A call to expand global change research in LTER coastal wetlands

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Abstract

Global change stressors are altering the structure of ecological communities with significant implications for the functions and services that ecosystems provide. Coastal zones are particularly susceptible to such stressors, yet our collective understanding of the long-term effects of global change on these systems and, in particular, the consumer species found within them, is limited. The US Long-Term Ecological Research (LTER) network provides an opportunity to address this research need. Leveraging publicly available LTER data, I summarize ongoing LTER research in coastal wetlands with an emphasis on studies assessing how global change variables impact consumer species and trophic interactions; identifies research gaps; and introduces a framework for future long-term global change research in coastal LTER sites. In so doing, this piece highlights important new directions for long-term ecological studies in coastal ecosystems and provides an impetus for future research to fill in crucial knowledge gaps.

Keywords

Coastal ecosystems; Consumers; Global change; Long-term ecological research; Species interactions

1. Introduction

Across the globe, ecosystems are experiencing an increase in the number and intensity of anthropogenic impacts, including climate change, eutrophication, pollution, and land-use change (Bellard et al. 2012, Diaz et al. 2019, van Moorsel al. 2022, IPCC 2023). While significant variation exists in how species and ecological communities respond to these impacts, the overall effects are negative and range from habitat degradation to biodiversity loss (Sage 2019, IPCC

2023). Coastal zones, which include salt marsh, mangrove, and seagrass ecosystems, are particularly susceptible to global change stressors as nearly 40% of the world’s population is concentrated along coastlines (Harley et al. 2006, Cloern et al. 2015). These ecosystems provide crucial functions and services, including food production, habitat refugia, and disturbance regulation, valued in the trillions of dollars annually (Costanza et al. 2017, Zedler 2000). However, despite their importance, various anthropogenic activities have resulted in large-scale losses of coastal wetlands and their associated ecosystem functions and services (Craft et al. 2009, Kirwin and Megonigal 2013, Giri et al. 2011). In a recent review of coastal impacts in the Anthropocene, He and Silliman (2019) summarize the scope of climate change and other human-induced effects that range in scale from genes and physiology to ecosystem functions and services. For example, rising sea-levels can increase inundation stress, reducing the photosynthesis and growth of salt marsh grasses and mangroves on their seaward edge (Donnelly and Bertness 2002). At the community level, climate change can reshuffle coastal marine communities; increased mortality of species occupying habitats outside their thermal tolerance, for instance, can lead to the simplification of ecological assemblages (He and Silliman 2019). Further, harmful algal blooms resulting from anthropogenic nutrient enrichment along with overfishing can make coastal ecosystems more sensitive to increasing seawater temperatures, which can lead to an increase in pathogen loads and cause phase shifts to barren states (Zaneveld 2016). Altogether, such impacts sharply reduce the capacity for coastal ecosystems to provide important functions and services with consequences for both people and nature.

As global climate change and other anthropogenic impacts continue, developing an understanding of the long-term effects on coastal ecological communities and the provision of ecosystem services is crucial. To date, the landscape of long-term research (defined here as a study conducted over a minimum five-year period) on global change in coastal environments has emphasized impacts on abiotic features and habitat-forming species, such as oysters and corals (Iwaniec et al. 2021, Rastetter et al. 2021, Zinnert et al. 2021). However, research over the last 30 years has increasingly highlighted the importance of other biotic factors, such as herbivory and trophic interactions, in the maintenance of ecosystem properties and functions within coastal wetlands (Cannicci et al. 2008, Hughes et al. 2013, Bertness et al. 2014, Moore 2018, Moore and Schmitz 2021, Sievers et al. 2022). He and Silliman (2016), for example, synthesized data from 443 studies and found that salt marsh and mangrove herbivores strongly influence plant survival, reproduction, and growth. Similarly, through a series of consumer presence/absence experiments, Hughes et al. (2016) observed a novel trophic cascade whereby sea otters increased seagrass nutrient thresholds by facilitating a reduction in harmful epiphyte loads. Despite these and other examples noting the importance of consumer species and trophic interactions in coastal systems, empirical assessments of the long-term effects of global change stressors on these features have been limited. Such studies can provide key insights into the lasting effects of global change on coastal ecological communities and have the potential to inform conservation and restoration efforts within these environments.

The US Long-Term Ecological Research (LTER) network provides a unique opportunity to address this research need. Established in 1980, the LTER network consists of 28 sites across the United States, Puerto Rico, and Antarctica, with over 1800 scientists and students studying ecological processes over extended temporal and spatial scales (Alber et al. 2013). Research studies conducted within this network, which include long-term observation data coupled with shorter-term experiments and other mechanistic studies, produce publicly available datasets that can be used in concert to address important large-scale ecological questions. These multi-decadal studies have played a disproportionate role in advancing the field of ecology, including transforming our understanding of long-term cycles in soil carbon decay and associated microbial responses in forested ecosystems and elucidating the influence of multi-year climate variability on net primary productivity in grasslands (LTER 2019 Decadal Review). Therefore, using this vast research network, I leverage LTER data to assess the current state of long-term research in coastal wetlands evaluating ecological responses to global change. Specifically, I aim to: 1. Summarize ongoing LTER research in coastal wetlands with an emphasis on studies assessing how global change variables impact consumer species and trophic interactions; 2. Identify important research gaps; and 3. Introduce a framework for future long-term global change research in coastal wetlands. In so doing, this piece highlights important new directions for long-term ecological studies in coastal wetlands and provides an impetus for future research to fill in crucial knowledge gaps.

2. Current state of LTER studies in coastal wetlands

2.1. LTER database review

Data on coastal wetland research conducted at LTER sites was compiled from the Environmental Data Initiative Portal on May 18, 2023. The following search terms were used in separate queries to gather data from studies conducted in vegetated coastal wetlands: “salt marshes”, “mangroves”, and “seagrass.” The EDI search engine takes plural and multi-word terms and provides results that include the singular and individual words such that “salt marshes,” for example, produces results that include “salt,” “marsh,” and “marshes” in the title, abstract, or keywords.

These searches produced 748 salt marsh, 49 mangrove, and 63 seagrass meadows datasets after removing studies that were not conducted in any of these ecosystems. Results from each search were compiled into one comprehensive spreadsheet and filtered to remove duplicates, resulting in 665 salt marsh, 44 mangrove, and 57 seagrass meadow datasets for a total of 767 studies. For each dataset, bibliographic information, study location, and details on the focus of the study were extracted from the title, abstract, and metadata. The data were further filtered to identify studies that incorporated evaluations of biotic factors, such as consumer species or trophic interactions, with additional information on the study duration, study type (e.g., experimental or observational), species type (e.g., vertebrate or invertebrate), and species taxonomic group extracted from this subset. A comprehensive summary of these datasets can be found in the Supplementary Materials.

2.2. Summary of LTER studies in salt marshes, seagrass meadows, and mangroves

Within the LTER network, there are four intertidal coastal research sites: the Florida Coastal Everglades (FCE, established in 2000), Georgia Coastal Ecosystems (GCE, established in 2000), Plum Island Ecosystems (PIE, established in 1998) in Massachusetts, and the Virginia Coast Reserve (VCR, established in 1987). Research studies were unevenly distributed across these locations, with 328 studies conducted in GCE, 187 in PIE, 127 in VCR, and 53 in FCE. The remaining 72 studies either encompassed multiple regions or were conducted in non-LTER sites supported by LTER-funding or affiliates, including locations in California, Mississippi, South Carolina (an archived LTER site), Texas, Australia, and the Caribbean (Fig. 1). The Santa Barbara Coastal LTER in California focuses on subtidal giant kelp forest ecosystems and is not included in this synthesis.

