PROJECT DESCRIPTION

I. INTRODUCTION & INTELLECTUAL MERIT

A. History, Growth, and New Directions of the VCR LTER Program

The Virginia Coast Reserve (VCR) LTER is an interdisciplinary research program dedicated to developing a predictive understanding of ecosystem state change in coastal barrier systems in response to long-term environmental drivers. This heterogeneous coastal landscape—including barrier islands, shallow coastal bays, and intertidal marshes—is the first line of defense against sea-level rise and storms, and at the same time, may be vulnerable to climate drivers (Fig. 1). The VCR exemplifies the ecological dynamics and management considerations of coastal barrier systems that comprise 15% of coastlines globally, and occur on all continents except Antarctica (Pilkey & Fraser 2003; Kennish & Paerl 2010). With more than half the world's population living within 100 km of the coast, and even more depending on coastal resources, ecosystem changes in these regions have significant consequences for coastal resilience and the provisioning of ecosystem services (Barbier et al. 2011).

The VCR provides a unique opportunity to study the mechanisms that underlie responses of coastal systems to climate variability and trends. The domain is the greatest expanse of undeveloped coastline along the U.S. Atlantic seaboard, and was designated as a Man and the Biosphere Reserve in 1979. It has been managed by The Nature Conservancy (TNC) since 1970, and thus is well protected and highly suitable for long-term research. There is little human footprint on the VCR landscape: the islands are undeveloped, the watersheds are largely rural, and water quality in the coastal bays is high (Hayden et al 1991; Stanhope et al. 2009; Giordano et al. 2011). **This makes climate, in large measure, the dominant driver of ecological change.** Sea-level rise in the region is about three times higher than the global average and is accelerating (Sallenger et al. 2012). Storms cause frequent disturbances that create an extremely dynamic landscape where ecosystem state change occurs on time scales of years to decades (e.g., Dolan et al. 1983; Fenster & Hayden 2007). Higher temperatures may push some species beyond tolerance thresholds, affect the competitive advantage of others including invasives, and expand the range of more southerly species into the VCR domain (Thomsen & McGlathery 2006; Lonard et al. 2011; Johnson 2014). The rates and intensities of these climate drivers are changing over time, and long-term research is needed to forecast how coastal systems will respond in the future.

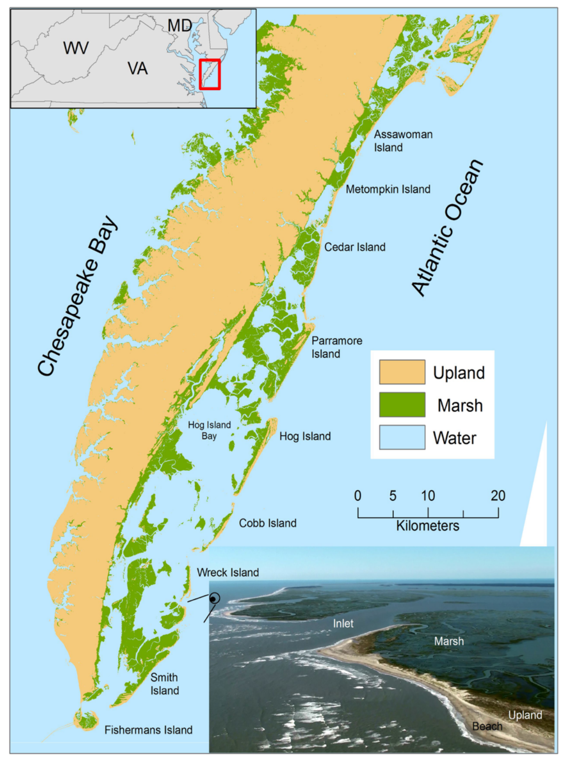

Fig. 1. Virginia Coast Reserve LTER includes 14 barrier islands and 9 shallow coastal bay systems, extending 110 km along the seaward margin of the Delmarva Peninsula. Exchange with the ocean is through narrow inlets between the islands.

Throughout the history of the VCR LTER, we have contributed to theoretical advances in understanding complex dynamics of state change in ecosystems dominated by foundation species (see definitions in Box 1; e.g., Brinson et al. 1995; Carr et al. 2012a,b; Durán Vinent & Moore 2015a; Kirwan et al. 2010, 2012, 2016a). Our research focuses on the major landscape units of the VCR and the ecosystems that comprise them (Fig. 2). On barrier islands, grasslands are transitioning to shrub thickets and dune grasses affect dune morphology; both influence island vulnerability to storms. In coastal bays, large-scale restoration of seagrass and oysters is reversing

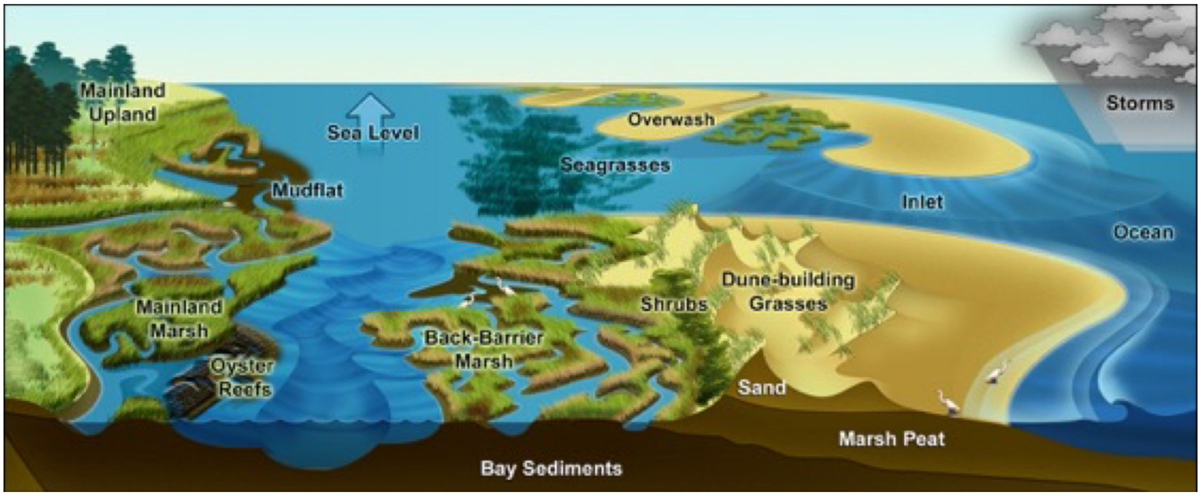

Fig. 2. Cross section of the VCR LTER domain. VCR research focuses on the mechanisms of ecosystem state change in each part of the coastal landscape, including barrier islands (dune-overwash fan, grassland swale-shrub thicket), subtidal (seagrass-tidal flat), intertidal (marsh-tidal flat, marsh-upland), and on connectivity and coupled dynamics between these landscape units (subtidal-intertidal, island-subtidal, across barrier island ecosystems) to achieve a holistic understanding of coastal barrier response to climate forcing.

the state change that occurred when these habitats were lost in the last century. For intertidal marshes, sea-level rise and storms cause migration into uplands and erosion at the seaward border. **Understanding these ecosystem transitions individually, and how the occurrence of a state change in one part of the landscape could propagate across the landscape through coupled dynamics is a critical frontier in projecting the long-term response of coastal systems to climate drivers.** Our strength is the integrated approach we take, linking ecological and physical (geomorphic, hydrologic) processes that are critical to ecosystem dynamics in coastal systems. For example, sediment transport and deposition allows marshes to keep pace with rising seas, oyster reefs and seagrass affect marsh erosion during storms, and vegetation (shrubs, grass) affects how barrier islands build elevation and migrate inland in response to sea-level rise and storms. We have made significant contributions to understanding ecological and physical processes, feedbacks that either maintain or facilitate transitions in ecosystem states, and have identified leading indicators of threshold responses (e.g., Blum & Christian 2004; Carr et al. 2010; Kirwan & Blum 2011; Hansen & Reidenbach 2012; Fagherazzi et al. 2013a; Wolner et al. 2013; Thompson et al. 2017). We are leaders in developing and testing mechanistic models with long- and short-term observations and experimental data, and using these to project state change and its ecological consequences across the landscape (e.g., Kirwan et al. 2010; Carr et al. 2012a,b; Fagherazzi et al. 2006; Mariotti & Fagherazzi 2010; Durán Vinent & Moore 2015a). This integrated long-term research informs management and conservation of coastal ecosystems at the VCR, and through synthesis and comparative work our research impact extends globally.

VCR research began in 1987 (**VCR I**, 1987-1992) with the hypothesis that large-scale events and persistent processes, such as storms and sea-level rise, drive ecosystem dynamics. We established that the redistribution of sediment by wind, waves, and currents is a critical process driving these dynamics (e.g., Hayden et al. 1991; Oertel et al. 1992), and showed that the region has extraordinarily rapid rates of landscape change driven primarily by storms (e.g., Hayden et al. 1991; Young et al. 1995a,b). In **VCR II** (1992-1994), we emphasized the interaction of 'press' (pervasive and gradual) and 'pulse' (sudden event or disturbance) dynamics that continues to be central to our thinking. We learned how gradual changes in ecosystems are punctuated by abrupt transitions to a different ecosystem state due to storm disturbance (e.g., Fahrig et al. 1993; Brinson et al. 1995). In **VCR III** (1994-2000), we developed the unifying theme that the mechanisms of ecosystem state change throughout the coastal bay system are linked to the relative elevations of the land, sea, and groundwater (e.g., Hayden et al. 1995; Shao & Shugart 1997; Christian et al. 2000). We quantified how the interaction of physical processes (storms, sea-level rise, precipitation) and biotic feedbacks of plant foundation species (on elevation and groundwater levels)

Box 1. Definition of Terms

Ecosystem state: dynamic equilibrium of an ecosystem under a set of drivers

Foundation species: species that have a strong role in structuring ecosystems through effects on other organisms and ecosystem processes

Resilience: ability of a population, community or ecosystem to respond to changing drivers (recovery from disturbance, absorb changes) and maintain state

Transgression: landward migration of coastal features in response to sea-level rise and storms

Hypsometry: distribution of elevation relative to mean sea level and its relationship to land area

influences these relative elevations, and thus ecosystem state transitions and ecological processes (e.g., Tolliver et al. 1997; Moncrief & Dueser 1998; Brinson & Christian 1999). We used the geomorphic concept of hypsometry (Box 1; Oertel et al. 2000) in **VCR IV** (2000-2006) to quantify long-term and spatially variable patterns of shifting ecosystem states related to vertical elevation changes. We also initiated the seagrass state-change experiment that has become a hallmark of VCR research. In **VCR V** (2006–2012), we introduced lateral processes (e.g., fluxes of organisms and material) into our conceptual framework (e.g., Lawson et al. 2012; Fagherazzi et al. 2013a,b,c). Our research in **VCR VI** (2012–2018) has built on this previous work to develop and test data-driven, mechanistic models of ecosystem state change, including alternative stable states, within landscape units (subtidal, intertidal, barrier island; Carr et al. 2010; Mariotti & Fagherazzi 2010; Durán Vinent & Moore 2013), and began to explore linkages between them (Mariotti & Carr 2014; Walters et al. 2014; Kirwan et al. 2016a; Zinnert et al. 2017).

Rationale for LTER VII and Conceptual Framework. It became clear in VCR VI that to achieve a holistic understanding of ecosystem state change across the coastal barrier system, we must better quantify and model how ecosystem dynamics in different landscape units are coupled. **These landscape linkages are the focus of VCR VII.** We will expand studies of system-wide fluxes of sediments and organisms and coupled state-change dynamics of adjacent systems (e.g., marsh–bay, island–back barrier marsh) to test and modify predictive models. We will also add new studies on the coupling of non-adjacent systems (e.g., island–mainland marsh) and on potential of cascading state change on the landscape (e.g., island–back barrier marsh–seagrass). **Our overarching goal for VCR VII is to understand, quantify, and predict how spatially integrated ecological and physical mechanisms drive ecosystem state change in coastal barrier systems in response to climate trends and variability, and to understand the consequences of these changes for ecosystem function.** We focus on carbon sequestration and habitat provisioning as two important functions that are valued in these coastal systems. We have modified our conceptual framework to reflect the recent advances in our understanding of state change dynamics that motivates our proposed research (Fig. 3). This includes the importance of spatial context, in

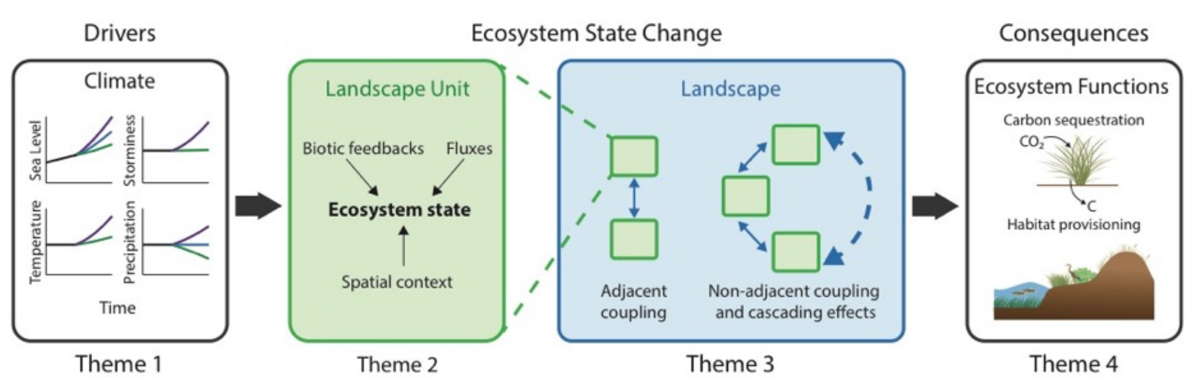

Fig. 3. The VCR VII conceptual framework focuses on the climatic drivers of change (Theme 1), the coupled ecological and physical processes that drive ecosystem state change dynamics (Themes 2 & 3), and the consequences for ecosystem function (Theme 4) on the coastal barrier landscape. We continue to investigate processes within landscape units (intertidal, subtidal, barrier island) and propose new studies to address connectivity of state change dynamics, including sediment and organism transport, and coupled processes of adjacent and non-adjacent systems. These dynamics affect the sensitivity and resilience of foundation species and their influence on ecosystem function.

addition to biotic feedbacks and fluxes, in magnifying or dampening ecosystem state change, and the hypothesized central role of connectivity and coupled dynamics at the landscape scale. Our long-term foundation of integrated interdisciplinary research makes us uniquely poised to move beyond studies of individual ecosystems and link landscape components to understand responses to climate drivers across spatial and temporal scales. We continue to take advantage of natural 'experiments' of pulse events (e.g., storm disturbance, marine heatwaves) that leverage our decadal-scale observations and experiments, and will conduct new experimental disturbances to investigate the sensitivity and resilience of foundation species and their functions. In addition, we will explore how species that are spreading into the VCR due to warming and unintentional introductions alter ecosystem responses to climate drivers.

B. The VCR Context – Research Site and Drivers of Change

The VCR LTER site is within the most extensive stretch of coastal barriers in the world (Allen et al. 2010), and is an ideal model for assessing climate impacts and ecosystem state change in shallow coastal systems. Our long-term data (1940 – 2006) show that the VCR is the most dynamic coastal barrier landscape on the U.S. Atlantic seaboard, with rates of change second only to the barrier islands of the Mississippi Delta (Dolan et al. 1983; Morton 2008). Shoreline erosion rates on the VCR barrier islands can be as high as 15–40 m yr^{-1} (Fig. 4; Fenster et al. 2015). **The VCR is a transgressive system** (Fig 5): over the long term, storms and sea-level rise cause the landward migration of the islands across back-barrier marshes and coastal bays (Hayden et al. 1990; Fenster & Hayden 2007; Moore et al. 2010; Deaton et al. 2017), and the encroachment of marshes into forests and agricultural land (Brinson et al. 1995; Shao et al. 1998; Kirwan et al. 2016b). The mid-term site review noted "*The opportunity provided by the VCR to examine a natural transgressive system is remarkable and has been a hallmark of previous LTER research at this site.*"

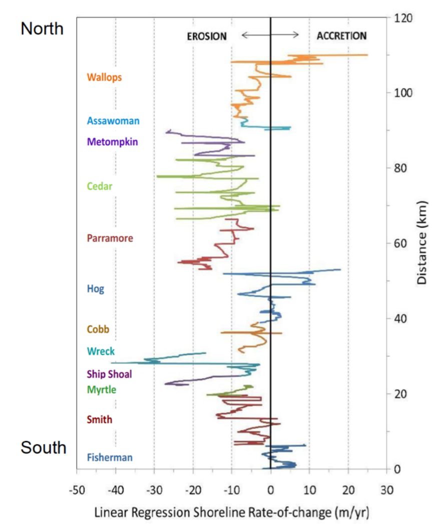

Fig. 4. Shoreline rates of change for the VCR barrier islands for the period 1940-2006.

