

Effects of overstory structure and fire regime upon diversity and abundance of selected understory species in longleaf pine (*Pinus palustris* Mill.) forests in southeastern Georgia

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ABSTRACT: We examined the impacts of variation in overstory structure and burning regime on understory vegetation in the longleaf pine (*Pinus palustris* Mill.) forest of the Okefenokee National Wildlife Refuge in southeastern Georgia, U.S.A. On sandy upland sites surrounding the Okefenokee Swamp and on islands, we established five randomly-located 0.04-ha plots within each of six study areas. The plots varied in overstory density, past management and fire regime. We measured overstory tree size of longleaf pines in the 0.04-ha plots and percent cover of ground cover species in five 1-m² subplots nested within each 0.04-ha plot. We also calculated diversity indices for the ground cover species. There was no significant relationship between overstory basal area and any diversity measure. Even at the subplot level, there was no significant relationship observed between the diversity measures and distance to the nearest tree, presumably a surrogate for overstory density. The diameter (DBH) of the nearest tree exhibited a slight influence over the Shannon Index, and the nearest tree's height was significantly related to evenness in each subplot. There were varied relationships between individual species and fire regime or nearest tree measurements. There was a definite, but statistically insignificant, trend of decreasing diversity with increasing years since the last burn. Height of the nearest tree positively influenced evenness, probably reflecting the influence of stochasticity and amount of needle deposition (influencing fire behavior) over a wide area. Within the generally equal fire-return interval across sites, individual fire-events and site-specific behavior apparently influence understory diversity. It is not surprising that the last burn would affect species richness, even more so than the number of growing-season burns, other studies support this observation. The presence of obligate seeding and (clonal) sprouting as dominants in the ground cover suggests that the fire-return interval is not regular. The cycling of fire-return intervals, even within the management-prescribed 2- to 4-year range, and the variation by microsite appear to provide sufficient variability of disturbance to create diversity in the ground-level cohort. Site-specific relationships between particular species and the nearest tree suggest that even a narrowly-prescribed fire management regime can provide sufficient diversity.

Keywords: longleaf pine; *Pinus palustris*; fire frequency; season of burn; understory diversity; overstory basal area; *Aristida beyrichiana*; *Gaylussacia dumosa*; *Gaylussacia frondosa*; *Ilex glabra*; *Pteridium aquilinum*; *Serenoa repens*; *Vaccinium myrsinites*

The conservation status of longleaf pine forests and intact native ground cover

Due to the drastic reduction in acreage of longleaf pine (*Pinus palustris* Mill.) forests of the southeastern United States, a great deal of attention has been paid to the species and its associated ecosystem (NOSS 1989). Estimates of the extent of pre-European settlement longleaf forests range up to 24 to 36 million hectares (FROST 1993), while there are just above 1.2 million hectares remaining (OUTCALT, OUTCALT 1994). Fire suppression, forest-type conversion and mechanical disturbance reduce the extent and diversity of native ground cover in longleaf pine systems (FROST 1993; PEET, ALLARD 1993).

Longleaf pine forests are noted for the diversity of the understory vegetation (CHRISTENSEN 1988; WALKER, PEET 1983; WALKER 1993; PLATT et al. 1988a; NOSS

1989). This diversity depends on frequent fires, primarily during the lightning season (WAHLENBERG 1946; PLATT et al. 1988b; LANDERS et al. 1995; GRELEN 1975, 1978). Before European settlement, fires in pine flatwoods like those in the Okefenokee area were estimated to have occurred every 1–10 years with a range of intensities (CHRISTENSEN 1988).

In these forests, variations in overstory density can influence species' responses. Their studies found that solar radiation and temperature (both soil and air) were higher in gap centers and especially in larger gaps. Species richness was greater in these larger gaps. PLATT et al. (1988a) and PLATT and RATHBUN (1993) found that patches of small trees formed away from larger trees, in areas where interference effects were low. Just as tree seedlings have their own particular response to overstory and disturbance influences (BOYER 1974; PLATT et al. 1988; GRACE,

