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PROGRAM ANNOUNCEMENT/SOLICITATION NO./ DUE DATE: **NSF 24-520** 03/14/2024

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OCE - LONG TERM ECOLOGICAL RESEARCH, (continued)

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TITLE OF PROPOSED PROJECT: **LTER: Georgia Coastal Ecosystems V**

SHOW LETTER OF INTENT ID IF APPLICABLE

REQUESTED AMOUNT	PROPOSED DURATION (1-60 MONTHS)	REQUESTED STARTING DATE	SHOW RELATED PRELIMINARY PROPOSAL NO. IF APPLICABLE
$ 7,542,000	72 months	02/01/2025	

THIS PROPOSAL INCLUDES ANY OF THE ITEMS LISTED BELOW

- ☒ TYPE OF PROPOSAL **Research**
- ☒ COLLABORATIVE STATUS **Collaborative from one organization**
- ☐ BEGINNING INVESTIGATOR
- ☐ DISCLOSURE OF LOBBYING ACTIVITIES
- ☐ PROPRIETARY & PRIVILEGED INFORMATION
- ☐ HISTORIC PLACES
- ☐ LIVE VERTEBRATE ANIMALS IACUC App. Date ______
  PHS AnimalWelfareAssurance Number ______
- ☐ HUMAN SUBJECTS Human Subjects Assurance Number______ Exemption Subsection______ or IRB App. Date______
- ☐ FUNDING OF INT'L BRANCH CAMPUS OF U.S IHE
- ☐ FUNDING OF FOREIGN ORGANIZATION OR FOREIGN INDIVIDUAL
- ☒ INTERNATIONAL ACTIVITIES: COUNTRY/COUNTRIES INVOLVED GR
- ☐ POTENTIAL LIFE SCIENCES DUAL USE RESEARCH OF CONCERN
- ☒ OFF-CAMPUS OR OFF-SITE RESEARCH

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GCE-V Project Summary

Overview. The overall goal of the Georgia Coastal Ecosystems (GCE) Long-Term Ecological Research program is to understand estuarine and intertidal ecosystems and how they respond to long-term change. Since the program began in 2000 the Principal Investigator (PI) team has established a robust program of long-term field observations, experiments, remote sensing, and modeling to understand wetland ecosystem functioning. The PIs will build on this in GCE-V, but with an overlay of new efforts focused on variability. The GCE-V project has 5 programmatic areas that map onto objectives (obj). Obj. 1 is to characterize spatial and temporal patterns in mean and variability of drivers and responses. This will be done by measuring external drivers (e.g., sea level), marsh and estuarine conditions, the wetland biophysical template, and modeling. Obj 2 is to evaluate linkages between external drivers and ecological responses, and determine whether assessing the variability of abiotic drivers improves explanatory power for predicting those responses. This will be done by analyzing long-term data and conducting field campaigns in areas with different salinity standard deviations and time-varying inundation, and complementary mechanistic experiments exploring effects of driver variability (e.g., salinity). Obj. 3 is to assess disturbances and their effects on patterns of variability in ecological responses. This will be done by tracking response to and recovery from natural disturbances in the field and in ongoing experimental manipulations. Obj. 4 is to evaluate how ecological properties change across abiotic gradients, and determine whether variability increases near habitat transitions. This will be done using remote sensing, sampling across gradients of salinity and inundation, and establishing new long-term monitoring sites in forested areas to track upland marsh migration. Obj. 5 is to determine the mechanisms by which coastal wetlands respond to changing drivers and assess whether variability informs this understanding. This will be done by conducting univariate and multivariate analyses relating key ecosystem variables (e.g., net ecosystem exchange, plant biomass) to drivers (salinity, inundation, temperature), using remote sensing to investigate spatial and temporal patterns in the mean and variability of marsh productivity and their relationship to variability in climate drivers, and synthesizing results to describe net daytime production and above- and below-ground C stocks and how they might change in response to future conditions.

Intellectual Merit. Ecologists generally describe drivers and responses using measures of central tendency, most commonly the mean. However, measures of variability, such as the range or coefficient of variation, may also be important for predicting the effects of global change. There is evidence that abiotic variability can be important for explaining ecological processes, that variability increases significantly during recovery after a disturbance, and that increased variability can indicate an underlying environmental stress that may be associated with an impending transition. The research proposed here is designed to determine 1) whether understanding of the GCE-LTER system and coastal wetlands generally can be improved by assessing driver variability in predicting ecological responses, and 2) the potential value of ecological variability as a fundamental metric of system behavior in ecosystem ecology. This effort will result in a comprehensive evaluation of the role of variability that will apply well beyond GCE and wetland ecosystems.

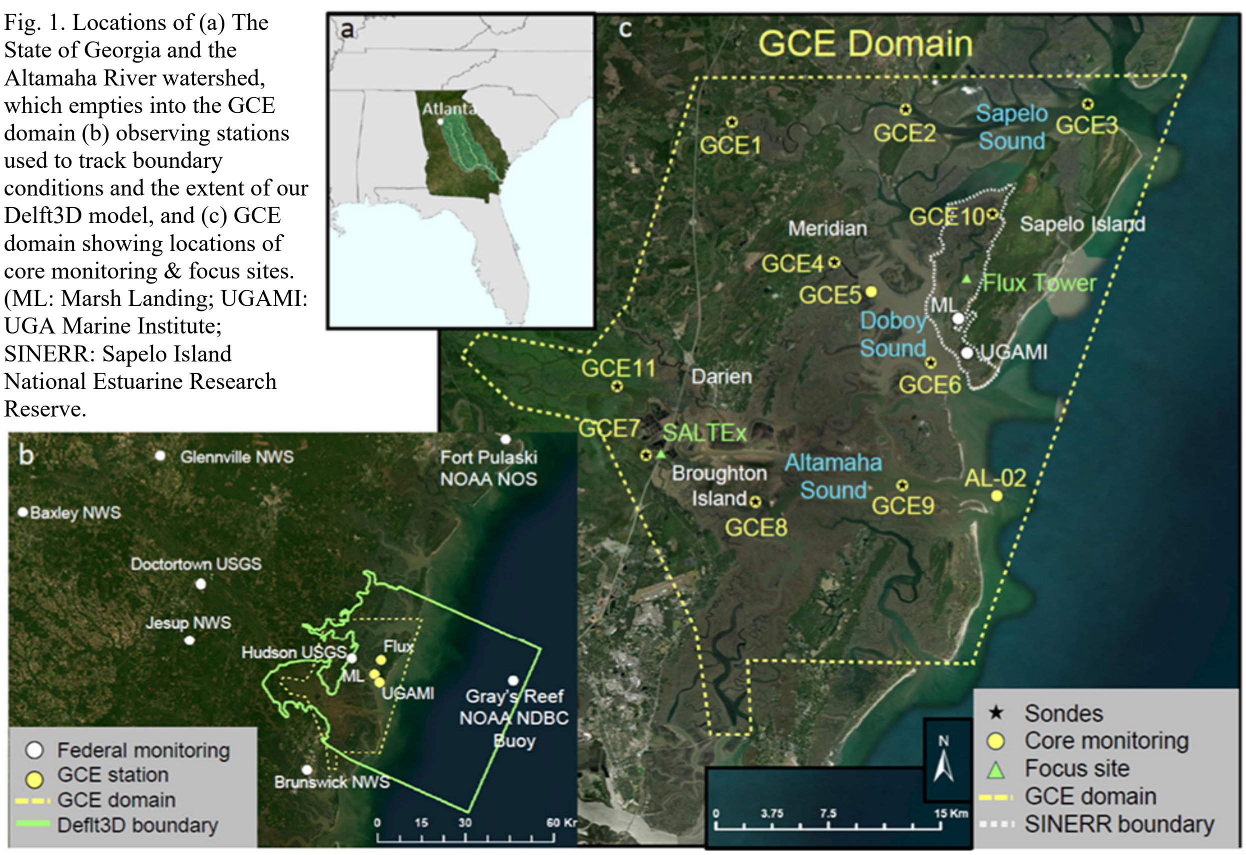
Broader Impacts. The proposed education and outreach activities are designed to enhance scientific literacy, expand opportunities in STEM, and broaden participation at all levels, from K12 to PIs. Proposed efforts aim to increase the diversity of GCE undergraduates, graduate students, and PIs, and the reach of educational and outreach activities. The GCE Schoolyard program, built around long-term contact and mentoring, will continue; and school visits will expand the curriculum and scope of K12 activities. The GCE REU program will provide research opportunities for a diverse group of undergraduates. A cross-site course will provide interdisciplinary training for graduate students. The PIs will work with collaborators from minority-serving institutions to improve graduate recruitment and identify new GCE investigators. A citizen science effort that will help delineate high tide flooding events in coastal uplands will involve Geechee descendants who live on Sapelo Island. The GCE project will continue to partner with the Georgia Coastal Research Council to exchange information with managers and promote science-based management of coastal resources.

Results from Prior Support (Georgia Coastal Ecosystems-IV, OCE-1832178)

The Georgia Coastal Ecosystems (GCE) LTER program was established in 2000 and we are now completing GCE-IV, which has 22 Principal and 12 Affiliated Investigators from 17 Institutions. The GCE-IV team published 121 journal articles and 28 books, theses, and other one-time publications, and has 742 publicly available data sets uploaded to the EDI data portal that are also discoverable through DataONE, BCO-DMO, and the GCE Data Catalog (*see Data Availability Report*). During GCE-IV we received NSF supplemental funding (denoted **Supp.**) that supported engagement with faculty from Savannah State University, post-baccalaureate students, and replacement of critical equipment. We have strong programs in information management, education, and outreach. These accomplishments lay the foundation for the ambitious plan we propose for GCE-V.

The GCE-LTER site (or "domain") is located on the Georgia (GA) coast (Fig. 1) and is representative of southeastern USA estuaries and associated intertidal wetland habitats (salt, brackish, and fresh marsh, tidal fresh forest). ***The overall goal of the GCE program is to understand estuarine and intertidal wetland ecosystems and how they respond to long-term change***. During GCE-I we began to describe the patterns of variability in the system and identified spatial variation in freshwater inflow as a primary environmental forcing of ecological structure and function across our domain. In GCE-II we expanded our understanding of water movement along the longitudinal axes of the estuaries, tidal exchange with the marsh platform, and the implications for landscape-level distributions of organisms (Fig. 2a). GCE-III focused on salinity and inundation as major structuring variables, and asked how long-term changes expected in these properties, due to climate change and anthropogenic factors, would affect biotic and ecosystem responses (Fig. 2b). In GCE-IV we added an explicit focus on the role of disturbance in coastal marshes (Fig. 2c). We worked to characterize disturbance events and their relationship to external drivers and to develop an understanding of ecosystem responses at the landscape scale. We divided GCE-IV research into 4 inter-related programmatic areas; our accomplishments in each are highlighted below.

Fig. 1. Locations of (a) The State of Georgia and the Altamaha River watershed, which empties into the GCE domain (b) observing stations used to track boundary conditions and the extent of our Delft3D model, and (c) GCE domain showing locations of core monitoring & focus sites. (ML: Marsh Landing; UGAMI: UGA Marine Institute; SINERR: Sapelo Island National Estuarine Research Reserve.



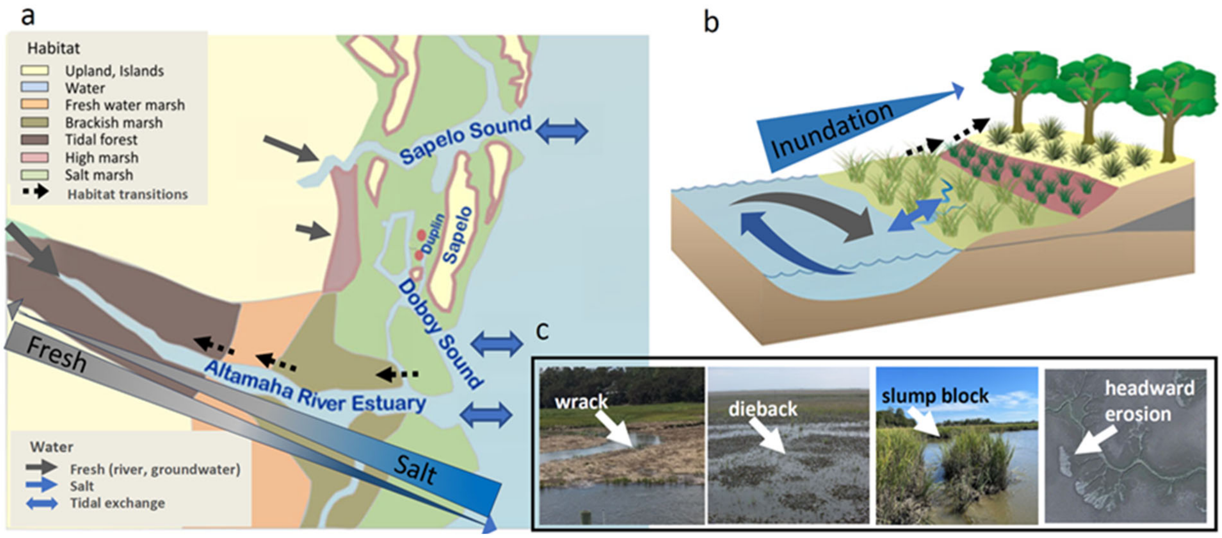


Fig. 2. GCE domain showing water movement and habitat distributions along (a) longitudinal and (b) lateral gradients of salinity and inundation across the landscape. With sea-level rise we expect salt and inundation tolerant habitats to migrate up-estuary and upslope, respectively (arrows). (c) Examples of common disturbances in marsh habitats.

References to our 10 most significant publications are in bold, <u>with findings underlined.</u>

Area 1: External drivers of change. Our goal for this area is to characterize external drivers such as climate change, sea-level rise, and human alterations of the landscape in terms of long-term trends, spatiotemporal variability, and extreme events (e.g., storms, droughts) so that we can investigate the links between external drivers and ecosystem responses. To accomplish this, we track changes in environmental drivers and human activities that influence conditions in the GCE domain. *These efforts will continue, with minor modifications, in GCE-V.*

Environmental patterns. Crotty et al. (2020) analyzed sea-level trends and accretion rates in the southeastern region and found that rates of sea-level rise during the 20 years since the GCE began (1999-2019) were double those from 1940-1999, causing the marsh to be submerged for 0.4 to 1.8 h more per day in 2019 than 1999, depending on the accretion scenario. At the same time (1999-present) the southeast has experienced record droughts and several large storm events (including two major hurricanes since 2016). We used a combination of approaches to evaluate dissolved organic matter (DOM) in Altamaha River water entering the GCE domain, and found that the dominant pattern of variability in DOM composition (FT-ICRMS) and microbial activity (using gene expression/meta-transcriptomics as a proxy) was associated with seasonality in discharge (Martineac et al. 2021), with large increases in terrigenous material and biodegradation during extreme events (Letourneau & Medeiros 2019; Medeiros 2022). These analyses suggest that future changes in river discharge could significantly impact DOM composition and cycling in coastal systems. Over much longer time scales, we used high-resolution radiocarbon dating to anchor the dendrochronological sequence of the GA Coast over the past 5,000 years, linking drought and sea level changes to tree die-offs (Napora et al. 2019, Napora 2021).

Human patterns. We conducted archaeological studies to characterize the changing relationships between humans and the environment. <u>Data from ~40,000 oyster shells from along the Atlantic Coast provided a long-term record demonstrating that Native shellfish harvesting practices were sustainable until the late 1800s</u> (**Thompson et al., Science Advances 2020**; Garland & Thompson 2023). However, sea-level modeling and isotope geochemistry suggest that the growth and decline of Native American villages were associated with changes in sea level, which caused regional shifts in village locations and permanence (Thompson et al. in review). We also focused on land use changes on Sapelo Island, which is the center of the GCE domain. We traced the history of property ownership and anthropogenic impacts (i.e., ditching and wetland draining) and the ramifications for the Saltwater Geechee, who are descended from West and Central Africans enslaved on sea islands in the southeastern US (Heynen 2020; Hardy & Heynen 2021;

Hardy et al. 2022). We are specifically evaluating flood risk in the Hogg Hummock community on Sapelo due to legacy infrastructure (e.g., drainage ditches) and sea-level rise (Hardy 2023), and collecting oral histories from Geechee descendants on changes in natural resources over time (with Savannah State, **Supp.**). *We will add a citizen science program in GCE-V to help document flooding patterns in this community.*

Area 2: Long-Term Patterns of Estuary and Intertidal Variation. Our goal for this area is to describe temporal and spatial changes in habitats within the GCE domain in order to evaluate ecosystem responses to disturbance and long-term changes in external drivers. We maintain time series of water and marsh attributes that span all 5 LTER core research areas, and collect digital imagery of habitat productivity and distributions. *These efforts will continue, with minor modifications, in GCE-V.*

Field monitoring. Our long-term time series include continuous estuarine conductivity, temperature, and pressure measurements from multi-sensor instruments (**Supp.**) distributed across the domain, and discrete measurements of surface water dissolved and particulate constituents collected during regular cruises. In the marsh we monitor vertical accretion and sedimentation, plant productivity, animal abundance, and disturbances at 11 core monitoring sites as well as in transitional areas where we expect habitat shifts. **Smith et al. (Ecosphere in press)** used these 20+ year time series to evaluate effects of storm surges from Hurricanes Matthew (2016) and Irma (2017) on coastal marshes, highlighting marsh resistance. **Liu & Pennings (Ecology 2021)** also leveraged the time series, and found no asynchrony in plant production across sites and marsh zones (creekbank and mid-marsh), suggesting that one species does not compensate for another during poor years. Adams et al. (2021) analyzed 20 years of insect densities, and Smith et al. (in review) found that both drought and *Littoraria irrorata* (periwinkle snails, hereafter: *Littoraria*) suppressed the biomass of *Spartina alterniflora* (salt marsh cord grass, hereafter: *Spartina*), although snails only had an effect when present at high densities. *These long-term observations provide essential data for our new work evaluating variability in both domain drivers and ecosystem responses, the central theme of the research proposed for GCE-V.* We also maintain an eddy covariance (hereafter, flux) tower that measures CO_2/H_2O (**Supp.**), weather conditions, radiation, tidal creek water levels, and soil temperature. Hawman et al. (in review) used these data to derive estimates of net ecosystem exchange (NEE) from 2014 to 2022 and found that annual CO_2 uptake was lowest in 2016 when there was a severe drought. *Ongoing data collection at the flux tower will be used to evaluate responses to environmental variability and to develop models of Spartina production that can be scaled up to the landscape with remote sensing.*

Digital imagery. We maintain two PhenoCams that collect oblique images every 30 min, which are contributed to the National Phenocam Network. The GCESapelo camera was established in GCE-III and is focused on a *Spartina* marsh while the GCEJuncus camera began in GCE-IV and includes stands of both *Spartina* and *Juncus roemerianus* (hereafter: *Juncus*). O'Connell et al. (2020) used PhenoCam images to develop a spring warm-up model for *Spartina* that suggests that winter warming has resulted in earlier green-up over the last 60 y. We also used PhenoCam images as ground truth data to develop tools to predict the presence or absence of marsh flooding in both MODIS (O'Connell et al. 2017) and Landsat (Narron et al. 2022) imagery. These open-source tools are widely used by other researchers and have been implemented in Google Earth Engine. We use high-resolution aerial photographs to evaluate patterns in creek configuration, creekbank slumping, shoreline armoring, and shifts in tidal marsh distribution. Currin (2023) applied a random forest classifier to orthoimagery collected in 2018 (15-cm scale) and, along with extensive ground data collected in 2021-2022, developed tidal marsh habitat maps for the GA coast. We also performed a community analysis of Altamaha tidal fresh forest vegetation based on hierarchical clustering to identify distinct freshwater forest communities (Costomiris et al. 2024). *These maps will form the basis of scaled-up productivity and transition analyses in GCE-V.*

Area 3: Process studies. Our goal for this area is to develop a mechanistic understanding of ecosystem function and response to long-term and episodic changes. We accomplish this through long-term manipulations and focused investigations.

