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Biotic and abiotic determinants of intermediate-consumer trophic diversity in the Florida everglades

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Abstract. Food-web structure can shape population dynamics and ecosystem functioning and stability. We investigated the structure of a food-web fragment consisting of dominant intermediate consumers (fishes and crayfishes) in the Florida Everglades, using stable isotope analysis to quantify trophic diversity along gradients of primary production (periphyton), disturbance (marsh drying) and intermediate-consumer density (a possible indicator of competition). We predicted that trophic diversity would increase with resource availability and decrease after disturbance, and that competition could result in greater trophic diversity by favouring resource partitioning. Total trophic diversity, measured by niche area, decreased with periphyton biomass and an ordination axis representing several bluegreen algae species. Consumers' basal resource diversity, estimated by $\delta^{13}C$ values, was similarly related to algal community structure. The range of trophic levels ($\delta^{15}N$ range) increased with time since the most recent drying and reflooding event, but decreased with intermediate-consumer density, and was positively related to the ordination axis reflecting increases in green algae and decreases in filamentous bluegreen algae. Our findings suggest that algal quality, independent of quantity, influences food-web structure and demonstrate an indirect role of nutrient enrichment mediated by its effects on periphyton palatability and biomass. These results reveal potential mechanisms for anthropogenic effects on Everglades communities.

Additional keywords: competition, disturbance, food web, nutrients.

Introduction

Determining factors that shape food-web structure has long been a central goal in ecology, and is especially critical given the increasing need to identify relationships among food-web structure, food-web stability and ecosystem functioning in the face of anthropogenic environmental changes (e.g. McCann 2000; Duffy *et al.* 2005; Rooney *et al.* 2006). Food webs reveal how abiotic and biotic interactions structure communities (e.g. Menge and Sutherland 1987) and mechanisms by which altering population densities or habitats can impact communities (e.g. Pace *et al.* 1999; Layman *et al.* 2007*b*). Food-web structure has been empirically linked to ecosystem functioning (e.g. Carpenter *et al.* 1987; Schindler *et al.* 1997; Duffy *et al.* 2005) and there is a general consensus that critical components of food webs, such as trophic interactions, complementarity and redundancy, have important effects on ecosystem properties (Hooper *et al.* 2005).

Trophic diversity, illustrated by realised food webs that represent feeding links and energy flow (Post 2002*a*), is a function of overall species richness and the range of trophic positions present (food-chain length). Decades of research seeking processes that determine biotic diversity have identified productivity, disturbance and competition as key mechanisms. However, the nature and strength of these relationships are highly context-dependent (Menge and Sutherland 1987; Mackey and Currie 2001; Mittelbach *et al.* 2001). Both productivity and disturbance have also been implicated in determining food-chain length, although evidence is mixed and the relationships can be positive or negative (Post 2002*a*). Thus, how productivity, disturbance and competition alter food-web structure, by modifying community structure and/or trophic interactions, remain important questions for most systems. Community-wide trophic metrics linking trophic diversity to environmental gradients offer one path towards improved understanding of these relationships (Layman *et al.* 2007*a*).

By measuring realised trophic roles with greater resolution than traditional functional groupings, stable isotopes may be more informative for studies of food-web structure than gut contents used alone (Layman *et al.* 2007*a*). Analysis of stable isotopes is a tool for examining diet when potential resources are associated with natural variation in isotope ratios. Nitrogen ratios ($\delta^{15}N$) tend to reflect trophic position because there is a stepwise enrichment in ^{15}N with each trophic level, whereas carbon ratios ($\delta^{13}C$) reflect basal carbon sources because there is relatively little change associated with trophic transfers (Minagawa and Wada 1984; Peterson and Fry 1987; Post 2002*b*). Trophic parameters measured using stable isotope ratios, including trophic diversity, trophic similarity, carbon range and nitrogen range, have been proposed as quantitative community-wide metrics for describing food-web structure (Layman *et al.* 2007*a*). Trophic diversity, the total size of a food web, can be estimated as the total area encompassing species in a $\delta^{13}C$–$\delta^{15}N$ bi-plot. Unlike food-chain length, both the range of trophic positions and

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diversity within trophic levels influence trophic diversity. The degree of trophic similarity among species in the food web can be measured as the mean nearest-neighbour distance between species points in δ^{13}C–δ^{15}N bi-plot space. As trophic diversity can be highly sensitive to outliers, this provides some measure of average similarity between species or 'packing' within the trophic niche. Additionally, ranges of δ^{13}C and δ^{15}N values estimate diversity of basal resources and vertical trophic positions, respectively. Therefore, geometric measurements based on isotope data offer a newly described approach for measuring functional features of food-web structure.

Oligotrophic marshes of the Florida Everglades have gradients of both limiting nutrients (phosphorus) and hydrological disturbance (seasonal drying of the marsh) (Noe *et al.* 2001; Trexler *et al.* 2005). These gradients result from natural topography, anthropogenic management of water levels and anthropogenic canals that act as conduits for nutrient-enriched water from urban and agricultural areas. Nutrient enrichment and hydrology have profound effects on algal community structure and abundance (McCormick *et al.* 1996; Gaiser *et al.* 2006; Gottlieb *et al.* 2006), which likely spread to consumers (e.g. King and Richardson 2007; Liston *et al.* 2008). Small fishes ($<$8 cm) and macroinvertebrates are key intermediate consumers in this ecosystem, representing a large portion of the biomass in aquatic communities (Rader 1999; Turner *et al.* 1999). They also comprise an important trophic link between basal primary producers (predominantly periphyton mats composed of benthic algae, bacteria, fungi and detritus) and larger vertebrates, such as wading birds (Rader 1999). Overall, densities of small fishes and invertebrates typically decrease with disturbance and increase with nutrient enrichment (Turner *et al.* 1999; Gaiser *et al.* 2005; Trexler *et al.* 2005), but eventually decline at highest phosphorus levels with the disappearance of periphyton (King and Richardson 2007; Liston *et al.* 2008). Trophic positions of intermediate consumers may also shift following a disturbance (Williams and Trexler 2006), suggesting that environmental gradients help determine trophic interactions in addition to simple abundance patterns.

Most studies in the Everglades and elsewhere have focussed on how abiotic gradients and biotic interactions alter abundances of species or taxonomic groups, which can dramatically affect food webs (e.g. keystone species). Yet, even without removing particular species, environmental gradients can influence available prey and/or diet selections in ways that change the patterns of energy flow through the food web (i.e. changes in functional diversity; Post *et al.* 2000). Species whose densities are resilient to environmental change may nonetheless play different roles in the community if their diets shift in response to altered prey distributions (Layman *et al.* 2007*b*). Competition can also modify trophic interactions by forcing species to further partition available prey (Schoener 1974), even when having little effect on density. Understanding foraging decisions of consumers is essential for obtaining biologically meaningful interpretations of food-web structure and stability (Beckerman *et al.* 2006; Uchida and Drossel 2007). To better understand how abiotic and biotic gradients influence food-web structure via trophic interactions in the Everglades, we examined trophic structure revealed by stable isotopes in a food-web fragment composed of small fishes and crayfishes (henceforth 'intermediate consumers'). We expected that trophic interactions would be strongly affected by nutrients and drying events, and possibly by competition. Specifically, we predicted that: (1) increases in food availability and quality (mediated by nutrient levels) would support more diverse trophic roles, (2) disturbance would have the opposite effect by reducing prey levels and (3) competition could increase trophic diversity by favouring resource partitioning.

