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RESEARCH ARTICLE

An apex predator engineers wetland food-web heterogeneity through nutrient enrichment and habitat modification

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Abstract

1. The potential for animals to modify spatial patterns of nutrient limitation for autotrophs and habitat availability for other members of their communities is increasingly recognized. However, net trophic effects of consumers acting as ecosystem engineers remain poorly known. The American Alligator *Alligator mississippiensis* is an abundant predator capable of dramatic modifications of physical habitat through the creation and maintenance of pond-like basins, but its role in influencing community structure and nutrient dynamics is less appreciated.
2. We investigated if alligators engineer differences in nutrient availability and changes to community structure by their creation of 'alligator ponds' compared to the surrounding phosphorus (P)-limited oligotrophic marsh.
3. We used a halo sampling design of three distinct habitats extending outward from 10 active alligator ponds across a hydrological gradient in the Everglades, USA. We performed nutrient analysis on basal food-web resources and quantitative community analyses, and stoichiometric analyses on plants and animals.
4. Our findings demonstrate that alligators act as ecosystem engineers and enhance food-web heterogeneity by increasing nutrient availability, manipulating physical structure and altering algal, plant and animal communities. Flocculent detritus, an unconsolidated layer of particulate organic matter and soil, showed strong patterns of P enrichment in ponds. Higher P availability in alligator ponds also resulted in bottom-up trophic transfer of nutrients as evidenced by higher growth rates (lower N:P) for plants and aquatic consumers. Edge habitats surrounding alligator ponds contained the most diverse communities of invertebrates and plants, but low total abundance of fishes, likely driven by high densities of emergent macrophytes. Pond communities exhibited higher abundance of fish compared to edge habitat and were dominated by compositions of small invertebrates that track high nutrient availability in the water column. Marshes contained high numbers of animals that are closely tied to periphyton mats, which were absent from other habitats.

5. Alligator-engineered habitats are ecologically important by providing nutrient-enriched 'hotspots' in an oligotrophic system, habitat heterogeneity to marshes, and refuges for other fauna during seasonal disturbances. This work adds to growing evidence that efforts to model community dynamics should routinely consider animal-mediated bottom-up processes like ecosystem engineering.

KEYWORDS
American alligator, animal-mediated nutrient dynamics, bottom-up effects, ecological stoichiometry, ecosystem engineer

1 | INTRODUCTION

A long-standing debate in food-web ecology is the extent to which communities and ecosystems are structured from the bottom-up and top-down (e.g. Lynam et al., 2017; Power, 1992). Empirical evidence supports the idea that nutrient availability impacts primary productivity and plant biomass, which controls the biomass of consumers (Polis, 1999; Power, 1992). Also, studies show that predators control herbivores and thus release plants from herbivory (e.g. Matson & Hunter, 1992; Wilkinson & Sherratt, 2016). Both top-down and bottom-up pressures serve to organize food webs (Dyer & Letourneau, 2003; Lynam et al., 2017), and animals may exert control in both directions (e.g. Meserve et al., 2003; Schmitz et al., 2010). The potential for animals to influence bottom-up control through impacts on nutrient availability and limitation, as well as habitat availability for basal autotrophic resources, is being increasingly recognized. There are two major themes in animal-mediated bottom-up effects on food webs: (1) effects of nutrient translocation and recycling including direct impacts and indirect consequences of altering behaviour of prey that serve as nutrient vectors (Polis et al., 1997; Schmitz et al., 2010); and (2) effects from physical ecosystem engineering (Sanders et al., 2014). We know little about the net effects of engineering on food-web structure and function (e.g. Sanders et al., 2014) and even less about the potential interactive effects of animals that are both a predator and an engineer (e.g. Sanders & van Veen, 2011).

Through egestion and excretion, consumers can transform and recycle limiting nutrients including phosphorus (P) and nitrogen (N) at rates comparable to other sources and induce landscape-level heterogeneity in nutrient patterns (Schmitz et al., 2010; Vanni, 2002). Organisms may move nutrients or energy against existing resource gradients and these subsidies can increase ecosystem productivity (Polis et al., 1997) and create trophic effects that may increase biodiversity and promote coexistence (Elser & Urabe, 1999; Flecker et al., 2002). Large-bodied organisms have potential to generate landscape-level nutrient heterogeneity from excretion because of their capacity for long-distance movements, consumption of considerable biomass and time lags between ingestion and excretion/egestion. For example, after feeding in deep waters, whales release iron-rich faecal plumes and nitrogen-rich urine in surface waters and enhance productivity at the surface (Roman & McCarthy, 2010). Transporters create hotspots where the magnitude of nutrient fluxes is particularly high compared to the surrounding matrix (McClain et al., 2003). Resting areas or feeding sites may feature increased nutrient regeneration from biodeposition. For instance, crows release about 27% of the annual nitrogen input of an evergreen forest mainly at roosting sites even though they were primarily feeding in a nearby urban landscape (Fujita & Koike, 2007).

Consumers may also trigger bottom-up effects by modifying the physical environment. Bioturbation from animal movement and digging can resuspend and regenerate nutrients buried in the substrate, making it available for bottom-up transfer (Vanni, 2002). Ecosystem engineers are organisms that make physical alterations to biotic or abiotic materials that are significant at the landscape level (Jones et al., 1994; Wright et al., 2002; Wright & Jones, 2006). For example, dam building beavers *Castor canadensis* create ponds and wetlands that have long-term implications for large-scale drainage networks, affect species diversity, increase habitat heterogeneity and may alter biogeochemical cycles (Naiman et al., 1994; Wright et al., 2002). Hippopotamuses *Hippopotamus amphibious* create trails during nighttime foraging excursions between rivers and riparian zones in southern Africa that increase habitat connectivity and provide movement corridors for diverse taxa (Naiman & Rogers, 1997). Engineering effects may result in both negative and positive impacts on primary producers but are generally net positive (Jones et al., 1997; Sanders et al., 2014).

The American Alligator *Alligator mississippiensis* is an abundant predator in most aquatic ecosystems throughout the southeastern United States (Delany & Abercrombie, 1986). Crocodilians may also play a role in nutrient dynamics. For instance, alligators may facilitate nutrient transport by moving across productivity gradients (Rosenblatt & Heithaus, 2011) and aquatic-terrestrial matrices (Subalusky et al., 2009). In a central Amazonian lake, caiman can release high amounts of allochthonous nutrients and through daily movement may stimulate primary production (Fittkau, 1973). Alligators can also physically modify the environment through their creation and maintenance of 'alligator ponds' (Craighead, 1968; Kushlan, 1974). In some wetlands, alligator ponds are an important open-water feature of otherwise vegetated marsh landscape. They may be originally formed by a natural depression in topography, dug by an alligator or caused by human activity, but are maintained in an open-water state by the presence of alligators (Campbell & Mazzotti, 2004; Fujisaki et al., 2012). In their ponds, alligators repeatedly remove vegetation and push sediment into the banks with their claws, snout and tail. These actions maintain a unique open-water area that would fill in with vegetation without the activities of alligators (Campbell & Mazzotti, 2004;

Kushlan, 1974). This disturbance of soil may affect establishment and recruitment of plant species by redistribution and regeneration of nutrients, particularly the remobilization of legacy P stored in sediment (Palmer & Mazzotti, 2004). The banks of alligator ponds provide higher elevation substrate used as nest sites for other reptiles (Kushlan, 1974) and hydrologic relief for woody vegetation (Palmer & Mazzotti, 2004). Ponds range in size and shape, but can hold water even in severe drought and function as refuges for fishes and invertebrates, which may attract foraging by other animals in the dry season (Campbell & Mazzotti, 2004).

