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Overview:

The Georgia Coastal Ecosystems (GCE) LTER program, which is located along three adjacent sounds on the Atlantic coast, was established in 2000. GCE research focuses on long-term change in estuarine and intertidal wetland ecosystems. In GCE-IV we will focus on disturbance. Our specific goals are to: 1) Track environmental and human drivers that can cause perturbations in our focal ecosystems. We will accomplish this through continuing long-term measurements of climate, water chemistry, oceanic exchange, and human activities on the landscape. 2) Describe temporal and spatial variability in physical, chemical, geological and biological characteristics of the domain and how they respond to external drivers. We will accomplish this through our field monitoring program in combination with remote sensing and modeling. 3) Characterize the ecological responses of intertidal marshes to disturbance. We will accomplish this by ongoing monitoring and experimental work to evaluate system response to major perturbations in three key marsh habitats (changes in inundation and top-down control in Spartinadominated salt marshes; increases in salinity in fresh marshes; changes in runoff in high marshes), by implementing standardized experimental disturbances along salinity and elevation gradients, and by tracking responses to natural disturbances. 4) Evaluate ecosystem properties at the landscape level (habitat distribution, net and gross primary production, C budgets) and assess the cumulative effects of disturbance on these properties. We will also develop relationships between drivers and response variables, which can be used to predict the effects of future changes. We will accomplish this through a combination of data synthesis, remote sensing and modeling.

Intellectual Merit:

The major external drivers that influence the GCE domain can cause perturbations that result in disturbance. Ecologists have a long-standing interest in disturbance, but different studies define it in different ways and it is rare to have a comprehensive understanding of multiple disturbance types across abiotic gradients. The research proposed here is designed to systematically characterize perturbation patterns and to evaluate disturbance responses with a standardized suite of population, community and ecosystem variables. Information on the spatial and temporal patterns in perturbations will be combined with observed disturbance effects to produce cumulative "disturbance-scapes". The end result will be a landscape scale synthesis of disturbance responses in intertidal marshes and their relationship with external drivers.

Broader Impacts:

The goal of the GCE education and outreach program is to share our understanding of coastal ecosystems with teachers and students, coastal managers, citizen scientist and the general public. The GCE Schoolyard program is built around long-term contact and mentoring of educators, and we are planning an assessment to evaluate its effectiveness and improve the program in the future. The GCE children's book is now in its second edition; a GCE comic book will be produced during GCE-IV. We have also launched two citizen science web applications to align and interpret marsh photographs and will work with Schoolyard teachers to develop additional educational content for these sites. The GCE REU program will provide research opportunities for a diverse group of undergraduates, and cross-site courses will provide interdisciplinary training for graduate students. We will partner with the Georgia Coastal Research Council to exchange information with managers and promote science-based management of coastal resources. GCE information will continue to be broadly available via our website, which uses a state-of-the art information system to manage and display information about study sites, research, taxonomy, data sets, publications, and project administration.

Results of Prior Support (LTER: Georgia Coastal Ecosystems-III, OCE-1237140)

The Georgia Coastal Ecosystems (GCE) LTER program was established in 2000. We are now completing GCE-III, which has 20 Principal and 11 Affiliated Investigators from 9 Institutions. During this funding cycle GCE scientists have published 118 journal publications and 49 books, theses, and other one-time publications and have obtained external grants from NSF, NOAA, NASA and elsewhere to leverage our overall efforts. In addition, we received 3 supplements from NSF that allowed us to purchase new equipment, including an infrared gas analyzer, an unmanned aerial system (drone), radon detectors and a computer cluster, all of which supported our research mission. We also have strong programs in information management, education, and outreach. These accomplishments lay the foundation for the ambitious plan we propose for GCE-IV.

The GCE domain is located on the central Georgia coast (Fig. 1). It encompasses three adjacent sounds (Altamaha, Doboy, Sapelo) as well as upland (mainland, barrier islands, marsh hammocks), intertidal (fresh, brackish and salt marsh) and submerged (river, estuary, continental shelf) habitats. Our overall approach to studying this landscape is to assess how spatial and temporal variations in fresh and salt water affect biotic and ecosystem properties, with a focus on intertidal habitats. During GCE-I we began to describe the patterns of variability in the system with an emphasis on the marked spatial variation in freshwater inflow as a primary environmental forcing in our domain. In GCE-II we added a more detailed understanding of the movement of water between subtidal, intertidal and terrestrial habitats, taking into account freshwater-marine gradients along the longitudinal axes of the estuaries as well as lateral gradients including tidal exchange on and off the marsh platform. In GCE-III we focused on salinity and inundation as the major structuring variables in the domain. We asked how variation in salinity and inundation, driven by climate change and anthropogenic factors, affect biotic and ecosystem responses at different spatial and temporal scales, and sought to evaluate the consequences of these changes for habitat distribution and C flow across the coastal landscape. We divided our research into 4 inter-related programmatic areas, and our accomplishments in each of them are highlighted below. References to our 10 signature publications are in bold.

Area 1: External Drivers of Change We collected long-term measurements of environmental (meteorology, riverine input, and oceanographic conditions) and human (land use and population density) drivers of change in order to document temporal variation in boundary conditions that affect the domain. *These measurements will continue, with minor modifications, in GCE-IV.*

Environmental patterns Sheldon & Burd (2014) investigated the effects of seven climate signals on the precipitation and river discharge patterns of the Altamaha River watershed, which provides most of the freshwater to the GCE domain. They found significant relationships between three climate signals (the Bermuda High, the El Nino/Southern Oscillation (ENSO) cycle, and the Atlantic Multidecadal Oscillation) and precipitation and river discharge, indicating that these large-scale climate patterns affect the amount and seasonality of freshwater entering the estuary. This translates to changes in downstream ecosystems: annual variation in river discharge is the most important driver of primary production of the salt marsh grass *Spartina alterniflora* at most GCE sites (Wieski & Pennings 2014). We also analyzed our long-term record of water quality observations in the tributaries of the Altamaha River and found that discharge was the primary driver of nutrient loading to the estuary (Takagi et al. 2017).

Human drivers We conducted several studies to evaluate anthropogenic change in McIntosh County, GA, where the GCE domain is located. We produced a GIS database of shoreline structures, and **Gehman et al. (2017)** found that bulkheads at the high marsh/upland border had small but detectable effects on marsh attributes. Interviews conducted as part of the LTER cross-site "Maps and Locals" project identified changes in freshwater inflow as one of the primary environmental concerns of long-time residents. Hauer et al. (2015) used the "sea level affecting marshes model" to estimate the number of people potentially affected by sea level rise along the GA coast. We also used a combination of geological and archeological techniques to evaluate changes in shoreline position (DePratter & Thompson 2013) and the ways in which human occupation of the coast over past millennia varied with sea level (Turck & Thompson 2016).

Area 2: Long-term Patterns within the Domain We collected and modeled data documenting key variables within the GCE domain. These include variables that describe abiotic conditions, such as salinity and temperature, as well as ecosystem responses that span all five of the LTER core research areas. Major activities in this area consist of A) field monitoring of water and marsh attributes at our core monitoring sites, B) remote sensing of productivity and habitat distributions, and C) hydrodynamic modeling of water and salt transport. *These activities will continue, with minor modifications, in GCE-IV.*

Field monitoring - water column We monitored conductivity, temperature, and pressure at 10 sites distributed across the GCE domain. We also ran regular cruises to measure the surface water concentrations of dissolved and particulate materials. Di Iorio & Castelao (2013) analyzed long-term salinity data and found that system-wide freshening is dominated by river forcing. However, changes in salinity due to wind forcing caused different responses in the three sounds, indicating that the complex network of connecting channels plays an important role in water exchange. A series of oceanographic cruises during GCE-III provided information on seasonal salinity variability and net exchange between the mouths of the estuaries and the coastal ocean (Richards 2018). Saltwater intrusion shifts with river discharge and affects organic matter composition: high river flow leads to significant increases in the terrigenous signature of DOM throughout the estuary, which has implications for the oceanic fate of this material and its role in the global carbon cycle (**Medeiros et al. 2015**, 2017).

Field monitoring - marshes We monitor vertical accretion and sedimentation, plant productivity, animal abundance, and disturbance at our core monitoring sites to document spatial and temporal patterns across the domain. During GCE-III we added measurements to track habitat transitions and also began quantifying barnacle recruitment. A retrospective analysis of our long-term measurements of primary production indicated that Altamaha River discharge was the most important driver of *S. alterniflora* end-of-year aboveground biomass at almost all GCE core sites, especially in creekbank vegetation (Wieski & Pennings 2014). In the mid-marsh zone, river discharge and maximum temperature had similar predictive power. Disturbance (loss of aboveground vegetation) varied up to 14-fold among years as a negative function of river discharge and sea level (Li & Pennings 2016). Wrack (floating detritus) and creekbank slumping were the most common causes of disturbance at the creekbank, whereas snail herbivory was the most common in the mid-marsh. *These long-term observations provide a context for our new work on disturbance, which is a central theme of the research proposed for GCE-IV*.

Remote sensing One of the key challenges in using remotely sensed data in intertidal areas is that tidal flooding reduces spectral reflectance, making existing satellite products inaccurate and noisy. We developed the Tidal Marsh Inundation Index, which identifies flooded pixels so they can be filtered from spectral reflectance vegetation time series. We demonstrated its use on MODIS imagery from the GCE LTER, PIE LTER, and Gulf coast marsh sites (O'Connell et al. 2017). We expect this index to be broadly useful for creating high quality vegetation time series in tidal marshes. O'Donnell & Schalles 2016 developed an algorithm for Landsat5 imagery (1984-2011) that produced landscape estimates of *S. alterniflora* aboveground biomass. River discharge, precipitation, and sea level were all positively correlated with biomass, a result that was consistent with plot-level data (Wieski & Pennings 2014). The 28-year record documented a long-term decline of ~34% in plant biomass that appears to be related to increased frequency of drought. *In GCE-IV we will extend this time series with the Landsat8 satellite and expand the analyses to include other plant species*.

We initiated two new photographic time series that will continue into GCE-IV. The <u>"GCESapelo"</u> <u>Phenocam</u> is a digital camera that auto-collects oblique images every half-hour and contributes them to the National Phenocam Network. We developed a method to extract a subset of optimal scenes for phenological analysis (O'Connell & Alber 2016). The first 4 years of data show interannual and spatial differences in *S. alterniflora* phenology that result from differences in winter soil temperatures (O'Connell et al. in prep.). *We will follow up on these observations in GCE-IV*. We also collected a series of <u>highresolution aerial photographs</u> (15 cm-scale) of Altamaha Sound and the Duplin River. *We will use these photographs to follow geomorphic changes over time and to support scaled up estimates of disturbance*. *Hydrodynamic modeling* One of our major accomplishments in GCE-III was the implementation of the hydrodynamic FVCOM model (Chen et al. 2006; Zhao et al. 2010) in both the GCE domain and the Duplin River. Both implementations have been extensively validated and can produce accurate predictions of salinity and inundation. **Y. Wang et al. 2017** used the domain model to show the effects of river discharge and wind forcing on surface salinity over the course of the year. We also used Lagrangian particle tracking to produce highly detailed maps of residence time and transport patterns in both models (Y. Wang et al. 2017; McKnight 2016). *These models provide us with a powerful tool that we will use in GCE-IV to evaluate patterns of material transport, salinity, and inundation in the domain.*

Area 3: Response of Marsh Habitats to Changes in Salinity and Inundation We work in three key marsh habitats to assess how they respond to pulses and presses in salinity and inundation: salt marshes dominated by *S. alterniflora* (hereafter, Spartina marsh); fresh/brackish marshes found in lower salinity areas; and high marsh areas found at the marsh/upland border. *We will build on these studies in GCE-IV to focus specifically on perturbations, disturbance, and recovery.*

Spartina marsh During GCE-III we set up an eddy covariance tower to measure vertical CO_2 flux between the marsh and atmosphere. Our analyses show that light response curves vary as a function of the ratio between plant height and inundation, and suggest that net ecosystem exchange (NEE) is reduced by 55% when the marsh is covered by water (Nahrawi et al. subm.). A comparison of NEE data from PIE, GCE, and several other Atlantic coast sites revealed latitudinal differences in the seasonality and magnitude of CO_2 fluxes. *During GCE-IV, the ongoing data collected at the flux tower will be used to develop models of Spartina marsh gross primary production that can be scaled up with remote sensing.*

We also conducted several studies of salt marsh dieback, which is an important drought-associated disturbance in the GCE domain. We found that the abundances of all invertebrate groups and the diversity of macroinfauna were lower in areas that had experienced dieback, with clear separation between infaunal assemblages in bare versus vegetated reference plots (McFarlin et al. 2015). Angelini et al. (2016) showed that *S. alterniflora* had a greater chance of surviving a severe drought and was able to recolonize dieback areas more rapidly if *G. demissa* mussel aggregations were present. An experimental manipulation of wrack disturbance to *S. alterniflora* found that the timing of disturbance affected plant recovery rates, flowering, and densities of stem-boring herbivores (Li & Pennings 2017). Another type of disturbance agent that affects *S. alterniflora* is the herbivorous crab, *Sesarma reticulatum*, which can excavate large amounts of soil and consume plants at creek heads, facilitating headward erosion of creeks (Hughes et al. 2009; Vu & Pennings 2017). *These studies provide motivation and context for the disturbance experiments and observations proposed in GCE-IV*.

We also conducted studies to assess top-down effects on salt marsh ecosystems. Manipulation of diversity and body size of infaunal mud crabs showed that they indirectly facilitate primary production and affect biogeochemical cycling by controlling densities of periwinkle snails (Griffin et al 2015; Soomdat et al 2015; Davidson et al. 2015). Experimental removal of snails showed that their effects depend on their body size and density (Atkins et al 2015; Silliman et al 2013). A cross-kingdom experiment revealed that marsh ecosystem multifunctionality (primary production, decomposition, infiltration) is higher with a diverse set of consumers present (pathogenic fungi, snails, and crabs) (Hensel and Silliman 2013). We also evaluated the role of top predators, which are often highly mobile and have the potential to link spatially distinct food webs. We found that American alligators cross between salt and fresh water and consume salt marsh species such as blue crabs (Nifong et al. 2012, 2015; Nifong & Silliman 2017). Moreover, the presence of alligators influenced blue crab behavior, resulting in reduced foraging. This translated to increased survival of snails and ribbed mussels, demonstrating the cascading effects of an apex predator through the salt marsh food web (Nifong & Silliman 2013). To follow up on these types of observations, we initiated a predator exclusion experiment in summer 2016 in the Spartina marsh adjacent to the Duplin River. Our initial 6 months of data show increases in densities of snails and fiddler crabs in the predator exclusion cage treatment. We will continue the predator exclusion experiment in GCE-IV.

Fresh/brackish marsh During GCE-III we began regular monitoring of the channel-edge vegetation along the Altamaha River and established an additional core monitoring site in the tidal fresh forest. We also initiated the Seawater Addition Long Term Experiment (SALTEx), which is a large-scale field manipulation to evaluate how pulses and presses of brackish water affect a tidal freshwater marsh.

Craft (2012) found that soil accretion rates (~1-2 mm/y) in tidal forests in coastal Georgia, measured using ¹³⁷Cs and ²¹⁰Pb, were substantially lower than that of sea level rise (SLR) in this area (3.2 mm/y, NOAA 2018), suggesting that accelerated SLR is likely to lead to decline of tidal forests due to submergence and expansion of oligohaline and brackish marshes. We also evaluated the short-term effect of saline intrusion on N and P storage in tidal forest soil: soils from areas that were not experiencing saltwater intrusion removed considerable inorganic N from freshwater, but released it when inundated with salt water (Jun et al. 2013). This suggests that tidal forest soils, which normally adsorb nutrients, could release them as a consequence of saltwater intrusion. SALTEx is designed to mimic saltwater intrusion caused by droughts and long-term sea level rise. We set up 30 plots (2.5 m²) in a freshwater marsh in 2013 and collected one season of background/pretreatment data. There are 5 treatments, with 6 replicates each: 1) Press plots were inundated with brackish water to maintain their porewater at target salinities of 2 - 5. 2) Pulse treatments received a 2-month pulse (September and October) of increased salinity. There is also 3) a freshwater addition, 4) a procedural control (with siding), and 5) an unmanipulated (unsided) control. We began treatments in April 2014 and continued them for four growing seasons (2014-2017).

