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Differential impacts of hurricanes on direct and complex life cycle parasites: a 42-year study of riverine fish

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ABSTRACT

Hurricanes have increased in frequency and magnitude due to anthropogenic climate change. These events can cause outbreaks of parasitic diseases in humans, but little is known about how they impact parasite abundances for wildlife hosts. The southeastern United States Gulf region has been affected by hundreds of hurricanes in the past 50 years, with frequency and intensity increasing through time. Prior studies have quantified the response of wildlife parasites to individual hurricanes, but have never systematically evaluated whether these effects are consistent across hurricanes or different from control conditions. From the Royal D. Suttkus Fish Collection at the Tulane University Biodiversity Research Institute, we selected and performed parasitological dissections of 1197 preserved fish across seven fish species collected between 1963 and 2005 from the Pearl River in Louisiana. We evaluated the effect of hurricanes on parasite abundance using generalized linear mixed models that contrasted responses of fish parasites to 24 hurricanes against control conditions. We found that change in parasite abundance in response to a hurricane was dependent upon parasite taxonomic group and transmission strategy, with direct life cycle parasites (copepods and monogeneans) negatively impacted by hurricanes on short time scales, while complex life cycle parasites (acanthocephalan, cestode, nematode, trematode adult and trematode metacercaria) were not affected by hurricanes. This investigation of hurricane impacts on parasitism in wildlife populations across a 42-year period identifies parasite traits that modulate resistance to hurricane conditions. Continued anthropogenic climate change will cause more frequent and intense hurricane events, which our research suggests could lead to decreased abundances of direct life cycle parasites, affecting riverine fish parasite community structure. Declines of parasites may signal broader ecosystem stress under increasing hurricane frequency, with cascading effects on fish hosts and other interacting species.

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Extreme weather; BACI design; lagged transmission effects; environmental resistance; metazoan parasites; shelter effect

Introduction

Anthropogenic climate change is increasing the frequency and intensity of extreme weather events like hurricanes (Michener et al. 1997), with the frequency of category four and five hurricanes increasing by 30% for every 1 °C increase in temperature (Holland and Bruyère 2014). Hurricanes can alter the physical structure of freshwater habitats, causing runoff pollution, salinity spikes, deposition and suspension of debris and direct destruction of structures including mangrove forests (Mallin and Corbett 2006; Patrick et al. 2020). Furthermore, storm surge from hurricanes can both force seawater upriver and deposit large amounts of marsh vegetation in the lower reaches of rivers (Cahoon 2006). Aquatic plant and animal

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Article highlights

- We investigated how parasite abundance in riverine fish is affected by hurricane events relative to control conditions using museum collections of fish collected from the Pearl River between 1963 and 2005.
- We found that hurricanes drove short-term declines in the abundance of direct life cycle parasites on short time scales (3 months), but this effect dissipated at longer (6-month) time scales.
- The abundance of complex life cycle parasites was not affected by hurricanes.
- The increasing frequency of hurricanes might pose a threat to populations of direct life cycle parasites.

populations are particularly impacted by floods, which can temporarily inundate a river or body of water with excess nutrients, leading to eutrophication (Patrick et al. 2020). High winds and rain can suspend sediment in the water column of rivers and lakes, obscuring light and leading to decreases in biomass of primary producers like phytoplankton (Havens et al. 2011). These conditions also lead to changes in predator-prey interactions, changes in the density of fishes, reductions in vegetative cover and an increase in the abundance of macro-zooplankton (Havens et al. 2011). These effects of hurricanes on physical habitat can in turn impact the composition of riverine communities (Mallin et al. 2002).

Hurricanes are known to affect the transmission dynamics of human-infecting parasites. Transmission of parasites to humans has been observed to increase after hurricane events, especially when hurricanes cause water to become contaminated (e.g. with *Leptospira* bacteria, which cause leptospirosis, and *Vibrio cholerae*, which causes cholera) (Nelson et al. 2009; Rebaudet et al. 2013; Al-orry et al. 2016). Hurricanes can force humans into closer contact with each other, facilitating the spread of directly transmitted parasitic diseases including cryptosporidiosis and giardiasis, which can be compounded by storm-induced disruptions to freshwater sources (Roman et al. 1994; Howard et al. 1996; Mallin and Corbett 2006; McMichael 2015; Lynch and Shaman 2023). Most studies that document the impact of hurricanes on the transmission of parasites find that hurricanes increase the frequency of infection.

But while hurricane effects on transmission have been well documented in human hosts, we know little about how hurricanes affect parasitic infections in wildlife populations (Cely 1991; Maness 2019; Filipe et al. 2020). Aguirre-Macedo et al. (2011) found that, following a hurricane, *Cerithideopsis* (syn. *Cerithidea*) *pliculosa* snails formerly abundant in a coastal lagoon of the Yucatán Peninsula were absent for 6 months. These snails are important intermediate hosts for fish-borne trematode parasites, which were themselves absent from this ecosystem for 14 months following the hurricane event (Aguirre-Macedo et al. 2011). The authors estimated that it would take between six and ten years for snail biomass to recover to 90% of before-hurricane values and that trematode infection prevalence would take between six and eleven years to recover to 90% of before-hurricane values (Aguirre-Macedo et al. 2011). Effects of hurricanes have been reported on direct life cycle protozoan parasites (specifically *Balantidium coli*) in rhesus macaques of Puerto Rico: *B. coli* infection intensity was lower following a hurricane event than before the event (Pavez-Fox et al. 2024). *Balantidium coli* cysts thrive in high-humidity environments protected from direct sunlight, conditions that became less common after Hurricane María, which reduced the island's vegetation cover (Schuster and Ramirez-Avila 2008; Pavez-Fox et al. 2024). For the same population of rhesus macaques, the prevalence of two nematode species, *Strongyloides fulleborni* (complex life cycle) and *Trichuris trichura* (direct life cycle), increased following the hurricane, suggesting that after-hurricane crowding may facilitate the spread of these parasites, a trend similar to those observed in human populations following hurricane events (Behie et al. 2014; Pavez-Fox et al. 2024). These examples illustrate that hurricanes impact parasite populations in wildlife (Aguirre-Macedo et al. 2011; Pavez-Fox et al. 2024). But, importantly, these studies have all focused on changes manifested in response to single hurricane events. To our knowledge, no study has synthesized data across hurricanes or compared hurricane-affected areas to unaffected controls; therefore, a gap remains in our understanding of how wildlife parasites respond to the disturbance caused by hurricanes.

The life cycle strategy a parasite employs can further modulate its ability to withstand environmental perturbations. For example, parasites of fish intestines were found to be unaffected by environmental salinity changes as internal osmoregularity remained fairly constant (Möller 1978). In contrast, salinity affected freshwater ectoparasite and external larval nematode development negatively, an effect which was compounded by high temperatures (Möller 1978). Taken together, ectoparasites like copepods and

monogeneans that are more directly exposed to the environment than endoparasitic nematodes, trematodes, or acanthocephalans, may be more sensitive to environmental changes independent of environmental effects on hosts themselves.

Prior studies have noted the importance of transmission strategy in modulating the response of parasites to hurricane events. Parasites can be categorized into two broad transmission strategies: complex life cycle parasites rely upon two or more host species to complete their life cycle, while direct life cycle parasites can be transmitted between conspecifics (Olsen 1986). Complex life cycle parasites are expected to be more prone to negative impacts from hurricanes. First, if any of the hosts involved in the life cycle are reduced in abundance following a hurricane, the parasite may not be able to persist in that particular environment. Moreover, free-living infective larvae are known to be sensitive to changes in abiotic conditions, potentially decreasing in lifespan after exposure to pollutants and salinity spikes, though relationships are species-specific (Cross et al. 2001; Koprivnikar et al. 2010; Prasopdee et al. 2020; Jones et al. 2020). However, other outcomes are possible: complex life cycle parasites may be at an advantage during a short-term disturbance like a hurricane, because, in a manner of speaking, their eggs are distributed across many baskets: different infectious stages of a complex life cycle parasite infect different hosts, so that if any one host is temporarily wiped out by hurricane conditions, there is a reservoir of infectious propagules in the upstream host ready to continue the life cycle once the extinguished host recovers. These parasites could therefore maintain their populations by sheltering in unaffected hosts, allowing them to ride out the hurricane and resist any short-term change in the system (Molnár et al. 2013; Aleuy and Kutz 2020). Direct life cycle parasites might have only one host species, and as such could be protected from hurricane events if their host is unaffected. Conversely, a direct life cycle parasite might not have any reservoir or back-up hosts in which they could ride out a hurricane, so if their host is affected, the parasite will be affected as well. Disruption in abundance or distribution of a host organism can manifest in spatio-temporal mismatches, wherein a misalignment of hosts and parasites encountering each other in space (e.g. range shifts, shifts in habitat use) or time (e.g. disruptions of normal seasonal patterns) detrimentally affects parasite development and reproduction (Saino et al. 2009; Paull and Johnson 2014; Poulin and Lagrue 2015; McDevitt-Galles et al. 2020). When sustained in an ecosystem for a long period of time, such mismatches can lead to a decrease in that parasite's abundance (O'Donnell et al. 2011).

