Title: Geomorphology and species interactions control facilitation cascade self-organization and strength

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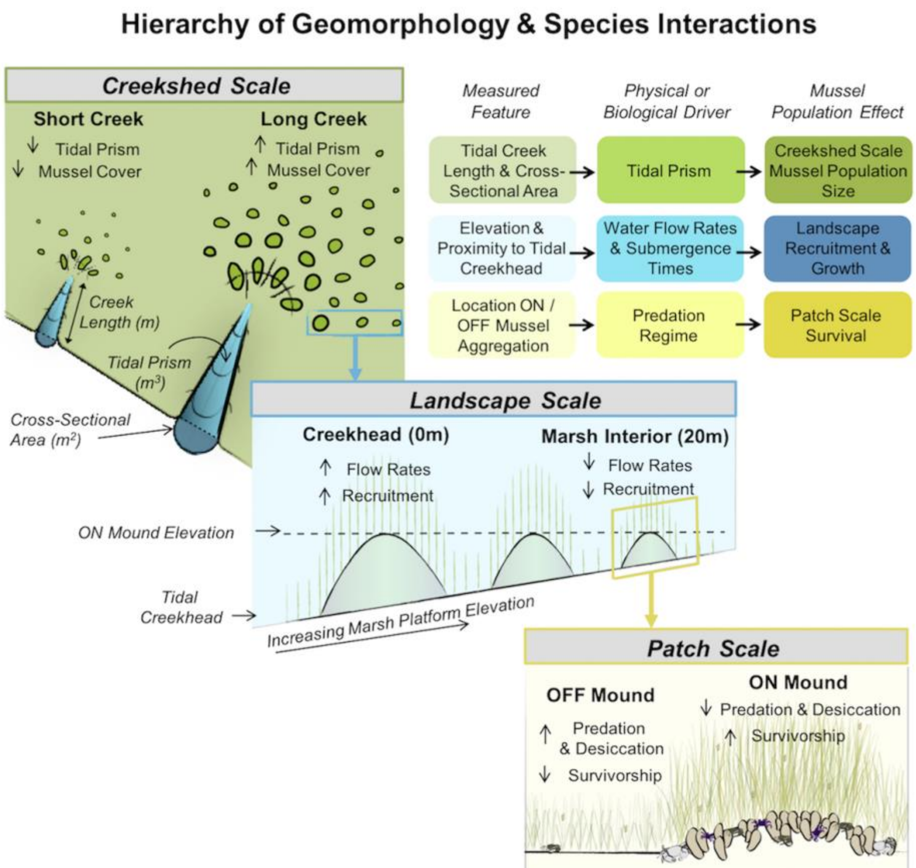
SUMMARY

Facilitation cascades are chains of positive interactions that occur as frequently as trophic cascades, and are equally important drivers of ecosystem function where they involve the overlap of primary and secondary, or dependent, habitat-forming foundation species [cite]. Although it is well-recognized that the size and configuration of secondary foundation species' patches are critical features modulating the ecological effects of facilitation cascades, the mechanisms governing their spatial distribution are often challenging to discern given that they operate across multiple spatial and temporal scales [cite]. We therefore combined regional surveys of southeastern US salt marsh geomorphology and invertebrate communities with a predator exclusion experiment to elucidate the drivers, both geomorphic and biotic, controlling the establishment, persistence, and ecosystem functioning impacts of a regionally-abundant facilitation cascade involving habitat-forming marsh cordgrass and aggregations of ribbed mussels. We discovered a hierarchy of physical and biological factors predictably controlling the strength and self-organization of this facilitation cascade across creekshed, landscape, and patch scales. These results significantly enhance our capacity to spatially predict coastal ecosystem function across scales based on easily identifiable metrics of geomorphology that are mechanistically linked to ecological processes [cite]. Replication of this approach across vegetated coastal ecosystems has the potential to support management efforts by elucidating the multi-scale linkages between geomorphology and ecology that, in turn, define spatially-explicit patterns in community assembly and ecosystem functioning.