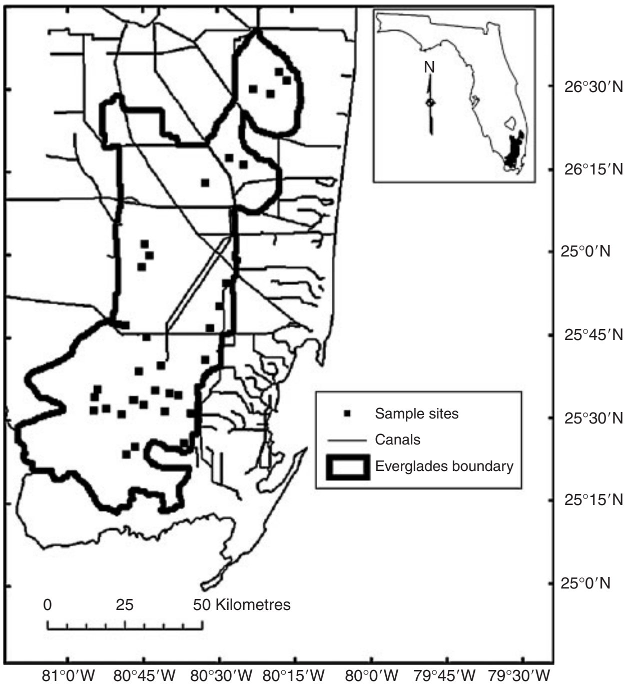

Fig. 1. Map of the study area with the location of sampling sites in Water Conservation Areas, Loxahatchee National Wildlife Refuge and Everglades National Park.

Materials and methods

Study system

In the Florida Everglades, communities in wet-prairie slough habitats are typically composed of large standing stocks of periphyton mats (Turner *et al.* 1999), spikerush-dominated (*Eleocharis cellulosa* Torr.) emergent vascular plants, infaunal macroinvertebrates (Liston 2006), larger invertebrates (crayfishes, insects), several species of small fishes (Trexler *et al.* 2002) and, in long-hydroperiod areas, large piscivorous fishes (Chick *et al.* 2004), as well as larger consumers such as amphibians, reptiles, mammals (muskrats and otters) and wading birds. We sampled aquatic communities in 34 sites across the Everglades (~25°19′N, 80°56′W) in November and December 2005 (Fig. 1). These sites were separated by 1.7–137.7 km and past research has indicated that sites separated at this scale can be treated as independent (Trexler *et al.* 2002; Ruetz *et al.* 2005).

Sampling procedure

We employed a standardised throw-trap sampling protocol (Jordan *et al.* 1997) with three replicates per site. We used 1-m^2

throw-traps constructed from copper pipe and covered on four sides with 1.5-mm mesh to collect small fishes (<8 cm standard length) and large invertebrates. Traps were cleared with a bar seine (1.5-mm mesh) and two dip nets (1- and 5-mm mesh). Vertebrates were killed upon collection by immersion in an MS-222 (tricaine methanesulfonate) bath. All aquatic animals captured were placed on ice in the field and then frozen at −17.7°C for ~7 months before sample processing.

We defined intermediate-consumer density as the total density of fishes and crayfishes, calculated for each site as the mean of the total counts (all species) over the three throw-trap replicates. We collected periphyton samples from within each throw trap and processed them for algal community composition, ash-free dry mass (AFDM) ($\mathrm{g\,m^{-2}}$), percentage of nitrogen and organic content, total phosphorus content (TP) ($\mu\mathrm{g\,g^{-1}}$ dry), and chlorophyll *a* mass ($\mu\mathrm{g\,m^{-2}}$) and concentration ($\mu\mathrm{g\,g^{-1}}$ dry) (as described in Gaiser *et al.* 2006). Because nutrients are rapidly absorbed by biota, periphyton TP is used as a biotic indicator of nutrient enrichment (Gaiser *et al.* 2006). Hydrological data were obtained using the Everglades Depth Estimation Network (EDEN) hydrological estimation tool (http://sofia.usgs.gov/eden/stationlist.php, accessed 16 April 2008). Disturbance was measured by time since flooding, calculated as the number of days since the marsh surface was flooded after the most recent drying event (water levels <5 cm). This estimate of disturbance measures the time a system has had to recover following a drought, such that sites with a short time since flooding have been subjected to more recent disturbance. The Everglades have distinct wet (May–November) and dry (December–April) seasons based on rainfall and our sampling was conducted in the late wet season, when marshes were near peak water depths after summer rains.

Isotope sampling and niche measures

Because complete isotopic sampling of an entire food web is generally impractical due to the number of species and size limitations for small organisms (e.g. Polis 1991), we measured a food-web fragment consisting of five species whose abundance reflects dominant trends in the community composed of medium-sized, intermediate consumers (small fishes and crayfishes). Thus, we included in our analysis three relatively common fish species that represent diverse roles in the food web: a predominantly herbivorous species (flagfish, *Jordanella floridae* Goode and Bean) and two omnivorous species that predominantly consume animals but also some algae, plants and detritus (eastern mosquitofish, *Gambusia holbrooki* Girard; golden topminnow, *Fundulus chrysotus* Günther). We also included the two species of omnivorous crayfish found in the Everglades, the Everglades crayfish (*Procambarus alleni* Faxon) and the slough crayfish (*P. fallax* Hagen), which were non-overlapping in our samples (i.e. were never both collected at the same site). Consistent with other studies (e.g. Dorn and Trexler 2007), Everglades crayfish were present only in short-hydroperiod sites, whereas slough crayfish were present in long-hydroperiod sites.

We selected this subset of intermediate consumers to allow maximum coverage of the large spatial scale sampled. Thus, our analysis encompasses a greater number of independent sites than similar studies, but may include fewer species at each site. Despite measuring isotopes for only five species, those species were common (average ~58% of the total abundance of small fishes and crayfishes) and their density and biomass were correlated with values for all small fishes and crayfish from throw-trap samples combined (Spearman rank correlations, $r_s = 0.69, P < 0.001$ and $r_s = 0.92, P < 0.001$, respectively). The relative abundances of the five species were correlated with the relative abundances of all small fishes and crayfish combined (Mantel test on Bray–Curtis dissimilarity matrices of standardised data, 2000 permutations, $r_s = 0.69$, $P = 0.05$). Thus, these species represent dominant trends in the density, biomass and community-structure patterns of the intermediate-consumer community at large. Furthermore, these species reflect the isotope range of common fishes (Loftus 2000). However, eastern mosquitofish, golden topminnows and flagfish were absent from throw-trap samples at 1, 4 and 13 sites, respectively (see ‘Data analysis’ below).

Fishes and crayfishes obtained from throw-trap samples were thawed and muscle was removed from each individual for isotope analysis (one to three individuals per species per site). Muscle tissue was removed from the caudal region on both sides of the fish and from the tail of the crayfish. Tissue was rinsed with deionised water and dried at 55–60°C for ≥24 h before being ground into a fine powder and analysed for δ^{13}C and δ^{15}N with an isotope ratio mass spectrometer (IRMS) (Finnigan, San Jose, CA, USA) at the Stable Isotope Laboratory at Florida International University. Isotope values are reported in standard delta (δ) notation (Peterson and Fry 1987), calculated using Pee Dee Belemnite as a standard for δ^{13}C and air as a standard for δ^{15}N. The standard deviation of sample replicates for this analysis was 0.08‰ for δ^{13}C and 0.05‰ for δ^{15}N. Past work revealed no impact of extracting lipids from muscle on δ^{13}C and δ^{15}N data from Everglades consumers (Williams and Trexler 2006). Additionally, the organisms in this study had average C : N values ≤3.5 with little variation between species and lipid extraction is thought to be unnecessary for aquatic animals with such low C : N values (Post *et al.* 2007). Based on these findings, we did not extract lipids because it was difficult to obtain sufficient tissue mass for isotope analysis for these small organisms.

Following Layman *et al.* (2007*a*), we measured several important aspects of the community's trophic niche as represented in δ^{13}C–δ^{15}N bi-plot space for each site, using mean δ^{13}C and δ^{15}N values from each species for each site. Total niche area was defined as the convex hull area (Cornwell *et al.* 2006) encompassing the trophic positions of the species and was calculated using the program QHULL (available from http://www.qhull.org/, accessed 16 January 2008; Barber *et al.* 1996). We defined mean nearest-neighbour distance as the mean of the Euclidean distances between each species and its nearest neighbour. We calculated δ^{13}C range and δ^{15}N range by subtracting the lowest δ^{13}C and δ^{15}N values from the highest δ^{13}C and δ^{15}N values, respectively. Potential pitfalls in applying stable isotope analyses to ecological data are well known (Gannes *et al.* 1997; Post 2002*b*; Barnes *et al.* 2008), but in many cases possible weaknesses are outweighed by benefits (e.g. long-term integration of complex trophic pathways; Post 2002*b*). Additionally community-wide metrics may be less vulnerable to biases caused by shifting isotopic baselines and species-specific patterns of isotope fractionation and routeing because they are measured on a relative scale, where relationships between the same set of species are of interest (Layman *et al.* 2007*a*). A potential problem with applying these niche metrics to isotope data is the arbitrary nature of the δ^{13}C axis – two resources may exhibit very large or very small differences in δ^{13}C while they are still simply two different resources (Hoeinghaus and Zeug 2008). However, major differences in niche metrics resulting from these arbitrary patterns are more likely when different systems are being compared and this approach still offers some insight when there are many resources that cannot be easily partitioned using isotopes (Layman and Post 2008).

