



Hydrology-mediated ecological function of a large wetland threatened by an invasive predator

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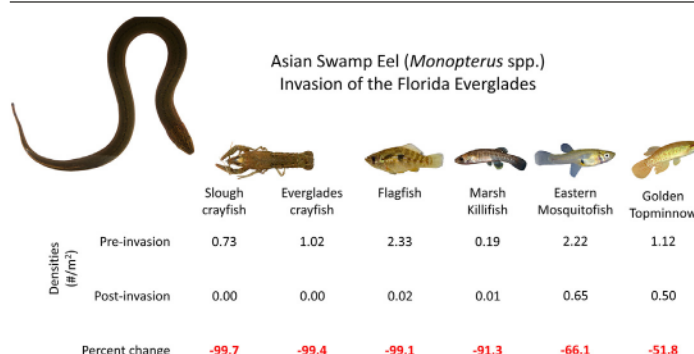
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HIGHLIGHTS

- Asian swamp eels have spread into Everglades marshes since 2010.
- Populations of native crayfish and small fish collapsed after invasion.
- Drought-resistant traits of swamp eels undermined natural environmental dynamics.
- Water management may have played a role in swamp eel spread.
- Everglades restoration and trophic dynamics may be threatened by this invasion.

GRAPHICAL ABSTRACT



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ABSTRACT

Invasive species are one of the greatest threats to ecosystems, disrupting ecosystem function and leading to the collapse and extinction of native species. While populations of native fishes in the Everglades are tied to the system's natural hydrological dynamics, Asian Swamp Eels (*Monopterus albus/javanensis*) are drought-resistant fish first reported from Florida in 1997 and the Everglades in 2007. Using a 26-year dataset that included a 13-year baseline period prior to swamp eel arrival in Taylor Slough, we assessed population changes of common small fishes and decapods that are important prey for larger vertebrate predators. After invasion, populations of two crayfishes collapsed by >95 %, two fishes declined by >80 %, two fishes had intermediate declines of 44–66 %, and three species remained unchanged. Species most strongly reduced were those dependent on predator-free habitats at the onset of the wet season, indicating drought-resistant swamp eels have introduced novel predator effects and disrupted the hydrology-mediated production of aquatic animals that are prey for many larger predators. Ongoing Everglades restoration is designed to restore hydrological conditions that support production of crayfishes and fishes, and nesting wading birds reliant on them. Water management may have facilitated the invasion of swamp eels. Our results suggest that the continued spread of swamp eels may result in adverse consequences for Everglades trophic dynamics and potentially diminish benefits expected from the \$20B+ restoration.

1. Introduction

Globally, the number of invasions by non-native species continues to increase and raise alarm among scientists as their effects on biological systems, human health, and economies grow (Seebens et al., 2017). Although effects of many non-native species are unknown, their impacts on populations, communities, habitats, and ecosystem process are becoming better

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documented (Hulme et al., 2013; Ricciardi et al., 2013). Species invasions have been implicated in the decline, collapse, and extinction of native species via competition, predation, habitat alteration, and other processes (Clavero and Garciaberthou, 2005; Kats and Ferrer, 2003; Medina et al., 2011). The spread and effects of newly introduced species are difficult to predict, but often the most successful have trait sets absent from an ecosystem's native species (Lawson and Hill, 2022), while native species lacking adaptations to the effects of non-native species are most vulnerable (Cox and Lima, 2006; Ricciardi and Atkinson, 2004; Sih et al., 2010).

Freshwater ecosystems have been invaded by a diversity of aquatic species, including algae, vascular plants, crustaceans, and molluscs (Strayer, 2010), but freshwater fishes have some of the most widespread and well-documented invasions because of the long history of humans facilitating their introductions through aquaculture, sport, pet trade, and construction of waterways (Haubrock et al., 2021; Hulme, 2015). Invasive fishes have precipitated the population collapse and extinction of native species (Cucherousset and Olden, 2011; Gunnell et al., 2008; Mills et al., 2004), while also changing trophic interactions, altering ecosystem function, and introducing pathogens (Capps and Flecker, 2013; Gozlan et al., 2005; Martin et al., 2010). Although many introduced non-native fishes have had no known effects on native taxa, extreme effects include population declines of 86–99 % of native cyprinids in Zimbabwe (Gratwicke and Marshall, 2001), local extirpation of small-bodied cyprinids in Ontario (MacRae and Jackson, 2001), and extinction of ~60 % of Lake Victoria's endemic cichlids (Witte et al., 1992). Benthic macroinvertebrates can also be strongly diminished by non-native predatory fish (Gallardo et al., 2016), with declines in populations (Matsuzaki et al., 2009; van Kleef et al., 2008) and shifts in community composition (Flecker and Townsend, 1994). However, a lack of historical population data on freshwater arthropods in most ecosystems makes detecting effects of new non-native species difficult for macroinvertebrates and possibly biased towards detecting effects on native fishes (Collier et al., 2016).

