Multiple drivers of fish community change on Bahamian coral reefs

Iris George

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Signed by the final examining committee:

________________________________ Chair

Dr. Dylan Fraser

________________________________ External Examiner

Dr. Rassim Khelifa

________________________________ Examiner

Dr. Dylan Fraser

________________________________ Examiner

Dr. Katalin Patonai

________________________________ Thesis Supervisor

Dr. Nicola Smith

Approved by ____

Dr. Robert Weladjij – Graduate Program Director

__________________________, 2025 ____

Dr. Pascale Sicotte, Dean of Faculty

Abstract

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Iris George, MSc

Coral reef fish communities are essential for ecosystem health but are threatened by many of the same environmental stressors as coral. Marine heatwaves and hurricanes are intensifying with climate change and can adversely affect reef fish via physiological stress or coral loss. Additionally, Caribbean reef fish are threatened by invasive Indo-Pacific lionfish predation. Here, I determine the impacts of invasive lionfish, marine heatwaves, and hurricane passage on patch reef fish communities from 2009-2024 in The Bahamas. Using a metacommunity framework, I also analyze shifts in fish community composition spatially via network analysis to determine whether reef connectivity reduces fish species turnover through time and following hurricanes. Lionfish biomass was positively related to native fish biomass and species richness, possibly driven by attraction of lionfish to reefs with abundant prey. Although marine heatwaves negatively affected fish biomass, they had a consistent, positive effect on species richness, suggesting a complex, possibly non-linear relationship of temperature to diversity. Hurricane passage negatively affected fish biomass but had no clear impacts on species richness or turnover. Over the timeseries, beta diversity significantly increased in the metacommunity with more central, connected reefs experiencing lower species turnover, likely driven by dispersal. My findings show predictable changes in reef fish biomass to multiple stressors but demonstrate more complex responses of species richness, supporting the use of multiple metrics to more fully understand drivers of environmental change. Further, by using a metacommunity framework, my findings reinforce the prominent paradigm of a dynamic nature of reef fish assemblages over time.

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Contribution of Authors

Study concept and design: Iris George, Nicola Smith and Katalin Patonai

Acquisition of data: Iris George, Nicola Smith, Katelyn Moffat and Stephanie Green

Analysis and interpretation of data: Iris George, Nicola Smith and Katalin Patonai

Drafting of manuscript: Iris George

Critical revisions: Iris George and Nicola Smith

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Introduction

Coral reefs are biodiversity hubs vital to coastal economies but are increasingly threatened by multiple stressors (Moberg and Folke 1999; Burke et al. 2011). Globally, coral reefs support the most biodiversity by unit area of any marine habitat and generate approximately $36 billion USD annually from tourism (Burke et al. 2011; Spalding et al. 2017). The physical structure of reefs provides shoreline protection to adjacent communities from storm surge and coastal erosion, and they hold immense cultural value for many groups (Moberg and Folke 1999). In addition to these functions, the health of coral reefs and the services they provide are closely tied to the diverse community of species they support.

Reefs provide habitat for vibrant communities of thousands of fish species. Many coastal communities rely on these coral reef fish to fuel commercial, recreational and subsistence fisheries and provide residents with an essential source of protein and micronutrients (Moberg and Folke 1999; Burke et al. 2011). Reef fish also provide coral with a key source of nutrient deposition via their excrement, which contributes to coral health and growth (Meyer et al. 1983; Allgeier et al. 2014; Francis and Côté 2018). Reef fish that closely associate with coral, such as butterflyfish (Chaetodontidae) also act as key indicator species for overall reef health, as their abundances decrease with declining healthy coral cover (Hourigan et al. 1988; Graham et al. 2009). Because of this, monitoring reef fish community composition over time and in relation to environmental stressors can provide insights to overall reef health.

A prominent threat to global biodiversity is the spread of invasive species (Mainka and Howard 2010). Invasive species are species introduced to ecosystems outside of their natural range, often via human mediation, that successfully establish viable populations, spread, and cause negative impacts to the local community (Roy et al. 2023). Their ability to successfully spread within their invaded range is due to a variety of shared traits, including a wide range of physiological tolerance, high fecundity, a lack of natural predators in their invaded range, or high competitive ability (Lockwood et al. 2013). The presence of invasive species can have devastating consequences for the invaded system, as the invader may dramatically alter food webs via competition with native species and consumption of naïve prey (Lockwood et al. 2013). This can permanently alter ecosystem functions and reduce the abundance of native species, potentially driving them to extinction (Roy et al. 2023). The impacts of invasive species may act in conjunction with climate change to cause increased damage to ecosystems, as climate change has the potential to alter the distribution of invasive species, impact their behaviours, and assist in the establishment of new invaders (Hellmann et al. 2008; Mainka and Howard 2010; Roy et al. 2023). In recent years more than 200 new invasive species have been recorded annually, indicating the highest global rate of invasion ever observed (Roy et al. 2023).

A particularly ecologically destructive invasive species on coral reefs are the Indo-Pacific lionfish (*Pterois volitans* and *P. miles*). Lionfish initially established off the coast of Florida in the mid-1980s, likely following aquarium releases, and have since spread throughout the

Caribbean and western Atlantic, with the first reports of presence in The Bahamas in 2004 (Whitfield et al. 2002; Schofield 2009; Mainka and Howard 2010; Côté and Smith 2018). Lionfish possess life history traits ideal for a successful invader: they mature early, grow quickly, and produce approximately 2 million eggs annually (Morris and Whitfield 2009; Côté and Smith 2018). These eggs drift via ocean currents to colonize new habitats, allowing for fast and extensive spread (Betancur-R. et al. 2011). Once established lionfish act as generalist opportunistic predators, feeding on a diversity of small-bodied fishes and invertebrates, and have reduced native prey fish biomass by 65% on natural reefs (Morris and Whitfield 2009; Green et al. 2012; Côté et al. 2013). Under climate change, lionfish are expected to spread into warming regions that were previously too cold for them to occupy and increase their consumption rates of prey, thereby further increasing their invaded range and impacts to natural ecosystems (Côté and Green 2012; Grieve et al. 2016). Thus far, culling efforts have been the primary method of managing invasive lionfish populations, but the labour and cost required to remove lionfish at the necessary frequency is difficult to sustain long-term (Smith et al. 2017). Continually monitoring lionfish populations and their impact on reef communities over time is imperative to better understand their long-term effects and population trends.

In addition to affecting the spread and impact of invasive species, climate change is causing major shifts to ocean conditions globally. Atmospheric changes are modifying ocean currents and weather patterns, carbonic acid created from dissolved carbon dioxide is leading to ocean acidification, and greenhouse gases trapped in the atmosphere are causing rapid warming of ocean waters (Reid et al. 2009). On Bahamian coral reefs, water temperatures have increased 0.17 °C on average per decade since 1988 (Bove et al. 2022). Warming ocean temperatures can impact a range of organismal processes, including survival, life history, metabolism, and immune responses (Yao and Somero 2014). Ocean warming may induce range shifts in mobile marine species attempting to remain within their optimal thermal range or create intense physiological stress for those that cannot move, ultimately leading to shifts in reef community composition (Yao and Somero 2014; Sunday et al. 2015).

In addition to increasing mean ocean temperatures globally, climate change is affecting the prevalence of extreme ocean temperature events known as marine heatwaves (MHWs; Frölicher et al. 2018). MHWs are extended periods of anomalously high ocean temperatures that can be especially damaging to marine ecosystems (Hobday et al. 2016). They create short-term but especially intense thermal stress for marine organisms which can be seen at the individual, population, and community level (Smith et al. 2023). Under climate change, the intensity, duration and frequency of MHWs is increasing globally (Oliver et al. 2018). Regionally in the Caribbean, MHW frequency has increased more than fivefold, and the duration of each heatwave event has approximately doubled since the 1980s (Bove et al. 2022).

Increasing ocean temperatures and more frequent marine heatwaves due to climate change can trigger mass coral bleaching events on reefs, ultimately causing widespread coral mortality on affected reefs (Hoegh-Guldberg 1999; Shlesinger and van Woesik 2023). Under normal conditions, corals derive much of their energy and colour via symbiotic zooxanthellae algae, which are single-celled dinoflagellates that produce nutrients via photosynthesis and live within coral tissue (Muscatine and Porter 1977; Hoegh-Guldberg 1999). However, in extreme environmental conditions zooxanthellae photosynthetic cells can be damaged, causing them to increase production of oxygen radicals which damage coral (Lesser 2006). Corals subsequently expel their zooxanthellae counterparts and lose this key source of nutrients and colour, hence the term “coral bleaching” (Hoegh-Guldberg 1999; Baker et al. 2008). If conditions improve, it is possible for coral to re-establish their zooxanthellae and reverse the bleaching process, but if bleaching occurs regularly or for longer periods it can result in coral death (Schoepf et al. 2015). Coral bleaching induced by MHWs has been found to be particularly detrimental, as the extreme heat can cause immediate mortality of coral colonies and more rapid damage to their skeletal structure (Leggat et al. 2019). Due to the increase in ocean temperatures and MHWs caused by climate change, coral bleaching events are an annual occurrence on most reefs globally (Oliver et al. 2018).

In addition to coral, increased ocean temperatures and MHWs will also directly impact the broader reef community (Magel et al. 2020). Reef fish, for example, are thought to possess narrow thermal ranges characteristic of the stable, low-latitude thermal ranges they are adapted to (Tewksbury et al. 2008; Vaughan et al. 2025). As climate change continues to alter the thermal seascape of reefs via increased ocean temperatures and MHWs, reef fish are more regularly exposed to thermal conditions outside of their preferred range, which can result in physiological stress, behavioural modifications and developmental changes (Spinks et al. 2019; Van Wert et al. 2024). Additionally, fish species pushed outside of their thermal range may migrate to reefs in cooler waters, resulting in range shifts and alterations to coral reef community composition (Feary et al. 2010).

Tropical coral reefs experience additional disturbance from passing hurricanes and tropical storms. Hurricanes are low-pressure storm cells that form over warm water and are characterised by high wind speeds (>32 m/s) and heavy rainfall (Rakhecha and Singh 2009). This generates increased wave and current action adjacent to the storm and additional changes to the turbidity and salinity of the water (Harmelin-Vivien 1994). Hurricanes damage coral reefs mainly via structural damage to coral itself, which can be observed up to 250 km away from the storm (Beeden et al. 2015). Increased wave action from storms has the potential to break off pieces of coral colonies, resulting in a decrease in coral cover and structural complexity of affected reefs (Harmelin-Vivien 1994; Gleason et al. 2007). The extent of reef damage depends on the size and intensity of the storm itself as well as the location of the reef, as shallow reefs are more susceptible to damage and surrounding topography may reduce hurricane force before it reaches reefs (Harmelin-Vivien 1994; Beeden et al. 2015; Puotinen et al. 2020). Recovery of coral following a hurricane can take decades and may never occur for some species (Harmelin-Vivien 1994; Gardner et al. 2005; Madden et al. 2023).

The relative intensity of hurricanes is increasing globally in response to climate change, thereby increasing the potential of these storms to damage marine habitats (Gardner et al. 2005; Holland and Bruyère 2014). There is evidence of wider community effects of hurricanes on coral reefs at least in the short term, where reef fish have been observed to temporarily migrate to deeper waters during intense storms for shelter from waves (Walsh 1983; Letourneur et al. 1993). Hurricanes have also been found to affect juvenile fish to a greater extent than adults, with higher levels of mortality and re-distribution observed in sub-adult individuals (Lassig 1983). Fish species richness on coral reefs has been observed to increase in the months following hurricane passage, with an increase in herbivorous and omnivorous fishes post-storm, indicating alterations to community structure induced by hurricanes (Letourneur et al. 1993). Longer-term community effects are also likely due to the loss of coral hurricanes cause.

Stressors to coral reefs such as increased ocean temperatures and hurricane intensity indirectly impact reef fish via reductions in coral cover. Coral colonies are key contributors to the structural complexity of reefs (Graham and Nash 2013; Darling et al. 2017). High structural complexity on coral reefs is closely tied to community richness, with high structure reefs able to support a greater density and biomass of fish due to the increased habitat and refuge from predators that they provide (Graham and Nash 2013; Darling et al. 2017). Environmental stressors such as hurricanes and MHWs cause increased coral mortality on reefs, which has been found to reduce structural complexity (Magel et al. 2019; Yuval et al. 2023). Coral loss of over 10% on reefs reduces reef fish abundances up to 75%, and the 8% of reef fish who utilize specific species of live coral as habitat (e.g., gobies [Gobiidae] and damselfish [Pomacentridae]) as well the many species who associate with coral as juveniles, may be impacted to an even higher degree (Jones et al. 2004; Pratchett et al. 2011; Coker et al. 2014).

The impact of coral loss on reefs due to MHWs and hurricanes may also impact fish trophic groups differently. Corallivores such as butterflyfish (Chaetodontidae) directly utilize coral as a food source and may suffer reductions to their populations or be forced to shift to alternate food sources if coral cover declines (Rotjan and Lewis 2008; Graham et al. 2009; Pratchett et al. 2011). Additionally, when coral is lost on reefs it is often replaced by macroalgae, which is a food source for many herbivorous fish such as parrotfish (Scaridae; McManus and Polsenberg 2004; Rotjan and Lewis 2008; Bruno et al. 2009). If benthic communities shift towards macroalgae, populations of herbivorous fishes may increase on reefs due to increased food availability (Pratchett et al. 2018). Selectively examining the impact of stressors on specific functional groups and their impact on functional diversity as a whole is essential to provide a more complete understanding of community change.

The spatial configuration of reefs is also critical in shaping the diversity and resilience of the fish community. Patch reefs are relatively small, discrete reef units often aggregated together and connected via the dispersal of organisms, thereby forming a metacommunity (Leibold et al. 2004). In reef fish, dispersal is species-specific. The larvae of fish may travel large distances via ocean currents, but once juveniles settle many species have limited dispersal, leading to high adult site fidelity (Jones et al. 2009; Green et al. 2015). Exceptions include pelagic groups such as jacks (Carangidae) which continue to travel as adults, and species such as grouper (Serranidae) which perform seasonal spawning migrations (Green et al. 2015; Dahlgren et al. 2016). However, dispersal distances for most smaller reef fish, such as those found mainly on patch reefs, are relatively short (0.1-3 km; Green et al. 2015).

The ease by which individuals move between patches in the network defines the connectivity of the fish metacommunity (Leibold et al. 2004). The spatial connectivity of patch reefs can influence their fish species composition, as well as how that composition changes through time and in relation to environmental stressors such as increasing SST, hurricane passage and species invasion. For example, high site connectivity has been linked to lower fish species turnover and higher resilience to disturbance, due to the "rescue effect" whereby species recolonize the site from surrounding patches (Eriksson et al. 2014; White et al. 2021). Conversely, isolated reefs may be more susceptible to community shifts and biodiversity loss in response to stressors (McLaughlin et al. 2013; Thompson et al. 2017; Chase et al. 2020; White et al. 2021). At the metacommunity scale, disturbance can lead to biotic differentiation in which beta diversity (i.e., differences in species composition between sites) increases due to variation in the response of local communities (Socolar et al. 2016; Chase et al. 2020). This can be caused by dispersal limitation leading to local extirpation at some sites (Hubbell 2011; Chase et al. 2020). Identifying shifts in beta diversity within a reef fish metacommunity and potential drivers of this change are necessary to predict the resilience of the metacommunity and locate where conservation resources may be most effective.

Here, I aim to quantify changes in coral reef fish communities in South Eleuthera, The Bahamas, in relation to key reef stressors. To do this, I compare historical fish community time series survey data from 2009-2018 to present-day community data collected at the same sites via the same survey methods in the summer of 2024. Specifically, I examine how the reef fish community has changed over time and in relation to invasive lionfish biomass, rising sea surface temperatures and marine heatwaves, and hurricane passage. I explore the impact of these stressors on reef fish biomass and species richness. *A priori* hypotheses are summarized in Table 1.

Additionally, I explore the spatial structure of patch reefs using network analysis, treating each reef as a node in the reef fish metacommunity. I examine the relationship between network structure and the fish community composition of each reef over time and in relation to environmental disturbance caused by hurricane passage. I expect that reefs will show changes in fish community composition over time and in relation to hurricane passage. Additionally, I expect that highly connected reefs will maintain similar fish community composition over time, indicating resilience to stressors (McLaughlin et al. 2013).

Methods

Sites

Twenty coral patch reefs were selected in 2024 and were resurveyed between August 29 and September 9, 2024. I selected for patches with the maximum number of years of historical survey data available while also aiming to maximize the area covered by the network of patches to account for spatial variation in fish and benthic community composition. All patches were between 2.39 and 5.37 km off the coast of Southern Eleuthera, The Bahamas (Figure 1). Patches ranged in size from 43-385 m^2 (mean = 124.5 m^2) and 2.7-3.8 m in depth (mean = 3.2 m). Maximum vertical relief of patches ranged from 0.8-2.3 m (mean = 1.6 m) and reef rugosity ranged from 1.1-1.6 (mean = 1.4). Both these metrics describe the structural complexity of coral reefs, with larger values indicating higher complexity.

Belt Transect Surveys

Present-Day Belt Transect Surveys

Two to three belt transect surveys per patch reef, depending on reef size, were performed using SCUBA in summer 2024 to determine present-day fish community composition on each reef. In cases of single, discrete reef patches, transects were consistently oriented and spaced to avoid spatial overlap in survey area. In cases of dispersed reef patches comprising multiple smaller patches, transects were placed running across individual patches, covering multiple patches with one transect wherever possible.

During belt transect surveys, a diver swam to the start of each transect and hovered, immobile, at least 1m from the start of the transect line for 3 minutes to allow fish to resettle on the reef after the disturbance caused by placing the transect line. The diver then swam at a slow, fixed speed along the transect line at a consistent height. The diver recorded species identity, abundance, and approximate total length (TL, rounded to the nearest 0.5 cm) of all fish observed within a 1 m width on either side of the transect line, for a total surveyed area of 16 m^2 per transect. Divers scanned the benthos and water column continuously along the transect line in order to record all species present. Belt transect surveys ranged from 2-7 minutes in duration.

Historic Belt Transect Surveys

From 2009-2018, belt transect surveys were performed regularly at all 20 patch reefs (at variable times of year, between 0-12 times annually; Table S1). All historic belt transect surveys were performed using the methodology outlined above (see Present-Day Belt Transect Surveys) and between 1-6 transects per patch reef were performed per survey.

Biomass Calculation

All fish lengths recorded on belt transect surveys were converted to biomass using the allometric function:

$$B = aL^b$$

where B = biomass (g), L = fish length (cm), and a and b are species-specific scaling parameters (Smith and Côté 2021). Conversion parameters were obtained from FishBase (Froese and Pauly 2025). When multiple parameters were available for a species, I selected those obtained geographically closest to the study site. However, if the sample size at a location identified on FishBase was < 5 individuals, I selected parameters with a larger sample size for the next closest location to the study site. If no parameters were available for a species, I selected parameters for a closely related species with similar diet and shape in the same genus (22.8% of species). If no conversion parameters were available for any species in the genus, Bayesian-estimated parameters for TL, calculated by Froese et al. (2014) and obtained via FishBase, were used (6.3% of species; Froese and Pauly 2025). Large, transient reef species (e.g., nurse shark [*Ginglymostoma cirratum*] and great barracuda [*Sphyraena barracuda*]) were not included in biomass calculations as they were not considered to be 'true' reef residents.

Environmental Stressor Data Collection

Invasive Lionfish & Grouper Biomass

Invasive lionfish and native grouper species biomass were obtained based on belt transect data.

Sea Surface Temperature (SST)

Daily SST values (°C) were obtained from NOAA Coral Reef Watch (2025) via the Environmental Research Division's Data Access Program. Each SST is a nighttime temperature value obtained from satellite data for a 5 km x 5 km grid cell. SST values for each survey were obtained from the 5 km cell encompassing the location of the patch reef on the date of the survey. For some historical surveys, a specific survey date was not recorded, only the month and year that the survey was conducted (5.4% of all surveys). In this latter instance, the average monthly SST was calculated and used as the SST value for these surveys.

Hurricane Passage

The historical path of hurricanes in a 300 km radius around the midpoint of all survey sites was examined from one year prior to the start of the time series (2008) to the end of the time series (2024) using NOAA's Historical Hurricane Tracks program (NOAA Office for Coastal Management 2025). A 300 km radius was chosen because severe damage from large, strong cyclones is restricted to this maximum distance away from the storm track (Puotinen et al. 2020). Fourteen hurricanes and tropical storms passed through the study area during the survey period. For each of these storms, their start and end dates were recorded (as the date on which the storm entered and exited the 300 km radius around survey sites) as well as their category (if they were hurricanes) which was defined as the category assigned to the storm at the time of its nearest passage to survey sites. The distance to survey sites was measured in Google Maps as the distance in km from the storm track to the approximate midpoint of all survey sites at the time of nearest passage to the sites (Google 2025). R64 values were gathered for each quadrant of every storm at the time of nearest passage to sites, which provide a measure of the maximum distance from the centre of the storm at which 64 knot winds (i.e. hurricane-speed winds) are felt in each hurricane quadrant (NOAA Office for Coastal Management 2025). R64 values per hurricane quadrant were cross-referenced with the minimum site distance from the storm to determine whether hurricane-speed winds were likely to have reached survey sites.

Based on the above method, I retained two hurricanes in my stressor dataset: Hurricane Irene (which entered the 300 km radius around sites on August 26, 2011 and passed 16 km away from sites at an R64 value of 96.56 km) and Hurricane Sandy (which entered the 300 km radius around sites on October 27, 2012 and passed 37 km away from sites at an R64 value of 48.28 km). I acknowledge the potential effects of water depth, currents, and surrounding topography on hurricane behaviour, which my current method does not account for, but I think that the ultimate impact of these features on the variability of hurricane intensity at the sites was diminished due to the uniformly shallow depth of all survey sites (maximum depth of 3.2 m) and the flat, narrow profile of Eleuthera, the only land that the storms would have passed over prior to reaching sites (Wu et al. 2002; Cangialosi and Chen 2004; Oey et al. 2007).

The time taken for reef fish communities to recover from hurricane passage is variable with no consensus in the literature (Harmelin-Vivien 1994). Based on past observed effects of hurricanes on reef fish communities, I chose to use a hurricane effect period of 6 months to examine relatively short-term impacts to the fish community. I dummy coded hurricane passage with value of 1 for six months from the date the hurricane entered the 300 km radius around survey sites, indicating potential hurricane effects, and a value of 0 on all other dates. In cases where a specific survey date was not recorded and only the month and year that the survey was completed were available, a hurricane effect was coded as present if the 6-month hurricane effect occurred at any time during that month and was coded as absent if not.

Statistical Analyses

Generalized Linear Mixed Effect Models (GLMMs)

All analyses were conducted using R v4.4.1 (R Core Team 2025; Table S2). I performed a series of GLMMs with the *glmmTMB* package (Brooks et al. 2017) to assess the impact of various environmental stressors on reef fish communities from 2009-2024. Models were estimated using maximum log likelihood. In all models, year and site were coded as random intercepts while environmental stressors were fixed effects. Reef rugosity was initially included as a fixed effect in all models, but its impact was found to be non-significant in all cases, and it was therefore removed prior to model selection. All models used a gaussian distribution except for lionfish prey and non-prey richness models, which used a Poisson distribution (Table S3). Fish biomass was log transformed in all models to improve model fit while continuous fixed effects (e.g., lionfish biomass and SST) were standardized by subtracting the mean and dividing by one standard deviation (Schielzeth 2010). I assessed for collinearity among fixed effects in models via a Variance Inflation Factor (VIF) with a threshold of 5 using the *car* package (Petrie 2016; Fox and Weisberg 2019). Temporal autocorrelation was also assessed via Autocorrelation Function (ACF) plots and a lag 1 threshold of 0.3. All models met the assumptions of normality of residuals and homogeneity of residual variance.

Model Selection

I created a series of candidate models based on my *a priori* hypotheses (Table S3). Model selection was then carried out using information theory. Specifically, I calculated Akaike Information Criterion corrected for small sample sizes (AICc), where smaller AICc values indicate higher support in the data for a model. The model with the lowest AICc value was considered to be the top model. Candidate models with an AICc difference <2 were assumed to be similarly supported by the data (Burnham and Anderson 2004; Symonds and Moussalli 2011). If multiple models were considered to be a top model based on ΔAICc values <2, the most parsimonious model was selected as the top model (i.e. the model with the fewest parameters). Additionally, I calculated conditional R^2 values for each top model to determine the amount of variance in the data explained by the top model (Lüdecke et al. 2021). Statistical significance of stressor effects was determined using an alpha value of 0.05.

Network Analysis

I created a network of the patch reef system surveyed in the time series using each reef site as a node in the metacommunity. Specifically, the Euclidean distance between each node was calculated in decimal degrees using the latitude and longitude coordinates of each patch. I then created a binary adjacency matrix of all nodes using a logical comparison and a connectivity threshold of 0.02 decimal degrees, which represents the maximum Euclidean distance between two nodes at which dispersal of species is considered likely (Urban and Keitt 2001). Two nodes within this distance from each other will therefore be connected by an edge in the network structure. A threshold of 0.02 decimal degrees corresponds to ~2.22 km between sites at the study latitude. All self-connections between nodes were removed from the adjacency matrix. Using an unweighted and undirected graph of the network, I then calculated several metrics for the patch reef network using the *igraph* package (Csárdi et al. 2025; Table 2).

