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ARTICLE

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Asymmetrical facilitation ameliorates environmental conditions through positive feedback in partner traits

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Abstract

Positive species interactions, including facilitation and mutualism, are important in shaping ecological communities through the amelioration of stressful conditions. Facilitation results from traits (e.g., plant growth form) that create benefits for one or more interacting partners. The outcomes of facilitation depend on positive or negative feedbacks between partners, which can determine the stability of interactions over time. We can expand our understanding of these dynamics through a bidirectional approach that identifies the specific mechanisms creating benefits for the associated species, the traits related to those benefits, and the potential for feedbacks to affect amelioration by modifying traits. We characterized an association between the salt marsh plant *Limonium carolinianum* and mussel *Geukensia* sp. in the northern Gulf of Mexico. We used a field survey and three field experiments to establish the bidirectional effects of the association, the underlying mechanisms, and the relevant traits for each partner species. Mussels benefitted from *Limonium* canopies, which ameliorated high temperatures and predation for mussels, increasing survival and recruitment. These positive effects were particularly evident under larger canopies. Mussels enriched sediment organic matter and thus over time are expected to alleviate nutrient limitation for *Limonium*. Changes in functional traits of both species contributed to facilitation. *Limonium* both benefitted from and promoted higher mussel density, and mussels both allowed *Limonium* to grow or retain more leaves and benefitted from stress amelioration under larger canopies. The benefits of the association appear asymmetrical: mussels consistently benefitted in both experiments, but we found only modest positive effects on *Limonium*, and only over the longer term. These differences likely reflect variation in the seasonality and/or timescale of the facilitative mechanisms. The bidirectional and mechanistic design of our study revealed positive feedbacks that reinforced the traits conferring benefits to each partner, potentially stabilizing this positive interaction. Understanding how feedbacks influence the outcomes of facilitation is increasingly important as anthropogenic stressors increase globally.

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KEYWORDS
environmental stress, facilitation, feedback, functional traits, *Geukensia*, habitat amelioration, *Limonium carolinianum*, reciprocal effects, refuge, salt marsh, temperature stress

INTRODUCTION

Positive species interactions such as mutualism and facilitation influence community structure and ecosystem processes (Callaway, 2007; Gribben et al., 2019; Hay et al., 2004) and may be key to maintaining resilience under stressful conditions with continued climate change (Angelini et al., 2016; Bulleri et al., 2018; Jurgens et al., 2022). Facilitation is a facultative species interaction with a positive outcome for at least one partner based on amelioration of physically or biologically stressful conditions (Stachowicz, 2001). Facilitation is generally expected to be more important under stressful environmental conditions (Bertness, 1985; Bertness & Shumway, 1993; Menge & Sutherland, 1987), as formalized in the Stress Gradient Hypothesis and supported by subsequent research (Bertness & Callaway, 1994; He et al., 2013).

Positive interactions depend on the traits of interactors, as species with different traits can create different types of benefits (Altieri et al., 2007; Stachowicz & Whitlatch, 2005) and vary in their degree of cooperation versus exploitation (Wulff, 2008). Facilitation often depends on traits that create mechanisms of habitat amelioration, such as density or size of plant structures (Bishop et al., 2013; Irving & Bertness, 2009; Schöb et al., 2013). The less stressful microhabitats created by facilitators can also change the functional traits of associated species (García-Cervigón et al., 2015; Schöb et al., 2012). Traits that ameliorate stressors or affect limiting resources are key to facilitative interactions, and more studies are needed that test mechanisms to determine which specific traits create benefits (Bulleri, 2009; Gribben et al., 2019) and how feedbacks between interactors may influence ameliorating traits (Michalet et al., 2011).

