Metacommunity Structure Along Resource and Disturbance Gradients in Everglades Wetlands

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Abstract We evaluated metacommunity hypotheses of landscape arrangement (indicative of dispersal limitation) and environmental gradients (hydroperiod and nutrients) in structuring macroinvertebrate and fish communities in the southern Everglades. We used samples collected at sites from the eastern boundary of the southern Everglades and from Shark River Slough, to evaluate the role of these factors in metacommunity structure. We used eigenfunction spatial analysis to model community structure among sites and distance-based redundancy analysis to partition the variability in communities between spatial and environmental filters. For most animal communities, hydrological parameters had a greater influence on structure than nutrient enrichment, however both had large effects. The influence of spatial effects indicative of dispersal limitation was weak and only periphyton infauna appeared to be limited by regional dispersal. At the landscape scale, communities were well-mixed, but strongly influenced by hydrology. Local-scale species dominance was influenced by water-permanence and nutrient enrichment. Nutrient enrichment is limited to water inflow points associated with canals, which may explain its impact in this data set. Hydroperiod and nutrient enrichment are controlled by water managers; our analysis indicates that the decisions they make have strong effects on the communities at the base of the Everglades food web.

Keywords Niche-based models · Dispersal · Metacommunity · Community structure · Community assembly · Variation partitioning

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Introduction

Niche-based models predict that environmental gradients structure community dynamics in predictable ways (Chase and Leibold 2003). Resource availability and disturbance, frequency and intensity, are two classes of environmental gradients that are commonly the focus of niche-based analyses. Wetlands fit well into this framework because they are spatially structured environments characterized by gradients of disturbance created by local topography that determines the frequency and intensity of drying events as the water table fluctuates. The impact of local disturbance on the aquatic fauna of a wetland is determined by the intersection of topography and hydrological fluctuation, and the dispersal abilities and drying tolerance of the regional species pool (Batzer et al. 2006). The metacommunity framework (Leibold et al. 2004; Holyoak et al. 2005) is useful to develop hypotheses about the origins of community assembly in such landscapes. Niche-based and dispersal-based (e.g., neutral models) assembly models provide competing hypotheses for the origin of community dynamics in wetlands, though few researchers have applied them there (e.g., Soininen et al. 2007). Niche-based assembly is deterministic and indicated by correlations

between community composition and environmental gradients. Dispersal-based hypotheses rely on dispersal limitation as the primary factor determining community structure and, though the link is difficult to prove, are consistent with spatially correlated community patterns that are not otherwise explained by known environmental gradients.

Hydrologic and phosphorus gradients have been shown to organize macroinvertebrate and small fish standing stocks and community composition in the Everglades through their direct effects on mortality and resource availability, and indirectly through cascading food web impacts (Chick et al. 2004; King and Richardson 2007; Liston et al. 2008; Liston 2006; Rader and Richardson 1994; Sargeant et al. 2011; Trexler et al. 2002, 2005). Water flows from agricultural land in the north, through the Everglades, and out to Florida Bay and the Gulf of Mexico in the south. Historically, the Everglades ecosystem was an oligotrophic wetland, with dissolved phosphorus (P) concentrations <6 μg L^{-1} (McCormick et al. 2002; Gaiser et al. 2012), and seasonal periodicity in water discharge and depth; P is the limiting element for plant growth in the Everglades. Flowing water has created a braided microtopography in the Everglades called a ridge and slough landscape (Larsen et al. 2007). In this landscape, hydrologic cycles result in large-scale (tens of kilometers) hydrologic gradients perpendicular to the direction of water flow and are a major organizer of metacommunity dynamics (Trexler et al. 2002; Gaiser et al. 2012). Historically, the landscape was dominated by long-hydroperiod deep-water sloughs forming the center of its two drainages, Shark River Slough (SRS) and Taylor Slough (TS) (Fig. 1). Short-hydroperiod habitats were located in high elevation areas (between 1 and 3 m above sea level) on the east and west borders of the sloughs. Compartmentalization by canals, levees, retention basins, and other water management structures has considerably altered the hydrology (McVoy et al. 2011). Canals and detention basins create heterogeneity in the hydroscape by adding deep-water refuges for aquatic animals where they did not previously exist and shape local mixing of animals driven by drying and re-wetting (Chick et al. 2004; McElroy et al. 2011). These changes may have created a finer scale (1 m to hundreds of meters) hydrologic heterogeneity in the landscape than was present historically.

Intense agriculture on the northern border of the Everglades has served as a nutrient source, creating enrichment gradients with decreasing total phosphorus (TP) concentrations downstream from inflows (Sklar et al. 2005). In the modern Everglades, spatial heterogeneity in nutrient availability is largely organized by canals, which tend to have elevated TP concentrations and act as local sources for P enrichment, creating nutrient gradients into the marsh ranging from less than one to several kilometers (Childers et al. 2003; Gaiser et al. 2012). Elevated TP concentrations are not always detectable in surface water, but elevated periphyton TP concentrations owing to low-level chronic P loading from canals are easily measured and create nutrient enrichment gradients that decrease to ambient levels over a spatial scale of 5 to 100 m downstream (Gaiser et al. 2013; Rehage and Trexler 2006).

We sought to capture the multi-scale spatial variation in hydrology and nutrient inflow to Everglades National Park (ENP), and evaluate the relative contribution of spatial processes and hydrological and nutrient gradients on structure of aquatic animal communities. We hypothesized that TP and hydrology are strong drivers of community structure (Sargeant et al. 2010, 2011), but their relative importance varies among taxa based on their dispersal ability (Trexler et al. 2002; Dorn 2008). We hypothesized that fish are the most mobile consumers sampled and quickly re-fill the sloughs at the outset of the dry season (DeAngelis et al. 2010), diminishing the effects of spatial factors in structuring their communities. Some members of the periphyton mat infauna are the least mobile of our study organisms (invertebrates lacking flying stages, such as amphipods and gastropods) and we hypothesized that these communities will show the greatest variation over the spatial gradient owing to dispersal limitation. We hypothesized that the effect of TP will be modified by the local hydroperiod for periphyton infauna (Liston 2006), but not for fish. TP effects were hypothesized to be limited in scope overall because only sites immediately adjacent to nutrient inputs (canal inflows) will be affected (Rehage and Trexler 2006).

