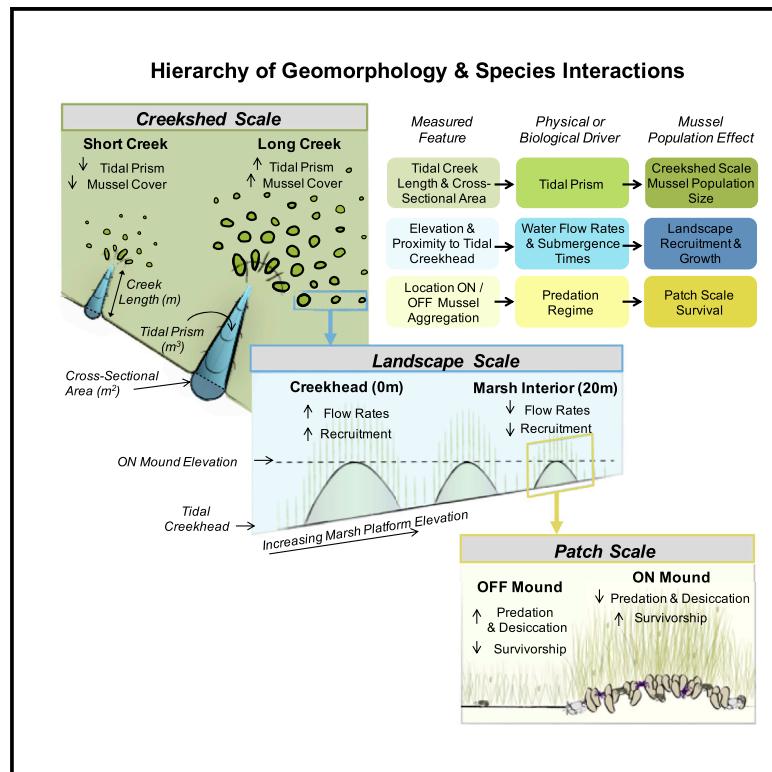


Geomorphology and Species Interactions Control Facilitation Cascades in a Salt Marsh Ecosystem

Graphical Abstract



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In Brief

Facilitation cascades widely enhance ecosystem function, but drivers of their spatially inconsistent patterning are unclear. Crotty and Angelini therefore elucidate the geomorphological, physical, and biological drivers that predictably control the presence and magnitude of the facilitation cascade between salt marsh cordgrass and ribbed mussels.

Highlights

- Tidal prism controls creekshed density of cordgrass-mussel facilitation cascade
- Elevation and creek proximity drive mussel recruitment and growth across landscapes
- Associational defenses control survivorship and aggregative behavior at patch scale
- Geomorphology can be used to predict population patterns and ecosystem function



Geomorphology and Species Interactions Control Facilitation Cascades in a Salt Marsh Ecosystem

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<https://doi.org/10.1016/j.cub.2020.02.031>

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 [1]. 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 [2], the mechanisms governing their spatial distribution are often challenging to discern given that they operate across multiple spatial and temporal scales [1, 3]. 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. 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.

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 hotspots of ecosystem function along the Atlantic coast of North America [2, 4–9]. Despite nuanced understanding of the population processes and ecosystem function effects of this secondary foundation species, why mussels vary in cover by orders of magnitude within and across marsh platforms in the region remains unexplored [4, 7, 9, 10]. Given the importance of mussel-derived ecosystem function hotspots to overall marsh multifunctionality [2, 9], we conducted a survey of creeksheds associated with short and long creeks (i.e., 50–75 m and 125–250 m from the creek mouth to creekhead, respectively) from northern Florida to central South Carolina (Figure 1A) with the goal of characterizing patterns in mussel abundance and distribution within and across salt marshes. Survey results revealed 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 size than creeksheds associated with shorter tidal creeks. All four of these mussel population metrics were highest at creekheads (0 m), where tidal water floods onto and drains off the marsh platform (Figure 1B), intermediate at 10 m, and lowest at 20 m onto marsh platforms (Figure S1; see figure insets for model results here and below). Further, at all three distances from the tidal creekhead, mussel population size increased with tidal creek length (Figure 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 across creeksheds (i.e., associated with long versus short creeks; 100 s–1,000 s of m²), 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 [11–14], or the volume of water conveyed by a creek per tidal cycle, to characterize the “first-order” features of the geomorphic template. Tidal prism controls flood versus ebb dominance and sediment import and export regimes; as a result, tidal prism is strongly related to the influx of both food and larvae that is conveyed by the tide over the marsh platform [15]. In agreement with morphology literature [11–14], we found that creek cross-sectional area increased as a linear function of creek length



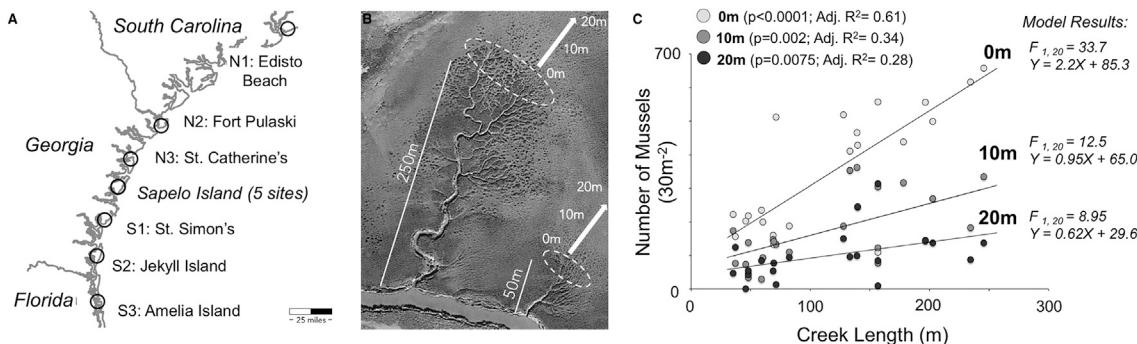


Figure 1. Regional Patterns in Mussel Cover

(A) Regional surveys were conducted at 11 sites, ranging from Edisto Beach, South Carolina to Amelia Island, Florida.