GRAPHICAL ABSTRACT



RESULTS

Regional Survey: Mussel Distribution Patterns across the Geomorphic Template

Habitat-forming salt marsh cordgrass (*Spartina alterniflora*) and suspension-feeding ribbed mussels (*Geukensia demissa*, hereafter mussels) commonly overlap to form facilitation cascades and hot spots of ecosystem function along the Atlantic coast of North America. Despite nuanced understanding of this secondary foundation species' population processes and effects on ecosystem function, why mussels vary in cover by orders of magnitude within and across marsh platforms in the region remains unexplored [1,4,6,13]. Given the importance of mussel-derived ecosystem function hot spots to overall marsh multifunctionality [6,7], we conducted a survey of creeksheds associated with long and short creeks (i.e. 125-250m and 50-75m from the creek mouth to creekhead, respectively) from northern Florida to central South Carolina (**Fig. 1A**) with the goal of characterizing patterns in mussel abundance and distribution within and across salt marshes. We found that creeksheds associated with long tidal creeks consistently support larger numbers of mussels, percent areal coverage of mussel aggregations, and both average and maximum aggregation sizes than creeksheds associated with shorter tidal creeks. All four of these mussel population metrics were highest at creekheads (0m), where tidal water floods onto and drains off of the marsh platform (**Fig. 1B**), intermediate at 10m, and lowest at 20m onto marsh platforms (**Fig. S1**; see figure insets for model results here and below), indicating that mussel population densities are highest at creekheads where flow rates and submergence times are highest [9,14-17].At all three distances from the tidal creekhead, mussel population size increased with tidal creek length (**Fig. 1C**).

Quantifying the Geomorphic Template

Creekshed Scale: Creek Length and Cross-Sectional Area

To evaluate how first-order features of the salt marsh geomorphic template may relate to one another and influence observed patterns in mussel population metrics at creekshed-scales (i.e. associated with long versus short creeks; 100s-1,000s of m^2), we measured both tidal creek length and cross-sectional area at the point of creek initiation from the main channel of each creek surveyed across the region. We use tidal creek length and cross-sectional area, a proxy for tidal prism [18-21], or the volume of water conveyed by a creek per tidal cycle, to characterize the 'first-order' features of the geomorphic template, which we define as features that control the timing and magnitude of tidal inundation across creeksheds. Tidal prism controls flood- versus ebb-dominance, sediment import and export regimes (CITE), and the influx of food and larvae conveyed by the tide over the marsh platform [22]. In agreement with prior studies[18-21], we found that creek cross-sectional area increased as a linear function of creek length ($p<0.0001$; Adj. $R^2=0.83$;**Fig. 2A**), indicating a tight physical relationship between the length of tidal creeks and the volume of water they convey each tide. Further, creekshed mussel population density increased as a log function of creek cross-sectional area ($p<0.0001$; Adj. $R^2=0.73$;**Fig. 2B**). Thus, these first-order features are highly correlated and can be used to predict mussel abundance and distribution patterns across marsh creeksheds (Graphical Abstract).

Landscape Scale: Marsh Surface Elevation and Proximity to Tidal Creekheads

We next used marsh surface elevation and proximity to creekheads to characterize the 'second-order' features of the geomorphic template (10s-100s of m^2). To evaluate how these second-order features may control observed patterns in mussel population metrics across landscapes (i.e. creekhead versus marsh interiors), we first identified five sites on Sapelo Island, GA representative of marshes across the southeast US (**Fig. S2**). At each site, to test the hypothesis that marsh surface elevation predictably varies with proximity to creekheads and structures water flow rates across marsh landscapes, surface elevation and water flow rates were measured on and off mussel aggregations at three distances from creekheads (0,10, 20m) associated with long and short tidal creeks (N=5 measurements per area type, distance, creek length, and site).

Mussel aggregation elevation was similar in all locations (+0.84±0.06m above sea level [ASL]; all Mean ± SD; $p>0.25$) indicating a potential optimal height or 'ceiling' for mussel growth, a phenomenon shown for oysters [23]. In contrast, off-aggregation marsh surface elevations were lowest at creekheads (+0.71±0.06mASL), intermediate at 10m (+0.75±0.04mASL), and highest at 20m onto marsh platforms (+0.77±0.05mASL; Tukey HSD, $p<0.001$; **Fig. 2C**). Corresponding to this spatial variation in marsh elevation, rates of chalk dissolution—a time-integrated measure of water flow—were highest at lower elevation creekheads and decreased linearly with increasing elevation onto marsh platforms ($p<0.0001$; Adj. $R^2=0.35$, **Fig. 2D**). Thus, second-order geomorphic template features predictably structure water flow rates and may act to secondarily control the delivery of mussel larvae and planktonic food available to mussel aggregations across marsh landscapes.

