Association of ecotones with relative elevation and fire in an upland Florida landscape

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Abstract

Question: What are the importance of elevation and fire in maintaining ecotones of Florida scrub assemblages along a gradual topographic gradient?
Location: Archbold Biological Station (ABS), 12 km south of Lake Placid, Florida, USA.
Methods: Vegetation cover of upland Florida shrublands was quantified using the line-intercept method along 20 transects traversing similar elevation gradients, stratified by time since fire (TSF). We objectively identified shrubland ecotones using a split moving windows boundary analysis (SMW) with three different window widths. Non-metric multidimensional scaling ordination was used to determine relationships among plant assemblages defined by SMW.
Results: We located up to four ecotones per transect, the majority of which were wide, highly heterogeneous zones. Relative elevation controlled the distribution of plant assemblages in upland Florida shrublands. Ecotones in shrublands > 30 years TSF had relatively low dissimilarity values in SMW, indicating that previously discrete plant assemblages with longer TSF were becoming more similar with time.
Conclusions: Split Moving Windows (SMW) analysis identified ecotones relatively well although patches generated by oak clonal growth were sometimes identified as ecotones. Fire suppression caused ecotones to become more diffuse, suggesting that without fire at least every 30 years, discrete plant assemblages within upland Florida shrublands will be more continuous.

Keywords: Boundary; Dissimilarity coefficient; Landscape gradient; Monte Carlo simulation; Ordination; Split moving window; Time since fire; Transition zone; Vegetation change.

Abbreviations: ABS = Archbold Biological Station; SMW = Split moving window; TSF =Time since fire; NMDS = Non-metric multi-dimensional scaling; OSF = Open Scrubby Flatwoods; RS = Rosemary Scrub; SF = Scrubby Flatwoods; F = Flatwoods; SCB = Squared city block dissimilarities.

Nomenclature: Wunderlin (1998); Abrahamson et al. (1984).

Introduction

Ecotones, heterogeneous transitional areas between plant assemblages (Risser 1995; Fortin & Drapeau 1995), are critical features of the landscape for many reasons including their role in ecosystem dynamics and sensitivity to environmental change (Naiman & Decamps 1990; Risser 1995; Camarero et al. 2000; Weltzin & McPherson 2000). We use 'plant assemblage' to describe a relatively uniform grouping of plants that occur together in a relatively similar location (Fauth et al. 1996). A challenge in the study of ecotones is to quantitatively identify where the transition is located (Fortin & Drapeau 1995). Numerous methods have been used to identify ecotones, including split moving windows analysis (SMW) and moving window regression analysis, which identify the highest rate of change between two habitats (Walker et al. 2003; Hennenberg et al. 2005). Other methods identify homogenous areas on either side of the ecotone to locate the transition (e.g. Lloyd et al. (2000). Recently, Hennenberg et al. (2005) used a combination of split moving window analysis and moving window regression analysis to assess the importance of edges. One limitation of SMW has been that this analysis is scale dependent and it may have difficulty detecting ecotones in patchy vegetation with irregular vegetation structure (Cornelius & Reynolds 1991). As this study demonstrates, using multiple window widths in the SMW analysis can alleviate the scale dependency of SMW.

Determining which factors maintain an ecotone provide insight into the dynamics of plant assemblages on either side of the ecotone (Williams-Linera 1990; Wilson & Agnew 1992; Agnew et al. 1993; Carter et al. 1994; Kirkman & Sharitz 1994; López-Barrera 2004). For example, ecotones may be created or maintained by disturbances such as fire (Myers 1985; Brown & Sieg 1999), high winds and snow avalanches (Camarero & Gutiérrez 2002) and tropical cyclones (Wilson & Bowman 1994). Recognizing the importance of these

disturbances for ecotone maintenance should be incorporated in management decisions, and conservation and restoration strategies.

