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RESEARCH ARTICLE

Habitat engineering by an apex predator generates spatial trophic dynamics across a temporal environmental stress gradient

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Abstract

1. Ecosystem engineering is a facilitative interaction that generates bottom-up extrinsic variability that may increase species coexistence, particularly along a stress/disturbance gradient. American alligators (*Alligator mississippiensis*) create and maintain 'alligator ponds' that serve as dry-season refuges for other animals. During seasonal water recession, these ponds present an opportunity to examine predictions of the stress-gradient (SGH) and intermediate disturbance hypotheses (IDH).
2. To test the assumption that engineering would facilitate species coexistence in ponds along a stress gradient (seasonal drying), we modelled fish catch-per-unit-effort (CPUE) in ponds and marshes using a long-term dataset (1997–2022). Stomach contents ($n=1677$ from 46 species) and stable isotopes of carbon and nitrogen ($n=3978$ representing 91 taxa) from 2018 to 2019 were used to evaluate effects of engineering on trophic dynamics. We quantified diets, trophic niche areas, trophic positions and basal-resource use among habitats and between seasons. As environmental stress increases, we used seasonal changes in trophic niche areas as a proxy for competition to examine SGH and IDH.
3. Across long-term data, fish CPUE increased by a factor of 12 in alligator ponds as the marsh dried. This validates the assumption that ponds are an important dry-season refuge. We found that 73% of diet shifts occurred during the dry season but that diets differed among habitats in only 11% of comparisons. From wet season to dry season, both stomach contents and stable isotopes revealed changes in niche areas. Direction of change depended on trophic guild but was opposite between stable-isotope and stomach-content niches, except for detritivores.
4. Stomach-content niches generally increased suggesting decreased competition in the dry season consistent with existing theory, but stable-isotope niches yielded the opposite. This may result from a temporal mismatch with stomach contents reflecting diets over hours, while stable isotopes integrate diet over weeks.

Consumptive effects may have a stronger effect than competition on niche areas over longer time intervals.

5. Overall, our results demonstrated that alligators ameliorated dry-season stress by engineering deep-water habitats and altering food-web dynamics. We propose that ecosystem engineers facilitate coexistence at intermediate values of stress/disturbance consistent with predictions of both the SGH and IDH.

KEYWORDS

American alligator, bottom-up effects, disturbance ecology, ecosystem engineer, food webs, stable isotopes, stomach contents, stress gradient hypothesis

1 | INTRODUCTION

Ecosystem engineers enhance habitat and resource availability, creating bottom-up effects that extend across trophic levels, altering species densities, diversity and food-web structure (Sanders & Van Veen, 2011; Van der Zee et al., 2016). Animal-engineered habitat modifications, such as nutrient enrichment, may result in trait-mediated indirect effects that can intensify direct bottom-up effects, diminish top-down effects and influence trophic dynamics (Wetzel et al., 2016; Zhong et al., 2017). Ecosystem engineers as diverse as mussels, seagrass, desert shrubs and marsh grasses have been shown to facilitate survival of other species by ameliorating physical stressors such as heat, nutrient limitation, osmotic stress and disturbance (Bertness & Callaway, 1994). These beneficial effects unfold across spatial and temporal gradients, with recent work highlighting reduction of competitive interactions (Lowney & Thomson, 2021, 2022). Despite the profound influences of animal engineering on food webs, we lack a mechanistic understanding of its effects on food-web structure and function (Sanders et al., 2014; Sanders & Van Veen, 2011).

Ecosystem engineering is an indirect source of extrinsic variability imposed by the engineered environment on species' realized niches that may facilitate species coexistence on finite resources (Chase & Leibold, 2003; Hutchinson, 1961; Sanders et al., 2014), particularly in harsh ecosystems or those that are regularly disturbed (Lowney & Thomson, 2021, 2022). These dynamics are encompassed in both the stress gradient hypothesis (SGH) and the intermediate disturbance hypothesis (IDH). The SGH states that intensity of facilitation and interspecific competition will be inversely related along environmental stress gradients, with competition decreasing under stressful conditions; most studies addressing these hypotheses have focused on plant communities (Bertness & Callaway, 1994; Malkinson & Tielbörger, 2010). Meanwhile, the IDH posits that diversity of competing species is greatest at intermediate frequencies and/or intensities of disturbance (Connell, 1978; Grime, 1973; Hutchinson, 1961). The IDH and potential underlying mechanisms have been heavily criticized with support in the literature being mixed and notably low in aquatic ecosystems (Fox, 2013; Moi et al., 2020). Facilitation via enhanced habitat and resource availability by ecosystem engineering is one potential mechanism for decreased interspecific competition during disturbance and/or environmental stress. In a food-web framework, trophic niches are inversely related to interspecific competition according to the niche variation hypothesis (NVH) (Bolnick et al., 2007; Van Valen, 1965) and can be used to inform our understanding of coexistence in combination with the SGH and IDH. Increased bottom-up effects that result from ecosystem engineering (e.g. nutrient enrichment, habitat availability) may facilitate a decrease in interspecific competition (SGH and IDH assumption) permitting larger trophic niche areas (increased intraspecific trophic variation based on NVH) along an environmental stress/disturbance gradient.

These three disturbance-based hypotheses of community assembly and stability have not been evaluated equally well across ecosystem types. Recent studies without facilitation by ecosystem engineers found trophic niche compression from disturbances in aquatic ecosystems (Burdon et al., 2020; Gutiérrez-Fonseca et al., 2024; Hansen et al., 2023). Meanwhile, Rahman et al. (2021) found an increase in trophic niche area for ground beetles following disturbance. Effects of disturbance and interactions of facilitation and disturbance on trophic niche area remain unclear and may vary between aquatic and terrestrial ecosystems. For example, the SGH comes from primarily terrestrial plant communities with recent support in bird and arthropod communities (Dangles et al., 2018; García-Navas et al., 2021; Lowney & Thomson, 2021, 2022). However, support varies among aquatic ecosystems and when considering communities that include diverse taxa.

In the Everglades, USA, American alligators (*Alligator mississippiensis*) create and maintain 'alligator ponds' through removal of vegetation and redistribution of sediment (Campbell & Mazzotti, 2004; Kushlan, 1974; Palmer & Mazzotti, 2004). These ponds have elevated nutrient levels that spill over to an enriched margin supporting dense emergent plant growth and aquatic animal communities that differ from those in surrounding marshes (Strickland et al., 2023). The Everglades experiences seasonal rainfall with dry seasons characterized by a dropping water table and concentration of mobile aquatic animals (Gaiser et al., 2012; Loftus & Kushlan, 1987) that currently depend on canals, alligator ponds and other deeper-water habitats as hydrological refuges in especially dry years (Kushlan, 1974). Despite occupying a fraction of the land cover, spatial heterogeneity provided by alligator ponds (increased nutrients, dry-season refuge) are thought to be critical to aquatic prey production on which apex predators (wading birds and alligators) rely (Kushlan, 1974; Strickland et al., 2023). Ameliorating drying-induced stress may be essential for maintaining ecosystem function in short-hydroperiod environments prone to drying (Crain & Bertness, 2006).

We used a 25-year electrofishing dataset to model fish catch per unit effort (CPUE) during different sampling periods to examine the assumption that ecosystem engineering facilitates coexistence along an environmental stress gradient (wet season to dry season). Within 1 year, we conducted an in-depth food-web study of stomach contents and stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) to assess impacts of alligator engineering on basal resource use (autotrophic vs. heterotrophic), trophic positions, diets and trophic niches of aquatic consumers across both spatial and seasonal environmental gradients. We examined the influence of facilitation via ecosystem engineering across a seasonal environmental stress/disturbance gradient (dry-season water recession) using trophic niches characterized by stable isotopes and stomach contents as a proxy for competition as assumed by the NVH. We predicted that (1) fishes would become concentrated in ponds during the dry season and (2) elevated nutrient levels in engineered habitats would generate bottom-up effects that lead to increased autotrophic energy use (Polis, 1999; Polis et al., 1997; Power, 1992), which facilitates increased fish CPUE under elevated environmental stress. As a result of trophic dynamics, we also hypothesized that (3) trophic position would increase in deeper water habitats (alligator-engineered ponds) (McHugh et al., 2015), (4) consumers would undergo dietary shifts in engineered habitats because of nutrient-enriched plant and consumer communities (Strickland et al., 2023) and (5) trophic niche areas would increase as competition decreases and environmental stress increases (in the dry season) (Figure 1) (Bolnick et al., 2010; Malkinson & Tielbörger, 2010).

2 | MATERIALS AND METHODS

2.1 | Study ecosystem

Everglades National Park, Florida, USA has two major drainages, Shark River Slough (SRS) and Taylor Slough (TS), which carry freshwater through the Everglades to Florida Bay. TS is smaller and dries faster than SRS, however the two sloughs have many similarities. These sloughs are predominantly wet prairie (spikerush-dominated sloughs, *Eleocharis* spp.) with large stocks of periphyton (Gunderson & Loftus, 1993; Turner et al., 1999). Throughout this landscape, alligators dig and maintain alligator ponds or alligator holes that constitute <1% of total land cover (Brandt et al., 2010; Campbell & Mazzotti, 2004). This alligator-engineering results in two distinct habitats: (1) a pool or semi-open water habitat that is typically 1-m deeper than surrounding marsh (hereafter 'pond') and (2) a dense ring of thick vegetation, including woody vegetation, immediately surrounding the pond (hereafter 'near-pond') (Campbell & Mazzotti, 2004; Palmer & Mazzotti, 2004). Alligator activity creates deeper channels through the near pond that allows connectivity, albeit more limited, between pond and marsh until the marsh has completely dried.

