

Research article

Winners and losers of reef flattening: an assessment of coral reef fish species and traits

David P. Kochan¹  ¹, Matthew D. Mitchell^{1,2}, Rachel Zuercher¹  and Alastair R. Harborne¹ ¹Institute of Environment and Department of Biological Sciences, Florida International University, Miami, FL, USA²Marine Biology Lab, Division of Science, New York University, Abu Dhabi, UAECorrespondence: David P. Kochan (dkoch010@fiu.edu)

Oikos

2023: e10011

doi: [10.1111/oik.10011](https://doi.org/10.1111/oik.10011)

Subject Editor: Jarrett Byrnes

Editor-in-Chief: Pedro Peres-Neto

Accepted 31 July 2023

Anthropogenic stressors are causing widespread coral mortality, leading to loss of coral cover and decreased structural complexity that threatens reef biodiversity, functioning, and ecosystem services. Reef fishes are intimately linked to coral reef complexity, but we lack a generic understanding of which species are particularly affected by reef flattening and what traits make them susceptible. We used extensive species- and trait-based analyses to build a framework for western Atlantic fish association with both structural complexity and coral cover to better understand the implications of reef degradation. These analyses also highlighted the relative importance of live coral versus the structure it provides to reef fishes, which currently remains unclear. We modeled how 25 biophysical and anthropogenic factors correlated with the densities of 109 fish species across 3292 Floridian reef sites. The importance of a metric of structural complexity and coral cover to the abundance of each species was then isolated. Species with positive associations were categorized as likely future ‘losers’ and negative associations as ‘winners’. We predicted that 53% of species will be losers on low-relief reefs, while only 11% were losers with decreased coral cover. We found morphological, behavioral, and ecological traits, not phylogeny, mediate species’ responses to reef degradation and that the loss of structure seemed more critical than the loss of coral cover. Eight traits explained 79.7% of the variation in species’ associations with relief and six traits explained 27.8% of associations with coral cover. Smaller, streamlined, habitat and trophic generalists are more likely winners on flattened reefs and large-bodied predators, among other taxa, are likely losers of reef flattening. Identifying these important traits provides insight into mechanisms that may link fish and complex habitats, which allows us to better predict assemblage-wide responses to future reef flattening.

Key words: coral reef, fish density, Florida’s Coral Reef, reef flattening, structural complexity, trait-based assessment

Introduction

Widespread increases in anthropogenic stressors have caused declines in biodiversity and altered community assemblages with serious consequences for ecosystem functioning

and resilience (McGill et al. 2015). Ecosystem changes often cause reshuffling of species assemblages and communities resulting from nonrandom 'winners' and 'losers', as species' responses to disturbances are dependent on the nature of those changes and the characteristics of the affected organisms (McKinney 1997, McKinney and Lockwood 1999, Graham et al. 2011). Identifying which species are likely to win or lose is critical for predicting how ecosystems will change after disturbances and the effect of those changes on important ecosystem services. Trait-based approaches, which categorize organisms into sets of quantitative and qualitative characteristics, allow generalization across taxa and geography (McGill et al. 2006) and provide a promising approach for identifying these winners and losers. Trait responses can be generalized from common or easily studied species to predict changes to the more data-deficient species of an assemblage (González-del-Pliego et al. 2019). Furthermore, linking traits to ecosystem changes may provide a mechanistic understanding of population-level responses to stressors, explaining why species are positively or negatively affected by changes (McGill et al. 2006). In addition to linking species' responses to ecosystem changes (Streit and Bellwood 2022), trait-based approaches can also connect assemblage shifts to changes in ecosystem function (Hadj-Hammou et al. 2021). Trait-based approaches have greatly increased in use over the last decade to predict effects of global change across habitats, taxa, and scales (Green et al. 2022). For example, such analyses have been used to predict the extinction risk of amphibians worldwide (González-del-Pliego et al. 2019), sensitivity to habitat loss of birds in the Atlantic forest of Brazil (Hatfield et al. 2018), responses of epifauna to seagrass fragmentation (Yeager et al. 2019), and plant community shifts with habitat patchiness (Miller et al. 2018).

Habitat degradation and loss, and specifically the simplification of three-dimensional structural complexity, is one of the most impactful consequences of human activity with drastic effects on biodiversity, species abundances and ecosystem function (Cloern et al. 2016, Borland et al. 2021). Understanding the role of habitat complexity in structuring communities is necessary to predict the effects of habitat degradation, particularly in systems such as coral reefs where structural complexity is central to ecosystem functioning (Graham and Nash 2013). For example, reef complexity plays an important role in supporting diverse reef fish assemblages, where structure provides spatial refuges from predation, creates niche space, increases food availability and supplies nesting sites (Robertson and Sheldon 1979, Hixon 1991, Bozec et al. 2013). Additionally, three-dimensional complexity of coral reefs provides protection from high water flow, likely lowering metabolic costs for reef fish and increasing long-term fitness (Binning and Roche 2015). Since 1970, coral cover on Caribbean reefs has decreased by an average of 80%, with degraded reefs shifting to novel species assemblages with limited populations of reef-building corals (Gardner et al. 2003, Toth et al. 2019). As reefs are increasingly subjected to anthropogenic and natural stressors, high coral mortality reduces carbonate production below erosion rates, removing critical structural complexity

(Graham and Nash 2013, Perry et al. 2013). As a result, flat, homogenous reefs with low coral cover and reduced structural complexity have increased in proportion across the Caribbean, from a low of 20% in the 1970s to 75% as of 2009 while structurally complex reefs have decreased in prevalence from 45% of Caribbean reefs to just 2% (Alvarez-Filip et al. 2009). The loss of structure on reefs from coral mortality has been repeatedly demonstrated to cause shifts in fish species assemblages (Alvarez-Filip et al. 2015) and could reduce fisheries productivity up to three-fold (Rogers et al. 2014). Reef degradation leads to the homogenization of fish assemblages and the loss of specialist species (Pratchett et al. 2014, Richardson et al. 2018). However, previous work has been largely limited to classifying species within a single family as generalists or specialists along a single trait axis, such as corallivory within Chaetodontidae (reviewed by Pratchett et al. 2008) or habitat breadth within Pomacentridae (Wilson et al. 2008). Using a trait-based analysis provides the ability to determine the effects of reef flattening on specialization across the reef fish assemblage and along several trait axes. Additionally, although coral cover and structure are often conflated, they represent different components of reef complexity (Coker et al. 2014). Species like parrotfishes have much higher abundances on reefs with high structural complexity (Almany 2004), but have been shown in the Pacific to experience short-term population growth in response to the proliferation of algae following bleaching events which kill corals (Adam et al. 2011). Therefore, it is critical to distinguish between the effects of lost coral cover versus declines in structure to determine how all reef species will respond to different stages of reef flattening.

For trait-based analyses to provide a useful predictive framework, a suite of easily measurable or observable characteristics that can be linked to responses to disturbances and effects on ecosystem function must be available (Cadotte et al. 2011, Bartomeus et al. 2018). There is often a tradeoff between availability or ease of measurement and specificity of a trait, especially when comparing across large data sets (Cadotte et al. 2011). Traits that are too broad are unlikely to be informative in explaining species responses or effects on ecosystem function, but very specific traits may be either difficult to measure or present challenges when generalizing to data-deficit species. Coral reef fishes are well suited for trait-based analyses (reviewed by Hadj-Hammou et al. 2021), and the more common and non-cryptic species tend to have well described traits in databases (FishBase, Froese and Pauly 2000) and the literature (Mouillot et al. 2014, Alvarez-Filip et al. 2015, Bridge et al. 2016). Indeed, the use of traits in coral reef fish research continues to grow (Anderson et al. 2022, Hodge and Price 2022, Ferrari et al. 2023). A second key consideration when conducting trait-based analyses is that traits and phylogeny are often inextricably linked as organisms evolve alongside changes in their environment (Li and Ives 2017). When traits and phylogeny are highly correlated it is difficult to untangle whether environment or evolution was the more important driver of assemblage along a trait axis (Schweikert et al. 2018). The well-described evolutionary relationships of reef fishes as part of the fish tree of life

(Rabosky et al. 2018) facilitates the inclusion of phylogeny in trait-based approaches.

Like many reefs close to large urban populations, the marine ecosystem of south Florida is highly threatened by a range of stressors including climate change (Manzello 2015), coral diseases (Precht et al. 2016), overfishing (Ault et al. 1998, McClenachan 2009), loss of grazing species (Chiappone et al. 2002), decreasing water quality (Ward-Paige et al. 2005), invasive species such as lionfish (Ruttenberg et al. 2012), and damage from hurricanes (Blair et al. 1994). The combination of the long-term degradation of reefs and recent acceleration by anthropogenic forces have led to region-wide low coral cover and the proliferation of flat, degraded reefs (Burman et al. 2012). Despite their decline, Florida's Coral Reef still supports productive reef fish assemblages that in turn support fisheries and tourism (Ault et al. 1998), and being able to predict further future changes to fish assemblages is critical. The aim of this study is to predict the winners and losers of reef flattening on Florida's Coral Reef by using comprehensive species- and trait-based approaches to link current estimates of structural complexity and coral cover to current fish densities and identify traits that predict those densities. We first combine fish survey data from a large-scale monitoring program with a range of biophysical and anthropogenic factors to build a well-parameterized and uniquely detailed model explaining variation of reef fish species' densities. We then extract the influence of relief and coral cover in explaining the variation in species' densities on reefs, thus identifying species which are likely to increase (winners) or decrease (losers) in abundance on less complex reefs. Finally, we test species' associations with relief and coral cover for phylogenetic relationships and determined if 13 easily measurable or observable morphological, behavioral, and ecological traits explained species' responses to loss of structure and coral cover. We predict that, across the entire fish assemblage, species with traits associated with movement in complex environments (small body size, maneuverability) or specialized functions (herbivory, piscivory) will be losers, and more generalist species (intermediate trophic levels, multiple habitats) will be winners of reef flattening.

Material and methods

Study area

Florida's Coral Reef contours the Atlantic coast of mainland southeast Florida and along the Florida Keys, stretching more than 550 km from Martin County to the Dry Tortugas (approximately 27°50' to 24°55'N, 80°28' to 83°00'W). We used geospatial maps created by the Florida Fish and Wildlife Conservation Commission (FWC) to identify coral reef (currently or historically associated with cover of stony corals) and hardbottom (low-relief calcium carbonate benthos typically dominated by gorgonians and algae) habitats deeper than 2 m. We included fish survey data collected on habitats categorized by the level two classification of Florida's Unified Reef

Map (URM) as one of the following types: Aggregate reef, Individual or Aggregated patch reef, Spur and groove, (Coral Reef) ridge, Reef rubble, Colonized reef rubble, Pavement, and Colonized pavement (FWC 2016). Pavement sites were included as low-relief, low-coral cover hardbottom habitats represent a potential outcome following loss of reef-building corals and long-term erosion of coral reef sites. Preliminary models separating each habitat group showed similar factors drive fish abundance (Zuercher et al. 2023).

