



OPEN Invasive swamp eels reduce aquatic animal diversity and disproportionately reduce prey for nesting wading birds

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Ecosystem restoration often aims to create environmental conditions that support communities of native organisms resembling those prior to alteration by humans. One focus of the multi-decade multi-billion-dollar Florida Everglades restoration effort is to recreate hydrologic conditions in Everglades National Park and associated pulses of aquatic animal prey to support the large colonies of seasonally nesting wading birds that are iconic predators in the ecosystem. Recent studies indicate that invasion of predatory Asian Swamp Eels (*Monopterus albus/javanensis*) has disrupted the hydrology-mediated production of crayfish and some small fishes in the drainage of first invasion (circa 2012). Here we used a complete community dataset of fish and decapods to report changes to the aquatic community diversity, composition, and biomass of prey produced for wading birds. After the establishment of swamp eels in Taylor Slough (Everglades National Park) average fish and decapod richness declined by 25% and communities shifted to a new state dominated by grass shrimp and a few species of small fishes. Swamp eels differentially reduced the production of primary wading bird resources; while there has been a 68% decline in total small fish and decapod biomass, the biomass of the most important prey species for nesting wading birds declined 80%. If similar impacts follow the spread of swamp eels into other major drainages of the Everglades, the invasion may precipitate an ecosystem collapse—fundamentally simplifying and restructuring the aquatic communities of this vast wetland ecosystem and limiting the trophic support for wading bird breeding aggregations that are important indicators for ecological restoration.

Keywords Everglades, Ecosystem collapse, *Procambarus*, Killifish, Ibis, Top-down effects

Biological invasions are one of the leading factors causing changes to ecosystems worldwide^{1–3}. Introduced predators are among the most destructive invaders⁴, and this is particularly apparent when predators fill a novel niche in the invaded ecosystem^{5,6}. Invasive predators can effectively lead to the formation of novel ecosystems by reducing the abundance, extirpating, or changing the behavior of native prey species^{7–9}. Despite the growing number of species introductions¹⁰, effects of introduced predators are often unreported or not apparent¹¹, and this is particularly the case for changes beyond individual populations when investigating changes to assemblages and communities¹². Assessment of species invasions often requires long-term data with extensive periods preceding and following invasion, while other regions that remain uninvaded or vary in their invasion timeline can serve as valuable reference regions^{13–15}. Long-term data are also needed to assess the persistence of ecosystem change to define an ecosystem as collapsed: ecosystems with a loss of biodiversity and widespread disruption of ecosystem function that will not recover unaided within decades (sensu Newton et al.²).

The Florida Everglades is a large (365,000 ha), topographically flat, oligotrophic, subtropical wetland ecosystem that experiences distinct wet/dry seasonality¹⁶. The hydrologic conditions at local (ha) and regional (1000s of ha) scales are direct and indirect drivers that regulate the populations of aquatic animals such as fish and decapods^{17–19}. At adult sizes, fish and decapods become important prey resources for larger predators such as wading birds (Pelecaniformes and Ciconiiformes; ibises, egrets, herons, storks) and alligators²⁰. Everglades National Park was established to preserve the southern end of this unique ecosystem, which seasonally supports aggregations of breeding wading birds when water levels are low^{21,22}. During the twentieth century, construction of canals, water diversion, impoundment of wetlands, and conversion of large areas for agriculture and other

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human development resulted in the alteration of the historical hydrologic conditions, a decline in the seasonally pulsed production of aquatic animals, and fewer numbers of breeding wading birds^{23,24} along with a multitude of other consequences to the wetland and connected ecosystems²⁵. An ongoing decades-long, multi-billion-dollar effort to restore the Everglades ecosystem was initiated in the 1990s^{25,26}. Restoration efforts include bringing back water flows to the two primary drainages of Everglades National Park, Shark River Slough and Taylor Slough (Fig. 1), to a state resembling conditions prior to human alteration that can support greater seasonal production of prey for nesting wading birds²⁷. Long-term biological monitoring projects were established during the 1990s and 2000s to assess progress towards restoration goals²⁶.

Over the past century, at the same time that the Everglades was being modified away from, and now back towards, its historic hydrologic conditions, a wide array of non-native species were introduced to the ecosystem²⁸. Several of these non-native species have become invasive species of great concern²⁹, but until

