

Multi-Scaled Grassland-Woody Plant Dynamics in the Heterogeneous Marl Prairies of the Southern Everglades

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ABSTRACT

The Everglades freshwater marl prairie is a dynamic and spatially heterogeneous landscape, containing thousands of tree islands nested within a marsh matrix. Spatial processes underlie population and community dynamics across the mosaic, especially the balance between woody and graminoid components, and landscape patterns reflect interactions among multiple biotic and abiotic drivers. To better understand these complex, multi-scaled relationships we employed a three-tiered hierarchical design to investigate the effects of seed source, hydrology, and more indirectly fire on the establishment of new woody recruits in the marsh, and to assess current tree island patterning across the landscape. Our analyses were conducted at the ground level at two scales, which we term the micro- and meso-scapes, and results were related to remotely detected tree island distributions assessed in the broader landscape, that is, the macro-scape. Seed source and hydrologic effects on recruitment in the micro- and meso-scapes were analyzed via

logistic regression, and spatial aggregation in the macro-scape was evaluated using a grid-based univariate O-ring function. Results varied among regions and scales but several general trends were observed. The patterning of adult populations was the strongest driver of recruitment in the micro- and meso-scape prairies, with recruits frequently aggregating around adults or tree islands. However in the macro-scape biologically associated (second order) aggregation was rare, suggesting that emergent woody patches are heavily controlled by underlying physical and environmental factors such as topography, hydrology, and fire.

Key words: woody plant invasion; recruitment; dispersal; hierarchical patch dynamics; univariate grid-based O-ring function; spatial patterning; community and landscape structure; shifting boundaries; tree islands; Cape Sable seaside sparrow habitat.

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INTRODUCTION

A century of drainage, compartmentalization, and fire suppression has irrevocably reduced the Everglades to half its original size, and despite recent restoration efforts, more than 2500 km of canals, levees, and water control structures threaten to slowly deteriorate what remains. Preservation of extant communities may require a restructuring of

hydrologic systems and a revision of fire management practices to better emulate natural conditions. However, natural environmental conditions are not always clearly defined and the historical distribution of landscape patches is not well documented. Although we know that both historical and present day landscapes contained thousands of tree islands embedded within marsh/grassland matrices, we do not clearly understand the extent to which management has altered the scale and pattern of this woody-graminoid mosaic, nor do we understand the sensitivity of patch dynamics to variation in management scenarios. Researchers suspect that the freshwater marl prairie landscapes comprising the outer regions of Everglades National Park (ENP) may be vulnerable to woody plant expansion (Jenkins and others 2003a, b) due to alterations in natural disturbance mechanisms (namely, flood and fire management). However, potential encroachment patterns and processes have not been examined in detail.

Spatial processes play an integral role in the dynamic balance between woody and graminoid cover in the Everglades marl prairie landscape, and these processes vary across scales. Although local-level studies provide valuable information on the distribution and abundance of interacting species within patches, neighborhood processes also inevitably influence within-patch conditions (Levin 1992; Wu and Levin 1994; Chase and Leibold 2002). Because increases in woody plant cover may be obscured or exaggerated in studies that focus specifically on patch-scale phenomena (With and King 2001), multi-scaled spatial detail is indispensable for conservation biologists who wish to effectively manage the unique habitat requirements of multiple interacting species. Preservation of habitat complexity within the Everglades heterogeneous marl prairies for example, necessarily requires a better understanding of the spatially explicit effects of seed source, hydrology and fire on woody plant recruitment and encroachment.

Marl prairies contain species-rich grasslands and tree islands that vary in size, density, and composition. The resident flora and fauna depend upon the persistence and connectivity of both grassland and woody community types, maintained through intertwining biotic and physical feedback mechanisms. The endemic Cape Sable seaside sparrow (CSSS; *Ammodramus maritimus mirabilis*) in particular requires extensive and well-connected prairie habitat patches (Nott and others 1998; Browder and Ogden 2000; Pimm and others 2002; Jenkins and others 2003a, b), whereas several wading bird species such as the woody stork (*Mycteria*

Americana) and white ibis (*Eudocimus albus*) utilize prairie regions for foraging, but require intermittent woody patches for nesting and roosting (Hoffman and others 1994). Cyclical shifts in the spatial patterning of habitat types are driven to various degrees by environmental dynamics and the physiological adaptations of local biota, such as flood and/or fire tolerance, life history traits, and phenological patterns. Woody plant establishment in the marsh may be the leading spatial process influencing habitat shifts across the landscape. The distribution of new woody recruits provides a template for successive processes that promote or inhibit woody patch nucleation and persistence (Nathan and Muller-Landau 2000).

Nucleation around woody stems involves multiple positive feedback mechanisms, which are limited by hydrology and disturbance. Tree island development frequently begins with soil accretion around newly established individuals or surface anomalies. As woody plants colonize these topographic rises, concomitant increases in peat production further alleviate flooding stress in support of continued patch expansion (Rietkerk and others 2004). In addition to altering the local topography, established individuals serve as magnets for seed-dispersing animals, which results in the development of mixed species assemblages. These assemblages exhibit higher transpiration rates than surrounding marshes, which increase the concentration of nutrients below their developing canopies. Transpirative nutrient accumulation and increased faunal input also contribute to the competitive advantage of woody plants over grasses (McCarthy and others 1993; Wetzel and others 2005; Ross and others 2006a; Givnish and others 2008; Hanan and Ross 2010). Newly developed tree islands promote woody plant expansion at landscape scales through seed production and physiochemical interactions with neighboring communities. Meanwhile, disturbance in the form of periodic fire serves to slow and set back tree island establishment and nucleation (Lockwood and others 2003).

The patterning of habitat patches within a landscape affects the ultimate size and distribution of emerging patches (Wu and Levin 1994). Therefore, to understand habitat change, it is necessary to assess both community-level processes such as those affecting recruitment, and landscape patterns. The Hierarchical Patch Dynamics Paradigm (HPDP) combines patch dynamics perspective (Watt 1947) and hierarchy theory to structure knowledge on multi-scaled heterogeneous systems (Wu and Loucks 1995). Within the HPDP framework, we integrated ground-level and remote

sensing data to investigate the effects of seed source, hydrology and more indirectly, fire on the recruitment of new woody stems in the marsh. We also mapped and analyzed the spatial patterning of existing forested area across the study region to test the following hypotheses:

- (1) Source effects (i.e., size and proximity of adult trees and tree islands) are a strong determinant of recruitment in the prairie. Specifically, establishment probability increases with proximity to conspecific adults and/or tree islands due to gradients in dispersal and/or habitat suitability.
- (2) Hydrology impacts establishment across scales and differing hydrologic scenarios favoring the establishment of some species over others at each location.
- (3) Tree islands are aggregated at multiple scales, due to biological and biogeochemical feedbacks (i.e., biogenesis).

Our ground-level analyses were conducted at two scales and levels of detail, which we term the micro-scape (i.e., single tree islands and their immediate surrounding environments) and the meso-scape (i.e., intermediately-sized prairie regions that include multiple tree islands). We also related our ground-level observations to remotely detected woody plant distributions assessed at the macro-scape (i.e., large landscapes that include a heterogeneous mosaic of high- and low-density patches of tree islands).

METHODS

Study Site

Our study was conducted within the short-hydro-period marl prairies located along the edges of the Shark and Taylor Sloughs in Everglades National Park. Sampling took place between 2006 and 2008 in six regions designated as subpopulations for the endangered Cape Sable seaside sparrow (subpopulations A–F; Figure 1). Soils range from calcitic marls classified as fluvaquents in the open marsh, to histosols found within tree islands and/or other densely vegetated patches. Marl prairies exhibit characteristically high graminoid diversity maintained by relatively short hydroperiods (inundated for approximately 3–7 months per year). In this part of the Everglades, tree islands typically form in conjunction with limestone bedrock highs, which reduce flooding stress that might otherwise inhibit woody growth.

Hydroperiods in the Everglades are influenced by climatic drivers, and modified by operations of the

South Florida Water Management District's (SFWMD) network of canals, levees, and water control structures. The primary controls of water redistribution to the study area are channeled through the S12 structures, located along Tamiami Trail, north of Shark Slough, and the S332 detention basins, located along the L31W and L31N canals (Figure 1). The South Florida wet season typically extends from May through early October, whereas the dry season occurs from the end of October through April. Mean annual precipitation ranges from 120 to 160 cm, and mean daily temperatures range from 17 to 25°C (Obeysekera and others 1999). A record-setting drought between 2006 and 2008 impacted hydroperiods across the southern Everglades (Meeker 2008).

Extensive burns (consuming more than 93 km² of vegetation) occur approximately every 10–15 years in the larger Everglades ecosystem, typically in late spring when conditions are still relatively dry (Gunderson and Snyder 1994). Smaller fires that occur more frequently tend to spark during wet season thunderstorms typical of June and July. The natural fire return interval is complicated by fire management practices, which both suppress large natural fires and ignite controlled burns to reduce fuel loads, maintain early successional stages, and inhibit the proliferation of invasive species (Lockwood and others 2003; La Puma and others 2007). The role of fire in the maintenance of species composition and structure within the marl prairie landscape is not fully understood.

