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## Examining gradients in ecosystem novelty: fish assemblage structure in an invaded Everglades canal system

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**Abstract.** Novel ecosystems result from a combination of altered historical abiotic regimes and new species assemblages. In freshwater systems, novel environmental conditions often result from large-scale changes to hydrological connectivity as well as species invasions. Novel environmental conditions may affect the survival of aquatic fauna by altering dispersal patterns and resource fluctuations, and/or may impose physiological constraints on native species evolutionarily adapted to particular environments. Further, novel systems can provide insight into processes driving community structure because re-sorting or filtering of regional biota is a likely consequence of decoupling from historical conditions. Although several studies document the presence of novel conditions, few examine variation or gradients in novelty. The Florida Everglades is a highly invaded and hydrologically altered system characterized by a large network of canals that compartmentalize the ecosystem and act to both increase and decrease connectivity. Little is known about how canals in this region function as habitat for native and nonnative fishes, the extent to which these canals may function as novel habitats, and how these habitat characteristics may influence distribution, abundance, and assembly patterns. In this study, we examined native and nonnative fish assemblages along a gradient of novelty, defined as the loss of wetland connectivity, influence of the natural hydrological regime, and habitat complexity (well connected to leveed canals). As novelty increased, native species richness and abundance strongly declined and the contribution of nonnatives increased to nearly 50%. Vast differences in community structure across the novelty gradient were strongly influenced by spatial factors and secondarily by hydrological factors, while habitat and abiotic factors were of very low relevance. Natives and nonnatives had opposing responses to key hydrological and habitat characteristics. Abundance of native fishes declined with decreased connectivity to adjacent marshes and canal littoral zone width, while nonnative fishes increased significantly in the most novel canals. Our results suggest that the inherent loss of natural environmental conditions and subsequent replacement by novel ones can lead to extensive changes in fish community structure. Success or failure at maintaining native assemblages will rely heavily on natural resource manager's ability to incorporate natural environmental characteristics with ecosystem restoration.

**Key words:** anthropogenic disturbance; canals; community structure; distance-based linear models; ecosystem novelty; Everglades; nonnatives; species invasions.

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## INTRODUCTION

The synergistic effects of anthropogenic disturbance and species invasions can rapidly alter both ecosystem structure and function (Milton 2003, Root and Schneider 2006, Didham et al. 2007). These changes can profoundly affect all levels of ecological organization and result in the emergence of biotic and abiotic conditions that bear little to no resemblance to their natural counterparts (Fox 2007, Kueffer 2015, Radeloff et al. 2015). Such systems have recently generated much discussion and are often referred to as “no-analog” or “novel” ecosystems (Milton 2003, Hobbs et al. 2006, 2013, Fox 2007, Williams and Jackson 2007). Novel ecosystems are defined by two key characteristics which include alterations to historical abiotic regimes and the presence of new species assemblages, both caused by a combination of varying degrees of environmental degradation (e.g., land use changes) and species invasions (Hobbs et al. 2006, 2009). Novel systems provide an opportunity for insight into community assembly processes since re-sorting or filtering of regional biotas is a likely consequence of this decoupling from historical conditions.

In freshwater systems, anthropogenic ecosystem degradation most often results from disruptions of natural hydrological regimes and spatially widespread disturbances (Pringle 2001, 2003, Vörösmarty et al. 2010, Arthington 2012). Alterations to the natural flow regime (Poff et al. 1997, Acreman et al. 2014) and aquatic species invasions (Ricciardi and Rasmussen 1999) are recognized as two of the most concerning global threats to aquatic biodiversity (Dudgeon et al. 2006). Altered hydrological connectivity from dams, impoundments, canals, and levees, created for both water retention and diversion, can result in novel conditions for aquatic fauna that can limit or enhance dispersal abilities, alter resource fluctuations, and impose physiological constraints on native species that are evolutionarily adapted to particular natural regimes (Conley et al. 2000, Freeman et al. 2007, Franssen et al. 2013).

An estimated 40% of the Earth’s land area may already be covered by novel ecosystems (Ellis et al. 2010, Foley et al. 2011, Barnosky et al. 2012), with many terrestrial examples (Cramer and Hobbs 2002, Lindenmayer et al. 2008, Mascaro

et al. 2008, Lugo 2009, Hobbs et al. 2013). In aquatic and marine systems, examples of novel ecosystems are increasingly being reported (Nilsson and Berggren 2000, Gido et al. 2009, King et al. 2011, Pandolfi et al. 2011). For instance, algal blooms from non-point source runoff in the Gulf of Mexico have resulted in extensive dead zones and novel species interactions (Rabalais et al. 2002). Similarly, human-induced ocean acidification combined with rising ocean temperatures and pollution has left novel ecosystems in the wake of once thriving coral reefs (Fabricius 2005, Hoegh-Guldberg et al. 2007, Pandolfi et al. 2011). Although these studies documented ecosystem novelty, they provide little detailed information of variation in novelty, in other words how truly novel these conditions are. This variation can have important implications for resource management, conservation and restoration efforts. Effective resource management requires that we understand how novel conditions are, in order to apply appropriate management targets (i.e., protect vs. restore; Woodworth 2013, and Wuerthner et al. 2014). One potentially helpful approach is the identification of gradients in novelty in the landscape as a function of varying degrees of both abiotic and biotic change (e.g., urbanization; King et al. 2011).

The Everglades is a rain-fed karstic wetland system, which due to drainage and impoundment, is presently bisected by an extensive network of canals and levees. Built for water supply and flood control beginning in the 1880s, nearly 2500 km of canals and levees presently surround and cut through wetlands, impeding sheet flow and compartmentalizing the entire ecosystem (Light and Dineen 1994, Sklar et al. 2002). Canals in this region offer an opportunity to better understand how these structures function as novel habitat for both native and nonnative fishes and how novel conditions influence the distribution, abundance, and assembly patterns in fish communities. Canals likely provide permanent deep-water faunal refuges which were historically rare or absent in the natural Everglades ecosystem (Gunderson and Loftus 1993), thus acting as novel aquatic habitats. Canals also vary in their attributes, which we expect will result in a novelty gradient (Fig. 1). Variation in (1) their connectivity to adjacent marshes, (2) in the influence of the natural seasonal hydrological