The Everglades ecosystem of southern Florida is a large subtropical wetland, has been invaded by a wide range of taxa (Ewel, 1986; Kline et al., 2014), and is the focus of the largest and most expensive environmental restoration effort in history (Sklar et al., 2005), with projected costs exceeding \$20 billion. Recovery of historical populations of large predators such as wading birds and alligators, along with their seasonally pulsed prey (primarily small fish and crayfish), through hydrological management is a major goal of this restoration (Doren et al., 2009; National Academies of Sciences, Engineering, and Medicine, 2021). Extensive monitoring programs were established to document responses of the Everglades to restoration, but data have also been used to study the biology of native freshwater animals and document the arrival and spread of non-native species (e.g., Kline et al., 2014; Ruetz et al., 2005), among many other studies. From this work it is clear that small fish and crayfish in the Everglades have variable responses to hydrological variation; while some small fish and macroinvertebrates reach peak densities with multi-year continuous inundation, others benefit from occasional wetland drying that differentially disturb predator populations and temporarily reduce top-down impacts of large native and non-native fishes (Dorn and Cook, 2015; Trexler et al., 2005).

Since the mid-2000s, Burmese pythons (*Python bivittatus*) have become the face of invasive species in the Everglades due in large part to the coincident dramatic declines of common terrestrial mammals (Dorcas et al., 2012). Pythons have garnered an immense amount of attention from the scientific and management communities in Florida, while ingraining in the public consciousness across the United States due to sensationalistic stories portrayed by the media. Yet, non-native fishes have been found in the Everglades since the late 1960s (Kline et al., 2014), and the Everglades is a wetland ecosystem noted more for its diversity and abundance of nesting wading birds than its mammal diversity or abundance (Brown et al., 2006; Doren et al., 2009). Fish are known to disrupt avian reproduction through competitive interactions in some shallow aquatic ecosystems (e.g., Haas et al., 2007; Kloskowski, 2012), and regular introductions of non-native fish may threaten the prey-producing function of the Everglades

for seasonal nesting wading birds. Despite widespread concern for the potential effects that non-native fishes could have in the Everglades, there has been little correlative evidence of detrimental effects on wild populations (Schofield and Loftus, 2015; Shafland et al., 2010; Trexler et al., 2000). Lack of obvious effects could be from the annual hydrological cycle that accompanies the wet/dry seasonality (Gaiser et al., 2012; Ruetz et al., 2005), functional similarity of the many non-native cichlids to native centrarchids (Montaña and Winemiller, 2013), or the effects of cold events on the mostly tropical non-native fish species (Rehage et al., 2016; Schofield and Kline, 2018). Lack of correlative evidence could be misconstrued to suggest there are no impacts, but few empirical studies have attempted to directly evaluate the effects of non-native fishes while simultaneously accounting for the major hydrologic drivers of fish and decapod populations (Schofield and Loftus, 2015).

Asian Swamp Eels (*Monopterus albus/javanensis* complex [Synbranchidae], hereafter 'swamp eels') are drought-resistant fish first recorded in Florida in 1997 from northern Miami-Dade County and Tampa (Collins et al., 2002; Liem, 1987; Schofield and Nico, 2009). A genetically distinct population was recorded in the C-113 Canal in Homestead in 1999 (Collins et al., 2002) and were spreading in, and largely restricted to, canals until they were first observed in Everglades National Park in the marsh/mangrove creek interface east of Taylor Slough south of the C-111 Canal in 2007 and subsequently in ponds at Royal Palm in northern Taylor Slough in 2009 (Kline et al., 2014). By October 2014, swamp eels had been collected throughout all of Taylor Slough and have since continued to spread in the Everglades (Fig. 1) and elsewhere in Florida. When swamp eels were first recorded in marshes of Everglades National Park, limited work on their presence in canals and ponds suggested they may have no effects on the native fauna (Hill and Watson, 2007; Shafland et al., 2010). However, swamp eels possess a set of traits that make them unlike any other predatory fish in the Everglades, as they are protogynous hermaphrodites (Matsumoto et al., 2011), somewhat salt-tolerant (Schofield and Nico, 2009), possibly capable of making overland movements (Liem, 1987), and most notably, are obligate air-breathers (Graham, 1997; Liem, 1987) that burrow into moist substrates during the dry season where they can survive prolonged drought (Chew et al., 2005). Therefore, swamp eels may be the most functionally unique predator in the Everglades and we hypothesize that they have more noticeable effects in the shallow, spatially expansive, and seasonally dry marshes, where some species are drought-adapted, than in the smaller but perennially wet canals, where many other fishes are often found in high abundance. Here, we use a 26-year dataset to document the spread of swamp eels and assess the potential effects that they have had on fish and decapods in marshes of the Everglades.