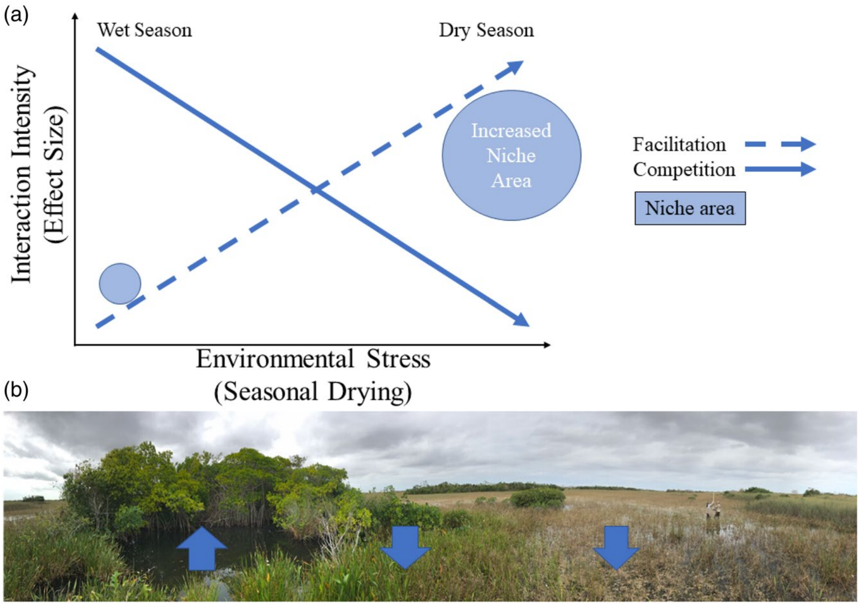

FIGURE 1 Conceptual model of predicted outcomes of ecosystem engineering from American alligators based on the Stress Gradient (SGH), Intermediate Disturbance (IDH), and Niche Variation (NVH) Hypotheses. (a) As environmental stress/ disturbance increases (i.e. water recession during the dry season), under SGH and IDH, competition will decrease. According to the NVH, a decrease in competition will result in an increase in niche area. (b) Alligator-engineered ponds act as dry-season refuges for aquatic fauna, thus ameliorating environmental stress. Therefore, we predicted that niche areas would increase in dry-season ponds as environmental stress increases and that the opposite trend would occur in marshes and near-ponds (represented by blue arrows).

2.2 | Long-term fish monitoring

Since 1997, long-term monitoring of fishes ≥8 cm standard length has been conducted in both ponds and marshes in SRS and TS (Figure 2) (Chick et al., 1999; Parkos et al., 2011). Four marsh sites in SRS and three marsh sites in TS with three 1-ha plots each have been sampled with three transects of 5 min of electrofishing (CPUE = individuals/5 min) twice in the wet season (July, October) and twice in the dry season (February, April). Ten alligator ponds, five in each slough, were sampled in the same manner. All ponds sampled both for food-web samples in this study and long-term monitoring showed signs of active use by alligators including trails, maintained entrances/exits, wallow, scat, bellowing and/or observation of alligator(s) (Strickland et al., 2023).

2.3 | Food-web sampling

Consumers and basal resources for trophic analyses were collected from ponds, near-ponds, and adjacent marshes at five ponds in SRS and five in TS (Figure 2). Each set of habitats was sampled once in the wet season (October–December 2018) and once in the dry season (March–April 2019) unless prevented by shallow water depth, which occurred when near-pond habitats in TS dried prior to dry-season sampling (Tables S1 and S2). TS dry-season food-web sampling was limited and did not include electrofishing because airboat trails dried, restricting access to helicopter transport. Alligator engineering created environmental gradients of depth (near-ponds were the shallowest habitat and ponds the deepest) and of environmental harshness (dry-season water recession decreases available marsh habitat concentrating animals in ponds).

We collected basal resources and aquatic consumers for analysis of $\delta^{13}C$, $\delta^{15}N$ and stomach contents of vertebrates. Basal resources included flocculent organic benthic matter (hereafter 'floc'), emergent vascular plants, *Utricularia* spp., *Nostoc* spp. and periphyton (Table S3). We used several methods to collect aquatic consumers including zooplankton, macroinvertebrates, fishes and amphibians (Appendix S1: Field collections). For simplification, we refer to all invertebrates collected in inverted funnel traps as zooplankton (Trexler & Loftus, 2016). Vertebrates were sorted into size classes based on length (Table S4) to account for ontogenetic diet shifts (Piet et al., 1999; Wainwright & Richard, 1995). Species size classes within a habitat-season-slough level with $n < 3$ were excluded from statistical analyses. Our target sample size per species size class per habitat-season-slough was 20 individuals and was 10.5 on average for stomach contents and 10 for stable isotopes for species size classes included in analyses (Table S3). In total, there were 3978 samples for $\delta^{13}C$ and $\delta^{15}N$ from 91 taxa and 1677 individuals from 46 species for stomach contents. Research and animal procedures were conducted under auspices of protocol #IACUC-18-067-CR01 from Institutional Animal Care and Use Committee (IACUC) at FIU 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.

2.4 | Statistical analyses—Long-term fish monitoring

To test the assumption that alligator-engineering facilitates coexistence in engineered ponds under elevated environmental stress during the dry season, we modelled fish CPUE from long-term data.

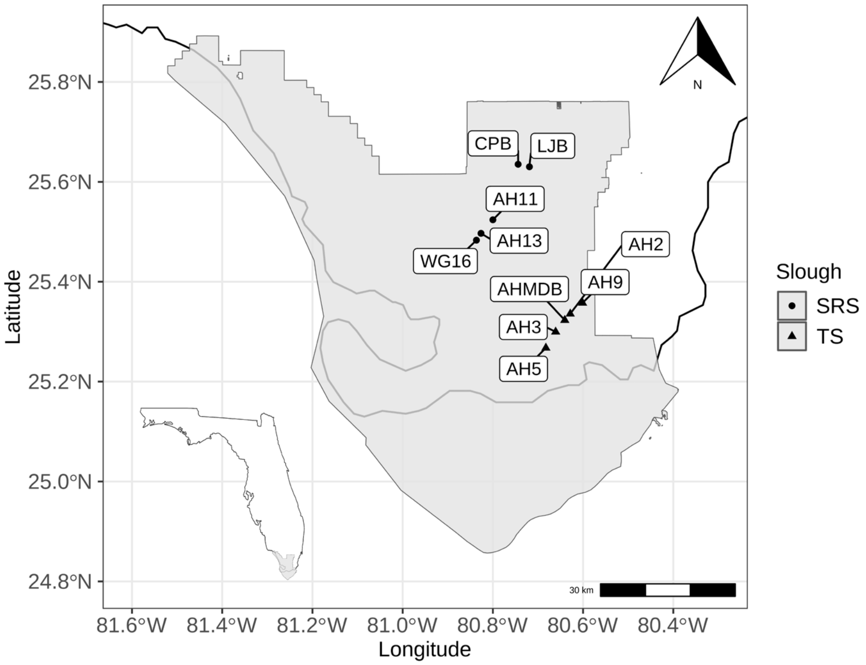

FIGURE 2 Location of alligator ponds that served as sites for food-web sampling within Everglades National Park (grey shaded area) in south Florida, USA (see inset).

Each year was treated as a replicate with four sampling periods (i.e. July, October, February, and April). Fish CPUE was modelled among periods using generalized linear mixed modelling (GLMM) with a Poisson distribution using the *glmer* function in the *lme4* package in R (Mangiafico, 2022; Wheeler & Torchiano, 2016). Habitat, sampling period, and their interaction were included as fixed effects with site as a random effect. Post-hoc pairwise comparisons were performed using the *emmeans* R package (Lenth, 2024).

2.5 | Statistical analyses—Food-web sampling

We modelled trophic positions separately for stomach contents (TP_{SCA}) and stable isotopes (TP_{SIA}; Table 1) and compared results across habitats and seasons to quantify impacts of alligator engineering. We used *tRophicPosition* package to model TP_{SIA} and a metric 'alpha' (Quezada-Romegialli et al., 2018). Alpha is the proportion of δ^{15}N in a consumer's tissues derived from detritus (floc, 'brown') and one minus alpha is the proportion derived from green algae ('green'). Thus, alpha represented a spectrum of green (<0.5) to brown (>0.5) energy use. TP_{SIA} and alpha were modelled using *multiSpeciesTP* function and compared across habitats and seasons with *pairwiseComparisons* function. TP_{SCA} was a function of prey trophic position following Adams et al. (1983). Permuted analysis of variance (permuted ANOVA) and subsequent pairwise permutation tests were used for habitat and season comparisons. These were conducted in R using *aovp* and *pairwisePermutationTest* function in *lmPerm* and *rcompanion* packages respectively (Mangiafico, 2022; Wheeler & Torchiano, 2016).

To explore diet shifts in alligator-engineered habitats, we quantified diets based on counts of stomach contents for both the entire consumer community and individual species size classes in all habitats and seasons. We used non-metric multidimensional scaling (NMDS, $k=2$) with Morisita-Horn distances (Jost et al., 2011) to visualize community-wide dynamics in prey consumption and assessed stress using a permutation-based ecological null model (Dexter et al., 2018). Permutational multivariate analysis of variance (PERMANOVA; 10,000 iterations) and similarity percentages (SIMPER) were used to determine differences in prey community of all consumers among habitats and seasons. Furthermore, spatiotemporal changes in diets of species size classes were examined using pairwise PERMANOVAs. These analyses were conducted using *vegan* and *RVAideMemoire* packages (*pariwise.perm.manova* function) and base R (Hervé, 2022; Oksanen et al., 2022; R Core Team, 2022).

To examine effects of alligator engineering on trophic niches of aquatic consumers, we separately modelled trophic niches for species size classes using stomach contents ($niche_{SCA}$) and δ^{15}N and δ^{13}C ($niche_{SIA}$). Trophic niches were modelled with *SIBER* package in R (Jackson et al., 2011). For $niche_{SCA}$, we used axes one and two from NMDS in place of δ^{13}C and δ^{15}N (Flood et al., 2023). Differences in trophic niche area for species size classes in different habitats and seasons were determined using *pairwiseComparisons* function from *tRophicPosition* package (Quezada-Romegialli et al., 2018). Changes or shifts in trophic niche area were defined as the probability of one niche area being larger or smaller than another exceeding 95%.

3 | RESULTS

3.1 | Dry-season crowding

Fishes concentrated in ponds during the dry season, with a corresponding decrease in CPUE in marshes. GLMM (R^2m = 0.26, R^2c = 0.9) revealed that CPUE in ponds increased with water recession. Median CPUE more than doubled in ponds in April (5.2 CPUE, peak dry-season sampling period) compared to July (1.2 CPUE,

TABLE 1 Definitions of terms and abbreviations for this study.

Term	Definition	Sources
TP_{SCA}	Trophic position based on stomach content analysis where a consumer is one trophic level higher than the weighted average of the trophic position of its prey	Adams et al. (1983)
TP_{SIA}	Trophic position based on stable isotope analysis relative to isotopic baselines	Quezada-Romegialli et al. (2018)
$Niche_{SCA}$	Trophic niche area based on Bayesian standard ellipse areas derived from ordination of stomach contents	Flood et al. (2023) and Jackson et al. (2011)
$Niche_{SIA}$	Trophic niche area based on Bayesian standard ellipse areas derived from stable isotopes	Jackson et al. (2011)
Shift	Probability that a given metric (e.g. niche area or trophic position) is larger or smaller than the same metric from another factor level exceeding 95% via Bayesian inference	Flood et al. (2023) and Quezada-Romegialli et al. (2018)

Note: Niche abbreviations are from Petta et al. (2020) and trophic position abbreviations follow that format. Sources are for the term definitions. 'Shift' is synonymous with a statistical difference.