Alternate network structures were generated using other connectivity threshold values from 0.01-0.025 decimal degrees to determine the impact this had on network structure (Figure S4; Tables S16-S20; Figures S7-S10). 0.02 decimal degrees was ultimately chosen as the final connectivity threshold as it did not create separate network clusters and produced the most reliable small-world network based on the small-world metric and small-world-ness values, showing a balance between high clustering and short average path lengths (Watts and Strogatz 1998; Humphries and Gurney 2008).

Jaccard Dissimilarity

Four comparisons of Jaccard dissimilarity index values were conducted to determine how fish species composition within patch reef sites changed over survey periods. Firstly, the species composition of each reef community was compared between the years 2011 and 2024 to capture how reef fish communities have changed from early in the time series to present-day. The year 2011 was selected as the "early" year because it was the first year in the time series during which all 20 patch reef sites was surveyed. Only one survey of each reef was conducted in 2024, so these surveys were selected as the 2024 dates for the comparison. To reduce the potential impact of seasonal variation in species composition, a corresponding 2011 survey for comparison was selected that most closely matched the month and day that the 2024 survey was conducted at the corresponding site.

I also compared pre- and post-hurricane surveys to determine if the passage of major storms impacted fish community composition on reefs. During the time series, Hurricane Irene passed near the patch reef sites in August of 2011 followed by Hurricane Sandy, which passed in October of 2012. To compare community composition before and after these storms, I selected the first survey conducted on each reef after the passage of Hurricane Sandy as the post-hurricane surveys. I then selected a survey performed in the year prior to the passage of Hurricane Irene which most closely matched the month and day of the post-hurricane survey at the same site to reduce the impact of any seasonal differences in species composition.

Finally, I compared two pre-hurricane surveys and two-post hurricane surveys to determine if similar community changes were observed over these periods (thus suggesting no 'true effect' of hurricane passage on community composition). The pre-Hurricane Irene survey dates selected for the pre- and post-hurricane comparison were paired with the most seasonally similar surveys conducted during the first year of the time series, from 2009-2010. Only 17 of the 20 total patch reef sites were utilized in this comparison (with sites 119, 99 and E3 excluded), as only these reefs were surveyed in the first year of the time series. To determine fish community composition changes post-hurricane, I selected the most seasonally similar surveys conducted in 2014 and 2015, more than one year after the passage of Hurricane Sandy. Only 10 of the 20 patch reefs were surveyed in these years (sites 101, 104_NF27, 106, 112_NF25, 55, 70, 74, 76, 79 and 93 were excluded from the comparison).

For each survey (i.e., 2011, 2024, pre-hurricane and post-hurricane, two pre-hurricane and two post-hurricane) a presence/absence species matrix was created. The pairwise Jaccard dissimilarity for each survey period was then calculated using the *vegan* package as:

$$Jaccard\ dissimilarity = \frac{B + C}{A + B + C}$$

where A = the number of species present in both survey periods (e.g., present in both the 2011 and 2024 survey), B = the number of species present in only the first survey period (e.g., only 2011) and C = the number of species present in only the second survey period (e.g., only 2024; Jaccard 1900; Oksanen et al. 2001). This provides a value from 0-1, where 0 = identical species compositions between survey periods and 1 = no shared species between survey periods.

Changes in species composition across reef sites over survey periods (i.e., 2011 vs. 2024, pre- vs. post-hurricane, two pre-hurricane and two post-hurricane surveys) were assessed using one-way permutational multidimensional analyses of variance (PERMANOVAs) on the Jaccard dissimilarity matrices generated. Statistical significance was assessed with 10,000 permutations of residuals with a reduced model using a type III sum of squares. Differences in beta diversity between survey periods were additionally assessed with tests of homogeneity of multivariate dispersions (PERMDISPs) and it's *a posteriori* test on the Jaccard dissimilarity matrices using 10,000 permutations of residuals (Anderson et al. 2006; Alonso-Domínguez et al. 2025). The PERMDISP allowed us to determine whether a significant difference in the variance of species composition was present between survey periods by assessing the deviation in the group from the centroid. PERMANOVA and PERMDISP analyses were performed using the *vegan* package (Oksanen et al. 2001). A Principal Coordinates Analysis (PCoA) was conducted on the Jaccard dissimilarity matrix to visualize the dissimilarity between each site in each survey period by plotting the first two ordination axes.

Finally, I investigated the correlation between Jaccard dissimilarity and two metacommunity network metrics, betweenness centrality and closeness centrality, between the two primary survey periods of interest: 2011 vs. 2024 and pre- vs. post-hurricane. This allowed me to determine whether reefs that played an important role in network connectivity were also more likely to have high or low similarity in community composition over time. Jaccard dissimilarity, betweenness centrality and closeness centrality were not normally distributed in either survey period comparison. Hence, I used Spearman rank correlation tests to assess the relationship between Jaccard dissimilarity and network metrics across survey periods, as well as the correlation between network metrics.

Results

Survey data spanned 14 years, 9 months, and 17 days starting on November 23, 2009, and ending on September 9, 2024. Patch reef surveys were conducted on 184 days, with a total of 1,755 individual transects. In total, 127 reef fish species were recorded from 38 Families.

Model Selection

Model predicting total fish biomass

The top model on the log-transformed biomass for all fish recorded on belt transect surveys from 2009-2024 contained all three stressors (lionfish biomass, SST and hurricane passage) and explained 7.5% of variance in fish biomass over fourteen years (Table 3; Table S4). Lionfish biomass was found to have a significant positive effect on fish biomass ($p < 0.001$), whereas SST and hurricane passage each had significant negative effects on biomass ($p < 0.001$ for both stressors; Figure 2A).

Model predicting total fish species richness

The top model for fish species richness for surveys from 2009-2024 contained lionfish biomass and SST as stressors, but excluded hurricane passage, and explained 29.3% of variance in richness (Table 3; Table S5). Lionfish biomass had a significant, positive effect on species richness ($p < 0.001$). However, contrary to the negative effect of SST on fish biomass, SST was also found to positively affect richness ($p < 0.001$; Figure 3A).

Models predicting lionfish, grouper & total mesopredator biomass

Top models on changes in total lionfish biomass recorded from 2009-2024 included the null model, suggesting that none of the examined factors explained changes in lionfish biomass over time (Table 3, Table S6). In contrast, the top model predicting total grouper biomass from 2009-2024 contained lionfish biomass as a significant predictor ($p < 0.001$), explaining 15.4% of variance in grouper biomass (Table 3; Table S7; Figure 2B). Model selection on total mesopredator biomass on reefs (i.e., lionfish and grouper biomass combined) also contained the null model, suggesting that none of the factors that I examined could explain variance in total mesopredator biomass over the survey period (Table 3; Table S8).

Models predicting total mesopredator prey & non-prey fish biomass

The top model predicting log-transformed mesopredator prey biomass (any fish ≤ 5 cm TL) contained three stressors (lionfish biomass, SST, and hurricane passage) and explained 9.0% of variance (Table 3; Table S9). Lionfish biomass had a significant positive effect ($p = 0.016$) while SST and hurricane passage had significant, negative effects ($p < 0.001$ and = 0.001, respectively; Figure 2C) on prey biomass. In terms of non-prey biomass (any fish >5 cm TL), the top model contained grouper biomass and hurricane passage as significant predictors and explained 5.0% of variance (Table 3; Table S11). Specifically, hurricane passage had a significant negative effect on non-prey biomass while grouper biomass had a significant positive effect ($p = 0.009$ and < 0.001, for hurricane passage and grouper biomass, respectively; Figure 2D).

Models predicting total mesopredator prey and non-prey fish species richness

Model selection performed on mesopredator prey and non-prey species richness from 2009-2024 revealed similar top models, with SST present as the only stressor in both cases. The top prey species richness model explained 38.7% of variance while the top non-prey species richness model explained 25.0% of variance in the data (Table 3; Table S10; Table S12). In both instances, SST was found to have a significant, positive effect on species richness ($p < 0.001$ and = 0.007, respectively; Figure 3B-C).

Models predicting corallivorous & herbivorous fish biomass

The top models predicting the log biomass of corallivorous and herbivorous fish species recorded from 2009-2024 contained SST and hurricane passage and explained 15.9% and 15.3% of variance in corallivore and herbivore biomass, respectively (Table 3; Table S13; Table S14). SST had a significant negative effect on both corallivore and herbivore biomass ($p = 0.010$ and < 0.001, respectively). Likewise, hurricane passage significantly, negatively affected corallivore and herbivore biomass ($p < 0.001$ for both corallivores and herbivores; Figure 2E-F).

Metacommunity Structure

Network Structure

Network analysis on the patch reef fish metacommunity using a connectivity threshold value of 0.02 revealed a network of 20 nodes (one per patch reef) with 88 edges connecting nodes to one another (Figure S15). The network had a connectance of 0.220, indicating that 22.0% of all possible connections between nodes were realized in the network. The network had a clustering coefficient of 0.707, meaning that if two reefs were connected to a common third reef, there was a 70.7% probability that they were also connected to one another. The network had a diameter of 3 and an average distance between nodes of 1.668, indicating that the network was compact with high local clustering. The network had an intermediate small-world metric of 0.424 and an average small-world-ness value of 1.475 when compared to three randomly generated networks with the same number of nodes and edges, indicating sufficient support for small-world behaviour of the network. The betweenness centrality of nodes ranged from 0 at sites 108, 74, 78 and 89 to 26.603 at site 55 (Table 4). Closeness centrality of nodes ranged from 0.026 at site 108 to 0.040 at site 55 (Table 4). Sites 93 and 55 had the highest degree, with 13 connections each, compared to site 70 which had the lowest degree value of 5 connections (Table 4). This indicates a range in the connectivity of reef patches, with some sites more highly connected in the network than others.

Changes in the fish metacommunity between 2011 vs. 2024

The comparison of fish species composition at sites in 2011 and 2024 showed a range in Jaccard dissimilarity from 0.469 at site 93 to 0.816 at site 104_NF27 (Figure 4A, Table S21). The results of the PERMANOVA revealed that survey period (2011 vs. 2024) explained 14.4% of the variation in site species composition ($p < 0.001$), indicating a significant shift in beta diversity across the metacommunity from the early years to end of the time series (Table 5). The PERMDISP revealed significant differences in the dispersion of species composition across sites between each survey period ($p = 0.0021$), with 2024 belt transect surveys showing higher variation in species composition compared to 2011 surveys (Table 5; Figure 4B). Together, the PERMANOVA and PERMDISP results indicate significant changes in reef fish community composition and variability from 2011 to 2024.

The relationship between the Jaccard dissimilarity of fish species composition on reefs in 2011 compared to 2024 and the betweenness and closeness centrality of sites at a connectivity threshold value of 0.02 was analyzed using a rank Spearman correlation test. This produced rho values of -0.442 and -0.389 for the relationship between Jaccard dissimilarity and betweenness and closeness centrality, respectively, though both relationships were marginally non-significant ($p = 0.051$ for Jaccard vs. betweenness centrality and 0.090 for Jaccard vs. closeness centrality; Figure 6).

Pre- vs. post-hurricane changes in the fish metacommunity

Pre-Hurricane Irene (August 2011) and post-Hurricane Sandy (October 2012) fish species composition on patch reefs was compared to assess the potential impact of hurricanes on reef fish community assemblages. Jaccard dissimilarity pre- and post-hurricane ranged from 0.481 at site 90 to 0.692 at site 106 (Figure 5A, Table S22). The PERMANOVA performed on reef Jaccard dissimilarity pre- and post-hurricane revealed a significant effect of survey period on metacommunity beta diversity, with pre- or post-hurricane explaining 6.9% of total variation in species composition on reefs ($p < 0.001$). However, the PERMDISP revealed no significant difference in the dispersion of community composition across sites pre- and post-hurricane ($p = 0.573$; Table 6, Figure 5B). Together, the PERMANOVA and PERMDISP suggest a significant shift in fish community composition between pre- and post-hurricane surveys but not driven by a change in variability.

To determine whether a 'true' pre/post-hurricane effect was present, I assessed changes in species composition between reefs in two pre-Hurricane Irene surveys and two post-Hurricane Sandy surveys. Pre-Hurricane Irene differences in species composition ranged from a Jaccard dissimilarity value of 0.316 at site 74 to 0.667 at site 94 (Table S23). A PERMANOVA performed on the Jaccard dissimilarity values of each site between surveys indicated a significant effect of survey period on beta diversity, with early pre-hurricane compared to later pre-hurricane explaining 6.6% of variation in species composition ($p = 0.001$). The corresponding PERMDISP test was not statistically significant, indicating no difference in variability in species composition across sites between survey periods ($p = 0.148$; Table 6; Figure S5). Similarly to the pre- vs. post-hurricane comparison, this suggests a significant shift in community composition between survey periods but no change in patch variability. In post-Hurricane Sandy surveys, Jaccard dissimilarity values for reef community composition ranged from 0.385 for site E3 to 0.632 for site 102 (Table S24). There was no significant difference in fish community composition between survey periods and no change in the variability of species composition across reefs (PERMANOVA $p = 0.977$ and PERMDISP $p = 0.483$; Table 6; Figure S6). Together, this suggests no significant change in patch community composition between the post-hurricane survey periods.

There was no relationship between the Jaccard dissimilarity of fish species composition in pre- and post-hurricane surveys compared to the betweenness and closeness centrality of the reef network. Similarly, no correlation was found between the Jaccard dissimilarity of species composition in the two pre-hurricane and two post-hurricane survey periods (Figure S11).

The correlation between dissimilarity in reef fish community composition between 2011/2024 surveys and pre/post-hurricane surveys was also examined. I found no relationship between dissimilarity over the two periods (Figure S12). Finally, the correlation between reef betweenness and closeness centrality was analyzed with a rank Spearman correlation test, revealing a significant, positive relationship between the metrics (rho = 0.983, $p < 0.001$; Figure 7).

Discussion

This study explored the impacts of environmental stressors and the network structure on patch reef fish assemblages from 2009 to 2024. I found that over a 15-year period, rising sea surface temperatures and hurricane passage negatively affected the total biomass of reef fish communities as well as specific trophic groups (corallivores and herbivores) and size classes (<5 cm TL, i.e., mesopredator prey fish). Contrary to expectations, I found a positive relationship between invasive lionfish biomass and native reef fish biomass and species richness, as well as a positive effect of SST on species richness. In terms of the structure of the patch reef fish metacommunity, my analyses suggested a well-connected network with high dispersal capacity between reefs. I saw a significant shift in community composition from 2011 to 2024, with an increase in beta diversity in 2024 fish surveys. I also found a weak, negative relationship between reef connectivity and dissimilarity in fish community composition, indicating lower species turnover on highly connected reefs. Although there was a change in reef fish species composition within the metacommunity with the passage of hurricanes, significant species turnover also occurred between years when hurricanes did not occur, making it difficult to discern the effect, if any, of hurricanes on the metacommunity.

Effects of Environmental Stressors on Reef Fish Assemblages

Opposite to my expectation, invasive lionfish biomass was consistently positively associated with reef fish community metrics (e.g., native prey fish species biomass, grouper competitor biomass, total fish biomass and total fish species richness; Figure 2 A,C, Figure 3A). These findings contrast with previous experimental and observational studies that revealed adverse effects of lionfish on prey fish communities (Green et al. 2012; Green and Côté 2014; Albins 2015) and grouper competitors in The Bahamas (Green et al. 2012; Curtis et al. 2017; but see Hackerott et al. 2013). A possible explanation for these findings is that lionfish are simply attracted to reefs that already possess high abundances and diversity of reef fish due either to specific habitat features of reefs (e.g., reef structural complexity [Beets and Hixon 1994]) or high prey availability. The former explanation also holds for my finding that grouper biomass was positively associated with non-prey fish biomass (Figure 2D). In contrast, grouper biomass was not linked to prey fish biomass, suggesting that other factors that I did not measure (e.g., grouper fishing pressure) may be more important (Figure 2C).

Sea surface temperature was a significant predictor of fish community metrics in most top models. This result reinforces the central role of temperature in marine ectotherm communities through its influence on individual metabolism, growth, reproduction, and behaviour (Munday et al. 2008; Spinks et al. 2019; Van Wert et al. 2024). Specifically, consistent with my expectations, SST acted as a significant, negative predictor of fish biomass and was present in total fish, prey fish and corallivore top models (Figure 2 A,C,E,F). However, a similar, negative effect of SST was found in the herbivorous fish top model, which contradicts my hypothesis (Table 1; Figure 2F). This negative effect may be because the adverse consequences of increased temperature (e.g., thermal stress) outweigh any benefits of subsequent increases in macroalgae (Pratchett et al. 2011; Shlesinger and van Woesik 2023).

Unlike its effect on biomass, and contrary to my prediction, SST was positively associated with fish species richness in all top models (Figure 3). This result contrasts with previous studies that showed negative impacts of SST on fish biomass and richness (e.g., Pratchett et al. 2011; Chaudhary et al. 2021; Shlesinger and van Woesik 2023). Although increased ocean temperatures have been linked to increases in species richness, these effects occurred on much larger spatial scales due to species range shifts caused by individuals trying to remain within their thermal optima, which is unlikely in this study of small, Bahamian patch reefs (Hiddink and Ter Hofstede 2008; Lloyd et al. 2012; Chaudhary et al. 2021). Instead, the positive association with SST found here with a simple, linear model may possibly mask a more complex relationship that is non-linear and beyond the scope of this study.

Hurricane passage had a large and consistently negative effect on reef fish biomass, being selected as a major stressor in five of the six top biomass models (Table 3). Further, when present, the hurricane effect size was greater than every other stressor present in top biomass models (Figure 2 A,C-F). This finding supports my hypothesis that hurricanes would negatively impact reef fish (Walsh 1983; Yuval et al. 2023; Table 1). In contrast to expectations, there was a negative impact of hurricanes on herbivore abundances which may, in part, be due to a time lag effect in which a period greater than 6-months post-storm may be necessary to detect increases in macroalgae sufficiently large to benefit herbivorous fishes. Examining a longer time scale may reveal a positive effect of hurricanes on herbivores, or a reduced negative effect. However, it is also possible that the negative impacts of hurricanes on coral cover and subsequent decreases in suitable habitat may outweigh any benefits accrued from increased macroalgae.

In the specific case of mesopredator biomass, which in these reef ecosystems refers to lionfish and grouper species, I found no support for my hypotheses. Model selection predicting lionfish biomass and total mesopredator biomass (i.e., lionfish and grouper biomass) in relation to all environmental stressors (excluding lionfish biomass) included the null model as a top model, indicating no effect of the stressors (Table 3). As discussed previously, the grouper biomass top model included lionfish biomass as a positive predictor, which was the only mesopredator top model to contain a stressor. The lack of a measurable impact of SST and hurricane passage on lionfish biomass and total mesopredator biomass may be because of the overriding effect of fishing pressure, which was not measured in this study. Both lionfish and groupers are heavily fished in The Bahamas (Cheung et al. 2013), including in the study area where there is a haphazard but ongoing lionfish culling program by the Cape Eleuthera Institute as well as the presence of subsistence fishers, who regularly fish on the patch reef network.

To better understand environmental influences on lionfish and their impact on reef fish communities, models could incorporate additional factors. The inclusion of reef-specific features such as rugosity or wave exposure may reveal patterns in their abundance (Côté & Smith 2018; Anton et al. 2014). As well, including lionfish size or body condition as response variables rather than biomass may better capture how their populations shift through time and in relation to stressors (Aguilar-Perera & Hernández-Landa 2022). Finally, exploring the relationship between lionfish biomass and fish species with functional traits selected for by lionfish, such as shallow bodies, solitary behaviour, or near-benthic habitat preference, could provide further insight into their role in shaping fish communities (Green & Côté 2014).

All top stressor models were found to have generally low to moderate conditional R^2 values, ranging from 0.05 for the top non-prey fish biomass model to 0.387 for the prey fish richness model (Table 3). Though large R^2 values are often a goal in model fitting, these results were not surprising given the nature of my dataset being a long time series collected across multiple sites (Nakagawa & Schielzeth 2012, Lin & Wiegand 2023). Additional predictors unrelated to my hypotheses may be needed to explain greater variance in my models, such as reef-specific habitat variables. Top models predicting species richness as a metric were also found to have higher conditional R^2 values than models predicting fish biomass (Table 3), and biomass top models generally contained more predictors (2-3 fixed effects; Fig 2) than species richness models (1-2 fixed effects; Fig 3). The generally lower R^2 values in biomass models might be due to greater error surrounding biomass estimates, which depended on length estimates in the field as well as species-specific parameters, which were not always available. In contrast, the observation that biomass models often contained more predictors than richness suggests that biomass may be a more sensitive metric than richness to a variety of stressors.

The Reef Fish Metacommunity

Network analysis on the patch reef metacommunity revealed a relatively connected network with high dispersal capacity, based on the moderate connectance and clustering coefficient values (Watts and Strogatz 1998; Dunne et al. 2002). The patch reef network was compact with generally short dispersal pathways linking reefs together, allowing many avenues for potential species dispersal between patches (Patonai et al. 2023). Together, the small-world metric and small-world-ness value indicated strong small-world behaviour of the network, characteristic of a sufficiently random and clustered network (Watts and Strogatz 1998; Humphries and Gurney 2008; Patonai et al. 2023). This agrees with past studies on reef metacommunities which found high connectivity (e.g., MacNeil et al. 2009). The avenues available for efficient dispersal of reef fish in the patch reef network suggest that the metacommunity may possess high resilience to disturbance.

Individual patch reefs varied in their connectivity and consequent dispersal capacity. The range in betweenness and closeness centrality values for reefs in the network suggest that some patches act as bridges in the network, allowing for increased connectivity and species dispersal (Bodin and Norberg 2007; Zhang and Luo 2017; Patonai et al. 2023; Table 4). This was partially supported by the comparison of 2011 compared to 2024 species composition on reefs, which found a weak negative relationship between reef connectivity and species turnover (Figure 6). Visually in the network structure, central reefs also appeared to have lower species turnover (Figure 4A). As hypothesized, this suggests that more central, highly connected reefs may experience lower species turnover through time due to consistent immigration of fish from surrounding patches (Mouquet and Loreau 2003; Leibold et al. 2004; Hillebrand et al. 2018). However, these connected patches may also act as source reefs by maintaining stable populations of fish that can then disperse to peripheral sink reefs, facilitating persistence of the metacommunity through rescue effects (Pulliam 1988; Chase et al. 2020). These findings align with studies that identify highly connected reefs as conservation priorities due to their high dispersal capacity (e.g., Hock et al. 2014; Schill et al. 2015).

Other studies report no correlation between reef connectivity and fish abundance (e.g., MacNeil et al. 2009). Similarly, in my reef network not all patches showed decreasing species turnover with increasing connectivity. For example, site 104_NF27 had the largest dissimilarity value of all reefs (dissimilarity = 0.816), indicating the highest level of species turnover from 2011 to 2024 (Table S21, Figure 6). However, this reef also had large betweenness and closeness centrality values, indicating high connectivity (betweenness centrality = 12.935, closeness centrality = 0.038; Table 4, Figure 6). Site 79 showed a similar pattern, with both large dissimilarity and connectivity values (Table S21, Table 4, Figure 6). This suggests that in some cases, factors other than connectivity may drive species turnover on reefs, such as patch-specific demographic parameters including habitat quality and survival rates (MacNeil et al. 2009; Figueira 2009; Hill et al. 2017). Thus, while connectivity can buffer against species turnover via dispersal and rescue effects, it may be overridden by local processes in some cases.

Some resilience of the reef metacommunity to local disturbance was suggested by the analysis of hurricane impacts, though the results are not definitive. A significant change in community composition was seen from the year before hurricanes Irene and Sandy passed compared to the year after, but no corresponding shift in beta diversity was observed (Figure 5). As well, the control comparison of two pre-hurricane surveys revealed similar results, indicating that differences in pre- and post-hurricane composition may not be driven by storm disturbance (Table 6). These findings may indicate some ability of well-connected source reefs to buffer against disturbance via rescue dispersal to sink reefs, providing some stability to the metacommunity in the face of discrete disturbance (Eriksson et al. 2014; White et al. 2021). Previous studies have identified a key role of dispersal in the recovery of metacommunities following a local disturbance (e.g., Altermatt et al. 2011; Mausbach and Dzialowski 2019), which may be a mechanism at play in this reef network. However, it is important to note that these results do not rule out any impact of hurricanes or other local disturbances on fish metacommunities and warrant further exploration.

Synthesis

My analyses revealed varying impacts of environmental stressors on the reef fish metacommunity depending on the response variable examined. Hurricane passage consistently had a strong, negative effect on fish biomass, but no clear effect was seen on species richness or species turnover (Figure 2A, Figure 3A, Table 6). As well, increased SST had conflicting effects on fish biomass versus species richness (Figure 2A, Figure 3A). These findings support previous work showing biomass to be a more sensitive indicator of community change compared to species richness (e.g., Hillebrand et al. 2018; Maureaud et al. 2019) and indicate the importance of exploring multiple community response metrics to gain a more complete understanding of the complexity of community change.

These findings also highlight the dynamic nature of reef fish communities. Community composition shifted over time and in relation to reef spatial position, and fish biomass was influenced by environmental stressors including SST, hurricane passage and mesopredator biomass (Figure 4, Figure 2). Since the 1990s, coral reefs have been thought to exist in multiple stable states, switching between coral and macroalgae-dominated forms (Knowlton 1992). However, little empirical evidence supports this paradigm (Dudgeon et al. 2010). Rather, more recent studies have shown support for phase shifts on reefs, in which the community changes continuously with environmental conditions until a threshold is reached (Dudgeon et al. 2010; Spinks et al. 2019). The results of this study support this phase shift hypothesis, with changing fish community composition and biomass through time, in response to environmental factors, and in relation to reef connectivity, and no evidence of prolonged assemblage stability.