Historic legacies related to storm disturbance and habitat loss have played an important role in shaping the present-day landscape. A series of severe storms convinced people to abandon the islands in the early 1930s. The island town of Broadwater, nestled in a maritime forest on Hog Island, was once a thriving community of 250 residents at the turn of the last century. Today, the former town site is 2 km offshore at the bottom of the ocean because the island has migrated toward the mainland (Hayden et al. 1991). Storms at that time also contributed to the extirpation of seagrass (eelgrass, *Zostera marina*) already weakened by a pandemic disease and the loss of the scallop fishery that depended on seagrass habitat

Fig. 5. The VCR is a transgressive system, where climate-driven sea-level rise and storms cause the landward migration of landscape features. Over time, islands "roll over" toward the mainland as sand is washed over island uplands and back-barrier marshes during storms leaving ghost forests and marsh peat on the barrier beaches, and on the mainland marshes migrate inland and replace forests.

(Orth & McGlathery 2012; Oreska et al. 2017a). Later in the century, large expanses of intertidal oyster (*Crassostrea virginica*) reefs were also lost due to disease and over-harvesting. Human population densities declined partly as a result of economic losses, and remain low (Peters et al. 2011). Recent large-scale restoration of seagrass and oysters is reversing these state changes.

Sea-level rise, and changes in the frequency and magnitude of storms and in the mean and variance in temperature and rainfall, are the main **climate** drivers of state change in the VCR. The shallow seaward slope of coastal barrier landscapes (typically <0.1%) makes them particularly vulnerable to sea-level rise and storms (e.g., Day et al. 2008). **Storm** frequency has changed along the U.S. Atlantic coast over the last century, and we are in a period of relatively high storminess, with some 15 extra-tropical storms per year hitting the VCR coast (Hayden & Hayden 2003). Larger, less frequent storms cause shoreline erosion and overwash on barrier islands (e.g., Wolner et al. 2013; Brantley et al. 2014; Walters & Kirwan 2016), and saltwater inundation that causes dieback of forests bordering marshes on the mainland (e.g., Brinson et al.1995; Kirwan et al. 2007; Middleton 2016; Fernandes et al. 2018). Smaller, more frequent storms cause marsh loss by erosion and increased bay turbidity by resuspending sediments (Lawson et al. 2007; Fagherazzi & Wiberg 2009; Hansen & Reidenbach 2013; Wiberg et al. 2015; Leonardi et al 2016). The rate of **relative sea-level rise** has been 5.4 mm yr^{-1} at the VCR over the last 40 years (NOAA), and reflects rising seas and land subsidence (2.5 to 2.9 mm yr^{-1}; Oertel et al. 1989; Emory & Aubrey 1991). Based on current rates and IPCC emission scenarios (Church et al. 2013), we estimate low, medium and high sea-level rise by 2100 to be 0.56 m, 0.75 m and 1.2 m, respectively (Fig. 6).

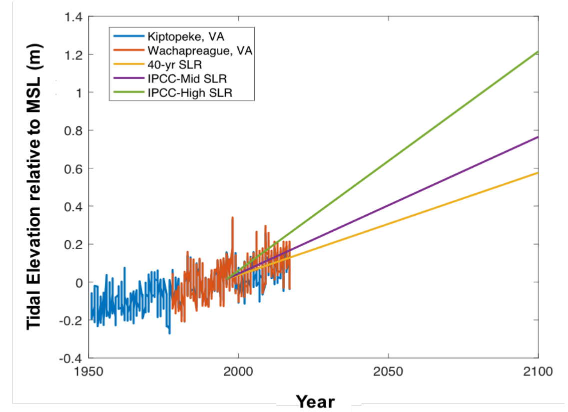

Fig. 6. Relative sea-level rise rates for the VCR domain. Projected rates are based on IPCC 5AR RCP 6.0 and RCP 8.5 emission scenarios.

Changes in **temperature** trends and extreme high-temperature events (marine heatwaves) will affect both species growth and abundance in the VCR (Lin et al. 2010; Zinnert et al. 2011; Carr et al. 2012b). Statistical downscaling from general circulation models for nearby Chesapeake Bay predict increases in surface water temperatures by the end of the century (Muhling et al. 2018). Some foundation species in this region are at, or near, the southern limit of their range (e.g., the seagrass *Z. marina* in coastal bays) and are vulnerable to high temperatures. Other more southerly species (e.g., sea oats, *Uniola paniculata*, a dune-building grass on the islands; and *Morella cerifera*, the dominant shrub on the barrier islands) are expanding into the VCR with warming temperatures. Temperature effects have been implicated in both the partial die-back of seagrass in 2015 and the subsequent recovery. Changes in **precipitation** influence the depth to the groundwater table

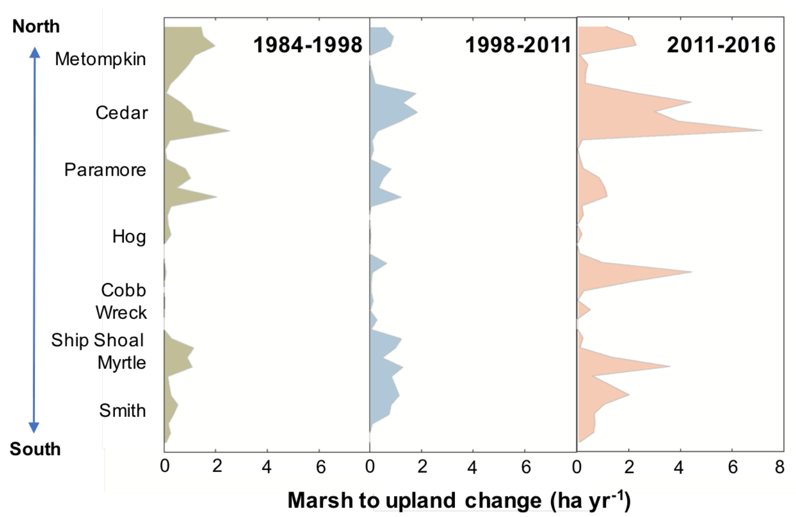

Fig. 7. Conversion of marsh on the islands to overwash fans (designated as upland) by storms has increased in the last decade.

for terrestrial vegetation and availability of freshwater and nutrients (Shao et al. 1995; Zinnert et al. 2011). Lower rainfall and warmer winters have been associated with a state change from grasslands to shrub thickets on the barrier islands over the last three decades (Zinnert et al. 2011). Similar climate-induced transitions to shrub dominance have been documented for other non-coastal arid regions, including LTER sites (JRN, SEV; e.g., D'Odorico et al. 2012; Laureano & Sala 2015).

Decades of integrated research at the VCR have increased our understanding of how these historical legacies and climate drivers affect ecosystems independently and interactively, and have positioned the VCR LTER as a global leader in describing coastal barrier dynamics. Our previous work documented how this undeveloped landscape acted as a shifting mosaic, where local transitions (between upland, intertidal marsh, and coastal bay) were frequent, but there was little change in total cover of each (McGlathery et al. 2013). A new 30-year retrospective (1984-2016), however, suggests more directional changes are underway. For example, barrier island area is declining, and conversion of marsh on the islands to overwash fans by storms has increased in the last decade (Fig. 7; Zinnert et al. 2016a). Understanding these changes and projecting future scenarios requires that we address complex system dynamics across spatial scales, from within ecosystems to across the landscape.

C. Theoretical Context

VCR research contributes to the development of theory on **ecosystem state change** in the context of coastal systems that are dominated by foundation species. We are particularly interested in how both gradual directional changes (e.g., sea-level rise, species' range expansions) and abrupt events (e.g., storms, high temperatures) associated with climate affect ecological systems and their functions. Responses to these climate-related forcing can lead to different trajectories. Changes may be linear or they may involve thresholds that lead to an abrupt, non-linear transition to a different ecological state (Scheffer et al. 2001; Bestelmeyer et al. 2011; Pace et al. 2015; Fig. 8). These threshold responses may involve feedbacks that stabilize the new state, prohibit a return to the initial state even if pre-transition conditions are reestablished (hysteresis), and result in the existence of alternate stable states (Carpenter 2001; Scheffer et al. 2009; D'Odorico et al. 2011). VCR research tests these conceptual models by quantifying mechanisms that either lead to, or resist, ecosystem state change across the coastal barrier landscape. Our previous work has shown: (1) abrupt transitions (marsh → intertidal flat with increased inundation related to sea-level rise (Kirwan et al. 2010; van Belzen et al. 2017); seagrass → bare sediment with extreme temperatures or low light (Carr et al. 2012a,b; McGlathery et al. 2012); (2) feedbacks that maintain alternate states after a transition has occurred (shrubs modifying local microclimate, Thompson et al. 2017); and (3) linear change (marsh → intertidal flat through erosion, Leonardi et al. 2016). We will explore these possible trajectories further in VCR VII by continuing to test mechanisms that underlie responses to climate drivers, by considering the role of ecological and physical interactions within and between landscape units, and by integrating these data with mechanistic models that yield predictions that can be tested with long-term observations and experiments. This has implications for managing ecosystems (e.g., restoration)

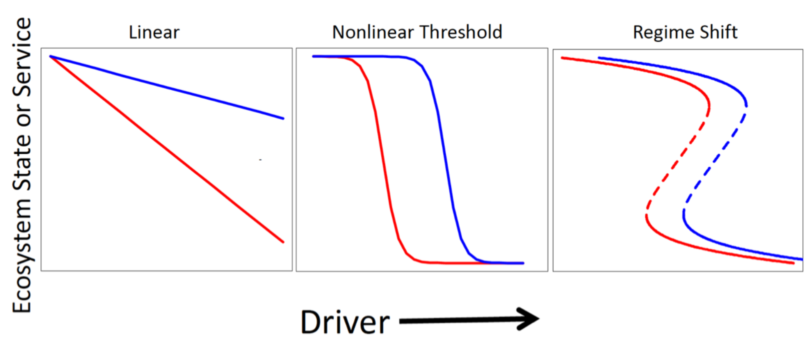

Fig. 8. An ecosystem state or service can respond to controlling drivers in multiple ways: linear (no feedback), non-linear (weak feedback), and regime shift (strong feedback leading to hysteresis). The difference between the red and blue lines reflects how management actions can increase resilience by reducing declines. For example, a shift in system dynamics that can lower the response rate to a driver (*left*), a shift in the threshold at which the driver causes a large decline (*middle*), and a shift from the red line to the blue line where a collapse to an alternate state occurs (*right*). Adapted from Pace et al. (2015).

to enhance resilience to environmental changes that are occurring at faster rates or with greater frequencies or magnitudes than in the recent past.

A critical feature of our conceptual framework is understanding the **coupled dynamics of ecosystems**, which represents an important advance in state change theory. Our ongoing work and that of others in diverse terrestrial and aquatic systems (e.g., Peters et al. 2006; Okin et al. 2009; Castorani et al. 2015, 2017) have addressed how connectivity of materials (sediment, water, organic matter, nutrients) and organisms affects state change dynamics. **We are now extending this connectivity framework to ask how state change in one ecosystem can propagate to other ecosystems—both adjacent and non-adjacent—and how this coupling can influence the landscape-scale response to environmental change.** For example, seagrass meadows and oyster reefs in coastal bays could affect the persistence of adjacent marshes positively (wave attenuation) or negatively (reduced sediment supply), and marsh-edge erosion could reduce light availability for seagrass growth. On the barrier islands, coupling between dunes and the swales behind them that are transitioning from grassland to shrubland can influence landward island migration during storms. This in turn could affect the size of coastal bays and the ability of mainland marshes to migrate inland. The mid-term review committee highlighted: *"The diverse nature of the site offers a huge added value that is unmatched by most other LTER sites and should be emphasized. The site provides a rare opportunity to examine linkages among multiple ecosystems that are not spatially juxtaposed—something that cannot be done anywhere else in the US because of habitat fragmentation and the destruction of linkages among different ecosystems by anthropogenic activities."* **Addressing the complexity and interdependence of landscape components is critical to projecting future scenarios.**

D. VCR LTER VII Research Themes and Questions

We organize our new and continuing research around four foundational themes that build on recent findings and integrate existing long- and short-term studies with new observations, new experiments, and model development and testing. Activities under these research themes are coordinated within and across research groups, integrating our work on the ecosystems that make up the coastal barrier landscape and facilitating broader-scale syntheses.

Theme 1. Drivers and Patterns of Long-term Change: ***How have the distribution, spatial extent, and characteristics of ecosystems changed over time and how are these changes related to climate trends and variability?*** VCR research to date has identified climate-related forcing as having the greatest impact on ecological and physical processes that cause ecosystem state change. Changes in the trends and variability of storm frequency and intensity, sea-level rise, rainfall, and temperature have the potential to transform the coastal barrier landscape. Climate change may shift disturbance frequency (e.g., storms, high-temperature events) as well as mean climate state values.

Theme 2. Dynamics within Landscape Units: ***How do ecological and physical processes interact to maintain ecosystem states or facilitate transitions to new ones?*** We build on our long-term research to identify and test mechanisms that can lead to different possible trajectories (linear, threshold, regime shift). Long- and short-term data are used to parameterize, test, and evaluate mechanistic models. Natural disburbance events (high temperatures and storms) provide valuable opportunities to test conceptual and theoretical models of state change and resilience in the context of climate-related forcing.

Theme 3. Dynamics between Landscape Units: ***How does connectivity influence ecosystem state change?*** The VCR is a model system in which to ask how ecosystems are connected through material and organismal transport and coupled state change dynamics. These integrated studies allow us to explore the relationship between local and broader-scale patterns and processes. Understanding how state change in one part of the landscape can propagate to another is critical to determining the holistic response of coastal barrier systems to present and future climate forcing.

Theme 4. Ecological Consequences of State Change: ***What are the consequences of ecosystem state change for ecosystem function?*** We focus on two important ecosystem functions of coastal barrier systems: carbon sequestration and habitat provisioning for consumers. Coastal systems are sites of high carbon sequestration, yet uncertainty exists on how ecosystem state change in response to climate forcing will affect carbon storage over the long term. Expansions of foundation species (i.e., *Z. marina* seagrass, *M. cerifera* shrub, *Gracilaria vermiculophylla* macroalga, *C. virginica* oysters) affect carbon cycling and also provide habitat for consumers that may alter predation, pathogens, and trophic dynamics. We address this question across multiple spatial and temporal scales, including mechanisms that can enhance responses to climate at the landscape scale. Our understanding of climate effects on ecosystem state change can inform management decisions that can avert undesirable changes (e.g., marsh loss) and reinforce positive ones (e.g., habitat restoration, wildlife conservation).

II. RESULTS OF PRIOR SUPPORT

INTELLECTUAL MERIT

VCR VI (2012-2018) research has produced 190 journal articles (including 9 in *Nature,* 1 in *Science*, 4 in *PNAS*), 24 book chapters, 2 books, and 40 graduate theses/dissertations to date. Over $10 million in additional funding has been leveraged to support LTER-related research. Here we summarize *selected* accomplishments of LTER-funded research from VCR VI and highlight in **bold** 10 significant publications that lay the foundation for VCR VII.

A. Long-term Landscape Change

We evaluated long-term trends in the distribution of ecosystems on the VCR landscape with data from Landsat TM5 satellite images, NOAA Coastal Change Analysis Program, aerial photographs, and historical records, and corroborated these with field data. On the barrier islands, over 40% of the upland area has changed from grassland to shrub thicket over the last 30 years, despite a 29% loss of island upland area (Fig. 9; **Zinnert et al. 2016a**). This conversion to shrublands may reduce the ability of islands to build upward/migrate landward in response to sea-level rise and storms. In the intertidal zone, 19% of marshes have been lost largely due to island migration over the last ~150 years (Deaton et al. 2017), and rates appear to be accelerating (Sun et al., in review). In the subtidal zone, the large-scale restoration experiment has resulted in 25 km^2 of seagrass meadows since 2001. *In VCR VII we will focus on linking state change to disturbances from individual events, including high temperatures and storms.*

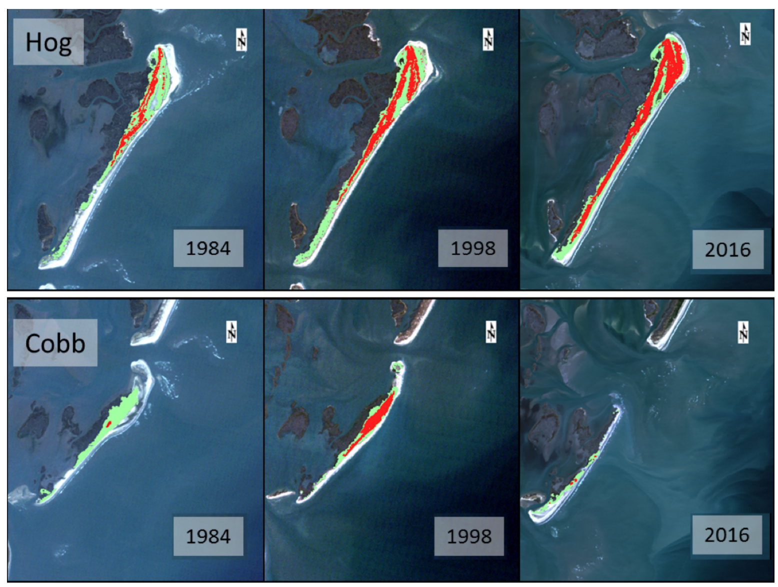

Fig. 9. Grasslands (green) have transitioned to shrub thickets (red) on VCR barrier island interior swales by 40% over the last 30 years, despite a significant (29%) loss of island upland area.