Reef and fish survey data

Since 1979, NOAA has conducted fishery-independent coral reef fish and benthic surveys across southeast Florida as part of the Reef Visual Census (RVC) and National Coral Reef Monitoring Program (NCRMP) (Bohnsack et al. 1999, Smith et al. 2011, NOAA 2017). Sites were surveyed annually (before 2014) or biennially (2014 to present) using a two-stage stratified random sampling scheme in conjunction with a 100 × 100 m resolution grid covering Florida's Coral Reef. The first stage stratified grid cells by habitat type within three sub-jurisdictions (Florida Keys, Dry Tortugas/Marquesas and southeast Florida), and survey sites were randomly selected within each 100 × 100 m cell. One or two diver pairs conduct stationary point counts and size assessments of over 500 species of fish (see Bohnsack and Bannerot 1986 for details of this approach), visually estimate benthic coral cover, and measure rugosity based on maximum vertical relief of the substrate within individual 7.5 m radius cylinders. Briefly, each diver created a list of fish identified to species level that entered the cylinder in the first five minutes, counting and sizing highly mobile species. The following ten minutes were used to count and size individuals remaining in the cylinder while adding any new fish entering the cylinder. The rest of the dive was used to assess the benthos, including measuring maximum height of hard relief visually estimating live hard coral cover from an overhead view within the cylinder (NOAA 2017). Maximum hard relief is a metric of reef complexity measured as the average of the highest rigid point within 8 segments of the 7.5 m survey cylinder. Coral cover was measured as the average of live hard coral visually estimated within eight segments of the 7.5 m survey cylinder. Data from the pair of divers (or from multiple pairs of divers where appropriate) at the same site were averaged. We used survey data from 2005 to 2018, excluding 2010 when a significant cold snap caused fish kills (Kemp et al. 2016). Out of 7046 unique sites in the region surveyed since 2005, using data from the most recent surveys if surveyed multiple times, 3292 sites were designated as coral reef or hardbottom by the FWC UFRTM level two classifications. We included 109 reef fish species from 25 families (Table 1), all of which were present at 4% or more of sites, which was experimentally determined as the minimum number of non-zero values necessary to run the density models. We excluded cryptic species that are difficult to survey with point counts (e.g. species in families Gobiidae, Blennidae and Muraenidae) (Willis 2001).

Table 1. Biophysical and anthropogenic predictors used to model individual species' densities

Variable	Description	Derivation
Area of reef within 20 km	Area of reef and pavement habitat within 20 km of reef cell	UFRTM habitat maps
Availability of mangrove nursery habitat	Reef connectivity to mangrove nursery habitat	Use of algorithm (Mumby 2006) in combination with UFRTM habitat maps
Availability of seagrass nursery habitat	Reef connectivity to seagrass nursery habitat	Use of algorithm (Mumby 2006) in combination with UFRTM habitat maps
Coral cover	Coral cover at survey site	From fish survey data set
Community fishing engagement and reliance	Metrics of fishing engagement and economic reliance on fishing by fishing community	Data provided by Michael Jepson (NOAA NMFS) (Jepson and Colburn 2013)
Depth	Depth of data collection	From fish survey data set
Distance to deep water habitats	Distance to 30 m depth contour	30 m contour derived from data available in Sbrocco and Barber (2013)
Distance to fish spawning aggregation	Distance to nearest known snapper or grouper spawning aggregation	Location data for spawning aggregations provided by Todd Kellison (NOAA NMFS) and Ben Binder (FIU)
Fishery activity: commercial	The number of class 1 federal snapper-grouper permits within 50 km of reef cell	Data provided by NOAA NMFS SEFSC
Fishery activity: charter	The number of federal snapper-grouper permits assigned to charter vessels within 50 km of reef cell	Data provided by NOAA NMFS SEFSC
Fishery activity: recreational 50 km	The number of marine recreational fishing license holders within 50 km of reef cell	Data provided by the FWC
Fishery activity: tourism-related	The estimated number of tourism reef fishing days per year on a reef cell	Data on tourist hotel units publicly available from FGDL; estimates of tourist fishing days by county from Johns et al. (2001) Cinner et al. 2018
Gravity of all potential fish markets (within a 500 km radius)	Market gravity defined as population size divided by the square of travel time (a proxy for distance)	
Habitat type	Level two classification of reef habitat type	UFRTM habitat maps
Human population within 50 km of reef	Number of people within 20 km of a reef cell	LandScan human population data
Human population per area reef within 50 km	Number of people within 50 km divided by area of fishable reef within 50 km	LandScan human population data
Marina slips	The number of marina slips (<14 m) within 25 km	FWC data layer available online
Month	Month of data collection	From fish survey data set
Number of larvae from upstream	Estimate of relative number of larvae arriving at each reef from upstream sources only	Biophysical model of ocean currents provided by Claire Paris (Univ. of Miami)
Oceanic net primary productivity (NPP)	Mean net primary productivity from monthly data 2012–2016	Oregon State University-modelled product derived from satellite data
Protected status	Whether the site is a no-take area or open to fishing; level of fishing protection	FWC and NOAA databases of marine protected areas
Relief	Reef complexity measured as maximum height above substrate	From fish survey data set
Sea surface temperature (SST)	Mean temperature of the coldest month	NOAA's CoRTAD satellite-based ocean temperature dataset
Wave exposure	Wave exposure based on fetch and mean wind data	Data layer provided by I. Chollett (Chollett et al. 2012)
Year	Year of data collection	From fish survey data set

Biophysical and anthropogenic predictors

To model species densities at each survey site, we compiled biophysical and anthropogenic explanatory variables (Table 2) from in situ, remotely sensed and published data sources. Justification for inclusion and full derivation of each predictor is available in the Supporting information. Maximum hard relief, coral cover and depth were all measured in situ by NOAA NCRMP divers. Maximum hard relief provides a proxy for large scale complexity, capturing boulders and drop offs, while coral cover generally captures small-scale complexity. Month and year of surveys were included as categorical

variables to account for seasonal and longer-term trends in species densities.

The remaining predictors were extracted (using the coordinates of the underwater surveys) from continuous geospatial data layers with a grid size of 100 × 100 m in ArcGIS Pro (ver. 10.7 ESRI). The biophysical variables used to predict individual species' densities from these layers included UFRTM habitat level two class, the total area of coral reef and hardbottom habitats within 20 km of each site, connectivity to mangrove and seagrass nursery habitats, distance to deep water habitats, lowest monthly mean sea surface temperature (SST), net primary productivity (NPP), larval connectivity,

Table 2. Traits used to determine if morphology, behavior, and ecology can explain associations between species' densities and relief or coral cover $A = h^2/s$, where h is height and s is surface area (Bridge et al. 2016) using lateral photos from FishBase (Froese and Pauly 2000) and Humann and Deloach 2002

Trait	Description	Derivation
Aspect ratio of caudal fin	Quantifiable analog of tail shape representing general tradeoff between speed and maneuverability	
Depth range	Maximum observed depth	Quimbayo et al. 2021
Group size	Classification into increasing group size: solitary, paired, small, medium, large groups	Quimbayo et al. 2021
Home range size	Categorized into sedentary, mobile, and highly mobile	Quimbayo et al. 2021
Maximum total length	Maximum observed length in cm from tip of head to longer lobe of caudal fin	FishBase (Froese and Pauly 2000)
Multihabitat	Observation in more than 1 habitat type	Luiz et al. 2013
Nocturnal	Activity at night	Green and Côté 2014, FishBase (Froese and Pauly 2000), and field observations
Physical or chemical defenses	Presence of defenses such as spines or toxins	Green and Côté 2014 and FishBase
Position in water column	Categorized into benthic (living in or on the bottom), demersal (<2 m from bottom), or pelagic (>2 m above bottom)	Green and Côté 2014 and FishBase
Spawning mode	Categorized into pelagic (eggs released in water column), demersal (slow-developing eggs or swimming young are guarded or brooded), or balistid (fast-developing eggs are guarded)	Luiz et al. 2013
Swim mode	Combination of body and fin movements used for routine activity (Fulton 2010)	Fulton 2010
Swim type	Combination of fin movements used for propulsion (Fulton 2010)	Fulton 2010
Total length to body depth ratio	Quantifiable analog of body roundness	$R = TL/BD$, where TL is total length and BD is linear distance from pelvic girdle to pectoral ridge using lateral photos from FishBase (Froese and Pauly 2000) and Humann and Deloach 2002
Trophic level	Estimation of mean weight of trophic level of food items (Froese and Pauly 2000)	FishBase (Froese and Pauly 2000)

wave exposure, and distance to the nearest mapped fish spawning aggregation (FSA). We also included 10 anthropogenic variables to account for human impacts, specifically impacts from fishing which has major effects on populations of reef fishes like snappers and groupers (Zuercher et al. 2023). These predictors included the number of recreational anglers within 50 km, human population within 50 km, human population per reef area within 50 km, the number of marina slips for boats under 14 m within 25 km, gravity of all potential fish markets (within 500 km), the number of federal commercial (within 50 km) and charter (within 25 km) snapper–grouper permits, metrics of community fishing engagement and reliance, the estimated number of tourist fishers, and the protected status of reefs.

Fish trait data compilation

We assembled 13 morphological, behavioral, and life history traits to identify which traits were predictive of a species' relationship to relief or coral cover. Justification for inclusion and full derivation of each set of fish traits is available in the Supporting information. Trait values were collected from a combination of published literature, online databases (particularly FishBase, Froese and Pauly 2000), and measurements from publicly available photographs. For morphological traits derived from photographs, a single value

was obtained from the mean of three lateral images of adults of the species of interest. Local values of traits (i.e. in Florida or northern Caribbean) were used where available. When possible, continuous, quantifiable analogs were used in place of categorical variables to produce higher quality functional spaces (Maire et al. 2015). Maximum total length, total length to body depth ratio, and presence of physical or chemical defenses were included based on the known importance of morphology in determining predation risk and availability of spatial refuge (Green and Côté 2014). Swim type (fin and body combination for propulsion) and aspect ratio (ratio of height squared to surface area) of the caudal fin were used to highlight the importance of swim performance for predator avoidance and maneuverability for navigating complex reefs (Fulton 2010). Additionally, schooling and nocturnality were included as each are common predator avoidance techniques, which may reduce the need for structure for refuge (Green and Côté 2014). Whether a species uses multiple habitat types (hereafter referred to as multihabitat), home range size and depth range were included as proxies for specialization to shallow coral reef habitats (Luiz et al. 2013), while specific associations with the benthos were determined by position in the water column and spawning mode. Finally, trophic level was included because reef structure has a variety of effects on feeding, for example, complexity may increase the surface area for herbivores to

graze (González-Rivero et al. 2017) or provide hiding places for ambush predators (Harborne et al. 2022).