We set out to quantify the effects of hurricanes on parasite populations in wildlife. Our goal was to understand how hurricanes affect the abundances of parasites and whether transmission strategy (direct versus complex life cycle) modulates that response. We hypothesized that complex life cycle parasites would be negatively affected, as they require more host species and more steps to successfully reproduce, meaning disruption at any stage could lead to declines in abundance (Rauch et al. 2005; Kutz et al. 2009; Poulin and Lagrue 2015; Aleuy and Kutz 2020). We also hypothesized that direct life cycle parasites would be less affected by hurricanes, since they do not require more than one host species and may be more flexible as host community composition shifts post-hurricane (Anderson 1980; Niewiadomska and Pojmańska 2011; Aleuy and Kutz 2020). To test these hypotheses, we parasitologically examined riverine fish collected from a hurricane-prone area over a 42-year period that encompassed 25 hurricane events. These data allowed us to quantify the effects of hurricane events on parasites of riverine fish and investigate whether transmission strategy, location of infection within the host, or parasite taxon modulates parasite responses to hurricanes.

Methods

Specimens

This study used the Royal D. Suttkus Fish Collection housed at the Tulane University Biodiversity Research Institute (TUBRI) in Belle Chasse, Louisiana, USA—a collection that includes numerous specimens collected from the Pearl River in Louisiana between 1963 and 2005 (Tulane University Biodiversity Research Institute n.d.) (Figure 1). Given the robustness of this collection, our team identified seven species of fishes that were sufficiently abundant across both space and time (*Gambusia affinis*, *Carpiodes velifer*, *Hybognathus nuchalis*, *Ictalurus punctatus*, *Notropis atherinoides*, *Percina vigil* and *Pimephales vigilax*). We selected fish with sufficient within-lot replication (more than four fish individuals

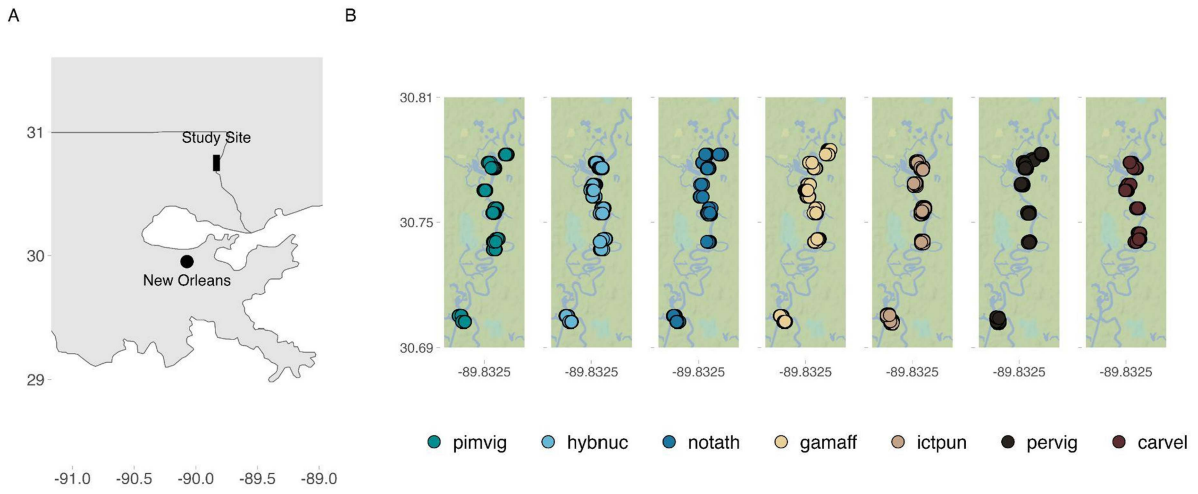

Figure 1. The sampling locations from which fish were originally collected are along the Pearl River in southern Louisiana, about 100 miles north of New Orleans, LA. Latitude and longitude are represented on the y and x axes, respectively. (A) Location of Pearl River study site in relation to New Orleans, Louisiana and the greater United States Gulf Region. (B) Collection location along the Pearl River for all lots of fish separated out by fish species with points jittered to show overlapping sampling sites (pimvig = *Pimephales vigilax*, hybnuc = *Hybognathus nuchalis*, notath = *Notropis atherinoides*, gamaff = *Gambusia affinis*, ictpun = *Ictalurus punctatus*, pervig = *Percina vigil* and carvel = *Carpiodes velifer*).

per jar) and instituted an upper and lower body size limit (total length) to keep body size constant through time, as we noticed a decrease in body size through time when fish were randomly selected (>27 mm for *G. affinis*; >30 mm for *C. velifer*, *P. vigil* and *P. vigilax*; >35 mm for *H. nuchalis* and *N. atherinoides*; and between 35 and 150 mm for *I. punctatus*—all fish except *I. punctatus* had no defined upper limit and the largest fish we analyzed measured 139 mm in length) (Supplemental Figure 9). We used stratified random sampling to select final lots from the total collection based on decade and location of collection. For example, we selected the same number of lots from the decade 1980–1989 as we did from the decade 1990–1999 for each of the two main sampling location criteria (see experimental design below), aiming for five lots per decade-location combination [see Diaz-Morales et al. 2026 for more details].

Data collection

We employed a semi-destructive method of dissection that would allow us to accurately inspect for parasites but preserve the host specimen for retention in the Fish Collection (Wood et al. 2023a). We focused on the right side of each fish, collecting the right eye, pectoral and pelvic fins and gills. We made an incision from just below the gill isthmus to the vent and removed all visceral organs. The organs and tissues were placed into a container with 70% ethanol and examined for parasites. Parasite counts from bilateral organs (i.e. eye) were doubled (Shaw et al. 2005). The skin, caudal fin, anal fin, dorsal fin, buccal cavity and body cavity were examined intact. Once all parasites had been removed and vouchered in 70% ethanol, the fish was placed in a container with its tissues and organs, labeled and returned to the museum collection jar (Wood et al. 2023a). Parasites were identified to the lowest possible taxonomic level and were sorted based on transmission strategy and higher taxonomic category for analysis as follows: direct (i.e. monogenean, copepod); complex (i.e. acanthocephalan, cestode, trematode adult, trematode metacercaria, myxozoan and nematode). In the case of myxozoans, species producing pseudocysts and species infecting the gall bladder of *C. velifer*, *G. affinis* and *P. vigil* were assessed. For pseudocyst-producing myxozoans, abundance was defined as the number of pseudocysts (containing hundreds of spores) per fish. Myxozoans infecting the gall bladder were recorded as present or absent.

Experimental design

This study was part of a larger project concerned with estimating the impacts of industrial pollution on parasite burdens of riverine fishes. As such, locations above (control) and below (impact) a pulp mill were

selected to test the effects of pollution on parasite communities through time. Pollution was not a central aspect of this sub-project. Therefore, we account in our models for the sampling location via inclusion of a 'mill_location' fixed effect, but do not explore the effects of pollution on parasite populations further.

Unlike the larger, pollution-focused project, the project described herein was designed to assess the effects of hurricanes on parasites in riverine fish. To that end, we used a before–after–control–impact (BACI) design, where the 'impact' is hurricane presence; the two main effects (before–after, control–impact) interact to create four categories (before hurricane, after hurricane, before control, after control). In order to split our data into BACI categories, we identified all hurricane events that occurred between the collection date of our first (1963) and last (2005) fish specimens, and identified appropriate control events, and ecologically relevant timeframes to append as buffers on either side (before and after) of both hurricane and control events, all of which were incorporated into our dataset based on date of occurrence.

Identifying hurricane events

Hurricane events were identified using the publicly available historical hurricane track dataset from the National Oceanic and Atmospheric Administration (NOAA n.d.). Using tools on this website, we generated a polygon that outlined the Pearl River from source to sea (from near Jackson, Mississippi to the Gulf of Mexico). We then assigned a 50-mile-radius buffer zone to this polygon, and recorded all historical hurricanes that intersected with it (NOAA n.d.). Due to our study system's position in the hurricane-prone US Gulf region, we were able to capture 25 hurricanes crossing this buffer zone during our focal time period (1963–2005) (Figure 2). Two hurricanes occurred within two months of each other—Hurricane Erin in late July 1995 and Hurricane Opal in late September 1995—and were combined into one hurricane that lasted from the beginning of Erin on 31 July 1995 to the end of Opal on 6 October 1995. This brought our total number of hurricanes to 24. Data collection ceased halfway through 2005 due to the disruption caused by Hurricane Katrina and as such that year was dropped from the analysis. Hurricanes occurred in 16 of 42 years (37%) sampled in this study, while the remaining 26 years (63%)

