# 1. Introduction

Anthropogenic activities continue to exert long-term, varied, and increasing pressures on ecosystems [1] causing alterations to biological diversity on local and global scales. Shifts in biodiversity at local scales are variable and potentially more nuanced than at global scales, but generally local changes manifest primarily as changes to community composition and structure rather than declines in richness [2]. These shifts in communities through time are difficult to predict, in part, due to the multidimensional nature of biodiversity [3]. Yet, understanding how communities change through time is crucial for predicting current and future changes to biological systems and ecosystem services.

Explaining the extent and pace of biodiversity change will require identifying the conditions that lead to divergent biological responses to environmental change, both natural and anthropogenic. In particular, it will be important to disentangle the roles of intrinsic (e.g., ecological) and extrinsic (e.g., environmental) drivers of biodiversity change. Intrinsic and extrinsic processes can interact, leading to temporal patterns of biodiversity change that vary in response to environmental change. For example, gradual environmental change over time can lead to gradual community shifts or these shifts may be undetectable or abrupt [4,5].

Disentangling the complexity of drivers and responses in community structure is especially pressing for marine systems. Marine systems have experienced greater changes than other habitats [6]. Yet, we currently lack linkages between ecological theory, primarily derived from terrestrial systems, and data in marine systems leaving unanswered questions about biodiversity changes in these habitats [7]. We propose a framework to explore the nature of biodiversity change in an estuary bay community and connect this change to intrinsic and extrinsic drivers. This research will build towards a more coherent theory of biodiversity change through time[8]**.**

**We propose to address four main questions in this work:**

1. **What are the temporal dynamics (magnitude, frequency, duration, predictability) of community change?**
2. How are the temporal dynamics of community change **linked to temporal dynamics of extrinsic drivers?**
3. How are the dynamics of community change linked to temporal dynamics of extrinsic drivers **altered by community cohesiveness?**
4. How are the dynamics of community change linked to temporal dynamics of extrinsic drivers altered by community cohesiveness **as determined by niche filtering and species interactions?**

# 2. Background

## 2.1 The Temporal Dynamics of Community and Environmental Change

Biological communities are changing [9,10]; however, we currently lack an understanding of the mechanisms underlying these changes [11–14]. Community change, like the broader concept of biodiversity, is multidimensional and responses can vary along single and multiple dimensions [3]. For instance, biodiversity change can manifest in the total number of species (*α*-diversity), species composition (*β*-diversity), or species’ relative abundance (community structure). Changes in diversity, richness, evenness, composition, abundance, and biomass may all occur, not occur all, or occur in combination in response to environmental variation in time. For example, multi-decadal changes in a California rocky intertidal community were primarily compositional, related to range shifts [15]. Following a punctuated period of high temperatures, local extinctions decreased *α*-diversity in the Mediterranean [16]. Decreases in abundance, and concordant species richness, were seen in Lake Pontchartrain, Louisiana after Hurricane Katrina however no changes in evenness or composition were observed [17]. Benthic compositional shifts and declines in richness and abundance highly correlate with duration of hypoxia events in the Northern Gulf of Mexico [18]. The effects of pollution are known to radically increase abundances in a few key taxa, ultimately leading to decreases in evenness (e.g. [19]). Yet, along pollution gradients compositional and structural changes are also observed [20]. *How these different community dynamics react can inform about the mechanisms occurring within the community.*

The uncertainty in predicting community responses reflects that both communities and disturbances can exhibit a range of temporal dynamics that vary in *magnitude, duration, frequency, and predictability*.

Magnitude is defined by how much the change departs from its original state [21]. Duration is the temporal length of change until it returns to the original state. Frequency is the rate of occurrence of the event. Last, predictability is the constancy in magnitude, duration, and frequency [22]. For disturbance, distinguishing between pulses and presses as end members has proven a useful heuristic, despite its limitations [21]. Here, pulse disturbances are short duration, high magnitude, and often unpredictable. In contrast, press disturbances are constant, of long-duration and often of low magnitude (but cumulative effects can be large), and more predictable [21].

Likewise, community change can occur over long durations and of low magnitude, i.e. gradual, or can be abrupt and of high magnitude, i.e. punctuated. The connection between the dynamics of environmental and community change has long guided and perplexed ecologists. In some cases, environmental variation imparts small amounts of random noise in population abundances around a longer-term mean. In others, the temporal dynamics of disturbance can be a dominant controlling factor, causing population extinction in extreme cases [23]. Large, punctuated community changes can reflect the influence of extrinsic processes like disturbance as well as the intrinsic dynamics of the community and its constituents [4]. Rapid community changes can be common and may occur in conjunction with gradual long-term changes [24], yet they need not arise from abrupt and/or large external forcings [4,5]. As long-term monitoring of marine systems is becoming more prevalent, the observation of these events is also becoming more common [25].

One of the most comprehensive studies on community change, the Portal Project [26], provides an excellent case study on the influence of different types of environmental variation on community change. Over the 40 years of high-frequency monitoring of a desert ecosystem (1977-present), the small mammal communities have undergone apparent gradual shifts in community composition in response to vegetation transitions [27]. In addition to these long-term trends, discrete climatic events have completely reorganized mammal communities [28]. Recently, novel analytical tools have shed a new light on these dynamics. Working with the complete time series of mammal monitoring, Christensen and coauthors [24] observed that the appearance of gradual community shifts, i.e. *see* [27], resulted from a more complex, repeated series of events. Community shifts were tied to environmental disturbance events that reduced community abundance, thereby disrupting entrenched community patterns of dominance, competition. Interestingly, not all instances of low abundance, nor all disturbance events, resulted in community shifts, however, all community shifts were associated with reduced community abundance and often disturbance events. These patterns show the important interactions between intrinsic ecological processes and extrinsic environmental variation in determining the patterns of community change over time.

**Community change is multidimensional, and the concordance between community change and extrinsic drivers is often unclear. Understanding the internal dynamics of communities may explain this disconnect.**

## 2.2. The Concept of Community Cohesiveness

Community dynamics in response to extrinsic drivers can vary based on the intrinsic dynamics of the community and its constituents. A long running debate in ecology centers around whether communities should be viewed as a loosely defined collection of individual species (individualist [29]) or as integrated units (organismic [30]). These two perspectives provide seemingly opposing viewpoints on the cohesiveness of community change, complete independence on one side and complete interdependence on the other. In reality, community change likely occurs through both individual species shifts in response to environmental variation and through changing interactions among interdependent species. Disentangling the conditions that modify community cohesiveness will help identify the underlying mechanisms of community change.

Incohesive communities take the shape of uncorrelated responses among populations at the species level. In the purest neutral version, species abundances, local extinctions, recruitment, and dispersal are stochastic processes [31]. As such, species show little to no interdependence and each species is generally considered ecologically equivalent. This concept has a long history in ecology, e.g., the Theory of Island Biogeography [32]. At a broad scale, empirical support of incohesive community assembly exists, in that species richness appears to be regulated at the community scale and the total number of species at a location is relatively fixed through time [33,34]. While fixed species richness aligns with neutral processes proposed in classical ecological theories [29,31,32], these initial theories, i.e. Gleason 1926, did not assume species niches did not exist. Rather, the associations in communities were largely determined by dispersal processes around species-specific environmental optima. In a simplified example, if temperature is changing through time and thermal tolerances vary among species in the community, species abundances smoothly track the temperature gradient.

These models of individualistic and incohesive community change may fail to capture rapid, correlated community shifts such as those observed across space in some well-studied plant communities [35] and documented regime shifts in marine fisheries [36]. These examples of dramatic synchronous changes in multiple species abundances, e.g., *see* [36], rest at the other end of the cohesiveness spectrum. In these examples, strong connections exist among species that create correlation in species abundances, both negative and positive, through time. Correlated (or cohesive) community dynamics can arise from a number of conditions: 1) strong environmental filtering selecting for similar species niches along a single dimension; 2) positive feedbacks such as mutualistic and other facultative interactions [37] may cause species to enter and exit communities together; 3) within trophic groups, “zero-sum” constraints mediated through competitive interactions lead to gains and losses in one species being compensated by losses and gains of other species, i.e. compensatory dynamics [27]; and 4) strong trophic interactions across multiple trophic levels, e.g. trophic cascades [38]. The influence of both niche filtering and species interactions can create both positive (synchrony) and negative (compensatory) species correlations in time, the strength and importance of which is dependent on the timescale [39] and level of organization [40].

**The temporal relationship of community change and extrinsic drivers depends on the constituent species, their niches, and interactions. We need to elucidate these linkages and the role of community cohesiveness to understand community dynamics.**

## 2.3 The Role of the Niche in Community Cohesiveness

Trait-based perspectives of ecology provide a framework to connect species’ niches to extrinsic drivers of community change. Species’ traits connect organisms to their environment and to their contribution towards important ecosystem processes [41], however they may also help disentangle random from functional community shifts. Community change through time is expected through even neutral processes [31,32]; therefore examining community trait distributions provides a higher-level lens, free of the noise of neutral taxonomic variability, to understand if community shifts represent neutral processes or a fundamental restructuring of the ecosystem [42,43]. Connecting trait shifts with taxonomic shifts on both short and long timescales may help disentangle the influence of stochastic processes from environmental filtering that can cause abrupt shifts in ecosystem dynamics. Indeed, integrating trait dynamics into models of community change may help predict systems approaching critical thresholds and regime shifts [44].