(B) Within each marsh, creeksheds associated with long and short tidal creeks were selected based on length and complexity. Mussel population metrics were quantified in transects perpendicular to the tidal creek at three locations on the marsh platform: the creekhead (dotted white oval; hereafter 0 m); 10 m onto the marsh platform (hereafter 10 m); and 20 m onto the marsh platform (hereafter 20 m).

(C) At all distances from creekheads, mussel abundance increased with tidal creek length. Results revealed that mussel population sizes are consistently higher closer to tidal creekheads (0 m; light gray circles) and decrease with distance onto marsh platforms (10 m and 20 m; intermediate gray and black, respectively). All model results are presented inset.

See also [Figure S1](#).

($p < 0.0001$; adj. $R^2 = 0.83$; [Figure 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. $R^2 = 0.73$; [Figure 2B](#)). Thus, these first-order features are highly correlated and can be used to predict mussel abundance and distribution patterns across marsh creeksheds.

Landscape Scale: Marsh Surface Elevation and Proximity to Tidal Creekheads

We next used marsh surface elevation and proximity to creekheads to characterize “second-order” features of the geomorphic template (10 s–100 s 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 ([Figure 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 the three distances from creekheads associated with both long and short tidal creeks ($n = 5$ measurements per unique combination of area type, distance, creek length, and site).

Mussel aggregation elevation was similar in all locations ($+0.84 \pm 0.06$ m above sea level [ASL]; all mean \pm SD; $p > 0.25$), indicating a potential optimal height or “ceiling” for mussel growth, a phenomenon shared with intertidal oysters [[16](#)]. In contrast, off-aggregation marsh surface elevations were lowest at creekheads ($+0.71 \pm 0.06$ m ASL), intermediate at 10 m ($+0.75 \pm 0.04$ m ASL), and highest at 20 m onto marsh platforms ($+0.77 \pm 0.05$ m ASL; Tukey’s Honest Significant Difference (HSD) test, $p < 0.001$; [Figure 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. $R^2 = 0.35$; [Figure 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 aggregations across the marsh landscape at the five Sapelo Island sites. Zero mussel recruits were observed off mussel aggregations at all distances from creekheads (0 total recruits; $n = 240$, 0.25-m^2 quadrats). At all sites and creek lengths, on-mound recruitment was highly variable (0.48 ± 0.87 recruits per aggregation; mean \pm SD) but consistently decreased with distance onto marsh platforms (distance: $F_{2,177} = 12.0$; $p < 0.0001$; [Figure S3A](#)). Linear regression further revealed that recruitment increased linearly with aggregation size ($F_{1,25} = 25.3$; $p < 0.0001$; [Figure S3B](#)). 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 [[7, 17, 18](#)].

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 20 m than both 10 m and 0 m (distance: $F_{2,177} = 11.9$; $p < 0.0001$; Tukey HSD; $p < 0.001$; [Figure S3C](#)). 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 [[19, 20](#)]. Alternatively, similar to other