Sampling Design

Our study was designed to analyze the woody plant encroachment process broadly across the marl prairie landscape and more intensively at specific invasion fronts within each CSSS subpopulation. Six study areas were established, one within each subpopulation (Figure 1), and sampling followed a hierarchical design (Figure 2). One macro-scape (i.e., a 3.2 km × 3.2 km cell comprising a single South Florida Water Management Model grid cell) was selected at random within each subpopulation, and then divided into nine 1 km × 1 km plots (leaving a buffer of 100 m on all sides). From these, a single 1-km² meso-scape was randomly selected in each subpopulation (Figure 1). To examine the demography of individual woody species in the vicinity of tree islands, one 100 m × 100 m (1 ha) micro-scape was centered on a randomly selected tree island within each meso-scape (Figure 1). Each micro-scape was partitioned into

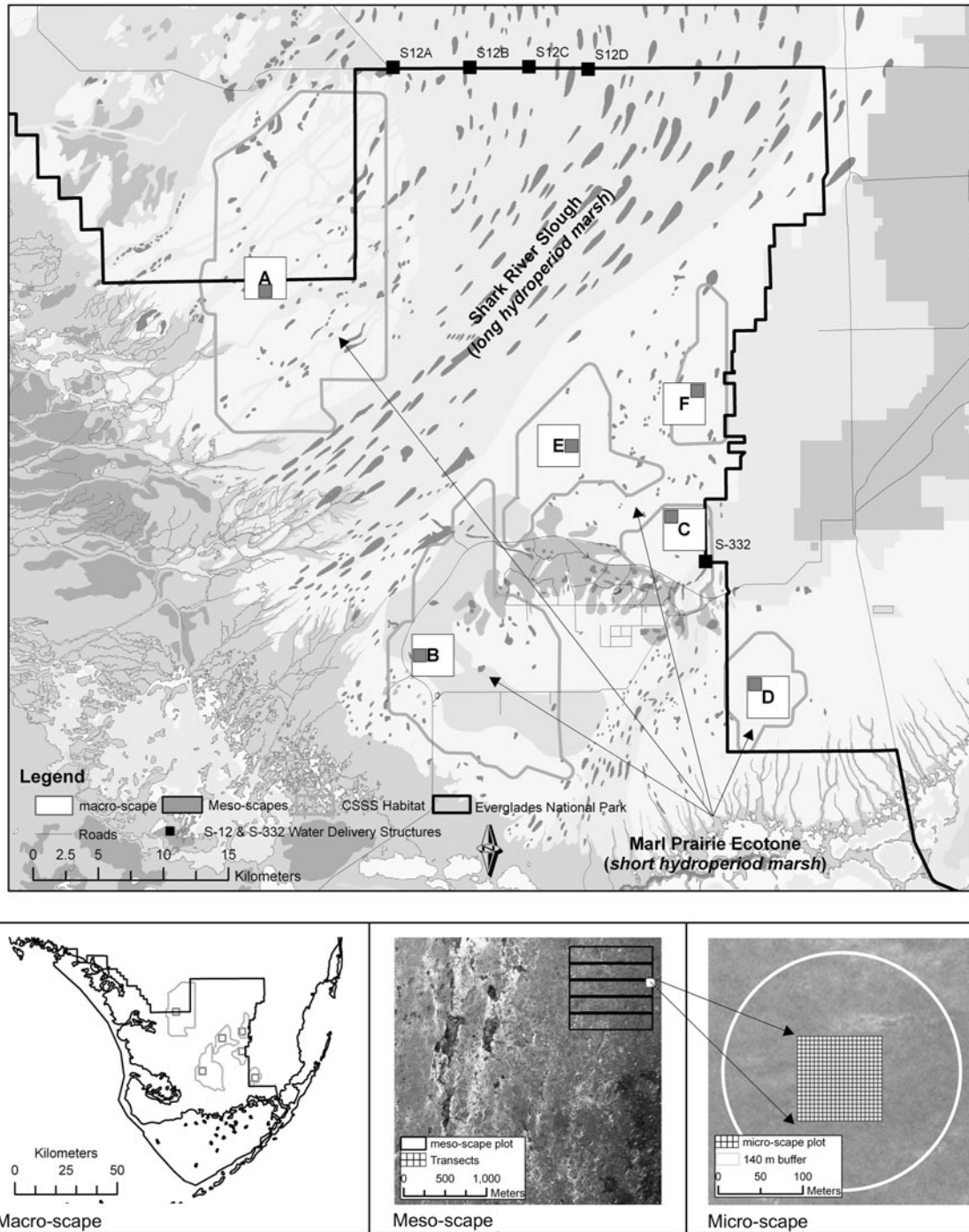


Figure 1. Location of the six macro-scale plots within the habitat of the Cape Sable seaside sparrow (CSSS) in Everglades National Park, FL, and sampling design for meso- and micro-scales.

100 10 m x 10 m subplots and those subplots were each further partitioned into four 5 m x 5 m grid cells (400 cells total per micro-scale; Figure 1).

In each micro-scale, all adult (height > 2 m) trees and recruits (height < 2 m) present outside the central tree island were identified to species, mapped to nearest 0.5 m, tagged, and measured by

height. Trees within the central tree islands were mapped and measured in similar fashion, but recruits were not. Elevations and soil depths were determined at the corners of each 10 m x 10 m subplot, by auto-level surveys from benchmarks of known elevation. Additional elevations were determined at random points within the central

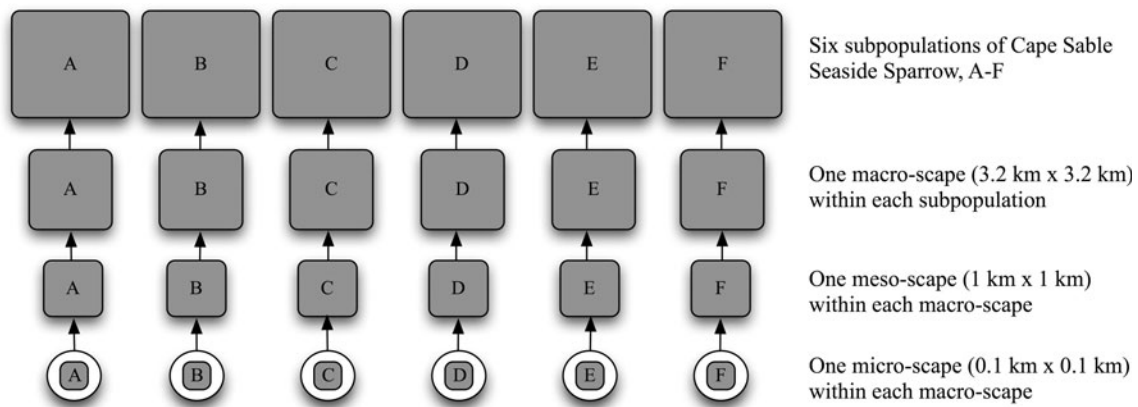


Figure 2. Schematic of study's nested scale hierarchy within the Everglades marl prairie landscape.

tree islands, and at the base of each woody recruit in the marsh. Elevation surfaces were created via ordinary kriging in ESRI[®] ArcMap[™] 9.3 using a spherical model, and elevations were extracted for each of the 400 5 m × 5 m cells within the 1-ha plot, based on the center of each cell's geometric axis. Radial distances between cell centroids and each adult tree were calculated and subsequently used to relate size and proximity of potential seed sources to the distribution of recruits outside the tree island. To identify additional potential seed sources, all tree islands and individual woody plants located within a 140-m buffer of each plot's centroid (Figure 1) were also identified, mapped, and measured.

Four 1-km long, E–W oriented strip transects were established across each meso-scale, equally spaced at 200-m intervals (Figure 1). Individual woody plants present within 10 m of the transect center were identified to species, mapped, and measured for height. GPS coordinates were recorded every 100 m along the transect. For analytical purposes, transects were divided into ten 90-m long segments (with 20-m unsampled spaces between segments to prevent overlap resulting from compass error), and each segment was divided into two rows of 10 m × 10 m cells (one on either side of the transect; 18 total per segment). Presence/absence and counts of woody plants within each 10 m × 10 m cell were determined. Radial distances between cell centroids and remotely digitized tree islands within 200 m of each cell were calculated and subsequently used to relate size and proximity of potential seed sources to mapped individuals found along each transect. Also, marsh vegetation community types were visually recorded every 20 m along each transect using designations outlined by Ross and others (2006b).

All landscape features within the six macro-scales were identified and mapped by soft-copy remote sensing techniques using a set of 2004 NAPP color infrared aerial photographs with a 1-m spatial resolution (1 × 1 m pixel). Because of the quality and spatial resolution of the imagery, a 5 m² minimum mapping unit (mmu) was considered to be the lowest resolution by which landscape features could be properly discerned and accurately classified. Features larger than the mmu were digitized on screen, using ESRI[®] ArcMap[™] 9.3. Landscape features that extended beyond the perimeter of the macro-scale were truncated at the macro-scale boundary.

