Silliman Research Statement

The majority of my work has been with plant and animal communities on temperate and tropical coasts, including salt marshes, rocky shores, mangroves, seagrasses, coral reefs, and maritime forests. My research primarily focuses on five questions:

1) What is the role of consumers and food web structure in controlling ecosystem structure and function?
2) How and why do top-down impacts vary across large spatial and temporal scales?
3) How do climate change, microbial, and human forces modify top-down control?
4) What is the role of facilitation in regulating biodiversity and ecosystem function?
5) What are the implications of these community-regulating interactions for conservation of coastal ecosystems and the critical services they provide?

Overturning one of the oldest paradigms in ecosystem ecology

In the 1940s and 50s, salt marshes acted in large part as the birthplace for modern-day ecosystem ecology. For nearly 6 decades, the prevailing paradigm in marsh ecology has been that bottom-up forces are the primary determinants of plant production. Results from my research in east coast U.S. marshes have overturned this long-entrenched dogma. By manipulating grazer densities, I demonstrated that the most abundant marsh grazer, the snail (*Littoraria irrorata*), exerts strong control over cordgrass growth (Silliman and Zieman 2001, *Ecology;* Silliman and Newell 2003*, PNAS*). Subsequent experiments demonstrated that marine predators (e.g., blue crabs), by controlling densities of plant-grazing snails, indirectly facilitate marsh primary production (Silliman and Bertness 2002*, PNAS*). In the absence of predators, *Littoraria* densities increase and convert lush intertidal marshes into exposed mudflats. Combined, these findings revealed that a simple trophic cascade regulates salt marsh production.

Over the last 15 yrs, > 250,000 acres of marsh have died back in the U.S. Physical factors (e.g., drought) were hypothesized to be the causal mechanisms. I surveyed > 20 die-back areas and found average *Littoraria* densities to exceed 400/ m^2, and 1000 m long fronts of snails grazing down cordgrass. With collaborators, I placed exclosures ahead of snail fronts. After 3 months, snail removal increased plant biomass, while continued snail access resulted in conversion to exposed mudflat. Model analyses revealed that localized drought stress intensified top-down control by snails on stressed plants, leading to mudflat formation and subsequent cascading vegetation loss (Silliman et al. 2005*, Science*). More currently, my work with the predator-keystone consumer-*Spartina* interactions has focused on both large spatial and temporal scales, and reveals that: (1) predator diversity stabilizes consumption rates on snails during wide-ranging temperature fluctuations (Griffin and Silliman 2011, *Biology Letters*)(2) during drought years, blue crab numbers drop drastically, leading to population build-up in plant-grazing snails Silliman et al. in review), (3) infaunal predators regulate biogeochemistry of marshes through a trophic cascade (Griffin and Silliman in review, Journal of Ecology) and (4) cross-kingdom primary consumer diversity regulates ecosystem functioning (Hensel and Silliman, 2013, *PNAS*). Our most recent work reveals that after reaching clear density thresholds during drought years, snails begin grazing down marshes, acting in concert with elevated soil salinities to generate mosaics of mudflats. In non-drought years that follow, blue crabs increase, snails decline, soil salinities drop, mussel mounds facilitate grass growth and the marsh begins recovery (Angelini and Silliman 2012*, Ecology,* Angelini et al 2015*, Nature Comm.*). Finally, we have just discovered the parasites in the snails protect salt marshes from climate change and indirectly regulate marsh ecosystem function (Morten and Silliman in prep, target journal *Nature Communications*). Parasite infection rates are regulated by their final hosts – migratory birds – whose increased presence in snail barrens facilitates the recovery of these inconic ecosystems (Morten and Silliman in prep, target journal *Science).*

Biogeography of top-down forcing and global change

Over the past 11 years and during the next 5, I have examined and will continue to test the generality of top-down control in salt marshes in New England, Argentina, Californian, Chile, Brazil, China, New Zealand, and South Africa. This work has already resulted in 23 publications (e.g., in *Ecology, J. Ecology, Ecology Letters, Ecological Monographs*) and reveals that intense consumer control is not a biogeographic anomaly of U.S. southern marshes but, instead, a worldwide phenomenon. This work also indicates that the worldwide decline in marine predators is contributing to increased grazer control in these systems, as it unleashes potent grazers from top-down control (He and Silliman 2016, *Ecol. Monographs*). Most recently, our work on salt marshes in temperate China (He, Silliman, et al. *Ecology Letters*) has revealed that grazing crabs can eliminate drought-stressed vegetation that could otherwise survive and recover from the climate extreme, transforming once lush marshes into persistent salt barrens. This is the first direct experimental demonstration for the obligatory role of top-down forcing across the initiation, expansion and recovery stages of a natural ecosystem's collapse. It highlights that top-down factors should no longer be considered ancillary to the primary force of drought but indeed a likely powerful counterpart that cannot only act additively to kill ecosystems but also suppress their recovery after drought subsides. This finding has implications for the resilience of ecosystems worldwide to drought.