Animals, including the alligators themselves, may transport nutrients and organic matter from the surrounding marsh and concentrate it in the pond. This enrichment may be significant, given that freshwater wetlands of the Everglades are sensitive to nutrient loading and respond rapidly to short-term, low-level P enrichment with noticeable differences in periphyton and flocculent detritus (Noe et al., 2002). Alligators are often cited as an example of ecosystem engineers through their activities creating ponds (e.g. Jones et al., 1994), though quantitative evidence is sparse. The work reported here expands our understanding of alligator engineering impacts and provides the first evaluation of their role in altering nutrient cycling. Our goal was to determine if alligator-engineered ponds differ in nutrient status and community structure compared to the surrounding marsh. We predicted that alligator ponds are P enriched from bioturbation of legacy P and animal-mediated nutrient recycling of N and P by alligators and other animals using engineered habitats. We also investigated the hypothesis that alligator ponds are associated with increased species richness and total abundance because of both enrichment and physical modification increasing habitat heterogeneity. We predicted that this relationship is stronger in the dry season when marsh-dwelling fish and invertebrates are forced into the aquatic refuges including alligator ponds to avoid desiccation.

2 | MATERIALS AND METHODS

2.1 | Study site and design

Shark River Slough and Taylor Slough, in Everglades National Park, are the two major drainage basins of freshwater through the Everglades to the Gulf of Mexico. Taylor Slough is a smaller, drier conduit basin than Shark River Slough, but shares many features (Kotun & Renshaw, 2014). These wet prairie habitats are dominated by spikerush (primarily *Eleocharis cellulosa*) and large stocks of periphyton (Daoust & Childers, 1999). Interspersed throughout these sloughs are alligator ponds, which are generally the only open-water areas deeper than the surrounding marsh and ringed by dense and distinct assemblages of emergent vegetation (Palmer & Mazzotti, 2004).

We sampled 10 active alligator ponds, five each in Shark River Slough and Taylor Slough (Figure 1; Table A1). Evidence of alligator activity included the presence of alligators, vegetation trails, worn basking areas, underwater dug-outs/trenches, alligator scat or alligator nests (found at the ridge of ponds). There are three distinct habitats associated with active alligator ponds extending outwards from the centre of the basin: (1) a pool or semiopen water habitat (hereafter 'pond'), (2) a dense ring of vegetation immediately surrounding the pond (hereafter 'near-pond') and (3) the surrounding marsh. Each site was sampled in November–December 2018 (high-water period, referred to as 'wet season') and March–April 2019 (low-water period, referred to as 'dry season').

2.2 | Water and flocculent detrital matter

We collected water and flocculent detrital matter ('floc') in three different locations within each habitat and aggregated these into a single sample. Floc, the unconsolidated layer of particulate organic matter, and the underlying soil in the oligotrophic Everglades is derived from decaying periphyton and macrophytes (Noe et al., 2002). We measured carbon, nitrogen and phosphorus using dry combustion and colorimetric methods (Solórzano & Sharp, 1980). We compared wet-season water total phosphorus (TP) across all three habitats and both sloughs using a repeated-measures analysis of variance (rm-ANOVA). The three habitats at a site were treated as the repeated measure (repeated over space rather than over time) and the within-site profile (or transect) of differences among habitats was the fundamental unit of observation for hypothesis tests. Although our rm-ANOVA is a special case of the GLMM and the results are virtually identical, we opted for the simpler rm-ANOVA framework because all variables were categorical, degrees of freedom calculations for *p* values are more straightforward, and

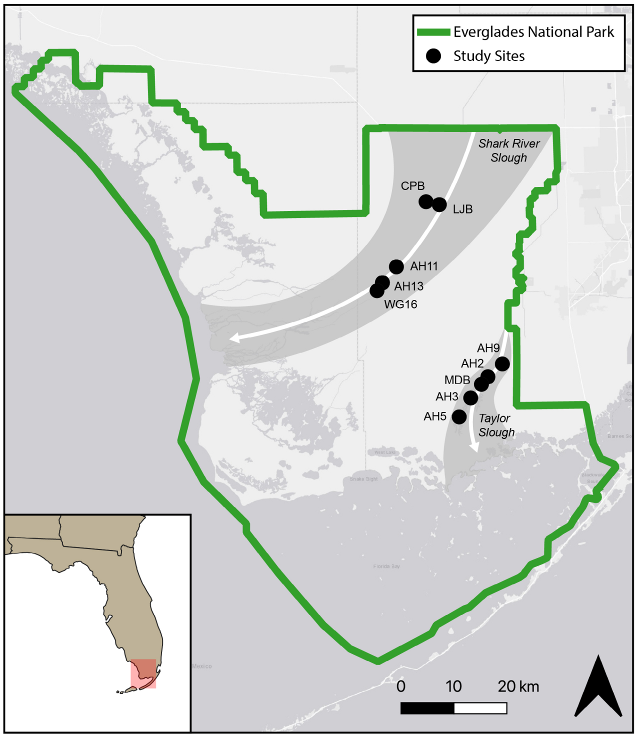

FIGURE 1 Alligator pond sites in Taylor Slough and Shark River Slough, Everglades, Florida, USA sampled in the 2018 wet and 2019 dry seasons.

coding of factor variables is less complex. We checked for outliers and extreme outliers using 1.5 and 3 times the interquartile range respectively. Because of the presence of extreme outliers in each group, we also used Friedman tests to check sensitivity of our overall results. The same model structure and procedure follows for each subsequent use of rm-ANOVA. We used a rm-ANOVA to compare dry-season mean TP across marsh and pond habitats. We compared wet- and dry-season mean TP for marsh and pond habitats using paired *t*-tests because of missing dry-season data from Taylor Slough. We also used separate rm-ANOVA to compare floc C:N, C:P and N:P across habitats and sloughs. For significant sources and interactions, we estimated marginal least-squares means of all contrasts. We compared wet- and dry-season C:N:P relationships within each habitat using paired *t*-tests.

2.3 | Basal resources

We collected floating mat-forming and epiphytic mat-forming periphyton. We used Fisher's exact tests for each season to determine if there was a relationship between habitat and the presence of mat-forming periphyton. We simulated *p* values from 2000 replicates because of small sample sizes (Agresti, 2002). We also report Pearson's chi-squared test statistic for sensitivity. We then used pairwise comparisons with a Bonferroni adjustment to find differences between habitats.

All dominant emergent vascular plant species in each habitat at all sites were collected as a composite of leaves or stems from multiple individuals. We also collected aggregates of submerged vegetation, including bladderworts (*Utricularia* spp.). We used Fisher's exact tests and the above procedure to determine if there were relationships between habitat and the presence of the most frequently observed plant species. We calculated species richness for the plant communities. To compare richness across habitats and visits, we used rm-ANOVA. Community analyses were conducted using the VEGAN package in R (Oksanen et al., 2019). We developed a Morisita–Horn distance matrix and used a permutational multivariate analysis of variance (PERMANOVA) set to 999 permutations to compare community composition among habitats and between seasons (Jost et al., 2011). We used post hoc pairwise comparisons on a binary distance matrix to further investigate significant effects of habitat. We calculated similarity percentages (SIMPER) with 999 permutations to investigate influential species in explaining dissimilarities between factor levels (Clarke & Warwick, 2001). Finally, we report nonmetric multidimensional scaling (NMDS) to illustrate differences in community composition by slough, habitat and season.

2.4 | Consumer communities

We used several types of sampling to capture the aquatic consumer community: Brakke's (1976) inverted-funnel traps, 1-m^2 throw-traps, 3-mm wire-mesh minnow-traps and omni-directional drift fences. All invertebrate taxa were in aquatic life stages except rare catches of spiders, crickets and grasshoppers (Table A10). For each sampling method, we developed dominance-diversity curves to visually assess differences in richness and abundance among habitats (Gotelli & Colwell, 2011). We interpolated and extrapolated species richness to yield asymptotic rarefied values using INEXT package in R (Hsieh et al., 2016). To compare richness across habitats and visits, we used a rm-ANOVA. We also compared total abundance across habitats, seasons and sloughs. Using NMDS, we explored differences in community composition by slough, habitat and season. We developed a Morisita–Horn distance matrix and used a PERMANOVA to compare community composition among habitats and visits. We used post hoc pairwise comparisons on a Canberra distance matrix for count data to further investigate significant effects of habitat. We performed SIMPER to investigate influential species in explaining dissimilarities between factor levels. We were unable to evaluate full models with slough (i.e. region) and season effects because of missing data at some sites, primarily from Taylor Slough in the dry season. Instead, we tested regional and seasonal hypotheses in separate analyses based on data availability.