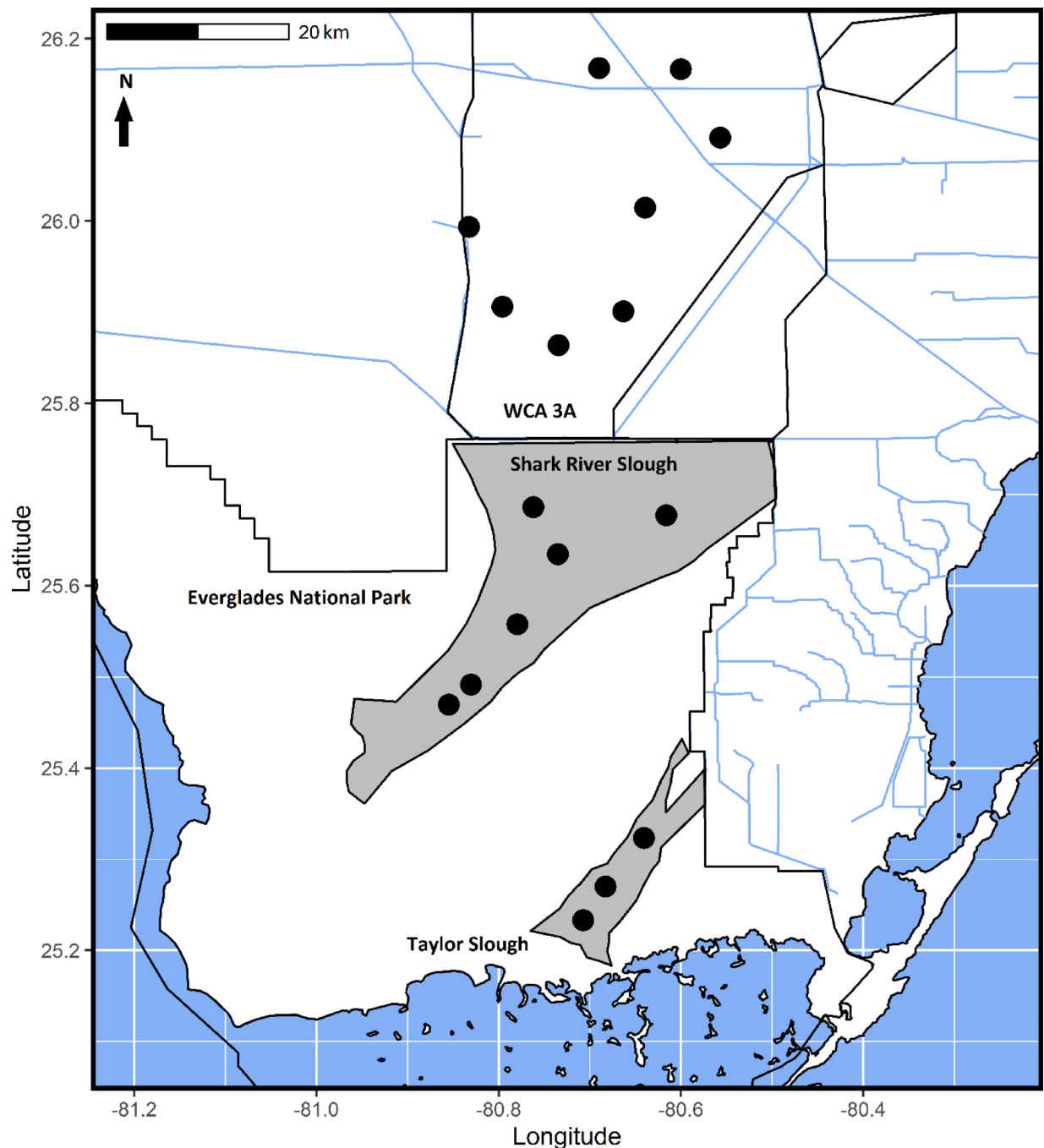


Fig. 1. Map of the southern Everglades illustrating the locations of Taylor and Shark River sloughs in Everglades National Park and the distribution of sample sites (black circles) in each slough and those in Water Conservation Area 3A. Blue lines are major canals; water flows through the sloughs from north to south.

recently the 16+ species of non-native fishes found in Everglades National Park did not garner as much attention or appear to have effects as noticeable as other taxa^{30,31}. The invasion of the Asian Swamp Eel (*Monopterus albus/javanensis* complex; hereafter 'swamp eels') to Taylor Slough has been linked to the near-complete loss of crayfish and two small fishes, as well as substantial declines in other fishes³². Swamp eels are functionally unique fishes in the Everglades, being salt-tolerant³³, protogynous hermaphrodites³⁴, and capable of surviving through the dry season buried in marsh sediments when all other large fishes must migrate to deeper refuges³⁵. Their drought tolerance has enabled swamp eels to disrupt population dynamics of taxa that were previously reliant on predator-free periods at the start of the dry season for breeding and population growth^{19,32}. The effects of swamp eels on populations of individual species have greatly exceeded potential effects of other invasive fishes³⁶ and created concern for the structure of Everglades food webs and restoration efforts aimed at increasing populations of aquatic animals that are prey for native wildlife.

The recent evidence that illustrated severe declines in population densities in six out of the nine most common small fish and decapod species in Taylor Slough following swamp eel invasion were dramatic effects on individual species³², but, concurrent changes among less common species might produce different community-wide effects than those of a single species may predict; over 40 species of fishes have been collected in Taylor Slough in the same dataset since monitoring began in the 1990s. Species-specific relationships with hydrologic conditions and seasonal population recruitment in the Everglades are critical to understanding changes to processes occurring because of invasion. The well-established link between aquatic animal populations and hydrologic conditions, and frequency of dry-down in particular^{17,19}, produces expectations of certain population-level changes as hydrologic conditions change. Therefore, any comparison of communities before and after invasion would need to consider the hydrologic context of the periods.

In this study, we examined a 26-year dataset of fish and decapod densities in the Everglades to document community-level changes (diversity and composition) and total biomass production changes following swamp eel invasion in Taylor Slough. We selected and compared communities at time periods before and after swamp eel invasion based on similarity of hydrologic conditions during which we expected to see relatively similar communities in the sloughs. While densities of several individual species had been reduced, the swamp eel-invaded wetland still supported modestly high densities of some species of small fishes and decapods³², but the trophic objectives for the Everglades restoration include the encouragement of prey that support nesting wading birds and such species feed predominately on larger (> 2 cm standard length) species of marsh fishes plus crayfishes^{20,37,38}. To quantify the change in the trophic function of the invaded wetland we compared the compositional biomasses of aquatic animals supported in the invaded and uninvaded periods with reference to the types of prey used by wading birds. Given the recent rapid expansion of swamp eels across Florida³⁹ and ongoing efforts to restore the Everglades, we discuss the implications of our findings in the context of Everglades food webs, restoration, ecosystem change, and the concept of ecosystem collapse.

Methods

Study system

Fish and aquatic macroinvertebrates (i.e., aquatic animals 1–8 cm body length; Table S1) were collected using 1-m², 2-mm mesh, throw traps following standardized protocols^{40,41} from July 1996 to the present (2025). Sampling occurred at 24 sites throughout the Everglades⁴², but here we focus on those in Taylor Slough (3 sites) and Shark River Slough (6 sites) of Everglades National Park (Fig. 1); data from 8 additional sites in Water Conservation Area 3A were used only for comparison of overall biomass changes. Most sites consisted of three 1-ha plots (with smaller 0.3-ha plots at three Shark River Slough sites) separated by several hundred meters, while the two upstream (northern) sites of Taylor Slough consisted of five plots per site, with two of the five plots having shorter hydroperiods on the margins of the slough^{42,43}. Seven throw-trap samples were collected at each plot during each sampling period, except when wetlands were drying and inaccessible by airboat; helicopters were used to access sites when airboats could not, and in such cases only five samples were collected. Samples were collected during five months of each year, starting after the onset of the wet season (begins in June), with wet-season samples collected in July and October, transition period samples collected in December, and dry-season samples collected in February and April. During the driest years, sites were occasionally completely dry during the dry season and/or early wet season and not sampled. Animals were removed from throw traps using bar seines and dip nets; vertebrates were euthanized using MS-222 and all animals were fixed in formalin before being transferred to ethanol and identified.

Taylor and Shark River sloughs are two similar yet different drainages in terms of their hydrologic conditions, size, and invasion history. The pool of species inhabiting the two sloughs were largely similar. Previous analyses^{32,36}, suggest all of the dramatic changes that have occurred in Taylor Slough were a result of swamp eel invasion after factoring out hydrologic drivers and comparing to Shark River Slough. Therefore, we focused here on changes in Taylor Slough and present complementary analyses of Shark River Slough data in the supplements. Taylor Slough experienced generally wetter conditions during the early and later years of our time series, with drier conditions during the mid- and late-2000s, when our sites dried (< 5 cm) every year or two and for longer times during the dry season (Fig. 2). Swamp eels were first detected at our sites in Taylor Slough in 2012 and have been found at all sites with regularity since 2014³².