The concept of differential species responses based on their ecological niches has a long historical legacy in ecology, e.g. r- versus K- selected organisms. In marine systems, the differential responses by different groups to perturbations, e.g., amphipods and polychaetes to pollution and hypoxia [18–20], are well documented. These higher-level taxonomic responses reflect the difference in ecological roles that taxonomy captures. Body size, even at coarsely measured levels, often captures differential responses. For example, the macrobenthic response to hypoxia is primarily driven by hypoxia tolerance, whereas the megabenthic response is affected by the ability to migrate and the availability/unavailability of macrobenthos prey [45]. Trait distributions, therefore, provide a tool to measure the potential role of extrinsic drivers in community change.

Capturing intrinsic controls on community changes requires understanding how species are “connected” to each other through ecological interactions. For example, competition for resources has long been recognized for its structuring role in communities, controlling species abundance and persistence [46,47]. The strength of competition and its variation within a community can have important implications for biodiversity and ecosystem dynamics [48]. Dynamics of community change in time will be modified by the patterns of competition within a community because these interactions create species interdependence around a resource. Further, species are connected across trophic levels directly and indirectly through predation and these species interactions can have cascading influence on species abundance throughout a community [38]. As such, cohesive responses in species’ abundance such as synchronous and compensatory dynamics will likely propagate through strong interspecific interactions. Therefore, if communities contain strong species interactions, changes may occur through cohesive multi-species shifts compared to communities with more diffuse and uniform interactions [49].

**Integrating species’ traits and interactions into concepts of community change is an important step towards identifying the roles of extrinsic and intrinsic drivers of change.**

# 3. Intellectual Merit

Coastal ecosystems are unique systems to explore the role of interacting environmental signals on biodiversity changes. These regions are the epicenter for a number of global change drivers, they are important components of regional ocean ecosystems, and therefore mirror the broader changes occurring across the global oceans. Here, we propose to leverage and continue two long-term datasets of benthic macroinvertebrates and demersal megafauna in a coastal Louisiana estuarine bay.

The goal of this project is to characterize the nature of biodiversity change in the communities of a shallow bay-estuary complex. We will integrate time series of environmental and disturbance data, community data, trait dimensions, and isotopic analysis of trophic niches to ask:

1. What are the temporal dynamics (magnitude, frequency, duration, predictability) of community change?
2. How are the temporal dynamics of community change linked to temporal dynamics of extrinsic drivers?
3. How are the dynamics of community change linked to temporal dynamics of extrinsic drivers altered by community cohesiveness?
4. How are the dynamics of community change linked to temporal dynamics of extrinsic drivers altered by community cohesiveness as determined by niche filtering and species interactions?

In seeking to address these questions, we pose a number of competing predictions:

## 3.1. Temporal Dynamics of Community Change

**P1.1:** Community changes are gradual reflecting uniform rates of species additions/losses or abundance redistributions,

**P1.2:** Community changes are punctuated reflecting non-uniform rates of species additions/losses or abundance redistributions characterized by sharp,

**P1.3:** Community changes are a mixture of gradual and punctuated shifts, **Pnull:** No change occurs in community structure/communities are fixed.

While “gradual” and “punctuated” shifts represent categorical bookends along a continuum of community change, we use them here to frame hypotheses. We propose to decompose the patterns of community change into its temporal dynamics, focusing on magnitude, frequency, duration, and predictability. We define “gradual” versus “punctuated” changes to reflect distinctive community rate changes. In the gradual change model, metrics of community change through time (reflecting composition and/or redistributions of abundance changes) are linear. In a punctuated model, distinctive changes in metrics of community change should be detectable through non-linear models, e.g., polynomial, break point regression, logistic, or exponential. Support for competing models can be evaluated through model selection criteria (e.g., loglikelihoods, AIC, or BIC). If community changes are gradual (**P1.1**), this may reflect either random community drift or, potentially, niche occupancy mirroring gradual environmental change. Punctuated shifts can suggest tipping points in environmental change or pulse disturbances (**P2.1**). These two patterns may both operate at different times reflecting varying responses to extrinsic and intrinsic drivers (**P1.3**), or not at all if communities are resistant to change, e.g. complex direct/indirect interactions stabilize community composition (**Pnull**). Detecting and decomposing community-level patterns, while coarse, is the vital first step to connecting drivers to community change.

**3.2. Linking community change to temporal dynamics of extrinsic drivers.**

**P.1:** Long-term disturbances, i.e. press disturbances, will induce gradual changes in the community structure,

**P2.2:** Pulse disturbances will induce punctuated changes in the community structure, but communities return to a pre-disturbance state,

**P2.3:** Press disturbances will induce punctuated changes in the community structure, i.e. regime shifts and tipping points,

**P2.4:** Pulse disturbances induce punctuated changes in the community structure, leading to a new stable community state,

**P2.5:** Pulse disturbances induce a gradual change in the community structure, **Pnull:** Community changes have no relation to extrinsic drivers.

The temporal dynamics of environmental variation can take a multitude of forms [21,50]. Our framework is flexible to varied temporal patterns in community and environmental change, yet for clarity we adopt a similar heuristic as above to distinguish between bookends of a continuum. “Pulse” disturbances are discrete events, e.g., an oil spill, compared to the long-duration, sustained pressures of a “press” disturbance. We will utilize a similar ‘variability’ framework as above to characterize extrinsic drivers (e.g., salinity, temperature, chlorophyll *a*, sediment grain size, sediment carbon content, current speed, wind speed, water height, storm frequency). Using multivariate decomposition tools and general additive models, we will explore the coherence between community change and extrinsic drivers. These changes will be compared against neutral models of community change. Here, gradual change in communities which track long-term press disturbances suggest species filtering by shifting environmental windows (**P2.1**). These states may be upset, briefly, by punctuated pulse events (**P2.2**), with long-term community states showing resilience around longer-term environmental conditions. In contrast, communities might resist press disturbances, until a critical threshold is reached causing punctuated change in the community (**P2.3**; i.e. regime shifts). These punctuated community changes may arise from intrinsic processes, or they may be induced by pulse disturbance events which upset the biological processes causing resistance (**P2.4**). Finally, pulse events may induce community change which appears gradual (**P2.5**), that arises from small, punctuated shifts or neutral community turnover through time (**Pnull**).

## 3.3. Linking community change to community cohesiveness

**P3.1:** Species exhibit positively correlated patterns in abundance changes through time, i.e. niche filtering or seasonal resource dynamics,

**P3.2:** Species exhibit negatively correlated patterns in abundance changes through time, i.e. compensatory dynamics or competitive interactions,

**P3.3**: Community changes occur from a combination of independent and interdependent species responses

**Pnull:** Species abundance changes are independent of other species’ responses.

A number of processes can cause the dynamics of species abundances to be correlated across space and time [51]. For example, seasonal periods of copious resource availability can shape the life-history and densities of populations on both local and regional scales. These conditions can lead to temporal synchrony in local species’ abundances (**P3.1**; positive correlations and increased community-level variation). Contrastingly, parallel lines of thought have highlighted the importance of compensating mechanisms (**P3.2**; compensatory dynamics, negative correlations among species abundance) in stabilizing aggregate processes. Each process can operate on different timescales, which creates varying temporal dynamics in the cohesiveness of community dynamics. These changes can be quantified with variance ratio methods that can capture the different timescales of synchrony and compensatory dynamics (**P3.3**; [39]). Finally, species abundances may also operate independent of each other and exhibit random noise (**Pnull**; zero correlation of abundances in aggregate).

## 3.4. Linking community change to niche filtering…

**P4.1:** Cohesive community changes (gains and losses/abundance increases and decreases) are associated with distinct traits, i.e. niche filtering,

**P4.2:** Incohesive community changes are associated with distinct traits,

**P4.3:** Cohesive community changes are associated with new traits, i.e. increases in niche novelty,

**P4.4:** Incohesive community changes are associated with new traits,

## ...and species interactions

**P4.5:** Cohesive community changes are mediated by strong species interactions,

**P4.6:** Cohesive community changes are mediated by weak, uniform species interactions,

**P4.7:** Incohesive community changes are mediated by strong species interactions,

**P4.8:** Incohesive community changes are mediated by weak, uniform species interactions,

**Pnull:** Community changes are neutral to distinct traits and independent of interactions strengths within the community.

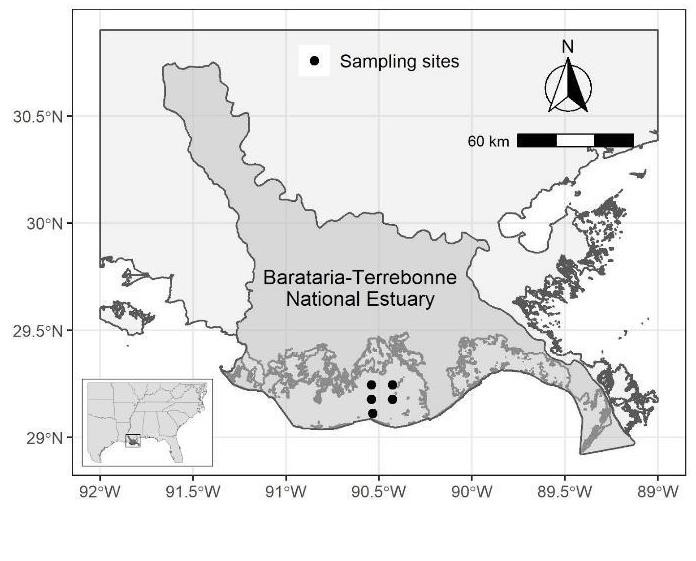
Species’ niches and interspecific interactions create connections between species and their environment and other species that can shape community change and cohesiveness. This is further shaped by how environmental variation, over short and long timescales, constrains or shifts the availability of niches or species interactions. As such, synchronized species responses may result from strong environmental filtering for distinct traits in the community (**P4.1**), or filtering may operate on distinct traits in a stochastic manner (**P4.2**). Additionally, environmental change can open new niche space for organisms to fill, leading to an expansion in community traits space. This new space may operate through synchronous changes of multiple organisms, thereby creating novel species interdependencies (**P4.3**), or independent species dynamics (**P4.4**). These patterns can be assessed by mapping the hypothetical trait space occupied by a community through time. Species traits are multidimensional and ordination techniques are well-suited to assess how the theoretical niche space of a community changes through time. These can further be compared with randomized models to assess functional vs random change. Comparing the dynamics of community change with trait-space and environmental changes will allow for the assessment of the general effects of extrinsic factors.