B. Mechanisms of State Change at the Local Scale

Intertidal – To keep pace with sea-level rise over the long term, marshes must increase in vertical elevation and erosion at the bayward edge must be balanced by migration into uplands. Marshes adapt to sea-level rise by producing organic matter belowground and accumulating sediment, the supply of which is controlled by wave-driven suspension in the bays and flooding. We developed a mechanistic model, parameterized with VCR data (sediment, biomass, erosion), short-term experiments, and long-term biomass records, which showed that there is a threshold sea-level rise rate beyond which marshes cannot keep pace (Kirwan et al. 2010; **Mariotti & Fagherazzi 2013**; **Kirwan et al. 2016a**). This is because plant productivity responds non-linearly to changes in sea level/flooding duration, and declines at high levels (Burns 2015). These data coupled with time-series analysis of marsh disturbance show that there is an early warning indicator of this state change, where recovery time following flooding disturbances increases close to the flooding threshold ("critical slowing down", van Belzen et al. 2017). At the marsh edge, loss rates by erosion has been linear over the last 60 yr (McLoughlin et al. 2015), vary with wave energy, with moderate-light driving 90% marsh-edge erosion (Fig. 10; Priestas et al. 2015; **Leonardi et al. 2016**). At the marsh-upland boundary, flooding from storm surge limits forest regeneration, but growth of adult trees in some areas can recover after 3 years (Fernandes et al. 2018). *In VCR VII, we propose new experiments to test mechanisms underlying the forest-marsh transition and biotic feedbacks controlling sediment deposition.*

Fig. 10. Average contribution of different wind categories to marsh edge erosion rates during 1991-2014. Extreme conditions (violent storms, hurricanes) accounted for <1% of marsh erosion (Leonardi et al. 2016).

In many regions of the VCR intertidal mudflats are now dominated by the non-native macrolga, *G. vermiculophylla*, creating a novel ecosystem that impacts nutrient cycling, productivity, and trophic dynamics. We have previously documented that this alga is successful in part because of its high tolerance to climate-related stressors, such as high temperatures and storm disturbance (Thomsen & McGlathery 2007; Thomsen et al. 2009, 2010). In VCR VI, we extended this work to describe its invasion history through genetic analysis, its impact on nitrogen cycling (denitrification and subsidies), and its role in supporting aquaculture clam production and in harboring pathogenic bacteria (Gulbransen & McGlathery 2013; Gonzalez et al. 2013, 2014; Hondula & Pace 2014). *In VCR VII, we will address how this invader alters primary production, consumer communities, and trophic dynamics.*

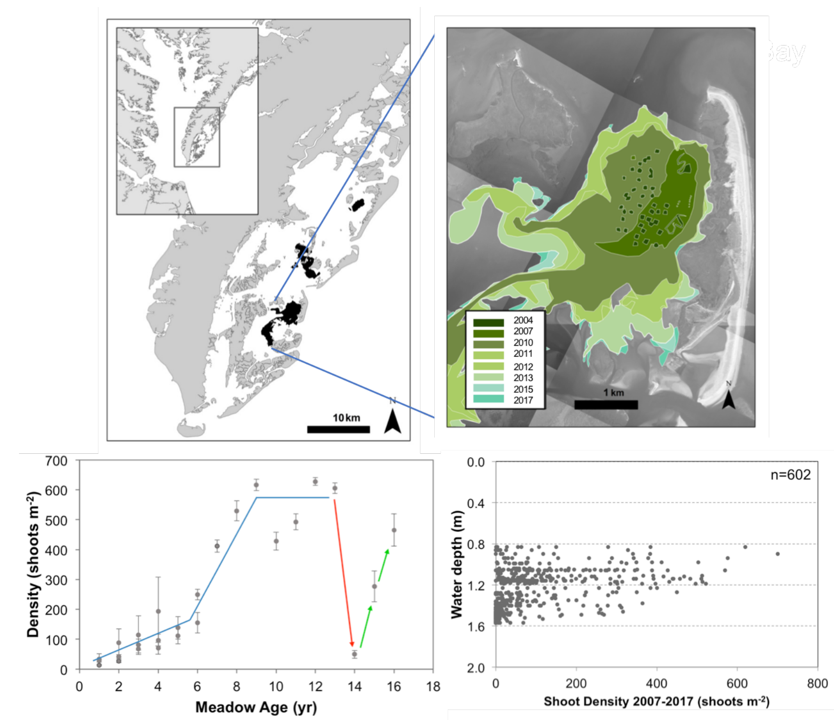

Fig. 11. Map of restored seagrass meadows in the entire VCR domain (*top left*) and in South Bay showing the initial 1.0 acre seeded plots and the natural extension of the meadow from those plots over 16 yr (*top right*). Ecosystem development (density) was non-linear, with an initial lag related to seed production / seedling recruitment and the meadow reaching maturity after ~9 yr (*bottom left*). A high-temperature event in 2015 caused meadow dieback, but with significant recovery after 2 yr. The long-term experiment confirmed the model-predicted depth limit of 0.8-1.6 MSL (Carr et al. 2012a,b) (*bottom right*).

Subtidal – In the coastal bays, seagrass meadows that once carpeted the seafloor were lost due to disease (slime mold, *Labryinthula* sp.) and storm disturbance in the early 1930s, and the system remained in a non-vegetated state due to seed limitation (Orth & McGlathery 2012; McGlathery et al. 2012; Oreska et al. 2017a). A landscape-scale restoration experiment in which over 6 million seeds were broadcast in 58 replicate 0.5 or 1.0 acre plots was initiated in 2001 to reverse the state change. We use this long-term experiment to test our mechanistic model for state change dynamics (Carr et al. 2012a,b) and to study long-term trajectories of ecosystem development and connectivity with adjacent marshes. The 16-year data set shows how seagrass state change results in the restoration of key ecosystem services: (1) increased primary production (**Rheuban et al. 2014a**,b); (2) sediment accumulation and carbon burial at rates similar to mature meadows after 12 years (Greiner et al 2013, 2016; **Oreska et al. 2017b**,c); and (3) 3–4× higher denitrification rates than unvegetated sediments (Aoki & McGlathery 2017). These data and short-term experiments agree with model predictions of the depth threshold between bare and vegetated states (Fig. 11; McGlathery et al. 2012; Al Haj 2014). *High-temperature events that occurred in 2012 and 2015 provide an unprecedented opportunity to use the long-term experiment to study mechanisms underlying seagrass sensitivity and resilience. This will be a focus of new research proposed for VCR VII.*

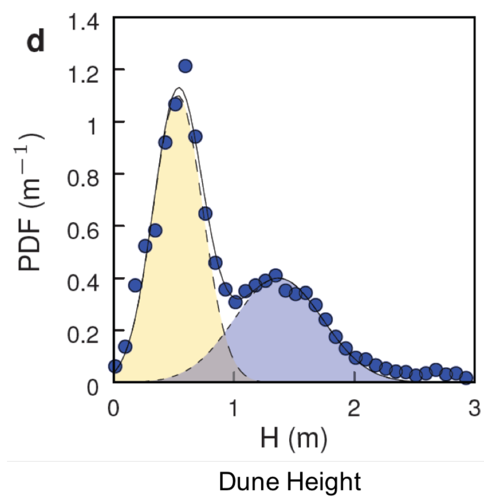

Fig. 12. Vegetation feedbacks on dune building interact with physical processes (storm disturbance, wind transport of sand) to reinforce either high dune (blue) or low overwash (yellow) states on barrier islands (Durán Vinent & Moore 2013).

Barrier Islands – Coastal dunes are critical in determining island vulnerability to storms. Their shape (height, width) and recovery following storms are determined by feedbacks between vegetation and sediment transport that cause sediment deposition. For example, different grasses are associated with different dune morphologies, in part because some grass species are stimulated more by burial than others (Wolner et al. 2013; Brantley et al. 2014; Harris et al. 2017; Goldstein et al., 2017; Mullins, in review). By controlling the patterns and fluxes of sediment delivery during storms (overwash) to the island interior and back-barrier marsh, dune shape ultimately affects long-term island change (e.g., **Walters et al. 2014**). In VCR VI, we developed the spatially explicit, numerical Coastal Dune model, parameterized with VCR data, that includes the effects of vegetation and topography on wind, the effect of sedimentation on vegetation growth, and dune erosion during storms (Durán Vinent & Moore 2013, 2015a,b, 2017). Our model and observations from the VCR and other regions (MD, FL, NC, WA) suggest that the relationship between dune building and storm disturbance frequency tends to reinforce either a dune (high) or overwash (low) state (Fig. 12; Durán Vinent & Moore 2103, 2015b; Goldstein & Moore 2016; Moore & Murray 2018). We also have evidence that the salt-tolerant dune grass (*Spartina patens*) which was previously thought to maintain the low overwash state is instead a dune builder that initiates recovery following storms. Expansion of the southern dune grass *(U. paniculata)*, which lab experiments suggest is competitively superior to local dune grasses (Harris et al. 2017; Brown et al. 2017) and an increase in storm frequency may lead to more hummocky (vs. high linear) dunes, increasing the vulnerability of island interiors to storm disturbance (Goldstein et al. 2017). *In VCR VII, we will integrate long-term field experiments and modeling to evaluate the effects of different grass species and abiotic factors (elevation, beach width, shoreline change rate, wind, precipitation) on dune formation and long-term island change.*

The transition from grassland to *M. cerifera* shrub thicket in the inland swales of the barrier islands is facilitated and maintained by positive feedbacks in which shrubs alter the microclimate, causing warmer winter and cooler summer temperatures that enhance shrub growth, and fewer extreme damaging temperatures (Thompson et al. 2017). This state change increases annual net primary productivity (by 3.5×), soil organic matter, and soil nitrogen and carbon stocks (Shiflett et al. 2014). After shrubs establish, there is no evidence of succession to maritime forest (Bissett et al. 2014, 2016). There is some evidence that *M. cerifera* shrublands can convert back to grasslands (**Zinnert et al. 2016a**), but this only occurs abruptly with sufficient storm disturbance to kill or removes shrubs. *In VCR VII, we plan a suite of experiments to test additional ecological feedbacks between dune grasses and shrubs that may facilitate shrub seedling establishment and survival. We will also explore connections between the dune/overwash and shrub/grassland states.*

C. Connectivity

Hydrologic Connectivity

Sediment Transport – Sediment distributions and fluxes between the coastal bays and marshes are important drivers for state change dynamics. We used newly acquired LiDAR topography and existing bathymetry to calculate residence times and circulation using the FVCOM coastal hydrodynamic model (Safak et al. 2015). We also characterized bottom sediment size and organic content using a novel method combining field measurements and hydrodynamic modeling (**Wiberg et al. 2015**). The combined results provide information, for example, on the spatial variation of sediment supply for back-barrier marshes and on light availability to support seagrass in coastal bays. We also used this approach to develop a sediment budget to study storm effects on sediment transport. From 2009 to 2016, 52 storms were identified and simulated using Delft3D, and found that strong storms import sediment from the ocean into the bays, determined primarily by the duration and magnitude of storm surge (Castagno et al., in review). This enhances resilience of the coastal bay system by providing sediment to counteract sea-level rise (Ganju et al. 2017). *In VCR VII, we will expand our system-wide hydrodynamic modeling to address sources and fates of transported sediment and effects on state change dynamics (e.g., seagrass expansion on sediment suspension, and redistribution of sediments from marsh edge erosion).*

Larval Transport – In VCR VI, we collaborated with TNC to initiate a new long-term experiment to restore oyster reefs (*C. virginica*) in intertidal regions that fringe mainland marshes using concrete structures that facilitate larval settlement. We found that settlement on these reefs is influenced by larval behavior in response to higher turbulence caused by reef topographic complexity (Fuchs & Reidenbach 2013). Landscape position is also important to larval recruitment: oyster reefs in higher velocity environments depend on connectivity with other areas, while reefs in low velocity regions have a higher probability of self-colonization (Hubbard & Reidenbach 2015). *In VCR VII, we will combine the hydrodynamic model with the reef restoration experiment to study how regional patterns of larval production, dispersal, and recruitment affect the establishment, growth, and metapopulation dynamics of restored reefs.*

Coupled Dynamics Integrating Ecology, Geomorphology and Hydrology

Oyster Reef-Marsh – Intertidal oyster reefs are effective at reducing wave height and energy for low to moderate water depths, and thus reduce marsh erosion (Taube 2013; **Leonardi et al. 2016**). Reefs also affect sediment transport on to the marsh. The effect is non-linear: sediment fluxes are reduced at low water velocities, and then increase over a critical threshold that resuspends sediments off the reef (Reidenbach et al. 2013). *VCR VII research will build on this research using the reef restoration experiment to understand how reef configuration (height, width) affects marsh state change dynamics.*

Seagrass-Marsh – Seagrass meadows adjacent to marshes also have the potential to affect sediment supply and wave energy (**Hansen & Reidenbach 2013**), and thus influence state change of adjacent marshes. We developed a mechanistic model (Mariotti & Carr 2014) that couples tidal flat and salt marsh processes (sediment suspension, wave attenuation, marsh accretion) to explore the long-term (decadal-to-century scale) marsh response to sea-level rise and storms at the VCR, PIE, and GCE LTER sites. The model results show that wave attenuation by seagrass meadows reduces marsh edge erosion, and only for very small tidal flats do seagrass have the potential to 'starve' the marsh of sediment and enhance the potential for loss. *In VCR VII, we will take advantage of marsh adjacency to the long-term seagrass restoration experimental sites to test the model of marsh erosion and sediment deposition on a multi-year time scale*.

Island-Marsh – When marshes are present behind barrier islands, they can reduce the rate of landward island migration because the islands can remain 'perched' on the marsh (Fig. 13; **Walters et al. 2014**). Storm overwash also supplies sediment that increases the resilience of narrow back-barrier marshes (100-500 m), allowing them to persist under conditions in which they would otherwise disappear. *In VCR VII, we propose integrated field experiment and modeling studies that further examine couplings between vegetation feedbacks and island morphology.*

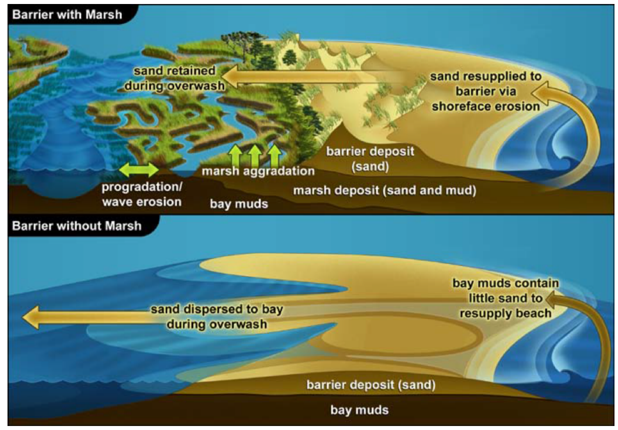

Fig. 13. Back-barrier marshes retain sand during overwash and slow island migration due to storms.