Methods

Field Collections

We collected fish and macroinvertebrates from 40 sites (Fig. 1a) during the wet season in September 2010 in and around ENP. Paired sites were located in SRS in long-hydroperiod sites, while near the eastern edge of ENP, triplicate sites were spaced ~200 m apart along transects originating near water control structures ("0-m sites") and extending ~400 m into the marsh (200-m and 400-m sites). These transects were located in the Rocky Glades region near the S332 B, C, and D impoundments, Context Road, and the L-31 W canal. Transects of triplicate sites were also located near the C-111 canal and canals bordering Aerojet Road (See Table S1 in electronic supplementary material 1 (ESM 1) for site coordinates).

These study sites cover much of the range of hydroperiods found in ENP. The long-hydroperiod sites were inundated for all 365 days of the year before we sampled (and most had been inundated continuously for several years before that), while the short-hydroperiod sites were inundated for as few as 180 days. Long-hydroperiod sites were located in spike rush-dominated sloughs (mostly *Eleocharis cellulosa*), while vegetation at short-hydroperiod sites was typically dominated
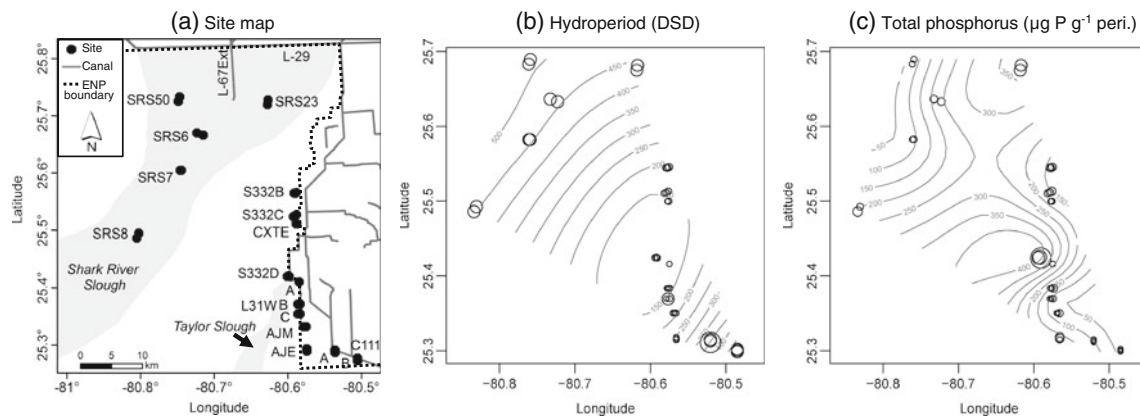
Fig. 1 Map of (**a**) site locations in Everglades National Park (ENP), and contour maps of (**b**) hydroperiod and (**c**) estimated periphyton total phosphorus levels. *Shaded areas* in (**a**) delineate sloughs. *Contour lines* represent hydroperiod (Days since dry-down, DSD) in (**b**) and periphyton Total Phosphorus (μg P g^{-1} dry mass periphyton) in (**c**), symbol size is proportional to hydroperiod length (**b**) or estimated TP concentration (**c**)

by sawgrass (*Cladium jamaicense*) and muhly grass (*Muhlenbergia capillaris*) (Armentano et al. 2006). Periphyton mats comprised of an assemblage of algae, bacteria, and fungi actively remove P from the water and incorporate it into their tissues, making their tissue TP an excellent metric for nutrient enrichment (Gaiser et al. 2006). Periphtyon tissue TP exceeding 150 μg P g^{-1} dry mass is considered indicative of anthropogenic enrichment, with 90–100 μg P g^{-1} dry mass is common in un-enriched short-hydroperiod wetlands. Long-hydroperiod areas of ENP generally have more TP than short-hydroperiod ones, but a concentration of 150 μg P g^{-1} dry mass is a reasonable cutoff to classify a site as having "elevated" TP loading. Anthropogenic nutrient enrichment is limited to areas on the edges of ENP where canal water from upstream flows in to hydrate the wetlands. We included study sites on the edge of Everglades wetlands that received nutrient enrichment, as well as ones that did not (Table 1).

We recorded 3 to 5 estimates of water depth at each sample site at the time of sampling. Plots were only sampled when water depth was >20 cm. A passive sampling device was used to collect fishes ranging in standard length from approximately 1 to 8 cm over a 24 h period at each site. Each passive sampler consisted of an X-shaped drift fence built from shade cloth and rebar and with four minnow traps placed in the center; these traps had one opening and sampled in each cardinal direction (Obaza et al. 2011). Fish that encountered the wings of the drift fence were corralled toward the minnow traps. After 24 h, fish were collected from the minnow traps, anesthetized using MS-222 and preserved in 10 % formalin, and counted and identified to species in the lab. Counts are reported per unit effort (catch per unit effort CPUE). This measure of CPUE is biased toward active fishes (Obaza et al. 2011), and we interpret it as the makeup of the fish community

encountering stationary prey, such as macroinvertebrate infauna.

The Everglades is home to a diverse macroinvertebrate fauna that cannot be well characterized by a single sampling device (Turner and Trexler 1997). Floating periphyton mats are home to the majority of macroinverbrates retained on a 250 um sieve, but not a 2 mm one, including *Hyalella azteca*, *Dasyhelea* spp., cladocerans, chironomids and planorbellid and physid snails (Liston and Trexler 2005). We sampled these animals using a 5-cm diameter coring device concurrent with the fish sampling. Three cores were collected at each site and preserved in the field in 70 % ethanol. Infaunal macroinvertebrates were removed and identified using 10 × magnification. Periphyton was dried at 60 °C for at least 24 h and weighed before being combusted at 500 °C for 2 h, and reweighed to calculate ash-free dry mass (AFDM, Eaton et al. 2005). Periphyton AFDM was used to calculate areal estimates of periphyton standing crop. Macroinvertebrate counts from each core were standardized to periphyton AFDM to provide estimates of infaunal crowding (Liston 2006). Periphyton standing crops reported here reflect the density and condition of the periphyton mats at a site, but are not meant to be extrapolated to landscape-scale estimates of periphyton standing crop.