This study uses a long-term monitoring dataset to explore the effects of multiple stressors on reef fish assemblages and integrates network analysis to further investigate the ecological dynamics of reef fish communities. Despite discussion of potential interactions between multiple environmental stressors, we remain uncertain of their relative effects on coral reef communities (Crain et al. 2008; Ban et al. 2014; Muthukrishnan and Fong 2014). Moreover, few studies have examined the impact of hurricane passage on fish rather than benthic communities (e.g., Wulff 1995; Gleason et al. 2007; Beeden et al. 2015; but see Lassig 1983 and Adams 2001). Studying the relative impacts of invasive lionfish biomass, SST, and hurricane passage on reef fish communities over a nearly 15-year time period provides novel insights into the dynamics shaping reef fish assemblages in the intermediate-term. These results reveal varying or opposite effects of stressors on some community response metrics (e.g., the response of fish biomass vs. richness to SST and the response of fish biomass vs. richness and species turnover to hurricane passage). This adds to a growing body of work highlighting that community responses are not uniform across metrics, which reinforces the need to consider multiple dimensions of biodiversity when evaluating ecological impacts (Santini et al. 2017; Maureaud et al. 2019).

Additionally, the use of network analysis on a coral reef metacommunity to examine the impact of environmental stressors on beta diversity is an analysis that to my knowledge has not previously been performed. While it can be difficult to explore coral reef metacommunity dynamics due to a general lack of discrete habitat patch structure, this patch reef system in southern Eleuthera provides an ideal network due to the proximity of many small, discrete reef units (Leibold et al. 2004). The analysis performed here uncovered possible evidence of reef connectivity buffering against species turnover in fish metacommunities, despite connectivity being typically unaccounted for in studies of reef community change unless exploring larval dispersal or reserve design (Mumby and Hastings 2008; Munday et al. 2009; Schill et al. 2015).

Future additions to this, or any, long-term dataset of reef fishes could benefit from several improvements. Firstly, many different surveyors with varying levels of expertise collected data over the course of the time series, leading to potential surveyor bias (Thompson and Mapstone 1997; Bernard et al. 2013). In future, surveying with two independent divers as recommended by Bernard et al. (2013) could be employed, and/or the adoption of standardized training practices across monitoring frameworks to help reduce bias (Thompson and Mapstone 1997). Additionally, in this dataset belt transect surveys were conducted around midday when crepuscular and nocturnal fish species, such as lionfish and grouper, have limited activity and generally shelter within reef structure (Green and Côté 2014; Khan et al. 2017; Harmelin-Vivien and Harmelin 2022). Green et al. (2013) found that >50% of lionfish detections were missed when using belt transect surveys as a monitoring technique. To avoid underestimation of important mesopredator species in future, I recommend the incorporation of roving predator surveys into monitoring practices, which cover the exterior and interior of the reef in greater detail (adapted from REEF [2025]; see Wartenberg 2012). Finally, benthic community change on reefs should be monitored in addition to shifts in fish communities to gain more detailed information on coral reef ecosystem shifts and the mechanisms behind change (Chong-Seng et al. 2012; Donovan et al. 2018). Reef fish and benthic communities are interconnected, with benthic structure providing habitat structure, refuge, and food for fish, and fish providing the benthos with a key source of nutrient deposition (Graham and Nash 2013; Allgeier et al. 2014). Looking at changes to both these groups simultaneously would greatly improve our understanding of community change in relation to stressors.

Reef fish communities are incredibly complex and sensitive to direct and indirect effects from environmental stressors. This study points to fish biomass as a key indicator of reef fish community change and highlights the role of the spatial structure of reefs as an additional factor important for assessing reef resilience. These findings demonstrate the importance of incorporating multiple community response metrics into analyses (in this case biomass, species richness, and community composition) to ensure that opposing effects and differences in metric sensitivities are accounted for. Additionally, these results emphasize the dynamic nature of reef fish communities, with temporal shifts in community composition and changes to fish biomass linked to environmental stressors. Recognizing that reef communities may not be as stable as previously thought and understanding how this is impacted by reef connectivity and exposure to environmental stressors is essential for explaining and predicting community change through time.

Tables and Figures

Table 1. Summary of hypotheses for each stressor: invasive species, sea surface temperature (SST), and hurricane passage. The community metrics tested for each hypothesis (fish biomass and/or species richness) are indicated.

Stressor	**Hypothesis**	**References**	**Metric**	
			Biomass	*Species Richness*
Invasive species	Invasive lionfish biomass will decrease native prey.	Green et al. 2012	✓	NA
Invasive species	Invasive lionfish biomass will reduce native prey diversity.	Albins 2015; Green & Côté 2014	NA	✓
Invasive species	Invasive lionfish biomass will decrease native predators.	Green et al. 2012	✓	NA
Native predators	Native grouper biomass will decrease native prey.	Harmelin-Vivien & Harmelin 2022	✓	NA
Native predators	Native grouper biomass will reduce native prey diversity.	Harmelin-Vivien & Harmelin 2022	NA	✓
SST	Increased SST will decrease corallivorous fishes.	Shlesinger & Van Woesik 2023; Pratchett et al. 2011	✓	NA
SST	Increased SST will increase herbivorous fishes.	Shlesinger & Van Woesik 2023; Pratchett et al. 2018	✓	NA
SST	Increased SST will decrease non-herbivorous fishes.	Shlesinger & Van Woesik 2023; Pratchett et al. 2011	✓	✓
Hurricanes	Hurricanes will decrease corallivorous fishes.	Gleason et al. 2007; Pratchett et al. 2011	✓	NA
Hurricanes	Hurricanes will increase herbivorous fishes.	Gleason et al. 2007; Pratchett et al. 2018	✓	NA
Hurricanes	Hurricanes will decrease non-herbivorous fishes.	Walsh 1983; Yuval eta l. 2023	✓	✓
Hurricanes	Hurricanes will decrease juvenile fishes.	Lassig 1983	✓	✓

Table 2. Description of network metrics calculated to describe the patch reef metacommunity.

Metric	Definition	Equation	References
Number of nodes	The number of patch reefs present in the network.	NA	Csárdi et al. 2025
Number of edges	The number of connections between nodes present in the network.	NA	Csárdi et al. 2025
Connectivity Threshold	The maximum Euclidean distance between two nodes, in decimal degrees, at which dispersal of species is considered likely. Two nodes within this distance from each other will therefore be connected by an edge in the network structure.	NA	Urban and Keitt 2001
Connectance	The proportion of possible edges present in the network.	$Connectance = \frac{Number\ of\ Edges}{(Number\ of\ Nodes)^2}$	Dunne et al. 2002
Clustering coefficient	A global measure of node clustering tendency calculated as the probability that two nodes both connected to a third node are also connected to each other.	$\mathrm{CL} = \frac{3 \text{ x Number of Triangles}}{\text{Number of Connected Triples}}$ where triangles = a set of three vertices where each vertex is connected to the other two and connected triples = a set of three vertices where at least two edges connect them in a path length of two.	Humphries and Gurney 2008; Csárdi et al. 2025
Diameter	Among the shortest path lengths connecting each pair of nodes in the network, the path with the greatest number of edges (i.e. the maximum number of edges required to get from one node to another in the network).	NA	Csárdi et al. 2025

Average distance	The average distance between each node in the network, measured in edges.	$d = \frac{1}{\frac{N(N-1)}{2}} \sum_{i<j} d(i,j)$ where N = the number of nodes in the network and $d(i,j)$ = is the shortest path length between nodes i and j.	West 1996
Small world metric	Characterizes the structure of a network based on how ordered or random it is. Small CL and d values indicate a random network while large CL and d values indicate a regular or lattice-like network. High CL and small d values indicate a small-world, more natural structure.	$SW = \frac{CL}{d}$ where CL = the clustering coefficient of the network and d = the average distance of the network.	Watts and Strogatz 1998; Patonai et al. 2023
Small-world-ness	Compares the network to randomly generated networks with the same number of nodes and edges to determine how small-world the network behaves. Values > 1 indicate small-world behaviour.	$SWI = \frac{CL_{observed}/\overline{CL}_{random}}{d_{observed}/\bar{d}_{random}}$ where $CL_{observed}$ = the clustering coefficient of your network, $\overline{CL}_{random}$ = the mean clustering coefficient of the randomly generated networks, $d_{observed}$ = the average distance of your network and $\bar{d}_{random}$ = the mean average distance of your randomly generated networks.	Humphries and Gurney 2008
Betweenness centrality	A per-node measure of how often a node lies on the shortest path between all other nodes. A high betweenness value indicates that the node acts as a "bridge" between other nodes.	$BC(v) = \sum_{s \neq v \neq t} \frac{g_{st}(v)}{g_{st}}$ where $BC(v)$ = betweenness centrality of node v, g_{st} = the total number of shortest paths from node s to t, and $g_{st}(v)$ = the	Freeman 1978; Brandes 2001

		number of those shortest paths from s to t that pass through node v. This is summed over all pairs of nodes in the network, excluding v.	
Closeness centrality	A per-node measurement of the inverse of the average shortest path length from the node to all other nodes in the network. A high closeness centrality indicates fast possible dispersal from the node throughout the network.	$$CC(v) = \frac{1}{\sum_{i \neq v} d_{vi}}$$ where $CC(v)$ = the closeness centrality of node v and d_{vi}= the shortest path distance from node v to i. This is summed over all other nodes in the network, excluding v.	Freeman 1978
Degree	A per-node measurement of the total number of connections each node has to other nodes in the network.	NA	Csárdi et al. 2025

Table 3. Summary of top models obtained for each reef fish community response metric following AICc model comparison. All fixed effects were found to be statistically significant. Marginal R^2 corresponds to the proportion of variance explained by the model when accounting for only fixed effects while conditional R^2 corresponds to the percentage of variance explained when accounting for both fixed and random effects.

Response Variable	**Fixed Effect Model Structure**	**Marginal R^2**	**Conditional R^2**
Total fish biomass	Lionfish biomass, SST, hurricane passage	0.009	0.075
Total fish richness	Lionfish biomass, SST	0.040	0.293
Lionfish biomass	NA	0.000	0.161
Grouper biomass	Lionfish biomass	0.025	0.154
Mesopredator biomass	NA	0.000	0.125
Prey fish biomass	Lionfish biomass, SST, hurricane passage	0.014	0.090
Prey fish richness	SST	0.033	0.387
Non-prey fish biomass	Grouper biomass, hurricane passage	0.005	0.050
Non-prey fish richness	SST	0.005	0.250
Corallivore biomass	SST, hurricane passage	0.008	0.159
Herbivore biomass	SST, hurricane passage	0.008	0.153

Table 4. Network metrics for each site in the patch reef metacommunity using a connectivity threshold of 0.02. Each site acts as a node in the network. Betweenness centrality measures how often a node lies on the shortest path between all other nodes, closeness centrality measures the inverse of the average shortest path length from the node to all other nodes in the network, and degree is equal to the total number of connections each node has to other nodes in the network.

Site	**Betweenness Centrality**	**Closeness Centrality**	**Degree**
108	0	0.0263	6
74	0	0.0270	7
78	0	0.0270	7
90	1.395	0.0303	8
93	24.472	0.0400	13
71	2.063	0.0323	7
104_NF27	12.935	0.0385	12
112_NF25	4.028	0.0323	10
102	9.659	0.0357	10
94	4.028	0.0323	10
119	1.747	0.0294	7
76	1.395	0.0303	8
55	26.603	0.0400	13
70	0.583	0.0294	5
101	16.621	0.0370	11
106	0.226	0.0278	7
E3	1.268	0.0286	8
89	0	0.0271	7
79	5.356	0.0345	9
99	14.624	0.0370	11

Table 5. PERMANOVA & PERMDISP results for 2011 vs. 2024.

Source of Variation	**PERMANOVA**			**PERMDISP**	
	F	*p-value*	R^2	*F*	*p-value*
Time period	6.468	<0.001	0.144	9.947	0.0021
Residuals			0.855		

Table 6. PERMANOVA & PERMDISP results for pre vs. post hurricane, pre-hurricane, and post-hurricane.

Source of Variation	**PERMANOVA**			**PERMDISP**	
	F	*p-value*	R^2	*F*	*p-value*
Time period (pre vs. post hurricane)	2.827	<0.001	0.0693	0.328	0.573
Residuals (pre vs. post hurricane)			0.931		
Time periods (pre hurricane)	2.254	0.0014	0.0658	2.124	0.148
Residuals (pre hurricane)			0.934		
Time period (post-hurricane)	0.438	0.977	0.0238	0.517	0.483
Residuals (post-hurricane)			0.976		

Figure 1. Map of 20 coral patch reef sites around Southern Eleuthera, The Bahamas. Each site is represented by a red circle and text labels are site names. Site 104_NF27 is shortened to 104 and site 112_NF25 is shortened to 112. The inset map shows the broader region, with the approximate location of the sites marked with the black square.

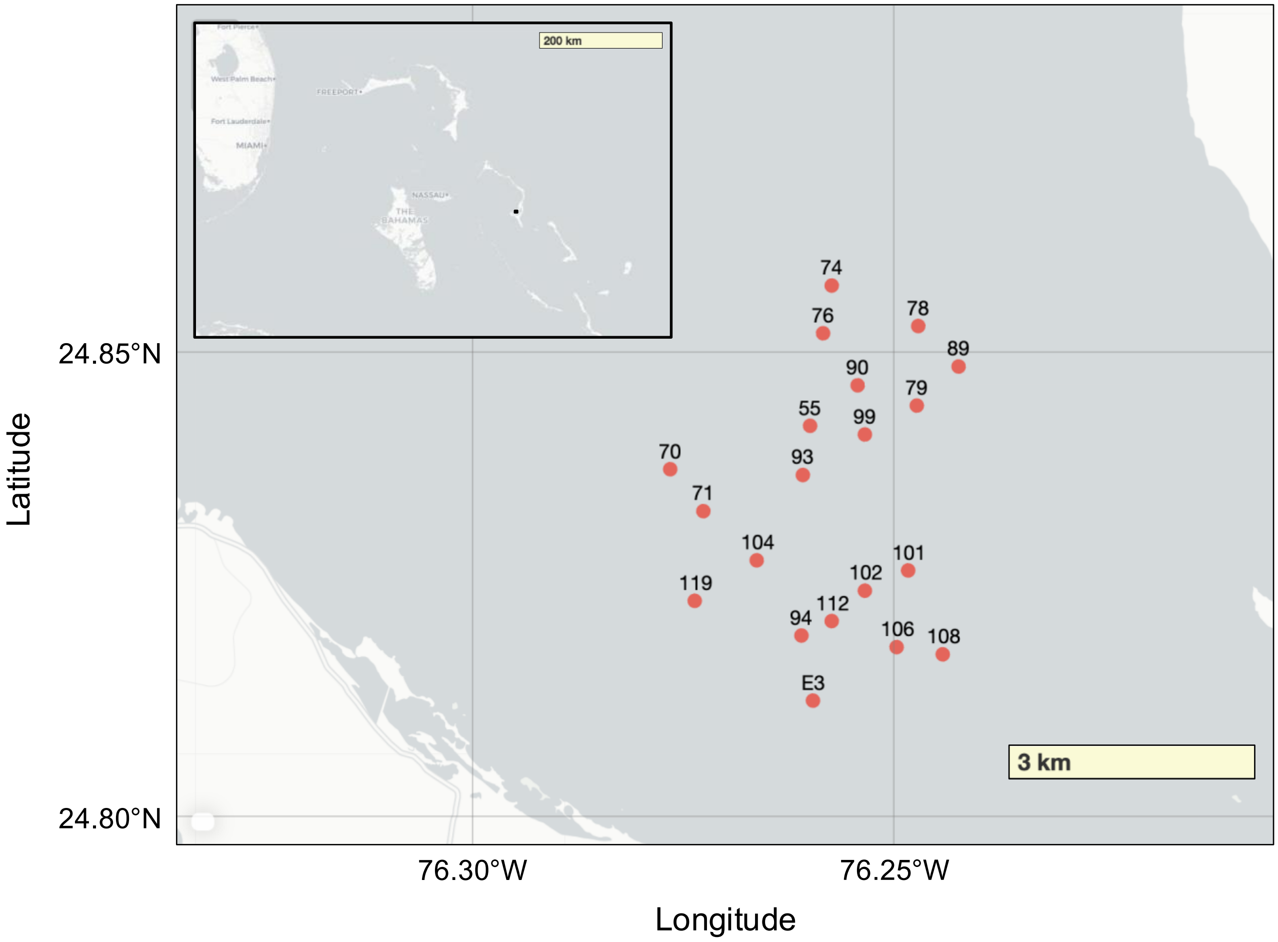


Figure 2. Coefficient plots of top fish biomass GLMMs. Y-axis labels indicate the stressors present in the top model and plot titles indicate the response variable used in the model. All models utilized log-transformed biomass as the response variable. Points indicate the estimated effect size of each stressor with tails representing the 95% confidence interval around this estimate. All stressor effects shown were significant in top models at an alpha value of 0.05. Values in brackets to the right of each effect show the sample size per model, calculated as the total number of surveys conducted. A. total fish biomass, B. grouper biomass, C. prey fish biomass (any fish ≤5 cm TL, excluding lionfish and grouper), D. non-prey fish biomass (any fish >5 cm TL, excluding lionfish and grouper), E. corallivorous fish biomass and F. herbivorous fish biomass.

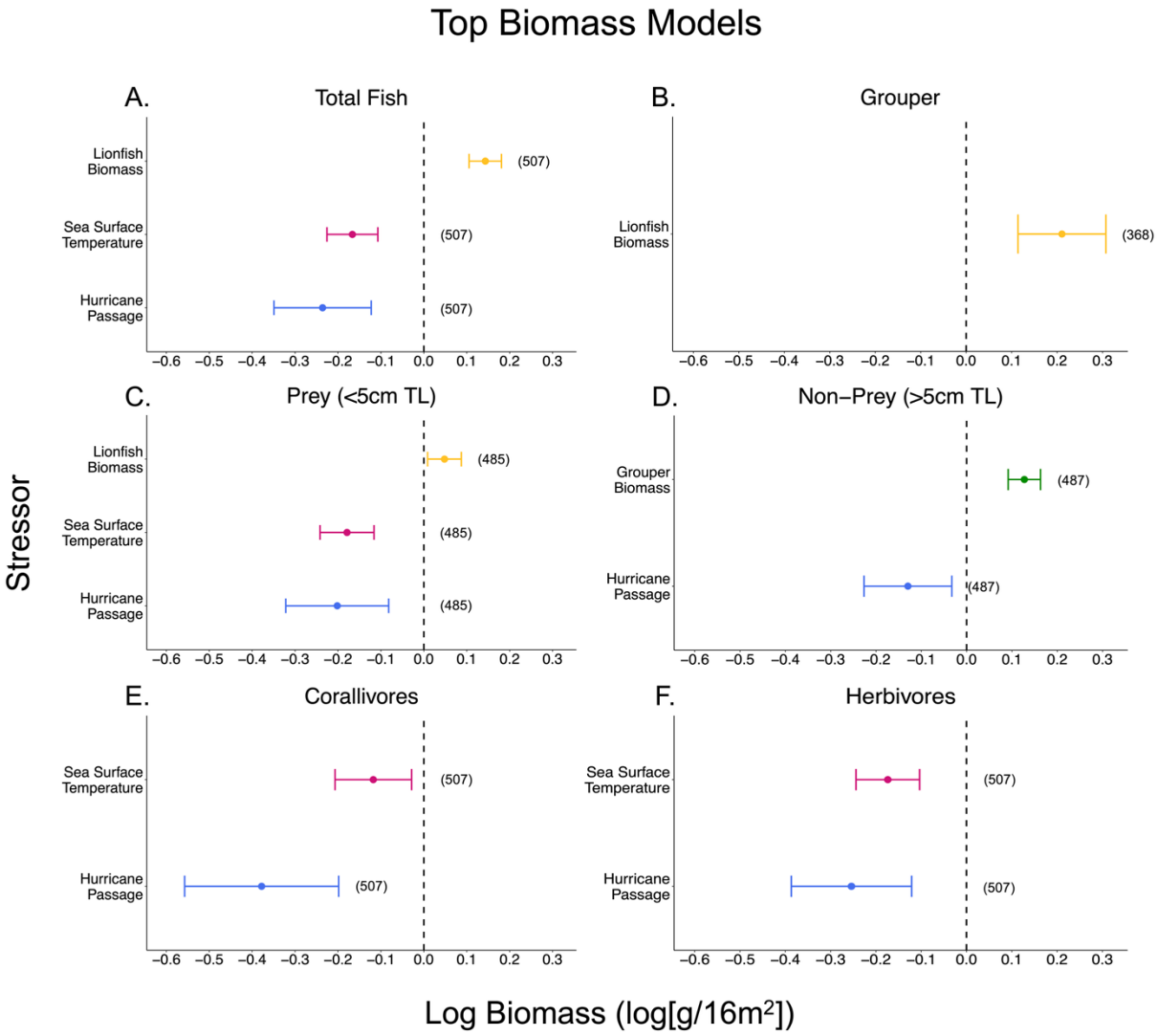


Figure 3. Coefficient plots of top fish species richness GLMMs. Y-axis labels indicate the stressors present in the top model and plot titles indicate the response variable used in the model. Points indicate the estimated effect size of each stressor with tails representing the 95% confidence interval around this estimate. All stressor effects shown were significant in top models at an alpha value of 0.05. Values in brackets to the right of each effect show the sample size per model, calculated as total number of surveys conducted. A. total fish species richness, B. prey fish species richness (any fish ≤5 cm TL, excluding lionfish and grouper) and C. non-prey fish species richness (any fish >5 cm TL, excluding lionfish and grouper).

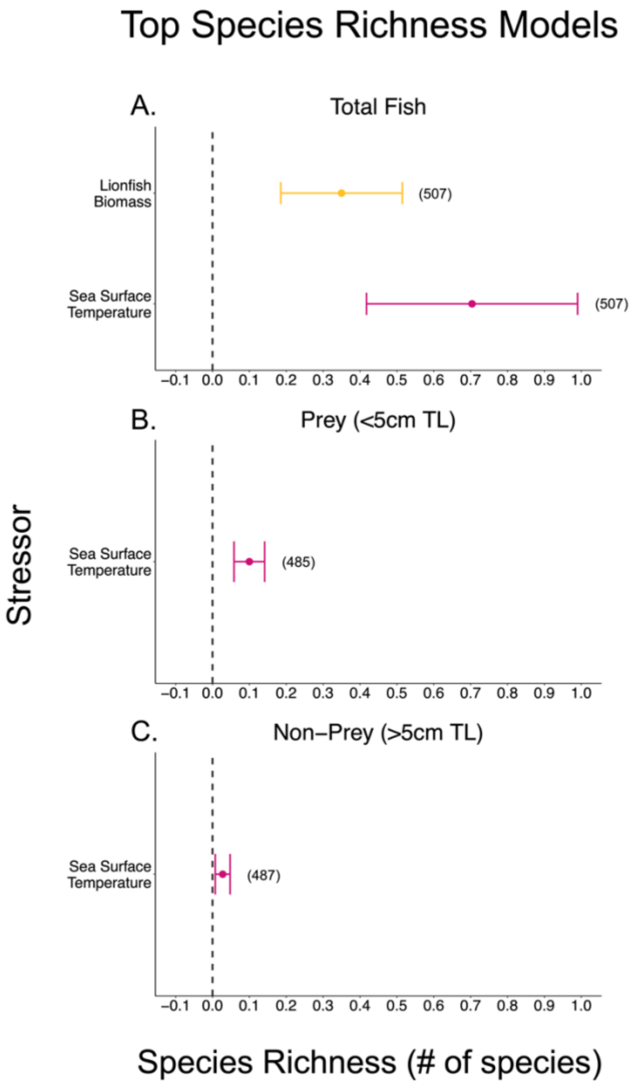


Figure 4. Changes in fish species composition of Bahamian patch reef sites between 2011 and 2024. A. the metacommunity network of patch reefs at a connectivity threshold of 0.02 decimal degrees with nodes (sites) coloured by Jaccard dissimilarity index values comparing community assemblages from belt transect surveys performed in 2011 and 2024. B. PCoA ordination plot showing the community composition of each site in 2011 compared to 2024. The distance between site points in 2011 compared to 2024 indicates their relative dissimilarity in species composition. Points are coloured by site, with circular points showing 2011 compositions and triangles showing 2024 compositions. Ellipses denote the confidence region around the centroid of each survey period based on a multivariate t-distribution and are patterned by survey period, with the solid ellipse showing 2011 surveys and the dashed ellipse showing 2024 surveys.

