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Springer



1432-9840(200402)7:1;1-E

10021 ISSN 1432 9840 ECOSFJ 7:1-108 (2004)

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# ECOSYSTEMS

Volume 7, Number 1, January 2004

*On the cover:* Slough community of white water lillies (*Nymphaea odorata*) and bladderworts (*Utricularia spp*) surrounded by dense stands of *Cladium jamaicense* (sawgrass) in the northern Everglades. Photo by R. S. King. See King and others, this issue.



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# Spatial Dependency of Vegetation–Environment Linkages in an Anthropogenically Influenced Wetland Ecosystem

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## ABSTRACT

Management and restoration of vegetation patterns in ecosystems depends on an understanding of allogenic environmental factors that organize species assemblages and autogenic processes linked to assemblages. However, our ability to make strong inferences about vegetation–environment linkages in field studies is often limited due to correlations among environmental variables, spatial autocorrelation, and scale dependency of observations. This is particularly true in large, heterogeneous ecosystems such as the Everglades. Here, an extensive canal-and-levee system has modified historical fire regimes and hydropatterns while contributing large inputs of surface-water phosphorus (P), nitrogen (N) and cations such as sodium (Na). Some of these anthropogenic influences have been implicated as factors leading to the shift of sawgrass (*Cladium jamaicense* Crantz) and slough communities to an assemblage of weedy species such as cattail (*Typha domingensis* Pers.). To untangle the independent effect of multiple variables, we used a spatially explicit, multivariate approach to identify linkages among spatial patterns, environmental factors, and vegetation composition along a 10-km gradient of anthropogenic influence in the Everglades, an area immediately downstream from canal inflow structures. Clusters of plots were stratified among three zones (*Impacted*, *Transition*, and *Reference*), a design

that allowed us to contrast vegetation–environment linkages and spatial patterns at multiple scales and degrees of ecosystem alteration. Along the 10-km gradient, partial Mantel tests showed that nutrients (phosphorus, nitrogen, and potassium) and hydropattern (frequency of dryness) were independently linked to patterns in fine-scale vegetation composition, but phosphorus was the only environmental variable linked to patterns of coarse-scale composition. Regardless of scale, the effect of distance from canal inflows accounted for variation in vegetation that could not be explained by other variables. A significant residual effect of spatial proximity among sampling locations also was detected and was highly suggestive of dispersal or other spatial determinants of vegetation pattern. However, this pure spatial effect was significantly stronger in the Transition and Impacted zones than in the Reference zone—fine-scale environmental variables explained all of the spatial structure in vegetation in the Reference zone. A further examination of spatial patterns in vegetation by using Mantel correlograms revealed significant heterogeneity at fine, local scales in the Reference zone, but this pattern progressively degraded toward homogeneity among closely neighboring locations in the Impacted zone. However, the fine-scale vegetation pattern in the Reference zone was hierarchically nested at a broader scale and yielded a similar coarse pattern across the landscape, whereas the coarse pattern in the Transition and Impacted zones

Received 10 July 2002; accepted 2 January 2003; published online 12 January 2004.

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was relatively heterogeneous and fragmented. Collectively, these results indicate that allogenic spatial and environmental factors related to the canal system have disrupted the coupling between pattern and process by altering fine-scale vegetation–environment linkages and spatial patterns characteristic of the natural Everglades ecosystem.

**Key words:** scale; pattern; hierarchy theory; macrophytes; partial Mantel test; ordination; spatial autocorrelation; hydropattern; nutrients; Everglades.

## INTRODUCTION

Environmental factors are traditionally considered one of the predominant determinants of vegetation pattern [for example, see Whittaker (1956) and Bray and Curtis (1957)], a view that has resulted in numerous observational studies of community–environment relationships in plant ecology. Unfortunately, studies of this type often produce equivocal results due to the confounded nature of ecological data [for example, see Legendre (1993) and Thomson and others (1997)]. Correlations among environmental variables, spatial autocorrelation, and scale dependency of observations all degrade the interpretative value of results produced from many analytical techniques in use today [see Legendre and Legendre (1998)]. This is especially true for large-scale observational studies in which supplementary experimental manipulations are either impractical or impossible to produce at the appropriate scale (Legendre and Fortin 1989; Wiens 1989), a fact that is troubling given our current awareness of the importance of landscape-scale processes in ecology (Levin 1992). Thus, conducting field studies that afford strong inference about vegetation–environment linkages can be a daunting task, particularly in large, heterogeneous ecosystems (Beyers 1998; Urban 2000).

The Everglades is an example of a large, heterogeneous ecosystem in which vegetation–environment linkages have received much attention. Vegetation in this wetland ecosystem has been affected by a variety of anthropogenic influences in the past several decades, which has led to a surge of recent studies designed to infer the causes of observed changes. Reputedly sustained by fire and hydropattern (Loveless 1959; Craighead 1971) while limited by phosphorus (Steward and Ornes 1975a, 1975b; Davis 1991; Noe and others 2001), the historic heterogeneous mosaic of vegetation communities described by Davis (1943) has been altered by disruption of natural environmental variation and degradation of water quality (SFWMD 1992; Davis

and Ogden 1994). However, intercorrelations and spatial autocorrelation of multiple factors have made it difficult to isolate the linkages between specific environmental variables and observed changes in vegetation patterns.

Although modifications to hydrology, fire frequency and intensity, and other environmental factors are suggested to play a role in the alteration of plant distributions in the Everglades, phosphorus (P)-enriched runoff from the Everglades Agricultural Area (EAA) has been identified as the primary stressor (SFWMD 1992). The extensive canal-and-levee system that compartmentalizes the remnant Everglades also serves as a conduit for P from the EAA, and water-control structures along the canals function as point sources of P to downstream portions of the wetland ecosystem. In areas near water-control structures, P has been found to be at least partially responsible for the transformation of *Cladium jamaicense* Crantz (sawgrass) stands and open-water sloughs to dense stands of invasive *Typha domingensis* Pers. (cattail) (Davis 1991; Urban and others 1993; Newman and others 1998). *Typha* distribution and growth is positively correlated with both soil and water total P and is limited in areas with low P (Craft and Richardson 1997; Doren and others 1997; Miao and Sklar 1998; Miao and others 2000). Mesocosm studies also have demonstrated that *Typha* is more competitive than *Cladium* under high P conditions [for example, see Newman and others (1996)]. However, fertilizer experiments have been unable to show that adding P alone necessarily results in competitive exclusion of *Cladium* (Craft and others 1995; Chiang and others 2000). These experimental findings suggest that other factors, such as hydropattern [for example, see Toth (1987), Urban and others (1993), and Newman and others (1996)], fire [for example, see Gunderson and Snyder (1994), Urban and others (1993), and Newman and others (1998)], or cations such as sodium (Craft and Richardson 1997) may be important synergists in *Typha* expansion.

Because the autecology of both *Typha* and *Cladium* has received most of the attention from researchers, few studies have examined patterns of entire macrophyte communities in response to these human influences. The general observation has been that high-P areas are dominated by monotypic stands of dense *Typha* [for example, see Jensen and others (1995) and Rutchey and Vilchek (1999)], resulting in a relatively homogeneous landscape pattern when compared to the reference *Cladium*–slough mosaic (Obeysekera and Rutchey 1997; Wu and others 1997). However, this observation has been largely based on photointerpreta-

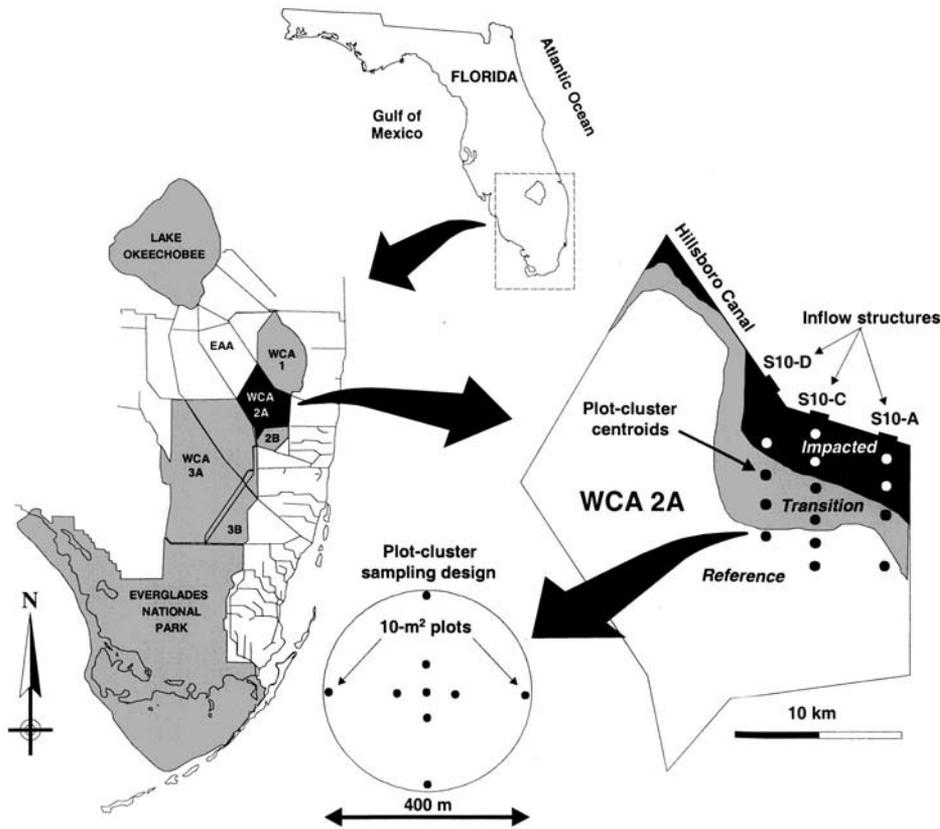


Figure 1. Map of south Florida showing the location of Water Conservation Area 2A (WCA-2A); Impacted, Transition, and Reference zones; locations of S-10 water-control structures on the Hillsboro Canal; centroids of sampling clusters; and plot-cluster sampling design. EAA, Everglades Agricultural Area.

tion of satellite imagery, which is limited in spatial resolution and is not appropriate for assessing fine-scale pattern in species composition (Obeysekera and Rutchey 1997; Richardson and others 1997). Recent field studies have indicated that many other macrophyte species coexist with *Typha* in high-P areas, and that diversity is actually greater near canals than in interior-wetland locations (Doren and others 1997; Vaithiyanathan and Richardson 1999). However, little is known about the spatial patterns of these communities, the environmental factors that are responsible for generating these patterns, or the influence of such spatial patterns on autogenic environmental variation [for example, biogeochemical properties of peat soils (Noe and others 2001)].

Despite the large body of research that continues to expand our understanding of the Everglades ecosystem, no field study has attempted to untangle the independent role of multiple abiotic factors in community-level changes in vegetation composition. Thus, we evaluated linkages among spatial factors, environmental conditions, and vegetation composition along a gradient of anthropogenic influence in the northern Everglades. We used a multiscale sampling approach (a) to examine vegetation–environment linkages along the full gradient

of anthropogenic influence, (b) to contrast linkages and spatial patterns in composition as a function of relatively discrete levels of impact to the ecosystem, and (c) to contrast linkages and spatial patterns across fine and coarse spatial scales. We contend that an understanding of the characteristic scales and patterns of vegetation–environment linkages is critical for the Everglades and other ecosystem restorations if these efforts are to facilitate natural processes effectively at multiple scales (Holling and others 1994; Redfield 2000).