Long-term manipulations. We completed a Seawater Addition Long-Term Experiment (SALTEx), continued a nekton exclusion experiment (Predex), and established 3 disturbance manipulations in GCE-V. SALTEx was a large-scale field manipulation (2013-2022) that evaluated how pulses and presses of brackish water affect a tidal freshwater marsh (Craft et al. 2016). We documented treatment effects on carbon dynamics (Herbert et al. 2018), nutrient cycling (Widney et al. 2019), microbial communities (Mobilian et al. 2020), and plant characteristics (Li et al. 2022). Of particular importance was **Solohin et al. (Ecology 2020),** who documented a decline in surface elevation and C loss in plots continuously exposed to seawater. We have now synthesized observations about post-treatment recovery (Thompson et al. in review). Top-down predator effects are being evaluated in Predex (begun in 2016), which excludes nekton (blue crabs and fish) from 20 m^2 plots in a *Spartina* marsh. Morton et al. (in review) found increased densities of snails and fiddler crabs after 2 years, followed by a 3-fold increase in mesopredator mud crabs in year 3 that erased the predation refuge. *We will continue the Predex experiment in GCE-V.*

Both the ‘Disturbance across Salinity’ and ‘Disturbance across Elevation’ experiments test the hypothesis that underlying abiotic gradients affect marsh recovery from a standardized disturbance (removal of all aboveground vegetation). These manipulations build on a 12-year study that found that plant community recovery time increased with increasing salinity (**Wang et al., Ecology 2024**). The new experiments are better replicated and include a wider suite of response variables. The ‘Disturbance across Salinity’ experiment established 20 paired plots (control and disturbed) in each of the four dominant vegetation types (*Zizaniopsis, Juncus, Spartina,* and *Sarcocornia* sp.) along the salinity gradient of the Altamaha estuary in 2023. We are currently following recovery, which we expect to take 10-15 years in less-resilient vegetation types. In the ‘Disturbance across Elevation’ experiment, 20 paired plots were established across an elevational gradient in a single vegetation type (*Spartina*) in 2022. We expect recovery to be complete by the end of 2025. (Note that these experiments were delayed due to COVID.) We are also participating in the DRAGNET experiment, a distributed global experiment examining grassland responses to disturbance and nutrients. We set up the experiment in a *Spartina* marsh in 2021. The DRAGNET disturbance (rototilling) mimics that of feral pigs in salt marshes (Hensel et al. 2021); we also added a treatment mimicking wrack disturbance (dead plant material deposited by tides). We expect that rototilling, which disturbs both above- and belowground material, will have a greater effect than simulated wrack disturbance, which only affects above-ground biomass. This experiment has an anticipated 10-y lifespan. *We will use these disturbance experiments to test whether variability increases during recovery (Q2 in GCE-V).*

Focused investigations. These studies were designed to better understand controls on plant production, relationships between marsh fauna and environmental variables, and soil carbon dynamics. Temperature and flooding are two key variables affecting plant production, and both are experiencing long-term change. Alber & O’Connell (2019) demonstrated that fine-scale elevation gradients correspond to microspatial differences in soil temperature, and in turn, result in spatial differences in *Spartina* green-up and phenophase length across the marsh (O’Connell et al. 2020). Submergence also affects photosynthetic performance. We used plot-level measurements of leaf area index (LAI) to determine how atmospheric exchange and light use efficiency change with inundation (Hawman et al. 2021). **Mao et al. (JGR Biogeoscience 2023)** found that Photosystem II reaction centers are active and able to transfer electrons when leaves are submerged, but only at ~20% of the typical daily rate. This fits with observations that tidal flooding depresses NEE, an effect that varies seasonally (Nahwari et al. 2020). *We will use these insights in GCE-V to evaluate how variable patterns of inundation affect marsh productivity.*

Our studies of marsh fauna have evaluated feedbacks between organisms and marsh geomorphology. The headward erosion of tidal creeks is associated with the herbivorous marsh crab, *Sesarma reticulatum* (hereafter: *Sesarma*), which excavates soils, consumes creekbank plants (increasing erodibility), and likely enhances decomposition of soil organic matter through burrow networks that increase oxygen penetration (Vu et al. 2017; Vu & Pennings 2018). The biomass of other marsh invertebrates is severely decreased adjacent to crab-grazed creeks, likely due to increased predator access to the marsh platform (Crotty et al. 2020). Crotty et al. (2023) quantified deposition associated with aggregations of ribbed mussels and their contribution to microspatial patterns of marsh accretion, which is relevant for coastal restoration (Sievers et al. 2022). We also looked at organismal response to environmental conditions: Atkins et al (2022) found variation in respiration and feeding among different size-classes of *Littoraria*, and our field measurements using biomimics show high spatio-temporal variation in temperature that could lead to divergent responses of *Littoraria* in different microhabitats. *We will continue to use biomimics in GCE-V to measure variation in temperature regimes experienced by organisms.*

Marsh soil studies focused on organic matter decomposition, which has implications for coastal wetland carbon (C) storage with climate change (Spivak et al. 2019). We found that microbial responses to repeated, simulated root C pulses increase over time, demonstrating anticipatory or acclimatization responses, but that oxygen availability has greater potential to regulate C mineralization than root exudates **(Spivak et al., Soil Biology & Biogeochemistry 2023**). We also found that organic matter decay rates vary predictably with relative elevation in the tidal frame (Reddy et al., in prep). *We will build on this in GCE-V to evaluate how variability in salinity and inundation affect soil processes.*

Area 4: Integration and scaling up. Our goal for this area is to evaluate disturbance and long-term change at the landscape scale and understand relationships between drivers and responses. We accomplish this through a combination of remote sensing, field investigations, and modeling.

Disturbance. We used a TerraView RangePro X8 Unmanned Aerial Vehicle (UAV, **Supp.**) coupled with a high-resolution multispectral camera (Micasense Altum) to assess the accumulation of *Spartina* wrack and the occurrence of creekbank slumping, both of which are common disturbances in southeastern marshes (Li & Pennings 2016, Fig. 2c). We began monthly UAV flights of the Dean Creek marsh (0.13 km^{-2} salt marsh) in Jan 2020 and added a second site, Belle Marsh (0.12 km^{-2}), which has a larger tidal prism and is more fragmented, in May 2022. The flights will continue through April 2025. Lynn et al. (2023) used the imagery to analyze temporal and spatial patterns of 2,100 wrack patches over 1 year. The imagery also helped guide field sampling to measure responses to and recovery from wrack disturbance at 35 plots across 16 wrack patches. Williams et al. (in prep) found that almost all measured response variables recovered within a year. We are using these results to develop estimates of wrack effects at the whole marsh scale (Pierce et al., in prep). The UAV imagery is also being used to describe the dynamics of slump blocks, which are sections of vegetated marsh that break off along creekbank edges. Yang et al. (in press) found that most slump blocks persist for only a short period of time (< 6 mon), and that block loss accounted for 66% of channel widening within the study area. Crotty et al. (2020) analyzed aerial imagery and found that headward-eroding creeks, which extend onto the marsh platform at a rate of 1 - 4.5 m y^{-1}, have increased drainage density by 8 - 35% across the southeast over the past 25 y. **Wu et al. (Limnology & Oceanography 2021)** took advantage of a space-for-time substitution to evaluate the effects of headward erosion on 19 marsh attributes and found multiple patterns of disturbance effect sizes and recovery trajectories that belied any simple univariate understanding. *We will continue to assess the implications of disturbance for marsh structure and function in GCE-V.*

Landscape Change. Assessing habitat distributions and landscape-level changes in marsh area and productivity is important for evaluating long-term responses of ecosystems to external drivers and disturbances. **Burns et al. (Estuaries & Coasts 2020a)** found that tidal channel widening and contraction over 70 y were largely balanced, resulting in no net change in the vegetated area of a *Spartina* marsh located near Sapelo Island. A model by Langston et al. (2020) indicated that natural "elevation capital" will help GCE marshes persist against sea-level rise through 2100, in contrast to marshes elsewhere that are perched lower in the tidal range. However, the long-term stability of salt marshes remains an area of active research as there are many unknowns regarding feedbacks among flooding depth, plant growth and sediment accretion. There is also considerable temporal and spatial variability in plant productivity. We used Landsat-derived vegetation indices to evaluate patterns in aboveground biomass (AGB) of *Spartina* in the GCE domain (O'Donnell & Schalles 2016; Bice et al. 2023) and are poised to expand this to the entire GA coast, and to conduct similar analyses for *Juncus* and *Zizaniopsis*. Our light-use efficiency model for *Spartina* at the flux tower site (Hawman et al. 2021; 2023) is an important step towards developing a gross primary production (GPP) model that we can use on a per-pixel basis for all salt marshes in the GCE domain. Finally, we are developing orthoimagery-based tools to classify tidal forest and marsh (fresh, brackish, salt) habitats using satellite imagery (Sentinel 2; Costomiris 2022; Pudil 2023) from which we can assess habitat change. *We will build on these efforts in GCE-V to evaluate habitat shifts and develop primary production estimates that can be scaled to the GCE domain and the GA coast.*

Modeling. Our models synthesize diverse data streams and provide mechanistic insight into GCE data and relationships between drivers and responses. Our 3-D hydrodynamic models (FVCOM, Delft3D) are forced using meteorology, river discharge, and sea surface height along with salinity from GCE hydrographic moorings. These models predict salinity, circulation and residence times (McKnight 2016; Wang et al. 2017) *and will help guide field sampling and other efforts in GCE-V*. Our soil model (Miklesh & Meile 2018) predicts porewater salinity--an important input for modeling plant growth--based on hydrology and evapotranspiration, *and will be expanded to include temperature in GCE-V*. Observations from an upland-marsh transitional site were used to construct a 2-D variable-density groundwater flow model (Sanders 2021; Rossiello 2023) *which will be refined in GCE-V*. Our empirical Belowground Ecosystem Resilience Model (BERM) uses extreme gradient boosting to predict *Spartina* below-ground biomass (BGB) from environmental (e.g., elevation, temperature) and biological (e.g., foliar nitrogen, plant phenology) variables (**O'Connell et al., New Phytologist 2021**, Runion et al. in review). One of the exciting things about this effort is that aboveground proxies can be used to provide spatially explicit estimates of BGB through readily available remote sensing and gridded spatial data. We will use BERM to test the hypothesis that declining BGB is an indicator of marsh vulnerability to stressors such as sea-level rise. Bice et al. (2023) assessed patterns in satellite-derived plant biomass using wavelet analysis, and identified causal connections with temperature, river discharge, drought, sea level, and river nutrients with cross-convergent mapping. These analyses highlight the power of long time series to identify ecological interactions in complex natural systems.

Cross-Site Research. During GCE-IV we participated in multiple cross-site research efforts. Alber and Alexander were part of a Coastal SEES project comparing the sustainability of the three Atlantic Coast salt marsh LTER sites (GCE, PIE, VCR). Mishra worked with collaborators at PIE, South Carolina, and Delaware to compare NEE along a latitudinal gradient. Spivak conducted lab and field experiments at GCE and PIE to test how sea-level rise and redox conditions affect soil carbon cycling; she is also part of the LTER Marine & Coastal Consumer Nutrient Synthesis Working Group and the Coastal Carbon Research Coordination Network. Medeiros participated in the "pulse dynamics in LTER" group. Our PIs contributed to cross-site papers within the LTER network (Harms et al. 2021; Zinnert et al. 2021; Gaiser et al. 2022; Reed et al. 2022) and beyond (e.g., Feagin et al. 2020; Temmink et al. 2022; Sharma et al. 2022; Holmquist et al. 2023). Pennings and Craft did comparative research on introduced *Spartina* in Chinese marshes (e.g., Liu et al. 2020; Chen et al. 2021; Zhang et al. 2020). *We will continue to pursue cross-site research opportunities in GCE-V.*

Broader Impacts. GCE education and outreach activities increase community engagement and facilitate understanding of coastal ecosystems. We provide training and professional opportunities to undergraduate and graduate students, K-12 students and teachers, citizen scientists, coastal managers, and the general public. *We will continue these efforts in GCE-V.*

Undergraduate and graduate students are deeply embedded in our research. Graduate students who participated in GCE-IV completed 9 MS theses and 8 PhD dissertations; our program currently includes 32 graduate students from 6 institutions. We led distributed graduate courses on *Foundation Species* (2019) and *Disturbance in Coastal Wetlands* (2023) that each reached more than 135 participants (students and coastal managers) across the country. The GCE-IV REU program supported 10 of 90 GCE undergraduates. We are working to broaden participation in our intern program through targeted recruiting, changes to our application (asking about perseverance in overcoming obstacles), covering costs of travel and field clothes, and improved orientation and mentor training. We had a post-baccalaureate student in 2022 (**Supp.**) who is now a PhD student at Stanford, and in 2023-2024 we piloted a cross-site RaMP-inspired program (**Supp.**) that provided proof-of-concept for the 2024 proposal led by the LTER Network Office. Our ongoing collaboration with SSU includes participation in GCE meetings, field trips to GCE, and undergraduate and graduate student support (**Supp.**).

Each year, ~12 K-12 teachers spend a week on Sapelo Island immersed in research alongside GCE investigators participating in our Schoolyard program, which is built on a model of long-term contact and mixes returning and new teachers. Participants report that working alongside scientists demystifies the scientific process and makes the program unique. Teachers develop lesson plans, "meet the scientist" videos (a suggestion from our 3-y review) and other materials that are available on our website, and share classroom activities based on GCE science throughout the year. We engage K-12 students through our children's book, *As the Tide Comes In* (now in its 2nd edition). The book is part of the LTER series and has been widely distributed to schools and environmental centers. We also wrote a comic book in English (*The Adventures of Jacob the Technician*) and Spanish (*Las Adventuras de Jacob el Técnico*) that shows a day in the life of the GCE technicians and includes word games and activities.

The GCE works with coastal managers through the Georgia Coastal Research Council (GCRC), which is a boundary organization that facilitates science-based management of coastal resources for GA and the southeast region. The GCRC has 149 affiliates from 19 universities and 17 federal and state agencies. During GCE-IV the GCRC organized biennial meetings for scientists and managers (2018, 2020 [virtual], and 2022), provided technical support for the state's response to the Golden Ray oil spill, wrote a report on the impacts of seismic activities on marine organisms, compiled literature on black mangrove expansion into salt marshes and wave attenuation by coastal forests and oysters, and produced an on-line spreadsheet of coastal resiliency funding opportunities for the GA Dept. of Natural Resources. The GCE also partners with the Sapelo Island National Estuarine Research Reserve (SINERR), the Nature Conservancy, and the USGS to collect data of mutual interest.

GCE scientists routinely participate in public forums and provide information about their research to the general public. In 2021 GCE research was featured by PBS on their "Changing Seas" program. We publish a weekly e-newsletter that is publicly available and the GCE website provides public access to information and data from the GCE program and decades of research on Sapelo Island and the GA coast. Since the beginning of GCE-IV we have logged 535,000 web visitors and over 8 million page views. (*See Data Management Plan for download statistics and details of our information management program*.)

Response to Reviewers. The GCE-IV mid-term review team found that "*GCE is making progress on all overarching goals and detailed objectives in the GCE IV proposal*", that "*[p]roject oversight is effective*", and that "*GCE is doing very well*". They had two recommendations: 1) Develop a code of conduct that includes zero tolerance of harassment or discrimination of any kind, and 2) Update the 2012 Diversity Plan with the goal of increasing coordination among complementary efforts and engaging more members of the GCE community in activities related to diversity, equity, and inclusion. In response, we formally adopted a code of conduct (2021), a field safety plan (2022), and a DEI implementation plan (2022), and expanded our DEI committee (*see Program Management*). There were no research recommendations, but the panel identified advances in remote sensing and the use of C dynamics to integrate across the landscape as program strengths, both of which we are building on in GCE-V.

Project Description

1 Introduction

The overall goal of the GCE-LTER is to understand estuarine and intertidal ecosystems and how they respond to long-term change. Over the past four funding cycles we have established a robust program of long-term field observations, experiments, remote sensing, and modeling to produce fundamental insights into coastal wetland ecosystem function. As we have deepened our knowledge of these systems we have added research explicitly focused on habitat transitions and the role of disturbance in structuring wetland landscapes. These efforts represent the ongoing core of our program and are essential for identifying the nature and mechanisms of long-term ecological change. ***In GCE-V, we are building on this foundation to determine 1) whether our understanding of the system can be improved by assessing driver variability in predicting ecological responses and 2) the potential value of ecological variability as a fundamental metric of system behavior***. This conceptual framework, which applies well beyond wetland ecosystems, provides the motivation for the new research described below.

1.A GCE Overview. The GCE study site is located on the coast of Georgia, USA, and is representative of estuarine and intertidal habitats in the southeast (Fig. 1). The Altamaha River, with a watershed of 36,700 km^2, is the largest undammed river east of the Mississippi and is the major source of freshwater to the region. On the ocean side the broad expanse of the continental shelf in the South Atlantic Bight helps to protect the coast from wave and storm activity and it also serves to funnel the tides, which are semi-diurnal and vary in range from 1.4 m (neap) to 2.9 m (spring). The habitats in the GCE domain are defined by gradients in both salinity and inundation, which are major structuring agents for coastal ecosystems (Figs. 1, 2). Salinities grade from polyhaline (15-30) to mesohaline (5-15) to oligohaline (<5) moving upstream in the estuary, and intertidal habitats shift from salt to brackish to freshwater marsh and then to tidal fresh forest (Fig. 2). Inundation defines the vertical boundaries of the intertidal zone, which lies between subtidal (always inundated) and upland areas (only inundated by extreme events such as hurricanes), with different organisms dominating areas of low versus high elevation. Patterns and processes in this complex landscape vary both spatially (within and between sites) and temporally (tidal, diurnal, biweekly, seasonal, and interannual). Overlain on this spatial and temporal heterogeneity is the long-term forcing of global climate change, which affects sea level as well as oceanic and atmospheric conditions. These drivers manifest as changes in key abiotic variables in the domain (inundation, salinity,

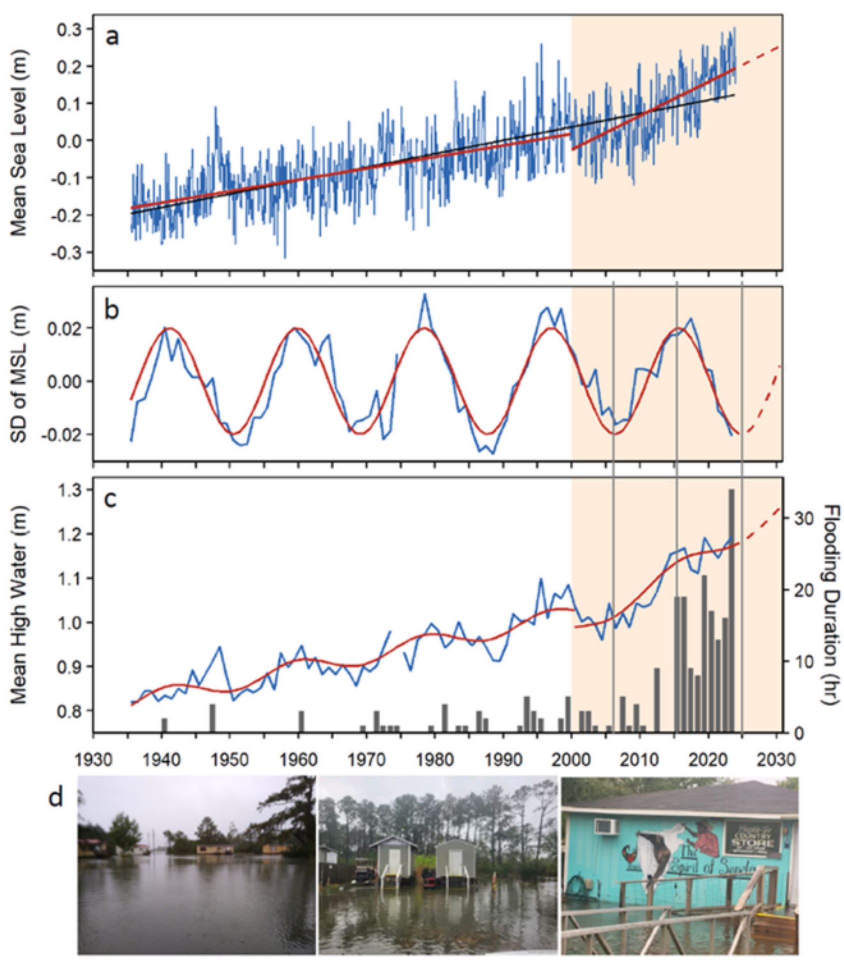


Fig. 3. Long-term trends in sea level on the Georgia coast (Fort Pulaski, GA). Period of the GCE project shaded in peach, with dashed lines showing projections through GCE-V (2030). (a) monthly mean sea level has increased over time. The slope of the anomaly in mean sea level was 3.6 mm y^{-1} over the period of record (1935-2023, black line), and has increased from 3.1 (1935-1999) to 9.1 mm y^{-1} since the start of the GCE project (2000-2023, red lines); (b) Annual standard deviation (SD) of daily mean sea level (MSL), blue line, reveals the 18.6 yr lunar nodal cycle (fitted with red line). This cycle is additive to SLR. Vertical grey lines show max and min of the cycle during the GCE project. (c) Annual mean high water levels are increasing (blue line, left-axis), along with the number of hours that tide levels exceeded the NOAA high-tide flooding threshold (>0.59 m above MHHW) (right-axis). Model line (red) fit by combining trends in MSL (panel a) and the lunar nodal cycle (panel b). (d) Photos of a high-tide flooding event on Sapelo Island (11/10/22).

and temperature) along with changes in the disturbance regime. Mean sea level has risen at a long-term rate of 3.6 mm y^{-1} since 1935 (NOAA station 8670870 at Ft. Pulaski, GA) but has increased to 9.1 mm y^{-1} (~ 20 cm total) since the GCE project began in 2000, with a corresponding increase in high tide flooding (duration and frequency) (Fig. 3). Sea levels in the southeast region are projected to increase by 40 to 58 cm between 2000 and 2050 under a range of global change scenarios (USGCRP 2023), and we expect even higher high tide levels over the next decade due to the lunar nodal cycle, which affects tides independently of sea- level rise. The lunar nodal cycle is reflected in the standard deviation of tide height, and will be in an upward phase during GCE-V, adding up to an additional 2 cm to high tide levels (Fig. 3b, c). Tidal flooding is linked with wetland disturbances such as wrack deposition (Li & Pennings 2016, Lynn et al. 2023), headward erosion of creeks (Hughes et al. 2009; Crotty et al. 2020) and the formation of slump blocks (Li & Pennings 2016; Yang et al. in press) (Fig. 2c). In recent decades the US southeast has also experienced prolonged, record droughts (1998-2002, 2006-2009) and variable precipitation, with record lows in Altamaha River streamflow interspersed with near-record highs (Fig. 4). Low river discharge and drought increase salinity throughout the domain, changing organic matter composition (Medeiros 2015), reducing plant productivity (Wieski & Pennings 2014), and causing vegetation dieback (Alber et al. 2008, Rolando et al. 2023). Rising atmospheric temperatures over the past 65 y observed at the UGA Marine Institute (UGAMI) have resulted in earlier spring green-up (O'Connell et al. 2020). Additional effects are expected across the domain, particularly since the National Climate Assessment predicts warming and more very hot days (>95ºF) in the southeast (USGCRP 2023). ***It is important for this proposal that in many cases these key abiotic drivers are changing in terms of not only their means but also their distributions (e.g., ranges, standard deviations).***

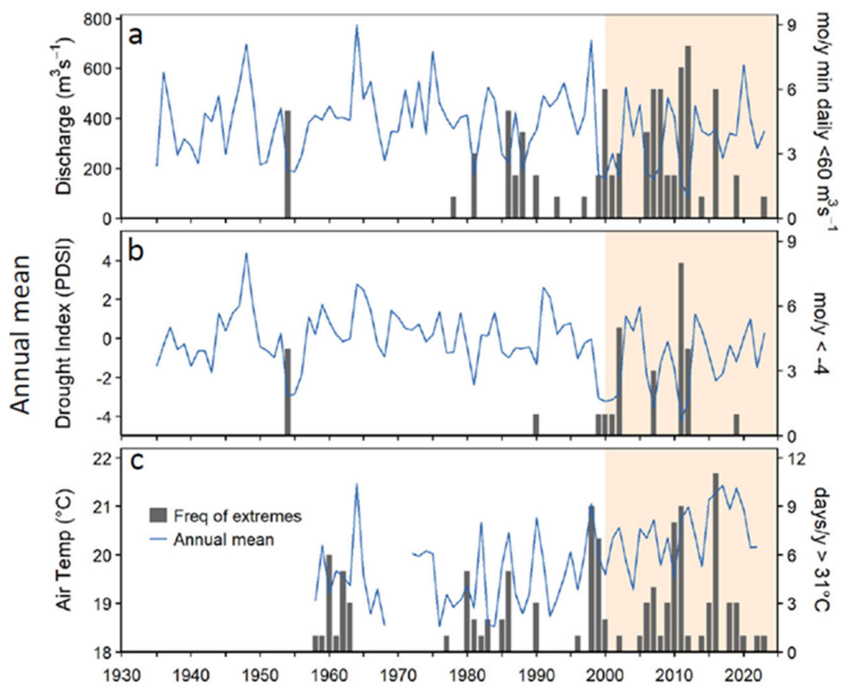


Fig. 4. Long-term patterns in (left axis) mean annual (a) river discharge (USGS gage at Doctortown), (b) Palmer Drought Severity Index (NOAA) and (c) air temperature (NWS UGAMI station), along with (right axis) frequency of (a) months in a given year when minimum daily discharge < 60 $m^3 s^{-1}$, (b) months in a year of extreme drought (PDSI < -4), (c) days in a year with mean temperature > 31°C. Period of the GCE project in peach.