The SALTEx press treatments have shown changes in: 1) inorganic constituents (elevated porewater N, P, and S, and an increase in reduced sulfur (i.e. pyrite-FeS₂); decreased levels of soil iron-bound P); 2) soil conditions (increased temperature and decreased redox potential) and 3) soil organic matter (shifts in bacterial and fungal biomarkers). There have also been changes in 4) greenhouse gas emissions (decreased CH₄ and net ecosystem production); 5) primary producers (almost complete loss of above- and belowground plant biomass and an increase in benthic microalgae); and 6) sediment elevation (decreasing by 1 cm/y). The press treatments are now essentially bare soil, but with some signs of encroachment by brackish emergent plants. The pulse treatments have shown intermediate responses (**Craft et al. 2016**; Li et al. in review; Herbert et al. in review). In accompanying mesocosm experiments, species richness and plant biomass decreased with increasing pulse duration and salinity (Li & Pennings in review). *We stopped SALTEx treatments in December 2017 and will follow recovery from these disturbances in GCE-IV*.

High marsh We documented the effects of shoreline armoring on high marsh ecosystems, evaluated time series data from instrumented groundwater wells, and initiated an experimental manipulation of freshwater input from upland habitats. We surveyed 60 high marsh sites, comparing residential sites with and without bulkhead structures to forested areas (**Gehman et al. 2017**). Marshes adjacent to bulkheads had lower elevations than those adjacent to unarmored or forested sites, with greater *S. alterniflora* coverage and crab burrow abundance. As part of a cross-site LTER effort characterizing ecological responses to armoring across a wide diversity of coastal settings, Dugan et al. (2017) found that 71% of the ecological effects of armoring were negative, 22% were positive, and 7% were not significant. Both of these papers are part of a special issue of *Estuaries and Coasts* on Shoreline/Land Use Effects.

Analyses of groundwater wells showed that submarine groundwater discharge to the marsh is proportional to tidal amplitude and varies with tidal stage and sea level (Wilson et al. 2015a). However, Ledoux (2015) found that precipitation-driven flow exceeds the impact of tidal forcing on net groundwater flow from the upland to the marsh. Differences in hydrologic regime can be linked to zonation in marsh plants, with *Juncus roemerianus*, *S. alterniflora*, and succulents found in areas with differing hydrological regimes and porewater salinities (Wilson et al. 2015b; Evans & Wilson 2016, 2017).

To assess the effect of water discharge from the upland on high marsh ecosystems, we initiated an upland manipulation in an area on Sapelo Island with a well-developed surface sandy layer that serves as a

potential conduit for freshwater to the marsh. We established five blocks, each containing three 7 m x 10 m plots, along the upland border. Plots were divided into five 10-m long lanes for different types of sampling (resistivity profiles, vegetation and macro-invertebrate transects, wells and soil cores, and future activities). We collected pre-manipulation vegetation and invertebrate data in July of 2015 and 2016 and imposed one of three treatments (reduced freshwater input, increased freshwater input, control) in March 2017, for a total of 5 replicates per treatment. To reduce surface flow and shallow groundwater flow into the reduced input plots, we trenched a 1-m deep diagonal cut across the upland border of each plot and installed a plastic barrier running from 1 m below to 10 cm above the soil surface. The barrier directs blocked water into an adjacent "addition" plot. Addition and control plots were trenched to control for disturbance, but do not have a barrier. We are tracking groundwater pressure continuously to characterize the horizontal hydraulic gradient, and are regularly sampling plants and invertebrates. *We will continue the upland manipulation in GCE-IV*.

Area 4: Integration and Forecasting We use a combination of integrative modeling, empirical observations, and remote sensing to assess habitat distribution and carbon flow across the landscape, and to evaluate how changes in salinity and inundation may change these services in the future.

Integrative modeling We use a suite of models that includes hydrodynamic models, a soil model, and a Spartina model. The GCE domain (**Y. Wang et al. 2017**) and Duplin River (McKnight 2016) hydrodynamic models (FVCOM, Area 2) produce high-resolution predictions of transport, water column salinity, and intertidal inundation over a range of scales and have been useful for evaluating salinity and inundation patterns in response to sea level rise and storm conditions. We also developed a process-based, spatially explicit soil model that predicts porewater salinity based on hydrology and evapotranspiration (Miklesh & Meile subm.). The Spartina model, which is a modification of Morris et al. (1984), was revised to include mechanistic transport from above- to belowground tissues based on field observations of non-structural carbohydrates (Jung & Burd 2017), salinity, inundation, and basic phenology. *These modeling activities will continue in GCE-IV to help interpret field data and make predictions about ecosystem responses to sea level rise, changes in freshwater inflow, and other drivers.*

Habitat provisioning Accurate habitat and elevation maps are critically important for flood inundation mapping, coastal hazard assessments, and modeling sea level rise. We used a combination of LiDAR and hyperspectral imagery to produce an accurate digital elevation map (DEM) and an improved habitat classification for the marshes on the Duplin River (**Hladik et al. 2013**). This served as the basis for a detailed evaluation of the relationship between marsh platform geomorphology, vegetation composition and biomass, and invertebrate densities (Schalles et al. 2013). The habitat map has now been extended with field observations obtained with an RTK GPS to include brackish and tidal fresh marshes. GCE investigators also worked with the developer of Sea Level Affecting Marshes Model (SLAMM) to incorporate ecogeomorphic feedbacks among flooding depth, biomass, and accretion. When the model was run using a variable accretion rate and improved elevation information, the predicted effects of sea level rise on intertidal marshes along the Altamaha River changed from marsh loss to marsh gain (Herbert 2015). *During GCE-IV, we will use the updated habitat map to study variation in S. alterniflora biomass along the entire GA coast.*

Carbon The sources and sinks of carbon in the coastal ocean are an important, but little understood, component of the global carbon budget (Cai 2011). **S. Wang et al. (2017)** published a complete budget of CO_2 exchange in the Duplin River estuary (based on DIC exchange in a small creek in combination with estuary metabolism measurements), which showed that the system was a net source of CO_2 to the atmosphere and coastal ocean and a net sink for oceanic and atmospheric O_2 . On a larger scale, we evaluated C export to the South Atlantic Bight and found that terrestrially derived CO_2 from both rivers and intertidal marshes was exported to the continental shelf, with highest inputs closest to shore (Jiang et al. 2013; Reimer et al. 2017a, b). GCE investigators were also part of several major review papers on the coastal ocean (Hopkinson et al. 2012; Bauer et al. 2013) that evaluated the overall importance of C storage (blue carbon) in wetland sediments. Although there is still much uncertainty in global estimates,

these papers point out that the coastal ocean may have become a net sink for atmospheric C and that changes in river discharge, the loss of coastal wetlands, and increasing atmospheric levels of CO_2 will continue to alter shelf-atmosphere-open ocean C exchange in the future. *During GCE-IV, we will continue to improve our estimates of the domain C budget.*

Cross-site Research During GCE-III we participated in a number of cross-site research efforts. Alber and Alexander are part of a Coastal SEES effort comparing marsh sustainability among the three Atlantic Coast salt marsh LTER sites (GCE, PIE and VCR). Mishra and the GCE flux tower group are working with PIE and investigators in South Carolina and Delaware to compare NEE along a latitudinal gradient. Byers, Alber and Alexander participated in a cross-site working group led by the SBC LTER on the ecological effects of armoring. Medeiros is collaborating with FCE scientists to characterize highly biorecalcitrant "black C" in the Altamaha River. Craft is participating in a coast-wide comparison of sediment delivery that includes both GCE and PIE. Craft and Pennings have active collaborations with scientists in China, and Meile is part of a project that is collaborating with the Luquillo Critical Zone Observatory. *We will continue to pursue cross-site research opportunities in GCE-IV*.

Education and Outreach Graduate students who participated in GCE-III completed 7 MS theses and 10 PhD dissertations; we currently have 31 graduate students from 7 institutions. We routinely involve undergraduate students in our research, many of whom have gone on to graduate school. During GCE-III, REU funds supported 14 of the 64 undergraduate students who have been part of the program. The GCE Schoolyard program provides in-service training in field ecology for K-12 educators. From 2000 to 2017, approximately 120 teachers participated in one or more Schoolyard sessions. We also published a children's book, "*And the Tide Comes In*," as part of the LTER children's book series. The book, along with supplemental materials targeted for K-12 educators, has been widely distributed through our partners in Marine Extension, 4H, and other environmental education centers, and was reprinted in 2017. We led a distributed graduate course on wetland ecology in 2013 and 2015 that reached more than 150 students and coastal managers across the country and participated in a similar course led by FCE in 2016.

The GCE provides outreach to coastal managers through partial support of the Georgia Coastal Research Council (GCRC), which promotes science-based management of Georgia coastal resources by facilitating information transfer between scientists and managers. The GCRC currently has 168 affiliates representing 19 universities and 17 federal and state agencies. GCRC activities during GCE-III have included holding meetings of scientists and managers, working on the development of numeric nutrient criteria, and writing technical summaries about vegetated buffers in the coastal zone, the effects of climate signals on shrimp and crab catch, disposal of dredge material, and living shorelines. The GCE also directly partners with the Sapelo Island National Estuarine Research Reserve (SINERR), the Nature Conservancy, and the USGS to collect data of mutual interest.

Finally, the GCE website provides public access to information and data from the GCE program as well as decades of research on Sapelo Island and the Georgia coast. Over 1.5 million visits from 234 countries and territories have been logged on the GCE website since its introduction in December 2000, accounting for over 5 million page views. *We will continue all of these efforts in GCE-IV*.

Information Management During GCE-III we continued an IM approach that met the highest LTER IM standards and served as a benchmark for the ecological informatics community. As of February 2018 there are 576 data sets registered in the GCE data catalog (comprised of 897 data objects), 567 of which are publicly accessible in the LTER Data Portal (EDI) and discoverable through DataONE and BCO-DMO. We have also added 763 publicly accessible ancillary data sets to the GCE data portal. Collectively, we have archived over 26 million data records that have been accessed by a diverse user community (>145,000 file downloads to date; see Data Download Statistics in Data Availability Report). Our information manager, Wade Sheldon, who served on the LTER IM Executive Committee and Executive Board and co-chaired the Network Information System Advisory Committee, also provided technical assistance and software tools to other sites. *During GCE-IV we will maintain high IM standards while transitioning to a more generic web platform (See Data Management Plan)*.

PROJECT DESCRIPTION

INTRODUCTION

The GCE LTER program focuses on estuarine and intertidal wetland ecosystems, and how they respond to long-term change. The study site is located on the coast of Georgia and encompasses three adjacent sounds (Altamaha, Doboy, Sapelo). The Altamaha River drains a watershed of 36,700 km² and is the largest source of freshwater to the area (Fig. 1). 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 also serves to funnel the tides, which are semi-diurnal and vary 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. Estuarine salinities grade from euryhaline to mesohaline to oligohaline as one moves upstream, and adjacent intertidal areas shift from salt to brackish to fresh marsh habitat, and then to tidal fresh forest (Fig. 2). Plant communities of salt marshes are dominated by the grass Spartina alterniflora, brackish marshes by the rush Juncus roemerianus, fresh marshes by the grass Zizaniopsis miliacea, and tidal fresh forests by the trees tupelo gum, Nyssa aquatica, and cypress, Taxodium distichum. Inundation defines the boundaries of the intertidal zone, which occurs between subtidal (always inundated) and upland areas (only inundated by extreme events such as hurricanes), with differing communities occurring along this elevation gradient. Patterns and processes in this complex landscape vary spatially (within and between sites) and temporally (tidal, diurnal, seasonal, and annual).

Overlain on this "normal" heterogeneity is long-term forcing due to both environmental change and human alteration of the landscape (Figs. 3, 4). Mean sea level is rising at a rate of 3.2 mm/y; this rate is expected to increase as higher global temperatures accelerate glacial melting and expansion of ocean and coastal waters (Meehl et al. 2007). The North Atlantic Oscillation, ENSO cycles, and variability in the Gulf Stream also generate localized hotspots of SLR along the Atlantic coast (Ezer et al. 2013; Valle-Levinson et al. 2017). The net effect of SLR is to push salt water further upstream and increase the depth and duration of flooding of intertidal areas. The Altamaha River watershed, which includes parts of metro Atlanta, is experiencing population growth and land use changes that affect both the quantity and quality of river discharge to the GCE domain (Tagaki et al. 2017). The coastal Georgia population is projected to increase by 33% between 2015 and 2050, with an accompanying 26% increase in water demand (Coastal Georgia Regional Council 2017). This growth will likely be accompanied by an increase in impervious surfaces as roads and other structures are built, along with an increase in the demand for shoreline structures such as bulkheads. This increased hardening of the uplands will alter runoff and infiltration patterns that can, in turn, affect marsh ecosystems (Gehman et al. 2017; Dugan et al. 2017). Although the southeast region has warmed only slightly over the last few decades, the National Climate Assessment predicts future warming with a significant increase in the number of very hot (>95°F) days (USGCRP 2017). These drivers can be characterized as "presses" to the system because they are ongoing. However, some of them (e.g. sea level rise, population growth) may more properly be called "ramps" (sensu Lake 2000) because they are not only ongoing but are also steadily increasing in magnitude over time.

The GCE domain is also subject to shorter-term "pulse" perturbations. Over the past 16 years it has experienced extremes in precipitation, including several major droughts and two hurricanes, which have caused increased environmental variability (e.g. as indexed by the Palmer Drought Severity Index; Fig. 3c). Decreases in river discharge associated with droughts influence estuarine salinity and residence time (Y. Wang et al. 2017), organic matter composition (Medeiros et al. 2015), plant distribution (White & Alber 2009), and plant production (Wieski & Pennings 2014) and are the likely cause of long-term decreases in *S. alterniflora* biomass (O'Donnell & Schalles 2016; Fig. 5). Droughts have also been linked to marsh dieback events in which distinct patches of *S. alterniflora* suddenly senesce, leaving bare exposed mud (Alber et al. 2008; Silliman et al. 2005; Angelini & Silliman 2012). Wrack deposition, creekbank slumping, and herbivory (Fig. 2c) are all common perturbations that affect plant biomass (Li & Pennings 2016). Characterizing the duration, frequency, and magnitude of these perturbations and

quantifying their effects on ecological processes is essential for evaluating their relative importance at the landscape level. For example, Macreadie et al. (2013) found that seagrass wrack affected 30% of a Florida salt marsh and that soil organic C in these areas was 30% lower than in unaffected areas. Overall, this resulted in an estimated 10% reduction in soil C across the entire marsh.

The ecological literature regarding disturbance uses a variety of terminology in inconsistent ways (Standish et al. 2014; Angeler & Allen 2016) For the purposes of this proposal, we use the following definitions (see also Fig. 6). We define a **perturbation** as a disruption in the environment that is outside the range of normal variability (which must be defined). For example, a hurricane would be considered a perturbation whereas seasonal variation in precipitation would not. Although they are often caused by external drivers, we are concerned here with how perturbations act within the GCE domain (e.g. a hurricane may manifest as a change in estuarine salinity or an increase in inundation). Perturbations can be either abiotic (e.g. increased temperature) or biotic (e.g. herbivore grazing). We define a **disturbance** as a perturbation that causes a significant response (which must be defined) in a population, community, or ecosystem property. The magnitude of a response to a given disturbance (measured by comparing a variable before and after the perturbation, or, for a localized disturbance, comparing affected and unaffected areas) is a measure of **resistance**, such that a variable that experiences a large change has low resistance. If a perturbation does not cause a significant biotic response, we define that as **persistence**. Once a system's property is disturbed it may **recover**, which can be quantified in terms of time or rate of return to pre-disturbance or control conditions. If multiple variables are being tracked they may show differing levels of resistance and recovery rates. Although these can be evaluated individually, ecologists often use multiple ecological variables, either separately or in combination, to evaluate system state (e.g. Spencer et al. 2011). Following Pimm (1984), we consider an ecosystem to be resilient if it has a fast recovery rate. If the system does not recover but instead transitions to a new habitat (e.g. salt marsh replacing brackish marsh or submerging marsh converting to unvegetated mud flat) we consider that a state change. Because we will evaluate state changes over a period of a few years, which is less than the generation time of many of the organisms involved, we will not be in a position to formally determine whether state changes are stable within the time frame of GCE-IV.