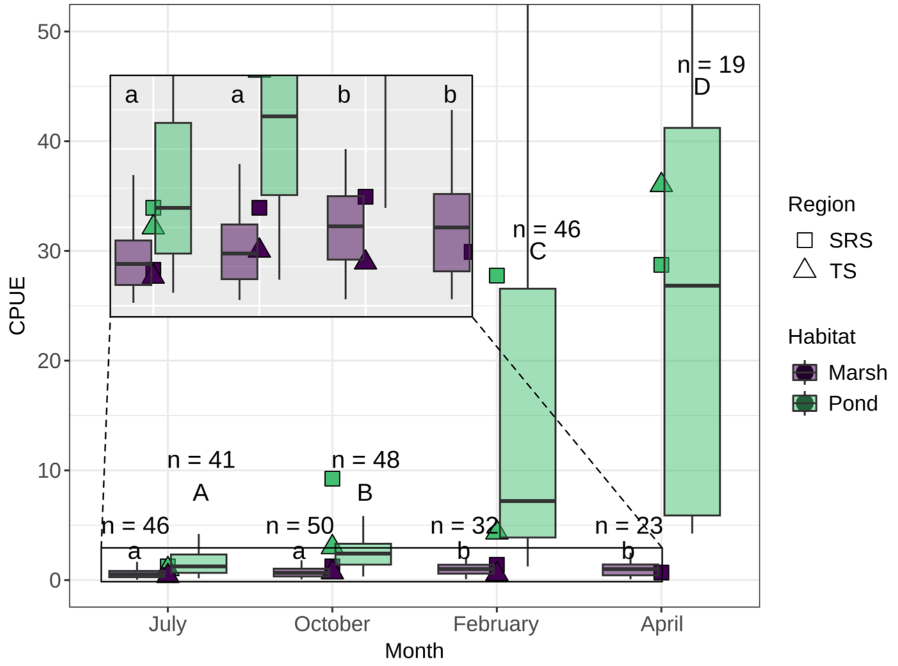

FIGURE 3 Boxplots of average total fish CPUE per sampling month in alligator ponds and marshes from 1997 to 2022. Letters represent results of post-hoc statistical comparisons (uppercase for ponds, lowercase for marshes). Shapes between boxplots represent total fish CPUE in ponds and marshes from long-term data corresponding to the time of this study in wet season 2018 and dry season 2019. Sample sizes represent the number of years a slough (SRS or TS) was sampled in that habitat and month (e.g. if both sloughs were sampled in that habitat and month in all years, then $n = 50$). Each sampling event included multiple sites with multiple plots within each slough.

early in the wet season), while mean CPUE increased from 1.5 in July to 17.8 in April (Figure 3; Table S5). In marshes, fish CPUE was statistically indistinguishable within a season but different between seasons (i.e. February and April were not significantly different from each other, but were statistically different from both July and October, which were also not statistically different from each other) Median CPUE in marshes was approximately six times greater in the wet season and early dry season with the lowest CPUE in April (0.1, dry season) and highest in October and February (0.6 in both, wet season and early dry season, respectively).

3.2 | Basal energy use

Shifts in basal energy use (alpha) were rare, but those that did occur were usually towards more green energy used in near-pond habitats (i.e. alpha decreased). We documented shifts in alpha in 14% of slough comparisons, 8% of seasonal comparisons and 4% of habitat comparisons (Figure S1). Alpha was higher in the wet season relative to the dry season in all habitats of both sloughs, except for SRS ponds.

3.3 | Trophic position

We found that shifts in both TP_{SCA} and TP_{SIA} were uncommon and that when changes in trophic position did occur, they were usually higher in alligator-engineered habitats. For TP_{SCA}, there were shifts for three species size classes in different habitats that on average increased half a trophic level (Table S6). TP_{SIA} shifted more frequently between sloughs (28% of comparisons) than between seasons (21%) or among habitats (18%) (Table 2). For comparisons across both sloughs and seasons, TP_{SIA} was generally higher in alligator-engineered habitats (59%) than in adjacent marshes (Table S7). Among habitats, TP_{SIA} was typically highest in ponds, intermediate in marshes, and lowest in near-pond habitats across species' size classes. Most seasonal shifts were decreases in TP_{SIA}, except in ponds where 66% were increases of approximately half of a trophic level.

3.4 | Dietary shifts

Our analyses of stomach contents revealed that consumer diets viewed from either community-wide or species-specific size-class levels, relied on different prey in alligator-engineered habitats compared to adjacent marshes. PERMANOVA revealed that prey ingestion was structured by an interaction among consumer size classes, slough, habitat, and season ($F = 1.75$, $p < 0.005$, Table S7) and NMDS ($k = 2$, stress $= 0.23$) separated prey by size on axis 1 (Figure S2). NMDS stress, though greater than preferred (McCune & Grace, 2002), was significantly lower ($Z = -10.4$, $p < 0.001$) than the mean (0.27) of the distribution of simulated stress values from null models (Figure S3). Zooplankton were the most abundant prey in

TABLE 2 Frequency (percent of comparisons that underwent a shift) and magnitude (percent change) of $\mathrm{TP}_{\mathrm{SIA}}$ for different spatiotemporal comparisons.

		Stable isotopes	
Comparison type	**Comparison**	**Frequency**	**Magnitude**
Habitat	All	18%	0.55±0.21
	Marsh–near-pond	23%	0.62±0.22
	Marsh–pond	15%	0.52±0.20
	Near-pond–pond	16%	0.42±0.15
Season	All	21%	0.59±0.62
	Marsh	11%	1.13±1.46
	Near-pond	36%	0.38±0.12
	Pond	26%	0.47±0.15
Slough	SRS versus TS	28%	0.67±0.62

Note: Mean percent change was calculated based on the absolute value for each comparison. Comparisons were made with other factor levels remaining constant. For example, the 'marsh–pond' habitat comparison represents shifts in $\mathrm{TP}_{\mathrm{SIA}}$ between marsh and pond fish within the same slough and season (only habitat varies) and the marsh row under season represents seasonal shifts in marshes within the same slough (only season varies).

TABLE 3 Frequency (percent of comparisons that underwent a shift) and magnitude (mean absolute value of percent change for comparisons that underwent a shift ±95% confidence interval) of changes in niche$_{\mathrm{SCA}}$ and niche$_{\mathrm{SIA}}$ for different spatiotemporal comparisons.

		Stomach contents		Stable isotopes	
Comparison type	**Comparison**	**Frequency**	**Magnitude**	**Frequency**	**Magnitude**
Habitat	All	37%	1039%±2086%	42%	836%±2099%
	Marsh–near-pond	33%	108%±67%	37%	1074%±2722%
	Marsh–pond	32%	888%±2035%	41%	894%±2222%
	Near-pond–pond	47%	1809%±2651%	52%	482%±739%
Season	All	47%	813%±1387%	43%	389%±966%
	Marsh	47%	415%±532%	47%	267%±568%
	Near-pond	75%	3230%±2139%	42%	70%±14%
	Pond	42%	256%±325%	39%	671%±1436%
Slough	SRS versus TS	40%	144%±118%	43%	1033%±2474%

Note: Comparisons follow structure of Table 2.

consumer guts across habitats and seasons; however, relative abundances of taxa shifted (Figure S4). For example, in SRS wet-season marsh consumers, ostracods and aquatic mites (Hydrachnidia) were the second and third most abundant prey items, while in ponds cladocerans were the second most abundant prey approximately tripling in average count per individual stomach from marsh consumers to pond consumers (Figure S4). Aquatic snails (Mollusca) were the most abundant prey item in guts of consumers from SRS wet-season marshes and ponds but were rare or absent in guts of consumers from other slough-habitat-season levels.

Dietary shifts (changes in gut contents defined by pairwise PERMANOVA $p \leq 0.05$) for species size classes occurred in 21% of seasonal comparisons, 11% of habitat comparisons, and 8% of slough comparisons (Table S8). Changes in diet among habitats (Tables S9 and S10) were more common in near-pond-pond comparisons (19%) than marsh-pond comparisons (13%) and more frequent during the dry season (73% of shifts). Dietary shifts between habitats (≥10% change in percent contribution to diet per prey category, Table S8) were driven by shifts in consumption of omnivorous invertebrates (100% of shifts), detritus (73%), carnivorous invertebrates (64%), herbivorous invertebrates (36%), and producers (9%).

3.5 | Trophic niche area—Stomach contents

We documented greater niche$_{\mathrm{SCA}}$ in dry-season ponds (Table 1) than in wet-season ponds and spatial shifts between ponds and near-ponds (the two alligator-engineered habitats) compared to other pairwise habitat comparisons (i.e. ponds vs. marshes and near-ponds vs. marshes). Shifts in trophic niche area occurred in 47% of seasonal comparisons, 40% of slough comparisons, and 37% of habitat comparisons (Table 3; Table S11; Figure S5). For seasonal comparisons in ponds, dry-season niche$_{\mathrm{SCA}}$ typically increased (63% of shifts) with an average increase of ~25%, yet typically decreased in all other habitats (Figures 4 and 5a). However, niche$_{\mathrm{SCA}}$ for mesopredators was approximately one-sixth the size in dry-season compared to wet-season