Patterns in Mussel Recruitment

To test the hypothesis that marsh surface elevation and proximity to creekheads dictate mussel recruitment patterns, we scored mussel recruits on and off of existing mussel aggregations across the marsh landscape at the five Sapelo Island sites. While zero mussel recruits were observed off of mussel aggregations at all distances from creekheads (0 total recruits; N=240, 0.25m^2 quadrats), recruitment to existing mussel aggregations mirrored the spatial distribution of adult mussels (**Fig. S3**). At all sites and creek lengths, on-mound recruitment was highly variable (0.48±0.87 recruits per aggregation; mean±SD), but consistently decreased with distance onto marsh platforms (Distance: $F_{2,177}=12.0$; $p<0.0001$; **Fig. S4A**). Linear regression further revealed that recruitment increased linearly with aggregation size ($F_{1,25}=25.3$; $p<0.0001$; **Fig. S4B**). These results are supported by previous work quantifying mussel settlement patterns which found that mussel recruitment occurs in spatially distributed clumps of multiple juveniles which exhibit a strong settlement preference for existing aggregations of conspecifics [4,24,25].

To next test whether recruitment decreases with distance onto platforms as a result of decreasing aggregation sizes, we standardized recruitment by dividing the number of recruits by the number of adult mussels observed in each surveyed aggregation. Standardized recruitment rates were similar across sites and creek lengths, but were significantly lower at 20m than both 10m and 0m (Distance: $F_{2,177}=11.9$; $p<0.0001$; Tukey HSD, $p<0.001$; **Fig. S4C**). This decrease in recruitment rate per mussel with distance onto the marsh platform may be the result of shorter submergence times at higher elevations restricting the frequency or duration of opportunities for recruits to settle [26,27]. Alternatively, similar to other self-organized systems where spatial patterning is the result of long-distance competition and local scale facilitation[28,29], long-distance competition among aggregations for mussel larvae may operate across the geomorphic template, whereby larvae settle upon first contact with conspecifics near creekheads and become increasing depleted in the water column with distance from their point of entry [12,30]. These patterns in recruitment likely act to reinforce differences in mussel cover and aggregation size distribution amongst long and short creeks (i.e. large mounds get larger faster), and contribute to the decreases in mussel cover observed with distance from creekhead at all creeks (Graphical Abstract).

Patterns in Mussel Survival and Growth: Experimental Results

Mussel Survival

To test the hypothesis that the relative importance of facilitation, predation, and competition are not uniform across the marsh but instead vary predictably with geomorphic template features , we deployed a mussel tethering experiment. Mussels were individually tagged, measured for length, tethered and deployed on and off of existing mussel aggregations at the five Sapelo Island sites in one of three experimental treatments: predator exclusion cage, procedural cage-control, and open control. At each site, mussels were deployed at three distances from creekheads associated with one long and one short creek (*N*=1,440 individually tethered mussels). Classification tree analysis [34](**Fig. 3**) revealed a significant effect of experimental treatment, such that mussels deployed in predator exclusion cages (96% survivorship) were >2-times more likely to survive than mussels deployed in open controls or cage-control treatments (42% survivorship). Within treatments exposed to predation, we found that associational defenses are activated at a threshold aggregation size and dictate the predation regime a mussel is exposed to. Specifically, the number of mussels in the recipient mussel aggregation strongly influenced survivorship, such that mussels deployed in aggregations with >6 individuals (70% survivorship) were >3-times more likely to survive than mussels deployed on aggregations with ≤6 individuals (23% survivorship). Within aggregations above the size threshold of 6 individuals, survivorship was high for all intermediate and large mussels >4.9cm (82% survivorship). For small mussels (≤4.9cm) on aggregations, survivorship of those deployed >8.5cm from the nearest predatory mud crab burrow (58% survivorship) was ~4-times higher than survivorship of those deployed in closer proximity (≤8.5cm; 15% survivorship).