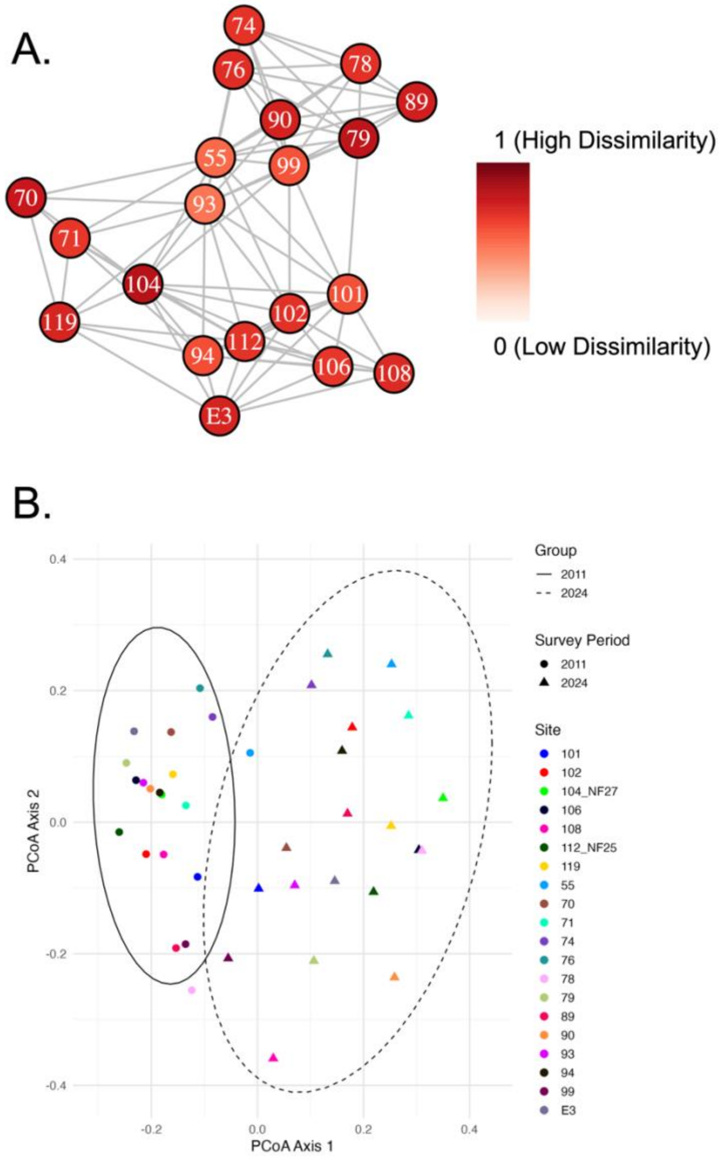


Figure 5. Changes in fish species composition of Bahamian patch reef sites between pre- and post-hurricane surveys. A. the metacommunity network of patch reefs at a connectivity threshold of 0.02 decimal degrees with nodes (sites) coloured by Jaccard dissimilarity index values comparing community assemblages from belt transect surveys performed in the year prior to Hurricane Irene in August 2011 and the year following Hurricane Sandy in 2012. B. PCoA ordination plot showing the community composition of each site in pre-hurricane surveys compared to post-hurricane. The distance between site points pre-hurricane compared to post-hurricane indicates their relative dissimilarity in species composition. Points are coloured by site, with circular points showing pre-hurricane compositions and triangles showing post-hurricane compositions. Ellipses denote the confidence region around the centroid of each survey period based on a multivariate t-distribution and are patterned by survey period, with the solid ellipse showing pre-hurricane surveys and the dashed ellipse showing post-hurricane surveys.

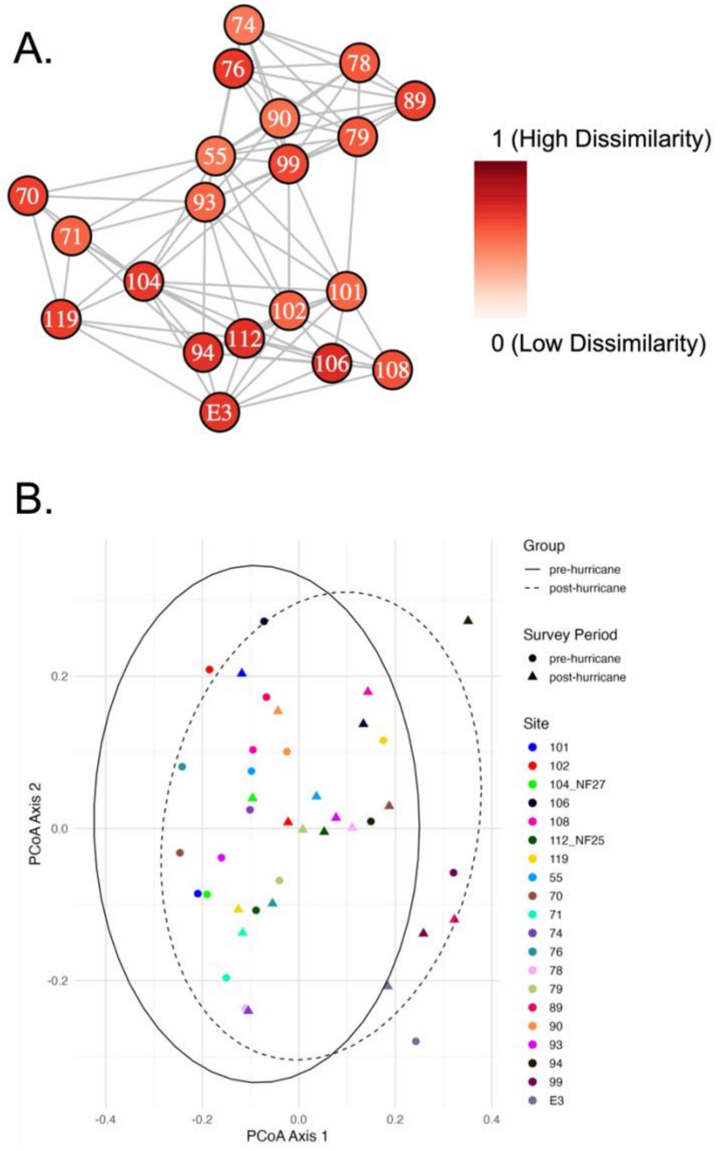


Figure 6. Correlation between patch reef metacommunity network metrics and Jaccard dissimilarity for fish species composition in 2011 compared to 2024 belt transect surveys. The network contains 20 total nodes, one per patch reef site surveyed. A connectivity threshold of 0.02 was utilized to calculate all network metrics. A. Jaccard dissimilarity vs. betweenness centrality of each node and B. Jaccard dissimilarity vs. closeness centrality of each node. The rho and *p*-value of the corresponding rank Spearman correlation test are reported in the figure boxes.

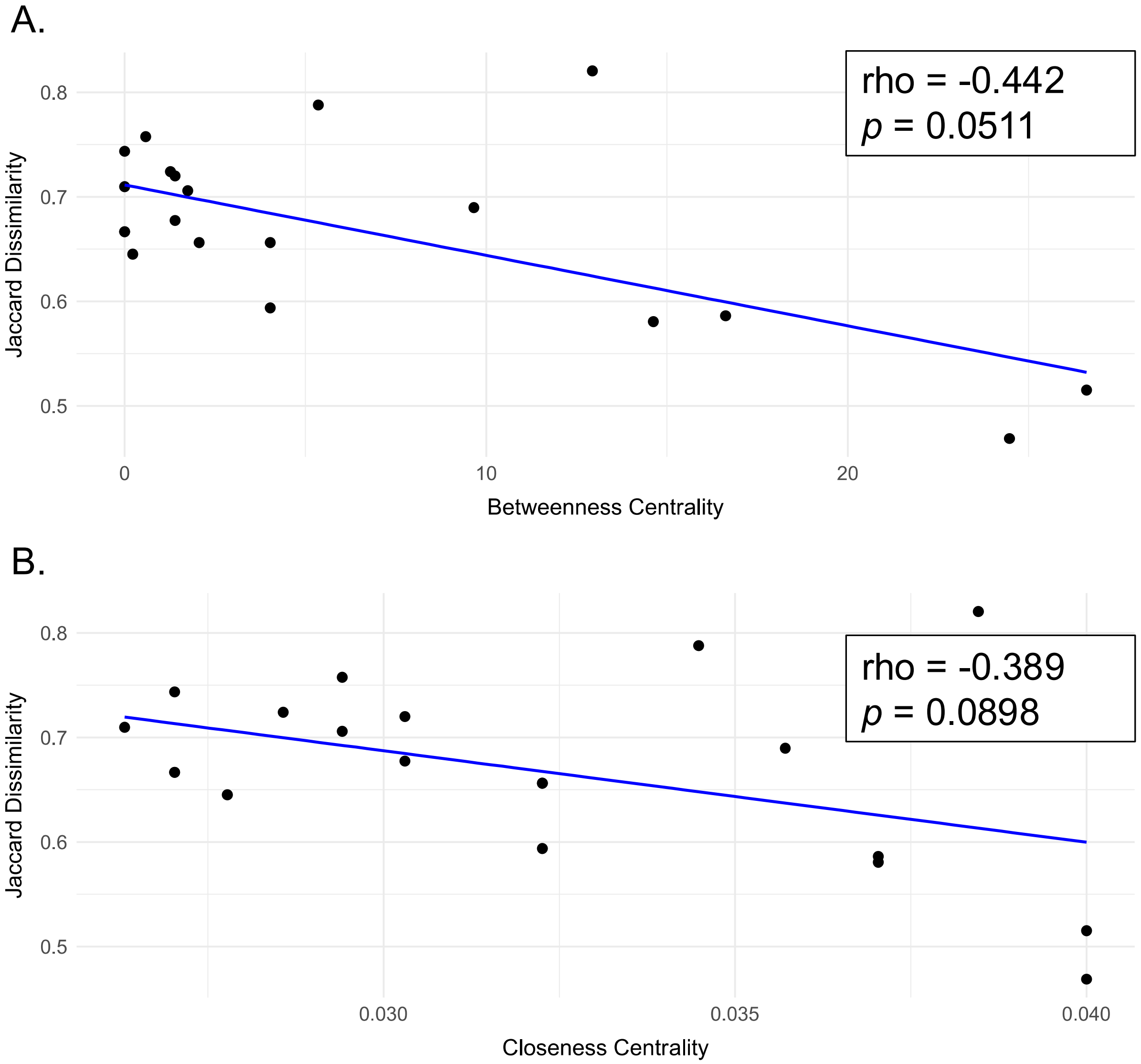
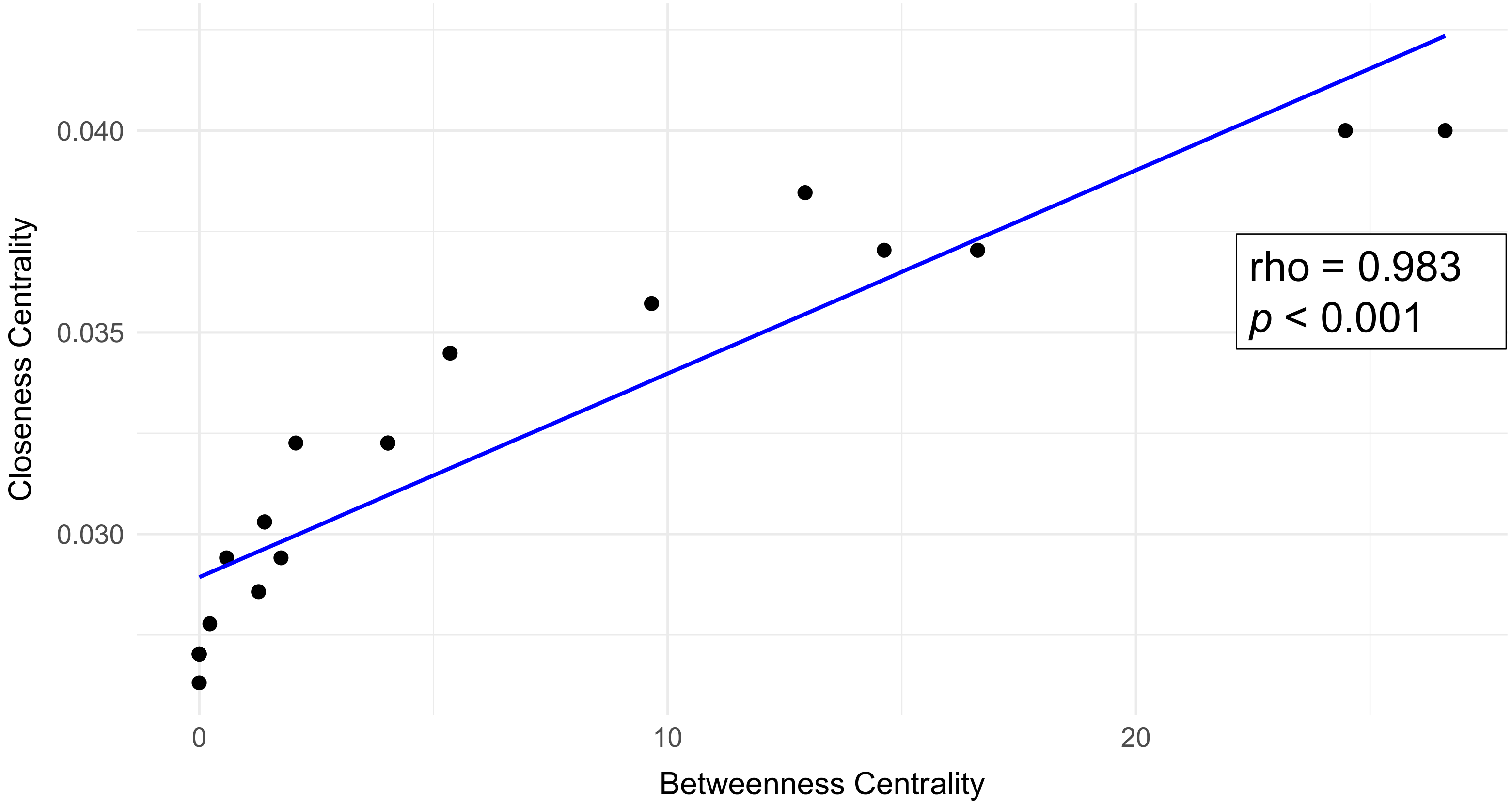


Figure 7. Relationship between betweenness centrality and closeness centrality of each network node at a connectivity threshold value of 0.02. The network contains 20 total nodes, one per patch reef site surveyed. The rho and *p*-value of the corresponding rank Spearman correlation test are reported in the figure box.



References

Adams A (2001) Effects of a hurricane on two assemblages of coral reef fishes: Multiple-year analysis reverses a false “snapshot” interpretation. Bull Mar Sci 69:341–356

Albins MA (2015) Invasive Pacific lionfish *Pterois volitans* reduce abundance and species richness of native Bahamian coral-reef fishes. Mar Ecol Prog Ser 522:231–243. https://doi.org/10.3354/meps11159

Allgeier JE, Layman CA, Mumby PJ, Rosemond AD (2014) Consistent nutrient storage and supply mediated by diverse fish communities in coral reef ecosystems. Glob Change Biol 20:2459–2472. https://doi.org/10.1111/gcb.12566

Alonso-Domínguez A, Ayón-Parente M, Ríos-Jara E, et al (2025) Gamma diversity partitioning of Pocillopora coral-associated crustaceans in the Mexican Central Pacific. Community Ecol. https://doi.org/10.1007/s42974-025-00251-8

Altermatt F, Bieger A, Carrara F, et al (2011) Effects of connectivity and recurrent local disturbances on community structure and population density in experimental metacommunities. PloS One 6:e19525. https://doi.org/10.1371/journal.pone.0019525

Anderson MJ, Ellingsen KE, McArdle BH (2006) Multivariate dispersion as a measure of beta diversity. Ecol Lett 9:683–693. https://doi.org/10.1111/j.1461-0248.2006.00926.x

Aguilar-Perera A, Hernández-Landa RC (2022) Variation in body length, length-weight relationship, and condition factor of lionfish (*Pterois volitans*) between years in a mesophotic coral ecosystem in Alacranes Reef, southern Gulf of Mexico. CJoS 52:142–151. https://doi.org/10.18475/cjos.v52i2.a1

Anton A, Simpson MS, Vu I (2014) Environmental and biotic correlates to lionfish invasion success in Bahamian coral reefs. PLoS ONE 9:e106229. https://doi.org/10.1371/journal.pone.0106229

Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. Estuar Coast Shelf Sci 80:435–471. https://doi.org/10.1016/j.ecss.2008.09.003

Ban SS, Graham NAJ, Connolly SR (2014) Evidence for multiple stressor interactions and effects on coral reefs. Glob Change Biol 20:681–697. https://doi.org/10.1111/gcb.12453

Beeden R, Maynard J, Puotinen M, et al (2015) Impacts and recovery from severe tropical cyclone Yasi on the Great Barrier Reef. PLOS ONE 10:e0121272. https://doi.org/10.1371/journal.pone.0121272

Beets J, Hixon MA (1994) Distribution, persistence, and growth of groupers (Pisces: Serranidae) on artificial and natural patch reefs in the Virgin Islands. Bull Mar Sci 55:470–483

Bernard ATF, Götz A, Kerwath SE, Wilke CG (2013) Observer bias and detection probability in underwater visual census of fish assemblages measured with independent double-observers. J Exp Mar Biol Ecol 443:75–84. https://doi.org/10.1016/j.jembe.2013.02.039

Betancur-R. R, Hines A, Acero P. A, et al (2011) Reconstructing the lionfish invasion: insights into Greater Caribbean biogeography: Reconstructing the lionfish invasion. J Biogeogr 38:1281–1293. https://doi.org/10.1111/j.1365-2699.2011.02496.x

Bodin Ö, Norberg J (2007) A network approach for analyzing spatially structured populations in fragmented landscape. Landsc Ecol 22:31–44. https://doi.org/10.1007/s10980-006-9015-0

Bove CB, Mudge L, Bruno JF (2022) A century of warming on Caribbean reefs. PLOS Clim 1:e0000002. https://doi.org/10.1371/journal.pclm.0000002

Brandes U (2001) A faster algorithm for betweenness centrality. J Math Sociol 25:163–177. https://doi.org/10.1080/0022250x.2001.9990249

Brooks ME, Kristensen K, Benthem KJ van, et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400

Bruno JF, Sweatman H, Precht WF, et al (2009) Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology 90:1478–1484. https://doi.org/10.1890/08-1781.1

Burke L, Reytar K, Spalding M, Perry A (2011) Reefs at risk revisited. World Resources Institute, Washington, D.C., United States

Burnham KP, Anderson DR (2004) Model selection and multimodel inference. Springer, New York, NY

Cangialosi J, Chen S (2004) A numerical study of the topographic effects on the structure and rainfall in Hurricane Georges (1998). In: Session 13D, Tropical cyclones at landfall II

Chase JM, Jeliazkov A, Ladouceur E, Viana DS (2020) Biodiversity conservation through the lens of metacommunity ecology. Ann N Y Acad Sci 1469:86–104. https://doi.org/10.1111/nyas.14378

Chaudhary C, Richardson AJ, Schoeman DS, Costello MJ (2021) Global warming is causing a more pronounced dip in marine species richness around the equator. Proc Natl Acad Sci 118:e2015094118. https://doi.org/10.1073/pnas.2015094118

Cheung WWL, de Mitcheson YS, Braynen MT, Gittens LG (2013) Are the last remaining Nassau grouper *Epinephelus striatus* fisheries sustainable? Status quo in the Bahamas. Endanger Species Res 20:27–39. https://doi.org/10.3354/esr00472

Chong-Seng KM, Mannering TD, Pratchett MS, et al (2012) The influence of coral reef benthic condition on associated fish assemblages. PLOS ONE 7:e42167. https://doi.org/10.1371/journal.pone.0042167

Coker DJ, Wilson SK, Pratchett MS (2014) Importance of live coral habitat for reef fishes. Rev Fish Biol Fish 24:89–126. https://doi.org/10.1007/s11160-013-9319-5

Côté IM, Green SJ (2012) Potential effects of climate change on a marine invasion: The importance of current context. Curr Zool 58:1–8. https://doi.org/10.1093/czoolo/58.1.1

Côté IM, Green SJ, Hixon MA (2013) Predatory fish invaders: Insights from Indo-Pacific lionfish in the western Atlantic and Caribbean. Biol Conserv 164:50–61. https://doi.org/10.1016/j.biocon.2013.04.014

Côté IM, Smith NS (2018) The lionfish *Pterois* sp. invasion: Has the worst-case scenario come to pass? J Fish Biol 92:660–689. https://doi.org/10.1111/jfb.13544

Crain CM, Kroeker K, Halpern BS (2008) Interactive and cumulative effects of multiple human stressors in marine systems. Ecol Lett 11:1304–1315. https://doi.org/10.1111/j.1461-0248.2008.01253.x

Csárdi G, Nepusz T, Müller K, et al (2025) igraph for R: R interface of the igraph library for graph theory and network analysis

Curtis JS, Wall KR, Albins MA, Stallings CD (2017) Diet shifts in a native mesopredator across a range of invasive lionfish biomass. Mar Ecol Prog Ser 573:215–228. https://doi.org/10.3354/meps12164

Dahlgren CP, Buch K, Rechisky E, Hixon MA (2016) Multiyear tracking of Nassau grouper spawning migrations. Mar Coast Fish 8:522–535. https://doi.org/10.1080/19425120.2016.1223233

Darling ES, Graham NAJ, Januchowski-Hartley FA, et al (2017) Relationships between structural complexity, coral traits, and reef fish assemblages. Coral Reefs 36:561–575. https://doi.org/10.1007/s00338-017-1539-z

Donovan MK, Friedlander AM, Lecky J, et al (2018) Combining fish and benthic communities into multiple regimes reveals complex reef dynamics. Sci Rep 8:16943. https://doi.org/10.1038/s41598-018-35057-4

Dudgeon S, Aronson R, Bruno J, Precht W (2010) Phase shifts and stable states on coral reefs. Mar Ecol Prog Ser 413:201–216. https://doi.org/10.3354/meps08751

Dunne JA, Williams RJ, Martinez ND (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecol Lett 5:558–567. https://doi.org/10.1046/j.1461-0248.2002.00354.x

Eriksson A, Elías-Wolff F, Mehlig B, Manica A (2014) The emergence of the rescue effect from explicit within- and between-patch dynamics in a metapopulation. Proc R Soc B Biol Sci 281:20133127. https://doi.org/10.1098/rspb.2013.3127

Feary DA, Cinner JE, Graham NAJ, Januchowski-Hartley FA (2010) Effects of customary marine closures on fish behavior, spear-fishing success, and underwater visual surveys: Customary closure effects. Conserv Biol no-no. https://doi.org/10.1111/j.1523-1739.2010.01613.x

Figueira WF (2009) Connectivity or demography: Defining sources and sinks in coral reef fish metapopulations. Ecol Model 220:1126–1137. https://doi.org/10.1016/j.ecolmodel.2009.01.021

Fox J, Weisberg S (2019) An R companion to applied regression. Sage Publications, Thousand Oaks

Francis FT, Côté IM (2018) Fish movement drives spatial and temporal patterns of nutrient provisioning on coral reef patches. Ecosphere 9:e02225. https://doi.org/10.1002/ecs2.2225

Freeman LC (1978) Centrality in social networks conceptual clarification. Soc Netw 1:215–239. https://doi.org/10.1016/0378-8733(78)90021-7

Froese R, Pauly D (2025) FishBase. https://fishbase.de/. Accessed 15 Jun 2025

Froese R, Thorson JT, Reyes Jr RB (2014) A Bayesian approach for estimating length-weight relationships in fishes. J Appl Ichthyol 30:78–85. https://doi.org/10.1111/jai.12299

Frölicher TL, Fischer EM, Gruber N (2018) Marine heatwaves under global warming. Nature 560:360–364. https://doi.org/10.1038/s41586-018-0383-9

Gardner TA, Côté IM, Gill JA, et al (2005) Hurricanes and Caribbean coral reefs: Impacts, recovery patterns, and role in long-term decline. Ecology 86:174–184. https://doi.org/10.1890/04-0141

Gleason ACR, Lirman D, Williams D, et al (2007) Documenting hurricane impacts on coral reefs using two-dimensional video-mosaic technology. Mar Ecol 28:254–258. https://doi.org/10.1111/j.1439-0485.2006.00140.x

Google (2025) Google Maps. https://www.google.com/maps. Accessed 20 Feb 2025

Graham NAJ, Nash KL (2013) The importance of structural complexity in coral reef ecosystems. Coral Reefs 32:315–326. https://doi.org/10.1007/s00338-012-0984-y

Graham NAJ, Wilson SK, Pratchett MS, et al (2009) Coral mortality versus structural collapse as drivers of corallivorous butterflyfish decline. Biodivers Conserv 18:3325–3336. https://doi.org/10.1007/s10531-009-9633-3

Green AL, Maypa AP, Almany GR, et al (2015) Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. Biol Rev 90:1215–1247. https://doi.org/10.1111/brv.12155

Green SJ, Akins JL, Maljković A, Côté IM (2012) Invasive lionfish drive Atlantic coral reef Fish declines. PLoS ONE 7:e32596. https://doi.org/10.1371/journal.pone.0032596

Green SJ, Côté IM (2014) Trait-based diet selection: Prey behaviour and morphology predict vulnerability to predation in reef fish communities. J Anim Ecol 83:1451–1460. https://doi.org/10.1111/1365-2656.12250

Green SJ, Tamburello N, Miller SE, et al (2013) Habitat complexity and fish size affect the detection of Indo-Pacific lionfish on invaded coral reefs. Coral Reefs 32:413–421. https://doi.org/10.1007/s00338-012-0987-8

Grieve B, Curchitser E, Rykaczewski R (2016) Range expansion of the invasive lionfish in the Northwest Atlantic with climate change. Mar Ecol Prog Ser 546:225–237. https://doi.org/10.3354/meps11638

Hackerott S, Valdivia A, Green SJ, et al (2013) Native predators do not influence invasion success of Pacific lionfish on Caribbean reefs. PLOS ONE 8:e68259. https://doi.org/10.1371/journal.pone.0068259

Harmelin-Vivien M, Harmelin JG (2022) Feeding biology of groupers. In: Biology and ecology of groupers. CRC Press

Harmelin-Vivien ML (1994) The effects of storms and cyclones on coral reefs: A review. J Coast Res 211–231