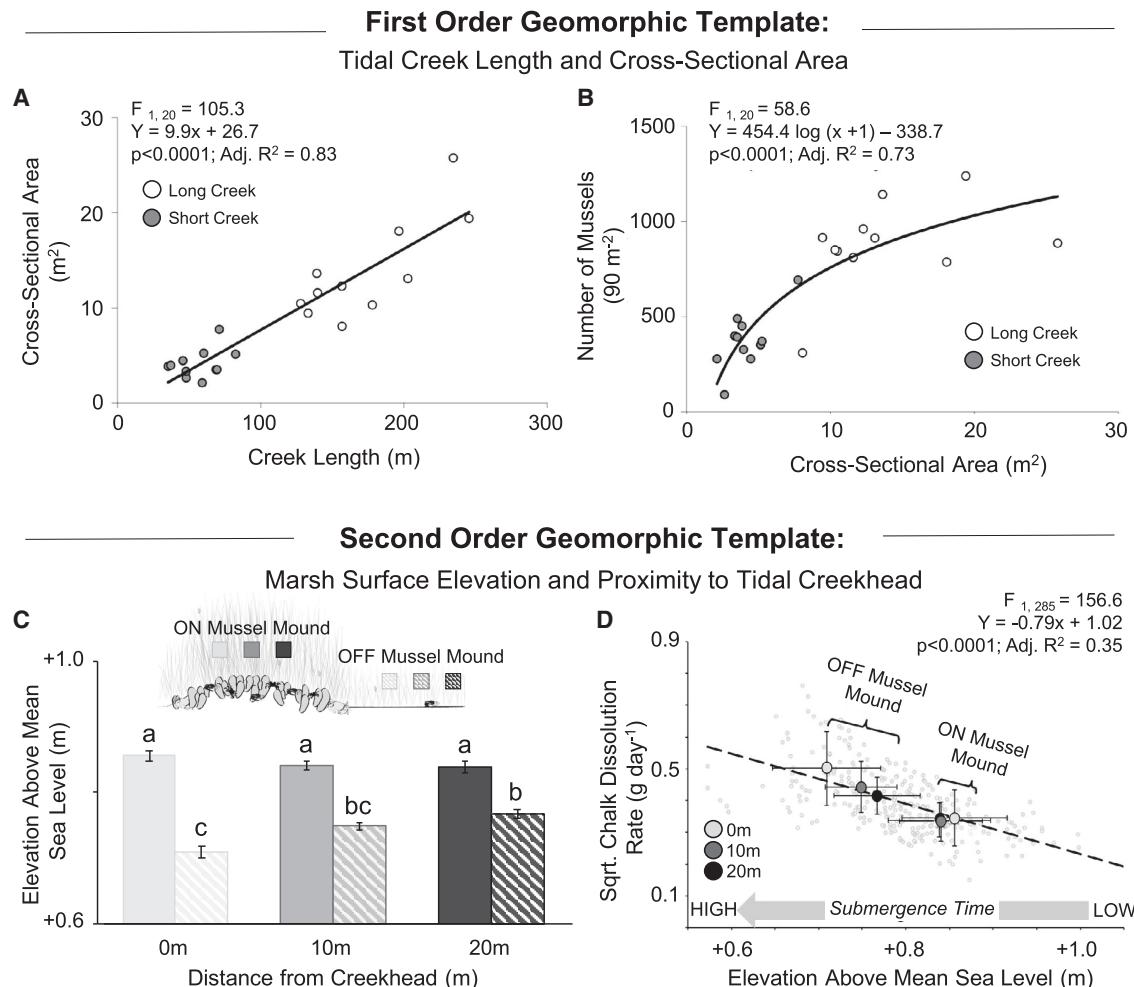


Figure 2. Quantifying the Geomorphic Template

(A and B) First-order geomorphic template feature, tidal creek cross-sectional area, increased linearly with tidal creek length (A), although mussel population sizes at the platform scale (90 m^2) increased as a log function of cross-sectional area (B). Individual data points from creekheads associated with long and short tidal creeks are presented as white and gray circles, respectively, and best-fitting model parameters are presented inset.

(C) Second-order geomorphic template feature, marsh surface elevation, increased with distance from creekhead when assessed on marsh platforms (i.e., off of existing mussel aggregations; $p < 0.001$) but remained at higher, more consistent elevations atop mussel aggregations. Data from 0-m, 10-m, and 20-m locations are presented in light, intermediate, and dark gray, respectively, with all on-mound results depicted by solid colored bars and off-mound results presented in hatch-patterned bars (all mean \pm SE).

(D) Water flow rates, as measured by magnesium calcite chalk blocks, decreased with increasing elevations onto marsh platforms and on mussel aggregations. All raw data are presented in panel background (white circles), although mean values \pm SD on and off existing mussel mounds are presented at creekheads (0 m, light gray), 10 m (intermediate gray), and 20 m (dark gray) onto marsh platforms. Best-fitting model parameters are presented inset.

See also Figures S2, S3, and S4.

self-organized systems where spatial patterning is the result of long-distance competition and local-scale facilitation [21, 22], 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 increasingly depleted in the water column with distance from their point of entry [23, 24]. These patterns in recruitment likely act to reinforce differences in mussel cover and aggregation size distribution among 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.

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 features of the geomorphic template, we deployed a predator exclusion 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 the three

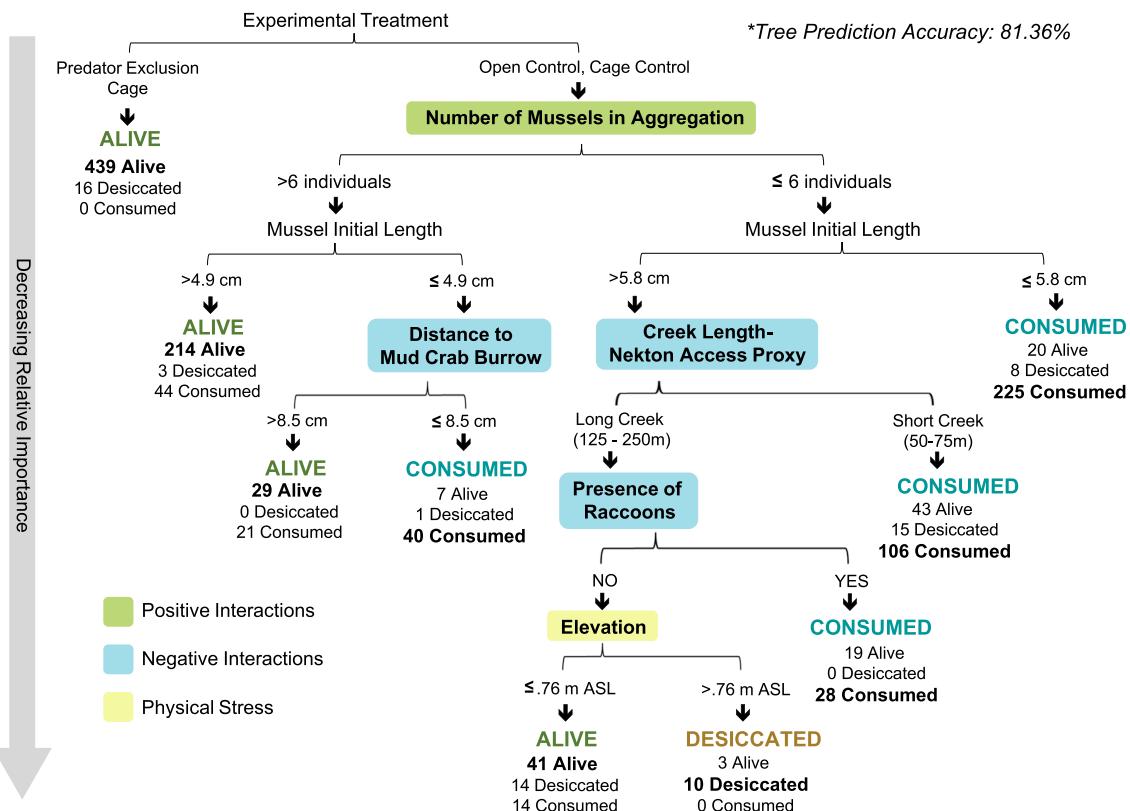
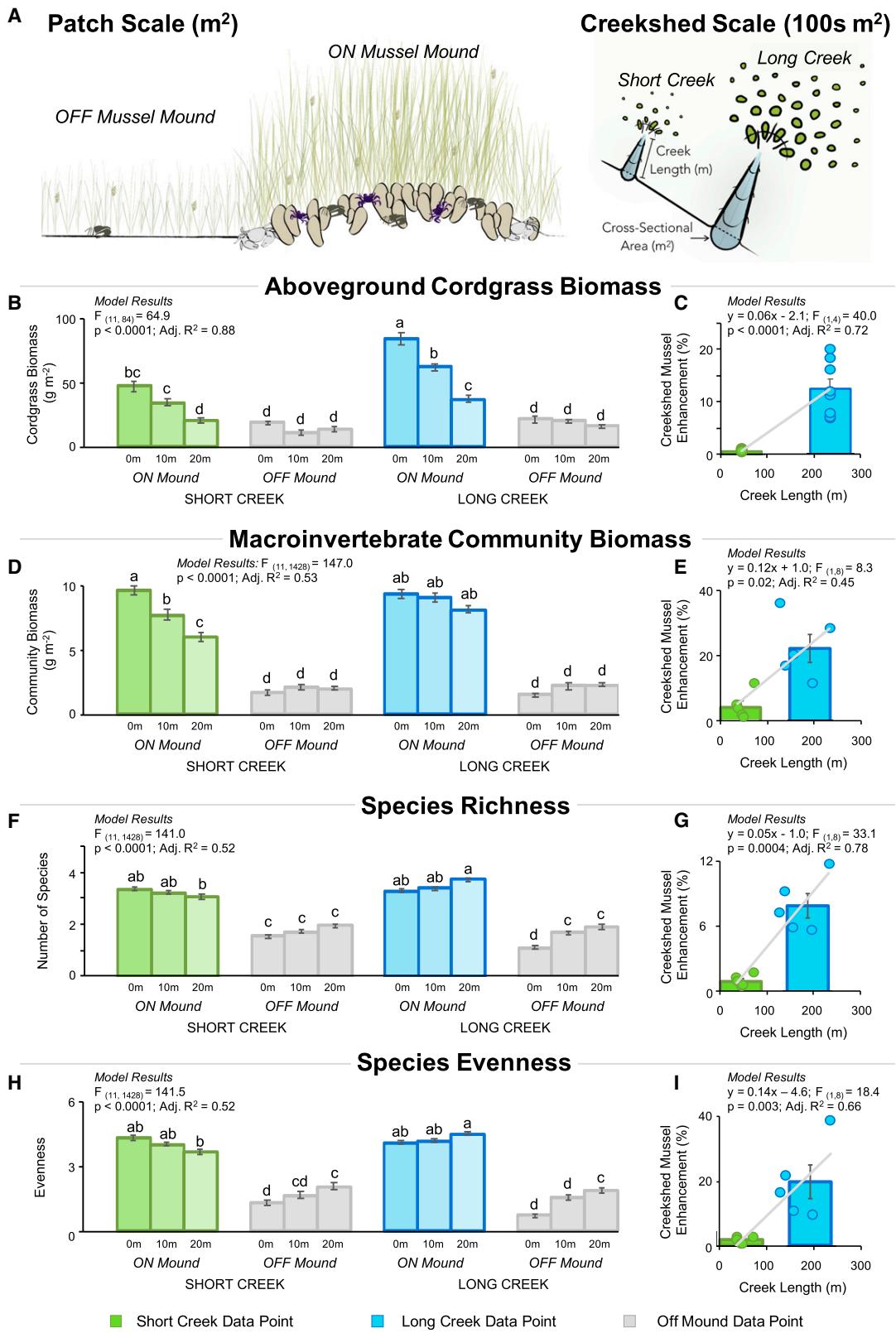


