Received: 29 June 2023 | Revised: 23 February 2024 | Accepted: 2 March 2024

DOI: 10.1111/gcb.17263

Global Change Biology WILEY

RESEARCH ARTICLE

Widespread habitat loss leads to ecosystem-scale decrease in trophic function

W. Ryan James[1,2,3] | Bradley T. Furman[4] | Jonathan R. Rodemann[1,3] | Sophia V. Costa[3] | Zachary W. Fratto[5] | James A. Nelson[6] | Jennifer S. Rehage[1,3] | Rolando O. Santos[1,2]

[1]Institute of Environment, Florida International University, Miami, Florida, USA

[2]Department of Biological Sciences, Florida International University, North Miami, Florida, USA

[3]Department of Earth and Environment, Florida International University, Miami, Florida, USA

[4]Florida Fish and Wildlife Conservation Commission, Florida Fish and Wildlife Research Institute, St. Petersburg, Florida, USA

[5]South Florida Natural Resources Center, National Park Service, Homestead, Florida, USA

[6]Department of Marine Science, University of Georgia, Athens, Georgia, USA

Correspondence
W. Ryan James, Institute of Environment, Florida International University, Miami, FL, USA.
Email: wjames@fiu.edu

Funding information
National Park Service Critical Ecosystem Study Initiative, Grant/Award Number: P16AC01437; Division of Environmental Biology, Grant/Award Number: DEB-1832229; U.S. Environmental Protection Agency, Grant/Award Number: SF-02D21022-0; National Centers for Coastal Ocean Science, Grant/Award Number: NA21NOS4780150; National Science Foundation, Grant/Award Number: HRD-1547798 and HRD-2111661

Abstract

Natural and anthropogenic disturbances have led to rapid declines in the amount and quality of available habitat in many ecosystems. Many studies have focused on how habitat loss has affected the composition and configuration of habitats, but there have been fewer studies that investigate how this loss affects ecosystem function. We investigated how a large-scale seagrass die-off altered the distribution of energetic resources of three seagrass-associated consumers with varied resource use patterns. Using long-term benthic habitat monitoring data and resource use data from Bayesian stable isotope mixing models, we generated energetic resource landscapes (*E*-scapes) annually between 2007 and 2019. *E*-scapes link the resources being used by a consumer to the habitats that produce those resources to calculate a habitat resource index as a measurement of energetic quality of the landscape. Overall, our results revealed that following the die-off there was a reduction in trophic function across all species in areas affected by the die-off event, but the response was species-specific and dependent on resource use and recovery patterns. This study highlights how habitat loss can lead to changes in ecosystem function. Incorporating changes in ecosystem function into models of habitat loss could improve understanding of how species will respond to future change.

KEYWORDS
ecosystem function, *E*-scapes, global change, habitat degradation, habitat resource index, seagrass die-off

1 | INTRODUCTION

Natural and anthropogenic disturbances, especially related to human land use change, have led to rapid declines in the amount and quality of available habitat (i.e., the resources and conditions in area needed for an organism to occupy; Hall et al., 1997) in many ecosystems (Bryan-Brown et al., 2020; Ellis et al., 2010; Hall et al., 2016). For example, the global distribution of seagrass meadows has declined by about 30% over the last 150 years due to coastal modification, poor water quality, and climate change (Waycott et al., 2009). Habitat loss changes the structure of habitats by decreasing the amount of available habitat and altering the composition (i.e., amount and types) and configuration (i.e., spatial arrangement) of habitats, which in turn can alter species distributions, movement, and interactions, often leading to changes in ecosystem function (Dobson et al., 2006; Fahrig, 1997, 2003; Thompson et al., 2017). Many studies have investigated how habitat loss is changing the structure of habitats (e.g., Bryan-Brown et al., 2020), but less is known about how these changes alter the function of habitats.

Ecosystem function is the processes that transform and translocate energy or materials in an ecosystem (e.g., primary production, nutrient cycling, trophic support for secondary production), and many of these processes are mediated through food web interactions (Naeem, 1998). Future global change is expected to rewire food webs through changes in species interactions and resource availability and distribution (Bartley et al., 2019; Lázaro & Gómez-Martínez, 2022). Habitat loss not only decreases the amount of structural habitat but also alters the energetic resources available to consumers (Harris et al., 2021; Jones et al., 1994). Because specific resources are produced within certain habitat types, there is a direct link between habitat distribution and resource availability. Resource availability is a major driver of consumer biomass, movement, and distribution (Abrahms et al., 2021; James, Santos, Rehage, et al., 2022; Ware & Thomson, 2005), and habitat loss could lead to changes in the trophic function (i.e., how habitats provide energetic resources for consumers) of habitats (Harris et al., 2021; James, Santos, Rehage, et al., 2022; Nelson et al., 2020). Habitat loss is a landscape-level phenomenon that will impact energetic resource distribution at the ecosystem scale, and therefore a spatial or landscape approach is needed to fully understand the impacts of habitat loss on the trophic function of habitats (James, Santos, Rehage, et al., 2022).

Coastal ecosystems are some of the most rapidly changing ecosystems on earth (Bryan-Brown et al., 2020; Scavia et al., 2002; Waycott et al., 2009). Both press and pulse disturbances, such as sea level rise, human modification, and hurricanes have led to large-scale habitat modification in these ecosystems (Bryan-Brown et al., 2020; Couvillion et al., 2016; Hall et al., 2016). Coastal ecosystems have ecological importance because their high productivity supports diverse food webs (many of which include key fisheries) and their role as nursery habitats for many species (Beck et al., 2001; Boström et al., 2011). Because of their high ecological importance, it is crucial to understand how ecosystem function responds to habitat loss in order to predict how these ecosystems will respond to future change.

Food webs are complex, and consumers often rely on energetic resources produced across multiple habitat types (Pimm, 1982; Polis et al., 2004). Understanding how habitat loss alters the distribution of energetic resources across the landscape and their importance to consumers is critical to understand how habitat loss will alter trophic function. The energetic resource landscape or *E*-scape, maps where energetic resources being used by a consumer are being produced across the landscape by combining habitat maps and stable isotope analysis (James, Santos, Rehage, et al., 2022). Stable isotope analysis when paired with Bayesian mixing models provides information about what resources a consumer is using (Layman et al., 2012), and habitat maps indicate where in the landscape resources are being produced. This method links energetic resources and habitats at a landscape scale and permits us to examine the consequences of habitat loss for trophic function. *E*-scapes are generated using an index (habitat resource index, HRI) that accounts for both the quantity (amount of each habitat type in a given area) and quality (how a consumer is using energetic resources being produced in those habitat types) of trophic function of an area (James, Santos, Rehage, et al., 2022). *E*-scapes are consumer-specific and have been used to show how consumer abundance, biomass, and body size relate to energetic resources (James, Santos, Rehage, et al., 2022), how tropicalization of salt marshes has decreased trophic function (Harris et al., 2021), and how trophic function recovers after restoration (Nelson et al., 2020).

We investigated how a large-scale seagrass die-off altered the distribution of energetic resources available to three seagrass-associated consumers. In 2015, a drought-related seagrass die-off occurred in Florida, resulting in an estimated 88 km^2 loss of seagrass habitat (Figure 1; Hall et al., 2016). Despite differences in habitat amount, a recent study found that seagrass consumers had the same resource use inside and outside the die-off boundary (James, Santos, Rodemann, et al., 2022). In this study, we expand on that work by investigating the impact of habitat loss on trophic function. We hypothesized that because consumers did not shift resource use, energetic resources would decrease in areas affected by the seagrass die-off, leading to a decrease in trophic function. Additionally, this loss in trophic function would be species-specific because of the unique resource use patterns of consumers (James, Santos, Rodemann, et al., 2022). We combined long-term seagrass monitoring data to construct benthic habitat maps with stable isotope data to generate *E*-scapes from 2007 to 2019.