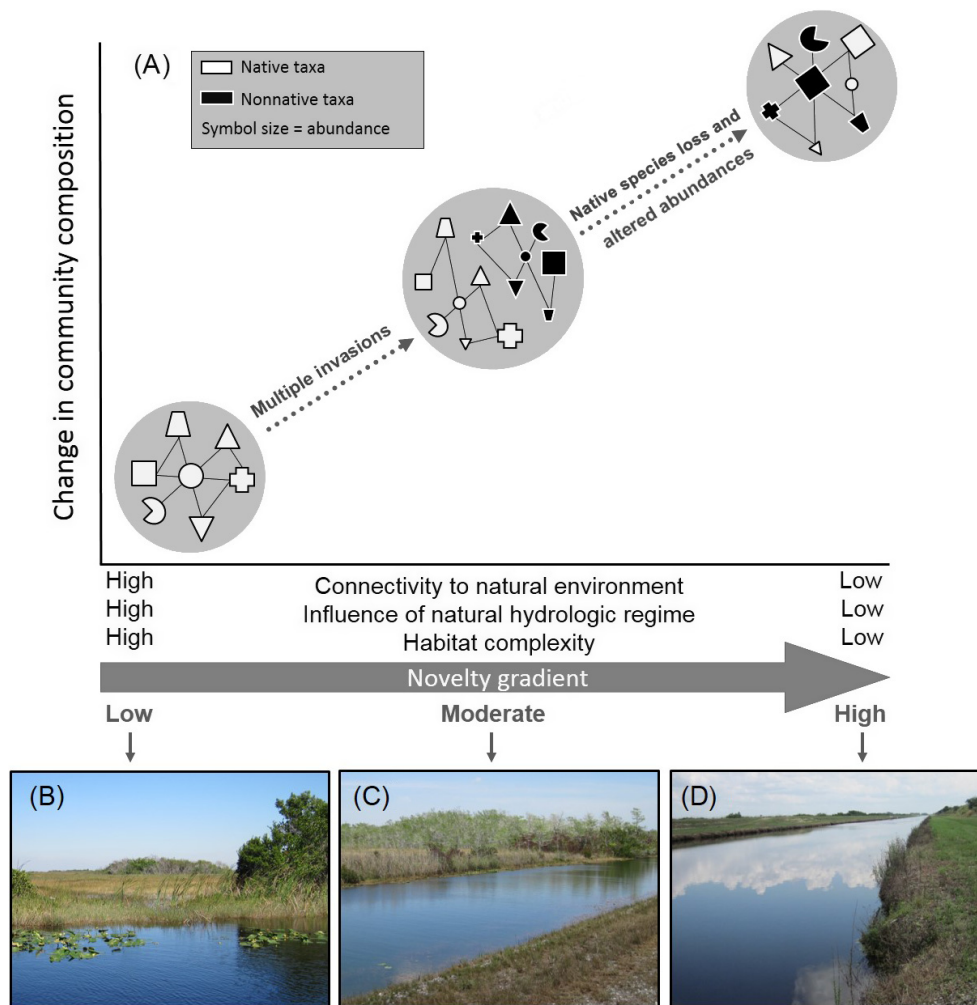


Fig. 1. (A) Conceptual diagram depicting hypothesized changes in fish community structure as a function of increasing novelty in Everglades canals. Native species are represented by white symbols, while nonnatives are represented by black symbols, and symbol size corresponds to species abundance. We expect the degree of invasion to increase with increasing novelty, leading to an increasing number of nonnative species (and higher nonnative abundances) and a lower number of native species (and lower abundance—at least for some native taxa). At the highest level of novelty, we hypothesize habitat quality to decrease for native species, and for nonnative species to dominate the community. Canals with higher novelty are characterized by lower connectivity to natural habitats, lower influence of the natural hydrological regime, and lower habitat complexity. Novelty increases from (B) well connected canals to (C) moderately connected canals and to (D) leveed canals.

regime, and (3) habitat complexity may drive gradients in novelty that we hypothesize relate to the degree of invasion.

Canals exhibit a range in connectivity with surrounding marshes (analogous to floodplains), ranging from those that are well connected and contain complex littoral zone habitats, to canals with only moderate connectivity (i.e., only

connected at high water levels and/or partially leveed), to those with no direct connectivity and virtually no habitat resemblance to Everglades freshwater habitats and thus higher novelty (fully leveed on both sides and isolated from surrounding wetlands; Fig. 1). Canals that are well connected to marshes should be more influenced by the natural wet dry pulsing seasonality of the

subtropical Everglades (Sklar et al. 2002, McVoy et al. 2011).

We expect then canals with lower connectivity to marshes, lower influence of the seasonal hydrological regime, and lower habitat complexity to be more novel and thus more invaded by nonnative fish species (Fig. 1). Fish invasions have been a persistent and prominent feature of the Everglades ecosystem (Fuller et al. 1999, Kline et al. 2014). This is particularly true in canals, which can act as a source of invasions to protected areas such as Everglades National Park (ENP; Kline et al. 2014). Presently, 34 nonnative fishes are considered established (i.e., they have reproductively viable populations; Shafland et al. 2008) in south Florida, of which 17 are established within ENP (Kline et al. 2014). These numbers are comparatively large relative to the low native fish diversity (35 species; Loftus 2000).

In this study, we examined native and nonnative fish community structure in an Everglades canal network as a function of a gradient in novelty, specifically the loss of wetland connectivity, the natural seasonal hydrology, and habitat complexity—conditions not reflective of the pre-drainage Everglades (McVoy et al. 2011). Our specific objectives were to (1) examine spatiotemporal variation in both the native and nonnative fish communities in relation to the degree of novelty in canals, and (2) determine the relative importance of hydrological, habitat, and spatiotemporal factors in driving community structure patterns. We expected that (1) increasing ecosystem novelty would result in a change in community structure driven by a loss in native species and replacement by nonnatives (Fig. 1) and (2) that the relative importance of structuring factors will differ between native and nonnative assemblages.

We hypothesized that native species may not be able to cope with increasingly more novel conditions, resulting in niche opportunities that allow for increased nonnative species richness and abundance (Fig. 1). When resource dynamics are altered via environmental disturbances, niche opportunities (e.g., increased resources, escape from enemies) may provide mechanisms by which nonnatives can increase from low densities and even become dominant (Shea and Chesson 2002). As ecosystem novelty increases in Everglades canals, we expected environmental conditions to shift to those that share little

resemblance to conditions found in Everglades marshes, resulting in a loss of native species and replacement by opportunistic invaders that could establish in these less favorable conditions (Fig. 1). We also expected hydrological variables to play a stronger role in structuring the native community, given that this community should be pre-adapted and thus responsive to hydrology, particularly the strong signature of seasonal hydrological variation (Trexler et al. 2005, Rehage and Trexler 2006).

## METHODS

### *Novelty gradient across Everglades canals*

We sampled five major canals (L-29, L-31N, L-31W, C-111, and L-67A) in the central and southern Everglades (Fig. 2). Canals were located along the eastern boundary of ENP, bordering agriculture areas to the east, and to the north of ENP and center of Water Conservation Area 3 (WCA 3) bisecting freshwater marshes. To account for variation in canal traits across space and time, we classified our focal canals into nine canal sampling units (Table 1) on the basis of connectivity within a canal (i.e., presence of water control structures between sections of a canal), and to surrounding marshes (i.e., presence of levees vs. direct connectivity to adjacent marshes; Fig. 1). When a water control structure was present in a canal, we examined 20 years of flow data from each structure in order to demarcate canal sampling units. For example, the L-29 canal is leveed in the eastern portion but not leveed in the western portion (Fig. 2), and the eastern and western sections of L-29 are separated by a gravity-fed water control structure (S-333) which moves water between them, but likely limits the exchange of biota since at times in any given year it is closed. Thus, we delineated these two canal sections as separate canal sampling units (Fig. 2, Table 1).

Since our focus was to understand how a gradient in novelty influences fish community structure, canal sampling units were classified into three categories (hereafter CANALTYPE): well-connected (WC), moderately connected (MC), and leveed (L) canals (Table 1). WC canals ( $n = 3$ ) are connected to longer hydroperiod marshes nearly year-round, experiencing a greater influence from the natural hydrological



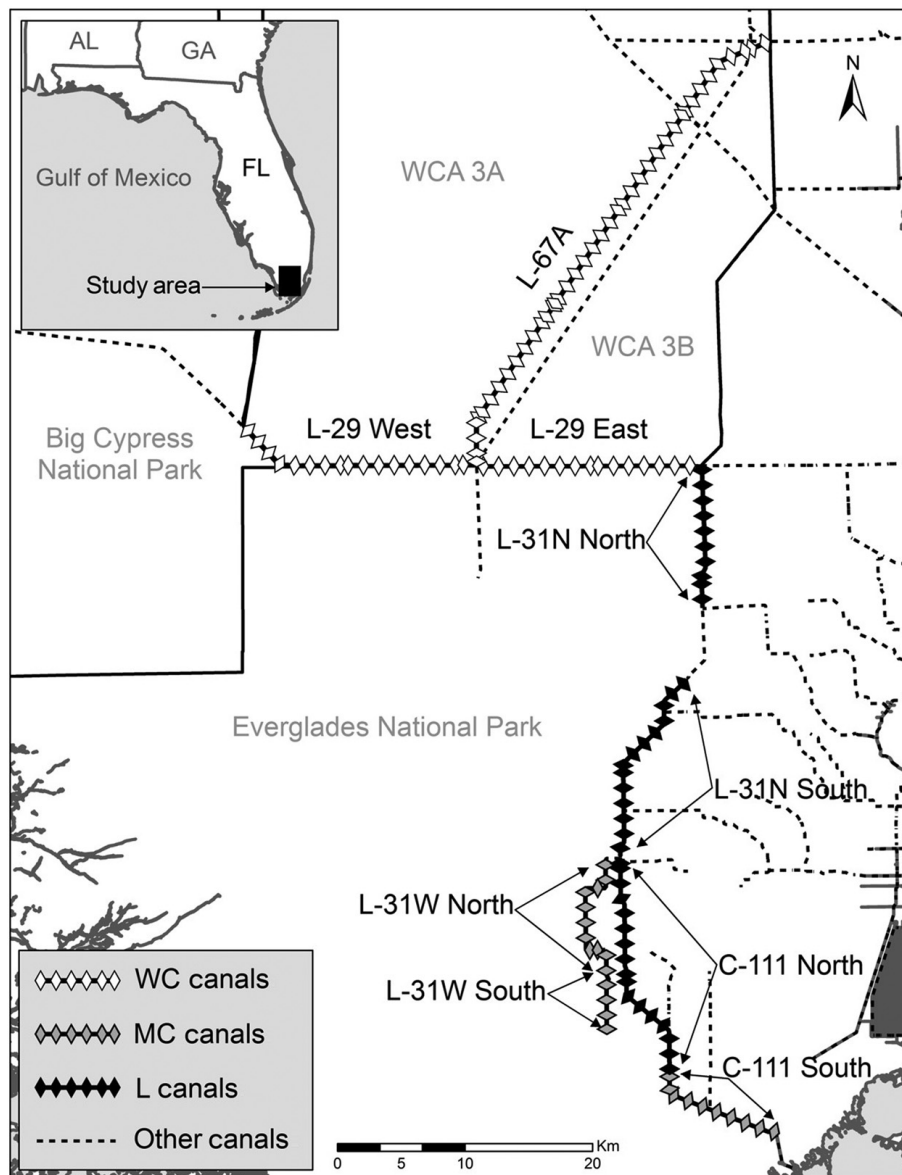


Fig. 2. Map showing the nine canal sampling units spanning across the southern and central portions of the Everglades and surrounding Everglades National Park. Sites are coded based on their connectivity to marshes: WC, well connected canals; MC, moderately connected canals; L, leveed canals. WC canals are connected to marshes year-round, MC canals are connected only at high water conditions, and L canals are completely disconnected from surrounding marsh habitats due to levees on both sides.