Studies that did not incorporate assessments of consumer species or trophic interactions represented 71% of the dataset and focused primarily on surveying changes in plant, soil, or water properties overtime or in response to experimental manipulations, such as nutrient enrichments (Table 1). Of the remaining 218 (28%) datasets, most focused on one of the following broad study areas: consumer density and abundance surveys, nutrient enrichment impacts, consumer impacts on vegetation or ecosystem functions, and food web and ecological community structure (Table 2). Within this subset of consumer-focused studies, the majority were observational with only 25 datasets derived from experimental investigations. Study duration ranged from less than 1 year to 38 years and nearly 50% of studies were conducted for up to 1 year while less than 20% continued for more than 10 years (Fig. 2). Further, LTER studies assessing consumer species exhibited a significant ecosystem bias and regional skew, with 204 salt marsh, 8 seagrass, and 5 mangrove datasets spread across GCE (137 studies), PIE (41 studies), VCR (15 studies), and FCE (7 studies). Similarly, the type of consumers evaluated were heavily biased towards invertebrates, while only 34 studies included vertebrate species (Table 3). Within these groupings, crustaceans and gastropods were the most commonly evaluated invertebrates and birds and fish were the most common vertebrates. Finally, 14 studies included assessments of herbivory and 4 addressed predator-prey interactions or predation, collectively representing only 6% of the consumer-focused datasets.

3. Global change impacts on consumer species in LTER coastal sites

In order to summarize coastal LTER studies focused on consumer species and trophic interactions, consumer-focused studies were filtered by research topic to identify those that evaluated global change stressors. This filtering process produced 24 studies with publicly available corresponding data that were placed into three global change categories: nutrient enrichment (15 studies), saltwater intrusion and range expansion (5 studies), and sea-level rise (4 studies). The following sub-sections summarize these data in two ways: 1. A meta-analysis was conducted to evaluate the overall effect of nutrient enrichments on consumers and biotic interactions; and 2. Narrative reviews of saltwater intrusion, range expansion, and sea-level rise impacts are provided based on the available data and associated publications.

3.1 Nutrient enrichment

3.1.1 Data extraction, effect size calculations, and data analysis

Studies included in this meta-analysis were required to meet three criteria: 1. They were observational or experimental studies that included a nutrient enrichment treatment and a control; 2. Consumer and/or trophic interaction responses, such as species abundance or density, were measured in each treatment; and 3. The experimental treatment and control contained at least 10 replicates. Using these criteria, 11 studies with 38 observations were retained (see Supplementary Materials for study details). Several studies conducted repeated measures within an experiment over various time periods – in these cases, only the most recent measurement, which represents the accumulation of treatment effects over time, were included in this analysis. Although this limits the ability to detect temporal variation in treatment effects, it nonetheless provides a snapshot of global change effects at a key moment in time across each experimental site.

For each observation, sample size, mean response of all measured variables, and the associated standard deviations were calculated. The effect size was calculated as the standardized mean difference (SMD) using Hedge’s *g*, which has a magnitude that can be interpreted using the following rule of thumb (Cohen 1988, 1992): 0.2 is considered to be a small effect, 0.5 is a medium effect, 0.8 is a large effect, and $g > 1.0$ is a very large effect. To calculate an overall mean effect size, a multi-level random effects model was constructed using the *metafor* package in RStudio (version 2022.07.2 + 576). Unlike standard random-effects models, multi-level models account for correlated or dependent effect sizes that may be present within or between studies by including nested random effects within the model. Here, ‘study’ was included as a random effect with individual observation ‘effect sizes’ nested within it.

Lastly, publication bias was assessed using funnel plots and an Egger test was conducted to measure plot asymmetry. These tests revealed a correlation between observed outcomes (SMD) and the corresponding sampling variances, suggesting a publication bias ($z = 2.0612$, $p < 0.0393$). However, Rosenberg’s fail-safe number – the estimated number of unpublished studies that would have to be included in the meta-analysis to change the significance of the result – was 4816, which is larger than the rule of thumb cut-off value for assessing publication bias (equal to $5N + 10$, where N is the number of studies included in synthesis). The large fail-safe number suggests that these results are robust to publication bias.

3.1.2. Data summary and meta-analysis results

Of the 11 studies included in this meta-analysis, all but one were conducted in salt marshes found at the Plum Island Ecosystems LTER. The remaining study (GCE LTER and McCall 2012) was conducted in several salt marshes across the Atlantic coast and the Gulf of Mexico. Study durations ranged from less than 1 year to 17 years with an average of 8.5 years. Finally, consumers evaluated within these studies included arthropods, crustaceans, gastropods, and fish. No study assessed herbivory, predation, or other species interactions.

The multi-level meta-analysis model results indicate that nutrient enrichment had a small but significant negative effect on consumer response variables (SMD = -0.2001, p = 0.0381). Specifically, consumer abundance, biomass, density, and size were lower under nutrient enrichment compared to the control (Fig. 3). As posited in two recent studies (Nessel et al. 2021, Nessel et al. 2022), the decline in invertebrate abundance and biomass may be due to nutrient enrichment changing the identity of the limiting nutrient, thereby causing elemental imbalances between consumers and their resources. Such mismatches can constrain consumer growth and reproduction, leading to changes in population abundance as well as the structure of the ecological community (Schade et al. 2003, Mulder 2010, Gonzalez et al. 2014, Lemoine et al. 2014).

Vertebrate responses to nutrient enrichment may be similarly mediated by vegetation impacts. Specifically, fish abundance and species richness have both been shown to decline with increasing nutrient availability in salt marshes and seagrass meadows due to attendant changes in ecosystem structure and function (Deegan 2002). For example, nutrient enrichment is associated with a decline in stem density in seagrass ecosystems, reducing the availability of preferred habitat structure for many nekton species. Conversely, in salt marsh ecosystems, nutrient enrichment allows for the rapid growth of algae, followed by a decline in dissolved oxygen availability, and a concomitant decline in fish abundance and diversity (Deegan 2002).

Altogether, although the overall effect was modest and varied across taxonomic groups, the meta-analysis results presented here suggest that nutrient additions may have important implications for community structure and function at higher order trophic levels.

3.2 Saltwater intrusion and range expansion

Coastal ecosystem responses to saltwater intrusion and range expansions were assessed in five studies included in this review, with two primary areas of focus: 1. Mangrove encroachment into higher latitudes due to increasing winter temperatures and sea-level rise, and 2. Upland migration of salt marsh species in response to sea-level rise and saltwater intrusion. These studies, each of which are briefly summarized below, evaluated a diversity of response variables, including dietary preferences and food quality, consumer species abundance and biometrics, and changes in ecological community structure.