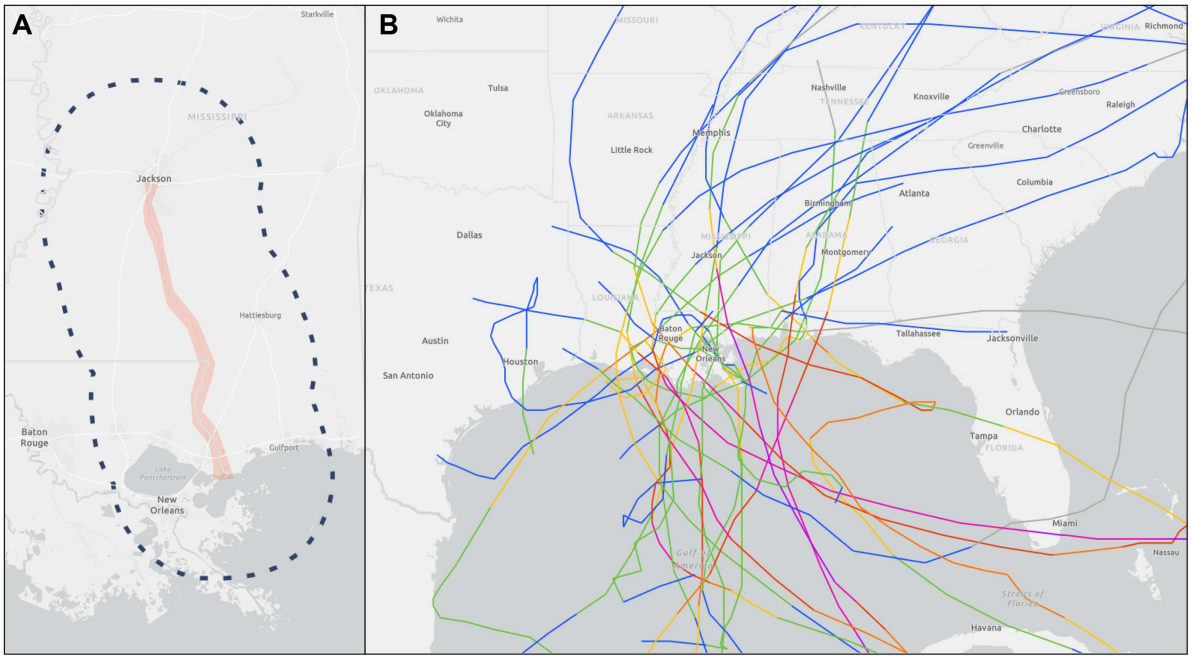

Figure 2. All hurricanes crossing a 50-mile buffer zone around the Pearl River were identified and collected for analysis. (A) A polygon was drawn around Pearl River from source to sea (in red) with a 50-mile buffer zone (dotted line) surrounding the polygon. (B) All storms crossing this polygon were included in this study (25 storms). The color of the lines corresponds to the intensity of the storm, with Category 5 storms represented in magenta and extratropical storms shown in gray (a gradient of decreasing intensity). Images collected from the NOAA hurricane watch website.

experienced no hurricanes. Start and end dates of each hurricane were recorded from the NOAA database and assigned to the dataframe using a 6-month buffer on either side of the hurricane (6 months before a hurricane [denoted 'before'] and 6 months after a hurricane [denoted 'after']). A second analysis was conducted using 3-month buffers to discriminate between the immediate effects of hurricane events (3-month buffer) and longer-term effects (6-month buffer). We chose a 3-month time buffer (3 months before an event and 3 months after the event) to capture direct and immediate effects of hurricanes on parasites (i.e. a time span just long enough to encompass a sufficient number of sampled fish). Similarly, we chose a 6-month buffer to capture potential longer-term effects of hurricanes on parasites of riverine fish, with the assumption that effects not immediately present (such as those affecting more nuanced dynamics like host populations or environmental pollution) would be evident on this longer time scale (Waddell et al. 2021). By incorporating both 3-month and 6-month buffer timeframes, we were able to examine both immediate and longer-term effects of hurricanes on parasite populations in these riverine fish.

Identifying appropriate control events

A before–after comparison can suggest what change occurred due to an impact, but it cannot rule out other explanations for that change (e.g. regular seasonal variability, coincident environmental shifts), which is why before–after–control–impact designs are so powerful (Christie et al. 2019). We chose to identify control periods against which we could contrast hurricane periods, allowing us to separate change due to hurricanes specifically from change due to other drivers. In this study, we use the term 'control' to denote years in which no hurricane occurred. To designate control periods, we started with the total span of data (1963–2004) and removed all the years when there was a hurricane. All remaining years (26 years) were randomly assigned an actual hurricane's start/end date (month and day only, not year). Because we had two more control years than we had hurricane events to assign (24 hurricane events in total versus 26 years of controls, with each control year being assigned one hurricane event only), this random assignment was conducted with replacement until all control years were assigned a corresponding hurricane start/end date. This allowed us to have 'control events' that mirrored the start, end and duration of real hurricane events, but occurred in years when there was no hurricane present, which would make comparisons between hurricane events and non-hurricane events consistent with respect to seasonal variation; in other words, hurricanes occur more typically in the summer months, and to make sure that we were comparing like with like, we ensured that the control periods mirrored hurricane periods with respect to time of year. We then placed all hurricane events (actual hurricane start/end dates in years the hurricane happened) and control events (hurricane start/end day/month timeframes but with control years—years in which no hurricane occurred—assigned to them) chronologically on a timeline to determine if there was any overlap between the start/end dates of hurricane or control events. If overlaps were found, that control period (the actual hurricane dates given to a non-hurricane year) was randomly resampled with replacement. This process was repeated until no overlaps existed between the hurricane and control periods. Figure 3 shows the assigned hurricane and control events as well as all sampled fish across our 42-year collection timeframe and Figure 4 depicts how both hurricane and control events were assigned.

Statistical analysis

All analyses were performed using R in RStudio (R 2025.09.2+418, The R Project for Statistical Computing n.d.). To determine whether parasite abundance was affected by hurricane events, we ran a series of generalized linear mixed models (GLMM), as outlined below using the function '*glmmTMB*' in the package 'glmmTMB' (Brooks et al. 2017). We constructed three models: one to test whether the response to hurricanes varied based on the parasite transmission strategy (Model 1), one to test whether the response to hurricanes varied among the most abundant taxonomic groups of parasites (Model 2), and one to quantify the response to hurricanes among myxozoans (Model 3). The transmission strategy analysis (Model 1) does not directly evaluate parasite taxonomic groups as a fixed effect in the models, only just whether the parasite has a direct or complex life cycle. Model 2 narrowed into the specific responses of those parasite taxonomic groups that were sufficiently abundant to be analyzed separately. Myxozoan

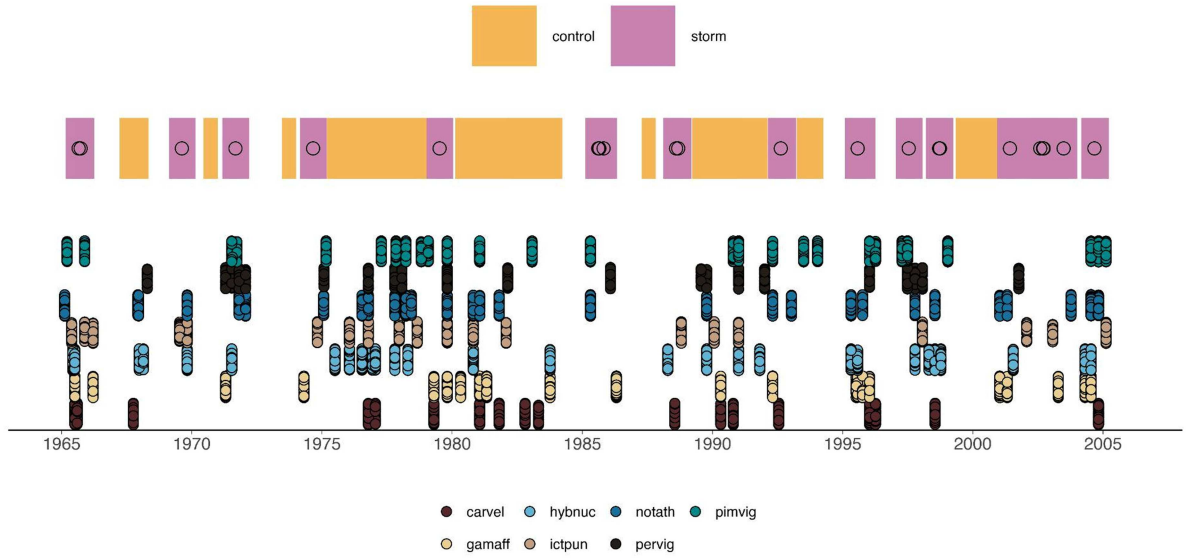

Figure 3. Timeline of hurricane and control events (top) with corresponding fish collected (bottom). Black circles represent actual periods of hurricane occurrence, with 3- or 6-month buffers applied to either side of that storm event to create 'before' and 'after' conditions. All rectangles represent hurricane (pink) or control (orange) events and their respective buffer zones, so larger rectangles represent longer stretches of storms or controls across multiple years. Though no circle is present in the control events, the same method was applied to controls—assigning a hurricane event to a control year and creating 3- or 6-month 'before' and 'after' conditions. pimvig = *Pimephales vigilax*, hybnuc = *Hybognathus nuchalis*, notath = *Notropis atherinoides*, gamaff = *Gambusia affinis*, ictpun = *Ictalurus punctatus*, pervig = *Percina vigil* and carvel = *Carpiodes velifer*.