Data analysis

We first modelled the density of each species against biophysical and anthropogenic predictors and extracted the association of each species' density with relief and coral cover to determine the importance of complexity for the species-based analysis (Fig. 1). The density models provided 1) the overall percentage of variation in individual species' densities explained by all included predictors and 2) the percentage contribution of each predictor to explaining the variation in species' densities. We multiplied the percentage contributions of relief and coral cover by the total variation explained in the model to get a value for the contributions of relief and coral cover to the overall species densities. This approach accounts for both the overall model fit and the relative importance of each variable while controlling for a range of other factors. We assigned a positive or negative score to these variables based on the relationship visualized in the partial dependency plots whereby species with positive associations with maximum hard relief or coral cover were considered losers in reef flattening, and negative associations considered winners. These results were the response variables for the trait-based analysis, where relief and coral cover were separately modeled to identify associations with species' traits. We also tested those associations for phylogenetic patterns.

Species' density and trait associations were each modeled using boosted regression trees (BRTs) which use boosting with an adaptive algorithm (combining many simple models to improve performance) to relate response variables to explanatory variables using recursive binary splits (Elith et al. 2008). BRTs are robust to different types of predictors (continuous, binary, factor), accommodate missing data, allow for non-linear relationships, automatically handle interactions and can fit large numbers of explanatory variables (Elith et al. 2008). BRTs also generate intuitive graphs (partial dependency plots) for visualizing relationships and display the contribution (percentage of total variance explained) of each explanatory variable to the model.

All numerical covariates were tested for co-linearity and we removed variables with correlations > 0.85 . We also ensured that no model variables had variance inflation factors (VIFs) > 10.0 . The same set of variables was then used for all species density models to maintain a common model architecture necessary for inter-species comparisons. Since the species-level models were generated to simply identify the importance of complexity and coral cover, no model simplification was conducted. However, for the trait analysis models, we included a variable comprised of randomly generated numbers as a guide to identify 'significant' variables (Soykan et al. 2014). Variables explaining less deviation than the random variable were removed from final models. BRT parameters (learning rate, tree complexity, and bag fraction) were calculated for the density models by testing a range of possible values and using the values which gave the lowest model

deviance for density of a representative species *Sparisoma viride*. Note that BRT parameters may affect model fitting efficiency but are highly unlikely to affect correlations with covariates. For 14 species that exhibited lower variance across sites, learning rates were decreased to improve better model performance, but tree complexity and bag fraction were unchanged. Model performance was assessed by the total deviance explained by the model and the correlation between observed and predicted values. Due to the stochasticity of BRTs, we ran multiple iterations of each model and averaged explanatory variable contributions. We ran 10 density models per species, and 1000 models for trait analysis of maximum hard relief and coral cover. All analyses were done in R ver. 4.1.1 (www.r-project.org) and RStudio ver. 2021.09.0, using the packages 'dismo' ver. 1.3-5 (Hijmans et al. 2021) and 'ggBRT' ver. 0.0.0.90 (Jouffray et al. 2019).

We modeled species counts using a Poisson distribution of abundance using an offset of total area surveyed to account for variation in survey area due to additional diver pairs. Whereas biomass is a metric well suited to functional analyses (e.g. predator-prey interactions), here we were particularly interested in species-specific abundance independent of fish size. The metric of fish density better captures smaller-bodied individuals thus increasing representation of the small-bodied species and juveniles more common on reefs. Large numbers of small species and young individuals of larger species also underpin complex coral reef food webs with important implications for reef fish assemblages (Alvarez-Filip et al. 2011, Rogers et al. 2014, Brandl et al. 2019, Siqueira et al. 2021). Furthermore, access to structure is typically a density- rather than biomass-dependent process where there is intra- and interspecific competition for refuge (Holbrook and Schmitt 2002). Although many species' densities were zero-inflated, hurdle models provide separate sets of results for species' presence on reefs and density on reefs where species are present, which limit comparisons across models. Preliminary analyses of species' densities showed similar results between hurdle and zero-inflated models, so we used the zero-inflated density models to simplify model interpretation and generalization. Trait-based analyses were modeled using a Gaussian error structure using each of the two separate response variables: association species' densities with relief or coral cover from the density models.

Phylogenetic signal

Closely related species often have similar traits, and ignoring phylogenetic relationships among traits can lead to increased statistical error and incorrect model conclusions (Li and Ives 2017). To account for the effects of species' relatedness, we constructed phylogenetic trees using The Fish Tree of Life (Rabosky et al. 2018) and the R package 'fishtree' ver. 0.3.2 (Chang et al. 2019). Of the 109 species used in the trait analysis, 103 were present in the phylogeny and used to create a phylogenetic tree for analysis with the R package 'ape' ver. 5.3 (Paradis and Schliep 2019). Using results from the models of species density, we estimated the phylogenetic signal among

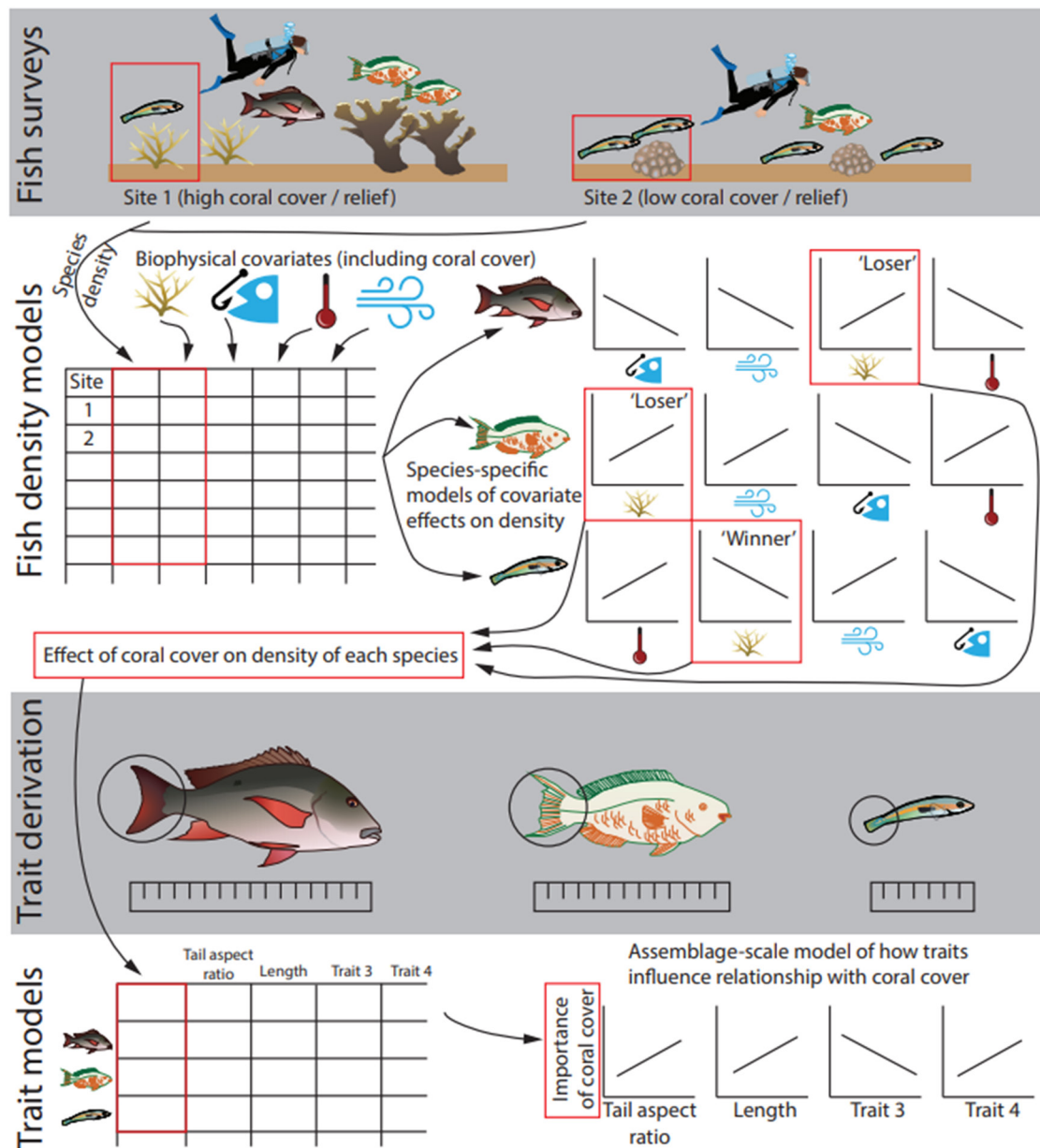


Figure 1. Schematic depicting the methods for the species- and trait-based analyses. The schematic depicts the methods for examining correlations with coral cover (highlighted by red boxes), but the analyses also included correlations maximum hard relief. Reef fish counts, relief, and coral cover were recorded in situ and combined with additional biophysical and anthropogenic covariates to create fish density models. The correlations of coral cover and relief with density were extracted from the fish density models and used as the response variables for the trait-based analyses.

species' responses to relief or coral cover by calculating Pagel's λ (Pagel 1999, Freckleton et al. 2002) and Blomberg's K using the 'phytools' package ver. 0.6-99 (Revell 2012). Pagel's λ is a measure of the phylogenetic correlation of a trait, where 0 represents complete independence and 1 shows covariance in proportion to shared evolutionary history. We tested Pagel's λ against a null hypothesis that $\lambda = 0$ using a likelihood ratio test. Blomberg's K tests the phylogenetic signal compared to expected evolution of a trait under Brownian motion (Blomberg et al. 2003). We tested Blomberg's K against a null hypothesis that $K = 0$, indicating species are less similar than

expected under Brownian motion evolution, using a likelihood ratio test with 1000 simulations.

Results

Density models and extracting contribution of relief and coral cover

Species-specific density models explained an average of 58.4% of the variation in species densities across Florida's

Coral Reef, ranging from 90.2% for *Chromis scotti* to 11.0% for *Scorpaena plumieri* (Supporting information). Correlations between observed and predicted values corresponded to deviance explained, averaging 0.789, with a maximum of 0.974 and a minimum of 0.166. Models for rarer species (those present on fewer reefs or in lower abundances) tended to have lower deviance explained or a weaker correlation between observed and predicted values; for example, species present at 10% or fewer survey sites had an average variance explained of 42.4% and correlation of 0.631. Overall species' responses to relief and coral cover had a weak positive correlation (p -value < 0.001, $R^2=0.157$) with a small number of species showing opposite relationships to each factor. The percentage of variation explained by maximum hard relief to the overall density of each species ranged from +21.2% for *C. scotti* to -14% for *Xyrichthys splendens* and a mean of +4.5%. The contribution of coral cover to the density of each species ranged from +41.5% for *Hypoplectrus nigricans* to -10.2% for *X. splendens* with a mean of +1.5%. A positive relationship between density and relief or coral cover means that the species was considered to be a 'loser' (density decreases with decreasing relief or coral cover). Conversely, species showing a negative relationship are designated as 'winners'. To identify the overall influence of relief to species' densities, the directions of the relationships were removed to calculate an average percentage of variation explained of 7.2%. The overall influence of coral cover to species' densities was 3.5%, approximately half that of relief. By setting a threshold of 5% of the total variance explained by the model that is correlated with relief or coral cover as indicating a demographically significant association, we identified 58 losers and 15 winners of flattening out of the 109 species, but only 12 losers and 8 winners of the loss of coral cover. Relief was not a significant predictor for the densities of 38 species and coral cover not significant for 91 species' densities. Only four species were indicated as winners of declines in both relief and coral cover.