Reciprocal effects between mutualistic or facilitative partners can be negative, neutral, or positive (Bronstein, 2001; Brooker et al., 2008). Positive reciprocal effects can stabilize an interaction over time, whereas negative feedbacks may lead to a breakdown of the interaction (Bronstein, 2009). Despite their importance, relatively few studies address these bidirectional effects (Bulleri, 2009; Schöb et al., 2014). Further, such reciprocal effects between interacting partners may influence the very traits that ameliorate stress for one another (Michalet et al., 2011), potentially determining which species or individuals ameliorate environmental conditions and which can benefit from this facilitation.

The bidirectional nature of facilitation may differ for interactions between functionally similar species and functionally different species (Bulleri, 2009). For example, outcomes of plant–plant facilitation often depend on a trade-off between stress amelioration and competition for common resources that can lead to negative feedbacks (Maestre et al., 2009). In contrast, species of different trophic levels are expected to have less overlap in resource use and therefore limited potential for competition, as well as different sensitivities to stressors, potentially increasing the likelihood of stress amelioration, even under extreme conditions (Bulleri, 2009). Such cross-trophic facilitation is common in marine ecosystems. For example, in the intertidal zone, marine vegetation can reduce temperature and desiccation stress for invertebrates (Dijkstra et al., 2011), provide refuge from predation (Peterson & Heck, 2001a), or both (He & Cui, 2015). In turn, invertebrates facilitate plant growth through excretion of nitrogenous waste and deposition of organic matter (Holdredge et al., 2010; Peterson & Heck, 2001b). Negative feedbacks can occur between species of different trophic levels due to competition for nonfood resources, such as attachment space (Connell, 1983; Tallis et al., 2009) and dissolved oxygen in seawater (Ferguson et al., 2013), or due to modification of a shared habitat by one species that makes it unsuitable for the other (Castorani et al., 2014). However, overall we expect more positive feedbacks between interacting species across trophic levels than within trophic levels.

Facilitation is a driving force in intertidal salt marsh ecosystems, which are characterized by strong physical stressors such as low nutrient levels, high salinity, and low sediment oxygen (Altieri & van de Koppel, 2013). One of the best documented facilitative interactions in this system involves the ribbed mussel *Geukensia* sp. (hereafter referred to as mussel), which benefits the dominant salt marsh plant *Spartina alterniflora*, with higher mussel densities leading to increased plant production (Bertness, 1984; Hughes et al., 2014) and plant resilience (Angelini et al., 2016; Hensel et al., 2021). Mussels deposit nutrient-rich organic matter from feces and pseudofeces at the sediment surface, where it can be an important source of nitrogen and phosphorous for plants (Newell, 2004). Mussels in turn benefit from the attachment sites provided by plant structures (Bertness & Grosholz, 1985) and reduced temperature stress from shading (Angelini et al., 2015). However, under some

conditions, *S. alterniflora* can also increase heat stress for mussels, potentially by baffling air flow with its upright stems (Jost & Helmuth, 2007).

Although the interaction between mussels and *S. atlerniflora* is well studied, we know little of mussel effects on or responses to other common marsh plants. Here, we examined an association between the salt marsh plant *Limonium carolinianum* (hereafter *Limonium*) and mussel using a bidirectional and mechanistic approach to identify potential feedbacks on partner traits. We documented the pattern of the association and manipulated *Limonium* and mussel co-occurrence and mussel density in field experiments to determine: (1) whether each species benefits from facilitation; (2) what mechanisms create benefits of the interaction; (3) what traits are involved in these mechanisms; and (4) whether the interaction may cause a positive or negative feedback on partner traits. We expected that the association may be based on mutual or commensal facilitation, given the probable low cost of the association for species with limited overlap in resource use and thus reduced potential for competition. We measured the effect of the interaction on potentially beneficial traits, including mussel aggregation and plant canopy characteristics, to determine how feedbacks may influence benefits to interacting species.