Data analysis

Algal species, important basal resources in this food web, are likely to vary in their quality as food and thus food quality may be represented by algal community composition. Nonmetric multidimensional scaling (NMDS) conducted with PRIMER-5 (Primer-E Ltd, Ivybridge, UK) was used to ordinate sites based on algal species, resulting in gradients where sites are positioned according to their dissimilarity in relative abundances of species (McCune and Grace 2002). Dissimilarity matrices were based on Bray–Curtis dissimilarity indices calculated on untransformed, standardised algal community data after rare species (present in $<5\%$ of sites) were removed (McCune and Grace 2002). Resulting axis scores from three-dimensional solutions were obtained ($\text{stress} = 0.10$) and used as independent variables in regression models (McCune and Grace 2002). We used Kendall's tau-b (τ) nonparametric correlations between NMDS axis scores and relative abundances of species to interpret the axes (Beals 2006). We considered a species to be strongly correlated with an axis if their correlation was $|\tau| \geq 0.40$.

We developed separate regression models for each niche metric that included terms representing measures of disturbance, resource availability and quality, and competition, factors that influence intermediate-consumer density and possibly trophic roles. Full models for each included: time since flooding, periphyton AFDM, periphyton algal NMDS axes, intermediate-consumer density and interaction terms for periphyton variables and density (after centering). We sought to examine trophic changes resulting from dietary shifts of co-occurring species, so to address possible biases caused by the occasional absence of one of the species we included flagfish presence as a binary variable in the analyses as they were missing from more than one-third of the sites. We also included interaction terms between flagfish and variables containing density (to check whether slopes were different depending on flagfish presence). Because eastern mosquitofish and golden topminnows were missing from only a few sites, we could not include them as explanatory variables and instead examined leverage and influence diagnostics (Belsley *et al.* 1980) to determine whether these sites had strong effects on parameter estimates obtained in regression analyses. Regressions were conducted using PROC GLM in SAS 9.1 (SAS Institute Inc., Cary, NC, USA) with Type III sums of squares (partial F tests). We used stepwise-backward elimination based on a criterion of $\alpha = 0.05$ for partial F tests to select final models, with main effects remaining in the model unless relevant interaction terms were first removed. Residuals were examined to ensure that assumptions of linear regression were met, and when assumptions were clearly violated, $\log_{10}(x+1)$ transformations were used to meet assumptions. Spearman correlations between main effects were $|r_s| \leq 0.75$ except for periphyton AFDM and density ($r_s = -0.76$), indicating that despite some correlation between environmental variables as is common in ecological data, there was sufficient variation to include these explanatory variables. Standardised β weights adjust parameter estimates by their standard deviations and thus can be helpful guides as to the relative importance of each variable (Tabachnick and Fidell 2007). The adjusted R^2 for each model is the total proportion of variance in the dependent variable explained by the model (adjusting for model complexity), while the squared semipartial coefficients express the variance explained that can be uniquely attributed to each explanatory variable (Tabachnick and Fidell 2007). When models contain multiple explanatory variables, simple plots of the dependent variable against an explanatory variable can be misleading since the effects of other explanatory variables have not been accounted for. Therefore, we illustrated the results of the regression models using partial regression plots, which plot the residuals of the dependent variable against the residuals of each explanatory variable after each has been separately regressed on the other explanatory variables in the model (Belsley *et al.* 1980). Although the axes are not in the same scale as the original variables, the plots accurately show the relationships tested by regression (i.e. the slope equals the partial regression coefficient) and allow visual inspection of the scatter of points and possible influential cases.

Results

Abiotic and biotic gradients

Our study sites spanned a range of disturbance (time since flooding), nutrient (periphyton TP) and biotic (periphyton AFDM and intermediate-consumer density) gradients typical of other studies of the Greater Everglades, with the exception of areas that have high nutrient levels and constant water inundation (cf. Trexler *et al.* 2002; Gaiser *et al.* 2006; King and Richardson 2007) (Table 1). The algal NMDS axes reflected changes in the relative abundance of species associated with phosphorus levels (Table 2). NMDS Axis 1 was strongly positively correlated with the filamentous bluegreen alga *Schizothrix* sp. and negatively correlated with several species of diatoms typically associated with low phosphorus levels (Gaiser *et al.* 2006). This pattern was also reflected by the correlation between Axis 1 and the relative abundances of physiognomic groupings. NMDS Axis 2 was negatively associated with the bluegreen alga *Aphanothece* sp. and several green algae and diatom species, including members of the genus *Eunotia*, which are indicators of moderate to high phosphorus levels (Gaiser *et al.* 2006). Across broader taxonomic categories, Axis 2 was most strongly related to the relative abundance of green algae and more weakly associated with filamentous bluegreen algae. NMDS Axis 3 increased with the relative abundance of bluegreen algae, particularly *Gloeothece* sp. and, although it decreased with some diatom species, it was not correlated with diatom relative abundance in general. NMDS Axes 1 and 2 were correlated with periphyton TP (Spearman correlation: $r_s = -0.62$ and -0.45, respectively) and to a lesser

Table 1. Descriptive statistics for environmental gradients, consumer density and niche metrics ($n = 34$)

Variables	Range of values	Mean (s.e.)
Periphyton total phosphorus ($\mu g\,g^{-1}$ dry)	53–617	239 (30)
Time since flooding (days)	147–2164	537 (107)
Periphyton ash-free dry mass ($g\,m^{-2}$)	0.6–540	139 (29)
Intermediate-consumer density ($\#\,m^{-2}$)	4–44	16 (1.8)
Total niche area	0.1–7.1	2.4 (0.31)
Mean nearest-neighbour distance	1.10–3.59	1.81 (0.084)
$\delta^{13}C$ range	0.3–3.8	1.6 (0.18)
$\delta^{15}N$ range	2.3–5.9	4.2 (0.14)

degree with time since flooding ($r_s = -0.42$ and -0.29). Axis 3 was not correlated with either gradient ($r_s = 0.08$ and -0.15).

Periphyton TP was negatively correlated with measures of periphyton biovolume and biomass, but increased with organic content and percentage nitrogen (Table 3). Phosphorus levels were positively correlated with the relative abundance of green algae and diatoms, but negatively correlated with the relative abundance of bluegreen algae and filamentous bluegreen algae (Table 3). Thus, our findings join those of several experimental and observational studies suggesting that phosphorus enrichment tends to decrease periphyton quantity (mass, biovolume, aerial cover), but increase periphyton quality (proportion of palatable algal species, C : N ratio, percentage of organic content).

Intermediate-consumer density was positively correlated with eastern mosquitofish density ($r_s = 0.70$, $P < 0.001$) and with golden topminnow ($r_s = 0.38$, $P = 0.027$), but not with flagfish ($r_s = 0.07$, $P = 0.693$) or crayfish density ($r_s = -0.22$, $P = 0.205$). The proportion of total density composed of fishes was significantly correlated with eastern mosquitofish ($r_s = 0.68$, $P < 0.001$), flagfish ($r_s = -0.41$, $P = 0.017$) and crayfish densities ($r_s = -0.84$, $P < 0.001$). Mean relative abundances of eastern mosquitofish and crayfish were 0.25 and 0.24, compared with 0.05 for golden topminnows and 0.04 for flagfish. Thus, eastern mosquitofish contributed strongly to high levels of intermediate-consumer density and crayfish predominated at lower intermediate-consumer densities.