Studying responses to disturbance is complicated by the fact that different types of perturbations can occur simultaneously and interact (Peters et al. 2004; Turner 2010; Foster et al. 2016). For example, the effect of a drought may be intensified by sea level rise or an increase in summer temperatures. The relationships between drivers and responses also may vary from linear to saturating to sigmoidal (Andersen et al. 2008; Bestlemeyer et al. 2011; Petraitis & Hoffman 2010; Hunsicker et al. 2016). We can begin to tease this apart by considering pulse, ramp and press perturbations, alone or in combination, together with different driver-response relationships, to develop a family of potential outcomes ranging from no response (i.e. persistence) to recovery to a state change (Figs. 6, 7). We can also test for interactions experimentally by evaluating the response to the same perturbation across a range of abiotic conditions. For example, we have found that *S. alterniflora* recovered from experimental clearing faster in low as compared to higher-salinity areas (Fig. 8), whereas the response was parabolic along an elevation gradient (Table 1; see also van Belzen et al. 2017). This indicates that the response of an ecosystem to a given pulse perturbation needs to be interpreted in the context of underlying abiotic gradients.

In this proposal we seek to advance ecological understanding of perturbations and disturbances. In a recent review, Donohue et al. (2016) made several important points regarding the limitations of previous research: 1) theoretical studies tend to focus on the effects of a single pulse perturbation; 2) few studies combine theory and empirical measurements; 3) most empirical studies focus on population or community characteristics rather than ecosystem functions and processes; and 4) there is a strong bias towards terrestrial systems (only 16% of the studies they evaluated were marine). Similar conclusions were reached by Sasaki et al. (2015), who found very few papers that examined press and pulse disturbances at the same time. This topic is particularly salient not only because many elements of global change show an increase in both mean and variance over time (Donahue et al. 2016), but also because the threshold for a state change may change with different underlying conditions (Scheffer & Carpenter 2003;

van Belzen et al. 2017). Our work addresses these knowledge gaps by focusing on multiple types of disturbances, combining theoretical and empirical approaches, and examining a suite of population, community, and ecosystem responses.

The research proposed for GCE-IV is designed to characterize perturbation patterns and their relationships to external drivers, to develop an understanding of disturbance responses, and to evaluate the consequences of these responses at the landscape scale. These ideas are summarized in our conceptual model of disturbance (Fig. 9; see also 2c), which lists the major external drivers that influence the GCE domain, which in turn interact with internal processes and manifest as domain perturbations (e.g. sea level rise may increase inundation; shoreline armoring may affect runoff). Whether or not the perturbation results in a disturbance, and the magnitude of the response to disturbance, is contextdependent, which is represented in the figure as a function (f) of both the domain perturbations and the biophysical characteristics of the system (e.g. short-term increases in salinity may be more important in fresh than in salt marshes). If the system is disturbed it will cause a response in abiotic, population, community, and ecosystem-level properties. Changes in these properties will likely feed back to affect the biophysical template (e.g. causing changes in population densities or in porewater ammonium concentrations), which will in turn alter how the system responds to ongoing or future perturbations. In response to a disturbance, the system may recover or transition to a new habitat. Information on the frequency, intensity, and duration of various perturbations can be combined with observed disturbance effects to produce cumulative "disturbance-scapes" that can be used to assess the landscape-scale consequences of disturbance in coastal wetlands.

INTELLECTUAL MERIT

During GCE-IV we seek to build on the major programmatic elements developed in the first three funding cycles but with an explicit focus on how perturbations affect the domain. We propose a combination of monitoring, focused studies, long-term field manipulations, and modeling to evaluate the conceptual model described above (Fig. 9). We divide our proposed research into 4 inter-related programmatic areas (Fig. 10, which also lists the PIs primarily responsible for each sub-project).

Area 1: External drivers of change External drivers such as climate change, sea level rise, and human alterations of the landscape all affect the estuaries and marshes in the GCE domain. In Area 1 we document their patterns over time and space. Most of our proposed activities are a direct continuation from GCE-III, but we will statistically characterize these external drivers in terms of long-term trends, spatio-temporal variability, and occurrence of extreme events (e. g. storms, droughts) so that we can investigate the links between external drivers, domain perturbations, and ecosystem response. We will also add studies of land use and human populations in the upland areas of the GCE domain to enhance our understanding of human drivers of change. *Our goals are to track long-term changes in environmental drivers and human effects (in both the adjacent uplands and the entire watershed*).

Area 2: Long-term patterns within the domain We follow spatial and temporal variability in physical (estuarine salt intrusion length, residence time, and inundation), chemical (salinity, nutrient concentration and speciation, dissolved inorganic C, and pH), geological (accretion) and biological (organism distribution, abundance, and productivity) characteristics within the GCE domain. This provides the long-term perspective necessary to understand how observations in the five core areas respond to changes in external drivers (Area 1). To understand these relationships, *and to be able to evaluate how the biophysical template of the domain sets the context for response to perturbations*, we will continue our core monitoring program, remote sensing, and modeling, all of which build on the foundational work of GCE I through III. For GCE-IV we will also sample soil temperatures and assess DOM transformations and the health of tidal fresh forest trees. *Our goals are to describe the biophysical template of the GCE domain in relation to external drivers and to evaluate responses to domain perturbations*.

Area 3: Marsh response to disturbance The research in this area is designed to characterize the responses of our three key marsh habitats—*S. alterniflora*-dominated salt marsh, fresh/brackish marsh,

and high marsh—to disturbance. We will take advantage of ongoing monitoring and experimental work to assess ecological responses to major perturbations in each habitat (i.e. changes in inundation and top down control in Spartina marshes; increases in salinity in fresh/brackish marshes; and changes in runoff and groundwater infiltration in high marshes). We will also **add new research** to evaluate how the responses of these three marsh types to a standardized disturbance vary across abiotic gradients of salinity and inundation. We hypothesize that both marsh resistance to and recovery from disturbance will be a function of underlying abiotic conditions (Fig. 11). Our goals are to track trajectories of response and recovery from disturbance and to characterize transitions to new states.

Area 4: Integration and forecasting The information on drivers (Area 1), the biophysical template (Area 2), and marsh response to disturbance (Area 3) all correspond to the components of our conceptual model (Fig. 9). In Area 4 we will synthesize this information to evaluate ecosystem properties at the landscape level (habitat distribution, net and gross primary production, C budgets) and assess the cumulative effects of disturbance. We will also use these results to develop relationships between drivers and response variables, which can be used to predict the effects of future changes. *Our goals are to produce synoptic estimates of ecosystem properties in the GCE domain, to quantify disturbance effects at the landscape scale, and to develop driver-response relationships for marsh ecosystems*. We will accomplish this through a combination of data synthesis, remote sensing, and modeling.

Ecologists have a long-standing interest in disturbance, but different studies define it in different ways and it is rare to have a comprehensive understanding of multiple disturbance types across abiotic gradients. By systematically quantifying perturbation patterns and evaluating disturbance responses, we will provide *one of the most comprehensive studies of disturbance effects at the landscape scale.* These efforts will result in a synthesis of disturbance effects and resilience in intertidal marsh ecosystems and their relationships with external drivers, thus positioning us to predict how the system may be influenced by future change. Below we describe the research proposed for each of our program areas.

Area 1: External Drivers of Change

We will continue to collect long-term measurements associated with both environmental and human drivers that influence conditions in the GCE domain.

Environmental drivers We use a series of meteorological stations to characterize the GCE domain (Fig. 1, Table 2). The station at Marsh Landing on Sapelo Island, which we operate in partnership with the Sapelo Island National Estuarine Research Reserve (SINERR), serves as our primary station for the LTER Climate database (ClimDB). The station at Hudson Creek in Meridian is operated in cooperation with the USGS. We make near-real-time and historic data and plots from these and other relevant climate stations publicly accessible on the GCE Data Portal. In GCE-III we established an eddy covariance flux tower, which also serves as a level 3 weather station.

The majority of freshwater input into the GCE domain enters via the Altamaha River. The USGS gage stations at Doctortown and Everett City provide near-real-time data on river discharge, and we collect monthly samples for analysis of dissolved inorganic nutrients (NO₃, NH₄, PO₄), organic constituents (DON, DOC, PN, PC), DIC, pH, and alkalinity to track changes in concentration and loading. Riverine input is the primary determinant of salinity at each of our core monitoring sites except station GCE1 (Fig.1), where groundwater and precipitation are locally important (Di Iorio & Castelao 2013; Y. Wang et al. 2017). We previously used Rn-222 surveys (Peterson et al., in prep) to quantify groundwater flux to the Duplin River and constrain total freshwater inputs for the hydrodynamic model. *In GCE-IV we will expand our Rn-222 surveys to GCE1* to improve our understanding of subsurface water inputs at this site.

We obtain real-time monitoring data on oceanographic conditions (including pH) from the National Data Buoy Center's station at the Gray's Reef National Marine Sanctuary, and sea level data from NOAA/NOS stations in Fort Pulaski GA and Fernandina FL. Our Meridian station also monitors local sea level height variations (Fig. 12a). These data are regularly retrieved from NOAA/NOS and processed for analysis. *Human drivers* The GCE is located in McIntosh County, GA. The county is rural, with a low population density (~13/km²), a median household income of \$43,000, and a poverty rate of 21% (DataUSA 2017). However, this is a rapidly exurbanizing and gentrifying area, and development is likely to result in shoreline alteration and additional impervious surface. There is also an increasing threat of flooding due to sea level rise and storms, which will increase pressure for shoreline armoring. During GCE-III, we created a GIS database of shoreline armoring along the GA coast and found that the extent of armoring was highly correlated with impervious surface coverage at the county scale (r = 0.98). *We will build on this in GCE-IV by evaluating trends in population density, demography, and property transactions and how they relate to land use, impervious surface cover, and shoreline structures*. This information will allow us to develop realistic scenarios for how human population increases in the GCE domain will affect freshwater input into marshes and potentially limit marsh migration into the upland. We will also use it to identify areas of pending development that could be used for high marsh studies (Area 3c).

The modern landscape also reflects a legacy of thousands of years of human alteration. Lulewicz et al. (2017) found evidence that the size of oysters in shell middens decreased around 3800 years ago. *In GCE-IV, we will focus on human modification of oyster reefs as a large-scale disturbance that persists today.* This will involve sampling historical (19th century) reefs, paleo-reefs, and shell middens to evaluate the age and size distributions of past oyster populations in comparison to current distributions. We hypothesize that contemporary oyster reefs are less prevalent in extent and are comprised of smaller oysters in comparison to historical and paleo-reefs.

Area 2: Long-Term Patterns within the Domain

We will continue to collect data documenting key ecosystem variables within the GCE domain. These data provide the large-scale and long-term context for our research questions, and stimulate new research questions as we seek to better understand ecosystem patterns and dynamics. Major activities in this area consist of A) field monitoring of water and marsh attributes, B) remote sensing, and C) modeling.

Field monitoring Our core monitoring program (Table 2), which addresses the **five LTER core areas**, will continue with only minor modifications for a total of 24 years by the end of GCE-IV. We have 11 core monitoring sites where we work in the water and the adjacent intertidal areas (Fig. 1c). We also have a water column station at an offshore site (AL-2) to characterize mixing of the Altamaha River plume with the ocean. We deploy sondes that monitor salinity, temperature, and pressure continuously at 10 of our sites (Figs. 1c, 12b) and obtain vertical CTD profiles at all sites during regular cruises. We measure nutrients, chlorophyll, particulate material, pH, and DIC monthly at two endmember stations (GCE7, a low salinity site upstream in the Altamaha River, and GCE6, a high and variable salinity site on Sapelo Island) and sample a more limited list of variables at the remaining stations quarterly (Table 2). We also collect continuous horizontal Acoustic Doppler Current Profiler (ADCP) measurements of water flux between the Duplin River and Doboy Sound. We obtain estuarine pH data from four sondes operated within our domain by SINERR. *In GCE-IV we will add regular sampling of DOM composition at the head and mouth of the Altamaha estuary* to identify dominant transformations as DOM transits toward the sea (Medeiros et al. 2015).

At the marsh sites we monitor soil accretion, accumulation, and compaction through SETs (Sediment Elevation Tables), and porewater salinity, plant community composition and biomass, and invertebrate community composition in permanent plots on an annual basis (Table 2, Fig. 12c). In the tidal fresh forest we measure productivity as well as sedimentation and soil elevation. To track transitions between habitats we currently conduct annual assessments of mixed vegetation plots and the distribution of fresh/brackish marsh vegetation. *We will augment this sampling in several ways during GCE-IV.* 1) Given that long-term changes in temperature have the potential to influence marsh processes, we will deploy soil temperature loggers at all core sites. We will also explore the use of biomimetic sensors (mimics of 1 gastropod and 2 bivalve species) to obtain biologically relevant measurements of temperature (Lima et al. 2011; Helmuth et al. 2016). 2) After Hurricane Irma, which brought a large pulse of salt water upstream in the Altamaha

River, we identified trees at each of 40 stations along a 10 km transect starting at the most downstream distribution of tidal fresh forest in our domain (30 km from the mouth). In 2018 we will track these trees quarterly for one year and classify each as dead (no leaves), stressed (brown leaves), or vigorous to document immediate hurricane impacts. We will then continue these transects on an annual basis during GCE-IV to document effects of salt water intrusion. We expect that tupelo gum (*Nyssa aquatica*) will be more vulnerable to salt water intrusion than cypress (*Taxodium distichum*), and that the highest level of tree mortality will occur at the downstream end of the transect (i.e. closest to the ocean).

Remote sensing We will continue to use multiple remote sensing platforms to collect information on patterns and processes in the GCE domain. 1) We operate the GCESapelo PhenoCam, which takes regular (30 min) measurements of plant phenology at the flux tower site. *In GCE-IV we will add a second Phenocam at a lower-salinity salt marsh site (GCE4)* to assess how salinity affects phenology. 2) We are in the process of purchasing a drone that can obtain high resolution (down to 1 cm) images using a variety of cameras (4 band color/NIR, thermal). *In GCE-IV we will use the drone to quantify disturbance patterns in Spartina marsh (Area 3a) and document shifts in high marsh plant zonation (Area 3c)*. 3) We collect periodic high-resolution aerial photographs (georeferenced, 15 cm resolution, in 4-band color/NIR) of Altamaha Sound and the Duplin River that we use to evaluate shifts in creek morphology, marsh area, and marsh habitats over time. *In GCE-IV we will reduce the frequency of these flights from annual to once every five years* because they are expensive, geomorphological change at this spatial scale has been slow, and the drone will replace some of this functionality. 4) We will continue to take advantage of publicly available satellite data such as MODIS, Sentinel-2 and -3, and Landsat8 to evaluate large-scale, long-term patterns in marsh production (Area 4).

Modeling Our goal is to have a series of linked models operating in the GCE domain such that the properties of estuarine water (e.g. salinity, inundation) can be used as an input for predictions of intertidal soil conditions (e.g. water content, porewater salinity), which can in turn be used to help drive plant productivity models. We now have implemented the hydrodynamic model (FVCOM) in both the Duplin River (McKnight 2016) and the GCE domain (Fig. 1b; Y. Wang et al. 2017). The domain model (FVCOM v2.7) has a horizontal resolution of ~10-40 m in tidal creeks, 50-100 m over salt marshes, and 0.15-2.5 km in the main water channels and near the open boundary over the shelf. The vertical resolution implements six sigma levels in order to capture the range of observed stratification. The **Duplin River** model (FVCOM v3.2) has a higher resolution (7-10 m horizontal resolution in tidal creeks, 10-30 m in tidal channels and marsh areas, and 30-50 m near the open water boundary); six sigma layers are again used to resolve stratification. Over the past year we have updated model topography with recent GA LIDAR data, providing improved predictions of inundation, circulation, and connectivity. We are also in the process of implementing a basic water quality model for the GCE domain (with leveraged funding from GA EPD). In GCE-IV we will upgrade both models to FVCOM v.4.0, which has options for multidomain nesting. Nesting the high resolution Duplin River model in the GCE domain model will allow us to interpret field observations in the context of large scale patterns and external drivers (Areas 1 and 2). We will also use the models to provide predictions at scales that match those of the various platforms used in the project (e.g. satellite, flux tower, drones).