Upland Florida shrublands are dominated by clonal oaks intermixed with palmettos and other shrubs forming a patchy mosaic. These shrublands are rapidly declining due to human development and agricultural activities and it is essential to properly manage the remnants of this ecosystem. Distance to the water table may be a major factor determining the distribution of the plant assemblages (Abrahamson et al. 1984) although water table may not always coincide with relative elevation. Fire also is expected to play a role in determining vegetation composition and ecotone location, as the Florida scrub vegetation represents a gradient in flammability (Menges 1999). In this study we use SMW analysis to identify ecotones and determine the importance of relative elevation and fire for the maintenance of Florida shrubland assemblages.

Methods

Study area and vegetation

The study was carried out at Archbold Biological Station (ABS), located 12 km south of the town of Lake Placid, FL (27°11' N, 81°21' W, 35-150 m a.s.l.). The ABS area is located on the Lake Wales Ridge and is characterized by a mosaic of scrub, flatwoods and seasonal ponds (Abrahamson et al. 1984; Menges 1999; Menges & Hawkes 1998). Upland Florida scrub vegetation is divided into three major assemblages described in detail by Abrahamson et al. (1984): (1) Sand Pine Scrub with *Ceratiola ericoides* (Florida rosemary) or oak – in this study we only sample Rosemary Scrub, (RS); (2) Scrubby Flatwoods (SF); and (3) Flatwoods (F). These three assemblages represent a gradient in flammability from the less frequently burned RS to the frequently burned F assemblage, with SF intermediate. RS is found at higher elevations on well-drained soil and is characterized by stands dominated by *Ceratiola ericoides*, (> 70%) with bare sand usually covering > 20% and often with an overstorey of *Pinus clausa*. The Scrubby Flatwoods type is found at intermediate elevations on well-drained soils and are dominated by shrubby xerophytic oaks: *Quercus inopina*, *Q. chapmanii* and *Q. geminata*, and *Serenoa repens* (palmettos) and *Sabal etonia*, with less than 10% bare sand and a variable overstorey. Flatwoods are found at lower elevations on poorly drained soils and are characterized by varying densities of *Pinus elliotii* and an understorey of grasses, e.g. *Aristida stricta*, palmettos and shrubs, e.g. *Befaria racemosa*.

Fire history

The plant assemblages at ABS have been influenced by fire (e.g. Abrahamson 1984a,b; Menges 1999; Maliakal et al. 2000). Flammability of each assemblage differs, leading to varying fire intensity and intervals in each assemblage (Abrahamson et al. 1984). Plant distributions are influenced by historical fire regimes combined with life history traits. For example, a slow-maturing, obligate seeding shrub (e.g. *C. ericoides*) often occurs in less frequently burned (every 15-100 year) RS (Menges 1999). Other species recover from fire through regeneration by sprouting (e.g. *Quercus* spp., *S. repens*; Menges 1999) and are more abundant in frequently burned scrubby flatwoods (5-20 years) and flatwoods (2-10 years). Archbold Biological Station is divided into different burn units of varying fire histories (Main & Menges 1997), allowing examination of vegetation with different time since fire (TSF). We stratified ABS burn units into four TSF categories: 1-2 years TSF, 5-8 years TSF, 15 years TSF, and >30 years TSF.

Transect site selection

We established 20 transects, varying in length from 30 m to 147 m, across upland Florida vegetation, stratified by TSF, beginning at a high elevation and ending at a lower elevation. This was achieved by creating two pools of UTM (Universal Transverse Mercator) coordinates based on the high elevations (ca. 147 m a.s.l.) and low elevations (ca. 143 m a.s.l.) High elevation coordinates were randomly shuffled within the four TSF categories and start points were selected. Low elevation coordinates were then randomly selected around each high point to create transects descending directly from a high point to a low point. Global Positioning System (0.5 m resolution, GPS Pathfinder Pro XRS) was used to navigate to high and low elevation coordinate locations, thus locating transect ends.

Data collection

We collected vegetation cover data from February to July 2002 using the line intercept method. All vascular plants were identified to species. We measured the canopy cover of each individual shrub or herb to the nearest cm. A point intercept was used to categorize ground surface every 10 cm as bare sand, litter, lichen, or *Selaginella arenicola*. A theodolite (Leitz Model 115) and range pole were used to measure relative elevation to the nearest cm at every meter along the transect using the known high point as a starting reference.