Human alterations to the landscape are also changing and can exacerbate or mitigate climate effects. The southeastern coast is one of the fastest developing regions in the country. The number of visitors to Sapelo Island, in the heart of the GCE, is at an all-time high and there is growing development pressure. The human population in the Altamaha River watershed increased 32% between 2000 and 2022, with the most growth around metro Atlanta (Fig. 5). Human activities in the watershed affect downstream water delivery and water quality, either directly via flow diversion, channel modifications, reservoirs, and point source discharges, or indirectly

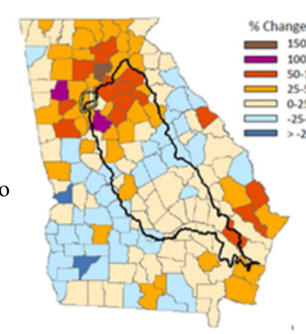


Fig. 5. 2000-2022 human population change in GA counties, with the Altamaha watershed indicated in black. (worldpopulationreview.com/states/georgia-population)

via changes in land cover (Roebuck et al. 2020). Humans also directly affect estuaries and intertidal areas: ditches alter flooding and draining patterns (Hardy 2023); docks shade plants and trap wrack (Alexander 2008); and bulkheads affect elevation, sediment composition, and animal communities in the upper marsh (Gehman et al. 2018).

We aim to understand how long-term global change affects ecological properties in estuarine and intertidal ecosystems. We anticipate that increases in extreme events in terms of tidal flooding, drought, and temperature (Figs. 3, 4) will increase the variability of salinity, inundation, and temperature in the GCE domain. We have also observed increased variability in ecosystem responses due to disturbance. ***The new research proposed for GCE-V, which is motivated by recent literature and our long-term observations, has an explicit focus on the insights to be gained by a) assessing both the means and variability of environmental drivers as predictors of ecological responses, and b) examining variability in ecological responses in relation to disturbance and habitat transitions.*** Below we provide background on how measures of variability have been used as predictors and their potential utility as outcomes. The implications of these new research foci are general and not limited to coastal systems.

1.B. Conceptual Framework. Ecologists generally describe drivers and responses using measures of central tendency, most commonly the mean. However, measures of variability, such as the range, standard deviation (SD), or coefficient of variation (CV), may also be important for predicting the effects of global change. For example, Rastetter et al. (2023) found that increasing the variance of temperature, precipitation, and light decreased C, N and P storage in the Arctic. Seddon et al. (2023) used sensitivity to climate variability to assess ecosystem resilience. The range of abiotic variation is likely to be important if there is a critical physiological limit (e.g. thermal, osmotic) or extreme that triggers a response (Jentsch et al. 2007; Swam et al. 2022). In a meta-analysis, Slein et al. (2023) found that increases in thermal variability tended to be detrimental to organismal performance. ***Here, we use "variability" to encompass the different measures of statistical spread associated with a data set.***

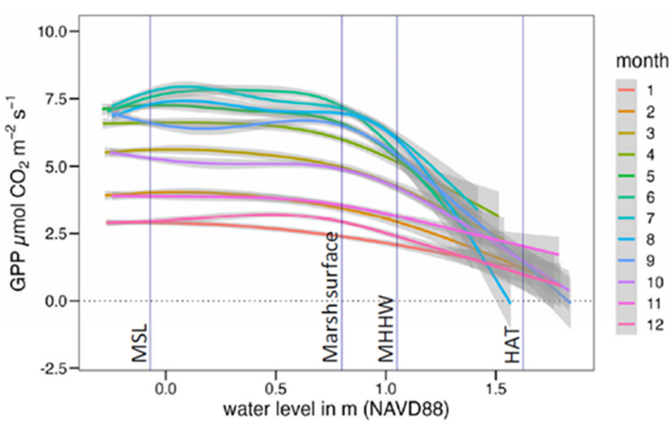


Fig. 6. An example non-linear response to an environmental driver. Daytime 30-minute Gross Primary Production (GPP) as a function of water level relative to NAVD88 at the GCE flux tower (2014-2023). GPP changes over the year, with the highest uptake during the growing season (April through August), and decreases non-linearly as the marsh surface is inundated by tides. Vertical lines show the marsh surface elevation at the site along with Mean Sea Level (MSL), Mean Higher High Water (MHHW) and Highest Astronomical Tide (HAT) measured at the Fort Pulaski tide gage.

Ecological responses to abiotic drivers are often non-linear (Fig. 6), and as a result the same average conditions can lead to different responses depending on the shape of the response curve (accelerating or decelerating) and the magnitude of the variance of the environmental driver due to Jensen's inequality (Ruel & Ayres 1999, Fig. 7). The value of considering variability in addition to the means of environmental *drivers* to explain patterns in ecological data has been highlighted in a number of systems (Benedetti-Cecchi 2003; Ruel & Ayres 1999; Floder et al. 2002; Lawson et al. 2015; Marshall et al. 2021), especially when responses are non-linear (e.g., Bernhardt et al. 2018). Osland et al. (2017) found that temperature extremes were better predictors of mangrove presence than mean temperature; Van Diggelen & Montagna (2016) found that benthic macrofauna diversity in a Texas estuary was better predicted by the standard deviation of salinity than the mean; Rudgers et al. (2018) showed the value of evaluating both mean and CV of environmental conditions to understand net primary production (NPP) in terrestrial grasslands. Moreover, environmental variance can have different effects depending on mean conditions (e.g., increased variance in temperature may be more stressful for a population living near its thermal maximum than for one living in the center of its thermal range) (Lawson et al. 2015).

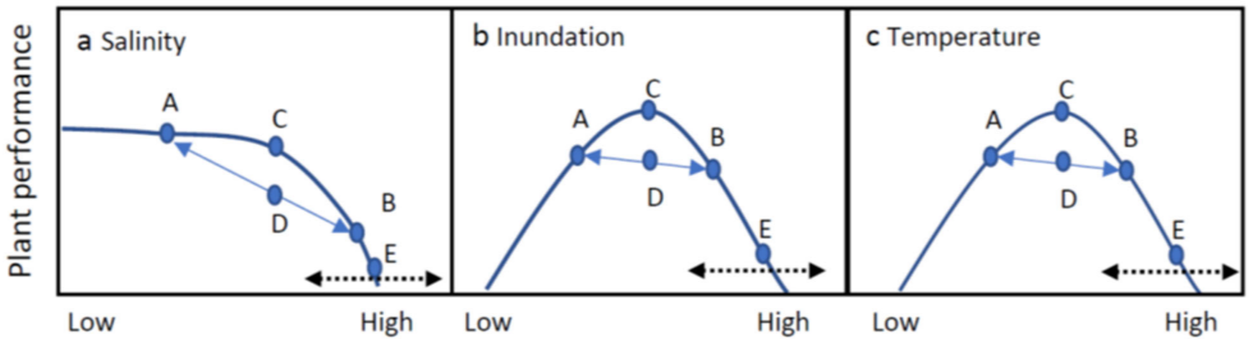


Fig. 7. Non-linear responses of *S. alterniflora (Spartina*) to salinity, inundation, and temperature suggest that variance in these abiotic drives will lead to lower plant performance than expected under constant conditions due to Jensen's inequality. Literature data show that *Spartina* productivity is relatively unaffected by low to medium values of salinity (a), but declines sharply as salinity ranges from 30 to 60, and is hump-shaped with respect to both inundation (b) and temperature (c). Because these curves are all concave down, plants experiencing fluctuating conditions (e.g., ranging between A and B) are predicted to be less productive (D) than expected based on the average conditions that they experience (C). In addition, plants experiencing high average salinities, inundation or temperature (E) are predicted to be extremely sensitive to variation (dotted arrow) because these high values may be lethal.

<u>*We have evidence that abiotic variance also matters for explaining processes in the GCE domain*</u>. We analyzed end-of-year plant biomass from the GCE long-term (22 y) monitoring sites and found that both mean and standard deviation of growing season salinity were significant in explaining *Spartina* biomass at the creekbank, with one site (GCE3) improving from an adjusted R^2 of 0.35 (mean salinity alone) to 0.49 (mean and standard deviation of salinity) (Fig. 8). Coefficients in these relationships were negative, indicating that plant production decreased in response to both increased salinity and increased *variability* in salinity, as would be predicted from the shape of the salinity response curve (Fig. 7a). ***We hypothesize that assessing the distributions of key abiotic variables in addition to their means will improve***

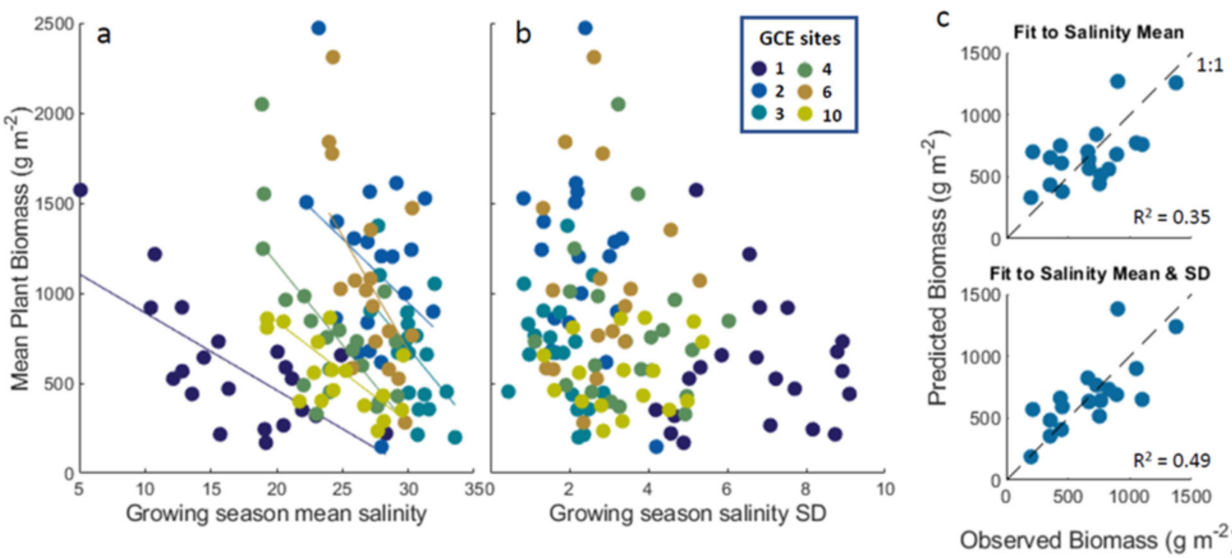


Fig. 8. Annual Spartina biomass observed in creekbank plots at GCE sites (colored circles) versus growing season (April-September) (a) mean daily salinity and (b) standard deviation (SD) of mean daily salinity. Lines in (a) represent linear mixed model fits to mean salinity for each site for the median year in the sample range. The model for all sites with salinity mean and SD as predictive factors was a slightly better fit (AIC 1659; R^2 0.55) than the model with mean only (AIC 1662; R^2 0.53 (c) The largest improvement was for site GCE3, where the adjusted R^2 increased from 0.35 with mean alone (top) to 0.49 when both mean and SD were included. Graphs depict modeled fits against 1:1 line.

explanatory power for predicting ecological responses. We are specifically interested in forecasting how changes in both the mean and variability will affect the GCE domain in the future.

Variability in ecological *responses* to abiotic drivers can also convey important information about a system (Fraterrigo & Rusak 2008; Underwood 1994; Fraterrigo et al. 2020). Ecological responses to disturbance are often characterized as effect sizes, quantified by comparing the means of a response variable between disturbed and control conditions. However, disturbance can also change variability in ecological responses (Fraterrigo & Rusak 2008). Cottingham et al. (2002) showed that fertilization increased variability of photosynthetic pigments in an experimental lake, and that this increased the uncertainty of forecasts. Braziunas et al. (2018) showed that variation in regeneration after a fire affected conifer stand structure for decades to centuries. We have evidence for a similar result in the GCE domain. *In a long-term experiment conducted at the GCE, we found that the CV of vegetation cover and height increased significantly during recovery after a disturbance compared to CV in control and post-recovery observations (**Wang et al. 2024;** Fig. 9a).* Moreover, the CV during recovery 1) increased with pore water salinity, which represents an underlying abiotic stress (Fig. 9b), and 2) was negatively correlated with recovery rate, such that sites that recovered more slowly had a higher CV (Fig. 9c). ***We hypothesize that disturbance increases variability in ecological responses, and that abiotic conditions affect both the extent to which this variability increases and the recovery rate following disturbance.*** Disturbance-driven changes in variability and recovery are particularly important to understand given expected increases in disturbance in an era of rapid global change (Turner 2010).

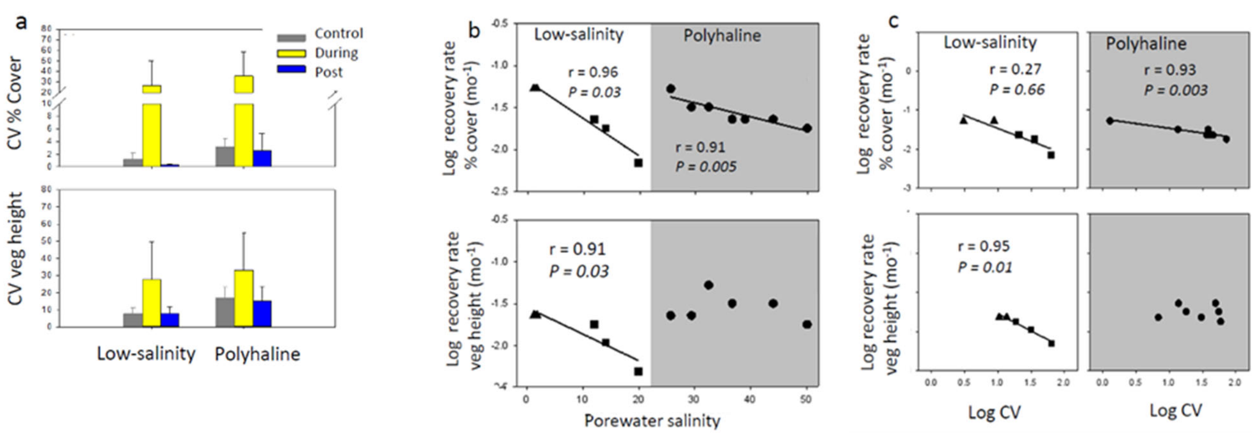


Fig. 9. Marsh plots subject to experimental disturbance across a salinity gradient, separated into low-salinity and polyhaline sites, showed (a) CV of % cover and vegetation height was elevated during recovery, (b) recovery rates decreased with increasing porewater salinity; and (c) CV during recovery was correlated with recovery rate except for vegetation height at polyhaline zones, where recovery rate was not related to salinity. Source: Wang et al. 2024

Patterns of variability can also be used to assess resilience and the potential for an impending state change. Increasing variance and autocorrelation in ecosystem variables have been proposed as early warnings that the system is destabilizing and approaching a threshold, either in space or time (Carpenter & Brock 2006; Scheffer et al. 2015; Dakos et al. 2011). These metrics have attracted a great deal of attention, and there are numerous examples where variance, autocorrelation, or both, serve as useful indicators of impending state changes (reviewed in Dakos et al. 2023, but see Hillebrand et al. 2020). Other metrics of variation, including changes in skewness, have also been used to evaluate transitions and characterize ecosystem resilience (Veldhuis et al. 2022; Seddon et al. 2016). *In coastal wetlands salinity and inundation are long-term drivers that could cause state changes,* which we define based on habitat transitions: shifts from salt to brackish to freshwater marsh and then tidal fresh forest along the salinity gradient, and from mud flats to low marsh to high marsh to upland along inundation gradients (Zinnert et al. 2021). Increases in flooding have also been linked to marsh fragmentation (Ganju et al. 2022). We anticipate changes in upstream and upland borders over the coming decades as the result of the lunar nodal cycle and long-term sea-level rise (Fig. 3) and are well-positioned to characterize these shifts both across the landscape and over time. ***We hypothesize that increased variability is an indication of an underlying environmental stress and is associated with an impending state (i.e., habitat) change.***

The GCE-V conceptual model (Fig. 10) depicts predicted relationships between drivers and responses. We start with connections between external environmental and human drivers (left gray panel) and internal drivers within the domain (middle blue panel), which are observed as changes in key abiotic variables and the disturbance regime. Ecological responses to internal drivers manifest as changes in population, community, and ecosystem properties (right yellow panel). These responses determine the overall system status (persistence, recovery, state change) within the context of the biophysical template (geomorphology, hydrology and habitat at a site). The proposed research will address variability within this framework by: Q1) quantifying the effects of mean and variability of drivers on mean ecological responses; Q2) evaluating how an extreme event (e.g., a disturbance) affects the mean and variability of ecological responses; and Q3) evaluating whether variability of the responses increase as a function of a change in the mean driver as the system approaches ecological transitions (both in time and space). *<u>This research will provide a comprehensive evaluation of the role of variability in coastal wetlands</u>.*

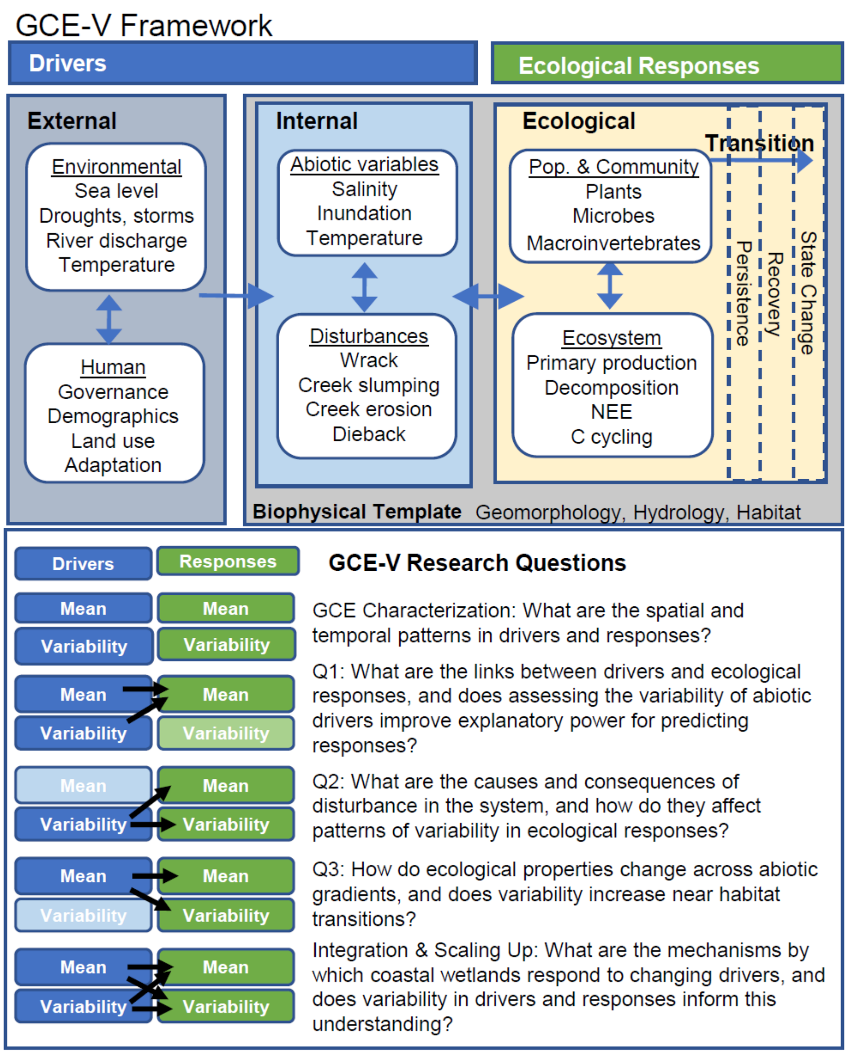


Fig. 10. Conceptual model of GCE-V research. (Top) Environmental and human drivers are altering key abiotic drivers and the disturbance regime in the GCE domain. These changes will result in ecological responses in the context of the biophysical template, which determine the overall system response and whether it transitions to a new state. (Bottom) GCE-V research will tease apart the effects of changes in mean and variability in both drivers and responses to inform our understanding of coastal wetlands and predict how they will respond to long-term change.