Additionally, intrinsic interdependencies among species (i.e. species interactions) can modify cohesiveness of community changes through time. Highly cohesive (synchronous or compensatory) community changes are expected with the presence of strong species interactions (**P4.5**); however, cohesive community changes may occur with weak species interactions in the presence of strong environmental filters (**P4.6**). Contrastingly, incohesive community changes when strong species interactions exist (**P4.7**) seem unlikely but would be associated with unstable ecosystem dynamics. Incohesive community changes are expected in the presence of weak interactions (**P4.8**) when extrinsic processes that create cohesion are also weak. Under this scenario, stochastic demographic processes dominate community changes. This prediction is indistinguishable from neutral processes, where the relationship between dynamics of community change and species’ traits and interactions is no different than random (**Pnull**). The distribution of interaction strengths among species can be inferred indirectly through time series [52] and isotopic methods [53]. We will combine these approaches to infer the distribution of species interactions through time. Randomized simulation models will be built to characterize the change in species interaction strength distributions expected under random change.

# 4.Methodological Approach

## 4.1 Terrebonne Bay as an Exemplar System for Change

|  |
| --- |
| Figure 1. Map of Terrebonne Bay (29°11.200’N 90°36.560’W) located in the northern Gulf of Mexico, Louisiana, USA. The five sampling locations for benthic trawls are shown in black dots. LUMCON’s environmental monitoring station is located approximately 5 km west of the western N-S transect. Map credit: S. K. Archer. |

We focus our research on Terrebonne Bay (Figure 1), experiencing a variety of anthropogenic and environmental drivers occurring over a spectrum of durations, intensity, frequency, and predictability. Terrebonne Bay, located along the Louisiana Gulf Coast, is a broad (1,761 km2), shallow estuary (average depth 2m). Terrebonne Bay is separated from the Gulf of Mexico by two barrier island chains and is connected by four tidal passes. The bayestuary complex is part of an abandoned distributary of the Mississippi River. The estuary therefore no longer receives any significant riverine inputs, and the majority of its freshwater inputs are from the local drainage basin [54]. While water column salinity and density are homogenous, strong salinity gradients exist seaward from the marsh to the barrier islands [54]. Tides in Terrebonne Bay are diurnal with a semidiurnal component, ranging 20-80 cm [55]. During the winter months, large amounts of sediment accumulation may occur just prior

to a cold front passage when the wind is blowing from the south [56]. Since Terrebonne Bay has very limited river flow, nutrient limitation is likely to be controlled by the connection between the fringing marshlands and/or sediments within the Bay’s water column.

In the last century the global oceans have experienced an unprecedented transformation precipitated by increased sea level rise and habitat loss. Coastal Louisiana has experienced 4,800 square kilometers of land loss since 1932. In Louisiana, relative sea level rise (the combined result of subsidence and global sea level rise) are substantially greater than the global average. Terrebonne Bay is at ground zero for this change and is currently transitioning from a semi-closed, estuary driven system to an open and enlarging bay. The wetlands of this region are being converted to open waters at rates exceeding 130 square kilometers per year. Historically, the primary mechanisms of water transport are by wind and microtidal fluctuation. Recently, the loss of wetlands and barrier islands has made this system more exposed to wave action and mixing with shelf waters [54]. Increases of cold fronts and tropical storms in the last decade are also prominent. These meteorological effects in the bay can mask the normal hydrological regimes of the bay [56]. During extended periods of southerly surface winds, higher salinity coastal ocean water moves into Terrebonne Bay and “pushes” water up onto the marsh resulting in extended periods of marsh flooding and higher salinity water throughout the Bay. Annual cold fronts can also equal the erosion of a single tropical storm [57]. These ephemeral events occur in Terrebonne Bay against a backdrop of a seasonal pattern that is driven by changes in discharge in the Mississippi-Atchafalaya River system. Typically, the Mississippi-Atchafalaya Rivers peak in discharge in late winter-early spring. This increased discharge can result in lower salinity throughout Terrebonne Bay.

## 4.2 Temporal Dynamics of Community Change

### 4.2.1 Quantifying the Communities of Terrebonne Bay

The proposed sampling design will leverage and extend ongoing data collection of benthic and demersal communities. This consists of >10 years continuous sampling of ship trawls and three years of benthic core sampling from the bay (Figure 2; see **Preliminary Results**).



Figure 2. Dates of historical sampling of demersal trawl and benthic core communities in Terrebonne Bay. Each black vertical line represents a unique sampling day for the ~439 trawls taken from 2007 to March 2020. Benthic core sampling dates are represented by dashed grey lines. Benthic core sampling dates are updated until August 2020.

Recurring **demersal megafauna trawl surveys** will be conducted in collaboration with LUMCON’s Education and Outreach department. Visiting school groups (K-12 and university level) incorporate a benthic trawling activity aboard the R/V *Acadiana* into their visits to LUMCON. These trawls occur on average weekly throughout the year, with some variation due to school visitation patterns. During the COVID-19 pandemic the trawl surveys occurred bimonthly, despite the lack of school group visits. Briefly, the bottom trawl is conducted with a 25-foot otter-trawl with ¾ inch mesh. The trawls are, on average, 7-10 minutes in duration and the vessel travels at approximately 3-4 knots while the net is in the water. All organisms caught in the trawl are sorted, identified, and counted. A subset of individuals for each taxonomic group identified are measured for length (or other appropriate measures of size). The dataset includes ~439 trawls taken from 2007 to the present (Figure 2). The proposed sampling will continue these trawls at minimum bi-monthly and more frequently as school groups visit. Species identifications are conducted by trained marine educators. Training and quality checks are overseen by two fisheries faculty members and the Associate Director of Education with two decades of experience.

**Sediment cores of soft bottom macrofaunal communities** in Terrebonne Bay will continue along N-S transects within the bay (Figure 1). Sampling of the B transect (westernmost N-S transect in Figure 1) began in 2018 and the C transect followed in 2019. Each transect has three stations at the same latitudes that move from the top of the bay South toward the barrier islands that divide the bay from the continental shelf. To date, additional samples were taken from TB3C, however coarse sediments and underwater hazards have prevented additional grabs. PONAR grabs (23 x 23 cm) are taken at each sample site. After recovery of a suitable grab, 4-6 sub-cores are taken. A total of 15+ sub-cores are taken per site. A previous power analysis and species accumulation curves indicated that ~12 sub-cores are needed per site. Prior to removal of sub-cores, a sample of surface mud (2-5 ccs) is gathered for sediment properties and total organic carbon. The overlying water from the core top along with the top 5 cm of the core are removed, sieved on a 300 μm mesh, and preserved in 80% ETOH for later identification of species. Species identification is conducted by trained ecologists with consultation with taxonomic experts (see Management Plan).

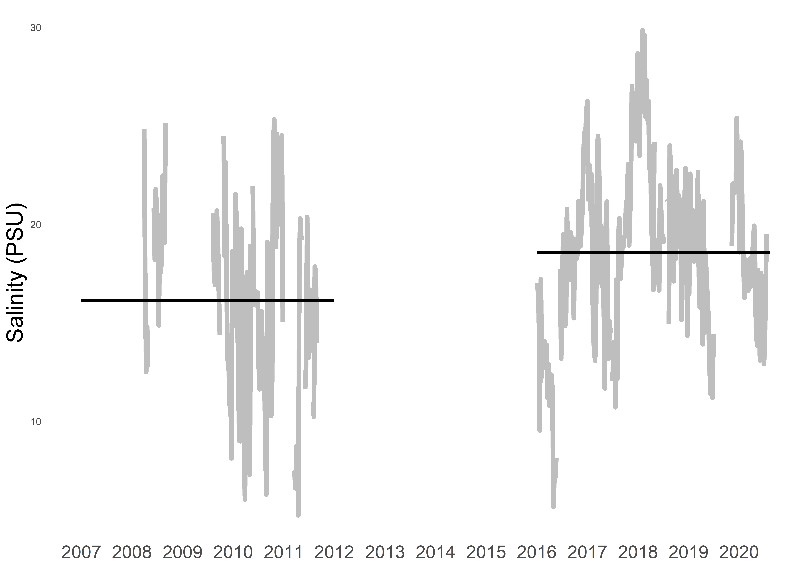
### 4.2.2 Quantifying and Analyzing Community Change

The dynamics of community change will be characterized using classical measurements of biodiversity in a temporal context [58,59] and emerging tools on temporal community shifts [24]. Specifically, to capture broad biodiversity shifts, biodiversity indices (species richness, dis/similarity indices, species abundance distributions) will be calculated on seasonal and longer-term time scales. Community composition will be visualized and assessed with multi-dimensional scaling (MDS) with appropriate distance indices (e.g., BrayCurtis). We will further characterize community changes by partitioning species gains and losses over time into its respective partitions of turnover and nestedness [60] These indices will be calculated with appropriate open source software [61]. We will test specifically for “gradual” versus “punctuated” changes in community rate changes. In the gradual change model, metrics of community change through time (reflecting composition and/or redistributions of abundance changes) are linear. In a punctuated model, distinctive changes in metrics of community change should be detectable through non-linear models, e.g., polynomial, break point regression, logistic, or exponential. Support for competing models will be evaluated through model selection criteria (e.g., log-likelihoods, AIC, or BIC).