2 | METHODS

2.1 | Site description

Florida Bay is an expansive estuary consisting of shallow mud banks and interconnected basins with vast seagrass beds mainly comprised of *Thalassia testudinum*, *Halodule wrightii*, and *Syringodium filiforme*, located between the Everglades and the Florida Keys (Krause et al., 2023). Human modification has drastically altered freshwater flows resulting in chronic hypersalinity, which in combination with high temperatures, has led to two large-scale die-offs in the last 40 years (Hall et al., 2016; Marshall et al., 2020; Robblee et al., 1991). The first die-off began in 1987 (Fourqurean & Robblee, 1999; Robblee et al., 1991), and recovery to pre-die-off benthic communities did not occur until 2010 (Hall et al., 2021). Another drought-associated seagrass die-off occurred in 2015, resulting in an estimated 88 km^2 loss in seagrass habitat (Figure 1; Hall et al., 2016). For this study, we focused on three basins (Johnson, Rankin, and Whipray) in Florida Bay with varied impacts from the 2015 seagrass die-off (Figure 1). Johnson and Rankin Basins were both heavily impacted by the die-off but followed

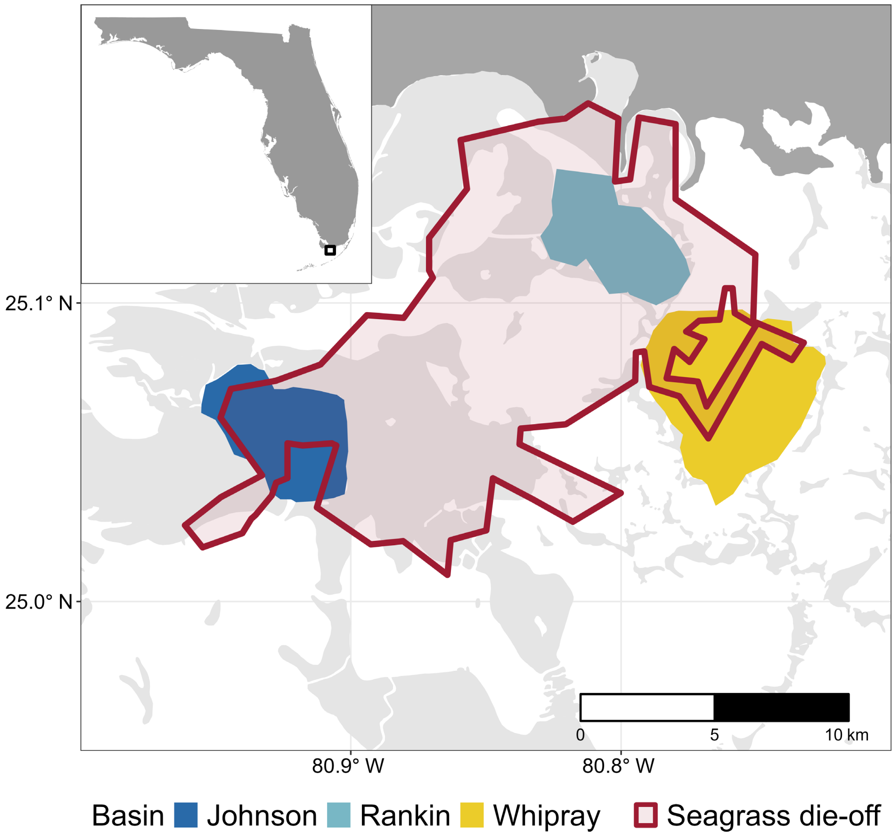

FIGURE 1 Seagrass die-off area (red) and the basins of interest in Florida Bay. Die-off footprint is based on field surveys post die-off (Hall et al., 2016). Johnson and Rankin Basin (blue) were heavily impacted by seagrass die-off, while Whipray (yellow) had minimal impact.

TABLE 1 Mixing model results of source contribution (mean ± SD) for all species collected in the dry season in Florida Bay from James, Santos, Rodemann, et al. (2022).

Species	Algae	Epiphytes	Seagrass	Mangrove
Bay anchovy	0.05 ± 0.01	0.33 ± 0.07	0.36 ± 0.12	0.27 ± 0.08
Pinfish	0.02 ± 0.01	0.58 ± 0.10	0.13 ± 0.06	0.26 ± 0.08
Pink shrimp	0.11 ± 0.02	0.12 ± 0.03	0.54 ± 0.06	0.23 ± 0.05

different recovery trajectories in the years following, and Whipray Basin was minimally affected by the seagrass die-off (Hall et al., 2016; Rodemann et al., 2021). Rankin Basin displayed signs of recovery of seagrass cover in the first years after the die-off, while Johnson Basin continued to lose seagrass (Rodemann et al., 2021).

2.2 | Generation of *E*-scapes

E-scapes for consumers in Florida Bay were generated by combining basal resource use from stable isotopes with habitat maps generated from long-term submerged aquatic vegetation monitoring data. *E*-scapes are generated by combining an index of relative use of a resource compared to the relative amount of habitat that generates that resource (index of energetic importance, IEI) with the amount of each habitat in a given area to calculate a relative metric of the energetic quality (HRI) (James, Santos, Rehage, et al., 2022). *E*-scapes were generated yearly for each species.

James, Santos, Rodemann, et al. (2022) investigated seasonal resource use in Florida Bay of seagrass consumer using stable isotopes ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) and Bayesian mixing models (MixSIAR; Stock et al., 2018). Therefore, resource use for this study was based on published mean basal resource use values of seagrass, epiphytes, algae, and mangroves for bay anchovy (*Anchoa mitchilli*), pinfish (*Lagodon rhomboides*), and pink shrimp (*Farfantepenaeus duorarum*) (Table 1; James, Santos, Rodemann, et al., 2022). These species displayed seasonality in basal resource use (James, Santos, Rodemann, et al., 2022), but only values from the dry season were used because that is when the data for the habitat maps were collected (see below). These species were chosen because of their ecological importance as prey species in the system, high biomass, and because of their different patterns of basal resource use (James, Santos, Rodemann, et al., 2022). The resource use of bay anchovy was similar between seagrass, epiphytes, and mangrove, while pinfish and pink shrimp relied heavily on a single basal resource, epiphytes and seagrass, respectively (Table 1).

Benthic habitat maps were generated based on spatial interpolation of benthic cover data from the Florida Fish and Wildlife Commission Fish Habitat Assessment Program (FHAP; Hall et al., 2016, 2021). Monitoring for FHAP is conducted once a year in May–June at 16 basins across Florida Bay (including Johnson, Ranking, and Whipray Basins, Figure 1; Figure S1). Monitoring is conducted across 29–31 sites in each basin. At each site, eight 0.5 × 0.5 m quadrats are deployed and benthic macrophyte surface cover/abundance is quantified using a modified Braun-Blanquet (BB) scale: 0 = no presence, 0.1 = 1 shoot, 0.5 = less than 5 shoots, 1 = many shoots but <5% cover, 2 = 5%–25% cover, 3 = 25%–50% cover, 4 = 50%–75% cover, 5 = 75%–100% cover (Hall et al., 2021). Each benthic macrophyte, including the major species of submerged aquatic vegetation, is scored, and a mean BB score is calculated for each taxonomic category. Along with the BB scores, 10 shoots of *Thalassia testudium* are also collected for shoot morphometrics (Furman et al., 2021).

Habitat maps for seagrass and benthic algae were generated from the BB scores of total seagrass cover (combined cover of all seagrass species) and total macroalgae (combined cover of all macroalgae species), respectively at each of the 30 surveyed sites within Johnson, Rankin, and Whipray Basins. BB scores were converted to proportional cover using the median cover for each score (BB median scores: 0 = 0, 0.1 = 0.03, 0.5 = 0.03, 1 = 0.03, 2 = 0.15, 3 = 0.375, 4 = 0.625, 5 = 87.5). BB scores of 0.1 (solitary), 0.5 (sparse), and 1 (numerous) all represent benthic cover <5% while describing the pattern of the vegetation, so they were given the same median value. Since epiphytes grow on seagrass, total leaf area of seagrass was used as a proxy for amount of habitat available for epiphyte production. We calculated the mean leaf area per shoot for seagrass using the measured seagrass shoot data from the long-term transects. At each site, we calculated a mean shoot count per m^2 for each unique combination of *T. testudium*, *Halodule wrightii*, and *Syringodium filiforme* across the entire timeseries (i.e., averaged all of the shoot counts for BB score of *x* for *T. testudium*, *y* for *H. wrightii*, and *z* for *S. filiforme*). Total leaf area was calculated at each site by multiplying the mean leaf area per shoot by the mean shoot count per m^2 for that unique cover score for *T. testudium*, *H. wrightii*, and *S. filiforme*. The total leaf area at each site was divided by the max total leaf area within that basin across all years, such that the maximum amount of surface area for epiphytes to grow was 1 and comparable to proportional seagrass and algal cover (Figure S1).

We used ordinary kriging with the *gstat* R package (Gräler et al., 2016; Pebesma, 2004) to create a habitat map for seagrass, algae, and total leaf area for each basin in each year from 2007 to 2019 (with the exception of 2013 due to not having data on leaf area) at a 10 × 10 m cell size (Figure S1). For each habitat map, the variogram was automatically fit with the 'autofitVariogram' function in the *automap* R package (Figures S2–S10; Hiemstra et al., 2009). To create a habitat map for mangrove, a 500 m width buffer was placed around the mangrove islands that bordered each basin. A 10 × 10 m raster was created for each basin, and cells were assigned as mangrove (value of 1) if they fell within the 500 m buffer and given a value of 0 if outside of the buffer (Figure S1).