2. Materials and methods

Long-term monitoring sites were established across the Everglades as part of the Modified Water Deliveries to Everglades National Park project (Doren et al., 2009). These sites were selected to track changes in abundance of aquatic animals related to changing hydrologic management as part of efforts to restore the greater Everglades ecosystem. The aquatic animals monitored were selected because of their role as prey for wading birds and alligators and their turn-over rate relative to management decision processes (Doren et al., 2009; Trexler and Goss, 2009). The biotic and hydrologic conditions of the sites (Trexler et al., 2001, 2003), rationale behind the sampling design (Chick et al., 1999; Jordan et al., 1997), and subsequent studies documenting the intricate hydrologic regulation of aquatic animal populations, among other ecological studies using the monitoring data, have been documented in the literature (e.g., Dorn and Trexler, 2007; Parkos et al., 2011; Ruetz et al., 2005; Trexler et al., 2005; among others). To summarize the study design, from July 1996 through February 2022 (26 years) fish and invertebrates were collected using 1-m², 2-mm mesh, throw traps following standardized protocols (Jordan et al., 1997) at three sites in Taylor Slough (Fig. 1). Sampling also occurs in the larger

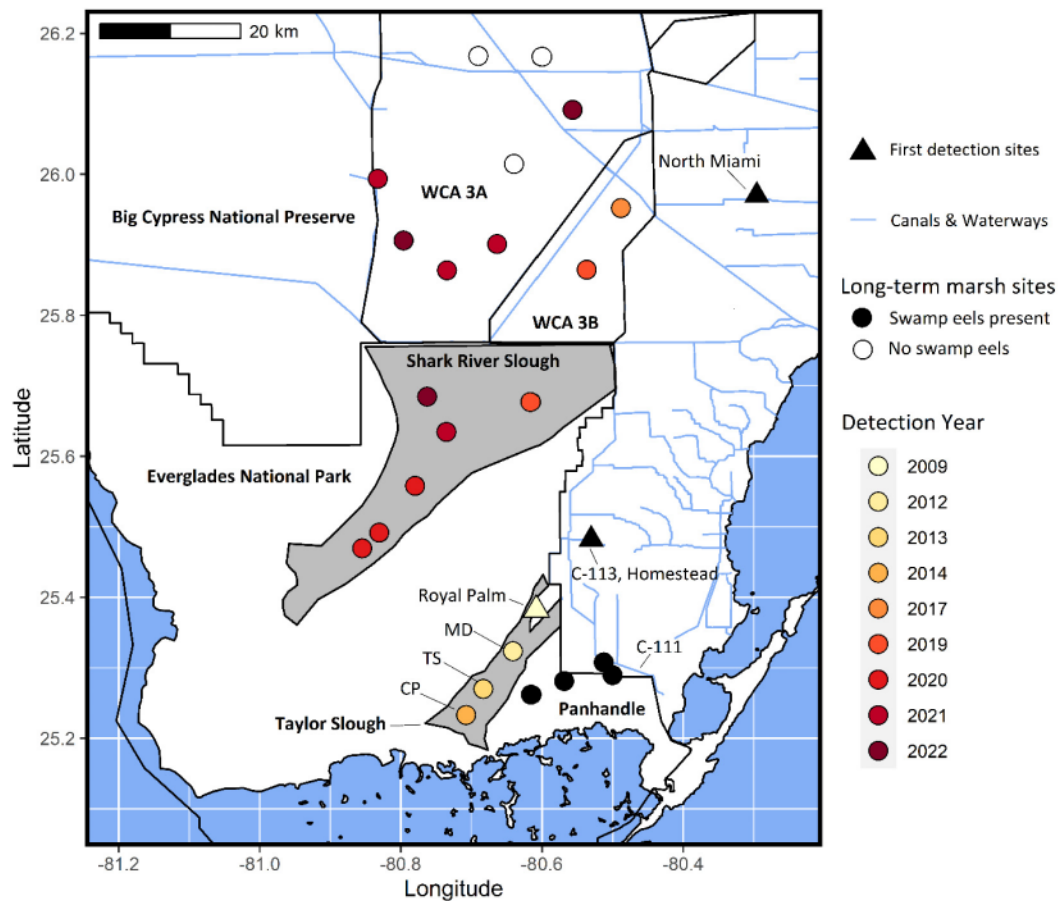


Fig. 1. Map of the study area in southern Florida, showing the location of Taylor Slough and Shark River Slough (gray polygons) within Everglades National Park, along with the Water Conservation Areas and major canals. Circles represent locations of monitoring sites that are regularly sampled by throw trapping and/or electrofishing, with color indicating the year swamp eels (*Monopterus albus/javanensis*) were first collected at each site. Triangles are the two locations where swamp eels were first detected; black circles indicate sites where swamp eels were present by 2011, but were not previously regularly sampled.

Shark River Slough drainage and Water Conservation Area 3A, which have been invaded since 2019 (Fig. 1), but we focused our analyses on Taylor Slough because of the longer history of swamp eel invasion. The southernmost, longest hydroperiod site (CP) in Taylor Slough consisted of three 1-ha plots, while the upstream sites (TS, MD) consisted of five plots per site with two of the five plots having shorter hydroperiods (Trexler et al., 2001, 2003). Seven throw-trap samples were collected at each plot during each sampling period except when sites were only accessible by helicopter and five throw-trap samples were collected; our analyses here are on plot-level mean densities of small fishes and decapods. 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. Animals were removed from throw traps following a standard protocol 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. From 1997 to 2022, the nine central/deeper plots in Taylor Slough were sampled with an airboat-mounted electrofisher for three transects of 5 min (pedal time) to assess large fishes (>8 cm standard length) providing catch-per-unit-effort (CPUE = # / 5-minute transect) relative abundance values (Chick et al., 2004; Parkos et al., 2011). Native fishes were released and non-native fishes were euthanized following each electrofishing transect. Electrofishing data in combination with throw-trap captures were used to document the first detection, spread, and abundance change of swamp eels (Figs. 1, 2a; see below).