Data Analysis

To analyze source and hydrologic effects on the establishment of woody species within each micro-scale, Species Source Factors (SSFs) and hydroperiods were calculated for all plot cells, and subsequently evaluated using stepwise logistic regressions. SSFs were calculated as follows:

$$SSF_{ij} = \sum \left(\frac{h_j}{r_{ij}} \right) \quad (1)$$

where h represents adult tree heights for species j , and r_{ij} is the radial distance from the centroid of cell i to potential source trees of species j within the 140-m buffer. Adult tree heights were normalized by calculating their percent of the maximum height for each species. Assumptions underlying SSF_1 include (1) seed outputs of individual trees are proportional to their size (Thomas 1996; Nathan and Muller-Landau 2000), and (2) because the number of cells at radial distance r from a source tree is proportional to $2\pi r$, the probability for recruitment within a given cell is proportional to $1/r$.

Hydroperiods (mean days per year flooded) were calculated for each cell using elevation estimates, coupled with Everglades Depth Estimation Network (EDEN 2008) daily water stage records for the 6-year period 2000–2006.

Using presence/absence of recruits within plot cells (outside tree islands), the effects of SSF and hydroperiod were evaluated by stepwise logistic regression using the following model:

$$P(m) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 \text{SSF}_{ij} + \beta_2 \text{Hydroperiod}_i)}} \quad (2)$$

where $P(m)$ is the probability of species j establishment within cell i . In our stepwise logistic regression, variables were selected in the order of their contribution to the model. If a variable did not contribute significantly, it was removed and a reduced model was then run. Logistic regressions were carried out for all species present in at least two cells in 2007 that had at least one potential parent tree within the 140-m buffer. To avoid potential confounding of hydroperiod with SSF we (1) omitted cells that were completely or partially within tree island boundaries and (2) tested for collinearity between hydroperiod and SSF.

Species-specific observations of saplings and adults were made along transects, but individual regressions were not possible in the meso-scape analysis because the species compositions of all tree islands within the 1 km² were not known. Likewise, the precise hydrology associated with each stem could not be estimated, due to the lack of a detailed and comprehensive topography for the region. Therefore, to analyze source and hydrologic effects on the establishment of woody plants within each meso-scape, we calculated a non-specific Woody Plant Source Factor (WPSF) and a vegetation-based Prairie Wetness Index (PWI) for each transect cell. WPSFs were calculated as follows:

$$\text{WPSF}_{ij} = \sum \left(\frac{a_j}{r_{ij}} \right) \quad (3)$$

where WPSF_{ij} is the Woody Plant Source Factor for cell i , and j represents tree islands within 100 m of cell i . Assumptions underlying WPSF are similar to those for SSF, namely that (1) seed outputs of tree islands are proportional to their area, and (2) the probability for recruitment within a given transect cell is proportional to $1/r$, where r is the distance between the source tree island's centroid and the centroid of each cell.

PWI was calculated from vegetation community observations made at 20-m intervals along each transect. For each herbaceous community

observed, a relativized wetness index ranging from 1 to 10 was derived from vegetation-inferred hydroperiods outlined in Ross and others (2006b). Communities at the lower end of the scale were less flood-tolerant than communities at the upper end of the scale; for example, the PWI of *Muhlenbergia* Wet Prairie and *Eleocharis-Rhynchospora* Marsh were 1 and 10, respectively.

Using presence/absence of individual woody recruits and/or adults within transect cells (outside tree islands), the effects of WPSF and PWI were evaluated by stepwise logistic regression using the following model:

$$P(m) = \frac{1}{1 + e^{-(\beta_0 + \beta_3 \text{WPSF}_{ij} + \beta_4 \text{PWI}_i)}} \quad (4)$$

where $P(m)$ is the probability of species j establishment within cell i . Logistic regressions were carried out for all species present in at least two cells along the transects. As with the micro-scape, we avoided potential confounding of PWI with WPSF by (1) omitting cells that were completely or partially inside tree islands and (2) testing for collinearity between PWI and WPSF. All logistic regressions were run in SPSS version 14.0 (SPSS Inc.) and plotted using Statistica (Statsoft Inc.).

The spatial patterning of tree islands within each of the six macro-scapes was analyzed using an O-ring statistic derived in Programita (Wiegand and Moloney 2004). The O-ring statistic is a second-order probability density function, similar to the more commonly used Ripley's K; however, the O-ring statistic uses annuli instead of circles, thus identifying the levels of aggregation or dispersion that occur at specific distance classes (Wiegand and Moloney 2004). In this study, second-order aggregation may be indicative of tree island biogenesis via positive feedback mechanisms.

Because tree island dimensions varied significantly across our macro-scapes, non-dimensional point patterns, which are frequently used in spatial analysis, were not suitable to represent their distribution and influence. Instead we converted our vector-based maps to ASCII grid-files (cell size = 5 m), which allowed us to randomize entire islands rather than just object centroids, thereby conserving their dimensional properties. Features that were not tree islands (for example, pine forest, roads, and so on) and tree islands that were truncated by the macro-scape boundary were masked from the analyses.

Complete spatial randomness (CSR) is the simplest and most commonly used null model in spatial pattern analyses (Wiegand and others 2006b).

CSR assumes that objects within a given study area follow a Poisson distribution and as such, the intensity λ of these objects is constant and no interactions occur between them. However, ecological systems rarely meet this assumption because observed spatial trends can result from both broad-scale first-order phenomena, such as hydrologic, topographic, and edaphic gradients, or from smaller-scale second-order processes, such as dispersal and establishment. The simplest alternative to CSR is the heterogeneous Poisson null model (Wiegand and Moloney 2004). Like CSR, the heterogeneous Poisson null model assumes that the occurrence of any object is independent of any other object within the landscape; however, the distribution of these objects follows an intensity function $\lambda(x, y)$ which varies by location (x, y) ; (Wiegand and Moloney 2004). Because the heterogeneous Poisson null model accounts for large-scale (first-order) aggregation, it is more suitable for identifying second-order patterns in non-homogeneous landscapes (Wiegand and Moloney 2004).

We tested each macro-scale for homogeneity using the two-step grid-based approach outlined by Wiegand and Moloney (2004). Step 1 utilized a large moving window, R set to 150 (i.e., 750 m; one-quarter the width of each macro-scale) to remove all sizeable gaps or regions with extremely low point densities within each macro-scale. Step 2 calculated a smaller moving window, R_{\min} that could discriminate between gaps and possible empty plots to further refine each study region. R_{\min} values were 10 (i.e., 50 m) for macro-scapes A, B, C, and F, 12 (i.e., 60 m) for macro-scale D and 15 (i.e., 75 m) for macro-scale E. The heterogeneous Poisson null model then randomized tree islands locally within their given neighborhood R_{\min} in each macro-scale. In other words, the heterogeneous Poisson null model applied CSR to newly delineated homogenous sub-regions, thereby conserving large-scale (first order) patterns.

A Monte Carlo approach was used to construct confidence limits for our null model. Ninety-nine Monte Carlo simulations were used to determine the general broad-scale patterning of tree islands within each macro-scale at a maximum distance of 750 m. This distance was approximately one-quarter the width of each macro-scale and extended well beyond the scale at which the observed spatial pattern of tree islands deviated from our null model. Once general patterns were established, we re-ran the analyses using 299 Monte Carlo simulations at a maximum distance of 325 m in each macro-scale. We used the 5th lowest and highest values of the simulation envelope to

determine whether the observed patterns deviated from our null model. Because Type I errors can occur when the observed values fall particularly close to the simulation envelopes, a Goodness of Fit test (Loosmore and Ford 2006; Wiegand and others 2007) was also applied.

Lastly, fire histories for all three landscape scales (macro, meso, and micro) were constructed from a geodatabase populated with Everglades National Park 1980 to 2008 fire records. This spatial dataset allowed for the identification and extraction of all fires that occurred within the boundaries of the study areas during the last 29 years. For each plot at each scale, a fire recurrence interval (i.e., fire frequency) was calculated using the following equation:

$$\text{Fire recurrence} = \frac{1}{A_b/Y/A_t} \quad (5)$$

where A_b is the sum total area of all burns, Y is the number of years being analyzed (29), and A_t is the total plot area (1036, 100, and 1 ha for the macro, meso, and micro-scapes, respectively).

Because of the error associated with fire boundary locations it was not practical to apply fire recurrence effects to our spatially explicit logistic regressions. However, general trends were derived for each plot at each scale and discussed within the context of our other analyses.

RESULTS

Thirty-five woody plant species were identified in varying densities across the micro- and meso-scapes (Tables 1, 2). Micro and meso-scapes also varied in their hydrology (Table 3), creating suitable conditions for the habitat preferences and dispersal mechanisms of each woody species (Table 4).

Recruitment in the Micro-Scape

Highest recruit densities typically occurred immediately adjacent to central tree islands in the micro-scale (Figure 3) and declined exponentially with distance. Some species such as *Annona glabra* and *Salix caroliniana* however were more broadly distributed into the prairies (Figure 3). A positive source effect was identified for seven of the eight species-site combinations that contained enough individuals to justify a logistic regression (Tables 5, 6; Figure 4A). Significant hydroperiod effects were observed in only three cases; contrary to expectation, higher recruitment probability was associated with longer periods of flooding in each case (Tables 5, 6; Figure 4B).