Swamp eel effects on species densities (#/m²) were detected using both presence/absence (pre- and post-establishment of swamp eels) and abundance-based modeling approaches based on combined swamp eel catches in throw traps and catch-per-unit-effort from paired large fish electrofishing sampling^{32,36}. Results based on the two approaches were largely equivalent and suggested swamp eel presence alone in our electrofishing dataset may be correlated with population establishment as it effectively accounted for observed changes in the prey populations. Therefore, in our comparisons of diversity and biomass/trophic function we adopted a categorical approach wherein we divided our time series into three six-year periods based on the hydrologic conditions

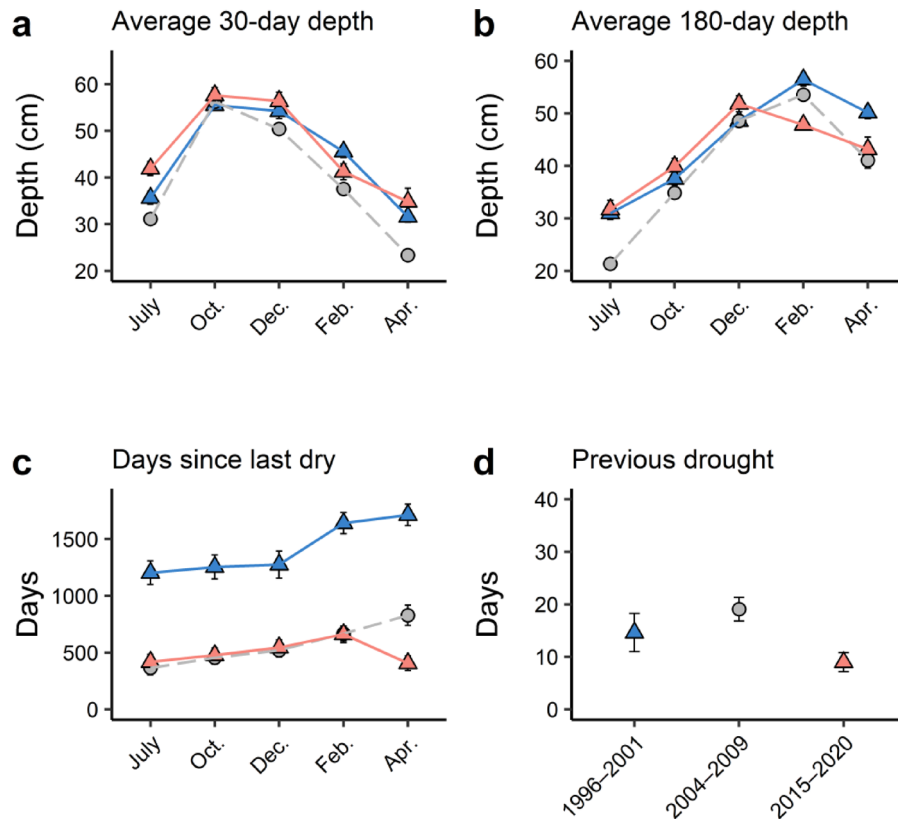


Fig. 2. Mean ($\pm$ SE) plot-level hydrologic conditions in Taylor Slough in Everglades National Park: **a** average water depth over the previous 30 days, **b** average water depth over the previous 180 days, **c** days since a site was last dry (depth < 5 cm), and **d** length of the previous hydrological drought (days with water depth < 5 cm during previous dry season). Data are separated into three 6-year periods based on the presence of swamp eels and hydrologic conditions in Taylor Slough: symbol colors and shapes in all panels correspond to year grouping in **(d)**. Swamp eels were present in Taylor Slough from 2015–2020 but absent in the other two periods. Our primary comparisons are between 1996–2001 and 2015–2020 due to similar frequency of drying in Taylor Slough (**c**); however, this frequency of drying was notably lower (more days since dry) during 2015–2020 in Shark River Slough. Sampling seasons (month) in **(a–c)** are ordered from the start of the wet season (July) through the end of the dry season (April).

and invasion history of Taylor Slough (Fig. 2): 1996–2001 was as a wet, pre-invasion period when swamp eels were absent; 2004–2009 was a dry, pre-invasion period; and 2015–2020 was a wet period when swamp eels were present at all sites within the slough. Given the importance of hydrologic conditions for regulating aquatic animal populations in the Everglades, we focused our comparisons for swamp eel impacts on contrasts of the wet pre-invasion period to the wet period with swamp eel establishment in Taylor Slough. The middle drier period was used to illustrate how drastic the effects of swamp eels have been relative to the hydrologic disturbances that previously affected the ecology of the system. Intervening years outside of these three periods were excluded from primary analyses and figures, and the most recent years (2021–2024) were excluded due to the swamp eel invasion of Shark River Slough during that time. The middle period of 2004–2009 was illustrated in figures, but not analyzed. Full time series data on densities of the common taxa have been assessed elsewhere^{32,36}.

Data analysis

In this paper we analyzed plot-level mean densities of small fishes (< 8 cm TL) and decapods ($N = 13$ plots in Taylor Slough, 18 plots in Shark River Slough); although other invertebrates and amphibians were collected, fishes and decapods were reliably identified to species level across the entire time series. The relatively few (~ 0.5%) fish and crayfish not identified to species (primarily tiny crayfish and sunfish) were included in abundance and biomass totals, but were excluded from composition and diversity analyses. While our focus was on community-level changes, the three common decapods and six most common fishes in Taylor Slough prior to swamp eel invasion were individually assessed in biomass analyses, play important roles in community analyses, are regularly discussed, and have had their populations individually modeled elsewhere. For decapods, these species were riverine grass shrimp (*Palaemon* [*Palaemonetes*] *paludosus*), Everglades crayfish (*Procambarus alleni*), and slough crayfish (*Procambarus fallax*). The six most common fishes were Golden Topminnow (*Fundulus chrysotus*), Marsh Killifish (*Fundulus confluentus*), Eastern Mosquitofish (*Gambusia holbrooki*), Least Killifish (*Heterandria formosa*), Flagfish (*Jordanella floridae*), and Bluefin Killifish (*Lucania goodei*). Swamp eels caught in

throw traps were excluded from all analyses. During our focal years of 2015–2020 in Taylor Slough, swamp eels accounted for 0.5% of total fish biomass caught in throw traps (of all size classes, including all fish > 8 cm that we otherwise did not analyze here); when excluding fish > 8 cm, swamp eels accounted for 0.05% of fish biomass.

In the analyses below we used three hydrologic covariates measured at the plot scale following Pintar et al.^{32,36}; see similar covariates in Trexler et al.¹⁸, Dorn and Trexler¹⁹). Data from the Everglades Depth Estimation Network^{44,45} were used to estimate hydrologic conditions at each plot at the time of sampling: the average water depth during the 30 or 180 days prior to throw-trap sampling ('30-day depth' or '180-day depth'; Fig. 2a, b), the days since a plot was last dry (depth < 5 cm; DSD; Fig. 2c), and the length of the last dry season (LDS: number of days water depth was < 5 cm during the previous dry season; Fig. 2d). Species respond to water depth on different temporal scales, so the better fitting depth measure was used for each species. Low-water conditions (depths < 5 cm) creates an abiotic disturbance (biomass reduction) by killing fish, but also increases the probability of exposure to avian predation^{46,47}. The seasonal reductions caused by low water disturbance is modeled with the DSD, LDS, and depth terms in different ways to accommodate the different life histories of the native taxa^{19,48}.