1.C Research Outline. The research proposed for GCE-V builds on the major programmatic elements from the first four GCE funding cycles and is designed to understand wetland ecosystem function, the connections between external drivers and ecological responses, and how ecological properties change in response to disturbance and underlying abiotic gradients, but with an overlay of new efforts that test the above hypotheses regarding the role of variability. We divide our proposed research into five interrelated programmatic areas (Figs. 10, 11).

GCE characterization. What are the spatial and temporal patterns in drivers and responses? Our long-term monitoring program provides context for all GCE research, addresses the five LTER core areas, and produces foundational information on the biophysical template and hydrodynamics of the GCE domain. We will continue to track sea level, river discharge, meteorological conditions, human population and land use, and will also maintain our time series of spatial and temporal patterns in estuarine and intertidal attributes. We will continue high-frequency NEE measurements at the GCE flux tower. We will characterize the biophysical template through digital imagery, including UAV (i.e., drone), satellite observations, and regular aerial flights that are used for habitat mapping, delineating marsh geomorphology, and tracking disturbance, and will add new measurements of soil properties. Our hydrodynamic model (Delft3D) provides information on salinity and water movement, and in GCE-V we will build a detailed model for the flux tower site to inform directed studies at that site. Together, these measurements will provide information on the mean and variability of the environmental drivers that affect the domain and enable us to characterize the disturbance regime. They will also allow us to track both the spatial and temporal patterns in ecological responses, and to document habitat transitions. ***These efforts document long-term change and provide the foundation for the question-driven research described below.***

Q1. What are the linkages between external drivers and ecological responses, and does assessing the variability of key abiotic drivers improve explanatory power for predicting ecological responses? We will approach this using long-term analyses, field campaigns, and experiments. We will determine if consideration of extremes or variance of abiotic drivers (e.g., sea level, river discharge) improves statistical models of temporal and spatial patterns in ecosystem responses at annual time scales (e.g., invertebrate densities, plant biomass, NEE). Context for these analyses will come from historical records of past climate variability (through dendrochronology and paleoanthropology) and by assessing the effects of large-scale climate patterns on sea level. We will run two field campaigns. One will be in paired polyhaline marshes with similar mean salinities but different growing season salinity variation where we will measure a full suite of ecosystem responses ranging from gas exchange to abundance and composition of microbes to invertebrates and higher plants. In the second, we will take diurnal measurements during different stages of the spring-neap cycle to evaluate how variability in tidal inundation affects vertical and lateral C exchange (i.e., to the

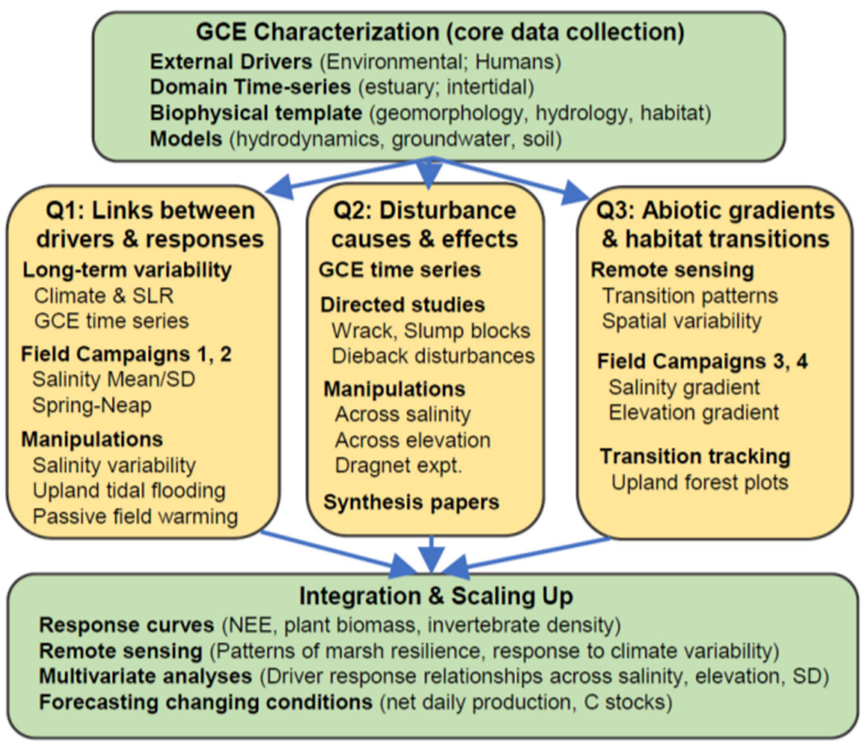


Fig. 11. GCE-V Research Portfolio. Investigators associated with each task are listed in the Budget Justification.

atmospheric and coastal ocean, respectively). We will conduct experiments with constant and fluctuating salinity (mesocosms with marsh plants and invertebrates, soil lab experiment) and air temperature (passive warming field chambers), as well as an inundation experiment at the upland edge (tree watering with salt water) that contrasts increased regular flooding due to an increase in the tidal range with that due to irregular flooding from storm events. ***Our goal is to understand how changes in both the mean and variability of salinity, inundation, and temperature affect ecological responses.***

Q2. What are the causes and consequences of disturbances in the system, and how do they affect patterns of variability in ecological responses? Wetlands in the GCE domain are subject to large-scale (droughts, storms) and small-scale (wrack, creekhead erosion, creekbank slumping, dieback) disturbance events. During GCE-IV we began an unprecedented time series of monthly UAV flights in conjunction with ground measurements of responses and recovery. In GCE-V we will use these data to build tools to identify disturbances from satellite imagery (PlanetScope). We will also continue three experimental manipulations evaluating disturbance responses across gradients of elevation, salinity and nutrient availability. We will use these results, along with the records of disturbance in our long-term monitoring plots, to evaluate patterns of disturbance over space and time, and add new analyses to determine how disturbance affects both the mean and variability of response variables. We will also leverage DRAGNET, a globally distributed disturbance experiment, to evaluate variability during recovery from a standardized disturbance across a broad range of environmental conditions. ***Our goals are to track variability during recovery from disturbance as well as how recovery changes along abiotic gradients, and to evaluate whether disturbance increases variability in ecological properties.***

Q3. How do ecological properties change across abiotic gradients, and does variability increase near habitat transitions? System "states" in the GCE domain (based on habitat types defined by the dominant plant species, which function as foundation species) change along salinity and inundation gradients. We expect the boundaries between them to shift in response to long-term change in these drivers. We will use remote sensing to assess multi-year habitat shifts on imagery classified by vegetation type, determine whether these shifts are persistent or transient over time, and assess whether variability in plant metrics (e.g., greenness) increases near a habitat boundary. We will conduct two field campaigns to understand spatial variability associated with habitat transitions: one with sites along the salinity gradient of the Altamaha River and the second across elevation gradients at three core GCE monitoring sites, with a similar suite of measurements as in Q1. At the top of each elevation transect we will establish new long-term plots in the upland forest to track potential marsh migration over time. We will also initiate a citizen science program to help document flooding in upland areas. ***Our goals are to track habitat transitions and evaluate whether increased variability in ecosystem characteristics is a signal of state change.***

Integration and Scaling Up. What are the mechanisms by which coastal wetlands respond to changing drivers, and does variability in drivers and responses inform this understanding? We will integrate and scale our results in several ways. We will use our field and experimental data to develop response curves for NEE, plant biomass, invertebrate density, and other key variables as functions of salinity, inundation, and temperature to develop a general understanding of how ecosystem performance is affected by abiotic variability. We will build on our remote sensing tools to produce time series estimates of productivity measures (above-ground biomass, BGB, NEE, GPP) at the same spatial scale and analyze spatial and temporal variability as well as patterns of autocorrelation to see how they change over time. We will also look at how climate means, variance, and extremes affect productivity. To advance our understanding of marsh function we will use structural equation models (SEM) and other multivariate approaches to synthesize results from the field campaigns to identify predictors of plant productivity across gradients of salinity and elevation and to compare marshes with different patterns of salinity variability. Finally, we will estimate net daytime production in a *Spartina* marsh (as NEE corrected for lateral export) and C stocks across the domain and forecast how they may change with increasing inundation and salinity. ***Our goal is to forecast how changes in the means and variabilities of salinity, inundation, and temperature will affect ecosystem properties and habitat distribution in intertidal wetlands.***

2 Plan of Work

2.1 GCE Characterization: What are the spatial and temporal patterns in drivers and responses?

We will continue to document and interpret estuarine and intertidal variation across the GCE. These data provide the large-scale and long-term context for our research questions as we seek to better understand ecosystem patterns and dynamics and the links between drivers and responses. Major activities in this area consist of A) tracking **external drivers**, B) continuing our long-term **time series** of estuary and marsh attributes, C) characterizing the **biophysical template**, and D) developing **mechanistic models**.

2***.1A1 External Drivers: Environmental.*** We use meteorological stations to characterize climate in the GCE domain (Fig. 1b, Table 1). The station at Marsh Landing on Sapelo Island, which we operate in partnership with SINERR, serves as our primary station for the LTER Climate database (ClimDB). We acquire near-real-time and historic data from this and other nearby climate stations, which are publicly accessible on the GCE Data Portal. We also operate the GCE eddy covariance flux tower, which serves as a level 3 weather station. Most freshwater input to the GCE domain enters via the Altamaha River, and is the primary determinant of salinity at our core monitoring sites (Di Iorio & Castelao 2013; Wang et al. 2017). The USGS gauge station at Doctortown provides near-real-time data on river discharge and we will continue characterizing the composition of freshwater entering the domain through monthly analyses of dissolved and particulate nutrients (Table 1A). Freshwater input to marshes via groundwater from upland habitats is characterized by wells at GCE6, and we will expand this effort in GCE-V by installing additional wells with conductivity, temperature, and depth sensors (CTDs) along elevation transects at GCE1, 3, and 7 (*see 2.4B2, 2.4C*). Oceanographic conditions are recorded by the National Data Buoy Center's station at the Gray's Reef National Marine Sanctuary and sea-level data by the nearest NOAA/NOS station (Fort Pulaski, GA). In addition to these publicly available data, we collaborate with SINERR and USGS on a hydrological station that records local sea-level height variations at GCE4 and maintain a tide gauge that we installed on Sapelo Island during GCE-IV. These data are regularly retrieved and processed for analysis.

2.1A2 External Drivers: Human. The GCE is located in McIntosh County, GA. The county is rural, with a low population density (~9 km^{-2}), a median household income of $49,951, and a 20% poverty rate (DataUSA 2024). However, this area is rapidly exurbanizing and gentrifying, and development will likely result in changes in demographics and land use, with implications for human-environment interactions. There is also an increasing threat of flooding due to sea-level rise and storms (Hardy 2023). During GCE-V, we will build on our existing geographical information systems (GIS) database of shoreline armoring along the GA coast to evaluate bulkheads, docks, and other coastal modifications in the context of trends in population density, demography, and land use in McIntosh County. <u>We hypothesize that household income will be correlated with the presence of coastal structures, and that there will be a surge in new structures after large storms.</u> We will also start a citizen scientist program to track upland flooding events (*see Broader Impacts*). This information will allow us to develop more realistic scenarios for marsh migration into the upland that account for the links between demographic changes and shoreline structures in the GCE domain.

2.1B1 Time-series: Estuarine water. Our core monitoring program consists of sites in the estuary and the adjacent marsh distributed across the GCE domain. It addresses the five LTER core areas and will continue with only minor modifications, for a total of 30 years by the end of GCE-V (Table 1). We maintain a distributed network of 10 sondes to track conductivity, temperature and depth of estuarine water throughout the domain (Fig. 1c). We collect vertical CTD profiles at each station during regular cruises, along with an additional station at an offshore site (AL-2) to characterize mixing of the Altamaha River plume with the South Atlantic Bight. Estuarine pH is recorded at four stations by YSI data sondes operated by SINERR. Discrete samples are collected monthly for analysis of nutrients, chlorophyll, particulate material, and dissolved inorganic carbon (DIC) at GCE7, a low salinity site upstream in the

Altamaha River, and GCE6, a high and variable salinity site on Sapelo Island. The same variables are measured quarterly at the remaining stations (Table 1B).

2.1B2 Time-series: Intertidal wetlands. In the fall of each year, we measure plant community composition and biomass, and invertebrate community composition and size structure in 8 permanent plots in 2 zones (creekbank and mid-marsh) at each of our marsh sites (GCE1-10). An additional *Juncus* zone is sampled at two sites, for a total of 178 plots. We note disturbances (wrack, slumping, herbivory) in each plot (Li & Pennings 2016), and in GCE-V will use these surveys to explicitly identify potential

Table 1. Monitoring program for GCE-V, mapped to LTER **core areas: 1**: primary production, **2**: populations, **3**: organic matter cycling, **4**: inorganic nutrients, **5**: disturbance. GCE PIs responsible for supervising each aspect of the monitoring program are indicated: AS: Spivak, AW: Wilson, CC: Craft, DD: Di Iorio, DM: Mishra, GM: Moore, JB: Byers, JO: O'Connell, LS: Sutter, MA: Alber, SP: Pennings. *See 2.1*, GCE Characterization and Fig 1.

Description	**Location**	**Freq**	**Core Area & Variables Measured**
2.1A1 External drivers			
Weather stations (DD, DM)	GCE4, 6, Flux tower	15 min	Abiotic driver of **1-5**. > level 2 stations: PAR, temp, rH, precip, wind speed and direction, barometric pressure, total solar and long wave radiation; flux tower also measures CO_2, humidity, and heat fluxes
Tide height (DD)	GCE6, Marsh Landing	15 min, 6 min	Abiotic driver of **1-5**. Water level, stage
Altamaha River chemistry (AS)	Head of tide	Monthly + storms	**3, 4**. Dissolved inorganic nutrients (NO_3^-, NO_2^-, NH_4^+, HPO_4^{2-}, $H_2SiO_4^{2-}$, DIC) and organics (DOC), particulate CN
Groundwater (AW)	GCE1, 3, 6, 7	30 min	Abiotic driver of **1-4**. Groundwater level, salinity, and temperature.
2.1B Estuary and marsh			
Sound chemistry (AS, MA)	GCE1-5; 8-11, AL-2	Quarterly	**1, 3, 4**. Dissolved inorganic nutrients (NO_3^-, NO_2^-, NH_4^+, HPO_4^{2-}, $H_2SiO_4^{2-}$, DIC) and organics (DOC), particulate CN, chl.*a*, total suspended sediment
(AS, MA)	GCE6-7	Monthly	**1, 3, 4**. Variables as above (quarterly sampling)
Sound hydrography (DD)	GCE1-4, 6-11	30 min	Abiotic driver of **1-5**. Salinity, temperature, pressure at moorings; CTD profiles in conjunction with sound chemistry
Soil accretion (LS)	GCE1-11	Annual	**3**. Sediment accretion, elevation, compaction
Plant productivity (SP)	GCE1-10	Annual	**1**. Stem density, height, flowering status, & calculated biomass in 2-3 marsh zones
(CC, GM)	GCE1, 3, 7, 11	Annual	**1**. Litterfall traps and stem wood growth of trees
(DM)	Flux tower	5 min	**1**. Net ecosystem exchange, GPP, NPP, respiration
(JO)	Flux tower	Monthly/ Quarterly	**1**. Above/ belowground biomass in short, medium, tall *Spartina*
(JO)	Flux tower, Dean Creek	30 min	**1**. PhenoCam observations of phenology in short, medium, tall *Spartina* and *Juncus*
Disturbance (SP)	GCE1-10	Annual	**5**. Disturbance in permanent vegetation plots
Plant composition (SP)	GCE6, 10	Annual	**2**. Community composition in 4 types of salt marsh, 2 types of high marsh vegetation mixtures
(SP, MA)	Altamaha	Annual	**2**. Community composition in marsh transitional areas (3 sites), mixed vegetation on Broughton Island (25 sites). Survey of creekbank vegetation (~50 stations), health and survival of tidal fresh forest trees (~40 stations) along the Altamaha River.
Marsh Invertebrates (SP, JB)	GCE1-10	Annual	**2**. Density and size of benthic macroinvertebrates (mollusks, crab burrows) in 2-3 marsh zones
Insects (SP)	GCE1-6, 9, 10	Annual	**2**. Density of grasshoppers in salt marsh transects
Recruitment (SP, JB)	GCE1-10	Annual	**2**. Recruitment of barnacles to standard substrates

range-expanding tropical species that have been observed in GA and may become abundant in the future (mangroves, *Avicennia germinans*; mangrove fiddler crab, *Leptuca thayerii*; mangrove crab, *Aratus pisonii*; and the blue land crab, *Cardisoma guanhumi*). Each site has a sediment elevation table (SET) with paired feldspar plots that together describe soil accretion, accumulation, and compaction. In the tidal fresh forest, we established a site in 2014 (GCE11) to measure tree growth (using dendrobands and litterfall) and sediment elevation (SETs), and in GCE-V we will add 3 additional forest sites associated with elevation transects to follow potential marsh migration at the upland border (*see 2.4B2*). Habitat transitions along the estuary are tracked through annual assessments of mixed vegetation plots (n=18 sites), assessments of the distribution of a dominant brackish grass (*Spartina cynosuroides*; 50 sites) and assessments of tidal fresh forest trees (40 sites) to identify signs of habitat shifts. Across the elevation gradient, where salt marsh vegetation transitions from *Spartina* to *Juncus* and marsh meadow (a mixture of salt-tolerant species), we again monitor plots with mixed vegetation and at one site (GCE6) we have observed a retreat of the *Juncus*/marsh meadow border by ~10 m since 1996 due to periodic drought.

One of the main ways we characterize primary production is through our eddy covariance flux tower, which has been in place since 2014 and is part of the Ameriflux network (Station US-GCE). It records high resolution (5 min) exchange of carbon dioxide (CO_2) and water between a *Spartina* marsh and the atmosphere as well as supporting atmospheric, soil, and water properties that are used to calculate net ecosystem exchange, gross primary production, and ecosystem respiration (NEE, GPP, R). Instrumentation on the tower includes a sonic anemometer, a closed-path gas analyzer (LI-7200), soil heat flux plates, an averaging thermocouple for soil temperature, soil water content reflectometer, up- and downward looking radiative sensors (total solar, PAR, and net radiation), and sensors measuring humidity, air temperature as a function of height, atmospheric pressure, rainfall, and creek and marsh water levels. An important initiative of GCE-V will be estimating net daytime production by combining NEE (i.e., vertical exchange with the atmosphere) with lateral exchange of dissolved and particulate organic and inorganic C in tidal waters *(see 2.2C2, 2.5D1*). Above- and below-ground biomass in 3 *Spartina* height forms (tall, medium, and short) is measured throughout the year near the tower. These data are used to inform flux measurements and our BERM model (**O'Connell et al. 2021;** Hawman et al. 2023; *see 2.5B*). We maintain two PhenoCams in marsh zones dominated by *Spartina* and *Juncus*, respectively, that provide information on plant phenology, habitat shifts and flooding patterns that is invaluable for scaling to satellite estimates.

2.1C Biophysical template. The biophysical template of intertidal areas – including topography, soil characteristics, creek network, and dominant vegetation – provides essential context for interpreting ecosystem dynamics and predicting future responses to climate change. We have developed a corrected digital elevation model and habitat map of the GA coast from 2018 that provides foundational information for much of our work. We collect 15-cm resolution, 4-band color/NIR aerial imagery of the Altamaha Sound and Duplin River every 6 years to evaluate shifts in creek morphology, marsh area, and marsh habitats (e.g., Burns et al. 2020a, b). A 2024 flight is scheduled, and we will collect additional imagery during the latter half of GCE-V. We will continue using publicly available satellite data to evaluate large-scale, long-term patterns in marsh extent. For 2022-2024 we have access to CNES VENμs (Vegetation and Environment monitoring) imagery (12 band, 4 m resolution) for the GCE domain. We use our UAV to generate multispectral imagery for multiple research efforts (e.g., annual flights of the DRAGNET experiment), and have access to a high-resolution LIDAR drone that can provide detailed 3D maps (2 cm resolution) of marsh topography that are crucial for understanding marsh geomorphic structure. We routinely obtain accurate elevation information at our study sites with our theodolite and RTK-GPS, as even small topographic differences can affect the extent and frequency of tidal inundation.

A long-term goal of the project is to parameterize a geomorphic model of creekbank dynamics to understand the changing biophysical template within GCE and draw comparisons with other systems. In GCE-V we will collect soil observations, including shear strength, in conjunction with our field campaigns (*see 2.3B*), to use in comparison with PIE-LTER and Louisiana marshes.

2.1D Mechanistic modeling. Our primary modeling effort is a 3-D mechanistic hydrodynamic model (Deltares Delft3D) forced with data on meteorology, discharge, and sea surface height, along with salinity from GCE sondes. It simulates water movement and salinity patterns in the GCE domain and can be used to predict how salinity and residence times vary seasonally and in response to events such as droughts, sea-level rise, and storms. We are currently running version 4.04.01 with orthogonal grid spacing that ranges from 50 m in the estuaries to 300 m at the eastern boundary, with 5 equal vertical sigma layers to capture the range of observed stratification. During GCE-V we will implement the recently released Flexible Mesh Suite (Delft3D-FM) with multi-domain nesting. This is a powerful tool that will be used to identify sites for the distributed field campaigns, characterize water movement and mixing at the flux tower site (*see 2.2C2*), and estimate salinity and inundation for our synthesis efforts (*see 2.5D1*). We will also combine our soil salinity model (Miklesh & Meile 2018) with soil temperature and water content simulations, focusing on the vertical variation of these properties across the rooting zone. Soil model expansion will be enabled by data collected during the field campaign at the flux tower (*s*ee 2*.2C2*), as multiple sensor deployments will allow us to better parameterize evapotranspiration, refine a soil heat budget, and validate the model. This will provide insight into the soil conditions experienced by plants, and allow us to quantify vertical solute exchange in the subsurface and how it varies with changes in inundation and temperature. The explicit resolution of temperature and salinity profiles also allows us to consider their potential impact on biogeochemical processes that can affect carbon cycling (*see 2.2C2*). We also have a process-based groundwater model (Evans & Wilson 2016, 2017) to estimate water flow from the upland to the marsh that informs our interpretation of high marsh plant composition (*see 2.4B2*).