Table 1. Density (stems/ha) of Individuals Present in Micro-scapes

Species	A		B		C		D		E		F	
	Adult	Recruit	Adult	Recruit	Adult	Recruit	Adult	Recruit	Adult	Recruit	Adult	Recruit
<i>Annona glabra</i>	1.6	41				1				23		1
<i>Baccharis halimifolia</i>			0.2	1							0.5	
<i>Baccharis</i> spp.											0.6	2
<i>Bursera simaruba</i>											0.8	
<i>Cephalanthus occidentalis</i>	0.2											
<i>Chiococca parvifolia</i>						1						
<i>Chrysobalanus icaco</i>	0.3	5								2		
<i>Coccoloba diversifolia</i>											0.2	
<i>Conocarpus erectus</i>					0.2	1					0.2	
<i>Eugenia axillaris</i>											1.1	
<i>Ficus aurea</i>	0.2				0.2			6			1.8	6
<i>Ilex cassine</i>	0.2				0.3	3				3	0.8	
<i>Magnolia virginiana</i>	0.2					1	2.0	59	0.3	3	1.6	
<i>Melaleuca quinquenervia</i> ¹											0.2	
<i>Morella cerifera</i>	3.9	2	0.8	11	2.1	4	4.1	34	1.6	6	18.7	
<i>Myrsine floridana</i>			0.2	1	0.8						5.7	24
<i>Persea borbonia</i>	2.6	66	0.2	9	2.8	29	5.9	423	1.5	105	17.1	
<i>Psychotria nervosa</i>											0.2	
<i>Randia aculeata</i>						3						
<i>Sabal palmetto</i>	0.7				0.2	9			0.5	9	7.1	4
<i>Salix caroliniana</i>		2			0.3				0.2		7.1	3
<i>Schinus terebinthifolius</i> ¹											8.6	1
<i>Sereinoa repens</i>			0.2									
<i>Sideroxylon reclinatum</i>						1					0.2	
<i>Sideroxylon salicifolium</i>					0.2						1.1	
<i>Solanum donianum</i>						1		1				155
<i>Taxodium distichum</i>					0.3		21.4	391				
Subtotals	9.7	116	1.5	22	7.3	54	33.3	914	4.1	151	73.6	211

Adults were greater than 2 m in height, found within 140-m buffer including central tree island. Recruits were less than 2 m in height, found within 1-ha plot. Recruit densities do not include those inside central tree island.

¹Invasive exotic species.

Recruitment in the Meso-Scape

In meso-scapes A, B, C, E, and F, a reduced model that included only Woody Plant Source Factor as a predictor of recruitment produced the strongest results (Tables 7, 8, Figure 5). In each case, the probability of establishment increased significantly with WPSF, that is, the area and proximity of tree islands. In meso-scape D, the probability of establishment increased with both PWI and WPSF (Tables 7, 8; Figure 5), namely, in wet locations near tree islands.

Tree Island Patterning in the Macro-Scape

Homogeneity tests revealed that tree islands in all six macro-scapes were heterogeneously distributed (i.e., aggregated at very large [>200 m] scales). Using the heterogeneous Poisson null model, our

O-ring function showed that tree islands in macro-scapes A, B, D, E, and F were more or less randomly structured with minor dispersion at some scales (Figure 6). Specifically, tree islands in macro-scapes A, B, and D were over-dispersed at intermediate scales (i.e., 30–140, 20–150, and 10–125 m, respectively), and tree islands in macro-scapes E and F were over-dispersed at smaller scales (i.e., below 95 and 5–25 m, respectively). Tree islands in macro-scape C were also over-dispersed at small scales (i.e., 5–25 m), and uniquely, they displayed aggregation at intermediate scales (i.e., 55–165 m).

Fire Patterns Across Micro-, Meso-, and Macro-Scapes

Seventy-eight fires burned 36,951 ha of marl prairie habitat across our study region over the last

Table 2. Density (stems/ha) of Individuals Present in Meso-scapes

Species	A			B			C			D			E			F				
	0.5-1	1-2	>2	0.5-1	1-2	>2	0.5-1	1-2	>2	0.5-1	1-2	>2	0.5-1	1-2	>2	0.5-1	1-2	>2		
<i>Acacia pinetorum</i>									1.1											
<i>Annona glabra</i>	5.0	0.2		0.6	0.2				1.7				1.1	0.4		3.9	1.6			
<i>Baccharis</i> spp.					0.0				2.8	1.8										
<i>Casuarina equisetifolia</i> ¹									0.2							30.6	24.7	2.4		
<i>Cephalanthus occidentalis</i>								6.7	5.8					0.2		3.9	1.6			
<i>Conocarpus erectus</i>				1.1	0.7			3.3	6.2	2.4								0.4		
<i>Eugenia axillaris</i>																		1.7		
<i>Ficus aurea</i>				2.8	1.3			0.6	0.4		2.2			3.9	0.4			1.1	2.0	
<i>Ilex cassine</i>				0.6	0.4			16.7	1.8	0.2	0.6			2.8				1.1		
<i>Magnolia virginiana</i>	1.1	0.9		16.7	18.4			5.0	6.4	0.2	0.6	0.2	1.6					1.1	0.9	
<i>Melaleuca quinquenervia</i> ¹															0.2			5.0	3.3	0.2
<i>Metopium toxiferum</i>				2.2	2.7				0.2	0.9	0.6	0.9	0.4						0.7	
<i>Morella cerifera</i>	4.4	3.3	1.6	7.8	4.4	2.7		8.3	4.4		5.0	0.7		1.1	3.6			2.8	3.1	1.1
<i>Myrsine floridana</i>		0.4		6.7	2.9			10.0	2.4			0.2		3.9				12.8	6.4	
<i>Persea borbonia</i>	0.6	2.0		12.2	13.3	0.2		20.6	5.1	1.6	5.0	2.4	0.2	1.7	2.2			10.6	4.9	
<i>Pinus elliotitii</i> var. <i>densa</i>				1.1	2.2															
<i>Randia aculeata</i>				12.8	2.0										1.1					
<i>Sabal palmetto</i>	0.6	0.4	0.7	3.9	2.4			7.2	14.0	1.3		1.3		3.3	1.8			15.0	10.9	2.9
<i>Salix caroliniana</i>								2.2	19.1	14.9								5.6	21.3	9.8
<i>Sideroxylon reclinatum</i>				10.6	0.4			5.0	8.2	3.1					0.2					
<i>Sideroxylon salicifolium</i>				1.1	0.9				0.9											
<i>Solanum donianum</i>				0.0				21.1	0.4									72.2	0.7	
<i>Stillingia sylvatica</i>				0.6																
<i>Swietenia mahogani</i>					0.2															
<i>Taxodium distichum</i>											56.1	77.3	82.9							
Subtotals	11.7	7.3	2.2	80.6	52.7	2.9	112.2	77.6	24.7	70.0	83.1	85.1	18.9	9.1		167.2	82.4	16.4		

¹Invasive exotic species.

Table 3. Mean Hydroperiod in Micro-Scapes, and Mean PWI in Meso-Scapes

Plot	Micro-scape		Meso-scape
	Average center tree island hydroperiod ± SD	Average marsh hydroperiod ± SD	
A	173.3 ± 11.2	219.7 ± 8.8	8.4 ± 1.5
B	47.4 ± 3.6	78.8 ± 13.8	2.91 ± 1.7
C	126.7 ± 5.3	171.4 ± 24.0	2.48 ± 1.8
D	90.2 ± 10.0	164.4 ± 23.7	6.12 ± 1.3
E	168.3 ± 18.6	179.2 ± 12.4	3.38 ± 1.8
F	166.3 ± 15.5	180.0 ± 16.4	2.80 ± 1.7

29 years. For the most part, fire occurrences were consistent across the micro-, meso-, and macro-scapes in each subpopulation (Table 9), suggesting that the processes observed at the smallest scales are representative of the general landscape. Fire occurrence intervals varied across the six micro-, meso-, and macro-scapes, with the longest fire occurrence interval in macro-scape A (one fire every 366.3 years), and fire occurrence was

undetectable within the meso- and micro-scapes (at least over the last 400 years using our 29 year dataset; Table 9). By contrast, macro-scapes B–F averaged one fire approximately every 14.5 years.