We also propose to continue and improve modeling of soil processes. Our existing soil salinity model (Miklesh & Meile subm.) considers tidal flooding, lateral groundwater exchange and drainage, and atmospheric exchange, using FVCOM simulation results or climatology data as input data. We are currently using the soil model to hindcast porewater salinity associated with both our long-term field monitoring and Landsat-derived estimates of plant production in the Upper Duplin River. *In GCE-IV we will expand the soil modeling effort to simulate soil temperature*, as that has been identified as a potential driver of spring green-up for *S. alterniflora*. As part of this effort, we will collect additional porewater salinity and temperature data that will be used for model calibration and validation. We will also use a process-based groundwater model (Evans & Wilson 2016, 2017) to estimate water flows in high marsh areas, which will improve our estimates of porewater salinities at these sites by providing lateral and vertical exchanges of groundwater between the marsh and upland (Area 3c).

We have explored several different process-based models for *S. alterniflora* production and found that they were unable to accurately predict long-term (> 2–3 years) changes in biomass in the domain, in part because they did not adequately account for changes in belowground allocation of resources (Jung & Burd 2017). In recognition of this we initiated additional field observations of belowground biomass at the flux tower, and these data will be used to improve the model and our understanding of plant growth and phenology. *In GCE-IV we will improve the mechanistic Spartina model* to include interactions between temperature, salinity, and plant response that can be used to simulate plant responses to changing conditions and various disturbance scenarios. To do this, we will combine our continuing field observations with data from experiments to evaluate above- and belowground biomass responses to changes in temperature, salinity, and nutrients (Area 3a). These observations will also inform our remotesensing based synoptic estimates of belowground biomass (Area 4).

Area 3: Disturbance Response

Area 3a: Spartina Marsh

S. alterniflora is the most important foundation species in salt marshes along the Atlantic and Gulf coasts of North America, and the marshes it dominates are the focus of our salt marsh studies. Spartina marsh is found between mean sea level and mean high water, with the tallest plants occurring at low elevations along creekbanks and shorter plants occurring at higher elevations in the mid-marsh. Plant performance is limited at very low elevations by flooding and at high elevations by desiccation and porewater salinity. Spartina marsh in the GCE domain is flooded and drained twice daily through a network of tidal creeks, which serve as the primary hydrological conduit between intertidal and open water areas. External drivers such as sea level rise, storms, changes in freshwater input, and increases in temperature are likely to result in <u>domain perturbations</u> such as increases in inundation and changes in salinity in Spartina marsh (Fig. 9). Other perturbations such as deposition of wrack (dead plant material), high densities of herbivores and burrowing organisms, and slumping of creek banks are also common.

We have chosen a suite of key **response variables** that will be quantified in all of our experiments (Fig. 9, Table 3). These encompass the LTER core areas and include measurements of abiotic variables, primary producers, invertebrates, decomposition, and soil organic material. Our inorganic nutrient response variable is porewater NH₄ concentration. This was chosen because it changes in response to disturbance in Spartina marshes: we have observed 10-fold higher concentrations in areas that have experienced dieback (Ogburn & Alber 2006) or wrack deposition (Alber, unpubl. data), presumably due to decomposition of belowground plant biomass and reduced uptake of NH₄ in the absence of plants. The responses will be evaluated individually, but we can also assess integrated "community responses" by calculating Bray-Curtis dissimilarity indices of disturbed vs. undisturbed communities (Avolio et al. 2015). In addition, we will explore multivariate techniques such as PCA (Donohue et al. 2013) and the computation of n-dimensional hypervolumes (Blonder et al. 2014; Barros et al. 2016) to allow us to characterize overall ecosystem response to perturbations and make comparisons among treatments. This will provide us with a proxy for "ecosystem state" that we can use to operationalize ecosystem resilience.

In response to disturbance, three outcomes are most likely in Spartina marshes: 1) recovery (*S. alterniflora* re-establishes as the dominant plant species), 2) a shift to a different plant community (e.g. to succulent-dominated marshes in saline areas), or 3) a complete loss of vegetation and conversion to bare mud (e.g. in areas of low elevation or affected by dieback). Below we describe our ongoing investigations of patterns in *S. alterniflora* productivity and top-down controls on marsh communities, as well as new research designed to evaluate how this habitat responds to various perturbations.

Spartina productivity We will continue to use our eddy covariance flux tower to provide continuous (every 5 min) measurements of CO_2 and H_2O flux along with atmospheric, soil, and water properties. Instrumentation associated with the tower includes a sonic anemometer, a closed-path gas analyzer (Li-7200), soil heat flux plates, an averaging thermocouple, soil water content reflectometer, up- and

downward looking radiative sensors, and sensors measuring humidity, vertical temperature variations, atmospheric pressure, rainfall, and creek and marsh water levels. In GCE-IV we will develop an automated workflow based on EddyPro software to calculate NEE from the flux tower—this will reduce costs of data processing and improve speed of access to data. *We will have multiple years of NEE data that we can use to identify responses to environmental drivers such as inundation, salinity, and temperature.* Finally, flux tower observations will be used to inform our synthesis of C exchange in marshes (Area 4).

We will also continue to operate the "GCESapelo" PhenoCam and to collect monthly observations of above- and belowground biomass at the flux tower. As described above (Area 2), we will add a new PhenoCam at a lower salinity site (GCE4) to help determine whether there are differences in phenology that are associated with porewater salinity, and will use this as an opportunity to collect additional measurements to validate the soil model.

In GCE-IV we will conduct a greenhouse experiment to evaluate how winter soil temperature interacts with salinity and nutrients to affect belowground processes and S. alterniflora phenology. We are adding this experiment because we have found that seasonal translocation of belowground resources is an important but poorly characterized process affecting S. alterniflora production (Jung & Burd 2017), and that the rate of belowground biomass loss was high during warm and wet winters (O'Connell et al., in prep). We will grow individual S. alterniflora plants hydroponically at two levels of winter soil temperature simulating cool and warm winters (ambient, $+2^{\circ}$ C), three levels of salinity spanning the range occupied by S. alterniflora (20, 30, 40), and two levels of nutrients typical of creekbank and midmarsh, with 5 plants per treatment combination for a total of 60 plants. Salinity and nutrient treatments will be administered starting in June; winter warming will run from December through February, and plants will be followed throughout the following growing season. We will measure total live biomass throughout the experiment, and estimate changes in above- and belowground biomass by displacement of hydroponic fluid. We will also measure the heights of all shoots at the beginning of the experiment, in November and March, and at the end of the second growing season, and use previously developed allometric relationships to estimate dry biomass. Finally, we will harvest plants at the end of the experiment to calibrate live biomass and the various non-destructive measures against actual dry biomass. The data collected in these efforts will be used to further develop empirical phenology models and provide detailed information on plant responses and resource allocation to help inform and calibrate the Spartina production model (Area 2).

Top-down control by predators We will continue a predator removal manipulation to evaluate top-down effects on marshes. As described above (Results of Prior Support), we excluded nekton (blue crabs and fish) from 27 m² plots in a Spartina marsh starting in summer 2016. We will continue to focus on the top-down response to this manipulation through regular field sampling (spring, summer, and fall). To determine which nekton species are likely affecting the outcome of the experiment, we will sample the relative abundance and diversity of nekton predators in creeks adjacent to the experiment with Fyke nets, and characterize the gut contents of numerically dominant predators. During spring tides, we will also use acoustic sampling and Go-Pro cameras to gain a better understanding of which predators are moving over our uncaged marsh plots. Within the plots, we will sample the response variables described above (Fig. 9, Table 3), as well as insect community composition and parasite loads of hydrobiid snails, to link changes in food web structure to ecosystem function.

Multiple outcomes are possible from this manipulation. Our early results indicate that snail densities are increasing, as is snail grazing on plants, which could ultimately reduce plant biomass, with potentially cascading effects to other indicators (e.g. increased benthic microalgal biomass, increased soil temperature and NH_4 concentrations, decreased organic matter storage). However, we anticipate that the increase in snails will be countered by a compensatory increase in mud crabs, a marsh meso-predator that eats snails (Griffin et al 2015). Alternatively (or simultaneously), mussel and fiddler crab densities might also increase from the removal of predators, improving habitat quality for plants and counteracting the

negative effects of snail grazing. Because snails and mussels can live for more than a decade, we anticipate that it will take at least that long for the disturbance response to manifest fully. At that point (likely in GCE-V), we will use this manipulation to investigate how changes in response variables due to predator exclusion affect the resistance of the system to an additional pulse perturbation such as a wrack addition. We hypothesize that 1) additional perturbations will amplify top-down effects on prey populations (He et al. 2017; Silliman & He in press), 2) high densities of mussels and fiddler crabs will result in increased resistance (i.e. perturbations will result in smaller magnitude changes) and resilience (i.e. the system will be faster to recover). In contrast, we predict that 3) high densities of snails will result in decreased resistance and resilience. We will use information gained from this experiment, combined with long-term invertebrate monitoring at the core sites, to predict how variation in predator densities affects Spartina marsh. This will help us understand the response of salt marshes to shifts in large predators, such as might result from human activities.

Perturbations, disturbance, and recovery We will conduct new research projects designed to characterize marsh response to naturally occurring perturbations and evaluate trajectories of response and recovery from standardized experimental disturbances.

Natural marsh perturbations We will use our drone (Area 2b) to conduct monthly flight surveys over ~1 km² stands of Spartina marsh at three sites around Sapelo Island (the flux tower, sites GCE 6 and GCE 10). At each site we will fly over the entire elevational gradient of the marsh, from the upland border to the lower, seaward extent of marsh vegetation. From these surveys we will track the frequency of occurrence, duration, and size of all observed perturbations. We will use our corrected digital elevation model and porewater salinity model to estimate elevation and salinity at these locations. A perturbation will be operationally defined as an area of at least 1 m^2 that either is covered by wrack, has slumped into the creek, or has unusually large amounts of standing dead vegetation (indicative of early phase of marsh dieback). Each month, we will identify a subset of newly perturbed areas in each survey area that we will visit on foot to measure the thickness of wrack (if present), and assign to likely causes: creekbank slumping (based on changes in morphology at the creekbank), wrack (based on the presence of wrack on the ground), snail grazing (based on the presence of high snail densities), headward-eroding creeks (based on creek morphology and the presence of marsh crabs), and dieback (bare or thinned patches that appear during drought with no other obvious cause). We will use drone surveys to quantify vegetation response to these events based on a greenness index (likely NDVI) to follow trajectories of each perturbed area over time. We expect some perturbed areas will show persistence (e.g. short-duration or thin wrack cover that may not cause a vegetation response), and will consider an area disturbed where live vegetation cover is less than 50% for > 1 mo. We expect that disturbed areas will vary in their resistance (e.g. the magnitude of NDVI decline) and rate of recovery to baseline NDVI levels, and that some may show a state change whereby previously vegetated areas shift to a different foundation species or to bare ground.

To explore mechanisms influencing this variability in resilience we will measure a wider suite of disturbance response variables in a subset of perturbations caused by wrack, snail herbivory, and dieback, because these are common and will be the most tractable to visit regularly on foot. At the beginning of each quarter we will use the drone observations to identify a set of newly disturbed areas of different sizes and proximate causes, a selection process that will continue until we have a total of 60 disturbed areas. We will delineate selected areas with an RTK-GPS and also mark permanent plots in adjacent reference areas (as controls). We will visit each disturbed and reference area (total of 120) 6 times per year (once per quarter, with 2 additional sampling events during summer to capture the growing season), and will measure our suite of response variables (Table 3) as well as elevation (annually). Disturbed and reference plots will be followed until the disturbed areas either return to control conditions (i.e. are not significantly different from reference areas) or convert to a new habitat type (i.e. are no longer Spartina marsh). For the purposes of these measurements, plots that convert to another habitat type and remain in it for 5 years will be considered to have undergone a state change and will not be measured further. (We will have the option of revisiting these plots during GCE-V if we decide that this would be informative.) *We hypothesize that marsh recovery will be faster after wrack than snail or dieback disturbances because*

wrack tends not to kill all vegetation, and that recovery rates will peak in intermediate elevations where inundation and salinity stress are both at moderate levels. The results from the 60 intensively sampled disturbances combined with the observations of several hundred areas that will be followed in the drone surveys will enable us to evaluate the response of Spartina marsh to disturbance with respect to natural gradients in patch size, event timing, elevation, and salinity, and to make comparisons among different disturbance types. These observations will be used in combination with our experimental manipulations to develop a disturbance-scape for Spartina marsh (Area 4).

Headward-eroding creeks that are created by very high densities of the marsh crab *Sesarma reticulatum* are too large, and progress too slowly, to follow with these methods (Hughes et al. 2009). Instead, we will use a space-for-time substitution to document response and recovery from these disturbances by sampling the response variables described above (Fig. 9, Table 3) along a parallel transect (30 plots) adjacent to three creeks. Transects will begin in front of the creek head and end at the intersection with the main channel. Distance along this transect reflects increasing time since the disturbance. Dates at which locations along the transect were perturbed and re-vegetated will be estimated from aerial photographs (Hughes et al. 2009). Control transects that were not affected by the creek (as determined from aerial photographs) will allow us to control for effects of marsh location (edge versus interior).

Experimental disturbance across abiotic gradients We hypothesize that underlying abiotic gradients in elevation and salinity affect the response of a marsh to a disturbance (i.e. the disturbance interacts with the biophysical template). To test this, we will conduct two experiments in which we implement a standardized 4 m^2 disturbance across natural gradients of 1) salinity and 2) elevation in four vegetation types (from low to high salinity along the estuarine gradient: Z. miliacea, J. roemerianus, S. alterniflora and succulents). We will kill plants within trenched plots by covering with tarps or applying herbicide (Brewer & Bertness 1996). These approaches do not precisely mimic disturbance caused by wrack, snails or dieback, but reliably kill both above- and belowground vegetation, and provide a standardized, generic disturbance that we can compare across vegetation types, salinity, and elevation. To test for responses across salinity gradients, we will establish 15-20 stations that vary in salinity within each of the four vegetation types, holding elevation constant. At each station we will establish a disturbed and a control plot, and measure the suite of disturbance response variables described above. We expect that there is likely a threshold of salinity beyond which a given plant species cannot survive (Guo & Pennings 2012; Gabler et al. 2017) and the habitat switches to a more tolerant plant species or bare mud (i.e. as salinity increases, Z. miliacea is replaced in turn by J. roemerianus, S. alterniflora, succulents and unvegetated salt pans), and hypothesize that resistance will decrease and recovery will be slower close to these thresholds (Fig. 11). However, recovery rates of the four vegetation types may differ due to plant architecture. Specifically, we expect clonal plant species with "runner" morphologies (S. alterniflora, Z. miliacea) to recover faster than those with "phalanx" morphologies (J. roemerianus). We have evidence from other experiments that J. roemerianus recovers very slowly after disturbance (Area 3c). This will represent a second type of interaction between a disturbance and the biophysical template.

To test for responses *across elevation gradients*, we will establish 20 stations that vary in elevation within each of a single marsh dominated by *S. alterniflora, J. roemerianus*, or *Z. miliacea*. At each station we will establish a disturbed plot and a control plot, as above, and will measure disturbance response variables. Productivity of a given marsh plant species can be described as a parabola across elevation (Morris et al. 2002), with plants at very low elevations stressed by flooding and at very high elevations stressed by desiccation. We expect that stations closer to the low and high elevation limits of each species will be less resistant (greater magnitude of change) and recover more slowly and at the extremes may transition to a different state following a perturbation (Fig. 9). We will use the results from both the salinity and elevation experiments to evaluate each disturbance response variable alone as well as with the combined dissimilarity and multivariate analyses. This will allow us to evaluate how marsh resilience varies as a function of salinity and elevation, and to characterize the "safe operating space" within each habitat type (Johnstone et al. 2016).