2.2 Q1: What are the linkages between external drivers and ecological responses, and does considering the variability of key abiotic drivers improve explanatory power for predicting ecological responses?

Mean effects of abiotic drivers such as salinity, inundation, and temperature on wetland ecosystems have been documented extensively. For example, air temperature, precipitation, and river discharge averaged over the growing season reasonably predict end-of-season plant biomass in GCE marshes (Liu & Pennings 2021). However, our new analyses indicate that variability in water column salinity helps explain residual variation in end-of-season biomass (Fig. 8). To follow up on this observation and address Q1, we will investigate how the mean and variability of abiotic drivers affect ecosystem responses at different temporal and spatial scales. Major activities in this area include A) examining **long-term variability** in climate and sea level, B) evaluating **ecological responses to abiotic variability** in our time-series data, C) conducting **field campaigns** in areas with variable salinity and inundation, and D) **experimental studies** with treatments that manipulate variance.

2.2A Long-term variability in climate and sea level. We will characterize past environmental conditions (~5,000 y) using dendrochronology, which provides information on climate (e.g., droughts), and oyster shell isotopes ($\delta^{18}O$), which can be used to infer water temperature and salinity. We will also develop geochronologies for sediment cores collected from ponds in the interiors of barrier islands to characterize long-term changes in vegetation (pollen, phytoliths) and fire disturbance (microscopic charcoal). In addition to providing long-term context, tree, oyster, and pond sediment data will be used with ongoing archeological surveys (Thompson & Turck 2010; Ritchison 2019) to test the hypothesis that during periods of high climate variability human population density decreased and its distribution changed.

To understand processes driving interannual patterns in sea-level variability, which respond to basin-scale oceanic forcing along the U.S. southeast coast (Volkov et al. 2019), we will use a sea level reconstruction built by combining satellite altimeter observations and tide gauge measurements, yielding a sea level dataset with the spatial resolution of the altimeter data and the record length of the tide gauge data (Hamlington et al. 2014). We can then disentangle the role that large-scale forcing has on this variability (e.g. North Atlantic Oscillation, Valle-Levinson et al. 2017; Atlantic Meridional Overturning Circulation, Volkov et al., 2023). We will use these analyses to predict how increased temperature, in combination with the periodicity of the lunar nodal cycle (Peng et al. 2019), will affect the mean and variability of flooding in the coming decades (Fig. 3).

2.2B Responses to abiotic variability in the GCE time series. We have analyzed our 20+ year record at our core monitoring sites to evaluate how average annual abiotic conditions determine end of season plant height, shoot density, flowering, and biomass (Li et al. 2018; Liu & Pennings 2019, 2021). We will build on this to evaluate whether variability in abiotic conditions over time (e.g., salinity SD at a site within a year, or the number of days exceeding temperatures of ~30°C) improves our predictions of annual plant performance. Similarly, we have examined relationships between NEE, GPP and R at the flux tower and abiotic conditions (Hawman et al. 2021; 2023; in review). Building on these "response curves" (e.g., NEE versus temperature or river discharge), we will ask how variability in abiotic conditions affects time-integrated C fluxes (e.g., how does within-month variability in temperature affect monthly cumulative NEE). We will also use our long-term data on abiotic conditions (e.g., water column salinity, temperature) in combination with invertebrate abundance and body size to generate spatially explicit species distribution models driven by not only mean but also the range and variability of these drivers.

2.2C Field campaigns. We will conduct two complementary field campaigns to better understand how variation in salinity and inundation affect salt marsh ecosystem functioning.

2.2C1 Field campaign 1: Similar mean salinity but different standard deviation. We will directly test the applicability of Jensen's inequality (Fig. 7a) by quantifying how variability around a given mean salinity affects *Spartina* marshes. The experimental design includes duplicate *Spartina* sites that experience a range of mean salinities from 15 to 25, but have high or low salinity variability (n=8 pairs). We will use the Delft3D hydrodynamic model to identify prospective sites with their suitability verified through deployment of CTDs in groundwater wells. Within each site, 8 replicate plots will be sampled for primary

Table 2. Summary of major response metrics to be measured in field efforts. Field Campaigns are denoted as 1: across SD of salinity (*see 2.2C1*), 2: variable inundation (*2.2C2*), 3: across salinity (*2.4B1*), and 4: across elevation (*2.4B2)*. Disturbance manipulations are denoted D and are across salinity, across elevation and in Dragnet (see 2.3C). Each effort includes replicated plots. Most variables will be measured in all plots; (S) after the response denotes it will be measured in a subset. GCE PIs are indicated: AS: Spivak, AW: Wilson, CO: Osenberg, DM: Mishra, GM: Moore, GM_2: Mariotti, JB: Byers, JK: Kostka, JN: Nelson, JO: O'Connell, LS: Sutter, PM: Medeiros

Response	Efforts	PI	Metric
Ecosystem metabolism			
Eddy covariance	2	DM	NEE, GPP, R
Plot-scale CO_2 fluxes (S)	1,3,4	AS	Summer light / dark CO_2 flux
pCO_2 (S)	2	DM	pCO_2 levels in creek
Tree stem CO_2 (S)	4	AS	Stem CO_2 flux
Plant community			
Aboveground	1-4, D	SP	Biomass, % cover, height
Photosynthetic performance	2	DM	Diving PAM
Belowground (S)	1-4	JO	Biomass of live roots and rhizomes
Trees (S)	4	GM	Biomass (tree bands)
Animal community			
Invertebrates	1-4, D	JB, SP	Species identity, abundance, size
Niche breadth	1,3,4	JN	Stable isotopes
Body temperature	2	CO	Snail and bivalve biomimics
Soils			
Bulk properties (S)	1-4	AS, GM_2	Bulk density, shear strength
Microbes (S)	3,4, D	JK	Diversity, composition, metabolic activity
Organic matter (S)	1-4, D	AS, SP	Carbon content, loss on ignition
Porewater	1-4, D	AS	Salinity, pH, redox, DIN, S^{2-}, DOC
DOM (S)	2,3	PM	DOM composition (FT-ICRMS)
Physical variables			
Elevation	1-4, D	AS, SP	RTK-GPS; total station
Temperature (S)	1-4, D	AS	Hobo loggers at 10 cm
Groundwater	1-4	AW, AS	Water level, conductivity, temperature

production, invertebrate abundance and composition, and soil properties (Table 2). Marsh metabolism estimates from light / dark CO_2 fluxes will be made at the plot-scale with a temperature-controlled clear chamber interfaced to an infrared gas analyzer (LI-7810; Ledford et al. 2020). We will also evaluate bivalve performance and gene expression so that we can identify the extent to which environmental fluctuation drives large effects in expression changes and thus plasticity in the face of environmental variation (Erlenbach & Wares 2023). Response-specific sampling will be hierarchical, reflecting field and laboratory resources, with some variables measured in every plot (n = 128), while others from a subset or as composites from the 8 plots/site. We hypothesize that sites with high salinity variation will have lower primary production (i.e., plot scale CO_2 fluxes, summer biomass) than sites with low variation, particularly at higher mean salinities. Decreased plant production will have cascading effects, such as reduced snail densities, broader invertebrate niche breadths (quantified via stable isotopes, Lesser et al. 2020), reduced microbial activity (Rolando et al. 2022) more reducing soil conditions (Howes et al. 1981), and higher pore water levels of reduced metabolites (e.g., ammonium, sulfide), with some of these variables also affected directly by salinity variability. This effort is targeted for year 1. We will unravel these relationships and differences between low and high standard deviation sites through SEM analysis (*see 2.5C*; Grace 2006; Fan et al. 2016).

2.2C2 Field campaign 2: Effects of variable inundation on ecosystem processes. Tides structure salt marshes, creating distinct zones over time (years to decades) that reflect inundation frequency (Odum 1988). But is variability in inundation useful for understanding processes over shorter (weeks) time scales? We will address this by evaluating how changing tidal inundation affects ecosystem C uptake and export (Fig. 12). As inundation increases from neap-to-spring, ecosystem C uptake will decrease because canopy submergence results in non-linear reductions in photosynthetic performance (Mao et al. 2023). Increasing inundation will also result in greater export of C via lateral (i.e., to the estuary) versus vertical (i.e., to the atmosphere) fluxes. Lateral C export will increase rapidly as neap transitions to spring but will slow as peak spring approaches. The initial increase will reflect flushing of porewater that accumulated DIC, DOC, and microbial metabolites since the last spring phase. Lateral DIC fluxes will slow or decrease as spring transitions to neap because inundation reduces soil redox and slows respiration (Fig. 12A; Fettrow et al. 2023). Lateral DOC fluxes will be smaller and follow a similar trajectory, but for a different reason: abiotic reduction of iron oxides that release DOC will happen quickly, depleting this reservoir (Fig. 12A). As a neap tide phase approaches, lateral fluxes will decrease, because the marsh is inundated less, and vertical C fluxes (uptake and loss) will increase. We therefore hypothesize that variability in inundation over alternating spring-neap cycles will affect net C uptake and the magnitude and direction of C export (i.e., vertical versus lateral; Fig. 12B). The balance between C uptake and export, as net daily production (*sensu* Wang et al. 2018), will change nonlinearly over spring-neap cycles and be predicated on whether inundation frequency and extent are increasing or decreasing (Fig. 12C).

This effort will be sited in the marshes and tidal creek within the footprint of the flux tower, where we previously measured lateral fluxes seasonally during moderate tides (Wang et al. 2018; McKnight 2016). We will build on methods in that study and, more recently in Turner et al. (2022), by measuring chemical and physical properties of tidal creek water, surface water over the marsh, and soil porewaters over complete tidal cycles (~12 hours). Six efforts are planned in summer, during different phases of the lunar cycle (peak spring, peak neap, and 4 intermediate increasing and decreasing periods), which will be used to generate response curves against inundation extent (*see 2.5A*, Fig. 12c), and two in winter, during peak spring and neap. Seasonal data will allow us to better understand plant – soil interactions and parse contributions to C export. In the tidal creek, we will deploy acoustic doppler current profilers (ADCPs), a partial pressure of CO_2 sensor (pCO_2), and a multi-sensor instrument recording conductivity, temperature, depth, oxidation-reduction potential, fluorescent DOM (proxy for DOC), pH, and dissolved oxygen. In the marsh, we will deploy underwater quantum sensors, pCO_2 sensors, soil redox probes, temperature loggers in bivalve mimics, and CTDs in wells. These sensors will be positioned at both ends of transects that extend between the creekbank and the marsh interior and along dominant tidal water flow paths (see below). At 5 stations along these transects and in the tidal creek we will collect discrete porewater and

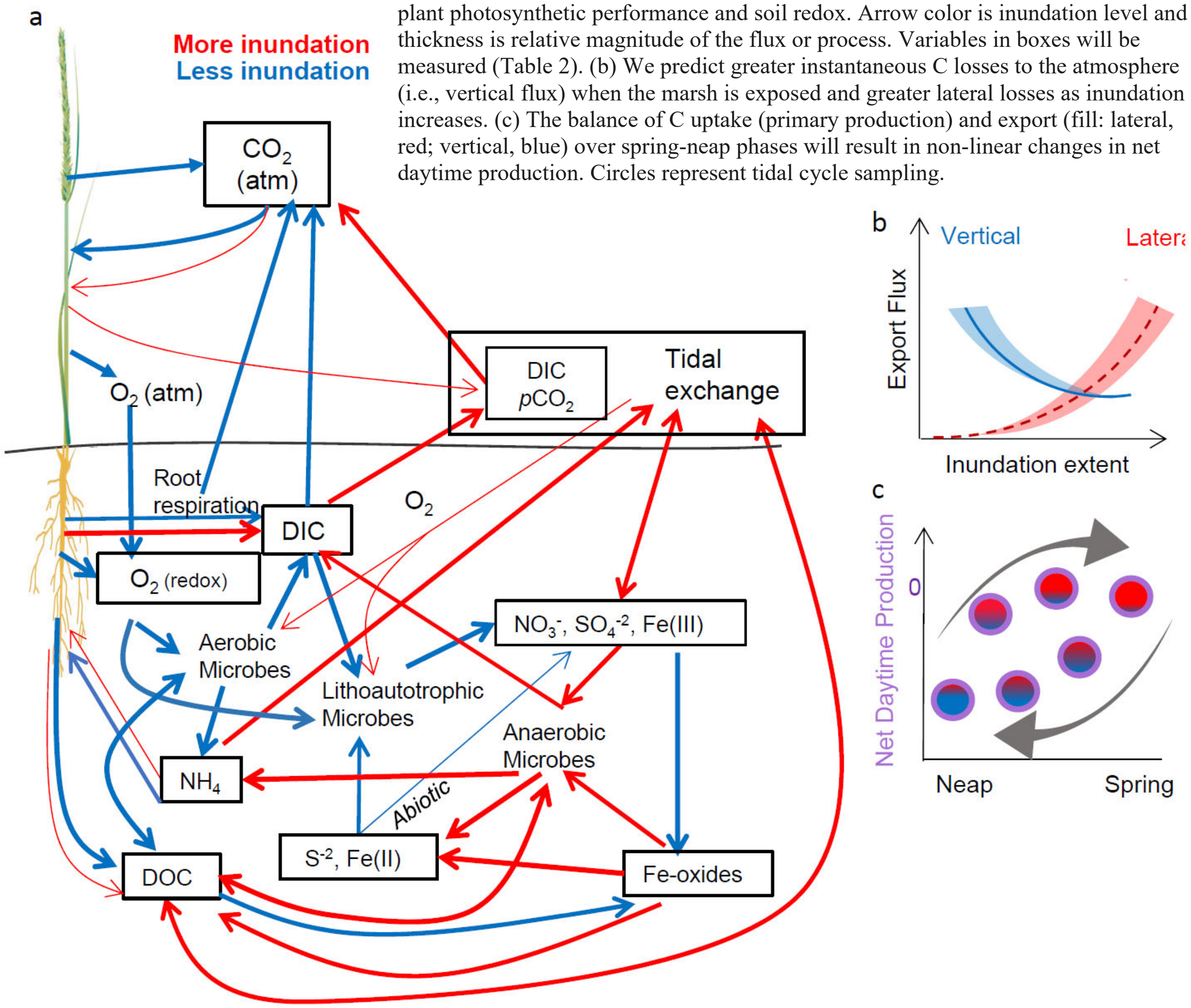


Fig 12. Conceptual model contrasting periods of more or less inundation over spring and neap tides. (a) Inundation alters C flows and soil biogeochemistry by changing plant photosynthetic performance and soil redox. Arrow color is inundation level and thickness is relative magnitude of the flux or process. Variables in boxes will be measured (Table 2). (b) We predict greater instantaneous C losses to the atmosphere (i.e., vertical flux) when the marsh is exposed and greater lateral losses as inundation increases. (c) The balance of C uptake (primary production) and export (fill: lateral, red; vertical, blue) over spring-neap phases will result in non-linear changes in net daytime production. Circles represent tidal cycle sampling.

surface water samples hourly for DOC, DIC, POC, pH, redox, and other properties to assess concentration and compositional changes in the water flooding into and off the marsh (Table 2; Fig. 12a boxes). These measurements will describe concentration changes, but partitioning processes contributing to DIC production (and consumption; Fig. 12a arrows) are not part of this Campaign. Plant photosynthetic performance will be measured at the same locations and resolution. Groundwater wells and compositional data will be used to assess subsurface water flow and porewater contributions through the creekbank walls. Complementary lab incubations with DOC from pore water, surface water, and tidal creek water will describe how microbial respiration is affected by C concentrations and composition, and vice-versa. Vertical CO_2 exchange between the marsh and atmosphere (NEE, R, GPP) will be estimated from flux tower data (Hawman et al. in review; s*ee 2.1B2*). We will calculate net daytime production as net vertical exchange (i.e., NEE) minus estimated lateral export (Wang et al. 2018). This effort is planned for year 5 and resulting data will be used to forecast potential changes in net daytime production in *Spartina* marshes with increasing inundation (*see 2.5D1)*.

Water transport, volume, and residence time in the tidal creek and across the marsh over tidal cycles will be described by a high-resolution (3 m) Delft3D-FM model. The model will be informed by our previous observations (Wang et al. 2018; McKnight 2016) along with a new high resolution digital elevation model from drone-based LIDAR and ADCP deployments. Simulated passive tracer releases in the model will be used to identify areas where water fluxes are largest in order to locate transects for quasi-quantitative water mass characterization. The high-resolution hydrodynamic model will be a major advance in coupling marsh-estuary interactions and valuable for forecasting ecological and geomorphic changes with continued sea-level rise.

We will also explore relationships between CO_2 fluxes in eddy covariance data and NASA OCO-3's XCO2 products (column-averaged dry-air mole fraction of CO_2), particularly during tidal flooding when a dampened CO_2 signal is expected. We anticipate that XCO2 captured over flooded marshes will demonstrate elevated CO_2 levels due to reduced photosynthesis, particularly in autumn after nighttime spring tides when the marsh is most net heterotrophic and CO_2 evasion is the greatest. We will isolate the differences in XCO2 by analyzing the OCO-3 pixel matching the eddy covariance footprint and comparing the variations in XCO2 at different tide heights during flooding days and consecutive dry days. We will also observe how XCO2 concentrations respond to tidal flooding throughout the growing season, enhancing our understanding of lateral flux dynamics. This will inform our NEE scaling efforts beyond the flux tower footprint to the entire study domain.

2.2D Experimental studies. We will support the field campaigns with mesocosm and field experiments that manipulate variability in salinity, flooding, and temperature while holding mean conditions constant. These experiments will also inform our integrated analyses (*see 2.5A*).

2.2D1 Experimental studies: Salinity variability. Field Campaign 1 (*see 2.2C1*) will describe biological and biogeochemical patterns at sites with different magnitudes of variability in salinity. This work will be complemented by mesocosm and lab experiments that manipulate variability in water-column salinity. The mesocosm experiment will consist of 3 components: 1) constant conditions in which we assess the response of monocultures of *Juncus* and *Spartina* to salinity (increments of 5, from 0-30), which will provide salinity-response curves for both species grown in isolation; 2) variable conditions with both low variation (weekly fluctuations from 10 to 20) and high variation (weekly fluctuations from 5 to 25) treatments for both monocultures, which will *test the applicability of Jensen's inequality as applied to monospecific plant dynamics*; and 3) mixtures of *Juncus* and *Spartina* under constant (15) and variable (10-20 and 5-25) conditions, which will allow us to assess how environmental variation alters the outcome of competition (Chesson et al. 2000). This experiment has 21 treatments, 9 of which comprise a crossed design: a plant treatment (*Juncus* only, *Spartina* only, *Juncus* and *Spartina* mixtures) crossed with a salinity treatment (no, low, or high variation). Response variables include plant traits (above- and below-ground biomass, stem height, proportion flowering, and PSII quantum yield). The experiment will run ~4 months during the growing season and include 8 replicates per treatment. In later years, we will use the mesocosm system for follow-up experiments based on results of this experiment and patterns observed in the field. We expect that these will focus on responses of other organisms (e.g., snails, crustaceans, bivalves) to salinity variation and on different vegetation transitions (e.g., *Spartina* to succulents in the high marsh).

A parallel laboratory experiment will test how constant and variable salinity affects soils from *Juncus* and *Spartina* marshes. The major effect on biogeochemistry will not be due to salinity per se, but to sulfate, which is a major seawater ion that alters the balance between microbial methanogenic and sulfate reducing metabolisms, which dominate in fresh and salt marshes, respectively. Flow through reactors will be filled with marsh-specific soils and continuously supplied with artificial seawater amended with nutrients to prevent limitation. Soil respiration rates will be determined based on concentration differences between inflow and outflow waters and turnover times within the reactors (Roychoudhury et al. 2003; Bulseco et al. 2020; Spivak et al. 2023). We will measure concentrations of DIC (net respiration), ammonium (mineralization), dissolved oxygen (aerobic respiration, abiotic oxidation), sulfides (sulfate reduction), and dissolved iron, as well as pH and redox. Data from this experiment will be valuable in informing our synthesis efforts (*see 2.5*).

2.2D2 Experimental studies: Upland tidal flooding. Increased tidal flooding into forested areas can cause tree mortality and result in "ghost forests" (Hall et al. 2022), and represents an upland expansion of the intertidal zone. This can be due to sea-level rise or to increased intensity (or frequency) of storms, both of which are expected to increase with climate change. To examine experimentally how variability in increased flooding affects upland forest retreat, we will manipulate tidal flooding adjacent to small *Juniperus virginiana* (Eastern red cedar) trees at the marsh edge (e.g., Hopple et al. 2023). Trees will receive one of three primary treatments (n=10 trees/treatment): 1) seawater added during the highest spring tides each month, 2) annual flooding with the same cumulative amount of seawater as treatment #1 added during 4 consecutive high tides in September, simulating a storm surge (e.g., extreme event), and 3) no added seawater (the control). Additional freshwater controls will allow us to separate out the effects of adding water alone. Seawater will be added manually and constrained to the target plant by a frame deployed around the tree. Response variables will include tree physiology (photosynthesis, osmotic stress, stem respiration), growth, and survival (Moore et al. 2004; Aparecido et al. 2017). We hypothesize that trees will initially be more vulnerable to annual flooding because it represents a more extreme event (Tolliver et al. 1997), but that surviving trees in this treatment will grow faster than those experiencing monthly inundation due to beneficial compensatory responses to extreme events (Kozlowski & Pallardy 2002).

2.2D3 Experimental studies: Passive field warming. Georgia is near *Spartina's* southern limit and has been shown to decrease photosynthetic activity above ~30°C (Giurgevich & Dunn 1979). We are seeing high temperatures with increasing frequency (Fig. 4c) and our long-term data show that *Spartina* production declines with increases in the annual maximum temperature (Wieski & Pennings 2014). To evaluate experimentally the importance of temperature variability on *Spartina* performance, we will deploy 0.5 x 0.5 m open-top chambers in the mid-marsh (Messerli et al. 2015). Chamber sides will have clear plastic walls with differential perforation to create five levels of increased daytime air temperature, ranging from control (no walls) to an increase of ~1.5°C. A high variability treatment with intermediate average warming will be created by taking the sides of the highest temperature chambers (~1.5°C) on and off the plots every two weeks. Temperature loggers and biomimics in each chamber will document actual temperature patterns. Tagged marsh mussels (*Geukensia*) will be embedded in each chamber so that we can assess effects on both plants and a common invertebrate (Erlenbach & Wares 2023). We hypothesize that increased temperature will reduce growth and survival, and that organisms in the variable treatment will have lower performance than those in the fixed treatment with the same average temperature.