## METHODS

### Study Area and Sampling Design

We sampled in Water Conservation Area 2A (WCA-2A) in the northern Everglades (Figure 1). WCA-2A is a 43,280-ha diked wetland landscape, with water-control structures governing the inflow and outflow of surface water. Inflow primarily occurs along the northern levee through three water-control structures (S10-A, C, and D) on the Hillsboro Canal, a conduit for outflow from Lake Okeechobee and P-enriched runoff from the EAA (Figure 1). Inflow from the Hillsboro Canal has induced a steep longitudinal eutrophication gradient in WCA-2A,

due primarily to large inputs of P (SFWMD 1992). Aerial photographs (US Geological Survey unpublished data) and descriptive studies [for example, see Davis (1943)] prior to impoundment have demonstrated that vegetation pattern and composition across this region of the WCA-2A landscape was once very similar. Today, however, three relatively distinct vegetation zones exist along this gradient (Figure 1): (a) an impacted zone (hereafter, Impacted) approximately 0–3 km downstream of the canal inflow structures, where surface water and soil are heavily enriched with P, and vegetation characteristic of the pristine Everglades reportedly has been all but replaced by dense stands of *Typha* and other invasive species; (b) a transition zone (hereafter, Transition) that ranges from 3–7 km from the canal, where P concentrations diminish but remain elevated, and vegetation is a mix of *Typha*, other invasive species, *Cladium*, and infrequent open-water slough habitats; and (c) a relatively unaffected reference zone (hereafter, Reference) beyond 7 km from the canal that exhibits water and soil chemistry representative of the historical Everglades, with vegetation structured as a mosaic of *Cladium* stands interlaced with open-water sloughs. Because boundaries among these three zones have been well established in recent studies [for example, see Doren and others (1997), Obeyesekera and Rutchev (1997), Van der Valk and Rosburg (1997), Wu and others (1997), Richardson and others (1999), Vaithyanathan and Richardson (1999), SFWMD (2000), and King and Richardson (2002)], we felt these zonal categorizations were valid and would provide us with an opportunity to make contrasts among three relatively discrete, yet contiguous, levels of ecosystem alteration.

Previous to this study, three 10-km-long transects were established, each aligned with one of the S-10 inflow structures and parallel to the vegetation gradient (Figure 1) (Richardson and others 1999). Six long-term sampling stations were marked along each transect, starting 1.0–1.5 km from the canal and spaced at 1.5-km intervals. We selected 14 of these stations as centroids for our sampling, with all six selected from the central transect (C transect), and random draw of four of the six from each of the A and D transects (Figure 1). In aggregate, five centroids were considered Impacted, five Transition, and four Reference based on the a priori zone classifications (Figure 1).

We used a stratified-cluster sampling design as described by Urban (2000). In this study area, we hypothesized that variation in vegetation pattern was likely to occur on fine, local scales (for example, tens of meters) as well as coarse or landscape

scales (thousands of meters). Conventional sampling designs such as random or stratified random would not have captured local patterns in variation if conducted with coarse or landscape-scale separation distances among plots; similarly, at fine scales, these designs would require thousands of plots and thus would not be practical at a large spatial extent. Thus, this cluster approach (see Figure 1) provided a highly efficient method for considering multiple scales in spatial, environmental, and compositional variables (Fortin and others 1989; Urban 2000).

A single plot at each of the 14 stations served as a plot-cluster centroid. Eight additional plots were marked in a constellation, with four plots placed at 50-m distances from centroids and four others at 200-m distances, each in the four cardinal directions (Figure 1). Separation distances among plots within clusters ranged from 50 to 400 m, with a total of nine plots per cluster and 126 plots across the landscape. Distances among plot clusters ranged from approximately 1000 to 10,000 m. Random allocation of plots within clusters was not practical, as this would have caused excessive damage to vegetation in the areas adjacent to plots because of the airboat used for transportation.

We chose a plot size of 10 m<sup>2</sup>, large enough to integrate across microhabitats and thus reduce noise, but not so large that they averaged across distinct patches of vegetation (Fortin and others 1989). Plots were semicircular to facilitate sampling from the perimeter and to minimize disturbance.

### Environmental and Vegetation Variables

One assumption inherent to our study was that the environmental variables that we measured were indeed important to variation in vegetation composition and expressed in an ecologically meaningful manner. We selected a suite of variables that we hypothesized were causing changes to vegetation patterns or were linked to patterns autogenically. We considered four types of variables: (a) spatial, (b) soil chemical, (c) hydrological, and (d) physical disturbance (that is, fire).

*Spatial Variables.* Relative proximity to inflow structures on the Hillsboro Canal was expected to be the underlying, indirect determinant of changes in vegetation in patterns in the study area. Distance (in meters) from these structures (hereafter, *Canal*) was calculated using Universal Trans-Mercator (UTM) coordinates of inflow structures and individual plots. Coordinates were estimated using a global positioning system (GPS) at inflow structures and plot-cluster centroids. For greater precision, coordinates of the eight additional plots per cluster were determined using direct measurements (in meters)

from a meter tape and bearings from plot-cluster centroids.

These coordinates were also used to calculate separation distances (in meters) among plots. Separation distances (hereafter, *Space*) were used for estimating the effect of spatial proximity among plots on vegetation–environment correlations. This was important because vegetation samples that are close together tend to be more similar than ones far apart, regardless of environmental determinants. In other words, we used *Space* to remove the confounding effect of spatial autocorrelation on the statistical significance of vegetation–environment linkages, as well as to detect spatial structure in vegetation that could not be accounted for by environmental variables (Legendre and Fortin 1989; Legendre 1993). Greater explanation on the use of the variable *Space* is presented in *Data Analysis: Vegetation–Environment Linkages*.

**Soil Chemical Variables.** We limited our chemical variables to those obtained from soils because soils are an integrator of long-term water-chemistry conditions and the variables of interest are highly correlated to both water chemistry and loading rates across the study area [for example, see DeBusk and others (1994), Craft and Richardson (1997), Richardson and others (1999), and King and Richardson (2002)]. Moreover, soil chemistry was shown by Pan and others (2000) to explain more variation in community attributes than did water chemistry in the Everglades, particularly for P, which was a nutrient of great interest for the present study. Preliminary analysis and results reported by King (2001), who used the same plots examined in this study, showed that soil chemistry was more strongly related to vegetation composition than was water chemistry data collected from 1995 to 1998 at these same locations. Specifically, soil total P (TP) explained all of the variation explained by either surface-water TP or soluble reactive P (SRP), while soil TP still remained significantly related to vegetation after removing the combined variance explained by surface-water TP and SRP ( $P \leq 0.0001$ , partial Mantel test—see *Data Analysis: Vegetation–Environment Linkages*). Finally, variation in many soil-chemical variables [for example, soil total carbon (C)] is a product of variation in vegetation composition; thus, soil chemistry enabled us to more directly evaluate the linkage between composition and potential autogenic processes.

Soil samples were collected for chemical analyses from every plot during 20–29 October 1998. Each sample was analyzed for total C, P, nitrogen (N), calcium (Ca), potassium (K), magnesium (Mg), and

sodium (Na). Field and laboratory methods are described by King (2001). Soil chemical concentrations were expressed per unit dry mass rather than volume because bulk density has been shown to be similar along the vegetation gradient (Reddy and others 1991). All soil variables were retained for analysis because no pair was deemed to be collinear (Kleinbaum and others 1988).

**Hydrological Variables.** The hydropattern in WCA-2A is regulated, and no longer occurs as natural response to precipitation and surface-water flow as it did before water control structures were built. Within WCA-2A, the hydropattern varies considerably (Romanowicz and Richardson 1997, 2004). Variations in hydropattern result from the relative rate of water flow through the water control structures, the topography of the peat surface, and equipotential surface of the water. We estimated hydropattern at each plot by linking field measurements to a spatially explicit hydrological model developed by Romanowicz and Richardson (1997, 2004) for the same study area.

The model was developed using historical surface-water stage and discharge data (SFWMD 1992) and a network of 11 continuous-recording stage recorders equipped with 10-psi pressure transducers (error,  $\pm 0.1\%$  full-scale reading). These stations were monitored for between 2 and 3 years to relate the equipotential surface of surface water to concurrent surface-water stage data and discharges through the canal inflow structures into WCA-2A ( $r^2 = 0.99$ ). This model was then used to predict water elevation at numerous locations in WCA-2A, including the 14 plot-cluster stations, using historical (1981–98) stage and discharge data (SFWMD 1995). Predicted water depths at plot-cluster centroids were validated using multiple field measurements in 1998–99 ( $r^2 = 0.98$ ).

To estimate hydropattern at each of our plots, water depths (in centimeters) were measured at three random locations within each plot and averaged during 20–29 October 1998. Field water-depth measurements taken from each plot were then linked to the water-depth estimates produced by the model at each of the respective plot-cluster centroid benchmarks. In other words, we used the validated water-depth estimates generated by the model at each of the 14 plot-cluster centroids as benchmarks, and the relative difference in instantaneous field measurements of water depth between the centroids and surrounding plots, to correct for differences in local elevation among plots in each respective cluster. The model was then used to generate temporal estimates of water depth for every plot for the period of 1981–98.

Using the temporal water-depth estimates, we considered metrics of (a) mean water depth, (b) frequency of exceeding or falling below certain depths (for example, percent of days at  $< 150$  cm), and (c) stability of water depth (for example, metrics of variance or range in water depth). We evaluated all metrics by using both short-term (1 year) and long-term (1981–98) data. Short-term hydrology was expected to have a greater influence on subtle compositional patterns (Gunderson 1989), whereas long-term hydrology was expected to have a greater influence on coarse-scale species distributions (Urban and others 1993; Busch and others 1998; Shay and others 1999). Preliminary results indicated that short-term mean water depth (hereafter, *Depth*), long-term frequency of depth less than  $-10$  cm (index of severe dryness calculated as the percent of days during 1981–98 in which water depth was less than  $-10$  cm; hereafter *Freq* $\leq 10$ cm), and long-term interquartile range of depth [a robust index of stability of water depth calculated as the range between the 25th and 75th percentiles of the distribution of daily water depths during 1981–98; hereafter *IQR*(*Depth*)] were most strongly related to vegetation. These three variables were not collinear, and each accounted for unique variation in vegetation composition along the anthropogenic influence gradient ( $P < 0.05$ , partial Mantel test—see *Data Analysis*). Thus, all three were retained for further analysis.

**Fire Variables.** Fire disturbance was expected to play a role in vegetation pattern because *Cladium* is considered fire tolerant (Steward and Ornes 1975b), and intense fires are believed to be partially responsible for maintaining the sawgrass–slough mosaic (Craighead 1971; Gunderson and Snyder 1994). A composite map of recent, large fires constructed using aerial photographs indicated that more than 50% of WCA-2A had burned at some point during 1981–98 (Florida Game and Freshwater Fish Commission unpublished data). We calculated an index of fire frequency for the period of 1981–98 by using these data. Coordinates of fire boundaries were related to plot coordinates and used to determine the presence of fires at each plot, following methods used by Newman and others (1998). Frequencies of large fires ranged from zero to two for individual plots during this period. Because the time since the last fire was potentially as important as the frequency of fires (Allen and Wyleto 1983; Gunderson and Snyder 1994), fire frequency was weighted as  $1/\log_{10}(t + 1)$ , where  $t$  = time since fire (years), and summed for all fires during the period 1981–98. Preliminary analysis indicated that vegetation composition had a higher

correlation to this fire index (hereafter, *Fire*) than did simple fire frequency; thus, the index was retained for analysis.

**Vegetation Composition.** We estimated vegetation species composition and cover within each plot by using Braun–Blanquet cover classes (Phillips 1959). This cover-estimation technique was used to minimize disturbance to vegetation within the plots and because it was ideal for our distance-based statistical analyses [for example, see Leduc and others (1992)]. Classes ranged from 0 to 6, and approximated a log-linear relationship with increasing percent cover. Two observers estimated cover by wading around the perimeter of the plot. All macrophytes were identified to the lowest practical level, usually species.