At the same time, we sampled larger macroinvertebrates using sweep nets (Turner and Trexler 1997). Sweeps were collected by passing a 0.5-cm mesh D-frame dip net through the water column in a 1-m long "U" shaped motion, and preserving the catch in 10 % formalin; animals were removed and identified in the laboratory without magnification. The sweep-net sampling method integrates the macroinvertebrate community throughout the entire water column providing a better estimate of the general aquatic macroinvertebrate community composition (i.e., surface and benthic periphyton, emergent macrophytes, water column) (Cheal et al. 1993; Rader and Richardson 1994). The resulting data are CPUE,

Table 1 Summary of environmental variables and consumer standing stocks in Shark River Slough, Taylor Slough, and the Rocky Glades region of the Everglades Ecosystem in September 2010. Means (standard errors in parentheses) are reported for long (Days since dry-down, DSD>300) and short-hydroperiod (DSD<300) with elevated (> 150 µg P g^{-1} dry mass) or normal (< 150 µg P g^{-1} dry mass) total phosphorus (TP) concentrations in periphyton tissue

		Long-hydroperiod		Short-hydroperiod	
		Elevated TP	Normal TP	Elevated TP	Normal TP
Environmental variables					
Depth	Standing water depth (cm)	56.8 (3.7) n=5	45 (2.2) n=12	30.2 (2.3) n=13	27.3 (1.3) n=10
DSD	Days Since Dry (d)	479.5 (3.7) n=5	523.6 (42.3) n=12	132.6 (7.3) n=13	100.2 (7.5) n=10
Yearwet	Prop. of year inundated	1 (0) n=5	1 (0) n=12	0.77 (0.03) n=13	0.71 (0.05) n=10
TP	Estimated total P in Peri. (µg P g^{-1} dry mass peri.)	267.7 (43.8) n=5	82.7 (8.6) n=12	262 (50.8) n=13	80.4 (6.5) n=10
Peri.	Periphyton standing crop (g AFDM)	119.6 (18.2) n=5	136.1 (11.9) n=6	190.9 (26.4) n=12	290.7 (50.5) n=7
Consumer standing stocks					
Infaunal	Crowding of infaunal macroinvertebrates in periphyton cores (no. g^{-1} AFDM peri)	28.9 (6.8) n=5	19.3 (5.6) n=6	24.4 (6.6) n=12	8.9 (2.1) n=7
Macroinvertebrates	Macroinvertebrates collected in sweep samples (CPUE)	104.6 (14.1) n=5	109.2 (39.1) n=6	64.3 (10.2) n=12	26.1 (6) n=7
Fish CPUE	Active fishes (CPUE)	73.8 (28.1) n=4	53.2 (19.7) n=12	66.5 (13.5) n=13	46 (16.6) n=9

which is the number of individual invertebrates caught in a~ 1 m sweep sample.

Estimates of Interpolated Environmental Variables

We retrieved water depth estimates for each of our sites for the entire sampling period and the preceding 365 days (September 2008–December 2011) from the Everglades Depth Estimation Network's (EDEN) xyLocator tool (http://sofia.usgs.gov/eden/edenapps/xylocator.php; Liu et al. 2009). We performed regression analysis to use the EDEN-generated depths to predict depths that we measured at the time of sampling. EDEN depths are estimated as the average of a 400×400 m grid, so we adjusted for smaller-scale, local topography at our sampling sites. We used the regressions to generate corrected depths for each day at all of our sites. From these corrected depths, we calculated hydroperiod (the proportion of the previous 365 days that a site had >1 cm depth) and days-since-dry (the number of days since that site had last been dry, DSD). Daily values averaged over the month of September in 2010 were used to represent hydrology at each site during the field collection period. A threshold of 300 DSD was used to distinguish between short and long hydroperiod sites (Trexler et al. 2002).

While periphyton was not explicitly collected for TP analysis during this survey, it was measured through several large sampling programs at nearby locations during or near the time of this study. To estimate the periphyton TP concentration for each location, we calculated the average concentration from the nearest 1 to 3 sites co-located with our study sites when possible, or when necessary, located in the same habitat type within 3 km of the location. Samples used for TP analysis were taken during the wet season between 2006 and 2011; in these data variance among years was lower than inter-site variance. For the S332, L31W, CXTE, AJM, AJE and C111 locations, we used periphyton TP values from co-located survey points for 0-m sites, and data from nearby S-332 monitoring (Gaiser et al. 2008), marl prairie survey (Sah et al. 2010) and Florida Coastal Everglades Long-Term Ecological Research (FCE LTER) program sites (http://fcelter.fiu.edu/research/sites/) to estimate values for the 200–400 m locations. Periphyton TP data for SRS were taken from nearby sites sampled by the Comprehensive Everglades Restoration Program Monitoring and Assessment (Gaiser et al. 2011) and the FCE LTER programs.

Statistical Analysis of Environmental and Spatial Filters

All analyses used "site" as the observational unit. When available, replicate values for a site were averaged to determine a site-level representative value. The R v2.13.1 statistical environment (R Development Core Team 2011) was used for all statistical analyses unless otherwise noted. For all

univariate statistical analyses, consumer standing values were log x+1 transformed (McCune and Grace 2002). Densities of individual species were not transformed prior to calculating distance metrics used in multivariate analysis. For univariate analyses of primary consumer standing stocks and multivariate analyses of primary consumer community composition, predictor variables representing environmental gradients were transformed when necessary (McCune and Grace 2002): TP, DSD, and Periphyton standing crop were log x+1 transformed, proportion of the year a site was inundated (yearwet) was arcsine-square-root transformed.

Multiple regression models describing the relationship between primary consumer standing stocks and environmental variables were constructed using stepwise model selection (Venables and Ripley 2002). We used the step() function in the stats package for R (R Development Core Team 2011) to select a set of predictor variables (representing environmental gradients) to create the best fit linear model describing variation in consumer standing stocks, given the set of possible predictor variables (scope). The stepwise algorithm (Hastie and Pregibon 1992) iteratively adds and/or removes predictor variables from the linear model, and returns the model with the minimum AIC value (Venables and Ripley 2002). The scope of predictor variables for macroinvertebrate standing stocks for periphyton core and sweep-net datasets used in model selection included TP, DSD, depth, periphyton standing crop, and yearwet, and the scope of variables used to predict active fish standing stocks included TP, DSD, depth, and yearwet.