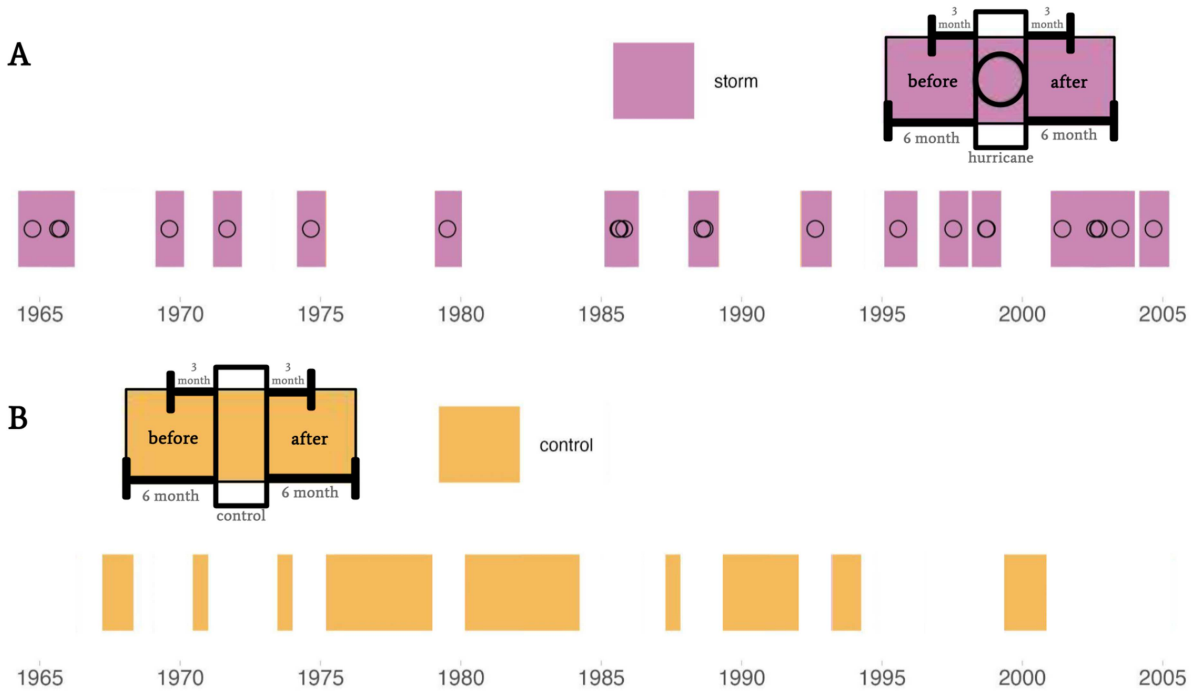

Figure 4. Representation of how control and hurricane 'before' and 'after' periods were generated. (A) Black circle hurricane events were assigned to non-hurricane (control) years and 3- or 6-month buffers were applied to either end of this event. (B) Control events were generated by applying an actual hurricane event start and end month and day to a year in which a hurricane event did not occur.

parasites were counted as abundance of pseudocysts and not as abundance of individual parasites (as required for inclusion in Models 1 and 2, where parasite abundance is the response variable), and as such myxozoans were analyzed separately and excluded from the transmission strategy analysis.

Models 1 and 2 were run using the family 'nbinom2', which typically provides a good fit to parasite data, given that parasites tend to be aggregated in their hosts: the negative binomial distribution models variance quadratically with the mean, which aids in situations where overdispersion and aggregation are present, as is the case here (Poulin 1993; Zuur 2009). Model 3, the myxozoan model, was run using family 'nbinom12', which combines both linear and quadratic parameters to maintain flexibility in lower replicate datasets and where overdispersion is present, as is the case with this myxozoan analysis (Lindén and Mäntyniemi 2011; Brooks and Kristensen 2017). We additionally fed the *'glmmTMB'* models into the function *'joint_tests'* in the package 'emmeans' to determine if each individual term or interaction was influential (Searle et al. 1980; Lenth and Piaskowski 2025), the full outputs of which can be found in Supplemental Table 4.

We tested model fit using residual Q–Q plot analysis, overdispersion, outlier and normality tests. The data were found to be zero-inflated, so we included a zero-inflated model component to our existing structure, which mirrors the given conditional effect model structure. The conditional model includes all observations and assumes all zeros result from true absence of a parasite (i.e. the parasite has been found in that species of fish, but not in that specific fish). The zero-inflated model factors in the possibility of both false and structural zeros resulting from either the inability to detect a given parasite in a fish or the fact that a given parasite is actually not present in a given fish (Zuur 2009). All models were run at a significance level of alpha = 0.05.

Two variants were run for each of the three models: one with a 3-month buffer around each event and another with a 6-month buffer around each event. Because the shorter 3-month window captured fewer observations, different subsets of data were included in each analysis. Control years were reassigned independently for each buffer timeframe length using the same range of control years available (i.e. the total number of years in which there was no hurricane). Therefore, the control years assigned to hurricane event periods differed between the two timeframes used in these analyses, but were generated from the same set of possible control years.

Our general model structure was selected after comparison of Akaike information criterion (AIC) values in converging models. In some instances, models with higher AIC values were selected if the lowest AIC model was determined to have overdispersion or related diagnostic issues. In addition to the triple interaction term (event*timing*transmission_strategy or event*timing*parasite_taxonomic_group), we used the fixed effect of 'MillLocation', which represents collection location along the Pearl River. We incorporated random effects of catalog number$_j$ (i.e. the unique identifier assigned to all lots in the collection, to account for autocorrelation among fish individuals collected at the same time and place), Season(year) $_{kl}$ to account for possible seasonal variation (see Supplemental Figures 10, 11 and 12, Supplemental Table 1), and FishSpecies$_m$ to account for host-specific variation in parasite burden. We also included FishParasiteCombo, a term that combines the fish species and the species of parasite for a given observation, which was a random intercept with a random slope of TotalLengthMM, the total length of the host fish individual in mm. This random effect was included to control for the fact that the slope of the relationship between fish body size and parasite abundance varies among fish–parasite species pairs (Poulin 2000). All random intercepts are normal distributions with mean 0 and variance σ^2_x. Our response variable Abundance$_{ijklm}$ represents the number of parasites found in fish individual i of species m from catalog number j in season l and year k (Zuur and Ieno 2016). The response variable Z_{ijklm} represents the zero-inflated distribution analysis using the same parameters as found in the above descriptions of the Abundance$_{ijklm}$ response variable. Figure 5 displays for each model the interactive effects and the number of samples that went into each analysis.

Model 1: transmission strategy

This analysis includes complex life cycle (i.e. acanthocephalan, cestode, nematode, trematode adult, trematode metacercaria) and direct life cycle (i.e. copepod and monogenean) parasites across all seven fish species.

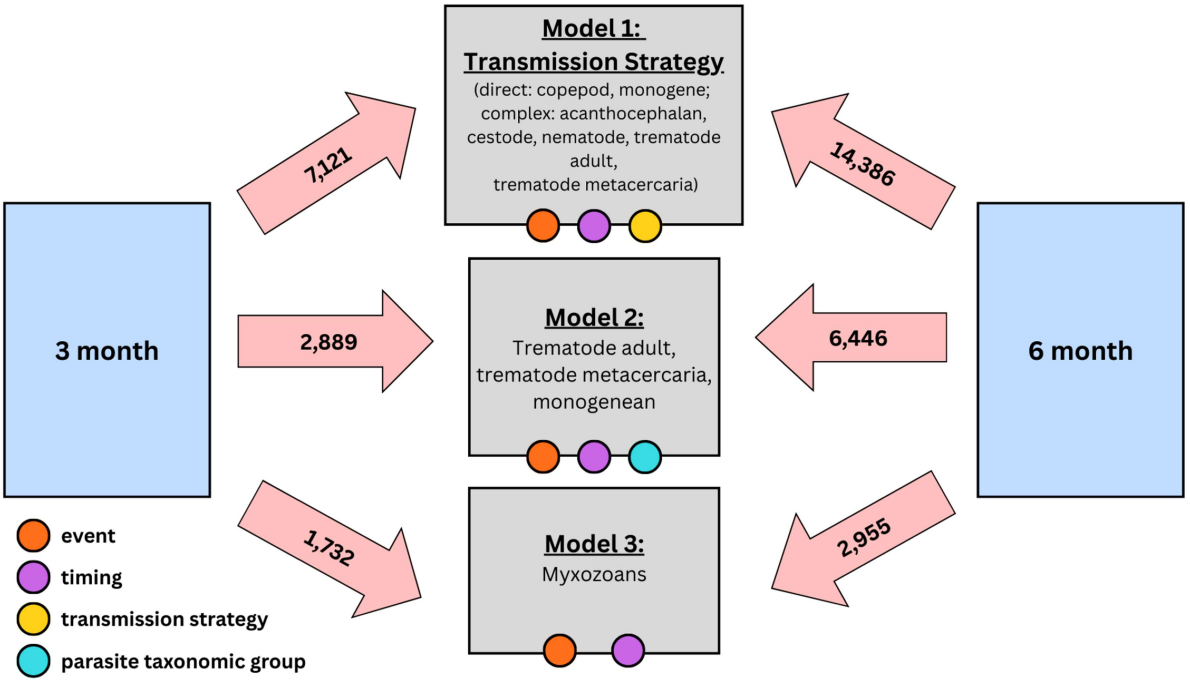

Figure 5. Different combinations of main interaction effects, sample sizes used in each analysis (inside red arrows), analytical subdivisions and timing of buffer zone on our three main models run. 'Event', 'timing' and 'transmission strategy' consist of two levels each: control and hurricane, before and after and complex and direct, respectively. 'Parasite taxonomic group' consists of three levels: Trematode adult, trematode metacercaria and monogenean.