Regression results for niche metrics

Mean $\delta^{13}C$ and $\delta^{15}N$ values across all sites are shown for each species in Fig. 2. Niche area was positively correlated with mean nearest-neighbour distance ($r_s = 0.52$, $P = 0.001$) and $\delta^{13}C$ range ($r_s = 0.81, P < 0.001$), but not $\delta^{15}N$ range ($r_s = 0.29$, $P = 0.101$). Mean nearest-neighbour distance increased with both $\delta^{13}C$ range ($r_s = 0.45$, $P = 0.008$) and $\delta^{15}N$ range ($r_s = 0.38$, $P = 0.026$), even though the latter were unrelated ($r_s = -0.10, P = 0.565$). Despite these correlations, niche metrics varied in their response to periphyton quantity (periphyton AFDM), periphyton quality (algal NMDS axes), disturbance (time since flooding) and competition (intermediate-consumer density) (Table 4). Log-transformed niche area increased when flagfish were present and decreased with increasing values of periphyton AFDM and algal NMDS Axis 3 (Fig. 3). Although the single site without eastern mosquitofish had high leverage and influenced the relationship between niche area and algal NMDS Axis 3 (Fig. 3*c*), this relationship was still significant when that observation was removed. Log-transformed mean nearest-neighbour distance depended only on algal NMDS Axis 2, but this relationship hinged entirely on a single site (the site with the highest nearest-neighbour distance) and may therefore be unimportant (i.e. the model contained no significant predictors when that site was excluded) (Fig. 4). Alternatively, low power may have limited our ability to document the strength of this effect since that site was one of only four with high nutrient levels and relatively low time since flooding. Algal NMDS Axis 3 was negatively related to log-transformed $\delta^{13}C$ range (Fig. 5). Like niche area, the site missing eastern mosquitofish heavily influenced, but did not solely determine, this relationship. Finally, $\delta^{15}N$ range increased with time since flooding (Fig. 6*b*) and decreased with algal NMDS Axis 2 (Fig. 6*c*). The regression model suggested that effects of intermediate-consumer density and flagfish presence on $\delta^{15}N$ range were related (Fig. 6*e*). The model is consistent with the hypothesis that, when flagfish were present, increasing density resulted in a decrease in the range of $\delta^{15}N$ values (Table 4).

Discussion

We found strong support for the different roles of disturbance, resources and consumer density in determining patterns of trophic structure for food webs in the Florida Everglades. Importantly, we identified changes in trophic diversity of dominant intermediate consumers resulting from apparent niche shifts, contributing to the understanding of how food webs change as a function of these gradients beyond what is known from studies of fish density and community structure.

General results for niche metrics

Our regression model suggests that the trophic diversity of intermediate consumers, as measured by total niche area, was influenced by algal community structure (NMDS Axis 3), was higher at lower levels of periphyton AFDM and increased when flagfish were present. The latter result was expected, since inclusion of flagfish in our food web should expand the community trophic niche (Fig. 2). By examining the algal species and

Table 2. Kendall's tau correlations between algal nonmetric multidimensional scaling axis scores and relative abundances for species and physiognomic groups

	Axis 1	Axis 2	Axis 3
Species (τ)	*Schizothrix* sp. (0.55)	*Aphanothece* sp. (−0.52)	*Gloeothece* sp. (0.48)
	Fragilaria synegrotesca (−0.62)	*Eunotia* sp. (−0.45)	*Encyonopsis egsp01* (−0.45)
	Encyonema ftsp01 (−0.57)	*Pinnularia gibba* (−0.44)	*Frustulia rhomboides* var. *crassinervia* (−0.45)
	Fragilaria nana (−0.53)	*Encyonopsis subminuta* (−0.44)	*Pinnularia gibba* (−0.44)
	Encyonema evergladianum (−0.51)	*Frustulia rhomboides* var. *crassinervia* (−0.44)	*Brachysira brebissonii* (−0.42)
	Mastogloia smithii (−0.48)	Bulbochaete filament (−0.42)	*Nitzschia palea* var. *debilis* (−0.40)
	Brachysira neoexilis (−0.40)	*Cosmarium phaseolus* (−0.42)	
		Gonatozygon sp. (−0.41)	
		Eunotia naegelii (−0.41)	
		Staurastrum connatum (−0.40)	
Physiognomic group (τ)			
Bluegreen algae	(0.36)	(−0.18)	(0.42)
Filamentous bluegreen algae	(0.55)	(0.34)	(−0.18)
Green algae	(−0.18)	(−0.42)	(−0.11)
Diatoms	(−0.80)	(0.11)	(−0.05)

physiognomic groups strongly correlated with Axis 3, it is clear that niche area was inversely correlated with the proportion of bluegreen algae (especially *Gloeothece* sp.). Additionally, niche area increased as the relative abundance of diatom species associated with Axis 3 increased. This suggests that the edibility of algal species plays an important role in food-web structure in the Everglades, and that increased availability of preferred foods increases trophic diversity. In a similar analysis of Bahamian tidal creek communities, Layman *et al.* (2007*b*) identified decreased niche areas in fragmented habitats. They suggested that fragmentation had resulted in a decrease in prey diversity and narrowing of the food web. Our results also point to the importance of resources in shaping trophic diversity. Interestingly, niche area declined with the amount of periphyton organic matter available at the 1 m^2-scale. While a decline in trophic diversity with increasing resource quantity was unexpected, changes in algal community structure and nutrients with increasing phosphorus reflect increased quality of periphyton (e.g. palatable species, percentage of organic content, percentage of nitrogen content) despite decreased quantity (e.g. AFDM, biovolume, aerial cover). Thus, our findings suggest trophic diversity in small consumers increases with phosphorus levels indirectly via increased food quality, despite decreased food quantity.

Our results suggest that the breadths of basal resources and trophic positions responded differently to the gradients. Like niche area, $\delta^{13}C$ range was negatively associated with algal NMDS Axis 3, suggesting that greater availability of palatable species contributed to the diversity of basal resources of the food web. The diversity of trophic levels, as estimated by $\delta^{15}N$ range, was associated with other variables. The regression model was consistent with the hypothesis that disturbance had a negative effect on $\delta^{15}N$ range because $\delta^{15}N$ range was positively correlated with time since flooding. Williams and Trexler (2006) reported a similar finding for eastern mosquitofish and grass shrimp (*Palaemonetes paludosus* Gibbes), in which trophic position (measured relative to a baseline primary consumer) increased with time since flooding. Separate gut content analyses also indicated a decrease in trophic position for eastern mosquitofish and flagfish, and, to a lesser extent, golden topminnows, in spikerush habitats during low water (Loftus 2000). These shifts were associated with a decreased reliance on invertebrate prey, greater consumption of lower trophic level invertebrates, and/or increased consumption of algal and plant material. After a drying event, macroinvertebrate and fish densities decline and may take 3–5 years to fully recover (Trexler *et al.* 2005; Liston 2006). Fish that survive or colonise rapidly may consume more algae or plants initially when alternative prey are scarce. Overall, then, at least some intermediate consumers in our food web were likely to switch to diets of lower trophic level following a disturbance, explaining the trends observed in our analyses. Changes in the algal community towards more palatable species appeared to increase $\delta^{15}N$ range. The range of $\delta^{15}N$ values was inversely related to algal NMDS Axis 2, such that it increased with the relative abundance of bluegreen algae (especially *Aphanothece* sp.), increased with the relative abundance of green algae and was associated with changes in the species compositions of green algae and diatoms. When flagfish were present, increasing intermediate-consumer densities

Table 3. Spearman rank correlations between periphyton total phosphorus (TP) and other periphyton measures ($n = 34$)

Periphyton measures	Periphtyon TP (r_s)	*P*
Total periphyton biovolume (mL)	−0.79	<0.001
Total periphyton aerial cover (%)	−0.86	<0.001
Periphyton ash-free dry mass ($\mathrm{g\,m^{-2}}$)	−0.82	<0.001
Percentage organic content (%)	0.84	<0.001
Percentage carbon (%)	0.84	<0.001
Percentage nitrogen (%)	0.85	<0.001
Chlorophyll *a* concentration ($\mu\mathrm{g\,g^{-1}}$ dry)	0.75	<0.001
Chlorophyll *a* mass ($\mu\mathrm{g\,m^{-2}}$)	−0.81	<0.001
Algal NMDS Axis 1	−0.62	<0.001
Algal NMDS Axis 2	−0.45	0.007
Algal NMDS Axis 3	0.08	0.666
Relative abundance of bluegreen algae	−0.38	0.028
Relative abundance of filamentous bluegreen algae	−0.87	<0.001
Relative abundance of green algae	0.54	0.001
Relative abundance of diatoms	0.55	0.001

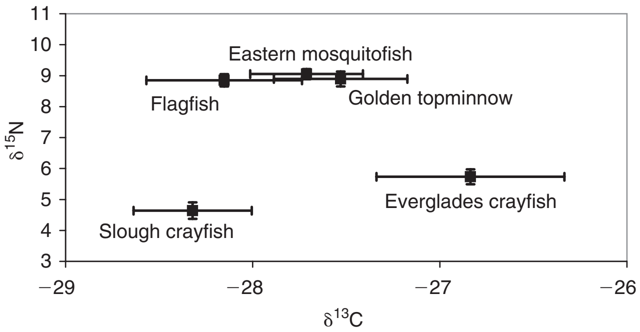

Fig. 2. $\delta^{13}C$–$\delta^{15}N$ bi-plot showing mean values and standard errors for each species across all sites.