Hellmann JJ, Byers JE, Bierwagen BG, Dukes JS (2008) Five potential consequences of climate change for invasive species. Conserv Biol 22:534–543. https://doi.org/10.1111/j.1523-1739.2008.00951.x

Hiddink JG, Ter Hofstede R (2008) Climate induced increases in species richness of marine fishes. Glob Change Biol 14:453–460. https://doi.org/10.1111/j.1365-2486.2007.01518.x

Hill MJ, Heino J, Thornhill I, et al (2017) Effects of dispersal mode on the environmental and spatial correlates of nestedness and species turnover in pond communities. Oikos 126:1575–1585. https://doi.org/10.1111/oik.04266

Hillebrand H, Blasius B, Borer ET, et al (2018) Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. J Appl Ecol 55:169–184. https://doi.org/10.1111/1365-2664.12959

Hobday AJ, Alexander LV, Perkins SE, et al (2016) A hierarchical approach to defining marine heatwaves. Prog Oceanogr 141:227–238. https://doi.org/10.1016/j.pocean.2015.12.014

Hock K, Wolff NH, Condie SA, et al (2014) Connectivity networks reveal the risks of crown-of-thorns starfish outbreaks on the Great Barrier Reef. J Appl Ecol 51:1188–1196. https://doi.org/10.1111/1365-2664.12320

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshw Res. https://doi.org/10.1071/MF99078

Holland G, Bruyère CL (2014) Recent intense hurricane response to global climate change. Clim Dyn 42:617–627. https://doi.org/10.1007/s00382-013-1713-0

Hourigan TF, Timothy CT, Reese ES (1988) Coral reef fishes as indicators of environmental stress in coral reefs. In: Soule DF, Kleppel GS (eds) Marine organisms as indicators. Springer, New York, NY, pp 107–135

Hubbell SP (2011) The unified neutral theory of biodiversity and biogeography. Princeton University Press

Humphries MD, Gurney K (2008) Network "small-world-ness": a quantitative method for determining canonical network equivalence. PloS One 3:e0002051. https://doi.org/10.1371/journal.pone.0002051

Jaccard P (1900) Contributions au problème de l'immigration post-glaciaire de la flore alpine. Bull Société Vaudoise Sci Nat 37:547–479

Jones GP, Almany GR, Russ GR, et al (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral Reefs 28:307–325. https://doi.org/10.1007/s00338-009-0469-9

Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. Proc Natl Acad Sci 101:8251–8253. https://doi.org/10.1073/pnas.0401277101

Khan JA, Goatley CHR, Brandl SJ, et al (2017) Shelter use by large reef fishes: long-term occupancy and the impacts of disturbance. Coral Reefs 36:1123–1132. https://doi.org/10.1007/s00338-017-1604-7

Knowlton N (1992) Thresholds and multiple stable states in coral reef community dynamics. Am Zool 32:674–682

Lassig BR (1983) The effects of a cyclonic storm on coral reef fish assemblages. Environ Biol Fishes 9:55–63. https://doi.org/10.1007/BF00001058

Leggat WP, Camp EF, Suggett DJ, et al (2019) Rapid coral decay is associated with marine heatwave mortality events on reefs. Curr Biol 29:2723-2730.e4. https://doi.org/10.1016/j.cub.2019.06.077

Leibold MA, Holyoak M, Mouquet N, et al (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecol Lett 7:601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Lesser MP (2006) Oxidative stress in marine environments: Biochemistry and physiological ecology. Annu Rev Physiol 68:253–278. https://doi.org/10.1146/annurev.physiol.68.040104.110001

Letourneur Y, Harmelin-Vivien M, Galzin R (1993) Impact of hurricane Firinga on fish community structure on fringing reefs of Reunion Island, S.W. Indian Ocean. Environ Biol Fishes 37:109–120. https://doi.org/10.1007/BF00000586

Lin Y, Wiegand K (2023) Low R^2 in ecology: Bitter, or B-side? Ecol Indic 153:110406. https://doi.org/10.1016/j.ecolind.2023.110406

Lloyd P, Plagányi ÉE, Weeks SJ, et al (2012) Ocean warming alters species abundance patterns and increases species diversity in an African sub-tropical reef-fish community. Fish Oceanogr 21:78–94. https://doi.org/10.1111/j.1365-2419.2011.00610.x

Lockwood JL, Hoopes MF, Marchetti MP (2013) Invasion Ecology, 2nd edn. Wiley-Blackwell, Hoboken, New Jersey, United States

Lüdecke D, Ben-Shachar MS, Patil I, et al (2021) performance: An R package for assessment, comparison and testing of statistical models. J Open Source Softw 6:3139. https://doi.org/10.21105/joss.03139

MacNeil MA, Graham NAJ, Polunin NVC, et al (2009) Hierarchical drivers of reef-fish metacommunity structure. Ecology 90:252–264. https://doi.org/10.1890/07-0487.1

Madden IA, Mariwala A, Lindhart M, et al (2023) Quantifying the fragility of coral reefs to hurricane impacts: a case study of the Florida Keys and Puerto Rico. Environ Res Lett 18:024034. https://doi.org/10.1088/1748-9326/acb451

Magel JMT, Burns JHR, Gates RD, Baum JK (2019) Effects of bleaching-associated mass coral mortality on reef structural complexity across a gradient of local disturbance. Sci Rep 9:2512. https://doi.org/10.1038/s41598-018-37713-1

Magel JMT, Dimoff SA, Baum JK (2020) Direct and indirect effects of climate change-amplified pulse heat stress events on coral reef fish communities. Ecol Appl 30:e02124. https://doi.org/10.1002/eap.2124

Mainka SA, Howard GW (2010) Climate change and invasive species: double jeopardy. Integr Zool 5:102–111. https://doi.org/10.1111/j.1749-4877.2010.00193.x

Maureaud A, Hodapp D, van Denderen PD, et al (2019) Biodiversity–ecosystem functioning relationships in fish communities: biomass is related to evenness and the environment, not to species richness. Proc R Soc B Biol Sci 286:20191189. https://doi.org/10.1098/rspb.2019.1189

Mausbach WE, Dzialowski AR (2019) Dispersal mitigates biologically induced disturbances in heterogeneous metacommunities. Ecosphere 10:e02662. https://doi.org/10.1002/ecs2.2662

McLaughlin ÓB, Emmerson MC, O'Gorman EJ (2013) Chapter four - Habitat isolation reduces the temporal stability of island ecosystems in the face of flood disturbance. In: Woodward G, O'Gorman EJ (eds) Advances in ecological research. Academic Press, pp 225–284

McManus JW, Polsenberg JF (2004) Coral–algal phase shifts on coral reefs: Ecological and environmental aspects. Prog Oceanogr 60:263–279. https://doi.org/10.1016/j.pocean.2004.02.014

Meyer JL, Schultz ET, Helfman GS (1983) Fish schools: An asset to corals. Science 220:1047–1049. https://doi.org/10.1126/science.220.4601.1047

Moberg F, Folke C (1999) Ecological goods and services of coral reef ecosystems. Ecol Econ 29:215–233. https://doi.org/10.1016/S0921-8009(99)00009-9

Morris JJr, Whitfield P (2009) Biology, ecology, control and management of the invasive Indo-Pacific lionfish: an updated integrated assessment. NOAA

Mouquet N, Loreau M (2003) Community patterns in source-sink metacommunities. Am Nat 162:544–557. https://doi.org/10.1086/378857

Mumby PJ, Hastings A (2008) The impact of ecosystem connectivity on coral reef resilience. J Appl Ecol 45:854–862. https://doi.org/10.1111/j.1365-2664.2008.01459.x

Munday PL, Jones GP, Pratchett MS, Williams AJ (2008) Climate change and the future for coral reef fishes. Fish Fish 9:261–285. https://doi.org/10.1111/j.1467-2979.2008.00281.x

Munday PL, Leis JM, Lough JM, et al (2009) Climate change and coral reef connectivity. Coral Reefs 28:379–395. https://doi.org/10.1007/s00338-008-0461-9

Muscatine L, Porter JW (1977) Reef corals: Mutualistic symbioses adapted to nutrient-poor environments. BioScience 27:454–460. https://doi.org/10.2307/1297526

Muthukrishnan R, Fong P (2014) Multiple anthropogenic stressors exert complex, interactive effects on a coral reef community. Coral Reefs 33:911–921. https://doi.org/10.1007/s00338-014-1199-1

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

NOAA Coral Reef Watch (2025) NOAA coral reef watch daily global 5km satellite sea surface temperature. https://coralreefwatch.noaa.gov/product/5km/. Accessed 5 Feb 2025

NOAA Office for Coastal Management (2025) NOAA Historical Hurricane Tracks. https://coast.noaa.gov/hurricanes/#map=4/32/-80. Accessed 20 Feb 2025

Oey L-Y, Ezer T, Wang D-P, et al (2007) Hurricane-induced motions and interaction with ocean currents. Cont Shelf Res 27:1249–1263. https://doi.org/10.1016/j.csr.2007.01.008

Oksanen J, Simpson GL, Blanchet FG, et al (2001) vegan: Community ecology package. 2.7–1

Oliver ECJ, Donat MG, Burrows MT, et al (2018) Longer and more frequent marine heatwaves over the past century. Nat Commun 9:1324. https://doi.org/10.1038/s41467-018-03732-9

Patonai K, Jordán F, Castaldelli G, et al (2023) Spatial variability of the Po River food web and its comparison with the Danube River food web. PLOS ONE 18:e0288652. https://doi.org/10.1371/journal.pone.0288652

Petrie A (2016) Introduction to Regression and Modeling with R. Cognella, Solana Beach

Pratchett MS, Hoey AS, Wilson SK, et al (2011) Changes in biodiversity and functioning of Reef fish assemblages following coral bleaching and coral loss. Diversity 3:424–452. https://doi.org/10.3390/d3030424

Pratchett MS, Thompson CA, Hoey AS, et al (2018) Effects of coral bleaching and coral loss on the structure and function of reef fish assemblages. In: van Oppen MJH, Lough JM (eds) Coral bleaching: Patterns, processes, causes and consequences. Springer International Publishing, Cham, pp 265–293

Pulliam HR (1988) Sources, sinks, and population regulation. Am Nat 132:652–661. https://doi.org/10.1086/284880

Puotinen M, Drost E, Lowe R, et al (2020) Towards modelling the future risk of cyclone wave damage to the world’s coral reefs. Glob Change Biol 26:4302–4315. https://doi.org/10.1111/gcb.15136

R Core Team (2025) R: A language and environment for statistical computing

Rakhecha PR, Singh VP (2009) Tropical storms and hurricanes. In: Rakhecha PR, Singh VP (eds) Applied hydrometeorology. Springer Netherlands, Dordrecht, pp 126–162

REEF (2025) Reef environmental education foundation volunteer fish survey project database. https://www.reef.org/database-reports. Accessed 25 March 2025

Reid PC, Fischer AC, Lewis-Brown E, et al (2009) Chapter 1 impacts of the oceans on climate change. In: Advances in marine biology. Academic Press, pp 1–150

Rotjan R, Lewis S (2008) Impact of coral predators on tropical reefs. Mar Ecol Prog Ser 367:73–91. https://doi.org/10.3354/meps07531

Roy HE, Pauchard A, Stoett P, et al (2023) IPBES invasive alien species assessment: Summary for policymakers. Zenodo. URL https://zenodo.org/record/7430692

Santini L, Belmaker J, Costello MJ, et al (2017) Assessing the suitability of diversity metrics to detect biodiversity change. Biol Conserv 213:341–350. https://doi.org/10.1016/j.biocon.2016.08.024

Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. Methods Ecol Evol 1:103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x

Schill SR, Raber GT, Roberts JJ, et al (2015) No reef is an island: Integrating coral reef connectivity data into the design of regional-scale marine protected area networks. PLOS ONE 10:e0144199. https://doi.org/10.1371/journal.pone.0144199

Schoepf V, Grottoli AG, Levas SJ, et al (2015) Annual coral bleaching and the long-term recovery capacity of coral. Proc R Soc B Biol Sci 282:20151887. https://doi.org/10.1098/rspb.2015.1887

Schofield P (2009) Geographic extent and chronology of the invasion of non-native lionfish (Pterois volitans [Linnaeus 1758] and P. miles [Bennett 1828]) in the Western North Atlantic and Caribbean Sea. Aquat Invasions 4:473–479. https://doi.org/10.3391/ai.2009.4.3.5

Shlesinger T, van Woesik R (2023) Oceanic differences in coral-bleaching responses to marine heatwaves. Sci Total Environ 871:162113. https://doi.org/10.1016/j.scitotenv.2023.162113

Smith KE, Burrows MT, Hobday AJ, et al (2023) Biological impacts of marine heatwaves. Annu Rev Mar Sci 15:119–145. https://doi.org/10.1146/annurev-marine-032122-121437

Smith NS, Côté IM (2021) Biotic resistance on coral reefs? Direct and indirect effects of native predators and competitors on invasive lionfish. Coral Reefs 40:1127–1136. https://doi.org/10.1007/s00338-021-02117-7

Smith NS, Green SJ, Akins JL, et al (2017) Density-dependent colonization and natural disturbance limit the effectiveness of invasive lionfish culling efforts. Biol Invasions 19:2385–2399. https://doi.org/10.1007/s10530-017-1449-6

Socolar JB, Gilroy JJ, Kunin WE, Edwards DP (2016) How should beta-diversity inform biodiversity conservation? Trends Ecol Evol 31:67–80. https://doi.org/10.1016/j.tree.2015.11.005

Spalding M, Burke L, Wood SA, et al (2017) Mapping the global value and distribution of coral reef tourism. Mar Policy 82:104–113. https://doi.org/10.1016/j.marpol.2017.05.014

Spinks RK, Munday PL, Donelson JM (2019) Developmental effects of heatwave conditions on the early life stages of a coral reef fish. J Exp Biol 222:jeb202713. https://doi.org/10.1242/jeb.202713

Sunday JM, Pecl GT, Frusher S, et al (2015) Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. Ecol Lett 18:944–953. https://doi.org/10.1111/ele.12474

Symonds MRE, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav Ecol Sociobiol 65:13–21. https://doi.org/10.1007/s00265-010-1037-6

Tewksbury JJ, Huey RB, Deutsch CA (2008) Putting the heat on tropical animals. Science 320:1296–1297. https://doi.org/10.1126/science.1159328

Thompson A, Mapstone B (1997) Observer effects and training in underwater visual surveys of reef fishes. Mar Ecol Prog Ser 154:53–63. https://doi.org/10.3354/meps154053

Thompson PL, Rayfield B, Gonzalez A (2017) Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. Ecography 40:98–108. https://doi.org/10.1111/ecog.02558

Urban D, Keitt T (2001) Landscape connectivity: A graph-theoretic perspective. Ecology 82:1205–1218. https://doi.org/10.1890/0012-9658(2001)082[1205:LCAGTP]2.0.CO;2

Van Wert JC, Birnie-Gauvin K, Gallagher J, et al (2024) Despite plasticity, heatwaves are costly for a coral reef fish. Sci Rep 14:13320. https://doi.org/10.1038/s41598-024-63273-8

Vaughan GO, Ripley DM, Mitchell MD, et al (2025) Narrow margins: Aerobic performance and temperature tolerance of coral reef fishes facing extreme thermal variability. Glob Change Biol 31:e70100. https://doi.org/10.1111/gcb.70100

Walsh WJ (1983) Stability of a coral reef fish community following a catastrophic storm. Coral Reefs 2:49–63. https://doi.org/10.1007/BF00304732

Wartenberg R (2012) On the underwater visual census of Western Indian Ocean coral reef fishes. MSc, Rhodes University

Watts DJ, Strogatz SH (1998) Collective dynamics of 'small-world' networks. Nature 393:440–442. https://doi.org/10.1038/30918

West DB (1996) Introduction to graph theory. Prentice Hall, Upper Saddle River, N.J.

White ER, Baskett ML, Hastings A (2021) Catastrophes, connectivity and Allee effects in the design of marine reserve networks. Oikos 130:366–376. https://doi.org/10.1111/oik.07770

Whitfield P, Gardner T, Vives S, et al (2002) Biological invasion of the Indo-Pacific lionfish Pterois volitans along the Atlantic coast of North America. Mar Ecol Prog Ser 235:289–297. https://doi.org/10.3354/meps235289

Wu C-C, Yen T-H, Kuo Y-H, Wang W (2002) Rainfall simulation associated with typhoon Herb (1996) near Taiwan. Part I: The topographic effect. Weather Forecast 17:1001–1015. https://doi.org/10.1175/1520-0434(2003)017<1001:RSAWTH>2.0.CO;2

Wulff JL (1995) Effects of a hurricane on survival and orientation of large erect coral reef sponges. Coral Reefs 14:55–61. https://doi.org/10.1007/BF00304073

Yao C-L, Somero GN (2014) The impact of ocean warming on marine organisms. Chin Sci Bull 59:468–479. https://doi.org/10.1007/s11434-014-0113-0

Yuval M, Pearl N, Tchernov D, et al (2023) Assessment of storm impact on coral reef structural complexity. Sci Total Environ 891:164493. https://doi.org/10.1016/j.scitotenv.2023.164493

Zhang J, Luo Y (2017) Degree centrality, betweenness centrality, and closeness centrality in social network. Atlantis Press, pp 300–303

Supplementary Material

Summary of Belt Transect Survey Data

Table S1. Summary of belt transect survey data used in “Multiple drivers of change on Bahamian coral reefs”. Each year with survey data is provided along with the number of surveys performed that year in brackets. Four survey data sources are provided: Present-Day Data collected in 2024, CEI Data collected by the Cape Eleuthera Institute, Green Data collected by Dr. Stephanie Green at CEI, Green December Data collected by Dr. Stephanie Green at CEI in December of several years, and Côté Data collected by Dr. Isabelle Côté at CEI. The Data Summary column shows the total number of surveys each year contained.

Site	**Present-Day Data**	**CEI Data**	**Green Data**	**Green December Data**	**Côté Data**	**Data Summary**
71	2024 (1)	2011 (3), 2012 (10), 2013 (5), 2014 (3), 2015 (4), 2016 (1)	2009 (2), 2010 (2)	2011(1), 2012 (1)	2011 (1), 2012 (1), 2013 (2), 2014 (2)	2009 (2), 2010 (2), 2011 (5), 2012 (12), 2013 (7), 2014 (5), 2015 (4), 2016 (1), 2024 (1)
102	2024 (1)	2011 (3), 2012 (10), 2013 (5), 2014 (4), 2015 (4), 2016 (1)	2009 (2), 2010 (2), 2011 (1)	2011 (1)	2011 (1), 2013 (2), 2014 (2)	2009 (2), 2010 (2), 2011 (6), 2012 (10), 2013 (7), 2014 (6), 2015 (4), 2016 (1), 2024 (1)
78	2024 (1)	2011 (3), 2012 (10), 2013 (4), 2014 (3), 2015 (4), 2016 (1), 2018 (1)	2009 (2), 2010 (2), 2011 (1)	2011 (1), 2014 (1)	2011 (2), 2013 (2), 2014 (2)	2009 (2), 2010 (2), 2011 (7), 2012 (10), 2013 (6), 2014 (6), 2015 (4), 2016 (1), 2018 (1), 2024 (1)
90	2024 (1)	2011 (3), 2012 (10), 2013 (5), 2014 (4), 2015 (4), 2016 (1)	2009 (2), 2010 (2), 2011 (1)	2011 (1)	2011 (2), 2013 (2)	2009 (2), 2010 (2), 2011 (7), 2012 (10), 2013 (7), 2014 (4), 2015 (4), 2016 (1), 2024 (1)
94	2024 (1)	2011 (4), 2012 (10), 2013 (5), 2014 (4), 2015 (4), 2016 (1)	2009 (2), 2010 (2), 2011 (1)	2011 (1), 2012 (1)	2011 (1), 2012 (1), 2013 (2)	2009 (2), 2010 (2), 2011 (7), 2012 (12), 2013 (7), 2014 (4), 2015 (4), 2016 (1), 2024 (1)

104_NF27	2024 (1)	2011 (4), 2012 (10), 2013 (1)	2009 (2), 2010 (2), 2011 (1)	2011 (1), 2012 (1)	2011 (1), 2012 (1)	2009 (2), 2010 (2), 2011 (7), 2012 (12), 2013 (1), 2024 (1)
112_NF25	2024 (1)	2011 (4), 2012 (10), 2013 (1)	2009 (2), 2010 (2)	2011 (1)	2011 (1)	2009 (2), 2010 (2), 2011 (6), 2012 (10), 2013 (1), 2024 (1)
74	2024 (1)	2011 (4), 2012 (10), 2013 (1)	2009 (2), 2010 (2)	2011 (1)	2011 (2)	2009 (2), 2010 (2), 2011 (7), 2012 (10), 2013 (1), 2024 (1)
93	2024 (1)	2011 (3), 2012 (10), 2013 (1)	2009 (2), 2010 (2), 2011 (1)	2011 (1)	2011 (1)	2009 (2), 2010 (2), 2011 (6), 2012 (10), 2013 (1), 2024 (1)
108	2024 (1)	2011 (2), 2012 (10), 2013 (5), 2014 (4), 2015 (4)	2009 (2), 2010 (2), 2011 (1)	2011 (1)	2011 (1), 2013 (2), 2015 (1), 2016 (1)	2009 (2), 2010 (2), 2011 (5), 2012 (10), 2013 (7), 2014 (4), 2015 (5), 2016 (1), 2024 (1)
119	2024 (1)	2011 (4), 2012 (4), 2014 (4), 2014 (3), 2015 (4), 2016 (1)	NA	2011 (1), 2012 (1)	2011 (1), 2012 (2), 2013 (2), 2014 (2)	2011 (6), 2012 (7), 2013 (2), 2014 (6), 2015 (4), 2016 (1), 2024 (1)
E3	2024 (1)	2011 (3), 2012 (3), 2013 (4), 2014 (3), 2015 (4), 2016 (1), 2018 (1)	NA	2014 (1)	2013 (2), 2014 (3)	2011 (3), 2012 (3), 2013 (6), 2014 (7), 2015 (4), 2016 (1), 2018 (1), 2024 (1)
89	2024 (1)	2011 (3), 2012 (10), 2013 (2), 2014 (3), 2015 (4), 2016 (1), 2018 (1)	2009 (2), 2010 (3), 2011 (1)	2011 (1), 2012 (1), 2014 (1)	2011 (2), 2012 (1), 2014 (2)	2009 (2), 2010 (3), 2011 (7), 2012 (12), 2013 (2), 2014 (6), 2015 (4), 2016 (1), 2018 (1), 2024 (1)
70	2024 (1)	2011 (2), 2012 (10), 2013 (1)	2009 (2), 2010 (2), 2011 (1)	2011 (1), 2012 (1)	2011 (1), 2012 (1)	2009 (2), 2010 (2), 2011 (6), 2012 (12), 2013 (1), 2024 (1)
79	2024 (1)	2011 (3), 2012 (10), 2013 (1)	2009 (2), 2010 (2)	2011 (1)	2011 (1)	2009 (2), 2010 (2), 2011 (5), 2012 (10), 2013 (1), 2024 (1)
55	2024 (1)	2011 (1), 2012 (10), 2013 (1)	2009 (2), 2010 (2), 2011 (1)	2011 (1)	2011 (1)	2009 (2), 2010 (2), 2011 (4), 2012 (10), 2013 (1), 2024 (1)
76	2024 (1)	2011 (5), 2012 (11), 2013 (2)	2009 (2), 2010 (2)	2011 (1)	2011 (1)	2009 (2), 2010 (2), 2011 (7), 2012 (11), 2013 (2), 2024 (1)

106	2024 (1)	2011 (2), 2012 (10), 2013 (2)	2009 (2), 2010 (2), 2011 (1)	2011 (1)	2011 (1), 2012 (1)	2009 (2), 2010 (2), 2011 (5), 2012 (11), 2013 (2), 2024 (1)
99	2024 (1)	2011 (3), 2012 (4), 2013 (4), 2014 (4), 2015 (4), 2016 (1)	NA	2011 (1)	2011 (1), 2013 (2), 2014 (1), 2015 (1)	2011 (5), 2012 (4), 2013 (6), 2014 (5), 2015 (5), 2016 (1), 2024 (1)
101	2024 (1)	2011 (3), 2012 (10), 2013 (1)	2009 (2), 2010 (2), 2011 (1)	2011 (1)	2011 (1)	2009 (2), 2010 (2), 2011 (6), 2012 (10), 2013 (1), 2024 (1)

Summary of R Packages

Table S2. R packages used in study.

Package	**Version**	**Reference**
glmmTMB	1.1.11	Brooks et al. 2017
car	3.1.3	Fox and Weisberg 2019
performance	0.13.0	Lüdecke et al. 2021
AICcmodavg	2.3.4	Mazerolle 2023
Broom.mixed	0.2.9.6	Bolker and Robinson 2018
MuMIn	1.48.4	Bartoń 2010
igraph	2.1.4	Csárdi et al. 2025
vegan	2.6.8	Oksanen et al. 2025
ggplot2	3.5.1	Wickham 2016
leaflet	2.2.2	Cheng et al. 2025
lubridate	1.9.4	Grolemund and Wickham 2011
Reshape2	1.4.4	Wickham 2007

Belt Transect Time Series Data Summary

Figure S1. Average per transect biomass of total fish observed per site per year of the belt transect time series. Values in brackets above each year indicate the total number of patch reef sites surveyed that year. Dotted blue lines indicate years where hurricanes passed near survey sites, with Hurricane Irene passing in August of 2011 and Hurricane Sandy passing in October of 2012.