Goeke et al. (2021a, 2021b, 2023) used feeding trials and food quality assays over a one year period to determine how key coastal wetland consumers, the marsh periwinkle (*Littoraria irrorata)* and mudflat fiddler crabs (*Uca rapax),* interact with the encroaching black mangrove (*Avicennia germinans*) in the Gulf of Mexico. They found that *Littoraria* avoided consuming *Avicennia* and selectively ingested leaf tissue from a common marsh grass instead, and that both *Littoraria* and *Uca* were found to store ~10% less energy when consuming *Avicennia*. Though outside the scope of their study, Goeke et al. (2023) note that the pattern of food preference and decreased physiological condition in two taxonomically distinct species may represent a general consequence of mangrove encroachment that is not species-specific, with significant implications for energy flow within these changing ecosystems. In particular, as *Spartina alterniflora* becomes less common, the attendant decrease in body condition of basal consumers may lead to a reduction in prey availability and destabilization of higher trophic levels (Goeke et al. 2023).

Separately, Armitage et al. (2021a) evaluated the impact of mangrove encroachment on associated plant and epifaunal assemblages over an eight-year period. The authors established several large survey areas at tidal wetland sites with and without black mangroves along the Texas coastline and annually recorded vascular plant cover and diversity as well as snail (*Littoraria* *irrorata*) and fiddler crab (*Uca spp.*) density along transects perpendicular to the shoreline. They observed a 50% reduction in marsh plant species richness at sites with mangroves, while snails and crabs were largely unaffected (Armitage 2021a). In an associated publication that expanded upon this work, the authors found that mangrove encroachment was also correlated with a decline in bird richness and a shift in the nekton community assemblage (Fig. 4 and 5) (Armitage et al. 2021b). The authors posit a number of potential explanations for these observations, including competition between mangroves and marsh vegetation leading to a decline in plant diversity that resulted in subsequent changes in faunal diversity (Armitage et al. 2021b). Altogether, the findings of these studies suggest that mangrove encroachment may have significant impacts on growth and survival at the individual-level and alter community assemblages with implications for the provision of functions and services at the ecosystem-level.

Two datasets included in this review assessed the impact of salt marsh migration and coastal forest retreat on invertebrate community assemblages. Johnson & Goetz (2022) and Goetz & Johnson (2023) surveyed arthropod communities over a one-year period across a forest-to-marsh gradient and evaluated the ecological equivalency between the retreating "ghost" forest and marsh habitats. Diet measurements for two common arthropods, a salt marsh amphipod (*Orchestia grillus*) and a marsh hunting spider (*Pardosa littoralis*), were also collected to assess the functional equivalency of the marsh and ghost forest as food sources. The authors found that community composition differed between habitats, driven largely by retreating forest species, marsh species migrating into the forest, and species unique to both habitats at the ecotone; these shifts in community assemblages resulted in greater species diversity in the ghost forest (Goetz 2022). Further, isotope analyses revealed that although *O. grillus* expanded its diet to include terrestrial detritus when in the ghost forest, both *O. grillus* and *P. littoralis* diets consisted primarily of salt marsh species regardless of which habitat they occupied. These results indicate that as rising seas and saltwater intrusion facilitate salt marsh migration and the formation of ghost forests, marsh invertebrates may be able to maintain their habitat extent in the face of marsh loss at the seaward edge.

3.3 Sea-level rise

The effect of sea-level rise on consumer species attributes was assessed in four studies using a space-for-time substitution method. Three studies (Byrnes 2019, 2021, 2022) were conducted at the Plum Island Ecosystems LTER, where permanent plots are arranged along the landscape at varying distances from the creekbank to simulate different stages of sea-level rise. A fourth study (Morris and Sundberg 2023) was conducted at the North Inlet, an archived LTER site in South Carolina, where sampling plots were similarly established in high and low marsh areas as proxies for sea-level rise treatments. It is important to note here that the summaries provided below are based on broad preliminary statistical analyses, as the aforementioned LTER datasets were not associated with any corresponding publications when the present article was written.

Using the space-for-time sea-level rise study salt marsh sites at PIE over a 5-year period, Byrnes (2019, 2021, 2022) deployed fishing traps and collected identity and abundance data on 17 common fish and crab species, as well as data on predation and herbivory rates using tethered baits at established experimental plots. Within this study, plot number indicates distance from the creekbank, with Plot 1 being the closest and Plot 5 being the furthest. The relationships between predation/herbivory rates, fish and crab abundance, and sea-level rise were analyzed using generalized linear models. To provide a broad overview of these data, only fish and crab abundance for the two most common species (the mummichog, *Fundulus heteroclitus* and the European green crab, *Carcinas maenas*) were included in this analysis. For each model, experimental plot and year were set as fixed effects and an experimental plot by year interaction term was included to identify year-specific differences. Finally, consumption rate models were fit to a binomial error distribution while the fish and crab abundance models were fit to a Poisson error distribution. Models were analyzed using the "glmmTMB" library (Brooks et al. 2017) along with the "multcomp" library (Hothorn et al. 2008) to get significance estimates.

Model results indicate that sea-level rise was not a significant predictor of predation ($p > 0.381$) or herbivory rates ($p > 0.489$). However, there were significant differences in the abundance of *F. heteroclitus* and *C. maenas* within and between years. Specifically, across the full dataset, *F. heteroclitus*, was present in lower numbers in Plots 2 and 3 compared to Plots 1 and 4 (Table 4). Conversely, *C. maenas* was present in greater numbers in plots further from the creekbank compared to plots closer to the creekbank, except for Plots 2 and 3, which were not statistically different from one another (Table 4). There were additional differences in species abundance patterns across experimental plots between years, but no generalizable trends were observed (Fig. 6). Altogether, though preliminary, these findings suggest that sea-level rise is not expected to be correlated with predictable changes in consumption rates or fish and crab abundances at PIE.

In a separate study, Morris and Sundberg (2023) compiled a 19-year dataset on plant traits and the habitat use of two species of snail, *Littoraria sp.* and *Melampus sp.*, in response to nutrient enrichment and sea-level rise in a South Carolina salt marsh. In the analysis of these data, nutrient enrichment treatments were excluded in order to focus exclusively on sea-level rise effects. Further, since *Melampus sp.* was rarely observed at this study site across years, only data for *Littoraria sp.* is summarized here. Across all years, the average abundance of *Littoraria sp.* was roughly equal between the high and low marsh, with 1.066 and 1.044 individuals per plot, respectively. There was, however, a significant difference in habitat use between the high and low marsh, though inter-annual variation was observed (Fig. 7). Specifically, *Littoraria sp.* in the low marsh was more likely to be found on vegetation than on the ground (F-value = 63.1, df = 1, $p < 0.0001$), while *Littoraria sp.* in the high marsh was more likely to be found on the ground than on vegetation (F-value = 43.25, df = 1, $p < 0.0001$). Such responses have been observed in other studies, where *Littoraria* occupies vegetation during high tide to avoid nekton predators, like the blue crab, which forages when the marsh is inundated (Hovel et al. 2001). Though limited in scope, these results highlight differential habitat use in marsh invertebrates in response to sea-level rise, with potential implications for survival and food-web structure under increasing and constant seal-level rise conditions.

3.4. Summary of global change LTER studies

The studies summarized above highlight the diversity of responses to global change within coastal systems across temporal and geographic scales. Specifically, nutrient enrichment was associated with a decrease in consumer density and abundance, though significant variation was present across consumer types and metrics. Saltwater intrusion and range expansion produced outcomes that ranged from reduced diversity and the simplification of the ecological community to the upland expansion of an ecosystem experiencing significant coastal losses. Finally, while sea-level rise did not strongly influence consumer abundance or herbivory/predation rates, there was an observed shift in the habitat use between low marsh and high marsh environments. This range of ecological responses underscores the importance of evaluating biotic factors and the concomitant impacts they may have on ecosystem functions and services.