To investigate potential effects of swamp eels on fishes and decapods, we first developed statistical models of hydrologic conditions on density using covariates at the plot scale (similar covariates in Dorn and Trexler, 2007; Trexler et al., 2005). Data from the Everglades Depth Estimation Network (Liu et al., 2009; Telis, 2006) were used to estimate hydrological conditions at each plot at the time of sampling: days since a site was dry (depth < 5 cm; DSD), length of previous dry season (= days a site was dry [depth < 5 cm] during previous dry season; LDS), and the average water depth during the 30 or 180 days prior to throw-trap sampling ('30-day depth' or '180-day depth'). Species respond to water depth on different temporal scales, so the better fitting depth measure was used for each species. A layer of dense flocculent material sits at the bottom of the water column such that when the water depth drops below 5 cm dissolved oxygen levels are too low to support many gilled aquatic animals, and most fish, in particular (Trexler et al., 2005).

2.1. Data analysis

We were interested in whether establishment of swamp eels in wetlands has reduced densities of other taxa, so rather than using catch-per-unit-effort data of swamp eels, which was limited to a couple seasons per year (i.e., water deep enough for electrofishing), we divided the time series into three time periods: prior to swamp eel invasion of Taylor Slough (1996–2009; 'before'), the intervening period during which swamp eel populations were spreading throughout Taylor Slough (2010–2014; 'during'), and the period following their complete spread around Taylor Slough (2015–2022; 'after'). The 'during' period consists of the years following