We also estimated cover classes of calcareous and noncalcareous periphyton mats, as calcareous mats have been indicated to be sensitive to P (Flora and others 1988; Vymazal and others 1994; McCormick and others 1998) and are an important feature of pristine slough habitats in the Everglades (Turner and others 1999a; Noe and others 2001). Periphyton mats either disappear or shift to noncalcareous forms where P is elevated (McCormick and others 1998). Coverage of open water (no vegetation in water column) was included as a cover type because reportedly it has been reduced in impacted areas due to invasive vegetation [for example, see Obeysekera and Rutchey (1997)]. All vegetation sampling was conducted during 20–29 October 1998 (end of wet season), a period when periphyton mats were at their peak biomass (McCormick and others 1998) and water levels were sufficient to allow airboat travel to most areas of WCA-2A.

## Data Analysis

**Environmental Variation Among Zones.** We used mixed-model nested analysis of variance (ANOVA) to compare means of soil chemical (C, Ca, K, Mg, N, Na, and P), hydrological (*Depth*, *Freq* $\leq 10$ cm, and *IQR*(*Depth*)), and fire (*Fire*) variables among the three vegetation impact zones to evaluate whether they differed environmentally at this relatively broad scale. Plots were replicates nested within clusters (Cluster, random effect), whereas clusters were replicates nested within zones (Zone, fixed effect). Means were contrasted using Tukey's HSD test for Zone effects deemed significant by ANOVAs; means for significant Cluster effects were not compared because this effect was considered random (Bennington and Thayne 1994). ANOVAs were conducted using the Variance Components module of Statistica 5.5 (Statsoft, Tulsa, OK, USA).

*Macrophyte Species Distributions Among Zones.* To assess affinities of macrophyte species to impact zones and test the hypothesis that the transition zone was truly an area of ecological transition, we performed Indicator Species Analysis (INSPAN) (Dufrêne and Legendre 1997) on vegetation cover data. INSPAN is a nonparametric technique used to identify species with a high fidelity for a particular group or class, as defined by the user. Indicator Values (IVs) were the percent of perfect indication among the three impact zones and were calculated using both the relative frequency and cover of each species [see Dufrêne and Legendre (1997) for analytical details]. Here, we hypothesized that the Transition zone would have fewer indicator species than either the Impacted or Reference zones because it should host patchy distributions of species more frequent to the other zones. Significance (Bonferroni-corrected  $P \leq 0.05$ ) of IVs was estimated using 10,000 random permutations of the vegetation data (Manly 1997). INSPAN was performed using PC-ORD 4.08 (MjM Software, Gleneden Beach, OR, USA).

*Vegetation–Environment Linkages.* We used two complementary distance-based procedures to estimate relationships between vegetation composition and environmental variables. First, we ordinated plots and species based on species composition by using nonmetric multidimensional scaling (nMDS) (Minchin 1987). Ordination provided a visual assessment of gradients in species composition among and within impact zones and was conducted to aid in the interpretation of partial Mantel tests, our second, more tactical approach to estimating spatial and environmental linkages to composition. We used Bray–Curtis dissimilarity (BCD) as the distance metric, a coefficient shown to be one of the most robust and ecologically interpretable (Faith and others 1987). Once plots were ordinated, species centroids were mapped into ordination space by using weighted averaging (Legendre and Legendre 1998). A two-dimensional solution was the most appropriate for all ordinations, as stress values (an indicator of agreement between BCDs and the configuration of the ordination) were relatively low and exhibited small decreases when additional axes were included in the ordination.

We performed ordinations for all plots ( $n = 126$ ) as well as three subsets of plots corresponding to each zone ( $n = 45$  for Impacted and Transition; and  $n = 36$  for Reference). We used subsets of data to examine potential interactions in vegetation–environment relationships among impact zones that would potentially be obscured when using the full data set. An additional coarse-scale ordination was

produced by using average composition of each of the 14 plot clusters in contrast to vegetation patterns produced at the fine scale (Allen and Wyleto 1983; Turner and others 1999b).

To relate environmental variables to gradients in composition in nMDS ordinations, we used rotational vector fitting (Faith and Norris 1989). Vector fitting was used to find the direction of the maximum correlation of an environmental variable in an ordination of the vegetation data. Vector fitting was performed on all ordinations. Environmental values from each plot were used in fine-scale vector fitting, whereas average values from within each plot cluster were used in the coarse-scale analysis. Significance ( $P \leq 0.05$ ) of environmental vectors was estimated using 10,000 random permutations of the data. Ordination and vector fitting were performed using DECODA 2.05 (University of Melbourne, Parkville, Victoria, Australia).

Partial Mantel tests were used to measure the partial correlation (Mantel  $r$ ) between spatial, environmental, and vegetation distance matrices (Mantel 1967; Smouse and others 1986). Fundamentally, the analysis examines whether plots that are similar environmentally also are similar compositionally (Urban and others 2002). Mantel  $r$  coefficients are typically relatively small in magnitude (usually  $< 0.5$  for all but the strongest relationships) because the analysis considers the full rather than reduced dimensionality in multivariate data [for example, see Legendre and Fortin (1989), Legendre and others (1992), and Foster and others (1999)]. Because it uses distance matrices, this approach enables the user to extract variation caused by spatial autocorrelation (Legendre 1993) as well as other environmental variables to yield pure-partial correlations—relationships that represent variation that cannot be explained by all other variables included in the analysis.

We used spatial (Space and Canal) and environmental (C, N, P, Ca, K, Mg, Na, Depth, IQR(Depth), Freq $\leq 10$ cm, and Fire) variables as individual predictors in the Mantel analysis. Individual variables were converted to distance matrices using euclidean distance (Legendre and Legendre 1998). Vegetation species composition was expressed using BCD, as in the nMDS analysis. We first examined simple relationships between Space and individual environmental variables, Canal and environmental variables, and each spatial or environmental variable and vegetation. We then examined the effect of spatial autocorrelation on vegetation–environment linkages by factoring out the effect of Space. Finally, we estimated pure-partial vegetation–environment linkages. Here, the strength of a relation-

ship between a predictor variable and vegetation was assessed after variation explained by all other variables had been removed (except for Canal, because it was assumed to be causing variation in several environmental variables). We also examined the pure-partial Space–vegetation relationship, which would indicate residual spatial pattern in vegetation that can be explained only by spatial processes such as dispersal or other unmeasured factors with spatial structure.

Partial Mantel tests were conducted by using data from all plots, three subsets of data corresponding to the impact zones, and coarse-scale averages of composition and the environment within the 14 plot clusters. Significance (Bonferroni-corrected  $P \leq 0.05$ ) of Mantel  $r$  coefficients was assessed using 10,000 permutations. As a visual framework for these results, linkages among spatial, environmental, and vegetation variables were synthesized using path diagrams, a schematic that depicts significant paths of relationships among variables (Leduc and others 1992; Zmyslony and Gagnon 2000).

Bootstrapped confidence limits (95% CLs) were estimated for partial Mantel  $r$  coefficients to allow for comparison of the strength of linkages among zones. Bootstrapping was conducted by resampling distance matrices at a level of 90%, with 1000 resamples (Manly 1997; King and Richardson 2002).

*Spatial Pattern of Vegetation Among Zones.* To assess spatial patterns in vegetation at multiple scales, we used an extension of the Mantel test called a Mantel correlogram (Oden and Sokal 1986). Correlograms produce an index of spatial autocorrelation for classes of separation distances—samples that are compositionally more similar than average—yield positive autocorrelation, while those that are less similar are negatively autocorrelated (Legendre and Fortin 1989).

We contrasted pattern in vegetation among the three zones at both fine and coarse scales. Fine-scale pattern was examined within clusters by using separation distances of 50–400 m, with 50 m intervals (for example, 251- to 300-m separation distances = 300-m distance class). Coarse-scale pattern was assessed by comparing autocorrelation among clusters (within-cluster versus among-cluster variation). Because we were interested in how the average pattern within each cluster differed with respect to the average pattern among remaining clusters, these correlograms were limited to only one 400-m interval. Significant differences in Mantel  $r$  values among distance classes were contrasted using 95% CLs estimated by bootstrapping. Distance classes were considered significantly different if CLs did not overlap (Manly 1997). Mantel

tests and bootstrapping were performed using S-Plus 5.0 for Unix.

## RESULTS

### Environmental Variation Among Impact Zones

Three of the 11 environmental variables analyzed by using ANOVA differed among landscape impact zones (Table 1). All three zones differed for P and IQR(Depth), while Na differed between Impacted and Reference zones. Values of Ca, Depth, and Freq $\leq$ 10cm tended to be greatest in the Reference zone but were not statistically different than other zones because of high heterogeneity among plots within clusters in that zone (reflecting the heterogeneity of the *Cladium*–slough mosaic). All 11 variables yielded a significant Cluster effect, indicating coarse-scale spatial differences in the environment among clusters within one, two, or all of the three zones.

### Macrophyte Species Distributions

Forty macrophyte species and three other cover types (open water, noncalcareous periphyton, and calcareous periphyton) were identified (Table 2). Eight species were significant indicators of the Impacted zone, whereas six were indicators of the Reference zone. Despite having the most species, no species or cover types were indicators of the Transition zone, reaffirming it to be an ecological area of transition between the Impacted and Reference zones because it hosted patchy distributions of species common to both other zones (Table 2). *Typha domingensis* and invasive vines, *Mikania scandens* and *Sarcostemma clausum*, were the best indicators of the Impacted zone, although small floating species, *Lemna* spp. and *Salvinia minima*, and the understory herb *Rumex verticillatus* also had strong affinities for sparse-canopied areas there. The invasive willow *Salix caroliniana* was the only woody shrub with a significant indicator value; it was common in the Impacted zone. *Cladium jamaicense* was a significant indicator of the Reference zone despite being fairly common in the Transition zone as well. Four slough-community species also showed high fidelity to the Reference zone: *Nymphaea odorata* (water lily), *Eleocharis elongata* (spikerush), and *Utricularia purpurea* and *U. fibrosa* (bladderworts). Calcareous periphyton mat also was a significant indicator and was almost exclusively found in the Reference zone.

**Table 1.** Results from Mixed-model Nested Analysis of Variance (ANOVA) on Selected Environmental Characteristics of Impacted, Transition, and Reference Zones

Variable <sup>a</sup>	Code	Units	$F_{(2,11)}$ <sup>b</sup>	P	Landscape Zone		
					Impacted (n = 45) <sup>c</sup>	Transition (n = 45)	Reference (n = 36)
Distance from canal	Canal	m	— <sup>d</sup>	—	2495 (869)	5541 (914)	9050 (924)
Total carbon (soil)	C	g/kg	0.15	NS	435.0 (20.3)	435.0 (27.1)	428.0 (47.7)
Total calcium (soil)	Ca	g/kg	0.46	NS	37.1 (16.5)	42.8 (20.8)	47.0 (34.5)
Total potassium (soil)	K	mg/kg	0.06	NS	581.7 (29.5)	557.4 (58.4)	527.0 (28.3)
Total magnesium (soil)	Mg	mg/kg	0.11	NS	3707 (111)	3859 (140)	3625 (146)
Total sodium (soil)	Na	mg/kg	4.31	0.032	3058 (160) <sup>A</sup>	2900 (173) <sup>AB</sup>	2162 (187) <sup>B</sup>
Total nitrogen (soil)	N	g/kg	0.02	NS	29.3 (2.2)	29.0 (3.7)	29.2 (4.4)
Total phosphorus (soil)	P	mg/kg	102.30	≤ 0.001	1434 (174) <sup>A</sup>	1198 (184) <sup>B</sup>	578 (152) <sup>C</sup>
Water depth (1 year)	Depth	cm	3.74	NS	35.7 (8.3)	41.8 (9.6)	46.4 (10.4)
Interquartile range, water depth <sup>e</sup>	IQR(Depth)	cm	20.90	≤ 0.001	28.2 (0.1) <sup>A</sup>	29.7 (0.2) <sup>B</sup>	33.6 (0.1) <sup>C</sup>
Frequency, water depth less than 10 cm <sup>e</sup>	Freq≤10cm	%	2.79	NS	3.1 (0.4)	3.1 (0.3)	6.0 (0.8)
Fire index <sup>e</sup>	Fire	Sum <sup>f</sup>	0.46	NS	0.2 (0.4)	0.4 (0.5)	0.3 (0.5)

<sup>a</sup>Canal, distance from Hillsboro Canal; Depth, short-term mean water depth; Fire, fire index; Freq≤10cm, water depth less than 10 cm, and IQR(Depth), interquartile range of depth. C, carbon; Ca, calcium; K, potassium; Mg, magnesium; N, nitrogen; Na, sodium; and P, phosphorus.