We also performed a global synthesis to test for the generality of top-down forcing in coastal wetlands including both salt marshes and mangroves. By synthesizing 1748 measures of consumer effects reported in 443 experiments/ observations on all continents except Antarctica, this work (He and Silliman 2016, *Ecol. Monographs*) reveals that top-down control is indeed general across a wide range of salt marshes globally. It also reveals potential generality of top-down control in mangroves. By synthesizing results of studies that factorially manipulated presence of consumers and environmental factors relevant to global change, this work further found that across a range of studies and salt marshes, nutrient, disturbance, and flooding often amplify the negative effects of herbivores on salt marsh plants.

If top-down control is prevalent across a range of salt marshes and mangroves, the next question is whether top-down control varies geographically. Theory has long predicted that herbivore pressure is more intense at lower than at higher latitudes. Analyzing how top-down control varies across latitude, we found that top-down control by endothermic vs. ectothermic herbivores varied differentially across latitude (He and Silliman 2016, *Ecol. Monographs).* Along latitudinal gradients, increased temperature enhances the negative effects of ectothermic herbivores, but has no effect on endothermic herbivores. This finding highlights the value of incorporating thermoregulation strategy into future models that predict the impact of rising temperature on trophic interactions. We also investigated if the effect of nutrient enrichment on top-down control varies geographically (He and Silliman 2015, Ecology Letters). We found that fertilization strongly increases herbivory in salt marshes, but not in mangroves, and that this effect increases with increasing latitude in salt marshes. The mechanism likely underlying this pattern is that nutrient enrichment has stronger effects on plant nitrogen concentration at higher latitudes and that higher increases in plant nitrogen concentration generally lead to higher increases in herbivory. This work provides a mechanistic understanding of how eutrophication affects plant–herbivore systems predictably across broad latitudinal gradients, and calls for incorporation of biogeography into understanding large-scale variability in the impact of environmental change.

Combined, my 10-year, 44-publication body of work on consumer control in marshes is serving as a template for rewriting the 60-year old, bottom-up paradigm of salt marsh ecology and for pushing the whole field of ecology forward by increasing predictive understanding of how top down control varies with spatial processes, geography, and physical forcing (Silliman et al 2013, Annual Review of Ecology, Evol. and Systematics; He and Silliman 2016, *Ecol. Monographs*).

Future work: Multi-predator impacts and alligators as marine top predators

Ecological theory implies that extinction of predator species, and the resulting erosion of predator diversity, may reduce the stability and strength of top-down control. The applicability of this theory to real-world scenarios remains unknown, however, because most empirical tests have not been conducted in the field. For example, experiments in laboratory mesocosms do not incorporate the seasonal environmental changes that characterize the world's temperate ecosystems, precluding temporal complementarity among species that arise owing to differential thermal tolerance. The insurance hypothesis states that differential responses of species to changing environmental conditions can have important benefits for the functioning of ecosystems, by buffering food webs against changes. Over the next 5-10 years, I will test the predator diversity insurance hypothesis in the field, under realistic scenarios, in marsh, mangrove and rocky shore communities. I hypothesize that predator diversity will be especially important in maintaining ecosystem function in temperate coastal communities characterized by marked seasonal environmental variation and host to potent grazers that, when left unchecked, can increase in numbers and transform ecosystems to barren flats.

Over the past 6 years, Silliman lab field studies have shown that the American alligator can: (1) live and feed (on, e.g., sharks, crabs, shrimp) in salt water for greater than 30 days (Nifong et al 2015, Journal of Animal Ecology) and (2) potentially generate a 4-level trophic cascade in marshes (Nifong and Silliman 2013, JEMBE). Surveys of marine protected areas in Florida indicate that alligators were likely a key marine predator in marsh and mangrove ecosystems, but have been eliminated by humans (Silliman et al in review, *Current Biology*). These results will likely overturn two storied paradigms in ecology: (1) alligators are purely freshwater animals and (2) apex predators play insignificant roles in the maintenance of coastal wetland plants. Future research will include installation of ~1000m x 1000m alligator enclosures and exclosures in marsh and mangrove ecosystems to test for the direct and indirect effects of their presence on ecosystem structure and function. In addition, as a co-PI at the GCR-LTER site, I just began a 6-year project of large-scale (50 m2) exclusions of nekton predators to experimentally test for their keystone impacts on marsh structure, function and stability.