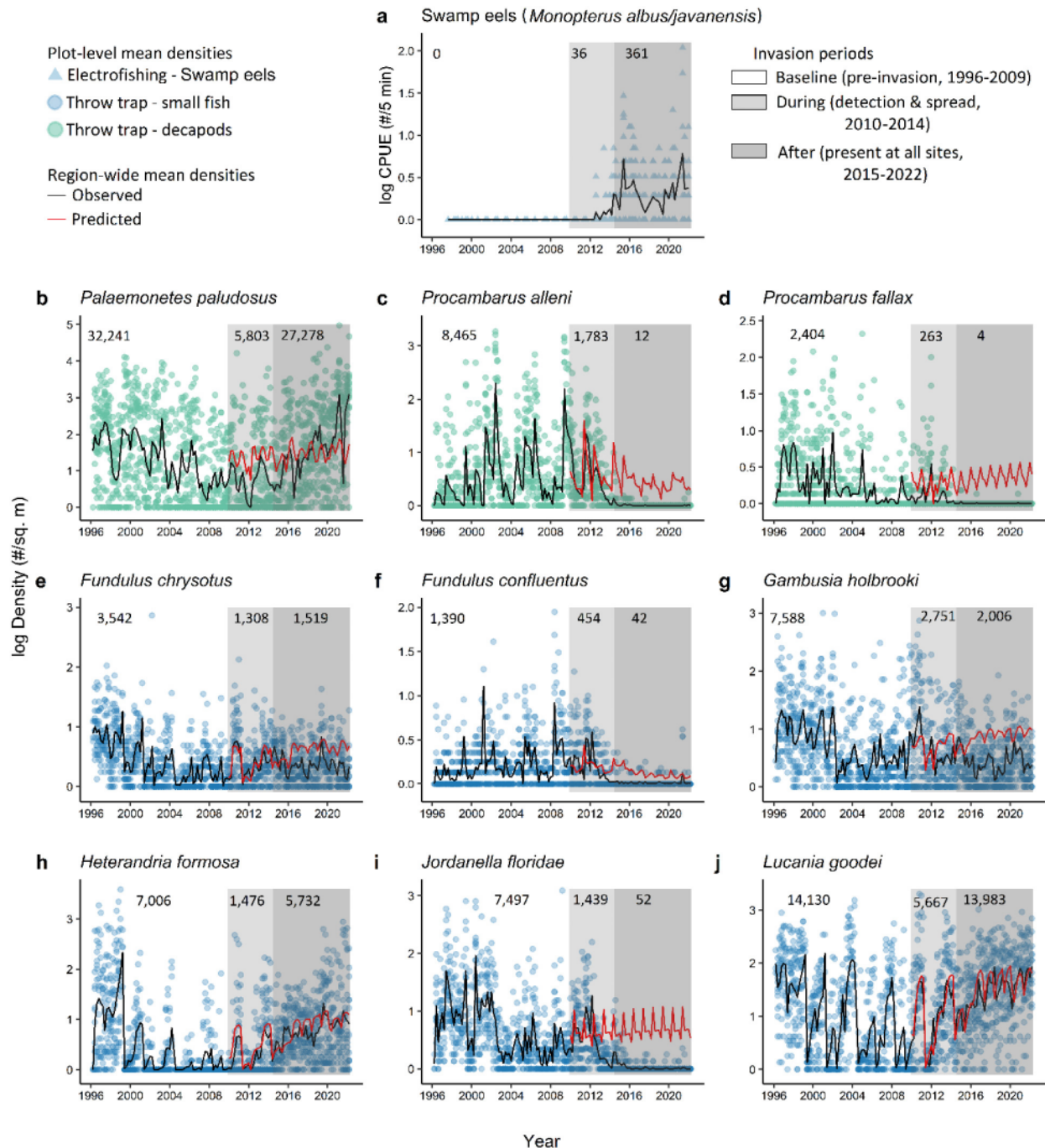


Fig. 2. (a) Densities (catch-per-unit-effort [CPUE]; # / 5-min transect) of swamp eels caught by electrofishing in Taylor Slough of Everglades National Park from 1997 to 2022. (b–j) Densities (log-transformed # / m²) of the three most common decapods (b–d) and six most common small fishes (e–j) collected from throw traps in Taylor Slough of Everglades National Park from 1996 to 2022. The light shaded area represents the “during” period when swamp eels were spreading (Figs. 1, 2a) through Taylor Slough (2010–2014), while the dark shaded area represents the “after” period when swamp eels were established across Taylor Slough (2015–2022). The black line is the mean density of all plots during each sampling period; the red line is the mean density of all plots following the arrival of swamp eels predicted by the parameterized models of hydrologic conditions from prior to swamp eel arrival (1996–2009); error bars are excluded for clarity. Numbers within plots are the total abundance of each species during the three invasion periods; mean densities during each period are listed in Table S1.

the first swamp eel detection in Taylor Slough (2009) at Royal Palm, which is north (upstream) of our northernmost site and an artificially deep area established for tourists, through the year when swamp eels were first detected at all of our sites in Taylor Slough (2014); ‘during’ period data were excluded from our primary analyses but are illustrated in figures. The 14-year ‘before’ period exhibited considerable hydrologic variation (Fig. S1) and served as a baseline period during which we could model relationships between hydrological variables and densities of

native species in the absence of swamp eels. Response species were the three most common decapods and the six most common fishes during the ‘before’ period (abundances in Table S1; shown in Fig. 2). We limited our analyses a priori to these nine species because (1) they were the nine most common fish/invertebrate species in the region, (2) they include decapods and native fishes that are the critical prey for seasonally nesting wading birds of restoration interest, and (3) other species are typically much less common in our throw trap

samples, which means their populations are not as effectively modeled over such a long time series. We used a model selection approach that compared the Akaike information criterion (AIC) among models to choose the best combination of the three hydrological variables (days since dry, either 30- or 180-day depth, length of the previous dry season), season (sampling month: July, October, December, February, April; a categorical variable), and the interaction between season and length of the previous dry season, which accounts for either diminishing effects of the previous dry season as the following water year (starting in June) progresses or lagged population responses (Dorn and Cook, 2015). The model with the lowest AIC was chosen as the best model using the *dredge* function in the MuMIn package 1.47.1 (Bartoń, 2020), even if there were competing models ($\Delta\text{AIC} < 2$). Overall model fit (marginal and conditional R^2) was determined using the *r.squaredGLMM* function from the MuMIn package.

Following parameterization of species responses to hydrologic variation during the 'before' period, we conducted subsequent analyses to assess the effects of swamp eels. We first fit the parameterized hydrologic variables to a dataset consisting of the 'before' period (1996–2009) and the 'after' period (2015–2022) while excluding the 'during' (i.e., colonizing) period. For each species, models included the density of that species in the prior time step and the best combination of the hydrological variables from the baseline analyses (including season). We tested for effects of the swamp eels by adding a categorical variable for the periods 'before' versus 'after' (hereafter 'before/after'). Our primary tests of an impact of swamp eels on densities of native taxa were obtained by testing whether the model fit was improved by contrasting these two models for each species (i.e., with vs without before/after) using a Chi-square test. Then we used the parameterized model from the pre-eel baseline data (1996–2009) to predict the density of each species for the following years (2010–2022) with the few negative predictions converted to zeroes; predicted means are illustrated on Fig. 2. Because the first six years of the time-series (1996–2001) were the most hydrologically similar portion of the 'before' period to the 'after' period, we used the differences in plot-level mean densities between these 'before' and 'after' years, along with the differences between the predicted and observed data during the 'after' period, to calculate two different estimates of percent changes in average population densities once swamp eels were established in Taylor Slough ('after' period).

All analyses were mixed-effects models that included site and plot nested within site as random effects. Dependent variables were densities of each species and were log-transformed to approximate normal error distributions of the models' fit; other error distributions (e.g., gamma) did not fit (lower log likelihood) or approximate assumptions as well as Gaussian. Independent variables length of the previous dry season and days since dry were log transformed, while depth was not transformed. All models were fit by maximum likelihood (using the Satterthwaite method) with the lme4 v 1.1–30 and lmerTest v 3.1–3 packages in R v 4.2.1 (Bates et al., 2015; Kuznetsova et al., 2017; R Core Team, 2022).