METHODS

Study system

We observed that mussels were closely associated with *Limonium* in salt marshes in the northern Gulf of Mexico in Florida. The marsh vegetation in this area is dominated by smooth cordgrass (*S. alterniflora*), which is intermixed with our focal species, *L. carolinianum*, and other plant species including pickleweed (*Salicornia virginica*) and needlerush (*Juncus roemerianus*). This area is characterized by mixed semidiurnal tides around St. Mark's National Wildlife Refuge and diurnal tides to the west in St. Joseph Bay (Kimbro, 2012). Mussels often occur in dense aggregations within and around the basal rosettes of *Limonium*, attached to the roots and stems of the plants (A. Moore, personal observation). Unlike the upright spikelet structure of *S. alterniflora*, *Limonium* has a basal rosette of leaves, which we expected to be effective in shading. *Limonium* also has woody stem and rhizome structures near the sediment surface, which may provide attachment substrate. We examined several potential mechanisms of facilitation, including (1) organic matter deposition by mussels improving nutrient conditions for *Limonium*, (2) shading by *Limonium* ameliorating temperature stress for mussels, (3) *Limonium* providing an attachment substrate for mussels, and (4) habitat structure created by *Limonium* reducing predation on mussels.

Field survey

We surveyed four field sites on the Gulf Coast of Florida, USA, where mussels and *Limonium* co-occur. We included two sites in St. Marks National Wildlife Refuge, Wakulla Beach (30°06′36.4″ N, 084°15′51.7″ W) and St. Mark's Lighthouse (30°04′24.4″ N, 84°10′42.6″ W), and two sites in St. Joseph Bay, SJB GD1 (29°41′04.4″, 085°20′24.4″) and SJB GD5 (29°41′00.8″, 085°21′08.3″). We surveyed within 0.25-m^2 plots at 10 randomly chosen points along two 25-m transects running parallel to the water within the mid-intertidal area where the species co-occur at each site. We estimated percent cover of *Limonium* and counted the number of mussels present within 0.25-m^2 gridded quadrats. We also collected one sediment core at 0–5 cm depth in the center of each quadrat for sediment organic matter (SOM) analysis, using a corer made from a 10-mL syringe with the top cut off.

We followed changes in plant size (number of leaves) and associated mussel abundance at a single site over time in 25 permanent plots with naturally occurring patches of both species within a plot of 0.125-m^2 area. In July 2013, we designated and marked 5 plots with mussels alone, 4 plots with *Limonium* alone, and 16 plots with the two species co-occurring at a range of mussel densities per 0.125-m^2 area plot (mussel densities groupings included low: mean = 10.2, range = 3–18; medium: mean = 38, range = 26–51; high: mean = 131.4, range = 63–180; $N = 5$–6 plots per density).

We analyzed the effects of field site and *Limonium* abundance on mussel densities from our field survey. We used analysis of covariance (ANCOVA) to test how mussel density varied by site with *Limonium* cover as a covariate, using the lm function in R. We then used regression to test the relationship between mussel density and *Limonium* cover across field sites that did not differ in mussel abundance. We included a quadratic term in models where it was significant (see *Results*). We used regression with the lm function to analyze the effect of plant size on mussel density and retention in naturally occurring *Limonium* patches.

Experiment 1: Partner presence/absence and mussel density manipulation

This experiment was conducted at Wakulla Beach, St. Marks National Wildlife Refuge, FL. Wakulla Beach