In general, wrasses and razorfishes (Family: Labridae) were winners of reef flattening and coral loss. In contrast, most parrotfishes (Subfamily: Scarinae), which are also in the Labridae family, were losers of flattening and had variable responses to coral cover. Fishes in the family Pomacentridae, which include damselfishes, were consistently linked with high relief and mostly positively associated with coral cover. Most grunts (Family: Haemulidae) had strong positive relationships with relief and weaker, but still positive, associations with coral cover. Most of the large- and small-bodied groupers (Subfamily: Epinephelinae; Family: Serranidae) were positively associated with relief and coral cover. In the remainder of the Serranidae family, there was a strong split between hamlets in the genus *Hypoplectrus* that appear to be losers of flattening and loss of coral and reef sea basses in the genus *Serranus* as winners. Butterflyfishes (Family: Chaetodontidae) and angelfishes (Family: Pomacanthidae) had positive associations with relief and coral cover and are thus likely losers of flattening.

Trait-based analysis

Species' traits explained 79.7% of variation in the association of species' densities on reefs and 27.8% of variation with coral cover. Eight traits (body roundness, multihabitat, caudal fin aspect ratio, swim mode, group size, total length, depth range and trophic level) were significant predictors of species' association with relief. The same traits, but not swim mode and group size, were correlated with responses to coral cover, but trait relationships varied between the two responses (Fig. 2, Table 3).

Body roundness was the strongest predictor of a species' association with relief, accounting for 17.3% of variance in the model. Rounder species, specifically species with total length to body depth ratios less than 4.0 (e.g. angelfishes and butterflyfishes), tended to be strongly associated with high relief (Fig. 2). Aspect ratio of the caudal fin (15.6% of variance) was the next most important predictor and showed a non-linear correlation with relief. Species with aspect ratios below ~ 1.2 (rounded caudal fins) were predicted to increase in density following flattening. Species with aspect ratios between 1.2 and 2 were predicted to decrease and species with ratios above 2.0 (caudal fins with larger heights and lower surface areas like in forked or lunate fins) were largely unaffected. Habitat generalists were much more likely to have positive associations with flatter reefs, with the multihabitat trait explaining 15.1% of the variance. Maximum total length (11.0%) generally had a positive relationship with relief, with species below 40 cm largely associated with flat reefs. Group size explained 10.5% of association with relief, with species found in small groups decreasing in density and solitary species increasing as relief decreased. Paired, medium groups, and large groups were largely unaffected by flattening. Trophic level explained 10.3% of variance with a positive relationship with relief. Herbivores were more likely to be winners of flattening, while piscivores in trophic levels above 3.7 were major losers. Swim mode explained 10.1% of the variance, with carangiform, chaetodontiform, and subcarangiform swimmers associated with complex reefs and tetraodontiform swimmers with flat reefs. Narrower depth ranges (10.0% of variance) were associated with a stronger association with relief, and species with ranges greater than 70 m tended to be unaffected by flattening.

Trophic level was the most important predictor of association with coral cover, accounting for 23.1% of the variance (Fig. 3). Trophic level showed a similar pattern to relief with piscivores being the biggest losers of coral loss; however, omnivores were more likely to be winners and herbivores were unaffected. Body roundness explained 22.6%, and the roundest species were most likely to be losers, but the threshold for positive association with coral was approximately a total length to body depth ratio of 3.0, with a small spike around 4.0. Maximum total length explained 20.7% of the association with coral cover. Like relief, there was generally a positive relationship between size and association with coral, except that species smaller than 20 cm had strong links to coral cover. Aspect ratio of the caudal fin explained 15.5%

of the association with coral cover but showed a much different relationship than with relief. Species with aspect ratios greater than 2.0 tended to be positively linked to coral cover, and those with ratios smaller than 2.0 were indicated as likely winners of flattening. Habitat generalists (10.0%) had a similar response to coral cover as with relief, with multihabitat species increasing in density with coral loss. Depth range (8.1%) had an opposite relationship with coral cover as with relief, with the narrowest depth ranges likely to be winners of coral loss.

Phylogeny

Using a phylogenetic tree of the 103 species available in the Fish Tree of Life database (Fig. 2, Supporting information), we estimated the phylogenetic signal of the contribution of relief and coral cover to species density. Estimation of Blomberg's K showed no phylogenetic relationship for species' association with either relief ($K=0.001$, $p\text{-value}=0.674$) or coral cover ($K=0.011$, $p\text{-value}=0.149$). Estimation of Pagel's λ supported a lack of phylogenetic signal a species' relationship

with coral cover ($\lambda=0.095$, $p\text{-value}=0.482$), but showed a weak but non-zero signal for relief ($\lambda=0.469$, $p\text{-value}=0.001$).

Discussion

The association between fishes and structurally complex coral reef habitats has been well established (Graham and Nash 2013), but predicting the long-term effects of reef flattening on fish assemblages and consequent ecosystem functioning is difficult without a species-specific understanding. Furthermore, with the many biophysical and anthropogenic factors affecting reef fishes it can be challenging to isolate the influence of relief and coral cover on fish abundance. By pairing a large fish survey data set with a wide range of biophysical and anthropogenic factors we have been able to quantify associations between densities and relief and coral cover separately for more than 100 species. This study has also developed a trait-based framework that identifies a suite of morphological, ecological, and behavioral traits which predict species' responses to reef flattening. Overall, traits that are strongly linked to maneuverability within complex reefs,

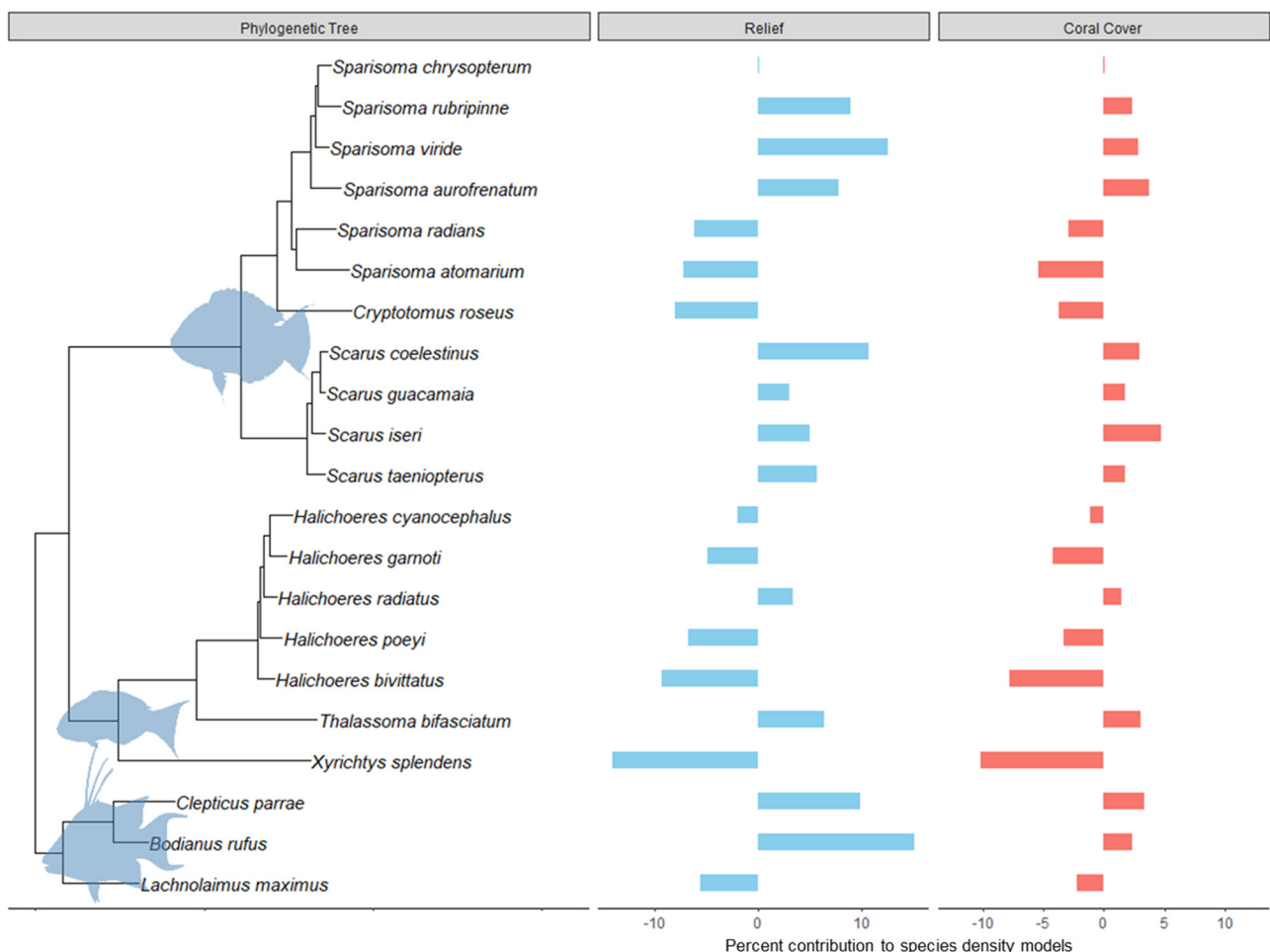


Figure 2. Example subset of phylogenetic tree showing the Labridae and their associations with relief and coral cover. For example, the abundance of *Sparisoma rubripinne* is positively correlated with both relief and coral cover across the sites surveyed.

Table 3. Results of boosted regression tree models for trait-based analyses for association with relief and association with coral cover averaged across 1000 iterations

Model	Variance explained (%)	Correlation between observed and predicted values	Significant predictors (% explained)
Association with relief	79.7	0.91	Total length body depth ratio (17.3) Aspect ratio of caudal fin (15.7) Multihabitat (15.1) Maximum length (11.0) Group size (10.6) Trophic level (10.3) Swim mode (10.1) Depth range (10.0)
Association with coral cover	27.8	0.64	Trophic level (23.1) Total length body depth ratio (22.6) Maximum length (20.7) Aspect ratio of caudal fin (15.5) Multihabitat (10.0) Depth range (8.1)

such as deep bodies and low aspect ratio fins, seem to be a tradeoff that lower the capacity to maintain similar population densities on flattened reefs.

Maximum hard relief explained more variation in the species' densities across Florida's Coral Reef and was linked to a larger number of species than coral cover. Measures of maximum hard relief better match the scale of complexity that typically drives reef fish densities by capturing large overhangs, crevices and holes that provide critical shelter (Wilson et al. 2007, Harborne et al. 2022). Although coral cover is positively associated with increased complexity and shelter space on reefs with high coral cover like those in the Pacific, there is a decoupling of live coral and complexity on low coral cover reefs (Graham and Nash 2013). Unlike Pacific reefs where coral cover may correspond with the presence of large, structure-providing corals (Kerry and Bellwood 2012), the drastic loss of reef-building corals on Caribbean reefs has led to reef ecosystems with unprecedentedly depauperate coral assemblages, so even reefs with relatively high coral cover are largely made up of weedy corals that provide little structure (Toth et al. 2019).