In contrast, when mussels were deployed off of aggregations or in aggregations with ≤6 mussels, intermediate and small mussels were highly likely to be consumed in all locations (8% survivorship). Meanwhile, survivorship of large mussels (>5.8cm) in this spatial context depended on creek length, such that mussels deployed on creeksheds associated with long creeks (49% survivorship) were twice as likely to survive as mussels deployed on short creeks (26% survivorship), potentially reflecting enhanced nekton predator access to creeksheds associated with short versus long creeks. Finally, within creeksheds associated with long creeks, off-mound large mussel survivorship was high (59% survivorship), unless the mussels were deployed at sites regularly accessed by raccoons (60% consumed), or deployed at high elevations (>0.76mASL) where desiccation stress was highest (77% desiccated). These results indicate that, while the first- and second-order geomorphic template features control the magnitude of larval delivery at both creekshed and landscape scales, they only minimally influence mussel patterning at the patch-scale. Instead, similar to other self-organized systems, the patch-scale distribution of mussels is largely driven by intraspecific facilitation in the form of associational defenses and physical stress amelioration that arises within aggregations of conspecifics [4,28](Graphical Abstract).

Mussel Growth

For mussels surviving the duration of the experiment, size-standardized growth rates were driven by site, distance from creekhead, and experimental treatment (Site: $F_{4,659} = 14.1$; $p<0.0001$; Distance: $F_{2,659} = 3.5$; $p=0.03$; Treatment: $F_{2,659} = 67.9$; $p<0.0001$; Tukey HSD, all $p<0.05$; **Fig. S4**). In agreement with earlier work [35], mussel growth was highest at the site positioned on the ocean-facing side of the barrier island where tidal exchange is higher [36] and marsh surface elevation is generally lower, intermediate at the three sites located on the lagoon side of the barrier island, and lowest at a relatively higher elevation inner lagoon site. Adult size distributions mirror these differences in growth rate across sites (**Fig. S3**), indicating that there is likely variability between creeksheds in phytoplankton food delivery and associated mussel growth rates. Further, at all sites, mussel growth was significantly higher closest to creekheads, and decreased with distance onto marsh platforms, suggesting a potential effect of long-distance competition for food resources operating at the creekshed scale (**Fig. S5**). Previous work has similarly suggested that intraspecific competition leads to depletion of food resources from the water column coincident with slower growth rates and higher mortality, with effects especially pronounced on smaller individuals [4]. Finally, mussels deployed in predator exclusion cages grew significantly faster than mussels deployed in controls or procedural cage controls, which did not differ ($p>0.76$).

Multi-Scale Effects of the Cordgrass-Mussel Facilitation Cascade on Ecosystem Function

Mussel aggregations have been experimentally and empirically shown to enhance patch-scale ecosystem functions including primary production of cordgrass, presence and abundance of mobile macroinvertebrates, and metrics of species diversity [6,7]. While mussel-derived enhancements to ecosystem function are significant at the patch-scale, it is unknown how these effects scale to larger landscapes and creeksheds given the patchy spatial coverage of the cordgrass-mussel facilitation cascade (**Fig. 4A**). To therefore test the hypothesis that mussel-derived enhancements in primary productivity are significant from patch to creekshed scales, we harvested aboveground cordgrass biomass across distances from creekheas of long/short creeks. At the patch ($0.11 m^2$ quadrat) scale, cordgrass biomass predictably followed patterns in mussel population metrics (**Fig. 4B,** see inset for model results here and below). Specifically, on-mound cordgrass biomass was highest at creekheads associated with long tidal creeks, and decreased with distance onto platforms associated with creeks of all lengths (Tukey HSD, $p<0.0025$). Off-mound cordgrass biomass was lower than on-mound biomass and was similar in all locations ($p>0.20$). Landscape mussel enhancements, i.e. the percent difference between a landscape with no mussel coverage (all off-mound biomass results) and a landscape (0m, 10m, and 20m transect areas) with natural mussel densities characteristic of the site, were averaged to calculate a measure of mussel-derived enhancement (%) at the creekshed scale. Mussel enhancement of creekshed-scale primary production was >17-times higher for creeksheds associated with long (12±2%) than short tidal creeks (0.7±0.2%; **Fig. 4C**).