harbors high densities of mussels relative to other sites in the FL Gulf Coast region (Figure 1). We manipulated plant and mussel presence and mussel density in the field from July 2012 to August 2013. Treatments included: *Limonium* alone, mussels alone at three mussel densities (5, 20, or 50 individuals per plot); and *Limonium* with mussels together at three mussel densities (5, 20, or 50 individuals per plot). We also included a procedural control treatment consisting of unmanipulated plants with naturally occurring mussels. Unmanipulated treatments were selected to have mussel densities comparable to the three controlled density treatments (Appendix S1: Table S1) and were replicated in the same manner as the manipulated treatments. To create these experimental treatments, we collected naturally occurring *Limonium* plants in discrete patches of 0.02-m^2 area with naturally occurring mussels attached and haphazardly assigned them to treatments. We removed mussels from plants to create plant and mussel alone treatments and replanted mussels on plants to create the treatments with plants and mussels together. The unmanipulated controls were maintained and handled similarly to the manipulated treatments, except that the mussels were not removed. After the treatments were established and within 14 days of collection, patches were planted in the naturally occurring vegetation in our experimental plots. Because each plant/animal presence treatment including mussels is replicated at three mussel densities per block, we also included three replicates of the *Limonium* alone treatment in each block, so that each presence treatment would be represented equally. The experiment consisted of 6 blocks with 12 plots each (see diagram in Appendix S1: Figure S1). Plot locations were randomized within each block.

We examined the effect of our treatments on the survival, leaf retention/growth, and flowering of *Limonium*. At the beginning of the experiment (July 2012), we measured the number of *Limonium* leaves within each patch. We then determined *Limonium* survival and the number of flowering stems per plant in August 2012 and August 2013. At the end of the experiment (August 2013), we harvested the experimental plants nondestructively and again counted the number of leaves per plant.

We measured changes in the abundance of mussels in response to our experimental treatments. To measure recruitment, we placed one small mussel recruit collector made from plastic mesh pot scrubbers (SOS Tuffy Pads) in each plot to measure recruitment in experimental treatments (Rilov & Schiel, 2011). We cut ~6-cm lengths from pot scrubbers to create recruit collectors small enough to fit in our mussel patches and used plastic zip ties to fasten the collectors to 4-inch steel garden staples, which were secured in the sediment.