In particular, Florida has seen major declines in branching *Acropora* corals that provide fine-scale complexity (Alvarez-Filip et al. 2009) and mounding *Orbicella* corals contributing to meso-scale complexity (Harborne et al. 2012). While the weeder coral species may still supply important functions like providing settlement cues for reef fishes, the lack of shelter space may be responsible for the weak relationship between reef fish densities and live coral cover (Coker et al. 2014). Additionally, there are no obligate corallivores that rely on corals as a major part of their diet in the Caribbean (Burkepile 2012). Indeed, current fish assemblages may already reflect a response to the near-single-digit coral cover recorded in the Florida Keys since the early 1980s (Schutte et al. 2010). However, the variation of coral cover captured in the data (0–55%) suggests that the patterns described here are not simply artifacts of current reef state. Instead, the stronger relationship between maximum hard relief and reef fish species

emphasizes the importance of scale-appropriate shelter space for fish densities and that long term reef flattening will likely result in more drastic reductions in reef fish abundances than loss of live coral cover. Indeed, predictions of Florida reef fish biomass under different management scenarios showed that the addition of relief with artificial reef structure is expected to result in significantly higher biomass for all reef fish than the restoration of coral alone (Zuercher et al. 2023), supporting our findings that relief has a higher relative importance than coral cover across the assemblage.

The lack of strong phylogenetic relationships in species' responses to relief and coral cover suggest fishes may have adapted to structure multiple times during their evolutionary history and use structure in different ways. This pattern is not unique among reef fish traits, as other functional traits including trophic level and extreme body sizes have evolved independently multiple times in reef fish lineages (reviewed by Floeter et al. 2018). Untangling phylogeny from traits is important when determining the drivers of community assemblages and potentially identifying mechanisms linking organisms to their environments (Li and Ives 2017). In the absence of a phylogenetic signal, species' densities can be tied more directly to the suitability of their morphological, behavioral, and ecological traits to their habitat than to outcomes of unknown historical processes. Thus, our results provide an understanding of the trait space reef fishes occupy, which allows us to predict how less common reef species (e.g. those not modeled in this study) may respond to long-term reef degradation based on how well their traits are adapted to reef environments.

The winners of reef flattening and coral loss (species with higher abundances on flatter reefs) tend to have generalist traits, including labriform swim mode, multihabitat use and wider depth ranges. Labriform swimming is a flexible form of locomotion that can be used to efficiently swim at a wide range of speeds, enabling the proliferation of labriform swimmers in both low- and high-flow habitats (Fulton et al. 2005, Fulton and Bellwood 2005). While evidence for deep reefs as refuge

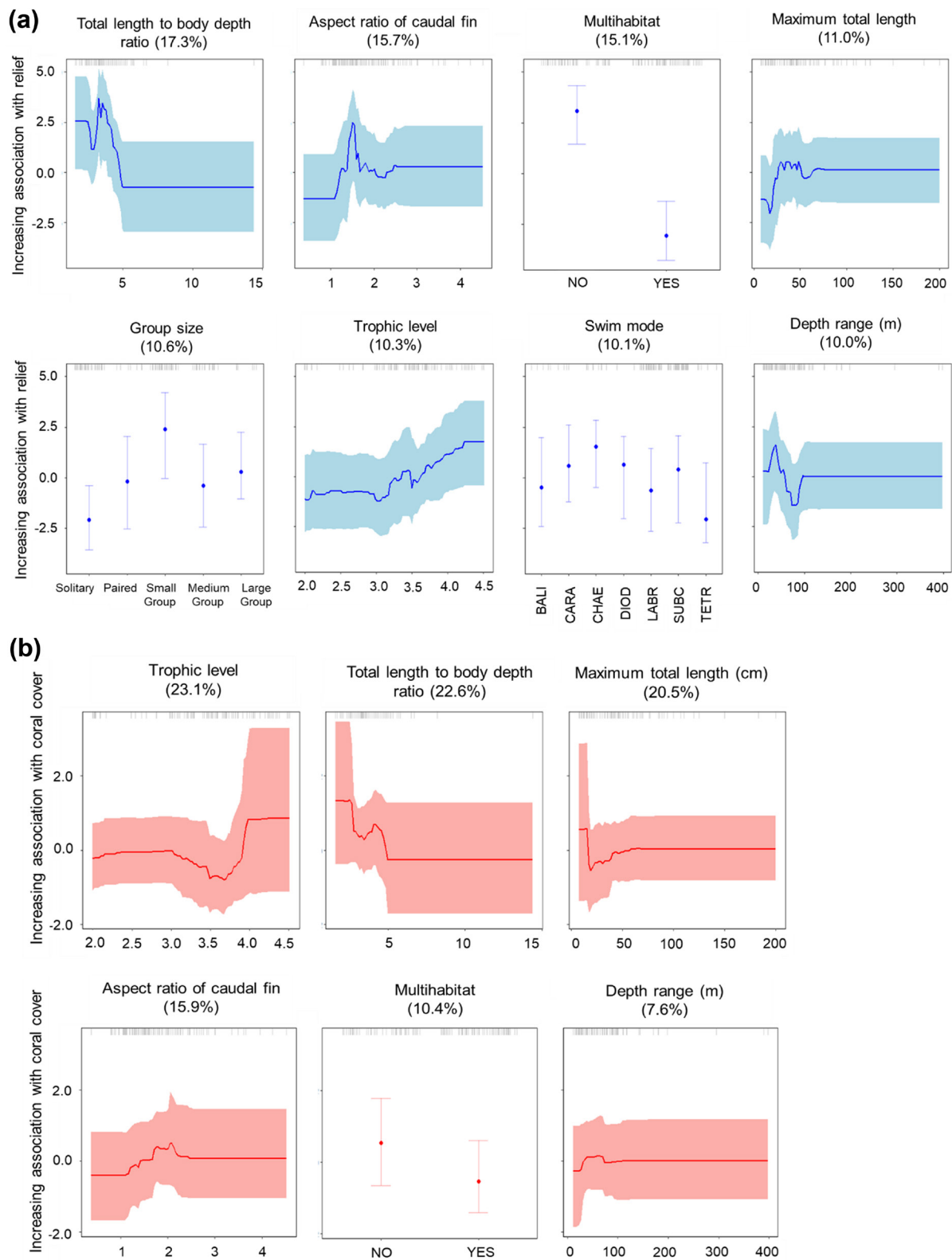


Figure 3. Results from boosted regression tree analysis testing for links between fish traits and (a) association with relief and (b) association with coral cover. Shaded areas and error bars represent 95% confidence intervals created by 1000 bootstrap replicates. Parentheses show average amount of model variance explained. Swim modes are balistiform (BALI), carangiform (CARA), chaetodontiform (CHAE), diodontiform (DIOD), labriform (LABR), subcarangiform (SUBC), tetraodontiform (TETR). Tick marks at top of each panel show distribution of data points.

for shallow-water species is minimal (Stefanoudis et al. 2019, Medeiros et al. 2021), species with wide depth ranges that are reliant on structure providing spatial refuge to persist in shallow, high-wave energy environments may be able to find refuge in deeper waters where surface currents and wave energy are weaker (Fulton et al. 2005). In contrast, populations of species with restricted depth ranges are likely to decline if structure is necessary to live in their preferred, high-energy zones (Johansen et al. 2008). Species found only on coral reef habitats throughout their life cycle (lacking the multihabitat trait) were major losers of flattening and had a lower, but still positive, association with coral cover. Specialists that fully rely on reef habitats throughout their life cycle have multiple possible disruption points during development, such as decreased larval settlement or increased competition for fewer refuges, which amplifies the effects of habitat degradation on mortality and reproduction (Stuart-Smith et al. 2021). As generalists become more dominant, assemblages on future flattened reefs are likely to be more resilient against additional stressors; however, the loss of specialists may have critical implications for ecosystem functioning on coral reefs.

The morphological and swimming traits of species predicted to decline on flatter reefs further suggest that refuges provided by both relief and coral cover may be more important than recognized for lowering metabolic costs, and perhaps equally or more important than for protection from predation. The importance of structure is likely driven by the mediation of water movement, as the location of reefs within relatively shallow water increases in the influence of water flow and wave energy on reef species (Bellwood et al. 2002). Traits that increase maneuverability in complex habitats, such as body shape and tail shape, have increased metabolic costs when swimming in high-flow environments. Body roundness and size are positively associated with both relief and coral cover, suggesting larger, rounder species may utilize complexity more for refuge from water movement as their morphology provides protection from gape-limited predators. The link between body roundness and relief and coral cover is present across a range of fish sizes, affecting smaller species that may rely on the intricacies of branching corals as well as larger species utilizing crevices, ledges, and overhangs for refuges created by reef topography. Additionally, diurnal species or those with physical or chemical defenses did not have a significant negative association with complexity as expected (Green and Côté 2014), providing additional evidence of the role of structure beyond predator avoidance. The swimming modes with the strongest positive association with structure, carangiform and subcarangiform, are generally described as high-speed, low-maneuverability swimmers (Fulton 2010). Even though these swimming modes are best suited for movement in open, low-complexity areas, these species rely on structure to provide refuge and decrease metabolic costs when recovering from fast, sustained swimming (Johansen et al. 2008).

Other morphological and behavioral traits associated with relief and coral cover support the established role of complexity in providing refuge from predation. Species with

caudal fins with intermediate aspect ratios are predicted to decline on flatter reefs. These intermediate aspect ratio species appear to tradeoff high speeds for increased maneuverability to access refuges from predators in high relief and coral cover environments. Species with high caudal fin aspect ratios, which decrease drag and increase speed at the cost of maneuverability (Pauly 1989, Sambilay 1990), likely use their quick acceleration for escape rather than structure for refuge. Schooling is used as a strategy by fishes to reduce vulnerability to predation by increasing vigilance and decreasing any individual's probability of mortality (Magurran 1990). As expected, medium and large groups were not associated with relief or coral cover, suggesting schooling may be their primary antipredator defense mechanism, as opposed to relying on refuges provided by structure (Eaton et al. 2016). However, species forming small groups had the strongest positive association with complexity. The decreased effectiveness of small group sizes for predator protection may require those species to use structure as refuge, and on flat reefs there would be more individuals within a group competing for fewer crevices (Holbrook and Schmitt 2002). The success of solitary species on flattened reefs may be linked to this reduction in competition.

Trophic level had a significant relationship with both relief and coral cover, with top level predators severely declining on flatter reefs, potentially driven by reductions in prey abundances and productivity. Homogenization of reef structure through bioerosion generally decreases the number and the diversity of crevices, increasing competition for refuge from predators and removing disproportionately high numbers of small and intermediate prey fish on which large piscivores rely, and young individuals of those larger predatory species may be competing for the reduced number of refuges on flattened reefs, further reducing their abundances (Rogers et al. 2014). Decreases in productivity driven by smaller surface areas for primary producers (González-Rivero et al. 2017) and fewer high points allowing access to plankton while maintaining access to refuge (Hurley and Hartline 1974) limit food for prey species, which may further reduce prey availability for higher trophic levels. The impacts of losing relief on piscivore hunting efficiency is also poorly understood. The association of higher trophic levels with both relief and coral cover suggests predator-prey interactions are mediated by the availability of both small- and large-scale refuges.