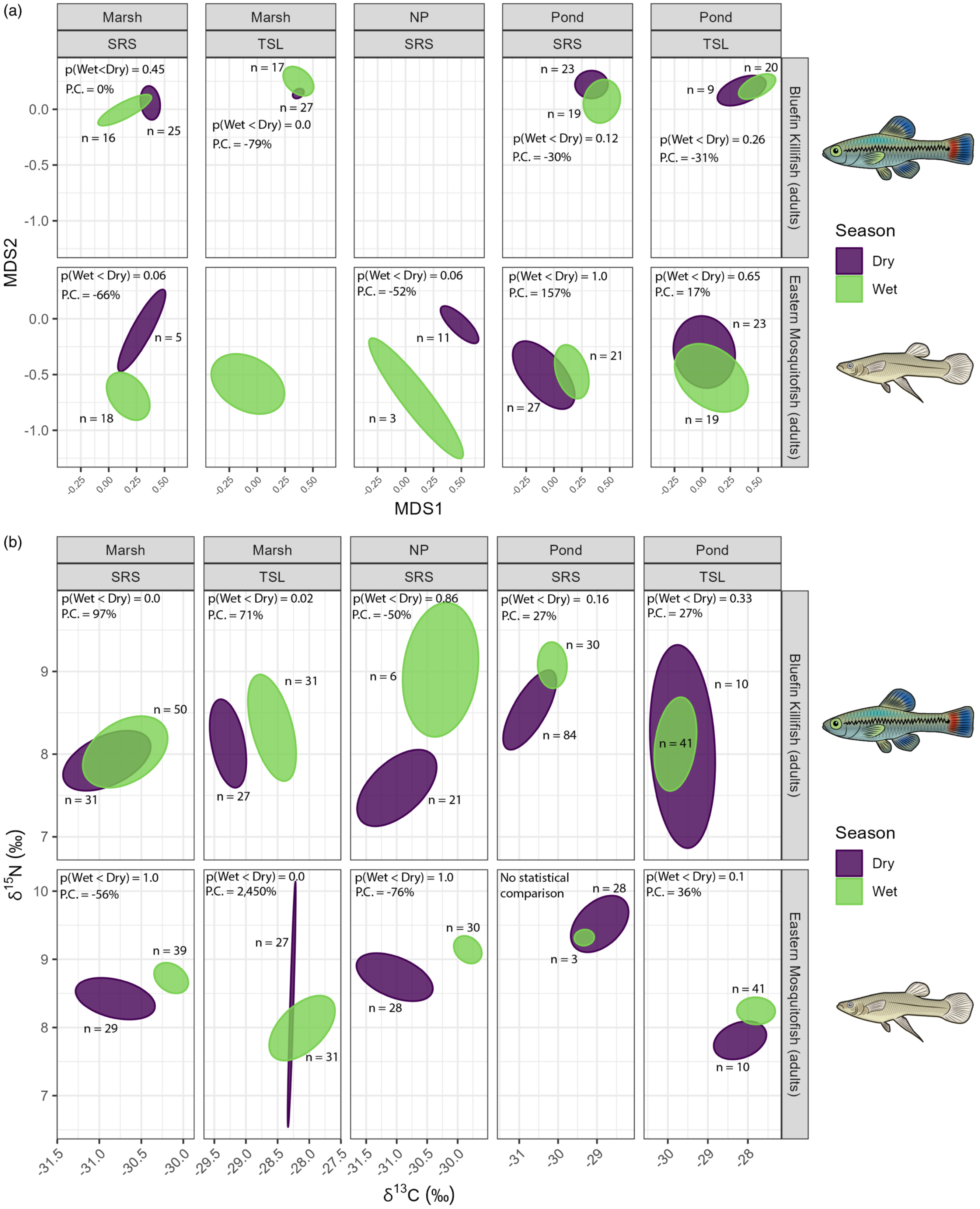

FIGURE 4 Seasonal changes in (a) niche$_{SCA}$ (Table S10) and (b) niche$_{SIA}$ (Table S11) for adult Bluefin Killifish and Eastern Mosquitofish. Probability of change—*p*(Wet < Dry)—is the probability the ellipse is smaller in the wet season than the dry season, while 'P.C.' represents percent change in ellipse area from wet season to dry season. Sample size (*n*) is the number of individuals per season per habitat.

ponds (Figure 5c). Average magnitude of seasonal changes was greatest in SRS near-ponds (3330%), relatively similar in SRS marshes (167%) and ponds (197%), but was more than twice as large in TS marshes (746%) compared to TS ponds (354%). Seasonal shifts occurred in 75% of comparisons in SRS near-ponds (TS near-ponds dried prior to dry season sampling), while seasonal shifts were more common in marsh comparisons (SRS marsh = 40%; TS marsh = 60%) than pond comparisons (SRS ponds = 38%; TS ponds = 50%) (Table S11). For shifts in niche$_{SCA}$ among habitats, changes were more likely in near-pond versus pond comparisons (47%) than either marsh versus pond (32%) or marsh versus near-pond (33%) comparisons (Table 3; Table S6). Niche$_{SCA}$ increased in ponds compared to marshes (70% of shifts) and near-ponds (100% of shifts) (Figure S5; see Table S11 for effect sizes of individual comparisons).

3.6 | Trophic niche area—Stable isotopes

Niche$_{SIA}$ typically decreased in dry-season ponds, while spatial trends were similar (shifts in niche$_{SIA}$ being more frequent in near-pond vs. pond comparisons). We documented shifts in niche$_{SIA}$ in 43% of seasonal comparisons, 42% of habitat comparisons, and 41% of slough comparisons (Table 3; Table S12; Figure S5). In the dry season relative to the wet season, niche$_{SIA}$ in ponds was nearly cut in half on average and with most species size classes (62%) decreasing in niche$_{SIA}$. In other habitats (marsh and near-pond), shifts in niche$_{SIA}$ were typically increases with niche$_{SIA}$ being approximately four times larger in dry-season than wet-season near ponds (Figure 5b; Table S12). Despite numerically having more dry-season increases in marshes, the average size difference was nearly zero. Shifts in niche$_{SIA}$ in dry-season ponds were increases for mesopredators (~3×), detritivores (~3×), and half of omnivores were increases, while shifts for remaining omnivores and numerically abundant invertivores (~1/2×) were decreases (Figure 5d). In both sloughs, magnitude of seasonal shifts was greatest in ponds (SRS = 343%; TS = 1762%) followed by marshes (SRS = 101%, TS = 414%) with the smallest changes found in near-pond habitats (SRS = 71%; TS = 67%). Like niche$_{SCA}$, shifts in niche$_{SIA}$ occurred more frequently in near-pond versus pond comparisons (52%) than either marsh versus pond (41%) or marsh versus near-pond comparisons (37%). However, for niche$_{SIA}$ we revealed the greatest magnitude of spatial change in area in marsh versus near-pond comparisons (1074%) and approximately half that in marsh versus pond (499%) and near-pond versus pond (482%) comparisons (see Table S11 for effect sizes of individual comparisons). Niche$_{SIA}$ typically increased in ponds relative to near-ponds (71% of shifts), while increases and decreases were equally likely in marshes relative to ponds (50% of shifts).

4 | DISCUSSION

Our study supported predictions of the SGH and IDH by documenting food-web and dietary shifts in aquatic communities impacted by an ecosystem engineer, the American alligator. We report evidence that ecosystem engineering by alligators facilitates species coexistence because fish CPUE increased in alligator ponds when dry-season water recession elevated environmental stress and loss of surrounding marsh habitat. We observed dietary shifts by aquatic consumers inhabiting ponds alligators created and maintained during dry-season stress, but that the basal resources supporting that food web did not change. For both niche$_{SCA}$ and niche$_{SIA}$, whether niche area increased (a proxy for a decrease in competition) depended on trophic guild. However, seasonal trends in ponds were opposite for niche$_{SCA}$ and niche$_{SIA}$ in invertivores, omnivores and mesopredators. This discrepancy may be the result of niche$_{SCA}$ and niche$_{SIA}$ representing different dimensions of an organism's ecology integrated over different time periods (Nielsen et al., 2018; Petta et al., 2020; Shipley & Matich, 2020). Based on NVH assumptions, niche$_{SCA}$ suggested that competition decreased in dry-season ponds for some trophic guilds, as predicted by the SGH and IDH (Bertness & Callaway, 1994; Grime, 1973; Van Valen, 1965). However, elevated mortality late in the dry season from predation and poor water quality may reduce benefits of alligator ponds. Below, we address two possible interconnected explanations for conflicting trends in niche$_{SCA}$ and niche$_{SIA}$: (1) stomach contents and stable isotopes represent diet integrated over different time periods (Nielsen et al., 2018) and (2) predation may be more influential than competition in aquatic ecosystems (Alofs & Jackson, 2014).

Stomach contents and stable isotopes reflect different aspects of trophic behaviour and are seldom comparable or interchangeable (Petta et al., 2020). Stomach contents reflect prey ingested over 24–48 h prior to collection, while stable isotopes represent diet integrated over several weeks (Nielsen et al., 2018). Competition may be most clearly revealed over shorter time scales, like those represented by stomach contents, while effects of predation on trophic behaviour may outweigh those of competition at the longer time scales reflected by stable isotopes. Additionally, physiological factors such as changes in growth rate and stress can lead to differences in isotopic signatures regardless of diet (Gorokhova, 2018; Karlson et al., 2018). Alligator-engineered depth and nutrient differences among habitats may influence physiological factors driving changes in stable isotope values unrelated to diet. At these study sites, some plants and animals have lower N:P in ponds compared to adjacent marshes, indicative of faster growth rates (Strickland et al., 2023; Vrede et al., 2004). Furthermore, it is possible that in the dry season, fishes caught in ponds had recently migrated from marshes where they were consuming prey. Given the month required for whole-animal tissue turnover (Vander Zanden et al., 2015), niche$_{SIA}$ measured in dry-season ponds may reflect assimilation from previous marsh (or near-pond) foraging (Abbey-Lee et al., 2013). Larger fishes become restricted to ponds early in the dry season (Parkos et al., 2011), while smaller fishes can swim among habitats later into the dry season, which may partially explain differences in niche area among trophic guilds.

Mechanisms influencing competition may differ between aquatic and terrestrial ecosystems (as indicated by decreased