DISCUSSION

Vegetation in the marl prairie landscape is heterogeneous over time and space, and multiple factors

Table 4. Habitat Preference and Dispersal Mechanisms for Species in Micro- and Meso-Scapes

Species	Habitat	Dispersal
<i>Acacia pinetorum</i>	Upland	Bird, mammal
<i>Annona glabra</i>	Wetland	Mammal, water
<i>Baccharis halimifolia</i>	Upland	Wind
<i>Baccharis spp.</i>	Upland	Wind
<i>Bursera simaruba</i>	Upland	Bird
<i>Casuarina equisetifolia</i> ¹	Exotic	Wind
<i>Cephalanthus occidentalis</i>	Wetland	Water
<i>Chiococca parvifolia</i>	Upland	Bird, mammal
<i>Chrysobalanus icaco</i>	Wetland	Mammal
<i>Coccoloba diversifolia</i>	Upland	Bird, mammal
<i>Conocarpus erectus</i>	Wetland	Water
<i>Eugenia axillaris</i>	Upland	Bird, mammal
<i>Ficus aurea</i>	Upland	Bird, mammal
<i>Ilex cassine</i>	Wetland	Bird, mammal
<i>Magnolia virginiana</i>	Wetland	Bird, mammal
<i>Melaleuca quinquenervia</i> ¹	Exotic	Wind, Water
<i>Metopium toxiferum</i>	Upland	Bird, mammal
<i>Morella cerifera</i>	Wetland	Bird, mammal, water
<i>Myrsine floridana</i>	Upland	Bird, mammal
<i>Persea borbonia</i>	Wetland	Bird, mammal
<i>Pinus elliotitii var. densa</i>	Upland	Wind
<i>Psychotria nervosa</i>	Upland	Bird, mammal
<i>Randia aculeata</i>	Upland	Bird, mammal
<i>Sabal palmetto</i>	Upland	Bird, mammal, water
<i>Salix caroliniana</i>	Wetland	Wind
<i>Schinus terebinthifolius</i> ¹	Exotic	Bird, mammal
<i>Serenoa repens</i>	Upland	Bird, mammal
<i>Sideroxylon reclinatum</i>	Upland	Bird, mammal
<i>Sideroxylon salicifolium</i>	Upland	Bird, mammal
<i>Solanum donianum</i>	Upland	Bird, mammal
<i>Taxodium distichum</i>	Wetland	Water

Dispersal for each species inferred from Wunderlin (1998) and/or Tomlinson (2001).

¹Invasive exotic species.

interact to drive the emergence, expansion, and contraction of woody assemblages at each scale. At local and intermediate scales recruits tend to aggregate around existing adults and/or tree islands, due to gradients in dispersal and/or smaller-scale gradients in habitat suitability. Early marsh invaders may eventually contribute to tree island growth, or serve as nucleation points for new neighboring communities. However, long-term nucleation and survival around recruits appears to be powerfully constrained by abiotic factors, so much so that tree islands at larger scales exhibit random and over-dispersed distributions in most macro-scapes.

Recruitment Patterns and Processes at Small and Intermediate Scales

Woody patch establishment begins with seedling recruitment in the marsh. Establishment success

depends upon several variables, including the spatial distribution of adult populations, spatial and temporal variation in seed vectors, and ambient environmental conditions (Bazzaz 1991; Schupp 1995). Logistic regressions at the micro and meso-scales uniformly support the premise that the size and distribution of tree islands in the landscape play a formative role in the patterning of germinant populations. In each model, source size and proximity increased the likelihood of establishment in the marsh. Seed densities are known to be highest in close proximity to parent trees across many ecosystems (Hughes and Fahey 1988; Campbell and others 1990; Clark and others 1999), although seedfall patterning can vary widely among species (Ribbens and others 1994). The interspecific variation observed in our logistic recruitment curves may result from factors known broadly to affect dispersal, including parental fecundity (Herrera

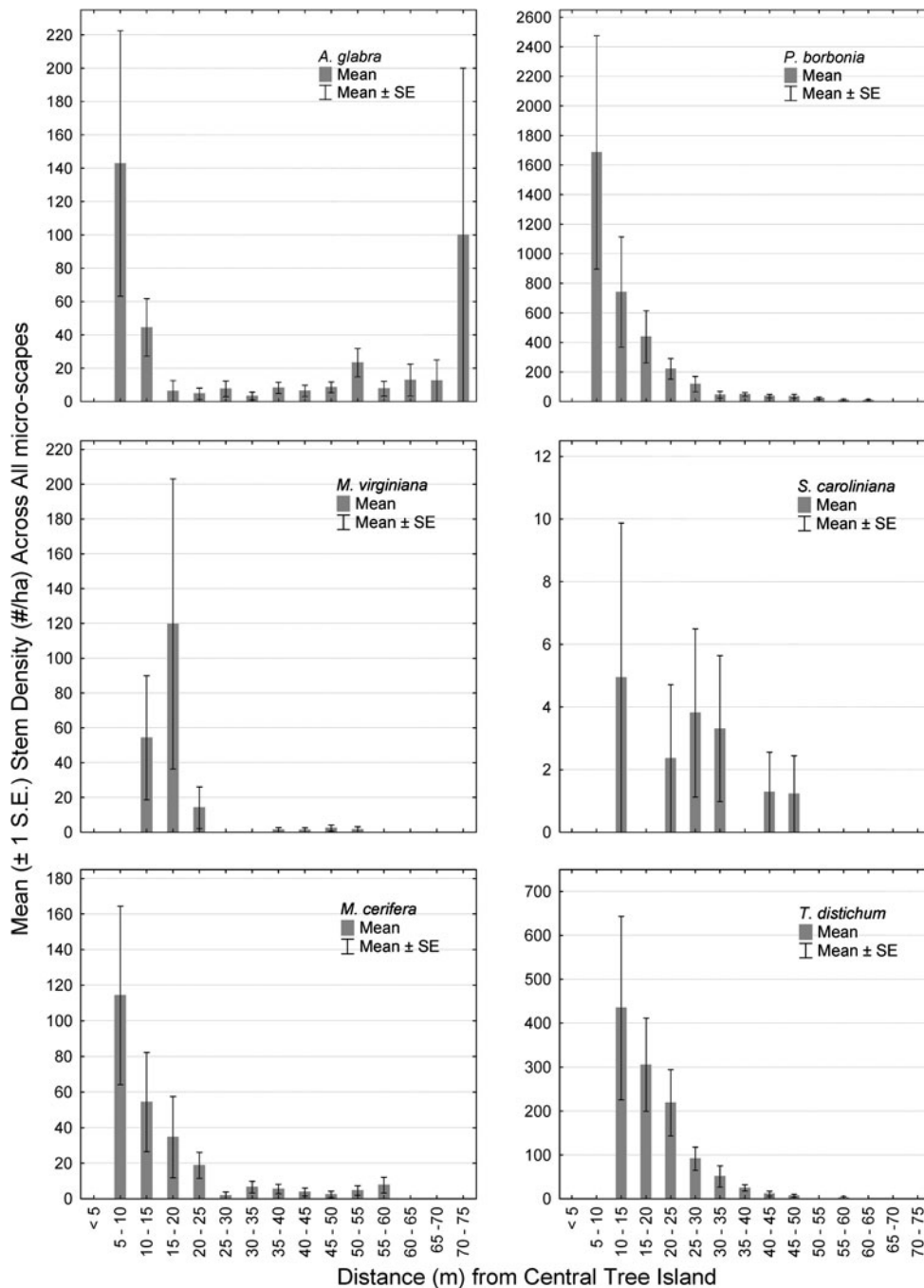


Figure 3. Mean (± 1 SE) *A. glabra*, *M. virginiana*, *M. cerifera*, *P. borbonia*, *S. caroliniana*, and *T. distichum* stem densities (#/ha) for all micro-scapes combined as a function of distance from tree island centroid. Seedlings were not sampled below tree island canopies.

1998), diaspore morphology (Howe and Smallwood 1982; Bazzaz 1996), disperser behavior (Nathan and Muller-Landau 2000), and substrate conditions (Fort and Richards 1998; van der Wall and Joyner 1998). Seed shadows serve as the template on which subsequent environmental processes further constrain germination, establishment, and survival (Nathan and Muller-Landau 2000). Such constraints include light, nutrient and water availability, seed predation, herbivory, competition, and disease. In addition to biotic and

abiotic source effects, environmental factors outside the zone of adult influence such as flooding and fire likely influence early recruitment success.

Hydrology can impact seedling establishment in several ways, and evidence for hydrologic impacts may depend on which metric is analyzed. For example, long flooding durations may favor one species over another during average hydrologic years; however, the same seedling populations may respond differently when hydrologic timing is altered (for example, inundation early in the

Table 5. Logistic Regression Results for Source and Hydroperiod Effects in Micro-Scapes

Plot	Species	Model <i>P</i>	Source effect (β_1)	SE	Wald	<i>P</i>	Exp (β_1)	Hydroperiod (β_2)	SE	Wald	<i>P</i>	Exp (β_2)
A	<i>A. glabra</i>	0.00*	44.82	8.54	27.55	0.00*	2.90E19	(-)	(-)	(-)	(-)	(-)
A	<i>P. borbonia</i>	0.00*	5.61	1.07	27.46	0.00*	273.46	(-)	(-)	(-)	(-)	(-)
B	<i>M. cerifera</i>	0.01*	4.72	1.54	9.45	0.00*	112.03	(-)	(-)	(-)	(-)	(-)
D	<i>M. cerifera</i>	0.01*	(-)	(-)	(-)	(-)	(-)	0.03	0.01	6.97	0.01*	1.03
D	<i>P. borbonia</i>	0.01*	0.70	0.22	9.69	0.00*	2.01	0.02	0.01	7.09	0.01*	1.02
D	<i>T. distichum</i>	0.00*	0.29	0.10	9.13	0.00*	1.33	0.03	0.01	27.17	0.00*	1.03
E	<i>M. cerifera</i>	0.03*	4.36	1.66	6.91	0.01*	78.07	(-)	(-)	(-)	(-)	(-)
E	<i>P. borbonia</i>	0.00*	5.57	1.85	9.08	0.00*	262.56	(-)	(-)	(-)	(-)	(-)

(-) indicates term was removed from model.