regime (i.e., seasonal rainfall patterns; Fig. 1). MC canals ( $n = 3$ ) are, on average, only connected to adjacent shorter hydroperiod marshes during the wet season and have intermediate habitat complexity in their littoral zones. All WC and MC canals have marsh connectivity on one side of the canal (leveed on only one side). In

contrast, L canals ( $n = 3$ ) have no direct connectivity to marsh habitats, receive little influence from the natural hydrological regime, and have low habitat complexity since they typically lack a littoral zone. These isolated, deep, and low-complexity habitats are unlike any natural aquatic habitat in the Everglades, and thus, we consider

Table 1. Summary of electrofishing sampling effort at each of the nine canal sampling units across years: years 1 (2010–2011), 2 (2011–2012), and 3 (2012–2013).

Canal unit name	Canal type	Available stations (N)	Year 1 (2010–2011)			Year 2 (2011–2012)			Year 3 (2012–2013)			
			Wet	Early dry	Late dry	Wet	Early dry	Late dry	Wet	Early dry	Late dry	
L-67A	WC	204	5	10	10	8	8	8	8	8	8	
L-29 East	WC	89	8	10	10	8	8	8	8	8	8	
L-29 West	WC	97	8	10	10	8	8	8	8	8	8	
L-31W North	MC	51	8	10	10	8	8	8	8	8	8	
L-31W South	MC	33	5	10	10	8	8	8	8	8	8	
C-111 South	MC	53	8	10	10	8	8	8	8	8	8	
L-31N North†	L	57	0	0	10	8	8	0	8	8	8	
L-31N South	L	84	8	5	10	8	8	8	8	8	8	
C-111 North	L	93	8	5	10	8	8	8	8	8	8	
Seasonal total			58	80	90	72	72	64	72	72	72	
Annual total				N = 228			N = 208			N = 216		

Notes: Shown are the number of electrofishing samples across the three seasonal sampling events per year. Canal units are classified into three canal types: WC, well connected; MC, moderately connected; L, leveed.

† L-31N North was not accessible at times with no samples.

them to exhibit the highest degree of novelty along our defined gradient (Fig. 1).

### Sampling design

We used a stratified random sampling design to allocate replicated electrofishing sampling effort across the nine canal sampling units over time (hydrological seasons and years). A stratified random sampling approach offers a robust design by accounting for variability among strata, increasing precision in generating estimates of fish abundance, and also meets the assumptions of probability statistics (Hansen et al. 2007, Bonar et al. 2009). At each canal sampling unit, we used ArcGIS to designate uniquely identified fixed sampling stations, each spaced 200 m apart (Table 1). At each seasonal sampling event, we randomly selected 8–10 sampling stations to sample from each canal sampling unit (and in a few rare exceptions only five stations; Table 1), and re-randomized for each sampling event. We conducted a total of nine sampling events (3 seasons  $\times$  3 yr) over the course of the study; seasonal sampling events included wet (June–November), early dry (December–February), and late dry (March–May) for each of year of the study. Between 2010 and 2013, sampling totaled 651 samples (9 canal sampling units  $\times$  8–10 replicate samples  $\times$  3 seasons  $\times$  3 yr = 651 samples; Table 1).

Across the 3 years of our study, prevailing La Nina conditions resulted in below-average

rainfall conditions in years 1 and 2 of sampling (Abteu et al. 2013). Climatic conditions in the dry season of 2010–2011 (year 1) resulted in severe region-wide drought conditions with prolonged drying and a late start to the wet season. In year 3, the system experienced above-average rainfall conditions, and thus the wettest conditions of the 3-year period. One site (L-31N north) was not accessible during the wet, and early dry samples of year 1 and late dry of year 2 (Table 1).

### Electrofishing sampling effort

Fishes were collected using a boat-mounted, generator-powered electrofisher (two spherical anodes, one-cathode system, Smith-Root GPP 9.0, Vancouver, Washington, USA). Electrofishing is an effective method for sampling fishes in freshwater habitats, including the Everglades, and electrofishing catch per unit effort (CPUE) has been shown to provide a reliable index of fish abundance (Chick et al. 1999, 2004, Moulton et al. 2002, Rehage and Trexler 2006, Zale et al. 2013). Boat electrofishing uses a flat-bottom aluminum boat to produce a standardized electrical field, so that fish may be electroshocked, immobilized, and easily collected. Each electrofishing sample consisted of 300 s of standardized, intermittent power application at 3000 W (Boucek and Rehage 2013). Since canal width is greater than the electric field, a shoreline side was targeted for each sample. If a canal had marsh connectivity, then the

marsh side of the canal was always sampled. If both sides were leveed, a shoreline was randomly selected for each sample. To ensure adequate sampling across the entire canal shoreline, samples began from two meters out from the littoral zone edge in deep water and crossed the littoral zone in a zigzag fashion at a 45 to 90° angle to the shore (Guy et al. 2009).

Fish were captured by two netters positioned at the front of the boat, and placed in a holding tank to be later identified and enumerated by species after each sample was completed. Electrofishing targeted all fish larger than 3 cm in length (Rehage and Loftus 2007). We used electrofishing CPUE as an index of abundance. We defined CPUE as the sum of fishes caught and shocked in each sample, adjusted for the length of canal shoreline sampled (measured with a GPS unit; Boucek and Rehage 2013). Shocked fishes included fish that were not caught by netters, but readily identified and counted while shocking. If fish identification was questionable, fish were not included in our CPUE, nor were fish from the opposite shoreline. Thus, electrofishing CPUE consisted of the number of fish per 100 m of canal shoreline sampled:

$$\text{CPUE} = \left[ \frac{\text{Fish netted} + \text{fish shocked}}{\text{distance sampled } (m)} \right] \times 100$$

#### *Habitat, abiotic, and hydrological attributes*

At the beginning of each sample, we measured habitat and abiotic conditions to examine their influence on community structure (Appendix S1). Submersed aquatic vegetation (SAV) characteristics were measured using a 0.5-m<sup>2</sup> quadrat every meter in a transect perpendicular to the shoreline out to 2 m into deep water. Within each quadrat, we measured SAV percent cover (PCOVER) and species richness (PRICH) as well as the average littoral zone depth (LZDEPTH) and width (LZWIDTH). At each sample, we also measured physicochemical conditions including dissolved oxygen (DO), temperature (TEMP), and ambient conductivity (COND) with a multisonder YSI unit, and water clarity using a Secchi disk (SECCHI).

To quantify hydrological connectivity between canals and surrounding marshes, we recorded two hydrological parameters (Appendix S1). First, we measured the local marsh connectivity

at the time of each sample as a categorical variable (LCON; connected or not connected to adjacent marsh at the time of sampling). Second, we estimated regional connectivity by calculating the proportion of days each canal unit was connected to marshes for the year prior to the date of each sample (DCON) using stage data provided by the Everglades Depth Estimation Network (<http://www.sofia.usgs.gov/eden/>). Data from the closest gauges to each canal unit were used. For both parameters, we defined a canal unit as connected if the average marsh depth was  $\geq 10$  cm. Marsh water depths lower than 10 cm in the Everglades have little remaining standing water that is not uniformly distributed across the marsh surface, making conditions unsuitable for many fishes (Chick et al. 2004).

#### *Statistical analyses*

We used a two-step approach to examine variation and structure in canal fish communities in relation to the degree of novelty of canals and hydrological, habitat, and spatiotemporal drivers. First, we fitted generalized linear models to examine spatiotemporal variation in abundance and richness of all fishes, and then of natives and nonnatives separately. We then used multivariate tools to test for variation in community structure across space and time, and for the relative contribution of predictor variables (hydrological, habitat, and abiotic variables).