Non-metric multidimensional scaling (NMDS) was used to determine site relationships based on taxonomic composition, and results were plotted using the vegan package (Oksanen et al. 2012). Two types of community dissimilarity matrices were calculated for each community type (infauna, macroinvertebrates, and active fishes). Jaccard dissimilarity matrices using presence/absence data emphasized differences in taxonomic composition and can be heavily influenced by rare taxa (rare-biased dissimilarity). Morisita-Horn distance matrices were calculated using standardized measures of abundance (infaunal crowding or CPUE) and emphasize differences in dominance (dominant-biased dissimilarity) of common taxonomic groups (Jost 2007; Jost et al. 2011). Both of these distance measures are based on "species equivalents", where the Jaccard distance measure gives more weight to rare taxa and the Morisita-Horn index gives more weight to common taxa. Vectors representing the correlation between environmental gradients and community composition were fit to the NMDS ordinations using the envfit() function in the vegan package.

Principal coordinates of neighbor matrices (PCNM, Borcard and Legendre 2002; Dray et al. 2006) were used to extract eigenvectors from geographic coordinates to create variables representing the organization of sites at different spatial scales (see ESM 2). The first PCNM eigenvector (PCNM1) represents the broadest scale spatial filter, and successive PCNM eigenvectors represent filters with increasingly finer scale spatial structure. To calculate spatial filters for the sites used in this study, a geographic distance matrix was calculated from latitude and longitude coordinates using Vincenty ellipsoid great circle distances with the distm() function in the geosphere package (Hijmans et al. 2011). Prior to calculating eigenvectors, a truncated distance matrix was created from the initial geographic distance matrix using a threshold distance that maintained a connected network, and all distances greater than the threshold were replaced by four times the threshold. Only eigenvectors with positive eigenvalues were used in the analysis. The Pearson's product moment correlation between each environmental variable and spatial variable (i.e., PCNM eigenvector) were calculated to assess the spatial scales at which each environmental variable was organized.

Among-site variation in community composition for infauna, macroinvertebrates, and active fishes was partitioned among spatial filters represented by the PCNM eigenvectors and environmental variables representing nutrient enrichment status and local hydrology (Beisner et al. 2006; Borcard et al. 1992; Heino et al. 2012; Landeiro et al. 2011, see electronic supplementary material 2 (ESM 2)). Distance-based redundancy analysis (dbRDA) was carried out separately for Jaccard and Morisita-Horn community dissimilarity matrices for each community type using the capscale() function in vegan (Oksanen et al. 2012). Forward stepwise model selection based on adjusted R^2 values using the ordiR2step() function in vegan (Blanchet et al. 2008; Oksanen et al. 2012) was used to select the PCNM vectors that created the best fit dbRDA spatial model that explained the variation in each community dissimilarity matrix (Heino et al. 2012). Stepwise model selection was also used to select the best environmental explanatory variables for dbRDA models for each community dissimilarity matrix. The selected spatial and environmental variables were then used in a variation partitioning analysis to determine the among-site variation for each community dissimilarity matrix that was explained purely by environmental variation (E | S), spatially structured environmental variation (E ∩ S), or purely spatial variation (S | E) (Borcard et al. 1992). This analysis indicates the environmental gradients that most influence variation in community composition, and the spatial scales at which communities are organized.

Results

Hydrology and nutrient enrichment status varied among sites (Table 1, Fig. 1). Interpolated DSD at the time of sampling for sites ranged from 74.5 to 988.5 days, and interpolated TP ranged from 51 to 780 μg P g^{-1} dry mass periphyton (Table S1 in ESM 1). Using the pre-determined cutoffs for TP

enrichment at short- and long-hydroperiod sites, one site (S332D 0 m) was classified as highly enriched, but seven additional sites had elevated TP levels. These included other sites located near S332D and Aerojet Road near the eastern edge of ENP, and SRS23 and SRS 8 in Shark River Slough. Three enriched sites were in long-hydroperiod habitats and five enriched sites were located in short-hydroperiod habitats. Overall, hydroperiod and TP concentrations were more heterogeneous among sites near the eastern edge of ENP, water control structures, and in Taylor Slough (Fig. 1).

Model selection indicated periphyton standing crop was negatively correlated with depth and TP, and positively correlated with yearwet (adj. R2=0.38, Table 2, Fig. 2a). Model selection on consumer abundance revealed different controls over infaunal macroinvertebrate crowding, macroinvertebrate CPUE from sweep samples, and active fish CPUE (Table 2). Neither hydrologic variables nor nutrient enrichment influenced infaunal crowding, but periphyton standing crop was negatively correlated with infaunal crowding (Fig. 1a, Table 2). Hydrology (DSD) and nutrient loading (TP) explained 55 % of the variation in macroinvertebrate CPUE from sweep samples (Fig. 2b, Table 2). Periphyton tissue TP was positively correlated (adj. R^2=0.14, Table 2, Fig. 2c) with active fish CPUE.

PCNM analysis yielded 19 positive eigenvectors that were used to represent spatial filters. Figure 3 illustrates 4 of the 19 spatial filters (also see Fig. 5 in ESM 1 for additional PCNM eigenvector maps), where PCNM variable numbers are ordered from broadest scale (PCNM1) to finest scale (PCNM19 not shown) spatial filters. Correlations (Pearson's r) between environmental gradients and PCNM vectors with a p-value <0.05 were considered relevant. TP (Pearson's r=−0.33) and depth (−0.46) were organized at the broadest scale, both negatively correlated with PCNM1, indicating greater TP concentration in periphyton and greater water depth in the northern section of ENP. Hydrologic variables (depth, DSD, and yearwet) were negatively correlated with PCNM2 (−0.6, −0.64, and −0.81, respectively). This still represents a relatively broad scale, and this spatial filter seems to reflect differences between sites in the Rocky Glades, Shark River Slough and Taylor Slough. TP was negatively correlated (−0.41) with PCNM4 and periphyton

standing crop was positively correlated (0.46) with PCNM4, indicating a negative correlation between TP and periphyton standing crop in the Rocky Glades and Taylor Slough. DSD is positively correlated (0.51) with PCNM9, which captured heterogeneity in the Rocky Glades and Taylor Slough sites along the southeastern edge of ENP.