Data analyses

Ecotone location

To quantitatively describe ecotone location, we used split moving window boundary analysis (SMW) (Ludwig & Cornelius 1987; Cornelius & Reynolds 1991). In SMW analysis, a dissimilarity coefficient is used to calculate the difference in floristic composition between two halves of a window of set size (window width). The 'window' is moved 1 m at a time across the length of transect and dissimilarity values are generated for each 'window'. Areas of high dissimilarity values indicate a discontinuity in vegetation composition (ecotones) and areas of lower dissimilarity values indicate gradual shifts in vegetation (Cornelius & Reynolds 1991). Squared city-block dissimilarity (SCB) coefficients were used to quantify vegetation cover change

$$SCB_{i,h} = \sum \left[\left| a_{i,j} - a_{h,j} \right| \right]^2 \qquad (1)$$

where a_{ij} is the abundance (cover) of species j in sample unit i and a_{hj} is the abundance of the same species in sample unit h (McCune & Grace 2002).

In SMW, small windows often create too much noise because they identify small changes in vegetation cover. After exploring window widths from 2 to 20 m, we chose to use larger window widths (12, 16 and 20 m) that reduced noise and focused on plant assemblage definition for the relevant scales of analysis. Multiple window widths were used to decrease scale dependence. When using SMW, a significance test determines whether or not discontinuities have higher values than expected under the null hypothesis of no distinct boundaries (Cornelius & Reynolds 1991; Fortin et al. 2000).

We assessed the significance of peaks found in SMW graphs by comparing them to peaks created in a random distribution, conducted following Cornelius & Reynolds (1991). The mean expected SMW dissimilarity and standard deviation between window halves for a given data series and window width were calculated using a Monte Carlo method computed with a MATLAB 6.5 (Mathworks). The method randomized each meter along a transect 1000 times, and repeated SMW calculations for the three window widths. We calculated overall expected means and standard deviations from the dissimilarity values for each window width and for each meter. We repeated this procedure for all 20 transects. Our non-restricted approach is conservative because it allows any combination of sampling units within each transect to be used to assess the level of background variation. Alternative procedures with restricted randomization can assess subtle changes but they require an a priori classification of the sampling units (Fagan et al. 2003).

For each window width, we calculated a normal Z-score by subtracting the overall expected mean from the observed dissimilarity value and dividing by the overall expected standard deviation. For each meter of a transect, we subsequently averaged the three Z-scores from three window sizes. Mean Z-score dissimilarity values were then plotted against transect position to identify points of greatest dissimilarity (high peaks). We defined as ecotones all peaks located above the 95% confidence interval ($Z = 1.65$) of the null distribution. Consecutive peaks with values of 1.65 and above were interpreted as wide ecotones. In some instances, consecutive peaks with values of 1.65 or more occurred interspersed with one or two meters of lower Z-scores; in these cases, we interpreted this area of high heterogeneity as a patchy ecotone.

Ecotone location and vegetation cover

To describe plant assemblages, we interpreted vegetation cover between two consecutive areas of high Z-scores as a relatively homogenous plant assemblage. We assigned these plant assemblages based on Abrahamson et al.'s (1984) classification.

To examine the consistency of this classification system, we entered vegetation cover data of defined plant assemblages (we corrected for differences in length of transects by taking the percent of the species cover for each assemblage) into a Non-metric Multidimensional Scaling (NMDS) ordination in PC-ORD 4 (Kruskal 1964). The ordination was conducted with the Sørensen distance measure (McCune & Grace 2000) and a random starting configuration. Sørensen distance is a city block distance measure expressed as a proportion of the maximum distance (McCune & Grace 2000). We used 50 runs with real data and the autopilot mode to determine the dimensions of the ordination. Three dimensions were included in the ordination after assessing the stability of these dimensions with a plot of stress vs. iteration. To assess the strength of the ordination, we selected a Monte Carlo option with 50 runs of randomized data. The final configuration of the ordination ran with 100 iterations with a probability of 0.02 that similar stress could be obtained randomly.