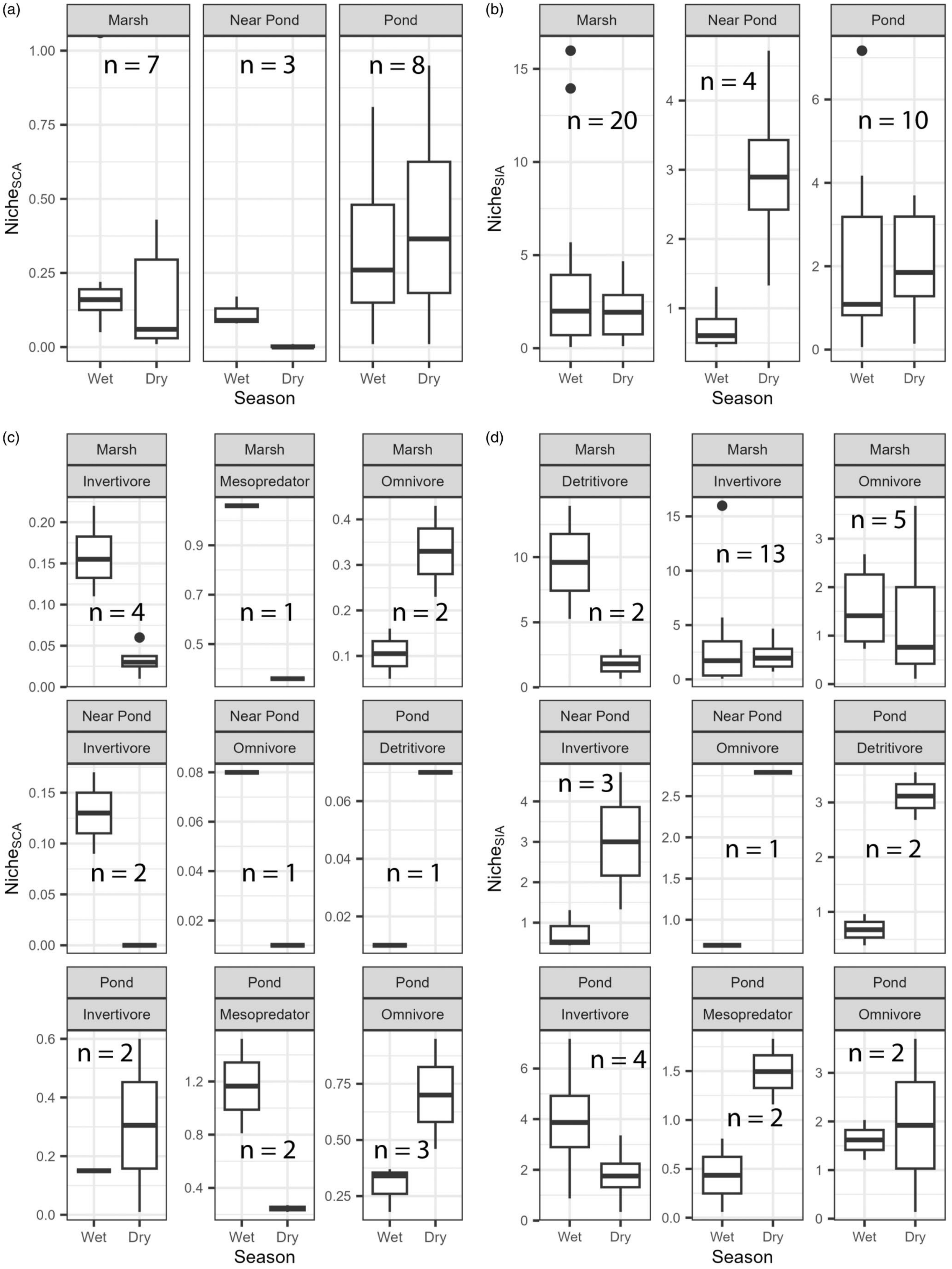
(a)
Marsh
Near Pond
Pond
n = 7
n = 3
n = 8
Niche$_{SCA}$
1.00
0.75
0.50
0.25
0.00
Wet
Dry
Season
(b)
Marsh
Near Pond
Pond
n = 20
n = 4
n = 10
Niche$_{SIA}$
Wet
Dry
Season
(c)
Marsh
Invertivore
Mesopredator
Omnivore
Near Pond
Pond
Detritivore
n = 4
n = 1
n = 2
n = 2
n = 1
n = 1
n = 2
n = 2
n = 3
Niche$_{SCA}$
Wet
Dry
Season
(d)
Marsh
Detritivore
Invertivore
Omnivore
Near Pond
Pond
Mesopredator
n = 2
n = 13
n = 5
n = 3
n = 1
n = 2
n = 4
n = 2
n = 2
Niche$_{SIA}$
Wet
Dry
Season

FIGURE 5 Boxplots of (a) $\text{niche}_{\text{SCA}}$ and (b) $\text{niche}_{\text{SIA}}$ for only species size classes that underwent a seasonal shift in niche area to visualize the direction of those shifts and subdivided by trophic guilds for (c) stomach contents and (d) stable isotopes. Sample sizes represent the number of species size classes within that habitat that underwent a seasonal shift in niche area. More comparisons were made but were not statistically different (Tables S10 and S11).

support for the IDH in aquatic ecosystems) and/or for mobile versus sedentary organisms (Barrio et al., 2013; Moi et al., 2020). Prior tests of the SGH have primarily been performed using terrestrial plant communities (Malkinson & Tielbörger, 2010). The relative importance of competition and predation in structuring freshwater communities and animal movement in response to those pressures may be opposite of terrestrial ecosystems (Alofs & Jackson, 2014; Jackson et al., 2001; Strong, 1992; Werner et al., 1983). For instance, a meta-analysis revealed that predation had a larger effect size than competition in structuring communities in freshwater environments compared to terrestrial ones (Alofs & Jackson, 2014). This finding aligns with another meta-analysis that demonstrated a trade-off between competition and predation where competition had a greater effect on growth rate, while predation had a greater effect on survival (Gurevitch et al., 2000). Furthermore, Fox (2013) observed that disturbance could slow species exclusion by increasing mortality rates just as by the more commonly assumed interruption of interspecific competition. As animals seek refuge in alligator-engineered ponds, predation risk and associated mortality inevitably increase as the dry season progresses. Mobile aquatic consumers may differentially use available habitats to optimize this trade-off among habitat and resource availability, competition, and predation. Over longer time intervals (weeks to months), there may be more variability in space use in response to predation risk than in reducing or avoiding competition (Heithaus & Dill, 2002; Werner et al., 1983). Foraging among habitats with different floral and faunal communities and nutrient levels (Strickland et al., 2023) may be an alternative strategy to diet switching for coping with environmental stress, expanding the spatial dimension of the animal's realized niche through movement and habitat choice that does not alter the trophic niche (neither stomach content nor isotopic).

Facilitation of coexistence and seasonal changes in trophic niche areas may be temporary, and our study cannot disentangle effects of competition from predation because alligator-created habitats attract fishes from multiple trophic levels. Environmental stress and predation can increase mortality rates, which inhibits competitive exclusion (Fox, 2013). Previous work demonstrated that fishes in alligator ponds late in the dry season may experience low dissolved oxygen, higher nitrogenous waste, and increased mortality from predation (Kushlan, 1974; Kushlan & Hunt, 1979). Similar community succession and mortality as the dry season progresses have been observed in solution holes (deeper pockets in the limestone in shorter-hydroperiod regions of the Everglades) (Kobza et al., 2004; Rehage et al., 2014). Since sampling of alligator ponds occurred early in the dry season, we did not document oxygen-stress induced mortality. There may be a tipping point at which environmental stress from drying and/or predation pressure becomes too intense, and facilitation of coexistence ceases in alligator ponds (Parkos et al., 2011). Taken together, this previous research suggests that instead of a linear relationship between environmental stress and competition (SGH), there may be a unimodal relationship, like the IDH, where competition increases at higher levels of environmental stress and/or because of additional stress or predation. Competition and predation may work in tandem to facilitate coexistence with their relative strength differing across time scales (as discussed above) and through time as stress/disturbance continues (Figure 6).

Dietary shifts among habitats were most common when comparing ponds to other habitats and in the dry season, when aquatic animal densities are high (Brauns et al., 2022; McHugh et al., 2015; Takimoto & Post, 2013). Shifts in diet among habitats were in part explained by differential consumption of omnivorous invertebrates, a group that contains zooplankton (e.g. copepods and cladocerans). In freshwater lakes, relative abundance of zooplankton changes based on the limiting nutrient (Sterner & Elser, 2002). This trend holds in our study system, an oligotrophic (phosphorus-limited) wetland, across this alligator-engineered habitat and phosphorus gradient with elevated zooplankton densities in ponds (Strickland et al., 2023). Therefore, it is not surprising that bottom-up effects of nutrient enrichment drive spatial variation in prey availability that extends across trophic levels to spatial variation in prey consumption. While facilitation by ecosystem engineers has been shown to have similar effects on trophic dynamics in other ecosystems (Sanders & Van Veen, 2011; Van der Zee et al., 2016), to our knowledge this is the first time such effects have been demonstrated for an ecosystem engineer that is also a large-bodied predator.

Everglades aquatic consumers mostly relied on detrital energy and, contrary to expectations, evidence of shifts in basal resource use was rare in this study. Previous work documented increased phosphorus levels, which is the primary limiting nutrient in the Everglades (McCormick et al., 2002), in alligator-engineered habitats (Strickland et al., 2023). Other work has also demonstrated that habitat modification by ecosystem engineers can increase strength of bottom-up effects (Zhong et al., 2017). It is possible that increased availability of phosphorus would lead to increased producer biomass and growth resulting in a bottom-up shift towards autotrophic energy throughout the food web (Polis, 1999; Polis et al., 1997; Power, 1992; Sterner & Elser, 2002). Instead of increased primary production in alligator-engineered habitats entering the food web through primary consumers, it may become incorporated into the