D. Ecological Consequences of State Change

Carbon Cycling and Sequestration – Ecosystem state changes across the coastal barrier landscape will likely influence long-term carbon sequestration. In marshes, our experiments and long-term data show that sediment carbon storage is driven more by rates of sea-level rise and flooding frequency than by either temperature or decomposition (Kirwan et al. 2012; Kirwan & Guntenspergen 2015; Burns 2015). Sediment carbon accumulation accelerates with sea-level rise up to a threshold rate of sea-level rise for marsh survival (Kirwan & Mudd 2012). For subtidal seagrass meadows, we were the first to show the role of restoration in reinstating sediment carbon stores (McGlathery et al. 2012; Greiner et al. 2013, 2016; Oreska et al. 2017b,c). Stable isotope analysis indicates that about half of the carbon stored in seagrass meadows is from other sources (microalgae produced *in situ*, marsh grass) and burial is determined by proximity to the meadow edge, not by either biomass or meadow age (Greiner et al. 2016; Oreska et al. 2017c). Carbon metabolism (production, respiration), measured by the novel aquatic eddy covariance method, increased 10–15× with restoration, with significant variance on hourly-to-seasonal time scales that is explained by variance in temperature, current flow, and light (**Rheuban 2014a**,b; Berg et al. 2015, 2016, 2017). *Understanding how state change affects carbon metabolism and sediment burial across the landscape is a focus on of VCR VII.*

Consumer Communities – Ecosystem state change also affects consumer communities across the coastal barrier landscape. On the barrier islands, changes in geomorphology and vegetation influence predator (fox, raccoon) and small mammal populations that are linked to the presence of shrub thickets and infrequent immigration. This is based on data from long-term field observations (Dueser et al. 2013), landscape modeling (**Porter et al. 2015**), and population genetics (Moncrief et al. 2017). Shorebird populations depend on vegetation- and predator-free sandy beaches and peat banks (for migrants) and also overwash fans and back-barrier tidal flats (for ground-nesting breeders). Each of these areas provides food, roosting, or nesting habitat (Gieder et al. 2014). In the coastal bays, state change resulting from the seagrass restoration experiment increased the biodiversity and abundance of fishes, epifaunal invertebrates, and bivalves (Lefcheck et al. 2017). *In VCR VII, we will address how changes in the distribution of ecosystems affects mammals, shorebirds, fish, and invertebrates.*

BROADER IMPACTS

Education, Outreach, and Diversity – VCR was the first LTER site in the network to develop a Diversity Plan for research and training. 54% of our faculty and students are from traditionally underrepresented groups. In VCR VI, we trained 76 graduate students and 51 undergraduate students from 15 institutions. The mid-term review noted the strong engagement, collegiality, and communication among the VCR students. The Schoolyard LTER (SLTER) program provides high-impact classroom and outdoor experiences for regional K-12 students and statewide teacher-training programs. Our SLTER supports five of the six public high school science courses offered in Northampton County where the VCR field station is located. Professional development workshops accommodate ~50 K-12 teachers each year from across VA and impact about 8000 students per year. Field opportunities for 3rd-12th grade students include an Oyster Gardening program, Summer Ecology Camp, and summer research internships through a Research Experience for High School Students program. We have collaborated with UVA's

Curry School of Education to develop on-line teaching modules with NSF's Web-based Interactive Science and Engineering (WISE) Learning Tool. The counties in which the VCR resides are among poorest counties in the state, and few of the local students have ventured into the marshes or bays, or onto the islands. It is therefore significant that *every Northampton High School student interacts with the VCR LTER program at least twice through classes and field activities; 64% of these are of minority groups.*

A key focus of our outreach activities is to communicate our research findings to NGOs, state and local agencies, and regional stakeholders to support management and conservation decisions and policies. We have a long-standing and close relationship with TNC, which uses our long-term data and models to inform conservation practices. Examples include 'best practices' for seagrass and oyster restoration, developing an index for marsh vulnerability, and co-developing a web-based Coastal Resilience decision-support tool for stakeholder use. We have co-authored the international protocol for issuing credits in the voluntary carbon market for seagrass and marsh restoration, adopted by Verified Carbon Standard, a global benchmark for carbon management. We also provide technical advising to the Eastern Shore Coastal Adaptation Working Group, Accomack and Northampton County Planning Commissions, NOAA Coastal Zone Management Program, and the Resource Conservation & Development Council. Our engagement with regional communities includes a public seminar series, Master Naturalists program, and Artist-in-Residence programs and exhibitions.

Information Management – The VCR is an active participant in information management activities within the LTER Network and the larger ecological information management community. Information Manager Porter has authored or co-authored numerous papers and book chapters on a broad range of issues. These include: sensor networks (Porter et al. 2012; Porter & Lin 2013), best practices for data (Campbell et al. 2013; Porter & Lin 2017; Porter 2018) and data sharing in ecology (Duke & Porter 2013; Hampton et al. 2013; Vanderbilt et al. 2015; Porter 2016; Vanderbilt et al. 2016). He has participated in or led numerous LTER workshops related to PASTA, NIMO (now EDI), Controlled Vocabularies, use of web services, and has given invited talks on data nationally (NSF, Perdue) and internationally (China, Korea). The VCR LTER provides 202 online datasets through EDI/PASTA, including 34 with durations ≥ 15 years. Data sets and access history are summarized in the Data Management Plan in this proposal. We also provide the web services that underlie the code generation functions on the LTER/EDI Data Portal.

Network Activities – McGlathery gave an invited talk at the 2017 NSF LTER Mini-Symposium, highlighting research at VCR and other coastal sites on carbon sequestration. Kirwan will be a keynote speaker at the 2018 LTER All Scientist Meeting, presenting VCR and collaborative research on wetland sensitivity to climate change. Our PIs have contributed to LTER Network governance and service, including the LTER Executive Board (McGlathery) and Education Committee (Schwarzschild), and serving as advisors to 3 LTER programs (FCE and MCR – McGlathery, LUQ – Porter) and on 4 mid-term review committees (CCE and MCM – Porter, MCR – McGlathery, SBC – Reidenbach).

Collaborative and Synthesis Activities – The impact of VCR research is leveraged by LTER cross-site studies and additional national/international collaborations. VCR scientists have been leaders in ***cross-site collaborations*** on marsh vulnerability to sea-level rise and storms (Mariotti & Carr 2014; Leonardi & Fagherazzi 2014; Kirwan et al. 2016b; Leonardi et al. 2016; van Belzen et al. 2017; Schepers et al. 2017), carbon sequestration (Fourqurean et al. 2012; Mudd & Fagherazzi 2016), and barrier island dynamics in response to climate drivers (Walters et al. 2014). VCR scientists are part of the Nutrient Network (NutNet) that includes comparative nutrient studies across diverse biomes, and the Ameriflux network of eddy covariance flux towers. Berg has pioneered the aquatic eddy covariance technique and trains national and international groups on its application (e.g., Berg et al. 2003, 2013, 2015, 2016, 2017). Our long-term data have contributed to ***syntheses led by VCR scientists*** on marsh response to sea-level rise and nature-based solutions to coastal flooding (Kirwan & Megonigal 2013; Temmerman & Kirwan 2015; Ganju et al. 2017), habitat restoration and blue carbon sequestration (Murphy et al. 2016), and shrub expansion and barrier island state change (Feagin et al. 2015; Zinnert et al. 2017). McGlathery co-edited the 2013 special issue in *Oceanography* on Coastal Long-term Ecological Research, which included two papers on VCR research (McGlathery et al. 2013; Fagherazzi et al. 2013a). Fagherazzi and Blum co-edited a book on *Ecogeomorphology of Tidal Marshes* (Fagherazzi et al. 2013d), and Moore recently co-edited a book on *Barrier Dynamics and Response to Changing Climate* (Moore & Murray 2018). VCR scientists are participating in two ***LTER synthesis working groups*** focused on the stability and synchrony of ecological communities, contributing long-term VCR data. VCR scientists have numerous ***international collaborations*** with researchers in 11 countries (Temmerman & Kirwan 2015; Azzoni et al. 2015; Emery et al. 2016; Kirwan et al. 2016a; Magri et al. 2017; van Belzen et al. 2017; Schepers et al. 2017). Our PIs are recognized leaders in coastal dynamics and have been keynote speakers, advisors, and participants with international groups focused on marshes (Christian, Fagherazzi, Kirwan), barrier island dynamics (Moore, Zinnert), sediment transport (Wiberg), and carbon sequestration (McGlathery, Pace).

Results of Supplemental Support – NSF provided $50K for equipment upgrades and $25K for a ROA to collaborator M. Fenster (Randolph Macon College). The equipment support was used to: (1) upgrade GPS units for real-time kinematic sampling to tie sites into a common elevation framework; (2) improve our ability to measure vegetation water balance to investigate shrub expansion; (3) remotely monitor mammals on the barrier islands using wildlife cameras; and (4) upgrade our meteorological stations to state-of-the-art loggers and digital sensors. The ROA project is using data on storms, shoreline change, and sediment texture to link storm intensity and frequency with erosion from 1980 to the present.

III. RESPONSE TO MID-TERM REVIEW RECOMMENDATIONS

The 2015 review team was impressed by the scale and scope of VCR research, and noted that the diverse coastal barrier landscape presents both research opportunities and challenges. Three main issues were identified as needing consideration.

1) Prioritization of research focus. The review committee cautioned that growth in programmatic scope over successive awards should be evaluated carefully with respect to benefits and costs of such expansion. We agree with this caution, and have focused this proposal on the primary climate drivers of ecosystem state change, including temperature, storms, and sea-level rise. This focus recognizes that the VCR landscape is minimally impacted by land-use changes and other human activities (Stanhope et al. 2009; Giordano et al. 2011; McGlathery et al. 2013). Across the landscape, our research program uses a shared conceptual framework to focus on mechanisms related to state transitions, connectivity, and two consequences of change (carbon sequestration and habitat provisioning). With these foci, we have moved further research related to upland watershed dynamics, aquaculture, and human attitudes/values to supplemental funding.

2) Integration across research themes. The review committee encouraged us to ensure that our research is integrated across proposed themes. Our unifying conceptual framework is key to this integration. It recognizes that spatial context (elevation, adjacency), biotic feedbacks, and fluxes drive state change dynamics at any point on the landscape. It then builds on a foundation of understanding ecosystem state change within landscape units (barrier island, coastal bay, marsh), to ask how connectivity and coupled dynamics affects state transitions across the landscape. This integration is achieved through long-term data collection and modeling, which was recognized as a core strength of the VCR. Our focus on climate drivers of ecosystem change described above also integrates research both between parts of the landscape and across themes. We acquired high-resolution LiDAR in LTER VI that allows us to link diverse ecosystems across the domain, and have developed the Delft3D hydrodynamic model to study connectivity, which was recommended by the review committee. These developments are critical to achieving a holistic understanding of coastal dynamics.

3) Efficacy of the alternative stable states framework for unifying the project. The review team was less convinced than the last proposal panel that alternative state change dynamics was the best working hypothesis for our integrated research, and recommended that we frame our research in terms of multiple possible trajectories (e.g., abrupt transitions, regime shifts (alternative states), and linear transitions). We agree with this recommendation. While we maintain a focus on ecosystem state change, we recognize that these transitions may occur in variable ways. We use experiments and observations to test the mechanisms that may lead to these different trajectories, and use these to develop and test models of state change across the landscape.

IV. NEW and CONTINUING RESEARCH FOR VCR VII (2018-2024)

Our research relies on integrating observations, experiments, and modeling (Fig. 14). Spatially, we conduct research at three scales: within landscape units (intertidal, coastal bay, barrier island), between landscape units (e.g., marsh and bay interactions), and across the entire landscape of islands and coastal bays. Temporally, we consider scales from a fraction of a day (e.g., element cycling), to years-decades (e.g., state change), to decades-century (e.g., sea-level rise, landscape change). Our conceptual framework also spans ecological scales from population studies of foundation species, to biotic interactions (facilitation, competition, predation) that structure communities, to ecosystem processes. A summary of core data sets and their relationship to the LTER five core areas is given in Table 1. We note in the text how these data sets are integrated with new and continuing research. Models are critical to our research, and the site review team recognized our strength in mechanistic modeling of coupled ecological and geomorphic processes. Data from our core observations, experiments, and analyses of remote-sensing imagery are linked with models to understand the dynamics of ecosystem state change. Based on our >20 years of observational and experimental data, we have developed, or are developing, mechanistic models for the major ecosystem transitions and the couplings between them (Table 2). The models play a central role in formulating new research questions and guide data collection; observations and experiments are used to test and modify the models. This data-model integration is critical to developing a predictive understanding of ecosystem responses to long-term environmental change. Most models are publicly available on the Community Surface Dynamics Modeling System website.

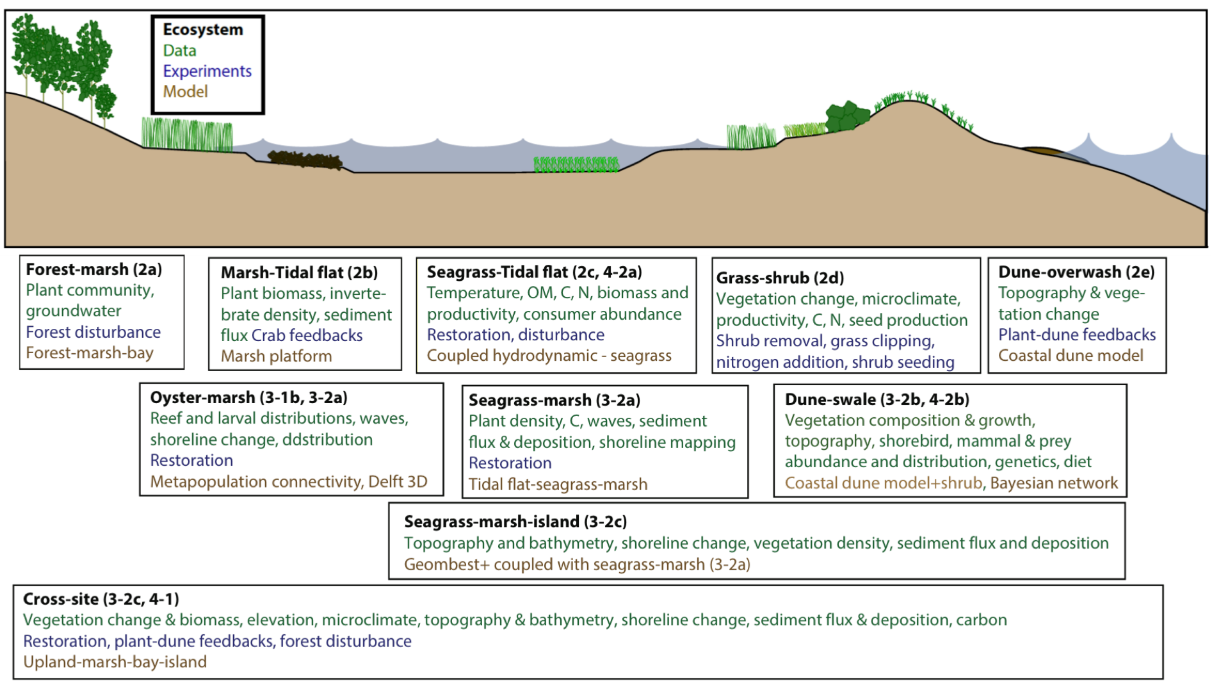

Fig. 14. Integrated data, experiments, and model development for the continuing and new research of VCR VII. Core data are described in Table 1, and models are described in more detail in Table 2. Long-term observations and experiments are used to motivate, parameterize, and test empirical mechanistic models of individual and coupled state change dynamics on the VCR landscape.

THEME 1. Drivers and Long-term Patterns of Change

Long-term observations over different spatial scales are needed to understand how climate drivers impact coastal ecosystems. The VCR program is committed to collecting, analyzing, and synthesizing a comprehensive set of data on climate variables and on ecological patterns and processes. Our goals are to:

(1) track long-term changes in average and extreme climate conditions (sea-level rise, storms, temperature, precipitation), and (2) describe trends and variation in ecosystem distribution, biogeochemical processes, organic matter, primary and secondary production, and community composition within the VCR domain, and to evaluate how these processes and trends are related to climate drivers. We also leverage related data sets from partners.

Habitat	Variables measured	Core Area	Spatial Extent	Sampling Frequency	Year Initiated
Intertidal	• Sediment and Organic Matter accumulation (Surface Elevation Tables)	OM	9 sites	Annual	1997
	• Root zone accretion – RSET	OM	9 sites	Annual	2003
	• Surface accretion - Marker horizons	OM	9 sites	Annual	1997
	• Aboveground biomass & diversity	PP, POP	26 sites	Annual	2007
	• Groundwater	N	4 sites	1 hour	2012
	• Meteorology	N,D	1 site	1 hour	1989
Coastal Bay	• Lagoon Water Quality (Temp, salinity, NH_4^+, NO_3^-, PO_4^{3-}, DON, PN, PC, PP, TSS, light, Chl)	N,OM	9 sites	Quarterly	1992
	• Seagrass Sediments (C, N, organic content, porosity)	OM,N	49 sites	Annual	2007
	• Seagrass density, biomass (above and below ground), canopy height, distribution	PP,POP,D	63 sites	Annual	2007
	• Benthic chlorophyll in seagrass	PP,N	63 sites	Annual	2008
	• Tides & water temperature	D	3 sites	6 minutes	1991
	• Fish abundance and diversity	POP	16 sites	Spring-Fall	2012
	• Seagrass meadow light & water temperature	D	31 sites	Spring-Fall	2012
Island	• Shrub growth, distribution	PP,POP	7 sites	1-5 years	1990
	• Mammal Populations	POP	3 sites	Semiannual	1989
	• Meteorology	N,D	1 site	1 hour	1989
	• Ground Water	N	9 sites	1 hour	1990
	• Shorelines	D	14 sites	~5 years	1852
Mainland	• Meteorology	N,D	1 site	1 hour	1989
	• Precipitation	N	4 sites	Daily	2001
All	• LiDAR elevation data	D	All sites	Periodic	1997
	• Bathymetry	D		Periodic	1997
	• Land Cover & Land Use Change	D		Periodic	1949
Data with Partners	• Shorebirds (Virginia Tech)	POP	225 sites	Annual	1998
	• Seagrass epifauna (VIMS, LTER)	POP		Quarterly	2001

Core areas: PP=Primary Production, OM=Organic Matter, N=Nutrient Movements, POP=Populations and D=Disturbance

Table 1. Core long-term measurements for VCR LTER

1a. Climate Drivers of Change

Storms and Sea-level Rise – Hayden & Hayden (2003) compiled historical storm records from 1880– 2002 for the VCR and other LTER sites using NOAA storm tracks (subsequently discontinued by NOAA). The historical VCR record was supplemented with wind- and wave-based storm analysis for 1990–2016 and will continue in the future. Relative sea-level rise for the VCR is determined from multi-decadal NOAA tide gauge records from Kiptopeke, VA, Wachapreague, VA (in VCR) and Atlantic City, NJ. We also monitor water levels at 3 additional tide gauge stations in the VCR. These data are used as input to the hydrodynamic and coupled ecological-geomorphic models of state change (Themes 2 and 3).