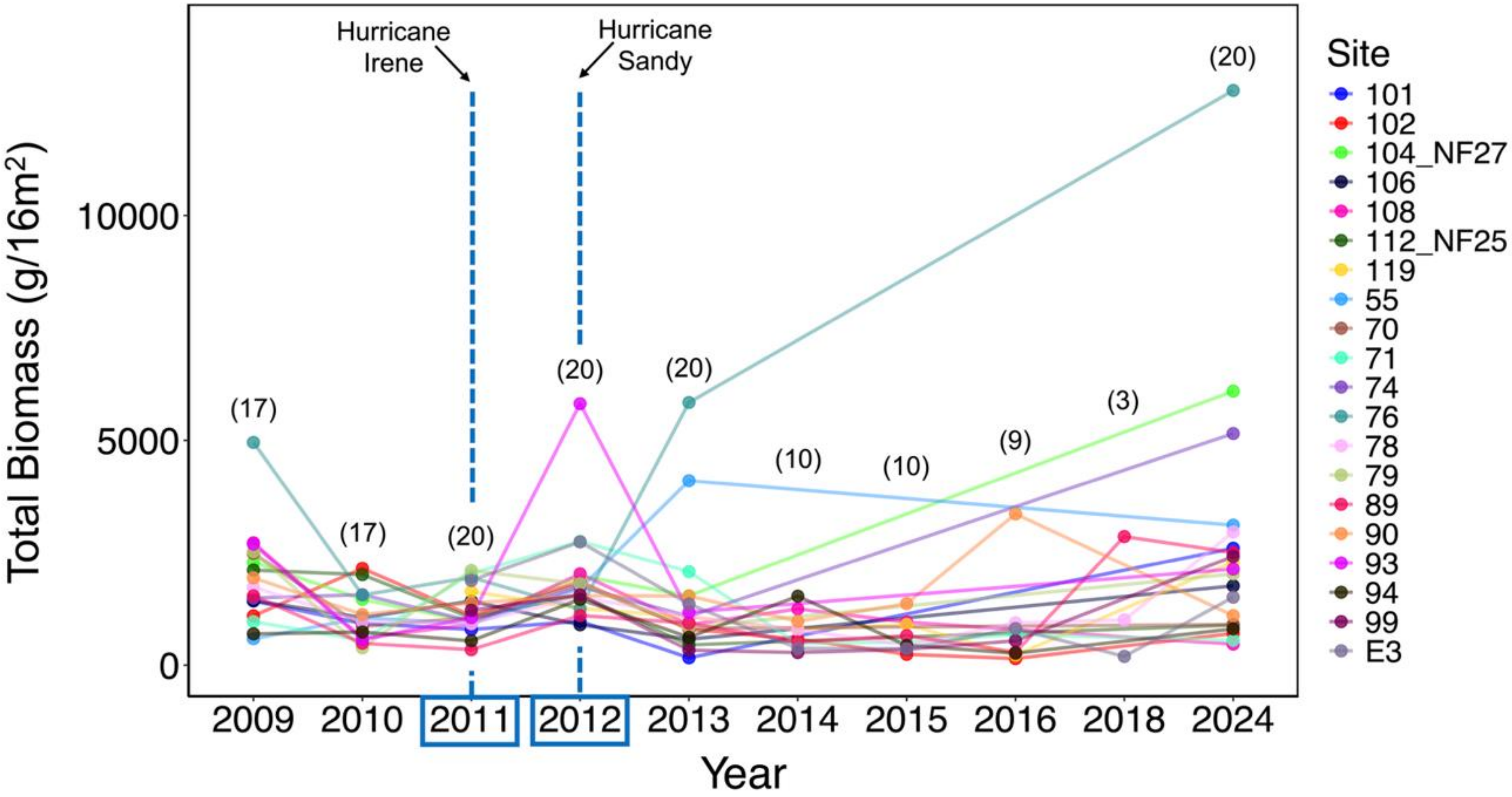


Figure S2. Average per transect biomass of lionfish per site per year of the belt transect time series. Values in brackets above each year indicate the total number of patch reef sites surveyed that year that recorded lionfish. Dotted blue lines indicate years where hurricanes passed near survey sites, with Hurricane Irene passing in August of 2011 and Hurricane Sandy passing in October of 2012.

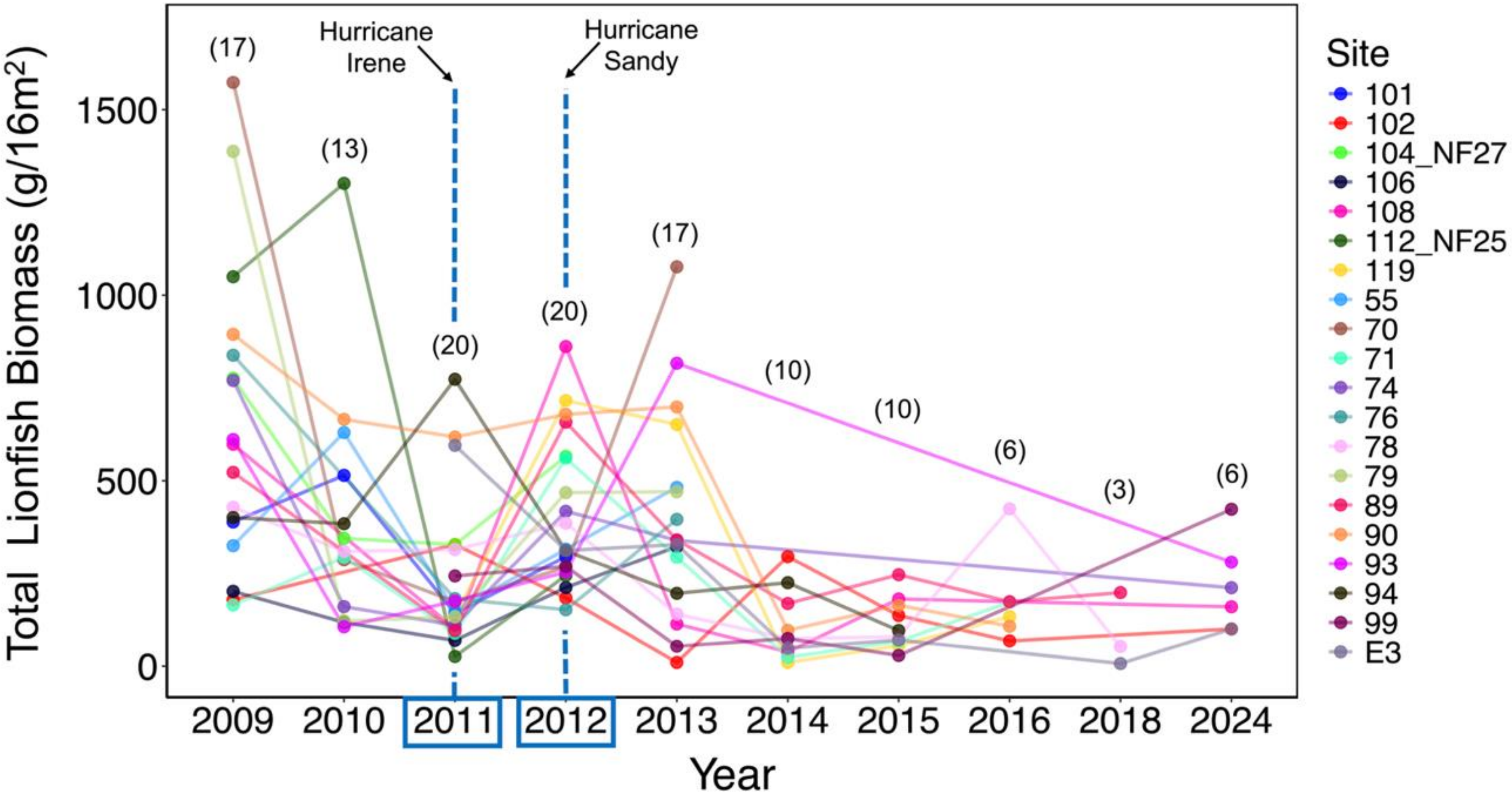
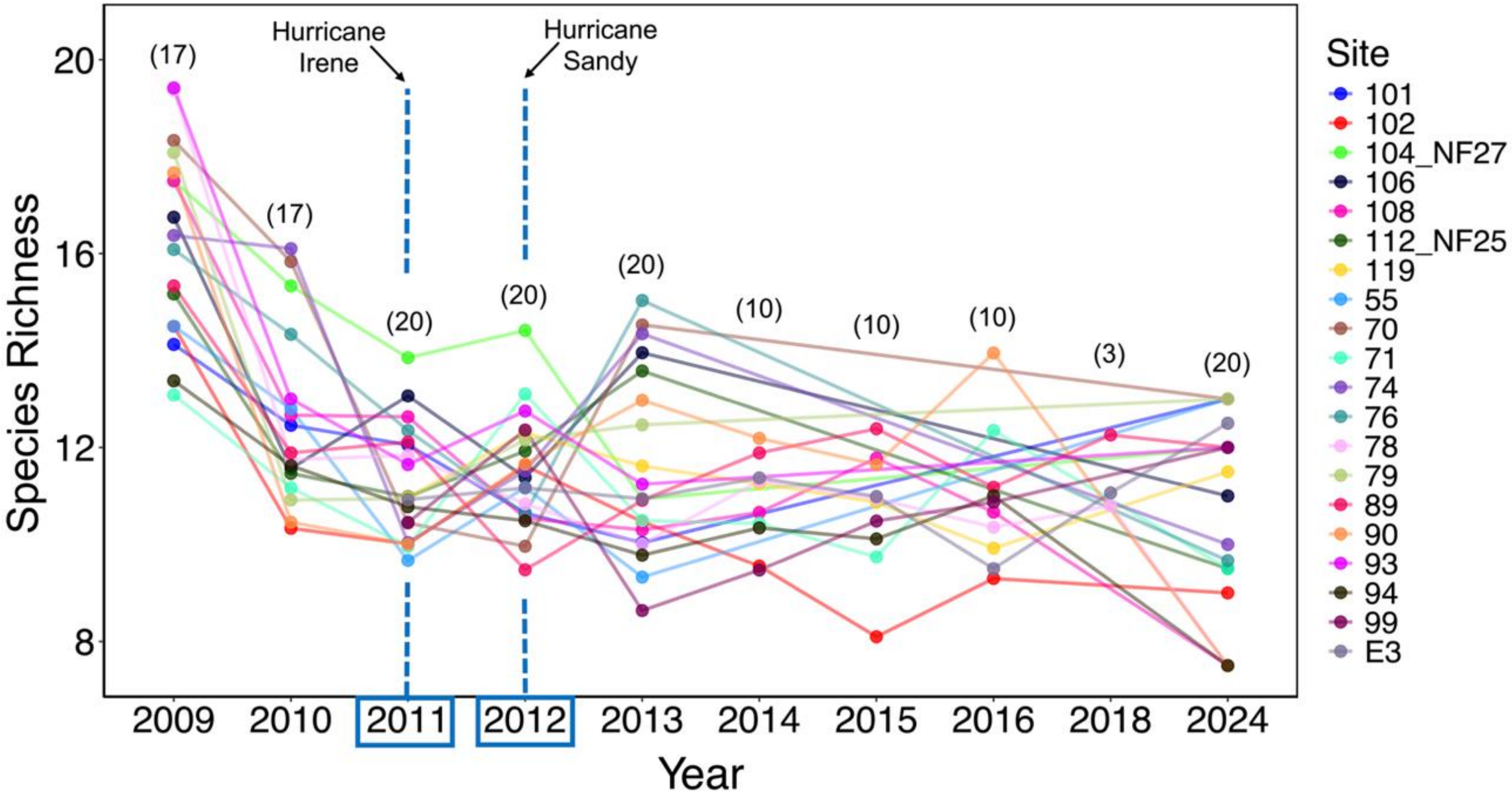


Figure S3. Average per transect fish species richness of total fish observed per site per year of the belt transect time series. Values in brackets above each year indicate the total number of patch reef sites surveyed that year. Dotted blue lines indicate years where hurricanes passed near survey sites, with Hurricane Irene passing in August of 2011 and Hurricane Sandy passing in October of 2012.



Model Selection Summary

Global Model Summary

Table S3. Details of generalized linear mixed effect models (GLMMs) used to test *a priori* hypotheses on the effect of environmental stressors on patch reef fish communities. Fixed effect codes: LF = lionfish biomass, GR = grouper biomass, SST = sea surface temperature and H = hurricane passage. All models contained survey year, survey site, and survey season as random intercepts.

Model number	Response variable	Fixed effects	Transformation of response	Residuals distribution
1	Total fish biomass	LF, SST, H	Log	Gaussian
2	Total fish richness	LF, SST, H	None	Gaussian
3	Lionfish biomass	SST, H	Log	Gaussian
4	Grouper biomass	LF, SST, H	Log	Gaussian
5	Mesopredator biomass	SST, H	Log	Gaussian
6	Prey fish biomass	LF, GR, SST, H	Log	Gaussian
7	Prey fish richness	LF, GR, SST, H	None	Poisson
8	Non-prey fish biomass	LF, GR, SST, H	Log	Gaussian
9	Non-prey fish richness	LF, GR, SST, H	None	Poisson
10	Corallivore biomass	SST, H	Log	Gaussian
11	Herbivore biomass	SST, H	Log	Gaussian

Total Fish Biomass Model

Table S4. Summary of model selection results for total fish biomass obtained via AICc comparison. LF = lionfish biomass, SST = sea surface temperature and H = hurricane passage. A ΔAICc <2 was assumed to indicate no difference between models. If multiple top models had ΔAIC values <2, the most parsimonious model was selected as the top model. The top model is in bold.

Fixed Effects	**Season included (Y/N)**	**K**	**AICc**	**ΔAICc**	**Weight**	**Cum. Weight**	**LL**
LF, SST, H	**Y**	**8**	**79157.82**	**0.00**	**0.97**	**0.97**	**-39569.63**
LF, SST, H	N	7	79164.95	7.13	0.03	1.00	-39574.49
LF, SST	Y	7	79171.92	14.09	0.00	1.00	-39577.98
LF, SST	N	6	79181.75	23.93	0.00	1.00	-39584.15
LF, H	Y	7	79185.73	27.90	0.00	1.00	-39584.88
LF	Y	6	79189.00	31.17	0.00	1.00	-39587.78
SST, H	Y	7	79210.62	52.79	0.00	1.00	-39597.33
LF, H	N	6	79217.88	60.06	0.00	1.00	-39602.22
LF	N	5	79218.65	60.83	0.00	1.00	-39603.82
SST, H	N	6	79221.29	63.47	0.00	1.00	-39603.92
SST	Y	6	79222.60	64.78	0.00	1.00	-39604.58
SST	N	5	79235.75	77.92	0.00	1.00	-39612.37
H	Y	6	79238.83	81.00	0.00	1.00	-39612.69
Null	Y	5	79240.82	83.00	0.00	1.00	-39614.90
Null	N	4	79278.82	121.00	0.00	1.00	-39635.08
H	N	5	79279.39	121.56	0.00	1.00	-39634.19

Total Fish Species Richness Model

Table S5. Summary of model selection results for all models on total fish species richness obtained via AICc comparison. LF = lionfish biomass, SST = sea surface temperature and H = hurricane passage. A ΔAICc <2 was assumed to indicate no difference between models. If multiple top models had ΔAIC values <2, the most parsimonious model was selected as the top model. The top model is in bold.

Fixed Effects	**Season included (Y/N)**	**K**	**AICc**	**ΔAICc**	**Weight**	**Cum. Weight**	**LL**
LF, SST	**Y**	**7**	**7701.31**	**0.00**	**0.75**	**0.75**	**-3842.67**
LF, SST, H	Y	8	7703.57	2.26	0.24	1.00	-3842.50
SST	Y	6	7715.41	14.10	0.00	1.00	-3850.98
SST, H	Y	7	7717.46	16.15	0.00	1.00	-3850.75
LF, H	Y	7	7723.42	22.11	0.00	1.00	-3853.73
LF, SST, H	N	7	7733.50	32.19	0.00	1.00	-3858.77
H	Y	6	7736.84	35.53	0.00	1.00	-3861.70
LF, SST	N	6	7737.76	36.45	0.00	1.00	-3862.16
SST, H	N	6	7744.80	43.49	0.00	1.00	-3865.68
SST	N	5	7749.34	48.03	0.00	1.00	-3869.16
LF, H	N	6	7753.50	52.19	0.00	1.00	-3870.03
H	N	5	7764.01	62.70	0.00	1.00	-3876.50
LF	Y	6	8683.00	981.69	0.00	1.00	-4334.77
Null	Y	5	8698.90	997.59	0.00	1.00	-4343.94
LF	N	5	8730.66	1029.35	0.00	1.00	-4359.82
Null	N	4	8743.58	1042.27	0.00	1.00	-4367.46

Lionfish Biomass Model

Table S6. Summary of model selection results for all lionfish biomass models obtained via AICc comparison. SST = sea surface temperature and H = hurricane passage. A ΔAICc <2 was assumed to indicate no difference between models. If multiple top models existed with ΔAIC values <2, the most parsimonious model was selected as the top model. The top model is in bold.

Fixed effects	**Season included (Y/N)**	**K**	**AICc**	**ΔAICc**	**Weight**	**Cum. Weight**	**LL**
Null	Y	5	2452.42	0.00	0.33	0.33	-1220.70
Null	**N**	**4**	**2453.75**	**1.33**	**0.17**	**0.50**	**-1222.54**
SST	Y	6	2453.82	1.40	0.16	0.67	-1220.18
H	Y	6	2454.74	2.32	0.10	0.77	-1220.65
SST	N	5	2455.06	2.64	0.09	0.86	-1222.02
SST, H	Y	7	2455.77	3.35	0.06	0.92	-1219.90
H	N	5	2456.09	3.67	0.05	0.97	-1222.54
SST, H	N	6	2457.43	5.01	0.03	1.00	-1221.99

Grouper Biomass Model

Table S7. Summary of model selection results for all grouper biomass models obtained via AICc comparison. LF = lionfish biomass, SST = sea surface temperature and H = hurricane passage. A ΔAICc <2 was assumed to indicate no difference between models. If multiple top models existed with ΔAIC values <2, the most parsimonious model was selected as the top model. The top model is in bold.

Fixed effects	**Season included (Y/N)**	**K**	**AICc**	**ΔAICc**	**Weight**	**Cum. Weight**	**LL**
LF, SST, H	N	7	2248.68	0.00	0.25	0.25	-1116.36
LF	**Y**	**6**	**2248.79**	**0.10**	**0.24**	**0.49**	**-1117.67**
LF, H	Y	7	2249.01	0.33	0.21	0.70	-1116.52
LF, SST, H	Y	8	2249.08	0.40	0.20	0.90	-1115.26
LF, SST	Y	7	2250.75	2.07	0.09	0.99	-1117.39
LF, H	N	6	2255.67	6.99	0.01	1.00	-1121.11
LF, SST	N	6	2261.23	12.55	0.00	1.00	-1123.89
LF	N	5	2261.70	13.02	0.00	1.00	-1125.34
SST, H	Y	7	2263.97	15.29	0.00	1.00	-1124.00
Null	Y	5	2264.37	15.69	0.00	1.00	-1126.68
SST, H	N	6	2264.42	15.73	0.00	1.00	-1125.49
H	Y	6	2264.79	16.11	0.00	1.00	-1125.67
SST	Y	6	2265.77	17.08	0.00	1.00	-1126.16
H	N	5	2274.00	25.32	0.00	1.00	-1131.49
SST	N	5	2277.73	29.05	0.00	1.00	-1133.36
Null	N	4	2279.73	31.05	0.00	1.00	-1135.53

Mesopredator Biomass Model

Table S8. Summary of model selection results for all mesopredator biomass models containing all lionfish and grouper species obtained via AICc comparison. SST = sea surface temperature and H = hurricane passage. A ΔAICc <2 was assumed to indicate no difference between models. If multiple top models existed with ΔAIC values <2, the most parsimonious model was selected as the top model. The top model is in bold.

Fixed effects	**Season included (Y/N)**	**K**	**AICc**	**ΔAICc**	**Weight**	**Cum. Weight**	**LL**
SST, H	Y	7	4746.44	0.00	0.29	0.29	-2365.24
Null	**Y**	**5**	**4746.55**	**0.10**	**0.28**	**0.57**	**-2367.76**
SST	Y	6	4746.85	0.40	0.24	0.81	-2366.70
H	Y	6	4747.94	1.49	0.14	0.94	-2367.24
SST, H	N	6	4750.01	3.56	0.05	0.99	-2368.28
SST	N	5	4755.23	8.78	0.00	1.00	-2372.10
H	N	5	4755.85	9.40	0.00	1.00	-2372.41
Null	N	4	4756.90	10.46	0.00	1.00	-2374.12

Prey Fish Biomass Model

Table S9. Summary of model selection results for all prey fish biomass models for all fish <5 cm TL obtained via AICc comparison. LF = lionfish biomass, GR = grouper biomass, SST = sea surface temperature and H = hurricane passage. A ΔAICc <2 was assumed to indicate no difference between models. If multiple top models existed with ΔAIC values <2, the most parsimonious model was selected as the top model. The top model is in bold.

Fixed effects	Season included (Y/N)	K	AICc	ΔAICc	Weight	Cum. Weight	LL
LF, SST, H	**Y**	**8**	**24960.79**	**0.00**	**0.82**	**0.82**	**-12471.11**
LF, GR, SST, H	Y	9	24961.93	1.14	0.29	0.79	-12470.33
SST, H	Y	7	24963.95	3.16	0.17	0.98	-12473.99
GR, SST, H	Y	8	24964.25	3.46	0.09	0.99	-12472.84
LF, SST	Y	7	24969.06	8.26	0.01	1.00	-12476.55
SST	Y	6	24971.90	11.11	0.00	1.00	-12479.23
GR, SST	Y	7	24972.26	11.47	0.00	1.00	-12478.15
LF, H	Y	7	24989.27	28.48	0.00	1.00	-12486.65
LF	Y	6	24989.80	29.01	0.00	1.00	-12488.18
LF, GR	Y	7	24990.76	29.96	0.00	1.00	-12487.40
H	Y	6	24992.61	31.82	0.00	1.00	-12489.58
GR, H	Y	7	24992.75	31.96	0.00	1.00	-12488.39
Null	Y	5	24992.99	32.20	0.00	1.00	-12490.99
GR	Y	6	24993.13	32.34	0.00	1.00	-12489.84
LF, SST	N	6	25011.81	51.02	0.00	1.00	-12499.18
LF, SST, H	N	7	25014.33	53.53	0.00	1.00	-12499.18
SST	N	5	25015.52	54.72	0.00	1.00	-12502.25
LF, GR, SST, H	N	8	25016.19	55.40	0.00	1.00	-12498.81
GR, SST	N	6	25016.64	55.85	0.00	1.00	-12501.60
SST, H	N	6	25017.94	57.15	0.00	1.00	-12502.25
GR, SST, H	N	7	25019.15	58.36	0.00	1.00	-12501.59
LF, H	N	6	25061.55	100.75	0.00	1.00	-12524.05
LF	N	5	25062.53	101.74	0.00	1.00	-12525.76
LF, GR	N	6	25063.59	102.80	0.00	1.00	-12525.07
H	N	5	25066.44	105.65	0.00	1.00	-12527.71
GR, H	N	6	25066.58	105.79	0.00	1.00	-12526.57
Null	N	4	25067.76	106.96	0.00	1.00	-12529.54
GR	N	5	25067.89	107.09	0.00	1.00	-12528.43

Prey Fish Richness Model

Table S10. Summary of model selection results for all prey fish species richness models for all fish <5 cm TL obtained via AICc comparison. LF = lionfish biomass, GR = grouper biomass, SST = sea surface temperature and H = hurricane passage. A ΔAICc <2 was assumed to indicate no difference between models. If multiple top models existed with ΔAIC values <2, the most parsimonious model was selected as the top model. The top model is in bold.

Fixed effects	Season included (Y/N)	K	AICc	ΔAICc	Weight	Cum. Weight	LL
SST	**Y**	**5**	**6488.17**	**0.0**	**0.30**	**0.30**	**-3238.58**
GR, SST	Y	6	6488.95	0.78	0.20	0.50	-3237.75
SST, H	Y	6	6489.52	1.36	0.15	0.65	-3238.04
LF, SST	Y	6	6489.75	1.58	0.14	0.79	-3238.15
GR, SST, H	Y	7	6490.39	2.22	0.10	0.89	-3237.21
LF, SST, H	Y	7	6491.23	3.06	0.06	0.95	-3237.63
LF, GR, SST, H	Y	8	6491.92	3.76	0.05	1.00	-3236.68
Null	Y	4	6509.01	10.85	0.00	1.00	-3250.17
GR	Y	5	6509.38	21.21	0.00	1.00	-3249.18
LF	Y	5	6510.63	22.46	0.00	1.00	-3249.81
LF, GR	Y	6	6510.80	22.63	0.00	1.00	-3248.67
H	Y	5	6511.26	23.10	0.00	1.00	-3250.12
GR, H	Y	6	6511.71	23.54	0.00	1.00	-3249.13
LF, H	Y	6	6512.95	24.78	0.00	1.00	-3249.75
SST, H	N	5	6522.99	34.82	0.00	1.00	-3255.99
GR, SST, H	N	6	6523.37	35.21	0.00	1.00	-3254.96
LF, SST, H	N	6	6525.07	36.90	0.00	1.00	-3255.81
LF, GR, SST, H	N	7	6525.34	37.18	0.00	1.00	-3254.69
GR, SST	N	5	6534.21	46.04	0.00	1.00	-3261.59
SST	N	4	6534.28	46.11	0.00	1.00	-3262.81
LF, SST	N	5	6536.27	48.10	0.00	1.00	-3262.62
GR, H	N	5	6544.84	56.67	0.00	1.00	-3266.91
H	N	4	6545.70	57.53	0.00	1.00	-3268.52
LF, H	N	5	6547.80	59.63	0.00	1.00	-3268.39
GR	N	4	6548.13	59.97	0.00	1.00	-3269.73
Null	N	3	6549.21	61.05	0.00	1.00	-3271.41
LF, GR	N	5	6549.97	61.80	0.00	1.00	-3269.48
LF	N	4	6551.22	63.05	0.00	1.00	-3271.28

Non-Prey Fish Biomass Model

Table S11. Summary of model selection results for all non-prey fish biomass models on all fish >5 cm TL obtained via AICc comparison. LF = lionfish biomass, GR = grouper biomass, SST = sea surface temperature and H = hurricane passage. A ΔAICc <2 was assumed to indicate no difference between models. If multiple top models existed with ΔAIC values <2, the most parsimonious model was selected as the top model. The top model is in bold.