Table 1. Study site histories at Okefenokee NWR. Study commenced in 1996, data from 1997*

| Study area | Soil type | Fire history | Most recent burn(s) before study |
|-----------------|------------------|--------------|----------------------------------|
| 3A | Leon Sand | Dormant | Growing (1995) |
| 3B | Mandarin Sand | Dormant | Dormant (1994), Growing (1996) |
| 3C | Leon Sand | Dormant | Growing (1994) |
| 15A | Sapelo Fine Sand | Dormant | Dormant (1995) |
| Billy's Island | Leon Sand | Dormant | Growing (1994) |
| Mitchell Island | Leon Sand | Dormant | Dormant (1995) |

*Soil data from unpublished maps. Charles Laquoyette, NRCS

PLATT 1995), ground cover species presumably have adapted to the particular mix structure and disturbance (MOORE et al. 1982; WALKER, PEET 1983; PLATT et al. 1988a; STRENG et al. 1993; TYLER, D'ANTONIO 1995). Some authors have warned that prescribed fires conducted in a consistent manner with the same seasonality and fire return interval will reduce diversity (ROBBINS, MYERS 1992). The objective of this study was to determine whether overstory basal area and a typical prescribed fire management regime were influential in determining species mix and abundance in second-growth longleaf pine forests in Georgia.

METHODOLOGY

Study sites

The Okefenokee National Wildlife Refuge (NWR) is located in Charlton, Ware, and Clinch counties, in southeastern Georgia, U.S.A. This area was extensively logged for cypress and longleaf pine early in this century. The remaining longleaf pine, most of it second- or third-generation natural stands as well as some planted stands, is located on numerous islands in the swamp and on surrounding uplands. The understory shrub layer includes such common flatwoods species as *Serenoa repens* (Bartr.) Small, *Lyonia fruticosa* (Michx.) G.S. Torr. in Robins., *Ilex glabra* (L.) Gray, *Myrica cerifera* L., *Gaylussacia dumosa* (Andrz.) T. & G. and *Aristida beyrichiana* Trin. & Rupr., sometimes in a two-layer structure, typical of flatwoods (ABRAHAMSON, HARTNETT 1990).

We selected six study sites for evaluation during the summer of 1997, two on islands in the middle of the swamp and four on the surrounding uplands, in an attempt to provide a variety of geographic locations throughout the refuge and a range in overstory density. Within each study site, five 0.04-hectare plots were randomly situated in pine habitat, for a total of thirty plots. Histories of prescribed burns for each study site were obtained from the Refuge Management (Table 1).

Measurements of overstory and ground cover

Each plot was 11.35 meters in radius or 0.04 hectare (0.1 acre) in area. We measured height, diameter and

crown spread of each tree and mapped each tree relative to plot center. We cored every tree greater than 10 cm in diameter at 1.37 meters. For ground cover measurements, we used a nested 10 m × 10 m grid in the center of the circular plots, randomly choosing 5 of the resulting 100 square meters for sampling of percent cover.

We also targeted seven species of special interest: *Aristida beyrichiana*, *Gaylussacia dumosa*, *Gaylussacia frondosa*, *Ilex glabra*, *Pteridium aquilinum*, *Serenoa repens* and *Vaccinium myrsinites*. These species were chosen for various reasons: because previous work suggested they were favored by particular fire regimes (*A. beyrichiana*, *P. aquilinum*, *V. myrsinites*) (CLEWELL 1989; ALONSO-AMELOT, RODULFO-BAECHLER 1996; OSTERTAG, MENGES 1994), because of the ecological and management interest in a particular threatened species (*A. beyrichiana*), because of their value as food for *Ursus americanus*, the endangered black bear (*I. glabra*, *S. repens*, *V. myrsinites*), or because they were present across all the sites and would provide a systematic overview of fire and overstory impacts.

We examined three common indicators of diversity: species richness, evenness and the Shannon Index (MAGURRAN 1988; PITKÄNEN 1998). Species richness is sensitive to the number of uncommon species. Evenness is less sensitive to sampling intensity than is richness or the Shannon Index. It is driven more by the proportional abundance of the most dominant species than by the number of species found (SILBAUGH, BETTERS 1995). The Shannon Index possesses advantages of each of the other indices and is commonly used in the literature.