In addition to providing a generic understanding of which species will be most affected by loss of structure, trait responses to loss of relief and coral cover provide important information for predicting how assemblage shifts and the potential loss of some traits will affect ecosystem functions. For example, predators have critical roles on reefs, shaping assemblages through consumptive and non-consumptive effects, driving trophic cascades and transporting and cycling nutrients (Hixon 1991, Heithaus et al. 2009, Williams et al. 2018). Thus the loss of piscivores may lead to a range of effects, such as the release of mesopredators with important consequences for juvenile fish and small species mortality and invertebrate abundances (Stallings 2008, Mumby et al. 2012).

Many predators are also large, and body size can be linked to important functions like nutrient cycling and transport, where larger species generally store more nutrients and move across wider spatial scales (Allgeier et al. 2014, Williams et al. 2018). Furthermore, body size provides an important link between ecosystem function and ecosystem services as fishers often target larger-bodied species with outsized functional roles on reefs (Bellwood et al. 2019).

In contrast to the decline of piscivory on flattened reefs, the trait-based analysis did not show a uniform positive association between herbivory and structural complexity as expected given previous work (Almany 2004). Instead, the density models showed differential impacts of reef flattening on grazing species with functionally important parrotfishes generally declining with loss of structure and some surgeonfish species increasing. Grazing, particularly by parrotfishes, is a critical ecosystem function that promotes resilience on coral reefs by removing macroalgae that may inhibit coral recruitment, increase mortality of juvenile and adult corals, and spread coral disease (Nugues et al. 2004, Nugues and Bak 2006, Box and Mumby 2007). While parrotfishes and surgeonfishes occupy the same trophic level, the differences in feeding modes, diet preferences and habitat usage among Caribbean grazers, and their opposing responses to loss of structure, has important implications for grazing as an ecosystem function on flattened reefs (Burkepile and Hay 2008, Adam et al. 2018, Duran et al. 2018). Individual parrotfish and surgeonfish species do not have interchangeable functions and graze differently (Burkepile and Hay 2010), so while the trait-based analysis predicts general abundances of grazers will not change on flattened reefs, it is important to consider herbivory in combination with other traits to demonstrate there will likely be serious functional implications caused by the loss of parrotfishes, as highlighted by a range of previous studies (Mumby 2006).

The results from this study provide critical information to move our understanding from broad positive relationships between reef structure and fish to identifying how structural complexity drives the densities of individual species. Furthermore, the trait-based analysis uncovered generic insights connecting morphology and behavior to structure and coral cover that allow us to hypothesize potential mechanisms linking complexity to fish species. While the generality of traits used in the analysis limits our ability to predict how specific functions may change on degraded reefs, there is value in extrapolating those results to data-deficient species. For example, the trait-based analysis provides information to build predictive models for rarer species not included in our analyses, such as the Goliath groupers *Epinephelus itajara* and Nassau groupers *Epinephelus striatus*. These iconic Caribbean species have been heavily fished and are absent throughout much of their historical range, making it difficult to predict how they would be affected by reef flattening. However, with traits including large, deep bodies, subcarangiform swim mode, and piscivorous diets (Froese and Pauly 2022), the trait-based analysis predicts strong positive associations with structure for both the Goliath and Nassau groupers. While

both species are protected from harvest by fishers, their continued recovery may be diminished without concurrent restoration of reef structure.

With the drastic decline in coral over the last several decades, fish assemblages may already be in a post coral paradigm across Florida's Coral Reef; however, strong associations between species and both relief and coral cover suggest that many species may become even less abundant with continued flattening. These results highlight the need to protect, and potentially artificially enhance, existing relief and coral cover to maintain crucial ecosystem services (Rogers et al. 2015, Zuercher et al. 2023). Additionally, the reliance on structure by commercially and recreationally important species suggests that limiting fishing pressure may not be sufficient for the recovery of those species. Finally, linking the responses of species and traits to habitat characteristics can provide crucial information for stakeholders designing management tools to achieve specific goals, such as increasing the density of parrotfishes to promote grazing or increasing piscivores available to fisheries. By continuing to build and incorporate trait-based mechanistic models into the management process, we improve our chances for preserving coral reefs and the species that rely on them into the future.

Acknowledgements – This work was made possible through support by Florida International University's Presidential Fellowship and Employer Supported Tuition Fellowship awarded by the University Graduate School and funding by The Nature Conservancy. Thank you to the divers and data management team for the NOAA RVC and NCRMP programs. Thanks to Claire Paris for the larval connectivity data and Iliana Chollett for exposure data. Thanks to Peter Cowman for consultation on reef fish phylogeny, and Eva McClure and Katie Sievers for their assistance with plots. The authors sincerely appreciate the thoughtful reviews by Jennifer Hodge and Matthew McLean, who waived their anonymity to support and improve this paper. This is contribution #1600 from the Institute of Environment at Florida International University.

Funding – Funding was provided to DPK by the University Graduate School at Florida International University by the Presidential Fellowship and Employer Supported Tuition Fellowship. Funding was provided by ARH by The Nature Conservancy.

Author contributions

David P. Kochan: Conceptualization (equal); Formal analysis (lead); Funding acquisition (equal); Investigation (equal); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Matthew D. Mitchell:** Conceptualization (equal); Writing – review and editing (equal). **Rachel Zuercher:** Data curation (equal); Writing – review and editing (equal). **Alastair R. Harborne:** Conceptualization (equal); Funding acquisition (equal); Resources (lead); Supervision (lead); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.xpnvx0kmn> (Kochan et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Adam, T. C., Schmitt, R. J., Holbrook, S. J., Brooks, A. J., Edmunds, P. J., Carpenter, R. C. and Bernardi, G. 2011. Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. – *PLoS One* 6: e23717.
- Adam, T. C., Duran, A., Fuchs, C. E., Roycroft, M., Rojas, M., Ruttenberg, B. and Burkipile, D. 2018. Comparative analysis of foraging behavior and bite mechanics reveals complex functional diversity among Caribbean parrotfishes. – *Mar. Ecol. Prog. Ser.* 597: 207–220.
- Allgeier, J. E., Layman, C. A., Mumby, P. J. and Rosemond, A. D. 2014. Consistent nutrient storage and supply mediated by diverse fish communities in coral reef ecosystems. – *Global Change Biol.* 20: 2459–2472.
- Almany, G. R. 2004. Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. – *Oecologia* 141: 105–113.
- Alvarez-Filip, L., Dulvy, N. K., Gill, J. A., Côté, I. M. and Watkinson, A. R. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. – *Proc. R. Soc. B* 276: 3019–25.
- Alvarez-Filip, L., Gill, J. A. and Dulvy, N. K. 2011. Complex reef architecture supports more small-bodied fishes and longer food chains on Caribbean reefs. – *Ecosphere* 2: art118.
- Alvarez-Filip, L., Paddock, M. J., Collen, B., Robertson, D. R. and Côté, I. M. 2015. Simplification of Caribbean reef-fish assemblages over decades of coral reef degradation. – *PLoS One* 10: e0126004.
- Anderson, L., McLean, M., Houk, P., Graham, C., Kanemoto, K., Terk, E., McLeod, E. and Beger, M. 2022. Co-variation of fish and coral traits in relation to habitat type and fishery status. – *Coral Reefs* 42: 279–284.
- Ault, J. S., Bohnsack, J. A. and Meester, G. A. 1998. A retrospective (1979–1996) multispecies assessment of coral reef fish stocks in the Florida keys. – *Fish. Bull.* 96: 395–414.
- Bartomeus, I., Cariveau, D. P., Harrison, T. and Winfree, R. 2018. On the inconsistency of pollinator species traits for predicting either response to land-use change or functional contribution. – *Oikos* 127: 306–315.
- Bellwood, D. R., Wainwright, P. C., Fulton, C. J. and Hoey, A. 2002. Assembly rules and functional groups at global biogeographical scales. – *Funct. Ecol.* 16: 557–562.
- Bellwood, D. R., Streit, R. P., Brandl, S. J. and Tebbett, S. B. 2019. The meaning of the term ‘function’ in ecology: a coral reef perspective. – *Funct. Ecol.* 33: 948–961.
- Binning, S. A. and Roche, D. G. 2015. Water flow and fin shape polymorphism in coral reef fishes. – *Ecology* 96: 828–839.
- Blair, S. M., McIntosh, T. L. and Mostkoff, B. J. 1994. Impacts of Hurricane Andrew on the offshore reef systems of central and northern Dade County, Florida. – *Bull. Mar. Sci.* 54: 961–973.
- Blomberg, S. P., Garland, T. and Ives, A. R. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. – *Evolution* 57: 717–745.
- Bohnsack, J. A. and Bannerot, S. P. 1986. A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. – NOAA Technical Report Nmfs 41. US Department of Commerce, National Oceanic and Atmospheric Administration.
- Bohnsack, J. A., McClellan, D. B., Harper, D. E., Davenport, G. S., Konoval, G. J., Eklund, A.-M., Contillo, J. P., Bolden, S. K., Fischel, P. C., Scott Sandorf, G., Javech, J. C., White, M. W., Pickett, M. H., Hulsbeck, M. W., Tobias, J. L., Ault, J. S., Meester, G. A., Smith, S. G. and Luo, J. 1999. Baseline data for evaluating reef fish populations in the Florida Keys, 1979–1998. – NOAA Tech. Memorandum NMFS-SEFSC, pp. 1–61.
- Borland, H. P., Gilby, B. L., Henderson, C. J., Leon, J. X., Schlacher, T. A., Connolly, R. M., Pittman, S. J., Sheaves, M. and Olds, A. D. 2021. The influence of seafloor terrain on fish and fisheries: a global synthesis. – *Fish. Fish.* 22: 1–28.
- Box, S. J. and Mumby, P. J. 2007. Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. – *Mar. Ecol. Prog. Ser.* 342: 139–149.
- Bozec, Y.-M., Yakob, L., Bejarano, S. and Mumby, P. J. 2013. Reciprocal facilitation and non-linearity maintain habitat engineering on coral reefs. – *Oikos* 122: 428–440.
- Brandl, S. J., Tornabene, L., Goatley, C. H. R., Casey, J. M., Morais, R. A., Côté, I. M., Baldwin, C. C., Parravicini, V., Schiettekatte, N. M. D. and Bellwood, D. R. 2019. Demographic dynamics of the smallest marine vertebrates fuel coral reef ecosystem functioning. – *Science* 364: 1189–1192.
- Bridge, T. C. L., Luiz, O. J., Coleman, R. R., Kane, C. N. and Kosaki, R. K. 2016. Ecological and morphological traits predict depth-generalist fishes on coral reefs. – *Proc. R. Soc. B* 283: 20152332.
- Burkipile, D. E. 2012. Context-dependent corallivory by parrotfishes in a Caribbean reef ecosystem. – *Coral Reefs* 31: 111–120.
- Burkipile, D. E. and Hay, M. E. 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. – *Proc. Natl Acad. Sci. USA* 105: 16201–16206.
- Burkipile, D. E. and Hay, M. E. 2010. Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. – *PLoS One* 5: e8963.
- Burman, S., Aronson, R. and van Woesik, R. 2012. Biotic homogenization of coral assemblages along the Florida reef tract. – *Mar. Ecol. Prog. Ser.* 467: 89–96.
- Cadotte, M. W., Carscadden, K. and Mirotnick, N. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. – *J. Appl. Ecol.* 48: 1079–1087.
- Chiappone, M., Swanson, D., Miller, S. and Smith, S. 2002. Large-scale surveys on the Florida Reef Tract indicate poor recovery of the long-spined sea urchin *Diadema antillarum*. – *Coral Reefs* 21: 155–159.
- Chang, J., Rabosky, D. L., Smith, S. A. and Alfaro, M. E. 2019. An R package and online resource for macroevolutionary studies using the ray-finned fish tree of life. – *Methods Ecol. Evol.* 10: 1118–1124. doi:10.1111/2041-210x.13182.
- Chollett, I., Mumby, P. J., Müller-Karger, F. E. and Hu, C. 2012. Physical environments of the Caribbean Sea. – *Limnol. Oceanogr.* 57: 1233–1244. <https://doi.org/10.4319/lo.2012.57.4.1233>
- Cinner, J. E. et al. 2018. Gravity of human impacts mediates coral reef conservation gains. – *Proc. Natl Acad. Sci. USA* 115: E6116–E6125.
- Cloern, J. E., Abreu, P. C., Carstensen, J., Chauvaud, L., Elmgren, R., Grall, J., Greening, H., Johansson, J. O., Kahru, M., Sher-