Fixed effects	Season included (Y/N)	K	AICc	ΔAICc	Weight	Cum. Weight	LL
GR, SST, H	N	7	47328.65	0.00	0.43	0.43	-23656.34
GR, H	**N**	**6**	**47330.33**	**1.68**	**0.19**	**0.62**	**-23658.44**
LF, GR, SST, H	N	8	47331.02	2.38	0.13	0.75	-23656.23
GR, SST, H	Y	8	47331.25	2.61	0.12	0.87	-23656.34
GR, H	Y	7	47332.85	4.20	0.05	0.92	-23658.44
LF, GR, SST, H	Y	9	47333.73	5.08	0.03	0.95	-23656.23
GR	N	5	47334.77	6.12	0.02	0.97	-23661.87
GR, SST	N	6	47336.23	7.59	0.01	0.98	-23661.39
LF, GR	N	6	47336.92	8.27	0.01	0.99	-23661.73
GR	Y	6	47337.16	8.52	0.01	1.00	-23661.86
GR, SST	Y	7	47338.75	10.10	0.00	1.00	-23661.39
LF, GR	Y	7	47339.40	10.75	0.00	1.00	-23661.72
SST, H	N	6	47372.22	43.58	0.00	1.00	-23679.39
LF, SST, H	N	7	47374.68	46.04	0.00	1.00	-23679.36
SST, H	Y	7	47374.74	46.09	0.00	1.00	-23679.39
H	N	5	47376.65	48.00	0.00	1.00	-23682.82
LF, SST, H	Y	8	47377.29	48.64	0.00	1.00	-23679.36
H	Y	6	47378.74	50.09	0.00	1.00	-23682.64
LF, H	N	6	47378.96	50.31	0.00	1.00	-23682.76
LF, H	Y	7	47381.15	52.50	0.00	1.00	-23682.59
Null	N	4	47381.62	52.97	0.00	1.00	-23686.48
SST	N	5	47381.75	53.10	0.00	1.00	-23685.37
LF	Y	5	47382.84	54.19	0.00	1.00	-23685.91
LF, SST	Y	6	47383.86	55.21	0.00	1.00	-23685.21
LF	N	5	47383.92	55.27	0.00	1.00	-23686.45
LF, SST	N	6	47384.16	55.51	0.00	1.00	-23685.36
LF	Y	6	47385.22	56.58	0.00	1.00	-23685.89
LF, SST	Y	7	47386.35	57.70	0.00	1.00	-23685.19

Non-Prey Fish Richness Model

Table S12. Summary of model selection results for all non-prey fish species richness models for all fish >5 cm TL obtained via AICc comparison. LF = lionfish biomass, GR = grouper biomass, SST = sea surface temperature and H = hurricane passage. A ΔAICc <2 was assumed to indicate no difference between models. If multiple top models existed with ΔAIC values <2, the most parsimonious model was selected as the top model. The top model is in bold.

Fixed effects	Season included (Y/N)	K	AICc	ΔAICc	Weight	Cum. Weight	LL
LF, SST	N	5	7358.30	0.00	0.16	0.16	-3673.64
SST	**N**	**4**	**7359.05**	**0.76**	**0.11**	**0.27**	**-3675.19**
GR, SST	N	5	7359.20	0.90	0.10	0.37	-3674.09
LF, SST, H	N	6	7359.82	1.52	0.07	0.44	-3673.18
LF, SST	Y	6	7360.46	2.16	0.05	0.49	-3673.50
LF, SST, H	Y	7	7360.53	2.24	0.05	0.55	-3672.28
SST, H	N	5	7360.55	2.25	0.05	0.60	-3674.77
LF, GR, SST, H	N	7	7360.76	2.46	0.05	0.64	-3672.40
GR, SST, H	N	6	7360.88	2.58	0.04	0.69	-3673.72
SST	Y	5	7361.20	2.91	0.04	0.72	-3675.09
GR, SST	Y	6	7361.32	3.02	0.03	0.76	-3673.93
LF, GR, SST, H	Y	8	7361.37	3.08	0.03	0.79	-3671.40
SST, H	Y	6	7361.42	3.12	0.03	0.82	-3673.98
GR, SST, H	Y	7	7361.60	3.31	0.03	0.85	-3672.82
LF, H	Y	6	7362.03	3.73	0.02	0.88	-3674.29
LF, H	N	5	7362.52	4.23	0.02	0.90	-3675.75
H	Y	5	7362.90	4.61	0.02	0.91	-3675.94
H	N	4	7363.13	4.83	0.01	0.93	-3677.23
GR, H	Y	6	7363.16	4.86	0.01	0.94	-3674.85
LF	N	4	7363.56	5.26	0.01	0.95	-3677.44
GR, H	N	5	7363.74	5.44	0.01	0.96	-3676.36
Null	N	3	7364.06	5.77	0.01	0.97	-3678.84
GR	N	4	7364.49	6.20	0.01	0.98	-3677.91
LF, GR	N	5	7364.53	6.23	0.01	0.99	-3676.76
LF	Y	5	7365.49	7.20	0.00	0.99	-3677.24
Null	Y	4	7366.04	7.75	0.00	0.99	-3678.69
GR	Y	5	7366.36	8.06	0.00	1.00	-3677.67
LF, GR	Y	6	7366.37	8.08	0.00	1.00	-3676.46

Corallivore Biomass Model

Table S13. Summary of model selection results for all corallivorous fish biomass models obtained via AICc comparison. SST = sea surface temperature and H = hurricane passage. A ΔAICc <2 was assumed to indicate no difference between models. If multiple top models existed with ΔAIC values <2, the most parsimonious model was selected as the top model. The top model is in bold.

Fixed effects	**Season included (Y/N)**	**K**	**AICc**	**ΔAICc**	**Weight**	**Cum. Weight**	**LL**
SST, H	**Y**	**7**	**13414.22**	**0.00**	**0.68**	**0.68**	**-6699.13**
SST, H	N	6	13416.62	2.40	0.20	0.88	-6701.58
H	Y	6	13417.76	3.55	0.12	1.00	-6702.16
Null	Y	5	13426.73	12.51	0.00	1.00	-6707.86
SST	Y	6	13428.02	13.81	0.00	1.00	-6707.29
H	N	5	13429.23	15.01	0.00	1.00	-6709.10
SST	N	5	13438.35	24.13	0.00	1.00	-6713.67
Null	N	4	13441.02	26.80	0.00	1.00	-6716.17

Herbivore Biomass Model

Table S14. Summary of model selection results for all herbivorous fish biomass models obtained via AICc comparison. SST = sea surface temperature and H = hurricane passage. A ΔAICc <2 was assumed to indicate no difference between models. If multiple top models existed with ΔAIC values <2, the most parsimonious model was selected as the top model. The top model is in bold.

Fixed effects	**Season included (Y/N)**	**K**	**AICc**	**ΔAICc**	**Weight**	**Cum. Weight**	**LL**
SST, H	**Y**	**7**	**27735.75**	**0.00**	**1.00**	**1.00**	**-13859.89**
SST	Y	6	27747.18	11.43	0.00	1.00	-13866.87
SST, H	N	6	27752.17	16.41	0.00	1.00	-13869.36
H	Y	6	27755.37	19.62	0.00	1.00	-13870.96
Null	Y	5	27757.97	22.22	0.00	1.00	-13873.48
SST	N	5	27793.02	57.27	0.00	1.00	-13891.00
H	N	5	27818.54	82.78	0.00	1.00	-13903.76
Null	N	4	27830.56	94.81	0.00	1.00	-13910.95

Community Response Variables Over Time

Table S15. Summary of GLMMs exploring the effect of survey year on each community response variable to determine trends in reef fish community change over time. All models include survey site as a random intercept but exclude survey season, as it was found to have a near zero variance that impacted convergence in some models. All biomass models utilized log-transformed biomass values to adhere to normality assumptions. All models were found to have sufficient fit based on diagnostic plots (residual scatterplots, residual histograms, QQ plots, and ACF plots).

Response Variable	**Estimated Effect**	**SE**	**Z-Value**	***P*-Value**
Total fish biomass	0.00717	0.000714	10.052	<0.001
Total fish richness	-0.247	0.0354	-6.972	<0.001
LF	-0.101	0.0274	-3.692	<0.001
GR	-0.0523	0.0236	-2.213	0.0269
Mesopredator biomass	-0.0648	0.0183	-3.533	0.000411
Prey biomass	-0.0124	0.00794	-1.562	0.118
Prey richness	-0.262	0.0272	-9.634	<0.001
Non-prey biomass	0.00715	0.000661	10.82	<0.001
Non-prey richness	-0.0752	0.0322	-2.334	0.0196
Corallivore biomass	0.0626	0.0115	5.422	<0.001
Herbivore biomass	0.00651	0.000804	8.105	<0.001

Network Connectivity Threshold Comparison

Various network connectivity threshold values were compared to determine which produced the best performing and most realistic network structure. We began by selecting standard threshold values that produced connectance values ranging from 0.05-0.3, similar to Dunne et al. (2002). Based on this, we compared threshold values of 0.01, 0.015, 0.02, and 0.025 decimal degrees (Table S16). Next, we examined the network structure that each threshold produced (Figure S4). The threshold of 0.01 decimal degrees produced a network structure that was disconnected and composed of two separate clusters of nodes (Figure S4 A). For further analyses, we wanted a fully connected network structure, so the threshold of 0.01 was removed from consideration.

We then examined the impact that each threshold value had on network metrics (Table S16). We were specifically interested in the effect of threshold on the small-world metric value, which calculates the ratio between network clustering coefficient and average distance. Smaller values indicate a more randomly behaving network, moderate to large values indicate a small-world structure, which is characteristic of natural networks, and high values indicate regular networks (Watts & Strogatz 1998). The threshold of 0.025 produced the largest small-world metric of 0.529 (Table S16).

For our final threshold comparison, we created three randomly generated networks at each threshold value with the same number of nodes and edges as in the natural patch reef network. We compared the structure of these random networks to the natural network by calculating the small-world-ness value for each threshold. This index also assesses the small-world behaviour of the network, with larger values indicating a more small-world network (Humphries & Gurney 2008). Based on the small-world-ness values, the network created with a threshold value of 0.015 had the highest small-world performance with an index of 1.796 (Table S20).

Overall, our comparison revealed contrasting results, with the small-world metric indicating the best network structure using a threshold of 0.025 and the small-world-ness value suggesting a threshold of 0.015. Because of this, we selected an intermediate connectivity threshold value of 0.02 decimal degrees as our final threshold to use in the main-text analyses. Though 0.02 was not the best performing metric in any of our comparisons, it consistently performed well and balanced network connectivity with high small-world network performance, producing a small-world metric value of 0.424 and a small-world-ness value of 1.409 (Figure S4, Table S16, and Table S20).

Figure S4. Comparison of the impact of varying connectivity thresholds on patch reef network structure and connectance. Thresholds for comparison were chosen to bound connectance between 0.05-0.3. Each connectivity threshold is in units of decimal degrees. Each patch reef site is represented by a light blue circle with the site name labelled. Sites 104_NF27 and 112_NF25 were shortened to 104 and 112, respectively, to fit within site nodes. Grey lines denote edges between nodes, indicating that species dispersal between these reefs is possible. A. network with a connectivity threshold of 0.01 decimal degrees (connects sites within ~1.11 km), B. network with a connectivity threshold of 0.015 decimal degrees (connects sites within ~1.167 km), C. network with a connectivity threshold of 0.02 decimal degrees (connects sites within ~2.22 km) and D. network with a connectivity threshold of 0.025 decimal degrees (connects sites within ~2.78 km).

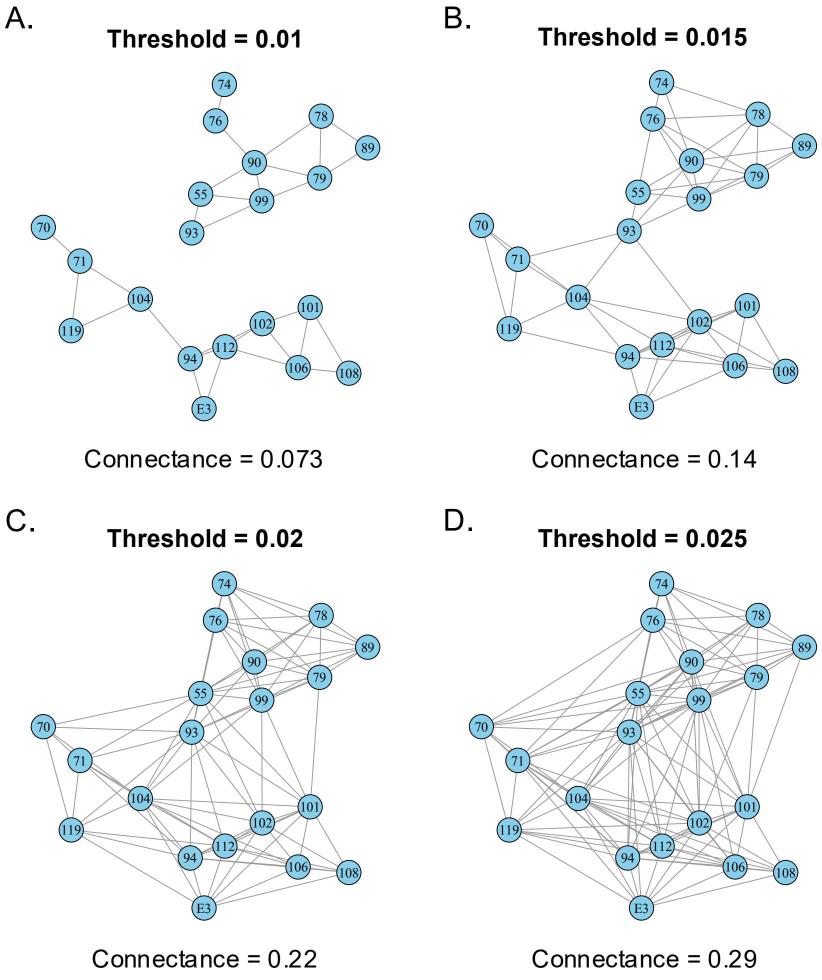


Table S16. Metacommunity network metrics at connectivity threshold values of 0.01, 0.015, 0.02, and 0.025 decimal degrees.

Metric	**0.01**	**0.015**	**0.02**	**0.025**
Number of edges	29	55	88	116
Connectance	0.073	0.138	0.220	0.290
Clustering coefficient	0.493	0.664	0.707	0.744
Diameter	6	4	3	3
Average distance	2.308	2.384	1.668	1.405
Small-world metric	0.213	0.279	0.424	0.529

Table S17. Betweenness centrality of each patch reef site at connectivity threshold values of 0.01, 0.015, 0.02 and 0.025 decimal degrees.

Site	**0.01**	**0.015**	**0.02**	**0.025**
108	0	0	0	0
74	0	0	0	0
78	1.833	1.417	0	0
90	15.33	34.500	1.395	4.583
93	0	89.433	24.472	17.342
71	9.000	9.000	2.063	3.158
104_NF27	21.000	29.550	12.935	4.753
112_NF25	7.333	4.850	4.028	2.102
102	12.000	50.783	9.659	5.651
94	24.833	8.617	4.028	3.469
119	0	2.350	1.747	1.043
76	7.000	1.417	1.395	1.567
55	1.833	8.000	26.603	10.394
70	0	0	0.583	1.084
101	2.167	0.417	16.621	6.929
106	6.667	1.000	0.226	1.068
E3	0	0	1.268	1.184
89	0	0	0	0.616
79	5.000	0.833	5.356	1.465
99	5.000	20.833	14.624	10.757

Table S18. Closeness centrality of each patch reef site at connectivity threshold values of 0.01, 0.015, 0.02 and 0.025 decimal degrees.

Site	**0.01**	**0.015**	**0.02**	**0.025**
108	0.0313	0.0200	0.0263	0.0294
74	0.0435	0.0185	0.0270	0.0323
78	0.0667	0.0196	0.0270	0.0323
90	0.0909	0.0263	0.0303	0.0400
93	0.0526	0.0313	0.0400	0.0500
71	0.0370	0.0233	0.0323	0.0385
104_NF27	0.0476	0.0278	0.0385	0.0416
112_NF25	0.0500	0.0227	0.0323	0.0385
102	0.0500	0.0286	0.0357	0.0417
94	0.0556	0.0227	0.0323	0.0400
119	0.0357	0.0208	0.0294	0.0357
76	0.0625	0.0196	0.0303	0.0345
55	0.0667	0.0244	0.0400	0.0455
70	0.0278	0.0192	0.0294	0.0345
101	0.0385	0.0208	0.0370	0.0400
106	0.0417	0.0213	0.0278	0.0357
E3	0.0417	0.0204	0.0286	0.0357
89	0.0526	0.0189	0.0271	0.0345
79	0.0769	0.0196	0.0345	0.0357
99	0.0769	0.0256	0.0370	0.0455

Table S19. Degree of each patch reef site at connectivity threshold values of 0.01, 0.015, 0.02 and 0.025 decimal degrees.

Site	0.01	0.015	0.02	0.025
108	2	4	6	7
74	1	3	7	8
78	3	6	7	8
90	5	8	8	13
93	2	6	13	18
71	3	4	7	12
104_NF27	3	7	12	14
112_NF25	4	7	10	12
102	4	8	10	14
94	4	7	10	13
119	2	4	7	10
76	2	6	8	10
55	3	5	13	16
70	1	3	5	9
101	3	5	11	13
106	4	6	7	10
E3	2	4	8	10
89	2	4	7	9
79	4	6	9	10
99	4	7	11	16

Table S20. Summary of small world index (SWI) calculation values for three randomly created networks at four connectivity thresholds: 0.01, 0.015, 0.02, and 0.025 decimal degrees. Random networks were created with the same number of nodes and edges as the natural patch reef network at the corresponding connectivity threshold value. Network metrics were averages to calculate the average SWI across all random networks.

Random Network	**Metric**	**0.01**	**0.015**	**0.02**	**0.025**
1	CL	0.043	0.238	0.454	0.612
	d	2.621	1.816	1.542	1.389
	SWI	13.053	1.231	1.439	1.201
2	CL	0.188	0.330	0.474	0.616
	d	2.668	1.889	1.537	1.389
	SWI	3.037	1.596	1.374	1.194
3	CL	0.080	0.296	0.462	0.564
	d	2.731	1.863	1.542	1.389
	SWI	7.286	1.756	1.416	1.303
Average	SWI Average	5.516	1.796	1.409	1.231

Jaccard Dissimilarity

Table S21. Jaccard dissimilarity per patch reef site of fish species composition between 2011 and 2024 belt transect surveys.

Site	Jaccard Dissimilarity
101	0.571
102	0.667
104_NF27	0.816
106	0.645
108	0.690
112_NF25	0.656
119	0.706
55	0.500
70	0.758
71	0.645
74	0.656
76	0.677
78	0.667
79	0.788
89	0.730
90	0.720
93	0.469
94	0.581
99	0.567
E3	0.714

Table S22. Jaccard dissimilarity per patch reef site of fish species composition between belt transect surveys performed one year prior to the passage of Hurricane Irene in August of 2011 to the first survey performed following Hurricane Sandy in October of 2012.

Site	**Jaccard Dissimilarity**
101	0.515
102	0.519
104_NF27	0.640
106	0.692
108	0.577
112_NF25	0.667
119	0.625
55	0.467
70	0.613
71	0.519
74	0.457
76	0.639
78	0.556
79	0.552
89	0.615
90	0.481
93	0.517
94	0.667
99	0.600
E3	0.652

Table S23. Jaccard dissimilarity per patch reef site of fish species composition between two surveys prior to the passage of Hurricane Irene near sites in August of 2011 and Hurricane Sandy in October of 2012. Surveys conducted in the year prior to the passage of Hurricane Irene were compared to surveys conducted in the first year of the survey time series, between 2009 and 2010. Only 17 of the 20 patch reef sites are compared, as only 17 sites were surveyed during the first year of the time series. Sites 119, 99 and E3 are excluded.

Site	**Jaccard Dissimilarity**
101	0.568
102	0.538
104_NF27	0.440
106	0.618
108	0.433
112_NF25	0.513
55	0.571
70	0.472
71	0.524
74	0.316
76	0.639
78	0.634
79	0.414
89	0.375
90	0.515
93	0.364
94	0.667

Figure S5. Changes in fish species composition of Bahamian patch reef sites between pre-Hurricane Irene (August 2011) belt transect surveys and surveys performed during the first year of the time series (2009-2010). A. the metacommunity network of patch reefs at a connectivity threshold of 0.02 decimal degrees with nodes (sites) coloured by Jaccard dissimilarity index values comparing community assemblages from belt transect surveys performed in the year prior to Hurricane Irene in August 2011 and the first year belt transect surveys were conducted at sites from 2009-2010. Grey nodes indicate sites with no Jaccard dissimilarity value calculated, as these patches were not surveyed in the first year of the time series. B. PCoA ordination plot showing the community composition of each site in pre-hurricane surveys compared to first year surveys. The distance between site points pre-hurricane compared to first year indicates their relative dissimilarity in species composition. Points are coloured by site, with circular points showing first year (2009-2010) compositions and triangles showing pre-hurricane compositions. Ellipses denote the confidence region around the centroid of each survey period based on a multivariate t-distribution and are patterned by survey period, with the solid ellipse showing first year surveys and the dashed ellipse showing pre-hurricane surveys.

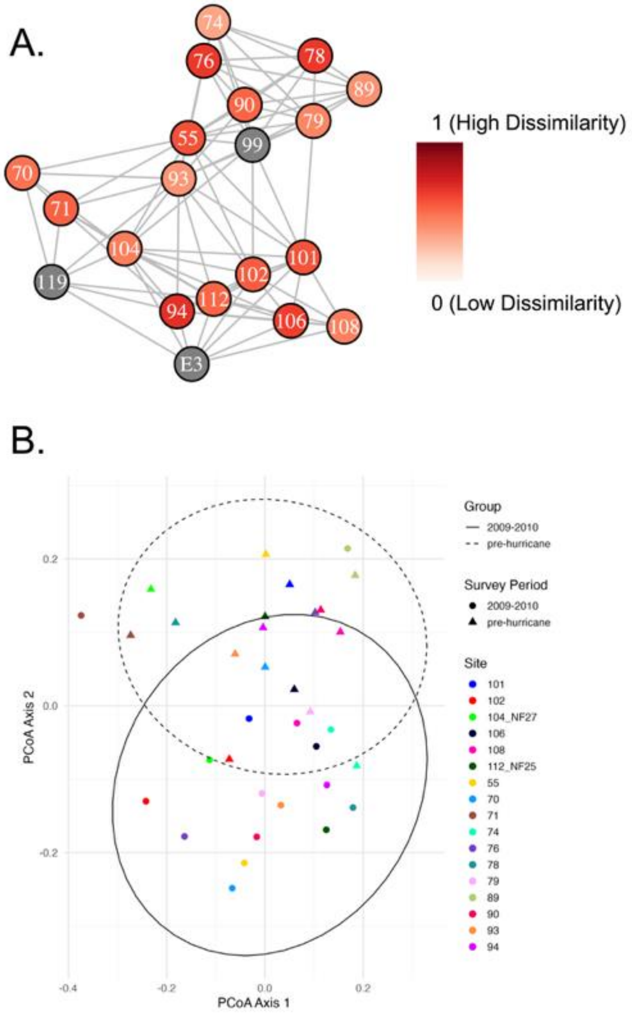
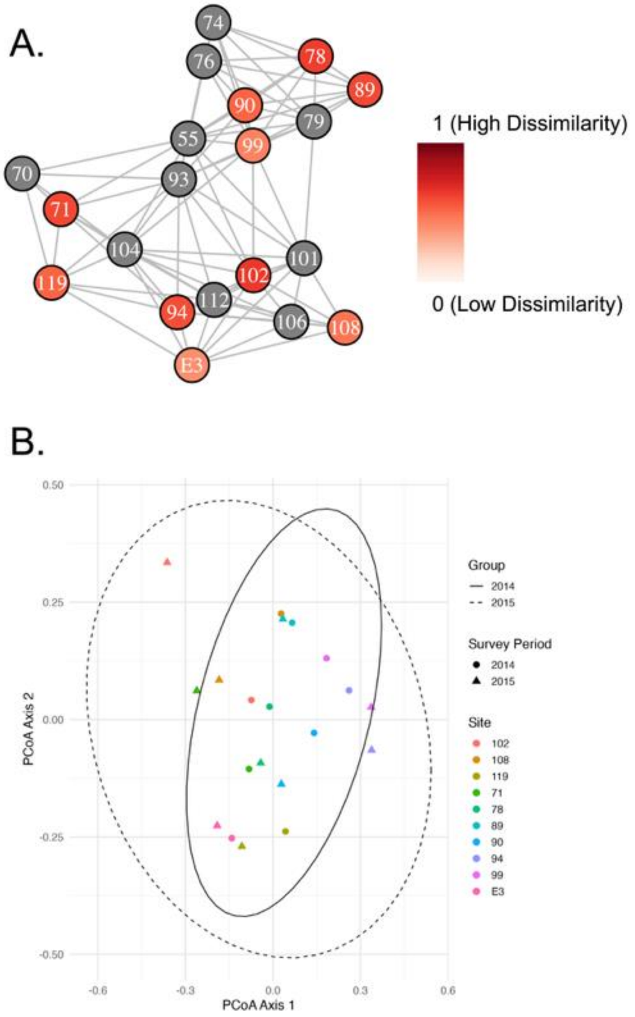


Table S24. Jaccard dissimilarity per patch reef site of fish species composition between two surveys after the passage of Hurricane Irene near sites in August of 2011 and Hurricane Sandy in October of 2012. Surveys conducted in 2014 were compared to surveys conducted 2015. Only 10 of the 20 patch reef sites are compared, as only these sites were surveyed in both 2014 and 2015. Sites 101, 104_NF27, 106, 112_NF25, 55, 70, 74, 76, 79 and 93 are excluded.