Analysis

We examined the effects of overstory and fire management upon ground cover diversity and abundance of the seven selected species. At the study site level (referred to here as the "compartment") ($N = 6$), we used a fixed-effects ANOVA on compartment means of the diversity and species abundance values to test categorical variables of fire management that do not vary within the site (Table 2). At the plot level ($N = 30$), we used linear regression on plot means to test for influence of overstory basal area (Table 3). At the square-meter subplot level ($N = 150$), we used linear regression to test the influences of size and

Table 2. Summary of means and standard errors (in parentheses) of selected variables vs. season of burn, number of growing season burns and years since the last burn, at the compartment level ($N = 6$). "Dormant" = dormant season burns (October through early April), "Growing" = growing season burns (mid-April through September). The three diversity indices have no units, the seven species' values are in percentages. Within each fire characteristic, those values without different subscripts are not significantly different at the 0.05 level

| | Season of burn | | | Number growing | | | Season burns | | | Years since | | | Last burn | | |
|-----------------------------|---------------------|---------------------|--------------------------|----------------------------|--------------------|----------------------------|----------------------------|--------------------|----------------------------|----------------------------|--------------------|----------------------------|----------------------------|--------------------|--|
| | Dormant ($N = 2$) | Growing ($N = 4$) | 0 ($N = 2$) | 1 ($N = 3$) | 2 ($N = 1$) | 1 ($N = 3$) | 2 ($N = 2$) | 3 ($N = 1$) | 1 ($N = 3$) | 2 ($N = 2$) | 3 ($N = 1$) | 1 ($N = 3$) | 2 ($N = 2$) | 3 ($N = 1$) | |
| Species richness | 7.20 (1.04) | 7.280 (0.345) | 7.20 (1.04) | 6.987 (0.258) | 8.16 | 7.853 (0.347) | 6.74 (0.58) | 6.48 | 7.853 (0.347) | 6.74 (0.58) | 6.48 | 7.853 (0.347) | 6.74 (0.58) | 6.48 | |
| Shannon Index | 1.520 (0.080) | 1.5400 (0.0627) | 1.52 (0.08) | 1.4933 (0.0593) | 1.68 | 1.62 (0.0306) | 1.48 (0.04) | 1.38 | 1.62 (0.0306) | 1.48 (0.04) | 1.38 | 1.62 (0.0306) | 1.48 (0.04) | 1.38 | |
| Evenness | 0.7850 (0.0150) | 0.7900 (0.0147) | 0.785 (0.015) | 0.7833 (0.0186) | 0.81 | 0.8 (0.0153) | 0.785 (0.015) | 0.76 | 0.8 (0.0153) | 0.785 (0.015) | 0.76 | 0.8 (0.0153) | 0.785 (0.015) | 0.76 | |
| <i>Aristida beyrichiana</i> | 3.46 (1.62) | 2.790 (0.664) | 3.46 (1.62) | 2.133 (0.141) | 4.76 | 3.973 (0.951) | 2.120 (0.280) | 1.92 | 3.973 (0.951) | 2.120 (0.280) | 1.92 | 3.973 (0.951) | 2.120 (0.280) | 1.92 | |
| <i>Gaylussacia dumosa</i> | 3.24 (1.16) | 3.360 (0.785) | 3.24 (1.16) | 3.03 (1.01) | 4.36 | 3.33 (1.05) | 2.600 (0.520) | 4.72 | 3.33 (1.05) | 2.600 (0.520) | 4.72 | 3.33 (1.05) | 2.600 (0.520) | 4.72 | |
| <i>Gaylussacia frondosa</i> | 8.74 (4.82) | 5.86 (1.80) | 8.74 (4.82) | 7.24 (1.63) | 1.72 | 3.293 (0.792) ^a | 11.70 (1.86) ^b | 7.64 ^{ab} | 3.293 (0.792) ^a | 11.70 (1.86) ^b | 7.64 ^{ab} | 3.293 (0.792) ^a | 11.70 (1.86) ^b | 7.64 ^{ab} | |
| <i>Ilex glabra</i> | 15.22 (3.82) | 15.910 (0.714) | 15.22 (3.82) | 14.333 (0.858) | 17.0 | 15.23 (1.91) | 16.78 (2.26) | 14.8 | 15.23 (1.91) | 16.78 (2.26) | 14.8 | 15.23 (1.91) | 16.78 (2.26) | 14.8 | |
| <i>Pteridium aquilinum</i> | 17.2 (10.0) | 2.41 (1.48) | 17.2 (10.0) ^a | 1.000 (0.615) ^b | 6.64 ^{ab} | 4.61 (2.31) ^{ab} | 14.7 (12.6) ^b | 0.88 ^a | 4.61 (2.31) ^{ab} | 14.7 (12.6) ^b | 0.88 ^a | 4.61 (2.31) ^{ab} | 14.7 (12.6) ^b | 0.88 ^a | |
| <i>Serenoa repens</i> | 16.64 (3.44) | 17.67 (4.45) | 16.64 (3.44) | 20.27 (5.11) | 9.88 | 15.19 (2.95) ^a | 13.96 (0.76) ^{ab} | 30.5 ^b | 15.19 (2.95) ^a | 13.96 (0.76) ^{ab} | 30.5 ^b | 15.19 (2.95) ^a | 13.96 (0.76) ^{ab} | 30.5 ^b | |
| <i>Vaccinium myrsinites</i> | 8.52 (5.52) | 10.22 (3.10) | 8.52 (5.52) | 7.68 (2.50) | 17.8 | 11.53 (4.54) | 6.86 (3.86) | 9.6 | 11.53 (4.54) | 6.86 (3.86) | 9.6 | 11.53 (4.54) | 6.86 (3.86) | 9.6 | |