To then test the hypothesis that mussel-derived enhancements in secondary productivity are significant from patch- to creekshed-scales, the five most common mobile macro-invertebrate consumer functional groups [6, 7, 37] were counted both on and off mussel aggregations at three distances from creekheads on one long and one short creek at each of five sites on Sapelo Island (**Fig. S6;** N=1,440 quadrats). Mirroring patterns in primary productivity, macroinvertebrate community biomass was higher on mussel aggregations and decreased with distance onto the marsh platform when associated with short tidal creeks in the region (**Fig. 4D**; Tukey HSD, $p<0.0025$). We then scaled these results to the creekshed, as above for primary production, and found that mussel-derived enhancements in secondary productivity increased with creek length and were on average ~4x higher when associated with long (17±3%) than short tidal creeks (4±2%; **Fig. 4E**).

Finally, to test the hypothesis that mussels drive significant community patterns across spatial scales, we calculated species richness and evenness in each quadrat where macroinvertebrates were surveyed (N=1,440 quadrats). Species richness and evenness were higher on than off mussel aggregations at the patch-scale (Tukey HSD, all $p<0.0025$) and both metrics increased with creek length (Richness: **Fig. 4F,G**; Evenness: **Fig. H,I**). At the creekshed scale, mussel-derived enhancements in species richness and evenness were on average ~8-10x higher when associated with long than short tidal creeks (Richness: 8±1% vs 1±0.2%; Evenness: 20±5% vs 2±0.5%, respectively). These results suggest that first-order geomorphic template features, such as creek length, can serve as valuable predictors of the locations and magnitude of the ecosystem function benefits of this regionally prevalent facilitation cascade.

DISCUSSION

In coupling regional quantification of coastal geomorphic templates and invertebrate population sizes with a predator exclusion field experiment, this study exposes simple rules governing the proliferation and spatial patterning of a regionally-abundant facilitation cascade. At the creekshed scale, salt marsh tidal creek length and cross-sectional area exert primary control over the across- and among-marsh variation in facilitation cascade strength, such that larger mussel populations establish and higher ecosystem functionality is supported near longer, deeper creeks that convey larger volumes of water. Within the marsh landscape scale, mussel population and aggregation size consistently decrease with distance onto the marsh platform of creeksheds associated with all tidal creeks, reflecting gradients in marsh platform elevation and time-integrated water flow. Within these governing population dynamics set by the geomorphic template, patch-scale biotic interactions, especially associational defenses, mediate individual mussel survivorship (**Fig. 3**). Although the mussel populations that arise via these hierarchical processes cover <1-5% of total marsh creekshed area, they increase creekshed-scale primary production, macroinvertebrate community biomass, and community metrics including species richness and evenness by up to 20%, 35%, 12%, and 39%, respectively, where the underlying geomorphology sustains larger populations of this secondary foundation species (**Fig. 4**). Together, these results highlight that simple, hierarchical rules defined by both geomorphic, physical drivers and biological interactions can be used to predict hotspots of this secondary foundation species and resulting enhancements in ecosystem function. We propose that similar mechanisms likely control the self-organization and strength of facilitation cascades across the many systems characterized by heterogeneous geomorphic templates, and should be widely utilized to generate informed spatial predictions of ecosystem function hotspots and areas of high conservation priority.

These results also inform the restoration and conservation of vegetated coastal ecosystems. Restoration efforts focused on cultivating foundation species have been used in many ecosystems [47-49], but are often costly and exhibit low success rates [50]. Further, there is commonly a disparity between the superficial recovery of the primary habitat-forming foundation species and the recovery of ecosystem functions [51]. Therefore, recent work has suggested that the layering of foundation species may be essential to restore both ecosystem structure and function, with both conceptual papers [48,52] and restoration-focused experimental studies in salt marshes [53] and high-elevation Mediterranean forests [54] arguing for the incorporation of these ideas into general ecological theory and restoration design. However, the success of restoration based on foundation species layering will require that secondary foundation species are deployed in areas where their survivorship, growth, and recruitment are high enough to support self-sustaining populations that promote ecosystem functions at the highest possible magnitudes. Therefore, understanding the hierarchy of drivers controlling the establishment and proliferation of these organisms will be critical in order for such restoration efforts to be successful over time.