<sup>b</sup>F ratios and associated P values correspond to the Zone main effect (fixed effect). Cluster was a random effect nested within Zone and was used as the error term. Cluster (random effect,  $F_{11,112}$ ) was significant ( $P \leq 0.05$ ) for all variables.

<sup>c</sup>Mean ( $\pm 1$  SD) values are based on measurements collected at individual plots within landscape zones. LSD tests were used to compare means among levels of the Zone effect when deemed significant from ANOVAs. Means with the same superscript letters do not differ ( $P > 0.05$ ).

<sup>d</sup>ANOVA not conducted on Canal since it was not independent of the landscape zones.

<sup>e</sup>1981–98.

<sup>f</sup>Sum of total number of fires/plot during 1981–98, weighted as  $1/\log_{10}(t + 1)$  for each fire, where  $t$  = time (years) since fire.

## Vegetation–Environment Linkages

**Ordination.** Ordination of fine-scale composition resulted in two gradients: a coarse-scale gradient significantly associated with Canal, P, IQR(Depth), and Depth; and a fine-scale gradient related to Freq≤10cm, Fire, K, N, and Na (Figure 2). Canal was most strongly linked to variation in composition but was closely followed by P and IQR(Depth) (Figure 2a).

Composition differed markedly among impact zones, as plots were sorted accordingly along nMDS axis 1 (Figure 2b). Reference-zone vegetation, although tightly banded at one end of nMDS axis 1, showed much fine-scale variation as evidenced by great dispersion ( $\beta$  diversity) along nMDS axis 2. However, the Transition zone showed the greatest overall variation in composition, with an extensive distribution of plots along nMDS axes 1 and 2, and several plots intermingling among Impacted and Reference zones.

Species centroids were unevenly dispersed in ordination space. Remarkably few species were projected in the region corresponding to the Transition zone; most centroids were clearly associated with the Impacted or Reference zones (Figure 2a and b).

In the Reference zone, slough-species centroids closely corresponded to vectors of Depth, N, and K, whereas *Cladium* (CLADJAMA) was at the opposite end of this within-zone gradient and corresponded to Freq≤10cm and Fire. Centroids were most tightly aggregated in the Impacted zone, suggesting less distinction of discrete communities.

Coarse-scale ordination of vegetation composition revealed that Canal, P, IQR(Depth), and Depth were the primary correlates of coarse-scale pattern (Figure 2c). Virtually all variation in composition occurred along nMDS Axis 1, and this gradient mirrored that of Axis 1 in the fine-scale ordination (Figure 2a and b). Ordination of average composition in clusters essentially eliminated fine-scale variation recovered by nMDS axis 2, subsequently eliminating fine-scale vegetation–environment relationships. Clusters were also completely separated into distinct strata corresponding to the three zones of impact, which provided further support for the dual gradient/zone concept in the study area (Figure 2c).

Ordinating subsets of data for each zone largely corroborated trends found in the full data set but revealed a few other potential relationships (Figure

**Table 2.** List of Macrophyte Species and Cover Types, Including Corresponding Codes (See Figures 2 and 3) and Indicator Values (IVs) for Each Landscape Zone

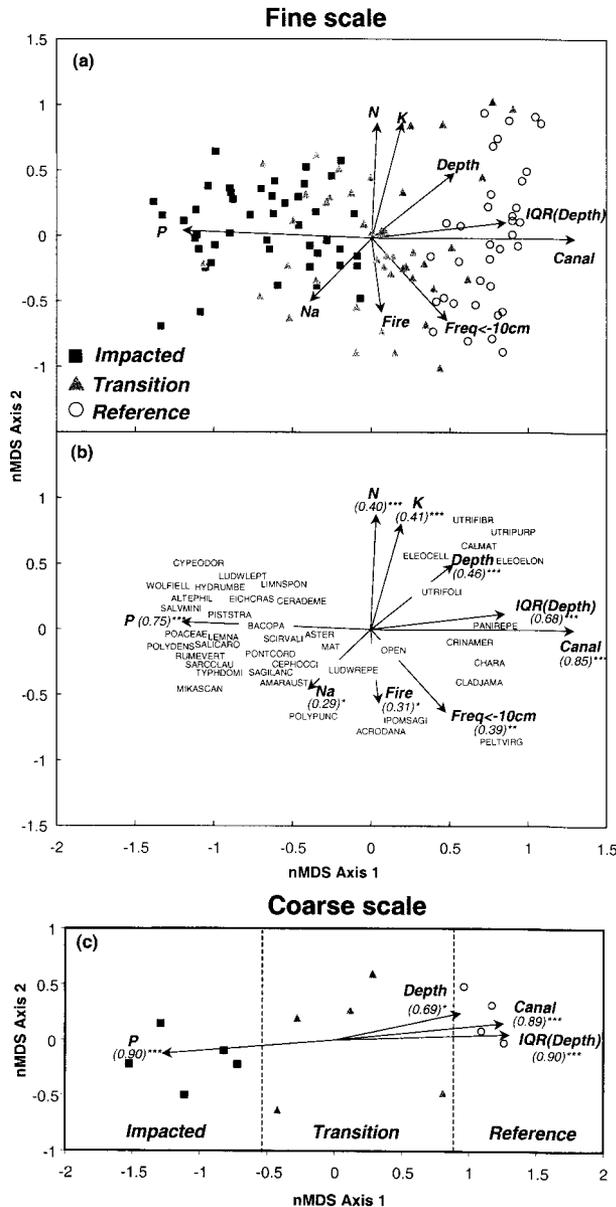
Species/Cover Type	Code	Indicator Value (IV)			
		Impacted	Transition	Reference	P
<i>Acrostichum danaeifolium</i> Langsd. and Fitch.	ACRODANA	0	6	0	NS <sup>a</sup>
<i>Alternanthera philoxeroides</i> (Mart.) Griseb.	ALTEPHIL	7	0	0	NS
<i>Amaranthus australis</i> (Gray) Sauer.	AMARAUST	1	1	0	NS
<i>Aster</i> sp.	ASTER	2	0	0	NS
<i>Bacopa</i> sp.	BACOPA	2	0	0	NS
Calcareous periphyton mat	CALMAT	0	2	37	≤ 0.0001
<i>Cephalanthus occidentalis</i> L.	CEPHOCCI	5	3	1	NS
<i>Ceratophyllum demersum</i> L.	CERADEME	0	4	0	NS
<i>Chara</i> sp.	CHARA	0	5	19	0.0055*
<i>Cladium jamaicense</i> Crantz.	CLADJAMA	6	28	46	≤ 0.0001
<i>Crinum americanum</i> L.	CRINAMER	0	1	8	0.0317*
<i>Cyperus odoratus</i> L.	CYPEODOR	2	0	0	NS
<i>Eichornia crassipes</i> (Mart.) Solms.	EICHCRAS	9	0	0	0.0353*
<i>Eleocharis cellulosa</i> Torr.	ELEOCELL	0	1	13	0.0107*
<i>Eleocharis elongata</i> Chapm.	ELEOELON	0	0	29	≤ 0.0001
<i>Hydrocotyle umbellata</i> Lamark.	HYDRUMBE	11	1	0	0.0190*
<i>Ipomoea sagittata</i> Poir.	IPOMSAGI	1	1	2	NS
<i>Lemna</i> sp.	LEMNA	30	4	0	≤ 0.0001
<i>Limnobium spongia</i> (Bosc.) Steud.	LIMNSPON	0	4	0	NS
<i>Ludwigia leptocarpa</i> (Nutt.)	LUDWLEPT	4	0	0	NS
<i>Ludwigia repens</i> Forst.	LUDWREPE	3	5	0	NS
Noncalcareous periphyton mat	MAT	3	20	0	0.0024*
<i>Mikania scandens</i> (L.) Willd.	MIKASCAN	61	8	0	≤ 0.0001
<i>Nymphaea odorata</i> Aiton.	NYMPODOR	0	9	39	≤ 0.0001
Open water—no cover	OPEN	19	34	34	NS
<i>Panicum repens</i> L.	PANIREPE	0	0	3	NS
<i>Peltandra virginica</i> (L.) Schott and Endl.	PELTVIRG	0	0	3	NS
<i>Pistia stratiotes</i> L.	PISTSTRA	7	2	0	NS
Poaceae sp.	POACEAE	13	0	0	0.0047*
<i>Polygonum densiflorum</i> Meisn.	POLYDENS	6	1	0	NS
<i>Polygonum punctatum</i> Ell.	POLYPUNC	25	16	0	0.0116*
<i>Pontederia cordata</i> L.	PONTCORD	8	6	0	NS
<i>Rumex</i> cf. <i>verticillatus</i> L.	RUMEVERT	36	0	0	≤ 0.0001
<i>Sagittaria lancifolia</i> L.	SAGILANC	31	14	1	0.0011
<i>Salix caroliniana</i> Michx.	SALICARO	20	1	1	≤ 0.0001
<i>Salvinia minima</i> Baker.	SALVMINI	25	0	0	≤ 0.0001
<i>Sarcostemma clausum</i> (Jacq.) Schult.	SARCCLAU	39	1	0	≤ 0.0001
<i>Scirpus validus</i> Vahl.	SCIRVALI	3	1	0	NS
<i>Typha domingensis</i> Pers.	TYPHDOMI	58	31	2	≤ 0.0001
<i>Utricularia fibrosa</i> Walt.	UTRIFIBR	0	10	37	≤ 0.0001
<i>Utricularia foliosa</i> L.	UTRIFOLI	0	6	14	0.0312*
<i>Utricularia purpurea</i> Walt.	UTRIPURP	0	0	48	≤ 0.0001
<i>Wolfiella</i> sp.	WOLFIELL	4	0	0	NS

<sup>a</sup>Indicates IVs that are not significant. IVs are percent of perfect indication, with significant (Bonferroni-corrected  $P \leq 0.05$ ) scores shown in bold.

\*Not significant after Bonferroni correction.