Combining the basal resource use and habitat maps, we calculated an IEI for each of the four resource/habitat type combinations for each consumer (James, Santos, Rehage, et al., 2022). Each IEI was calculated with the following formula:

$$\mathrm{IEI}_i = \frac{f_{\mathrm{source}_i}}{f_{\mathrm{habitat}_i}}$$

where f_{source_i} is the fraction of the contribution of source *i* to the total resource use of the consumer based on the results of the mixing model and f_{habitat_i} is the fraction of habitat type *i* that produces source *i* to the overall area at a scale relevant to the movement range of the consumer (i.e., area of the circle around the sampling point). An example of resource/habitat type combination is amount of seagrass-derived production and the cover area of seagrass habitat. An IEI around one means that the consumer is using a resource (f_{source_i}) around the same amount as the proportion of that resource's habitat type (f_{habitat_i}) relative to total area that the consumer forages (James, Santos, Rehage, et al., 2022). An IEI greater than one means that the consumer is using that source more than expected based on the proportion of that habitat type in the total foraging area, while the opposite is true for an IEI below one. IEI is a relative variable since f_{source_i} and f_{habitat_i} range 0–1. For f_{source_i}, the sum of all values =1, but since not all habitat types produce resources and some habitat types produce multiple resources, f_{habitat_i} values do not always =1 (James, Santos, Rehage, et al., 2022). We calculated IEIs for each of the 3 consumer species by randomly generating 50 points within the kriged habitat maps for Johnson, Rankin, and Whipray Basins ($n = 150$ for each species). The f_{habitat_i} was calculated by taking the mean proportion cover of the habitat map within a 300 m radius buffer of the point with the *exactextractr* package (Baston, 2022). Some of the kriging models led to values for habitat cover that were <0, and if this was the case, f_{habitat_i} values <0 were converted to 0 before calculating IEI values. IEI values were calculated using the habitat maps from 2019 to closely match when the sampling for basal resource use was conducted (James, Santos, Rodemann, et al., 2022). Therefore, IEI values are specifically representative of 2019, offering a snapshot of ecosystem function relative to habitat availability and consumer resource use at the time.

E-scapes were generated for each species at each basin between 2007 and 2019 (with the exception of 2013, 3 species × 12 years = 36 *E*-scapes). IEI values were combined with habitat cover areas within a landscape foraging unit (grid cell with an area that corresponds to the movement range of the consumer; James, Santos, Rehage, et al., 2022) to calculate the HRI. HRI was calculated with the following formula:

$$\mathrm{HRI}_x = \sum_{i=1}^{n} \widetilde{\mathrm{IEI}}_i \times f_{\mathrm{habitat}_i}$$

where $\widetilde{\mathrm{IEI}}_i$ is the median of the IEI for the species-specific source/habitat combination *i* and f_{habitat_i} is the fraction of habitat *i* to the overall area within landscape foraging unit *x*. HRI is an index that represents a relative measurement of the quality of the habitats for producing the resources used by the consumer based on stable isotope analysis. An HRI value of 1 means that the area is producing the average amount of resources for the consumer. HRI values >1 mean that the area is better for producing resources (i.e., more energetic resources) being used by the consumer, while HRI values <1 shows that the habitats most important to the production of resources being used by the consumer are underrepresented within the landscape foraging unit (James, Santos, Rehage, et al., 2022). The f_{habitat_i} was calculated by taking the mean value of the habitat map within each landscape foraging unit with the *exactextractr* package (Baston, 2022). Some of the kriging models led to values for habitat cover that were <0, and if this was the case, f_{habitat_i} values <0 were converted to 0 before calculating HRI values. Each basin was subdivided into a grid of 600m×600m landscape foraging units to generate an *E*-scape. This size was chosen to correspond to the 300m radius (600m diameter) buffer that was used to calculate the IEIs. Given the singular temporal point of resource use data, IEI values calculated for 2019 were applied across the entire time series. This approach necessitates the assumption that the relative energetic importance of each habitat to the consumers did not vary significantly throughout the timeseries.

2.3 | Statistical analyses

We conducted an analysis of variance (ANOVA) to compare the differences in HRI values across species, basins, and before and after the die-off. We created categorical term for if the HRI value was from before or after the seagrass die-off for the ANOVA. The years before 2015 were assigned as pre-die-off, and the years after 2015 were designated as post-die-off for our model. Species, basin, the categorical term for before or after the die-off, and all interactions were used as predictor terms in the ANOVA. For significant terms in our model, pairwise comparisons using model contrasts with a Bonferroni correction were analyzed to test for significance among factor groups using the *emmeans* package (Lenth, 2023).

Spatiotemporal trends in trophic function for each species were determined by averaging the HRI values of each landscape foraging unit to generate a basin-wide mean for each basin and year. We conducted breakpoint analysis across years on the mean trends in HRI value for each species using the R package *strucchange* (Zeileis et al., 2002). This package uses simple linear regression to estimate data breakpoints and test for differences in mean conditions using an intercept-only model. We assessed the optimal number of breakpoints for each model based on the lowest Bayesian information criterion score.

We conducted both the ANOVA and breakpoint analyses with all years. Due to the uneven sample size in years before and after the die-off, we also ran the analyses using the first 4 years before the die-off (2011, 2012, 2014, 2015) and 4 years after (2016–2019). The results were the same, therefore we only report analyses using all years. All data were analyzed in R v 4.2.3 (R Core Team, 2023).

3 | RESULTS

IEI values varied across species (Table 2; Figure 2). Bay anchovy had IEI values for epiphytes and seagrass >1 indicating these basal resources are used more than expected. For pinfish, epiphytes were the only resource/habitat with IEI values >1. Seagrass and algae IEI values for pink shrimp were >1. Mangrove IEI values were <1 for all species indicating they are used less than expected by consumers based on habitat availability.

HRI values varied across species, basins, and due to the seagrass die-off indicating variation in the production of resources being used across species, basins, and due to the die-off (Table S1; Figures 3 and 4). Across all years and basins, pinfish had the highest HRI values, followed by bay anchovy, with pink shrimp having the lowest HRI values (Table 3; Figure 3). For each species, HRI values varied across basins (Figure 3). Before the seagrass die-off in 2015, Johnson and Rankin Basins had higher HRI values than Whipray Basin across all species (Table 3; Figures 3 and 4). After the seagrass die-off, HRI values across the basins were similar for pink shrimp but higher in Whipray for bay anchovy and pinfish (Table 3; Figures 3 and 4).

Bay anchovy had a significant breakpoint in mean HRI values in 2015 (95% CI, 2012–2016) for both Johnson and Rankin Basins (Table 3; Figure 5a). Similar to bay anchovy, pinfish had significant breakpoints in Johnson and Rankin Basins. In Rankin Basin, the breakpoint for pinfish was in 2015 (2014–2016), but in Johnson Basin, the breakpoint occurred in 2016 (2014–2017, Table 3; Figure 5b). There was a breakpoint for pink shrimp in mean HRI values in Johnson Basin in 2015 (2012–2016), but unlike the other species, there was not a significant breakpoint in Rankin Basin (Table 3; Figure 5c). There were no breakpoints in mean HRI values for any species in Whipray Basin.

4 | DISCUSSION

In Florida Bay, there are species-specific patterns of resource use, but the major energy pathways for seagrass consumers are derived from seagrass and seagrass-associated epiphyte (that grow on seagrass blades) production (James, Santos, Rodemann, et al., 2022).

TABLE 2 Median (interquartile range) of the index of energetic importance (IEI) value for each resource/habitat combination for each species. IEI values >1 means that the consumer is using that source more than expected based on the proportion of that habitat in the total foraging area, while the opposite is true for an IEI <1.

Species	Algae IEI	Epiphyte IEI	Mangrove IEI	Seagrass IEI
Bay anchovy	0.40 (0.27–0.68)	1.55 (1.10–3.45)	0.31 (0.27–0.49)	1.64 (1.29–2.17)
Pinfish	0.20 (0.14–0.34)	3.16 (2.17–5.92)	0.55 (0.26–2.05)	0.62 (0.51–0.80)
Pink shrimp	1.25 (0.93–2.18)	0.58 (0.39–1.00)	0.42 (0.24–1.15)	2.21 (1.89–2.81)