Figure 3. Mussel Survivorship

Classification tree analysis (prediction accuracy 81.36%) revealed significant hierarchical effects of experimental treatment (i.e., total predator exclusion), intraspecific facilitation (i.e., number of mussels in aggregation), mussel initial length, predation (i.e., resident, nekton, and terrestrial predation proxies), and physical stress (i.e., elevation and desiccation-related mortality). Model parameters signifying positive intraspecific interactions are highlighted in green, parameters of negative interspecific interactions (including resident marsh, nekton, and raccoon predators) are highlighted in blue, and parameters controlling physical stress (such as exposure to heat and desiccation-related stress) are highlighted in yellow. All total counts are reported below mussel outcomes, with the dominant result highlighted in bolded font. See also Figure S4.

distances from creekheads associated with one long and one short creek of similar complexity ($n = 1,440$ individually tethered mussels). Classification tree analysis [25] (Figure 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 on larger aggregations with >6 individuals (70% survivorship) were >3 times more likely to survive than mussels deployed on smaller aggregations with ≤ 6 individuals (23% survivorship). Within mussel aggregations above the size threshold of 6 individuals, survivorship was high for all intermediate and large mussels >4.9 cm (82% survivorship). For small mussels (≤ 4.9 cm) on aggregations, survivorship of those deployed >8.5 cm from the nearest predatory mud crab burrow (58% survivorship) was ~4 times higher than survivorship of those deployed in closer proximity (≤ 8.5 cm; 15% survivorship). In contrast, when mussels were deployed off

aggregations or in aggregations with ≤ 6 individuals, intermediate and small mussels were highly likely to be consumed in all locations (8% survivorship). Meanwhile, survivorship of large mussels (>5.8 cm) in this spatial context depended on creek length, such that mussels deployed on creekheads 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 creekheads associated with short versus long creeks. Finally, within creekheads 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 (>0.76 m ASL), where desiccation stress was highest (77% desiccated). These results indicate that, although 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 [7, 21].