We examined spatiotemporal variation in fish abundance and richness of all fishes, natives only, and nonnatives only, as well as habitat and abiotic variables, using univariate two-way nonparametric permutational analysis of variance (PERMANOVA; Anderson 2001) to test for the fixed effects of CANALTYPE (WC, MC, and L) and SEASON (wet, early dry, late dry), the random effect year (YEAR), and the interactions of fixed effects.

To examine community structure, we conducted two-way nonparametric permutational analysis of variance (PERMANOVA; Anderson 2001, Anderson and Robinson 2003, Anderson et al. 2008) on three assemblage models: all fishes, natives only, and nonnatives only. Each model was based on fourth-root-transformed (to account for rare species) Bray–Curtis similarity matrices (Clarke and Warwick 2001). Models tested for the fixed effects CANALTYPE and



SEASON, the random effect YEAR, and the interactions of fixed effects. We followed significant main effects with PERMANOVA post hoc pairwise comparison tests. All PERMANOVA tests were based on 999 unrestricted permutations of the residuals under a reduced model to obtain a pseudo- $F$ -statistic and subsequent  $P$  value using type I sums of squares in PERMANOVA+ for Primer 6.0 (Anderson et al. 2008).

To examine the relationship between fish community structure and predictor variables, we used distance-based linear models (DISTLMs; Legendre and Anderson 1999). The DISTLM procedure is a distance-based redundancy analysis (dbRDA) that uses multivariate multiple regressions and performs a permutation test to model the variability of an assemblage matrix against multiple predictor variables (Anderson et al. 2008). We used DISTLMs to assess the relative contribution of five predictor variable sets: (1) spatial, (2) temporal, (3) hydrological, (4) habitat, and (5) abiotic factors (Appendix S1). Spatial variables included each canal unit (CANALUNIT) and CANALTYPE (WC, MC, L), temporal factors included YEAR, and hydrological variables included the annual proportion of days each CANALUNIT was connected to marshes (DCON), the local connectivity of the sampled area to adjacent marshes (LCON), and SEASON (wet, early dry, late dry). Habitat variables included PCOVER, PRICH, LZWIDTH, and LZDEPTH (averaged for each sample), and abiotic variables included DO, COND, TEMP, and SECCHI (Appendix S1).

Models were fitted using a stepwise selection procedure. We used the Akaike's information criterion for selecting the most parsimonious model corrected for small sample size ( $AIC_c$ ), and  $R^2$  to evaluate the % of variation explained by each variable set (Anderson et al. 2008). We conducted DISTLM separately for the three assemblages: all fishes, natives only, and nonnatives only, using Bray-Curtis resemblance matrices (Faith et al. 1987, Legendre and Gallagher 2001). Prior to analysis, all predictor variables were examined for collinearity to eliminate redundant variables ( $r > 0.6$ ) using principal components analysis and draftsman plots (Legendre and Anderson 1999, McArdle and Anderson 2001). Last, we used dbRDA plots to visualize the results of DISTLMs with vectors of predictor variables overlaid.

Statistical significance of predictor sets was assessed at  $\alpha = 0.05$  with 999 random permutations. DISTLMs were conducted using PERMANOVA+ for Primer 6.0 (Anderson et al. 2008). We then fitted simple regressions to better understand the relationship between native and nonnative abundance aggregated across the nine canal sampling units and key predictor variables identified in DISTLM analyses and dbRDAs in SigmaPlot 11.0, San Jose, California, USA.

## RESULTS

### *Spatiotemporal variation in habitat and abiotic attributes*

We found marked differences across CANALTYPE, SEASON, and YEAR in the littoral habitats of sampled canals (Table 2). We detected a gradient in habitat complexity of canal littoral zones, such that PCOVER, PRICH, LZWIDTH, and LZDEPTH declined as the degree of canal connectivity to surrounding marshes decreased (Appendix S2). Overall, littoral habitats in L canals were markedly less complex and nearly absent, with steep banks and sparse vegetation providing less cover for fish (Appendix S2). Average LZW and LZD decreased from  $2.3 \pm 0.1$  m and  $1.0 \pm 0.0$  m in WC canals to an average of  $0.6 \pm 0.1$  m and  $0.7 \pm 0.0$  m in L canals, respectively. Littoral zone PCOVER and PRICH declined nearly threefold from WC canals to L canals with MC canals showing intermediate conditions ( $\bar{x}_{\text{COVER}} = 43.6 \pm 1.6$  and  $\bar{x}_{\text{PRICH}} = 4.0 \pm 0.2$  to  $\bar{x}_{\text{COVER}} = 15.3 \pm 1.7$  and  $\bar{x}_{\text{PRICH}} = 1.3 \pm 0.1$ , respectively). Seasonally, we detected a general shrinking of the littoral zone, especially between the wet and the late dry, but the magnitude of this effect was not the same across canal types (Table 2). MC canals showed the greatest seasonal reduction in habitat complexity (37% reduction in COVER and 45% reduction in PRICH).

Variation in abiotic conditions was mainly a product of seasonality and sampling YEARS and not CANALTYPE (Table 2). Average DO levels were lowest in the wet season (2.0 mg/L) and highest in the late dry (4.4 mg/L). Although lower wet season DO values were contrary to what we would expect, previous work has found DO to be highly correlated with phosphorus (McCormick and Laing 2003); we suspect our results here to be driven by phosphorus-enriched

Table 2. Results of PERMANOVAs testing the fixed effects CANALTYPE (WC, MC, and L) and SEASON (wet, early dry, and late dry), the random effect hydrological year (YEAR), and the interactions of fixed effects (CT × S) on habitat and abiotic variables.

Effects by variable	df	F	P	Effects by variable	df	F	P
PCOVER (%)				DO (mg/L)			
CANALTYPE (CT)	2, 622	52.1	<b>0.005</b>	CANALTYPE (CT)	2, 622	1.4	0.403
SEASON (S)	2, 622	3.2	0.159	SEASON (S)	2, 622	7.6	<b>0.048</b>
YEAR	2, 622	17.9	<b>0.001</b>	YEAR	2, 622	5.1	<b>0.005</b>
CT × S	4, 622	8.5	<b>0.004</b>	CT × S	4, 622	0.6	0.647
PRICH				TEMP (°C)			
CANALTYPE (CT)	2, 622	199.6	<b>0.010</b>	CANALTYPE (CT)	2, 622	2.0	0.248
SEASON (S)	2, 622	5.0	0.084	SEASON (S)	2, 622	7.1	<b>0.043</b>
YEAR	2, 622	12.0	<b>0.001</b>	YEAR	2, 622	13.6	<b>0.001</b>
CT × S	4, 622	5.3	<b>0.026</b>	CT × S	4, 622	0.8	0.531
LZWIDTH (m)				COND (µS/cm)			
CANALTYPE (CT)	2, 622	75.4	<b>0.004</b>	CANALTYPE (CT)	2, 622	1.4	0.396
SEASON (S)	2, 622	6.1	0.065	SEASON (S)	2, 622	0.4	0.730
YEAR	2, 622	6.3	<b>0.001</b>	YEAR	2, 622	17.3	<b>0.001</b>
CT × S	4, 622	1.4	0.291	CT × S	4, 622	0.7	0.567
LZDEPTH (m)				SECCHI (m)			
CANALTYPE (CT)	2, 622	6.9	0.077	CANALTYPE (CT)	2, 622	2.7	0.150
SEASON (S)	2, 622	8.3	<b>0.038</b>	SEASON (S)	2, 622	2.6	0.225
YEAR	2, 622	8.4	<b>0.030</b>	YEAR	2, 622	2.3	0.088
CT × S	4, 622	0.6	0.660	CT × S	4, 622	1.9	0.226

Notes: Significant results ( $P < 0.01$ ) are bolded. Habitat variables include littoral percent vegetation cover (PCOVER), plant species richness (PRICH), littoral zone width (LZWIDTH), and littoral zone depth (LZDEPTH). WC, well connected canals; MC, moderately connected canals; L, leveed canals.

waters being flushed out of upstream agricultural areas into canals during high water periods. For TEMP, mean values were higher in the wet (27.5°C) and lowest in the early dry season (23.7°C,  $P \leq 0.001$ ).