2.3 Q2: What are the causes and consequences of disturbances in the system, and how do they affect patterns of variability in ecological responses?

Disturbances are one of the major factors structuring natural systems (Pickett & White 1985), but ecologists have struggled to settle on a consistent terminology to describe them. The term disturbance can be used to describe an unusual discrete event that can disrupt an ecosystem (e.g., a hurricane), but it can also be used in the context of the impact it has on an ecosystem: an ecosystem responding to an event can be considered disturbed whereas one that does not is resistant (Lake 2000; Graham et al. 2021). Regardless, if a system has been disturbed (or perturbed), one can then characterize the ecosystem response and track its recovery (resilience) or transition to a new state. Our proposed research will build on the idea that recovery rates can be used to assess the potential for state change (Scheffer et al. 2015; van de Leemput et al. 2018) and that variability following disturbances provides insight into resilience (Wang et al. 2024). During GCE-IV we documented the frequency, intensity, and duration of disturbance events as well as their effect size, recovery rate, and recovery trajectory after perturbations. During GCE-V we will use A) GCE **time-series data**, B) **directed studies** of natural disturbance events, C) **experimental manipulations**, and D) **cross-site-comparisons** to evaluate relationships between abiotic drivers and disturbance events and to test the hypothesis that variability increases following disturbances that perturb the system.

2.3A Patterns in the GCE time-series. Our long-term marsh monitoring includes annual measurements of disturbance from wrack, creekbank slumping, and other sources (Table 1). Disturbance frequency varies among sites due to differences in tidal elevation and landscape position, and there are large interannual differences in disturbance frequency (Li & Pennings 2016). We will now use these data to test the hypotheses that 1) disturbances increase the variability of plant biomass and invertebrate densities compared to undisturbed plots, and 2) recovery rates are slower under more stressful abiotic conditions (i.e., sites with higher salinities or greater flooding). These analyses will provide context for our experimental studies of disturbance *(see 2.3C)*.

2.3B Directed studies. The most common disturbance that affects GCE marshes is wrack. As described above (*Results from Prior Support*), we have used monthly UAV (drone) flights in combination with field observations to understand wrack occurrence in space and time, and its effects on a suite of marsh properties. These observations are scheduled to run through April 2025. We will use them to quantify plant biomass during recovery and how it varies with marsh elevation, wrack packet size, duration of wrack coverage, and season, based on an algorithm we developed for the UAV imagery. We will also use these observations to ground truth remote sensing imagery (PlanetScope) and scale up our understanding of wrack occurrence. As part of this we will evaluate how the patterns of wrack distribution affects configurational and functional landscape heterogeneity (*sensu* Tonetti et al. 2023) and test the hypothesis that different types of spatial heterogeneity lead to differential effects on plant productivity, with consequences for variability of plant biomass at the whole marsh scale. The UAV imagery also revealed the prevalence and high turnover of slump blocks along creekbanks (Yang et al. in press). We are now sampling slump blocks in the field to evaluate the effects of these transient, structured habitats on plants and invertebrates, and how they contribute to landscape heterogeneity (and thus increased habitat variability) in the creeks. To better understand slump block dynamics, we will deploy extensometers in combination with reference pipes (Mariotti et al. 2019) at selected sites within the UAV polygon to measure sediment movement. We are collaborating with Mariotti, who conducted similar observations at PIE, and will use these observations to develop a mechanistic model of sediment slumping and to test the hypothesis that lower soil shear strength contributes to increased sediment loss and faster turnover of slump blocks at GCE than at PIE. Finally, we continue to observe occasional areas of marsh dieback**,** which can lead to mortality of both above- and below-ground plant biomass and a local loss of sediment elevation, again leading to increased landscape variability. Although dieback is associated with drought conditions, the causal mechanism for this disturbance has not been identified (Alber et al. 2008; Hughes et al. 2012). We are currently monitoring a dieback patch that occurred in the Dean Creek study site, and we will continue to sample dieback patches opportunistically in GCE-V.

2.3C Experimental manipulations. As described in the *Results from Prior Support*, we have several ongoing experimental manipulations of disturbance that started in GCE-IV. The 'Disturbance across Salinity' and 'Disturbance across Elevation' experiments test the effects of standardized disturbances across abiotic gradients, and we are measuring the impact of these disturbances in terms of resistance (no effect) and resilience (magnitude of effect, recovery time) of a suite of response variables that includes soils, plants and animals (Table 2). In GCE-V we will add measurements of microbial dynamics based on sequencing of rRNA (Kolton et al., 2020; Rolando et al., 2022, 2023). The DRAGNET manipulation is evaluating combinations of disturbance (three years of tilling) and nutrients as part of a distributed global experiment, with the same response variables (Table 2). In addition to testing the original hypotheses that motivated these experiments in GCE-IV, we will use them to test three new hypotheses related to variance. 1) Spatial variability is greater in disturbed plots during recovery than after recovery or in control plots. 2) Spatial variability in disturbed plots undergoing recovery is greater under conditions of high versus low abiotic stress. 3) High variability among disturbed plots undergoing recovery is correlated with low resilience (i.e., long recovery times).

2.3D Generality and cross-site comparisons. We will expand the scope of these disturbance studies in two ways. First, we will generalize our results by synthesizing data on disturbance in coastal wetlands to contrast the effects of wrack, creekbank slumping, ice rafting, dieback, and herbivores, and how each type of disturbance affects both the mean and variability of marsh attributes. Second, we will leverage the DRAGNET network to evaluate variability in response variables during recovery from a standardized disturbance across a broad range of environmental conditions, and to contrast marshes with terrestrial grasslands. Based on preliminary results across the DRAGNET network, we hypothesize that the disturbance treatment (3 years of tilling) will increase plant species richness in terrestrial grasslands due to germination from the seedbank, but decrease species richness (often to zero) in marshes, which typically lack a seedbank.

2.4 Q3: How do ecological properties change across abiotic gradients, and does variability increase near habitat transitions?

Salinity and inundation are major structuring agents for coastal ecosystems. Plant are largely determined by salinity along the estuary (Higginbotham et al. 2004; Guo & Pennings 2012), and by inundation across elevation (Pennings et al. 2005; Simon et al. 2022), with parallel shifts in community structure, plant-microbe interactions, and biogeochemical processes (Craft 2007; Craft et al. 2009; Kolton et al 2020; Hyun et al. 2007). As sea levels rise, we expect marsh habitats to shift longitudinally (as salt water is pushed upstream into tidal fresh areas) and vertically (into uplands). *Our goal is to understand how ecosystem properties change along these gradients and assess whether there is a signal of increased spatial and/or temporal variation associated with transitions between habitats*. We will use A) **remote sensing**, B) **distributed field sampling**, and C) new long-term **upland forest plots** to track habitat transitions and evaluate whether variability increases at these transitions.

2.4A Remote sensing of transitions along salinity and elevation gradients. Our long-term observations from the monitoring plots will be coupled with remote sensing analyses to document habitat shifts and determine whether variability increases near transitions. Although these are not classic regime shifts in the sense of alternative states, marsh habitats occur as near monocultures with abrupt transitions along both salinity and elevation gradients and some of the tools developed to identify regime shifts are relevant here (Kefi et al. 2014; Scheffer et al. 2015). This work will consist of three objectives. *1) We will assess habitat shifts across salinity gradients* using our classification of orthoimagery of the tidal marshes (1-m pixel size), focusing on 5 major vegetation types: *Juncus*, *Spartina*, *Schoenoplectus*, *Zizaniopsis,* and tidal forest. We will use these images to develop random forest classification of Sentinel 2 multispectral imagery (10-m pixel size) of the gradient from salt marsh through tidal fresh forest to categorize shifts along the Altamaha estuary and will calculate spatial covariation between vegetation types as a way to objectively detect transitions and assess whether they are persistent or transient over time (Uden et al. 2019). We hypothesize that we will see upstream shifts in salt marsh habitat over time. 2) *We will assess changes in plant community composition on Broughton Island, which is in a transitional area*. Broughton Island is located in the mid-salinity zone of the Altamaha estuary and is projected to shift from brackish to salt marsh as sea level rises (Craft et al. 2009; Fig 1). We conduct annual surveys of the plant community at 15 sites on Broughton as part of our core monitoring, and will use these data to develop a fractional vegetation algorithm compatible with different satellite platforms (we have classifications for Sentinel 2 and will develop them for other platforms, including WorldView (leveraged from the NASA CSDA program)). We will use these observations to examine how plant community composition and relative abundance changes at these sites in association with landscape-level habitat shifts. *3) We will assess variability in species-agnostic (unclassified) Landsat Vegetation Indices of biomass* (e.g., NDVI, NIRv) along salinity and elevation transects that correspond with the distributed sampling campaigns (*see 2.4B*). This analysis will be conducted on cloud-free, low tide (Narron et al. 2022) Landsat images from the seasonal peak of biomass in October (1985-present), with data from different Landsat missions cross-calibrated before analysis. We will calculate Moran's *I*, a measure of spatial autocorrelation, along with spatial skewness (Veldhuis et al. 2022), to test the hypotheses that these metrics of biomass variability 1) increase at or near habitat shifts identified from the field campaigns and in our classified vegetation maps, and 2) vary predictably with salinity and elevation.

2.4B Distributed field sampling. We will conduct distributed field campaigns across gradients of salinity and inundation. These efforts will provide field data to test whether ecological variability increases in proximity to a habitat transition, and will also be valuable in charactering patterns in the GCE domain and developing space-for-time predictions of responses, such as changing C stocks, to sea-level rise (*see 2.5D2*).

2.4B1 Field Campaign 3: Distributed sampling across salinity. Along the estuarine salinity gradient, we will select areas where the dominant creekbank vegetation transitions 1) between fresh (*Zizaniopsis*) and brackish (*Spartina cynosuroides*) and 2) between brackish and salt (*Spartina*) marsh plants, based on long-term observations and habitat distribution maps. We hypothesize that spatial variability will increase approaching each transition and will be greatest in fresh marshes. The latter reflects the expectation that minor variability in tidal water salinity and sulfate concentrations will create variation in osmotic stress and substantially alter marsh processes in freshwater areas (i.e., switch from methanogenesis to sulfate reduction; Janousek et al. 2013; Herbert et al. 2018; Wang et al. 2019). On each side of a transition, we will select 3 marsh sites based on creekbank vegetation that extend from within the dominant monoculture to near the transition. Environmental conditions will be characterized by deploying groundwater wells, redox sensors, and temperature loggers and by measuring elevation. At each site we will sample 5 replicate plots in each of 2 zones (creekbank and mid-marsh), for a total of 120 plots (2 transitions x 6 marsh sites x 2 zones x 5 plots); values from replicate plots will be used to estimate spatial variation. Each plot will be sampled for most of the same response variables described for Field Campaign 1 (Table 2), as well as microbial dynamics (diversity, composition, metabolic activity). We will also sample nekton along the estuarine salinity gradient (trawl surveys) to characterize community composition, biomass and abundance, and diets (i.e. prey selection, gut contents, stable isotopes; Ziegler 2019) and to test how variability in predation activity (consumption assays) changes along environmental stress gradients (Duffy et al. 2015). This effort is targeted for year 3.

2.4B2 Field Campaign 4: Distributed sampling across elevation. We will sample 3 long-term monitoring sites that span a range of fresh (GCE7), brackish (GCE1), and salt (GCE3) marshes. Within each marsh site we will sample two vegetation transitions along the elevation gradient: mid-marsh to high-marsh and high-marsh to upland. At GCE3, for example, this would represent transitions from *Spartina* to succulents to shrubs. We will use a similar design as in Field Campaign 3, (*see 2.4B1*), and sample a similar set of response variables (Table 2). At each marsh site we will sample from 3 locations on either side of a transition along a transect that extends from within the marsh zone to close to the transition, and again sample from 5 replicate plots, for a total of 180 samples (3 marsh sites x 2 transitions x 6 locations along the elevation gradient x 5 plots). Environmental conditions in each site will be characterized similar to that outlined for Field Campaign 3 (see Table 2). We hypothesize that spatial variability will increase approaching each transition and will be greater at higher elevations because of greater groundwater input and heterogeneity in flow paths. This sampling will be conducted in year 1 and repeated in year 6 when the lunar nodal cycle will have increased the range of tidal inundation (Fig. 3), providing an opportunity to assess the effects of increased flooding. This design and measurement suite are comparable to DOE's COMPASS program focused on terrestrial-aquatic interfaces and will allow for intercomparison. Coordination with COMPASS will be facilitated by Dr. Pat Megonigal who is the Chief Scientist; he is also an external advisor to GCE and collaborates with GCE-V PI A. Spivak (e.g., **Spivak et al. 2023**; Holmquist et al. 2023).

2.4C Upland forest plots. In tandem with the above effort, we will incorporate plots at the forested edge of upland borders into our long-term monitoring efforts at GCE1, 3, and 7. We will install wells across the marsh-upland border to measure water levels and salinity to characterize groundwater flow, and conduct annual surveys of trees (dendrometer bands) and litter-fall. We will also map the location of vegetation transitions in the marsh, with the expectation that transitions will shift towards the upland edge over time and be linked to changes in porewater salinity. We will also analyze growth rings from cores collected in live and dead marsh boundary trees to assess impacts of historic stressors (e.g., drought, tidal flooding; Deshpande et al. 2020). Adding these new plots to our core monitoring efforts will establish permanent creekbank-to-upland transects that will allow us to characterize future marsh migration with sea-level rise.

2.5 Integration and scaling up: What are the mechanisms by which coastal wetlands respond to changing drivers, and does variability in drivers and responses inform this understanding?

The proposed field sampling and experimental efforts are designed to mechanistically describe how changing drivers affect the GCE domain and coastal marshes, provide insight into the role of driver variability in producing ecological responses, and explore the potential value of ecosystem variability as a descriptor of system behavior. To integrate these findings, we will A) develop **response curves** to evaluate the importance of variability in our major drivers for organism and ecosystem performance, B) use **remote sensing** to assess the relationships between scaled-up estimates of marsh productivity and climate variability and to determine whether increased variability in productivity is an indicator of reduced resilience, C) apply **multivariate analyses** to assess interactions and feedbacks between abiotic drivers and ecosystem responses and D) forecast how **C exchange and stocks** might change under future scenarios of increased salinity and inundation. Some of these synthetic efforts focus on variability more than others, but all will advance our general understanding of marsh responses to global change.

2.5A Response curves. With data from our experiments and field sampling efforts we will create response curves for plant biomass, invertebrate density, and other key variables as functions of salinity (i.e., mesocosm experiments, Field Campaign 3, fall monitoring), inundation (i.e., Field Campaign 4), and temperature (i.e., warming experiment). We will generate curves for NEE, GPP and net daytime production in response to inundation and temperature by using the high-frequency flux tower time series and the results of Field Campaign 2 (*see 2.2C2*). In some cases, we will incorporate literature data or previous work to strengthen this process. For example, we previously found a non-linear relationship between *Littoraria* metabolic demands and temperature (Atkins et al. 2022), suggesting that temperature variation has consequences for metabolism via Jensen's inequality (e.g., Bernhardt et al. 2020). We will use these response curves to predict organismal performance by applying non-linear averaging (e.g., based on Jensen's inequality), and explore performance under increasingly variable abiotic time-series. These abiotic time-series will include simulated data sets, in which we can tightly control the mean and variance, as well as data from our study sites (e.g., based on biomimics, field campaigns, long-term monitoring, flux tower). We will use these simulations to develop a general understanding of how abiotic variability affects time-integrated performance of organisms and ecosystem processes in coastal marshes.

2.5B Remote Sensing. We will use our remote-sensing tools to scale up and assess changes in productivity across the GCE domain. We have tools that predict marsh flooding from MODIS and Landsat, which can be used to assess flooding patterns and to filter out high tide imagery for improved estimates of marsh productivity (O'Connell et al. 2017; Narron et al. 2022). We have used Landsat-derived vegetation indices to estimate patterns in *Spartina* aboveground biomass (AGB) (O'Donnell & Schalles 2016; Bice et al. 2023), and are developing similar algorithms for *Juncus* and *Zizaniopsis*. Our data-driven BERM model (O'Connell et al. 2021) uses remotely-sensed above-ground biophysical characteristics and gridded climate data to estimate *Spartina* BGB, and we now have an improved version, BERM2, that captures a greater range of environmental conditions and belowground dynamics (Runion et al., in review). We are using our UAV data as ground-truthing for the development of Landsat-based estimates of the ratio of unvegetated to vegetated area (UVVR, Ganju et al. 2022) that can be applied to the southeast. Finally, we have remote sensing based machine learning techniques that can produce spatially explicit models of emergent leaf area index, NEE, and GPP for the flux tower site (Alber & O'Connell 2019; Hawman et al. 2023; in review) that can be scaled up with area-weighted mapping (Rey-Sanchez et al. 2022) that reflects different *Spartina* growth forms**.**

We propose to integrate the spatially-explicit productivity measures described above to address three questions. *1) Do patterns in productivity indicate marsh resilience?* We will use remote sensing models to produce time series estimates of AGB, BGB, NEE, GPP, and UVVR at the same spatial scale, and identify spatial and temporal patterns of critical gains and declines. Our field observations show evidence for a 5-year decrease in BGB that corresponds to an increase in sea level, and the BERM model output shows net losses in BGB despite net gains in AGB (Runion et al., in prep). We hypothesize that loss of BGB is an early indicator of marsh response to flooding, and that increasing sea level will lead to decreased BGB followed by decreased AGB and increased UVVR, with concurrent declines in GPP. 2*) Is declining resilience associated with increased variability in productivity?* Several authors have used the long-term trajectories of temporal autocorrelation (TAC) and its change over time (δTAC) as indicators of resiliency in forests (e.g. Forzieri et al. 2022; Boulton et al. 2022). We will examine each of our productivity measures to test whether this same approach can be applied in salt marshes (e.g., do areas with high δTAC correspond to areas where productivity is decreasing). We will also explore other analytical techniques to identify areas of high variability (e.g. hot spot/hot moment analysis, ecological control point analysis (Kannenberg et al. 2020; Bernhardt et al. 2017; Vargas et al. 2018)). *3) How does variability in climate drivers affect marsh productivity?* We will evaluate how climate means, variation and extremes influence productivity measures through predictive models, such as generalized additive models (GAMs), or machine learning models such as BERM. As part of this we will assess whether we can improve productivity predictions by informing models with variation, minima and maxima in addition to means for important drivers such as soil temperature, winter precipitation, and flooding duration. We will also use our estimates to evaluate spatial covariance between productivity estimates (e.g., NEE) and drivers (e.g., % flooding, soil temperature).

2.5C Multivariate analysis. We will gain a better understanding of tidal salinity and inundation effects on marsh ecosystem functioning and habitat distributions by synthesizing results from Field Campaigns 3 and 4 using structural equation models (SEM) designed to assess relationships between drivers (e.g., tidal salinity, inundation), soil properties (e.g., bulk density, porewater chemistry), and ecological responses (e.g., plant species and biomass, CO_2 fluxes, invertebrate and microbial communities; Table 2; *see 2.4*; Angelini et al. 2017; Damgaard 2019; Fan et al. 2016), with coefficients estimated from correlation matrices using a reticular action model method (Boyce et al. 2015). Salinity and inundation effects on ecological responses are somewhat confounded; the integrated SEMs will be key tools for describing the relative importance of each driver, allowing us to predict potential responses to future scenarios (*see 2.5D*). We will conduct similar analyses to compare sites with high versus low salinity SD from Field Campaign 1. We will continue using information theory and empirical dynamical system analysis (Bice et al. 2023) to assess connections between environmental drivers and ecosystem properties, focusing on our most data-rich time series (e.g., long-term plant productivity from satellite and flux tower data).

2.5D Forecasting changing conditions. Sea-level rise will alter functioning within habitats and the distribution of habitats along estuaries. We will synthesize results from the Field Campaigns and remote sensing to describe current, and potential future, net daytime production (see 2.2C) and above- and below-ground C stocks (*see 2.4B1,2*)

2.5D1 Net Daytime Production. We hypothesize greater tidal flooding will reduce photosynthetic C fixation and result in higher C losses via lateral (i.e., estuary) compared to vertical (i.e., atmosphere) export (Fig. 12; Bogard et al. 2020; Mao et al. 2023). This is important, because it means that sea-level rise will cause greater export of recently produced C to the coastal ocean (e.g., Cai 2011). We will determine how increasing tidal inundation affects net daytime production by correcting NEE for lateral C export using vertical and lateral exchange measurements made over complete tidal cycles (~12 h) and neap-to-spring periods in Field Campaign 2 (*see 2.2C*; Wang et al. 2018; Richardson et al. 2023; Hawman et al. in review). Contributions from areas with greater or lesser inundation will be determined from transect data, eddy covariance modeling, and the high resolution Delft3D-FM model.

To forecast how increased inundation duration and extent affects net daytime production, we will use dynamic structural equation models (DSEM), integrating multilevel time series analysis and time-varying effects modeling, as demonstrated by Asparouhov et al. (2018). This approach will update our conceptual plant-soil-inundation model (Fig. 12a) by incorporating observational data and will be informed by spatially explicit predictions of inundation from the high resolution Delft3D-FM model. We aim to discern diurnal from flooding effects (e.g., Selonen et al. 2021) and assess direct (e.g., inundation, temperature) and indirect (e.g., redox conditions) effects of tidal and seasonal variations on C fluxes. Our multi-level modeling strategy will detail the hierarchical structure of marsh ecosystems, from individual plants to creekbank and mid-marsh zones, facilitating nuanced analysis of C uptake and export (but not potential erosive or drowning losses) across and within tide stages and seasons. This methodological framework is adept at handling our dataset's repeated measures and will enable robust forecasting under various sea-level rise scenarios, thereby enhancing our understanding of the complex interplay between plant, soil, and hydrological processes.