Table 3. Results of plot-level linear regressions of the form (species of special interest) = overstory basal area in m²/ha. There was no significant influence upon any measure of diversity due to overstory basal area. Symbols in parentheses represent level and direction of significance, e.g. "+++" means positive influence significant at the 0.01 level, "--" means negative influence significant at the 0.05 level, "+" means positive influence significant at the 0.1 level, "(-)" means negative influence significant at the 0.25 level. $N = 30$

| | Overstory basal area (m ² /ha) |
|-----------------------------|---|
| <i>Aristida beyrichiana</i> | (-) |
| <i>Gaylussacia dumosa</i> | - |
| <i>Gaylussacia frondosa</i> | (+) |
| <i>Ilex glabra</i> | |
| <i>Pteridium aquilinum</i> | ++ |
| <i>Serenoa repens</i> | |
| <i>Vaccinium myrsinites</i> | -- |

distance to nearest tree with a dummy variable to account for plot means (Table 4). We also used linear regression to search for interrelationships between the diversity indices and percent cover of the 8 species (Table 5). Correlation tables between all variables provided the direction of any influences. All statistical analysis used the S-Plus 2000 statistical software package (INSIGHTFUL CORP. 2001).

RESULTS

Fire and diversity

Longer fire intervals have been shown to influence species richness in other sites (OSTERTAG, MENGES 1994). Poor sites are particularly affected by changes in fire interval, while very productive sites showed less of an increase in richness with a shorter fire interval. While the Okefenokee sites are nutrient-poor, the fire-return intervals fairly constant and did not appear to trigger changes in overall diversity (Table 2). Although our data suggested that years since the last burn provided a consistent negative influence over diversity, the actual fire interval has not appreciably changed in these stands in recent times (Phernetton, Refuge Forester, pers. comm.). There was no significant change in diversity due to season of fire, a finding supported by other studies (STRENG et al. 1993).

The fire regime was found to impact ground cover slightly more than did overstory basal area. The three diversity measures generally trended upward as a function of increasing number of growing season burns, although the results were not significant. The diversity measures trended downward as years since the last burn increased, although again not significant, mirroring results found in other studies (BROCKWAY, LEWIS 1997; WALDROP et al. 1992).

The diameter of the nearest tree had a slight positive influence ($P < 0.25$) on the Shannon Index and a slight

negative influence ($P < 0.25$) on evenness. Height of the nearest tree had a significant effect on evenness ($P < 0.05$). Tree diameter is generally a function of site quality, available growing space and age (OLIVER, LARSON 1995) for a given density. If larger diameter trees have larger crowns (and are taller, as is often the case), then the understory in a pine stand would have higher levels of needle fuel. This high fuel loading would result in higher-intensity fires. We discovered no significant relationship between evenness and distance to the nearest tree, which would suggest that fire intensity, a function in part of fuel accumulation, was not a determining factor for evenness. A tree with a given crown size is more likely to drop the needles on a near-tree site if it is shorter, less likely if it is taller. Evenness, therefore, might result from a more stochastic application of needle fuel than would species richness.