For our univariate community and biomass analyses, we set a baseline period prior to swamp eel invasion of Taylor Slough (1996–2009) to model relationships between response variables (described separately in the following sections) and hydrologic covariates. We used a model selection approach that compared the Akaike Information Criterion corrected (AICc) among models using the *dredge* function in the MuMin package v 1.47.1⁴⁹ to choose the relatively best combination of the three hydrological variables (DSD, either 30- or 180-day depth, LDS), season (sampling month: July, October, December, February, April), and the interaction between season and LDS, which accounts for either diminishing effects of the previous dry conditions as the water year progresses or lagged population responses⁵⁰. The model with the lowest AICc was chosen as the best model, even if there were competing equally effective models ($\Delta\text{AICc} < 2$), as our objective was to best account for (model) hydrologic conditions before exploring predator effects. Following selection of the best combination of covariates during the baseline period, we used these covariates in models comparing the two wet periods before and following swamp eel invasion.

Univariate models were mixed-effects models that included site and plot nested within site as a random effect. Dependent variables were typically (except as noted below) log-transformed to approximate normal error distributions of the models' fit. Independent variables LDS and DSD were log-transformed, while depth was not transformed. All univariate models were fit by maximum likelihood (using the Satterthwaite method) with the lme4 v 1.1–35.1 and lmerTest v 3.1–3 packages in R v 4.3.3^{51–53}.

Univariate community metrics

We assessed three univariate measures of communities at the plot scale: species richness, alpha diversity (inverse Simpson), and evenness. These metrics were calculated using the vegan package v 2.6–4⁵⁴; none were transformed for analyses. The analysis of species richness included log-transformed total density of fish and decapods as a covariate as the two were expected to covary (but see⁵⁵ and their relationships were linear, which presented a simple and intuitive manner for comparing richness (Fig. S4). Following selection of hydrologic covariates during the baseline period as described above, we compared the pre-invasion wet period to the wet period following invasion by including the selected hydrologic covariates in a model with the categorical invasion period (swamp eel presence/absence) and the interaction between the invasion period and season.

Species turnover

We analyzed species turnover to assess whether the seasonal rate of species change (appearance or disappearance of species from a plot) shifted after swamp eel invasion. Species turnover (total turnover, appearance, and disappearance) was calculated using the *turnover* function in the codyn package v 2.0.5⁵⁶. Because analyzing species turnover requires calculation of differences in species occurrences between consecutive sampling periods, the four shorter hydroperiod plots in Taylor Slough were excluded from the turnover analysis due to a greater incidence of dates when it was too dry to collect samples. We modeled the effects of environmental conditions on turnover for the entire baseline period, fit the selected hydrologic covariates to a dataset consisting of the two different (pre- and post-invasion) wet periods, and tested for categorical effects of invasion as described previously.

Multivariate community analyses

We used Primer v 7.0.23 and the PERMANOVA+ add-on^{57,58}, to analyze multivariate community structure (PERMANOVA) with a before-after-control-impact (BACI) design on plot-level communities. This PERMANOVA used the first six years (1996–2001) as the before period and 2015–2020 as the after period (following swamp eel invasion) with Shark River Slough serving as the control (reference region) for Taylor Slough. We analyzed data from each of the five sampling periods (months) separately; restricting these analyses within a single season helps to reduce variation in communities attributable to seasonal changes in species composition and abundance. We included 30-day depth, DSD, and LDS as covariates in PERMANOVA (non-significant terms were dropped from models), site and plot nested within site were random effects, and the interaction between categorical invasion period and region was our primary variable of interest. We performed analyses on fourth-root-transformed densities (Bray-Curtis similarity), species proportions standardized within plot-level samples (Bray-Curtis similarity), and presence/absence data (Jaccard similarity). Each of these analyses provides an alternate view of the community: the fourth-root transformed densities downweigh common species, but still directly analyze density data, BC similarity on proportions eliminates density effects but still allows for effects of relatively dominant species, and presence/absence data treats each species equally. There were 9999 permutations for each PERMANOVA, which were performed under a reduced model using type III sums of squares. We further examined the species responsible for compositional differences using similarity/

dissimilarity measures (SIMPER) on proportional and presence/absence data and conducted visualizations using non-metric multidimensional scaling (NMDS) with density (fourth-root) and proportional data. The composition during the intervening dry period (2004–2009) was included in tables of similarity/dissimilarity and NMDS figures for illustrative purposes, but was not analyzed.

Biomass

Lengths of all fish (standard length, SL) and crayfish (carapace length, CL) were measured in the lab, and wet weights were obtained using published length-to-wet weight regression equations or equations previously developed from measurements taken from our Everglades collections (Table S2). Mean masses for each species were used for unmeasured fish (typically damaged specimens; 0.07% of fish). Fish with lengths > 8 cm were excluded from biomass estimates since they are the focus of separate electrofishing sampling, are more of chance encounters in throw traps, and a single individual of species like Florida Bass (*Micropterus salmoides*) may heavily affect overall biomass estimates. Grass shrimp were not measured and instead we obtained biomass estimates by using the average wet weight of a grass shrimp in southern Florida (0.069974 g) based on⁵⁹; this dry season estimate may be biased towards larger individuals. With univariate analyses, we individually analyzed the six common fishes and two crayfishes, along with total fish biomass, total crayfish biomass, and total sunfish (*Lepomis* spp.) biomass. We also analyzed the total estimated biomass (fish + crayfish + grass shrimp), but we did not assess grass shrimp individually given their estimated biomass is a linear transformation of abundance (abundance assessed previously in Pintar et al., 2023a). We analyzed biomass changes in the same manner as other univariate analyses above by first selecting the best hydrologic model during the baseline period and then testing for differences between the two wet periods (before versus after invasion).

The overall changes in total fish and total crayfish biomass were assessed using pairwise comparisons among the three regions (Taylor Slough, Shark River Slough, and Water Conservation Area 3A) under a BACI framework after modeling hydrologic effects during the baseline period as described for other analyses. The significance and magnitude of the coefficients of the region-by-invasion period interaction were used to compare the relative changes in total biomass that occurred between regions and invasion periods. Lastly, we calculated and illustrated the change in overall fish and decapod biomass and the estimated biomass of wading bird prey, which was defined as crayfish with CL > 10 mm and fish with SL > 20 mm; grass shrimp were excluded. Exclusion of small crayfish, small fish, and grass shrimp were based on the known common prey characteristics of White Ibis (*Eudocimus albus*), Wood Stork (*Mycteria americana*), Snowy Egret (*Egretta thula*), and Tri-colored Heron (*Egretta tricolor*)^{20,37,38,60,61}. We focus on these prey size classes because White Ibis and Wood Stork colony sizes/ nesting numbers and success, in particular, are foci of Everglades restoration efforts²².

Results

Univariate community metrics

Species richness positively covaried with abundance (Fig. S4), but strongly declined following invasion ($F_{1,673} = 321$; $P < 0.0001$) in Taylor Slough (Fig. 3a, Table S7). Species diversity (inverse Simpson) and evenness both significantly declined in Taylor Slough following swamp eel invasion (Fig. 3b, c; Table S7).