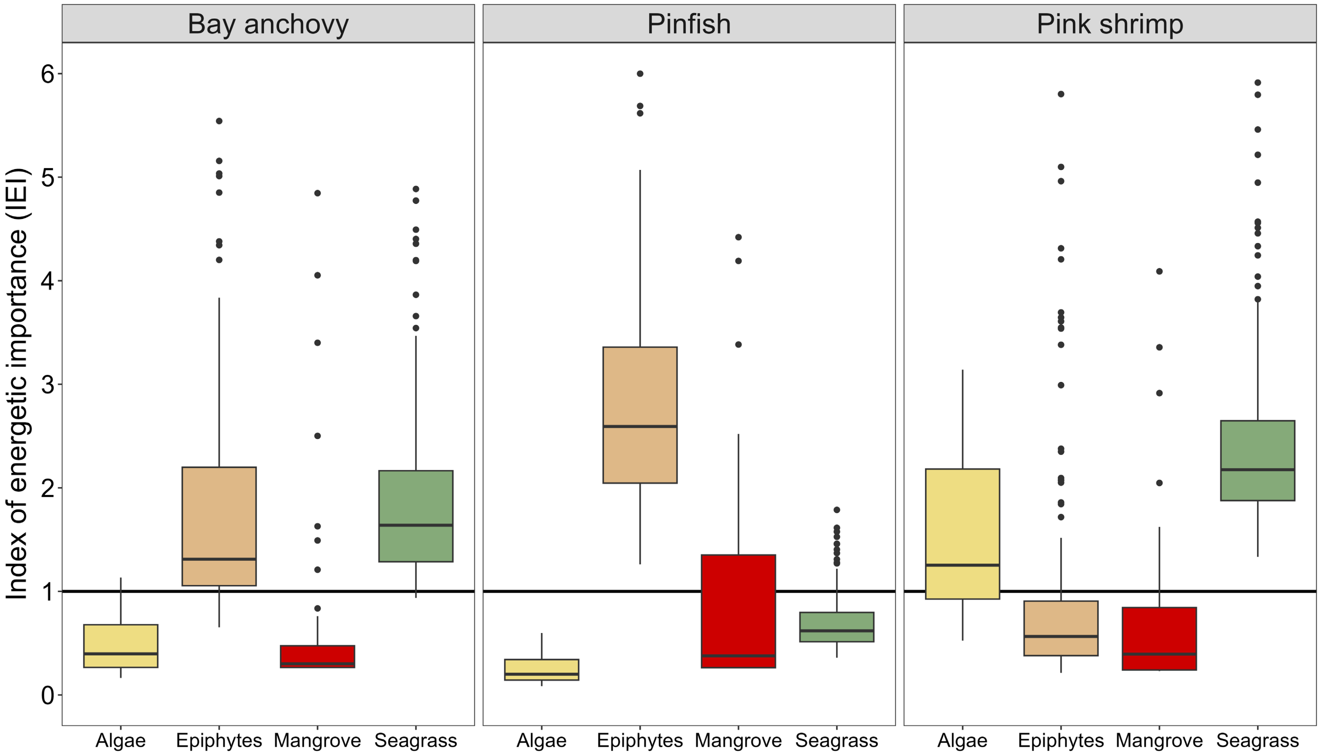

FIGURE 2 Boxplot of the index of energetic (IEI) values for each resource/habitat based on the 50 random points in each basin for each species calculated using the habitat maps for 2019. The horizontal black line represents IEI value of 1. IEI values >1 means that the consumer is using that source more than expected based on the proportion of that habitat in the total foraging area, while the opposite is true for an IEI <1.

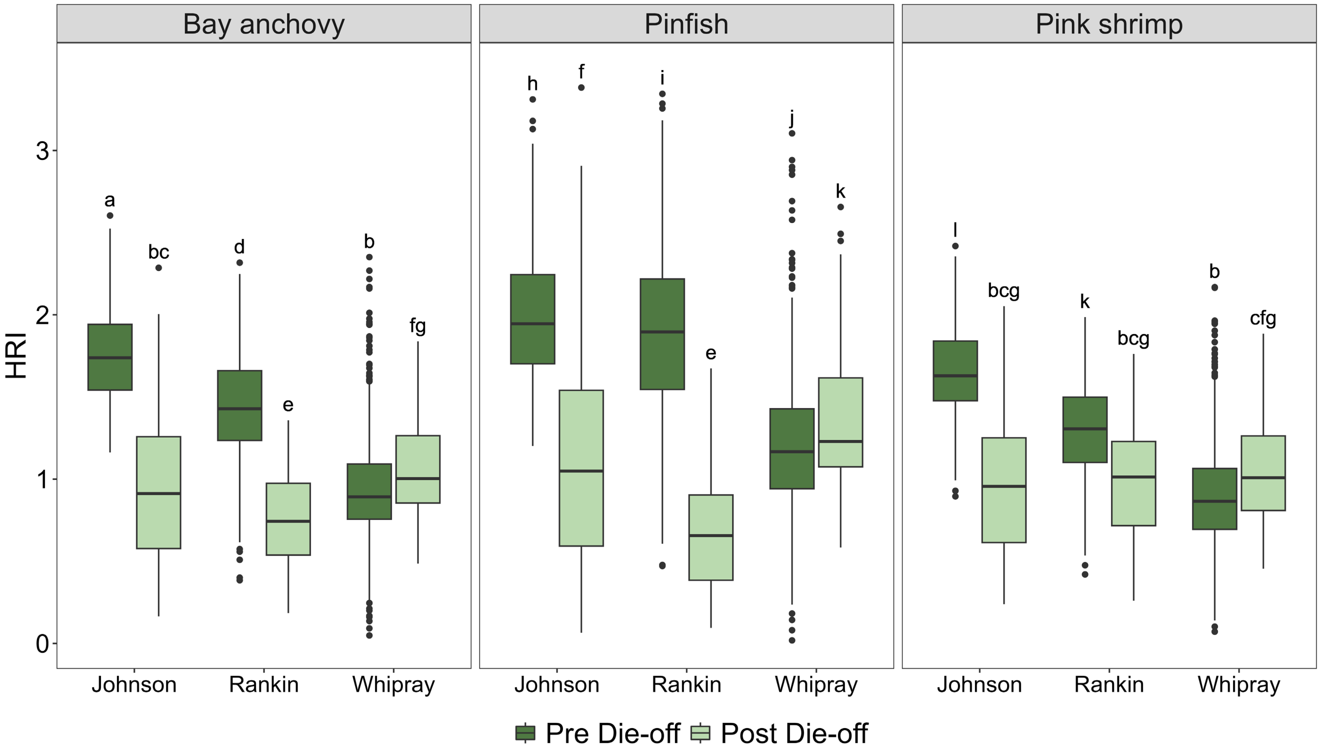

FIGURE 3 Boxplot for habitat resource index (HRI) values for each species and basin pre and post-2015 seagrass die-off. Different letters indicate significantly different ($p < .05$) groups based on model contrast comparisons with a Bonferroni correction.

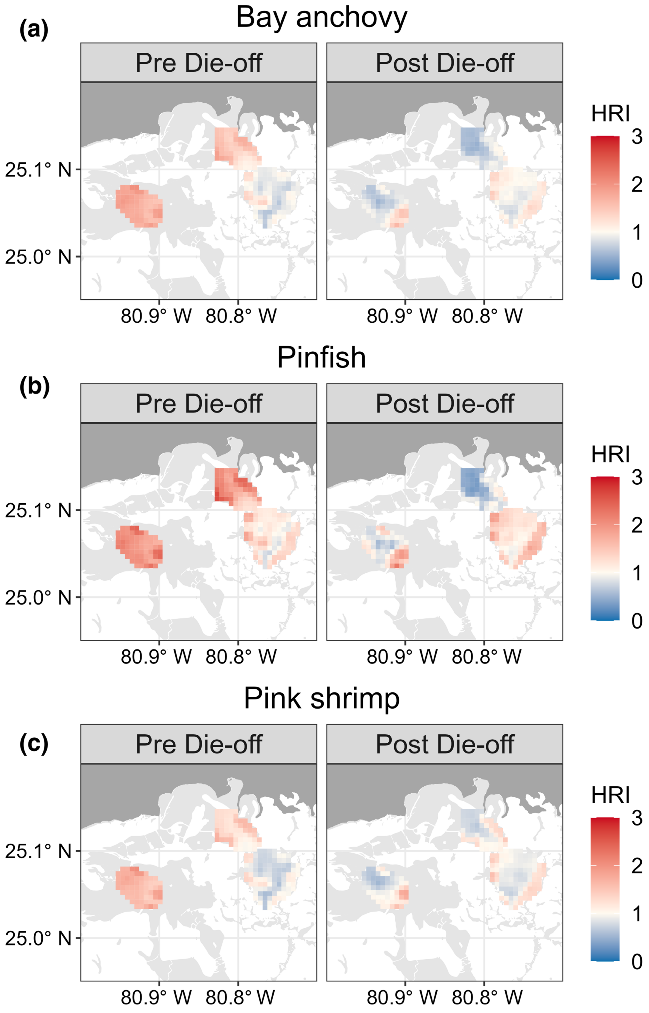

FIGURE 4 *E*-scapes for (a) bay anchovy, (b) pinfish, and (c) pink shrimp before and after the 2015 seagrass die-off for Johnson, Rankin, and Whipray Basins in Florida Bay. Habitat resource index (HRI) values from all years before and after were averaged for each landscape foraging unit. Warm colors (reds) represent HRI values >1 and cool colors (blues) represent HRI values <1. HRI values >1 indicate greater production of resources (i.e., more energetic resources) being used by the consumer, while the opposite is true for HRI values <1.

Therefore, the seagrass die-off not only decreased structural habitat, but also decreased primary production available to food webs. Overall, we found that HRI values decreased in areas most affected by the seagrass die-off (Johnson and Rankin Basins) but not in areas minimally affected by die-off (Whipray Basin). Our results show that the widespread habitat loss resulting from seagrass die-off led to ecosystem level reductions in trophic functioning.

There was a reduction of energetic resources in 2015 following the die-off event in the two heavily impacted basins (Johnson and Rankin, Figures 3–5). Bay anchovy, pinfish, and pink shrimp display interspecific basal resource use patterns (Table 1; James, Santos, Rodemann, et al., 2022). Despite differences in basal resource use, each species had IEI values >1 for seagrass, epiphytes, or both (Figure 2). IEI values >1 indicate that these resources are being used in a relative scale more than they are available by consumers. This notion is supported by the strong correlation of HRI values with both the amount of seagrass and amount of leaf area (Figure 6). Because species relied heavily on seagrass-associated production, it is not surprising that a large loss of seagrass led to a decrease in trophic functioning. Algae and mangrove IEI values (except for algae IEI values for pink shrimp) were <1 for all species. A large-scale loss of these habitat types (e.g., declines due to climate change) would not result in the loss of energetic resource distribution for these consumers because these are not energetically important habitats. Therefore, not all types of habitat loss results in changes to ecosystem function, and there is a need to identify which habitats are the most important producers of energy (i.e., IEI value >1) in order to fully understand the implication of habitat loss for the ecosystem.