Site	**Jaccard Dissimilarity**
102	0.632
108	0.464
119	0.519
71	0.593
78	0.618
89	0.593
90	0.516
94	0.581
99	0.423
E3	0.381

Figure S6. Changes in fish species composition of Bahamian patch reef sites between post-Hurricane Sandy (October 2012) belt transect surveys performed in 2014 and 2015. A. the metacommunity network of patch reefs at a connectivity threshold of 0.02 decimal degrees with nodes (sites) coloured by Jaccard dissimilarity index values comparing community assemblages from belt transect surveys performed in 2014 to those performed in 2015. Grey nodes indicate sites with no Jaccard dissimilarity value calculated, as these patches were not surveyed during these years. B. PCoA ordination plot showing the community composition of each site in 2014 compared to 2015. The distance between site points in each year indicates their relative dissimilarity in species composition. Points are coloured by site, with circular points showing 2014 compositions and triangles showing 2015 compositions. Ellipses denote the confidence region around the centroid of each survey period based on a multivariate t-distribution and are patterned by survey period, with the solid ellipse showing 2014 surveys and the dashed ellipse showing 2015 surveys.



Dissimilarity and Connectivity Correlation: Connectivity Threshold Comparison

2011 vs. 2024

Figure S7. Relationship between betweenness centrality and Jaccard dissimilarity of fish species composition from belt transect surveys performed in 2011 compared to 2024 on 20 patch reefs. A. connectivity threshold = 0.015 decimal degrees, B. connectivity threshold = 0.02 and C. connectivity threshold = 0.025. A Spearman correlation test was performed using each threshold. Corresponding rho and *p*-values are reported in boxes.

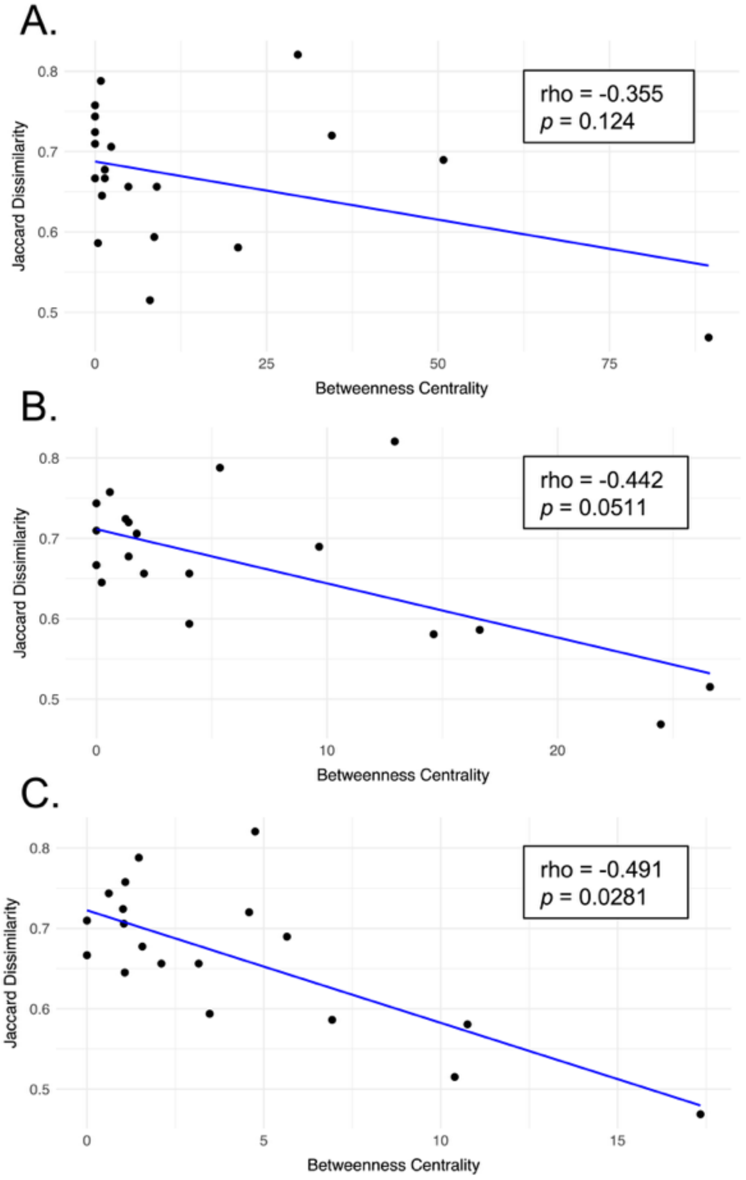
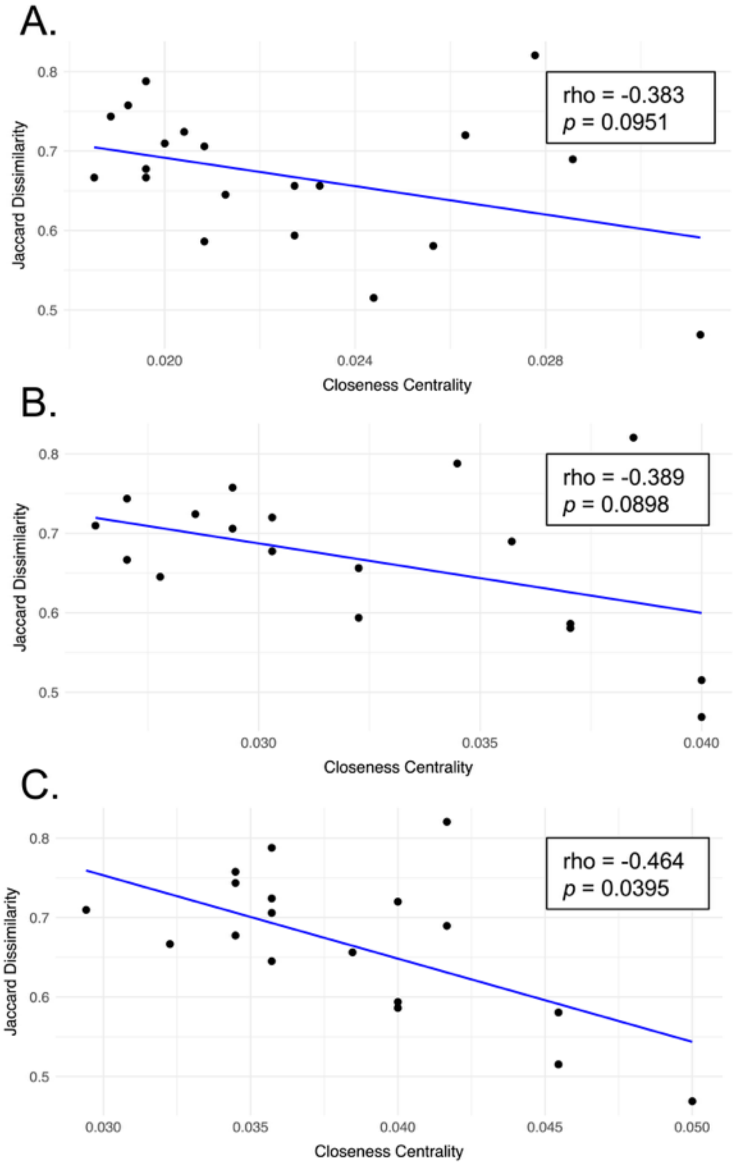


Figure S8. Relationship between closeness centrality and Jaccard dissimilarity of fish species composition from belt transect surveys performed in 2011 compared to 2024 on 20 patch reefs. A. connectivity threshold = 0.015 decimal degrees, B. connectivity threshold = 0.02 and C. connectivity threshold = 0.025. A Spearman correlation test was performed using each threshold. Corresponding rho and *p*-values are reported in boxes.



Pre vs. Post-Hurricane

Figure S9. Relationship between betweenness centrality and Jaccard dissimilarity of fish species composition from belt transect surveys performed before the passage of Hurricane Irene in August 2011 and after the passage of Hurricane Sandy in October 2012 on 20 patch reefs. A. connectivity threshold = 0.015 decimal degrees, B. connectivity threshold = 0.02 and C. connectivity threshold = 0.025. A Spearman correlation test was performed using each threshold. Corresponding rho and *p*-values are reported in boxes.

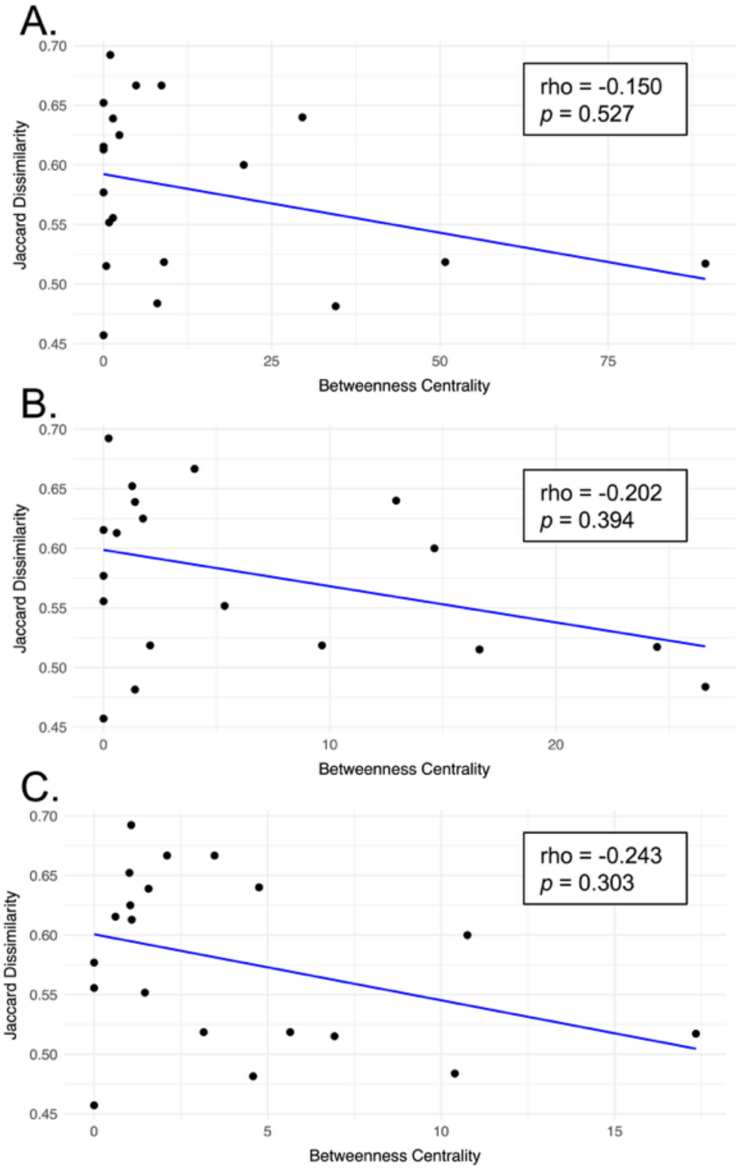
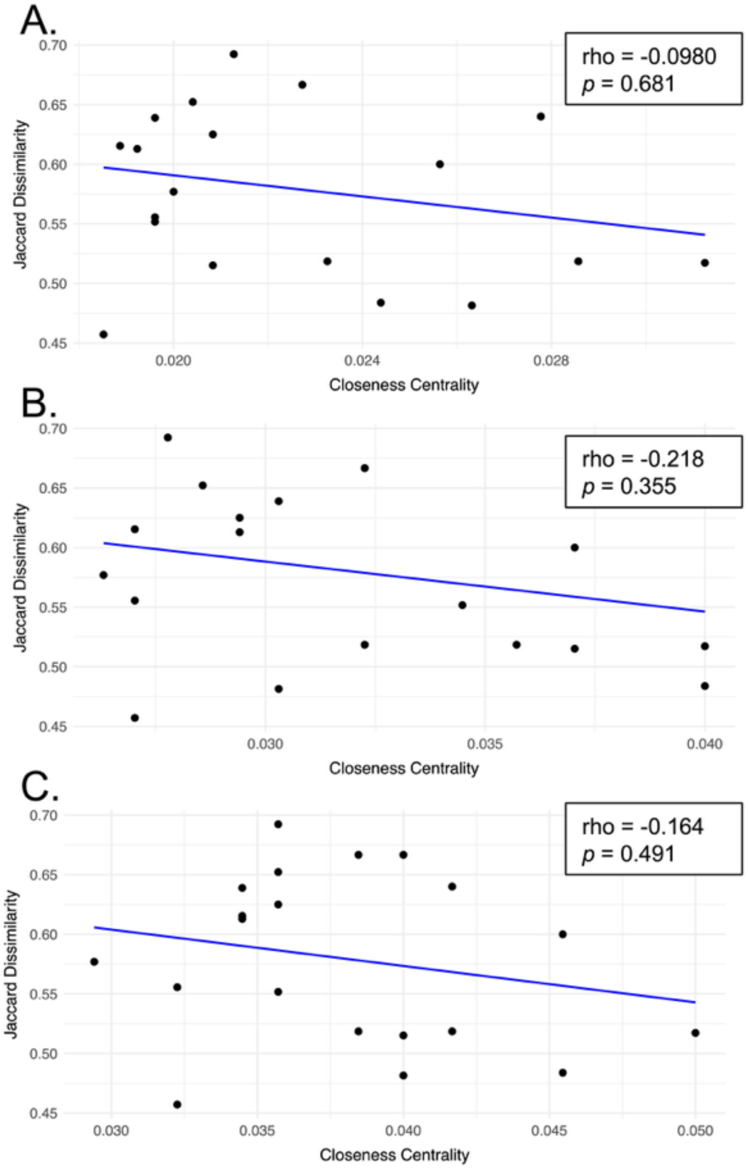
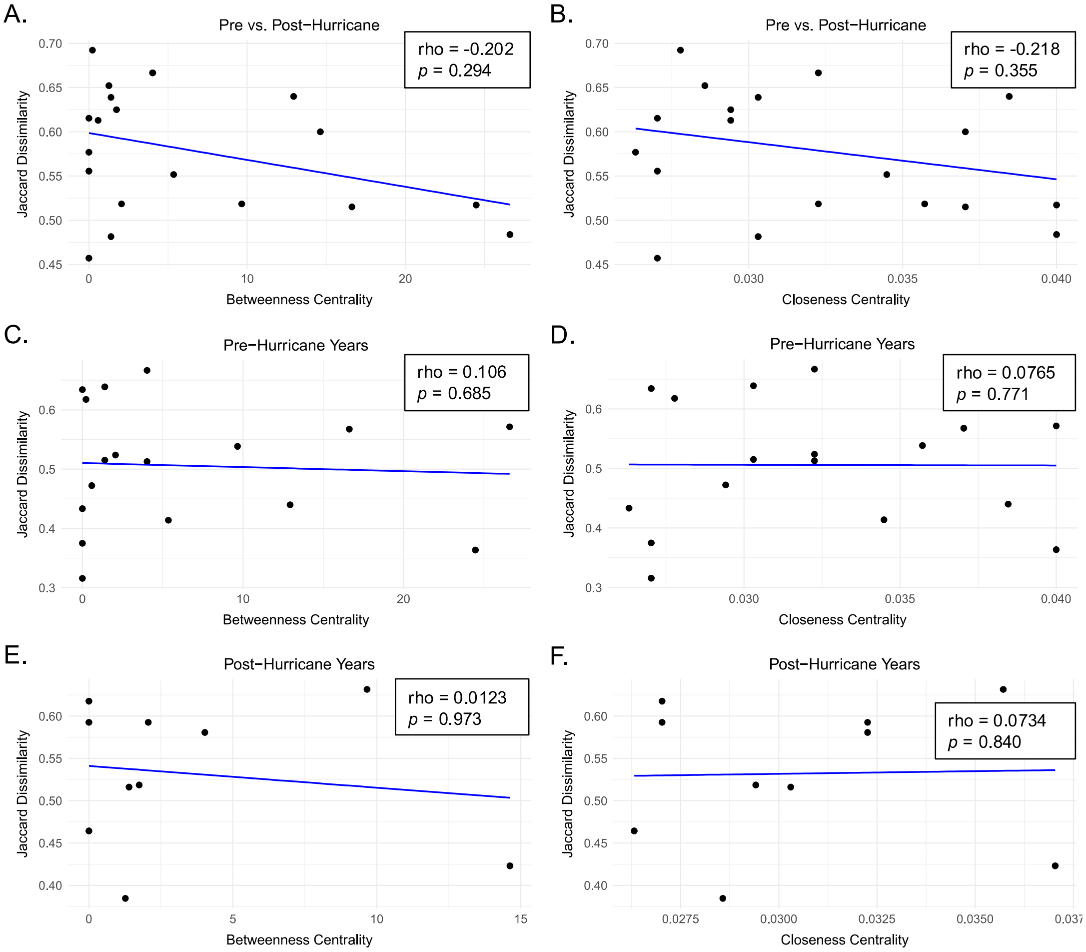


Figure S10. Relationship between closeness centrality and Jaccard dissimilarity of fish species composition from belt transect surveys performed before the passage of Hurricane Irene in August 2011 and after the passage of Hurricane Sandy in October 2012 on 20 patch reefs. A. connectivity threshold = 0.015 decimal degrees, B. connectivity threshold = 0.02 and C. connectivity threshold = 0.025. A Spearman correlation test was performed using each threshold. Corresponding rho and *p*-values are reported in boxes.



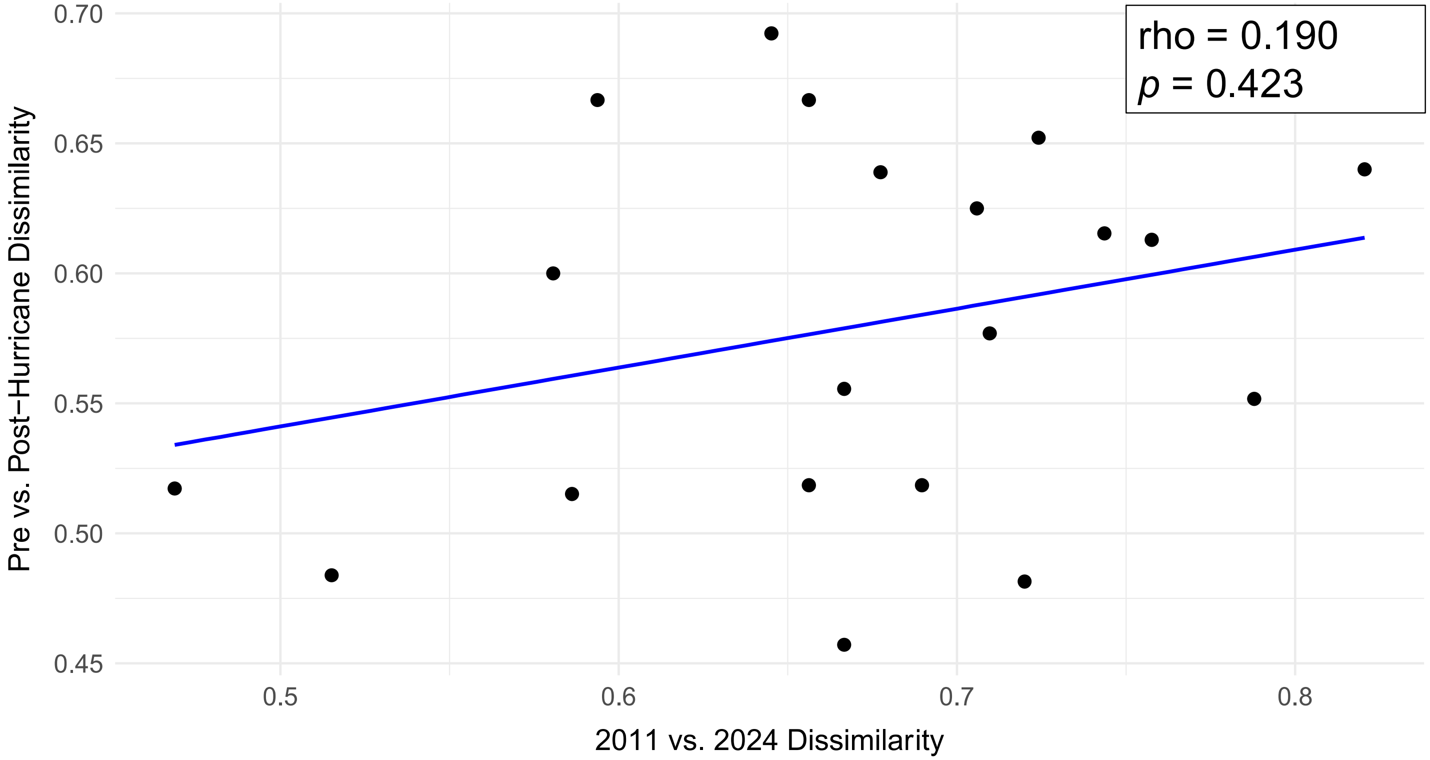
Pre- and Post-Hurricane Network Metric Correlation

Figure S11. Correlation between patch reef metacommunity network metrics and Jaccard dissimilarity for fish species composition on pre-Hurricane Irene (August 2011) compared to post-Hurricane Sandy (October 2012) belt transect surveys. The network contains 20 total nodes, one per patch reef site surveyed. A connectivity threshold of 0.02 was utilized to calculate all network metrics. A. Jaccard dissimilarity vs. betweenness centrality for pre-Hurricane Irene (August 2011) compared to post-Hurricane Sandy (October 2012) belt transect surveys, B. Jaccard dissimilarity vs. closeness centrality for pre-hurricane compared to post-hurricane belt transect surveys, C. Jaccard dissimilarity vs. betweenness centrality for two pre-Hurricane Irene belt transect surveys, D. Jaccard dissimilarity vs. closeness centrality for two pre-Hurricane Irene belt transect surveys, E. Jaccard dissimilarity vs. betweenness centrality for two post-Hurricane Sandy belt transect surveys and F. Jaccard dissimilarity vs. closeness centrality for two post-Hurricane Sandy belt transect surveys. The rho and *p*-value of the corresponding rank Spearman correlation test are reported in the figure boxes.



<u>Survey Period Dissimilarity Correlation</u>

Figure S12. Correlation between Jaccard dissimilarities of each network node for the comparison of 2011 vs. 2024 belt transect surveys and pre-Hurricane Irene (August 2011) and post-Hurricane Sandy (October 2012) belt transect survey fish species composition at a connectivity threshold value of 0.02. The network contains 20 total nodes, one per patch reef site surveyed. The rho and *p*-value of the corresponding rank Spearman correlation test are reported in the figure box.



Supplementary References

Bartoń K (2020) MuMIn: Multi-model inference

Bolker B, Robinson D (2018) broom.mixed: Tidying methods for mixed models. 0.2.9.6

Brooks ME, Kristensen K, Benthem KJ van, et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400

Cheng J, Schloerke B, Karambelkar B, Xie Y (2025) leaflet: Create interactive web maps with the JavaScript “Leaflet” library

Csárdi G, Nepusz T, Müller K, et al (2025) igraph for R: R interface of the igraph library for graph theory and network analysis

Dunne JA, Williams RJ, Martinez ND (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecol Lett 5:558–567. https://doi.org/10.1046/j.1461-0248.2002.00354.x

Fox J, Weisberg S (2019) An R companion to applied regression. Sage Publications, Thousand Oaks

Grolemund G, Wickham H (2011) Dates and times made easy with lubridate. J Stat Softw 40:1–25

Humphries MD, Gurney K (2008) Network “small-world-ness”: a quantitative method for determining canonical network equivalence. PloS One 3:e0002051. https://doi.org/10.1371/journal.pone.0002051

Lüdecke D, Ben-Shachar MS, Patil I, et al (2021) performance: An R package for assessment, comparison and testing of statistical models. J Open Source Softw 6:3139. https://doi.org/10.21105/joss.03139

Mazerolle MJ (2023) Model selection and multimodel inference based on (Q)AIC(c)

Oksanen J, Simpson GL, Blanchet FG, et al (2001) vegan: Community ecology package. 2.7–1

Watts DJ, Strogatz SH (1998) Collective dynamics of ‘small-world’ networks. Nature 393:440–442. https://doi.org/10.1038/30918

Wickham H (2016) ggplot2: Elegant graphics for data analysis

Wickham H (2007) Reshaping data with the reshape package. J Stat Softw 21:1–20. https://doi.org/10.18637/jss.v021.i12