Similar taxonomic groups were dominant (>5 % mean relative abundance) across hydrologic and TP gradients for the three community types, but rank-orders differed among habitat types (Table 3). Biting midges (*Dasyhelea spp.*) were dominant at all sites except for long-hydroperiod ones with ambient TP concentrations. In addition to biting midges, infaunal communities were primarily composed of chironomids, ostracods, and physid snails (*Hatia spp.*) at long-hydroperiod sites with elevated TP, and nematodes were abundant at short-hydroperiod-sites with elevated TP. Chironomids, biting midges, and amphipods (*Hyalella azteca*) were abundant in sweep samples from all habitat types, and planorbid snails (*Planorbella spp.*) were common at long-hydroperiod sites with ambient TP levels. The active fish community was dominated by eastern mosquitofish (*Gambusia holbrooki*) and sailfin mollies (*Poecilia latipinna*) in all habitat types. Golden topminnows (*Fundulus chrysotus*) were prominent at long-hydroperiod sites, irrespective of TP loading, and flagfish (*Jordanella floridae*) were abundant in all habitat types excluding short-hydoperiod sites with ambient TP loading.

NMDS ordinations showed variation in community composition for all consumers was associated with hydrology (Fig. 4). Environmental predictor variables chosen in dbRDA model selection appear as vector overlays in the ordinations. Similar patterns appear in ordinations plotted using rare-biased (Jaccard) and dominant-biased (Morisita-Horn) measures of community dissimilarity. Macroinvertebrate community composition differed between short and long-hydroperiod habitats. This was reflected in dbRDA model selection, which primarily selected hydrologic variables as the best predictors of variation in community composition (Table 4). Among-site variation in active fish dominance (Morisita-Horn distances, Fig. 4c) was influenced by both hydrology (yearwet) and TP concentrations, and rare-biased diversity (Jaccard distances based on presence/absence data, Fig. 4f) was only organized by hydrology (yearwet).

Table 2 Univariate regression models predicting periphyton standing crop in cores and consumer standing stocks for infaunal macroinvertebrates in periphyton cores, macroinvertebrates in sweep samples, and active fishes. Predictor variables (see Table 1) were selected using two-direction stepwise model selection (the step function in R). Periphyton standing stock was not used as a predictor for fish standing stock

Response variable	Adj. R^2	df1	df2	F	p-value	Selected predictor variables
Periphyton standing crop (log [g AFDM m^{-2}]+1)	0.38	3	26	12.39	<0.001	log(depth) + log(TP) + arcsine(yearwet$^{1/2}$)
Infauna standing stock (log crowding+1)	0.60	1	28	44.22	<0.001	log(peri.)
Macroinvertebrate standing stock (log CPUE+1)	0.55	2	27	18.85	<0.001	log(DSD) + log(TP)
Active fish standing stock (log CPUE+1)	0.14	1	36	7.19	0.011	log(TP)

Fig. 2 Partial regression plots for periphyton standing crop (**a**) and consumer standing stocks (**b**, **c**, and **d**) responses to selected environmental variables. Variables are described in Table 1, models are described in Table 2
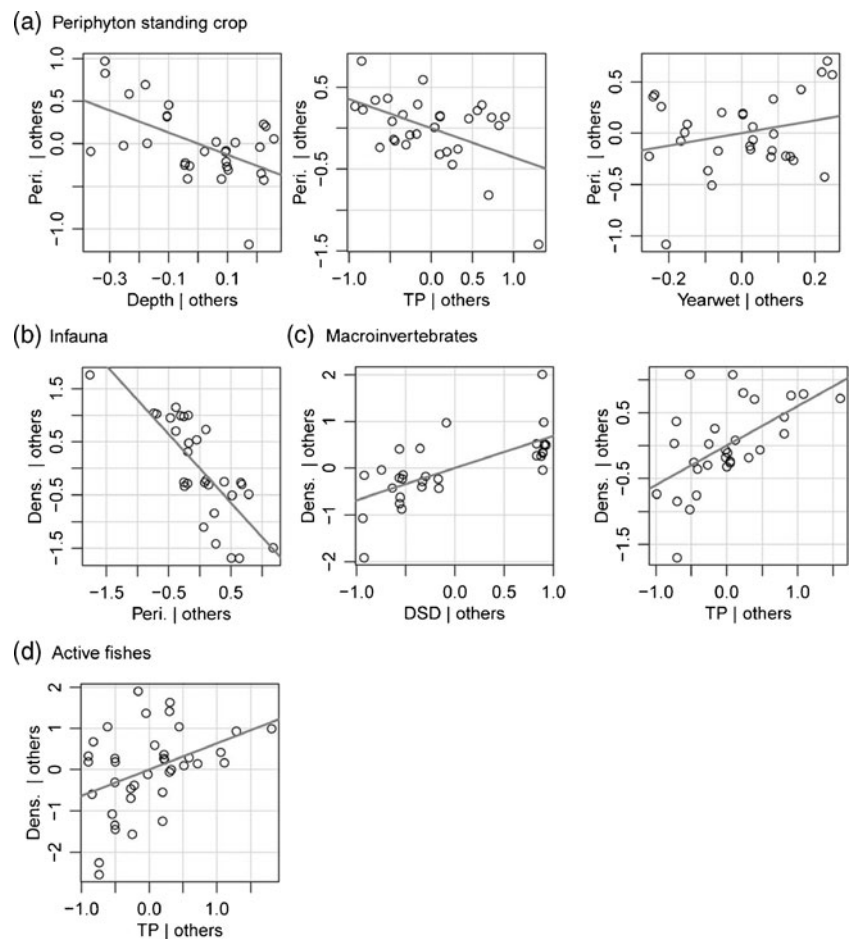
Variation partitioning (Table 4) showed the community composition of infauna, macroinvertebrates in sweep samples, and active fishes were primarily influenced by hydroperiod. Dominant-biased diversity (Morisita-Horn) responded more strongly to environmental gradients than rare-biased diversity (Jaccard index). A large proportion of the spatial structure in community composition was related to spatially structured environmental gradients (E ∩ S). Infaunal macroinvertebrate community composition was only influenced by hydroperiod, specifically DSD. Rare-biased infaunal diversity only showed structure at the broadest spatial scale (PCNM1), and this was not independent of environmental variation. Dominant-biased diversity had a significant spatial component (adj. $R^2=0.089$). Rare-biased diversity of macroinvertebrates in sweep samples was influenced by depth, and spatial filters independent of depth. Dominant-biased diversity was not correlated with spatial filters, but was strongly correlated with depth and periphyton standing crop ($R^2=0.359$). Rare-biased diversity of the active fish community was related to the proportion of a year a site was inundated (yearwet), and was not spatially structured independent of yearwet. Dominant-biased diversity of active fishes was not spatially structured, but was related to yearwet and TP.