Statistical tools developed for time series of high-dimensional data such as biological communities will also be used to capture temporal change points. Latent Dirichlet Allocation (LDA) is a dimension reduction analysis that operates on collections of discrete data [62,63]. Importantly for this application, LDA can classify biological communities into specific types based on their co-occurrence. The relative abundance of specific community types can then be mapped through time. Using packages implemented in R [64], we will apply change-point models to identify changes in mean and variance in community types through time. While these models are useful for detecting change in time-series, directly quantifying the rates of change is an ongoing pursuit. Analyzing the spread of the posterior distribution around the estimated change point has been suggested as an ad hoc inference [24]; however, we will also assess the utility of emerging approaches for detecting the rates of change in high-dimensional data, e.g., derivative-based methods [65].

**4.3 Linking community change to temporal dynamics of extrinsic drivers.**

### 4.3.1 Quantifying environmental variables in Terrebonne Bay

The LUMCON Environmental Monitoring network currently consists of three monitoring stations, each equipped with its own power source to ensure that data is collected simultaneously at 15-minute intervals. Stations are designed to endure extreme weather events such as hurricanes. The cell modem sends the dataset to a server located at LUMCON every 15 minutes. Each station contains the same suite of sensors measuring a total of 13 meteorological and hydrographic parameters (wind direction and speed, air temperature, humidity, barometric pressure, rainfall, photosynthetically active radiation, total solar radiation, water height, water temperature, salinity, specific conductivity, dissolved oxygen concentration [mg/L and % saturation], and chlorophyll fluorescence).

|  |
| --- |
| Figure 3. Partial time series of measured salinity in Terrebonne Bay, Louisiana from 2007 to 2020. Black lines represent the mean salinity in the bay from 2007-2012 and from 2016-2020. Data gaps represent periods currently under QA/QC within LUMCON’s environmental monitoring department. QA/QC process will be completed in December 2020. |

Meteorological instruments are calibrated annually, and hydrographic instruments are retrieved and calibrated in-house weekly or biweekly during the warmer months (when fouling rate is greatest) and bi-weekly or monthly during colder months. When instruments are retrieved or deployed, secondary readings are made using a handheld instrument for quality assurance and control. Daily

monitoring of operational status and data quality is completed to help identify issues so they can be resolved quickly. Additionally, weekly sampling of the station was initiated in 2018 by the Roberts lab to assess water temperature, conductivity, salinity, total dissolved solids, nutrients, carbon, and chlorophyll to provide an external check on data and augment monitored parameters. Data from the Terrebonne Bay monitoring station (29°11.200’N 90°36.560’W) will be utilized with data from 2000 to present to classify extrinsic drivers.

For proposed future sampling we will take additional measurements of physicochemical variables at local sampling locations to identify station offsets from the monitoring station. Further, we will quantify the carbon content of sediments as a proxy of local energy availability. From each sediment core, a subsample will be taken for carbon content. Carbon content will be measured directly on the sediments using a Carlo Erba NA-1500 Elemental Analyzer [66]. Sediment texture and composition will be quantified with the combined use of a laser particle sizer carried out on a Beckman-Coulter laser particle size analyzer attached to an aqueous module equipped with a pump and a built-in ultrasound unit.

In addition to LUMCON's environmental monitoring data and *in situ* measurements, we will also incorporate macroscale data to the analysis. Oil spill data will be taken from the Louisiana Oil Spill Coordinator’s Office that maintains an inventory of locations of past and current spills both over and under 10,000 gallons. Historical land loss data within Terrebonne Basin, will be gathered from USGS’s *Land Area Change in Coastal Louisiana (1932 to 2016)* report [67]. Updated data will be taken from initiatives form USGS and Louisiana's Coastal Protection and Resource Authority.

### 4.3.2 Quantifying and Analyzing Environmental Change

These time series will allow for the characterization of temporal dynamics of environmental variation over the observation period, specifically characterizing seasonal, directional, stochastic, and extreme components. There are many techniques used to analyze time series, including autoregressive integrated moving average (ARIMA) techniques and Fourier analysis tools [68]. We will employ such tools to extract the seasonal frequencies, amplitudes, and phases of change in environmental variables. Further, these tools will be used to identify extreme events, such as heatwaves, hurricanes, and tropical storms.

### 4.3.2 Linking environmental change to community change

The connection between community change and environmental variables is potentially complex and nonlinear. We will connect broad metrics of community change through time (e.g., turnover, nestedness, community type composition) to environmental change through time using flexible statistical tools. Here, generalized additive models (GAMs) provide an ideal modeling framework, allowing for hierarchical data structure, flexible distributions in response and explanatory variables, linear and non-linear responses, correlated errors, etc. [69,70]. These models can be implemented using a number of open source software in the R environment, e.g., mgcv [69], brms [71]. We will explore linkages using multivariate approaches such as a redundancy and partial-redundancy analyses (RDA), that combines regression and principal component analysis, using the ade4 [72] and vegan [73] packages in the R environment. We will implement a permutation test of the RDA results.

## 4.4. Linking community change to community cohesiveness

4.4.1 Quantifying and Analyzing Cohesiveness.

For the purpose of this proposal, community cohesiveness is defined as the extent to which species abundances change in concert. This can occur in two ways: 1) species abundances can increase at the same time showing positive correlation, or, 2) abundances of some species increase while others decrease, showing negative correlations. These two different outcomes are in contrast to an incohesive community in which species abundances fluctuate randomly. Therefore, community cohesiveness can be summarized conceptually as the differences in correlation of species abundances, positive or negative, from random expectations. However, these two processes may both occur depending on the timescale of measurement [39]. To account for both synchronous and compensatory processes, we will employ recently developed variance ratio methods that allow the partitioning of synchronous and compensatory processes on different timescales. Specifically, these methods build on previous variance ratio methods e.g., [74] and use spectral analysis to decompose population and community variability on different timescales. This analysis will be conducted using open-source software developed in the R environment [75].

## 4.4. Linking community change to niche filtering and species interactions

### 4.1.1 Quantifying Functional Traits

We will use the framework for functional traits based on the first principles of functional morphology as developed by Bush and Bambach [76,77]. The functional mode of a species is defined by three axes: tiering, motility, and feeding. Each axis consists of six categorical states. The tiering axis consists of pelagic, erect, surficial, semi-infaunal, shallow infaunal, and deep infaunal. The motility axis consists of freely motile/ fast, freely motile/slow, facultatively motile/unattached, facultatively motile/attached, non-motile/unattached, and non-motile/attached. The feeding axis consists of suspension feeding, surficial deposit feeding, mining, grazing, predatory, and other (for feeding strategies that do not fit into the previous five feeding modes). Functional traits assignments will be made based on published natural history of the taxa. For each functional group, we will quantity total biomass, number of individuals, and number of species. For each species, we will quantify mass as the geometric mean of wet and dry weight across all individuals of species.

### 4.1.2 Quantifying the Trophic Niche

Characterizing trophic relationships can be done in a number of ways, including stable isotope analysis [53]. Animal isotope signatures represent an integrated signature of the food resources assimilated and therefore can capture the food consumed. Increasingly, these tools have been used to infer the potential overlap in species resource use, and subsequently the potential for competition among species. Isotope ratios exhibit consistent and predictable discrimination in metabolic processes. For example, while the ratio of carbon (C) isotopes is relatively conserved, lighter nitrogen (N) isotopes are disproportionately excreted during metabolic processes. This discrimination leads to the accumulation of heavy isotopes in higher trophic positions. The combination of C and N isotopes can provide information on which food resources are consumed and the broader trophic structure in a community. Sulphur (S) isotopes in marine environments generally track salinity gradients from freshwater, brackish, and saline environments. Sulphur stable isotopes can provide another dimension to track food resources derived from remote or local estuarine sources [78]. They add additional information by which unique trophic niches can be distinguished among species. Combined, this information can help map out the major pathways of energy flux and the potential for species interactions (e.g., competition, predation) to occur. A minimum of 10 samples of each species and feeding mode bin will be run for each site in addition to the sediment cores collected from every site. All isotope samples will be rinsed with deionized water, dried at 60 °C, and ground to a fine powder with a Retchs MM400 mixer mill. All samples will be sent to the Washington State University stable isotope core facility and analyzed for C, N, and S stable isotopes. Internal standards and 10% duplicate samples will be utilized to ensure precision and replication of isotope values.

C, N, and S stable isotope data will be compared with the isotopic space shared among species using bayesian mixing models and isotopic hypervolume methods developed in the R environment, i.e. SIBER [79]. These data will be used as a proxy for food resource overlap and trophic structure to estimate the distributions of species interactions in the community.