(as measured by total fish and crayfish abundance) appeared to decrease their $\delta^{15}N$ range, contrary to our predictions based on resource partitioning. This suggests that as consumer density, and possibly competition, increases, the range of trophic levels nonetheless declines rather than increases as would be expected by decreasing trophic overlap through niche partitioning. A possible explanation for this is that high consumer density actually decreased the abundance of preferred prey and forced fish to feed on lower trophic levels, as niche partitioning may only be possible when alternative niches are actually available. Others have suggested that fish predation can limit macroinvertebrate abundances in the Everglades (Turner *et al.* 1999; Liston 2006).

Mean nearest-neighbour distance was significantly predicted by algal NMDS Axis 2, but this relationship was contingent on a single site, suggesting this pattern is not robust. However, because the site was one of only four sites with short times since flooding and high nutrient levels, it is possible that this trend is genuine and would be better evaluated with increased representation of such sites. The observation that $\delta^{15}N$ range was also negatively related to Axis 2 provides some support for this conclusion.

Interestingly, some factors that likely affected $\delta^{13}C$ and/or $\delta^{15}N$ range were not significant in the final models for total niche area or mean nearest-neighbour distance, or vice versa. Because total niche area and nearest-neighbour distance integrate changes in both $\delta^{13}C$ and $\delta^{15}N$ and niche area does so multiplicatively, they may possess emergent properties that are not evident for either $\delta^{13}C$ or $\delta^{15}N$ range alone. This is likely because $\delta^{13}C$ and $\delta^{15}N$ ranges were uncorrelated, suggesting that niche area and neighbour distances can increase via different combinations of mechanisms. Thus, even though the niche metrics were generally correlated, if $\delta^{13}C$ and $\delta^{15}N$ ranges change along different environmental gradients, their effects on neighbour distances and total area may cancel each other out.

Roles of algal biomass and species composition

In this study, the relative abundances of algal species were associated with an increase in the trophic diversity of intermediate consumers. Compositional changes associated with phosphorus enrichment (NMDS Axis 2) and others apparently unrelated to nutrients (NMDS Axis 3) contributed to their trophic diversity, likely by increasing the availability of preferred prey species and decreasing the availability of unpalatable ones. Most of the consumer species in the present study are omnivorous, so periphyton availability and composition may affect them directly as food, and also indirectly as food and habitat for their invertebrate prey (e.g. McCormick *et al.* 2004; Liston 2006). Algal community structure was an important predictor for more measures of intermediate-consumer trophic diversity (niche area, carbon range, nitrogen range) than periphyton biomass (niche area only), and explained a similar amount of variance in niche area as periphyton biomass, demonstrating a key role for resource quality. Thus, relative abundances of algal species may be of greater importance in determining trophic diversity and consumer relative abundance than the total amount of algae at certain nutrient levels. Other studies examining the effect of productivity on food-chain length reveal contradictory patterns and it

Table 4. Final regression models for niche metrics ($n = 34$)

Dependent variable	Significant terms	$\beta \pm$ s.e. (P)	β weights	Squared semipartial correlation	Global F (P)	Adjusted R^2
Log total niche area	Flagfish	0.20 ± 0.064 (0.0035)	0.44	0.20	$F_{3,30} = 7.22$ (0.0009)	0.36
	Periphyton AFDM	0.0005 ± 0.00018 (0.0127)	−0.37	0.14		
	Algal NMDS Axis 3	0.15 ± 0.062 (0.0228)	−0.33	0.11		
Log mean nearest-neighbour distance	Algal NMDS Axis 2	−0.04 ± 0.019 (0.0447)	−0.35		$F_{1,32} = 4.37$ (0.0447)	0.09
Log δ^{13}C range	Algal NMDS Axis 3	−0.12 ± 0.054 (0.0291)	−0.37		$F_{1,32} = 5.22$ (0.0291)	0.11
δ^{15}N range	Flagfish	0.9 ± 0.40 (0.0295)	0.57	0.09	$F_{5,28} = 6.65$ (0.0003)	0.46
	Time since flooding	0.0006 ± 0.00020 (0.0052)	0.48	0.15		
	Algal NMDS Axis 2	−0.6 ± 0.21 (0.0063)	−0.48	0.14		
	Density	0.00 ± 0.019 (0.9917)	0.0007	1×10^{-7}		
	Flagfish × density	−0.05 ± 0.023 (0.0298)	−0.79	0.09		

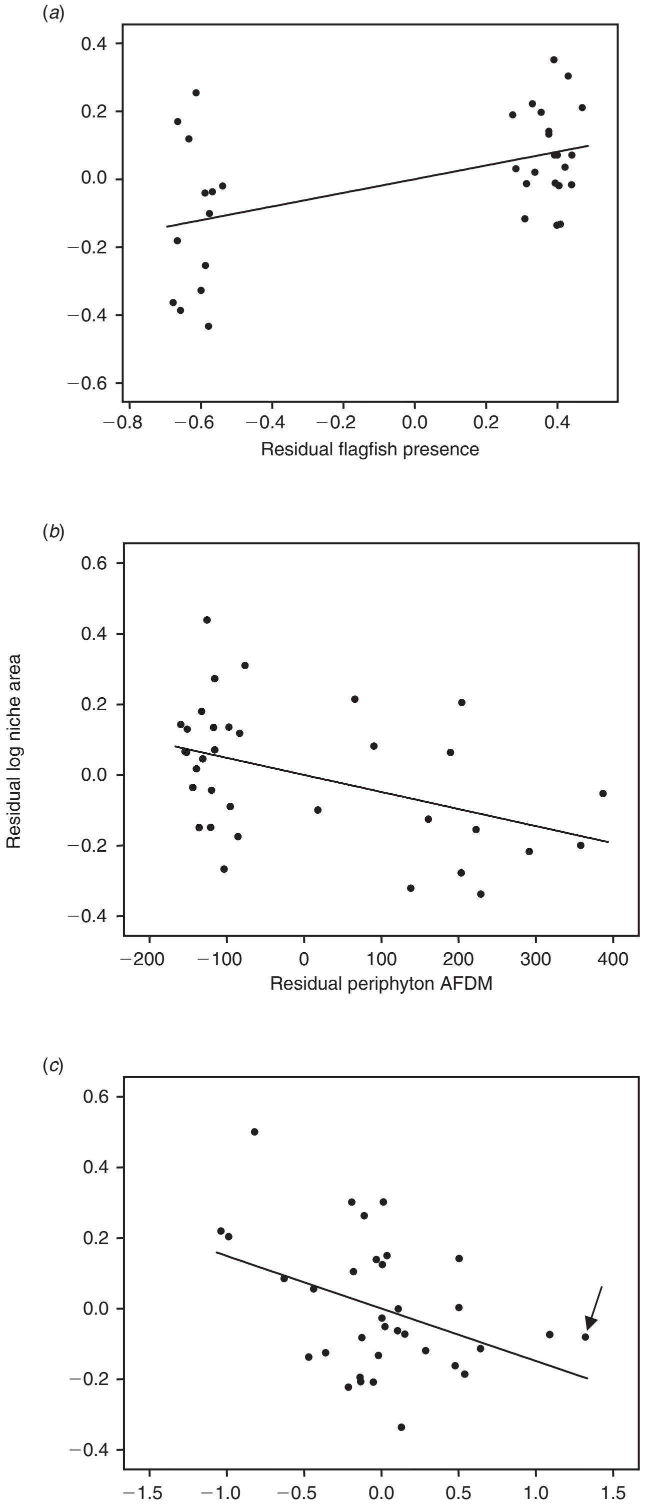

Fig. 3. Partial regression plots for log-transformed niche area and (*a*) flagfish presence, (*b*) periphyton ash-free dry mass (AFDM) and (*c*) algal nonmetric multidimensional scaling Axis 3. Plots show residuals for the dependent and independent variables after each was regressed separately on the other independent variables. Note that the *y*-axis scale varies among panels. In (*c*), the arrow points to a high-leverage site that lacked eastern mosquitofish.