2.5D2 Domain-scale C stocks. The above effort will describe potential responses in C exchange over short time (e.g., hours-days) and constrained spatial (*Spartina* marshes) scales. We will take a longer-term (10s to 100s of years) and larger-scale (across the domain) view by estimating C stocks, which represent an integrated metric (ecological-to-hydrodynamic) of ecosystem functioning and an important service provided by coastal marshes. We will estimate C stored in above and belowground biomass and soils across the GCE domain and how they might change with sea-level rise. Estimates of current stocks will be generated by combining habitat distributions with field observations across salinity and elevation gradients (*see 2.4*) and by leveraging a related project to estimate C stocks at depth (led by Mishra and Sutter, *see section 3*). Stock estimates will be based on above- and below-ground C pools measured within and across habitat types and across transitions (Table 2) and calculated using approaches described by Krauss et al. (2018) and Kirwan et al. (2023). Potential sea-level rise effects on domain-scale C stocks will be estimated by combining maps of projected wetland habitat change, from NOAA's Coastal Change Analysis Program and Sea-Level Rise Viewer (Osland et al. 2022), with time-resolved estimates of habitat-specific soil stocks that account for vertical accretion. Maps will be developed for several time horizons and informed by habitat-specific accretion rates from GCE and the Coastal Carbon Atlas (Holmquist et al. 2023). Comparisons between current and projected maps will allow us to estimate potential sea-level rise effects on coastal marsh C stocks. These maps will support partners at GA Department of Natural Resources who are interested in quantifying the state's 'blue carbon' resources and how they may change.

3. Related Research Projects

All the research described above will be funded as part of GCE-V, and is not dependent on other efforts. However, GCE investigators are involved in a number of projects with funding from NSF, NASA, NOAA and others that will extend the research proposed here and, in some cases, allow us to expand the scope of our inferences. The three most germane to this proposal follow. 1) Mishra and Sutter have NSF Signals in the Soils funding to develop machine learning-enabled predictive modeling of belowground soil organic carbon (SOC) using a combination of field sensor networks, soil cores, drone data, and satellite data. This project will produce estimates of the spatial distribution of both surficial and belowground SOC, which will generate new information for our domain-wide carbon budget research (*see 2.5D2*). 2) Sutter and Mishra have NOAA Effects of Sea Level Rise funding to parameterize a coupled hydrodynamic and ecological model (Hydro-Mem) for the South Atlantic Bight region to project marsh evolution to varying sea-level rise scenarios in a spatially-explicit manner at discrete time steps into the future (e.g. years 2050 and 2100). This project will generate complimentary field data on soil organic carbon and below-ground plant biomass in brackish and tidal freshwater marshes in our domain, and will be leveraged in our modeling exercises incorporating biophysical feedbacks to estimate marsh response to sea-level rise (*see 2.3D2*). 3) Spivak has a new Simons Foundation grant to study how redox conditions and marsh plant root exudates affect C preservation at PIE-LTER. Insights from this cross-site collaboration will be useful in interpreting soil processes observed in Field Campaign 2 (*see 2.2C2)*.

4. Broader Impacts

The education and outreach activities proposed for GCE-V are designed to enhance scientific literacy, expand opportunities in STEM, and broaden participation to people of all backgrounds. This includes working to increase the diversity of our undergraduates, graduate students, and PIs, to increase the reach of our Schoolyard and K-12 educational activities, and to strengthen ties with the local Hogg Hummock community on Sapelo Island. We are also planning a new citizen science effort and will continue our partnership with coastal managers. Our progress in each of these efforts will be tracked by our DEI committee, which conducts an annual review of our activities and will oversee a demographic survey of the membership in year 4 of the project.

The GCE supports summer *undergraduate interns* through our REU program and other leveraged funding, most of whom work at the field site on Sapelo Island. We have taken several steps to broaden participation in the program through targeted recruiting and changes to our application (asking about perseverance in overcoming obstacles, which provides additional insight into the applicants' motivation, resilience and "grit"), and improved orientation and mentor training. We have budgeted support for additional REU students during the summer and academic year in GCE-V to provide more opportunities, and included funds for graduating seniors so they can gain additional experience as they consider a career in research. We will continue working with colleagues at Savannah State Univ (SSU*; see Other Personnel*), which runs an NSF Bridge REU program, to recruit students to the GCE, and work with the UGA Graduate School to ensure that GCE opportunities are advertised as part of the "Graduate School 101" workshops, which improve access to graduate education for undergraduates at minority-serving institutions. *Graduate student* recruitment to GCE-V will be enhanced by leveraging UGA's Graduate FUSE Program, an educational pipeline partnership with 6 HBCUs: Albany State, Florida A&M, Fort Valley, Morehouse, North Carolina A&T, and Spelman. The UGA Graduate School provides workshops on admissions at these institutions and waives application fees. Uniquely, UGA offers a summer bridge program to help FUSE students with the transition to graduate school and we have budgeted funds to support GCE student participation in this program. Once at UGA, there are professional workshops and organizations aimed at retaining underrepresented students, including "Graduate Research Assistants Diversifying STEM". Another graduate-centered activity is our distributed graduate seminars, which are offered for credit at universities across the country and feature lectures by leading scientists in our field. The reach of these courses goes well beyond graduate students, and includes participants from across the LTER and National Estuarine Reserve Networks. In GCE-V we plan to offer a course on variability in ecological studies. Identifying strategies to increase the diversity of the GCE PIs is more challenging, but we have budgeted funds to bring potential collaborators from underrepresented groups to Sapelo and to our annual meeting, and will encourage them to join us as Affiliated Investigators.

The GCE Schoolyard program is our foundational activity for K-12 educators. In GCE-V we will continue the program but with more robust recruitment of diverse teachers from underserved school districts. We will leverage relationships with school and community leaders in coastal counties and HBCUs (SSU, Spelman College, connections with local educators) to recruit teachers and develop engagement opportunities during the academic year to broaden the participation of teachers who cannot afford the time during the summer. We will leverage our new Science Cafe (see below) to expand interactions between Schoolyard teachers and community members. We currently gauge effectiveness by surveying teachers and tracking teacher and school demographic information, and will incorporate more rigorous documentation of how teachers translate their experience to the classroom and estimate the number of students reached.

We will work with K-12 students by expanding the curriculum and reach of our children's book (*And the Tide Comes In: Exploring a Coastal Salt Marsh*) and comic book (*The Adventures of Jacob the Technician*). Our new education coordinator (Heil) will work with a team of teachers and students to develop lesson plans and bring the salt marsh to life (e.g., using live organisms) for ~1,500 third-graders per year across the 14 underserved, diverse public schools in Athens, GA. These schools surround UGA and we will leverage University education and outreach organizations to reach them (i.e., EcoReach, Sea Dawgs, Marine Extension and Georgia Sea Grant). We will also continue our collaboration with Atlanta Public Schools to bring high school students to Sapelo Island for field courses in coastal ecology. We will track the number of students reached, student and school demographics, curriculum effectiveness (i.e., content understanding), and teacher feedback. Lesson plans will also be posted on our website.

We will establish a *Citizen Science program* to help delineate high tide flooding events in coastal uplands, which we expect to increase due to sea-level rise and the lunar nodal cycle (Fig 3). On Sapelo Island we will recruit members of the Hogg Hummock community, including Geechee descendants, to be part of "*The Flood Patrol.*" Crest gauges will be deployed with water-soluble paint and cork particles to mark the high-water level and the Flood Patrol will be asked to record the data after each spring tide (every 2 weeks). Sites will be located in areas that have experienced upland flooding, based on community observations and our hydrodynamic models, and we will use our RTK-GPS to obtain precise elevation measurements. This builds on our existing work with a community member who maintains pressure loggers in remnant ditches that serve as conduits of estuarine water into the area (often into people's backyards). Recorded water level data will be used to reference Flood Patrol sampling. We have budgeted modest stipend support to incentivize participation in the Flood Patrol, which will also track marsh vegetation encroachment into the upland. We will also initiate a semiannual *Science Café* to increase dialog with a larger group of community members. These events will provide opportunities for the Flood Patrol to discuss their observations with other community members and the GCE team, thereby creating space for deliberate engagement. At the scale of the GCE domain, we will engage citizens across McIntosh County to collect data with the "*Sea-Level Rise app*", which uses GPS to delineate the boundaries of flood events. This app is available through NOAA's "Communities Tracking Coastal Change" program. This is a novel effort because no GA communities currently participate in this program; we will work with the Sapelo Island National Estuarine Research Reserve to publicize this effort. Citizen-generated data will be posted on both the NOAA and GCE website.

The GCE works with *coastal managers* by partnering with the Georgia Coastal Research Council (GCRC), which is headed by Alber. The GCRC is a boundary organization that works to overcome institutional barriers between scientists and managers (Osmond et al. 2010; Cvitanovic et al. 2015). The GCRC hosts workshops and meetings that bring together coastal researchers and managers, assists management agencies with scientific assessments, and synthesizes coastal research (e.g., we are currently compiling data on vertical change in salt marshes throughout GA). The GCRC provides a direct mechanism for sharing the results from GCE research with State managers and for alerting us to new resource issues (e.g., invasive species, the efficacy of marsh buffers). The GCRC recruits faculty from research and primarily undergraduate serving institutions (e.g., College of Coastal Georgia), and has a successful track record of connecting new faculty with coastal managers and more senior researchers (e.g., collaborations between SSU, GA Southern, UGA, and GA Tech).

We reach the *general public* through the GCE program website and public data portal, which disseminate information and products including publications, data, photographs, and remote sensing imagery. GCE data are downloaded by diverse users, including researchers from around the world, educators, and students. We publish a weekly e-newsletter of GCE activities that is publicly available. In addition, GCE scientists participate in public forums and provide information about their research to the media. For example, we will continue to host a "Marsh Madness" booth at the annual Atlanta Science Festival Expo, which regularly has >12,000 people in attendance.

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Project Management Plan

Project Organization. The GCE follows a co-project director (PD) model, with shared responsibility for project management (Fig. 1). Merryl Alber has been part of the GCE-LTER since its inception and has served as Lead PD since the start of GCE-II (2006); Steve Pennings has served as co-PD since the start of GCE-I (2000). Alber is responsible for overall project coordination, communication with NSF and the LTER network, overseeing GCE staff at UGA, taking the lead on annual reports and other program documents, and managing the budget. Pennings serves as director of field operations at UGAMI, oversees the monitoring program, and shares responsibility for personnel decisions, coordinating education and outreach efforts, and framing the scientific goals of the program. Although he holds a faculty position at the University of Houston, Pennings is in residence at the UGA Marine Institute (UGAMI) on Sapelo Island for most of the summer. Alber is also at UGAMI for one week a month. Day-to-day GCE operations at the field site are supervised by our lead technician, John Williams, who is in regular contact with Pennings in person during the summer and by email and telephone during the academic year. This structure is functioning well. However, we *are planning a leadership change during GCE-V, with Amanda Spivak coming on as co-PD now and assuming the Lead PD role during the third-year review.* In anticipation of this change, Spivak has been involved with the GCE since her arrival at UGA in 2019, and Alber, Pennings and Spivak have been working together over the past several years to oversee the project and this proposal. Our plan is for *Alber to transition to co-PD and remain involved in leadership as part of the Executive Committee (Pennings will remain as co-PD).*

The GCE is governed by a set of bylaws (available on our website), which describe roles and responsibilities as well as provisions for election and membership changes. As described in the bylaws, the overall research direction of the project is vested in an Executive Committee (EC), which makes major decisions about project direction. The PIs and EC members are elected for 6-year terms that begin one year before the renewal proposal is due. Having an Executive Committee helps to distribute decision-making and to engage additional PIs in project management. It also provides a way to train future PDs. The Committee stays on top of the business end of the program (comings and goings of field technicians; infrastructure needs), helps to set the agenda for annual meetings and other project events (e.g. 3-year review), and weighs in on potential collaborations and other opportunities. Executive Committee members are actively involved in drafting the proposal and they take the lead on specific sub-projects. The EC currently consists of Alber, Pennings, Spivak, Mishra (who will oversee flux tower and remote sensing research in GCE-V), and Osenberg (who will oversee the mesocosm experiments), the Information Manager (Sapp), and a graduate student representative. Having the Information Manager involved at this level of project management gives him a perspective that informs our data management structure and keeps the ECs apprised of NSF data requirements and any data issues that arise. The graduate student provides a voice for student concerns and serves as a liaison to the larger student community. The EC meets monthly and members are in touch regularly by email.

GCE scientists are classified as either Project Investigators (PI) or Affiliated Investigators (AI), as defined in our bylaws. Project Investigators are listed as Senior Personnel on the proposal. They fully participate in site research, attend project meetings, submit information for annual reports, and provide data and meta-data to the GCE IM program. Affiliated Investigators have an interest in GCE research and work on related projects but are not directly funded by the GCE. Affiliated Investigators are invited to meetings and can take advantage of our data reporting protocols, but are not expected to participate in GCE activities at the same level as PIs. Project postdocs (see mentoring plan) attend project meetings and interact with GCE scientists and students in accordance with their research tasks. GCE graduate students are defined as students working in the domain with a PI, AI, or external collaborator, which is a larger group than those directly funded by the project. A graduate student representative attends EC meetings as a non-voting representative, and serves as a bridge between GCE Investigators, GCE students, and the network. *This structure is functioning well and we will continue it in GCE-V.*

The GCE initially had a six-person Advisory Committee composed of scientists from within and outside LTER. Advisory Committee members attend our annual meeting and provide feedback and advice on project research and administration. This input was invaluable as the GCE was getting established, but by GCE-IV the project had matured such that the Advisory Committee was reduced to two people. Our current Advisors are Elizabeth Borer (Univ. of Minnesota) and Pat Megonigal (Smithsonian Environmental Research Center).

Project Meetings. The entire GCE membership, including postdocs, students, and technicians, meets annually, usually in January. Meetings last 2-3 days and focus on research results and planning. These annual meetings allow us to formally evaluate our progress and have been instrumental in helping plan research activities, prepare for our mid-term site review, and discuss new ideas. The meetings typically include a poster session during which we encourage students and postdocs to present their research. We also hold a business meeting to discuss administrative updates and project business (e.g., bylaws and project leadership votes). The annual meetings provide opportunities for small groups to work on papers, receive training on information management, and discuss leveraged proposal ideas. We invite partners from state agencies and potential new collaborators to attend the meetings. *We will continue annual meetings in GCE-V.*

Subsets of investigators within the project meet monthly or as needed by Zoom to advance collective projects or analyses and keep sub-projects on task. During GCE-IV we had monthly meetings of the flux tower, remote sensing, and disturbance groups, and as-needed meetings of other groups such as those involved with the SALTex and PREDex manipulations. Alber and Pennings (and recently Spivak) run and/or participate in most of these meetings. These meetings have improved communication and helped the groups stay on task. Sub-project meetings are also a good way to involve graduate students and technicians in decisions. *Over the course of GCE-V we anticipate continued regular meetings of project groups.*

The four Atlantic coast wetland LTER sites (PIE, VCR, GCE, FCE) regularly seek opportunities to collaborate and address topics ripe for cross-site work. The PIs and co-PIs of these projects see each other regularly at scientific meetings, and we have also found it valuable to send representatives to each other's site meetings. *GCE will continue to work with the other Atlantic coast wetland sites to exchange participants at annual meetings and promote cross-site interactions.*

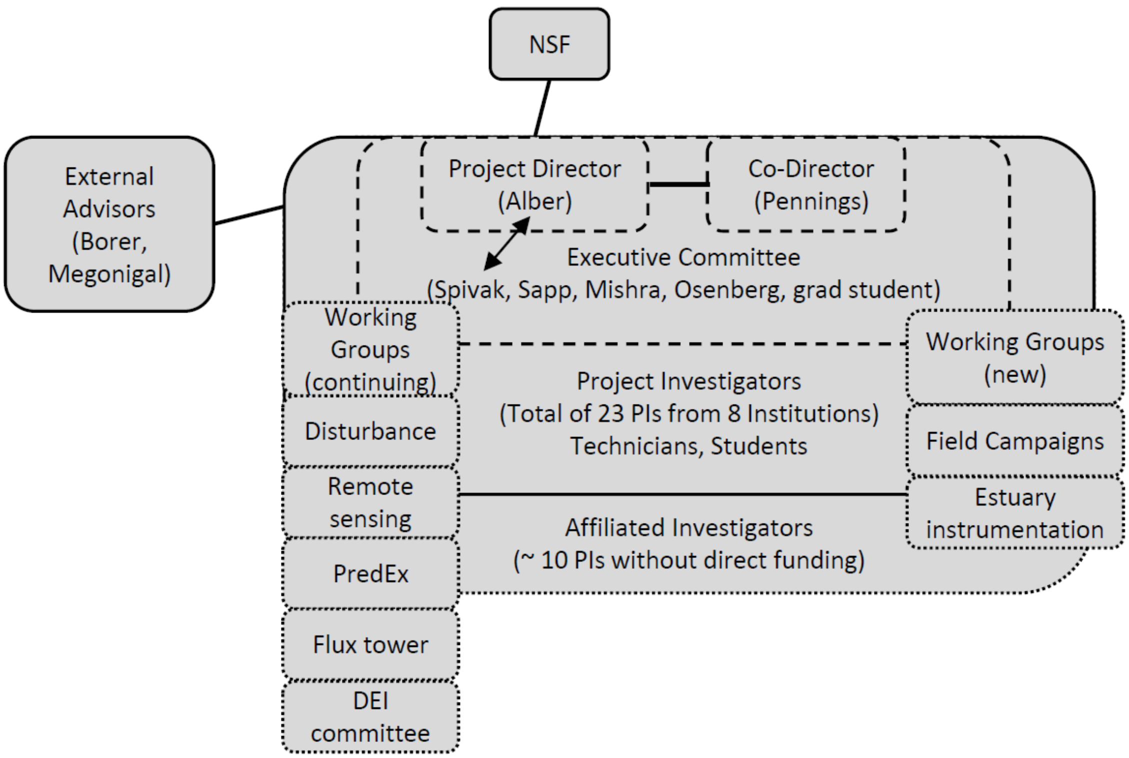
New Scientists. We are adding four new PIs in GCE-V: Kostka (GA Tech, microbiology), Moore (GA Southern, ecohydrology), Nelson (UGA, community ecology), Sutter (UNC Wilmington, wetland ecology), and have brought on two new AIs (Giulio Mariotti, LSU, geomorphology; Shelby Ziegler, Villanova, fisheries science). Wares (UGA, genetics) who was involved in GCE-I and II, is returning as a PI.

W*e will continue to encourage non-LTER scientists to become affiliated with the GCE site* by extolling the twin benefits of working at Sapelo Island and with the LTER. The UGA Marine Institute is a world-renowned center for tidal marsh research embedded in the Sapelo Island National Estuarine Research Reserve, and provides access to field sites with a rich history of previous research and GCE data that provide context for new studies. The LTER network offers the opportunity to coordinate with other sites as well, along with ready access to data. We expose new scientists to GCE research by inviting them to our annual meetings, and many have gone on to become AIs, and eventually PIs (e.g., Kostka, Moore, Sutter in this funding cycle). We also work with these scientists to develop leveraged research proposals.

Diversity. To date, the GCE has been successful at including female participants, but less successful at recruiting members of groups historically under-represented in science. The GCE is led by a woman, and in GCE-V almost half (9 of 19) of the PIs are female. Our current graduate students include several from under-represented groups and international students from Brazil, China, Ghana, Iran, Nigeria and Turkey. We conducted a survey in 2021 of all past participants in GCE research that we could contact. Of the respondents (n=117), ~81% of participants in GCE research from 2000 to 2021 were white, ~10% Asian,

~3% Black, ~4% were Hispanic or Latino, ~48% were female, and ~7% preferred not to respond. Our plan for broadening participation (see proposal) emphasizes partnerships and programs at every level—undergraduate students, graduate students, faculty, K-12 teachers and students, and the local community—to expand opportunities to engage with GCE research. The GCE DEI committee includes personnel from all ranks and is led by Pennings. They have developed a Code of Conduct, a DEI Implementation Plan, and various field safety and orientation documents. The GCE DEI committee reviews our progress on DEI implementation and adds new implementation steps annually. Some examples of steps taken over the past few years include adding a question about overcoming obstacles to our REU applications to help broaden access, holding a pre-summer orientation meeting for interns and graduate students working on Sapelo, and providing safety vests that identify researchers as official workers during field work in neighborhoods. We plan to repeat the demographic survey during GCE-V.

Fig. 1. GCE Administrative Structure. We are planning for Alber and Spivak to switch roles mid-way through GCE-V.



Safe & Inclusive Fieldwork Plan

This document constitutes a plan for nurturing a safe and inclusive off-campus or off-site research environment, and for how abuse by any person (including, but not limited to, harassment, stalking, bullying or hazing of any kind, whether the behavior is carried out verbally, physically, electronically or in written form), or non-inclusive conduct (including biased, unwelcome, offensive, indecent, obscene or disorderly), will be addressed.

1. Description of field setting and challenges for ensuring safe and inclusive working conditions. GCE-LTER researchers will conduct fieldwork on Sapelo Island and the Georgia coast. On Sapelo Island, researchers are housed at the UGA Marine Institute (UGAMI); most researchers have private bedrooms. Researchers will be made aware that Sapelo Island is home to a historic Geechee community in Hog Hammock and instructed to be respectful of the local culture and the people who call Sapelo Island their home. Another unique challenge is the extensive scope of the GCE-LTER and the multiple organizations involved, each with their own policies and procedures for incident reporting. We address this challenge in item 4 below.