$$
\begin{aligned}
&Abundance_{ijklm} \sim NegBin\left(\mu_{ijklm},\ \theta\right) \log\left(\mu_{ijklm}\right) \\
&= \beta_0 + \beta_1 Event_i + \beta_2 Timing_i + \beta_3 LifeHistory_i + \beta_4 MillLocation_i + \beta_5 \left(Event \times Timing\right)_i \\
&+ \beta_6 \left(Event \times LifeHistory\right)_i + \beta_7 \left(Timing \times LifeHistory\right)_i + \beta_8 \left(Event \times Timing \times LifeHistory\right)_i \\
&+ u_j + v_{kl} + w_m + b_{0n} + b_{1n}.\ TotalLengthMM_{ijklm} Z_{ijklm} \sim Bernoulli\left(\pi_{ijklm}\right) logit\left(\pi_{ijklm}\right) \\
&= \gamma_0 + \gamma_1 Event_i + \gamma_2 Timing_i + \gamma_3 LifeHistory_i + \gamma_4 MillLocation_i + \gamma_5 \left(Event \times Timing\right)_i \\
&+ \gamma_6 \left(Event \times LifeHistory\right)_i + \gamma_7 \left(Timing \times LifeHistory\right)_i + \gamma_8 \left(Event \times Timing \times LifeHistory\right) \\
&+ CatalogNumber_j + Season\left(year\right)_{kl} + FishSpecies_m + FishParasiteCombo_{0n} \\
&+ FishParasiteCombo_{1n} \cdot TotalLengthMM_{ijklm} CatalogNumber_j \sim N\left(0,\ \sigma^2{}_{CatalogNumber}\right) Season\left(year\right)_{kl} \\
&\sim N\left(0,\ \sigma^2{}_{Season\left(year\right)}\right) FishSpecies_m \sim N\left(0,\ \sigma^2{}_{FishSpecies}\right) \left(FishParasiteCombo_{0n},\ FishParasiteCombo_{01}\right) \\
&\sim MVN\left(0,\ \Sigma_{FishParasiteCombo}\right)
\end{aligned}
\tag{1}
$$

Model 2: trematode adult, trematode metacercaria and monogenean

This model included data only from taxonomic groups with high numbers of replicate observations (>200 possible instances of occurrence in a fish) or total parasite counts (>1000 individual parasites counted across all sampled fish). This allowed us to draw conclusions at the lowest possible taxonomic levels wherever we had sufficient replication to allow model convergence. The groups with sufficient replication were trematode adults, trematode metacercaria and monogeneans. *Carpiodes velifer* and *Percina vigil* did not host all three parasite groups assessed in this model and as such were dropped from Model 2 analyzes. Further, *Ictalurus punctatus* and *Gambusia affinis* were found to lack enough observations (<50 total observations) and were subsequently dropped from the 3-month analysis. Therefore, the 6-month analysis excluded *C. velifer* and *P. vigil* while the 3-month analysis excluded *C. velifer*, *P. vigil*, *I. punctatus* and *G. affinis*.

$$
\begin{aligned}
&Abundance_{ijklm} \sim NegBin\left(\mu_{ijklm},\ \theta\right)\log\left(\mu_{ijklm}\right)\\
&= \beta_0 + \beta_1 Event_i + \beta_2 Timing_i + \beta_3 ParasiteTaxonomicGroup_i + \beta_4 MillLocation_i\\
&+ \beta_5 \left(Event \times Timing\right)_i + \beta_6 \left(Event \times ParasiteTaxonomicGroup\right)_i\\
&+ \beta_7 \left(Timing \times ParasiteTaxonomicGroup\right)_i + \beta_8 \left(Event \times Timing \times ParasiteTaxonomicGroup\right)_i\\
&+ u_j + v_{kl} + w_m + b_{0n} + b_{1n} \cdot TotalLengthMM_{ijklm} Z_{ijklm} \sim Bernoulli\left(\pi_{ijklm}\right) logit\left(\pi_{ijklm}\right)\\
&= \gamma_0 + \gamma_1 Event_i + \gamma_2 Timing_i + \gamma_3 ParasiteTaxonomicGroup_i + \gamma_4 MillLocation_i\\
&+ \gamma_5 \left(Event \times Timing\right)_i + \gamma_6 \left(Event \times ParasiteTaxonomicGroup\right)_i\\
&+ \gamma_7 \left(Timing \times ParasiteTaxonomicGroup\right)_i + \gamma_8 \left(Event \times Timing \times ParasiteTaxonomicGroup\right)_i\\
&+ CatalogNumber_j + Season\left(year\right)_{kl} + FishSpecies_m + FishParasiteCombo_{0n}\\
&+ FishParasiteCombo_{1n} \cdot TotalLengthMM_{ijklm} CatalogNumber_j\\
&\sim N\left(0,\ \sigma^2{}_{CatalogNumber}\right) Season\left(year\right)_{kl} \sim N\left(0,\ \sigma^2{}_{Season\left(year\right)}\right) FishSpecies_m\\
&\sim N\left(0,\ \sigma^2{}_{FishSpecies}\right)\left(FishParasiteCombo_{0n},\ FishParasiteCombo_{01}\right) \sim MVN\left(0,\ \Sigma_{FishParasiteCombo}\right)
\end{aligned}
\tag{2}
$$

Model 3: myxozoans

Myxozoan parasites, counted as pseudocysts and not as individual parasites, were analyzed separately from other parasite taxonomic groups. After checking AIC in model validation, $Offset_{ijklm}$ was incorporated into the model as a log offset to account for the fact that larger fish tend to have more parasites (Poulin 1999; Luque et al. 2004). No myxozoan parasites were identified in *Percina vigil*, so this host species was not included in this analysis. Additionally, *Ictalurus punctatus* was found to have fewer than 100 total observations, and was subsequently excluded from the 3-month analysis. Gall bladder-infecting myxozoans were not found with high enough replication (<200 total observations at the 3-month buffer) to be included in this study, so the myxozoan models only measure myxozoan pseudocyst abundance and do not include gall bladder myxozoan presence/absence.

$$
\begin{aligned}
&Abundance_{ijklm} \sim NegBin\left(\mu_{ijklm},\ \theta\right)\log\left(\mu_{ijklm}\right)\\
&= \beta_0 + \beta_1 Event_i + \beta_2 Timing_i + \beta_3 MillLocation_i + \beta_4 \left(Event \times Timing\right)_i\\
&+ \beta_5 Offset_{ijklm} + \beta_6 \left(Event \times Timing\right)_i + \ CatalogNumber_j + Season\left(year\right)_{kl}\\
&+ FishSpecies_m + FishParasiteCombo_n Z_{ijklm} \sim Bernoulli\left(\pi_{ijklm}\right) logit\left(\pi_{ijklm}\right)\\
&= \gamma_0 + \gamma_1 Event_i + \gamma_2 Timing_i + \gamma_3 MillLocation_i + \gamma_4 \left(Event \times Timing\right)_i\\
&+ \gamma_5 Offset_{ijklm} + \gamma_6 \left(Event \times Timing\right)_i + \ u_j + v_{kl} + w_m + r_n CatalogNumber_j\\
&\sim N\left(0,\ \sigma^2{}_{CatalogNumber}\right) Season\left(year\right)_{kl} \sim N\left(0,\ \sigma^2{}_{Season\left(year\right)}\right) FishSpecies_m\\
&\sim N\left(0,\ \sigma^2{}_{FishSpecies}\right) FishParasiteComb_{on} \sim N\left(0,\ \ \sigma^2\ FishParasiteCombo\right)
\end{aligned}
\tag{3}
$$

Results

We dissected 1197 fluid-preserved fish across seven species (209 *Gambusia affinis*, 181 *Carpiodes velifer*, 221 *Hybognathus nuchalis*, 89 *Ictalurus punctatus*, 208 *Notropis atherinoides*, 92 *Percina vigil* and 197 *Pimephales vigilax*). From these fish we identified 151 parasite taxa comprising a total of over 36,171 individual parasites (this number includes myxozoan parasites, recorded as individual pseudocysts and not individual parasites). The dataset for Model 1 (transmission strategy) consisted of 14,386 parasite-host combinations for the 6-month analysis and 7121 combinations for the 3-month analysis. The dataset for Model 2 (trematode adult, trematode metacercaria and monogenean) included 6446 parasite-host combinations for the 6-month analysis, and 2889 combinations for the 3-month analysis. For Model 3 (myxozoan), the dataset included 2955 parasite-host combinations for the 6-month analysis, and 1732 combinations for the 3-month analysis (Figure 5). Complete model outputs for conditional and zero-inflated results are available in Supplemental Tables 2 and 3.

Model 1: transmission strategy

Direct life cycle parasites declined more precipitously in the three months following a hurricane than during comparable control time periods relative to complex life cycle parasites (3-month buffer, estimate = 0.1988, df = 7088, $p = 0.0169$) but this effect was not significant at 6 months (estimate = 0.3853, df = 12380, $p = 0.0632$) (Figure 6). However, at 6 months, a higher non-significant effect size was detected with higher/lower variability compared to the 3-month model.

Model 2: trematode adult, trematode metacercaria and monogenean

The abundance of trematode adults did not respond to hurricanes at either short (3-month buffer; estimate = 4.4669, df = 2848, $p = 0.0660$) or long (6-month buffer; estimate = 2.1532, df = 6405, $p = 0.1609$) time scales (Figure 7).