Unlike bay anchovy and pinfish, pink shrimp did not have a breakpoint in mean HRI values in Rankin Basin following the seagrass die-off. Pink shrimp HRI values did decrease in 2016 directly following the die-off, but by 2017, mean values were similar to before the die-off (Figure 5c). During the study period, Rankin Basin showed signs of seagrass recovery, which is not the case for Johnson Basin (Rodemann et al., 2021). Additionally, pink shrimp was the only species with an IEI value >1 for a basal resource that was unaffected by the die-off (algae, Table 2; Figure 2). The combination of the recovery trajectory of seagrass and the importance of algae likely led to pink shrimp not displaying a shift in annual trophic function (i.e., no breakpoint in annual HRI value) in Rankin Basin. Thus, *E*-scapes demonstrate that species-specific resource preferences result in markedly different resource distributions within the same seascape (Harris et al., 2021; James, Santos, Rehage, et al., 2022). Habitat loss has been widely shown to have species-specific responses (Betts et al., 2014; Mantyka-pringle et al., 2012; Powers & Jetz, 2019; Püttker et al., 2015; Stuart-Smith et al., 2021), and our results support previous findings that the effects of habitat loss are species-specific.

The two basins impacted by the seagrass die-off (Johnson and Rankin) displayed a decrease in trophic function following the seagrass die-off because of the decline of energetic resource distribution. Although not directly measured, this decline in trophic function likely has an impact on the populations of bay anchovy, pinfish, and pink shrimp. White shrimp in Louisiana marshes displayed decreases in biomass, abundance, and body size with decreases in HRI values (James, Santos, Rehage, et al., 2022), and it is possible that seagrass consumers in Florida Bay had a similar response. Additionally, resource distribution influences variability in resource use and competition between species (Lesser et al., 2020; Santos et al., 2022), as well as consumer movement and distribution (Abrahms et al., 2019, 2021; Geary et al., 2020). Changes in species interactions can result in altered food web structure and function and ultimately affect the stability of consumer populations (Dobson et al., 2006; McCann et al., 1998; Melián & Bascompte, 2002; Valladares et al., 2012). Because of the link between habitats and energy production, loss in structural habitat typically results in loss of energetic production. Decreases in populations and/or biodiversity related to habitat loss are not

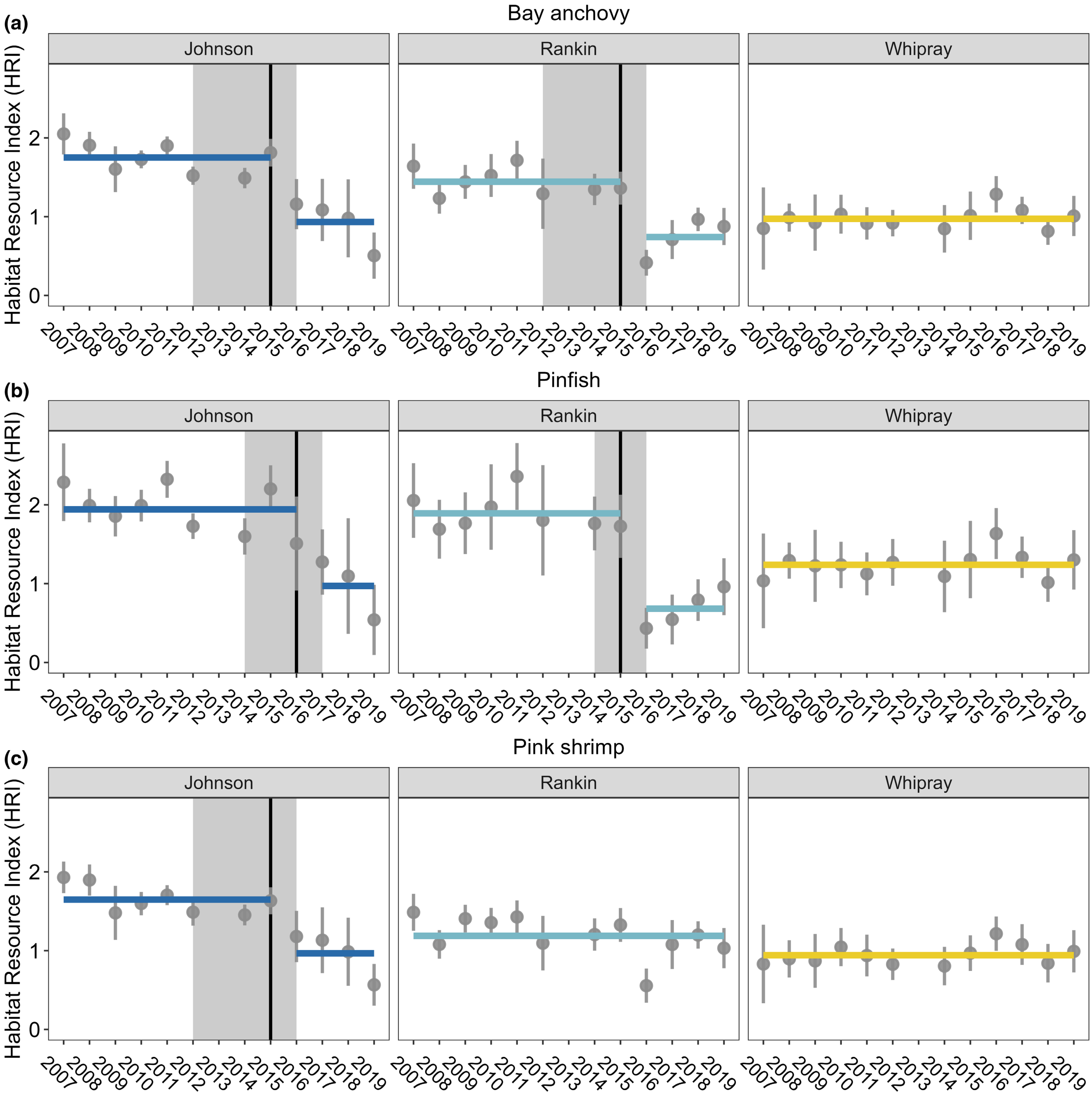

FIGURE 5 Breakpoints based on intercept model for mean habitat resource index (HRI) values for (a) bay anchovy, (b) pinfish, and (c) pigfish for each basin. Vertical black line indicates break point and grey shade represents the 95% confidence interval. Horizontal line indicates model prediction and gray points indicate mean ± SD HRI values for basin.

always linear with habitat amount, often showing nonlinear responses (Swift & Hannon, 2010). Habitat loss does not always decrease resource distribution, as it depends on resource use, as seen in pink shrimp in Rankin Basin. It is possible that trophic function could be a mechanism for the non-linearity between species declines and habitat amount. For example, HRI values for marsh consumers in Louisiana had a nonlinear (maximum at intermediate values) relationship between the proportional amount of water (Harris et al., 2021). Decreases in the amount of this habitat type could either increase trophic function or decrease, potentially leading to nonlinear responses by consumers. However, more research is needed to understand how consumers respond to changes in trophic function at the ecosystem scale.

Seagrass consumers in Florida Bay did not shift resource use in response to decreased seagrass cover from the seagrass die-off (James, Santos, Rodemann, et al., 2022), which led to decreases in provision of energy for the food web once seagrass cover was lost (Figures 3–5). Similar to seagrass consumers in Florida Bay (James, Santos, Rodemann, et al., 2022), marsh consumers in Louisiana did not alter food web structure in response to mangrove encroachment

(Nelson et al., 2019), and increases in mangrove habitat over a 5-year period led to decreases in trophic function of the seascape (Harris et al., 2021). Mangrove production was not an energy source to the food web and therefore, mangroves replacing other habitats that did produce energy sources important to the food web led to decrease in the amount of resources being used by consumers (Harris et al., 2021; Nelson et al., 2019). In these two examples, consumers did not shift resource use across space resulting in a decrease in trophic function, but optimal foraging theory predicts that consumers may either switch to more abundant resources or change behavior to forage in areas with more abundant resources in order to maximize energy intake (McCann et al., 2005; McCann & Rooney, 2009). This switch in foraging is thought to increase food web stability (McCann & Rooney, 2009; McMeans et al., 2015). Seagrass consumers in Florida Bay do show variation in resource use, both seasonally (James, Santos, Rodemann, et al., 2022) and compared to historic values (Calhoun-Grosch et al., 2023), but this variation is related to shifts in the amount of seagrass-associated production (i.e., shifts between epiphyte and seagrass production). Because consumers did not shift away from seagrass-associated production following the large-scale seagrass loss led to the decrease in trophic function seen in this study. There is evidence, however, of other consumers shifting resource use based on resource availability (Deegan & Garritt, 1997; Moncreiff & Sullivan, 2001; Olin et al., 2012). For example, neotropical birds rely heavily on forest-derived resources in heavily forested areas but shift to non-forest resources as forest habitat is lost (Navarro et al., 2021). Shifting resources could mitigate the loss of trophic function related to habitat loss, but further investigation is needed.