3). In the Impacted zone, cations (Ca and Mg) and Fire were associated with the few plots in which *Cladium* occurred (Figure 3a). However, of these three environmental variables, only Mg was signif-

icant after Bonferroni correction. IQR(Depth), N, and C were inversely related to this *Cladium* gradient, with the floating plants *Salvinia minima* (SALVMINI) and *Lemna* spp. (LEMNA) along with



**Figure 2.** Nonmetric multidimensional scaling (nMDS) ordination of individual (a) plots and (b) species/cover-type centroids using fine-scale vegetation species composition, and (c) clusters using coarse-scale species composition (calculated as averages of the 14 plot clusters). Symbols indicate membership among the three impact zones. Environmental vectors show the direction and magnitude of significant correlations ( $r$  values are adjacent to vectors) within the ordination space. See Tables 1 and 2 for codes for environmental and species variables, respectively. \* $P \leq 0.05$ , \*\* $P \leq 0.001$ , and \*\*\* $P \leq 0.0001$ . Canal, distance from Hillsboro Canal; Depth, short-term mean water depth; Fire, fire index; Freq $\leq 10$ cm, water depth less than  $-10$  cm; and IQR(Depth), interquartile range of depth. K, potassium; N, nitrogen; Na, sodium; and P, phosphorus.

the willow *Salix caroliniana* (SALICARO) reaching greatest abundance here. *Typha* (TYPHDOMI) was widespread throughout; thus, its centroid was located at the midpoint of the ordination. Neither P nor Canal was linked to composition in the Impacted zone.

In the Transition zone, N, K, Na, Depth, and Canal were the variables most closely linked to composition (Figure 3b). Noncalcareous periphyton mat (MAT) and *Nymphaea odorata* (NYMPODOR) were the two most notable centroids associated with these variables; their cover was chiefly located in slough habitats or other deep, open-canopied areas. *Cladium* abundance was inversely related to these variables.

Ordination of Reference-zone vegetation reproduced the *Cladium*–slough gradient revealed in the full landscape ordination (Figures 2 and 3c). Slough species were associated with deeper water, but also N. *Cladium* stands were more likely to experience periods of dryness and also had greater soil C and P relative to sloughs.

**Partial Mantel Tests.** Partial Mantel tests on fine-scale data from the full vegetation gradient indicated that most environmental variables were spatially autocorrelated (column Space in Table 3 and Figure 4). However, only four variables, Na, P, IQR(Depth), and Depth, were directly related to Canal (column Canal in Table 3), corroborating results from ANOVA among the landscape zones (Table 1). Considering simple relationships, vegetation composition was significantly related to all but two variables (Na and Fire; column Veg in Table 3). However, after extracting spatial autocorrelation (Space), Ca and Mg were no longer significant (column Veg/Space in Table 3). The variables that corresponded to nMDS axis 1 (Figure 2)—Canal, P, and IQR(Depth)—were most closely tied to composition regardless of spatial dependencies. N, K, and C exhibited the strongest link to composition of the remaining fine-scale variables, although Depth and Freq $\leq 10$ cm remained significantly correlated to vegetation as well.

Pure-partial tests revealed that C, Depth, and IQR(Depth) could not account for unique variation in the vegetation composition (column Veg/\* in Table 3 and Figure 4). However, P remained highly significant. The relationship between Freq $\leq 10$ cm and vegetation actually improved slightly after variation from all other variables had been removed. N and K also remained highly significant as pure partials. Confidence limits (95% CLs) generated by bootstrapping indicated that Canal was the strongest factor (partial Mantel  $r = 0.26$ , lower 2.5% = 0.24, and upper 2.5% = 0.28)—a relationship that

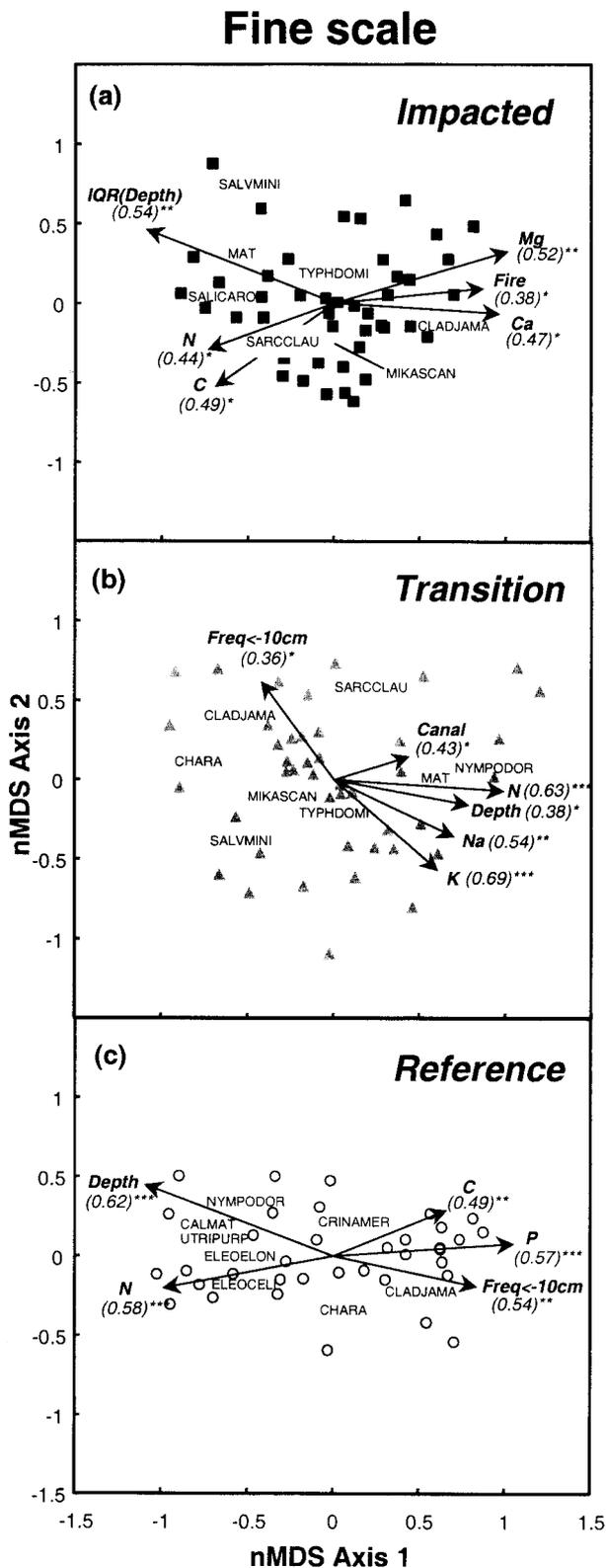


Figure 3. Nonmetric multidimensional scaling (nMDS) ordinations of plots using fine-scale vegetation composition (Bray–Curtis dissimilarity) within the (a) Impacted, (b) Transition, and (c) Reference zones. For clarity, only common species or cover-type centroids were projected.

was indicative of variation in composition caused by the canal-and-levee system but unexplained by any of the other measured spatial or environmental variables. Finally, a highly significant spatial residual suggested that spatial factors contributed to variation in vegetation pattern that could not be explained by the environment or Canal.

Mantel results from the coarse-scale analysis generally supported those of the coarse-scale nMDS ordination, as Canal, P, and IQR(Depth) were highly associated with vegetation (Table 3 and Figure 4). However, IQR(Depth) was not significant as a pure partial. Canal and P were the only variables that significantly accounted for coarse-scale variation that could not be accounted for by other variables. Although spatially autocorrelated, coarse-scale composition did not exhibit a significant spatial residual, indicating that coarse spatial patterns were mostly attributed to Canal and the environment.

Mantel analysis of data from just the Impacted zone revealed that fewer environmental variables were dependent upon Space or Canal than in the full data set, reflecting greater homogeneity in the environment (Table 4 and Figure 5a). Vegetation also had weaker linkages to the environment in this zone. N was the only environmental variable that was significant as a pure partial. Space explained the most variation in composition in the Impacted zone.

Environmental variables measured in Transition plots showed greater spatial dependency than in the Impacted zone (Table 4 and Figure 5b). Nevertheless, numerous environmental variables were linked to vegetation even after correcting for spatial autocorrelation and mutual correlations among variables. N and K had the strongest relationships to vegetation, although Depth, Freq $\leq$ 10cm, and C also were significant. Space was the most influential factor, with lower confidence limits of its pure-partial Mantel coefficient exceeding the upper limits of any other variable (partial Mantel  $r = 0.48$ , lower 2.5% = 0.45, and upper 2.5% = 0.50).

Environmental vectors show the direction and magnitude of significant correlations ( $r$  values are adjacent to vector labels) within the ordination space. See Tables 1 and 2 for codes for environmental and species variables, respectively. \* $P \leq 0.05$ , \*\* $P \leq 0.001$ , and \*\*\* $P \leq 0.0001$ . Canal, distance from Hillsboro Canal; Depth, short-term mean water depth; Fire, fire index; Freq $\leq$ 10cm, water depth less than -10 cm; and IQR(Depth), interquartile range of depth. C, carbon; Ca, calcium; K, potassium; Mg, magnesium; N, nitrogen; Na, sodium; and P, phosphorus.

**Table 3.** Results from Simple ( $r$ ) and Partial ( $\rho$ ) Mantel Tests Among Spatial, Environmental, and Vegetation (Veg) Distance Matrices at Fine and Coarse Scales Along the Full Vegetation Gradient

Variable (X) <sup>a</sup>	Space (S) <sup>b</sup>		Canal (C) <sup>c</sup>		Veg (Y) <sup>d</sup>		Veg/Space <sup>e</sup>		Veg/* (Pure Partial) <sup>f</sup>	
	$r_{SX}$	$P$	$r_{CX}$	$P$	$r_{XY}$	$P$	$\rho_{XY S}$	$P$	$\rho_{XY *}$	$P$
Fine scale ( $n = 126$ plots)										
Space	—	—	0.624	$\leq 0.0001$	0.392	$\leq 0.0001$	—	—	0.178	$\leq 0.0001$
Canal <sup>h</sup>	0.624	$\leq 0.0001$	—	—	0.502	$\leq 0.0001$	0.349	$\leq 0.0001$	0.262	$\leq 0.0001$
C	NS <sup>g</sup>		NS		0.104	$\leq 0.0001$	0.108	$\leq 0.0001$	NS	
Ca	0.115	$\leq 0.0001$	NS		0.071	0.0004	NS		NS	
K	NS		NS		0.088	$\leq 0.0001$	0.127	$\leq 0.0001$	0.187	$\leq 0.0001$
Mg	0.315	$\leq 0.0001$	NS		0.050	0.0021	NS		NS	
Na	0.060	0.0030	0.064	0.0002	NS		NS		NS	
N	0.067	$\leq 0.0001$	NS		0.230	$\leq 0.0001$	0.222	$\leq 0.0001$	0.210	$\leq 0.0001$
P	0.444	$\leq 0.0001$	0.714	$\leq 0.0001$	0.397	$\leq 0.0001$	0.266	$\leq 0.0001$	0.178	$\leq 0.0001$
Depth	0.215	$\leq 0.0001$	0.160	$\leq 0.0001$	0.140	$\leq 0.0001$	0.062	$\leq 0.0001$	NS	
Freq<-10cm	NS		NS		0.080	$\leq 0.0001$	0.071	$\leq 0.0001$	0.121	$\leq 0.0001$
IQR(Depth)	0.593	$\leq 0.0001$	0.786	$\leq 0.0001$	0.376	$\leq 0.0001$	0.193	$\leq 0.0001$	NS	
Fire	0.166	$\leq 0.0001$	NS		NS		NS		NS	
Coarse scale ( $n = 14$ clusters)										
Space	—	—	0.551	$\leq 0.0001$	0.527	$\leq 0.0001$	—	—	NS	
Canal	0.551	$\leq 0.0001$	—	—	0.763	$\leq 0.0001$	0.668	$\leq 0.0001$	0.406	$\leq 0.0001$
C	NS		NS		NS		NS		NS	
Ca	0.406	$\leq 0.0001$	NS		NS		NS		NS	
K	NS		NS		NS		NS		NS	
Mg	0.509	$\leq 0.0001$	NS		NS		NS		NS	
Na	NS		NS		NS		NS		NS	
N	NS		NS		NS		NS		NS	
P	0.503	$\leq 0.0001$	0.859	$\leq 0.0001$	0.658	$\leq 0.0001$	0.536	$\leq 0.0001$	0.465	$\leq 0.0001$
Depth	0.420	$\leq 0.0001$	0.297	0.0031	NS		NS		NS	
Freq<-10cm	NS		NS		NS		NS		NS	
IQR(Depth)	0.526	$\leq 0.0001$	0.775	$\leq 0.0001$	0.543	$\leq 0.0001$	0.370	0.0003	NS	
Fire	NS		NS		NS		NS		NS	

<sup>a</sup>Canal, distance from Hillsboro Canal; Depth, short-term mean water depth; Fire, fire index; Freq $\leq$ 10cm, water depth less than 10 cm; and IQR(Depth), interquartile range of depth; and Space, separation distance. C, carbon; Ca, calcium; K, potassium; Mg, magnesium; N, nitrogen; Na, sodium; and P, phosphorus.