2.5 | Plant and animal stoichiometry

Plant composites and animal specimens were chosen based on availability of dried material for measuring total N, P and C using dry-combustion methods and analysing colorometrically (Solórzano & Sharp, 1980). For plants, we report comparisons for spikerush, maidencane *Panicum hemitonum*, duck potato *Sagittaria lancifolia* and the leafy bladderwort *Utricularia foliosa*. The consumers targeted were eastern grass shrimp *Palaemonetes paludosus*, Bluefin Killifish *Lucania goodei* and Eastern Mosquitofish *Gambusia holbrooki*. These taxa were chosen because of their high relative abundance across habitats and their importance to the food web (Flood et al., 2023). C:N, C:P and N:P ratios were calculated as molar ratios. For plants, ratios were compared across two habitats using a paired *t*-test when group sizes were at least three. For consumers, ratios were compared across habitats at a site using a Welch two-sample *t*-test.

We used R (version 4.0.2) for statistical analyses (R Core Team, 2020), reported means with one standard deviation, and used a significance level of $\alpha = 0.05$. Research and animal procedures were conducted under the auspices of protocol #IACUC-18-067-CR01 from the Institutional Animal Care and Use Committee of the University of Florida and in accordance with scientific research permit #EVER-2017-SCI-0060 authorized by Everglades National Park and scientific collector's permits #S-18-06 and #S-19-05 granted by Florida Fish and Wildlife Conservation Commission.

3 | RESULTS

3.1 | Floc, water and periphyton

Habitats varied in mean floc C:N, C:P and N:P (Figures 2 and 3; Table 1) revealing that ponds were P enriched. For both C:P and N:P, all pairwise comparisons were significant (Table 2a). For instance, in

Response	Alligator Pond	Near-pond (edge)	Marsh
Floc	P-enriched	Intermediately P-enriched	P-limited
Periphyton	No mats present	No mats present	High cover of mats
Plants	Floating plants	Dense ring of nutrient-loving plants	Dominated by spikerush
Consumers	High density of zooplankton	High invertebrate density and richness in wet season, but low in dry season; few fishes	High abundance of consumers associated with periphyton mats
Stoichiometry	Plants had low N:P (faster growth rate)	Plants and fish had low N:P (faster growth rate)	Plants and fish had high N:P (slower growth rate)

FIGURE 2 Summary of results from this study conducted at 10 sites in Taylor Slough and Shark River Slough across marsh, near-pond (edge) and alligator pond habitats. Photo credit: Erin McCarthy.

both seasons, marsh C:P and N:P were about twice pond C:P and N:P respectively. When comparing ratios across seasons for different habitats, there were no differences except near-pond C:N was less in the dry than in the wet season (Table 2b). Mean water TP had considerable variation within each habitat (Figure A1) and did not differ among habitats (Table A2). For both seasons, mat-forming periphyton was more common in marshes (marsh–pond, $p < 0.01$; marsh–near-pond, $p < 0.01$) compared to near absence in near-ponds and ponds ($p = 1.00$).

3.2 | Plant communities

We identified 21 species of plants across all of our study sites (Table A3). ANOVA did not reveal any effects of habitat, season or slough on plant richness (Table A4). NMDS ($k = 2$, stress = 0.183) for community composition revealed overlap and compositional similarity among all three habitats, but marsh was the most dissimilar (Figure A2). PERMANOVA revealed that slough, habitat and the interaction of slough and habitat predicted dissimilarity observed in the community while season and other interactions were not significant (Table 3). Post hoc pairwise comparisons show that composition of marsh and pond (pseudo-$F = 8.0$, $r^2 = 0.17$, $p < 0.01$) and marsh and near-pond (pseudo-$F = 8.9$, $r^2 = 0.19$, $p < 0.01$) differed, but not pond and near-pond (pseudo-$F = 1.7$, $r^2 = 0.04$, $p = 0.13$). Fisher's exact test and SIMPER revealed that presence or absence of some plant species characterized dissimilarities among habitats (Table A5). Spikerush was present in 100% of marshes but was collected in only about half of near-ponds and ponds ($\chi^2 = 12.9$; marsh–near-pond and marsh–pond, $p < 0.01$). Bladderworts were observed more often in marshes compared to other habitats ($\chi^2 = 26.1$; marsh–pond and marsh–near-pond, $p < 0.01$; pond–near-pond, $p = 0.04$). In near-ponds and ponds, green arrow arum *Peltandra virginica* (40% near-pond, 45% pond surveys; $\chi^2 = 12.0$; marsh–pond and marsh–near-pond, $p < 0.01$; pond–near-pond, $p = 1$) and pickerelweed *Pontedaria cordata* (65% near-pond, 85% pond; $\chi^2 = 31.6$; marsh–pond and marsh–near-pond, $p < 0.01$; pond–near-pond, $p = 0.82$) were present, despite being absent from marshes. Across species, vascular plants in marsh habitats generally exhibited higher N:P than in other habitats (Table A6).

3.3 | Zooplankton communities

We collected a total of 9985 invertebrates from funnel traps divided into 16 taxonomic groups (Tables A7 and A8). Mean site total abundance was greater in the pond (299 ± 191 individuals/1000 mL) compared to near-pond (61 ± 147) but did not differ from marsh (175 ± 216; Table A7). Season and interaction of season and habitat explained zooplankton richness (Table 4). Across habitats, richness was almost three species greater in the wet season compared to the dry season ($d = 3.0 \pm 1.1$, $t_8 = 2.7$, $p = 0.03$). Comparing means across the contrasts of the interaction, we saw that near-pond was driving seasonal differences with estimates that were five taxa greater in the wet season compared to dry season (Table A9).