Overstory and diversity

Taken as a whole, the diversity measurements were not significantly affected by overstory basal area. The range of overstories (2.5–20 m²/ha) was broad enough to test the hypothesis.

Species of special interest

Species and overstory

We searched for any significant relationship between percent cover of the seven species of interest and site, prescribed burning and overstory variables. Within the range of stands examined, there was a significant relationship between overstory density and percent cover for *Pteridium aquilinum* (positive) and *Vaccinium myrsinites* (negative) (Table 3). For most species, however, overstory density had little or no influence on percent cover. These results seemed contrary to those of ABRAHAMSON

(1995), who concluded that canopy coverage by overstory trees strongly influenced *S. repens* densities. We found no evidence here.

Species and fire

In our study, a more important factor was the fire regime (Table 2). The number of growing-season burns had a significant positive influence over *P. aquilinum*. On the one hand, bracken fern can be perpetuated by fires that remove earlier growth bracken litter, which would otherwise suppress the development of new pinnae (WATT 1976). On the other hand, the more intense growing-season fires damage the rhizomes, the source of the carbohydrates that fuel early development of fronds (ALONSO-AMELOT, RODULFO-BAECHLER 1996), and reduce the effective growing season of the new fronds. *Pteridium aquilinum* starts to increase in abundance as the time since the last burn increases, but then declines, presumably the result of growth suppression by bracken litter and increased competition by neighboring woody species. SCHMALZER AND HINKLE (1992) found that *P. aquilinum* peaked 18 months after a burn, then dropped out on both oak-dominated and saw-palmetto scrub sites.

While this study did not show significant influence of the number of growing-season burns on *Aristida beyrichiana* abundance, the species has been found more likely to flower and produce viable seeds with frequent growing-season fires (CLEWELL 1989). Frequency may be more important than season of burn, as other studies have suggested (BROCKWAY, LEWIS 1997; ABRAHAMSON, HARTNETT 1990; LANDERS et al. 1995; WALDROP et al. 1992) but again, we found no evidence here. Grasses seem well-adapted to fire, because they maintain significant nutrient storage below-ground, have their leaf meristem at least 4 cm below the surface and can produce abundant production and distribution of reproductive bodies (LEMON 1949).

Table 4. Results of sub-plot level linear regressions of the form (species of special interest) = distance to the nearest tree + height of the nearest tree + diameter of the nearest tree + difference in distance between the nearest and the next nearest tree ("delta distance"). Variables separated by colon (":") represent interaction terms. Symbols in parentheses represent level and direction of significance, e.g. "+++" means positive influence significant at the 0.01 level, "--" means negative influence significant at the 0.05 level, "+" means positive influence significant at the 0.1 level, "-" means negative influence significant at the 0.25 level. $N = 150$

| Variable | N | R^2 | Distance | Height | Diameter | Delta distance |
|-----------------------------|-----|--------|----------|--------|----------|----------------|
| Species richness | 150 | 0.0431 | | | (+) | |
| Shannon Index | 150 | 0.0453 | | | | (+) |
| Evenness | 150 | 0.0437 | | ++ | (-) | |
| <i>Aristida beyrichiana</i> | 103 | 0.0229 | | | | |
| <i>Gaylussacia dumosa</i> | 79 | 0.181 | +++ | | | |
| <i>Gaylussacia frondosa</i> | 73 | 0.149 | +++ | | | |
| <i>Ilex glabra</i> | 124 | 0.0192 | | (+) | | |
| <i>Pteridium aquilinum</i> | 64 | 0.122 | (-) | | | (-) |
| <i>Serenoa repens</i> | 101 | 0.0911 | (+) | (-) | | (+) |
| <i>Vaccinium myrsinites</i> | 111 | 0.0523 | (+) | | | |