Weather Stations and Groundwater Wells – Three meteorological stations—two on the mainland and one on a barrier island—are equipped with Vaisala WXT-520 integrated digital weather sensors and record air temperature, humidity, air pressure, wind speed and direction, soil temperature and precipitation hourly. One mainland station also records solar radiation and photosynthetically active radiation (PAR). Four additional precipitation stations are deployed on the mainland. We maintain an eddy covariance flux tower on a *Spartina*-dominated marsh equipped with a open-path gas analyzer (LiCor LI-7500), sonic anemometer, light and temperature sensors. We operate several networks of groundwater wells on one of the barrier islands, at our long-term mainland marsh site, and at sites where we began monitoring marsh expansion into upland areas in VCR VI (Section 2a). In VCR VII, we will add new groundwater wells to support the mainland-marsh transition experiment and the new dune grass experiments on the barrier islands (Section 2d). We will also add an open-path methane analyzer to the eddy covariance flux tower (LiCor LI-1700).

Water Temperature – We use *in situ* sensors and remote sensing data to monitor water temperature in the VCR coastal bays over different temporal and spatial scales. Much of our *in situ* monitoring efforts are focused on the restored seagrass meadows where exposure to high temperatures appears to drive localized decline and recovery (Section 2c). These high-temperature events provide the opportunity for before-and-after disturbance experiments. *In situ* temperature sensors are deployed at >50 gridded locations during the spring–fall growing season. We are using a newly available data base going back a decade on sea-surface temperatures derived from AVHRR images (1 km^2 resolution) that are processed by the Rutgers Coastal Ocean Lab and cover the entire VCR domain. We also partner with the Virginia Institute of Marine Sciences (VIMS) in maintaining a network of Datasonde temperature sensors in the VCR coastal bays and measure water temperatures at our tide stations. In VCR VII, we will expand our monitoring to include high-resolution (10 cm) seascape-scale (>5 km^2) opportunistic measurements taken during high-temperature events using a compact autonomous underwater vehicle.

Water Chemistry – Our long-term data on dissolved oxygen and nutrients (inorganic nitrogen and phosphorus), chlorophyll, total suspended solids, and light indicates that water quality in the VCR coastal bays remains high with no trends since the record began in 1992. We continue to measure water quality seasonally at nine stations throughout the VCR domain. In VCR VII, we will add measurements of dissolved inorganic carbon, pH, and pCO_2 in the seagrass meadows to initiate studies on possible ocean acidification effects, described in Section 4-1.

	Brief description	Data used as input	Output	Data used to test
Delft3D Coastal Hydrodynamic Model Theme 3, Section 3-1	Open-source, flow, sediment transport & wave models. Options for effects of vegetation & morphologic change.	Wind speed & direction, tides, bathymetry, sediment properties.	Current speed & direction, wave height & period, water level, suspended sediments & flux.	Waves, currents, suspended sediments (Lawson et al. 2007; Mariotti et al. 2010)
Coastal Dune Model Theme 3, Section 3-2b	2D model of coastal foredune formation including vegetation dynamics, storm erosion, shoreline change, & sea-level rise. (Duran Vinent & Moore 2015b, 2017)	Vegetation growth rate, shape, size, cover density, winds, threshold dune height for shrub growth.	Vegetation density and DEM of the model domain at specified time intervals.	Dune height (Oster et al., 2011) & shape (Moore et al., 2016), shrub habitat polygons (Zinnert et al.,
Barrier Island GEOMBEST + Marsh Model Theme 3, Section 3-2c	2D cross-shore, model for barrier island change (including marsh and back bay) in response to changes in sea level & sediment supply. (Walters et al. 2015)	DEM, SLR, waves, sediment supply, rates of shoreface erosion & bay sedimentation, stratigraphy, marsh vegetation.	Cross-sectional profiles of barrier island/offshore stratigraphy & morphology, island volume & migration rate.	Marsh width (Walters et al., 2014); shoreline change (Johnson et al., 2015)
Seagrass - Marsh Coupled Behavior Model Theme 3, Section 3-2b	3-point coupled marsh-tidal flat-seagrass model to explore long-term coupled dynamics. Incorporates Carr et al. (2012b) model on seagrass-tidal flat transition. (Marriotti & Carr 2014)	Waves, seagrass density, light, water temperature.	Shoot density, light, tidal flat depth-width, marsh depth-width.	Shoot density (McGlathery et al., 2012)
Marsh Platform Evolution Model Theme 2, Section 2b	2D model of tidal marsh accretion with sediment transport a& vegetation growth to predict long-term changes in marsh habitat. (Kirwan et al. 2016a)	DEM, vegetation cover, tidal range, channel suspended sediment concentrations.	Maps of marsh elevation, vegetation type, biomass, carbon accumulation, a& accretion.	Long-term SET, accretion, & soil organic content; available as VCR datasets
Upland - Marsh - Bay Transgression Model Theme 2, Section 2a, 2c Theme 4, Section 4-1	1D transect model spanning tidal flats to uplands to examine how SLR drives transgression of coastal ecosystems. (Kirwan et al. 2016a; Marriotti & Carr 2014)	Initial bay width & depth, wind speed, tidal range, bay suspended sediment concentration.	Rates of forest retreat, marsh erosion, and marsh accretion. Changes in bay and marsh size.	Long-term SET & accretion datasets, trends in habitat size from historical maps & photographs (Deaton et al., 2017)

Table 2. Brief description of models used in VCR VII research and the data used to parameterize and test models.

1b. Patterns of Change

Ecosystem State Change – We maintain GIS databases to identify the spatial distribution (area, location) of ecosystem states and landforms (i.e., barrier islands uplands) on annual to decadal time scales. We use aerial photos, LiDAR, multispectral and hyperspectral satellite imagery to document long-term, landscape-level change at the VCR now for >30 years, including expansion of shrubs on barrier islands, loss of back-barrier marshes, and expansion of seagrass and oyster reefs. Our collaborators at VIMS maintain a data base of aerial photographs to map annual trends in seagrass meadow area. We will use high-resolution photography from drone surveys to document shorter-term landscape-scale changes (e.g., seagrass loss due to temperature; shrub loss due to storms; Themes 2 and 3). Within each ecosystem, we quantify biogeochemical processes, organic matter, primary production, and community composition.

Elevation – Changes in land elevation, relative to sea and groundwater levels, is a key driver of state change for all ecosystems in the VCR domain. The LiDAR survey of the VCR land surface completed in VCR VI coupled with detailed bathymetry of the coastal bays gives us the domain-wide integrated data set necessary for the hydrodynamic modeling of water circulation, residence time, and sediment transport (Fig. 15; Section 3-1). It is also a critical template for the ecosystem state change modeling, both within landscape units and for coupled dynamics across the landscape. We also have a network of nine sites with surface elevation tables (SET) to measure marsh vertical accretion, some of which extend 20 years.

Barrier Island and Marsh Shorelines – In VCR VI, we published a synthesis of long-term rates of shoreline change on the oceanfront of the barrier island across the VCR domain (see Fig. 4; Fenster et al. 2015). We use these data to test our models of island geomorphic and vegetation change. We have also established a long-term database on rates of marsh change due to erosion and accretion using historical photos and charts beginning in the late 1840s (T-sheets, US Coast and Geodetic Survey; Deaton et al. 2017). In VCR VII, we will use repeated drone-based high-resolution photography and structure-from-motion analysis (James et al. 2017; Warrick et al. 2017) to add to both databases to capture the effects of individual storm events.

Long-term Experiments – In addition to following natural rates of ecosystem state change, we have established several long-term experiments. These include the seagrass restoration in the subtidal, now in its 16th year, and two experiments established in VCR VI: oyster restoration to test the bay-marsh coupling, and shrub removal on barrier islands to test feedbacks on microclimate. We will add new long-term experiments in VCR VII, including: (1) forest disturbance to test resilience of the upland forest and mechanisms of the marsh-upland state change; (2) seagrass removal to assess resilience related to temperature conditions; and (3) on barrier islands, removal of grass to test effects on shrub seedling establishment in interior swales, and dune grass planting to test species-specific feedbacks on dune growth. These are discussed in Themes 2 and 3.

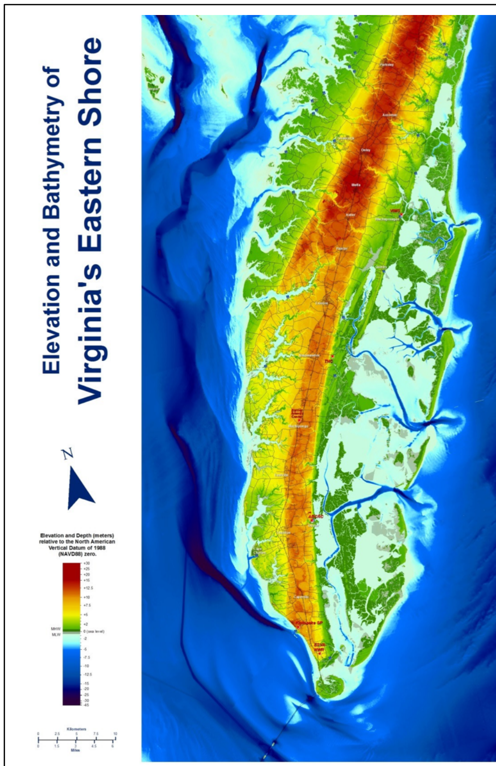

Fig. 15. Integrated land topography and marine bathymetry for the VCR LTER.

THEME 2: Dynamics within Landscape Units

We will build on VCR VI to test and model mechanisms underlying state changes at the major ecosystem transitions within the landscape units of the VCR (see Fig. 2; forest-marsh, marsh-tidal flat in the intertidal; seagrass-subtidal flat in the subtidal; dune-overwash, grassland-shrubland on the islands).

How do ecological and physical processes and feedbacks interact to maintain ecosystem states or facilitate transitions to new ones?

2a. Forest–Marsh Transition *(PIs: Gedan, Kirwan, Fagherazzi, Johnson, Carr)*

Coastal forests are retreating and being replaced by marshes as sea level rises (e.g., Brinson et al., 1995; Raabe & Stumpf 2015; Schieder et al., 2018). The mechanisms that drive this transition are poorly understood, especially spatial variability in response to storms. For example, current LTER modeling of marsh migration assumes forest retreat is linear and a function of slope (Kirwan et al. 2016b). However, we documented in VCR VI a zone of coastal pine (*Pinus taeda*) forest where mature trees survived the inundation and salinity stress of coastal flooding, but there was no regeneration by seedlings (Fernandes et al. 2018). This is consistent with earlier studies showing that seedlings are more sensitive to flooding (e.g., Conner & Askew 1992; Williams et al. 1999; Kirwan et al. 2007). At the same time, light availability in the understory may limit regeneration and recruitment of marsh grasses and shrubs in stands of mature trees (Schultz 1997). Thus, it may take a canopy disturbance by storms to drive a transition from coastal forests to marsh, which would be abrupt and non-linear.

New studies – In VCR VII, we will establish a new long-term disturbance experiment at the forest-marsh boundary to test feedbacks that govern this transition and to inform ongoing modeling (Kirwan et al. 2016b). After establishing baseline conditions for two years, we will ring-girdle all trees in four replicate forest plots (20 m × 20 m) and compare these to control plots at each of three elevations spanning the transition zone from salt marsh to coastal forest (Fig. 16). *We hypothesize that the response will vary along the elevation gradient: at low elevations, the forest is unable to regenerate; at mid-elevations, seedlings germinate but are unlikely to recruit into the adult population; high-elevation forests will recover without interruption to coastal forest.* We predict that only when pine regeneration ceases and adult trees die from storm disturbance or are experimentally killed, light availability will be sufficient for marsh grass (*S. patens*, *Distichlis spicata*) and salt-tolerant shrubs (*Baccharis halimifolia*, *Iva frutescens*) to colonize. Lower evapotranspiration rates in these communities relative to pine trees, and development of an organic, water-retaining soil layer, will promote waterlogged conditions that reinforce the marsh state. A suite of monitoring groundwater wells, sensors, and SETs will be deployed in each plot to measure depth to water table and salinity, vertical accretion, and light and temperature in the understory and at canopy height (Theme 1; Table 1). We will measure soil organic matter, soil moisture, abundance and height of trees and shrubs >1m tall, and identify species composition and percent cover of understory plants and pine seedlings (in 3 m × 3 m subplots). These long-term data will help advance the model's current simplistic treatment of marsh migration into upland forests with sea-level rise and storms (Sections 3-2c, 4-1).

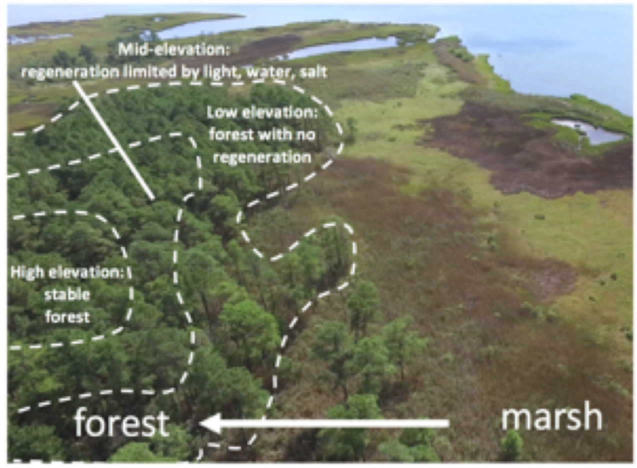

Fig. 16. We propose a new long-term experiment in three elevation zones spanning the transition from salt marsh to coastal forest to understand the role of disturbance in governing state change at the marsh-forest boundary.

2b. Marsh–Tidal Flat Transition *(PIs: Wiberg, Johnson, Fagherazzi)*

Our previous work documented widespread erosion of marsh edges (McLoughlin et al. 2015; Priestas et al. 2015; Leonardi et al. 2016) and increased marsh elevation that is keeping pace with sea-level rise (Kirwan et al. 2016b). These results raise important questions concerning the fate of sediment eroded from the marsh edge, the source of sediment depositing on the marsh, the role of biotic feedbacks, and the sensitivity of these processes to climate drivers. We propose to supplement continuing long-term studies with new observations of marsh edge dynamics to address these questions.

Continuing long-term studies – Over the past decade, we have used several techniques to quantify rates of marsh vertical accretion and edge erosion, and the processes controlling the transition from marsh to tidal flat, including: (1) historical aerial photography (McLoughlin et al. 2015; Theme 1); (2) annual measurements of marsh surface elevation and edge position (Priestas et al. 2015); and (3) morphodynamic and hydrodynamic modeling (Mariotti & Fagherazzi 2013; Tonelli et al. 2014; Leonardi et al. 2016). We will continue our core long-term measurements of marsh accretion using SETs at mainland and marsh island sites (Theme 1; Table 1). We will also continue to monitor marsh-edge retreat at mainland, marsh island, and back-barrier marsh sites using surveys and aerial photographs.

New studies – The time-scale of observed change in marsh-edge morphology from aerial photos and surveys (years – decades) is long relative to the time scale of forcing (e.g. storms). In VCR VII, we will use new technologies to quantify morphological change at time scales comparable to individual erosional events. We will use repeated drone-based high-resolution photography coupled with structure-from-motion techniques to determine storm-driven change in the morphology of the marsh-tidal flat boundary in response to individual storms. We will maintain several wave-tide gauges that record wave conditions and water levels to quantify hydrodynamic forcing. In combination with the continued monitoring outlined above, these data will provide unprecedented detail on the morphodynamic response of marsh boundaries to known forcing conditions. *The dataset will test the predictions of modeled marsh edge erosion for different storm conditions that is used to forecast future scenarios of change.*

We will also examine the role of ecological interactions that can influence plant production and marsh accretion rates, but are not currently included in geomorphic models of marsh response to sea-level rise (Bertness 1985; Thomas & Blum 2010; Coverdale et al. 2012; Gittman & Keller 2013). We propose a set of observations and experiments that will test the indirect effects on marsh sediment accretion by the two dominant marsh crabs, the fiddler crab (*Uca pugnax*) and the purple marsh crab (*Sesarma reticulatum)* that differentially affect plant growth. *We hypothesize that fiddler crabs that stimulate aboveground plant growth through nutrient regeneration and biodeposits will enhance marsh accretion, whereas purple marsh crabs, which graze plant biomass, will reduce accretion.* We will conduct a caging experiment in 0.5 m × 0.5 m plots using mean crab densities of the experimental area (80 m^{-2} for *U. pugnax*, 1 m^{-2} for *S. reticulatum*), with the following treatments (n=5 per treatment): fiddler crabs only, purple marsh crabs only, both crabs, and no crabs. We will measure above- and below-ground biomass, soil strength, decomposition, and sediment deposition using standard methods of the VCR (Blum & Christian 2013; McLoughlin et al. 2015). In field surveys, we will estimate crab densities in three marshes where we monitor marsh grass biomass and surface accretion using SETs (Theme 1). These biotic feedbacks will be evaluated for their potential influence on marsh threshold responses to sea-level rise.