#### Spatiotemporal variation in fish relative abundance and richness

Over 3 years, we collected 28,817 fishes: 23,771 natives (33 spp.) and 5046 nonnatives (16 spp.; Appendix S3). Patterns of fish abundance and species richness in Everglades canals varied significantly as a function of both space (CANALTYPE) and time (SEASON and YEAR). This was true when considering all taxa combined, as well as native and nonnative fishes separately (Table 3). Total fish CPUE decreased as canals became more novel (WC to L), particularly as a result of reductions in native fishes (Fig. 3A). On average, we caught  $125.6 \pm 11.7$  fish/100 m in WC canals,  $76.7 \pm 7.5$  fish/100 m in MC canals, and only  $27.8 \pm 4.1$  fish/100 m in L canals. The relative ratio of native to nonnative fishes also decreased with increased novelty. Native fishes

represented 99% of total CPUE in WC canals and 68% in MC canals, but only 53% L in canals. Notable is the fact that in L canals, total fish CPUE was four times lower than in WC canals, and close to half of fish caught were nonnative (47%). Mean nonnative fish CPUE was also similar between MC and L canals, an average of 16.7 fish/100 m ( $P = 0.730$ ).

Patterns in species richness across CANALTYPE generally mirrored those of CPUE (Table 3). Total species richness (mean per 100 m of shoreline sampled) was highest in WC canals (8.9 spp.), intermediate in MC canals (8.1 spp.), and lowest in L canals (5.5 spp.; Fig. 3B). As expected, mean native richness decreased from WC to L canals (WC = 8.3 spp., MC = 5.1 spp., L = 3.1 spp.). But, contrary to expectations, nonnative richness was highest in MC canals (3.1 spp.), relative to L (2.4 spp.) vs. <1 spp. on average per 100 m in WC canals.

Over time, variation in canal fish assemblages was detected both as a function of SEASON, YEAR, and a differential effect of SEASON and as a function of CANALTYPE (Table 3). Seasonally

Table 3. Results of PERMANOVAs testing the main fixed effects CANALTYPE (WC, MC, and L), SEASON (wet, early dry, and late dry), the random effect YEAR (HY1, HY2, and HY3), and the CANALTYPE  $\times$  YEAR interaction on total CPUE, species richness, and fish composition.

Effects by assemblage	CPUE			Species richness		Composition (Bray–Curtis dissimilarity)		
	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	df	Pseudo- <i>F</i>	<i>P</i> (perm)
All taxa								
CANALTYPE (CT)	2, 622	<b>31.9</b>	<b>0.010</b>	23.1	<b>0.024</b>	2, 621	16.5	<b>0.004</b>
SEASON (S)	2, 622	<b>26.1</b>	<b>0.012</b>	34.5	<b>0.038</b>	2, 621	3.5	<b>0.044</b>
YEAR	2, 622	<b>16.8</b>	<b>0.001</b>	13.6	<b>0.001</b>	2, 621	8.7	<b>0.001</b>
CT $\times$ S	4, 622	9.5	<b>0.004</b>	5.1	<b>0.032</b>	4, 621	2.5	<b>0.004</b>
Natives only								
CANALTYPE (CT)	2, 622	57.5	<b>0.005</b>	74.5	<b>0.005</b>	2, 610	11.5	<b>0.009</b>
SEASON (S)	2, 622	19.5	<b>0.011</b>	22.6	<b>0.034</b>	2, 610	4.0	<b>0.021</b>
YEAR	2, 622	11.9	<b>0.001</b>	12.8	<b>0.001</b>	2, 610	9.7	<b>0.001</b>
CT $\times$ S	4, 622	8.4	<b>0.010</b>	4.1	<b>0.045</b>	4, 610	2.7	<b>0.001</b>
Nonnatives only								
CANALTYPE (CT)	2, 622	47.0	<b>0.025</b>	52.7	<b>0.004</b>	2, 472	13.4	<b>0.002</b>
SEASON (S)	2, 622	9.1	<b>0.036</b>	8.4	<b>0.047</b>	2, 472	1.4	0.318
YEAR	2, 622	10.8	<b>0.001</b>	4.3	<b>0.014</b>	2, 472	1.1	0.362
CT $\times$ S	4, 622	11.6	<b>0.004</b>	8.9	<b>0.003</b>	4, 472	3.2	<b>0.001</b>

Notes: Significant results ( $P < 0.01$ ) are bolded. PERMANOVA models were run separately for all taxa, native fishes only, and nonnative fishes only. WC, well connected canals; MC, moderately connected canals; L, leveed canals.

and across all CANALTYPES combined, CPUE generally increased from an average of 33 fish/100 m in the wet season to 83 fish/100 m in the early dry, and to a peak abundance of 115 fish/100 m in the late dry season (Fig. 4). This three- to fourfold increase in fish CPUE over the dry season was primarily driven by large increases in the native fauna, and particularly in WC canals (Fig. 4A–C). Thus, the effect of seasonality varied as a function of CANALTYPE (Table 3). In WC canals, native fishes peaked in the late dry season with a nearly 4.5-fold increase relative to the wet season, while increases in MC canals (7.5-fold) occurred earlier in the early dry season ( $\bar{x}_{\text{wet}} = 14.2$  to  $\bar{x}_{\text{early dry}} = 105.0$  fish/100 m; Fig. 4B). In contrast, we noted no seasonality in native fish CPUE in L canals ( $P = 0.690$ ).

For nonnatives, we detected no seasonality in WC canals where nonnative numbers were very low (<1.8 fish/100 m; Fig. 4C); however, we did detect seasonality in MC and L canals ( $P < 0.001$ ; Fig. 4C). In MC canals, nonnative fishes increased sixfold between the wet and early dry, and then decreased by half in the late dry, very similar to the pattern seen in native fishes. In L canals, nonnative numbers increased by nearly twofold between the early dry and late.

Temporal patterns in species richness generally followed CPUE patterns (Table 3), with more species caught in the dry season but variation in the timing of peak richness (early vs. late dry season), and minor seasonality in L canals (Fig. 4D–F). Native fish richness (mean per sample) peaked in the early dry season in MC canals (6.2 vs. 3.9 spp. in the wet season,  $P < 0.01$ ), but in the late dry in WC canals (9.4 vs. 6.6 spp. in wet season,  $P = 0.03$ ; Fig. 4E). Nonnative richness showed seasonality only in MC canals, peaking in the early dry season (3.8 in early dry vs. 2.1 in wet,  $P = 0.01$ ) and matching the behavior of native richness in MC canals. In L canals, we observed a significant but small-magnitude SEASON effect for native species richness between the early and late dry seasons (2.6–3.6 spp.,  $P = 0.034$ ), and no seasonality in nonnative richness ( $P > 0.152$ ).

#### Spatiotemporal variation in fish community structure

As a whole, fish community structure showed marked dissimilarity as a function of all effects tested (Table 3). However, the influence of these structuring drivers varied between the native and nonnative components of the fauna. For

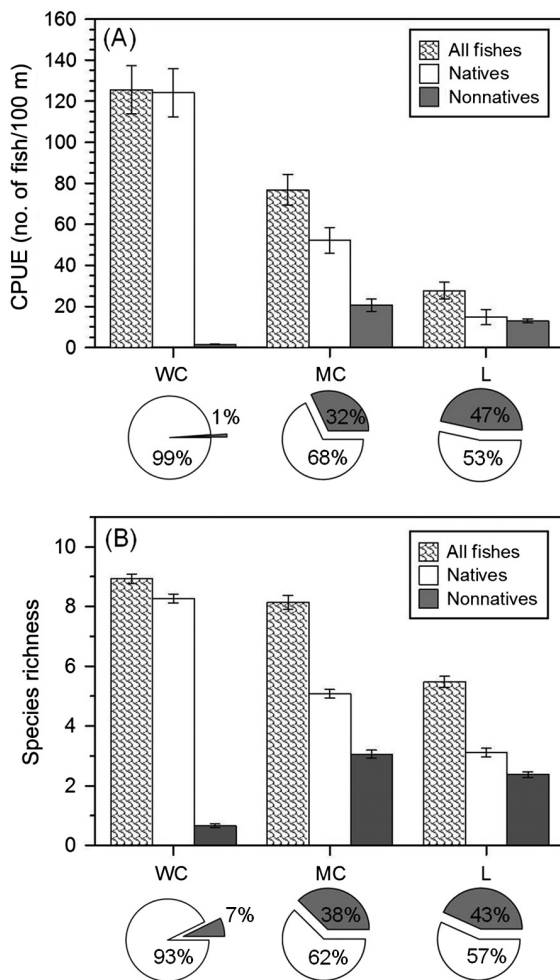


Fig. 3. Total catch per unit effort (CPUE) (no. of fish/100 m; A) and species richness (B) for all fishes (scale pattern bars), natives only (white bars), and nonnatives only (gray bars) across the CANALTYPE novelty gradient; WC, well connected canals; MC, moderately connected canals; L, leveed canals. Shown are means  $\pm$  SE.

native fishes, community dissimilarity was driven by both spatial and temporal stressors, while nonnative community structure was more spatial than temporally influenced; only CANALTYPE and the CANALTYPE  $\times$  SEASON interaction were significant effects (Table 3).