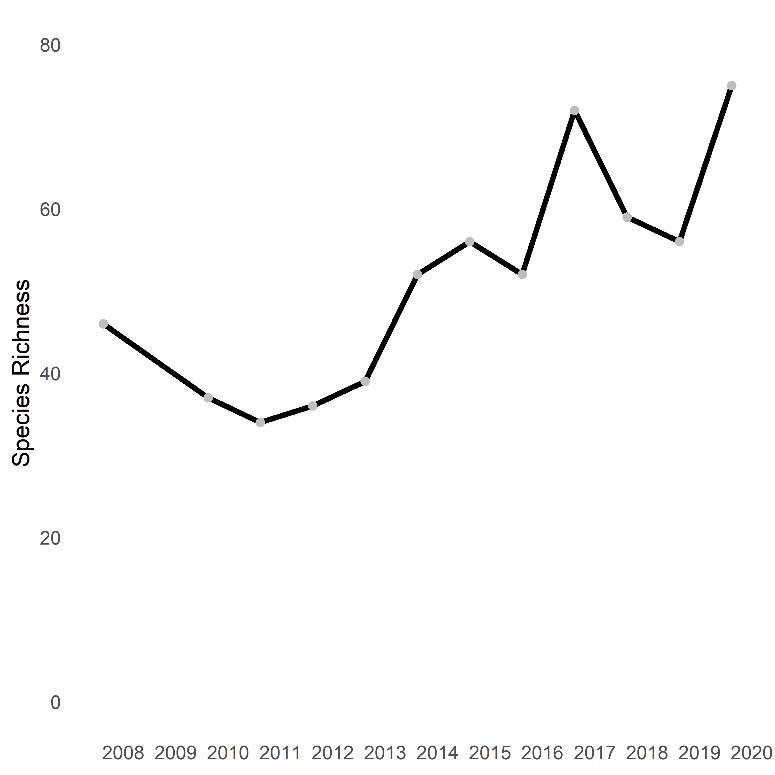
### 4.1.3 Analyzing niche filtering and species interactions

To quantify the functional diversity and niche space of communities through time, we will use distancebased approaches based on species traits [76,77,80]. From this we will calculate a number of metrics: functional richness, functional overlap, functional dispersion, functional evenness, and functional divergence. These metrics each capture aspects of functional change which can be related to biodiversity change. As an example, functional richness calculates the minimum volume of trait space occupied by a community. Expansion of cumulative trait space with increasing cumulative species richness in time would signify functional species additions. Alternatively, species packing into niche/trait space can be represented if temporal trends of functional richness are decoupled from species richness in time. We will further decompose these changes into components of turnover and nestedness to understand functional and neutral species additions/losses. The functional evenness and divergence through time in conjunction with environmental variables will be measured to better understand environmental niche filtering of community traits. These metrics will be calculated using open source software in the R environment [81,82]. Time series of community functional trait/niche dynamics will be compared against community diversity and community change to quantify relationship between community changes and functional changes or niche filtering.

We will use information from multiple sources to characterize the distribution of intra- and interspecific interaction strengths in trawl communities. Identifying species interactions and the role of densitydependent and density-independent processes on population abundances [56] is a central problem of ecology and coupling time series of ecological communities and environmental variables represent an appealing approach to accomplish this [33,57,58]. Multivariate Autoregressive models (MAR, also termed vector autoregressive models) are one approach to extract information about species interactions from time series [57,58]. MAR and related models (state-space MAR, [59]; dynamic linear models, [60]) allow options for increasing complexity and flexibility (i.e. accounting for spatial replicates, difference in sampling intervals, time-varying interactions). These models have been implemented in the R environment [61]. However, these models are often computationally restrictive, which has limited their use for the highdimensional data found in many ecological situations. These restrictions can be mitigated by limiting the potential interactions [62] and/or providing prior information. Information from stable isotope analysis will be used to constrain potential interactions. Isotope data will be available only for the time period overlapping the study. Therefore, prior information from isotope ratios will have increasingly diffuse influence when back-casting species interactions from the time series. Importantly, co-occurrence patterns themselves may be misleading signals of ecological interaction [63]. Therefore, necessary environmental covariates (e.g., temperature, salinity) will be included to account for environmental drivers of species abundance.

# 5. Preliminary results

|  |
| --- |
| Figure 4. Annual species richness measured in Terrebonne bay trawl communities during the period 2007-2019. |

Environmental monitoring of Terrebonne Bay has been ongoing since ~2000. Current efforts at LUMCON have begun to compile and QA/QC different data streams collected over the past two decades. Completion of this undertaken is expected by the end of 2020. Preliminary data are revealing a bay undergoing change. As a single example, we show the preliminary time series of salinity during the 2016-2020 time period when compared to the 2008-2012 time period (Figure 3). Although analyzing the complete dataset more rigorously will provide clearer support, this change is in line with increased connection between the bay and the open ocean due to a combination of sea level rise and erosion of barrier islands. Along with the ‘press’ change in background salinity, we also capture specific events, such as the notably low salinity in 2016 associated with increased rainfall and substantial flooding in Louisiana.

Sampling of trawl communities has been ongoing since ~2007 through the present. An initial analysis of the trawl community composition data through the time series showed cumulative species richness has increased through time. There is also evidence that *α*-diversity (as measured by annual species richness) has increased from ~50 to ~60 species over the 13 years of sampling, or about 1% per year (Figure 4). A principal component analysis (PCA) was conducted on Bray-Curtis distances of monthly-aggregated trawl community data to visualize the broad patterns of community change through time (Figure 5). Community composition varied through time both seasonally within a year and among years. The change in ordination space suggests both directional and abrupt changes in composition. Particularly conspicuous in this visualization is the transition from 2017 to 2018. Interestingly, in 2018 the Mississippi River, the dominant regional waterway and an important driver of local conditions in Terrebonne Bay, experienced its 6th longest flood since 1927.

This is a single example of the unique event histories that may contribute to biodiversity change. LUMCON data records note the trawl data set encompasses a number of tropical storms, six named hurricanes, the 6th longest flood since 1927, and the construction of a new levy system on the Mississippi River. Similarly, the benthic core data, while capturing a shorter time period, encompasses the responses and recovery of Hurricane Barry which made landfall ~150 km west of Terrebonne Bay.

# 6. Management Plan

Co-PI McClain will provide leadership for the overall project and ensure completion of the proposal goals (Table 1). PI Junker, co-PI McClain, senior staff Nunnally, and a research technician, aided by undergraduates, will be responsible for collecting and sorting sediment cores. PI

Junker will oversee database development, management, and storage, including all taxonomic, trait, and environmental data collected. PI Junker will lead the stable isotope analyses. PI Junker and Co-PI McClain will oversee analyses and modeling. Development of



Figure 5. Principal component analysis of monthly aggregated trawl community composition based on Bray-Curtis distance. The x and y axis represent the first and second principal components. The arrow connects the centroids for each year of sampling. Data for 2020 is updated until March 2020 and therefore does not fully capture annual community patterns.

the trait database will be accomplished by students with guidance from Co-PI McClain. Additionally, we have budgeted a salary for a LUMCON marine educator who will oversee the trawl collection and outreach components. PI Junker will oversee the data management for the trawl data. McClain and Nunnally who have expertise with Gulf of Mexico macrofauna based on ongoing projects will conduct preliminary taxonomic assignments. Additional taxonomic expertise will be provided by Adrian Glover (Natural History Museum, London)-polychaetes; Tammy Horton (National Oceanography Centre, UK)-amphipods; Stefanie Kaiser (Universitat Hamburg)-isopods. PI McClain has expertise in gastropod and bivalve taxonomy.

|  |  |
| --- | --- |
| Table 1. Tentative annual timeline of tasks to accomplish project goals. Manuscript preparation will occur throughout as data analysis are completed. | |
| **Year** | **Tasks** |
| 1 | Analysis of temporal dynamics of demersal trawl data (Q1)  Analysis of temporal dynamics of environmental data (Q2)  Linking temporal dynamics of demersal trawl data to environmental data (Q2)  Sorting and identification taxa from sediment cores  Stable isotope data collection |
| 2 | Analysis of temporal dynamics of benthic core data (Q1)  Linking temporal dynamics of benthic core to environmental data (Q2)  Joint analysis of cohesiveness of trawl and benthic community data (Q3)  Functional trait database development  Stable isotope data collection |
| 3 | Analysis of functional trait and stable isotope data (Q4) |

Benthic and demersal sampling will continue to occur during the grant. Trawls will occur at minimum of twice monthly and benthic coring occurring every other month.

Several manuscripts are planned to result from this work with emphasis on the following sub-topics: (1) Temporal dynamics of demersal communities of Terrebonne Bay, (2) Temporal dynamics of benthic communities of Terrebonne Bay, (3) Linking temporal community drivers to changes in extrinsic drivers, (4) Changes in community cohesiveness through time, (5) The role of niche dynamics in community change, (6) The role of trophic dynamics in community change, (7) Synthesis of theory on community change.

# 7. Intellectual Merit

The proposed work addresses three fundamental questions about temporal components of biodiversity [81] (1) what is the “natural” level of temporal change in community structure; (2) what is the change in community structure beyond this background change in response to anthropogenic drivers; (3) what are the mechanisms that underlie these linkages. As such, the proposed research will contribute substantially to ecological theory on temporal community dynamics and responses of marine communities to anthropogenic changes. The proposed research will also continue the development of two long-term environmental and ecological datasets. These types of data are comparatively uncommon for marine systems [84] but of vital importance as baseline data in efforts to reduce biodiversity loss [83]. The lack of information on the background rates and direction of change in ecological systems can make it difficult to detect the signature of anthropogenic impacts. For example, “the IPCC Fourth Assessment Report noted 28,586 significant biological changes in terrestrial systems, but only 85 from marine and freshwater systems [84]. By traversing longer timescales, the datasets will be able address both a multitude of current management challenges, e.g. land loss in Louisiana, as well as emergent challenges, e.g. major oil spills [84].