*Significant at $\alpha = 0.05$.

Table 6. Meso-Scape Logistic Regression Model Assessments

Plot	Species	Omnibus test (<i>P</i>)	Classification accuracy (%)	Tolerance	Variance inflation factor	Occupied cells	Adults
A	<i>A. glabra</i>	0.00	92.1	1.00	1.00	36	10
A	<i>P. borbonia</i>	0.00	92.4	0.97	1.04	41	16
B	<i>M. cerifera</i>	0.01	98.7	0.99	1.01	6	27
D	<i>M. cerifera</i>	0.01	94.3	1.00	1.00	24	25
D	<i>P. borbonia</i>	0.00	83.8	1.00	1.00	73	36
D	<i>T. distichum</i>	0.00	77.5	0.99	1.01	97	132
E	<i>M. cerifera</i>	0.03	99.0	1.00	1.00	5	10
E	<i>P. borbonia</i>	0.00	92.3	1.00	1.00	34	9

growing season; Reed 2007). In this study, we focused on annual duration of inundation (hydroperiod) in the micro-scape and a vegetation-derived wetness index (PWI) in the meso-scape. However, variation in hydroperiod and PWI at these scales showed weak and non-significant correlations with establishment in all but one area. High densities of hydrophilic species in our wettest populations, and positive effects of flooding on establishment in micro-scape D do suggest that surface hydrology plays an important role in large-scale woody species distributions. The lack of evidence for finer-scale hydrologic impacts could result from a scale mismatch between species response and hydrologic cell size (5×5 or 10×10 m for micro- and meso-scapes, respectively); although, source effects clearly play a stronger role in recruitment patterns in the marsh. Furthermore, source effects may incorporate some hydrologic impacts, where metrics such as duration, depth, and timing are most optimal in close proximity to adult populations.

Local scale interactions between hydrology, community composition, and ignition sources promote a heterogeneous fire regime across the

southern Everglades (Wade and others 1980). As one might expect, fire frequency was highest in our dry populations (i.e., C and F) and decreased with flooding duration. Effects of the heterogeneous fire regime may be magnified by the differential responses of woody species, which depend upon their physiological traits and local environmental conditions. *R*-strategists and species with clonal and vegetative growth patterns typically recover quickly, whereas woody stems that can only invade under a narrow set of conditions (for example, dry periods such as 2006–2008) may be removed for decades by fire. Ross and others (2009) found that the combination of fire and flooding can drastically alter community composition in the marl prairies. A prime example occurred in micro-scape B, which burned intensively in 2005, followed within days by flooding associated with Hurricane Katrina. In 2007, only four new recruits were found in the 1-ha plot, suggesting that the fire–flood interaction interrupted the annual recruitment process surrounding the small tree island. Very few reproductive trees survived the fire and flooding inhibited the establishment and survival of the propagules that remained.

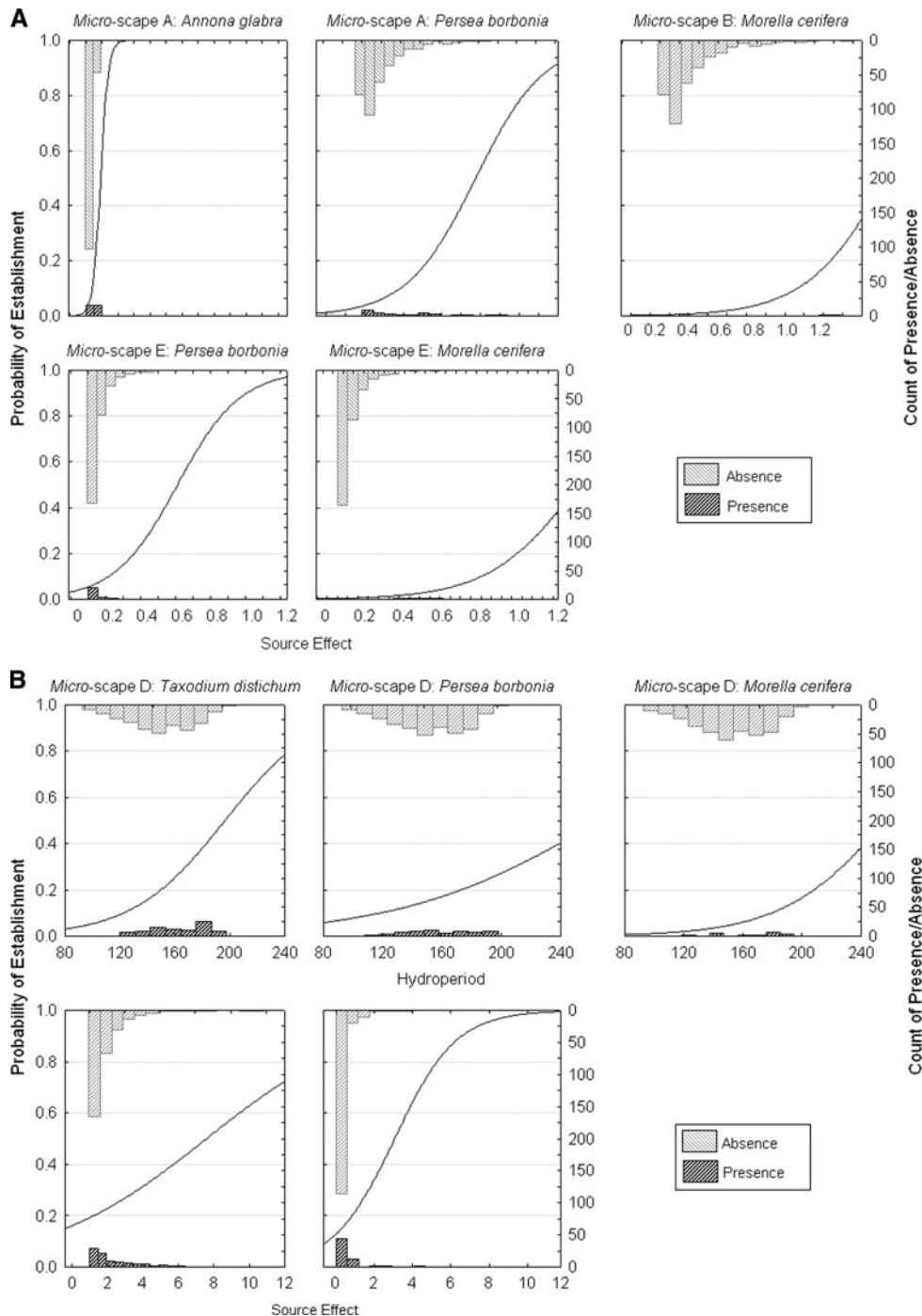


Figure 4. **A** Significant source effects for all reduced model logistic regressions in micro-scapes (A, B and E). **B** Source and hydroperiod effects for all significant logistic regressions in micro-scape D. *M. cerifera* establishment was best expressed with a reduced model using hydroperiod only. Both source effects and hydrology significantly influence the establishment of *P. borbonia* and *T. distichum*.

Large-Scale Patterning of Tree Islands in the Marl Prairie Landscape

According to the HPDP patterns observed at large scales, such as tree island distributions across the macro-scale, impose constraints on smaller-scale processes such as recruitment in the prairie. At the same time, lower-level processes give rise to higher-level patterns (Wu 1999). Using this logic, one

might expect woody plants to aggregate at multiple scales across the marl prairie landscape, resulting from (1) first order, abiotic-driven association of tree islands at very large scales, which limits dispersal to regions in which tree islands are present, and (2) smaller-scale dispersal patterns, where short distance dispersal contributes to the growth of existing tree islands, and longer distance dispersal

Table 7. Logistic Regression Results for Source and Hydrology Effects in Meso-Scapes

Plot	Model <i>P</i>	Source effect (β_3)	SE	Wald	<i>P</i>	Exp (β_3)	Hydroperiod (β_4)	SE	Wald	<i>P</i>	Exp (β_4)
A	0.00*	0.08	0.01	42.97	0.00*	1.09	(-)	(-)	(-)	(-)	(-)
B	0.00*	0.02	0.00	25.55	0.00*	1.02	(-)	(-)	(-)	(-)	(-)
C	0.00*	0.05	0.01	30.25	0.00*	1.05	(-)	(-)	(-)	(-)	(-)
D	0.00*	0.31	0.00	49.72	0.00*	1.03	0.29	0.08	12.25	0.00*	1.34
E	0.03*	0.06	0.02	6.39	0.00*	1.06	(-)	(-)	(-)	(-)	(-)
F	0.00*	0.03	0.01	19.80	0.00*	1.04	(-)	(-)	(-)	(-)	(-)

Plots A, B, C, E, and F employ a reduced model; plot D employs a complete model. (-) indicates term was removed from model.
*Significant at $\alpha = 0.05$.