Species turnover

While there was a significant interaction between invasion period and season for total turnover and disappearance in Taylor Slough ($F_{8,446} = 3.4$; $P = 0.008$; Table S7), this appeared to largely reflect a decline in species disappearance at the start of the wet season in July and an increase later during the wet season (October) (Fig. S5). This decline in turnover in Taylor Slough particularly reflects a lack of compositional change from April (late dry season) to July (early wet season) after the swamp eel invasion.

Multivariate community analyses

All before-after-control-impact PERMANOVA analyses indicated community composition changed during all seasons following swamp eel invasion (Table S10). Effect sizes approximated by pseudo- F values of the interaction between invasion period and region exceeded all other factors in 12 out of 15 models except for the main effect of invasion period. In NMDS figures, spatial separation between the two wet periods was clear in Taylor Slough (Fig. 4). Between-group similarities were low (Table S11): the species accounting for the most within-group similarity and dissimilarity varied between the wet and dry periods prior to swamp eel invasion in Taylor Slough (Tables S12–S15), and these differences were expected based on known hydrologic responses and relative abundances of these species. Prior to invasion, four or five species were needed to account for 80% of the similarity between plots, but following invasion only three species accounted for > 80% of the variation in density-based analyses. Dissimilarity in the communities between the pre-invasion (wet period, 1996–2001) and the post-invasion period (2015–2020) were fairly consistent across seasons but the import taxa (contributing the most to dissimilarity) depended on the analyses. Considering the dominant species (i.e., the proportional makeup) the post-swamp eel invasion community was more thoroughly dominated by grass shrimp, Bluefin Killifish, and Least Killifish (relative increases; Table S13) and with declines in both crayfish, Eastern Mosquitofish, and Flagfish. The presence-absence dataset also indicated some lower-density native fishes had essentially disappeared (Marsh Killifish and Everglades Pygmy Sunfish, *Elassoma evergladei*) while the non-native Mayan Cichlid (*Mayaheros urophthalmus*) was more commonly encountered in the post invasion community.

Biomass

Overall, biomass (g/m^2) declined in Taylor Slough across the invasion periods (Figs. 5, S9, S10; Tables S3,S4). Crayfish biomass was effectively eliminated from Taylor Slough (99.5% declines; Fig. 5c). Estimated biomass of

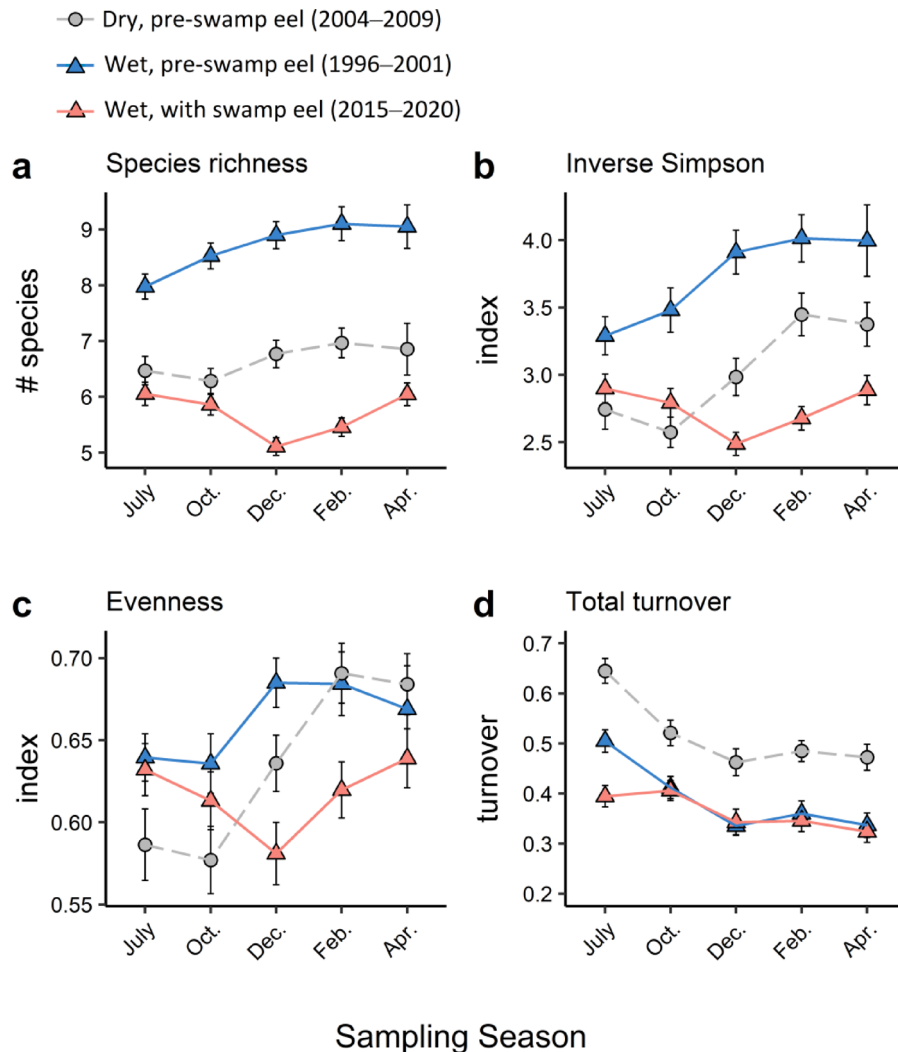


Fig. 3. Mean ($\pm$ SE) plot-level community indices of small fish and decapods across seasons in Taylor Slough in Everglades National Park: **a** species richness, **b** alpha diversity (inverse Simpson), **c** evenness, and **d** total species turnover. Data are separated into three 6-year periods based on the presence of swamp eels and hydrologic conditions in Taylor Slough. Sampling seasons (month) are ordered from the start of the wet season (July) through the end of the dry season (April).

grass shrimp showed little overall change in Taylor Slough except for a decline at the start of the wet season. Total fish biomass declined in the latter years following swamp eel invasion ($F_{1,699} = 335$, $P < 0.0001$), and the rate of seasonal increases (season over season within a year) in fish biomass was reduced (invasion: season: $F_{4,686} = 3$, $P = 0.014$). Total biomass of sunfishes declined by $> 80\%$ ($F_{1,623} = 51.6$, $P < 0.0001$). Biomass changes of individual fish species were illustrated in Fig. S10 and listed in Tables S3 and S4.

Paired BACI analyses of total fish biomass showed significant declines in Taylor Slough compared to Shark River Slough (region $\times$ invasion period interaction: $F_{1,1630} = 17$, $P < 0.0001$) and Water Conservation Area 3A ($F_{1,1837} = 13$, $P < 0.0001$), but there were no differences between Shark River Slough and Water Conservation Area 3A ($F_{1,2075} = 0.1$, $P = 0.92$; Table S5). While total crayfish biomass in Taylor Slough declined significantly relative to Shark River Slough ($F_{1,1546} = 165$, $P < 0.0001$), crayfish biomass also declined in Water Conservation Area 3A relative to Shark River Slough ($F_{1,1969} = 79$, $P < 0.0001$; Table S6). The decline in Taylor Slough (99.5%) was significantly greater than the decline in Water Conservation Area 3A (68.6%; $F_{1,1778} = 15$, $P = 0.0001$).