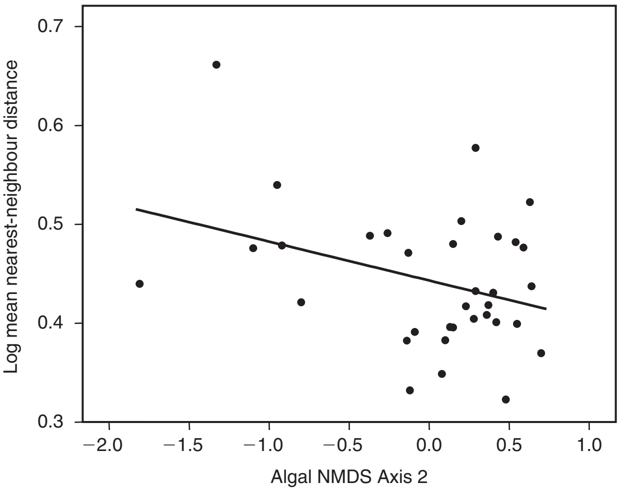

Fig. 4. Plot of log-transformed mean nearest-neighbour distance against algal nonmetric multidimensional scaling Axis 2.

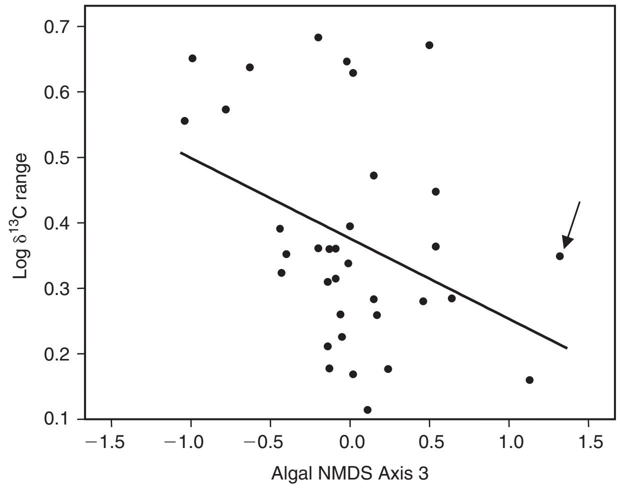

Fig. 5. Plot of log-transformed δ^{13}C range against algal nonmetric multidimensional scaling Axis 3. The arrow points to a high-leverage site that lacked eastern mosquitofish.

has been suggested that it rarely plays a role, except in systems with low productivity (Post 2002*a*). Our findings, however, are consistent with studies that have identified increased diversity or food-chain length with higher quality basal resources (De Deyn *et al.* 2004; Bukovinszky *et al.* 2008). In the oligotrophic Everglades, it appears that the trophic diversity of intermediate consumers is associated with nutrient availability (phosphorus) indirectly via basal resource species, but is less related to total primary production.

Consistent with other studies in the Everglades, periphyton TP was strongly correlated with algal community structure, suggesting that nutrient enrichment may influence the consumer community by altering resource quality (relative abundance of palatable algal species) and quantity (periphyton AFDM). Phosphorus enrichment causes a shift in algal community structure marked by the loss of filamentous bluegreen algae and their calcite precipitate and the resulting breakdown of the calcareous mat, an increase in green algae and changes in diatom composition (McCormick *et al.* 1996; Gaiser *et al.* 2005, 2006). Eastern mosquitofish have been shown to increase their feeding rates on diatoms after periphyton mats are physically broken up, allowing them to selectively choose palatable species and avoid unpalatable, physically difficult to eat filamentous bluegreen algae and calcium carbonate components of the mat (Geddes and Trexler 2003). We also observed the decrease in total algal biomass but increases in percentage of nitrogen and organic content coincident with increasing phosphorus observed by others (Gaiser *et al.* 2006; King and Richardson 2007).

Influence of droughts on Everglades food webs

In many aquatic ecosystems, disturbance in the form of periodic drying is thought to be a critical factor in structuring communities (Wellborn *et al.* 1996). Both densities and community structure of fish and invertebrates in the Everglades are often associated with hydrological parameters such as time since flooding and hydroperiod (Trexler *et al.* 2005; Liston 2006; Dorn and Trexler 2007). Like Williams and Trexler (2006), we found additional support for an effect of disturbance (drying events) on trophic position as approximated by δ^{15}N range, but we also found no effect on total niche area. Not only are large predators excluded by drying events (Chick *et al.* 2004; Trexler *et al.* 2005), but smaller consumers appear to feed at lower trophic levels following a disturbance when invertebrate standing stocks are reduced. Venturelli and Tonn (2006) documented similar decreases in trophic position of pike following removal of prey fish; pike switched to consuming invertebrates following the loss of their preferred prey. While studies of how disturbance affects diversity and food-chain length show no general consensus (Mackey and Currie 2001; Post 2002*a*), food webs in the Everglades may be expected to display strong relationships with disturbance given the intensity of hydrological disturbance and the resulting impacts on community structure.

Competition and resource partitioning

Resource partitioning is one mechanism by which coexisting species can respond to high interspecific competition (Schoener 1974) and diet shifts in response to the presence of a competitor have been shown in a variety of systems (e.g. Holbrook and Schmitt 1989; Nakano *et al.* 1999; Bonesi *et al.* 2004). In a previous study of Everglades fishes, juvenile eastern mosquitofish changed their diets in response to high intraspecific competition (Taylor *et al.* 2001). Although we measured competition indirectly, the relationship between δ^{15}N range and fish and crayfish density suggests that competition may decrease trophic position. Decreased trophic diversity with increasing consumer densities was unexpected if competition generally acts to increase trophic diversity. The most likely explanation for our results is that at high densities, consumers actually overwhelmed their preferred prey and were forced to feed on lower trophic levels.