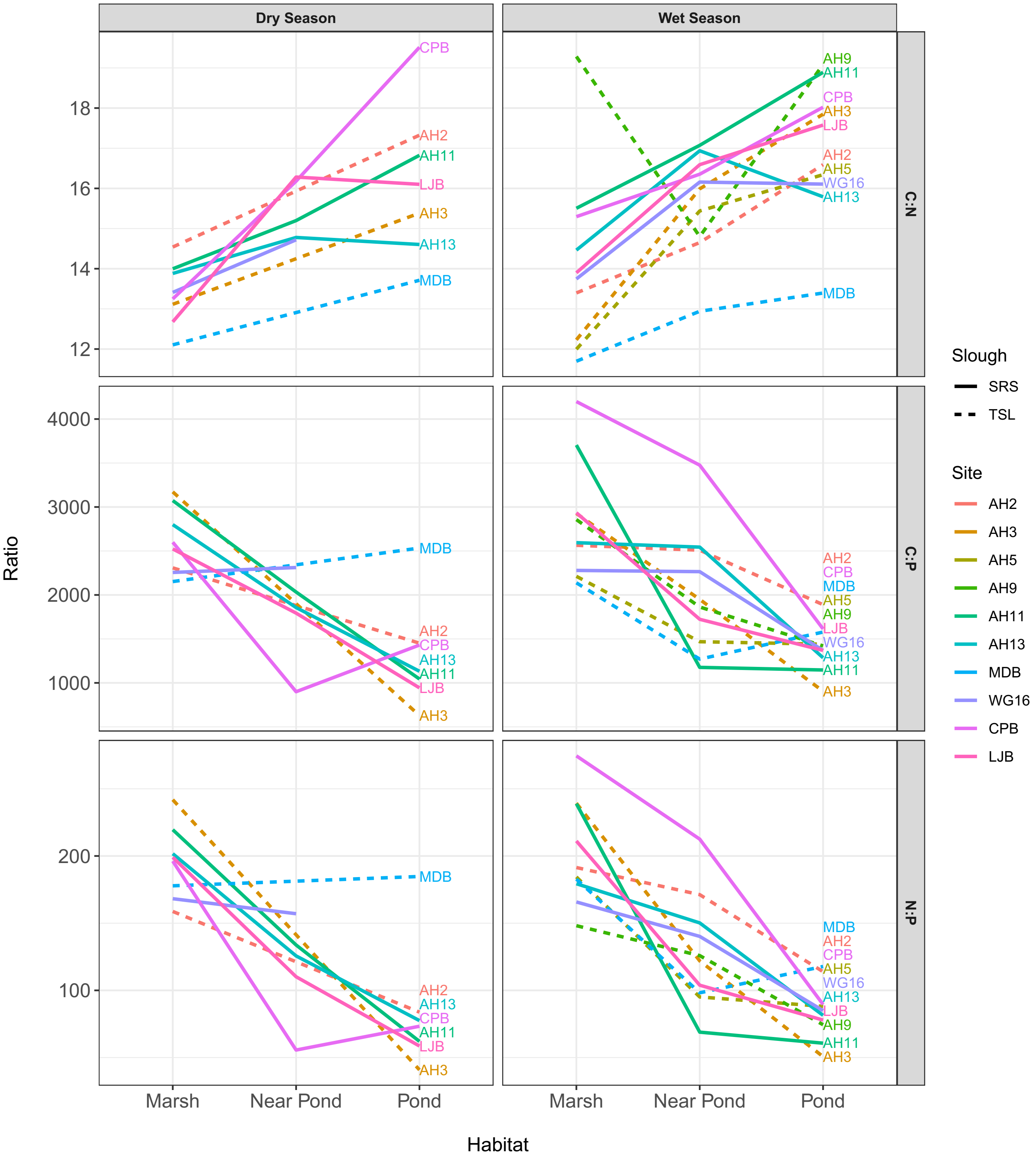

FIGURE 3 Floc C:N:P in alligator pond sites in Shark River Slough (SRS) and Taylor Slough (TSL)—the dry and wet seasons. Some Taylor Slough dry-season samples could not be collected in near-ponds.

NMDS ($k=2$, stress = 0.194) showed some compositional similarity among all three habitats, but ponds were most distinct (Figure A4). PERMANOVA revealed that slough, season and habitat predicted community dissimilarity (Table 3). Community compositions between marsh and pond (pseudo-$F=2.2$, $r^2=0.06$, $p=0.02$) and pond and near-pond (pseudo-$F=2.1$, $r^2=0.07$, $p=0.03$) were different, but not marsh and near-pond (pseudo-$F=0.9$, $r^2=0.03$, $p=0.55$).

Large differences in catches of several key taxa were observed in the composition of zooplankton across habitats (Figure 4). The largest differences in relative abundance between marshes and near-ponds were driven by almost double near-pond catches of copepods and aquatic mites. In ponds, catches of ostracods, copepods and aquatic mites were roughly twice as high as marshes. Compared to near-ponds, ostracod catches were double and roughly 30% greater

TABLE 1 Repeated-measures analysis of variance of floc C:N:P. Some sites and pond habitats were not able to be sampled in the dry season. Results are presented from analyses with detected outliers. Hypothesis test result was unchanged when outliers were removed. Bolded *p* values indicate significance level of $\alpha = 0.05$.

Season	Response	Error	Source	*df*	SSq	MSq	*F*	*p*
Wet	C:P	Site	Slough	1	732,281	732,281	1.6	0.24
			Residuals	8	3,628,001	453,500		
		Site*Habitat	Habitat	2	10,417,631	5,208,815	21.0	**<0.01**
			Slough*Habitat	2	646,849	323,424	1.3	0.30
			Residuals	16	3,971,792	248,237		
	C:N	Site	Slough	1	9.32	9.322	1.6	0.24
			Residuals	8	45.43	5.679		
		Site*Habitat	Habitat	2	39.71	19.855	11.2	**<0.01**
			Slough*Habitat	2	2.14	1.071	0.6	0.56
			Residuals	16	28.25	1.765		
	N:P	Site	Slough	1	622	621.5	0.4	0.55
			Residuals	8	12,734	1591.8		
		Site*Habitat	Habitat	2	70,484	35,242	30.8	**<0.01**
			Slough*Habitat	2	1563	782	0.7	0.52
			Residuals	16	18,292	1143		
Dry	C:P	Site	Slough	1	32,740	32,740	0.4	0.55
			Residuals	5	399,644	79,929		
		Site*Habitat	Habitat	1	6,397,625	6,397,625	13.7	**0.01**
			Slough*Habitat	1	313,712	313,712	0.7	0.45
			Residuals	5	2,342,429	468,486		
	C:N	Site	Slough	1	1.9	1.9	0.6	0.47
			Residuals	5	15.1	3.0		
		Site*Habitat	Habitat	1	28.3	28.3	17.3	**<0.01**
			Slough*Habitat	1	1.0	1.0	0.6	0.47
			Residuals	5	8.2	1.6		
	N:P	Site	Slough	1	491	491	0.6	0.46
			Residuals	5	3910	782		
		Site*Habitat	Habitat	1	47,333	47,333	20.8	**<0.01**
			Slough*Habitat	1	1858	1858	0.8	0.41
			Residuals	5	11,371	2274		

for copepods in ponds. Amphipod catches (2 individuals/1000 mL) in ponds were much lower compared to other habitats (marsh = 28; near-pond = 25 individuals/1000 mL).

3.4 | Aquatic consumer communities

Summarizing across all sampling methods, seasons and habitats, we identified 38 vertebrate species and 34 invertebrate taxa and captured 7875 individuals (Tables A10 and A11). After partitioning data to account for unequal sampling effort between sloughs and seasons, rarefaction analysis revealed that all three habitats were relatively close to an asymptote. Rarefaction curves for near-pond and marsh had considerable overlap of 95% confidence intervals, but pond richness was lower than other habitats. When accounting for unequal sampling between seasons, habitat but not slough explained richness (Table 4). Post hoc tests showed that mean richness in near-ponds and ponds was different with near-ponds averaging almost 15 more taxa than ponds (Table A12). When accounting for unequal sampling between sloughs, only the interaction of season and habitat was significant factors (Table 4), but post hoc tests did not reveal any significant pairwise contrasts (Table A12). Total abundance of fishes and invertebrates was generally explained by habitat and season (Table A13). For throw-trap data, near-ponds in the dry season had low mean catches of aquatic consumers (13 ± 38 individuals/CPUE), which was much lower than marsh (174 ± 133) but not different from pond catches (50 ± 39). Minnow traps did not show seasonal differences, but marsh catches (40 ± 43 individuals/CPUE) were higher than pond (7 ± 10) and near-pond (7 ± 10). Neither habitat nor season explained drift fence catches. Overall, total abundance per CPUE failed to support

TABLE 2 Estimated marginal least-squares means of floc total phosphorus compared among habitats (a) and season (b). Table b only includes Shark River Slough data. Bolded *p* values indicate significance level of $\alpha = 0.05$.

(a)

Season	Response	Contrast	Estimate ± SE	*df*	*t* ratio	*p*
Wet	C:P	marsh–near-pond	816 ± 223	16	3.7	**0.01**
		marsh–pond	1439 ± 223	16	6.5	**<0.01**
		near-pond–pond	623 ± 223	16	2.8	**0.03**
	C:N	marsh–near-pond	−1.5 ± 0.6	16	−2.6	**<0.05**
		marsh–pond	−2.8 ± 0.6	16	−4.7	**<0.01**
		near-pond–pond	−1.3 ± 0.6	16	−2.1	0.11
	N:P	marsh–near-pond	72.8 ± 15.1	16	4.8	**<0.01**
		marsh–pond	117.6 ± 15.1	16	7.8	**<0.01**
		near-pond–pond	44.8 ± 15.1	16	3.0	**0.02**
Dry	C:P	marsh–pond	1309 ± 370	5	3.5	**0.02**
	C:N	marsh–pond	−2.8 ± 0.7	5	−4.0	**0.01**
	N:P	marsh–pond	113 ± 26	5	4.4	**<0.01**

(b)

Contrast	Response	Habitat	*t*	*df*	*p*
Dry–Wet	C:P	Marsh	−0.9	11.8	0.39
		Near-pond	−1.0	6.6	0.35
		Pond	−0.4	10.7	0.70
	C:N	Marsh	−0.7	14.6	0.51
		Near-pond	−0.6	7.2	0.55
		Pond	−0.1	10.7	0.94
	N:P	Marsh	−0.7	13.4	0.51
		Near-pond	−3.1	5.9	**0.01**
		Pond	−0.8	14.0	0.43

TABLE 3 Permutational multivariate analysis of variance results from Morisita–Horn dissimilarity matrices of plant, zooplankton and aquatic consumer communities. Bolded *p* values indicate signifcance level of $\alpha = 0.05$.