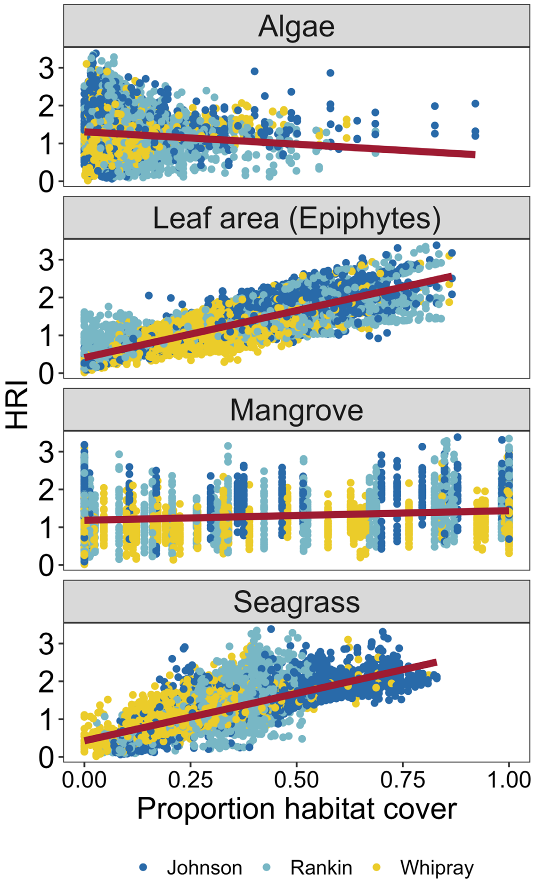

FIGURE 6 Correlation for the proportional habitat cover and habitat resource index (HRI) values for each landscape foraging unit across all species and seasons. There was a positive correlation between seagrass ($r=.75$, $t=105.9$, $p<.001$) and leaf area ($r=.80$, $t=125.2$, $p<.001$) habitat cover with HRI values. There was a slightly positive correlation between mangrove habitat cover and HRI values ($r=.23$, $t=22.0$, $p<.001$). Algal habitat cover and HRI values had a slightly negative correlation ($r=-.10$, $t=-9.5$, $p<.001$).

To build the *E*-scapes for this study, habitat maps were made from kriging points from monitoring data. This approach allowed us to take advantage of a large-scale monitoring effort and assess trends in trophic functioning over time. However, as with all kriging models, spatial uncertainty increases as distance extends away from sampling locations, and seagrass habitats can display abrupt changes within a seascape (Lloyd & Atkinson, 2001; Santos et al., 2015). Remote sensing approaches (e.g., satellite and aerial imagery) to generate habitat maps would increase the accuracy of resource distribution (Harris et al., 2021; James, Santos, Rodemann, et al., 2022; Nelson et al., 2020). We chose to use spatial interpolation to take advantage of the vast spatiotemporal dataset (increasing the number

TABLE 3 The mean (±SD) habitat resource index (HRI) values pre and post-2015 seagrass die-off and output from breakpoint intercept model for each species and basin for HRI values. Breakpoint indicates the year where breakpoint occurred with 95% confidence intervals. Empty value indicates there was not a significant ($p>.05$) breakpoint in the timeseries for mean HRI values.

Species	Basin	Pre die-off	Post die-off	Break point	*F*	*p* Value
Bay anchovy	Johnson	1.75 ± 0.26	0.93 ± 0.46	2015 (2012–2016)	32.9	<.001
	Rankin	1.44 ± 0.31	0.74 ± 0.29	2015 (2012–2016)	34.7	<.001
	Whipray	0.94 ± 0.31	1.05 ± 0.27		2.8	.59
Pinfish	Johnson	2.00 ± 0.37	1.11 ± 0.66	2016 (2014–2017)	21.5	<.001
	Rankin	1.89 ± 0.51	0.68 ± 0.37	2015 (2014–2016)	73.6	<.001
	Whipray	1.20 ± 0.41	1.32 ± 0.38		2.2	.73
Pink shrimp	Johnson	1.65 ± 0.26	0.97 ± 0.44	2015 (2012–2016)	26.2	<.001
	Rankin	1.30 ± 0.27	0.97 ± 0.34		7.2	.09
	Whipray	0.90 ± 0.30	1.03 ± 0.28		4.2	.33

of years *E*-scapes could be generated) and because decreased water clarity following the seagrass die-off made remote sensing more difficult (Rodemann et al., 2021). Our maps provide a robust overview of broad spatiotemporal trends in trophic function, but due to the unequal spatial uncertainty of habitat cover, we would caution against using these maps for fine-scale spatially explicit questions (i.e., fine-scale animal tracking). Additionally, our models make the assumption that seagrass leaf surface area is directly correlated to epiphyte production, although there can be heterogeneity in production (Frankovich & Zieman, 2005). Development of methods that can better estimate the spatial distribution of epiphyte production would improve estimates of resource distribution. To temporally match the resource use and habitat maps, we only calculated IEI values in 2019. Therefore, we assumed that the energetic importance of each resource/habitat type was constant throughout the timeseries. Even if this assumption is not true, patterns observed in this study would likely not change because consumers in Florida Bay do not use non-seagrass-associated production (Calhoun-Grosch et al., 2023; James, Santos, Rodemann, et al., 2022). However, temporal changes in energetic importance of resources are likely important in many systems and should be investigated.

Incorporating changes in ecosystem function into models of habitat loss could improve understanding of how species will respond to future change. Food webs are expected to shift architecture and/or energy sources in response to future global change, such as habitat loss (Bartley et al., 2019). This is already occurring in seagrass food webs, as food webs in areas with increased disturbance have different food web function than less impacted areas (Coll et al., 2011) and food webs have shifted functioning over time (Calhoun-Grosch et al., 2023). Our study provides evidence that differences in resource use, as seen through species-specific resource use, can lead to different ecosystem function within the same seascape. As global change leads to changes in food webs, trophic linkages could shift to make ecosystems have lower overall trophic function. Therefore, consumer species could face stressors from two fronts: the loss of habitat leading to decrease in available resources and changes in food web function that decrease the importance of available habitats. Multi-year studies that pair temporal food web sampling with temporal changes in habitat distribution are needed to understand how these two stressors will alter the trophic function of habitats.

AUTHOR CONTRIBUTIONS

W. Ryan James: Conceptualization; formal analysis; methodology; writing – original draft; writing – review and editing. **Bradley T. Furman:** Conceptualization; methodology; resources; writing – review and editing. **Jonathan R. Rodemann:** Conceptualization; methodology; writing – review and editing. **Sophia V. Costa:** Conceptualization; methodology; writing – review and editing. **Zachary W. Fratto:** Conceptualization; methodology; project administration; writing – review and editing. **James A. Nelson:** Conceptualization; funding acquisition; methodology; writing – review and editing. **Jennifer S. Rehage:** Conceptualization; funding acquisition; methodology; project administration; writing – review and editing. **Rolando O. Santos:** Conceptualization; funding acquisition; methodology; project administration; writing – review and editing.

ACKNOWLEDGEMENTS

This manuscript is the result of research funded by the National Park Service Critical Ecosystems Study Initiative (CESI) task agreement P16AC01437 and in collaboration with projects funded by EPA (SF-02D21022-0), NSF (DEB-1832229, HRD-1547798, HRD-2111661), and NOAA's National Centers for Coastal Ocean Science, Competitive Research Program under award NA21NOS4780150 to Florida International University through the South Florida-Caribbean Cooperative Ecosystems Studies Unit. NSF Grants No. HRD-1547798 and No. HRD-2111661 were awarded to Florida International University as part of the Centers of Research Excellence in Science and Technology (CREST) Program. This is contribution #1690 from the Coastlines and Oceans Division in the Institute of Environment at Florida International University.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available on Github at https://github.com/CoastalFishScience/James_etal_sgE-scape_GCB and archived on Zenodo at https://doi.org/10.5281/zenodo.10802560 (James et al., 2024).