Discussion

We found that hydrological factors explained more variation in the aquatic community structure than did nutrient gradients, though effects of both factors were pervasive. TP enrichment in ENP is currently limited to boundary areas, including new sources of water inflow created for hydrological restoration (Gaiser et al. 2013) and impacts we documented were primarily on consumer abundance (Table 2). The impact of TP enrichment on ENP aquatic community structure may be relatively limited because it has not reached the high levels found in other areas of the Everglades, which have a long history of high concentration inputs (Rader and Richardson 1994; Rader 1999; McCormick et al 2004). The strength and nature of the relationship between hydrologic gradients and community structure for aquatic macroinvertebrates and fishes is contingent on the scale at which each metacommunity interacted with the Everglades hydroscape (Wellborn et al. 1996). Below, we elaborate on these relationships in ENP and their broader implications.

Spatial filters represented by PCNM eigenvectors (Fig. 3) captured variation from broad to fine scales in both hydrological and TP gradients (Fig. 1b and c). Hydrologic gradients
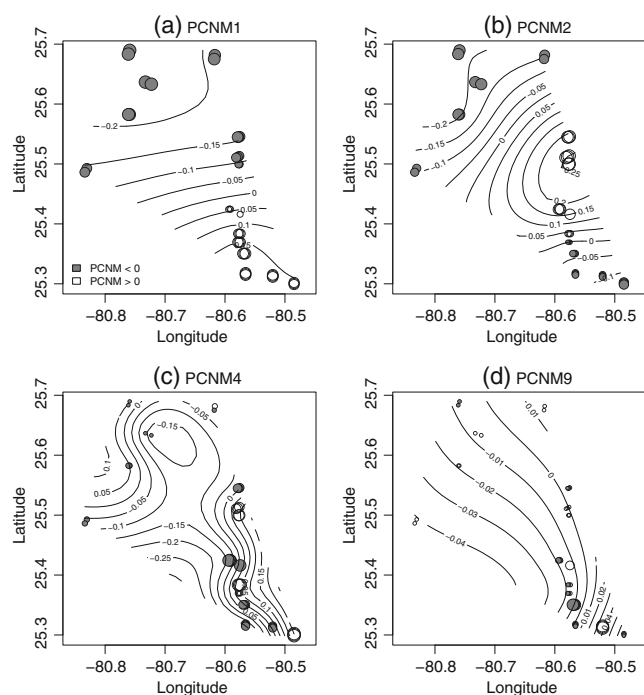
Fig. 3 Maps representing spatial filters (eigenvectors calculated using principal coordinate analysis of neighbor matrices, PCNM) used in variation partitioning. Symbol size is proportional to the absolute value of the of the spatial filter at the site. Sites with positive values are plotted with open circles, negative values are plotted with solid circles. Note that the scale of the spatial gradient described by a PCNM filter decreases with increasing PCNM number. See Fig. 5 in ESM 1 for maps of PCNM15 and PCNM19

were associated with PCNM vectors 1, 2, and 9. PCNM 1 corresponded with water depth, reflecting the broad scale organization of the hydroscape, with long-hydroperiod sites located in the middle of Shark River Slough and shallower short-hydroperiod sites near the edge of the wetland. PCNM 2 separates short-hydroperiod sites in the Rocky Glades from sites located in longer hydroperiod habitats in or near Shark River Slough and Taylor Slough. PCNM 9 was associated with finer scale gradients that correspond to within-transect heterogeneity, and represent spatial gradients on the order of hundreds of meters. The spatial heterogeneity in periphyton TP corresponded with spatial filters representing organization at broad (PCNM 1) and intermediate (PCNM 4, Fig. 3) spatial scales. These spatial patterns in elevated TP concentration correspond with inputs of P-enriched water near water control structures (Gaiser et al. 2013), specifically, the L-29 canal near the northeast edge of the park and the S332D pump station near the headwaters of Taylor Slough.

TP gradients in ENP were primarily associated with variation in consumer standing stocks, rather than community composition. Infaunal crowding in periphyton mats was higher at sites with elevated TP concentrations and longer hydroperiods (Table 1). However, the best-fit model shows this variation in crowding is a negative function of local periphyton mat standing crop (Fig. 2b, Table 2). Because infaunal crowding is standardized to periphyton core AFDM, and periphyton standing crops are responding to environmental gradients, infaunal crowding is probably most representative of local biotic and

Table 3 Relative abundances of dominant taxonomic groups (> 5 % mean relative abundance). See Table S2 in ESM 1 for all taxonomic groups and Table S3 in ESM 1 for a description of taxon codes