- wood, E. T., Xu, J. and Yin, K. 2016. Human activities and climate variability drive fast-paced change across the world's estuarine-coastal ecosystems. – *Global Change Biol.* 22: 513–529.
- Coker, D. J., Wilson, S. K. and Pratchett, M. S. 2014. Importance of live coral habitat for reef fishes. – *Rev. Fish. Biol. Fish.* 24: 89–126.
- Duran, A., Collado-Vides, L., Palma, L. and Burkepile, D. E. 2018. Interactive effects of herbivory and substrate orientation on algal community dynamics on a coral reef. – *Mar. Biol.* 165: 156.
- Eaton, L., Sloman, K. A., Wilson, R. W., Gill, A. B. and Harborne, A. R. 2016. Non-consumptive effects of native and invasive predators on juvenile Caribbean parrotfish. – *Environ. Biol. Fish.* 99: 499–508.
- Elith, J., Leathwick, J. R. and Hastie, T. 2008. A working guide to boosted regression trees. – *J. Anim. Ecol.* 77: 802–813. <https://doi.org/10.1111/j.1365-2656.2008.01390.x>
- Ferrari, D. S., Floeter, S. R., Leprieur, F. and Quimbayo, J. P. 2023. A trait-based approach to marine island biogeography. – *J. Biogeogr.* 50: 528–538.
- Floeter, S. R., Bender, M. G., Siqueira, A. C. and Cowman, P. F. 2018. Phylogenetic perspectives on reef fish functional traits. – *Biol. Rev.* 93: 131–151.
- Freckleton, R. P., Harvey, P. H. and Pagel, M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. – *Am. Nat.* 160: 712–26. doi: [10.1086/343873](https://doi.org/10.1086/343873).
- Froese, R. and Pauly, D. (eds) 2000. FishBase 2000: concepts, design and data sources. – ICLARM, Los Baños, Laguna, Philippines.
- Fulton, C. 2010. The role of swimming in reef fish ecology. – In: Domenici, P. and Kapoor, B. (eds), *Fish locomotion: an ethological perspective*. Science Publishers., USA, pp.374–406.
- Fulton, C. J. and Bellwood, D. R. 2005. Wave-induced water motion and the functional implications for coral reef fish assemblages. – *Limnol. Oceanogr.* 50: 255–264.
- Fulton, C. J., Bellwood, D. R. and Wainwright, P. C. 2005. Wave energy and swimming performance shape coral reef fish assemblages. – *Proc. R. Soc. B* 272: 827–832.
- FWC 2016. Users guide to the unified Florida Reef tract map. p. 14.
- Gardner, T. A., Côté, I. M., Gill, J. A., Grant, A. and Watkinson, A. R. 2003. Long-term region-wide declines in Caribbean corals. – *Science* 301: 958–960.
- González-Rivero, M., Harborne, A. R., Herrera-Reveles, A., Bozec, Y. M., Rogers, A., Friedman, A., Ganase, A. and Hoegh-Guldberg, O. 2017. Linking fishes to multiple metrics of coral reef structural complexity using three-dimensional technology. – *Sci. Rep.* 7: 13965.
- González-del-Pliego, P., Freckleton, R. P., Edwards, D. P., Koo, M. S., Scheffers, B. R., Pyron, R. A. and Jetz, W. 2019. phylogenetic and trait-based prediction of extinction risk for data-deficient amphibians. – *Curr. Biol.* 29: 1557–1563.e3.
- Graham, N. A. J. and Nash, K. L. 2013. The importance of structural complexity in coral reef ecosystems. – *Coral Reefs* 32: 315–326.
- Graham, N. A. J., Chabanet, P., Evans, R. D., Jennings, S., Letourneur, Y., Aaron Macneil, M., McClanahan, T. R., Ohman, M. C., Polunin, N. V. and Wilson, S. K. 2011. Extinction vulnerability of coral reef fishes. – *Ecol. Lett.* 14: 341–348.
- Green, S. J. and Côté, I. M. 2014. Trait-based diet selection: prey behaviour and morphology predict vulnerability to predation in reef fish communities. – *J. Anim. Ecol.* 83: 1451–1460.
- Green, S. J., Brookson, C. B., Hardy, N. A. and Crowder, L. B. 2022. Trait-based approaches to global change ecology: moving from description to prediction. – *Proc. R. Soc. B* 289: 20220071.
- Hadj-Hammou, J., Mouillot, D. and Graham, N. A. J. 2021. Response and effect traits of coral reef fish. – *Front. Mar. Sci.* 8: 640619.
- Harborne, A. R., Mumby, P. J. and Ferrari, R. 2012. The effectiveness of different meso-scale rugosity metrics for predicting intra-habitat variation in coral-reef fish assemblages. – *Environ. Biol. Fish.* 94: 431–442.
- Harborne, A. R., Kochan, D. P., Esch, M. M., Fidler, R. Y., Mitchell, M. D., Butkowski, D. W. and González-Rivero, M. 2022. Drivers of fine-scale diurnal space use by a coral-reef mesopredatory fish. – *J. Fish Biol.* 100: 1009–1024.
- Hatfield, J. H., Orme, C. D. L., Tobias, J. A. and Banks-Leite, C. 2018. Trait-based indicators of bird species sensitivity to habitat loss are effective within but not across data sets. – *Ecol. Appl.* 28: 28–34.
- Heithaus, M. R., Wirsing, A. J., Burkholder, D., Thomson, J. and Dill, L. M. 2009. Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. – *J. Anim. Ecol.* 78: 556–562.
- Hijmans, R. J., Phillips, S., Leathwick, J. and Elith, J. 2021. Dismo: species distribution modeling. – R package ver. 1.3-5. <http://CRAN.R-project.org/package=dismo>
- Hixon, M. A. 1991. Predation as a process structuring coral reef fish communities. – In: Sale, P. (ed.), *The ecology of fishes on coral reefs*. Elsevier, pp. 475–508.
- Hodge, J. R. and Price, S. A. 2022. Biotic interactions and the future of fishes on coral reefs: the importance of trait-based approaches. – *Integr. Compar. Biol.* 62: 1734–1747.
- Holbrook, S. J. and Schmitt, R. J. 2002. competition for shelter space causes density-dependent predation mortality in damselfishes. – *Ecology* 83: 2855–2868.
- Humann, P. and DeLoach, N. 2002. Reef creature identification: Florida, Caribbean, Bahamas. – New World Publications, Inc., Vaughan Press.
- Hurley, A. C. and Hartline, P. H. 1974. Escape response in the damselfish *Chromis cyanea* (Pisces: Pomacentridae): a quantitative study. – *Anim. Behav.* 22: 430–437.
- Jepson, M. and Colburn, L. L. 2013. Development of social indicators of fishing community vulnerability and resilience in the U.S. Southeast and Northeast regions. – NOAA Tech. Memorandum NMFS NMFSF/SPO-129.
- Johansen, J., Bellwood, D. and Fulton, C. 2008. Coral reef fishes exploit flow refuges in high-flow habitats. – *Mar. Ecol. Prog. Ser.* 360: 219–226.
- Johns, G. M., Leeworthy, V. R., Bell, F. W. and Bonn, M. A. 2001. Socioeconomic study of reefs in southeast Florida. – Florida Fish and Wildlife Conservation Commission and National Oceanic Atmospheric Administration. Hazen and Sawyer, P.C. Hollywood, FL.
- Jouffray, J., Wedding, L. M., Norstro, A. V., Donovan, M. K., Williams, G. J., Crowder, L. B., Erickson, A. L., Friedlander, A. M., Graham, N. A. J., Gove, J. M., Kappel, C. V., Kittinger, Lecky, J. and Oleson, K. L. L. 2019. Parsing human and biophysical drivers of coral reef regimes. – *Proc. R. Soc. B* 286: 20182544.
- Kemp, D. W., Colella, M. A., Bartlett, L. A., Ruzicka, R. R., Porter, J. W. and Fitt, W. K. 2016. Life after cold death: reef coral and coral reef responses to the 2010 cold water anomaly in the Florida Keys. – *Ecosphere* 7: e01373.