<u>Marsh-fauna interactions</u> The performance of salt marsh plants is mediated by benthic macroinvertebrates. Invertebrates have been shown to both benefit (Bertness 1984, 1985) and harm (Silliman & Zieman 2001) plants, and are likely to interact with perturbations in important ways. For example, Angelini et al. (2016) observed that the presence of mussel mounds (marsh mussels occur in ~0.25 m² aggregations in Spartina marshes) served both to reduce plant loss during a naturally occurring dieback and to enhance recovery. Fiddler crabs have also been shown to affect soil conditions, with important feedbacks to plant growth (Bertness 1985; Kristensen & Kostka 2005). It is beyond the scope of this proposal to investigate all of these interactions, but we will assess the drone imagery collected during the natural marsh perturbation observations to determine whether we can quantify mussel aggregations, fiddler crab burrow density, and snail distribution, and relate these factors to disturbance parameters. For example, we might expect fewer mussel aggregations associated with disturbed than with undisturbed areas during a drought. If this area of research proves fruitful, we will follow up with leveraged proposals.

Area 3b: Tidal forest/fresh/brackish marsh

Riverine estuaries such as the Altamaha have a longitudinal gradient of habitats (tidal fresh forest, fresh marsh, brackish marsh, salt marsh) that is largely controlled by salinity (Higinbotham et al. 2004) and that vary in their delivery of ecosystem services (Craft et al. 2009; Guo & Pennings 2012; Wieski et al. 2010). <u>External drivers</u> such as sea level rise, changes in river discharge and precipitation, or upstream alterations such as dams are likely to result in <u>domain perturbations</u> within tidal forest/fresh/brackish marsh, the most important being increases in salinity (Ensign & Noe 2018). Increasing salinity in these areas may cause disturbances, such as changes in plant biomass, that may lead to state changes, such as converting tidal forest to fresh marsh and then to brackish marsh. Disturbances can also feed back to affect abiotic conditions. In particular, increasing salinity may cause the release of inorganic N from freshwater soils (Jun et al. 2013). Below we describe our ongoing investigations of patterns in plant distributions along the estuary and our plan to use our ongoing experimental manipulation to evaluate the response and recovery of a tidal fresh marsh to varying periods of increased salinity. Fresh (*Z. miliacea*) and brackish (*J. roemerianus*) marsh will also be included in the "*Experimental disturbance across abiotic gradients*" manipulation described in Area 3a.

Field observations As described in Area 2, our existing core monitoring sites along the Altamaha River (GCE 11, 7, 8, & 9) include tidal fresh forest, fresh marsh, brackish marsh and salt marsh, respectively. We also have permanent vegetation monitoring plots at the transitions between fresh and brackish marsh (Z. miliacea/Spartina cynosuroides) and between brackish and salt marsh (S. cynosuroides/S. alterniflora). We conduct annual assessments of the distribution of S. cynosuroides at 50 stations along the estuary, and have recently added 40 stations where we have established photo-stations to rapidly assess tidal fresh forest trees. We are also working to track forest canopy cover via remote sensing (Landsat). We have also used remote sensing to identify transitional areas where the dominant vegetation changes frequently between oligohaline (primarily Z. miliacea) and mesohaline (primarily J. *roemerianus*) species. We have established monitoring plots in this area that we will follow on an annual basis. In GCE-IV we will use these observations to evaluate the relationship between river flow and other external drivers and plant distributions. In addition, we are constructing a high-resolution dendrochronology sequence of bald cypress (Taxodium distichum) to use as a proxy to assess the timing of major climate changes (warming, precipitation, sea level rise) over the past 7000 years. This will provide us with baseline information about the historic disturbance regime and will also be useful for interpreting the archeological record (Area 1).

SALTEx The ongoing SALTEx manipulation has found that the addition of brackish water to a fresh (*Z. miliacea*-dominated) marsh caused changes in microbial, plant, and soil processes as porewater salinity and sulfate increased. As summarized in the Results of Prior Support, results from four years of dosing have provided evidence for multiple responses in the press treatments whereas many variables were either unaffected or recovered quickly in the pulse treatment. *This experiment has already provided us with rich*

information on how a perturbation disturbed a tidal fresh marsh, and we can now use it to evaluate the time-scales and trajectories of recovery. Some of these outcomes are highlighted in Fig. 13, which shows that *Z. miliacea* biomass did not respond to the pulse treatment (i.e. it was persistent) but did decline in the press (i.e. it was disturbed); *Ludwigia repens* (creeping primrose-willow) responded to both pulse and press treatments with no signs of recovery in either treatment; whereas porewater NH_4 responded to both treatments and was able to recover from pulses but not the press.

Dosing ceased in December 2017, and *during GCE-IV we will track recovery as the plots readjust to the normal freshwater river flooding regime*. Based on results from the pulse treatment, we predict that porewater salinity, sulfate and inorganic N and P in the press treatment will recover within 4-8 weeks. We further hypothesize that greenhouse gas emissions (CH₄ and NEP) will recover within 3-6 months. Based on other experiments in this habitat (Guo & Pennings, unpubl.), we expect plant communities will take 2-3 years to recover fully. Recovery of vegetation may not follow the reverse pathway as vegetation loss, because salt-sensitive forbs *L. repens* and *Polygonum* sp, which were lost before *Z. miliacea* in the press treatment, may also recover faster than *Z. miliacea* because they grow faster. We predict that soil elevation will stabilize during year 1 and then increase rapidly in years 2 and 3 as the plant community recovers, because of the increase in belowground plant biomass. There is also the possibility that some variables will not return to baseline conditions. In particular, we expect that some soil characteristics such as increases in reduced forms of sulfur and decreases in iron-bound P will retain long-term legacies indicative of experimental salinization.

Hurricane Irma delivered an acute, short-term perturbation in terms of both high salinity water and high inundation to all of the SALTEx treatments in September 2017 (plots were underwater for 2 days and porewater salinities reached ~23). We are using this opportunity *to evaluate how a pulse perturbation (the hurricane) interacts with prior salinity disturbance*. Although it was a short-lived perturbation, we hypothesize that the pulse plots may show less resistance to the hurricane than the control plots because they have already experienced a series of salinity perturbations. We are also evaluating whether the control plots respond in the same way to the hurricane as the pulse treatments responded to experimental saline pulses. For example, we expect the loss of *L. repens* across all treatments in the 2018 growing season as a result of the hurricane.

We expect that the SALTEx plots will recover from the experimental treatments over the next 3-6 years, which we define as a return of plant biomass, plant composition, and sediment elevation to control/ baseline conditions. If so, we will then subject the plots to an additional perturbation. We will apply a strong saline pulse to simulate another hurricane or a drought. This will again—but in a more controlled way—test the hypothesis that legacies of previous disturbance reduce resistance and lengthen recovery to subsequent events (Schwalm et al. 2017). We expect that the press plots will be the most affected by the subsequent disturbance, followed by the pulse plots, with little to no effect on the other treatments.

Area 3c: High marsh/upland border

The high marsh is distinct from the low marsh in that it is flooded irregularly by only the higher high tides, and soils can range from hypersaline to brackish depending on freshwater input from the upland (Wilson et al. 2015b). The vegetation can be dominated by *Borrichia frutescens*, *J. roemerianus*, or the succulents *Batis maritima* and *Sarcocornia* sp.; the most hypersaline areas are unvegetated salt pans. High marsh plant and animal communities are more diverse than those found in other habitats. <u>External drivers</u> such as sea level rise, changes in precipitation, and upland land use patterns are likely to result in <u>domain perturbations</u> within high marsh/upland border areas, the most important being changes in inundation, freshwater infiltration, and runoff (Fig. 9). The presence of bulkheads or docks will also affect the distribution of wrack in these areas (Alexander 2011, 2012; Gehman et al. 2017). Disturbance to the high marsh may cause state changes, such as conversion from *J. roemerianus*-dominated marsh to *S. alterniflora* or to bare mud. *In GCE-IV we will continue several ongoing activities to evaluate high marsh vegetation dynamics and continue our upland manipulation in the high marsh*.

Long-term vegetation dynamics We continue to monitor vegetation dynamics at the borders between vegetation types, with two sites at each of the following transitions: *J. roemerianus*/marsh meadow, *S. alterniflora*/ marsh meadow and *J. roemerianus*/*S. alterniflora*, where "marsh meadow" is a mixture of several salt-tolerant species. Vegetation composition has changed dramatically over the past two decades at all of these edges. For example, plots originally located at the *J. roemerianus*/meadow border showed a sharp decrease in *J. roemerianus* cover that correlated with an extended (1998-2002) drought (Fig. 12d), and the border itself has now shifted by 10 m. We will formally analyze these data to assess vegetation response to environmental drivers and to identify the conditions under which the borders shift. Because we do not have data over this time period on porewater salinity, we will use the soil model (Area 2c) and the high-marsh groundwater model (described below) to hind-cast salinities to help interpret changes in vegetation. *In GCE-IV we will add instrumented wells at these monitoring sites to better understand groundwater flow and interpret vegetation changes going forward*.

We will also continue to follow two long-term disturbance experiments that involve high marsh vegetation. The first is a manipulation begun in 1999 to evaluate vegetation response to removal of J. roemerianus, which is the competitive dominant in this habitat. Three treatments were imposed at eight sites that vary in salinity: unmanipulated controls, a pulse treatment (J. roemerianus removed but allowed to reinvade) and a press treatment (J. roemerianus removed and not allowed to reinvade). The removal of J. roemerianus led to increases in other plant species in all plots, but J. roemerianus is slowly regrowing in the pulse treatment, and we will continue to track recovery. More interestingly, the manipulation gives us an opportunity to evaluate whether the rate of recovery varies with salinity, and how recovery rate influences vegetation composition. The second experiment was designed to examine the response of five types of marsh vegetation to wrack perturbations. Wrack was applied to 1.2 m x 1.2 m plots in five different vegetation zones in 2011 and removed after one year. Both the response and recovery to this disturbance varied with vegetation zone and elevation (Table 1). All plots have recovered except those in the J. roemerianus zone, which we will continue to track. The wrack experiment also showed that recovery rates were slower when the disturbance was applied in the fall rather than the spring. Thus, we will examine the effects of natural disturbances that occur in different times of the year (Area 3a, Natural marsh perturbations).

We will evaluate high marsh patterns at a landscape scale by taking advantage of our high-resolution aerial photographs (Area 2b) to delineate borders between *J. roemerianus*, meadow vegetation, salt pans and *S. alterniflora*. We will extend this record through GCE-IV with annual drone flights over the high marsh at three sites (which will include the long-term vegetation plots described above). We expect that shifts in plant borders will vary between wet and dry years in a manner that is consistent with the plot observations, and will use these observations to scale up these dynamics from a few sites to the landscape.

Upland manipulation We will continue a long-term experiment started in GCE-III to evaluate the effects of altered water flow from the upland to the high marsh. As described in the Results from Previous Research, we established a series of plots in the high marsh in 2015 with three treatments: reduced input, double input, and control. We installed shallow (90 cm) and deep (150 cm) wells inside and above each plot, instrumented ~20 wells with pressure loggers, and manually collected salinity data from the wells monthly. These data are providing an unprecedented understanding of shallow groundwater dynamics at the high marsh/upland border. To date, however, they have not shown a strong treatment effect on groundwater or plants. We will continue to monitor the experiment for at least one more year. This will give us a long-term record of groundwater flow and a detailed understanding of how the plant and macro-invertebrate community responds to temporal variation in groundwater inputs. We will also supplement well data with annual electrical resistivity tomograms that can provide vertically and horizontally synoptic information on groundwater dynamics from wells, tomograms and the groundwater model (described below), we will evaluate options and benefits of increasing the magnitude of the treatments (e.g., a deeper barrier, pumping groundwater, etc.).

If the manipulation results in biotic responses in the high marsh, we will use it to investigate how changes in water inflow affect the response to and recovery from disturbance. We will add one or two disturbance treatments (1 m^2 plots) inside each 7 m x 10 m plot. We will select these based on our drone measurements of disturbance frequency described above, but likely candidates are drought and wrack. This would not be done until the experiment is stabilized (likely in GCE-V).

We will use these data to parameterize a process-based model of groundwater flow at the upland-marsh boundary. The model will build on methods developed for intertidal systems (Wilson & Morris 2012; Evans & Wilson 2016, 2017) and will be calibrated and validated using well data from the high marsh experiment. We will use the model to estimate the magnitude of groundwater flows into the high marsh and to evaluate the extent to which changes in external drivers (tides and rainfall) lead to perturbations in system conditions (level and salinity of shallow groundwater). We will also use it in parallel with the soil model (Area 2) to hindcast porewater conditions in high marsh areas such as the long-term vegetation dynamics sites.

Area 4: Integration and Forecasting

We will use the information collected in Areas 1-3, along with modeling and remote sensing, to 1) produce synoptic descriptions of ecosystem properties (habitat provisioning [defined as the distribution of habitat across the landscape], net and gross primary production, and C budgets) in the GCE domain, 2) characterize the disturbance-scape based on temporal and spatial patterns of perturbations and their cumulative effects, and 3) investigate relationships between drivers and ecosystem response.

Ecosystem Properties

Habitat provisioning Productivity, carbon sequestration, nutrient retention, and other ecosystem properties differ across intertidal habitat types (Craft 2007; Craft et al. 2009; Wieski et al. 2010), and several studies have valued ecosystem services based on marsh type (Woodward & Wui 2001; Brander et al. 2006). Identifying habitat type is also necessary for correcting LIDAR-derived DEMs to produce accurate elevation maps (Hladik & Alber 2012), which can be used to identify areas that are potentially vulnerable to coastal flooding and serve as the basis for hydrodynamic modeling. Information on habitat distribution and how it changes over time is therefore important for evaluating ecosystem response to long-term drivers. We currently have a 2013 vegetation map that used ortho-imagery and a random forest classifier to predict the distribution of intertidal habitats along the GA coast. In late 2017 we re-flew the Altamaha River corridor at a higher resolution (with funding from a RAPID grant) to evaluate whether the vegetation borders shifted upstream or plants died back in response to the unprecedented influx of salt water associated with the storm surge from Hurricane Irma. We plan a follow-up flight in 2018 (with RAPID funds) and a flight in 2021 as part of GCE-IV. We are also following mixed vegetation plots to document shifts in habitat borders (Areas 3b, 3c) in the tidal fresh forest/fresh/brackish marsh through a combination of field and aerial surveys (Area 3b). In GCE-IV we will produce updated vegetation maps and evaluate how these habitat types have changed over time. These analyses will provide us with a synoptic picture of habitat distribution across the domain and the tools to evaluate changes in other ecosystem services. For example, we can overlay measurements of plant productivity or C sequestration in different marsh types to produce scaled-up estimates for the domain.

Biomass patterns During GCE-III we developed an algorithm to estimate aboveground *S. alterniflora* biomass from remotely sensed vegetation indices, and used the period of record of Landsat5 (1984 - 2011) to hindcast annual variation in *S. alterniflora* biomass in the GCE domain and its relationship with environmental drivers (Fig. 5). In GCE-IV we will extend this analysis in several ways. First, we will use the updated habitat distribution map to extend analyses of *S. alterniflora* biomass to the entire GA coast. Pilot analyses indicate that long-term declines in biomass are not as severe in low-salinity salt marshes along the Altamaha River as in higher-salinity marshes elsewhere. This result is consistent with the hypothesis that Spartina marshes are less affected by, or recover faster from, perturbations such as

drought at lower salinities. Second, we will use newer satellites (Landsat8) to extend the aboveground biomass time series to the present. Our initial calibration suggests that *S. alterniflora* biomass in the GCE domain has not recovered from the decline observed from 1984 to 2011. Third, we will use the same methodology that we applied to *S. alterniflora* to develop satellite-based biomass time series for additional marsh species (*J. roemerianus*, *Z. miliacea*) so that we can conduct similar long-term analyses for brackish and fresh tidal marshes. *We hypothesize that brackish and fresh plants will be more responsive than Spartina to increased salinity and will show steeper declines in biomass over time.*

We are also working to develop a Landsat-based algorithm that can estimate *belowground* biomass in S. alterniflora based on spectral reflectance of aboveground properties. Belowground biomass represents 50-75% of total biomass and productivity (Morris et al. 1984; Jung & Burd 2017) and is a key parameter determining marsh vertical accretion, but it is rarely estimated because the measurements are laborious and destructive. The remote sensing approach that we propose has been successful in other wetland species (O'Connell et al. 2014), and our preliminary results for S. alterniflora are promising. Our initial model, which used spectral data from Landsat8 to estimate aboveground biomass and foliar N, explained 80% of the variability in belowground biomass measured at the flux tower site (Fig. 14). This is an exciting avenue of research because translocation of resources between above- and belowground biomass is likely a key process explaining variation in plant phenology and productivity across elevation and among sites, but we know little about it, even at the m^2 plot scale. Moreover, areas with increased below ground biomass also have increased soil organic matter and can sequester more C (Mudd et al. 2009), so identifying areas that vary in belowground biomass may provide insight into carbon cycling and storage potential in different marsh locations. Remotely sensed estimates of both above- and belowground biomass at the landscape scale could transform our understanding of productivity patterns and carbon sequestration potential in coastal wetlands.