	Long hydroperiod Elevated TP		Long hydroperiod Normal TP		Short hydroperiod Elevated TP		Short hydroperiod Normal TP	
Infauna	DASSPP	0.286	TANYPO	0.18	DASSPP	0.179	DASSPP	0.374
	TANYPO	0.245	DASSPP	0.143	NEMATO	0.158	CHIRON	0.155
	TANYTA	0.108	OLIGOC	0.131	OLIGOC	0.122	TANYPO	0.088
	CHIRON	0.077	OSTRAC	0.11	TANYPO	0.096	OLIGOC	0.084
	HAISPP	0.072	TANYTA	0.095	OSTRAC	0.093	OSTRAC	0.083
	OSTRAC	0.065	CHIRON	0.08	CHIRON	0.08		
Macroinvertebrates	DASSPP	0.247	CHIRON	0.221	DASSPP	0.383	DASSPP	0.46
	CHIRON	0.185	TANYTA	0.221	CHIRON	0.107	CHIRON	0.086
	AMPHIP	0.171	DASSPP	0.141	AMPHIP	0.095	DIPPUP	0.084
	TANYTA	0.146	PLASPP	0.107	DIPPUP	0.093	AMPHIP	0.066
	TANYPO	0.07	AMPHIP	0.081	TANYPO	0.066		
			TANYPO	0.053				
Active fishes	GAMHOL	0.514	GAMHOL	0.576	GAMHOL	0.422	GAMHOL	0.63
	LUCGOO	0.22	POELAT	0.153	POELAT	0.286	POELAT	0.157
	JORFLO	0.087	LUCGOO	0.08	JORFLO	0.104	HEMLET	0.07
	POELAT	0.065	JORFLO	0.068			LUCGOO	0.051
	FUNCHR	0.053	FUNCHR	0.051				

Fig. 4 Non-metric multidimensional scaling (NMDS) ordinations using Morisita-Horn distances calculated from densities (**a–c**) and Jaccard distances calculated from presence/absence data (**d–f**), representing community composition of infaunal macroinvertebrates in periphyton cores (**a, d**), macroinvertebrates collected in sweep samples (**b, e**), and active fishes (**c, f**). *Vectors* represent correlations between community composition and environmental variables (described in Table 1). *Points* represent sites in taxonomic space. Morisita-Horn distances emphasize the influence of differences in relative abundances of dominant taxonomic groups, and Jaccard distances are more strongly affected by rare taxonomic groups
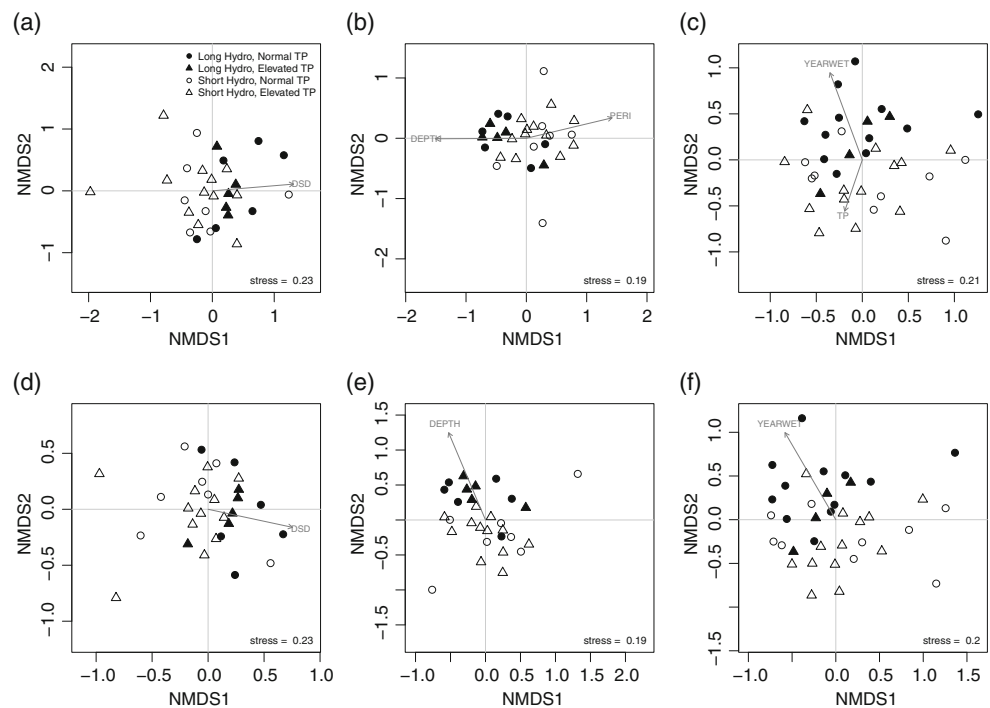
resource interactions (Liston 2006). As TP increases, Everglades periphyton mats deteriorate, and the loss of periphyton biomass results in increased macroinvertebrate crowding. At very high TP enrichment levels (beyond concentrations observed in this study) periphyton mats completely dissociate and lack of cover leads to a crash in local density of mat-dwelling taxa (King and Richardson 2007), possibly because of predation by fish (Liston et al. 2008). Macroinvertebrate CPUE from sweep samples provides a more appropriate variable to describe landscape-scale response to environmental variables (Rader and Richardson 1994; Turner and Trexler 1997).

Both macroinvertebrate CPUE and active fish CPUE increased in response to elevated TP (Table 2, Fig. 2c and d), which are similar to results observed in the Water Conservation Areas north of ENP (Rader and Richardson 1994; Rehage and Trexler 2006). The macroinvertebrate response to TP appeared to be modified by hydroperiod. As shown by Liston (2006), the disparity in macroinvertebrate standing stocks between sites with enriched and normal

Table 4 Variation partitioning of community composition for infaunal macroinvertebrates in periphyton cores, macroinvertebrates in sweep samples, and active fishes. Variation was partitioned using dbRDA for presence/absence data using Jaccard distances (emphasizes the influence of rare taxa) and for density data using Morisita-Horn distances (emphasizes the influence of abundant taxa). Environmental and spatial explanatory variables were identified with a forward, stepwise selection. Adjusted R^2 is the proportion of variation in community composition explained by environmental (E) or spatial (S) variables, where E | S is environmental influence independent of spatial variables, E ∩ S is the intersection between E and S (variation explained by spatially structured environmental variables), S | E represents the influence of spatial variables independent of environmental variation (purely spatial variation), and E + S is the total variation explained by environmental and spatial variables