<sup>b</sup>Simple Mantel test between Space and individual variables.

<sup>c</sup>Simple Mantel test between Canal and individual variables.

<sup>d</sup>Simple Mantel test between vegetation and individual variables.

<sup>e</sup>Partial Mantel test between vegetation and individual variables after accounting for variation explained by spatial autocorrelation.

<sup>f</sup>Partial Mantel test between vegetation and individual-variables after accounting for variation explained by remaining variables. Variation explained by Canal was not removed in pure-partial tests on vegetation since it was assumed to have caused changes to several environmental variables. However, variation explained by all other variables was removed from the estimate of the pure-partial effect of Space and Canal on vegetation.

<sup>g</sup>Indicates Mantel coefficients that are not significant (Bonferroni-corrected  $P > 0.05$ ).

<sup>h</sup>The effect of distance from canal inflow structures.

In the Reference zone, most environmental variables were spatially autocorrelated (Table 4 and Figure 5c). However, Depth, Freq $\leq$ 10cm, C, Ca, N, and P were significantly linked to vegetation regardless of spatial dependencies. Freq $\leq$ 10cm, C, K, N, and P all remained linked to vegetation after variance explained by other variables had been removed. Vegetation was not spatially autocorrelated, nor was there a significant spatial residual, which indicated that the spatial distribution of macrophyte

species was similar across the Reference landscape. Based on 95% CLs of partial Mantel coefficients, Space was significantly more important to vegetation patterns in Transition and Impacted zones than in the Reference zone.

### Contrasting Vegetation Pattern Among Impact Zones

Mantel correlograms showed that fine-scale pattern (within clusters) differed significantly among zones

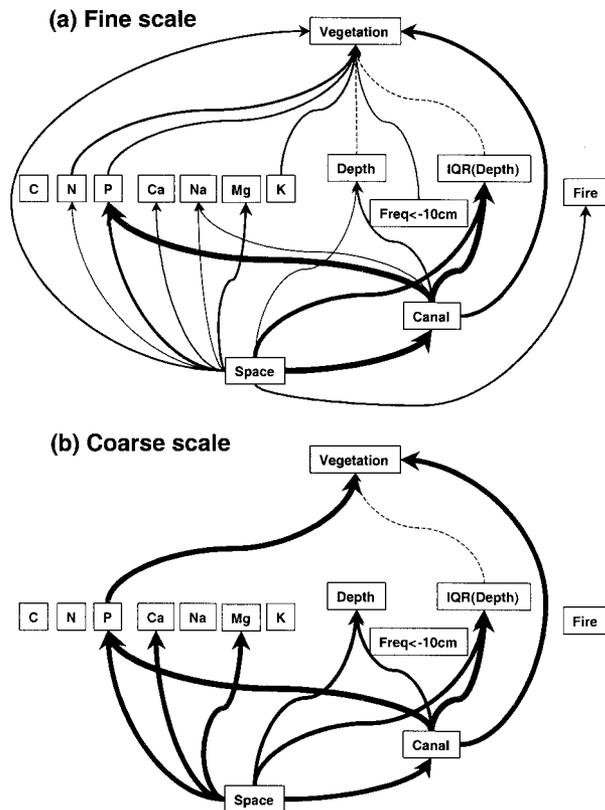


Figure 4. Path diagram depicting the linkages among spatial factors, environmental variables, and vegetation composition at (a) fine and (b) coarse scales along the vegetation gradient, as estimated using Mantel tests. Significant pure-partial linkages between variables and vegetation are shown by *solid arrows*, while linkages that were significant after accounting for spatial autocorrelation, but not as pure partials, are shown as *dotted arrows*. *Arrow thickness* is proportional to magnitude of relationship (see Table 3). Canal, distance from Hillsboro Canal; Depth, short-term mean water depth; Fire, fire index;  $\text{Freq} \leq 10\text{cm}$ , water depth less than  $-10\text{ cm}$ ;  $\text{IQR}(\text{Depth})$ , interquartile range of depth; and Space, separation distance. C, carbon; Ca, calcium; K, potassium; Mg, magnesium; N, nitrogen; Na, sodium; and P, phosphorus.

of differing impact (Figure 6a). Neither Impacted nor Transition zones displayed much local variation in composition, which manifested itself as relatively similar levels of autocorrelation among distance classes. However, all distance classes for these two zones exhibited positive autocorrelation, indicating that within-cluster composition, regardless of separation distance, was more similar than average composition in other areas of their respective zones. A subtle spike of positive autocorrelation occurred at the 250-m distance class in both Impacted and Transition zones.

In contrast, the Reference zone showed much fine-scale variation in composition, with the correlogram effectively capturing pattern of the natural vegetation mosaic. Vegetation was positively autocorrelated at the smallest separation distances (50 and 100 m), whereas no autocorrelation was observed at intermediate distances (Figure 6a). Plots separated by 400 m were negatively autocorrelated. Spatial pattern in the Reference zone differed significantly from that of the Transition and Impacted zones at 150-, 300-, and 400-m distance classes. Similar to the other two zones, the Reference zone exhibited a distinct and significant spike of positive autocorrelation at the 250-m distance class.

Coarse vegetation pattern differed among impact zones. At the cluster scale, the Transition zone had the highest degree of autocorrelation but was not significantly different from the Impacted zone (Figure 6b). Positive autocorrelation also was detected at this coarse scale in the Reference zone but to a significantly lesser degree than in the other two zones.

## DISCUSSION

### Vegetation–Environment Linkages: Allogenic or Autogenic?

Results from partial Mantel tests suggested that several of the spatial and environmental variables were independently related to vegetation composition. Although our approach effectively removed variation accounted for by space or other variables and thus provided strong evidence for variables directly linked to vegetation patterns, it did not conclusively establish the nature of these relationships. That is, were environmental factors causing variation in vegetation composition (allogenic), or were existing patterns in composition causing observed environmental variation (autogenic)?

The variables most closely related to the primary vegetation gradient—P, Canal, and  $\text{IQR}(\text{Depth})$ —were allogenic factors. In the case of P, it is well established that Everglades vegetation is P limited, with most species adapted to highly oligotrophic conditions [reviewed by Noe and others (2001)]. Several species, particularly those comprising the slough community, have been shown to be sensitive to elevated P in both observational (Vaithyanathan and Richardson 1999) and experimental (Walker and others 1989; Craft and others 1995; Chiang and others 2000) settings. Conversely, many species found to be most abundant in the Impacted and Transition zones are opportunistic, “weedy” species that are highly competitive in

**Table 4.** Results from Simple ( $r$ ) and Partial ( $\rho$ ) Mantel Tests Among Fine-scale Spatial, Environmental, and Vegetation (Veg) Distance Matrices within Each of the Three Impact Zones (See Table 3 for Details)

Variable	Space (S)		Canal (C)		Veg (Y)		Veg/Space		Veg/* (Pure Partial)	
	$r_{SX}$	$P$	$r_{CX}$	$P$	$r_{XY}$	$P$	$\rho_{XY S}$	$P$	$\rho_{XY *}$	$P$
Impacted ( $n = 45$ )										
Space	—	—	0.171	0.0025	0.286	$\leq 0.0001$	—	—	0.186	$\leq 0.0001$
Canal	0.171	$\leq 0.0001$	—	—	NS		NS		NS	
C	NS		NS		NS		NS		NS	
Ca	0.591	$\leq 0.0001$	NS		0.185	$\leq 0.0001$	NS		NS	
K	NS		NS		NS		NS		NS	
Mg	0.455	$\leq 0.0001$	NS		NS		NS		NS	
Na	NS		0.110	0.0026	NS		NS		NS	
N	NS		NS		0.085	0.0007	NS		0.116	0.0005
P	NS		NS		NS		NS		NS	
Depth	NS		NS		NS		NS		NS	
Freq<-10cm	NS		NS		NS		NS		NS	
IQR(Depth)	0.837	$\leq 0.0001$	0.286	$\leq 0.0001$	0.222	$\leq 0.0001$	NS		NS	
Fire	0.470	$\leq 0.0001$	NS		NS		NS		NS	
Transition ( $n = 45$ )										
Space	—	—	0.216	$\leq 0.0001$	0.376	$\leq 0.0001$	—	—	0.480	$\leq 0.0001$
Canal	0.216	$\leq 0.0001$	—	—	0.178	$\leq 0.0001$	0.107	0.0034	NS	
C	0.117	0.0004	NS		0.220	$\leq 0.0001$	0.191	0.0107	0.139	$\leq 0.0001$
Ca	0.177	$\leq 0.0001$	NS		NS		NS		NS	
K	NS		0.310	$\leq 0.0001$	0.298	$\leq 0.0001$	0.321	$\leq 0.0001$	0.261	$\leq 0.0001$
Mg	0.342	$\leq 0.0001$	NS		0.178	$\leq 0.0001$	NS		NS	
Na	0.166	$\leq 0.0001$	0.165	$\leq 0.0001$	0.210	$\leq 0.0001$	0.162	0.0002	NS	
N	NS		0.198	$\leq 0.0001$	0.458	$\leq 0.0001$	0.465	$\leq 0.0001$	0.370	$\leq 0.0001$
P	NS		NS		NS		NS		NS	
Depth	0.114	0.0013	0.208	$\leq 0.0001$	0.137	$\leq 0.0001$	0.103	0.0030	0.117	0.0003
Freq<-10cm	NS		NS		NS		NS		0.114	0.0012
IQR(Depth)	0.516	$\leq 0.0001$	0.543	$\leq 0.0001$	0.194	$\leq 0.0001$	NS		NS	
Fire	0.501	$\leq 0.0001$	0.274	$\leq 0.0001$	NS		NS		NS	
Reference ( $n = 36$ )										
Space	—	—	0.318	$\leq 0.0001$	NS		—	—	NS	
Canal	0.318	$\leq 0.0001$	—	—	NS		NS		NS	
C	NS		NS		0.149	0.0004	0.147	0.0006	0.120	0.0020
Ca	NS		NS		0.121	0.0018	0.118	0.0020	NS	
K	NS		NS		NS		NS		0.212	$\leq 0.0001$
Mg	0.484	$\leq 0.0001$	NS		NS		NS		NS	
Na	0.310	$\leq 0.0001$	NS		NS		NS		NS	
N	0.208	$\leq 0.0001$	NS		0.246	$\leq 0.0001$	0.239	$\leq 0.0001$	0.166	$\leq 0.0001$
P	NS		0.184	0.0006	0.231	$\leq 0.0001$	0.227	$\leq 0.0001$	0.102	0.0028
Depth	0.399	$\leq 0.0001$	NS		0.336	$\leq 0.0001$	0.342	$\leq 0.0001$	NS	
Freq<-10cm	0.424	$\leq 0.0001$	0.184	0.0004	0.228	$\leq 0.0001$	0.225	$\leq 0.0001$	0.103	0.0022
IQR(Depth)	0.440	$\leq 0.0001$	0.667	$\leq 0.0001$	NS		NS		NS	
Fire	0.471	$\leq 0.0001$	0.367	$\leq 0.0001$	NS		NS		NS	