Hurricanes did not have a significant effect on trematode metacercariae, but the climate conditions of control years did appear to contribute to high metacercarial abundances in early summer. At three months, trematode metacercaria declined under control conditions with a notably high abundance in the 'before-control' level (Table 1, Figure 7). This suggests that trematode metacercariae abundance is elevated in non-hurricane years in the months before hurricane season (see further explanation in the Discussion). On longer, 6-month timescales, we found no significant relationships between trematode metacercaria abundance and hurricane presence or timing (estimate = 5.2435, df = 6405, $p = 0.0503$).

Monogenean parasites declined more precipitously in the three months following a hurricane than during comparable control periods relative to other parasites, both at 3-month (3-month buffer; estimate = 0.0956, df = 2848, $p = 0.0186$) and at 6-month (estimate = 0.2159, df = 6405, $p = 0.0449$) time scales, though the effect was less pronounced at six months than at three.

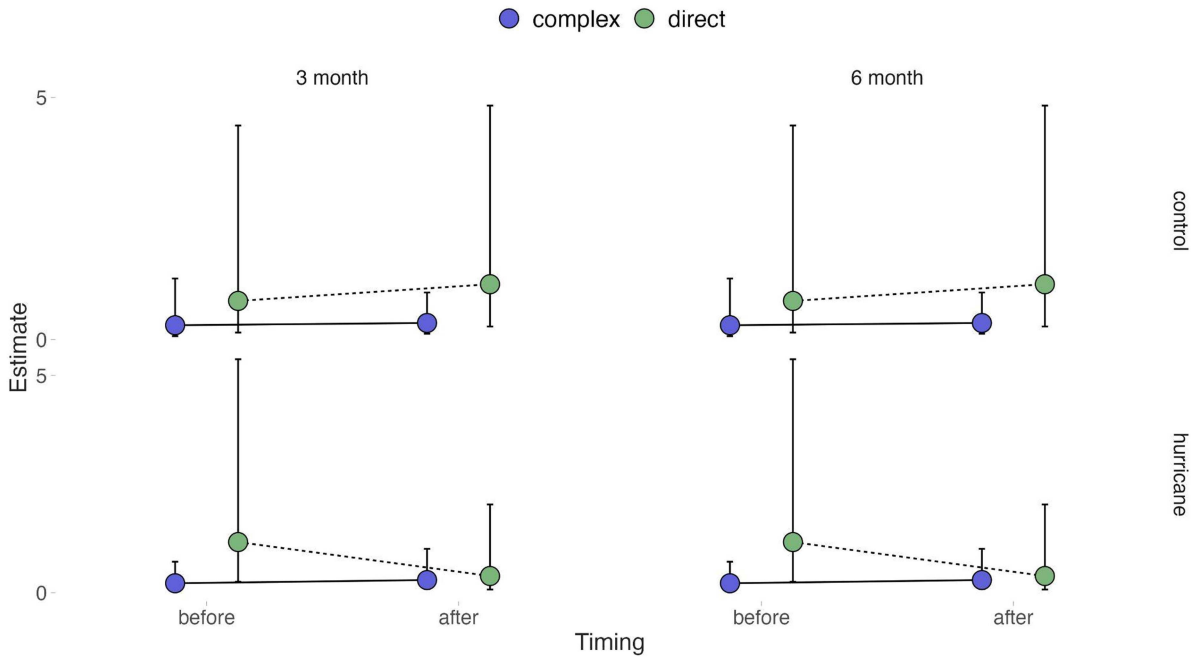

Figure 6. Result of transmission strategy analysis generated from the '*glmmmTMB*' model and visualized using '*ggpredict*' where the dots represent the predicted estimate of parasite abundance and the error bars indicate the 95% confidence interval. The y-axis represents the estimated abundance of parasites per fish in each given category between control (top) and hurricane (bottom) events on both pre and post-event timescales (as shown on the x-axis). Direct life cycle parasite abundance (green) was negatively affected by hurricane presence on short time scales, but this effect diminished on long time scales. Complex life cycle parasites (blue) were not as negatively affected by hurricanes on either time scale.

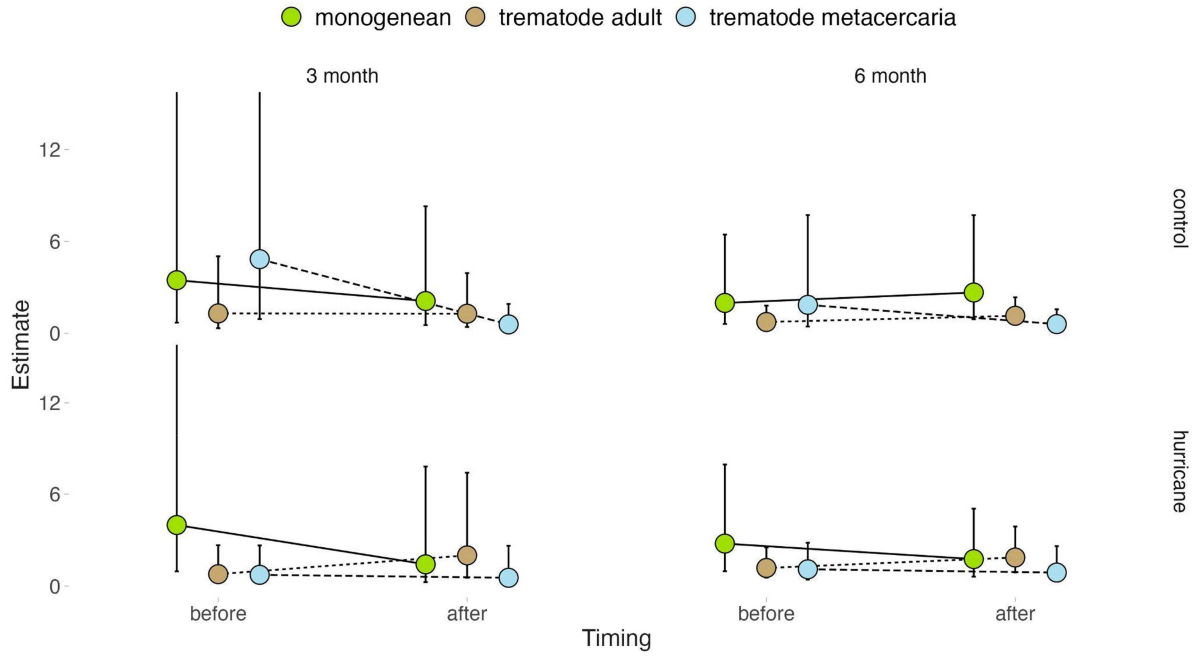

Figure 7. Effects of hurricane events on parasite abundance generated from the '*glmmmTMB*' model and visualized using '*ggpredict*' where the dots represent the predicted estimate of parasite abundance per fish and the error bars indicate the 95% confidence interval. The y-axis represents the estimated abundance of parasites in each given category between control and hurricane events on both before and after event timescales (as shown on the x-axis). Monogenean parasites declined in abundance following a hurricane on both short- and long-time scales. Trematode metacercaria were not negatively affected by hurricanes, but experienced a decrease in before-event abundance between hurricane and control years. Trematode adults were not affected by hurricanes on either time scale.

Table 1. Summarized model outputs for all models. Gray boxes represent the '*joint_tests*' model outputs which signify which terms and interactions are influential in predicting parasite abundance, while white boxes represent the direct outputs of the '*glmmTMB*' models indicating specific estimated effects of each term and interaction on parasite abundance. Bolded values are significant and bolded model term items indicate significance at both 3-and 6-month timeframes.

		3 month				6 month			
Response variable	Model term	Estimate	Chi2	F. ratio	*p* value	Estimate	Chi2	F. ratio	*p* value
direct or complex life cycle	event*timing*transmission_strategy	**NA**	**5.7050**	**5.7050**	**0.0169**	NA	3.4520	3.4520	0.0632
	hurricane*post*direct	**0.1988**	**NA**	**NA**	**0.0169**	0.3853	NA	NA	0.0632
	hurricane*post*complex	**5.0303**	**NA**	**NA**	**0.0169**	2.5956	NA	NA	0.0632
monogenean, trematode adult, trematode metacercaria	event*timing*parasite_taxonomic_group	**NA**	**6.6260**	**3.3130**	**0.0364**	NA	4.5580	2.2790	0.1024
	hurricane*post*monogenean	**0.0956**	**NA**	**NA**	**0.0186**	**0.2159**	**NA**	**NA**	**0.0449**
	hurricane*post*trematode_metacercaria	**10.4622**	**NA**	**NA**	**0.0186**	5.2435	NA	NA	0.0503
	hurricane*post*trematode_adult	4.4669	NA	NA	0.0660	2.1532	NA	NA	0.1609
myxozoan	hurricane*post	0.9773	NA	NA	0.9851	0.6187	NA	NA	0.5473

Model 3: myxozoans

Myxozoan parasites were unaffected by hurricanes at both short (3-month buffer; estimate = 0.9773, df = 1710, $p = 0.9851$) and long (6-month buffer; estimate = 0.6187, df = 2933, $p = 0.5473$) time scales, when compared to control conditions (Figure 8).