3. Results

Within three years of being collected at three long-term monitoring sites in Taylor Slough (Figs. 1, 2a), swamp eels dominated samples of large fishes, and populations of four common native species had collapsed (Fig. 2b–j). Populations of both crayfish species significantly declined, *Procambarus alleni* (Everglades Crayfish; $\chi^2 = 142.6$, $P < 0.0001$) and *Procambarus fallax* (Slough Crayfish; $\chi^2 = 216.6$, $P < 0.0001$). Average densities of *P. alleni* fell by $99.4 \pm 0.2\%$ (mean \pm SE) during the last eight years (Fig. 2c; swamp eel establishment = 'after' period) from the first six years (a similarly wet period) and by $96.1 \pm 3.4\%$ from densities predicted by our parameterized statistical models. *Procambarus fallax* densities fell by $99.7 \pm 0.2\%$ from the first six years and $99.6 \pm 0.2\%$ from predicted densities (Fig. 2d). Two fish species also experienced drastic declines ($\geq 80\%$): *Jordanella floridae* (Flagfish; $\chi^2 = 383.1$, $P < 0.0001$) fell by $99.1 \pm 0.4\%$ and $98.3 \pm 0.7\%$ (Fig. 2i) and *Fundulus confluentus* (Marsh Killifish; $\chi^2 = 88.1$, $P < 0.0001$) fell by $91.3 \pm 2.1\%$ and 84.4

$\pm 5.3\%$ (Fig. 2f) relative to the first six years and predicted densities, respectively. Two fishes experienced intermediate population declines: *Gambusia holbrooki* (Eastern Mosquitofish; $\chi^2 = 152.8$, $P < 0.0001$) densities declined by $66.1 \pm 5.3\%$ and $55.0 \pm 4.1\%$ (Fig. 2g) and *Fundulus chrysotus* (Golden Topminnow; $\chi^2 = 72.7$, $P < 0.0001$) densities declined by $51.8 \pm 4.6\%$ and $44.5 \pm 3.8\%$ (Fig. 2e) relative to the first six years of the time series and predicted densities, respectively. No population changes were detected for *Heterandria formosa* (Least Killifish; Fig. 2h; $\chi^2 = 0.4$, $P = 0.54$). *Lucania goodei* (Bluefin Killifish; Fig. 2j; $\chi^2 = 3.1$, $P = 0.079$) densities trended towards being higher after invasion than the first six years ($+55.0 \pm 21.2\%$), but did not differ from predictions based on hydrologic conditions ($-4.4 \pm 11.7\%$). Population densities of *Palaemonetes* [*Palaemon*] *paludosus* (Grass Shrimp; Fig. 2b) have also trended towards higher since swamp eel invasion ($\chi^2 = 4.4$, $P = 0.035$), being $150 \pm 42.7\%$ higher than predicted by hydrologic models, but they were not different from the first six years of the time series ($+20.9 \pm 27.9\%$). No similar declines of these taxa were observed in two other major regions of the Everglades, where swamp eels were largely absent during the "after" period of the Taylor Slough analysis (Appendices S1, S2).

Although first observed in wetlands east of Taylor Slough in 2007 and in northern Taylor Slough in 2009, swamp eels were first captured at our sites during electrofishing sampling in October 2012 and have been consistently found at all three sites since 2014 (Fig. 2a); since establishing in Taylor Slough ('after' period 2015–2022), they have been the most commonly caught fish electrofishing ($N = 361$) and more common than all other large fishes (>8 cm SL) combined ($N = 241$). During the study period, hydrologic conditions in Taylor Slough were relatively wet on the two ends of the time series and drier from ~2000–2010 (Fig. S1). Statistical models of hydrologic conditions during the baseline period (Table S2) indicated species-specific responses to hydrologic conditions, with three species that responded positively to hydrologic drought or were most common immediately after the dry season ended (*F. confluentus*, *J. floridae*, *P. alleni*) and six species responding negatively to drought (*G. holbrooki*, *F. chrysotus*, *H. formosa*, *L. goodei*, *P. fallax*, *P. paludosus*).

4. Discussion

The collapse of populations of four common native species within three years of swamp eel invasion suggests that swamp eels have imposed stronger top-down effects on most of the small fish and decapods than native predators and have undermined the hydrology-mediated production of aquatic animals. Until this analysis, the potential impacts of swamp eels on the trophic dynamics of the Everglades and implications for its restoration had gone unnoticed, but they are comparable to or exceeding the effects of the Burmese python invasion, which has received copious attention from scientists, managers, politicians, and the public. In the Everglades, hydrologic and seasonal (phenological) variation drives most changes in aquatic animal populations, from invertebrates and small fishes to larger predatory fishes (Boucek and Rehage, 2013; Chick et al., 2004; Dorn and Trexler, 2007; Gaiser et al., 2012; Ruetz et al., 2005). Our statistical models of species responses to hydrological variation parameterized prior to swamp eel invasion support a similar conclusion (Table S2). A monitoring program established to evaluate benefits from hydrological restoration has fortuitously demonstrated an unexpected and dramatic impact of a biological invasion resulting as an unintended outcome of restoration.