Future Work: Top predator expansion and impacts in novel ecosystems.
Over the past five years, I have been studying range expansion of top-predators into novel ecosystems (Silliman et al. *in review Current Bioogy*). By collecting long-term data and conducting surveys in protected and non-protected areas, my lab and I found that following long-term protection, sea otters along the northeast Pacific coast expanded into salt marshes and seagrasses, and alligators on the US east coast expanded into marine ecosystems - habitats presently thought beyond their niche space. A literature analysis shows that there is also evidence that seals have expanded into subtropical climates, mountain lions into grasslands, grey whales into lagoons, orangutans into disturbed forests, wolves into the rocky intertidal, orcas into rivers, and bobcats and wolves into beach systems. Historical records, surveys of protected areas, and patterns of animals moving into habitats that were former hotspots for hunting indicate that rather than occupying them for the first time, most of these animals are recolonizing ecosystems. This work brings to light that our baseline understanding of large consumer habitat niche-breadth is likely to be limited in many cases and that large consumer species richness for many ecosystems - especially for habitats along the coast and those in temperate and tropical seas - is greater than we imagined or predicted. This finding is incredibly important, because it not only suggests that there is much more space in which large consumers can be saved, but also means that the positive effects that predators may have on an ecosystem's resilience to environmental change are potentially available for a much greater diversity of habitats. Over the next decade I will focus on otters and alligators as model systems for testing impacts of expansion of top predators. Unlike most top predators, we can effectively exclude these animals and within the inclusions house prey items whose range is not larger than the cage's size (i.e. crabs, snails, worms).

Microbiomes, small grazers, and the control of plant communities

Relationships between fungal-farming animals and fungi are models of how co-evolution can drive positive interactions, and establish some species as keystone ecosystem engineers. My experimental work on *Littoraria* feeding demonstrates, for the first time, low-level fungal farming in a marine animal and outside class Insecta (Silliman and Newell 2003, *PNAS*). This work has now generated a new line of experimentally driven research, testing whether or not detritivores are non- or active-participants in the proliferation of fungi in plant tissues in aquatic and marine systems (Daleo, Silliman, et al., 2009, *Journal of Ecology*). This first demonstration of low-level microbial farming has also inspired new lines of research in microbial-consumer interactions that has quickly had large impacts on the field of evolutionary biology (see research and associated discussion papers in *Nature 393-396, 2011: Primitive agriculture in an amoeba*).

Over the past 8 years, I have examined generality of how this interaction affects host plants. In terrestrial communities, grazer-facilitation of fungal disease in plants has been studied for over a century. At times, this interaction can lead to massive loss of plant ecosystems (e.g., bark beetles in pine forests). Despite the prevalence of this interaction in terrestrial systems, it was not considered relevant to the structure of marine plant communities until my work in marshes. By manipulating both grazer and fungal presence, I demonstrated that snail grazing and subsequent fungal infection in live grass led to drastic reductions in plant growth and, at high grazer densities, destruction of canopy. If grazer promotion of fungal disease in marine plants is not limited to marshes, then small grazers that take small bites out of plants (e.g., fish, crabs) could be exerting similarly strong, but undetected control over marine plants globally. I tested this idea with funding from a NSF CAREER Award 2011 and focused on the following questions: *1) Is grazer facilitation of fungal disease in marine plants common, but overlooked? 2) What is the resultant impact of grazer-facilitated fungal infection on marine plant growth? 3) How do multiple stressors (i.e., warming, drought) impact the strength of grazer facilitation of fungal disease in marine plants?* Results so far have shown that cross-kingdom grazer diversity (including fungi) regulates ecosystems function (Hensel and Silliman 2013, *PNAS*), that nutrients and grazers facilitate disease causing pathogens in corals (Shaver et al 2017, *Ecology*) and that around the world in seagrass, marshes, mangroves and kelp bed communities grazers commonly increase microbial infection in plants and that global change stressors such as warming, nutrients, and drought amplify this affect (Silliman et al, *in prep*, target journal Ecology Letters).

To what extent do facilitation cascades control biodiversity?

Foundation species, such as kelps and trees, are defined as organisms that ameliorate physical (i.e., desiccation, heat) and biological (i.e., competition, predation) stress to enhance species diversity and productivity. To date, experimental studies have revealed direct, obligate interactions between foundation species and associated organisms in a variety of ecosystems, suggesting the presence of a single, dominant facilitator can give rise to an entire community.