A framework for future coastal LTER global change research

The data and summaries presented here uncover important limitations and gaps in current research on the long-term effects of global change on coastal wetland communities. Most notably, nearly half of all coastal wetland LTER research was conducted over a period lasting one year or less. While many of these studies were situated within larger research efforts conducted over longer time periods, numerous others were short duration experiments/observations independent of larger efforts. Short-term LTER experiments are often used to elucidate the mechanisms that underly large-scale spatial and temporal effects, but such studies are still limited in their ability to accurately reflect patterns and dynamics that occur over broad temporal scales. This may be especially true for biotic effects, which are known to shift seasonally and in response to cycles of disturbance and recovery (Reed et al. 2022). It is therefore essential for LTER studies on biotic factors to increase in duration in order to truly assess the long-term consequences of global change on coastal ecological communities.

Another important limitation identified through this assessment is the significant bias in the types of ecosystems and consumers under study. Nearly 88% of the studies included here were conducted in salt marshes and 82% of consumer-focused studies evaluated invertebrates. These biases restrict our ability to fully understand the long-term effects of global change across diverse vegetated coastal environments and the species found therein. As such, it is imperative that future efforts expand to include mangroves and seagrass meadows, as well as the vertebrate species that occupy these environments.

Finally, the research topics and variables measured in the datasets summarized here were relatively narrow. Roughly 76% of studies that assessed consumer species were presence/absence or abundance surveys; only 6% included consumer impacts on vegetation and just one study explicitly evaluated predator-prey interactions. While such studies provide invaluable information on population change and coastal ecosystem attributes over time, new research directions are needed. Therefore, in order to develop a comprehensive understanding of how global change will affect coastal ecological communities, a framework for future coastal LTER research is outlined in Figure 8. There is a pressing need for global change research to explicitly incorporate ecological complexity, additional and multiple global change stressors, context-dependency, relevant temporal scales, and their interactions (Orr et al. 2020). In particular, research in coastal LTER sites should investigate the role of species identity and interactions, as well as bottom-up and abiotic forces, in the maintenance of ecosystems functions and services, evaluate how multiple change stressors both independently and synergistically alter these dynamics, and assess the ways in which these relationships change across various temporal and spatial scales. Such assessments should explicitly incorporate response metrics across various scales, including species-level, community-level, and ecosystem-level responses in order to more accurately and holistically reflect environmental impacts. This framework aims to guide future studies within coastal LTER sites, thus leveraging this spatially, temporally, and collaboratively expansive network to its fullest potential.

Conclusions

The US LTER network provides an unparalleled opportunity to evaluate ecological processes at large spatial and temporal scales. While the insights derived from studies conducted across LTER sites have reshaped numerous ecological paradigms, research within this network must be expanded. Global change stressors are altering the structure of ecological communities with significant implications for the functions and services they provide. This is particularly true for coastal environments, which often experience multiple stressors simultaneously. In order to fully understand these impacts, research efforts that integrate long-term holistic assessments of ecosystem responses to global change are required. This article provides an impetus for future research to fill in critical knowledge gaps utilizing the LTER network, thereby improving our collective ability to understand and respond to global change.

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Table 1. Summary of coastal LTER studies that did not include assessments of consumer species. Values in parentheses indicate the number of studies included in that category.

Summary Variable	Category and Number of Studies
Site	Georgia Coastal Ecosystems LTER (190)
	Plum Island Ecosystems LTER (150)
	Virginia Coast Reserve LTER (111)
	Florida Coastal Everglades LTER (45)
	Non-LTER Sites (25)
Habitat	Saltmarsh (458)
	Seagrass Meadows (44)
	Mangrove Forests (32)
Study Focus	Plant Properties (152)
	Water Properties (123)
	Landscape Patterns (90)
	Soil Properties (70)
	Atmospheric Properties (43)
	Plant Community (36)
	Ecosystem Properties (15)
	Genetics (3)
	Socio-Ecological (1)
	Restoration (1)
	Carbon Storage (1)

Table 2. Summary of coastal LTER consumer-focused studies. Values in parentheses indicate the number of studies included in that category.

Summary Variable	Category and Number of Studies
Site	Georgia Coastal Ecosystems LTER (138)
	Non-LTER Sites (45)
	Plum Island Ecosystems LTER (39)
	Virginia Coast Reserve LTER (16)
	Florida Coastal Everglades LTER (8)
Habitat	Saltmarsh (205)
	Seagrass Meadows (8)
	Mangrove Forests (5)
Study Focus	Surveys (166)
	Fertilizer Experiment (15)
	Consumer Impacts on Vegetation/Ecosystem Properties (14)
	Food Web/Community Structure (8)
	Sea-level Rise (4)
	Ecosystem Engineers (3)
	Species Biometrics (2)
	Predation/Herbivory Rates (1)
	Predator Impacts on Prey (1)
	Parasite Impacts on Hosts (1)
	Trophic Cascades (1)

Table 3. Type of consumers evaluated in coastal LTER studies. Values in parentheses indicate the number of studies included in that category. The "Multiple" designation describes studies that evaluated more than two taxonomic groups.

Consumer Type	**Consumer Taxonomic Group**
Invertebrate (191)	Bivalves (14)
	Crustaceans (53)
	Gastropods (35)
	Insects (26)
	Zooplankton (2)
	Multiple (74)
Vertebrate (34)	Birds (10)
	Fish (14)
	Reptiles (3)
	Multiple (7)

Table 4. Generalized linear model results for *F. heteroclitus* and *C. maenas*, assessing the relationship between species abundance and experimental plot. Bold values indicate statistical significance at $p < 0.05$.

F. heteroclitus Model Results				
Experimental Plot Comparisons	**Estimate**	**Standard Error**	**z-value**	**p-value**
Plot 2 – Plot 1	-0.77596	0.07658	-10.133	**<1e-04**
Plot 3 – Plot 1	-1.40306	0.09678	-14.497	**<1e-04**
Plot 4 – Plot 1	0.05221	0.06002	0.870	0.815
Plot 3 – Plot 2	-0.62709	0.10740	-5.839	**<1e-04**
Plot 4 – Plot 2	0.82818	0.07596	10.902	**<1e-04**
Plot 4 – Plot 3	1.45527	0.09630	15.112	**<1e-04**
C. maenas Model Results				
Experimental Plot Comparisons	**Estimate**	**Standard Error**	**z-value**	**p-value**
Plot 2 – Plot 1	0.60217	0.12970	4.643	**<0.001**
Plot 3 – Plot 1	0.68770	0.12780	5.381	**<0.001**
Plot 4 – Plot 1	0.98354	0.12221	8.048	**<0.001**
Plot 3 – Plot 2	0.08553	0.10685	0.800	0.8525
Plot 4 – Plot 2	0.38137	0.10009	3.810	**<0.001**
Plot 4 – Plot 3	0.29584	0.09762	3.031	**0.0129**

Figure Legends

Figure 1. Map indicating location of coastal LTER or LTER-affiliated sites. Red represents current LTER sites; yellow represents either archived LTER sites or LTER-supported research sites.