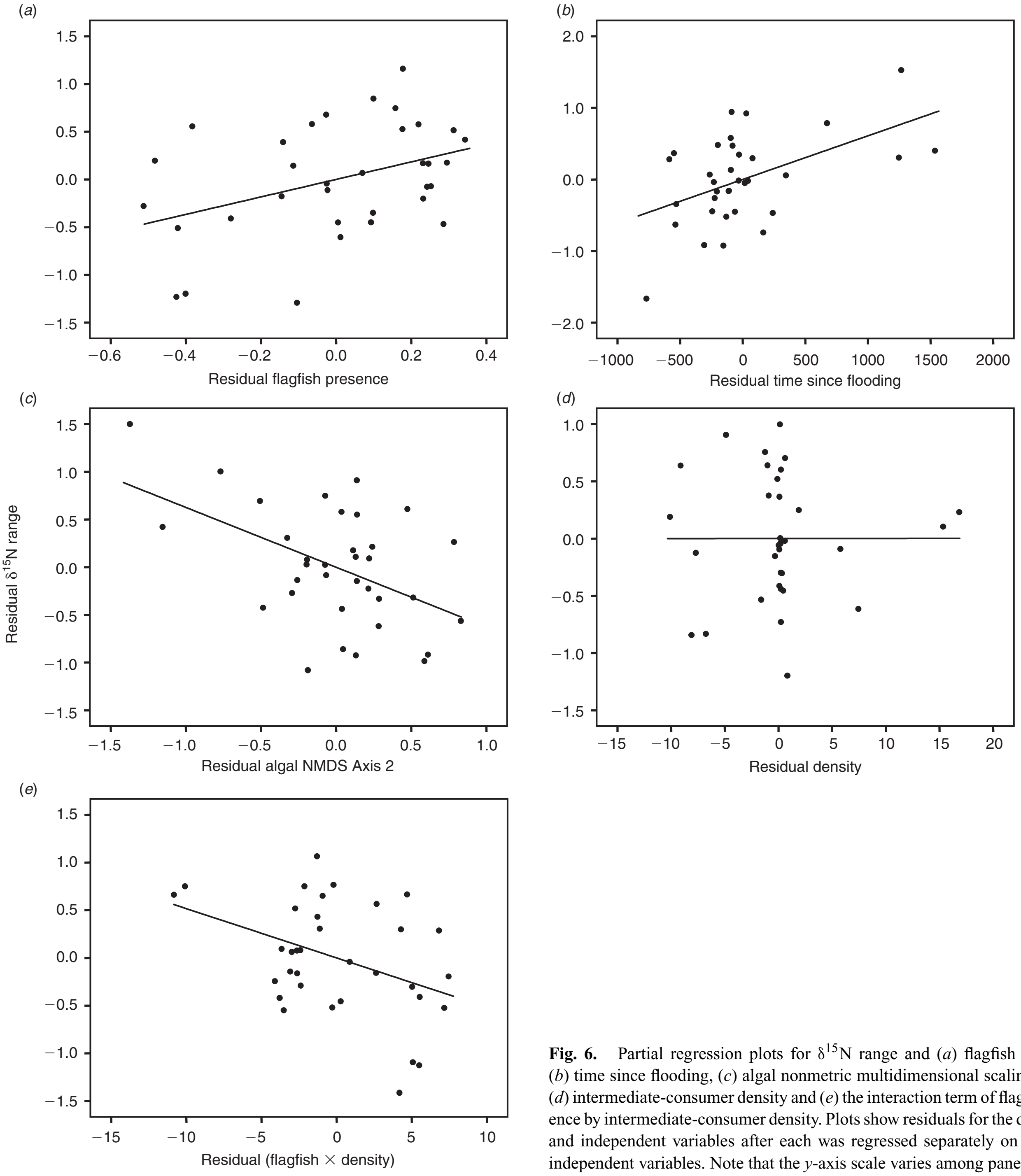

Fig. 6. Partial regression plots for $\delta^{15}N$ range and (*a*) flagfish presence, (*b*) time since flooding, (*c*) algal nonmetric multidimensional scaling Axis 2, (*d*) intermediate-consumer density and (*e*) the interaction term of flagfish presence by intermediate-consumer density. Plots show residuals for the dependent and independent variables after each was regressed separately on the other independent variables. Note that the *y*-axis scale varies among panels.

Conclusions

This study demonstrates effects of disturbance and productivity on the trophic structure of small consumers in the Everglades. Water flow through the Everglades has been anthropogenically altered in ways that affect disturbance rates and intensity, and a goal of current management is to restore historical water levels. Additionally, restoration of water flow will import nutrients from areas of*agriculturaland* urban development. These changes will not only affect the density and community structure of consumers, but our findings suggest they will also alter dominant trends in trophic interactions and energy flow through the food web. Thus, future studies should attempt to quantify the functional outcomes of these shifts on population dynamics and community structure.

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References

Barber, C. B., Dobkin, D. P., and Huhdanpaa, H. (1996). The Quickhull algorithm for convex hulls. *Association for Computing Machinery Transactions on Mathematical Software* **22**, 469–483. doi:10.1145/235815.235821

Barnes, C., Jennings, S., Polunin, N. V. C., and Lancaster, J. E. (2008). The importance of quantifying inherent variability when interpreting stable isotope field data. *Oecologia* **155**, 227–235. doi:10.1007/S00442-007-0904-Y

Beals, M. L. (2006). Understanding community structure: A data-driven multivariate approach. *Oecologia* **150**, 484–495. doi:10.1007/S00442-006-0551-8

Beckerman, A. P., Petchey, O. L., and Warren, P. H. (2006). Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 13 745–13 749. doi:10.1073/PNAS.0603039103

Belsley, D. A., Kuh, E., and Welsch, R. E. (1980). 'Regression Diagnostics. Identifying Influential Data and Sources of Collinearity.' (John Wiley & Sons: New York.)

Bonesi, L., Chanin, P., and Macdonald, D. W. (2004). Competition between Eurasian otter *Lutra lutra* and American mink *Mustela vison* probed by niche shift. *Oikos* **106**, 19–26. doi:10.1111/J.0030-1299.2004.12763.X

Bukovinszky, T., van Veen, F. J. F., Jongema, Y., and Dicke, M. (2008). Direct and indirect effects of resource quality on food web structure. *Science* **319**, 804–807. doi:10.1126/SCIENCE.1148310

Carpenter, S. R., Kitchell, J. F., Hodgson, J. R., Cochran, P. A., Elser, J. J., *et al.* (1987). Regulation of lake primary productivity by food web structure. *Ecology* **68**, 1863–1876. doi:10.2307/1939878

Chick, J. H., Ruetz, C. R., III, and Trexler, J. C. (2004). Spatial scale and abundance patterns of large fish communities in freshwater marshes of the Florida Everglades. *Wetlands* **24**, 652–664. doi:10.1672/0277-5212(2004)024[0652:SSAAPO]2.0.CO;2

Cornwell, W. K., Schwilk, D. W., and Ackerly, D. D. (2006). A trait-based test for habitat filtering: Convex hull volume. *Ecology* **87**, 1465–1471. doi:10.1890/0012-9658(2006)87[1465:ATTFHF]2.0.CO;2

De Deyn, G. B., Raaijmakers, C. E., van Ruijven, J., Berendse, F., and van der Putten, W. H. (2004). Plant species identity and diversity effects on different trophic levels of nematodes in the soil food web. *Oikos* **106**, 576–586. doi:10.1111/J.0030-1299.2004.13265.X

Dorn, N. J., and Trexler, J. C. (2007). Crayfish assemblage shifts in a large drought-prone wetland: The roles of hydrology and competition. *Freshwater Biology* **52**, 2399–2411. doi:10.1111/J.1365-2427.2007.01860.X

Duffy, J. E., Richardson, J. P., and France, K. E. (2005). Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. *Ecology Letters* **8**, 301–309. doi:10.1111/J.1461-0248.2005.00725.X

Gaiser, E. E., Childers, D. L., Jones, R. D., Richards, J. H., Scinto, L. J., *et al.* (2006). Periphyton responses to eutrophication in the Florida Everglades: Cross-system patterns of structural and compositional change. *Limnology and Oceanography* **51**, 617–630.

Gaiser, E. E., Trexler, J. C., Richards, J. H., Childers, D. L., Lee, D., *et al.* (2005). Cascading ecological effects of low-level phosphorus enrichment in the Florida Everglades. *Journal of Environmental Quality* **34**, 717–723.

Gannes, L. Z., O'Brien, D. M., and Martinez Del Rio, C. (1997). Stable isotopes in animal ecology: Assumptions, caveats, and a call for more laboratory experiments. *Ecology* **78**, 1271–1276.