Dataset	Source	*df*	SS	R^2	*F*	*p*
Plants	Slough	1	1.67	0.13	10.88	**<0.01**
	Season	1	0.05	0.00	0.35	0.83
	Habitat	2	2.95	0.22	9.64	**<0.01**
	Slough*Season	1	0.09	0.01	0.60	0.65
	Slough*Habitat	2	0.75	0.06	2.45	**0.02**
	Season*Habitat	2	0.18	0.01	0.58	0.79
	Slough*Season*Habitat	2	0.14	0.01	0.45	0.86
	Residual	48	7.33	0.56		
	Total	59	13.15	1.00		
Zooplankton	Slough	1	0.46	0.07	4.62	**<0.01**
	Season	1	0.34	0.05	3.40	**0.03**
	Habitat	2	1.41	0.21	7.04	**<0.01**
	Slough*Season	1	0.13	0.02	1.32	0.26
	Slough*Habitat	2	0.28	0.04	1.42	0.23
	Season*Habitat	2	0.21	0.03	1.03	0.40
	Slough*Season*Habitat	2	0.26	0.04	1.32	0.27
	Residual	37	3.71	0.54		
	Total	48	6.81	1.00		
Aquatic consumers (wet season only)	Slough	1	0.28	0.07	3.92	**0.01**
	Habitat	2	1.22	0.30	8.71	**<0.01**
	Slough*Habitat	2	1.01	0.25	7.20	**<0.01**
	Residual	23	1.61	0.39		
	Total	28	4.12	1.00		
Aquatic consumers (SRS only)	Season	1	0.04	0.02	0.57	0.67
	Habitat	2	0.50	0.20	3.43	**<0.01**
	Season*Habitat	2	0.34	0.13	2.32	**0.02**
	Residual	23	1.68	0.66		
	Total	28	2.56	1.00		

our prediction of an increased number of individuals in ponds during the dry season (Figure 5 and Figure A6).

NMDS (slough comparison, $k = 2$, stress = 0.130; season comparison, $k = 2$, stress = 0.202) showed there were compositional similarities between near-pond and marsh with considerable separation of ponds (Figure A7). In the wet season, PERMANOVA revealed that slough, habitat and interaction of slough and habitat predicted dissimilarity (Table 3). Considering only the effect of habitat averaged over sloughs, community composition differed across all habitats. SIMPER revealed that the most abundant taxa were most influential in driving dissimilarities. Compared to ponds, marshes yielded nearly three times the catch of grass shrimp and higher catches of creeping water bug *Pelocoris femoratus*, which were almost absent from ponds. Except for these two taxa, mean invertebrate catches were higher in near-ponds compared to marshes. Ponds had higher fish catches, but lower invertebrate catches compared to near-ponds. In Shark River Slough, PERMANOVA revealed that habitat and habitat-by-season interaction predicted community dissimilarity (Table 3). Averaged over seasons, community composition differed between marsh and pond (pseudo-$F = 3.0$, $r^2 = 0.15$, $p < 0.01$) and pond and near-pond (pseudo-$F = 2.5$, $r^2 = 0.13$, $p < 0.01$), but not marsh and near-pond (pseudo-$F = 1.4$, $r^2 = 0.07$, $p = 0.07$). Ponds generally had lower invertebrate catches, but 50% higher Eastern Mosquitofish and higher Sailfin Molly *Poecilia latipinna* catches than near-ponds. Creeping water bug catches were roughly 60% greater and average Bluefin Killifish catches in marshes were about four times those in near-ponds. Compared to ponds, marsh Golden Topminnow *Fundulus chrysotus* catches were about eight times greater and creeping water bug catches were more than 20 times

TABLE 4 Repeated-measures analysis of variance of asymptotic richness of zooplankton and aquatic consumer communities. Datasets were parsed for aquatic consumers to account for unequal sampling. Bolded *p* values indicate significance level of $\alpha = 0.05$.

Dataset	Error	Source	*df*	SSq	MSq	*F*	*p*
Zooplankton	Site	Slough	1	35.1	35.1	1.4	0.28
		Residuals	8	204.2	25.5		
	Site*Season	Season	1	134.0	134.0	7.2	**0.03**
		Slough*Season	1	4.4	4.4	0.2	0.64
		Residuals	8	149.5	18.7		
	Site*Habitat	Habitat	2	75.5	37.8	1.6	0.24
		Slough*Habitat	2	59.4	29.7	1.2	0.31
		Residuals	16	380.5	23.8		
	Site*Season*Habitat	Season*Habitat	2	158.6	79.3	6.9	**<0.01**
		Slough*Season*Habitat	2	2.5	1.2	0.1	0.90
		Residuals	16	183.9	11.5		
Aquatic consumers (wet season only)	Site	Slough	1	457.7	457.7	1.8	0.22
		Residuals	8	2049.9	256.2		
	Site*Habitat	Habitat	2	1091.8	545.9	5.8	**0.01**
		Slough*Habitat	2	123.2	61.6	0.7	0.53
		Residuals	16	1501.4	93.8		
Aquatic consumers (SRS only)	Site	Residuals	4	649.3	162.3		
	Site*Season	Season	1	325.2	325.2	1.0	0.38
		Residuals	4	1316.0	329.0		
	Site*Habitat	Habitat	2	722.0	361.0	1.8	0.23
		Residuals	8	1623.0	202.8		
	Site*Habitat*Season	Season*Habitat	2	623.1	311.56	5.9	**0.03**
		Residuals	8	420.2	52.5		

greater than those in ponds. Across sites, consumer stoichiometry deviated from homoeostasis for both fish consumers, but not grass shrimp. Eastern Mosquitofish C:P and N:P were higher in marsh than near-pond habitats, and Bluefin Killifish C:N was higher in marshes compared to ponds.

4 | DISCUSSION

Our findings (summarized in Figure 2) demonstrate that alligators act as ecosystem engineers through their maintenance of deep-water basins and influence nutrient availability in oligotrophic freshwater marshes. Engineering activities of alligators and the subsequent changes to their ponds result in spatial heterogeneity in nutrient availability and create hotspots of P enrichment. Alligator-engineered habitats demonstrated significant changes in plant and animal community structure and trophic organization likely brought about through bottom-up mechanisms including altering nutrient availability and habitat structure. Our work supports inclusion of alligators with other examples of the multifaceted roles of animals in mediating bottom-up controls of community dynamics.

Alligator-engineered habitats exhibited nutrient enrichment compared to the surrounding marsh. Floc C:P and N:P ratios were lowest in ponds and highest in marshes in both seasons indicating that P is less limited in ponds. Organic-matter-rich floc is reincorporated in biota through its role as a basal source for the detrital food web (Belicka et al., 2012). Field experiments in oligotrophic wetlands reveal that floc stores much of the accumulated P compared to soil, periphyton, plants and surface water (Noe et al., 2002). Water-column TP did not demonstrate nutrient enrichment in pond or near-pond habitats, although some sites displayed orders of magnitude higher TP in ponds compared to marshes in the dry season. P is readily concentrated into heterotrophic and autotrophic microbes at low levels of enrichment, but only in P-saturated conditions can elevated water-column TP be detectable (Gaiser et al., 2005).

Alligator-engineered habitats were less likely to have mat-forming periphyton present than the marsh. We hypothesize that the lack of periphyton in ponds and near-ponds was related to engineering activities that cause unfavourable environmental conditions such as increased water depth, shade and nutrient availability, as well as providing regular disturbances that limit mat formation. Everglades periphyton mats, which are comprised of autotrophic and heterotrophic bacteria, fungi and detritus, generally dissociate when P loading exceeds $10\,\mu\text{g}\,\text{L}^{-1}$ (Gaiser et al., 2005). These mats are an important energy source and habitat structure in the oligotrophic Everglades (Liston et al., 2008) and their absence requires animals that depend on them to inhabit less-structured and riskier habitats.