Table 5. Results of sub-plot level linear regressions of the form (species of special interest) = species richness * Shannon Index * evenness + plot, where plot is a dummy variable representing the plot means of each of the thirty plots. Variables separated by a colon (“:”) represent interaction terms. Symbols in parentheses represent level and direction of significance, e.g. (– –) means negative influence significant at the 0.05 level, (+) means positive influence significant at the 0.1 level. Total possible $N = 150$

| Variable | N | R^2 | Significant influences |
|-----------------------------|-----|-------|--|
| <i>Aristida beyrichiana</i> | 103 | 0.544 | Shannon Index (++) , Species richness:evenness (+) |
| <i>Gaylussacia dumosa</i> | 79 | 0.557 | |
| <i>Gaylussacia frondosa</i> | 73 | 0.412 | |
| <i>Ilex glabra</i> | 124 | 0.634 | Species richness (– –) |
| <i>Pteridium aquilinum</i> | 64 | 0.477 | Shannon Index (–), Shannon:evenness (–) |
| <i>Serenoa repens</i> | 101 | 0.649 | Species richness (++) , Species richness:Shannon:evenness (++) |
| <i>Vaccinium myrsinites</i> | 111 | 0.600 | |

One answer could be that the particular dormant season burns were of greater intensity, due either to weather or to fuel conditions.

In our study, *S. repens*, *P. aquilinum* and *G. frondosa* were all positively influenced by the number of years since the last burn, with the latter two peaking at two years after a fire, whereas *S. repens*' highest mean percentage was in year 3 (Table 2). *Serenoa repens* is known to increase in abundance as the time since the last fire increases (CLEWELL 1989). SCHMALZER and HINKLE (1992) noted that percent cover of *S. repens* peaked 24 months after a burn in oak-dominated scrub habitat and 3 years after a burn in saw-palmetto dominated habitat. Other studies have also shown that growth of *S. repens* is reduced with increased fire frequency and intensity (ABRAHAMSON 1995). Still, while intense fires, which are more likely during the growing season, may impact *S. repens* recovery because the species' carbohydrate reserves are lowest in the early summer (HILMON 1968), the rhizomes appear to be “armored” against fire damage, and intense fires inhibit *S. repens*' competitors' growth more. GREENBERG et al. (1995) found fire stimulated rapid postburn production of fronds. In saw palmetto scrub, *I. glabra* had peaked in abundance 3 years after a burn (SCHMALZER, HINKLE 1992). This positive correlation between abundance and fire-return interval is to be expected for woody plants, particularly clonal ones (OSTERTAG, MENGES 1994), although *S. repens* can regain its cover by the year following the burn (SCHMALZER, HINKLE 1992). However, our method for estimating abundance – percent cover – may have given undue influence to large-leaved species such as *S. repens*. Nonetheless, the data suggest that both *G. frondosa* and *S. repens* decline with a frequent growing-season fire regime.

A decrease in the years since the last burn did appear to influence *V. myrsinites* percent cover, but, unlike other studies (BROCKWAY, LEWIS 1997; WALDROP et al. 1992), the relationship was not significant. In a scrub habitat study, SCHMALZER and HINKLE (1992) found that *V. myrsinites* increased in percent cover on oak-dominated sites up to the 3-year (after a fire) limit of the study. As mentioned earlier, OSTERTAG and MENGES (1994) found

that *V. myrsinites* exhibited peak reproductive effort within one year of a fire.

Gaylussacia dumosa and *G. frondosa* were extremely significantly and positively influenced by distance to the nearest tree (Table 4). As mentioned above, *Gaylussacia frondosa* was significantly and positively influenced by years since the last burn. Since both of these species are common on wetter sites within the southeastern coastal plain, they would not have developed a strategy of rapid regrowth after fire. Thus, they would have been more adversely impacted by the higher intensity fires more likely present closer to a tree. None of the other species were influenced by any characteristic of the nearest tree above the $P < 0.25$ level.

Arista beyrichiana was significantly and positively influenced by diversity (Table 5). Oddly enough, so was *S. repens*. *Ilex glabra* was significantly and negatively affected by species richness. Since *S. repens* regrew fronds from the belowground caudex quite quickly after fire, the species would not be so negatively impacted by frequent fires (which facilitate diversity), as would *I. glabra*, which would first grow a shoot from the root collar, then replace the main stem, then the primary branches, and so on.

CONCLUSIONS

The variation in overstory cover, at least within the range studied here, did not significantly impact measures of diversity (Table 3). This conclusion has significant implications for managers desiring to reinstitute a multi-aged (or, at least, multi-sized) structure in the forest, as openings in the canopy are necessary to promote *P. palustris* regeneration.