Effect of elevation and time since fire

We investigated the relationships of ordination axes with median relative elevation and TSF. At ABS, the northern half of the property occurs at a higher absolute elevation than the lower half of the property. Water table is unrelated to absolute elevation; therefore, we used only relative elevation in our analyses. We calculated median relative elevation for each plant assemblage (defined between significant peaks) and for each

ecotone identified by the SMW analysis. We then assessed if plant assemblages occurred at different relative elevations (ANOVA; Tukey's *post hoc* test).

To test if TSF affected the presence of ecotones, dissimilarity values calculated in the SMW analysis for all 20 transects were grouped by TSF categories (1 year, 5-8 years, 15 years and > 30 years) and compared for differences (ANOVA; Tukey's *post hoc* test). We predicted that if TSF has an effect on ecotones, dissimilarity values would differ among TSF categories.

Results

Ecotone location

Split moving windows analysis identified ecotones in 19 of 20 transects (Fig. 1). The number of ecotones per transect ranged from 1 to 4, with 9 of 20 transects containing two ecotones. Between ecotones we identified six homogeneous plant assemblages (Table 1).
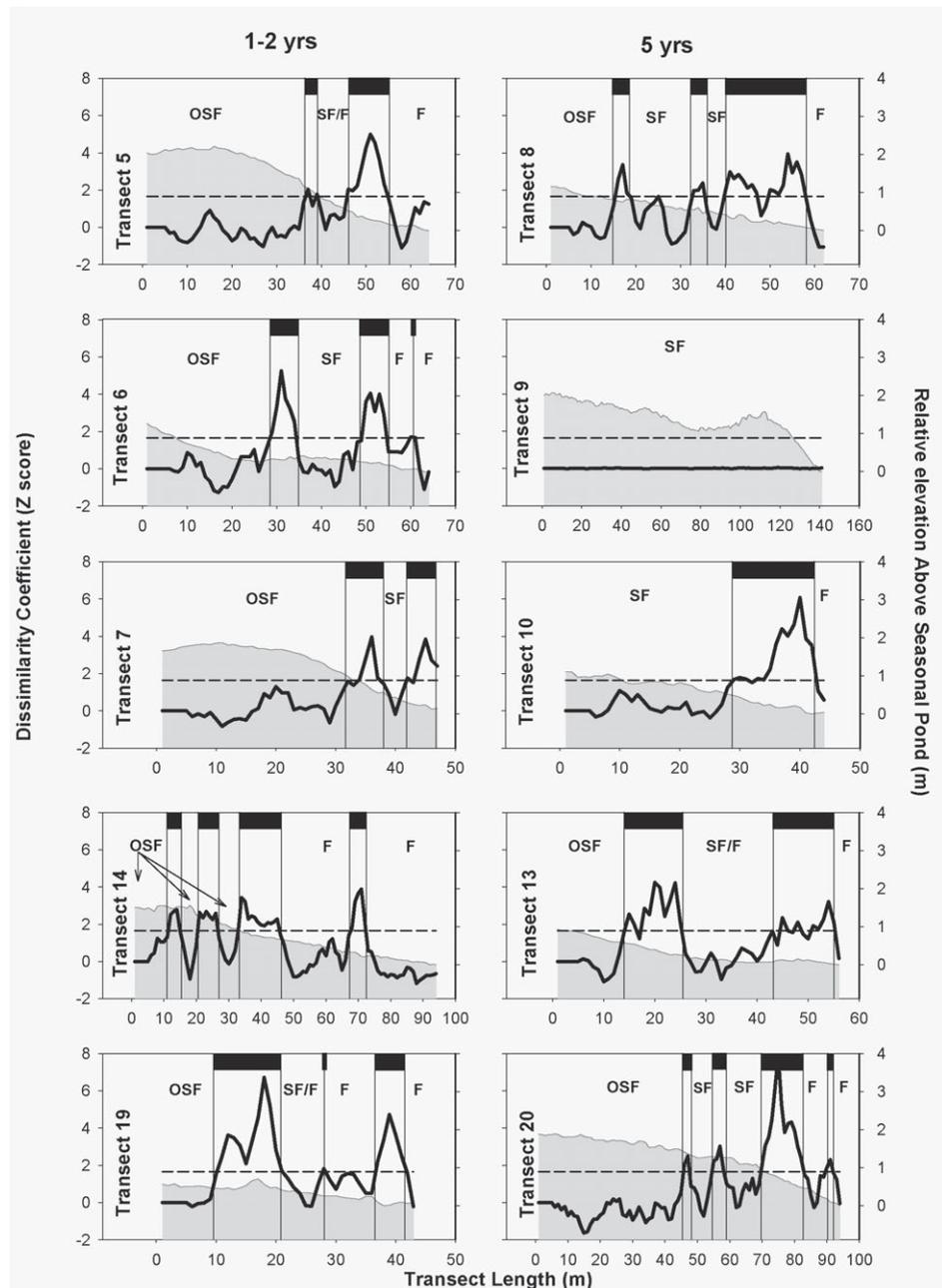