Table 8. Meso-Scape Logistic Regression Model Assessments

Plot	Omnibus test for model coefficients (<i>P</i>)	Classification accuracy (%)	Tolerance	Variance inflation factor	Occupied cells	Islands
A	0.00	99.2	0.90	1.12	15	19
B	0.00	93.8	0.95	1.05	38	69
C	0.00	84.2	0.99	1.01	117	50
D	0.00	86.0	0.99	1.02	105	18
E	0.03	97.9	0.93	1.07	15	27
F	0.00	87.2	0.99	1.01	92	33

creates nucleation points for new, spatially associated communities. Much to our surprise however tree islands in the macro-scape were mostly randomly distributed, with over-dispersion at small scales. The lack of second-order aggregation suggests that biological feedbacks, such as those promoting the aggregation of new recruits around adult populations are not sufficiently strong to promote nucleation and subsequent tree island aggregation over time in the face of external constraints.

Over-dispersion or “repulsion” is usually observed with individual organisms, and is normally the result of biological processes such as competition or allelopathy. It is not easy to imagine a biological process that would cause one tree island to be repelled by another. Instead, we suggest that the observed over-dispersion may result from interplay between environmental constraints such as fire, flooding, and existing tree island patterning across the landscape.

Hydrologic patterns in the marl prairies are defined by long-term variables including climate and geology, and modified by anthropogenic alterations such as compartmentalization and drainage. Under natural hydrologic regimes, flooding stress may limit tree island establishment to micro-topographic highs where hydroperiods are much more abbreviated than elsewhere in the marsh. Bedrock

outcrops in the marsh are often precursors to surface topographic rises, though it remains unclear to what degree tree island patterning depends upon bedrock topography. Observed recruitment patterns in the micro- and meso-scapes and tree island distributions across the macro-scape suggest that although second-order (biological) feedbacks might allow woody stems to colonize new environmentally favorable habitats throughout the prairie, tree island establishment, a much more prolonged process, could be limited to topographic outcrops, which may or may not exhibit aggregation at different scales. However, tree island size, distribution, and overall landscape complexity may change or have changed rapidly in regions where hydrologic conditions have been drastically altered.

Fire is another important constraint on woody plant patterning in mixed landscapes (Bond and others 2005), and may be particularly important in the fire-prone marl prairies of the southern Everglades. As tree islands form and increase in size they develop more humid microclimates, and become increasingly resistant to fire (van der Valk and Sklar 2004), whereas nearby recruits and small woody plant aggregates remain extremely vulnerable. In fast-moving head-fires, flow paths may diverge on approach to large islands, intensifying along their flanks. Such an effect on fire behavior could serve to eliminate previously established recruits from an

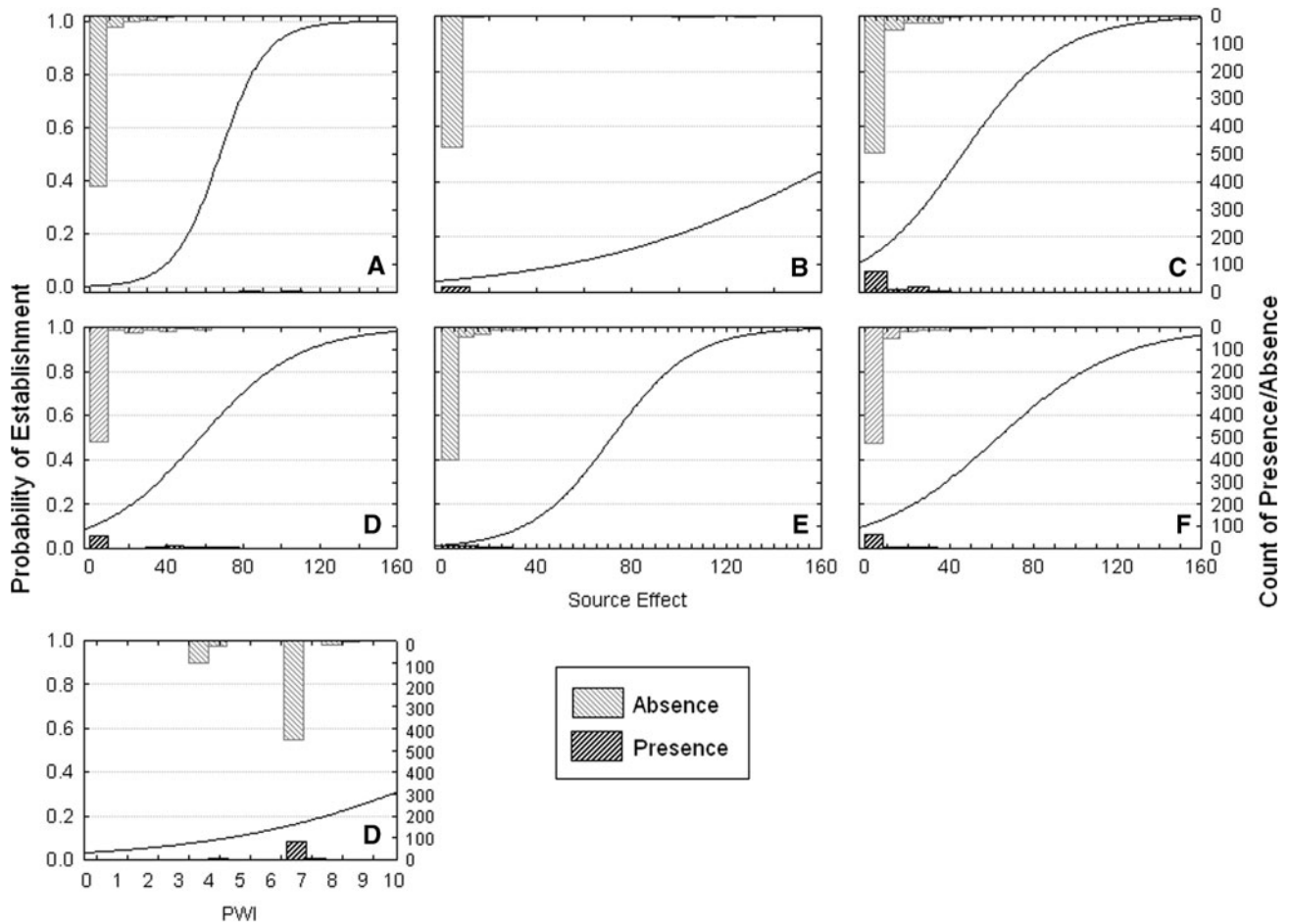


Figure 5. Source and PWI effects for all significant logistic regressions across all meso-scapes.

island’s vicinity, short-circuit fuel buildup nearby, and limit island size. Over time, it could perhaps lead to over-dispersion of islands at small scales.

Paradoxically, the only area in which local tree island patterning indicated aggregation instead of over-dispersion was the area in which fire frequency was greatest. Second-order tree island aggregation in the relatively dry macro-scape C may have progressed similarly to invasion processes that sometimes occur in open savannas. Mass recruitment of woody seedlings can occur in savannas when fire and subsequent rain storms reduce the graminoid layer and moisten the soil (Danthu and others 2003; Wiegand and others 2006a). These new woody patches can subsequently expand and aggregate over time because reduced grass layers can no longer sustain intense burns (Menaut and others 1990; Wiegand and others 2006a). Similarly in macro-scape C, fire and reduced flooding may have created optimal environments for tree island establishment, expansion, and aggregation. Perhaps, when recruitment occurs

in localized mass events (due to fire-drought interplay) longer-term tree island growth and survival is more probable. Furthermore, frequent fires in population C likely prevent fuel accumulation, thus reducing the probability of intense burns that would otherwise consume more woody resources. Lastly, large aggregates of tree islands are known to deflect fires, and interfere with their movement through the prairie (personal communication, Rick Anderson, ENP Fire Management Officer), so in dry regions, frequent low-intensity fires may allow aggregation to become an autogenic process.