Biomass of primary bird prey following invasion in Taylor Slough declined 80% from the pre-swamp eel wet period (1996–2001) and 76% from the preceding dry period (2004–2009, Fig. 6). Biomass decreases in Taylor Slough during the dry season (during and just prior to the wading bird breeding season) were relatively similar to those changes that occurred over the entire year (Fig. S11).

Discussion

Following the invasion of swamp eels in Taylor Slough, the fish and decapod community shifted to a state not previously seen across the range of hydrologic conditions experienced in the region. Species richness of fish

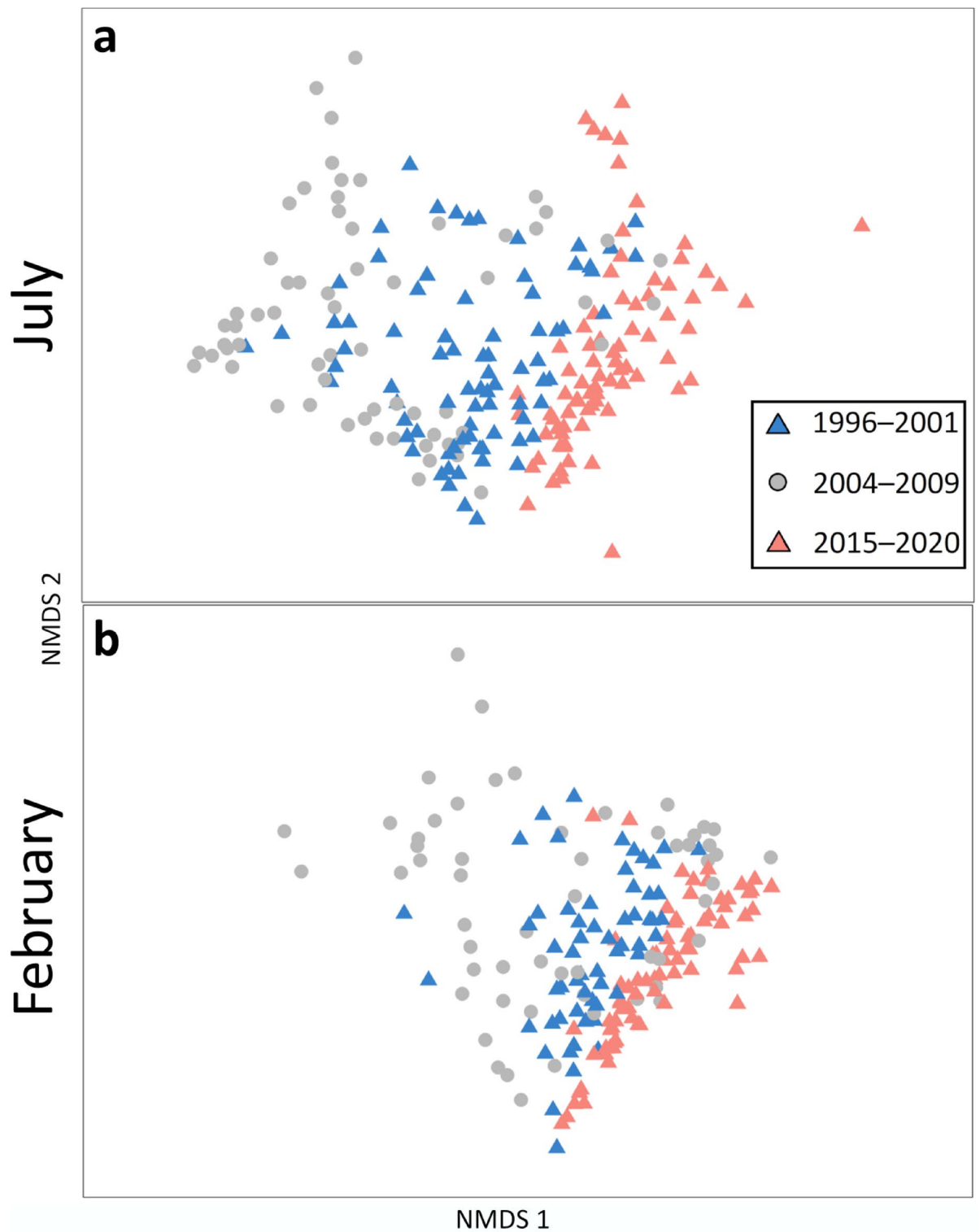


Fig. 4. Non-metric multi-dimensional scaling figures (based on proportion data) of the fish and decapod community in Taylor Slough during one wet season sampling period (July) and one dry season sampling period (February). Data are separated into three 6-year periods based on the presence of swamp eels and hydrologic conditions in Taylor Slough.