- Kerry, J. T. and Bellwood, D. R. 2012. The effect of coral morphology on shelter selection by coral reef fishes. – *Coral Reefs* 31: 415–424.
- Kochan, D. P., Mitchell, M. D., Zuercher, R. and Harborne, A. R. 2023. Data from: Winners and losers of reef flattening: an assessment of coral reef fish species and traits. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.xpnvx0kmn>.
- Li, D. and Ives, A. R. 2017. The statistical need to include phylogeny in trait-based analyses of community composition. – *Methods Ecol. Evol.* 8: 1192–1199.
- Luiz, O. J., Allen, A. P., Robertson, D. R., Floeter, S. R., Kulbicki, M., Vigliola, L., Becheler, R. and Madin, J. S. 2013. Adult and larval traits as determinants of geographic range size among tropical reef fishes. – *Proc. Natl Acad. Sci. USA* 110: 16498–16502.
- Magurran, A. E. 1990. The adaptive significance of schooling as an anti-predator defence in fish. – *Ann. Zool. Fenn.* 27: 51–66.
- Maire, E., Grenouillet, G., Brosse, S. and Villéger, S. 2015. How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. – *Global Ecol. Biogeogr.* 24: 728–740.
- Manzello, D. P. 2015. Rapid recent warming of coral reefs in the Florida keys. – *Sci. Rep.* 5: 16762.
- McClenachan, L. 2009. Documenting loss of large trophy fish from the Florida Keys with historical photographs. – *Conserv. Biol.* 23: 636–643.
- McGill, B. J., Enquist, B. J., Weiher, E. and Westoby, M. 2006. Rebuilding community ecology from functional traits. – *Trends Ecol. Evol.* 21: 178–185.
- McGill, B. J., Dornelas, M., Gotelli, N. J. and Magurran, A. E. 2015. Fifteen forms of biodiversity trend in the Anthropocene. – *Trends Ecol. Evol.* 30: 104–113.
- McKinney, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. – *Annu. Rev. Ecol. Syst.* 28: 495–516.
- McKinney, M. L. and Lockwood, J. L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. – *Trends Ecol. Evol.* 14: 450–453.
- Medeiros, A. P. M., Ferreira, B. P., Alvarado, F., Betancur-R, R., Soares, M. O. and Santos, B. A. 2021. Deep reefs are not refugia for shallow-water fish communities in the southwestern Atlantic. – *Ecol. Evol.* 11: 4413–4427.
- Miller, J. E. D., Ives, A. R., Harrison, S. P. and Damschen, E. I. 2018. Early- and late-flowering guilds respond differently to landscape spatial structure. – *J. Ecol.* 106: 1033–1045.
- Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J. E., Bender, M., Chabanet, P., Floeter, S. R., Friedlander, A., Vigliola, L., and Bellwood, D. R. 2014. Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. – *Proc. Natl Acad. Sci. USA* 111: 13757–13762.
- Mumby, P. J. 2006. The impact of exploiting grazers (Scaridae) on the dynamics of caribbean coral reefs. – *Ecol. Appl.* 16: 747–769.
- Mumby, P. J., Steneck, R. S., Edwards, A. J., Ferrari, R., Coleman, R., Harborne, A. and Gibson, J. 2012. Fishing down a Caribbean food web relaxes trophic cascades. – *Mar. Ecol. Prog. Ser.* 445: 13–24.
- NOAA 2017. Reef visual census (RVC) fish survey protocol for U.S. Caribbean and Gulf of Mexico. – National Oceanic and Atmospheric Administration.
- Nugues, M. M. and Bak, R. P. M. 2006. Differential competitive abilities between Caribbean coral species and a brown alga: a year of experiments and a long-term perspective. – *Mar. Ecol. Prog. Ser.* 315: 75–86.
- Nugues, M. M., Smith, G. W., Hooideonk, R. J. van, Seabra, M. I. and Bak, R. P. M. 2004. Algal contact as a trigger for coral disease. – *Ecol. Lett.* 7: 919–923.
- Pagel, M. 1999. Inferring the historical patterns of biological evolution. – *Nature* 401: 877–884. <https://doi.org/10.1038/44766>
- Paradis, E. and Schliep, K. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. – *Bioinformatics* 35: 526–528.
- Pauly, D. 1989. Food consumption by tropical and temperate fish populations: some generalizations. – *J. Fish Biol.* 35: 11–20.
- Perry, C. T., Murphy, G. N., Kench, P. S., Smithers, S. G., Edinger, E. N., Steneck, R. S. and Mumby, P. J. 2013. Caribbean-wide decline in carbonate production threatens coral reef growth. – *Nat. Commun.* 4: 1402.
- Pratchett, M. S., Munday, P. L., Wilson, S. K., Graham, N. A. J., Cinner, J. E., Bellwood, D. R., Jones, G. P., Polunin, N. V. C. and McClanahan, T. R. 2008. Effects of climate-induced coral bleaching on coral-reef fishes—ecological and economic consequences. – In: Gibson, R. J., Atkinson, J. A., Gordon, D. M. (eds), *Oceanography and marine biology*. CRC Press, pp. 257–302.
- Pratchett, M. S., Hoey, A. S. and Wilson, S. K. 2014. Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. – *Curr. Opin. Environ. Sustain.* 7: 37–43.
- Quimbayo, J. P., Silva, F. C., Mendes, T. C., Ferrari, D. S., Danielski, S. L., Bender, M. G., Parravicini, V., Kulbicki, M. and Floeter, S. R. 2021. Life-history traits, geographical range, and conservation aspects of reef fishes from the Atlantic and Eastern Pacific. – *Ecology* 102: e03298.
- Precht, W. F., Gintert, B. E., Robbatt, M. L., Fura, R. and van Woessik, R. 2016. Unprecedented disease-related coral mortality in southeastern Florida. – *Sci. Rep.* 6: 31374.
- Rabosky, D. L., Chang, J., Title, P. O., Cowman, P. F., Sallan, L., Friedman, M., Kaschner, K., Garilao, C., Near, T. J., Coll, M. and Alfaro, M. E. 2018. An inverse latitudinal gradient in speciation rate for marine fishes. – *Nature* 559: 392–395.
- Revell, L. 2012. phytools: an R package for phylogenetic comparative biology (and other things). – *Methods Ecol. Evol.* 3: 217–223. doi:10.1111/j.2041-210X.2011.00169.x.
- Richardson, L. E., Graham, N. A. J., Pratchett, M. S., Eurich, J. G. and Hoey, A. S. 2018. Mass coral bleaching causes biotic homogenization of reef fish assemblages. – *Global Change Biol.* 24: 3117–3129.
- Robertson, D. R. and Sheldon, J. M. 1979. Competitive interactions and the availability of sleeping sites for a diurnal coral reef fish. – *J. Exp. Mar. Biol. Ecol.* 40: 285–298.
- Rogers, A., Blanchard, J. L. and Mumby, P. J. 2014. vulnerability of Coral Reef fisheries to a loss of structural complexity. – *Curr. Biol.* 24: 1000–1005.
- Rogers, A., Harborne, A. R., Brown, C. J., Bozec, Y. M., Castro, C., Chollett, I., Hock, K., Knowland, C. A., Marshall, A., Ortiz, J. C., Razak, T., Roff, G., Samper-Villarreal, J., Saunders, M. I., Wolff, N. H. and Mumby, P. J. 2015. Anticipative management for coral reef ecosystem services in the 21st century. – *Global Change Biol.* 21: 504–514.
- Ruttenberg, B. I., Schofield, P. J., Akins, J. L., Acosta, A., Feeley, M. W., Blondeau, J., Smith, S. G. and Ault, J. S. 2012. Rapid invasion of Indo-Pacific Lionfishes (*Pterois volitans* and *Pterois miles*) in the Florida keys, USA: evidence from multiple pre- and post-invasion data sets. – *Bull. Mar. Sci.* 88: 1051–1059.

- Sambily, V. C. J. 1990. Interrelationships between swimming speed, caudal fin aspect ratio and body length in fishes. – *Fish-bite* 8: 16–20.
- Sbrocco, E. J. and Barber, P. H. 2013. MARSPEC: ocean climate layers for marine spatial ecology: ecological Archives E094-086. – *Ecology* 94: 979. <https://doi.org/10.1890/12-1358.1>
- Schutte, V. G. W., Selig, E. R. and Bruno, J. F. 2010. Regional spatio-temporal trends in Caribbean coral reef benthic communities. – *Mar. Ecol. Prog. Ser.* 402: 115–122.
- Schweikert, L. E., Caves, E. M., Solie, S. E., Sutton, T. T. and Johnsen, S. 2018. Variation in rod spectral sensitivity of fishes is best predicted by habitat and depth. – *J. Fish Biol.* 95: 179–185.
- Siqueira, A. C., Morais, R. A., Bellwood, D. R. and Cowman, P. F. 2021. Planktivores as trophic drivers of global coral reef fish diversity patterns. – *Proc. Natl Acad. Sci. USA* 118: e2019404118.
- Smith, S. G., Ault, J. S., Bohnsack, J. A., Harper, D. E., Luo, J. and McClellan, D. B. 2011. Multispecies survey design for assessing reef-fish stocks, spatially explicit management performance, and ecosystem condition. – *Fish. Res.* 109: 25–41.
- Soykan, C. U., Eguchi, T., Kohin, S. and Dewar, H. 2014. Prediction of fishing effort distributions using boosted regression trees. – *Ecol. Appl.* 24: 71–83. <https://doi.org/10.1890/12-0826.1>
- Stallings, C. D. 2008. Indirect effects of an exploited predator on recruitment of coral-reef fishes. – *Ecology* 89: 2090–2095.
- Stefanoudis, P. V., Gress, E., Pitt, J. M., Andradi-Brown, D., Rowlands, G., Woodall, L., Rogers, A. 2019. Depth-dependent structuring of reef fish assemblages from the shallows to the Rariphotic zone. – *Front. Mar. Sci.* 6: 307.
- Streit, R. P. and Bellwood, D. R. 2022. To harness traits for ecology, let's abandon 'functionality'. – *Trends Ecol. Evol.* 38: 402–411
- Stuart-Smith, R. D., Mellin, C., Bates, A. E. and Edgar, G. J. 2021. Habitat loss and range shifts contribute to ecological generalization among reef fishes. – *Nat. Ecol. Evol.* 5: 656–662.
- Toth, L. T., Stathakopoulos, A., Kuffner, I. B., Ruzicka, R. R., Colella, M. A. and Shinn, E. A. 2019. The unprecedented loss of Florida's reef-building corals and the emergence of a novel coral-reef assemblage. – *Ecology* 100: e02781.
- Ward-Paige, C. A., Risk, M. J., Sherwood, O. A. and Jaap, W. C. 2005. Clionid sponge surveys on the Florida Reef Tract suggest land-based nutrient inputs. – *Mar. Pollut. Bull.* 51: 570–579.
- Williams, J. J., Papastamatiou, Y. P., Caselle, J. E., Bradley, D. and Jacoby, D. M. P. 2018. Mobile marine predators: an understudied source of nutrients to coral reefs in an unfished atoll. – *Proc. R. Soc. B* 285: 20172456.
- Willis, T. J. 2001. Visual census methods underestimate density and diversity of cryptic reef fishes. – *J. Fish Biol.* 59: 1408–1411.
- Wilson, S. K., Graham, N. A. J. and Polunin, N. V. C. 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. – *Mar. Biol.* 151: 1069–1076.
- Wilson, S. K., Burgess, S. C., Cheal, A. J., Emslie, M., Fisher, R., Miller, I., Polunin, N. V. and Sweatman, H. P. 2008. Habitat utilization by coral reef fish: implications for specialists vs generalists in a changing environment. – *J. Anim. Ecol.* 77: 220–228.
- Yeager, L. A., Geyer, J. K. and Fodrie, F. J. 2019. Trait sensitivities to seagrass fragmentation across spatial scales shape benthic community structure. – *J. Anim. Ecol.* 88: 1–12.
- Zuercher, R., Kochan, D. P., Brumbaugh, R. D., Freeman, K., Layko, R. and Harborne, A. R. 2023. Identifying correlates of coral-reef fish biomass on Florida's Coral Reef to assess potential management actions. – *Aquat. Conserv. Mar. Freshwater Ecosyst.* 33: 246–263.