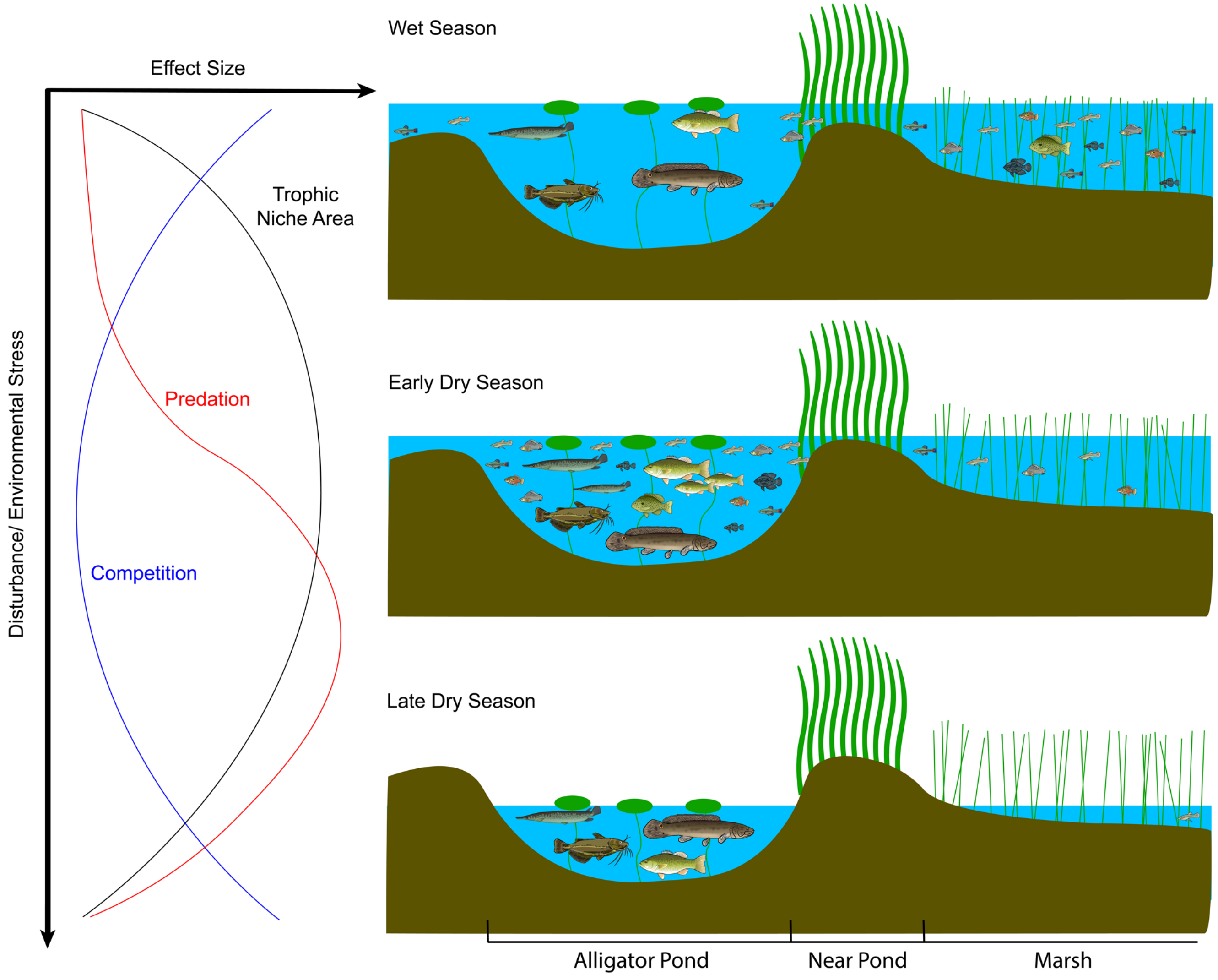

FIGURE 6 Theoretical relationships between trophic niche area, competition, and predation in alligator-engineered ponds as the dry season progresses represented by our data (wet season, early dry season) and beyond (late dry season). In the wet season, ponds are occupied by a relatively low density of prey resulting in higher competition for relatively few resources (low prey availability) and larger trophic niches. In the early dry season, fishes of all trophic levels are concentrated in ponds. Ecosystem engineering of ponds facilitates coexistence by providing refuge from marsh drying and elevated nutrient levels to support higher densities of consumers. Higher order consumers exert increasing predation pressure on prey, which may cause their prey to use what remains of adjacent habitats to avoid predation, reducing competition in ponds and increasing trophic niche area. The increased species richness in ponds means a higher diversity of available prey, also increasing trophic niche areas. Predation pressure peaks after trophic niche as densities decline and predation starts to have a higher per capita effect. Late in the dry season, small fishes are thought to have undergone high mortality. Remaining species are suffering from elevated environmental stress (low dissolved oxygen, high nitrogenous waste) and become more generalist in the absence of ideal prey.

microbial loop via positive algal priming of decomposition (Halvorson et al., 2019; Kuehn et al., 2014; Trexler et al., 2015). Moreover, dry-season strengthening of a detrital loop in alligator ponds could explain observed contraction of $\text{niche}_{\text{SIA}}$ (more energy flowing through the detrital loop homogenizing δ^{13}C values) and increased trophic position (microbial loop adding a trophic step between primary producers and first-order consumers). Further research is needed to measure changes in primary production and quantify its incorporation into different food-web compartments among alligator-engineered habitats.

In this study we demonstrated that ecosystem engineering by alligators alters resource availability with food-web effects that result in prey being attracted to sites of high predation. Combined with other work (Strickland et al., 2023), the role alligators play in these habitats by increasing nutrients and having bottom-up trophic effects are similar to those of hippopotami (Dutton et al., 2018; Subalusky et al., 2015). While observed nutrient increases from alligators are likely much smaller than those reported for hippopotami, the increases associated with alligator-engineering are ecologically important to the function of a nutrient-poor ecosystem such as the Everglades. In terrestrial ecosystems, predators, like Artic foxes (*Vulpes lagopus*) and Red foxes (*V. vulpes*), have been shown to create similar biogeochemical hotspots that attract their prey (Gharajehdaghipour & Roth, 2018; Zhao et al., 2022). Predator-induced nutrient enrichment can create a risk–reward trade-off or even a positive feedback loop between resources and risk (Johnson-Bice, Gable, et al., 2023; Johnson-Bice, Roth, & Markham, 2023; Monk & Schmitz, 2022). In the case of alligator-engineered ponds, bottom-up effects facilitate predators and prey across multiple trophic levels.

Despite the small spatial coverage of alligator ponds, this work adds to a growing body of evidence that these ponds are pivotal to the function of the Everglades ecosystem (DeAngelis et al., 1997; Kushlan, 1974; Strickland et al., 2023). Efforts should be made to quantify landscape-scale effects of alligator ponds using remote sensing (e.g. Johnson-Bice, Roth, & Markham, 2023). Additionally, questions remain about how far into the dry season positive effects of alligator ponds persist before negative effects related to crowding become dominant (Figure 6) and what the consequences may be for marsh recolonization in the wet season and subsequent secondary production. To address this, future research should visit ponds at multiple time points during both the wet and dry seasons across multiple years that encompass a diversity of hydrological conditions. Alligators may be as important to the Everglades and its restoration as beavers (*Castor canadensis*) for North American streams (Naiman et al., 1986). Effects of ecosystem engineering, such as by alligators in this study, should be directly included in restoration planning (He et al., 2024).

5 | CONCLUSIONS

Our data provided new insights on the SGH that arise from studying animal communities as opposed to plants, including potential effects of mobility and relative influence of predation and competition on niche$_{SCA}$ and niche$_{SIA}$ among trophic guilds. Moreover, we propose that the SGH may be a special case of the IDH where ecosystem engineering facilitates coexistence. Except for Lowney and Thomson (2021, 2022), previous community-wide tests of the SGH have been in plant communities (Holzapfel et al., 2006; Tewksbury & Lloyd, 2001). Mechanistic understanding and theory surrounding the SGH in communities of mobile organisms with differing feeding modes is just beginning to be developed (e.g. Barrio et al., 2013), which may explain why the connection between the SGH and IDH has not previously been made. This study was, to our knowledge, the first to examine facilitation impacting trophic dynamics by an ecosystem engineer that is also a large predator. Additional theoretical, empirical, and modelling studies are required to fill in these gaps (Soliveres et al., 2015), particularly concerning interactions between predation risk and facilitation of coexistence when ecosystem engineers benefit predators and prey. Increased mechanistic understanding of positive interactions in animal communities and how these processes are maintained within ecosystems is critical to conserving biodiversity in response to global increases in anthropogenic disturbance and directional environmental change (Coggan et al., 2018; Ratajczak et al., 2018). These questions should be a priority for future research to inform restoration and conservation efforts that need to consider the role of engineers on maintaining biodiversity and ecosystem functions and services as global change progresses.

AUTHOR CONTRIBUTIONS

Peter J. Flood, Bradley A. Strickland, Joel C. Trexler and Jeffrey L. Kline conceived the ideas and designed methodology; Trexler obtained and managed project funding; Flood, Strickland and Trexler collected the data; Flood analysed the data and 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 conflicts of interests.

DATA AVAILABILITY STATEMENT

Data available from the Florida Coastal Everglades Long-Term Ecological Research database—stable isotope and stomach content data: https://doi.org/10.6073/pasta/306f6b68dd46ae201f628b0a240d1673 (Flood et al., 2025) and long-term fish monitoring data: https://doi.org/10.6073/pasta/70379cfaa3572272bfd5e6e7d0d7840c (Pintar et al., 2022). R scripts for statistical analyses are available at https://github.com/pjflood/diet_and_pond_enrichment.

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REFERENCES

Abbey-Lee, R. N., Gaiser, E. E., & Trexler, J. C. (2013). Relative roles of dispersal dynamics and competition in determining the isotopic niche breadth of a wetland fish. *Freshwater Biology*, *58*(4), 780–792. https://doi.org/10.1111/fwb.12084

Adams, S. M., Kimmel, B. L., & Ploskey, G. R. (1983). Sources of organic matter for reservoir fish production: A trophic-dynamics analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, *40*(9), 1480–1495. https://doi.org/10.1139/f83-170

Alofs, K. M., & Jackson, D. A. (2014). Meta-analysis suggests biotic resistance in freshwater environments is driven by consumption rather than competition. *Ecology*, *95*(12), 3259–3270.

Barrio, I. C., Hik, D. S., Bueno, C. G., & Cahill, J. F. (2013). Extending the stress-gradient hypothesis - is competition among animals less common in harsh environments? *Oikos*, *122*(4), 516–523. https://doi.org/10.1111/j.1600-0706.2012.00355.x

Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, *9*(5), 191–193. https://doi.org/10.1016/0169-5347(94)90088-4

Bolnick, D. I., Ingram, T., Stutz, W. E., Snowberg, L. K., Lau, O. L., & Pauli, J. S. (2010). Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1689), 1789–1797. https://doi.org/10.1098/rspb.2010.0018

Bolnick, D. I., Svanbäck, R., Araújo, M. S., & Persson, L. (2007). Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(24), 10075–10079. https://www.pnas.org

Brandt, L. A., Campbell, M. R., & Mazzotti, F. J. (2010). Spatial distribution of alligator holes in the central Everglades. *Southeastern Naturalist*, *9*(3), 487–496.

Brauns, M., Kneis, D., Brabender, M., & Weitere, M. (2022). Habitat availability determines food chain length and interaction strength in food webs of a large lowland river. *River Research and Applications*, *38*(2), 323–333. https://doi.org/10.1002/rra.3908

Burdon, F. J., McIntosh, A. R., & Harding, J. S. (2020). Mechanisms of trophic niche compression: Evidence from landscape disturbance. *Journal of Animal Ecology*, *89*(3), 730–744. https://doi.org/10.1111/1365-2656.13142

Campbell, M. R., & Mazzotti, F. J. (2004). Characterization of natural and artificial alligator holes. *Southeastern Naturalist*, *3*(4), 583–594.

Chase, J. M., & Leibold, M. A. (2003). Environmental variability in time and space. In J. N. Thompson (Ed.), *Ecological niches: Linking classical and contemporary approaches* (pp. 95–105). The University of Chicago Press.