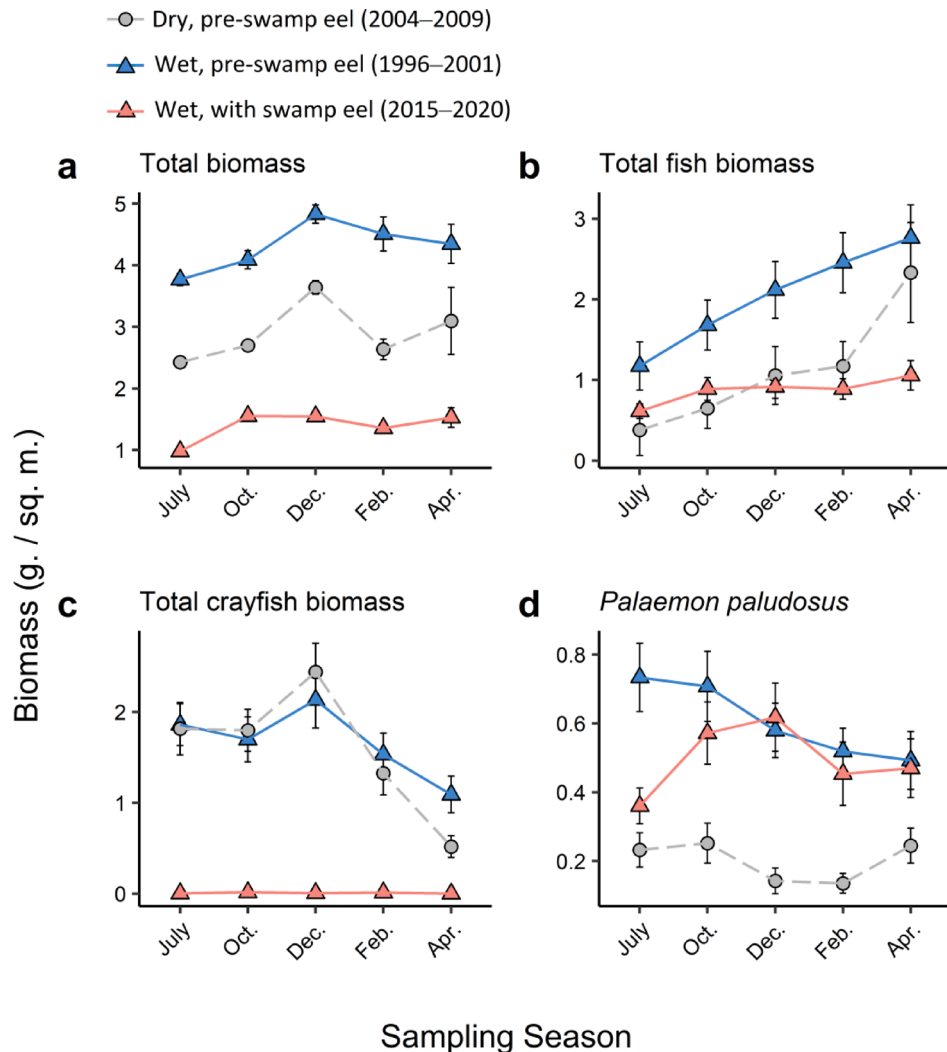


Fig. 5. Biomass densities (mean ± SE) across seasons in Taylor Slough in Everglades National Park: **a** total biomass of all small fishes (< 80 mm SL), crayfish, and grass shrimp, **b** total small fish biomass, **c** total crayfish biomass, and **d** estimated biomass of grass shrimp. Data are separated into three 6-year periods based on the presence of swamp eels and hydrologic conditions in Taylor Slough. Sampling seasons (month) are ordered from the start of the wet season (July) through the end of the dry season (April).

and decapods declined by almost 25%, with similar declines in alpha diversity and evenness and a minimal shift in seasonal turnover. After swamp eels established, small aquatic animal communities became dominated by grass shrimp and fewer species of marsh fishes, with relatively little seasonal change in the most dominant species (grass shrimp, Bluefin Killifish) over the course of the water year. The Taylor Slough community-level changes have been more permanent than changes seen in the reference region where changes largely followed expectations based on hydrologic conditions (see supplements) and have implications for long-term biodiversity support and production of prey critical for nesting wading birds.

Frequency of drought-related disturbances in the Everglades (modeled here with days since dry) has historically been a major driver of aquatic animal population dynamics in the Everglades¹⁸. Hydrologic drivers produced the expected changes to the communities in Taylor Slough from the initial period (1996–2001), which was wetter, to the drier middle period (2004–2009). During the relatively dry (frequently disturbed) middle period in Taylor Slough, there was a relatively modest decline in total biomass (32%) from the initial wet period. In our final post-invasion time period (2015–2020), Taylor Slough returned to the lower hydrologic disturbance frequencies observed during the initial period. Therefore, during the final time period, we would have expected a recovery of aquatic animal biomass in Taylor Slough. Yet, total biomass declined by an additional 53% from the middle period (Fig. 6b), while bird prey biomass collapsed following swamp eel invasion. The declines of both crayfishes, Marsh Killifish, Flagfish, and sunfishes accounted for most of the loss of available bird prey (Figs. 6, S11).

Communities in the adjacent drainage, Shark River Slough, also varied across the invasion periods, but changes there generally differed in direction, species composition, or magnitude from what occurred in Taylor Slough. Analyses indicated community structure shifted somewhat in the reference Shark River Slough drainage,

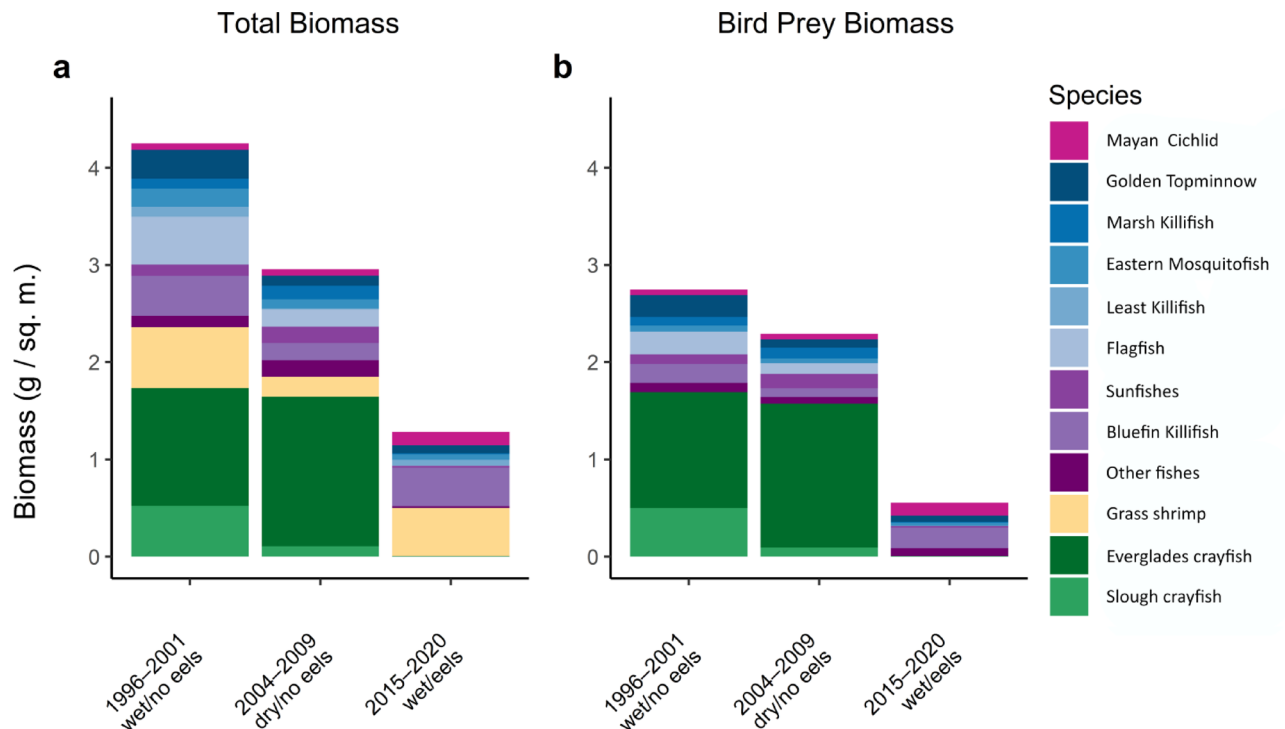


Fig. 6. Stacked bar charts of species contributions to biomass densities in Taylor Slough during all sampling seasons. Data are separated into three 6-year periods based on the presence of swamp eels and prevailing hydrologic conditions in Taylor Slough. There were five species of *Lepomis* and other fishes include 32 species found in Taylor Slough, excluding juvenile swamp eels during the invaded time period. **a** is the total biomass of all fishes and decapods; **b** is the biomass of bird prey (fish > 20 mm SL, crayfish carapace length > 10 mm).

but the magnitude was not as drastic as in Taylor Slough. Biomass also declined in Shark River Slough: paired comparisons of biomass changes to Water Conservation Area 3A indicate fish biomass changes there followed what occurred in Shark River Slough, but Taylor Slough experienced a more substantial decline beyond what occurred in those regions (see supplements). Similarly, while crayfish biomass declined in Water Conservation Area 3A relative to Shark River Slough, the changes in Taylor Slough exceeded what occurred in either reference region.