2c. Seagrass–Subtidal Flat Transition *(PIs: McGlathery, Castorani, Wiberg, Berg, Carr, Yang, Pace)*

In the coastal bays, our landscape-scale seagrass restoration experiment provides an extraordinary opportunity to quantify the effects of state change on ecosystem structure and function, and to test how spatial context (depth, ocean exchange) affects seagrass resilience to climate forcing. Our integrated long-term observations and modeling show that depth and hydrodynamics mediate seagrass stability through feedbacks between sediment suspension and light availability, and identify temperature as a critical driver of seagrass loss (Carr et al. 2012a,b; Hansen & Reidenbach 2012). Marine heatwaves have caused local declines and range contractions of coastal foundation species and associated biodiversity in many regions (Wernberg et al. 2013; Smale & Wernberg 2013; Reed et al. 2016). After a high-temperature event in 2015, we observed spatial variation in seagrass loss and recovery that suggested water residence time, as reflected in proximity to inlets that bring in cooler ocean water during the summer, is a key factor driving seagrass resilience to temperature extremes (Fig. 17). Given expected increases in the frequency and magnitude of temperature extremes (Ummenhofer & Meehl 2017), VCR research is well poised to advance understanding of climate warming effects on seagrass resilience and ecosystem function.

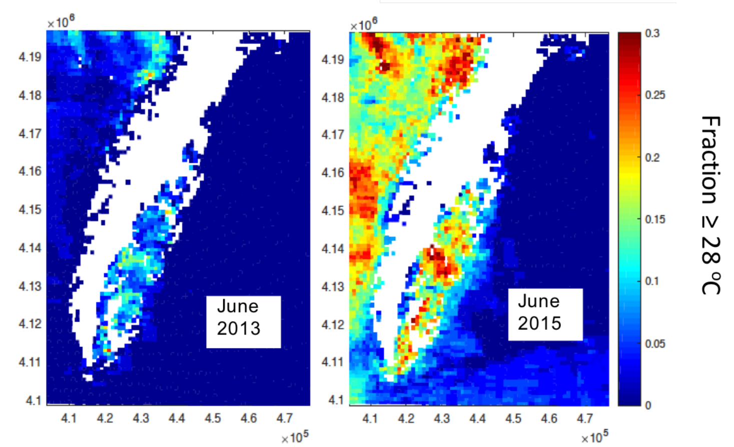

Fig. 17. Sea-surface temperatures in the VCR coastal bays from AVHRR images showing high temperatures in June 2015 associated with the seagrass die-off.

Continuing long-term studies – We will continue to monitor the seagrass restoration experiment which includes a period of ecosystem development following initial seeding, and a period before, during, and after a temperature disturbance to mature meadows. This time series highlights the value of long-term research and provides a strong test of temperature constraints on seagrass populations. Simultaneous measurements of metabolism by aquatic eddy covariance and temperature at high-temporal resolution will allow us to quantify both threshold responses to high-temperature events and recovery rates. We will relate changes in seagrass density and metabolism to variations in carbon sequestration (in plant biomass) and storage (sediments) over time, and to habitat use by consumers (Sections 4-1 and 4-2).

New studies – To understand and predict how landscape position mediates risk from exposure to high temperatures, we will establish a new spatial time series of seagrass population dynamics. We will collect high-resolution (<10 cm) optical and multispectral imagery during monthly surveys (>20 km^2) from May to September, calibrated with measurements of seagrass biomass. These images will be related to temperature determined at three spatiotemporal scales: (1) satellite imagery (1 km^2, 8× per day); (2) near-continuous (1 min) measurements *in situ* by loggers in gridded arrays; and (3) high-resolution meadow-scale (>5 km^2) opportunistic measurements taken during high-temperature events using a compact autonomous underwater vehicle (Section 1a). Changes in spatial population dynamics will be related to variation in the magnitude and duration of local warming using mixed effects models that account for autocorrelation and control for confounding environmental covariates.

We will add a new experiment to the long-term restoration experiment to *test the hypothesis that resilience will be greater (faster recovery) at sites with greater oceanic exchange and lower temperature stress.* We will establish replicate paired seagrass removal and control plots in two locations in the six km^2 meadow where we have established temperature differences based on calculated water residence time and *in situ* sampling. We will remove all seagrass in six replicate 3 m × 3 m plots and follow the mechanism and rate of recovery over time relative to six nearby control plots and relate to *in situ* temperature. To determine recovery mechanism, we will measure seed density and vegetative growth. To capture the long-term recovery rates, we will measure seagrass shoot density and biomass, shoot and root demographics, sediment organic matter, carbon and nitrogen stocks, and epifaunal community structure.

2d. Dune–Overwash Transition *(PIs: Moore, Zinnert, Young)*

Understanding how the distribution of dune-building grasses affects dune shape and how abiotic factors (elevation, beach width, shoreline change rate, wind, precipitation) influence long-term rates of dune building and recovery following storms is critical to developing models capable of forecasting the response of barrier island ecosystems to climate forcing (Fig. 18). Our coastal dune model resolves key interactions between wind, topography and vegetation, yet critical vegetation parameters (growth rates of dune-building grasses and feedbacks on dune recovery following storm disturbance) are generic and also do not include species interactions. In VCR VII, we will add new field experiments and time-series observations to test how species-specific growth rates of dune grasses affect the ecological feedback on dune dynamics. These data will be incorporated into the coastal dune model to improved its predictive capability.

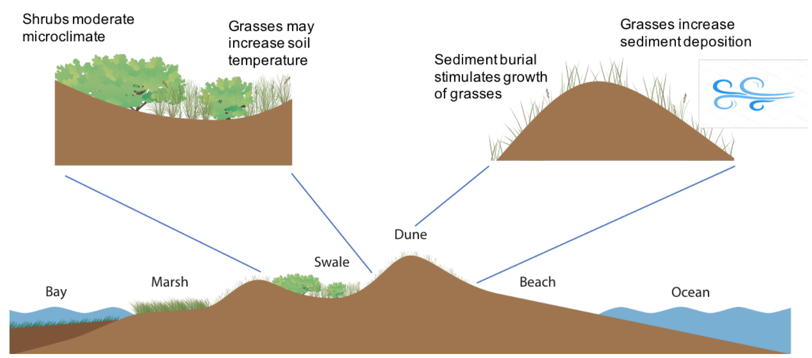

Fig. 18. Barrier island cross section showing ecological feedbacks on dunes and interior swales that affect geomorophology and island vulnerability to storms.

New field studies – New observations and experiments will *test the hypothesis that dunes with different dominant grass species will build at different rates and have different shapes (height, width, hummocky vs. linear).* To quantify species-specific growth rates as a function of elevation and time, we will begin a new long-term experiment in which we will plant monocultures of the three foundation dune-grass species in an area of seaward beach growth (to insure sand supply and to reduce disturbance) in replicate plots established at the same distance from shore but at different elevations. We will measure vegetation growth (longest leaf length, stem count, % cover) and topography through time leveraging our meteorological data, tide gauge data, and new groundwater wells to account for the effect of abiotic factors (Theme 1). We will also measure species composition and topography along transects at 1-km spacing on three islands that vary in beach width, shoreline change rate, and elevation. We will test a second hypothesis that *because the salt-tolerant grass (S. patens) thrives in overwash areas and is stimulated by burial, it increases the rate of* *dune recovery after storms by building elevation faster than aeolian processes alone, allowing for more rapid establishment of the dominant dune-building grasses (A. breviligulata and U. paniculata).* To test this hypothesis, we will initiate a new long-term experiment in recent overwash sites colonized by *S. patens* and compare dune growth (rate and form as described above) over time with paired adjacent sites where the grass is removed by clipping until the dominant dune-building grass becomes established (n=10 paired plots, each 2 m × 2 m). We will integrate experimental results into new parameterizations for vegetation growth and species interactions in the coastal dune model. Revisiting overwash sites surveyed in 2009 (Wolner et al. 2013; Brantley et al. 2014) to assess changes in species composition and topography will provide a hindcast data set for model testing. We will then use the model to forecast effects of these couplings on future island vulnerability to changes in storm frequency and sea-level rise.

2e. Grass–Shrub Transition *(PIs: Zinnert, Young)*

The state change from grasslands to *M. cerifera* shrub thickets occurs in the interior swales located behind the dunes (Fig. 18). Our previous work has shown that this transition is driven by regional-scale climate (higher winter temperatures and lower precipitation; Zinnert et al. 2011), shrub feedbacks on microclimate (warmer winter and cooler summer temperatures; Zinnert et al. 2016a), and seed supply (Crawford & Young 1998; Dows 2014). In addition, this foundation species forms dense mono-specific thickets that limit colonization by other species (Brantley & Young 2010). Our work for VCR VII builds on these findings to focus on how feedbacks from the presence of grasses may facilitate shrub seedling establishment and survival by moderating soil temperature (Maestre et al. 2001) and thereby promoting the state change to shrub thicket. We have also shown that successful growth of *M. cerifera* seedlings depends on the nitrogen fixing symbiont, *Frankia* sp. (Wijnholds & Young 2000), suggesting that nitrogen inputs also may facilitate woody expansion. *We propose integrated observations and experiments that will test the hypotheses that: (1) grasses facilitate growth of shrub seedlings in early development; and (2) nitrogen inputs from shrub litterfall provides a positive feedback that enhances grass density, favoring shrub seedling recruitment.*

Continuing long-term studies – We will continue to monitor long-term 5 × 5 m plots (n=5 per treatment) established in VCR VI (with and without experimental shrub removal) across the grass/shrub ecotone for species composition, annual net primary productivity (Brantley & Young 2007), and microclimate (temperature, soil water content, light) (Theme 1). We will add new measurements of available soil nitrogen using standard methods (Binkley &Hart 1989) to quantify input from shrub expansion. These measurements will capture the time period from initial transition to full thicket and associated changes in microclimate. We will add measurements of seed production to determine how age and interannual climate variability affect shrub fitness.

New studies – We will initiate new long-term experiments that will follow individual shrubs from seedlings through thicket formation. We will create 2 × 2 m plots (n=10 per treatment) with and without grass clipped to assess shrub growth, changes in microclimate (as above), and available soil nitrogen. Shrub height, crown diameter, and seasonal physiology (i.e., photosynthesis, stomatal conductance, and fluorescence) will be measured. Clipping will be maintained until re-sprouting no longer occurs (Bruno et al. 2017). In a second experiment, we will add nitrogen and *M. cerifera* shrub seeds in 1 × 1 m plots at three distances (50 m apart) along transects from the thicket edge into grassland (n = 5). We will measure grass height and density, microclimate, emergent seedlings, survivorship at the end of the growing season, and seedling height. We will reseed yearly to capture annual variations in precipitation. These studies will determine the role of biotic interactions and possible ecological feedbacks in the grass-shrub transition.

THEME 3: Dynamics between Landscape Units

We are building system-wide characterizations of vegetation, fauna, sediment, hydrodynamics, and geomorphology to support studies of ecosystem change (Theme 2). These studies are based on advances in VCR VI on coupled dynamics of adjacent ecosystems, and on the well-tested implementation of the Delft3D hydrodynamic model for the entire system to study sediment and larval transport. We focus on dynamics that link landscape units, including hydrologic connectivity, and coupled dynamics whereby state change in one ecosystem can propagate to another.

3-1. Hydrologic Connectivity: How do sediment and organism fluxes modulate state change dynamics, ecosystem properties, and biotic communities?

3-1a. Sediment Transport *(PIs: Wiberg, Fagherazzi, Reidenbach)*

New studies – Our results to date indicated that large storms import sediment to the coastal bay system, and that the amount is potentially enough to allow marshes to keep pace with sea-level rise (Castagno et al., in review). In VCR VII, we will use our Delft3D model to: (1) construct a sediment budget to study the sources and spatial variation in sediment transported to the bays and marshes; (2) quantify effects of seagrass on sediment transport; and (3) model marsh-edge morphodynamics, which requires higher spatial resolution that we have now built into our model. Our work on a sediment budget will explore how the variations in frequency and intensity of storm events affect sediment redistribution within the system and exchange with the ocean via tidal inlets. This will build on previous work in which we related hydrodynamics, water residence times, and sediment characteristics (Fig. 19). Based on the results of our *in situ* measurements of how seagrass reduces flow and sediment suspension (Hansen & Reidenbach 2012, 2013), we are including the effects of marsh grass and seagrass roughness in the Delft3D model using the approach of Baptist et al. (2007). We will examine how storm strength and frequency and seagrass biomass affect sediment import and redistribution within the entire VCR domain, and how this affects sediment supply for marshes to keep pace with sea-level rise. New locally refined grids in Delft3D will allow us to model coupled hydrodynamics, sediment dynamics, and morphological change in more detail than previously possible (Section 3-2a). We will relate these transport studies to sediment-associated transfer of organic carbon between seagrass and marsh ecosystems (Section 4-1).

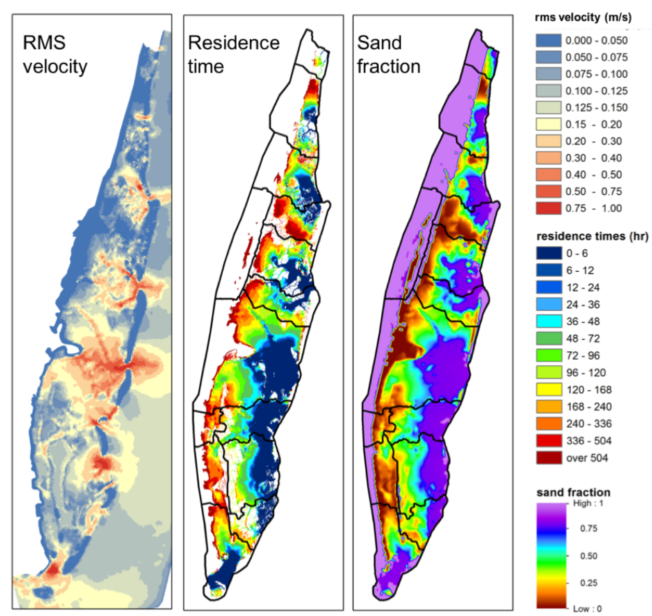

Fig. 19. Bottom sediment size and organic content determined using a novel method combining field measurements and hydrodynamic modeling throughout the VCR domain is used to develop a sediment budget and study storm effects on sediment transport. (Wiberg et al. 2015)

3-1b. Oyster Larval Transport and Metapopulation Dynamics *(PIs: Castorani, Reidenbach)*

The dynamics of marsh-bay coupling depends on connectivity via the colonization and growth of intertidal oyster reefs (Section 3-2a). Oyster populations may function as spatially-distributed meta-populations in which long-term stability, persistence, and expansion depends on demographic connectivity through larval dispersal (Lipcius et al. 2008; Schulte et al. 2009). The VCR is ideal for testing metapopulation theory because nearly all populations can be measured using remote sensing, and larval dispersal can be estimated using our existing Delft3D hydrodynamic model. Experimental work in VCR VI demonstrated that local-scale reef hydrodynamics and sediment loading constrain larval supply and recruitment (Whitman & Reidenbach 2012). Our proposed research for VCR VII builds on this work and *tests the hypotheses: (1) population fecundity, dispersal via water transport, and larval behavior structure demographic connectivity among reefs; and (2) the strength of this connectivity mediates local population growth, colonization and extinction, and regional patterns of metapopulation stability.*

New studies – We will conduct annual low-tide aerial surveys for a subset of intertidal oyster reefs in VCR using high-resolution drone imagery and structure-from-motion analysis that will be validated with field measurements and LiDAR data. These data will be used to develop correlations among reef size and elevation, and population abundance and fecundity (egg mass) for the study reefs, which then will be used to scale up to the VCR system (Castorani et al. 2017). We will estimate larval dispersal probabilities using our Delft3D hydrodynamic model with knowledge of pelagic larval dispersal duration and settlement behavior in response to environmental cues (Hubbard & Reidenbach 2015; Fuchs & Reidenbach 2013). To determine how local physical parameters constrain larval settlement and recruitment, we will compare reef location and elevation with model output, including mean tidal currents, wave intensity, and sediment properties. We will integrate estimates of fecundity, dispersal, settlement, and recruitment to quantify demographic connectivity and relate this to observed population dynamics, colonization, and extinction using generalized mixed models (Castorani et al. 2015). To validate connectivity estimates, we will quantify spatial variation in larval recruitment by counting oyster spat on settlement plates during the June–October spawning season. This data-model integration will improve our understanding of larval recruitment and population dynamics on oyster reefs and will enable VCR-wide assessments for selection of restoration sites.