Towards this goal of applying our results and strategies to future restoration and management efforts, we suggest that heterogeneous geomorphologies define the strength of scale-dependent feedbacks, and the scales over which they operate, in systems beyond southeastern US salt marshes [55]. While the identity of the geomorphic features exerting control over secondary foundation species' distributions will differ among systems, we hypothesize that the features of greatest importance will consistently be both those that control the spatial and temporal fluxes in larvae/propagules, as well as those that structure the stress gradients most limiting to the foundation species. In many coastal ecosystems, both delivery of larvae/propagules and the stressors that subsequently control their survivorship and growth are often tightly coupled to the hydrological regime [e.g. 56-58]. As a result, the establishment and proliferation of secondary foundation species within mangrove forests, rocky shores, intertidal mudflats, seagrass meadows and other coastal systems may be similarly controlled by exposure to tidal flows and underlying elevational gradients, given that these features are key modulators of propagule delivery and often define both predation and desiccation stress gradients [59-62]. However, whether there are well-defined conduits for tidal flow, such as tidal creeks in many coastal wetlands and tidal inlets in coastal bays, or whether the fluxes of propagules/larvae and planktonic food transported in water are more diffusely distributed across a landscape, as may occur in intertidal mudflats or rocky shores, will likely dictate whether secondary foundation species, and the hotspots of ecosystem function they support, are concentrated around water delivery features or arranged in elevational bands reflecting stress gradients across intertidal landscapes, respectively.

As these applications of our major findings to other coastal systems have yet to be tested, it is clear that additional studies that quantify the relative importance of geomorphic and biological drivers across spatial scales and a deep natural history understanding of the system of interest to identify the critical factors controlling the self-organization of facilitation cascades are needed. This process of developing a more holistic understanding of how populations and communities are deterministically structured across spatial scales is an important endeavor, especially in the Anthropocene [64]. This is because humans are pervasively altering species composition—via e.g. agriculture and aquaculture, species' introductions, and overexploitation [65-67]—and manipulating ecosystem geomorphology through actions such as channel dredging, river damming, land clearing, sediment infilling, shoreline hardening, and urbanization [68,69]. Excavation of drainage ditches in tidal and freshwater marshes, for example, alters water flow regimes, shifts plant growth strategies and/or species composition, increases edge exposure to physical and biological stressors, and lowers the water table—effects which likely to alter the magnitude and spatial distribution of fluxes of larvae, food, and stressors across coastal landscapes [70,71]. Along more heavily developed coastlines, shoreline hardening, channelization and dredging are altering sediment transport processes and shifting wave energy down shore, causing cascading changes to both the identity and distribution of benthic and shoreline habitats [72,73]. Changes to sediment budgets, whether through shoreline modifications, land clearance, urbanization, or river damming, can also elicit reverberating effects on ecosystems, including but not limited to the infilling of marsh habitats, reduction of dissolved oxygen concentrations, prevention of emergent plant germination and/or enhanced faunal mortality, increased turbidity, and associated decreases in primary productivity [68,74]. Together, this growing body of research demonstrating the pervasiveness with which humans are modifying ecogeomorphic feedbacks, in combination with this study quantifying the importance of such feedbacks to facilitation cascade distribution and ecological importance, highlight the intrinsic value of identifying the hierarchical rules governing community organization for informing the design of ecosystem management and restoration efforts. Finally, as climate change is altering physical stress dynamics and species' range distributions [75,76], management and restoration efforts will be challenged to predict and prepare for how climate change is reshuffling the hierarchical rules that once defined scale-dependent feedbacks and the resulting organization of ecological communities. Ultimately, to accurately predict directionality of climate change and other anthropogenic effects on ecosystem function and proactively establish and protect high priority areas for biodiversity conservation and ecosystem service provisioning, a more nuanced understanding of pattern formation of foundation species and the facilitation cascades they support is required.

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AUTHOR CONTRIBUTIONS

S.C. designed the experiment, conducted the field work, analyzed the data, and wrote the manuscript. All authors revised the manuscript.

DECLARATION OF INTERESTS

The authors have no competing interests to declare**.**

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