If overstory basal area, an indicator of competition for light and soil resources, was did not have a significant effect upon diversity, yet the size of the nearest tree did, then it is logical to assume that the nearest-tree size is an indicator of needle fall and, hence, a surrogate for fire intensity and periodicity. If tree diameter, related to crown size and volume of needle fall, were related to particular species, that would suggest that fire intensity was an important disturbance in the life history strategy of these

species. For those species more significantly influenced by tree height or some measure of diversity, then stochasticity and “spread” of the fire effects might be the most significant factor.

Within the generally equal fire return interval across sites, individual fire-events and site-specific behavior drive diversity. The potential for taller trees to drop needles over larger areas, and thus create small fuel “hotspots,” contributes to the overall evenness of the ground cover diversity. And again given the relatively similar fire-return intervals, it is not surprising that the last burn would affect species richness.

Four explanations of the species’ responses to fire and/or diversity suggest themselves. First, diversity is lower on sites with *P. aquilinum* because their large fronds capture more growing space (and might be more likely to obscure other species from observation). Second, diversity is lower on sites with higher *I. glabra* abundance because the same factor that facilitates the species, less frequent or intense fires, also negatively impacts diversity. Third, *Ilex glabra* is often indicative of wetter sites. Its presence may indicate a slight change in topography that would reduce fire intensity below a level completely lethal to their belowground structures while still killing its more shallow-rooted competitors. Finally, *A. beyrichiana* is pyrogenic, maintaining and benefiting from a more intense fire regime. Like most bunchgrasses, it is “clumped” in distribution, resulting in “micro-hot-spots” that provide disturbance diversity over a small scale (i.e., evenness).

Fire, either natural or prescribed, as it is applied in the Okefenokee NWR, is varied enough, even within the narrow range of behaviors studied here, to favor species who pattern their reproduction on non-regular disturbances (the “broad peak” model of reproductive effort – OSTERTAG, MENGES 1994). This conclusion seems particularly relevant when the influence of stand characteristics on evenness is taken into account. The presence of obligate seeding and (clonal) sprouting as dominants in the ground cover would suggest that the fire-return interval is irregular. Given the relatively rigid prescribed fire regime on the Refuge, however, the best explanation lies in the stochasticity of ground-level and tree-crown-level fuel production. The cycling of fire-return intervals and the variation on a microsite-by-microsite basis, even in a tight 2- to 5-year range, provides sufficient diversity of disturbance to create diversity in the ground-level cohort. Ecological prescribed fire regimes place great emphasis on varying the seasonal timing of burns (ROBBINS, MYERS 1992). Our evidence suggests that, at least in these conditions and for the principle species studied, such contrived variation is unnecessary.

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Vliv porostní struktury a režimu řízeného vypalování na diverzitu a početnost druhů podrostu v porostech *Pinus palustris* Mill. na jihovýchodě Georgie

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ABSTRAKT: Byl sledován dopad variability struktury porostu a režimu vypalování na přízemní vegetaci v porostech *Pinus palustris* Mill. na území Okefenokee National Wildlife Refuge na JV Georgie (USA). Na šesti různých lokalitách bylo založeno po pěti náhodně rozmístěných plochách o výměře 0,04 ha. Plochy se lišily hustotou porostu, dřívějším typem hospodaření a režimem vypalování. Byly stanoveny biometrické parametry dřevinné složky a pokryv přízemní vegetace na pěti dílčích plochách o velikosti 1 m² na každé ploše. Byly rovněž počítány indexy diverzity pro jednotlivé druhy podrostu. Mezi výčetní kruhovou základnou a parametry diverzity nebyl nalezen žádný významný vztah, ani na úrovni nižší než mezi plochami nebyly významné závislosti mezi diverzitou a vzdáleností od nejbližšího stromu. Průměr nejbližšího kmene vykazoval slabý vliv na Shannonův index a jeho výška ovlivňovala rovnoměrnost zastoupení druhů. Byly patrné vztahy mezi jednotlivými druhy a režimem požárů nebo charakterem nejbližšího stromu. Byl zde patrný, i když statisticky nevýznamný, vztah klesající diverzity a doby uplynulé od posledního požáru.