Canal, distance from Hillsboro Canal; Depth, short-term mean water depth; Fire, fire index; Freq $\leq$ 10cm, water depth less than 10 cm and IQR(Depth), interquartile range of depth; and Space, separation distance. C, carbon; Ca, calcium; K, potassium; Mg, magnesium; N, nitrogen; Na, sodium; and P, phosphorus.

high-P environments (Davis 1994). *Typha* in particular is clearly most competitive under elevated nutrient conditions (Urban and others 1993; Newman and others 1996; Miao and Sklar 1998; Miao and others 2000) and has been positively associated

with P gradients in many locations in the Everglades [for example, see Doren and others (1997)]. Thus, that P was significantly and independently linked to variation in vegetation pattern is not surprising and corroborates results from other studies

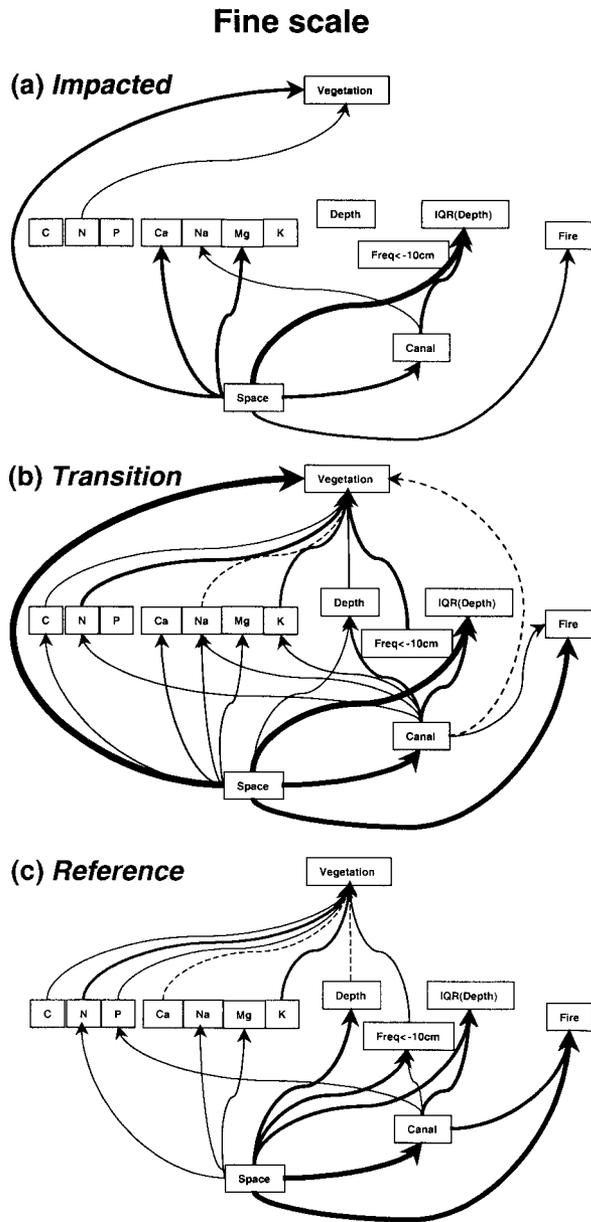


Figure 5. Path diagrams depicting the linkages among spatial factors, environmental variables, and fine-scale vegetation composition within (a) Impacted, (b) Transition, and (c) Reference zones, as estimated using Mantel tests. Significant pure-partial linkages between variables and vegetation are shown by *solid arrows*, while linkages that were significant after accounting for spatial autocorrelation, but not as pure partials, are shown as *dotted arrows*. *Arrow thickness* is proportional to magnitude of relationship (see Table 4). Canal, distance from Hillsboro Canal; Depth, short-term mean water depth; Fire, fire index; Freq $\leq$ 10cm, water depth less than -10 cm; IQR(Depth), interquartile range of depth; and Space, separation distance. C, carbon; Ca, calcium; K, potassium; Mg, magnesium; N, nitrogen; Na, sodium; and P, phosphorus.

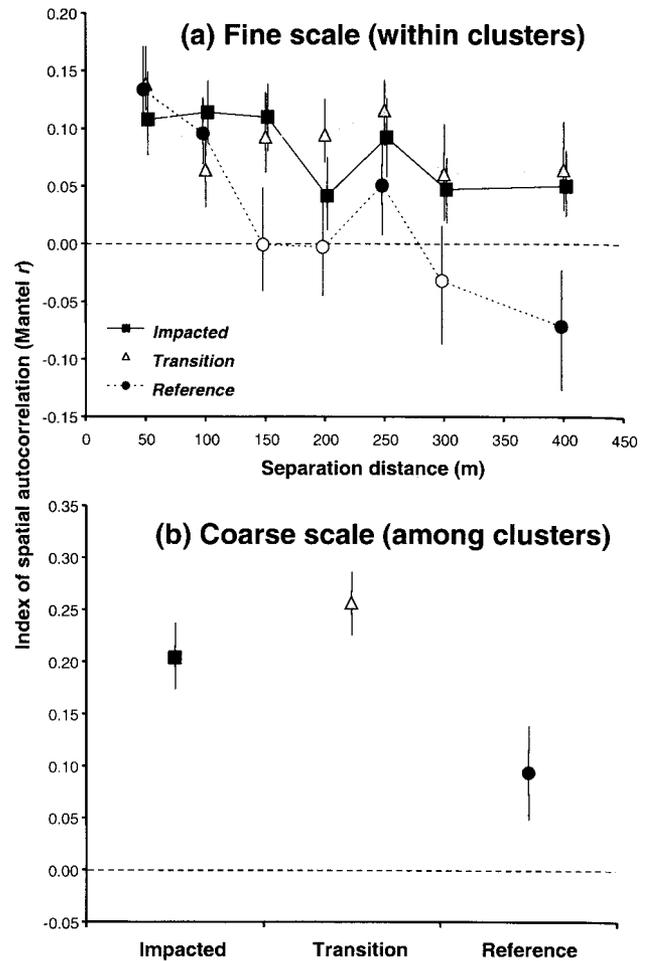


Figure 6. Mantel correlogram of vegetation composition showing spatial autocorrelation among impact zones using (a) fine-scale (within-cluster) separation distances (50 m), and (b) coarse-scale (among-cluster) separation distance (400-m distance class only). Significantly auto-correlated distance classes are indicated by the *filled symbols*, and *unfilled symbols* indicate no autocorrelation. Error bars indicate bootstrapped 95% confidence limits.

that suggest P enrichment is a major source of perturbation to Everglades plant communities.

Stability in water depth may have acted in concert with P to promote the establishment of invasive species such as *Typha*. Frequency of severe dryness (Freq $\leq$ 10cm) and variability of water depth [IQR(Depth)] were significantly related to vegetation composition along this gradient, although IQR(Depth) was not significant as a pure-partial coefficient. Several authors have suggested that hydroperiod plays a role in the observed expansion of *Typha* in the Everglades, as *Typha* is highly competitive in deeper, more stable water conditions but intolerant of drought (Toth 1988; Urban and others 1993; Newman and others 1996). *Cladium*, on the

other hand, is well adapted for dynamic hydrological conditions but exhibits a diminished capacity to resist invasion by *Typha* under deep, stable water conditions (Toth 1987; Davis 1994; Newman and others 1996). Our data showed that mean water depths from the previous year actually were greater with increasing distance from the canal, whereas variation in water depth was most stable near the canal inflow structures where *Typha* was most prolific. Severe dryness tended to be experienced more frequently in the Reference zone, and plots in this area also exhibited the greatest fluctuation in water levels. Concomitantly, *Cladium* dominated these drought-susceptible and hydrologically dynamic plots, as evidenced in the nMDS ordinations. The significant relationship between vegetation and hydrological variability supports the hypothesis that modifications to the hydropattern related to the canal-and-levee system have at least partially contributed to observed vegetation patterns. It further supports the hypothesis that hydrology may act synergistically with P to promote *Typha* and other invaders, since experimental fertilizer studies have been unable to demonstrate that P enrichment alone results in competitive exclusion of *Cladium* (Craft and others 1995; Chiang and others 2000).

Perhaps the most interesting linkage revealed along the full vegetation gradient was the residual variation in composition that could only be explained by distance from the canal inflow structures (Canal). Canal had a direct effect on P and IQR(Depth), a strong indication that variation in these factors was due to water entering the wetland through canal inflow structures (SFWMD 1992; Romanowicz and Richardson 1997, 2004). However, even after variation from these and all other remaining variables was removed, Canal remained a significant correlate of composition—its partial correlation was greater than any other variable. Possibly, Canal captured the synergistic effect of P and hydropattern that was not accounted for when those respective factors were considered individually. In addition, this observation may have resulted from one or a combination of several other factors: (a) environmental variables not measured but directly influenced by the canal were acting to structure vegetation (for example, micronutrients) (G. M. Ferrell unpublished data); (b) proximity to the canal affected seed and/or floating plant dispersal (Vaithyanathan and Richardson 1999); (c) a “front” of succeeding vegetation assemblages that began near the canal has progressed into the interior of the study area but asynchronously with environmental changes (that is, level of P enrichment) (Wu and others 1997; C. J. Richardson unpublished

data); and (d) other contagious spatial effects directly related to proximity to canal (for example, herbivory or disease (Richardson and others 1999). Indeed, other potential factors beyond these surely exist and warrant examination in future research. At a minimum, it seems reasonable to conclude that influences directly attributable to canal-and-levee systems represent a serious threat to the long-term integrity of the Everglades and other large, wetland ecosystems (for example, delta marsh) (Shay and others 1999).

Whereas proximity to the canal inflow structures, elevated P, and modified hydropatterns were allogenic determinants of vegetation patterns along the anthropogenic influence gradient, the nature of the linkages between significant fine-scale environmental variables and vegetation was much less clear. Of particular interest was the significant linkage between N and vegetation composition. Several studies have shown that N additions do not stimulate growth in Everglades plant communities (Steward and Ornes 1975a; Walker and others 1988; Craft and others 1995; Chiang and others 2000) and that all but the most heavily P-enriched locations are P limited (Richardson and others 1999). Nevertheless, N accounted for variation in vegetation that no other variable could, along the full vegetation gradient and within all three impact zones. Within the Transition and Reference zones, highest N (and K) concentrations were associated with periphyton mats and slough-community species, particularly the water lily *Nymphaea odorata*. Decomposing *Nymphaea* tissue has been shown to have greater N concentrations than more recalcitrant species like *Cladium* (Steward and Ornes 1975b; J. Vymazal unpublished data). Periphyton mats are largely composed of blue-green algae, many of which are heterocystic N fixers (Swift and Nicholas 1987; Browder and others 1994), and also tend to have relatively high tissue N concentrations (Vymazal and Richardson 1995). Indeed, Gleason and Stone (1994) describe two principal sediment types in the Everglades that closely correspond to our observations: Everglades peat, generated by *Cladium*, and Loxahatchee peat, a product of *Nymphaea* slough communities. Thus, N may have been an excellent indicator of fine-scale composition because the vegetation itself may have been causing variation in N concentrations—an excellent illustration of the effect of pattern on process (Watt 1947).