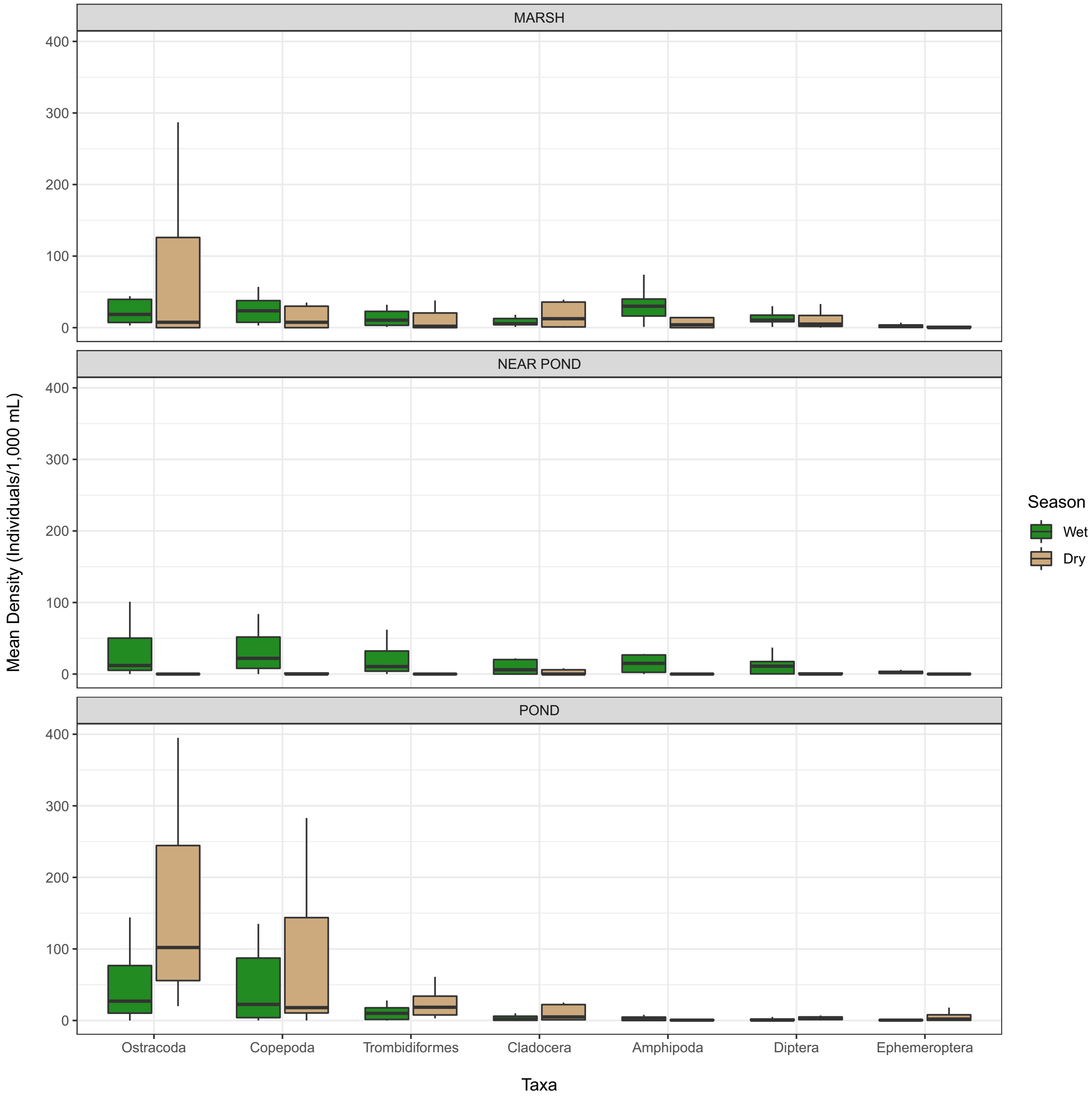

FIGURE 4 Dominance-diversity curves for mean density (individuals per 1000 mL) of invertebrate communities from funnel-trap sampling. Means appear as black lines, the coloured boxes contain the 25th and 75th percentiles, and whiskers extend to 1.5*Interquartile Range. Only the seven most abundant taxa are presented.

Marsh plant communities differed from communities in alligator-engineered habitats. Marshes were dominated by spikerush and more frequently had carnivorous bladderworts that typically provide the structural basis for periphyton mats in the Everglades (Busch et al., 1998). Near-ponds were densely vegetated, and, at times, dried completely when adjacent marshes did not. This relief gradient caused from modestly higher elevation is important for the assemblage of different plant communities including species tolerant of shorter hydroperiods and those that grow fast to avoid shading. Near-ponds were characterized by green arrow arum and pickerelweed. The abundance and growth of both plants respond well to N and P enrichment (Daoust & Childers, 1999) and have been previously associated with alligator ponds (Palmer & Mazzotti, 2004).

Although Everglades vascular plants are generally slow to respond to enrichment (Noe et al., 2002), some species were strongly associated with nutrient gradients. N:P ratios of the three most common plants tested across the gradient were higher in marshes than engineered habitats indicating slower growth rates (Vrede et al., 2004). In wetlands, it is thought that cattail is an indicator of nutrient enrichment (Vaithiyanathan & Richardson, 1999). Cattail was only detected at three sites, but in all three it was largely monotypic and these sites had some of the highest water-column TP values. Small-scale disturbances from pond maintenance and other biological activity from alligators and associated biota likely increase topographic heterogeneity, alter soil characteristics and nutrient dynamics, and manipulate plant communities through physical destruction and changes in herbivore populations. We hypothesize that actions such as these are

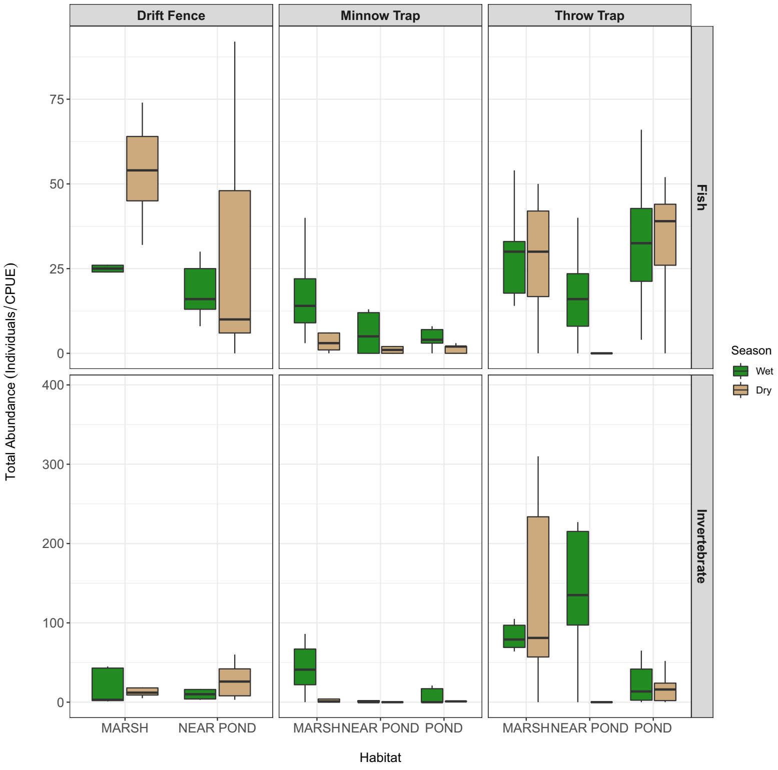

FIGURE 5 Total abundance per CPUE of aquatic consumer communities (fishes and invertebrates) from drift fence, minnow-trap and throw-trap sampling. Drift fence and minnow-trap data did not include Taylor Slough dry-season samples. Drift fences were not deployed in ponds.

responsible for the marked differences in plant communities observed at alligator ponds compared to the surrounding marsh.