Figure 2. Distribution of study duration for consumer-focused coastal LTER research studies.

Figure 3. Forest plot of the mean effect size for consumer variables in response to nutrient enrichment. Lines indicate 95% confidence intervals. The value of the overall mean effect size with 95% confidence intervals in brackets is shown in the bottom right-hand side of the figure.

Figure 4. Rarefaction curves for (a) shorebirds and (b) waders over all observations during the four-year study period. Reprinted from Armitage A.R., Weaver C.A., Whitt A.A., and Pennings S.C. 2021b. Effects of mangrove encroachment on tidal wetland plant, nekton, and bird communities in the Western Gulf of Mexico. *Estuarine, Coastal and Shelf Science* 248: 106767. Copyright 2021 by Elsevier.

Figure 5. Nonmetric multidimensional scaling plot depicting differences between nekton (a) fish and (b) invertebrate assemblages in sites with (black symbols) and without (grey symbols) mangroves over four years. Reprinted from Armitage A.R., Weaver C.A., Whitt A.A., and Pennings S.C. 2021b. Effects of mangrove encroachment on tidal wetland plant, nekton, and bird communities in the Western Gulf of Mexico. *Estuarine, Coastal and Shelf Science* 248: 106767. Copyright 2021 by Elsevier.

Figure 6. Average abundance of (a) *F. heteroclitus* and (b) *C. maenas* at each experimental plot between 2017 and 2021. Bars represent standard error. Data from: Byrnes 2019 and 2021.

Figure 7. Habitat use by *Litorraria sp.* in low marsh (LM) vs high marsh (HM) experimental plots. Panel (a) summarizes individuals found on the plant; Panel (b) summarizes individuals found on the ground. Bars represent standard error. Data from: Morris J. and Sundberg K. 2023.

Figure 8. Framework for future research in coastal LTER sites. Arrows indicate interactions among the broad research areas. EFS = Ecosystem functions and services.

Figure 1

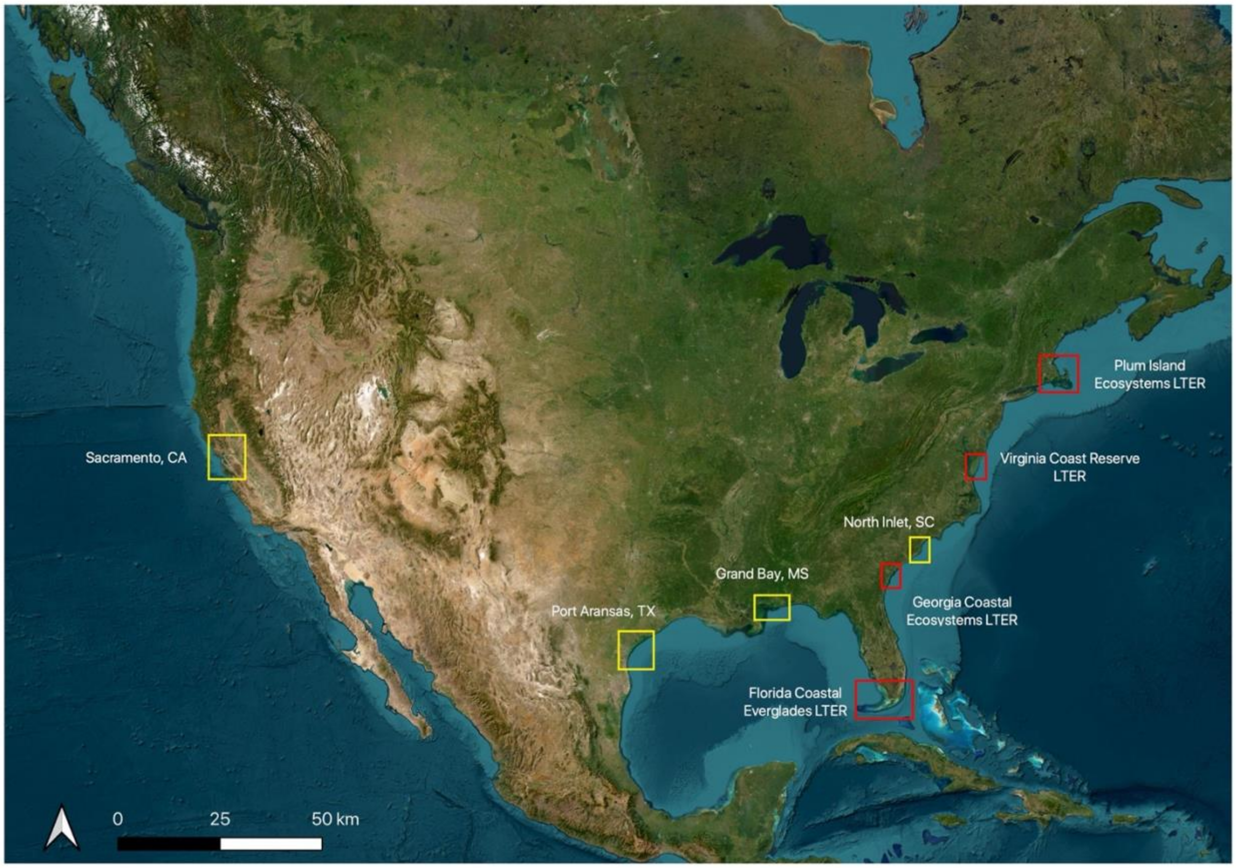
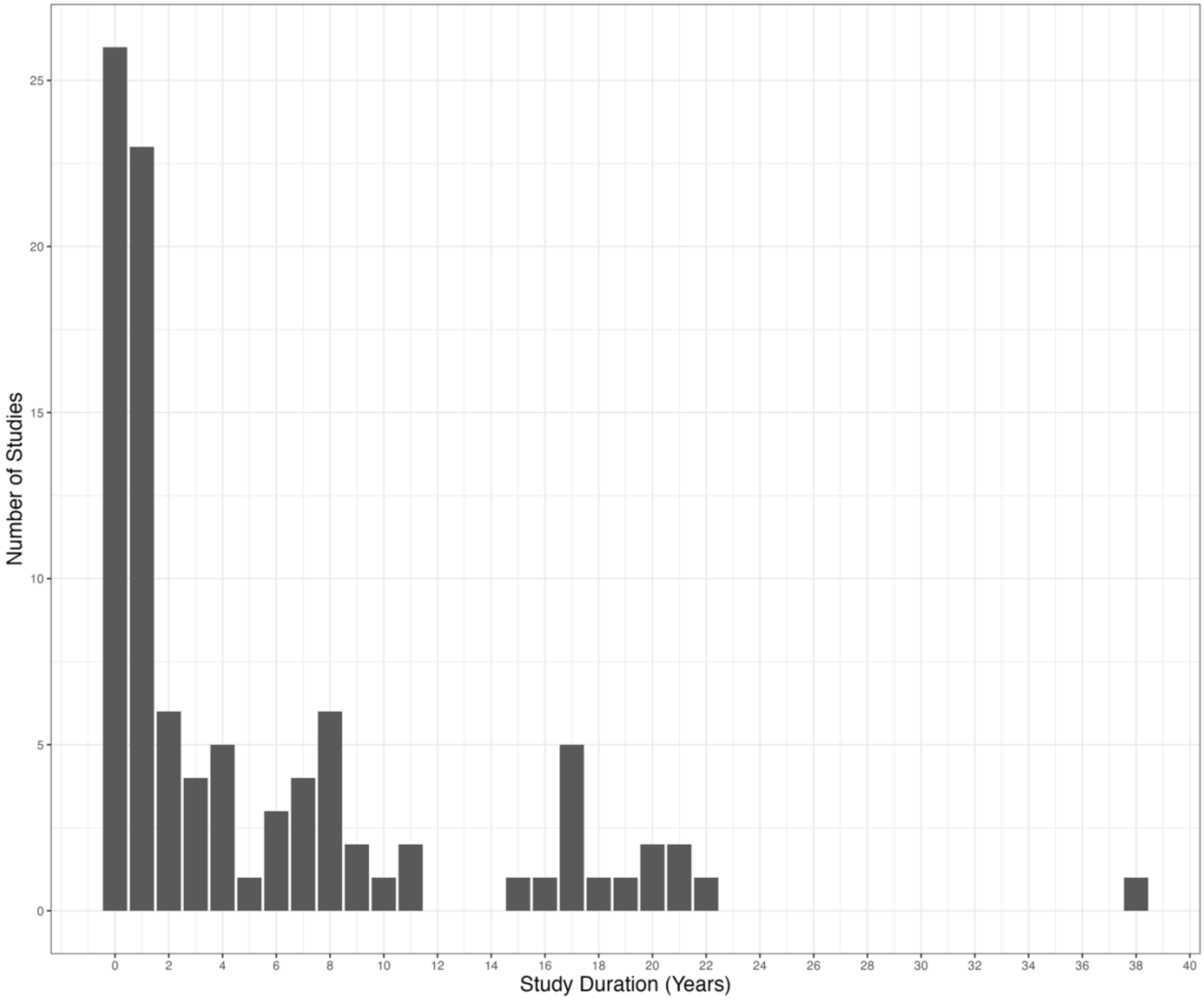