3-2. Coupled State Change Dynamics: *How do transitions in one ecosystem propagate on the landscape between systems that are adjacent and non-adjacent?*

3-2a. Subtidal–Intertidal Coupling *(PIs: Reidenbach, Wiberg, McGlathery)*

Marsh erosion and accretion depends on sediment supply and wave energy, both of which are influenced by the adjacent subtidal flat (Mariotti & Carr 2014; Duvall et al. 2018). The presence of either oyster reefs or seagrass meadows on the tidal flats can attenuate the wave energy reaching the marsh edge and impact erosion rates (Taube 2013; Carr et al. in review). At the same time reefs and meadows can act as sediment traps, thereby altering the amount of sediment suspended in the water flooding the marsh. *We hypothesize that by affecting both sediment supply and wave energy, oyster reefs and seagrass meadows impact state change dynamics of adjacent salt marshes* (Fig. 20).

New studies – We will use the long-term seagrass and oyster restoration experiments to initiate new studies that test how these systems affect lateral erosion and vertical accretion of adjacent marshes. For both types of systems, we will characterize hydrodynamic conditions and sediment supply with a combination of *in situ* measurements of waves, currents, suspended sediments and water-level, long-term NOAA measurements of winds and water levels, and wave modeling (Fagherazzi & Wiberg 2009; Mariotti et al. 2010). These parameters will be compared with control sites near the restoration experiments. Analysis of historical aerial photos (available beginning around 1960) will be used to establish rates of shoreline change over the last 50-60 years (e.g., McLoughlin et al. 2015; Section 1b) to compare with new surveys of marsh edge erosion and elevation at the experimental and control sites.

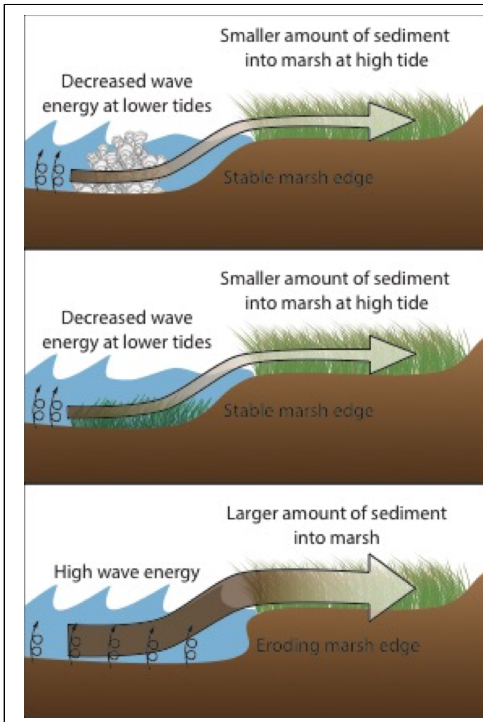

Fig. 20. The presence of seagrass and oysters affect sediment supply and marsh edge erosion.

Oyster-Marsh – The concrete "oyster castles" that are used in the reef restoration experiment to create vertical structure and provides hard substrate for oyster larvae to attach and grow also dissipate wave energy (Fig. 21). In VCR VI, eight 25 m reefs of four different designs were constructed that vary with respect to height relative to mean sea level (number of tiers) and width (number of rows 1 m apart). Wave gauges, optical backscatter sensors (to measure suspended sediments), and acoustic Doppler profilers (to measure current profiles) will be placed both in front and behind constructed reefs. These sensors will give information about wave attenuation and drag imposed on flow by the reef, and will be integrated with information on general circulation determined by the hydrodynamic model. Instruments will be deployed during summer and winter to capture typical and extreme storm conditions.

Seagrass-Marsh – We will take advantage of the seagrass restoration experiment to test the predictions of the coupled tidal flat-seagrass model developed in VCR VI (Mariotti & Carr 2014) where seagrass meadows have grown adjacent to back-barrier marshes of the adjacent island. We will monitor flow and suspended sediment concentrations in early summer (maximum seagrass biomass) and winter (minimum seagrass biomass). Observed seasonal differences in response to similar forcing but varying seagrass density will be compared to results from the coupled model (multi-year time scale) and from detailed morphodynamic modeling on the time scale of weeks-months using the Delft3D model (Section 3.1a).

Fig. 21. Restoration experiments with oyster reefs constructed of concrete "oyster castles".

3-2b. Barrier Island Ecosystem Coupling *(PIs: Moore, Zinnert, Young)*

To accurately project barrier island response to climate forcing, we need to understand how the dynamics of adjacent systems (dune and interior swale, Sections 2d,e) are coupled (see Figs. 2, 18; Zinnert et al. 2017). Over short time scales (days to months), storms erode islands and salinity exposure and physical disturbance (overwash) affect vegetation in dunes and swales. Regions where dunes are low experience more overwash (Houser et al. 2008; Gutierrez et al. 2015), and have swales with little to no shrub cover. Areas with high dune ridges create protected, low saline swales with higher plant cover and shrub establishment (Miller et al. 2010; Young et al. 2011; Bissett et al. 2014). Over longer time scales (decades to centuries), expansive shrub thickets can block overwash sediment transport during major storms (Morton & Sallenger 2003; Wang & Horwitz 2007) similar to the effect of buildings on developed coastlines (Rogers et al. 2015), and affect sediment connectivity with back-barrier marshes (Walters et al. 2014; Walters & Kirwan 2017). However, we lack an understanding of how dunes affect swale vegetation, how foundational *M. cerifera* shrubs affect sediment processes, and how interactions between dunes and swales affect island dynamics. These processes are critical to projecting future barrier island response to changes in forcing, especially given the potential for barrier islands to evolve at a faster pace than has been observed historically (FitzGerald et al. 2018; Rodriguez et al. 2018). In VCR VII, we will initiate new field studies and incorporate dune-swale dynamics into ecogeomorphic models to assess the effects of these dynamics on barrier island ecosystem coupling.

New field studies and modeling – We will *test our hypothesis that dune height determines plant productivity and community composition in the swale* by establishing three cross-island transects across the dunes and swales in each of two islands, Hog and Metompkin, that vary in topography and dune morphology. We will monitor permanent plots (1 m × 1 m, spaced at ~20 m intervals) for vegetation (species composition, percent cover, productivity) and elevation. We predict that there is a critical dune height required for the establishment of shrub thickets, and will quantify the relationship between dune height and shrub growth using existing and new dune height data (from LiDAR) and vegetation data (from remote sensing). Understanding these relationships will allow us to add dune-shrub relationships to the coastal dune model (Durán & Moore 2013; Durán Vinent & Moore 2015; Goldstein & Moore 2016; Table 2), which we will test using historical data on shrub expansion from remote sensing data. This will allow us to explore how storms (Section 1a) and dune dynamics (VCR LiDAR; Section 1b) control the pattern of shrub encroachment and test how the frequency and magnitude of storms controls the time scale for shrub expansion. Once we have tested and refined the expanded version of the coastal dune model, we will seek leveraged funding to merge it with a compatible cross-shore barrier-island model (e.g., Lorenzo-Trueba & Ashton 2015) to assess the time scales and conditions under which shrubs are predicted to promote or prevent islands from keeping up with sea-level rise.

3-2c. Cascading Effects and Coupling Between Non-adjacent Systems
(PIs: Kirwan, Moore, Fagherazzi, Wiberg, Zinnert, Gedan)

We will extend our state change research beyond adjacent systems to *address how state change in one location may cascade across the landscape as a whole, and potentially influence the dynamics of non-adjacent ecosystems.* Because non-adjacent couplings are difficult to observe in the field, we will initially explore them through numerical modeling. The opportunity to develop and test data-driven models in the vast and spatially connected coastal landscape is one of the distinct advantages of the VCR highlighted by the mid-term review committee. We will develop two process-based transect models that link multiple ecosystems and emphasize couplings between non-adjacent ecosystems. First, we will use the data and modeling on seagrass-marsh coupling (Section 3.2a) to link dynamics in coastal bays with the existing marsh-barrier island model (GEOMBEST+, Table 2; Walters et al. 2015). We will explore how the establishment of seagrass meadows could increase or decrease the persistence of marshes, which in turn influence the migration rate of barrier islands. Similarly, since barrier island overwash influences the width of marshes (Walters et al. 2015), changes in island morphology could control the width and depth of coastal bays in ways that influence the distribution of seagrass. Second, we will develop a new model that connects the components of the entire coastal landscape (forest, marsh, bay, barrier island) that conceptually follows the existing forest-marsh-bay model (Kirwan et al. 2016b; Sections 2a and 4-1; Table 2), where marsh edge erosion depends on bay depth and fetch, marsh accretion depends on the supply of sediment from the adjacent bay, and marsh migration depends on the slope of adjacent uplands. We will add a simple barrier island component to that model, informed by more detailed GEOMBEST+ experiments showing that migration depends on sand supply and sea-level rise rate, so that bay size depends both on marsh erosion and barrier migration. Bay size, in turn, plays a primary role in barrier island migration rate through its effect on the grain size of sediment feeding barrier migration (Brenner et al. 2015; Safak et al. 2015). Therefore, marshes far from barrier islands influence the island migration rate, and vice-versa, through their mutual influences on bay size. Modeling efforts will focus on exploring adjacent and non-adjacent couplings between ecosystems, and predicting how competition between the migration of different boundaries will influence the total width and size of the coastal landscape. For example, an acceleration in the rate of sea-level rise influences both landward (marsh migration into uplands) and seaward (barrier island migration into bays) boundaries, and the difference between them determines the width of the coastal landscape.

Both models will be parameterized using VCR data (e.g. measurements of seagrass flow attenuation, turbidity, seagrass and marsh biomass, marsh elevation change, barrier island overwash flux; Table 2). Both models will be tested by simulating landscape response to historical sea level rise, and by making comparisons between model output and observations from maps and aerial photographs (Zinnert et al., 2016a; Deaton et al., 2017). Model-field comparisons could potentially include changes in the relative size of each ecosystem, the overall width of the coastal landscape, or responses to the historic dieback and restoration of seagrasses. We anticipate that both models will lead to unforeseen relationships that can then be tested (e.g. previous GEOMBEST+ modeling revealed an unforseen relationship between island migration rate and marsh width which was verified with field observations). Finally, we will simulate coastal transgression under future accelerated sea-level rise, where we specifically probe landscape-scale response to fundamental changes in individual components (e.g. presence or absence of seagrass, marsh migration prevented by anthropogenic barriers, no barrier islands) which influence habitat diversity. Together, *these data-driven models represent an important advance of our conceptual framework to include coupled dynamics whereby local state change can propagate across the landscape.*

THEME 4: Ecological Consequences of State Change

4-1. Carbon Cycling and Sequestration

How does ecosystem state change affect carbon sequestration across the coastal landscape?
(PIs: Kirwan, Pace, Berg, Doney, McGlathery, Yang, Zinnert, Pusede)

How ecosystem processes and transitions influence total carbon sequestration at the landscape scale is unknown at the VCR or elsewhere, and represents a critical gap in understanding how climate forcing will affect the coastal carbon sink. Approximately half of all long-term carbon burial in marine sediments takes place in vegetated, coastal ecosystems where prolific organic matter production and slow decomposition leads to accumulation of organic matter (Duarte 2017). Our recent work, and that of others, quantifying carbon burial in marsh, mangrove, and seagrass sediments has demonstrated the importance of these coastal carbon pools relative to terrestrial and deep ocean systems (Fig. 22; Mcleod et al. 2011; Fourqurean et al. 2012; Hopkinson et al. 2012). This work has identified two main challenges to incorporating coastal carbon into global models: estimating stocks and rates of sequestration in biomass (short-term) and sediments (long-term), and understanding the effects of ecosystem loss and recovery. Our proposed research for VCR VII addresses these needs.

Continuing and new studies on carbon metabolism – We will continue our eddy covariance flux measurements of CO_2 in a *Spartina*-dominated salt marsh and underwater eddy covariance (of oxygen, as proxy for CO_2) in seagrass meadows now extending over a decade (Kathilankal 2011; Hume et al. 2007; Rheuban et al. 2014a,b). These high-frequency data will allow us to characterize temporal variability in net ecosystem metabolism (NEM) in response to changes in environmental controls, especially temperature and inundation (for marshes). Plant growth, and plant and soil/sediment carbon stocks, are included in our core measurements (Table 1). For the marsh, we will add measurements using a drone-based sensing platform developed by PI Yang that uses a thermal infrared camera and a spectrometer to measure solar-induced fluorescence (SIF) as an indicator of photosynthesis (Yang et al. 2015). For seagrass, we will add continuous measurements of pCO_2 and pH, and discrete sampling of dissolved inorganic carbon to integrate with the eddy covariance measurements. These data will allow us to link carbon cycling determined from water column biogeochemistry with processed-based biological rates (NEM, carbon burial), and to explore dissolved carbon export from marshes to coastal bays. Quantifying *in situ* variation in the carbonate system is a necessary first step to considering the potential role of ocean acidification, another accelerating climate driver, on seagrass metabolism.

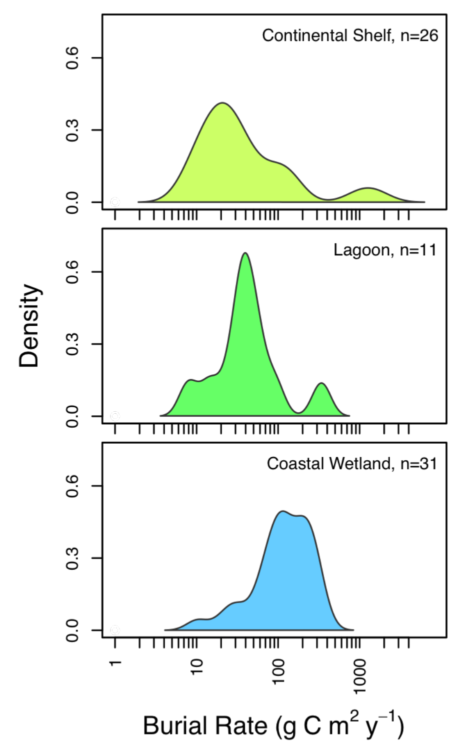

Fig. 22. Distribution of mean carbon burial rate for three categories of marine systems determined from the literature.

New and continuing studies on carbon burial – For sediment carbon stocks and accumulation rates, existing point-based estimates in each ecosystem will be synthesized and supplemented with targeted measurements that will allow us to extrapolate to large portions of the VCR landscape. For example, marsh carbon burial rates inferred from sediment cores and long-term SET measurements likely decrease with increasing elevation; such a relationship would allow us to use LiDAR to project marsh carbon burial rates across the entire VCR. Seagrass carbon burial rates vary as a function of location within the meadow (proximity to edges, water residence time), plant density, and age of the meadow (Oreska et al. 2017a). Carbon accumulation in soils on barrier island uplands varies as a function of vegetation type and elevation (obtained through existing LiDAR and spectral imagery). The total carbon burial rate in each ecosystem will be summed to estimate the total carbon buried across the VCR landscape in its current configuration, and other possible landscape configurations identified in Themes 1-3 from long-term data integrated with model predictions (e.g. expansion of seagrass, limits to marsh migration or marsh loss to storm overwash on barrier islands, reduction in barrier island area).

We will also evaluate the connectivity of carbon pools between intertidal and subtidal ecosystems. For example, organic carbon eroded from marsh edges can be transported and deposited on the marsh platform or in subtidal seagrass meadows (Section 3-1a). Oreska et al. (2017b) determined that

S. alterniflora marsh grass accounted for ~10% of buried organic carbon in seagrass meadows using $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ isotope ratios in a Bayesian mixing model. We propose to use a similar approach to determine how much *Z. marina* seagrass contributes to sediment organic carbon buried in marshes at sites where experimental seagrass meadows do and do not extend close to the marsh (Section 3-2a). Time series measurements also allow us to quantify the resilience of the sediment carbon pool to the high-temperature disturbance of the seagrass meadows in 2015.

To explore the conditions under which carbon burial in surviving and newly created marshes can compensate for carbon lost from marshes during erosion and drowning at the landscape scale, we will use a recently developed model that considers a 1D transect connecting marshes with uplands and coastal bays (Fig. 23), and is based on research addressed in Themes 2 and 3, including the in-situ production and decomposition of carbon on the marsh platform (Kirwan & Mudd 2012), the migration of marshes into adjacent coastal forests (Section 2a; Kirwan et al. 2016b), wave-driven erosion at the lagoon edge (Mariotti & Carr 2014), and coupling between-back barrier marshes and storm overwash (Section 3-1a). Data from the VCR will be collected to parameterize and test the model.

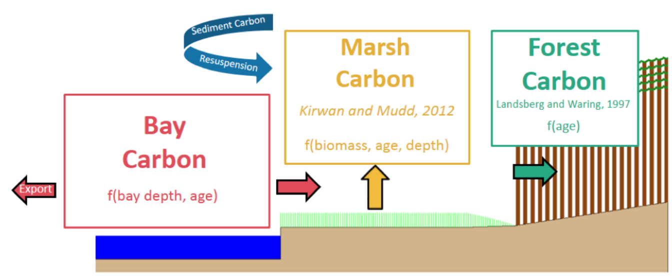

Fig. 23. 1D transect model of coupled physical and ecological processes that control marsh carbon burial rates related to marsh migration and loss.