Many ecosystems, however, are structured by multiple foundation species (i.e., corals-sponges, macroalgae-clams), whose interactions can produce emergent effects on community structure and diversity. My collaborative study in New England cobble beaches (Altieri, Silliman, Bertness 2007, *American Naturalist*), for example, found that facilitation cascades arise when an independent foundation species, cordgrass, harbors a second, dependent foundation species, mussels, and combined they generate conditions amenable to other plants and animals. Although this was the first-ever experimental demonstration of a facilitation cascade, these positive interactions among foundation species, or facilitation cascades, may be pervasive phenomena that organize communities, and explain biodiversity patterns on regional scales. Over the past three years, experimental work in my lab (Angelini and Silliman 2015, *Ecology*) in coastal oak tree hammocks along the Southeastern Atlantic coast provides evidence for this possibility, and reveals that the rich diversity of micro-animals (insects, spiders, reptiles) associated with oak tree canopies are in large part maintained via a facilitation cascade, where live oak trees (*Quercus virginiana*) facilitate Spanish moss (by ameliorating heat stress), which in turn facilitate local insect communities by protecting them from both predation and desiccation stress. Over the past 5 years, we have tested for occurrence of facilitation cascades and their impacts on food web structure in mangrove-oyster and bivalve-seagrass systems (Tjisse, H.,et al, 2016, *Proceedings of the Royal Society*), shown that facilitation cascades regulate marsh ecosystem function and these impacts are density dependent (Angelini et al, 2015, *Proceedings of the Royal Society*) and tested for global meta-analysis (Thomsen et al, in revision, *Nature Ecology and Evolution*). Combined, these results are supporting the idea show that positive interactions hierarchically organize associated animal communities, an idea not currently incorporated into ecological theory.

Alternate community states and climate change impacts on rocky shores

I am currently pursuing two theoretical questions in rocky shore systems: *(1) Can natural communities exist as alternative stable states* and *(2) How does the nature of species interactions that maintain local biodiversity change with increasing stress?* Both lines of research challenge current theory. Long-term work (12 years) on Maine rocky shores with mussel bed and seaweed communities indicates that alternative community stable states may be an interesting theoretical idea that is lacking a definitive empirical example, calling into question its widespread incorporation into conservation theory and practice (Bertness et al. 2003, 2004 *Ecology*, Silliman et al., *in review, Ecology*). Work on highly stressed, wind-swept Patagonia shores in Argentina (avg. speed: 62km/hr, <15% humidity) indicates that biodiversity patterns throughout the entire intertidal are maintained not by keystone predators (starfish), but by keystone facilitators (mussels) (Silliman et al., *PLoS ONE*, 2011). Thus, positive interactions may become relatively more important than keystone predation in maintaining biodiversity under extreme climatic stress. Over the next 5 years, I will be working with two Ph.D. students from the University of Patagonia to test experimentally for the latitudinal extent of these interactions and the physical conditions under which predation returns as a primary, controlling force of biodiversity.

Non-linearities in ecosystem services

A common assumption in conservation is that ecosystem services respond linearly to changes in habitat size. This assumption leads frequently to an “all or none” choice of either preserving habitats or converting them to human use. However, my collaborative research on coastal protection services (i.e., wave attenuation) reveals that these relationships are rarely linear, and that optimal land use occurs through the integration of development and conservation consistent with ecosystem-based management goals (Barbier, Koch, Silliman et al. 2008*, Science;* 2009 *Frontiers*). Thus, reconciling competing demands on coastal habitats should not always result in stark preservation-versus-conversion choices. Over the next 5 years, I will experimentally test for non-linearities in ecosystem generation of fishery and shoreline protection services in seagrass, mangrove, oyster and salt marsh communities.

Overturning paradigms in coastal restoration and resilience.