Changes to biomass in Taylor Slough indicate an important trophic ecosystem function⁵⁹ is being lost even as the region is being rehydrated. The total biomass reduction was particularly dramatic when accounting for the species that are most important prey for nesting wading birds. Grass shrimp were as abundant after invasion as during the wet period prior to swamp eel invasion and accounted for 35% of the remaining biomass in Taylor Slough (Fig. 4), but grass shrimp are a tiny component of wading bird diets, accounting for ~2% of prey fed to chicks of White Ibises, Snowy Egrets, and Tri-colored Herons^{37,60} and < 1% of prey for Wood Storks^{62,63}. Similarly, because even the smaller egrets select relatively larger fish prey (≥ 2 cm SL) small-bodied species do not provide a resource. The fish species with the highest abundance in Taylor Slough following swamp eel invasion was Least Killifish (Fig. S10 d), and even as an adult most Least Killifish are so small that they are not a meaningful component of bird prey biomass (Fig. S10f). During both the hydrologically dry and wet periods prior to invasion in Taylor Slough, crayfish accounted for > 58% of prey biomass for wading birds, but this source of food that dominates the diet of White Ibis chicks and has been associated with their breeding success^{38,60}, has functionally been eliminated from Taylor Slough since the establishment of the swamp eel. Whether these biomass declines will be observed across the landscape and reduce nesting activity remains to be seen. Swamp eels continue to spread westward into regions of the Everglades that are more commonly used as nesting wading bird foraging grounds³⁹. Herons, egrets, and storks prefer to feed on fish that grow to sizes > 2 cm long^{20,37,63} such as fundulids, poeciliids, and sunfishes. White Ibis feed heavily on crayfish and typically feed on fish only when they become highly concentrated and crayfish are scarce^{20,38,64,65}, but the dramatic declines in crayfish, several small fishes, plus sunfishes in Taylor Slough leave little opportunity for feeding by ibises, egrets, or storks during any season. The few larger Great Blue Herons and Great Egrets that are known to feed on larger swamp eels⁶⁶ may be the most likely species to benefit from the new resource.

We included some comparisons with adjacent regions (with different invasion histories) in the results and supplements (see also³⁶). For Taylor Slough, the adjacent Shark River Slough was the closest wetland to a natural reference available^{13,67}. The changes between the same time periods we observed in that drainage system illustrate the difficulty in finding reference regions and fully attributing community-scale changes to an invading species. In aquatic ecosystems like the Everglades, hydrologic variation affects the populations of aquatic animals; comparisons become more complex with hydrologic variation between impacted and reference

drainages, especially when they can be caused by natural climatic changes and the results of changing water management and ecosystem restoration. Biomass reductions and community shifts were stronger in Taylor Slough, but our comparisons to Shark River Slough were complicated by the impacts of another invasive species, the African Jewelfish boom-and-bust in the latter reference period in Shark River Slough that coincided with the swamp eel invasion of Taylor Slough³⁶. Swamp eel colonization of Shark River Slough (first detected in 2018) and their spread across the sites from (2018–2021) prevented us from using the most recent data from that region for comparisons. While we can model common individual species and account for hydrologic conditions before attributing predator effects³⁶, that is not that case for community-scale changes. In the end there was no perfect reference region when comparing community changes. Nevertheless, the mechanism responsible and predator-prey relationships seem fairly clear; large swamp eels are generalists known to feed on crayfish and small fishes⁶⁸. Given everything we know about the ecology of the species and responses to hydrologic variation^{19,32}, other factors cannot readily account for the multi-species coordinated and dramatic losses in the Taylor Slough animal community.

The unchecked spread of swamp eels across southern Florida has accelerated since around 2017 and may be in part tied to changes in water management³⁹. The spread of swamp eels now threatens the structure of the Everglades food web. The standing biomass of available 2+ cm aquatic prey during both the wet and the dry seasons in Taylor Slough was not only far below what would be expected with greater water deliveries as part of restoration but was also far lower than what was observed during the dry years prior to swamp eel invasion. Crayfish contributions were lost along with those of some larger fish, while shrimp and small killifishes remain. The results suggest there are fundamental population-level differences in predator sensitivity similar to suggestions in experimental work⁶⁹ when comparing sensitivities of shrimp (least sensitive), mosquitofish, and crayfish (most sensitive) populations to predator impacts. Evidence for declines will need to be further examined in regions that have recently been invaded by swamp eels and also have similar long-term monitoring data to examine the severity of the effects for the entire wetland landscape. Shark River Slough, which historically was a more diverse region with higher prey densities than Taylor Slough, may be the first to show signs of change. Additionally, wetlands in Water Conservation Area 3 upstream of Everglades National Park, have had characteristically longer hydroperiods and somewhat greater productivity⁷⁰ and will need to be monitored to determine whether the effects of swamp eels can be just as strong in areas with deeper water, longer hydroperiods, and greater productivity.

The loss of prey biomass for birds, the shift in communities to a composition never previously observed, and the loss of diversity have persisted over the past decade since swamp eels established in Taylor Slough. By some definitions these persistent shifts in characteristics of the aquatic animal community could be termed an ecosystem collapse² for this portion of the Everglades. Taylor Slough may continue in this state unless this shift can be reversed through a bust of swamp eel population, as was observed with African Jewelfish³⁶ or other adaptations of the community/ecosystem to the incorporation of swamp eels. Currently, swamp eels are so common, widespread, and difficult to capture that there are no known conservation actions that can be taken that might reverse these changes. Although Taylor Slough is not the most important drainage in the Everglades ecosystem for nesting wading birds, it serves as a warning about potential future conditions. Persistent monitoring will be needed to determine (1) whether populations of swamp eels and their effects continue to persist in Taylor Slough and (2) whether similar reductions to biomass production and biodiversity are spreading with the expanding range of swamp eels into the larger Everglades drainages. If the effects spread it will be vital to monitor and model wading bird nesting trends to see if abundances of breeding wading birds and other taxa match predictions based on hydrologic conditions⁷¹ or if effects of swamp eels are effectively short-circuiting the wading bird nesting conditions that water managers and restoration scientists aspire to produce. The implications of swamp eels changing community structure, altering seasonal prey production, and disrupting food webs may threaten progress on trophic functions of the multi-billion-dollar effort to restore the Everglades.

Data availability

Data are archived in Figshare (<https://doi.org/10.6084/m9.figshare.28876034>).

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Author contributions

Both authors contributed to study conception and design. Data analysis and visualization was led by MRP with input from NJD. The first draft of the manuscript was written by MRP and both authors contributed to revisions. Both authors read and approved the final manuscript.

Declarations

Competing interests

The authors declare no competing interests.

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Additional information

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