While most aquatic animal species in the Everglades, both native and non-native, rely on lifecycle characteristics or migration to/from refuges to survive the dry season (Dorn and Volin, 2009; Loftus and Kushlan, 1987; Parkos et al., 2011), swamp eels possess multiple physiological capacities that in combination are unlike other fishes in the Everglades and enable them to persist through drought (Chew et al., 2005; Graham, 1997; Liem, 1987). No native taxa were expected to decline precipitously after accounting for these hydrological influences on population dynamics in the post-swamp-eel invasion period and none revealed such declines in nearby habitats lacking swamp eels (Appendix S2). Therefore, all signs indicate that swamp eels caused the collapse of these formerly abundant

taxa, whose loss implies marked re-organization of the Taylor Slough food web and food-production system for apex predators including wading birds and alligators.

Limited dietary studies of populations in canals/ponds suggest swamp eels are opportunistic predators, feeding on insects, crayfish, and fish (Hill and Watson, 2007; Sakaris et al., 2019; Shafland et al., 2010); data on their diets in Everglades marshes suggest the same (P. Flood, unpublished data). Crayfish burrow into substrates when wetland surfaces dry (Dorn and Volin, 2009), emerge with re-inundation, and experience low predation and high recruitment following hydrologic droughts (Dorn and Cook, 2015; Dorn and Trexler, 2007) when predatory fishes are temporarily reduced by the drought disturbance (Chick et al., 2004; Parkos et al., 2011). The shared drought resilience of crayfishes and swamp eels may mean that the normal correlation between wetland drying and subsequent predator-free times has been broken. In contrast to crayfish, grass shrimp consistently respond positively to increasing water depth and time since the marsh dried (Table S2) and experimental work suggests they are relatively insensitive to predatory fish (Knorp and Dorn, 2014). Among the fishes, *J. floridae* and *F. confluentus* were reduced most strongly, and they are the only common small marsh fishes that seem to respond positively to drought (Ruetz et al., 2005; Trexler et al., 2005); they may have similar predator sensitivities as crayfish, co-occurring with larger fish predators in the system by growing fast during predator-free periods in places and times with system-wide drying.

The intermediate declines in abundances detected in *G. holbrooki* and *F. chrysotus*, but not *L. goodei* or *H. formosa*, may be tied to their abundance immediately after re-flooding. The three fastest colonizing fish species in the Everglades are *J. floridae*, *G. holbrooki*, and *F. chrysotus*; *F. confluentus* and possibly *J. floridae* lay desiccation-resistant eggs that hatch upon re-flooding, while *G. holbrooki* and *F. chrysotus* are highly exploratory and swim into reflooded areas from distant refuges (Gatto and Trexler, 2020). Recurrent immigration by *G. holbrooki* and *F. chrysotus* could buffer their populations from swamp eel impacts, while *J. floridae* and *F. confluentus* may experience persistent impacts from predation at the crucial post-drought recovery period without rescue from immigrants within their shared demersal microhabitats. Hence, the most strongly affected species are those independently thought to be sensitive to fish predation and/or adapted for rapid recovery following drought. Swamp eels reduced densities of species with a variety of life histories, suggesting they are more efficient predators than the rest of the community of predators, but the species most affected were those less sensitive to drought-disturbances (i.e., those responding positively or weakly to dry conditions). Frequency of drought-disturbance covaries inversely with top-down effects of aquatic predators in the Everglades (Trexler et al., 2005; Dorn and Cook, 2015), but swamp eels, with novel ability to withstand drying, may be flattening the inverse relationship in the two stressors. This supports the idea that species most vulnerable to a novel invasive species are those that occupy similar habitats and lack defenses to the novel predator (Cox and Lima, 2006; Ricciardi and Atkinson, 2004). In this case, invasive swamp eels appear to be eliminating predator-free spaces/times (Jeffries and Lawton, 1984) (i.e., shorter hydroperiod slough edges/immediately after re-inundation) from Taylor Slough, which is functionally extirpating taxa that require seasonal wetlands in order to co-occur with larger fish predators.

Our conclusions from Taylor Slough are supported by data from three other regions of the Everglades. The marshes of the eastern Panhandle region of Everglades National Park (Fig. 1) are where swamp eels were first detected outside of canals in 2007, but intensive sampling there did not begin until 2008 (Fig. S2). Panhandle data show near complete collapses of populations of *P. alleni*, *J. floridae*, and *F. confluentus* (Fig. S3; *P. fallax* were always uncommon), but these data were excluded from statistical analyses because we lacked any baseline period prior to swamp eel arrival. Conversely, swamp eels were only recently detected in our sampling efforts in Shark River Slough (2019) and Water Conservation Area 3A (2021) (Fig. 1), which is likely too soon to detect drastic changes. These regions effectively serve as reference regions for the changes observed in Taylor

Slough (see Appendix S2), and no species experienced concurrent population collapses in those regions (Figs. S4, S5).