Geddes, P., and Trexler, J. C. (2003). Uncoupling of omnivore-mediated positive and negative effects on periphyton mats. *Oecologia* **136**, 585–595. doi:10.1007/S00442-003-1294-4

Gottlieb, A. D., Richards, J. H., and Gaiser, E. E. (2006). Comparative study of periphyton community structure in long and short-hydroperiod Everglades marshes. *Hydrobiologia* **569**, 195–207. doi:10.1007/S10750-006-0132-1

Hoeinghaus, D. J., and Zeug, S. C. (2008). Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* **89**, 2353–2357. [Comment] doi:10.1890/07-1143.1

Holbrook, S. J., and Schmitt, R. J. (1989). Resource overlap, prey dynamics, and the strength of competition. *Ecology* **70**, 1943–1953. doi:10.2307/1938124

Hooper, D. U., Chapen, F. S., III, Ewel, J. J., Hector, A., Inchausti, P., *et al.* (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* **75**, 3–35. doi:10.1890/04-0922

Jordan, F., Coyne, S., and Trexler, J. C. (1997). Sampling fishes in vegetated habitats: Effects of habitat structure on sampling characteristics of the 1-m^2 throw trap. *Transactions of the American Fisheries Society* **126**, 1012–1020. doi:10.1577/1548-8659(1997)126<1012:SFIVHE>2.3.CO;2

King, R. S., and Richardson, C. J. (2007). Subsidy–stress response of macroinvertebrate community biomass to a phosphorus gradient in an oligotrophic wetland ecosystem. *Journal of the North American Benthological Society* **26**, 491–508. doi:10.1899/06-002R.1

Layman, C. A., and Post, D. M. (2008). Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* **89**, 2358–2359. [Reply] doi:10.1890/08-0167.1

Layman, C. A., Arrington, D. A., Montaña, C. G., and Post, D. M. (2007*a*). Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* **88**, 42–48. doi:10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2

Layman, C. A., Quattrochi, J. P., Peyer, C. M., and Allgeier, J. E. (2007*b*). Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecology Letters* **10**, 937–944. doi:10.1111/J.1461-0248.2007.01087.X

Liston, S. E. (2006). Interactions between nutrient availability and hydroperiod shape macroinvertebrate communities in Florida Everglades marshes. *Hydrobiologia* **569**, 343–357. doi:10.1007/S10750-006-0141-0

Liston, S. E., Newman, S., and Trexler, J. C. (2008). Macroinvertebrate community response to eutrophication in an oligotrophic wetland: An *in situ* mesocosm experiment. *Wetlands* **28**, 686–694. doi:10.1672/07-224.1

Loftus, W. F. (2000). Accumulation and fate of mercury in an Everglades aquatic food web. PhD Thesis, Florida International University, Miami, USA.

Mackey, R. L., and Currie, D. J. (2001). The diversity-disturbance relationship: Is it generally strong and peaked? *Ecology* **82**, 3479–3492.

McCann, K. S. (2000). The diversity–stability debate. *Nature* **405**, 228–233. doi:10.1038/35012234

McCormick, P. V., Rawlik, P. S., Lurding, K., Smith, E. P., and Sklar, F. H. (1996). Periphyton-water quality relationships along a nutrient gradient in the northern Florida Everglades. *Journal of the North American Benthological Society* **15**, 433–449. doi:10.2307/1467797

McCormick, P. V., Shuford, R. B. E., III, and Rawlik, P. S. (2004). Changes in macroinvertebrate community structure and function along a phosphorus gradient in the Florida Everglades. *Hydrobiologia* **529**, 113–132. doi:10.1007/S10750-004-5737-7

McCune, B., and Grace, J. B. (2002). 'Analysis of Ecological Communities.' (MjM Software Design: Gleneden Beach, OR, USA.)

Menge, B. A., and Sutherland, J. P. (1987). Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* **130**, 730–757. doi:10.1086/284741

Minagawa, M., and Wada, E. (1984). Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between ^{15}N and animal age. *Geochimica et Cosmochimica Acta* **48**, 1135–1140. doi:10.1016/0016-7037(84)90204-7

Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L., Reynolds, H. L., *et al.* (2001). What is the observed relationship between species richness and productivity? *Ecology* **82**, 2381–2396.

Nakano, S., Fausch, K. D., and Kitano, S. (1999). Flexible niche partitioning via a foraging mode shift: A proposed mechanism for coexistence in stream-dwelling charrs. *Journal of Animal Ecology* **68**, 1079–1092. doi:10.1046/J.1365-2656.1999.00355.X

Noe, G. B., Childers, D. L., and Jones, R. D. (2001). Phosphorus biogeochemistry and the impact of phosphorus enrichment: Why is the Everglades so unique? *Ecosystems* **4**, 603–624. doi:10.1007/S10021-001-0032-1

Pace, M. L., Cole, J. J., Carpenter, S. R., and Kitchell, J. F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution* **14**, 483–488. doi:10.1016/S0169-5347(99)01723-1

Peterson, B. J., and Fry, B. (1987). Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* **18**, 293–320. doi:10.1146/ANNUREV.ES.18.110187.001453

Polis, G. A. (1991). Complex trophic interactions in deserts: An empirical critique of food-web theory. *American Naturalist* **138**, 123–155. doi:10.1086/285208

Post, D. M. (2002*a*). The long and short of food-chain length. *Trends in Ecology & Evolution* **17**, 269–277. doi:10.1016/S0169-5347(02)02455-2

Post, D. M. (2002*b*). Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology* **83**, 703–718.

Post, D. M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J., *et al.* (2007). Getting to the fat of the matter: Models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* **152**, 179–189. doi:10.1007/S00442-006-0630-X

Post, D. M., Pace, M. L., and Hairston, N. G., Jr (2000). Ecosystem size determines food-chain length in lakes. *Nature* **405**, 1047–1049. doi:10.1038/35016565

Rader, R. B. (1999). The Florida Everglades: Natural variability, invertebrate diversity, and foodweb stability. In 'Invertebrates in Freshwater Wetlands of North America: Ecology and Management'. (Eds D. P. Batzer, R. B. Rader and S. A. Wissinger.) pp. 25–54. (John Wiley & Sons: New York.)

Rooney, N., McCann, K., Gellner, G., and Moore, J. C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature* **442**, 265–269. doi:10.1038/NATURE04887

Ruetz, C. R., III, Trexler, J. C., Jordan, F., Loftus, W. F., and Perry, S. A. (2005). Population dynamics of wetland fishes: Spatio-temporal patterns synchronized by hydrological disturbance? *Journal of Animal Ecology* **74**, 322–332. doi:10.1111/J.1365-2656.2005.00926.X

Schindler, D. E., Cole, J. J., Kitchell, J. F., and Pace, M. L. (1997). Influence of food web structure on carbon exchange between lakes and the atmosphere. *Science* **277**, 248–251. doi:10.1126/SCIENCE.277.5323.248

Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science* **185**, 27–39. doi:10.1126/SCIENCE.185.4145.27

Tabachnick, B. G., and Fidell, L. S. (2007). 'Using Multivariate Statistics.' 5th edn. (Pearson Education: Boston, MA, USA.)

Taylor, R. C., Trexler, J. C., and Loftus, W. F. (2001). Separating the effects of intra- and interspecific age structured interactions in an experimental fish assemblage. *Oecologia* **127**, 143–152. doi:10.1007/S004420000575

Trexler, J. C., Loftus, W. F., Jordan, F., Chick, J. H., Kandl, K. L., *et al.* (2002). Ecological scale and its implications for freshwater fishes in the Florida Everglades. In 'The Everglades, Florida Bay, and Coral Reefs of the Florida Keys. An Ecosystem Sourcebook'. (Eds J. W. Porter and K. G. Porter.) pp. 153–181. (CRC Press: Boca Raton, FL, USA.)

Trexler, J. C., Loftus, W. F., and Perry, S. (2005). Disturbance frequency and community structure in a twenty-five year intervention study. *Oecologia* **145**, 140–152. doi:10.1007/S00442-005-0094-4

Turner, A. M., Trexler, J. C., Jordan, C. F., Slack, S. J., Geddes, P., *et al.* (1999). Targeting ecosystem features for conservation: Standing crops in the Florida Everglades. *Conservation Biology* **13**, 898–911. doi:10.1046/J.1523-1739.1999.97513.X

Uchida, S., and Drossel, B. (2007). Relation between complexity and stability in food webs with adaptive behavior. *Journal of Theoretical Biology* **247**, 713–722. doi:10.1016/J.JTBI.2007.04.019

Venturelli, P. A., and Tonn, W. M. (2006). Diet and growth of northern pike in the absence of prey fishes: Initial consequences for persisting in disturbance-prone lakes. *Transactions of the American Fisheries Society* **135**, 1512–1522. doi:10.1577/T05-228.1

Wellborn, G. A., Skelly, D. K., and Werner, E. E. (1996). Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* **27**, 337–363. doi:10.1146/ANNUREV.ECOLSYS.27.1.337

Williams, A. J., and Trexler, J. C. (2006). A preliminary analysis of the correlation of food-web characteristics with hydrology and nutrient gradients in the southern Everglades. *Hydrobiologia* **569**, 493–504. doi:10.1007/S10750-006-0151-Y

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