(legend on next page)

Mussel Growth

For mussels surviving the duration of the experiment, size-standardized growth rates were driven by site, distance from creek-head, 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 $p < 0.05$; **Figure S4**). In agreement with earlier work [26], mussel growth was highest at the site positioned on the ocean-facing side of the barrier island where tidal exchange is higher [27] 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, 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 (**Figure S4**). 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 [7]. 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 [2, 9]. Although 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 (**Figure 4A**). To therefore test the hypothesis that mussel-derived enhancements in primary productivity are significant from patch to creekshed scales, we harvested above-ground cordgrass biomass across all aforementioned habitat types. At the patch (0.11-m^2 quadrat) scale, cordgrass biomass predictably followed patterns in mussel population metrics (**Figure 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 (0 m, 10 m, and 20 m transect areas) with natural densities of mussel aggregations characteristic of the site, were averaged to calculate a measure of mussel-derived enhancement (%) at the creekshed scale. Enhancements in primary production at the creekshed scale were >17 times higher on creeksheds associated with long ($12\% \pm 2\%$) than short tidal creeks ($0.7\% \pm 0.2\%$; **Figure 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 [2, 9, 28] were counted non-destructively 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 ($N = 1,440$ 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 (**Figure 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 $\sim 4\times$ higher when associated with long ($17\% \pm 3\%$) than short tidal creeks ($4\% \pm 2\%$; **Figure 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 tidal creek length (richness: **Figures 4F** and **4G**; evenness: **Figures 4H** and **4I**). At the creekshed scale, mussel-derived enhancements in species richness and evenness were on average $\sim 8\text{--}10\times$ higher when associated with long than short creeks (richness: $8\% \pm 1\%$ versus $1\% \pm 0.2\%$; evenness: $20\% \pm 5\%$ versus $2\% \pm 0.5\%$, 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

Figure 4. Multi-scale Effects of Cordgrass-Mussel Facilitation Cascade on Ecosystem Function

(A) Patch results in each case are scaled to the creekshed scale based on average areal coverage of mussel populations across marsh landscapes. (B–I) Aboveground cordgrass biomass (B and C), macroinvertebrate community biomass (D and E), species richness (F and G), and evenness (H and I) are each presented. Raw patch scale results from 0.11-m^2 quadrats (all mean \pm SE; B, D, F, and H) are presented for each response variable both on (green and blue bars) and off (gray bars) of existing mussel aggregations at 0 m, 10 m, and 20 m from tidal creekheads and associated with both short (green coloring) and long (blue coloring) tidal creeks. Significant differences are denoted with letters. Linear regression further revealed a significant positive relationship between creek length (m) and creekshed scale mussel enhancements in each ecosystem function (C, E, G, and I). Individual data points are overlaid on bars (mean \pm SE) depicting average values for all short (green) and all long (blue) creeks combined. All model results are presented inset.

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 (Figure 3). Although the mussel populations that arise via these hierarchical processes cover <1%–5% of total creekshed area, we show that they disproportionately 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 (Figure 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 the resulting enhancements in ecosystem function across spatial scales. 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 importantly inform the restoration and conservation of vegetated coastal ecosystems. Restoration efforts utilizing foundation species have been widely deployed across ecosystems [29–31] but are often costly and exhibit low success rates [32]. Further, there is commonly a disparity between the superficial recovery of the primary habitat-forming foundation species and the recovery of ecosystem functions [33]. 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 [30, 34] and restoration-focused experimental studies in salt marshes [35] and high-elevation Mediterranean forests [36] 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 these restoration strategies to be successful over time.

Toward this goal of applying our results and strategies to future restoration and management efforts, we suggest that heterogeneous geomorphologies likely define the strength of scale-dependent feedbacks and the scales over which they operate in many other systems beyond southeastern US salt marshes [37]. Although 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 [38–40]. 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 planktonic larvae delivery and often define both predation and desiccation stress gradients [41–44]. 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 are arranged in predictable hotspots of ecosystem function 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 will be needed in concert with a deep natural history understanding of the system of interest to identify the critical factors controlling the self-organization of facilitation cascades and their consequential effects on ecosystem functionality. 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 [45]. This is because humans are pervasively altering species composition—via, e.g., agriculture and aquaculture, species' introductions, and overexploitation [46–48]—and manipulating ecosystem geomorphology through actions such as channel dredging, river damming, land clearing, sediment infilling, shoreline hardening, and urbanization [49, 50]. 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 alter the magnitude and spatial distribution of fluxes of larvae, food, and stressors across coastal landscapes [51, 52]. 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 [53, 54]. 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 [49, 55]. 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 [56, 57], 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.

STAR METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- **QUANTIFICATION AND STATISTICAL ANALYSIS**
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SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.cub.2020.02.031>.

ACKNOWLEDGMENTS

We thank A. Bersoza and T. Pettengill for assistance in the field and the University of Georgia Marine Institute for research facilities. This work was funded by the NSF CAREER (no. 1652628) and NSF EAGER (no. 1546638) awarded to C.A. and the NSF GRFP (nos. 1315138 and 1842473) awarded to S.M.C.

AUTHOR CONTRIBUTIONS

S.M.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 declare no competing interests.

Received: October 14, 2019

Revised: December 20, 2019

Accepted: February 12, 2020

Published: March 19, 2020

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Raw data	This paper	https://doi.org/10.6084/m9.figshare.7977497.v1
Software and Algorithms		
ARTool software	[58]	http://depts.washington.edu/acelab/proj/art/index.html
Stata SE 13.1	StataCorp 1985	https://www.stata.com/
R: A language and environment of statistical computing	R	https://www.r-project.org/
rpart, R version 3.1.0	[25]	http://CRAN.R-project.org/package&equals;rpart

LEAD CONTACT AND MATERIALS AVAILABILITY

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Sinéad M. Crotty (sinead.crotty@yale.edu). This study did not generate unique reagents.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Subject Details

Salt marsh smooth cordgrass (*Spartina alterniflora*) and suspension-feeding ribbed mussels (*Geukensia demissa*) commonly overlap along the Atlantic coast of North America, in locations ranging from the Gulf of St. Lawrence (Canada) to western Florida (USA) [2, 4–9]. Across their geographic range, the abundance, spatial distribution, and size structure of mussel populations are a complex product of interactions between recruitment and settlement processes, individual growth, and both biological (e.g., competition, predation) and physical factors (e.g., submergence time, larval delivery, desiccation stress) that vary across marsh elevations and habitat types [4, 7, 59–62]. Within the southeast US, tidal creeks incise into marsh platforms terminating at ‘creekheads’ and function as conduits of water flow into and out of the system as tides flood and ebb. On shallow sloping marsh platforms, mussels, which disperse via planktonic larvae, form aggregations on marsh platforms ranging in size from 1 to 200 individuals. Embedded in marsh mud and attached by byssal threads to both conspecifics and the stems and rhizomes of cordgrass, mussel distribution is thought to be the result of high rates of predation outside of established aggregations, intraspecific competition for filtrate food sources, and by larval recruitment controlling the influx of new individuals [7, 9, 23, 62].