Gross Primary Production The MODIS satellite provides a powerful tool for evaluating broad-scale patterns of GPP (Running & Zhao 2015). However, the currently available MODIS algorithm for GPP (MOD17A2) lacks lookup table values for light use efficiency in wetlands and so is not accurate in those areas. An additional difficulty for estimating GPP in tidal areas is that flooding reduces spectral reflectance (particularly in the near IR), adding noise to vegetation spectral reflectance time series and obscuring gas fluxes on which GPP estimates are based. We have already developed a tool to filter out flooded MODIS imagery (O'Connell et al. 2017), and will use it in conjunction with eddy covariance carbon flux data and field measurements to improve MODIS predictions of GPP in Spartina marshes. The remote sensing GPP models will be based on two approaches; production efficiency models (Monteith 1972), which compute GPP from a combination of light use efficiency and absorbed solar radiation, and canopy photosynthesis models (Gitelson et al. 2006), which are based on biophysical variables including leaf area index, vegetation fraction, and canopy chlorophyll concentration. We will parameterize and test both models and use the best one to generate regional-scale GPP maps based on 500 m tide-indexed MODIS daily surface reflectance data. By the end of GCE-IV we aim to produce regional tidal marsh GPP maps for the period 2000-2020, which we will use to perform a comprehensive analysis of spatial and temporal patterns in productivity. Trends in productivity can then be related to long-term drivers such as salinity and inundation. For example, we can evaluate whether GPP at the regional scale is responsive to changes in river flow.

Carbon budgets The information on NPP and GPP described above will be useful for estimating the amount of C fixed by coastal wetlands. We can use these results, in conjunction with estimates of C accumulation based on soil cores and accretion based on SET data, to estimate long-term C storage in marshes. We are also continuing to measure DIC and alkalinity in the water entering the domain (Area 1) and in the estuary (Area 2), which provides us with information on inorganic C as it transits through the system. Inorganic C is important to track, as Reimer et al. (2017b) observed a long-term increase in pCO₂ in the coastal ocean and accompanying decrease in pH over the last 25 years, which they suggest is due to increases in both riverine DIC concentration and flux from intertidal areas, possibly as a consequence of sea level rise and increased marsh inundation. We also have continuous measurements of NEE from the

flux tower, and results of GCE-III studies estimating lateral transport of DIC through tidal creeks. We will use these observations to continue to improve our estimates of C transport and mass balance for the region. In combination with modeling scenarios, we will evaluate how the changes that might occur in response to changes in external drivers will affect these conclusions, with the goal of developing new hypotheses about the implications of climate and human activities for the coastal C budget.

Disturbance-scape

To create a disturbance-scape, we will use the drone flights and field measurements to quantify perturbations (frequency, size, and duration) in each of three 1 km² Spartina marshes and identify their causes (wrack deposition, dieback, creekbank slumping, snail grazing). As described in Area 3a, we will consider an area disturbed if at least 1 m² experiences at least 50% vegetation loss for > 1 month, and we will develop an automated protocol to identify affected areas (measured by a change in NDVI or a similar index) and track the rate of recovery (defined by vegetation regrowth). This will give us a measure of the proportion of each study marsh that is affected by different disturbance types at any given time. We will couple this with our field and experimental data on response variables (Table 3). For each variable we will calculate a disturbance effect (i.e. taking into account the magnitude of the change as well as the recovery trajectory), and use that to estimate the cumulative effect of disturbance on the study marsh. This will allow us to characterize the relative importance of each disturbance type to each response variable. For example, if we find that wrack disturbance reduces NPP by 50% and an average of 30% of a marsh is disturbed by wrack at any given time, that would mean that disturbance induces a 15% decrease in NPP at the landscape scale. Finally, we can combine the various disturbance types to provide an assessment of the cumulative effects of disturbance on ecosystem properties.

We are also interested in determining whether disturbances can be tracked via satellite. We will use three MODIS test pixels by the flux tower that are dominated by Spartina marsh (see O'Connell et al. 2017), and map the drone flights to the scale of the pixel (500 x 500 m), which equates to approximately 100 Landsat pixels (30 x 30 m for most bands). We will evaluate whether the disturbed areas recorded by the drone are visible from either satellite. The proportion of disturbed area vs vegetated area can then provide a base map on top of which NPP (Landsat8) and GPP (MODIS) can be calculated. By combining these remote sensing productivity estimates with changing vegetated area, we can observe whether there is an overall reduction in NPP and GPP associated with a higher proportion of disturbed area. We expect that this will open new avenues for evaluating the effects of disturbance on the landscape.

Finally, we will use our models in concert with the disturbance-scape. We will focus on the three 1 km² areas that will be regularly surveyed by the drone and evaluate the observed patterns of disturbance in the context of model simulations. We are specifically interested in determining whether the various disturbance types can be associated with particular flow patterns. For example, we might expect to see creek slumping in areas with high flow velocity or accumulations of wrack deposited at the spring tide line. We are particularly interested in evaluating whether these disturbances affect hydraulic connectivity and porewater characteristics, which will in turn influence plant dynamics.

Driver-Response relationships

Understanding how an ecosystem changes over time depends not only on the changes in drivers over time but also on the relationship between the driver and the ecosystem response (Fig. 7). This is important, as a threshold response in an ecological time series might not be indicative of a threshold in the driver-response relationship but may instead result from a jump in the time series of the driver (Andersen et al. 2008; Fig. 7). Bestlemeyer et al. (2011) found evidence that observed ecological "threshold" responses in the time series at three LTER sites were consistent with an underlying threshold or non-linearity in the driver-response relationship, whereas in a fourth example (population anomaly in krill abundance at the CCE LTER) the driver-response relationship was linear and the change in krill densities was due to changes in the driver over time. As described below, we will use the data collected by the GCE to evaluate driver-response relationships in marsh ecosystems.

Our characterization of external drivers (Area 1) provides a record of changes in drivers over time, and the results from our core monitoring program (Area 2; 18 years of field data to date) provides long-term data on ecosystem properties (some of which can be extended with remote sensing and historical mapping). We have already begun analyzing patterns of plant production and their relationships with environmental factors (Wieski & Pennings 2014; O'Donnell & Schalles 2016), and we can conduct similar analyses of invertebrates and other core monitoring variables. We will use these observations as well as the results of our disturbance research (Area 3) to develop empirical driver-response curves that can be used to interpret ecosystem change over time. We are particularly interested in using these relationships to predict how changes in salinity and inundation (two major drivers), interacting with disturbances, will affect ecosystem state.

The data collected here will also give us the opportunity to parameterize simple mechanistic models to evaluate the effects of multiple interacting drivers and responses. We can use the observations of natural marsh perturbations (Area 3a) to develop realistic time series of the frequency of different disturbance types and to parameterize equations that describe the responses of the different variables that are being tracked. We will use dynamical systems theory (e.g. Gurney & Nisbet 1998) to explore the sensitivity of each variable to interactions between multiple drivers and different combinations of perturbations. We will also use this approach with our multivariate characterization of ecosystem state in order to mathematically characterize ecosystem resilience to perturbation (Meyer 2016). This exercise will represent an advance because it will be informed by field data, whereas most theoretical ecological models use idealized perturbations.

Finally, we will use our suite of models to evaluate, through hindcasting and forecasting, how changes in external drivers will affect the domain. We will develop scenarios for potential changes in large scale external drivers based on our analysis of existing long-term records (Area 1) and bias-corrected, downscaled projections of IPCC model results (Maurer et al, 2007). Human alterations will be evaluated by simulating modifications in the greater Altamaha watershed (e.g. new reservoirs upstream). The FVCOM model will be used to predict changes in salinity and inundation patterns, which can then be used as input to our porewater salinity model, which can in turn predict conditions that can be related to plant response. Model results and predicted changes in drivers can also be assessed in terms of the driver-response relationships described above, providing us with an additional tool for evaluating the ecosystem consequences of future changes.

RELATED RESEARCH PROJECTS

All the research described above will be funded as part of GCE-IV, and is not dependent on other agencies. However, GCE investigators are involved in several projects that will extend the research proposed here and in some cases allow us to extend the scope of our inferences. In particular, 1) Our long-term observations of inorganic nutrients are being used by Medeiros, Castelao, and Alber for a project funded by the GA Environmental Protection Division in which we are modeling nutrients and dissolved oxygen to help establish numeric nutrient criteria for the State. This will expand the capacity of the FVCOM domain model. 2) Mishra is working on a NASA ROSES project to develop GPP models for other species (Spartina patens and J. roemerianus in Gulf coast marshes) with the goal of developing MODIS GPP predictors that can be used across multiple wetland species, thereby allowing the prediction of GPP for coastal habitats well beyond the GCE domain. 3) Heynen has NSF funding to investigate how uneven racial development, exurban growth, and sea level rise affect Sapelo Island, which will provide greater insight into human drivers. 4) Craft is part of an NSF-funded project to evaluate how tidal marshes along the US east coast have responded to changes in sediment delivery over time. This study will allow a comparison of GCE with other coastal sites. 5) Alexander and Alber are part of a coastal SEES project to evaluate salt marsh vulnerability and human adaptation responses to sea level rise at the three Atlantic coast LTER salt marsh sites (PIE, VCR, GCE). This study is allowing us to make comparisons across a gradient of biophysical and social characteristics. 6) A team of GCE investigators are using RAPID funds

to assess the effects of the storm surge from Hurricane Irma on the GCE domain. This funding is allowing us to augment sampling after a large perturbation and will inform the work proposed for GCE-IV. (See Facilities statement for a complete list of associated research projects.)

RESPONSE TO PREVIOUS REVIEWS

The GCE-III mid-term review team felt that the program had "clear, compelling science questions and objectives that are well-integrated intellectually across the project." They gave us no "recommendations" but did provide a number of "suggestions", three of which were emphasized in the cover letter from NSF. 1) Although understanding physical drivers is necessary, the primary focus of the work needs to be on ecological questions. *Response*: We will also continue our physical measurements as they are important for interpreting biological results and tracking drivers of change. However, the current proposal is focused on advancing our understanding of disturbance, which is a fundamental ecological concept. 2) Develop a plan for evaluating education activities. *Response*: As described under education and outreach, we are planning to improve integration amongst our education activities and begin to formally evaluate them. 3) Plan for future transitions in personnel. *Response*: As described in the management section, we are recruiting a new faculty member to UGA to assist with GCE and are planning to rotate younger scientists onto the executive committee.

BROADER IMPACTS

Education and Outreach The goal of the GCE education and outreach program is to share our understanding of coastal ecosystems with a wide variety of audiences, including undergraduate and graduate students, K-12 students and teachers, citizen scientists, coastal managers, and the general public. Although we will continue to use multiple platforms and diverse partnerships to accomplish this goal, *in GCE-IV we plan to better integrate these activities and to add more formal assessment measures*.

We routinely incorporate undergraduate and graduate students in our research, and expect to maintain an excellent record in this area. We will continue to support summer interns, most of whom work at the field site on Sapelo Island through our REU program (which we advertise through the Peach State Louis Stokes Alliance for Minority Participation, see Site Management). We will also continue our summer brown-bag seminar series, which features informal presentations by graduate students, undergraduates, postdocs, and faculty working at the field site. We have found that this is one of the most productive ways to help students grasp the scope of the entire project. To enhance graduate training, GCE organized and led distributed graduate courses in 2013 and 2015 that were formally offered at multiple universities across the country and featured lectures by world leaders in their fields. We will offer two similar courses during GCE-IV, with one of the courses focusing on disturbance in coastal habitats.

The GCE Schoolyard program serves as the core of our education activities. Each year approximately 12 K-12 teachers spend a week at the GCE field site on Sapelo Island immersed in hands-on research activities alongside GCE scientists and graduate students. The program is built around a model of long-term contact: we use a mix of returning and new teachers as a way to promote mentoring and continuing engagement of veteran teachers. Participants are supported throughout the year by electronic contacts and return trips to Sapelo Island to share classroom activities developed based on GCE science. We have always asked teachers to fill out evaluation forms, and we receive feedback such as "*I will use more inquiry based learning & process based activities*" and " *I will be able to use the concepts & alter them to fit my curriculum.* " However, we have never followed up on these statements. During the first year of GCE-IV we will work with a marine educator to formally assess how the program has affected practices of the teachers who have participated over the years (now more than 100) and to recommend ways we might improve its effectiveness going forward. For example, we are considering requiring teachers to develop lesson plans that are aligned with Next Generation Science Standards and submitted to the LTER Education Digital Library in order to qualify as a mentor during return visits. We will also evaluate ways to promote connections amongst participants (e.g. via social media and other outlets).

The GCE children's book, *As the Tide Comes In*, is now in its second edition. The book is part of the LTER book series and is aimed at teaching upper elementary children about salt marshes. The first edition is widely used in GA, in both the classroom and at environmental centers. The new edition has a wider geographic reach and we will work with our partners at the National Estuarine Research Reserves and state Sea Grant programs to distribute it more broadly. We have records of the educators who have received the book to date, and will develop a survey to determine the ways in which the book and accompanying lesson plans are being used. We are also developing a comic book, *The adventures of Jacob the technician*, aimed at middle school children, and will work with the Schoolyard teachers to develop accompanying educational materials for this project. All of these lesson plans will be aligned with standards and submitted to the LTER Education Digital Library.

We have developed two web applications in which we ask citizen scientists to help us align thousands of photographs into a mosaic of the marsh (this cannot be done with standard software due to parallax and the lack of strong features), and to then use these photo transects to collect data on community structure. We will use the data to document spatial relationships among all the species at multiple spatial scales and evaluate their relationships with external drivers. Both web applications (Scaling up Marsh Science and Marsh Explorer) are online and generating data, and both have educational content that informs users about salt marshes and promotes the children's book. During GCE-IV we will work with the Schoolyard Teachers to improve the educational content of both sites. We will also continue to track the number of users of each site.

The GCE works directly with coastal managers through partial support of the Georgia Coastal Research Council (GCRC), which is headed by Alber. The GCRC is a boundary organization that facilitates science-based management of coastal resources for Georgia and the southeast region. It hosts workshops and other meetings, assists management agencies with scientific assessments, and synthesizes coastal research. The GCRC provides a direct mechanism for sharing the results of GCE research with State managers and for alerting us to new resource issues as they arise (e.g. we received a recent request for information on thin layer placement in marshes). During GCE-IV the GCRC will create summary reports of GCE findings specifically geared to managers and will also provide opportunities for GCE researchers to participate in meetings with the GA DNR Coastal Resources Division.

Other Activities The GCE maintains samples of marine invertebrates collected during our fall monitoring efforts that date back to 2000, which are available to other researchers. We also contribute specimens to an extensive herbarium collection at the University of Georgia Marine Institute that focuses on vegetation of the Georgia coast, and maintain a species list (with photographs) on the GCE website.

Our broadest reach is through the GCE program website and public data portal, which disseminate information and products including publications, research data, photographs, and remote sensing imagery. GCE data are downloaded by a diverse group of web visitors, including researchers from around the world, educators, and students. The GCE IM program has developed a number of software products, database systems, and web applications that have been released as open source software. To date, the GCE Data Toolbox software has been downloaded by over 4000 registered users. The website also provides access to decades of research on Sapelo Island and the Georgia coast as well as a data catalog and bibliographic, taxonomic, and geographic databases for the Savannah River Ecology Laboratory. We also publish a weekly newsletter detailing GCE activities that is available to interested parties.