Fig. 1 (and overleaf). Dissimilarity coefficients (represented as Z-scores) of all 20 transects plotted against transect length (m). Classified vegetation zones (labeled in text) and ecotones (in black) are found along the top of each graph. The single dashed horizontal line denotes the 95% confidence limit criterion above which SMW peaks were significant. The filled gray profile represents the elevation gradients traversed by each transect. Transect 9 does not contain any ecotones and covers a uniform assemblage; the dissimilarity coefficients appear as a solid black line. Transect 9 was the longest transect (147 m) and therefore the elevation change was extremely gradual compared to other transects.

Classifying plant assemblages

We identified three homogeneous plant assemblages corresponding to those described by Abrahamson et al. (1984): Rosemary Scrub (RS), Scrubby Flatwoods (SF), and Flatwoods (F). Other homogeneous assemblages identified in our study did not concur with Abrahamson et al.'s (1984) descriptions. In some transects, areas between ecotones grouped into one of three new assemblages, each containing a mixture of species from two of the previously described associations. We termed these new assemblages Open Scrubby Flatwoods (OSF), Rose-

mary Scrub/Scrubby Flatwoods (RS/SF), and Scrubby Flatwoods/Flatwoods (SF/F; see Fig. 1). The Open Scrubby Flatwoods type (OSF) is found at high elevations typical of RS but with lower cover of *Ceratiola ericoides* and higher cover of oaks. Rosemary Scrub/ Scrubby Flatwoods (RS/SF) was characterized by a large amount of bare sand, almost no *C. ericoides* and high cover of oaks compared to RS. The RS/SF assemblage differed from SF in having lower oak coverage and high palmetto coverage. Finally, the SF/F assemblage occurred at the same elevations as F but SF/F had higher oak coverage than F, combined with high palmetto
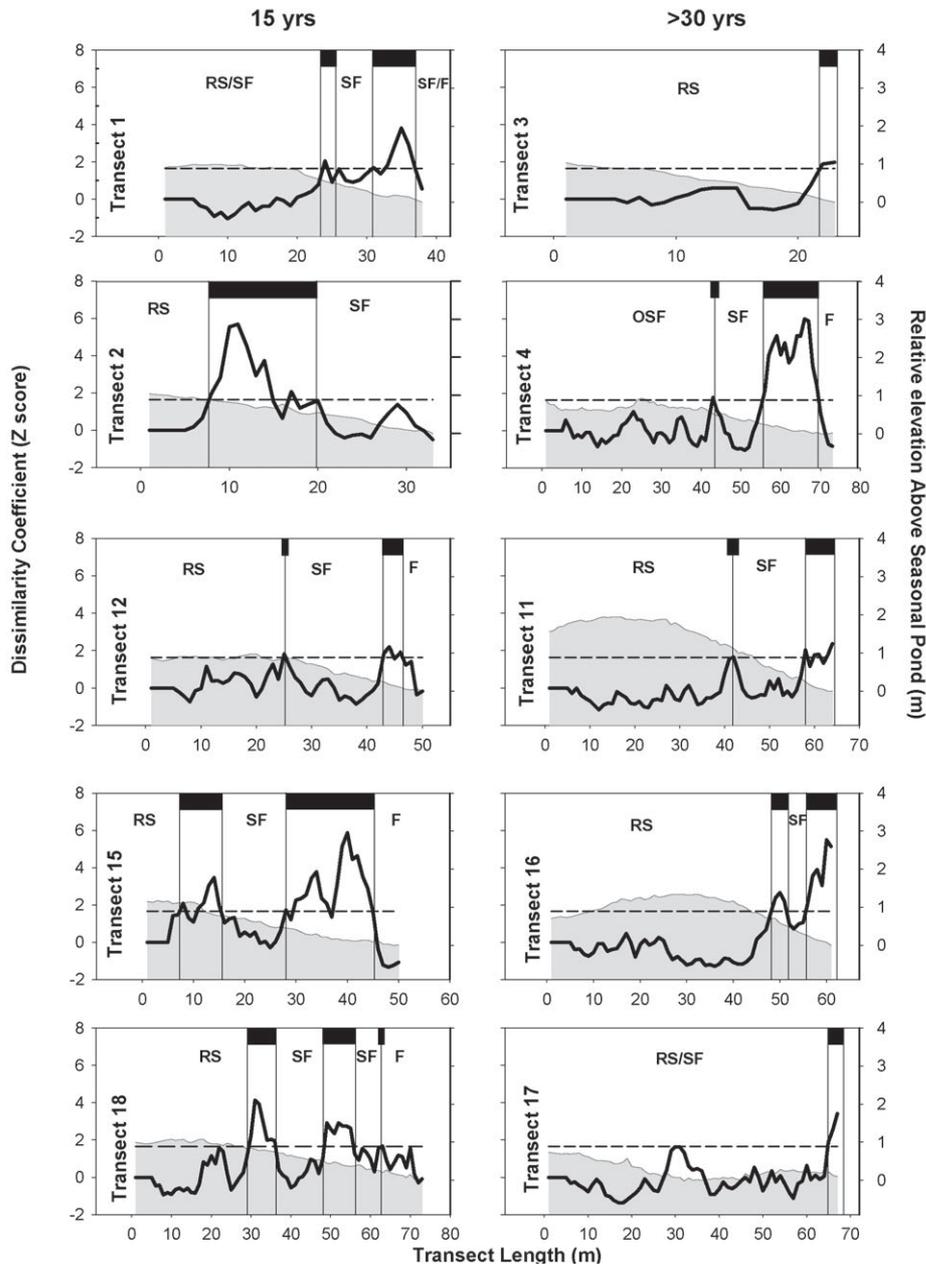
Table 1. Mean cover (%) of dominant vegetation types from all transects within each of six homogenous plant assemblages identified by split moving window analysis (SMW). 'Scrubby oaks' include *Quercus inopina*, *Q. chapmania*, *Q. geminata*; 'Other shrubs' is all other woody species; 'Palms' include *Serenoa repens*, and *Sabal etonia*. Values in [ ] are percent cover estimations from Table 3 in Abrahamson et al. (1984).

	Litter	Oaks	*Ceratiola ericoides*	Other shrubs	Palms
RS ($n = 7$)	61.4 [80]	28.4 [55]	14.0 [8]	3.7 [6-7]	7.7 [3]
OSF ($n = 11$)	40.0	0.8	30.5	8.9	20.1
RS/SF ($n = 2$)	80.0	19.0	31.5	1.5	7.5
SF ($n = 17$)	85.3 [90]	1.7 [0]	43.8 [57]	19.2 [8-10]	19.2 [30]
SF/F (4)	90.0	0	33.0	12.3	41.5
F ($n = 16$)	88.8 [90]	0.9 [0]	5.9 [1-3]	32.3 [30]	59.6 [36-77]

and other shrub coverage (Table 1). Often, a significant peak divided either SF or F because of change in a dominant species of oak or grass occurred.