Plum Island Ecosystems LTER
Sacramento, CA
Virginia Coast Reserve LTER
North Inlet, SC
Grand Bay, MS
Georgia Coastal Ecosystems LTER
Port Aransas, TX
Florida Coastal Everglades LTER
0
25
50 km

Figure 2


Number of Studies
0
5
10
15
20
25
Study Duration (Years)
0
2
4
6
8
10
12
14
16
18
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22
24
26
28
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32
34
36
38
40

Figure 3

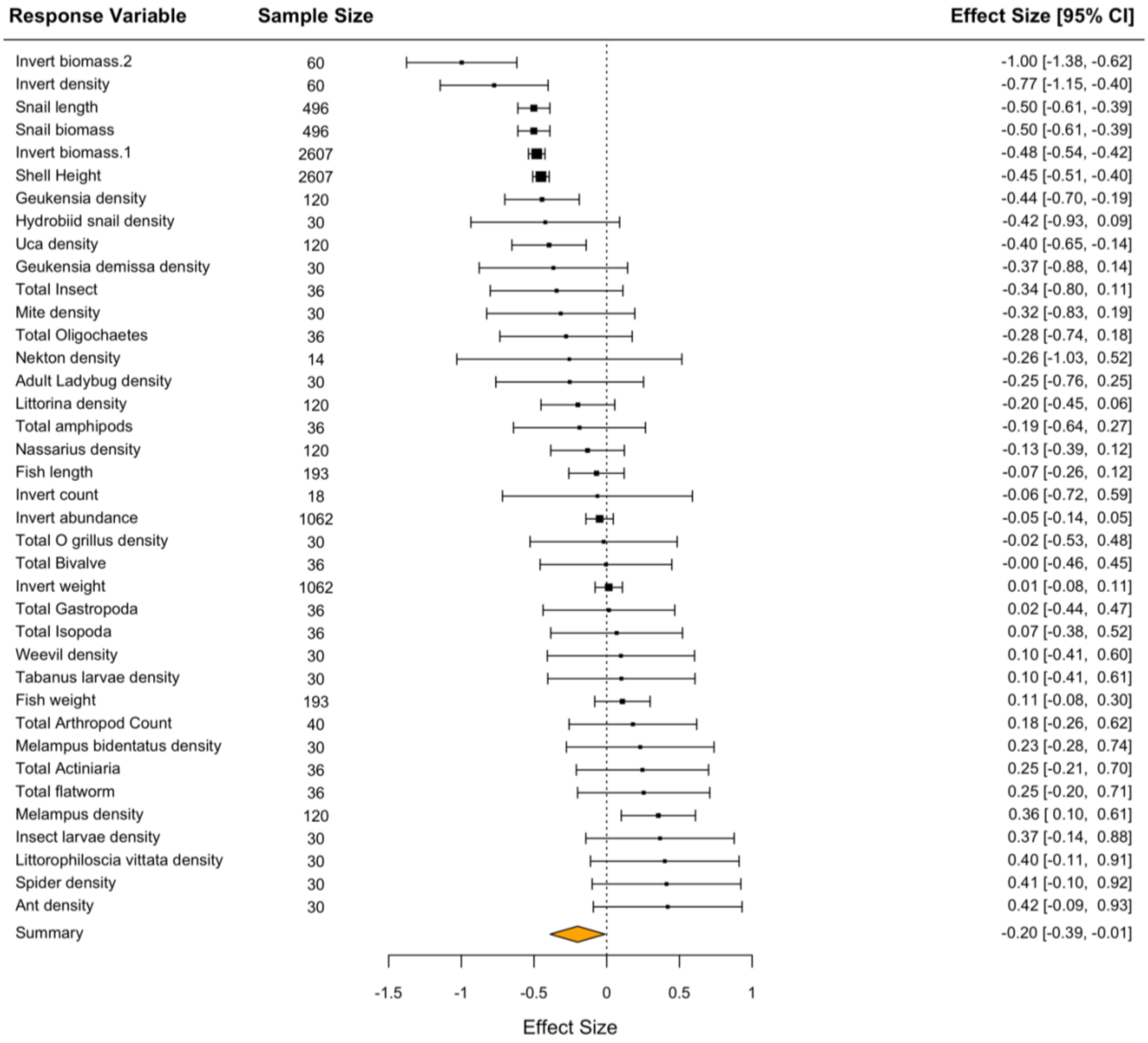
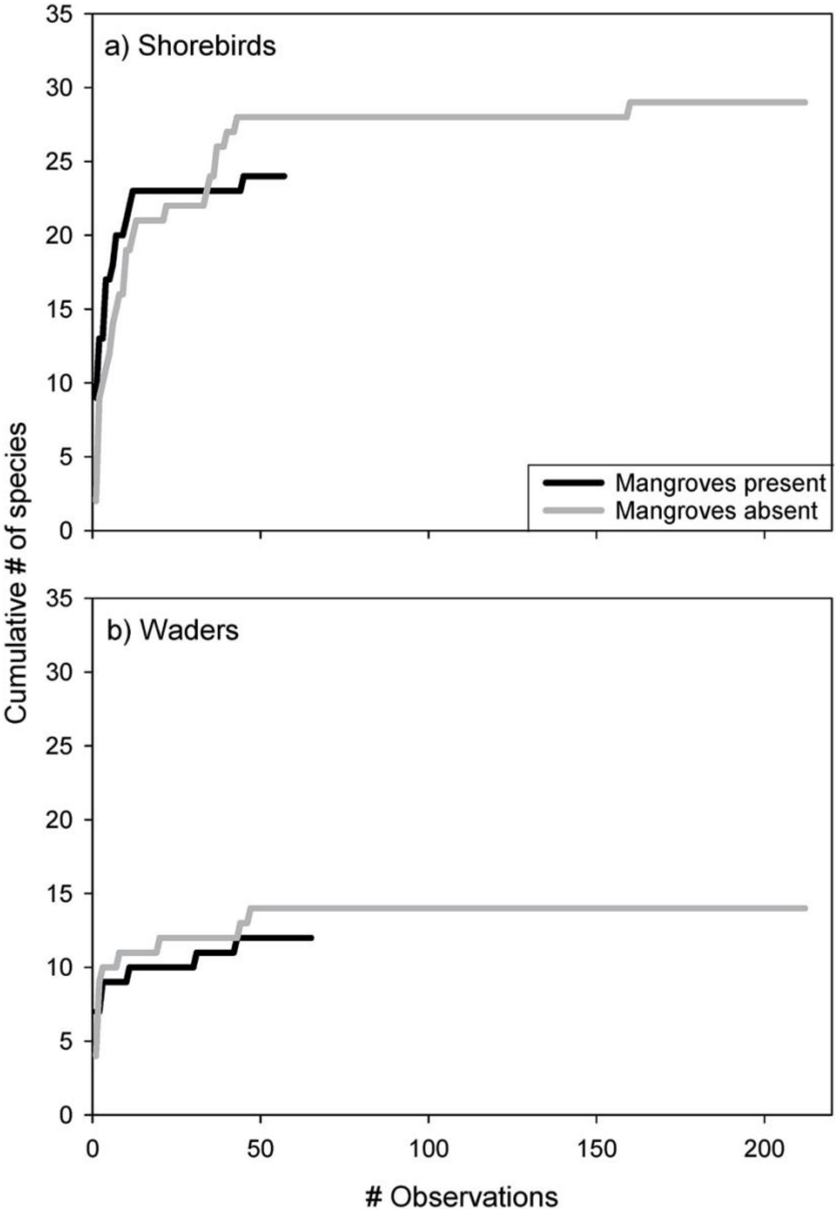