#### Relative contribution of predictor variable sets

The best fitted DISTLMs explained 40.8%, 36.9%, and 33.4% of the variation in community structure across all fishes, natives only,

and nonnatives only assemblages, respectively (Fig. 5A). For all three groups, spatial factors (CANALUNIT and CANALTYPE) consistently explained a much larger proportion of the variance relative to the other variable sets (32.1% for all fishes, 26.7% for natives, and 26.9% for nonnatives). Second in importance, although explaining a much smaller proportion of the variation, were hydrological variables across the three groups (5.1%, 6.5%, and 3.6%, respectively), while temporal, habitat, and abiotic variables explained a minimal amount of variance (<2%; Fig. 5A). Habitat variables were only important predictors for the all fishes and natives only models ( $P = 0.001$ ). Abiotic variables had slightly greater explanatory power for nonnatives than for natives (1.9% vs. 1.3%), whereas hydrological variables explained more variance for natives than for nonnatives (6.5% vs. 3.6%).

The dbRDA ordinations were considered to be a good representation of fish community structure since axes 1 and 2 combined represented 63.4%, 67.5%, and 59.3% of the fitted variation in all fishes, natives only, and nonnatives only models (Fig. 5B–D). Three continuous variables were identified as explaining the most variation in community structure in all three analyses (Fig. 5B–D). The hydrological variable DCON independently explained the most variance consistently for all three models (16.1% all fishes, 13.3% natives only, 8.5% nonnatives only). Among the habitat and abiotic variables, LZW explained the most variation (5.7%) in the natives model, but DO independently explained the most variation (2%) in the nonnatives model (Fig. 5C, D). Regressing CPUE as a function of DCON, LZW, and DO showed varying relationships with respect to native vs. nonnative fishes. Native fishes were more abundant as connectivity to surrounding marshes increased and followed a linear relationship, whereas nonnatives decreased with connectivity in a nonlinear fashion (Fig. 6A, B). Similarly, natives and nonnatives also exhibited opposing relationships as a function of habitat complexity (LZW; Fig. 6C, D). Natives were more abundant as the width of the littoral zone increased, while the opposite was true for nonnatives. No significant relationship was detected for both native and nonnative abundance as a function of DO (Fig. 6E, F).



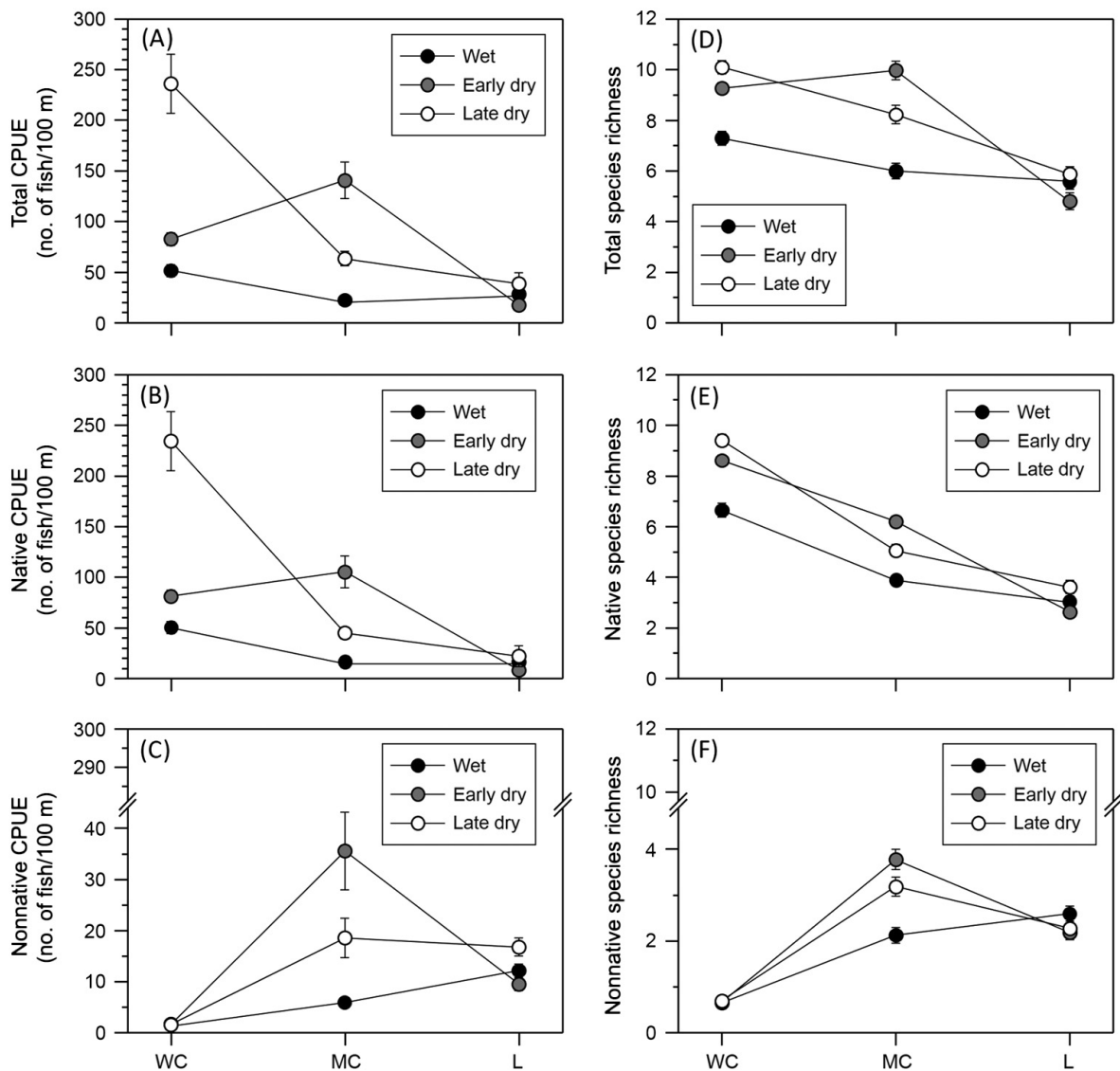


Fig. 4. Catch per unit effort (CPUE; no. of fish/100 m; A–C) and species richness (D–F) by SEASON for all fishes, natives only, and nonnatives only across the CANALTYPE novelty gradient; WC, well connected canals; MC, moderately connected canals; L, leveed canals. Shown are means  $\pm$  SE.

## DISCUSSION

Human-caused modifications to both abiotic conditions and biotic composition are increasingly leading to novel ecosystems (Milton 2003, Hobbs et al. 2006, 2009, 2013, Williams and Jackson 2007), and possibly to gradients in such novelty that directly relate to the degree of alteration (King et al. 2011). We hypothesized a gradient in novelty in Everglades canals that related to

variation in canal traits and to the degree of fish invasion, such that not all man-made canals are created equal. We expected a lower invasion rate in canals with higher connectivity (i.e., year-around) to nearby marshes and higher habitat complexity, and thus lower novelty, and a higher invasion rate associated with canals with low connectivity to marshes (higher novelty). Our findings matched this prediction well for native taxa, but the pattern deviated for nonnative