Predator Exclusion Experiment

In May 2016, we collected mussels between 3 and 7cm in length from a common site on Sapelo Island, GA (31°23'46.9"N 81°17'10.6"W). Mussel length was measured using a digital caliper, and a unique numbered tag was attached to the umbo of each mussel with super glue. Following tagging, 8cm tethers made of 50-lb. fishing line were super glued to each tagged mussel and attached to 6-in. sod staples. Tethered mussels were then deployed in late May 2016 at the five experimental sites across Sapelo Island, GA. At each site, one long and one short creek were chosen based on length, complexity, and distance from other creeks. At each creek, we established experimental zones at 0 m, 10 m, and 20 m from creek heads. At each distance, mussels were deployed both on and off existing mussel aggregations in one of three experimental treatments: predator exclusion cages, procedural cage controls, and open controls ($n = 8$ replicates / treatment; 1,440 total mussels deployed). All deployed mussels were deployed > 1 m apart such that only one tethered mussel was deployed per aggregation. In locations where no mussel aggregations were available given low mussel coverage (e.g., 20 m onto marsh platform from short creek entry point), ‘on-mound’ mussels were deployed with two co-transplanted neighboring adult mussels, each measuring > 8 cm in length. These neighboring mussels were deployed to mimic the effects of having adult conspecifics in an aggregation. However, the tethered mussels deployed in this setting were not included in survivorship analysis (72 out of 1,440 mussels) so as to not underestimate the effect of established mound structures on tethered mussel outcomes, given the potential transplantation effects and lack of byssal thread attachments between the transplants and conspecifics that we deployed and the surrounding cordgrass.

Predator exclusion cages were constructed using two polypropylene baskets, each measuring 4.5in x 3.75in x 2.6in (LxWxD). Predator exclusion cages had holes (0.83in x 0.45in) large enough to allow water flow and colonization by smaller marsh invertebrates, such as juvenile fiddler crabs, but small enough to obstruct all predator access. The cage bottom was filled with marsh mud, one tagged mussel, and two neighbor mussels if deployed on a mound. Cage tops were attached with four cable zip ties, and the predator exclusion cage was deployed into a recipient hole, the size and depth of one cage bottom. Procedural cage controls

were the same as the predator exclusion cages, but had two sides and the top removed from the aboveground basket to allow predator access. Predator exclusion cages were designed to exclude resident, nekton, and terrestrial predators. Resident predators primarily include mud crabs (*Eurytium limosum* and *Panopeus obesus*), which have been shown to preferentially consume mussels ranging from 1-3cm in length, but rarely exceeding 3.5cm [59]. Nekton predators, in contrast, include a diversity of swimming crabs and fish that migrate into marshes to forage at higher tides [7]. Blue crabs (*Callinectes sapidus*), in particular, have been shown to be an important predator of mussel populations, as they have several techniques for opening mussel shells that are adapted for different size classes of prey. These decapod predators exhibit a positive linear relationship between their carapace width and the maximum mussel length that they are able to consume, with a maximum reported mussel prey size of 8cm in length [59]. Other prevalent nekton predators include red drum (*Sciaenops ocellatus*) and sheepshead (*Archosargus probatocephalus*), both of which are likely to forage on ribbed mussels and/or their associated assemblages of macroinvertebrates given their hardened pallets that are able to crush bivalve shells. We predicted that creek length would control nekton predator access, such that the relative importance of predation and facilitation would be higher in creeksheds associated with short tidal creeks than those associated with long tidal creeks. This prediction was based on the perception that nekton predators may forage more intensively in creeksheds associated with short creeks because they would have shorter distances to travel from the main channel to access the marsh platform and, thus, would spend more time foraging for invertebrate prey in this spatial context [61, 63-65]. Finally, terrestrial predators, such as shore birds and terrestrial mammals (e.g., raccoons, *Procyon lotor*), are known to consume mussels, although evidence for size preferences and relative community importance is lacking.

The coordinates and elevation of each tethered mussel were quantified using a Trimble R6 RTK GPS unit in June 2016 after the initial deployment. Tethered mussel survival was then scored at each site after 2, 4, 8, and 16 weeks. Mussel mortality was scored as desiccated if the mussel was open/dead, with no evidence of shell damage [66, 67]. Conversely, the mussel was scored as predated if the shell was broken into fragments. At a subset of creeks in close proximity to the terrestrial border, we found evidence of raccoon predation on mussel mounds containing tethered mussels (i.e., raccoon tracks on and around partially deconstructed and consumed aggregations, with crushed shells in the vicinity) during the week 4 data collection. We therefore recorded locations of clear raccoon activity and associated mussel predation for the two following monitoring dates (weeks 8 and 16).