The NMDS ordination showed assemblages with some overlap. The ordination explains 0.77 of variance in species relative cover (Axis 1, $r^2 = 0.20$; Axis 2, $r^2 = 0.31$; Axis 3, $r^2 = 0.26$).

Relative elevation and fire

Separation of plant assemblages was greatest on ordination Axis 2, which was significantly correlated with median relative elevation ($r^2 = 0.30, p < 0.001$; Fig. 2). This relationship was stronger when TSF was added to the regression ($r^2 = 0.42, p < 0.001$). Axis 1 and Axis 3 were weakly or not significantly correlated with median relative elevation (Axis 1 ($r^2 = 0.05, p = 0.02$); Axis 3 ($r^2 = 0.003, p = 0.56$)) and were unrelated to TSF (Axis 1 ($r^2 = 0.02, p = 0.17$); Axis 3 ($r^2 = 0.04, p = 0.39$)).
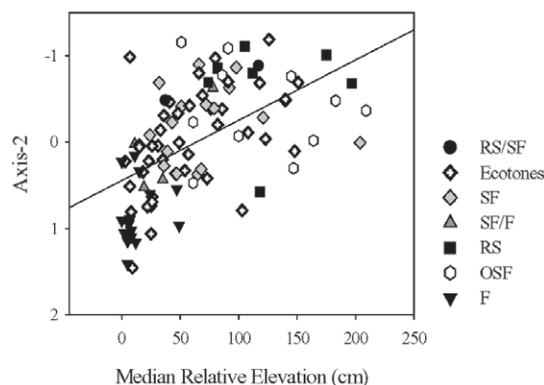

Fig. 2. Axis 2 of the NMDS ordination was negatively correlated with median relative elevation ($r^2 = 0.30, p < 0.001$).
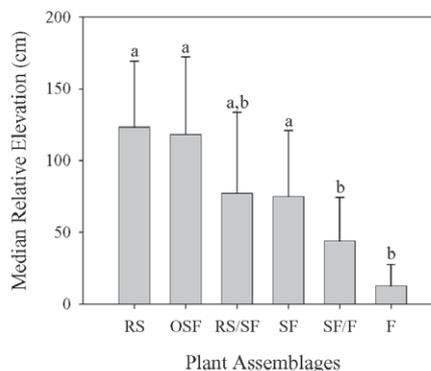

Fig. 3. Plant assemblages occurred at different relative elevations (ANOVA $F_{(5,56)} = 12.35, p < 0.001$, Mean + SE). Letters denote significant differences in elevation between groups ($p < 0.05$). RS/SF is statistically non-significant in median elevation to all other groups.

Plant assemblages were found in different locations along the gradient of relative elevation (ANOVA, $F_{(5,56)} = 12.35, p < 0.001$; Fig. 4). RS and OSF occurred at the same elevation ca. 1.2 m above seasonal ponds. SF typically occurred 0.75 m above seasonal ponds, SF/F occurred at 0.48 m and F occurred at ca. 0.14 m above seasonal ponds. Not all these differences were significant (Fig. 4).

Normalized dissimilarity coefficient values (Z-scores) differed among TSF categories (ANOVA, $F_{(3,16)} = 36.603, p < 0.001$; Fig. 4). Z-scores were significantly lower in > 30 years TSF than Z-scores in 1-2, 5-8 and 15 years TSF (Tukey's $p < 0.05$).
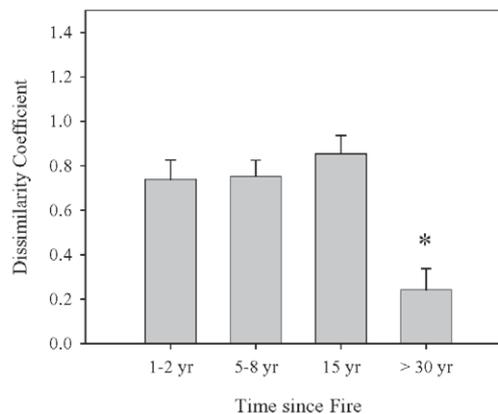

Fig. 4. Comparison of mean dissimilarity among TSF categories. Assemblages in transects > 30 a TSF had significantly (* = $p < 0.05$) lower dissimilarity values than 1-2 a, 5-8 a and 15 a TSF (ANOVA: $F_{(3,16)} = 36.603, p < 0.001$, Mean +SE).