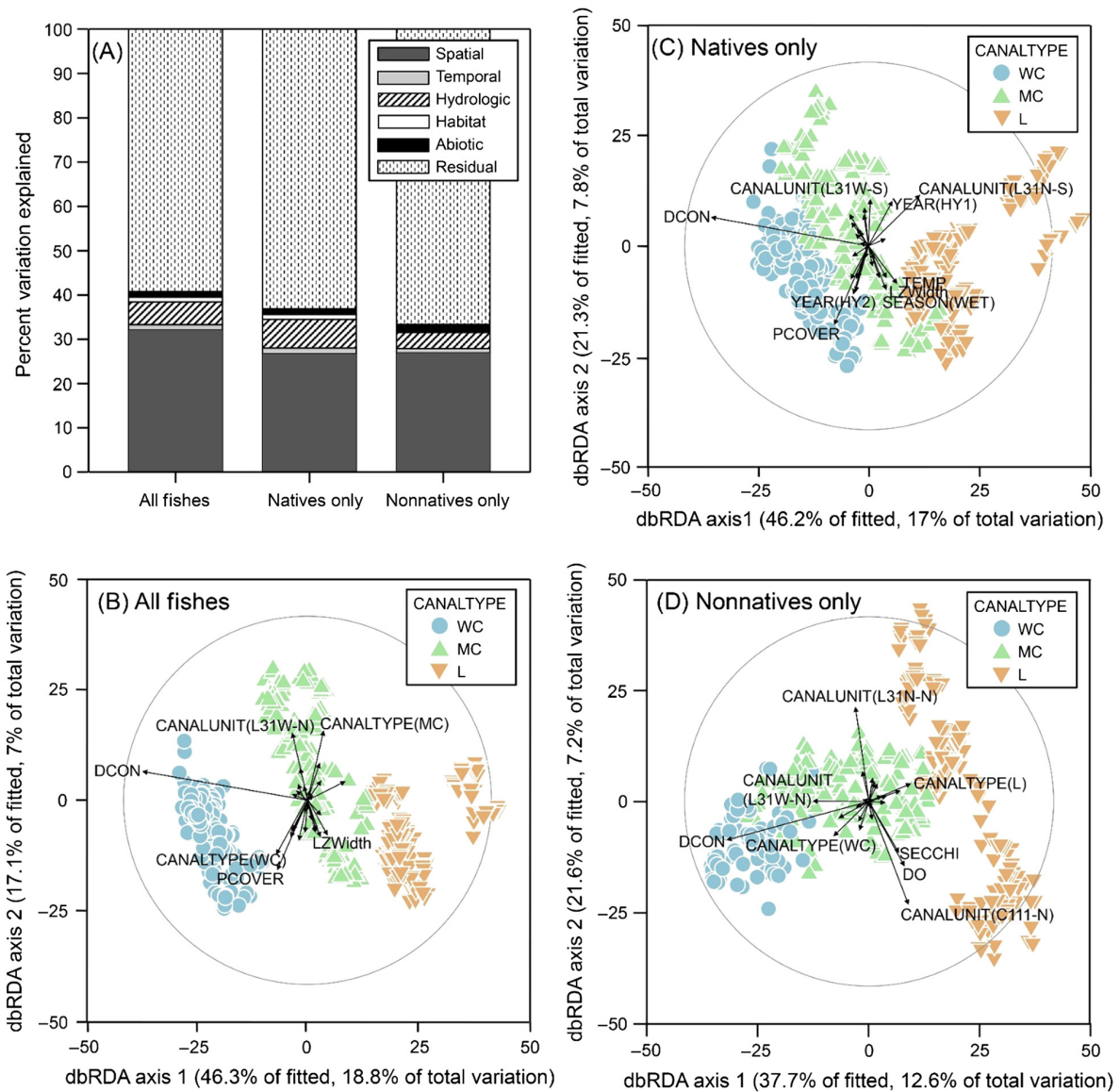


Fig. 5. Summary of distance-based linear models (A) showing the contribution of spatial, temporal, hydrological, habitat, and abiotic predictor variable sets in explaining differences in fish community structure for each assemblage model. Distance-based redundancy ordinations of the (B) all fishes model, (C) natives only model, and (D) nonnatives only model showing the independent contribution of predictor variables (Appendix S1) from the most parsimonious models ( $P < 0.01$  significance). Vectors represent the direction and strength of each predictor variables relationship against the dbRDA axes. WC, well connected canals; MC, moderately connected canals; L, leveed canals; dbRDA, distance-based redundancy analysis

fishes. Native fish communities were more abundant and speciose as novelty decreased (WC > MC > L canals). However, nonnative abundance was lowest in WC canals, but similar between MC and L canals. Nonnative richness

was lowest in WC canals and, contrary to predictions, peaked in MC and was intermediate in L canals. Community structure differed vastly as a function of CANALTYPE, and this structure was primarily influenced by spatial factors and to a

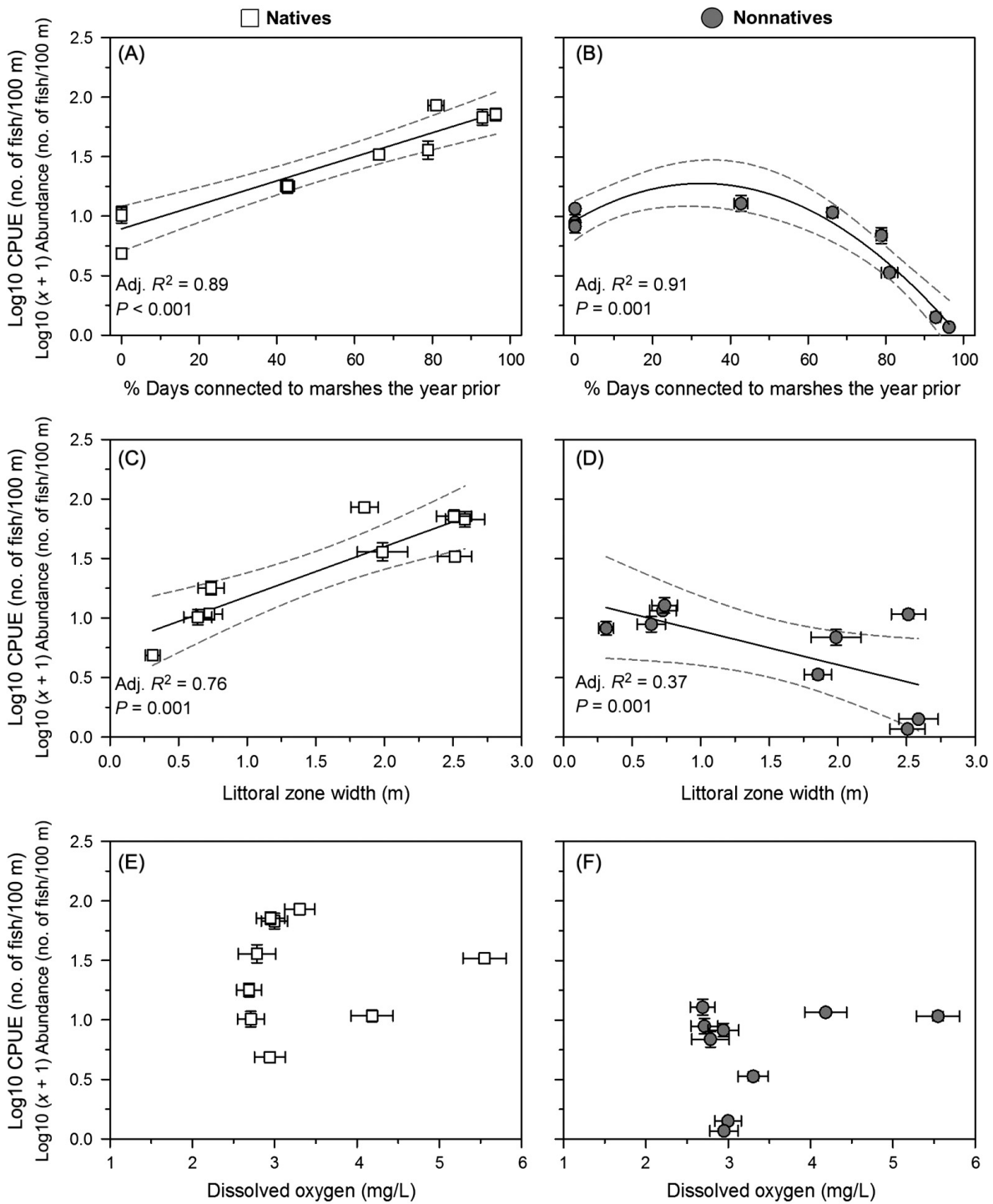


Fig. 6. Best fit regression models (linear and quadratic) fitted to native (A, C, and E) and nonnative (B, D, and F) fish abundance (no. of fish/100 m) against the top hydrological (% days connected to the marsh the year prior), habitat complexity (littoral zone width), and abiotic variables (dissolved oxygen) that explained the most independent variation in community structure from distance-based linear models/redundancy analysis (see Fig. 5). Regressions were fitted to the nine canal sampling unit seasonal means. CPUE, catch per unit effort.

much lesser extent by other factors (hydrological, habitat, and abiotic). Importantly, we noted contrasting responses between native and nonnative fish abundance and key hydrological and habitat factors. Across sampling events, native fish abundance was positively related to the hydrological connectivity of canals to surrounding marshes and size of the canal littoral zones, while the opposite was true for the nonnative fishes.

The most salient finding of our study was that spatial factors appeared to be the most significant driver of assembly patterns in canal fishes. The location of a canal and the marsh it bisects, as well as the degree of canal connectivity to the marsh habitat, appeared to have a strong influence on fish assemblages. This finding agrees with previous work showing that anthropogenic gradients can result in a divergence in fish communities. For instance, Slawski et al. (2008) found that urbanization in the upper Des Plaines River watershed had a strong influence on fish species composition, shifting from cool-water riverine specialist to warm-water riverine generalist as urbanization in undammed tributaries increased. However, in our study we expected that given the relatively uniform nature of canals as aquatic habitats (i.e., extensive with similar depth and width and relatively low structure except for littoral zones), we would see a high degree of biotic homogenization across the canal domain sampled (e.g., McKinney and Lockwood 1999, Rahel 2002). Gido et al. (2009) found that in the novel habitat of reservoirs, patterns of fish community structure were homogenous across drainage basins and more so relative to natural stream assemblages. In contrast, our Everglades canal fish community was markedly spatially segregated, with distinct fish assemblages along canals and even along sections of the same canal, despite the fact that all sites were part of an interconnected canal network.