In June 2016, to additionally quantify invertebrate community characteristics both on and off existing mussel aggregations, we placed a 33cm x 33cm quadrat centered on each tethered mussel and counted the total number of mussels, snails, juvenile and adult fiddler crab burrows, marsh crab burrows, and mud crab burrows occurring within the quadrat area [2, 9]. Periwinkle snail individuals were counted both on the cordgrass canopy and on the marsh surface. Juvenile and adult burrows of deposit-feeding fiddler crabs were counted separately given the functional disparity between these life stages and differences in burrow width and depth. Finally, counts of the predatory mud crab functional group's U-shaped burrows and the burrow complex openings for the omnivorous marsh crab were made in each quadrat. Counts were scaled by average number of individuals per burrow for each functional group derived from previous burrow excavations [9]. On mussel aggregations, we additionally scored all metrics on the entire mussel aggregation and recorded aggregation dimensions (LxWxH). To quantify proximity of each tagged mussel to resident predators, distance to nearest mud crab burrow was recorded. After 16 weeks in the field, all live mussels were harvested and returned to the laboratory where they were measured again for length (n = 828 surviving mussels). To size standardize mussel growth rates, we used the Von Bertalanffy growth curve [68] where growth rate declines with increasing mussel size, adapted for mark-recapture data:

$$k = (\ln((L_{t2} - L_{\infty}) / (-L_{\infty} + L_{t1}))) / (t_1 - t_2) \quad (\text{Equation 1})$$

where k is the growth constant (year⁻¹), L_{t1} is mussel shell length (mm) in May 2016, L_{t2} is mussel shell length (mm) in September 2016, L_{∞} is the maximum length mussels can attain in this system, $t_1 = 0$ and $t_2 = 0.30$ year (May to September 2016, 110 days). L_{∞} was set at 100 mm as this was the maximum mussel shell length found at the common source site where mussels were collected. Growth rates differed by experimental treatment. We expect this result occurred because predator exclusion cages provided more shade and relief from desiccation and solar stress than did procedural cage-controls, and may have additionally baffled water flow, thereby altering mussel feeding.

METHOD DETAILS

Regional Survey

To quantify regional patterns in mussel cover, we selected 11 salt marsh sites located between Edisto Beach, SC and Amelia Island, FL in May 2016 (Figure 1A). Five of these sites were distinct, non-contiguous marsh site located in the vicinity of Sapelo island (i.e., hundreds to thousands of meters apart). At each of the regional sites, we chose two creeks, one long (125-250 m) and one short (50-75 m). Creeks were standardized for complexity, with each having a sinuosity ratio between 1.1 and 1.3. To quantify mussel cover on marsh platforms with distance from creekheads, we established 30 m² transects (30 m x 1 m; LxW) perpendicular to the creekhead entry point onto the marsh platform (hereafter, 0 m), 10 m onto marsh platform (hereafter, 10 m), and 20 m onto marsh platform (hereafter, 20 m; n = 3 transects per creek; 66 total transects; Figure 1B). Within each transect, we counted all singleton mussels and aggregations, measured aggregation dimensions (LxWxH), and scored total number of mussels per aggregation. As variation in mussel population metrics within Sapelo Island marshes was equally as high as the variation among regional sites (Figure S2, all p > 0.05), we consider all sites to be distinct and independent in the analyses.

Creekshed Scale Geomorphic Template: Creek Length and Cross-Sectional Area

To quantify the creekshed scale features of the geomorphic template, we used a combination of GoogleEarth imagery and field measurements at the 11 regional salt marsh sites. First, we utilized the path measurement tool in GoogleEarth to quantify the length of each tidal creek (m) from the point of bifurcation from the main channel to the tidal creekhead. For the same tidal creeks, we measured inlet cross-sectional area in the field. Specifically, at the creek initiation point, or the point where the creek first bifurcates from the main channel, we measured creek width as distance between two levee crests, and depth as the distance between the bottom of the creek and the top of the levee. Creek cross-sectional area was calculated using the equation for half the area of an ellipse ($\Omega = \frac{1}{2} D [\frac{1}{2}W]$), where Ω is creek cross-sectional area (m^2), D is tidal creek depth (m), and W is tidal creek width (m).

Landscape Scale Geomorphic Template: Platform Elevation and Proximity to Creekheads

To quantify landscape scale features of the geomorphic template, we utilized the subset of five representative sites on Sapelo Island, GA for further analysis. Within these sites, at each long and short creek, we established monitoring locations at 3 distances from the creekheads (0 m, 10 m, and 20 m). At each of these locations, we measured marsh surface elevation with a Trimble R6 RTK GPS unit (2cm vertical accuracy) both on and off existing mussel aggregations (n = 5 measurements per unique combination of area type, distance, creek length, and site; n = 300 total measurements).

To next test the hypothesis that water flow rates predictably vary with gradients in elevation, we deployed pre-weighed and individually marked magnesium calcite chalk blocks in the same monitoring locations, both on and off of existing mussel aggregations. After 12 weeks in the field, chalk blocks were collected and reweighed in the lab. To calculate rates of chalk dissolution, as a proxy for relative time-integrated water flow [69], block final mass was subtracted from initial mass and divided by the number of days in the field.

Patterns in Mussel Recruitment

To quantify recruitment rates at each of the five Sapelo Island sites, we scored mussel recruits (≤ 20 mm in length) on and off of existing mussel aggregations across the marsh landscape in October 2016. To do so, we harvested 8 haphazardly-selected mussel mounds per distance (0 m, 10 m and 20 m) per creek, for a total of 240 mussel aggregations. Recruits were harvested in October 2016, as previous work demonstrated that the greatest biomass of mussel recruitment occurs in the months of September and October [4, 23]. All mussels, both new recruits and adults, were measured for length using a digital caliper. To quantify off-mound mussel recruitment, we harvested all mussels occurring with a 50cm x 50cm quadrat haphazardly placed in non-mound areas adjacent (~ 1 m away) to the aforementioned harvested mussel mounds (n = 240 total quadrats). We found zero recruits in these areas and we therefore only analyze patterns among recruitment in harvested mounds.

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

In late October 2016, to quantify primary productivity of the foundation species cordgrass on and off of mussel aggregations, we placed a 33cm x 33cm quadrat centered on control mussel locations from the predator exclusion experiment at one site ($31^{\circ}25'20.3''N$ $81^{\circ}17'30.7''W$; n = 96 total quadrats harvested). Since mussel effects on primary productivity are well documented [2, 9], we only harvested cordgrass at this one representative site to limit habitat destruction across all experimental sites. All cordgrass originating within the quadrat was harvested, and returned to the lab where it was cleaned and dried in an oven at $60^{\circ}C$ for 3 days, after which time it was weighed.