Zooplankton abundance and taxon richness were generally greatest in wet-season near-ponds. These thick stands of emergent macrophytes likely provide an abundance of food and habitat structure for aquatic invertebrates (Batzer & Wissinger, 1996), but in the dry season these habitats may dry completely and become unsuitable (Rader, 1994). Several near-ponds completely dried during the dry season. Inverted-funnel traps showed greater richness of zooplankton in dry-season ponds compared to near-ponds implying dispersal to avoid desiccation or movement to capitalize on enhanced biological activity and resources in the pond.

Invertebrate community composition differed greatly between ponds and marshes following expectations associated with the nutrient gradient. For instance, inverted-funnel traps showed that amphipods were most abundant in marshes. Amphipod abundance has previously been negatively associated with P enrichment and declined dramatically across a gradient of enrichment with abundance 10 times higher in unenriched marshes (McCormick et al., 2004). In addition, amphipods are tightly coupled with periphyton mats (Liston et al., 2008), which might make marshes preferable. Our other sampling gears also showed high capture rates of grass shrimp and creeping water bugs in marshes but not in other habitats; both taxa are thought to have strong ties to periphyton mats (Liston et al., 2008). Inverted-funnel traps showed that ostracods, copepods and aquatic mites were more abundant in ponds compared to other habitats. Elser et al. (1988) observed a shift from *Daphnia* to copepod dominance when P was no longer limiting in a whole lake food-web manipulation. Liston (2006) found that for both ostracods and copepods, the interaction of P availability and hydroperiod was associated with benthic infaunal crowding. Ponds had the longest hydroperiod regime of habitats we studied, staying relatively deep year-round and P enriched compared to marshes. At enriched sites in the Everglades, Rader and Richardson (1994) found that ostracods were 14 times more abundant than unenriched sites. In our study, mean site CPUE was twice as high for ostracods in ponds compared to marshes.

Ponds appeared to be dominated by only a few species of fishes, all of which were observed across other habitats. Our sampling methods only allowed us to capture relatively small fishes, but larger fishes like Florida Gar *Lepisosteus platyrhincus* and Largemouth Bass *Micropterus salmoides* were present and captured within ponds using electrofishing at the same sites we studied (Pintar et al., 2023). Large-bodied fishes were observed in many of the ponds, but rarely in marshes and never in near-pond habitats (personal observation). These fishes are primarily carnivorous, and mostly piscivorous, and their presence likely scares smaller fishes and large invertebrates into more structured habitats like near-ponds and marshes (Savino & Stein, 1982), potentially explaining lower consumer richness in ponds and greater abundance of zooplankton. Near-pond habitats were shallow or completely dry in the dry season making them unsuitable habitat for most fishes. Pond habitats are thought to provide a refuge for many aquatic animals during seasonal drying; thus, we predicted greater abundance and more diverse communities in ponds during drydown. In our sampling, we did not observe the expected seasonal migrations—perhaps because it was a relatively wet year (Figure A11) decreasing the need for a refuge from desiccation. Multiple samples within a season would be better suited to detect and track potential migrations across habitats.

Consumers did not exhibit stoichiometric homoeostasis across habitats, indicating food-web changes in stoichiometry and demonstrating that P availability engineered by alligators extends beyond greater nutrient availability for primary producers. For instance, Eastern Mosquitofish caught in marshes had higher C:P and N:P than those in the near-pond, which follows patterns of P enrichment associated with ponds. Lower C:P and N:P seen in the pond may be indicative of better food quality because of the closer stoichiometric tracking of a consumer and its prey (Cross et al., 2003). In addition, lower C:P and N:P is associated with faster growth rates (Vrede et al., 2004). These assumptions would mean that consumers such as Eastern Mosquitofish caught by predators in ponds would be higher quality food items and exhibit faster biomass turnover than individuals captured in marshes, creating a spatial mismatch of food quality, nutrients and energy across the habitat gradient. Bluefin Killifish did not show the same patterns of higher C:P and N:P in marsh habitats. Omnivorous and herbivorous fishes are more likely to be nutrient limited, while carnivores are more likely to experience energy limitation (Schindler & Eby, 1997). Dietary evidence suggests that Eastern Mosquitofish consume more primary producers and detritus (more omnivory) than Bluefin Killifish, which eat primarily omnivorous invertebrates (more carnivory; Flood et al., 2023), possibly explaining Eastern Mosquitofish's closer tracking of differences in P stoichiometry across habitats. Eastern grass shrimp were largely stoichiometrically invariant, and we detected no differences in stoichiometry among habitats. Our findings match those of Bornhoeft (2016) who observed Eastern Mosquitofish tracking stoichiometric changes in their food in experimental conditions but found no effect of diet on grass shrimp stoichiometry.

We have shown that alligator engineering effects on nutrient dynamics move up the food web, which could provide benefits to targets of wetland restoration like mobile predators and wading birds that are able to use these hotspots of food resources (Hagerthey et al., 2014). Increased P limitation in the oligotrophic marsh may create a cascade of ecological effects starting with consumer demand for P, greater P assimilation and lower excretion rates of P, which result in low P uptake by algae and microbes (Hagerthey et al., 2014; Hood et al., 2005). At scale, the stoichiometric patterns we observed in some of our consumers provide a potential mechanism for alligator engineering activities to change patterns of secondary production and energetic constraints on organisms living in an oligotrophic environment.

Beyond recycling and bioturbation by animals, alligator engineering may induce abiotic biogeochemical mechanisms that influence nutrient dynamics. A study of an alligator pond in Big Cypress Swamp in Florida showed high temperature stratification during some parts of the year and strong diurnal fluctuations in dissolved oxygen from photosynthetic activity (Kushlan & Hunt, 1979). During the dry season, it is suspected that animal activity brought dissolved oxygen so low that it resulted in a fish kill (Kushlan & Hunt, 1979). In our study, we did not measure dissolved oxygen or temperature, but these and other variables may influence biogeochemical dynamics in the ponds. Alligator ponds vary in hydrology, bathometry and morphometry (Campbell & Mazzotti, 2004) and these physical parameters may also influence the strength of changes that alligators cause in local nutrient cycling. In fact, depth, one of the most obvious changes by alligators to the landscape, is often considered the main driver of P dynamics in the Everglades (Sarker et al., 2020). Regardless, the associated changes in abiotic conditions in alligator ponds are ultimately caused by their engineering activities. Future studies could enhance our understanding of the consequences of alligator engineering by isolating these emergent mechanisms for further study.

5 | CONCLUSIONS

Ecosystem restoration generally focuses on abiotic variables or vegetation with the assumption that animal communities and food webs will recover and return in response to habitat recovery (Vander Zanden et al., 2016). However, often not considered in restoration plans is the role key animals play in engineering habitats and influencing ecosystem processes. Alligators are an important indicator of restoration success, and their abundance, distribution and behaviour have been impacted by drainage and subsequently restoration (Mazzotti et al., 2009; Strickland et al., 2022). They are considered an iconic species of the Everglades and their importance in creating alligator ponds is often used to justify their status as a restoration target. This work provides strong evidence for that rationale and demonstrates their roles in influencing both nutrient and trophic dynamics. Ecosystem restoration without recovery of ecosystem engineers may risk failure to recover fundamental ecological functions and services (Hastings et al., 2007). This study supports better inclusion of ecosystem engineers in efforts to include food-web function more fully in restoration planning (Vander Zanden et al., 2016).

AUTHOR CONTRIBUTIONS

Bradley A. Strickland, Joel C. Trexler, Peter J. Flood, Frank J. Mazzotti, Michael R. Heithaus and Jeffrey L. Kline conceived the ideas and designed the methodology; Joel C. Trexler obtained and managed the project funding; Bradley A. Strickland, Peter J. Flood and Joel C. Trexler collected and analysed the data; Bradley A. Strickland led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Environmental Data Initiative https://doi.org/10.6073/pasta/3b303590e5f6834661cf9002ec2594f4 (Strickland et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table A1. Alligator pond site descriptions and evidence of alligator activity in Taylor Slough and Shark River Slough, Everglades, Florida, USA.