Discussion

Our results showed that hurricanes affected the abundance of wildlife parasites, but that the direction of the effect was dependent on the parasite's transmission strategy, and that the impact attenuated over the months after the hurricane had passed. Direct life cycle parasites were negatively affected by hurricane events, while complex life cycle parasites were not, but effects were limited to the 3-month post-hurricane

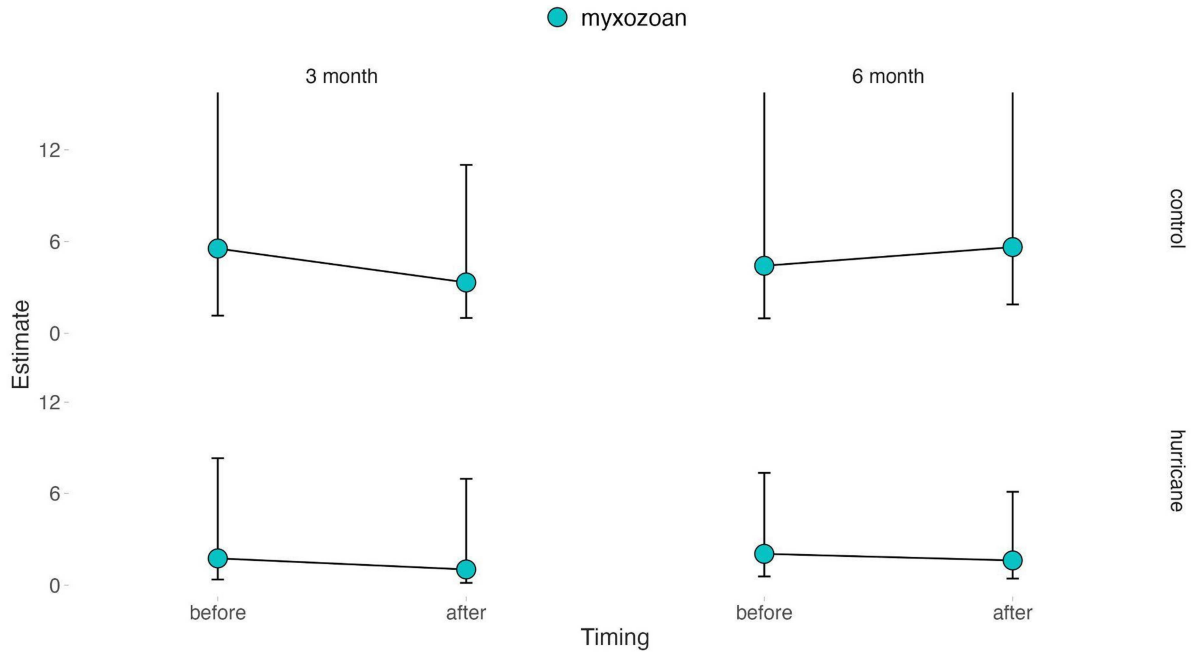

Figure 8. Effects of hurricane events on myxozoan abundance generated from the '*glmmmTMB*' model and visualized using '*ggpredict*' where the dots represent the predicted estimate of parasite abundance and the error bars indicate the 95% confidence interval. Myxozoan parasite prevalence was not affected by hurricanes on either time scale as indicated by no significant change in slope of the predicted effect between any sampled condition parameters.

timeframe. This result was at odds with our initial hypothesis that direct life cycle parasites would be unaffected by hurricane events. Complex life cycle parasites, which we expected to decrease following hurricane events, were unaffected by hurricane events, according to our data. This research provides new insight into the responses of wildlife parasites to hurricanes by evaluating whether parasite responses are consistent across hurricanes and different from control conditions.

Direct life cycle parasites declined in abundance in response to hurricanes, but this effect diminished when assessed on longer time scales, indicating an immediate but temporary reduction in monogenean and copepod abundance compared to non-hurricane controls. Reliant on only one host species for their life history, direct life cycle parasites could have been more susceptible to short-term change produced by hurricanes, as a product of having no reservoir hosts to shelter them from hurricane effects. Complex life cycle parasites were unaffected by these hurricanes, possibly because, at any one time, these parasites are present in an ecosystem in multiple host species; if one of these host species is temporarily lost, it can be reinfected as soon as it returns, because other life stages have remained in other host species. Our results suggest that the strategy of using a single host is hazardous during periods of intense and rapid change. When considering monogenean parasites on their own (Model 2), we found that monogeneans declined following a hurricane on both short and long time scales, although the effect attenuated between the 3- and 6-month mark. Because our results indicated that direct life cycle parasites no longer showed hurricane-related effects at the 6-month mark (Model 1), it is possible that these effects dissipated once hurricane-associated environmental conditions subsided and river systems stabilized.

Direct life cycle parasites were more susceptible to short-term hurricane effects than were complex life cycle parasites. Momentary disruptions in host-parasite interactions, such as fragmentation of the host population or reduction in host density, could render transmission between hosts ineffective, thus driving parasite abundance down. If host density decreases below a certain threshold, even temporarily, intra-specific transmission cannot occur (Saino et al. 2009; Paull and Johnson 2014; Poulin and Lagrue 2015; McDevitt-Galles et al. 2020; Anderson and May 1979a). In the case of direct life cycle parasites, where the parasite needs a single host species, if that host's presence is jeopardized by the hurricane, that will result in the complete interruption of the life cycle, especially for highly host-specific parasites. This effect was seen

in Belize, where directly transmitted helminth parasites and their howler monkey hosts were found to decrease in abundance after a hurricane (Behie et al. 2014). In contrast, complex life cycle parasites have multiple host species and it is possible that not all hosts are equally affected by hurricanes. Therefore, complex life cycle parasites could remain sheltered in unaffected host populations and resume transmission once favorable conditions return. River refugia, which provide short-term microhabitats for aquatic organisms with stable conditions, can shelter both hosts and associated parasites during severe weather events and can act as sources from which host and parasites alike can recolonize impacted river sections after the hurricane has subsided (Dolloff et al. 1994; Magoulick and Kobza 2003). While this can be beneficial for both direct and complex life cycle parasites, the latter have a better chance of benefiting from this refugia given the higher number of hosts involved in the life cycle (Perret et al. 2010; O'Connell et al. 2014). While this potential ability to 'hide out' in unaffected hosts could buffer parasites in general from hurricane effects, it could be particularly advantageous to complex life cycle parasites, who have a greater likelihood of maintaining at least one host at high density through a hurricane, as a product of using more hosts in their life cycle, though the current study was not able to evaluate these hypotheses directly.

All of the direct life cycle parasites detected were ectoparasites and all of the complex life cycle parasites were endoparasites, which means that our results cannot decouple transmission strategy and infection location from each other and one or both of these elements could be responsible for the patterns we observed. It is possible that environmental exposure experienced by ectoparasitic direct life cycle parasites (copepods and monogeneans) is greater than that experienced by endoparasitic complex life cycle parasites (acanthocephalans, cestodes, nematodes, trematode adults, trematode metacercariae), and that this degree of exposure is driving the observed effects. Under this hypothesis, the stronger declines observed in direct life cycle parasites may not necessarily reflect differences in transmission strategy, but rather differences in the degree to which parasites are shielded from environmental disturbance by their hosts. Occupying gills and fins, monogeneans and copepods could be vulnerable to changes in water quality caused by hurricane events. Changes in pH, sediment load and pollutant influx could have a disproportionate effect on after-hurricane parasite abundance for ectoparasites and drive down their abundances by forcing them into conditions in which they cannot survive, though these effects are species- and ecosystem-specific and can depend on the fish host's immune response to these conditions (Lafferty and Kuris 1999). For example, the monogenean *Gyrodactylus cichlidarum* from tilapia in Mexico experienced a die-off following a pulse heat stress event, where water temperatures were 34°C over the course of one week, killing the parasites within seven hours of exposure (Miranda-Aguirre et al. 2025). Such disruptions might reduce survival, reproduction and transmission opportunities, and an endoparasitic lifestyle might buffer against the sudden water quality shifts that occur after a hurricane. These mechanisms could help explain why direct life cycle parasites showed stronger declines following hurricanes than complex life cycle parasites. This study was unable to elucidate which of these competing factors (direct or complex vs. ectoparasitic or endoparasitic) are most strongly correlated with response to hurricanes and future studies should focus on decoupling these factors from each other.

Adult trematodes were unaffected by hurricanes across both short and long time scales (Figure 7). Abundances of adult trematodes, which develop when a larval trematode metacercaria is consumed by a definitive host fish, remain stable within the definitive host: one trematode metacercaria develops into one adult trematode in the definitive host, with no within-host replication (Poulin and Lagrue 2015). Therefore, changes in the abundance of adult trematodes were probably determined by changes either to trematode metacercaria abundance in intermediate prey fish or by the rate of predation on intermediate prey fish. The stability of adult trematodes that we observed across both short and long time scales suggests fish hosts may have continued to have access to trematode larvae, allowing them to develop into adult trematodes as normal within the definitive host regardless of external hurricane influences. This, in turn, may help buffer trematodes against long-term population declines despite short-term disruptions in transmission should adult trematode populations continue producing eggs within their definitive hosts, especially if the first intermediate host populations are stable and reinfection can happen quickly once hurricane effects dissipate (Poulin and Lagrue 2015). Future studies should incorporate intermediate host abundance estimates to form a clearer picture of the specific importance of these aspects of riverine ecosystem community structure.