To quantify community biomass of mobile macroinvertebrate consumers, as a proxy for marsh secondary production, 30 individuals of a range of sizes reflecting the natural size distributions of each functional group were harvested from a common site and returned to the lab where non-shell tissues were dried at $60^{\circ}C$, and weighed [9]. The five functional groups scored were periwinkle snails (*Littorina irrorata*), deposit-feeding juvenile and adult fiddler crabs (*Uca pugnax*), omnivorous marsh crabs (*Sesarma reticulatum*), and predatory mud crabs (*Eurytium limosum* and *Panopeus obesus*). Since we sought to quantify mussel effects on associated community biomass, mussel biomass was not included in these secondary production calculations. Invertebrate community biomass was then calculated for each plot by multiplying summed invertebrate counts from quadrats (33cm x 33cm, conducted in June 2016; n = 1,440 quadrats) by biomass per individual of each functional group [9]. In each quadrat, species richness (S) was calculated as the number of functional groups present. Finally, species evenness was calculated as the Shannon diversity index (H) divided by the natural log of functional group richness (lnS) in each quadrat.

QUANTIFICATION AND STATISTICAL ANALYSIS

To quantify the regional patterns in mussel population metrics (number of mussels, areal coverage of mussel aggregations, and average and maximum mound size) we ran a linear regression analysis at each distance from creekhead (0 m, 10 m, and 20 m), using tidal creek length (m) as the independent variable and mussel population metrics as the response variables in each case (R v. 3.0.2). To next quantify the relationships between creekshed scale geomorphic template features and mussel cover at the platform scale, we fit null ($Y = a$), linear ($Y = a + bP$), and log [$Y = a + b \cdot \log(P + 1)$] relationships among creekshed variables (i.e., creek length and cross-sectional area) and between creekshed variables and mussel cover response variables (i.e., number of mussels per 90 m^2). We fit linear and non-linear models to first assess whether the predictor had an effect on the response variable, and if so, which model best characterized the relationship between the variables [9]. We then used a fully factorial four-way ANOVA with main factors

site, creek length, distance from creek head, and location on/off mound to assess how marsh surface elevation varies across the landscape geomorphic template. To then assess the relationship between marsh surface elevation and time integrated water flow rates, we first square root transformed chalk dissolution rate data to meet the assumptions of parametric statistics. We then again fit null ($Y = a$), linear ($Y = a + bP$), and log [$Y = a + b \cdot \log(P + 1)$] relationships between elevation and transformed water flow data. In each case, we selected the best-fitting model using Akaike's information criterion corrected for low sample size, AICc (AICmodavg package; R v. 3.0.2) [70, 71].

To quantify patterns in recruitment across marsh landscapes, we first calculated the recruitment rate per mussel in each harvested aggregation. Next, both raw and standardized recruitment rates were transformed to meet assumptions of parametric statistics using the align rank transform method [58] since the raw data was zero-inflated (as recruitment was highly spatially variable). Transformed data was then analyzed with fully-factorial three-way ANOVAs, with factors site, creek length, and distance from creekhead in Stata SE 13.1. All post hoc analyses were performed using Tukey HSD tests with Bonferroni corrected p values. To assess the relationship between aggregation size and recruitment, we then used a linear regression with aggregation size as the independent variable and number of recruits as the dependent variable.

To assess the relative roles of facilitation, predation, and competition, experimental mussel survivorship data was analyzed using a classification tree using rpart in R version 3.1.0. Models treated endpoint survivorship outcome (i.e., alive, consumed, or desiccated) as the response variable, and selected the following predictor variables as significant: 1) experimental treatment, 2) number of neighbor mussels, 3) tethered mussel initial length, 4) distance of tethered mussel from mud crab burrow, 5) creek length, 6) presence of raccoon predation, and 7) elevation. The following variables did not have a significant effect on survivorship results despite being included in the model: 1) distance from creekhead, 2) site, 3) number of mud crabs, and 4) number of marsh crabs. Over-fitted trees were pruned using k fold cross-validation [25]. Growth of surviving mussels was then analyzed with a five-way fully factorial ANOVA with main effects: site, creek length, distance from creekhead, experimental treatment, and location on/off mussel mounds (Stata SE 13.1). All post hoc analyses were performed using Tukey HSD tests with Bonferroni corrected p values.

Primary productivity of aboveground cordgrass biomass was analyzed using a three-way ANOVA, with main effects: creek length, distance from creek head, and location on/off mussel mounds. Macroinvertebrate community biomass, used as a proxy for secondary productivity, as well as species richness and evenness were analyzed using a four-way ANOVA with main effects (site, creek length, distance from creek head, and location on/off mound; Stata SE 13.1). All pairwise comparisons were completed using Tukey HSD post hoc tests with Bonferroni corrected P values. To next scale the patch results to the landscape (i.e., 30 m²), we calculated the percent difference between areas characterized by natural mussel densities and an area with cordgrass but devoid of mussel aggregations. To do this for primary and secondary productivity, as well as species richness and evenness, we used the following equation:

$$E_L = \left[\frac{(30 \times P_M \times B_M) + (30 \times P_O \times B_O)}{(30 \times B_O)} - 1 \right] \times 100 \quad (\text{Equation 2})$$

where E_L is the mussel-derived enhancement (%) at the landscape scale (30 m²) and P_M and P_O are the proportion of the transect area covered by mussel aggregations (M), and by off-mound areas (O). To then scale these landscape results up to the marsh creekshed scale (90 m²), we calculated the mean percent enhancements in primary and secondary production across 0 m, 10 m, and 20 m separately for each creekshed. Finally, we ran linear regression analyses using creek length as the predictor variable and creekshed mussel enhancement (%) as the response variable for each of the ecosystem function variables (i.e., primary production, secondary production, species richness, and evenness).

DATA AND CODE AVAILABILITY

All data are archived and freely available through the Figshare online data portal (<https://doi.org/10.6084/m9.figshare.7977497.v1>). All code can be obtained from the Lead Contact upon request.