2. Steps to nurture an inclusive off-campus or off-site working environment. The University of Georgia (is committed to creating and maintaining a safe and inclusive environment, including in off-campus settings. This commitment extends to all campuses, field sites and anywhere UGA research and education are conducted. For this project, the following considerations, activities, and trainings will be used to further promote an inclusive off-campus or off-site working environment:

2.1 GCE Code of Conduct. All GCE members, including students, faculty, and staff, are expected to adhere to both the GCE Code of Conduct and the policies of their home institution. These expectations apply everywhere and whenever GCE activities are conducted, including in the field, laboratories, offices, and meetings. The Code of Conduct describes expected behavior – being welcoming and inclusive; abiding by principles of academic integrity; accommodating colleagues' individual needs -- and unacceptable behavior, including harassment, intimidation, discrimination, and sexual misconduct.

2.2 Orientation. Team members will be assured that their emotional and physical safety is the first priority and that they should exit the field site if they feel unsafe, for any reason. Before any fieldwork, we will ask the work group to review the GCE Code of Conduct and co-create a set of group norms concerning inclusion and belonging. The norms include: clear and honest communication; inclusion of researchers in making decisions about fieldwork; respecting personal boundaries; respecting and celebrating individual identities; support of team members; being aware of power differentials and how that might affect interactions; being aware of privilege; and expectations for working hours. In a meeting prior to the beginning of fieldwork, everyone will have the opportunity to participate in setting the tone of our team interactions. We will also adjust work tasks and housing assignments to allow individuals to avoid being alone with someone they don't feel comfortable with.

3. Communication processes within the off-site team and to the organization(s). Individuals participating in field research will have access to personal phones and personal computers, and regular internet or cell service, minimizing singular points of communication.

4. Organizational mechanisms that for reporting, responding to, and resolving issues of abuse or other misconduct. All participating individuals will be provided the following information:

a) Local law enforcement contact: 911.

b) Reporting sexual misconduct, harassment, discrimination, or retaliation: A challenge to reporting is that multiple institutions are involved in GCE work. Team members will be encouraged to report suspected or alleged misconduct to any or all of the following: their immediate supervisor, Merryl Alber (GCE PD), Steven Pennings (GCE co-PD), or any one of the GCE PIs; these reports will be conveyed to GCE or UGAMI leadership or relevant university offices as appropriate depending on the nature of the offense and the institutions involved. *Note that all University employees are required under federal law to report sexual misconduct to their Title IX office.* Team members can also report directly to the Human Resources or Equal Opportunity offices at their institution or the offender's institution. We will also inform participants to whom a report should be submitted and what to expect after a report is made.

c) In addition, individuals have the option to report "abuse of any person" that they are subjected to, have witnessed, or became aware of involving an NSF-funded program or activity to the NSF Office of Equity & Civil Rights at programcomplaints@nsf.gov.

d) Special considerations if third-party partners involved. Reports of abuse and/or non-inclusive behavior by third parties in the working environment will be reported to UGA's Equal Opportunity Office 706-542-7912, ugaeoo@uga.edu, which will assess the situation, provide support, contact equivalent offices at other universities and report cases to third-party entities when appropriate. Third parties who wish to report prohibited conduct by UGA or partner organizations' faculty, staff or students may follow their entities' codes of conduct and reporting structures or report incidents to Equal Opportunity Offices at relevant universities.

5. Physical safety. All participants in GCE research will be made aware of physical risks involved in the work, and steps to reduce these risks, during orientation meetings. Key points are as follows.

a) Interactions with the public. Fieldwork will be done in groups rather than alone to minimize risks from members of the public. Groups will be encouraged to wear clothing that identifies them as researchers; be prepared to introduce themselves and their purpose if questioned; be prepared to share study information or credentials, including a photo ID from the university and collecting permits. Hunting season information will be shared, and workers will wear red vests (available from GCE technicians) when in areas where people might be hunting. Participants will be told that they may leave if they feel afraid or are asked to leave, and that work will be re-scheduled.

b) Natural risks. The most significant natural risks of coastal fieldwork are heat and humidity, lightning, swift currents, diseases carried by ticks and insects, and wildlife (alligators, snakes, oysters). Supervisors will discuss precautions to be taken with their group and take appropriate steps to ensure their safety. Phone numbers for co-workers, the UGAMI office, and first responders will be provided to everyone. Boat work will not take place if there is a risk of lightning or high waves. The team will avoid physical labor in excessive heat. Researchers will wear clothing that protects from sun and vegetation and use sunscreen. They will wear a personal flotation device when working in a boat and take drinking water and a fully charged cell phone into the field. Benadryl will be on hand for allergic reactions to insect stings. Insect repellant and daily tick scans will be encouraged. Working alone on a field site is not required, and technicians will carry a first aid kit when groups are working at remote locations.

c) Float plans. Before each excursion, researchers will tell someone where they are going and when they expect to return from the field. That person will initiate a search if the researcher does not return on time and cannot be reached by phone.

d) Injuries and illness. In the event of a serious injury or illness, researchers will call 911, whether on the mainland or Sapelo Island. If the phone signal is poor, they will send a text with complete information (names, location, nature of problem) to a colleague who will call 911 (texting is often operational even when the phone signal is too weak for a call). On Sapelo Island, an automated external defibrillator (AED) is mounted on the first floor of the lab next to the restrooms. Researchers will be encouraged to learn first aid and CPR/AED and tell their co-workers about any medical conditions they have that could potentially need attention in the field.

6. Plan Dissemination. This plan, and the much more extensive documents that it summarizes, will be disseminated to all individuals participating in GCE research at multiple times, including annual meetings, a pre-summer orientation event conducted over zoom, and a summer orientation event located at the field site. Information will also be posted in UGAMI facilities.

Data Management Plan

1. **Overview**. The GCE has established a comprehensive information management program that supports the entire research enterprise as well as project logistics, administration, and governance. During GCE-I to -IV we developed efficient procedures and technology for acquisition, standardization, documentation, analysis, and synthesis of all GCE data. Our integrated information management system (GCE-IMS) is based on relational database and dynamic web application technology to manage, archive, and distribute data, metadata, and other research products. We also support GIS and remote sensing data products in the GCE-IMS and assist researchers with geospatial data processing, analysis, and archiving. *All LTER network standards and protocols are fully supported by the GCE-IMS*, and EML 2.2 described data sets are regularly synchronized with the LTER Data Portal (EDI) for automatic registration in DataONE and BCO-DMO, supporting data search and download through all these repositories. As of March 2024, GCE had uploaded 742 publicly available data sets to the EDI data portal representing almost 25 million tabular data records in 1214 files. An additional 1109 public data sets are also available through the GCE Data Portal. During GCE-V we will build on our established IM system and approaches to continue core data management efforts while further streamlining data submission. We will continue to transition our public-facing websites away from custom code to an industry standard content management system for improved maintainability and alignment with emerging LTER web design standards and practices.

2. **Data and Information Management System**.

GCE IT Resources. We maintain a strong IT infrastructure at UGA that we will maintain and expand to meet GCE-V information management needs. Current systems include a 10-core Dell server with 9.6TB drive array that runs Windows Server 2019 Hyper-V and hosts three virtual Windows servers (database, web and file) plus an Ubuntu Linux server for WordPress, a 12-core Dell server with 12TB drive array that serves as a backup server and host for additional virtual machines, and a 60TB Synology RAID server with 2 external 12TB backup drives for system backups, data archiving and workgroup data collaboration. All servers are equipped with redundant power supplies, UPS and RAID-5 or -10 drive configurations, collectively providing >100TB of fault-tolerant hard drive storage. We also maintain multiple workstation and laptop computers at UGA and UGAMI used for data processing, as well as a network file server at UGAMI for local computer backups. *In GCE-V we will migrate our production virtual servers to a new physical server to ensure system reliability and align with new software requirements.*

Basic networking, email, Listserv and VTC services will be provided by UGA, and each sub-contracting institution will provide network connectivity and computer support. Network- and application-layer firewalls, intrusion protection systems and secure transport protocols will be used to prevent unauthorized access to GCE systems. We will also operate and maintain the wireless data hub established on Sapelo Island during GCE-III to provide on-site storage, real-time data telemetry and remote management of the GCE flux tower, PHENOCAM, tide gauge and other instruments installed on the Island. The system includes a waterproof computer, outdoor UPS, 900MHz radio modem, WiFi router and 4G cellular modem for internet access, and streams over 300Mb of data to UGA daily for post-processing and analysis.

Software, Database and Website Development. Pre-built environmental data management software was not available when our program began in 2000, so we developed the GCE-IMS using general purpose scientific software (e.g. MATLAB, Python), commercial database systems (e.g. Microsoft SQL Server, ESRI ArcGIS) and web application frameworks (Microsoft IIS/ASP, eXist, Trac). *We will continue to use and maintain this software stack during GCE-V unless better community solutions emerge*, managing custom software code in a centralized Subversion repository (SVN) and following best practices (Wilson, 2006). We will also continue to make GCE software code available to the community as open source.

A major component of the GCE-IMS that we will continue to use in GCE-V is the GCE Data Toolbox, a MATLAB software library for metadata-based processing, analysis, quality control and synthesis of ecological data sets (https://gce-svn.marsci.uga.edu/trac/GCE_Toolbox). This software supports advanced, rule-based quality control analysis (Sheldon, 2008) and can import data from a wide variety of environmental data logger formats and data systems, making it ideal for developing automated data processing workflows. It also natively supports the EML 2.2 metadata specification, providing full interoperability with the EDI PASTA Framework and DataONE for both data archiving and synthesis.

We will also maintain the existing relational databases used to manage all project information, as well as related software and middleware tools that support automated metadata generation and access to GCE research products and associated information through applications, web services and websites (Fig. 1).

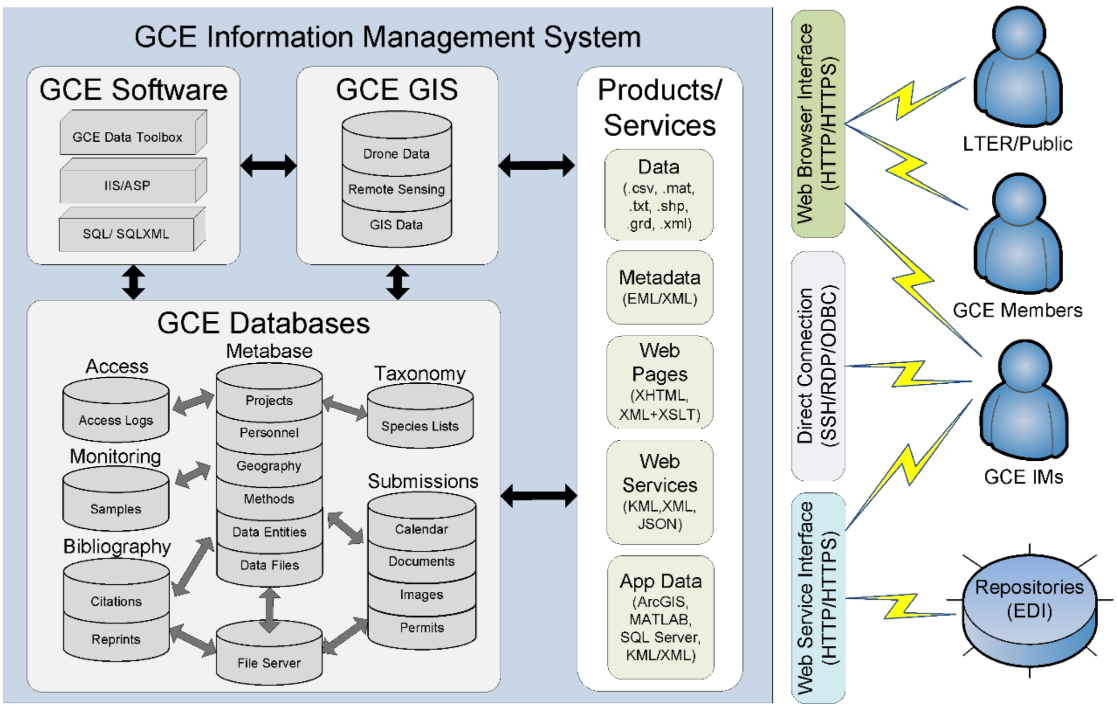


Figure 1. Overview of GCE Information Management System components and interfaces.

The GCE has a comprehensive public website (https://gce-lter.marsci.uga.edu) as well as a password-protected website for project participants containing submission forms, proprietary files, provisional data and other project resources. Visitors can search for data, publications and other research products directly, or discover them based on dynamic cross-links on pages across the GCE website (e.g. research projects, personnel pages, study site descriptions, Google maps, and species list entries). In addition, we have a public "Data Portal" website (https://gce-lter.marsci.uga.edu/portal/) to provide access to relevant ancillary data from federal programs and monitoring partners, documented and standardized for comparison with GCE data. We also maintain a dedicated WordPress site for our Education and Outreach activities (https://gce-schoolyard.uga.edu/). *These websites will be maintained and expanded in GCE-V, and we will continue efforts begun in GCE-IV to integrate these systems with a new public-facing WordPress 6.5 website to improve mobile device support, accessibility and maintainability moving forward.*

3. **Support for Site Science**

Integration of IM with the Research Program. *Information Management (IM) is integrated into all phases of the GCE research program and this will continue in GCE-V.* The Information Manager (Adam Sapp) serves on the GCE Executive Committee, regularly interacts with PIs and students in research planning, data analysis, and publication and proposal development (Table 1). He also routinely process, quality control and document routine monitoring data, providing Data-as-a-Service to the project.

Table 1. Integration of Information Management with the GCE Research Program.

Research Phase	**Information Management Support**
Study Design	Provide data, logistical resources (e.g. GPS, tide tables, maps, reg forms)
Data Collection	Provide advice on standards/practices, data harvesting, import filters
Data Analysis	Provide data processing, software tools, statistical reports, re-scaling
Quality Control	Provide guidance, software tools for data validation and QA/QC, reports
Publication	Provide analytical assistance, ancillary data, statistics, maps and aerial photos
Metadata	Provide metadata forms, templates, metadata importing, EML generation
Archival	Provide data and metadata cataloging, document/reprint archive, secured storage systems, offsite replication and backup, LTER/EDI synchronization
Reporting	Compile personnel information, publication lists and data usership profiles
Synthesis	Provide ancillary data, software for data search, re-sampling and integration
Governance	Manage email lists, databases for votes and research reg., IM on GCE-Exec

Data Acquisition and Submission. The GCE-IM works proactively with GCE investigators, technicians and students to develop workflows that ensure data are preserved, processed and documented as efficiently as possible, and *this will continue in GCE-V*. Electronic sensor data will continue to be automatically harvested from data loggers or online databases via network telemetry for automated processing whenever practical (e.g., flux tower, weather stations, streamflow gauges and VENμS satellite images). Sensor data that require manual downloading (e.g., sondes, well loggers and hand-deployed instruments) and drone imagery are synchronized to GCE servers on a routine basis for semi-automated processing. Monitoring data that are collected infrequently or are derived from laboratory analyses are submitted to the IM office at varying intervals, with sample information organized in a centralized database. Existing web forms and spreadsheet templates are used for preparing metadata from directed study and student research projects not amenable to automated processing, including non-tabular data from remote sensing, GIS, modeling, and mass spec. studies. All submitted data and support files are organized in hierarchical server directories, backed up daily, mirrored between servers and copied to external SSDs for off-site storage. Data submission and publication status is tracked and reviewed annually in conjunction with NSF reporting.

Data Processing and Quality Control. Tabular data from instruments and spreadsheets will continue to be processed using the GCE Data Toolbox, utilizing data parsing and quality control workflows designed in collaboration with GCE investigators. Metadata are added from pre-defined templates or imported directly from the GCE metadata database and then augmented with information derived from analyzing the data set. All transformations and data changes are automatically documented, resulting in metadata that describe the complete processing lineage. Finalized tabular data are archived in both standard text and MATLAB formats to provide broad compatibility. Geospatial (GIS) data, remote sensing imagery and other non-tabular data are processed, documented and quality controlled by investigators prior to submission using domain-specific software (e.g., Trimble Geomatics Office, ESRI ArcGIS, ENVI). Finalized data and metadata are then archived in domain-appropriate formats (e.g., file geodatabases, shapefiles, raster images, array formats).

Data Synthesis. Data integration, gap-filling and re-scaling protocols will be developed by IM staff in close collaboration with cognizant research teams, and long-term synthetic data sets will be updated on an annual basis. We will also archive more supporting information to capture the complete provenance of research findings, including research protocols, log sheets, computer code (e.g., R and MATLAB scripts), reference imagery and calibration data.

Data Distribution. All finalized data sets will continue to be versioned and distributed through the GCE Data Catalog (**https://gce-lter.marsci.uga.edu/public/app/data_search.asp**). Publicly released data sets are also synchronized to the LTER Data Portal (EDI) monthly for federated distribution through EDI, DataONE, BCO-DMO and related repositories. Data summaries and metadata are publicly available as soon as data sets are added to the GCE Data Catalog. The accompanying data files are available to GCE participants immediately, then automatically released to the public (and synchronized to EDI) within 2 years in compliance with LTER and NSF data access policies. Data downloads from the GCE Data Catalog and LTER Data Portal are tracked by research theme and user affiliation for reporting purposes, as possible. *See Tables 2-4 for a summary of planned GCE-V data products.*

4. **Support for LTER Standards**.

GCE has actively participated in and contributed to all LTER IM initiatives, and the GCE-IMS fully supports all LTER network protocols and standards. W*e expect this to continue in GCE-V.*

5. **Data Products**.

Anticipated data products for GCE-V are summarized in the tables below.

Table 2. Data acquisition from core monitoring outlined in Table 1 of proposed work. All data will be deposited annually into the EDI data repository (except for PhenoCam images, which are deposited in the PhenoCam network). Section corresponds to the first mention in the Plan of Work.

Section	Description	Data Sets	Acquisition Frequency
2.1A1	Weather stations	atmospheric conditions	Near-real-time
2.1A1	Tide height	water level, stage	Near-real-time
2.1A1	Altamaha River chemistry	nutrient concentrations	Monthly
2.1A1	Groundwater	salinity, temperature, pressure	Quarterly
2.1A1	Sound chemistry	nutrient concentrations	Monthly/Quarterly
2.1A1	Sound hydrography	water level, salinity, temperature	Quarterly
2.1B2	Soil accretion	sediment elevation	Annually
2.1B2	Marsh Monitoring	plants, invertebrates, insects, barnacles	Annually
2.1B2	Tidal Forest Monitoring	litter fall, tree growth	Annually
2.1B2	Flux Tower Fluxes	NEE, GPP, NPP, respiration	Quarterly
2.1B2	Flux Tower Biomass	plant biomass	Monthly/Quarterly
2.1B2	PhenoCam	imagery/phenology index	Near-real-time
2.1B2	Disturbance	disturbance to vegetation plots	Annually
2.1B2	Plant composition	plant community composition	Annually

Table 3. Data acquisition from field efforts outlined in Table 2 of proposed work. These data, which will be collected at varying times and frequencies (see proposal) will be deposited in the EDI data repository within 2 years of collection. Section corresponds to the first mention in the Plan of Work.

Section	Description	Data Sets
2.2C1	Plant and soil respiration	Plot-scale CO2 fluxes
2.2C2	pCO2	pCO2 levels in creek
2.4B2	Tree stem CO2	Stem CO2 flux
2.2C1	Aboveground biomass	Biomass, % cover, height
2.2C1	Belowground biomass	Biomass of live roots and rhizomes

2.4B2	Trees	Biomass (tree bands)
2.2C1	Invertebrates	Species identity, abundance, size
2.2C1	Niche breadth	Stable isotopes
2.2C2	Body temperature	Snail and bivalve biomimics
2.4B1	Microbes	Diversity, composition, metabolic activity
2.2C1	Soil properties	Bulk density, shear strength
2.2C1	Organic matter	Carbon content, loss on ignition
2.2C1	Porewater	Salinity, pH, redox, DIN, S2-, DOC
2.2C2	DOM	DOM composition (FT-ICRMS)
2.1C1	Elevation	RTK-GPS; total station
2.1C1	Temperature	Hobo loggers at 10 cm
2.1C1	Groundwater	Water level, conductivity, temp

Table 4. Additional data streams not covered in the tables above. These data will be collected at varying times and frequencies and deposited in the EDI data repository within 2 years of collection. High volume imagery and model output will be archived following best practices (Gries et al. 2021). Section corresponds to the first mention in the Plan of Work.

Section	Description	Data Sets
2.1A2	Shoreline armoring	GIS data of bulkheads, docks, coastal modifications
2.1A2	Citizen Science	Upland flooding events
2.1C	Aerial imagery	Aerial photographs, drone imagery
2.1C	DEM	GIS layers
2.1D	Model output	Delft-3D, soil salinity, groundwater
2.2A	Past environmental conditions	dendrochronology, oyster shell isotopes, geochronology
2.2A	Sea level	high-resolution spatial sea level
2.2C1	Gene expression	mRNA & rRNA sequencing
2.2C2	Water movement	ADCP
2.2D1	Soil respiration rates	DIC, ammonium, dissolved oxygen, sulfides, dissolved iron
2.3B	Sediment movement	extensometers with reference pipes
2.3C	Dragnet	Plant composition, light availability, soil chemistry
2.4B2	Nekton	community composition, biomass, abundance
2.5B	Model output	BERM model results

6. Physical Specimens

The GCE-LTER collects molluscs (snails and bivalves) as part of the annual fall monitoring effort (50 or more samples per year depending on which species are present). Organisms are measured and preserved in alcohol at the University of Georgia Marine Institute. Availability of these samples is advertised on the GCE web page (https://gce-lter.marsci.uga.edu/public/app/physical_specimens.asp). Lower-priority samples are progressively discarded after 3, 15 and 20 years due to limited storage space. *During GCE-V we will begin to transfer higher-priority samples* (starting with *Littoraria* snails from sites GCE3 and GCE6) *to the Collections Annex of the Georgia Museum of Natural History* (GMNH), which is located on the main campus of UGA in Athens. Each sample will be labeled internally with durable printed labels. Metadata will be stored in the Grace Thomas Invertebrates Collection database (invertebrates.uga.edu), which will allow internal organization/contextualization of the specimens as well as access to samples by outside researchers using standard GMNH policies. John Wares, who is a co-PI on the GCE project, is Curator of Genomics and Aquatic Invertebrates at the Museum and will oversee this effort.