraceae	Ironweed	0.22	0.05	4.4	Wind	Fall forb
<i>Vaccinium myrsinites</i>	Ericaceae	Shiny blueberry	0.28	0.06	4.4	Consumed	Woody
<i>Lechea sessiliflora</i>	Cistaceae	Pineland pinweed	0.26	0.06	4.3	Gravity	Fall forb
<i>Aristolochia serpentaria</i>	Aristolochiaceae	Snakeroot	0.04	0.01	3.3	Gravity	Summer forb
<i>Euphorbia pubentissima</i>	Euphorbiaceae	False flowering spurge	0.34	0.11	3.1	Gravity	Summer forb
<i>Dichanthelium aciculare</i>	Poaceae	Witchweed	0.54	0.19	2.8	Ant &/or explosive	C3 grass
<i>Hedyotis procumbens</i>	Rubiaceae	Innocence	0.15	0.05	2.7	Gravity	Summer forb
<i>Galactia mollis</i>	Fabaceae	Soft milkpea	0.14	0.05	2.7	Gravity	Legume
<i>Polygala grandiflora</i>	Polygalaceae	Showy milkwort	0.08	0.03	2.5	Ant &/or explosive	Summer forb

For sites without agricultural soil disturbance, but degradation primarily resulting from fire suppression, the persistence of species as rootstocks or buried seed in shaded conditions may play a more critical role in the recovery process following introduction of frequent fire regimes. The establishment of hardwoods in the understorey due to infrequent fire undoubtedly interacts with the recruitment process in influencing rates of vegetation establishment.

While this study addresses the importance of understanding life-history traits in determining the diversity and abundance of species in plant communities, we recognize that such information cannot provide a simple prescription for restoring a damaged or destroyed community. In fact, it underscores the need for co-directed approaches of basic and applied research to bridge the gaps in understanding natural and managed communities (Gross 1987; Sharitz *et al.* 1992; Willson 1996). Information from this study regarding life history traits may be useful in guiding efforts to understand the ecological mechanisms of recovery of communities in other species-rich savannas following disturbance. For disturbances that extirpate species and propagules, a longer period for re-establishment will be expected for those species with spatially limited dissemination of seeds relative to those with wind or animal dispersal mechanisms.

We have provided some explanation as to why groups of species behave as they do in community reassemblies, information that is potentially important in devising appropriate management or restoration plans for the longleaf pine-wiregrass community. However, other key factors in the recovery process, such as critical thresholds of soil disturbance intensity and persistence of seed banks, rates of recovery relative to soil types, and interactions with hardwood encroachment resulting from fire suppression, remain to be examined.

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