GCE investigators routinely host students and scholars from a variety of countries. We also have active collaborations with scientists in the Netherlands (Angelini) and China (Craft, Pennings) that include bidirectional visits and provide opportunities for international networking. In addition, GCE scientists regularly participate in public forums and provide information about their research to the media. GCE research has been featured in NSF Discoveries articles and picked up by major news outlets. We also provide tours of the research site to visitors to Sapelo Island, which have included legislators (US House and Senate), personnel from state (DNR, EPD) and federal (NOAA, EPA) agencies, and students and scientists from multiple Universities. Fig. 1. Locations of a) Altamaha River watershed within the state of GA, b) observing stations used to track boundary conditions (ML is Marsh Landing; UGAMI is UGA Marine Institute), and c) GCE domain showing locations of core monitoring & experimental sites.









Fig. 2. GCE domain, showing a) longitudinal and b) lateral distribution of habitat and water flows across the landscape, and c) examples of marsh disturbance.











Fig. 3. Long-term patterns in abiotic drivers on the Georgia coast. Average annual values for a) sea level (Fort Pulaski); b) river discharge (USGS gage at Doctortown), and c) the Palmer Drought Severity Index (NOAA). Shading denotes time period of GCE program.

Fig. 4. Long-term patterns in human usage of the Georgia coast.
a) Measured and projected population density in coastal counties (Coastal GA Regional Council 2017). Shading denotes time-period of GCE program.
b) % increase in the number and length of vertical (bulkhead) and lateral (revetment) shoreline structures along the entire Georgia coast and in McIntosh County, which is where GCE is located (Alexander 2016).



Biomass (g dwt m⁻²)

Fig. 5. Patterns in annual biomass of tall (red), medium (blue) and short (green) Spartina, estimated from Landsat5 (solid lines,with dotted regression lines). Slopes of trend lines are -13; -8.5 and -6.5 g/m²/y for tall, medium and short Spartina. Shading indicates drought periods as indicated by the Palmer Drought Severity Index. Modified from O'Donnell & Schalles 2016





Time

Fig. 7. The ecosystem response to a change in a driver depends on the type of perturbation (a-d) and the relationship between the driver and response (1-2). Combining perturbations (column d) leads to complex behavior. A hysteresis driver-response relationship (not shown) would affect the return trajectories for pulse perturbations.



Fig. 8. Time for Spartina recovery from a clearance experiment increased as a function of salinity. All plots are mid-marsh plots with medium/short Spartina. (Guo & Pennings, unpubl. data)



Table 1. Time for marsh plant recovery from a wrack perturbation varies with plant species and elevation. Spartina recovery is fastest at intermediate elevations. (Alber, unpubl. data)

Vegetation Zone	Elevation	Recovery time
S. alterniflora - tall	0.41 m	2 y
S. alterniflora - med	0.59 m	1 y
S. alterniflora - short	0.66 m	2 y
Juncus roemerianus	0.91 m	> 6 y
Marsh meadow	0.97 m	3 у



Fig. 9. Conceptual Model of Disturbance. Domain perturbations can be caused by external drivers and internal processes. Abiotic and disturbance (biotic) responses to these events are a function (f) of the interaction between domain perturbations and the system state (biophysical template), which can feed back to the biophysical template. Information on both perturbations and disturbance responses are used to produce a cumulative disturbance-scape.



Environmental (weather stations, freshwater inflow, ocean conditions) [DD, AB, WS, MA, RP, WC, PM] **Human** (population trends, land use, shoreline structures, archeology) [MA, CA, NH, VT]

Patterns within the domain (Area 2)

Field Monitoring Hydrology [DD, WS] Water chemistry [MA,WC, PM] Soils [CC] Flora & fauna [SP, BS, CHA, CO]

Remote sensing Aerial photography [CA, CH] Drones [CA, MA, JS] Satellite imagery [JS, DM, MA]

Modeling FVCOM [DD, RC] Soil model [CM] Plant model [AB]

Responses to disturbance (Area 3)

Spartina marsh Productivity [DM, WS, JO, SP] Predator exclusion [BS, JB, SP, CO] Disturbance [SP, CHA, MA]

Tidal Forest/fresh/brackish marsh Altamaha habitat [MA, SP, CH, VT] SALTEx [CC, SP, SB, JB, PM, CHA]

High marsh/upland border Vegetation dynamics [SP, MA] Upland manip [SP, AW, RV, CM, CA] **Integration & forecasting**

(Area 4)

Ecosystem properties Habitat provisioning [CH, JS] Biomass patterns [JS, CH, JO] GPP [DM, JO] C budgets [WC, DM, PM, CC]

Disturbance-scape Disturbance effects [MA, All] Remote sensing [MA, CA, JS, DM] Modeling [DD, RC, MA, AB]

Driver-response relationships Data synthesis [AB, SP, MA] Dynamical systems models [AB] Scenarios [All]

Fig. 10. GCE-IV Research Portfolio, showing major program components and the initials of the primary PIs involved in each activity - AB: Burd; AW: Wilson; BS: Silliman; CA: Alexander; CC: Craft; CH: Hladik; CHA: Angelini; CM: Meile; CO: Osenberg; DD: Di Iorio; DM: Mishra; JB: Byers; JS: Schalles; MA: Alber; NH: Heynen; PM: Medeiros, RC: Castelao; RP: Peterson; RV: Viso; JO: O'Connell; SP: Pennings; VT: Thompson; WC: Cai; WS: Sheldon.

Table 2. Monitoring program for GCE-IV. Initials of PIs responsible for supervising each aspect of the monitoring program are indicated in parentheses. LTER core areas are 1: primary production, 2: populations, 3: organic matter cycling, 4: inorganic nutrients, 5: disturbance. PI initials as in Fig. 10.

Туре	Location	Frequency	Core Area & Variables Measured
Area 1			
Weather stations, with SINERR, USGS (DD)	Sites 4, 6, flux tower	15 min	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
Altamaha River chemistry (MA, WC)	Head of tide	Monthly	3, 4. Dissolved inorganic nutrients (NO _x , NH ₄ ⁺ , HPO ₄ ⁻²⁻ , H ₂ SiO ₄ ⁻²⁻) and organics (DOC, TDN, DON, TDP, DOP), particulate CN, DIC, alkalinity, pH
Area 2 Water			
Sound chemistry (MA, WC, PM)	Sites 1-5, 8- 11, AL-2	Quarterly	1, 3, 4. Dissolved inorganic nutrients (NO _x , HPO ₄ ²⁻) and organics (DOC, TDN, DON), particulate CN, DIC, alkalinity, pH, chlorophyll a
	Sites 6-7	Monthly	1, 3, 4. Dissolved inorganic nutrients (NO_2^- , NO_3^- , NH_4^+ , HPO_4^{2-} , $H_2SiO_4^{2-}$) and organics (DOC, TDN, DON, TDP, DOP), particulate CN, DIC, alkalinity, pH, chlorophyll <i>a</i> , total suspended sediment
	Sites 7, AL-2	Quarterly	3. DOM composition
Sound hydrography (DD)	Sites 1-4, 6- 11	30 min	Driver of 1-5. Salinity, temperature, pressure at moorings; CTD profiles at all stations in conjunction with sound chemistry; sea level station at GCE4
Duplin-domain exchange (DD)	Mouth of Duplin R.	15 min	Abiotic driver of 1-5. Horizontal ADCP measurements of water flux
Area 2 Marshes			
Soil accretion (CC)	Sites 1-11	Annual	3. Sediment accretion, elevation, compaction
Soil temperature (JO, CM)	Sites 1-11	15 min	Abiotic driver of 1-4. Loggers in root zone (10 cm deep), in 2 marsh zones adjacent to vegetation plots.
Plant productivity (SP, CC, DM, JO)	Sites 1-10	Annual	1. Stem density, height, flowering status, calculated biomass, in 2 marsh zones
	Site 11	Annual	1. Litterfall traps and stem wood growth of tupelo gum and bald cypress
	Flux tower	5 min	1. Net ecosystem exchange
	Flux tower	Monthly	1. Above- and belowground biomass in short, medium, tall Spartina
	Flux tower, site 4	30 min	1. Phenocam estimates of aboveground biomass in short, medium, tall <i>Spartina</i>
Disturbance (SP)	Sites 1-10	Annual	5. Disturbance in permanent vegetation plots
Plant composition (SP, MA, CC)	Sites 6, 10	Annual	2. Community composition in 4 types of salt marsh, 2 types of high marsh vegetation mixtures
	Altamaha	Annual	2. Community composition in 2 types of low-salinity marsh vegetation (3 sites). Distribution of Altamaha marsh types (~50 stations), health and survival of tidal fresh forest trees (~50 stations).
Marsh Invertebrates (CHA, SP)	Sites 1-11	Annual	2. Density and size of benthic macroinvertebrates (mollusks, crab burrows) in 2 marsh zones.
Insects (SP)	Sites 1-6, 9, 10	Annual	2. Density of grasshoppers in salt marsh transects
Recruitment (CHA)	Sites 1-11	Annual	2. Recruitment of barnacles to standard substrates

Fig. 11. Predicted rate of recovery (fraction/y) from disturbance of different vegetation types across gradients of a) salinity and b) inundation. Vertical dotted lines in **panel a** indicate transitions between vegetation types where recovery rates of the lower-salinity vegetation type are low and a state change may occur. In **panel b** a state change may occur at the lowest elevation occupied by each plant species.

Fig. 12. Examples of GCE core monitoring data. a) water level at Hudson Creek; b) average monthly salinities at sites GCE3 (blue); GCE4 (grey); GCE8 (green) and GCE7 (red); c) average annual biomass of Zizaniopsis at creekbank (blue) and mid-marsh (red) at site GCE7; e) % cover of Sarcocornia (red), Juncus (blue) and Batis (green) in transitional area. Shading indicates drought periods as indicated by the Palmer Drought Severity Index. Error bars represent standard errors.



Table 3. Response variables, methodology, sampling frequency, and responsible PI (initials as in Fig. 10) of proposed measurements in disturbance experiments.

Variable	Methodology	Frequency	PI
Aboveground biomass	Stem density & height, flowering status	Each visit	SP
Belowground biomass	Cores	2x/year	CC
Plant production	Aboveground growth; root ingrowth	Annual	SP
Benthic algae	Benthotorch	Each visit	SP
Macroinfauna	Densities of snails & crab burrows	Each visit	SP
Decomposition	Tea bag weight loss (Keuskamp et al. 2013)	Annual	SP
Organic material	Soil C & N content	2x/year	CC
Inorganic nutrients	Porewater NH ₄ concentration	Each visit	MA
Abiotic conditions	Soil temp, pore water salinity, redox, pH	Each visit	SP



Fig. 13. Selected responses observed in SALTEx experiment. a) Porewater NH₄ concentration; b) % Ludwigia cover (note that Ludwigia cover was high in all treatments in 2014 but data were not collected until 2015); c) % Zizaniopsis cover; d) elevation as measured by SETs. The press treatment began in April 2014 and is shaded grey; pulse periods (Sept-Oct each year) are shaded blue. Black lines on each graph denote measurements made in press treatments; blue lines denote measurements made in pulse treatments; green lines denote measurements made in untreated controls (procedural controls not shown). Error bars represent standard errors.

Fig. 14. Example of using Landsat 8 spectral information to estimate a) aboveground biomass $(g m^{-2})$ and b) % foliar N at the GCE flux tower site (see Fig. 1). These two estimates (groundtruthed with field observations) are then combined using partial least squares linear regression as predictors of c) below-ground biomass $(g m^{-2})$ for May 2016. Note the locations in the lower right where above- and belowground patterns differ. (O'Connell et al., in prep.)



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DATA MANAGEMENT PLAN

Overview

The GCE has a comprehensive information management program that supports the entire research enterprise as well as project logistics, administration and governance. During GCE-I to -III we developed efficient procedures and technology for acquisition, standardization, documentation, analysis and synthesis of all GCE data. We developed an integrated information management system (GCE-IMS) based on relational database and dynamic web application technology to manage, archive and distribute data, metadata and other research products. We also established a GIS for managing geospatial data and developed software to link the GIS to the GCE-IMS to support unified metadata generation for tabular and spatial data. All LTER network standards and protocols are fully supported by the GCE-IMS, and our data sets (described in EML 2.1) are regularly synchronized with the LTER Data Portal (EDI) for automatic registration in DataONE and the Biological and Chemical Oceanography Data Management Office (BCO-DMO), thereby supporting data search and download through all of these repositories. During GCE-IV we will build on our established IM system to continue core data management efforts while further streamlining data submission and expanding support for routine archiving of drone imagery, remote sensing data and model output. We will also transition our public-facing websites from custom code to an industry standard content management system for improved maintainability and alignment with emerging LTER web design standards and practices.

Data and Information Management System.

GCE IT Resources We maintain a strong IT infrastructure at UGA that we will expand to meet GCE-IV information management needs. Current systems include a new 10-core Dell server with 9.6TB drive array that hosts four production virtual servers (database, web, file and software development), and a 12-core Dell server with 12TB drive array and 16-slot LTO-5 tape library that functions as a backup server and host for additional virtual machines. Both servers are equipped with redundant power supplies, UPS and RAID-5 or -10 drive configurations, collectively providing >14TB of fault-tolerant hard drive storage and >24TB of tape storage for off-site backups. We also maintain workstation and laptop computers at UGA and UGAMI for data processing, and a network file server at UGAMI for local computer backups. *In GCE-IV we will acquire a 48TB network-attached storage server to provide centralized shared storage for drone and satellite imagery, modeling output and working files generated by research groups.*

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 continue to share IT resources with the CWT LTER program (administered at UGA), including backup storage and reciprocal web application hosting.

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, H-ADCP and other instruments installed near the ferry landing. 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.

Other IT Resources We also leverage additional IT resources managed by GCE investigators:

- Satellite Remote Sensing (Mishra): 8 high speed workstations, 26TB server storage, high resolution scanner/plotter, image processing and GIS software
- Satellite Remote Sensing (Schalles): 4 notebooks/workstations, 15 teaching lab computers, 17TB server storage, large format UltraHD monitors, image analysis software (ENVI)
- Simulation Modeling (Castelao/DiIorio/Meile): UGA HPC cluster node (48cpu, 10GB RAM), 32cpu Dell server cluster, 24TB server storage

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-IV 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-IV is the GCE Data Toolbox, a MATLAB software library for metadata-based processing, analysis, quality control and synthesis of ecological data sets. 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 2.1 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 web sites (Fig. 1).



The GCE has a comprehensive public web site as well as a password-protected intranet site 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 web site (e.g. research projects, personnel pages, study site descriptions, Google maps, and species list entries). In addition, we have a public "Data Portal" web site to provide access to relevant ancillary data from federal programs and monitoring partners, documented and standardized for comparison with GCE data. *These web sites will be maintained and expanded in*

GCE-IV, but we will transition public-facing web sites to a modern content-management system (e.g. WordPress 4.9 or Drupal 8) during year 1 to improve mobile device support, accessibility and maintainability moving forward. We will pair the CMS with the GCE-IMS via web services integration.

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-IV. The Information Manager is a voting member on the GCE Exec and IM staff will regularly interact with PIs and students in research planning, data analysis, and publication and proposal development (Table 1). IM staff also routinely process, quality control and document routine monitoring data, providing Data-as-a-Service to the project.

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

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

Data Acquisition and Submission IM staff work 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-IV*. Electronic sensor data will be automatically harvested from data loggers or online data systems via network telemetry for automated processing whenever practical (e.g. flux tower, weather stations, streamflow gauges and H-ADCP). Sensor data that require manual downloading (e.g. sondes, well loggers and hand-deployed instruments) will be synchronized to GCE servers on a routine basis for semi-automated processing. Monitoring data that are collected infrequently or are derived from laboratory analyses will be submitted to the IM office at varying intervals, with sample information organized in a centralized database. Existing web forms and spreadsheet templates will be 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, mass spectrometers and other instrumentation. All submitted data and support files will be organized in hierarchical server directories, backed up daily, mirrored between servers and copied to LTO-5 tapes for off-site storage. All protocols will be documented and data submission and publication status will be tracked and reviewed yearly in conjunction with annual NSF reporting.