Discussion

Classification of plant assemblages

Overall, SMW was successful in locating ecotones and six areas of relatively homogenous vegetation composition along transects of Florida shrubland vegetation. SMW was sensitive to patchiness in vegetation and infrequently identified significant peaks in areas that were not true ecotones We limited this effect of the SMW technique by using three window widths to decrease scale dependency and sensitivity to patchiness (Cornelius & Reynolds 1991). Our analysis did not clearly define the width of these ecotones. Hennenberg et al. (2005) performed a combination of SMW and a moving window regression analysis to identify both ecotone location and width.

Relative elevation and fire

Our analysis supports distance to the water table as the primary environmental factor determining plant assemblages as suggested by previous studies. Rosemary Scrub occupies the most xeric sites, Scrubby Flatwoods intermediate and Flatwoods occupies mesic areas.

Time since fire also influenced the distribution of plant assemblages. RS occurred more frequently in longer unburned areas. The dominant species in RS, *Ceratiola ericoides*, is an obligate seeder that is killed by fire and requires 10 to 15 years to reach reproductive maturity (Johnson 1982). In contrast, SF and F are dominated primarily by obligate re-sprouters (Abrahamson 1984b; Menges & Kohfeldt 1995) and composition of these assemblages is not greatly changed after fire because dominants quickly re-sprout. Our results suggest that vegetation composition is relatively continuous along the elevational gradient in the absence of fire, while fire sharpens ecotones.

Mechanisms maintaining ecotones

Why do ecotones become more diffuse after 30 year? One possible explanation could be that dominant species from plant assemblages on either side of the ecotones invade each other, causing vegetation to become more similar. Alternatively, within a plant assemblage, the dominant plants may become larger, causing a decrease in bare ground and suppression of subordinate species. Menges et al. (1993) concluded that upland species composition is maintained over time and that invasion between plant assemblages is rare. Furthermore the abundance of oaks did not increase significantly with TSF in RS, while abundance of some oaks and palmettos (in particular *Q. geminata* and *S. repens*)

increased in SF (Menges & Kohfeldt 1995). These studies support the hypothesis of structural change within assemblages, rather than invasion between assemblages, as the reason for less distinct ecotones with greater than 30 years time since fire.

The transects surveyed in this study contained broad ecotones that were highly heterogeneous, indicated by low dissimilarity values interspersed between consecutive significant peaks. Ecotones may be areas that contain a series of transitions by different life-forms. These transitions, although they occur in the same general area, are spread out, creating a broad ecotone. Hennenberg et al. (2005) showed that trees, grasses, herbs, shrubs, etc. transition as an 'interlocked sequence of ecotones' within forest-savanna ecotones creating a broad ecotone.

Variable flammability of vegetation assemblages resulting in heterogeneous burn pattern may also be responsible for the observed structure of ecotones. Many boundaries act as barriers to the spread of disturbance due to combination of species (Gosz 1991). A barrier to the spread of fire is likely to occur where frequently burned productive vegetation interdigitates with xeric, less frequently burned vegetation. Spatial heterogeneous burn patterns within an ecotone would create a more distinct boundary between vegetation assemblages as species recover at different rates.

Maintaining heterogeneity in habitat structure (i.e. maintaining discrete plant assemblages with distinct ecotones) has been shown to promote diversity in many systems. This is important in areas where many species are endemic and endangered, as in upland Florida shrublands. In the absence of fire, slow structural changes occur in Florida vegetation resulting in diffuse ecotones and less habitat heterogeneity with consequences for species unique to Florida shrublands.

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