Chick, J. H., Coyne, S., & Trexler, J. C. (1999). Effectiveness of airboat electrofishing for sampling fishes in shallow, vegetated habitats. *North American Journal of Fisheries Management*, *19*(4), 957–967. https://doi.org/10.1577/1548-8675(1999)019⟨0957:eoaefs⟩2.0.co;2

Coggan, N. V., Hayward, M. W., & Gibb, H. (2018). A global database and 'state of the field' review of research into ecosystem engineering by land animals. *Journal of Animal Ecology*, *87*(4), 974–994. https://doi.org/10.1111/1365-2656.12819

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, *199*(4335), 1302–1310. www.sciencemag.org

Crain, C. M., & Bertness, M. D. (2006). Ecosystem engineering across environmental gradients: Implications for conservation and management. *BioScience*, *56*(3), 211–218. https://academic.oup.com/bioscience/article/56/3/211/333064

Dangles, O., Herrera, M., Carpio, C., & Lortie, C. J. (2018). Facilitation costs and benefits function simultaneously on stress gradients for animals. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1885), 20180983. https://doi.org/10.1098/rspb.2018.0983

DeAngelis, D. L., Loftus, W. F., Trexler, J. C., & Ulanowicz, R. E. (1997). Modeling fish dynamics and effects of stress in a hydrologically pulsed ecosystem. *Journal of Aquatic Ecosystem Stress and Recovery*, *6*, 1–13.

Dexter, E., Rollwagen-Bollens, G., & Bollens, S. M. (2018). The trouble with stress: A flexible method for the evaluation of nonmetric multidimensional scaling. *Limnology and Oceanography: Methods*, *16*(7), 434–443. https://doi.org/10.1002/lom3.10257

Dutton, C. L., Subalusky, A. L., Hamilton, S. K., Rosi, E. J., & Post, D. M. (2018). Organic matter loading by hippopotami causes subsidy overload resulting in downstream hypoxia and fish kills. *Nature Communications*, *9*(1), 1951. https://doi.org/10.1038/s41467-018-04391-6

Flood, P. J., Loftus, W. F., & Trexler, J. C. (2023). Fishes in a seasonally pulsed wetland show spatiotemporal shifts in diet and trophic niche but not shifts in trophic position. *Food Webs*, *34*, e00265. https://doi.org/10.1016/j.fooweb.2022.e00265

Flood, P. J., Strickland, B. A., & Trexler, J. C. (2025). *Stomach contents and stable isotopes from the aquatic food web in Everglades National Park, Florida, USA, 2018-2019 ver 1*. Environmental Data Initiative. https://doi.org/10.6073/pasta/306f6b68dd46ae201f628b0a240d1673

Fox, J. W. (2013). The intermediate disturbance hypothesis should be abandoned. *Trends in Ecology & Evolution*, *28*(2), 86–92. https://doi.org/10.1016/j.tree.2012.08.014

Gaiser, E. E., Trexler, J. C., & Wetzel, P. R. (2012). The Florida everglades. In D. P. Batzer & A. H. Baldwin (Eds.), *The Florida everglades* (pp. 231–252). University of California Press. https://doi.org/10.5749/minnesota/9780816670260.003.0001

García-Navas, V., Sattler, T., Schmid, H., & Ozgul, A. (2021). Bird species co-occurrence patterns in an alpine environment supports the stress-gradient hypothesis. *Oikos*, *130*(11), 1905–1918. https://doi.org/10.1111/oik.08588

Gharajehdaghipour, T., & Roth, J. D. (2018). Predators attract prey through ecosystem engineering in the arctic. *Ecosphere*, *9*(1), e02077. https://doi.org/10.1002/ecs2.2077

Gorokhova, E. (2018). Individual growth as a non-dietary determinant of the isotopic niche metrics. *Methods in Ecology and Evolution*, *9*(2), 269–277. https://doi.org/10.1111/2041-210X.12887

Grime, J. P. (1973). Competitive exclusion in herbaceous vegetation. *Nature*, *242*(5396), 344–347.

Gunderson, L. H., & Loftus, W. F. (1993). The Everglades. In W. H. Martin, S. G. Boyce, & E. G. Echternacht (Eds.), *Biodiversity of the southeastern United States* (Vol. 2, pp. 199–255). John Wiley and Sons Inc. https://www.researchgate.net/publication/258238657

Gurevitch, J., Morrison, J. A., & Hedges, L. V. (2000). The interaction between competition and predation: A meta-analysis of field experiments. *American Naturalist*, *155*, 435–453.

Gutiérrez-Fonseca, P. E., Pringle, C. M., Ramírez, A., Gómez, J. E., & García, P. (2024). Hurricane disturbance drives trophic changes in neotropical mountain stream food webs. *Ecology*, *105*(1), e4202. https://doi.org/10.1002/ecy.4202

Halvorson, H. M., Francoeur, S. N., Findlay, R. H., & Kuehn, K. A. (2019). Algal-mediated priming effects on the ecological stoichiometry of leaf litter decomposition: A meta-analysis. *Frontiers in Earth Science*, *7*. https://doi.org/10.3389/feart.2019.00076

Hansen, L. E., Yackulic, C. B., Dickson, B. G., Deemer, B. R., & Best, R. J. (2023). Linking ecosystem processes to consumer growth rates: Gross primary productivity as a driver of freshwater fish somatic growth in a resource-limited river. *Canadian Journal of Fisheries and Aquatic Sciences*, *80*, 1456–1469. https://doi.org/10.1139/cjfas-2022-0229

He, F., Svenning, J. C., Chen, X., Tockner, K., Kuemmerle, T., le Roux, E., Moleón, M., Gessner, J., & Jähnig, S. C. (2024). Freshwater megafauna shape ecosystems and facilitate restoration. *Biological Reviews*, *99*(4), 1141–1163. https://doi.org/10.1111/brv.13062

Heithaus, M. R., & Dill, L. M. (2002). Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology*, *83*(2), 480–491.

Hervé, M. (2022). *RVAidMemoire: Testing and plotting procedures for biostatistics* (R package version 0.9-79). https://cran.r-project.org/package=RVAideMemoire

Holzapfel, C., Tielbörger, K., Parag, H. A., Kigel, J., & Sternberg, M. (2006). Annual plant-shrub interactions along an aridity gradient. *Basic and Applied Ecology*, *7*(3), 268–279. https://doi.org/10.1016/j.baae.2005.08.003

Hutchinson, G. E. (1961). The paradox of the plankton. *The American Naturalist*, *95*(882), 137–145.

Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER—Stable isotope Bayesian ellipses in R. *Journal of Animal Ecology*, *80*(3), 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jackson, D. A., Peres-Neto, P. R., & Olden, J. D. (2001). What controls who is where in freshwater fish communities—The roles of biotic, abiotic, and spatial factors? *Canadian Journal of Fisheries and Aquatic Sciences*, *58*, 157–170.

Johnson-Bice, S. M., Gable, T. D., Roth, J. D., & Bump, J. K. (2023). Patchy indirect effects of predation: Predators contribute to landscape heterogeneity and ecosystem function via localized pathways. *Oikos*, *2023*(10), e10065. https://doi.org/10.1111/oik.10065

Johnson-Bice, S. M., Roth, J. D., & Markham, J. H. (2023). A cosmic view of 'tundra gardens': Satellite imagery provides a landscape-scale perspective of arctic fox ecosystem engineering. *Ecosystems*, *26*, 1670–1684. https://doi.org/10.1007/s10021-023-0085

Jost, L., Chao, A., & Chazdon, R. L. (2011). Compositional similarity and beta diversity. In A. E. Magurran & B. J. McGill (Eds.), *Biological diversity. Frontiers in measurement and assessment* (pp. 66–84). Oxford University Press (OUP).

Karlson, A. M. L., Reutgard, M., Garbaras, A., & Gorokhova, E. (2018). Isotopic niche reflects stress-induced variability in physiological status. *Royal Society Open Science*, *5*(2), 171398. https://doi.org/10.1098/rsos.171398

Kobza, R. M., Trexler, J. C., Loftus, W. F., & Perry, S. A. (2004). Community structure of fishes inhabiting aquatic refuges in a threatened Karst wetland and its implications for ecosystem management. *Biological Conservation*, *116*(2), 153–165. https://doi.org/10.1016/S0006-3207(03)00186-1

Kuehn, K. A., Francoeur, S. N., Findlay, R. H., & Neely, R. K. (2014). Priming in the microbial landscape: Periphytic algal stimulation of litter-associated microbial decomposers. *Ecology*, *95*(3), 749–762.

Kushlan, J. A. (1974). Observations on the role of the American alligator in the southern Florida wetlands. *Copeia*, *1974*(4), 993–996.

Kushlan, J. A., & Hunt, B. P. (1979). Limnology of an alligator pond in south Florida. *Florida Scientist*, *42*(2), 65–84.

Lenth, R. V. (2024). *emmeans: Estimated marginal means, aka least-squares means* (1.10.1).

Loftus, W. F., & Kushlan, J. A. (1987). Freshwater fishes of southern Florida. *Bulletin of the Florida State Museum, Biological Sciences*, *31*, 147–344.

Lowney, A. M., & Thomson, R. L. (2021). Ecological engineering across a temporal gradient: Sociable weaver colonies create year-round animal biodiversity hotspots. *Journal of Animal Ecology*, *90*(10), 2362–2376. https://doi.org/10.1111/1365-2656.13544

Lowney, A. M., & Thomson, R. L. (2022). Ecological engineering across a spatial gradient: Sociable weaver colonies facilitate animal associations with increasing environmental harshness. *Journal of Animal Ecology*, *91*(7), 1385–1399. https://doi.org/10.1111/1365-2656.13688

Malkinson, D., & Tielbörger, K. (2010). What does the stress-gradient hypothesis predict? Resolving the discrepancies. *Oikos*, *119*(10), 1546–1552. https://doi.org/10.1111/j.1600-0706.2010.18375.x

Mangiafico, S. (2022). *rcompanion: Functions to support extension education program evaluation* (R package version 2.3.27). https://cran.r-project.org/package=rcompanion

McCormick, P. V., Newman, S., Miao, S., Gawlik, D. E., Marley, D., Reddy, K. R., & Fontaine, T. D. (2002). Effects of anthropogenic phosphorus inputs on the Everglades. In J. Porter (Ed.), *The Everglades, Florida bay, and coral reefs of the Florida keys: An ecosystem sourcebook* (pp. 83–126). CRC Press.

McCune, B., & Grace, J. B. (2002). *Analysis of ecological communities*. MjM Software Design.