Data Processing and Quality Control Tabular data from instruments and spreadsheets will be processed using the GCE Data Toolbox, utilizing data parsing and quality control workflows designed in collaboration with GCE investigators. Metadata will be 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 will be automatically documented, resulting in

metadata that describe the complete processing lineage. Finalized tabular data will be archived in both standard text and MATLAB formats to provide broad compatibility. Geospatial (GIS) data, remote sensing imagery and other non-tabular data will be 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 will then be archived in domain-appropriate formats determined in consultation with IM staff (e.g. file geodatabases, shapefiles, raster images, array formats).

Data Synthesis During GCE-III we began systematically creating and archiving long-term data sets to simplify use of GCE data for synthesis projects, linking long-term data sets to the primary observational data. *This effort will continue and be expanded in GCE-IV*. 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 additional 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 be distributed through the GCE Data Catalog. Publicly released data sets will also be synchronized to the LTER Data Portal (EDI) monthly for federated distribution through EDI, DataONE, BCO-DMO and related repositories. Data summaries and metadata will be publicly available immediately. The accompanying data files will be 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 will be tracked by research theme and user affiliation for reporting purposes, as possible. *See Table 2 for a summary of planned GCE-IV data products and release timelines.*

Support for LTER Standards

GCE has actively contributed to standardization and cyber infrastructure development in LTER and the broader community, and *we expect this to continue in GCE-IV*. We played a major role in adoption of the EML metadata standard in LTER and fully support EML 2.1 throughout the GCE-IMS, and we will participate in future development of this standard. We also developed the EML-based MATLAB script generation tools deployed in the LTER/EDI Data Portal, added EML-based data mining and synthesis tools to the GCE Data Toolbox to support the EDI Portal, and improved MATLAB functionality in the Open Source Data Turbine software and will sustain these efforts as funding allows.

We developed a data harvesting service for the LTER HydroDB database that automatically contributes streamflow data from USGS stations near 13 LTER sites and 2 USFS sites weekly. We also helped 3 LTER sites (CWT, SBC and MCR) adapt GCE-IMS components for their use, and facilitated use of the GCE Data Toolbox at 7 other LTER sites, notably AND, CWT, NWT and HBR where this software is used extensively. *We will continue to facilitate these cross-site technology transfers in GCE-IV*.

Data Products

Anticipated data products and data release timelines for the research proposed in GCE-IV are summarized in Table 2. Because the suitability of the LTER Data Portal (EDI) for archiving high volume imagery and model output has not been established we will store high volume data at UGA and make them available as "offline" data referenced in summary data sets that are discoverable at EDI, DataONE and BCO-DMO until community archival practices for these data are identified.

Literature Cited

Sheldon, W.M. Jr. 2008. Dynamic, Rule-based Quality Control Framework for Real-time Sensor Data. Pages 145-150 in: Gries, C. and Jones, M.B. (editors). Proceedings of the Environmental Information Management Conference 2008 (EIM 2008): Sensor Networks. Albuquerque, New Mexico.

Wilson, G. 2006. Software Carpentry: Getting Scientists to Write Better Code by Making Them More Productive. Computing in Science & Engineering, November/December 2006, p. 66-69.

Table 2. Planned data acquisition and release time frames by research area and repository, where Freq = acquisition frequency, GCE = GCE release, Pub = public release, Repo = target repository, NRT = near-real-time, M = monthly, Q = quarterly, A = annual updates, S = special study, V = varying, <2Y = within 2 years, EDI = Environmental Data Initiative, GCE = GCE servers, PHENO = PhenoCam Network.

Area	Data Collection	Data Sets	Freq	GCE	Pub	Repo
1	USGS Streamflow	long-term streamflow	NRT	NRT	А	EDI
	River Chemistry	nutrient concentrations	М	Q	А	EDI
	Rn-222 Surveys	groundwater inputs	S	Α	<2Y	EDI
	NOAA/NOS Tides	long-term sea level	Q	Q	Α	EDI
	Demographics/Land Use	land use maps, trends	S	Α	<2Y	EDI
2	Sonde Moorings	long-term hydrography	Q	Q	А	EDI
	CTD Profiles	long-term hydrography	М	М	Α	EDI
	Water Column Organics	DOM characteristics	М	Q	<2Y	EDI
	Marsh Monitoring	plants, inverts	Α	Α	<2Y	EDI
	Tidal Forest Monitoring	litter fall, tree growth	Α	Α	<2Y	EDI
	Temp Loggers (mimics)	Temperature	S	Α	<2Y	EDI
	PhenoCam	imagery/phenology index	NRT	NRT	NRT	PHENO
	Drone Flights	marsh imagery	Q	Q	<2Y	GCE/EDI
	Aerial Photos	landscape imagery	S	Α	<2Y	GCE/EDI
	Landsat/MODIS	landscape imagery	Α	Α	<2Y	GCE/EDI
	Hydrodynamic Model	model conditions/results	V	V	<2Y	GCE/EDI
	Soil Model	model conditions/results	V	V	<2Y	GCE/EDI
	Plant Model	model conditions/results	V	V	<2Y	GCE/EDI
3	Disturbance Responses	disturbance data sets	Α	Α	<2Y	EDI
	Flux Tower Data	atm, soil, water params	NRT	NRT	<2Y	EDI
	Flux Tower Fluxes	NEE, footprint	М	М	<2Y	EDI
	Flux Tower Biomass	plant biomass	М	М	<2Y	EDI
	Greenhouse Experiment	plant biomass	S	Α	<2Y	EDI
	Predator Removal	inverts and plants	Α	Α	<2Y	EDI
	Marsh Perturb Images	drone imagery/ analysis	M/A	M/A	<2Y	GCE/EDI
	Marsh Perturb Sampling	elevation, disturbance	Q	Α	<2Y	EDI
	Dendrochronology	tree abundance/growth	S	Α	<2Y	EDI
	SALTEx Recovery	groundwater, nuts, soils,	M/A	Α	<2Y	EDI
	Leve Terry Merceletter	plant biomass, elevation	C		-017	EDI
	Long-Term vegetation	vegetation cover (plots),	3	A	<2 Y	EDI
	Upland Manipulation	wells, soils, plants, inverts	M/A	M/A	<2Y	EDI
4	Habitat Distribution	vegetation map	S	A	<2Y	EDI
	Biomass Patterns	satellite/NPP estimates	S	A	<2Y	EDI
	Belowground Biomass	satellite/biomass	S	A	<2Y	EDI
	Gross Primary Prod	MODIS/GPP maps	S	Α	<2Y	EDI
	Carbon Budgets	DIC/NEE	S	A	<2Y	EDI
	Disturbance-Scape	drone imagery/MODIS	S	A	<2Y	GCE/EDI
	Driver-Response	synthesized data/models	V	V	<2Y	GCE/EDI

PROJECT MANAGEMENT PLAN

Project Organization Alber has been a PI of the GCE-LTER since its inception and has served as Lead PI since the start of GCE-II (2006); Pennings has served as co-PI since the start of GCE-I (2000). Alber and Pennings work together to oversee the project. They handle routine administrative issues and are in touch on a daily basis. Alber is responsible for communication with NSF and the LTER network, overseeing GCE staff at UGA, and managing the budget. Pennings serves as director of field operations at the UGA Marine Institute on Sapelo Island (UGAMI), which is the base of our field program. Although he holds a faculty position at the University of Houston, Pennings is in residence at UGAMI 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, Jacob Shalack, 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, and we will continue it in GCE-IV*.

The GCE is governed by a set of bylaws, which describes the roles and responsibilities of the project as well as provisions for election and removal of individuals. A copy of the bylaws is available on our website. 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. Almost all major funding and research decisions are made by the EC, with the rare exception of items that are highly sensitive, which are handled in confidence by Alber and Pennings. Both the PI and the members of the EC are elected for 6-year terms that begin a year before the proposal is due. The EC members take the lead in writing the proposal and also take administrative responsibility for specific aspects of the project. The EC currently consists of Alber, Pennings, Burd, Di Iorio, Craft, and the Information Manager (Sheldon) (Table 1). EC members are in touch regularly via e-mail, and meet approximately every month (non-UGA participants attend by video-conference or travel to UGA when necessary). GCE scientists are classified as either Project Investigators or Affiliated Investigators, 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 Project Investigators. Project level post-docs (see post-doc mentoring plan) attend project meetings and interact with various GCE scientists and students in accordance with their research tasks. GCE graduate students are defined as students working in the domain with a Project Investigator. There is a graduate student liaison (elected by the students), who serves as a bridge between GCE Investigators, GCE students, and the network. This structure is functioning well, and we will continue it in GCE-IV.

The GCE has traditionally had a 6-person Advisory Committee comprised of scientists from both inside and outside LTER. Advisory Committee members attend our annual meeting and provide feedback and advice on project research and administration. Their participation was invaluable as the GCE was getting established, but the project has matured to the point where we can now reduce the size of the Committee. Therefore, *in GCE-IV we will rely on a 2-person Advisory Committee*.

Project Meetings The entire GCE membership, including postdocs, students and technicians, meets once a year, usually in January. Meetings last 2½ days and focus on sharing research results and planning future activities. These annual meetings allow us to formally evaluate our progress and have been instrumental in helping us plan research activities, prepare for our mid-term site review, and discuss new ideas. The meeting typically includes a poster session during which we encourage students and post-docs to present their research. We also hold a business meeting during the annual meeting to discuss project business, such as bylaws and project leadership. The annual meetings also provide an opportunity for small groups to work on papers, receive training on information management, and discuss leveraged proposal ideas. We invite our partners from state agencies to attend the meeting as well as potential new collaborators. *We will continue annual meetings in GCE-IV*.

Subsets of investigators within the project meet regularly, usually by conference call, to advance collective field projects or analysis tasks and to keep sub-projects on track. During GCE-III researchers involved in the SALTEx experiment, the high marsh experiment, and flux tower research met approximately monthly; other groups (remote sensing, modeling) met as needed. Alber or Pennings participated in most of these calls. *Over the course of GCE-IV we anticipate continued regular meetings of project groups*.

The four Atlantic coast wetland sites (PIE, VCR, GCE, FCE) regularly seek opportunities to collaborate and to address topics ripe for cross-site work. The PIs and co-PIs of these projects see each other on a regular basis 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 sites to exchange participants at annual meetings and promote cross-site interactions*.

New Scientists One of the suggestions during our mid-term review was to consider transitions in personnel, particularly with respect to long-term leadership of the project. In response, the UGA Dept. of Marine Sciences is currently in the middle of a search for a coastal scientist with a research focus on the ecology of coastal systems. The goal of the search is to hire a faculty member at the Assistant or Associate Professor level who will actively participate in the GCE, with the potential to take a leadership role in the project. We have budgeted funding for supplies and student support for the new hire, who is expected to be in place in Fall 2018. It is our expectation that this new hire will transition onto the Executive Committee mid-way through the GCE-IV proposal cycle and be a cover page investigator on the GCE-V proposal. We are also adding 6 new researchers in GCE-IV: Angelini (Univ. of Florida, community ecology); Heynen (UGA, human geography); Hladik (Georgia Southern, remote sensing); Mishra (UGA, C budgets); Osenberg (UGA, ecology); Wilson (Univ. of South Carolina, ecohydrology). Both Angelini and Hladik were previously graduate students at the GCE.

We will also continue to encourage non-LTER scientists to become affiliated with the GCE site by extolling the twin benefits of working at Sapelo Island and working 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 site as wells, along with ready access to data. We expose new scientists to GCE research by inviting them to our meetings, with the hope that they will be able to become Affiliated and, eventually, Project Investigators. We work with these scientists to develop leveraged research proposals and we write letters of support for related proposals.

<u>Diversity</u> - To date, the GCE has been successful at including female participants. The GCE is led by a woman, and women currently represent 27% of the PI and AI ranks and 40% of the participants at the level of graduate students and above. The PIs for GCE-IV include 2 investigators from Brazil, 1 from India and 1 from China. Our diversity plan emphasizes our partnership with the Peach State Louis Stokes Alliance for Minority Participation program, a collaborative effort between six colleges and universities in Georgia, led by UGA, to increase minority participation in STEM fields. We work with Peach State LSAMP to recruit undergraduates into our program as REUs and to encourage them to consider postgraduate studies in science. We also ensure that our REU and technician positions are advertised at Savannah State University, which is a historically black college near the GCE study area with a Marine Sciences undergraduate and MS program.

Table 1. Executive Committee. Members are elected for renewable 6-year terms, to include the year preceding and the first five years of each NSF proposal, following procedures detailed in GCE bylaws.

Personnel	Administrative Responsibilities		
Merryl Alber, Lead PI	Represent GCE to NSF and LTER network		
	Lead administrator		
	Oversee UGA management staff		
	Oversee entire program		
	Oversee Area 1: External drivers of change		
	Oversee Area 4: Integration and forecasting		
	Oversee outreach and education		
Steven Pennings, Co-PI	Oversee field operations		
	Oversee Area 2: Long-term patterns within the domain		
	Oversee Area 3a: Spartina marsh research		
	Oversee Area 3c: High marsh/upland border research		
Daniela Di Iorio	Oversee weather stations and flux tower (Area 1)		
	Oversee hydrological monitoring (Area 2)		
Christopher Craft	Oversee Area 3b: Tidal forest/fresh/brackish marsh research		
Adrian Burd	Oversee integrated modeling (Areas 2, 3, 4)		
Wade Sheldon	Information Management		

POSTDOCTORAL RESEARCHER MENTORING PLAN

The GCE will support at least 6 postdoctoral researchers over the time period of this award (supervised by Alber, Burd, Cai, Heynen, Mishra and Pennings). GCE postdoctoral researchers report to both the GCE Executive Committee (to monitor overall progress) and to their specific research mentors (for detailed technical progress). Participation in the GCE provides postdocs with experience in a large interdisciplinary project and multiple opportunities for advancement. During GCE-IV each postdoc will work with their research mentor, in consultation with the GCE Executive Committee, to develop an **individual career development plan** tailored to meet his or her career goals and experience. The plan will include specific expectations for research topics and products while funded by the GCE. The career development plan will take advantage of the *strengths of the GCE environment for postdoctoral training*:

Communication GCE Postdocs will gain experience in both oral and written communication through their participation in the project. They will have the opportunity to communicate with researchers from different fields at GCE and national meetings, with educators and students through our Schoolyard workshop, and with natural resource managers through the Georgia Coastal Research Council. They will take the lead on preparing scientific manuscripts based on their work, contribute to the GCE annual report, and write pieces for a more general audience through the GCE Newsletter.

Collaborations Because GCE postdocs will be nested within a large collaborative group and will work with multiple PIs, they will directly experience both the benefits and challenges of collaborative science. They will participate in GCE working groups and meetings as well as the LTER All-Scientists meeting and other network-level activities. We anticipate that most work by GCE postdocs will be collaborative and most publications multi-authored.

Career guidance The postdoc's primary research mentor will have responsibility for providing guidance in career planning; however, postdocs will also be required to submit an annual report to the GCE Executive committee, who will intervene if progress appears inadequate. We will encourage postdocs to participate in career development workshops offered by host institutions and at a national level, including workshops at national meetings and stand-alone career-development workshops. In addition, each host institution has requirements for evaluations of personnel that will provide an additional layer of progress evaluation.

Research competencies Each postdoc's research mentors will have responsibility for providing technical training as appropriate to the needs of the project and individual postdoc. Being part of an interdisciplinary group will provide multiple opportunities for the postdocs to gain broad exposure to a variety of scientific disciplines through regular research interactions and project meetings.

Teaching and mentoring GCE postdocs will be embedded in individual laboratories, and will help mentor graduate and undergraduate students within those laboratories and in the interdisciplinary research groups that develop around the postdoctoral projects.

Outreach GCE postdocs will have opportunities to participate in the Georgia Coastal Research Council meetings, the GCE schoolyard program, and other outreach activities as appropriate, given their individual research and career goals.

Responsible conduct of research GCE postdocs will be required to complete training in responsible research conduct, such as the Responsible Conduct of Research course offered by the Collaborative Institutional Training Initiative, or equivalent. The collaborative nature of the GCE will provide exposure to the specific ethical issues that arise in collaborative groups, in particular issues surrounding data sharing and authorship on multi-authored and multi-institution manuscripts.

Transition to faculty positions As postdocs transition to faculty and other higher level positions, we will provide guidance on job applications and startup negotiations, and will provide opportunities for them to remain involved with the GCE project as appropriate.