This high degree of heterogeneity detected in both the native and nonnative fish assemblages points to the potential for (1) limited dispersal abilities in fish species, (2) the ability of water control structures and water management to prevent fish movement and thus increase heterogeneity, and/or (3) an overwhelming effect of the surrounding marsh characteristics and not canals per se to drive the community structure of canal fish communities. Recent work in Everglades

canals comparing movement patterns between native largemouth bass and nonnative Mayan cichlids showed similar and relatively small linear movements within canals (<1 to 4 km), but did detect higher frequencies of movement over greater distances from canals into adjacent marshes in the nonnative Mayan cichlid (Parkos and Trexler 2014).

Human alterations to aquatic systems can lower habitat quality by disrupting natural geomorphologic processes, spatial heterogeneity patterns, and the natural fluctuation of resources (Ligon et al. 1995, Humborg et al. 1997, Poff et al. 1997, Rosenberg et al. 2000, Bunn and Arthington 2002). In Everglades canals, native fish richness and abundance declined sharply as hydrological and habitat complexity became more novel with extremely low numbers in the most novel L canals. We suspect this pattern is indicative of poorer habitat quality for natives as canal littoral zones become smaller and less complex, and as productivity and prey availability associated with the loss of connectivity to marshes are reduced. Although canals may provide deep, suitable habitat for larger taxa, it is the connectivity to marshes and the presence of littoral zones that enhance fish numbers (including prey), as told by the larger increases in fish abundance in the dry season as surrounding marshes went dry. More complex littoral zones within reservoirs can support a higher diversity in fish communities and have a greater potential for maintaining native populations, especially juveniles that use these areas to avoid predation (Fernando and Holčík 1991, Matthews et al. 2004).

The higher native species richness and abundance and lowest degree of invasion in WC canals, and conversely the highest degree of invasion in L canals, are congruent with the biotic resistance hypothesis (Elton 1958) and its more recent formulation of the diversity–invasibility hypothesis (Tilman 1999). These hypotheses postulate that invasive species are expected to fail to invade or have reduced invasion success in more diverse communities. This is due to a lack of open niche opportunities, lower resources, and/or increased competition or other antagonistic interactions as the number of native species and previous invaders increases (Shea and Chesson 2002, Levine et al. 2004). In aquatic

systems, studies have found evidence in support of this hypothesis (e.g., Stachowicz et al. 1999, Dunstan and Johnson 2004). However, other mechanisms may also be operating (e.g., Moyle and Marchetti 2006). For instance, Henriksson et al. (2015) found that the presence of one single species (i.e., species identity hypothesis; Crawley et al. 1999, Emery and Gross 2007) better explained Arctic char invasion success into Swedish lakes compared to native species richness or the community saturation level.

Along those lines, differences in native fish abundance between WC and MC canals likely reflect the variation in fish prey productivity of the marshes they bisect. WC canals connect to longer hydroperiod marshes almost year-round, which have been shown to have higher fish abundances than the shorter hydroperiod marshes that connect to MC canals only during the wet season (Chick et al. 2004, Green et al. 2006). Additionally, canal connectivity to marsh species pools with different community structure may have contributed to the observed patterns in this study. For instance, Parkos et al. (2011) documented differences in fish community structure in WCA 3A marshes that connect to WC canals compared to fishes within ENP marshes which connect to moderately connected canals.

Variation in the degree of marsh connectivity across canals also likely influences the role of canals as dry-down refuges. In pulsing systems, seasonal variation in rainfall drives patterns of inundation and thus habitat availability for fishes and other aquatic taxa, such that fish survival is highly dependent on refuge size, the intensity of the dry-down period, and mobility (Magoulick and Kobza 2003, Robson et al. 2013). The recurrent pattern of seasonal drying in Everglades marshes is a major driver of fish community dynamics as fish move to both natural (i.e., alligator holes, solution holes, and estuarine mangrove creeks; Loftus and Kushlan 1987, Kobza et al. 2004, Rehage and Loftus 2007, Parkos et al. 2011) and artificial (i.e., canals; Rehage and Trexler 2006) refuges as water levels recede. In this study, we saw further evidence of the use of canals as dry-down habitats. Fish abundance increased by fivefold in WC and sevenfold in MC in the dry season, with no such increases observed in L canals. The timing of these increases in abundance varied among CANALTYPE, matching what we

would expect from the hydroperiod of surrounding marshes. In MC canals, abundance of natives peaked sooner reflecting earlier drying of the surrounding shorter hydroperiod marshes followed by reductions by ~50% in the late dry season, likely attributed to predation.

Similar decreases in fish abundance later in the dry season have been documented in mangrove creeks, which serve as important dry-down habitats in the southern Everglades, and which have been attributed to predation by the larger piscivores. For example, Boucek and Rehage (2013) found that the arrival of a marsh prey subsidy in southern Everglades mangrove creeks during the onset of the dry season resulted in fitness gains for both marsh (largemouth bass) and estuarine (snook) consumers. Interestingly, nonnative taxa showed a similar increase in MC canals, indicating that they are also likely entering canals from marshes as native fishes do, but their numbers did not experience a decrease later in the season. In WC canals, seasonal increases occurred later in the dry season. Although canals may be lower quality habitats because of the high abundance of predators and low habitat complexity, they could provide better habitat in extreme droughts, playing a greater role in the re-colonization of marshes during these events and under the increased frequency of such events with climate change.

For nonnatives, a notable pattern was the increase in their relative contribution as novelty increased, representing nearly 50% of total fish in L canals. We hypothesize that this finding relates to the fact that these leveed canals provide lower quality habitats for native fishes, lowering competition or biotic resistance (Lowry et al. 2013) and thus favoring the establishment of opportunistic invaders. Otherwise, given the known broad environmental tolerances of nonnative fishes (Moyle and Marchetti 2006), nonnative taxa may be better able to withstand the less favorable conditions of L canals. In lotic systems, novel conditions have often been linked to shifts in assemblages from natives to phenotypically plastic and more tolerant nonnatives (Weaver and Garman 1994, Onorato et al. 1998, Walters et al. 2003). The extremely low contribution of nonnatives in WC canals may relate to variation in the role of canals as thermal refugia. Prior to the beginning of this study in 2010, a severe cold



snap led to a large mortality event for temperature sensitive taxa (Adams et al. 2012, Matich and Heithaus 2012), including nonnatives such as the Mayan cichlid, blue tilapia, and spotfin spiny eel (Boucek and Rehage 2014, Rehage et al. 2016). We suspect nonnatives contributed to a larger although still small part of the fish community in WC canals prior to the 2010 cold snap. Unpublished records from the Florida Fish and Wildlife Conservation Commission point to nonnatives accounting for about 8.1% of fishes caught in the L-67A canal (2006–2009), a WC canal sampled in this study. Temperature records from the cold snap indicated that in WC canal units, the pattern of water flow (from marshes into canals) reached low temperatures in the range of lethal limits of many nonnatives (e.g., Schofield et al. 2010, Schofield and Huges 2011), while canals elsewhere remained warmer (J. Kline, *personal communication*).

Environmental disturbance is often implicated as a key factor in facilitating species invasions (D'Antonio et al. 1999, Bando 2006, Clark and Johnston 2011). Disturbance can facilitate invasion by releasing resource opportunities, escapement from natural predators, or indirectly reducing native species abundance and thus resources consumption (Davis et al. 2000, Shea and Chesson 2002). Previous work in aquatic systems also points to the relation and feedback between hydrological disturbance and invasions (Marchetti et al. 2004, Leprieur et al. 2008). Not unlike these studies, we documented opposing relationships between marsh connectivity and the abundance of native vs. nonnative taxa. These relationships suggest, at minimum, that natives and nonnatives are responding to the natural hydrology of the system in different ways. Kiernan et al. (2012) showed that restoration of the natural hydrological regime can lead to the recovery of natives in heavily invaded California streams. Whether Everglades restoration could have the same detrimental effects on nonnatives to the benefit of native taxa is not known and merits further work. Regardless, canals are permanent features of the Everglades landscape, since most of this conveyance network that provides water supply and flood control and reroutes water delivery into natural areas will remain in place after ecosystem restoration. Our results suggest that the inherent loss of natural

environmental conditions and subsequent replacement by novel ones may result in wholesale changes in fish community structure.

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