Response Variable
Sample Size
Effect Size [95% CI]
Invert biomass.2 60 -1.00 [-1.38, -0.62]
Invert density 60 -0.77 [-1.15, -0.40]
Snail length 496 -0.50 [-0.61, -0.39]
Snail biomass 496 -0.50 [-0.61, -0.39]
Invert biomass.1 2607 -0.48 [-0.54, -0.42]
Shell Height 2607 -0.45 [-0.51, -0.40]
Geukensia density 120 -0.44 [-0.70, -0.19]
Hydrobiid snail density 30 -0.42 [-0.93, 0.09]
Uca density 120 -0.40 [-0.65, -0.14]
Geukensia demissa density 30 -0.37 [-0.88, 0.14]
Total Insect 36 -0.34 [-0.80, 0.11]
Mite density 30 -0.32 [-0.83, 0.19]
Total Oligochaetes 36 -0.28 [-0.74, 0.18]
Nekton density 14 -0.26 [-1.03, 0.52]
Adult Ladybug density 30 -0.25 [-0.76, 0.25]
Littorina density 120 -0.20 [-0.45, 0.06]
Total amphipods 36 -0.19 [-0.64, 0.27]
Nassarius density 120 -0.13 [-0.39, 0.12]
Fish length 193 -0.07 [-0.26, 0.12]
Invert count 18 -0.06 [-0.72, 0.59]
Invert abundance 1062 -0.05 [-0.14, 0.05]
Total O grillus density 30 -0.02 [-0.53, 0.48]
Total Bivalve 36 -0.00 [-0.46, 0.45]
Invert weight 1062 0.01 [-0.08, 0.11]
Total Gastropoda 36 0.02 [-0.44, 0.47]
Total Isopoda 36 0.07 [-0.38, 0.52]
Weevil density 30 0.10 [-0.41, 0.60]
Tabanus larvae density 30 0.10 [-0.41, 0.61]
Fish weight 193 0.11 [-0.08, 0.30]
Total Arthropod Count 40 0.18 [-0.26, 0.62]
Melampus bidentatus density 30 0.23 [-0.28, 0.74]
Total Actiniaria 36 0.25 [-0.21, 0.70]
Total flatworm 36 0.25 [-0.20, 0.71]
Melampus density 120 0.36 [0.10, 0.61]
Insect larvae density 30 0.37 [-0.14, 0.88]
Littorophiloscia vittata density 30 0.40 [-0.11, 0.91]
Spider density 30 0.41 [-0.10, 0.92]
Ant density 30 0.42 [-0.09, 0.93]
Summary -0.20 [-0.39, -0.01]
-1.5
-1
-0.5
0
0.5
1
Effect Size

Figure 4



a) Shorebirds
b) Waders
Mangroves present
Mangroves absent
Cumulative # of species
Observations
0
5
10
15
20
25
30
35
0
50
100
150
200

Figure 5

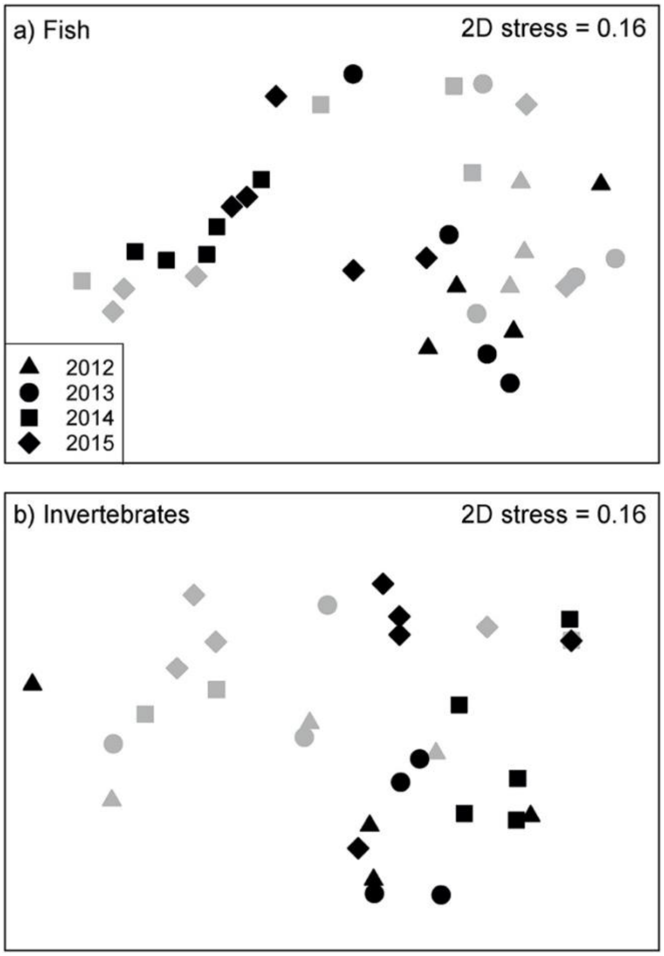

a) Fish
2D stress = 0.16
▲ 2012
● 2013
■ 2014
◆ 2015
b) Invertebrates
2D stress = 0.16