Assessment of our common nine species in Taylor Slough using electrofishing catch-per-unit-effort of swamp eels (9 of 13 plots in Taylor Slough were electrofished), other non-native fishes, and large native fishes corroborate the effects of swamp eels documented here for all of the species that experienced population declines and suggest no other taxa have played major roles in the declines of any of our nine assessed species in Taylor Slough (Appendix S1; Table S3). The two species that had intermediate declines in presence/absence analyses also had weaker associated declines with swamp eel densities. This may indicate that the presence of swamp eels is having an effect on them, but one that is only becoming more apparent as time since swamp eel establishment proceeds and the most dramatically affected species have been functionally eliminated from the system, potentially placing greater predation pressure on other taxa. Overall, our results document effects on the invasion front, and future production of crayfish and small fishes may depend on the stability of swamp eel populations and their ability to establish in habitats across the full range of hydroperiods characteristic of the Everglades.

Despite limited prior work suggesting that swamp eels had little potential for ecological or economic impacts (Hill and Watson, 2007; Shafland et al., 2010), our results do not bode well for the freshwater trophic functions and goals of restoration of the Everglades in light of the recent rapid expansion of swamp eels. The Everglades is recognized as important breeding grounds of wading birds such as the White Ibis (*Eudocimus albus*), and recent work has linked irruptive White Ibis breeding to crayfish populations in the southwestern Everglades (Cocoves et al., 2021). Restoration success is commonly linked to bringing back irruptive dynamics of breeding wading birds and regular re-establishment of large breeding aggregations in Everglades National Park (Frederick et al., 2009; National Academies of Sciences, Engineering, and Medicine, 2021). If crayfish populations collapse throughout the Everglades following swamp eel spread, breeding of White Ibis and other wading birds that prey on crayfish or fishes like *J. floridae* and fundulids (Klassen et al., 2016) could be curtailed or greatly limited despite monumental efforts at hydrologic restoration.

Restoration of historical hydrological flows to the southern Everglades are explicitly targeted to increase populations of invertebrates and small fishes that are prey of wading birds (Sklar et al., 2005). Although attributing the wetter conditions observed during the latter portions of this study to the relative contributions of water management, rainfall, and potential influence of sea level rise (Dessu et al., 2018) will require further analyses, water management actions prior to and early in this study increased the flow and hydroperiod within Taylor Slough (Kotun and Renshaw, 2014). Prior work suggested restoration could facilitate the introduction of non-native species by increasing connectivity of human-dominated canal habitats and marshes (Kline et al., 2014; Loftus, 1988). Introductions of several non-native fishes, including swamp eels, into Everglades National Park corresponded spatiotemporally with management changes, connectivity, and overflow of canals into marshes (Kline et al., 2014). Our results suggest the reduction of native prey populations following introduction of non-native species could compromise an aim of restoration – increasing wading bird prey availability.

There were limited control efforts (some data included in Sakaris et al. (2019)) to slow the spread of swamp eels beyond the canals before they were found in Everglades National Park. Unfortunately, removing a common, difficult to capture species like swamp eels from a large, open wetland seems unlikely (Loftus, 1988). Efforts should be focused on restoring unnatural habitats, in this case canals, to reduce their role as a refuge and corridor for spreading non-native species, along with preventing the future arrival of additional non-native species, despite how innocuous they may seem in other habitats. Species with unique sets of traits should raise the most alarm and be the focus of control efforts immediately after detection (Lawson and Hill, 2022). Past efforts to predict the risk of impacts from swamp eels (Hill and Watson, 2007; Shafland et al., 2010) failed to predict the vulnerability of species documented here. This study highlights how

little is known about the environmental drivers of non-native fish populations following introduction and establishment, or the ability to predict impacts of invasive fishes in wetlands.

It remains to be seen whether swamp eels will persist and have effects across southern Florida similar to those we report here, and many of these other regions lack long-term monitoring programs with the capacity to detect changes in prey populations and establishment of swamp eels. There should be similar concern for synbranchid introductions in other wetland ecosystems that lack functionally similar predators. Natural conditions such as disease or cold sensitivity could lead to drops in populations of swamp eels (Rehage et al., 2016; Saylor et al., 2021; Schofield and Kline, 2018), and it is possible that some larger wading birds will modify their diet to include swamp eels and replace a portion the lost native prey. The magnitude of the declines observed here underscore the need to more aggressively consider risk and prevent the spread of non-native species in the design of water management structures and operations, proactive risk assessments, monitoring, and possible management of non-native species at the edges of protected natural ecosystems before introductions occur and deleterious effects have been detected. In addition, targeted long-term monitoring of key performance measures, in this case populations of aquatic animals, will be invaluable to evaluate potential ecosystem-level effects of invasive species as ecosystem restoration progresses. An invasion eliminating an important hydrologically-mediated function of the Everglades has the potential to result in a dramatic loss of key ecosystem services and diminish the benefits of this historic wetland restoration effort.

CRedit authorship contribution statement

JCT and JLK managed the project and data collection; MRP analyzed data with input from NJD and JCT; MRP led the writing of the manuscript and all authors contributed to revisions.

Data availability

Data are archived at the FIU Florida Coastal Everglades LTER website (<https://doi.org/10.6073/pasta/70379cfac3572272bdf5e6e7d0d7840c>).

Declaration of competing interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.159245>.

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