Sediment cores will be used to parameterize carbon burial and loss rates at upland and lagoon edges, respectively. Long-term biomass data and previous experiments will be used to parameterize organic matter production and decomposition rates, and their response to increased flooding and sea-level rise. Finally, the proposed forest disturbance experiment (Section 2a) will help advance the model's treatment of marsh migration. We will simulate carbon burial rates for marshes under a variety of sea-level rise scenarios and geomorphic settings to explore the conditions under which marshes shift from sinks to sources of carbon, and the degree to which carbon burial in surviving marshes can compensate for carbon loss in drowning and eroding marshes. *This holistic treatment tests the hypothesis that the loss of ecosystem function in one part of the system can be offset by gains elsewhere.*

4-2. Habitat Provisioning for Consumer Communities

How do habitat cascades related to ecosystem state change affect consumer communities and food webs?

Ecosystem transitions also may have important and cascading consequences for consumers (Thomsen et al. 2010). Many consumers use multiple ecosystems, and because consumers integrate changes, patterns can emerge at the landscape scale if change in one system compensates for change in another. In VCR VII, we will evaluate the long-term dynamics of key consumer communities in relation to two major ecosystem state transitions: (1) the effects of increasing subtidal and intertidal vegetation on invertebrates and their predators (fish, birds); and (2) the effects of changing island geomorphology (storm overwash) and vegetation (shrub increase) on shorebirds and mammals.

4-2a. Consumer Responses to Subtidal and Intertidal Transitions *(PIs: Pace, Castorani, Johnson, McGlathery)*

The large-scale restoration of seagrass meadows and proliferation of non-native macroalgae (*G. vermiculophylla*) influence consumer communities. In the subtidal, we have shown that seagrass enhances the abundance and biodiversity of epifaunal invertebrates by forming complex habitat that increases recruitment, survival, and food availability (epiphytic algae; Lefcheck et al. 2017; Reynolds et al. 2018). Similarly, on intertidal mudflats, macroalgae increase epifaunal abundance and biodiversity by reducing predation and ameliorating harsh abiotic conditions (Byers et al. 2012; Wright et al. 2014; Ramus et al.

2017). However, in both cases the extent to which these ecosystem shifts propagate upwards to predator communities via increases in complex habitat and epifaunal prey are not well understood.

New studies – In VCR VII we will initiate two new long-term studies that build on our previous research (e.g., Thomsen & McGlathery 2006; Thomsen et al. 2009; Lefcheck et al. 2017) to determine how state transitions to seagrass and macroalgal dominance affect consumer communities. First, we will initiate new time series measurements of invertebrate communities to determine the direct and indirect effects of seagrass recovery and macroalgal proliferation on subtidal and intertidal consumers, respectively. In the subtidal, we will carry out replicated sampling of epifauna and infauna within our existing long-term seagrass restoration experiment that comprises paired vegetated and unvegetated areas. In the interidal, we will sample epifauna and infauna using paired cores over macroalgal and unvegetated mudflat patches at the sites and times described above. We will also visually quantify the abundance and foraging behavior of wading shorebirds (Section 4-2b), and will quantify the abundance of pathogenic *Vibrio* bacteria associated with intertidal mudflats that vary in macroalgal coverage. This is a continuation of work began in VCR VI (Gonzalez et al. 2014). We will bring these new measurements together with our ongoing decadal-scale time series of seagrass and fishes (Table 1), and new monthly summer seagrass drone surveys (Section 2c). We will relate variation in consumer communities to ecosystem zone (intertidal vs. subtidal), prey availability, habitat type (vegetated vs. unvegetated), habitat history (i.e., time since the shift in ecosystem state), environmental covariates (e.g., temperature), and their interactions using mixed models and piecewise structural equation models (Zuur et al. 2009; Lefcheck 2016). *We hypothesize that the transition of unvegetated sediments to seagrass dominance enhances fish abundance and richness directly by providing sheltering habitat and indirectly by improving prey abundance, but that these changes are strongly mediated by warming events* (Douglass et al. 2010). Likewise, *we hypothesize that transition of mudflats to macroalgal dominance will enhance the abundance and richness of epifaunal invertebrates, will have differential effects on shorebirds related to their foraging strategies, and will increase the abundance of pathogenic bacteria* (Section 4-2b).

The second study will focus on how shifts in these plant foundation species may alter food webs. Specifically, seagrass and macroalgae may increase trophic resources of consumers directly via their living and detrital tissue and indirectly by enhancing the growth of epiphytic microalgae. We will collect and analyze samples of detritus, primary producers (seagrass, epiphytic algae, benthic algae, macroalgae, phytoplankton), and consumers for isotopic ratios of carbon, nitrogen, sulfur, and hydrogen as well as compound-specific stable isotopes (e.g., Thorp & Bowes 2017). We will calculate the contribution of organic matter sources for key invertebrates and fishes in each habitat using Bayesian mixing models (Philips et al. 2014; Hondula & Pace 2014). By examining areas with and without vegetation, we will test how vegetation state is related to resources supporting consumers. For the subtidal (seagrass vs. bare state), we will compare our new results with those of Harbeson (2010) who conducted isotope studies in the same areas in 2005 during the early phase of meadow development.

4-2b. Consumer Responses to Barrier Island Transitions *(PIs: Karpanty, Porter, Dueser, Moncrief)*

Changes in island geomorphology and vegetation influence mammals, shorebirds, and their interactions. For example, expanding shrub habitat provides shelter for mammalian predators of ground-nesting bird eggs, such as the raccoon (*Procyon lotor*) and red fox (*Vulpes vulpes*) (Erwin et al. 2001; Dueser et al. 2013). Both migratory and ground-nesting shorebirds must adapt to changes in island geomorphology and vegetation structure, and associated variations in food/nest site availability and predation risk, both of which are crucial to migration and reproductive success (Fransson et al. 2002; Guglielmo et al. 2005). Using decadal-scale data on birds and mammals combined with new observations and modeling, we will study links between island geomorphology, ecosystem states, and long-term population dynamics.

Mammals – Prior work indicates mammalian populations on barrier islands are driven by changes in island area/elevation and extent of woody vegetation and by the effect of isolation on species occurrence, movement, and population genetics (Porter et al. 2015; Moncrief et al. 2017). In VCR VI, we will build on this research to evaluate how relative changes in barrier island habitat (beach, marsh, shrubland, forest) affect populations. For example, for islands that become more structurally simple (low islands, Section 2d) with increased storm impact and overwash, we expect the loss of red fox with forest decline followed by the loss of raccoons if shrubs are lost. *Our research tests the hypothesis that mammalian habitat generalists (e.g., raccoon) will be less vulnerable to the effects of climate-related changes in ecosystem structure than more specialized mammals (e.g., red fox).* We will continue our studies of species occurrence and genetic composition to analyze persistence of mammals on individual islands and metapopulation dynamics in terms of dispersal and abundance related to ecosystem state change. We will take advantage of: (1) past and ongoing removals of predators by TNC; (2) frozen tissue samples and museum specimens collected on the barrier islands and the mainland during the past 30 years; and (3) time-series ecosystem distribution data (Section 1a).

Ground-nesting shorebirds **–** Sea-level rise and storms are expected to have some positive effects on ground-nesting shorebirds that rely on sandy beaches, interdune areas, and overwash fans because frequent storm overwash and elimination of vegetation (grass, shrubs) creates predator-free nesting and foraging areas for these birds (Cohen et al. 2009b). *We hypothesize that abundance, distribution, and community structure of ground-nesting shorebirds is related to the relative availability of overwash and interdune areas, which is predicted by the frequency and extent of storms.* We will focus on piping plover (*Charadrius melodus*), American Oystercatcher (*Haematopus palliates*), and Wilson's plover (*Charadrius wilsonia*). We will continue to collaborate with TNC, Virginia Department of Game and Inland Fisheries, USFWS, and USGS to collect and analyze long-term data on habitat selection and breeding success that began in the mid-1990s. We will add new sampling focused on overwash fans identified using storm histories, orthophotography, and LiDAR (Section 1b). Three cross-island transects will be established to: (1) quantify the amount and quality of shorebird nesting and foraging habitat and prey; and (2) monitor how available nesting habitat and prey changes over time with colonization of vegetation and growth of dunes (Section 3-2b). We will work with our collaborators to apply a Bayesian network model of shoreline change and habitat selection that we have used in other regions (MD, NY) to relate shorebird abundance and nesting success to storms.

Fig. 24. Migratory birds track changes in ecosystem states, including overwash fans interdune areas with shrubs, and bay tidal flats (*top*), and sandy beaches and exposed marsh peat banks (*bottom*).

Migratory birds **–** Migrant shorebirds rely on sandy beaches, ocean-front marsh peat banks (exposed as islands migrate landward), and bay tidal flats for food to refuel. We maintain a database on the full suite of 19 spring migrants, and will focus our proposed new studies on three species that vary in their habitat use, migratory strategies, and life history traits. These are the long-distance migrant red knot (*Calidris canutus rufa*), and the short-distance migrants, Dunlin (*C. alpine*), and Sanderling (*C. alba*). Two bivalves—blue mussel in ocean-front peat banks and *Coquina* clams on sandy beaches—are the main prey for long-distance migrants, and birds track changes in these prey resources in space and time (Cohen et al. 2010a,b 2011; Karpanty et al. 2011). Low-lying islands that are frequently overwashed during storms have exposed marsh peat banks; more stable high islands have more sandy beachfronts (Fig. 24). The short-distance migrants also feed on invertebrates on bay tidal flats. *We hypothesize that short-distance migrants that have a broader foraging niche compensate for changes in ecosystem state or prey resources by shifting foraging strategy, and are less vulnerable to climate-driven changes than long-distance migrants.* We will continue long-term shorebird counts, invertebrate prey sampling (abundance, biomass), scat collection, banding, and resighting during the April–June spring migration season at 150 sites in sandy beach and peat bank habitats, and will add 75 sites in bay tidal flat habitats used by short-distance migrants. We will do next-generation DNA sequencing of scat to identify the origin and identity of prey the migrants are consuming (Kruger et al. 2014; Novcic 2014; Gerwing et al. 2016). Resighting methodology allows tracking individual phenology and habitat use. We will use generalized linear models to predict the relationships between migrant species, prey, and habitat use to quantify variability in migrant response to ecosystem state changes and prey availabilities associated with climate forcing.

V. SYNTHESIS

Our proposed work addresses the fundamental goal of long-term research—to build ecological knowledge at all levels of organization that will provide a baseline upon which to detect change, and to develop data-informed models that can be used to forecast future changes. We need decadal-scale studies to understand how long-term trends and short-term disturbance related to climate drive ecological structure and function. We ask fundamental questions about state change dynamics in ecosystems dominated by foundation species, including thresholds and critical transitions, landscape connectivity, vulnerability and resilience, and consequences for carbon sequestration and habitat provisioning. Our research provides a framework for understanding state change in other regions with a larger human footprint and where there could be a range of management options (i.e., systems that are more developed/engineered and where connectivity is interrupted, or where there are limits to transgression such as hardened shorelines).

VCR LTER provides comprehensive place-based, globally relevant, research that combines field observations, experiments, and modeling to advance understanding of climate-driven coastal change. Our proposal builds on long-term data and experiments, integrated with shorter-term experiments and predictive models, to address theory related to ecosystem state change in response to climate drivers. A strength of the VCR is the close collaboration of ecological and physical scientists necessary to develop an integrated understanding of long-term environmental change in these coastal systems. Based on our long-term foundation of integrated research, we have developed a unifying conceptual framework that state change at any point on the coastal barrier landscape (marsh, coastal bay, barrier island) is driven by the three factors: landscape position (elevation, adjacency), biotic feedbacks, and fluxes (sediment, organisms). We use our experiments and models to test how these mechanisms can lead to different trajectories: non-linear abrupt transitions, with or without hysteresis, and linear transitions. **In VCR VII, we extend this framework to take advantage of the unique opportunity at the VCR site to address how state change can propagate across the landscape through coupled dynamics. This is a critical frontier in achieving a holistic understanding of coastal dynamics and resilience in response to climate change.** Our theoretical advances related to state change, connectivity, and coupled dynamics will ultimately extend beyond coastal barrier systems to provide new insights on drivers and mechanisms of ecological state change that can be compared with other biomes where these types of transitions are important (for example, in the LTER sites KNZ, JRN, and MCR). Cross-fertilization of ideas across the LTER Network provides a critical opportunity to advance general ecological theory.

VI. RELATED RESEARCH PROJECTS

VCR has a strong track record of leveraging other funding sources to support complementary research related to core LTER foci. These studies are a valuable addition to LTER core activities, and several have involved collaborative, cross-site research. For example, VCR is the lead on a cross-site NSF-funded Coastal SEES project to compare marsh persistence in response to different social adaptation strategies to sea-level rise (with GCE and PIE). One ongoing related research project that contributes directly to the objectives described in this proposal is the collaboration between VCR LTER, VA Tech University, TNC, VA Department of Game and Inland Fisheries, USFWS, and USGS to collect and analyze long-term data on population dynamics, habitat selection, and breeding success of migratory shorebirds (Theme 4-2b).

VII. BROADER IMPACTS: EDUCATION and OUTREACH

Undergraduate and Graduate Education – Student training is a priority of the VCR LTER program. Each year, we support about 20 M.S. and Ph.D. students who are advised by PIs from seven institutions. Our collaborative model is to provide graduate student support for all our PIs. Graduate students are involved in all aspects of the research, and benefit by being trained in an interdisciplinary, collaborative environment. They are actively engaged in VCR education and outreach activities through mentoring, public seminars, and K-12 activities. The students are organized with a student leader, and have regular meetings, and an annual peer-mentoring workshop. In addition, we support at least four undergraduate REU students each year for 10-weeks of summer field-based research. Additional private sources provide opportunities for high school and undergraduates students to engage in field research. We have a formal *tiered peer-mentoring* program where we partner undergraduate researchers with graduate students and faculty supervisors. Many of these undergraduate students continue to work on LTER research through the academic year and complete theses.

K-12 Education – Our SLTER program has a high impact on the local community, one of the poorest counties in the state where m*ore than half of the students are from traditionally under-represented groups.* Since 2007, we have provided Summer Science Internships through our Research Experience for High School Students (REHS) program, which partners two local high school students with VCR graduate students to conduct field-based research projects. During VCR VI, we expanded our SLTER program to build new partnerships with local elementary schools that will continue in VCR VII. For example, we have designed field activities for 3^{rd}-12^{th} grade students to fulfill the VA Department of Education requirement for a Meaningful Watershed Experience. As part of our collaboration with TNC, we co-teach a Summer Ecology Camp. We have co-designed with a local teacher an Oyster Gardening Program that involves all local public and private schools. In 2017, we constructed a demonstration oyster restoration reef adjacent to the VCR LTER lab, and regularly host elementary school classes.

Teacher Training – The VCR SLTER program provides professional development and training programs for public school science teachers throughout the state of Virginia, and involves ~50 teachers each year who then connect with some 8000 students in their classrooms. Two science teacher workshops are held, one on Coastal Bay Ecology and a second on Fall Migration Ecology. In addition, three Art and Ecology teacher workshops are supported each year: two couple instruction in Plein Aire landscape painting techniques with an introduction to salt marsh ecology, and the other combines instruction in Observational Drawing techniques with discussions on environmental monitoring and long-term data. Artwork and essays generated from the workshops are displayed in public exhibitions at the Barrier Islands Center Museum on the Eastern Shore and in the Science and Engineering library at the University of Virginia. We also provide training and curriculum for K-12 teachers in the Oyster Gardening program, prepare classroom materials, and run field trips partnering with VA Oyster Reef Keepers.

Network-Level and Synergistic Activities – We plan to continue our cross-disciplinary, on-line graduate course started in the last funding cycle between the four Atlantic coastal sites (FCE, GCE, PIE, VCR). Typically, at least 100 students from over 10 institutions participate. We are continuing to build art/humanities-science collaborations. We will continue our successful Artist-in-Residence program at the LTER field site. In addition, we are developing an Environmental Listening Lab which brings faculty and students together from Music, Environmental Sciences, Ethics, and Religious Studies in field settings. We are a partner in a new Coastal Resilience NSF National Research Training Grant to train graduate students in the 'science of team science' and will use VCR LTER research as a foundation for that work.

Public Outreach, Policy, and Management – We will continue to build on our strong partnership with TNC, the Barrier Islands Center Museum and other local agencies to disseminate our findings to stakeholders. We have a monthly seminar series, and plan to expand our communication and outreach activities through other public media. We have launched our web-based Coastal Resilience decision-support tool, developed with TNC and based on VCR data and models. Along with TNC, we hold workshops with citizens and local/regional agencies to train them in using the tool to inform policy and decision making. We continue to be part of the Eastern Shore Coastal Adaptation Working Group that includes members from regional Planning Commissions, NOAA Coastal Zone Management Program, and Resource Conservation & Development Council. VCR experiments inform conservation projects and test ecological theory relevant to coastal restoration (e.g., coupled dynamics of oyster reefs/seagrass and marshes, seagrass resilience to temperature, marsh transgression). Collectively, our research will help develop more effective management approaches to enhance coastal protection and resilience and will position us to better forecast the responses of coastal barrier systems to long-term environmental change.