I am actively involved with studying causes, consequences and remediation of human impacts in marsh and mangrove ecosystems. In 2009, this effort culminated with the publication of a well-received, co-edited book: Human Impacts on Salt Marshes: A Global Perspective. I have also investigated impacts of the BP oil spill on marsh ecosystems. My lab’s research shows that marshes display both resilience and intense degradation (shoreline erosion) after oil-driven die-off (Silliman et al. 2012 *PNAS*). Although marshes are generally thought to be resilient to oiling, this assertion is based largely on small-scale field and laboratory studies. Our field observations and experimental manipulations indicate that: (1) there are clear thresholds of oil coverage that determine the severity of marsh ecosystem damage, (2) recovery can be rapid but it is highly location dependent, and (3) at the seaward edge of marshes oil-driven die-off sets in motion an accelerated erosion process, fueling marsh losses that are likely to be permanent. This work represents the first to reveal the importance of disturbance location as a key factor in resilience in marsh ecosystems, and to identify clear thresholds, that if crossed, can greatly hinder marsh system recovery. More recently, using data collected as part of the natural resource damage assessment (NRDA), I investigated the spatial generality of and thresholds in in the effect of oiling on marsh edge erosion across 103 salt marsh sites spanning ~430 kilometers of shoreline in coastal Louisiana, Alabama, and Mississippi. This work revealed a threshold for oil impacts on marsh edge erosion, with higher erosion rates occurring for ~1–2 years after the spill at sites with the highest amounts of plant stem oiling (Silliman et al 2016, *Scientific Reports*). These results provide compelling evidence showing large-scale ecosystem loss following the Deepwater Horizon oil spill.

Resilience of coastal wetlands is also challenged by rising seas and more and more frequent storms, yet intense debate has recently emerged over whether or not wetland vegetation actually suppresses coastal erosion. I have conducted a three-year vegetation removal experiment in a salt marsh in Florida to experimentally test if wetland vegetation presence reduces the lateral erosion of shorelines (Silliman et al. *in review Proc. Roy. Society*). This work reveals that loss of wetland plants increases erosion rates and that extensive root systems, not aboveground stems, are primarily responsible for this protective effect. This work provides experimental evidence that edge disturbances (e.g. oil spills) that kill wetland plants are powerful agents that can accelerate shoreline loss. This work thus substantiate a coastal protection paradigm that incorporates preservation of shoreline vegetation.

I have also worked in Florida and the Netherlands to incorporate positive interactions into marsh restoration efforts – a new and emerging paradigm in coastal conservation I co-framed (Halpern, Silliman et al. 2007, *Frontiers in Ecology and Env*.). My experiments reveal that a simple change in planting configuration (placing propagules next to, rather than at a distance from, each other) results in harnessing facilitation and increased yields by 107% on average (Silliman et al. 2015, PNAS). Although such small adjustments in restoration design may catalyze positive species interactions and result in significantly higher restoration success with no added cost, our survey of 25 restoration organizations in 14 states in the United States revealed that >95% of these agencies assume minimizing negative interactions (i.e., competition) between outplants will maximize propagule growth. This work thus highlights the potential importance of incorporating facilitation theory in wetland conservation efforts.

Future Research: Bringing food webs into Eco-Geomorphology

Coastal erosion is one of the most pressing environmental challenges many coastal communities face. While salt marsh ecosystems are highly valued for many ecosystem services, marsh erosion has been accelerated worldwide due to human-driven environmental change. The impacts of nutrient loading on marsh erosion have been experimentally demonstrated in east coast marshes. The hypothesized mechanism is that when nutrients are no longer limiting, marsh plants shift tissue allocation from belowground to roots that both acquire nitrogen and stabilize the marsh soils to aboveground leaves that gather more light. Another increasingly recognized cause of marsh erosion is grazer-driven marsh vegetation loss. Studies on multiple continents have shown that marsh grazers, including many burrowing crabs, can strongly suppress marsh vegetation and kill all vegetation when their abundance increases in the absence of predator control. Whether predator recovery, one of my major research areas outlined above may help halt marsh erosion due to runaway grazer-driven vegetation losses, however, is unknown.

On the west coast of the U.S., where trophic feedbacks are thought to be weak, marshes are experiencing high levels of loss due to intense edge erosion (0.5-1.5 m/yr)[1] without regrowth. As these are highly eutrophic estuaries, intense nutrient loading is purported to be a major driving factor in marsh loss. In those west coast marshes, however, we have observed high densities (50-100 burrows/m^2) of burrowing crabs on marsh edges. These crabs actively eat marsh plants and their roots, likely contributing to bank erosion as well. In collaboration with my post doc (Brent Hughes) and incoming graduate student Lindsay Ghaskin, we will experimentally investigate the extent to which top-predator expansion (sea otters) can halt marsh erosion through trophic control of runaway grazer impacts. We predict that although nutrient loading and outbreak of burrowing crabs have increased coastal erosion in Elkhorn Slough marshes, top-predator recovery due to recent predator conservation efforts will significantly help halt marsh erosion. This work will be ground breaking in that it will be the first to experimentally test how top predators can change the geomorphology of an ecosystem.