The linked environmental, species diversity, and species trait datasets will also be made publicly available and will provide a rich resource for testing a host of ecological and evolutionary theories. These trait data will be provided to other marine trait databases, e.g. Encyclopedia of Life, and the species locality data provided to Ocean Biogeographic Information System.

# 8. Broader Impacts

We propose a full integration of the education and outreach activities of the grant with the research program. One the proposed datasets, trawl data, are enabling the construction of impactful Scientific research projects around the existing education activities. For decades, students that visit the LUMCON marine center have collected a vast amount of data about the surrounding coastal habits of Terrebonne parish. Roughly 2,500 students participate in trawl collections of Terrebonne Bay on scientific research cruises aboard the R/V *Acadiana* annually. These education activities have produced a unique historical dataset from the benthic trawl samples. In this regard, the proposed project would have two levels of impact.

1. **In-person, place-based experiences:** The students that participate in the boat trips will have the benefit of participating in a research project and learn first-hand how their effort fits into a much larger effort to understand the local ecosystem. With both onboard and land-based activities, students will assess the population on the bay community and how their data fits into the larger dataset. Salary funding is budgeted for a marine educator to develop further curriculum materials. We also propose a tablet/phone application that allows students to enter data on the cruise and see real time updates to graphs and temporal patterns.
2. **Remotely learning through online delivery:** The models used to educate students are currently changing. The need to reach students with diverse and changing needs means the delivery methods of content and experiences also needs to change. We additionally propose activities that will result in the ability to create content-rich educational products specifically designed for online delivery. A virtual experience that incorporates content designed to teach students the need for biological monitoring, the importance of the bay (environmentally, culturally, and economically), and about ship-based research methods will be developed. Products will be designed to engage students with image analysis resulting in length/size data for organisms collected during the benthic trawl. Students will learn to measure fishes and invertebrates in images through an online interface with downloadable resources. This method of content delivery and student engagement activities will provide a way for students to interact with marine science through informal instruction while becoming engaged with an active research program. These online resources will also mean that LUMCON can reach students whose circumstances do not permit them to visit personally due to financial limitations, health concerns/limitations, or work/family obligations. Specific salary funding has been requested for a marine educator to develop these materials.

The educational mission of LUMCON is to enable the next generation of marine scientists and ocean literate citizens while aiming to have significant impacts on those populations underrepresented and underserved in marine science. Through partnerships with HBCUs, Grambling State University and Southern University, Baton Rouge as well as institutions that serve lower socioeconomic and first-generation students such as McNeese and Nicholls Universities, LUMCON and the McClain lab have **actively recruited and provided research experiences to underserved groups.** As part of this grant and through these formal relationships, LUMCON and its partners aim to provide undergraduate research opportunities.

# 9. Results from previous NSF

**PI-McClain. The energetic assembly of invertebrate communities: A test with experimental wood fall systems. NSF/OCE 1634586** ($833,270; 5/1/2016-current)—The overarching goal of this project is to identify the interactions in energetic processes that regulate community structure, using ROV deployed wood falls. The grant led to 196 deployed and collected woodfalls and 12 manuscripts published, in press/review, and in preparation. A manuscript that focused on the theory development of scaling metabolic niches to biodiversity patterns was published providing the theoretical basis of this grant. The project supported research for 2 yearly undergraduate researchers, 4 REU students, and 1 graduate student and provided at sea opportunities for 8 undergraduates, 5 graduate students, 2 post-doctoral fellows, and 4 artists/writers. Broader impact focused on social media during the cruises: Facebook- 30 cruise-related posts seen 42,665; Twitter: 90 cruise-related tweets seen 100,733 times; Reddit: Am Ask Me Anything (AMA) 78,000 unique viewers, more than 10,000 votes, and more than 1,000 comments.

**Co-PI McClain. REU Site: Interdisciplinary Research Experiences in Changing Coastal Environments NSF/OCE 1757887** ($238,102; 04/01/2018–03/31/2021) This REU site grant has supported a total of 15 undergraduates (12 through direct NSF support and 3 through leveraged support) to participate in REU program activities over the first two years of the grant. 2018 REU program alumni were lead author or co-author on a total of 8 oral or poster presentations at 4 different scientific meetings and 1 REU is completing an honors thesis after continuing work on their project at their home institutions. Seven early scientists (3 assistant professors, 2 research scientists, and 2 postdoctoral research associates) have served as leads or co-mentors for REU interns thus far.

1. Steffen, W., Broadgate, W., Deutsch, L., Gaffney, O., and Ludwig, C. (2015). The trajectory of the Anthropocene: The Great Acceleration. Anthr. Rev. *2*, 81–98. Available at:

https://doi.org/10.1177/2053019614564785.

1. Hillebrand, H., Blasius, B., Borer, E.T., Chase, J.M., Downing, J.A., Eriksson, B.K., Filstrup, C.T.,

Harpole, W.S., Hodapp, D., Larsen, S. Lewandowska, A., Seabloom, E. W., Van de Waal, D. B., Ryabov, A. B. (2018). Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. J. Appl. Ecol. *55*, 169–184. Available at: http://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365-2664.12959.

1. Chase, J.M., McGill, B.J., McGlinn, D.J., May, F., Blowes, S.A., Xiao, X., Knight, T.M., Purschke, O., and Gotelli, N.J. (2018). Embracing scale-dependence to achieve a deeper understanding of biodiversity and its change across communities. Ecol. Lett. *21*, 1737–1751. Available at: http://onlinelibrary.wiley.com/doi/abs/10.1111/ele.13151.
2. Williams, J.W., Blois, J.L., and Shuman, B.N. (2011). Extrinsic and intrinsic forcing of abrupt ecological change: case studies from the late Quaternary. J. Ecol. *99*, 664–677. Available at: http://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2745.2011.01810.x.
3. Scheffer, M., and Carpenter, S.R. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol. Evol. *18*, 648–656. Available at: https://linkinghub.elsevier.com/retrieve/pii/S0169534703002787.
4. Antão, L.H., Bates, A.E., Blowes, S.A., Waldock, C., Supp, S.R., Magurran, A.E., Dornelas, M., and Schipper, A.M. (2020). Temperature-related biodiversity change across temperate marine and terrestrial systems. Nat. Ecol. Evol., 1–7. Available at: http://www.nature.com/articles/s41559-020-1185-7.
5. Blowes, S.A., Supp, S.R., Antão, L.H., Bates, A., Bruelheide, H., Chase, J.M., Moyes, F.,

Magurran, A., McGill, B., Myers-Smith, I.H., Winter, M. Bjorkman, A. D., Bowler, D. E., Byrnes, J. E. K., Gonzalez, A., Hines, J. Isbell, F., Jones, H. P., Navarro, L. M., Thompson, P.L., Vellend, M., Waldock, C., Dornelas, M*.* (2019). The geography of biodiversity change in marine and terrestrial assemblages. Science *366*, 339–345. Available at: https://science.sciencemag.org/content/366/6463/339.

1. Shoemaker, L.G., Sullivan, L.L., Donohue, I., Cabral, J.S., Williams, R.J., Mayfield, M.M., Chase, J.M., Chu, C., Harpole, W.S., Huth, A., Hille Ris Lambers, J., James, A.R.M., Kraft, N.J.B., May, F.,

Muthukrishnan, R., Satterlee, S., Taubert, F., Wang, X., Weigand, T., Yang, Q., Abbott, K.C. (2020).

Integrating the underlying structure of stochasticity into community ecology. Ecology *101*, e02922. Available at: https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecy.2922.

1. Díaz, S., Settele, J., Brondízio, E., Ngo, H.T., Guèze, M., Agard, J., Arneth, A., Balvanera, P.,

Brauman, K., Watson, R.T., Baste, I.A., Larigauderie, A., Leadly, P. Pasual, U., Baptiste, B., Demissew,

S., Dziba, L., Erpul, G., Fazel, A., Fischer, M., Maria, A., Karki, M., Mathur, V., Pataridze, T., Pinto, I.S., Stenseke, M., Torok, K., Vila, B. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. 45.

1. Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., and Sexton, J.O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. Science *344*. Available at: http://science.sciencemag.org/content/344/6187/1246752.
2. Murphy, G.E.P., and Romanuk, T.N. (2012). A meta-analysis of community response predictability to anthropogenic disturbances. Am. Nat. *180*, 316–327. Available at: https://www.journals.uchicago.edu/doi/10.1086/666986.
3. Fox, J.W. (2013). The intermediate disturbance hypothesis should be abandoned. Trends Ecol. Evol. *28*, 86–92. Available at: http://www.sciencedirect.com/science/article/pii/S0169534712002091.
4. Adler, P.B., Seabloom, E.W., Borer, E.T., Hillebrand, H., Hautier, Y., Hector, A., Harpole, W.S.,

O’Halloran, L.R., Grace, J.B., Anderson, T.M., Bakker, J. D., Biederman, L. A., Brown, C.S., Buckley,

Y.M., Calabrese, L.B., Chu, C., Cleland, E.E., Collins, S.L., Cottingham, K.L., Crawley, M.J., Damschen,

E.I., Davies, K.F., DeCrappeo, N.M., Fay, P.A., Firn, J., Frater, P., Gasarch, E.I., Gruner, D.S., Hagenah,

N., Hille Ris Lambers, J., Humphries, H., Jin, V.L., Kay, A.D., Kirkman, K.P., Klein, J.A., Knops, J.M.H.,

La Pierre, K.J., Lambrinos, J.G., Li, W., MacDougall, A.S., McCulley, R.L., Melbourne, B.A., Mitchell, C.E., Moore, J.L., Morgan, J.W., Mortensen, B., Orrock, J.L., Prober,. S.M., Pyke, D.A., Risch, A.C., Schuetz., M., Smith, M.D., Stevens, C.J., Sullivan, L.L., Wang, G., Wragg, P.D., Wright,. J.P., Yang., L.H. (2011). Productivity Is a poor predictor of plant species richness. Science *333*, 1750–1753. Available at: http://science.sciencemag.org/content/333/6050/1750.