ORCID

W. Ryan James https://orcid.org/0000-0002-4829-7742
Bradley T. Furman https://orcid.org/0000-0002-9284-8388
Jonathan R. Rodemann https://orcid.org/0009-0006-9740-8599
Sophia V. Costa https://orcid.org/0009-0007-3344-3659
Zachary W. Fratto https://orcid.org/0009-0005-1605-2272
James A. Nelson https://orcid.org/0000-0003-4607-3953
Jennifer S. Rehage https://orcid.org/0000-0003-0009-6906
Rolando O. Santos https://orcid.org/0000-0002-3885-9406

REFERENCES

Abrahms, B., Aikens, E. O., Armstrong, J. B., Deacy, W. W., Kauffman, M. J., & Merkle, J. A. (2021). Emerging perspectives on resource tracking and animal movement ecology. *Trends in Ecology & Evolution*, *36*(4), 308–320. https://doi.org/10.1016/j.tree.2020.10.018

Abrahms, B., Hazen, E. L., Aikens, E. O., Savoca, M. S., Goldbogen, J. A., Bograd, S. J., Jacox, M. G., Irvine, L. M., Palacios, D. M., & Mate, B. R. (2019). Memory and resource tracking drive blue whale migrations. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(12), 5582–5587. https://doi.org/10.1073/pnas.1819031116

Bartley, T. J., McCann, K. S., Bieg, C., Cazelles, K., Granados, M., Guzzo, M. M., MacDougall, A. S., Tunney, T. D., & McMeans, B. C. (2019). Food web rewiring in a changing world. *Nature Ecology & Evolution*, *3*(3), 345–354. https://doi.org/10.1038/s41559-018-0772-3

Baston, D. (2022). *Exactextractr: Fast extraction from raster datasets using polygons*. https://CRAN.R-project.org/package=exactextractr

Beck, M. W., Heck, K. L., Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., Halpern, B., Hays, C. G., Hoshino, K., Minello, T.

J., Orth, R. J., Sheridan, P. F., & Weinstein, M. P. (2001). The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience*, *51*(8), 633. https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2

Betts, M. G., Fahrig, L., Hadley, A. S., Halstead, K. E., Bowman, J., Robinson, W. D., Wiens, J. A., & Lindenmayer, D. B. (2014). A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. *Ecography*, *37*(6), 517–527. https://doi.org/10.1111/ecog.00740

Boström, C., Pittman, S. J., Simenstad, C., & Kneib, R. T. (2011). Seascape ecology of coastal biogenic habitats: Advances, gaps, and challenges. *Marine Ecology Progress Series*, *427*, 191–217.

Bryan-Brown, D. N., Connolly, R. M., Richards, D. R., Adame, F., Friess, D. A., & Brown, C. J. (2020). Global trends in mangrove forest fragmentation. *Scientific Reports*, *10*(1), 7117. https://doi.org/10.1038/s41598-020-63880-1

Calhoun-Grosch, S., Foster, E. M., James, W. R., Santos, R. O., Rehage, J. S., & Nelson, J. A. (2023). Trophic niche metrics reveal long-term shift in Florida Bay food webs. *Ecosystems*, *26*, 1183–1194. https://doi.org/10.1007/s10021-023-00825-5

Coll, M., Schmidt, A., Romanuk, T., & Lotze, H. K. (2011). Food-web structure of seagrass communities across different spatial scales and human impacts. *PLoS One*, *6*(7), e22591. https://doi.org/10.1371/journal.pone.0022591

Couvillion, B. R., Fischer, M. R., Beck, H. J., & Sleavin, W. J. (2016). Spatial configuration trends in coastal Louisiana from 1985 to 2010. *Wetlands*, *36*(2), 347–359. https://doi.org/10.1007/s13157-016-0744-9

Deegan, L. A., & Garritt, R. H. (1997). Evidence for spatial variability in estuarine food webs. *Marine Ecology-Progress Series*, *147*(1–3), 31–47. https://doi.org/10.3354/meps147031

Dobson, A., Lodge, D., Alder, J., Cumming, G. S., Keymer, J., McGlade, J., Mooney, H., Rusak, J. A., Sala, O., Wolters, V., Wall, D., Winfree, R., & Xenopoulos, M. A. (2006). Habitat loss, trophic collapse, and the decline of ecosystem services. *Ecology*, *87*(8), 1915–1924. https://doi.org/10.1890/0012-9658(2006)87[1915:HLTCAT]2.0.CO;2

Ellis, E. C., Klein Goldewijk, K., Siebert, S., Lightman, D., & Ramankutty, N. (2010). Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography*, *19*(5), 589–606. https://doi.org/10.1111/j.1466-8238.2010.00540.x

Fahrig, L. (1997). Relative effects of habitat loss and fragmentation on population extinction. *The Journal of Wildlife Management*, *61*(3), 603–610. https://doi.org/10.2307/3802168

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fourqurean, J. W., & Robblee, M. B. (1999). Florida Bay: A history of recent ecological changes. *Estuaries*, *22*(2), 345–357. https://doi.org/10.2307/1353203

Frankovich, T. A., & Zieman, J. C. (2005). A temporal investigation of grazer dynamics, nutrients, seagrass leaf productivity, and epiphyte standing stock. *Estuaries*, *28*(1), 41–52. https://doi.org/10.1007/BF02732752

Furman, B. T., Durako, M. J., & Hall, M. O. (2021). *South Florida Fisheries Habitat Assessment Program 2020 annual report* (FWC/FWRI File Code: F4491-19-I8).

Geary, B., Leberg, P. L., Purcell, K. M., Walter, S. T., & Karubian, J. (2020). Breeding brown pelicans improve foraging performance as energetic needs rise. *Scientific Reports*, *10*(1), 1–9. https://doi.org/10.1038/s41598-020-58528-z

Gräler, B., Pebesma, E., & Heuvelink, G. (2016). Spatio-temporal interpolation using gstat. *The R Journal*, *8*(1), 204–218.

Hall, L. S., Krausman, P. R., & Morrison, M. L. (1997). The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin (1973–2006)*, *25*(1), 173–182.

Hall, M. O., Bell, S. S., Furman, B. T., & Durako, M. J. (2021). Natural recovery of a marine foundation species emerges decades after landscape-scale mortality. *Scientific Reports*, *11*(1), 6973. https://doi.org/10.1038/s41598-021-86160-y

Hall, M. O., Furman, B. T., Merello, M., & Durako, M. J. (2016). Recurrence of *Thalassia testudinum* seagrass die-off in Florida Bay, USA: Initial observations. *Marine Ecology Progress Series*, *560*, 243–249. https://doi.org/10.3354/meps11923

Harris, J. M., James, W. R., Lesser, J. S., Doerr, J. C., & Nelson, J. A. (2021). Foundation species shift alters the energetic landscape of marsh nekton. *Estuaries and Coasts*, *44*, 1671–1680. https://doi.org/10.1007/s12237-020-00852-8

Hiemstra, P. H., Pebesma, E. J., Twenhöfel, C. J. W., & Heuvelink, G. B. M. (2009). Real-time automatic interpolation of ambient gamma dose rates from the Dutch radioactivity monitoring network. *Computers & Geosciences*, *35*(8), 1711–1721. https://doi.org/10.1016/j.cageo.2008.10.011

James, W. R., Furman, B. T., Rodemann, J. R., Costa, S. V., Fratto, Z. W., Nelson, J. A., Rehage, J. S., & Santos, R. O. (2024). Data and code for James et al. "Widespread habitat loss leads to ecosystem-scale decrease in trophic function" [dataset]. *Zenodo*. https://doi.org/10.5281/zenodo.10802560

James, W. R., Santos, R. O., Rehage, J. S., Doerr, J. C., & Nelson, J. A. (2022). *E*-scape: Consumer specific landscapes of energetic resources derived from stable isotope analysis and remote sensing. *Journal of Animal Ecology*, *91*(2), 381–390. https://doi.org/10.1111/1365-2656.13637

James, W. R., Santos, R. O., Rodemann, J. R., Rezek, R. J., Fratto, Z. W., Furman, B. T., Hall, M. O., Kelble, C. R., Rehage, J. S., & Nelson, J. A. (2022). Widespread seagrass die-off has no legacy effect on basal resource use of seagrass food webs in Florida Bay, USA. *ICES Journal of Marine Science*, *79*(6), 1831–1842. https://doi.org/10.1093/icesjms/fsac112

Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, *69*(3), 373–386. https://doi.org/10.2307/3545850

Krause, J. R., Lopes, C. C., Wilson, S. S., Boyer, J. N., Briceño, H. O., & Fourqurean, J. W. (2023). Status and trajectories of soft-bottom benthic communities of the South Florida seascape revealed by 25 years of seagrass and water quality monitoring. *Estuaries and Coasts*, *46*(2), 477–493. https://doi.org/10.1007/s12237-022-01158-7

Layman, C. A., Araujo, M. S., Boucek, R., Hammerschlag-Peyer, C. M., Harrison, E., Jud, Z. R., Matich, P., Rosenblatt, A. E., Vaudo, J. J., & Yeager, L. A. (2012). Applying stable isotopes to examine food-web structure: An overview of analytical tools. *Biological Reviews*, *87*(3), 545–562. https://doi.org/10.1111/j.1469-185X.2011.00208.x

Lázaro, A., & Gómez-Martínez, C. (2022). Habitat loss increases seasonal interaction rewiring in plant–pollinator networks. *Functional Ecology*, *36*(10), 2673–2684. https://doi.org/10.1111/1365-2435.14160

Lenth, R. V. (2023). *emmeans: Estimated marginal means, aka least-squares means*. https://CRAN.R-project.org/package=emmeans