Nitrogen may have played a more direct role in generating fine-scale compositional patterns in the Impacted zone, however. It was the only environmental variable that was independently linked to vegetation composition in this zone. High soil P

concentrations adjacent to canal inflows have been suggested to result in some instances of N limitation [for example, see Richardson and others (1999)]. This fact, coupled with the autogenic soil legacies described by Gleason and Stone (1994), suggests that remnant patches of soil containing elevated N may influence vegetation patterns in locations where P is no longer limiting. *Salix caroliniana* (willow), an indicator of the Impacted zone, was particularly abundant in areas of elevated N. Understorey species (*Rumex verticillatus*, *Lemna* spp., and *Salvinia minima*) were closely associated with *Salix* stands, an indication that these species may have benefited from the reduction in canopy cover imposed by *Typha* (Grimshaw and others 1997). The pre-impact physical template may have influenced observed fine-scale pattern in the Impacted zone and subsequently may have contributed to the significant relationship between N and vegetation (Peterson 2002). A closer examination of spatial patterns of N and vegetation is needed to better evaluate its role in structuring fine-scale community composition in P-enriched areas of the Everglades.

Considering cation–vegetation relationships, our results support the conclusions of Craft and Richardson (1997), who examined the potential relationship between *Typha* expansion and elevated Na, Ca, and Mg in soils near inflow structures. Using simple correlations, they showed that *Typha* was most strongly related to soil P and concluded that cations were not important to its distribution even though *Typha* also was significantly correlated Na. In our study, none of these cations was able to account for unexplained variation in vegetation. Although Na and other cations cannot be completely ruled out as partial determinants, our results suggest that they may not be significant agents of pattern formation.

Fire has been shown to be an important disturbance in the maintaining of the mosaic of Everglades plant communities (Craighead 1971; Gunderson and Snyder 1994). A wide variety of responses of vegetation to fire have been reported, primarily focusing on *Typha* and *Cladium*. These responses have depended largely on intensity of fires and the presence of nutrient enrichment [for example, see Urban and others (1993), Richardson and others (1997), and Newman and others (1998)]. In our study, Fire was weakly but significantly correlated to composition in the ordination of the full vegetation gradient. Fire also covaried with  $\text{Freq} \leq 10\text{cm}$ , as plots that were dry most frequently tended to burn most frequently. Additionally, *Cladium* was the dominant species in plots that

were most susceptible to both drying and burning. However, Fire was not linked to vegetation composition in the partial Mantel analysis. Thus, our results are equivocal. In general, these findings imply that Fire covaries with other, stronger patterns of environmental variation and thus is not able to explain a unique component of variation in the vegetation. It is important to note that our fire index only considered large fires and only those that had occurred since 1981. Fires also were spatially contagious; hence, autocorrelation inhibited our ability to detect fire effects. Due to the tremendous number of potential interactions with other variables and the high variability of fire frequency, intensity, and spatial extent, it is highly unlikely that simple patterns will emerge [for example, see Newman and others (1998)]. For long-term management and restoration of Everglades vegetation to succeed, a better understanding of the influence of fire on vegetation patterns is needed.

### Implications of Spatial Pattern and Scale

One of the greatest limitations of conclusions drawn from observational studies in ecology has been the phenomenon known as spatial autocorrelation (Legendre 1993). Our Mantel test results revealed some implications of spatial structuring in the environment and the observed effect it can have on descriptive vegetation–environment relationships. Had Space not been considered, we may have erroneously concluded that virtually every variable measured was directly related to vegetation composition. On the contrary, many of these relationships were artifacts of spatial autocorrelation in both the environment and vegetation. Simply put, samples that were close together tended to be more similar environmentally and ecologically than ones far apart, regardless of whether the environment was mechanistically causing the observed vegetation patterns or vice-versa (Legendre 1993). Although the finding of nonsignificance after accounting for Space does not rule out the possibility that these variables were causally linked to vegetation, it does suggest that many observed “significant” relationships reported in the Everglades and elsewhere may have been due to spurious correlations that arose from spatially structured data (Thomson and others 1997). Factoring out variation explained by other variables provides further evidence that a significant variable indeed may be a determinant of observed pattern because its independent contribution can be more accurately assessed (Leduc and others 1992). Thus, our Mantel approach did not establish causation (Beyers 1998) but, we believe, represented an improvement in analytical ap-

proaches used to infer direct linkages between species and their environment, particularly in large, spatially heterogeneous landscapes.

An added benefit afforded by the partial Mantel approach was the ability to assess spatial variation in vegetation composition not accounted for by the environment—a spatially autocorrelated residual. We were able to show that spatial proximity among sampling locations (Space) accounted for significant variation in vegetation pattern across the landscape, particularly in the Impacted and Transition zones. In both of these zones, Space accounted for the most variation in composition, highly suggestive of dispersal- or disturbance-influenced pattern [for example, see Pickett and White (1985) and Pacala and Levin (1997)]. Moreover, other than a weak linkage to N, Space was the only variable to explain variation in vegetation in the Impacted zone. On the contrary, all of the spatial structure in the Reference zone was explained by environmental variation. Thus, these results suggest that, with increasing impact to the ecosystem, spatial factors overwhelmed and decoupled the linkages between fine-scale vegetation pattern and environmental factors observed in the Reference zone.

We further examined spatial pattern in vegetation between scales by using Mantel correlograms, which indicated that the spatial structure in the Transition and Impacted zones was occurring primarily at coarse rather than fine scales. The Transition zone exhibited the greatest degree of coarse-scale heterogeneity, as plots within clusters tended to be much more similar than plots among clusters. Coarse-scale heterogeneity diminished slightly in the Impacted zone, but not to a statistically significant degree (95% CLs). That spatial pattern in the Impacted zone was so prevalent was surprising, especially considering the widespread opinion that this area is almost exclusively composed of monotypic stands of dense *Typha* [for example, see Wu and others (1997) and Rutchey and Vilchek (1999)]. However, these earlier studies relied on remotely sensed data that may not have been sufficient in resolution to detect all but the most dominant species. It is likely that the resolution necessary to quantify the patterns we observed would be cost prohibitive and unrealistic to obtain by remote sensing (Obeysekera and Rutchey 1997). Thus, our results reinforce the importance of field studies in landscape ecology and suggest that synergy between field and remote-sensing approaches is needed to better understand the role of pattern and process across multiple scales (Levin 1992).

Historical data indicate that vegetation in the Impacted and Transition zones was very similar to that

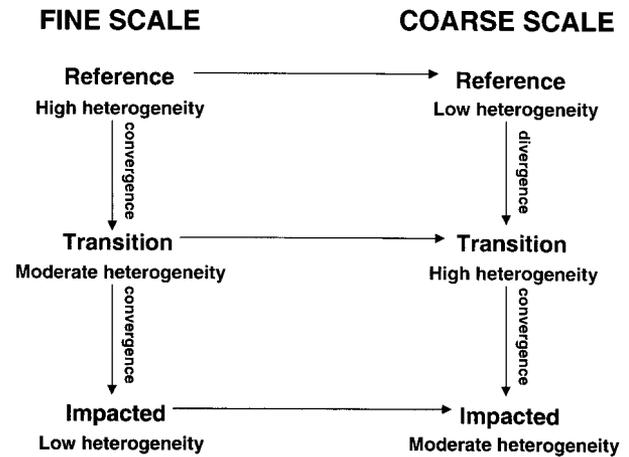


Figure 7. Conceptual diagram showing generalized trajectories of Everglades vegetation pattern among impact zones at fine and coarse scales.

of the Reference zone prior to the construction of the canal-and-levee system (Davis 1943; US Geological Survey unpublished data). Using the Reference zone as a benchmark, an examination of patterns between scales and among impact zones revealed an intriguing paradox—one that suggested different patterns through time and space, depending on scale. In Figure 7, we illustrate a conceptual model based on our results showing generalized trajectories of Everglades vegetation pattern at fine and coarse scales, and as intensity of human influence increases. Our results suggest that the fine-scale mosaic of *Cladium* stands and slough communities was degraded by locally invasive vegetation through time in the Transition zone, converging toward greater similarity among closely neighboring locations. The once-heterogeneous fine-scale pattern in the Impacted zone was degraded even further, with local pattern converging toward greater homogeneity.

Moving across scales, however, the Reference mosaic was homogeneous at a coarse scale (Figure 7). Here, fine-scale heterogeneity was repeated across the landscape, and coarse scales integrated this nested pattern much like Watt's (1947) *unit pattern*—fine-scale elements undergo shifts through time and space, but the aggregate coarse pattern essentially appears constant. In the presence of human influence, however, this was disrupted, and fine-scale components gave rise to different patterns at broader scales. In the Transition zone, coarse pattern diverged from the Reference landscape, moving in many different trajectories based on a variety of possible factors such as dispersal and interspecific competition (Smith and Huston 1989;

White 1994). Possibly, as different plants invaded and competed here, early colonists amplified coarse pattern through seed dispersal and vegetative propagation, reinforcing their presence through positive feedback (Pacala and Levin 1997; He and Mladenoff 1999). *Typha*, *Mikania scandens*, and *Sarcostemma clausum*, three of the dominant species near the canal inflow structures, effectively propagate vegetatively; thus, they may have contributed to coarse-scale variation by differentially proliferating in areas of the Transition zone. This high degree of fragmentation at a coarse scale was a divergence from fine-scale pattern in the Transition zone.

Finally, in the Impacted zone, coarse pattern converged toward greater homogeneity from that observed in the Transition zone but still remained fragmented relative to the Reference zone (Figures 2c and 7). Similar to the Transition zone, the Impacted zone was not dominated exclusively by *Typha* but also by a host of other invasive species. Thus, residual coarse pattern from its previous transitional phase, coupled with contagious disturbances and dispersal processes, may have been responsible for significantly greater heterogeneity at a coarse scale than that observed in the Reference landscape.

Using a hierarchical approach (Urban and others 1987), we took a "snapshot" of vegetation composition at multiple scales and described the potential trajectories of vegetation pattern as a function of anthropogenic influence. Our results indicate that human effects on the Everglades have resulted in more than just a replacement of *Cladium* with *Typha*. Collectively, these results indicate that allogenic spatial and environmental factors related to the canal system have disrupted the coupling between pattern and process by altering fine-scale vegetation–environment linkages and spatial patterns characteristic of the natural Everglades ecosystem. These alterations certainly affect the spatial ecology of higher organisms, such as invertebrates, fish, birds, reptiles, and other wildlife, in a variety of ways that may depend largely on landscape connectivity and critical scales in their individual life histories [for example, see MacArthur and Wilson (1967) and Levin (1976)]. The implications of this are great for restoration and management of vegetation, and suggest that serious attention needs to be given toward mimicking the characteristic spatial and temporal scales of pattern in the environment (DeAngelis 1994; Holling and others 1994), as these patterns ultimately drive self-organization in landscapes (Phillips 1999). The field of landscape ecology has already begun to address many of these scaling issues for terrestrial wildlife (for example,

spotted owl); such management approaches should be extended to aquatic systems as well. One simple management application of our findings could be the use of correlograms of vegetation and environmental spatial patterns from reference areas as models to guide restoration efforts in disturbed areas of the Everglades ecosystem. Principles of hierarchy theory [for example, see Allen and Star (1982) and O'Neill and others (1986)] may provide a framework for such efforts. In conclusion, our study indicates a need for more research on the spatial and temporal scales that are responsible for vegetation patterns, and the role these patterns play in the demographic processes of the flora and fauna across the Everglades and other anthropogenically influenced ecosystems.

#### ACKNOWLEDGEMENTS

We thank P. Heine, J. Rice, and W. Willis for help with soil chemical analyses, J. Johnson and L. Karppi for contributing long hours of assistance in the field, and P. Vaithyanathan for logistical support and study design suggestions. The article was improved by comments from M. Baker, B. Bedford, G. Bruland, D. DeAngelis, M. Hanchey, J. Vymazal, D. Whigham, and three anonymous reviewers. Funding was provided by a grant from the EAA Environmental Protection District to the Duke University Wetland Center.

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