Trematode metacercaria were sensitive not to hurricanes themselves, but to the climatic conditions leading up to the hurricane season. Specifically, we found that trematode metacercaria abundance was high in control years before a control event and low before a hurricane event. Hurricanes did not negatively affect trematode metacercaria abundance. What we did observe, however, was greater trematode metacercaria abundances in before-control periods. Environmental conditions associated with non-hurricane years may benefit early-year (winter and spring) transmission of trematode cercaria to fish second intermediate hosts. Hurricane events result in temporarily increased sea surface temperature (SST) locally, with decreased SST after an event (Cione and Uhlhorn 2003). Furthermore, multiseasonal and decadal variations in SST and ocean circulation trends are influential in predicting the occurrence of hurricanes in the US Gulf South region, with global and specific regional temperature increases correlated to an increase in intense storm surge activity associated with hurricanes (Gray et al. 1997; Grinsted et al. 2013). Cercarial production is influenced by temperature, as are population abundances of intermediate host snails (Pechenik and Fried 1995; Poulin 2006). As such, the seasonal variation in temperature in control years could be increasing the abundances of these parasites (Figure 7).

We examined trematode adults and trematode metacercaria in this study. Though these groupings encompass all the adult and all the larval trematodes we detected in this study, the groups are not necessarily composed of the same species, and therefore, we do not necessarily expect that the two groups will respond in the same way to BACI main effects and interactions. We found adult trematodes of 36 taxa and a further 10 taxa of trematode metacercaria in this study. Trematode cercariae in first intermediate hosts undergo clonal amplification, whereas trophic transmission of metacercariae from intermediate to definitive host do not yield amplification of trematode adult abundance (Poulin and Lagrue 2015). Therefore, first intermediate hosts are important for downstream adult trematode abundances and while we do not evaluate the impacts of hurricanes on these first intermediate hosts in this study, those dynamics could be influencing downstream abundances of both adult and metacercarial trematodes detected here (Anderson and May Poulin and Lagrue 2015; Anderson et al. 2021, 1979b). Poulin and Lagrue (Poulin and Lagrue 2015) suggest that this asexual reproduction of cercarial trematode stages in intermediate hosts can buffer adult population abundances downstream, which could explain why we found trematodes to have been largely unaffected by hurricanes.

Acute events like hurricanes have a different effect on parasite transmission than longer-term changes like the temperature shifts caused by climate change. We expected direct life cycle parasites to be resilient to hurricanes because prior studies investigating their responses to climate change found that to be the case; for example, Wood et al. (2023b) found that direct life cycle parasites were unaffected by rising sea surface temperature, while complex life cycle parasites declined in response to this stressor. Aleuy and Kutz (2020) similarly found that climate change has more net-negative effects on complex life cycle parasites than on direct life cycle parasites, due to the fact that having multiple hosts means that there are more opportunities for these hosts to be impacted by a changing environment, leading to disruptions in parasite transmission efficacy (Aleuy and Kutz 2020). While these previous studies suggest that the complex life cycle parasites are especially vulnerable to environmental change, our study suggests the opposite. This apparent tension can be reconciled by considering that complex life cycle parasites might be susceptible to long-term change but resilient to short-term change. This could arise because complex life cycle parasites' risk is spread across multiple hosts during a short-term event like a hurricane, whereas direct life cycle parasites might have all their eggs in one (host species) basket. This has been posited as the 'shelter effect' by Molnar et al. (2008). Previous research tracking reestablishment of parasites following host species eradication found that direct life cycle parasites of fish were slower to recolonize than complex life cycle parasites, suggesting that direct perturbations such as reductions in host abundance, can impact direct life cycle parasites in the short term, resulting in longer rebound times for these parasites compared to complex life cycle parasites (Rochat 2024). This supports our results, showing the short-term vulnerability of direct life cycle parasites to intense and drastic environmental perturbation. Taken together, these results suggest that direct life cycle parasites may be more vulnerable than complex life cycle parasites to short-term environmental perturbations, whereas the opposite may be true in the long-term (Wood et al. 2023b; Rochat 2024).

Though this study generates interesting insights into the effects of hurricanes on parasite communities, its findings are necessarily limited by its observational nature and opportunistic use of existing specimens.

Using museum specimens allowed us to develop a long time series, but it also limited our scope of inference. For example, the fishes used in this study were collected using seine nets, which favors capture of smaller fish. Larger fish support more parasites than smaller fish (Luque et al. 2004; Poulin and George-Nascimento 2007), so the exclusion of larger fish from this study could result in an underestimate of total parasite abundances and suggest that fewer parasites within the system than are actually present. Bounding the sizes of these fishes using upper and lower limits as we have done in this study has the advantage of ensuring comparisons across species are consistent, but also restricts our understanding of hurricane effects on larger fish, which are not analyzed here. It is possible that larger fish are both more resilient to hurricane impacts (such as salinity spikes) and harbor more parasites than smaller fish. However, assuming parasite species are shared across host size classes, the inclusion of larger hosts in this study would affect the total number of parasites observed, but there is no clear mechanism by which stable parasite populations in larger fish would buffer or reduce the impacts of hurricanes on parasite populations in smaller fish. If hurricane effects are truly mitigated by the persistence of parasites in larger hosts, similar stability would be expected across all host size classes, which was not observed. Parasite counts from bilateral organs like gills and eyes were assessed only on the left size and that count doubled to represent the estimated total abundance in that fish, which could introduce error if parasites are not equally distributed between left and right bilateral organs in each host. However, previous studies of fish parasites found no significantly asymmetrical distributions of parasites across bilateral organs (Baker et al. 2005; Kumar et al. 2017). We are also limited by only examining specific riverine fishes, and not the complete broad range of potential intermediate and definitive hosts for all parasites found. As such, the parasite-fish combinations we identify in this study represent a snapshot of the total ecology of these interactions, limiting our ability to make broad ecosystem inferences or predictions. The fishes dissected for this study were fixed in formalin, stored in ethanol and shelved in the TUBRI collection for between 19 and 61 years before being examined for parasites by our team. This fixation process preserves both host and parasite tissue, allowing parasites to be identified for many years after fixation (Harmon et al. 2019; Fiorenza et al. 2020). While validation studies confirm that there is little difference in detectability of parasites between fixed and fresh host specimens, it is possible that some parasite taxa might decay in detectability through time post-fixation. This would not influence our results, however, since our before–after contrast was made between specimens collected only months apart.

The final source of potential bias stems from climate change. Hurricanes are increasing in frequency and intensity with time (Michener et al. 1997; Holland and Bruyère 2014), which means that, in our study, control events were more likely to occur in the past when hurricanes were less frequent (Figure 3). Had our study been a CI rather than BACI design, this arrangement of hurricane and control events would have resulted in confounding between hurricane/control and time. However, our BACI design takes a long-term dataset (42 years) and breaks it down into smaller pieces (approximately 6 or 12 months at a time, depending on the size of the buffer period and the duration of the hurricane), allowing us to measure how parasite abundance changes from baseline for each hurricane or control event. As such, this greater density of hurricanes in more recent times does not impact our results. If the proportion of hurricanes relative to controls is changing through time, the BACI design still captures what a hurricane does to parasites in riverine fish.

The long-term effects of climate change on the environment are impacting parasite populations (Marcogliese 2008; Behie et al. 2014; Dobson et al. 2015; Byers 2021; Wood et al. 2023b). We found that hurricanes disrupted parasite transmission and survival in predictable, transmission strategy-specific ways. Direct life cycle parasites were immediately and temporarily reduced in abundance, while complex life cycle parasites were not affected. Taken together with previous research, parasites are vulnerable to both the long- and short-term effects of climate change, placing them in immediate and prolonged risk of resultant adverse effects. This increased understanding of parasite responses to hurricanes highlights the need for continued surveillance of parasite populations wherever they could be affected by climate change, whether effects are long-term as is the case with changes to temperatures or short-term, as we find with hurricanes. As anthropogenic climate change continues to manifest in earlier, longer, more frequent and more intense hurricane seasons, ignoring parasite response to extreme weather events like hurricanes risks overlooking cascading effects that may only become apparent once parasite-host dynamics have already been fundamentally altered.

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Author contributions

CRediT: **Connor Whalen:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing; **Desmond Boyd:** Investigation, Writing – review & editing; **Gabriella Commisso:** Data curation, Investigation, Writing – review & editing; **Shyanne Christner:** Investigation, Writing – review & editing; **Imani Jones:** Investigation, Writing – review & editing; **Katie Leslie:** Data curation, Investigation, Writing – review & editing; **Jolee Thirtyacre:** Investigation, Writing – review & editing; **Dakeishla M. Díaz-Morales:** Data curation, Investigation, Writing – review & editing; **Armand M. Kuris:** Conceptualization, Writing – review & editing; **Justin Mann:** Data curation, Resources, Writing – review & editing; **Henry Bart:** Data curation, Resources, Writing – review & editing; **Chelsea L. Wood:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Writing – review & editing.

Disclosure statement

The authors declare no competing interests.

Data availability statement

All code used in analysis can be found on GitHub via the Wood Lab GitHub page and all data are available on Dryad, accessible through the GitHub page: https://github.com/wood-lab/Whalen_et_al_2026_JFE.

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