1. Chase, J.M., and Knight, T.M. (2013). Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. Ecol. Lett. *16*, 17–26. Available at: http://onlinelibrary.wiley.com/doi/abs/10.1111/ele.12112.
2. Barry, J.P., Baxter, C.H., Sagarin, R.D., and Gilman, S.E. (1995). Climate-related, long-term faunal changes in a california rocky intertidal community. Science *267*, 672–675.
3. Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Chevaldonné, P., Cigliano, M., Diaz, D., Harmelin, J.G., Gambi, M.C., Kersting, D.K., Ledoux, J.B., Lejeusne, C., Linares, C., Marschal, C., Pérez, T., Ribes, M., Romano, J.C., Serrano, E., Teixido, N., Torrents, O., Zabala., M., Zuberer, F., Cerrano, C. (2009). Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. Glob. Change Biol. *15*, 1090–1103. Available at: http://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2486.2008.01823.x.
4. Engle, V.D., Hyland, J.L., and Cooksey, C. (2008). Effects of Hurricane Katrina on benthic macroinvertebrate communities along the northern Gulf of Mexico coast. Environ. Monit. Assess. *150*, 193. Available at: https://doi.org/10.1007/s10661-008-0677-8.
5. Baustian, M.M., and Rabalais, N.N. (2009). Seasonal composition of benthic macroinfauna exposed to hypoxia in the northern Gulf of Mexico. Estuaries Coasts *32*, 975–983. Available at: https://www.jstor.org/stable/40663599.
6. Simboura, N., Zenetos, A., Panayotidis, P., and Makra, A. (1995). Changes in benthic community structure along an environmental pollution gradient. Mar. Pollut. Bull. *30*, 470–474. Available at: https://linkinghub.elsevier.com/retrieve/pii/0025326X9500237H.
7. Ferraro, S.P., Swartz, R.C., Cole, F.A., and Schults, D.W. (1991). Temporal changes in the benthos along a pollution gradient: Discriminating the effect of natural phenomena from sewage-industrial wastewater effects. Estuar. Coast. Shelf Sci. *33*, 383–407. Available at: http://www.sciencedirect.com/science/article/pii/027277149190064I.
8. Donohue, I., Hillebrand, H., Montoya, J.M., Petchey, O.L., Pimm, S.L., Fowler, M.S., Healy, K., Jackson, A.L., Lurgi, M., McClean, D., O’Connor, N.E., O’Gorman, E.J*.* (2016). Navigating the complexity of ecological stability. Ecol. Lett. *19*, 1172–1185. Available at: http://onlinelibrary.wiley.com/doi/abs/10.1111/ele.12648.
9. Colwell, R.K. (1974). Predictability, constancy, and contingency of periodic phenomena. Ecology *55*, 1148–1153. Available at: http://esajournals.onlinelibrary.wiley.com/doi/abs/10.2307/1940366.
10. Wan, X., Jiang, G., Yan, C., He, F., Wen, R., Gu, J., Li, X., Ma, J., Stenseth, N.C., and Zhang, Z. (2019). Historical records reveal the distinctive associations of human disturbance and extreme climate change with local extinction of mammals. Proc. Natl. Acad. Sci. *116*, 19001–19008. Available at: http://www.pnas.org/content/116/38/19001.
11. Christensen, E.M., Harris, D.J., and Ernest, S.K.M. (2018). Long-term community change through multiple rapid transitions in a desert rodent community. Ecology *99*, 1523–1529. Available at: https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecy.2373.
12. Rocha, J., Yletyinen, J., Biggs, R., Blenckner, T., and Peterson, G. (2015). Marine regime shifts:

Drivers and impacts on ecosystems services. Philos. Trans. R. Soc. B Biol. Sci. *370*. Available at:

https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4247408/.

1. Ernest, S.K.M., Yenni, G.M., Allington, G., Bledsoe, E.K., Christensen, E.M., Diaz, R.M., Geluso,

K., Goheen, J.R., Guo, Q., Heske, E., Kelt, D., Meiners, J.M., Munger, J., Restrepo, C., Samson, D.A.,

Schutzenhofer, M.R., Skupski, M., Supp, S.R., Thibault, K., Taylor, S., White, E., Davidson, D.W., Brown,

J.H., Valone, T.J. (2018). The Portal Project: A long-term study of a Chihuahuan desert ecosystem. bioRxiv, 332783. Available at: https://www.biorxiv.org/content/10.1101/332783v2.

1. Ernest, S.K.M., Brown, J.H., Thibault, K.M., White, E.P., and Goheen, J.R. (2008). Zero sum, the niche, and metacommunities: LongǦterm dynamics of community assembly. Am. Nat. *172*, E257–E269. Available at: https://www.journals.uchicago.edu/doi/10.1086/592402.
2. Thibault, K.M., and Brown, J.H. (2008). Impact of an extreme climatic event on community assembly. Proc. Natl. Acad. Sci. *105*, 3410–3415. Available at: http://www.pnas.org/cgi/doi/10.1073/pnas.0712282105.
3. Gleason, H.A. (1926). The individualistic concept of the plant association. Bull. Torrey Bot. Club *53*, 7–26. Available at: http://www.jstor.com/stable/2479933.
4. Clements, F.E. (1936). Nature and structure of the climax. J. Ecol. *24*, 252. Available at: https://www.jstor.org/stable/2256278?origin=crossref.
5. Hubbell, S.P. (2001). The unified neutral theory of biodiversity and biogeography (Princeton University Press).
6. MacArthur, R.H., and Wilson, E.O. (1967). The theory of island biogeography (Princeton University Press).
7. Brown, J.H., Ernest, S.K.M., Parody, J.M., and Haskell, J.P. (2001). Regulation of diversity:

Maintenance of species richness in changing environments. Oecologia *126*, 321–332. Available at: http://link.springer.com/10.1007/s004420000536.

1. Gotelli, N.J., Shimadzu, H., Dornelas, M., McGill, B., Moyes, F., and Magurran, A.E. (2017).

Community-level regulation of temporal trends in biodiversity. Sci. Adv. *3*, e1700315. Available at:

https://advances.sciencemag.org/content/3/7/e1700315.

1. Adler, P.B. (2004). Neutral models fail to reproduce observed species–area and species–time relationships in Kansas grasslands. Ecology *85*, 1265–1272. Available at: http://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/03-0602.
2. Hare, S.R., and Mantua, N.J. (2000). Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog. Oceanogr. *47*, 103–145. Available at: http://www.sciencedirect.com/science/article/pii/S0079661100000331.
3. Bruno, J.F., Stachowicz, J.J., and Bertness, M.D. (2003). Inclusion of facilitation into ecological theory. Trends Ecol. Evol. *18*, 119–125. Available at: http://www.sciencedirect.com/science/article/pii/S0169534702000459.
4. Estes, J.A., and Palmisano, J.F. (1974). Sea otters: Their role in structuring nearshore communities. Science *185*, 1058–1060. Available at: http://science.sciencemag.org/content/185/4156/1058.
5. Zhao, L., Wang, S., Hallett, L.M., Rypel, A.L., Sheppard, L.W., Castorani, M.C.N., Shoemaker, L.G., Cottingham, K.L., Suding, K., and Reuman, D.C. (2020). A new variance ratio metric to detect the timescale of compensatory dynamics. Ecosphere *11*, e03114. Available at: http://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecs2.3114.
6. Wang, S., Lamy, T., Hallett, L.M., and Loreau, M. (2019). Stability and synchrony across ecological hierarchies in heterogeneous metacommunities: Linking theory to data. Ecography *42*, 1200– 1211. Available at: http://onlinelibrary.wiley.com/doi/abs/10.1111/ecog.04290.
7. Boersma, K.S., Dee, L.E., Miller, S.J., Bogan, M.T., Lytle, D.A., and Gitelman, A.I. (2016). Linking multidimensional functional diversity to quantitative methods: A graphical hypothesis-evaluation framework. Ecology *97*, 583–593. Available at: http://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/15-0688.
8. Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., and Bellwood, D.R. (2013). A functional approach reveals community responses to disturbances. Trends Ecol. Evol. *28*, 167–177. Available at: http://www.sciencedirect.com/science/article/pii/S0169534712002650.
9. Pimiento, C., Bacon, C.D., Silvestro, D., Hendy, A., Jaramillo, C., Zizka, A., Meyer, X., and Antonelli, A. (2020). Selective extinction against redundant species buffers functional diversity. Proc. R. Soc. B Biol. Sci. *287*, 20201162. Available at:

https://royalsocietypublishing.org/doi/10.1098/rspb.2020.1162

1. Clements, C.F., and Ozgul, A. (2016). Including trait-based early warning signals helps predict population collapse. Nat. Commun. *7*, 10984. Available at: http://www.nature.com/articles/ncomms10984.
2. Briggs, K.B., Craig, J.K., Shivarudrappa, S., and Richards, T.M. (2017). Macrobenthos and megabenthos responses to long-term, large-scale hypoxia on the Louisiana continental shelf. Mar. Environ. Res. *123*, 38–52. Available at:

http://www.sciencedirect.com/science/article/pii/S0141113616302951.