McHugh, P. A., Thompson, R. M., Greig, H. S., Warburton, H. J., & Mcintosh, A. R. (2015). Habitat size influences food web structure in drying streams. *Ecography*, *38*(7), 700–712. https://doi.org/10.1111/ecog.01193

Moi, D. A., García-Ríos, R., Hong, Z., Daquila, B. V., & Mormul, R. P. (2020). Intermediate disturbance hypothesis in ecology: A literature review. *Annales Zoologici Fennici*, *57*(1–6), 67–78. https://doi.org/10.5735/086.057.0108

Monk, J. D., & Schmitz, O. J. (2022). Landscapes shaped from the top down: Predicting cascading predator effects on spatial biogeochemistry. *Oikos*, *2022*(5), e08554. https://doi.org/10.1111/oik.08554

Naiman, R. J., Melillo, J. M., & Hobbie, J. E. (1986). Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology*, *67*(5), 1254–1269. https://doi.org/10.2307/1938681

Nielsen, J. M., Clare, E. L., Hayden, B., Brett, M. T., & Kratina, P. (2018). Diet tracing in ecology: Method comparison and selection. *Methods in Ecology and Evolution*, *9*(2), 278–291. https://doi.org/10.1111/2041-210X.12869

Oksanen, J., Gullaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. M., Szoecs, E., & Wagner, H. (2022). *vegan: Community ecology package* (R package version 2.5-7). https://cran.r-project.org/package=vegan

Palmer, M. L., & Mazzotti, F. J. (2004). Structure of Everglades alligator holes. *Wetlands*, *24*(1), 115–122.

Parkos, J. J., Ruetz, C. R., & Trexler, J. C. (2011). Disturbance regime and limits on benefits of refuge use for fishes in a fluctuating hydroscape. *Oikos*, *120*(10), 1519–1530. https://doi.org/10.1111/j.1600-0706.2011.19178.x

Petta, J. C., Shipley, O. N., Wintner, S. P., Cliff, G., Dicken, M. L., & Hussey, N. E. (2020). Are you really what you eat? Stomach content analysis and stable isotope ratios do not uniformly estimate dietary niche characteristics in three marine predators. *Oecologia*, *192*(4), 1111–1126. https://doi.org/10.1007/s00442-020-04628-6

Piet, G. J., Pet, J. S., Guruge, W. A. H. P., Vijverberg, J., & Van Densen, W. L. T. (1999). Resource partitioning along three niche dimensions in a size-structured tropical fish assemblage. *Canadian Journal of Fisheries and Aquatic Sciences*, *56*(7), 1241–1254. https://doi.org/10.1139/cjfas-56-7-1241

Pintar, M., Dorn, N., Kline, J., & Trexler, J. (2022). *Throw trap and electrofishing data collected during 1996–2022 from the Everglades, Florida, United States for the publication 'Hydrology-mediated ecological function of a large wetland threatened by an invasive predator'*. Environmental Data Initiative. https://doi.org/10.6073/pasta/70379cfaa3572272bfd5e6e7d0d7840c

Polis, G. A. (1999). Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos*, *86*(1), 3–15. https://www.jstor.org/stable/3546565

Polis, G. A., Anderson, W. B., & Holt, R. D. (1997). Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, *28*, 289–316. https://about.jstor.org/terms

Power, M. E. (1992). Top-down and bottom-up forces in food webs: Do plants have primacy. *Ecology*, *73*(3), 733–746.

Quezada-Romegialli, C., Jackson, A. L., Hayden, B., Kahilainen, K. K., Lopes, C., & Harrod, C. (2018). TrophicPosition, an r package for the Bayesian estimation of trophic position from consumer stable isotope ratios. *Methods in Ecology and Evolution*, *9*(6), 1592–1599. https://doi.org/10.1111/2041-210X.13009

R Core Team. (2022). *R: A language and environment for statistical computing* (4.2.2). R Foundation for Statistical Computing. https://www.r-project.org/

Rahman, A. U., Jones, H. P., Hosler, S. C., Geddes, S., Nelson, M., & Barber, N. A. (2021). Disturbance-induced trophic niche shifts in ground beetles (Coleoptera: Carabidae) in restored grasslands. *Environmental Entomology*, *50*(5), 1075–1087. https://doi.org/10.1093/ee/nvab065

Ratajczak, Z., Carpenter, S. R., Ives, A. R., Kucharik, C. J., Ramiadantsoa, T., Stegner, M. A., Williams, J. W., Zhang, J., & Turner, M. G. (2018). Abrupt change in ecological systems: Inference and diagnosis. *Trends in Ecology & Evolution*, *33*(7), 513–526. https://doi.org/10.1016/j.tree.2018.04.013

Rehage, J. S., Liston, S. E., Dunker, K. J., & Loftus, W. F. (2014). Fish community responses to the combined effects of decreased hydroperiod and nonnative fish invasions in a karst wetland: Are Everglades solution holes sinks for native fishes? *Wetlands*, *34*(Suppl. 1), S159–S173. https://doi.org/10.1007/s13157-012-0361-1

Sanders, D., Jones, C. G., Thébault, E., Bouma, T. J., van der Heide, T., van Belzen, J., & Barot, S. (2014). Integrating ecosystem engineering and food webs. *Oikos*, *123*(5), 513–524. https://doi.org/10.1111/j.1600-0706.2013.01011.x

Sanders, D., & Van Veen, F. J. F. (2011). Ecosystem engineering and predation: The multi-trophic impact of two ant species. *Journal of Animal Ecology*, *80*(3), 569–576. https://doi.org/10.1111/j.1365-2656.2010.01796.x

Shipley, O. N., & Matich, P. (2020). Studying animal niches using bulk stable isotope ratios: An updated synthesis. *Oecologia*, *193*(1), 27–51. https://doi.org/10.1007/s00442-020-04654-4

Soliveres, S., Smit, C., & Maestre, F. T. (2015). Moving forward on facilitation research: Response to changing environments and effects on the diversity, functioning and evolution of plant communities. *Biological Reviews of the Cambridge Philosophical Society*, *90*(1), 297–313. https://doi.org/10.1111/brv.12110

Sterner, R. W., & Elser, J. J. (2002). *Ecological stoichiometry: The biology of elements from molecules to the biosphere* (Sterner, R. W. & Elser, J. J., Eds.). Princeton University Press.

Strickland, B. A., Flood, P. J., Kline, J. L., Mazzotti, F. J., Heithaus, M. R., & Trexler, J. C. (2023). An apex predator engineers wetland food-web heterogeneity through nutrient enrichment and habitat modification. *Journal of Animal Ecology*, *92*, 1388–1403. https://doi.org/10.1111/1365-2656.13939

Strong, D. R. (1992). Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology*, *73*(3), 747–754. https://doi.org/10.2307/1940154

Subalusky, A. L., Dutton, C. L., Rosi-Marshall, E. J., & Post, D. M. (2015). The hippopotamus conveyor belt: Vectors of carbon and nutrients from terrestrial grasslands to aquatic systems in sub-Saharan Africa. *Freshwater Biology*, *60*(3), 512–525. https://doi.org/10.1111/fwb.12474

Takimoto, G., & Post, D. M. (2013). Environmental determinants of food-chain length: A meta-analysis. *Ecological Research*, *28*(5), 675–681. https://doi.org/10.1007/s11284-012-0943-7

Tewksbury, J. J., & Lloyd, J. D. (2001). Positive interactions under nurse-plants: Spatial scale, stress gradients and benefactor size. *Oecologia*, *127*(3), 425–434. https://doi.org/10.1007/s004420000614

Trexler, J. C., Gaiser, E. E., Kominoski, J. S., & Sanchez, J. L. (2015). The role of periphyton mats in consumer community structure and function in calcareous wetlands: Lessons from the Everglades. In J. A. Entry, A. D. Gottlieb, K. Javachandrahan, & A. Ogram (Eds.), *Microbiology of the everglades ecosystem* (pp. 155–179). Science Publishers, CRC Press.

Trexler, J. C., & Loftus, W. F. (2016). Invertebrates of the Florida Everglades. In D. Batzer & D. Boix (Eds.), *Invertebrates in freshwater wetlands: An international perspective on their ecology* (pp. 321–356). Springer.

Turner, A. M., Trexler, J. C., Jordan, F. C., Slack, S. J., Geddes, P., Chick, J. H., & Loftus, W. F. (1999). Targeting ecosystem features for conservation: Standing crops in the Florida Everglades. *Conservation Biology*, *13*(4), 898–911.

Van der Zee, E. M., Angelini, C., Govers, L. L., Christianen, M. J. A., Altieri, A. H., van der Reijden, K. J., Silliman, B. R., van de Koppel, J., van der Geest, M., van Gils, J. A., van der Veer, H. W., Piersma, T., de Ruiter, P. C., Olff, H., & van der Heide, T. (2016). How habitat-modifying organisms structure the food web of two coastal ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1826), 20152326. https://doi.org/10.1098/rspb.2015.2326

Van Valen, L. (1965). Morphological variation and width of ecological niche. *The American Naturalist*, *99*(908), 377–390. https://about.jstor.org/terms

Vander Zanden, M. J., Clayton, M. K., Moody, E. K., Solomon, C. T., & Weidel, B. C. (2015). Stable isotope turnover and half-life in animal tissues: A literature synthesis. *PLoS One*, *10*(1), e0116182. https://doi.org/10.1371/journal.pone.0116182

Vrede, T., Dobberfuhl, D. R., Kooijman, S. A. L. M., & Elser, J. J. (2004). Fundamental connections among organism C:N:P stoichiometry, macromolecular composition, and growth. *Ecology*, *85*(5), 1217–1229. https://doi.org/10.1890/02-0249

Wainwright, P. C., & Richard, B. A. (1995). Predicting patterns of prey use from morphology of fishes. *Environmental Biology of Fishes*, *44*(1–3), 97–113. https://doi.org/10.1007/BF00005909

Werner, E. E., Gilliam, J. F., Hall, D. J., & Mittelbach, G. G. (1983). An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, *64*(6), 1540–1548.

Wetzel, W. C., Screen, R. M., Li, I., Mckenzie, J., Phillips, K. A., Cruz, M., Zhang, W., Greene, A., Lee, E., Singh, N., Tran, C., & Yang, L. H. (2016). Ecosystem engineering by a gall-forming wasp indirectly suppresses diversity and density of herbivores on oak trees. *Ecology*, *97*(2), 427–438.

Wheeler, B., & Torchiano, M. (2016). *ImPerm: Permutation tests for linear models* (R package version 2.1.0). https://cran.r-project.org/package=lmPerm

Zhao, S. T., Johnson-Bice, S. M., & Roth, J. D. (2022). Foxes engineer hotspots of wildlife activity on the nutrient-limited Arctic tundra. *Global Ecology and Conservation*, *40*, e02310. https://doi.org/10.1016/j.gecco.2022.e02310

Zhong, Z., Li, X., Pearson, D., Wang, D., Sanders, D., Zhu, Y., & Wang, L. (2017). Ecosystem engineering strengthens bottom-up and weakens top-down effects via trait-mediated indirect interactions. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1863), 20170894. https://doi.org/10.1098/rspb.2017.0894

SUPPORTING INFORMATION

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

Appendix S1: Methods.

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