Community type	Community dissimilarity distance	Environmental variables	Spatial variables (PCNM eigenvectors)	Fraction of variation (adj. R^2)					
				E	S	E | S	E ∩ S	S | E	E + S
Infauna	Jaccard	DSD	PCNM 1	0.066*	0.046*	0.025**	0.041	0.005**	0.071*
	Morisita-Horn	DSD	PCNM 19, 4	0.106*	0.254*	0	0.165	0.089*	0.195*
Macroinvertebrates	Jaccard	depth	PCNM 2, 15, 1, 9	0.088*	0.103*	0.085**	0.003	0.100*	0.188*
	Morisita-Horn	depth, peri.		0.359*	0	0.359*	0	0	0.359*
Active fishes	Jaccard	yearwet	PCNM 2	0.099*	0.062*	0.054*	0.045	0.017**	0.116*
	Morisita-Horn	yearwet, TP		0.164*	0	0.164*	0	0	0.164*

*Indicates a significant adjusted R^2 (*p*-value<0.05) based on a permutation test, **Indicates a *p*-value>0.05

nutrient status was more pronounced in the short-hydroperiod habitat, where overall standing stocks were lower (Table 1). Fish standing stock response to the TP gradient was consistent across the hydrologic gradient. Different life history strategies to deal with the spatial and temporal heterogeneity of drying in the Everglades hydroscape may explain the different response patterns between macroinvertebrates and fishes. However, the ubiquitous positive correlation between nutrient enrichment and consumer standing stocks supports the notion that bottom-up trophic effects are driving consumer responses to TP, rather than-top down controls (Sargeant et al. 2011).

Regional-scale hydrologic gradients (tens of kilometers) have been shown to correspond with diversity patterns in the Everglades ecosystem (Chick et al. 2004; Rehage and Trexler 2006). Variation partitioning of beta-diversity between environmental and spatial filters (Borcard et al. 1992; Borcard and Legendre 2002; Dray et al. 2006; Beisner et al. 2006; Heino et al. 2012; Landeiro et al. 2011) showed hydrologic variables were associated with macroinvertebrate and active fish beta-diversity in ENP, but the spatial scales of variation in community composition differed between the two groups (Table 4). Rare-biased diversity showed macroinvertebrate assemblages (associated with PCNM 2, 15, 1, and 9) exhibited broad and fine scale heterogeneity in the landscape, whereas fishes were only associated with a broad scale spatial filter (PCNM 2). Dominant-biased diversity reflects compositional shifts in the local assemblages that were more closely tied to local habitat characteristics, and showed macroinvertebrate communities were more strongly correlated with the local environment than fishes (E in Table 4). Distinct macroinvertebrate assemblages (e.g., larval dipterans, amphipods, physid snails, etc.), were associated with periphyton mats, which serve as a refuge to avoid desiccation during the dry season (Browder et al. 1994; Liston et al. 2008). Thus, macroinvertebrate assemblage composition exhibits an integrative, niche-based response to the local microtopography, which determines the frequency a site dries, and the coverage of periphyton mats, which respond nonlinearly to hydrology and nutrient enrichment (Liston 2006; Gaiser et al. 2006; King and Richardson 2007; Liston et al. 2008).

In contrast, small fishes in the Everglades ecosystem have been shown to be a highly mobile and well mixed metacommunity (Trexler et al. 2002; DeAngelis et al. 2010; McElroy et al. 2011). For small fishes, the ability to readily disperse through the Everglades hydroscape has been hypothesized to be an important life history strategy to escape predation pressure from larger fishes, find food, and escape desiccation when the water recedes at the onset of the dry season (Trexler et al. 2002, 2005; DeAngelis et al. 2010). Thus, it follows that the highly mobile community represented in samples collected in this study respond less strongly to local environmental conditions and fine scale spatial filters.

Community composition is organized at a broader scale, and probably influenced by the proximity of deep-water refuges, such as canals (Rehage and Trexler 2006). Because canals are also a source of P enrichment, TP concentrations in the marsh probably co-vary with metacommunity connectivity between fish assemblages in the marsh and canals. Indeed, fish community composition was related to both hydroperiod and TP concentrations in Table 4, suggesting interspecific variation in fish movement between source and sink habitats is organizing beta-diversity patterns in ENP (Trexler et al. 2005; DeAngelis et al. 2010; Goss et al. 2013).

The relationship between body size and the balance of dispersal- and niche-based controls over local assemblage composition in ENP is a stark contrast to that observed in other ecosystems. The negative relationship between body size and dispersal ability for passive dispersers is a general pattern in ecology (Martiny et al. 2006) that has been observed in aquatic habitats (Beisner et al. 2006; Shurin et al. 2009; De Bie et al. 2012). Larger bodied, passively dispersing organisms are expected to have a patchy distribution when organized by source-sink dynamics. It follows that an increase in body size will correspond with an increase in the purely spatial (S | E in Table 4) component of beta-diversity, whereas, a decrease in body size will coincide with an increase in the purely environmental (E | S in Table 4) component of beta-diversity (De Bie et al. 2012). However, for actively dispersing animals, body size is positively correlated with dispersal (Jenkins et al. 2007), and thus larger organisms will show a weaker relationship with spatial filters. Variation partitioning data for aquatic consumers in this study support the notion that fishes are active dispersers in a highly interconnected hydroscape. Fishes, like other non-flying aquatic animals, act as passive dispersers in highly compartmentalized ecosystems (De Bie et al. 2012; Jenkins et al. 2007). Thus, the relationships between body size and the relative importance of dispersal- and niche-based controls may be reversed in ENP if the habitat is further compartmentalized. Under such a scenario, local habitat characteristics would have a much stronger influence over the composition of fish assemblages.

The spatial patterns in environmental gradients and communities of aquatic consumers render a complex relationship between hydrologic and nutrient enrichment gradients in the Everglades ecosystem. Results reported here indicate that elevated nutrient levels in and around ENP are influencing standing stocks of macroinvertebrates and small fishes, and hydrologic gradients, as well as TP influx, influence community composition at both broad and local scales. Further, different community types represented in three common collection techniques used in Everglades monitoring programs (periphyton cores, sweep samples, and active fishes collected using passive samplers) illustrated that animals respond to different environmental gradients at different spatial scales, probably tied to dispersal abilities. In spite

of the different responses exhibited by consumer groups, all exhibited responses to hydrologic and periphyton TP gradients that result from water control structures meant to restore flow between the Rocky Glades and Taylor Slough. These data from the base of the Everglades food web clearly delineate the pervasive impact of management decisions on ecosystem processes throughout wetlands of the ENP.

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