Figure 6

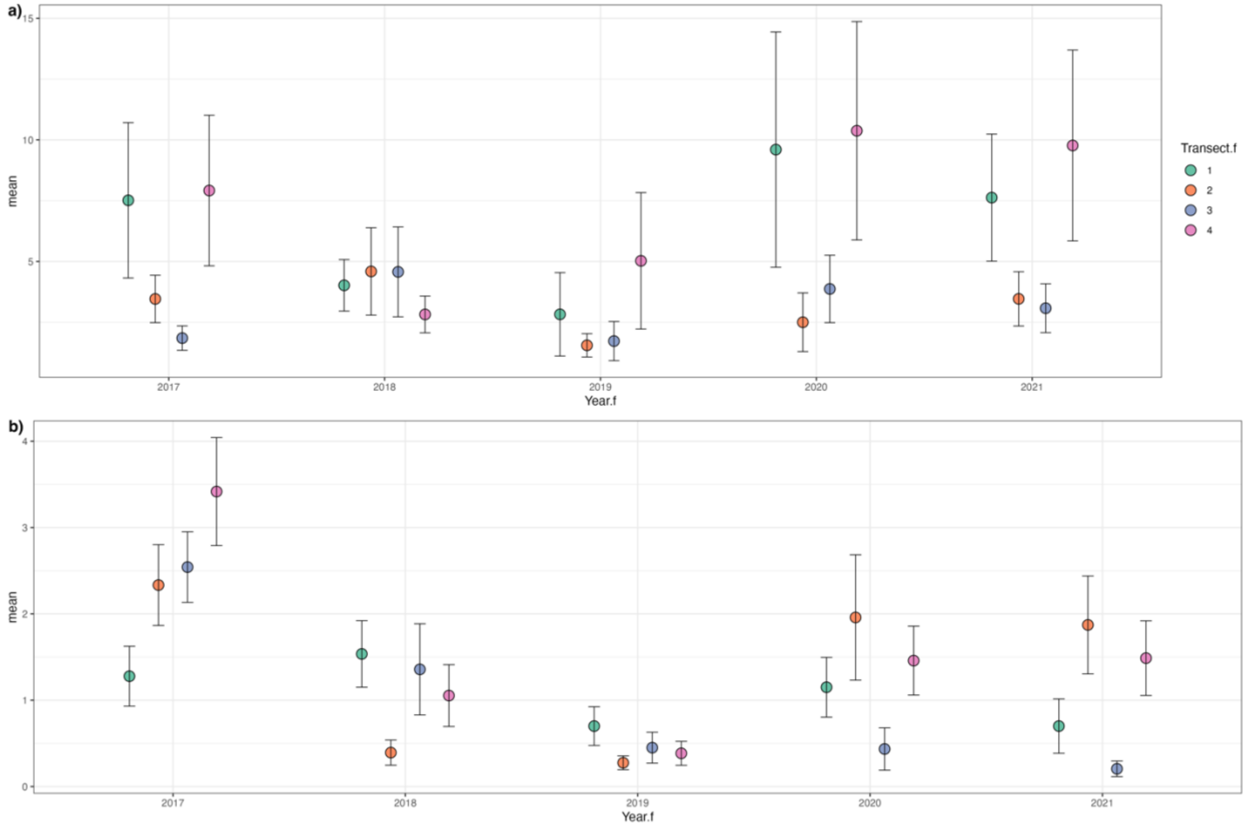
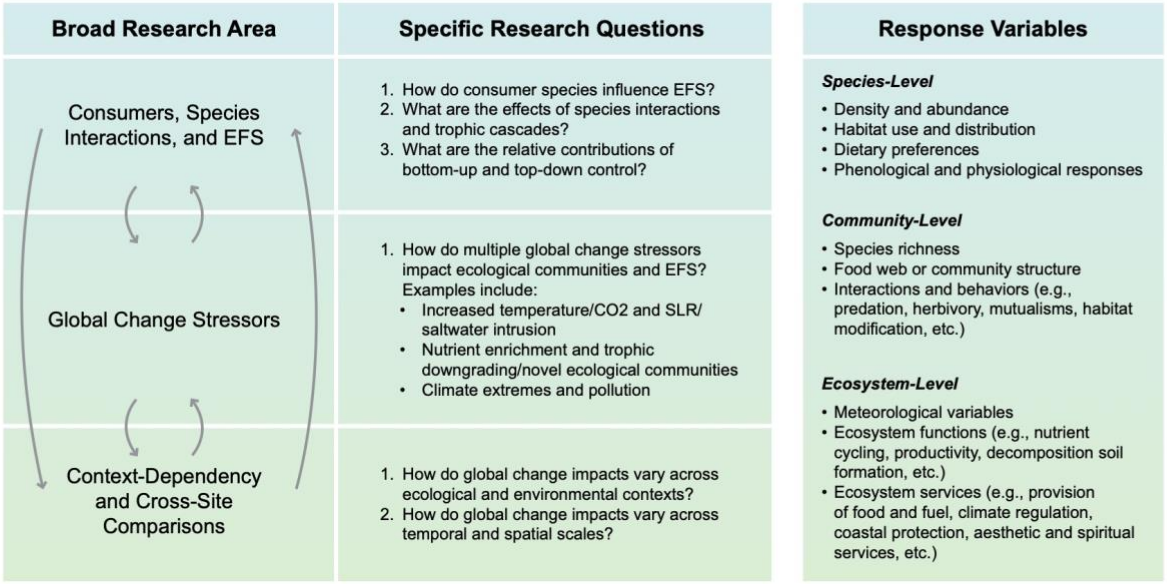

a)
15
10
5
mean
2017
2018
2019
2020
2021
Year.f
Transect.f
1
2
3
4
b)
4
3
2
1
0
mean
2017
2018
2019
2020
2021
Year.f

Figure 7


a)
2.0
1.5
1.0
0.5
mean
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019
2020
2021
2022
Year.f
Location.f
HM
LM
b)
0.6
0.4
0.2
0.0
mean
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019
2020
2021
2022
Year.f

Figure 8



Broad Research Area	Specific Research Questions
Consumers, Species Interactions, and EFS	1. How do consumer species influence EFS? 2. What are the effects of species interactions and trophic cascades? 3. What are the relative contributions of bottom-up and top-down control?
Global Change Stressors	1. How do multiple global change stressors impact ecological communities and EFS? Examples include: • Increased temperature/CO2 and SLR/ saltwater intrusion • Nutrient enrichment and trophic downgrading/novel ecological communities • Climate extremes and pollution
Context-Dependency and Cross-Site Comparisons	1. How do global change impacts vary across ecological and environmental contexts? 2. How do global change impacts vary across temporal and spatial scales?

Response Variables

Species-Level

- Density and abundance
- Habitat use and distribution
- Dietary preferences
- Phenological and physiological responses

Community-Level

- Species richness
- Food web or community structure
- Interactions and behaviors (e.g., predation, herbivory, mutualisms, habitat modification, etc.)

Ecosystem-Level

- Meteorological variables
- Ecosystem functions (e.g., nutrient cycling, productivity, decomposition soil formation, etc.)
- Ecosystem services (e.g., provision of food and fuel, climate regulation, coastal protection, aesthetic and spiritual services, etc.)