1. MacArthur, R.H., Diamond, J.M., and Karr, J.R. (1972). Density compensation in Island Faunas. Ecology *53*, 330–342. Available at: http://esajournals.onlinelibrary.wiley.com/doi/abs/10.2307/1934090.
2. Tilman, D. (1982). Resource competition and community structure (Princeton university press).
3. Kokkoris, G.D., Jansen, V.A.A., Loreau, M., and Troumbis, A.Y. (2002). Variability in interaction strength and implications for biodiversity. J. Anim. Ecol. *71*, 362–371. Available at: http://doi.wiley.com/10.1046/j.1365-2656.2002.00604.x.
4. Liautaud, K., van Nes, E.H., Barbier, M., Scheffer, M., and Loreau, M. (2019). Superorganisms or loose collections of species? A unifying theory of community patterns along environmental gradients. Ecol. Lett., ele.13289. Available at: https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.13289.
5. Vasseur, D.A., and Yodzis, P. (2004). The color of environmental noise. Ecology *85*, 1146–1152. Available at: http://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/02-3122.
6. Moran, P.A. (1953). The statistical analysis of the Canadian lynx cycle. Aust. J. Zool. *1*, 291–298.
7. Ives, A.R. (1995). Predicting the response of populations to environmental change. Ecology *76*, 926–941.
8. Newsome, S.D., Yeakel, J.D., Wheatley, P.V., and Tinker, M.T. (2012). Tools for quantifying isotopic niche space and dietary variation at the individual and population level. J. Mammal. *93*, 329–341. Available at: https://academic.oup.com/jmammal/article-lookup/doi/10.1644/11-MAMM-S-187.1.
9. Bianchi, T.S., DiMarco, S.F., Smith, R.W., and Schreiner, K.M. (2009). A gradient of dissolved organic carbon and lignin from Terrebonne–Timbalier Bay estuary to the Louisiana shelf (USA). Mar. Chem. *117*, 32–41. Available at: http://www.sciencedirect.com/science/article/pii/S0304420309001066.
10. Inoue, M., and Wiseman, W.J. (2000). Transport, mixing and stirring processes in a Louisiana estuary: A model study. Estuar. Coast. Shelf Sci. *50*, 449–466. Available at: http://www.sciencedirect.com/science/article/pii/S0272771400905870.
11. Reed, D.J. (1989). Patterns of sediment deposition in subsiding coastal salt marshes, Terrebonne Bay, Louisiana: The role of winter storms. Estuaries *12*, 222–227. Available at:

https://doi.org/10.2307/1351901.

1. Watzke, D. (2004). Short-term evolution of a marsh island system and the importance of cold front forcing, Terrebonne Bay, Louisiana. LSU Masters Theses. Available at: https://digitalcommons.lsu.edu/gradschool\_theses/3139.
2. Magurran, A.E., Dornelas, M., Moyes, F., and Henderson, P.A. (2019). Temporal β diversity—A macroecological perspective. Glob. Ecol. Biogeogr. *28*, 1949–1960. Available at: http://onlinelibrary.wiley.com/doi/abs/10.1111/geb.13026.
3. Legendre, P., and Gauthier, O. (2014). Statistical methods for temporal and space–time analysis of community composition data†. Proc. R. Soc. B Biol. Sci. *281*, 20132728. Available at: https://royalsocietypublishing.org/doi/full/10.1098/rspb.2013.2728.
4. Baselga, A., and Orme, C.D.L. (2012). Betapart: An R package for the study of beta diversity.

Methods Ecol. Evol. *3*, 808–812. Available at:

http://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/j.2041-210X.2012.00224.x.

1. R Core Team (2020). R: A Language and Environment for Statistical Computing (Vienna, Austria: R Foundation for Statistical Computing) Available at: https://www.R-project.org/.
2. Blei, D.M. (2003). Latent Dirichlet allocation. J. Mach. Learn. Res. *3*, 993–1022.
3. Valle, D., Baiser, B., Woodall, C.W., and Chazdon, R. (2014). Decomposing biodiversity data using the latent Dirichlet allocation model, a probabilistic multivariate statistical method. Ecol. Lett. *17*, 1591–1601. Available at: http://onlinelibrary.wiley.com/doi/abs/10.1111/ele.12380.
4. Simonis, J.L., Christensen, E.M., Harris, D.J., Diaz, R.M., Ye, H., White, E.P., and Ernest, S.K.M.

(2020). LDATS: Latent Dirichlet allocation coupled with time series analyses. Available at: https://CRAN.R-project.org/package=LDATS.

1. Pedersen, E.J., Koen-Alonso, M., and Tunney, T.D. (2020). Detecting regime shifts in communities using estimated rates of change. ICES J. Mar. Sci. *77*, 1546–1555. Available at: https://academic.oup.com/icesjms/article/77/4/1546/5835266.
2. Verardo, D.J., Froelich, P.N., and McIntyre, A. (1990). Determination of organic carbon and nitrogen in marine sediments using the Carlo Erba NA-1500 analyzer. Deep Sea Res. A *37*, 157–165. Available at: http://adsabs.harvard.edu/abs/1990DSRA...37..157V.
3. Couvillion, B.R., Beck, H., Schoolmaster, D., and Fischer, M. (2017). Land area change in coastal Louisiana (1932 to 2016) (Reston, VA: U.S. Geological Survey) Available at:

http://pubs.er.usgs.gov/publication/sim3381.

1. Sabo, J.L., and Post, D.M. (2008). Quantifying periodic, stochastic, and catastrophic environmental variation. Ecol. Monogr. *78*, 19–40. Available at: http://doi.wiley.com/10.1890/06-1340.1.
2. Wood, S. (2017). Generalized additive models: An introduction in R 2nd edition. (Boco Raton: CRC Press).
3. Pedersen, E.J., Miller, D.L., Simpson, G.L., and Ross, N. (2019). Hierarchical generalized additive models in ecology: An introduction with mgcv. PeerJ *7*. Available at: https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6542350/.
4. Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using stan. J. Stat. Softw. *80*, 1–28. Available at: https://www.jstatsoft.org/index.php/jss/article/view/v080i01.
5. Dray, S., and Dufour, A.-B. (2007). The ade4 Package: Implementing the Duality Diagram for Ecologists. J. Stat. Softw. *22*, 1–20. Available at:

https://www.jstatsoft.org/index.php/jss/article/view/v022i04.

1. Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O’Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H. (2019). vegan: Community Ecology Package Available at: https://CRAN.R-project.org/package=vegan.
2. Schluter, D. (1984). A variance test for detecting species associations, with some example applications. Ecology *65*, 998–1005. Available at: http://doi.wiley.com/10.2307/1938071.
3. Reuman, D.C., Zhao, L., and Wang, S. (2019). tsvr: Timescale-specific variance ratio for use in community ecology Available at: https://CRAN.R-project.org/package=tsvr.
4. Bambach, R.K., Bush, A.M., and Erwin, D.H. (2007). Autecology and the filling of ecospace: Key metazoan radiations. Palaeontology *50*, 1–22. Available at: http://onlinelibrary.wiley.com/doi/abs/10.1111/j.1475-4983.2006.00611.x.
5. Bush, A.M., Bambach, R.K., and Daley, G.M. (2007). Changes in theoretical ecospace utilization in marine fossil assemblages between the mid-Paleozoic and late Cenozoic. Paleobiology *33*, 76–97.

Available at: https://www.cambridge.org/core/product/identifier/S0094837300018972/type/journal\_article.

1. Peterson, B.J., and Fry, B. (1987). Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. *18*, 293–320.
2. Jackson, A.L., Inger, R., Parnell, A.C., and Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER – Stable isotope Bayesian ellipses in R. J. Anim. Ecol. *80*, 595– 602. Available at: http://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2656.2011.01806.x.
3. Froese, R., and Pauly, D. (2019). Fishbase. Available at: www.fishbase.org.
4. Laliberté, E., and Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. Ecology *91*, 299–305. Available at: https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/08-2244.1.
5. Keyel, A.C., and Wiegand, K. (2016). Validating the use of unique trait combinations for measuring multivariate functional richness. Methods Ecol. Evol. *7*, 929–936. Available at: http://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/2041-210X.12558.
6. Magurran, A.E., Baillie, S.R., Buckland, S.T., Dick, J.McP., Elston, D.A., Scott, E.M., Smith, R.I., Somerfield, P.J., and Watt, A.D. (2010). Long-term datasets in biodiversity research and monitoring: Assessing change in ecological communities through time. Trends Ecol. Evol. *25*, 574–582. Available at:

http://www.sciencedirect.com/science/article/pii/S0169534710001552.

1. Edwards, M., Beaugrand, G., Hays, G.C., Koslow, J.A., and Richardson, A.J. (2010). Multidecadal oceanic ecological datasets and their application in marine policy and management. Trends Ecol. Evol. *25*, 602–610. Available at: http://www.sciencedirect.com/science/article/pii/S016953471000162X.