In their discussion of multi-scaled patch and boundary dynamics, Peters and others (2006) defined three types of biotic transitions: directional, stationary, and shifting. Directional transitions such as those associated with woody plant invasion involve patch succession from one end state to another. These shifts are strongly influenced by abiotic drivers such as changes in climate, in addition to biotic and abiotic feedbacks. Over time, directional transitions create larger and more

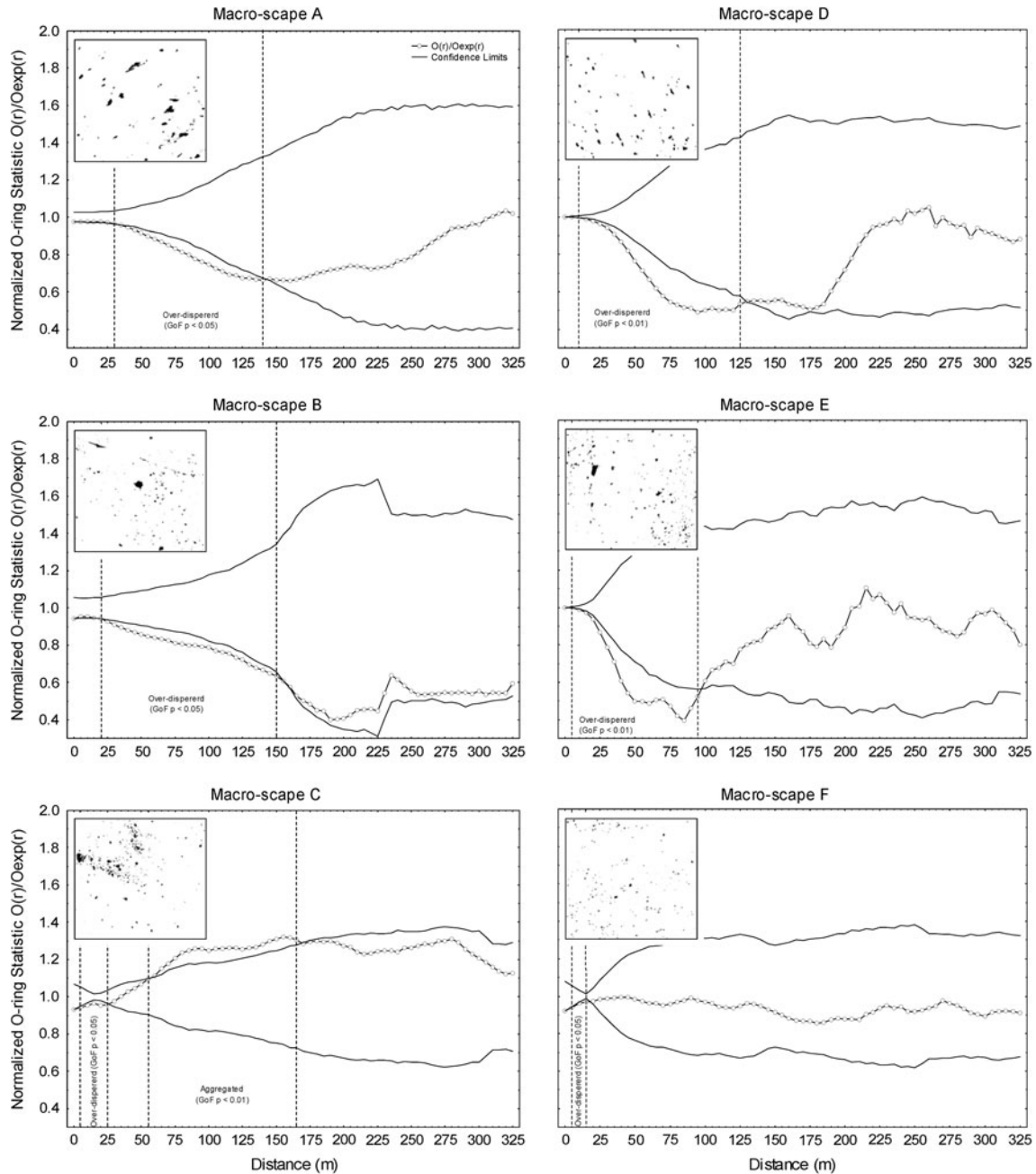


Figure 6. Univariate analysis of tree island aggregation within each of the six macro-scapes using the O-ring function, results from goodness of fit tests and inlay map of all macro-scapes. To better see the positive or negative departures from the null model $O(r)$ is normalized by $O_{exp}(r)$ under the homogeneous Poisson null model. The $O_{exp}(r)$ is the average $O(r)$ of the simulations of the null model. *Black* features in inlay represent tree islands that were used in our o-ring analyses, whereas *gray* features represent other communities (for example, pine forests) or islands truncated by the plot boundary, and were masked from the analyses.

spatially aggregated patches, which eventually may coalesce (Peters and others 2006). Stationary transitions remain somewhat stable over decades with little patch movement from one state to another. Stationary boundaries are controlled by intrinsic abiotic constraints including topographic anomalies, and are strengthened over time by

biotic feedbacks. Shifting transitions involve no net long-term change in boundary locations, though patch boundaries shift over shorter timescales. Shifting transitions are strongly affected by abiotic drivers such as flooding, drought and fire, and are not reinforced over time by biotic or abiotic feedback mechanisms (Peters and others 2006).

Table 9. Fire Occurrence Interval for All Three Landscape Scales

CSSS subpopulations	Fire occurrence interval (years)		
	Macro-scape	Meso-scape	Micro-scape
A	366.3	>400	>400
B	10.5	17.9	14.5
C	8.3	10.9	9.7
D	21.5	11.0	7.3
E	16.9	11.2	9.7
F	15.5	7.3	4.9

In interpreting this study, multiple transition types likely exist across the Everglades marl prairie landscape. The observed disconnect between aggregation of recruits around tree islands and tree island over-dispersion at larger scales however suggests that directional transitions are rare in most macro-scapes. Although nucleation feedbacks promote the recruitment of woody stems near conspecific adults in populations A, B, D, E, and F, they do not appear to be sufficiently strong to reinforce directional patch aggregation over time. Tree island over dispersion may result from the patterning of underlying bedrock highs and/or the distribution of

fire and water through the prairie. Such factors are likely associated with stationary and shifting boundaries, respectively. However, when natural hydrologic and disturbance regimes are directionally altered (for example, flow diversion and long-term fire suppression), shifting transitions might become directional (Peters and others 2006). Large-scale tree island aggregation in population C may result from directional shifts, triggered by dry conditions.

CONCLUSION

The Everglades grassland-woody plant mosaic is heterogeneous and dynamic across multiple scales. Despite the adaptive capacities of resident biota, landscape patches are perpetually subject to expansion, contraction, or replacement. Similar to other grasslands worldwide, woody encroachment into Everglades prairies may involve a chain of spatially dependent processes, beginning with the dispersal and establishment of individual propagules, the subsequent aggregation of individuals into tree islands and finally the potential coalescence of tree islands into more extensive forests (Peters and others 2006; Allen and Breshears 1998). Conversely, woody patch contraction may

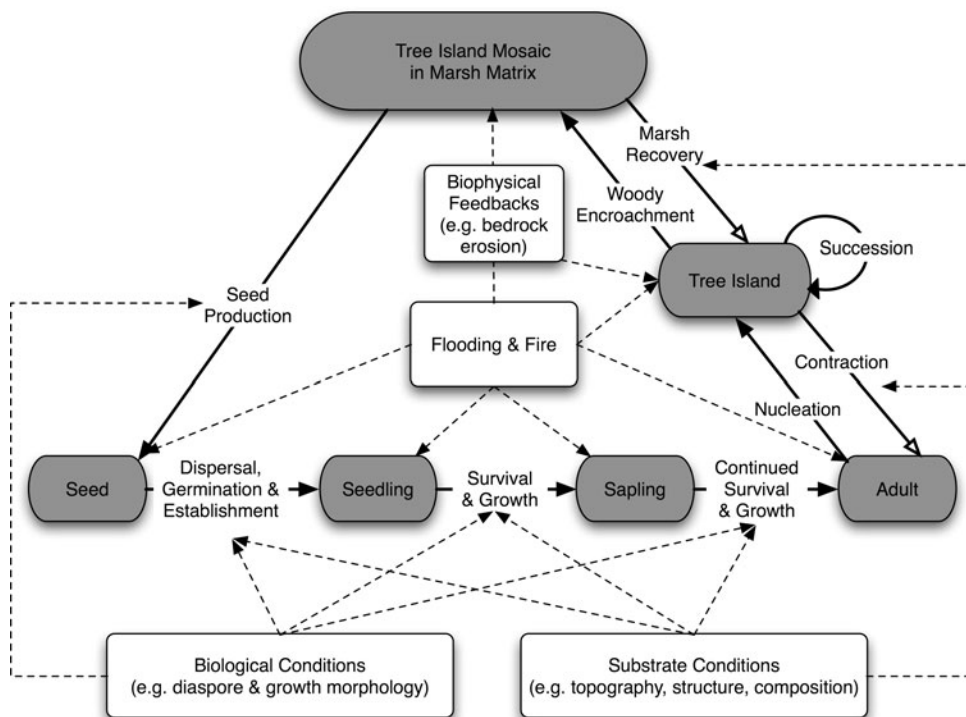


Figure 7. The major controls and feedbacks influencing patterns among woody plants at various life stages. *Solid boxes* indicate stages of woody encroachment/contraction. *Hollow boxes* indicate environmental factors influencing the two processes. *Solid filled arrows* represent encroachment processes, whereas *hollow arrows* denote marsh recovery. *Dashed arrows* indicate influences upon each process and/or stage.

result from environmental constraints such as nutrient limitation, flooding, and fire (Lockwood et al 2003; Figure 7). Therefore, a proper balance between environmental feedbacks and stressors is required to maintain a landscape mosaic suitable to the diverse requirements of its component species.

The patterning of adult populations within the Everglades marl prairies appears to be the most significant driver of tree island development and growth. However, following initial recruitment in the marsh, establishment of new tree islands may be extremely slow and relatively rare, with most early marsh invaders being eliminated over time by disturbance. Under this scenario, general tree island distributions may date back to the origins of the grassland-woody mosaic, approximately 2,000 years (Willard and others 2006). Nevertheless, pronounced changes in hydrology or fire regime, such as those resulting from development and drainage, might dramatically restructure this legacy tree island pattern.

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