Table A2. Repeated-measures analysis of variance of water-column total phosphorus. Sampling was performed in marsh, near-pond, and pond habitats in ten sites in Taylor Slough and Shark River Slough in the 2018 wet and 2019 dry seasons. Seasonal models were run separately because we were unable to collect dry season near-pond samples.

Table A3. Presence of aquatic plants sampled in marsh, near-pond, and pond habitats at ten sites in Taylor Slough and Shark River Slough in the 2018 wet and 2019 dry seasons. Presence is expressed as the proportion of visits to each habitat at ten sites across two seasons.

Table A4. Repeated-measures analysis of variance of richness of plant communities. Sampling was performed in marsh, near-pond, and pond habitats at ten sites in Taylor Slough and Shark River Slough in the 2018 wet and 2019 dry seasons.

Table A5. SIMPER analysis results following multiple PERMANOVAs across marsh, near-pond, and pond habitats at ten sites in Taylor Slough and Shark River Slough in the 2018 wet and 2019 dry seasons. Includes only the top species explaining at least 70% of the dissimilarity.

Table A6. Stoichiometric comparisons among marsh, near-pond, and pond habitats at ten sites in Taylor Slough and Shark River Slough in the 2018 wet season only for plants and aquatic consumers. Datasets were parsed to account for unequal sampling. Dry season comparisons are reported in the text.

Table A7. Repeated-measures analysis of variance of total abundance of zooplankton communities (A). Estimated marginal least-squares means of total abundance for the interaction of season and habitat (B). Funnel trap sampling was performed in marsh, near-pond, and pond habitats at ten sites in Taylor Slough and Shark River Slough in the 2018 wet and 2019 dry seasons.

Table A8. Relative abundance of zooplankton sampled in marsh, near-pond, and pond habitats at ten sites in Taylor Slough and Shark River Slough in the 2018 wet and 2019 dry seasons.

Table A9. Estimated marginal least-squares means of asymptotic richness of zooplankton community for the interaction of season and habitat. Funnel trap sampling was performed in marsh, near-pond, and pond habitats at ten sites in Taylor Slough and Shark River Slough in the 2018 wet and 2019 dry seasons.

Table A10. Count by taxa of aquatic consumers sampled in marsh, near-pond, and pond habitats at ten sites in Taylor Slough and Shark River Slough in the 2018 wet and 2019 dry seasons. Sampling was performed using throw traps, unbaited minnow traps, and drift fences.

Table A11. Aquatic consumers captured from throw trap, minnow trap, and drift fence sampling performed in marsh, near-pond, and pond habitats at ten sites in Taylor Slough and Shark River Slough, Everglades, Florida, USA in the 2018 wet and 2019 dry seasons.

Table A12. Estimated marginal least-squares means of aquatic consumer asymptotic richness for significant effects from throw trap, minnow trap, and drift fence sampling performed in marsh, near-pond, and pond habitats at ten sites in Taylor Slough and Shark River Slough in the 2018 wet and 2019 dry seasons. Datasets were parsed to account for unequal sampling.

Table A13. Repeated-measures analysis of variance of total abundance of aquatic consumer communities (A). Estimated marginal least-squares means of total abundance for significant interactions (B). Throw trap, minnow trap, and drift fence sampling was performed in marsh, near-pond, and pond habitats at ten sites in Taylor Slough and Shark River Slough in the 2018 wet and 2019 dry seasons. Datasets were parsed to account for unequal sampling.

Figure A1. Water-column total phosphorus for marsh, near-pond, and pond habitats at ten sites in Taylor Slough and Shark River Slough in the 2018 wet (A) and 2019 dry seasons (B). Wet season site MDB for the near-pond was an extreme outlier at 30.85 μmol/L and was not plotted. The near-pond habitat was not sampled during the dry season because of marsh drydown.

Figure A2. Non-metric multidimensional scaling biplot revealing plant compositional similarity among marsh, near-pond, and pond habitats. Sampling was performed at ten sites in Taylor Slough (represented by a circle) and Shark River Slough (square) in the 2018 wet (green) and 2019 dry (brown) seasons. Ellipses represent 1 standard deviation and are outlined and shaded to represent habitats: pond (blue), near-pond (green), and marsh (brown). Generally, taxa are abbreviated in the plot as the first three letters of genus and species. Taxa are abbreviated in the plot as the first three letters of genus followed by first three letters of species.

Figure A3. Rarefaction curves displaying species richness for zooplankton communities from funnel trap sampling performed in marsh, near-pond, and pond habitats at ten sites in Taylor Slough and Shark River Slough in the 2018 wet and 2019 dry seasons. The left plot shows all individuals sampled and the right plot shows a truncation to 2250 individuals.

Figure A4. Non-metric multidimensional scaling biplot revealing zooplankton compositional similarity among marsh, near-pond, and pond habitats. Funnel trap sampling was performed at ten sites in Taylor Slough (represented by a circle) and Shark River Slough (square) in the 2018 wet (green) and 2019 dry (brown) seasons. Ellipses represent 1 standard deviation and are outlined and shaded to represent habitats: pond (blue), near-pond (green), and marsh (brown). Generally, taxa are abbreviated in the plot as the first three letters of genus and species. Taxa are abbreviated in the plot as the first four letters: Copepoda, Ostracoda, Mollusca, Cladocera, Amphipoda, Diptera, Ephemeroptera, Nematoda, Platyhelminthes, Hemiptera, Odonata, and HYDR = Trombidiformes.

Figure A5. Rarefaction curves showing taxa richness of aquatic consumer communities from throw trap, minnow trap, and drift fence sampling performed in marsh, near-pond, and pond habitats at ten sites in Taylor Slough and Shark River Slough in the 2018 wet and 2019 dry seasons. The left plot shows all individuals sampled and the right plot shows a truncation to 1,150 individuals.

Figure A6. Total abundance as mean catch per unit effort of aquatic consumer communities from throw trap sampling performed in marsh, near-pond, and pond habitats at ten sites in Taylor Slough and Shark River Slough in the 2018 wet and 2019 dry seasons.

Figure A7. Non-metric multidimensional scaling biplot revealing aquatic consumer compositional similarity among marsh, near-pond, and pond habitats from throw trap, minnow trap, and drift fence sampling performed at five sites in Shark River Slough in the 2018 wet (green) and 2019 dry seasons (brown). Ellipses represent 1 standard deviation and are outlined and shaded to represent habitats: pond (blue), near-pond (green), and marsh (brown). Generally, taxa are abbreviated in the plot as the first three letters of genus and species. Light gray plus signs indicate taxa whose text overlapped another taxa with higher total abundance.

Figure A8. Dominance-diversity curves for mean density (individuals per m^2) of aquatic consumer communities from throw trap sampling performed in marsh, near-pond, and pond habitats at ten sites in Taylor Slough and Shark River Slough in the 2018 wet and 2019 dry seasons. Generally, taxa are abbreviated in the plot as the first three letters of genus and species.

Figure A9. Dominance-diversity curves for mean catch per unit effort of aquatic consumer communities from un-baited minnow trap sampling performed in marsh, near-pond, and pond habitats at ten sites in Taylor Slough and Shark River Slough in the 2018 wet and 2019 dry seasons. Generally, taxa are abbreviated in the plot as the first three letters of genus and species.

Figure A10. Dominance-diversity curves for mean catch per unit effort of aquatic consumer communities from drift fence sampling performed in marsh and near-pond habitats at ten sites in Taylor Slough and Shark River Slough in the 2018 wet and 2019 dry seasons. Generally, taxa are abbreviated in the plot as the first three letters of genus and species.

Figure A11. Mean annual hydroperiod (days with water depth ≥ 5 cm) in the marsh at each alligator pond (site) we sampled over the decade prior to 2017 (2007–2016). Boxes and whiskers represent 50% and 95% confidence intervals respectively. Water years start in June and end in May to capture one wet-dry cycle. Water year 2019, the water year in which we sampled, exceeded the 50% confidence interval at most sites, while the previous two water years were closer to the decadal mean.

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