Charakter individuálních požárů a charakter stanoviště ovlivňují patrně diverzitu vegetace. Výraznější vliv mají požáry vzniklé během růstového období. Přítomnost semenáčků a výhonů indikuje nepravidelnost ohně. Cyklické ohňové epizody a variabilita stanoviště vytvářejí dostatečné podmínky pro biodiverzitu na úrovni podrostu a nejmladší kohorty.

Klíčová slova: *Pinus palustris*; řízené lesní požáry; doba požáru; diverzita porostu; výčetní kruhová základna; *Aristida beyrichiana*; *Gaylussacia dumosa*; *Gaylussacia frondosa*; *Ilex glabra*; *Pteridium aquilinum*; *Serenoa repens*; *Vaccinium myrsinites*

Cílem studie bylo vyhodnocení vlivu proměnlivosti struktury porostu a režimu řízeného vypalování na přízemní vegetaci v porostech borovice *Pinus palustris* Mill. v oblasti Okefenokee National Wildlife Refuge na JV Georgie v USA. Na písčitých půdách kolem bažin Okefenokee a na ostrovech uvnitř bylo založeno na šesti lokalitách vždy pět ploch o velikosti 0,04 ha. Plochy se lišily zakmeněním (výčetní kruhová základna 2,5 až 20 m²/ha), pěstebními opatřeními (probírané a bez zásahu) a režimem řízeného vypalování (doba požáru, periodičita, doba od posledního požáru). Na jednotlivých plochách o velikosti 0,04 ha byly měřeny biometrické parametry stromů, v rámci těchto ploch se pak stanovila pokryvnost jednotlivých druhů přízemní vegetace na pěti ploškách o velikosti 1 m². Pro jednotlivé druhy byly počítány indexy diverzity. Výsledky jsou shrnuty v tab. 1–5. Tab. 1 uvádí shrnutí záznamů o označení a minulém vypalování, další tabulky uvádějí vlastní výsledky šetření. Mezi zakmeněním porostů a diverzitou podrostu nebyly prokázány významné vztahy – dokonce ani na úrovni dílčích ploch nebyly prokázány významné souvislosti mezi charakteristikami diverzity a vzdáleností od nejbližšího stromu, což byly pravděpodobně vzájemně závislé parametry. Výčetní průměr nejbližšího kmene vykazoval slabý vliv na Shannonův index a výška tohoto stromu byla ve vztahu s pravidelností zastoupení druhů. Vztahy mezi jednotlivými druhy a a režimem vypalování nebo parametry nejbližšího stromu byly různé. Byla prokázá-

na výrazná, nikoli však významná souvislost mezi poklesem druhu *Aristida beyrichiana* a dobou od posledního požáru (pokles). Pokryvnost *Gaylussacia dumosa* a *G. frondosa* byla významně a pozitivně ovlivněna rostoucí vzdáleností od nejbližšího stromu, což pravděpodobně odráží intenzitu vypalování. Pokryvnost *Pteridium aquilinum* a *Serenoa repens* významně a negativně souvisela s dobou od posledního požáru; odráží tak souvislost se způsobem vytváření a růstu listů těchto druhů. *Vaccinium myrsinites* byla významně negativně ovlivněna zakmeněním porostu a průměrem nejbližšího kmene. Byl patrný jednoznačný trend poklesu diverzity podrostu v závislosti na rostoucí době od posledního vypalování, i když nebyl statisticky významný. Výška nejbližšího stromu pozitivně ovlivňovala rovnoměrnost zastoupení druhů. Poslední parametr pravděpodobně odráží vliv stochastivity, dané množstvím opadu (ovlivňujícím chování ohně) na větší ploše.

Za předpokladu rovnoměrné frekvence požárů na jednotlivých lokalitách byla druhová diverzita dána především ekologickými nároky jednotlivých druhů a posledním požárem. Proměnlivost intervalů požárů, i když pouze v předepsaném rozmezí 2–4 let, a variability mikrostanovišť vytvářejí dostatečný rozptyl intenzity disturbance k vytvoření odpovídající variability podrostu. Stanovištní nároky, různé pro jednotlivé druhy, a vliv jednotlivých stromů vytvářejí dostatečný předpoklad zajištění diverzity přízemní vegetace.

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