Lesser, J. S., James, W. R., Stallings, C. D., Wilson, R. M., & Nelson, J. A. (2020). Trophic niche size and overlap decreases with increasing ecosystem productivity. *Oikos*, *129*(9), 1303–1313. https://doi.org/10.1111/oik.07026

Lloyd, C. D., & Atkinson, P. M. (2001). Assessing uncertainty in estimates with ordinary and indicator kriging. *Computers & Geosciences*, *27*(8), 929–937. https://doi.org/10.1016/S0098-3004(00)00132-1

Mantyka-pringle, C. S., Martin, T. G., & Rhodes, J. R. (2012). Interactions between climate and habitat loss effects on biodiversity: A systematic review and meta-analysis. *Global Change Biology*, *18*(4), 1239–1252. https://doi.org/10.1111/j.1365-2486.2011.02593.x

Marshall, F. E., Bernhardt, C. E., & Wingard, G. L. (2020). Estimating late 19th century hydrology in the greater Everglades ecosystem: An integration of paleoecologic data and models. *Frontiers in Environmental Science*, *8*, 1–21. https://doi.org/10.3389/fenvs.2020.00003

McCann, K. S., Hastings, A., & Huxel, G. R. (1998). Weak trophic interactions and the balance of nature. *Nature*, *395*(6704), 794–798. https://doi.org/10.1038/27427

McCann, K. S., Rasmussen, J. B., & Umbanhowar, J. (2005). The dynamics of spatially coupled food webs. *Ecology Letters*, *8*(5), 513–523. https://doi.org/10.1111/j.1461-0248.2005.00742.x

McCann, K. S., & Rooney, N. (2009). The more food webs change, the more they stay the same. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *364*(1524), 1789–1801. https://doi.org/10.1098/rstb.2008.0273

McMeans, B. C., McCann, K. S., Humphries, M., Rooney, N., & Fisk, A. T. (2015). Food web structure in temporally-forced ecosystems. *Trends in Ecology & Evolution*, *30*(11), 662–672. https://doi.org/10.1016/j.tree.2015.09.001

Melián, C. J., & Bascompte, J. (2002). Food web structure and habitat loss. *Ecology Letters*, *5*(1), 37–46. https://doi.org/10.1046/j.1461-0248.2002.00280.x

Moncreiff, C., & Sullivan, M. (2001). Trophic importance of epiphytic algae in subtropical seagrass beds: Evidence from multiple stable isotope analyses. *Marine Ecology Progress Series*, *215*, 93–106. https://doi.org/10.3354/meps215093

Naeem, S. (1998). Species redundancy and ecosystem reliability. *Conservation Biology*, *12*(1), 39–45. https://doi.org/10.1111/j.1523-1739.1998.96379.x

Navarro, A. B., Magioli, M., Bogoni, J. A., Moreira, M. Z., Silveira, L. F., Alexandrino, E. R., da Luz, D. T. A., Pizo, M. A., Silva, W. R., de Oliveira, V. C., Donatelli, R. J., Christianini, A. V., Piratelli, A. J., & Ferraz, K. M. P. M. B. (2021). Human-modified landscapes narrow the isotopic niche of neotropical birds. *Oecologia*, *196*(1), 171–184. https://doi.org/10.1007/s00442-021-04908-9

Nelson, J. A., Harris, J. M., Lesser, J. S., James, W. R., Suir, G. M., & Broussard, W. P. (2020). New mapping metrics to test functional response of food webs to coastal restoration. *Food Webs*, *25*, e00179. https://doi.org/10.1016/j.fooweb.2020.e00179

Nelson, J. A., Lesser, J., James, W. R., Behringer, D. P., Furka, V., & Doerr, J. C. (2019). Food web response to foundation species change in a coastal ecosystem. *Food Webs*, *21*, e00125. https://doi.org/10.1016/j.fooweb.2019.e00125

Olin, J. A., Rush, S. A., MacNeil, M. A., & Fisk, A. T. (2012). Isotopic ratios reveal mixed seasonal variation among fishes from two subtropical estuarine systems. *Estuaries and Coasts*, *35*(3), 811–820. https://doi.org/10.1007/s12237-011-9467-6

Pebesma, E. J. (2004). Multivariable geostatistics in S: The gstat package. *Computers & Geosciences*, *30*, 683–691.

Pimm, S. L. (1982). *Food webs*. Springer.

Polis, G. A., Power, M. E., Huxel, G. R., & Huxel, G. R. (Eds.). (2004). *Food webs at the landscape level*. University of Chicago Press.

Powers, R. P., & Jetz, W. (2019). Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nature Climate Change*, *9*(4), 323–329. https://doi.org/10.1038/s41558-019-0406-z

Püttker, T., de Arruda Bueno, A., Prado, P. I., & Pardini, R. (2015). Ecological filtering or random extinction? Beta-diversity patterns and the importance of niche-based and neutral processes following habitat loss. *Oikos*, *124*(2), 206–215. https://doi.org/10.1111/oik.01018

R Core Team. (2023). *R: A language and environment for statistical computing [Computer software]*. R Foundation for Statistical Computing. https://www.R-project.org/

Robblee, M., Barber, T., Carlson, P., Durako, M., Fourqurean, J., Muehlstein, L., Porter, D., Yarbro, L., Zieman, R., & Zieman, J. (1991). Mass mortality of the tropical seagrass Thalassia testudinum in Florida Bay (USA). *Marine Ecology Progress Series*, *71*, 297–299. https://doi.org/10.3354/meps071297

Rodemann, J. R., James, W. R., Santos, R. O., Furman, B. T., Fratto, Z. W., Bautista, V., Lara Hernandez, J., Viadero, N. M., Linenfelser, J. O., Lacy, L. A., Hall, M. O., Kelble, C. R., Kavanagh, C., & Rehage, J. S. (2021). Impact of extreme disturbances on suspended sediment in Western Florida Bay: Implications for seagrass resilience. *Frontiers in Marine Science*, *8*, 980. https://doi.org/10.3389/fmars.2021.633240

Santos, R. O., James, W. R., Nelson, J. A., Rehage, J. S., Serafy, J., Pittman, S. J., & Lirman, D. (2022). Influence of seascape spatial pattern on the trophic niche of an omnivorous fish. *Ecosphere*, *13*(2), e3944. https://doi.org/10.1002/ecs2.3944

Santos, R. O., Lirman, D., & Pittman, S. J. (2015). Long-term spatial dynamics in vegetated seascapes: Fragmentation and habitat loss in a human-impacted subtropical lagoon. *Marine Ecology*, *37*(1), 200–214. https://doi.org/10.1111/maec.12259

Scavia, D., Field, J. C., Boesch, D. F., Buddemeier, R. W., Burkett, V., Cayan, D. R., Fogarty, M., Harwell, M. A., Howarth, R. W., Mason, C., Reed, D. J., Royer, T. C., Sallenger, A. H., & Titus, J. G. (2002). Climate change impacts on U.S. coastal and marine ecosystems. *Estuaries*, *25*(2), 149–164. https://doi.org/10.1007/BF02691304

Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L., & Semmens, B. X. (2018). Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ*, *6*, e5096. https://doi.org/10.7717/peerj.5096

Stuart-Smith, R. D., Mellin, C., Bates, A. E., & Edgar, G. J. (2021). Habitat loss and range shifts contribute to ecological generalization among reef fishes. *Nature Ecology & Evolution*, *5*(5), 656–662. https://doi.org/10.1038/s41559-020-01342-7

Swift, T. L., & Hannon, S. J. (2010). Critical thresholds associated with habitat loss: A review of the concepts, evidence, and applications. *Biological Reviews*, *85*(1), 35–53. https://doi.org/10.1111/j.1469-185X.2009.00093.x

Thompson, P. L., Rayfield, B., & Gonzalez, A. (2017). Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. *Ecography*, *40*(1), 98–108. https://doi.org/10.1111/ecog.02558

Valladares, G., Cagnolo, L., & Salvo, A. (2012). Forest fragmentation leads to food web contraction. *Oikos*, *121*(2), 299–305. https://doi.org/10.1111/j.1600-0706.2011.19671.x

Ware, D. M., & Thomson, R. E. (2005). Ecology: Bottom-up ecosystem trophic dynamics determine fish production in the northeast Pacific. *Science*, *308*(5726), 1280–1284. https://doi.org/10.1126/science.1109049

Waycott, M., Duarte, C. M., Carruthers, T. J. B., Orth, R. J., Dennison, W. C., Olyarnik, S., Calladine, A., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Short, F. T., & Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(30), 12377–12381. https://doi.org/10.1073/pnas.0905620106

Zeileis, A., Leisch, F., Hornik, K., & Kleiber, C. (2002). Strucchange: An R package for testing for structural change in linear regression models. *Journal of Statistical Software*, *7*(2), 1–38. https://doi.org/10.18637/jss.v007.i02

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: James, W. R., Furman, B. T., Rodemann, J. R., Costa, S. V., Fratto, Z. W., Nelson, J. A., Rehage, J. S., & Santos, R. O. (2024). Widespread habitat loss leads to ecosystem-scale decrease in trophic function. *Global Change Biology*, *30*, e17263. https://doi.org/10.1111/gcb.17263