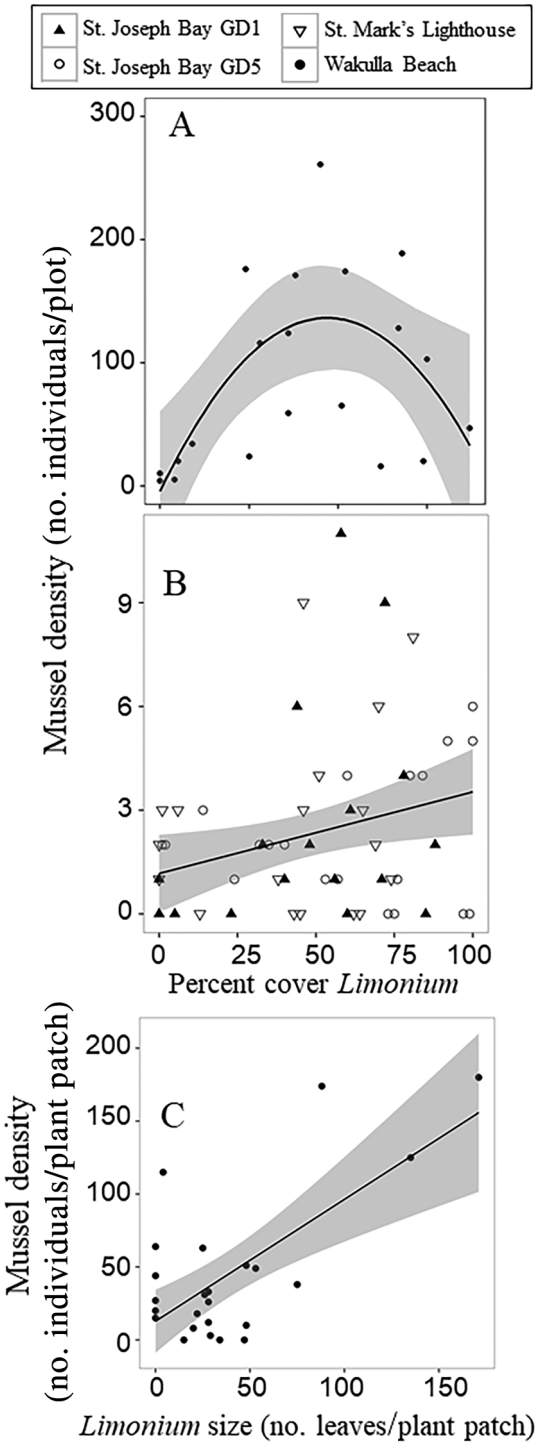


FIGURE 1 Relationship between *Limonium* percent cover and mussel density per plot sampled in scatterplots with fitted line and 95% CIs (gray shading) (A) at Wakulla beach, the field site with the highest mussel densities, and (B) the other three field sites: St. Joseph Bay GD1, St. Joseph Bay GD5, and St. Mark's Lighthouse. (C) Number of naturally occurring mussels versus number of *Limonium* leaves per plant patch in plots at Wakulla Beach. Note the different axes for panels.

In August 2012, there was a tropical storm that caused significant mussel mortality due to smothering of our plots by seagrass wrack, which we removed after the

storm had passed. We nondestructively counted plant presence and mussel density in the experimental plots soon after this disturbance to quantify plant survival and changes in mussel abundance in our treatments (Appendix S1: Table S2). At this time, we also collected sediment cores at 5-cm depth in each experimental plot for SOM analysis. We used organic matter content as a proxy for sediment nutrient input from mussel biodeposition, as has been shown for marsh cordgrass (Hughes et al., 2014). To determine SOM, we dried the sediment at 105°C for at least 3 h, combusted the sediment at 525°C for 3 h, and calculated percent mass lost.

We analyzed the effects of experimental treatments on all continuous metrics, including size, growth, and change in number, using linear mixed-effects models (LMMs) with experimental block as a random variable. We analyzed final plant size as number of leaves using initial number of leaves as a covariate to account for initial size. During Experiment 1, there was significant mussel mortality early in the experiment across all treatments (Appendix S1: Table S2), so we analyzed *Limonium* responses based on the presence and density of mussels immediately after this mortality event (August 2012). We also report analyses based on initial treatments (see *Results*) for comparison. We analyzed the effects of experimental treatments on survival of *Limonium* plants in Experiment 1 using generalized linear mixed-effects models (GLMMs) with a binomial distribution, including experimental block as a random variable. Counts of *Limonium* flowering stems were analyzed using GLMMs with a Poisson distribution. *p* values for GLMMs were determined using the Anova function in the car package in R, which uses type II Wald chi-square tests. We made multiple comparisons for mixed models with Tukey's honestly significant difference (HSD) tests, using the glht function in the multcomp package. We analyzed the proportion of initial mussels per plot remaining at the end of Experiment 1, which represents a combination of survival and recruitment, with initial mussel density as a covariate. We logit transformed the proportion of mussels remaining before analysis using the logit function in the car package. We used the mussels that settled in our recruitment collectors to estimate the maximum size for mussel recruits in Experiment 1, and then we counted all mussels less than or equal to that size in the collectors or the plot to estimate total recruitment.

Experiment 2: Partner presence/absence, plant structure, and nutrient manipulations

We used a second manipulative field experiment at the same site to test the predicted mechanisms underlying the *Limonium*–mussel facilitation: (1) mussels benefit *Limonium* through organic matter deposition that alleviates nutrient limitation; and (2) *Limonium* benefits mussels via habitat amelioration by the plant canopy and/or by providing a substrate for attachment to roots and woody shoots at the base of the plant. We included the following treatments ($N = 10$): intact *Limonium* alone; mussels alone; intact *Limonium* and mussels; *Limonium* belowground (roots and woody shoots) and mussels; artificial *Limonium* canopy and mussels; and intact *Limonium* with nutrient addition (see diagram in Appendix S1: Figure S2). We used a randomized blocked design with 10 blocks for a total of 60 plots in the experiment. Plots within blocks were separated by 1 m, with 2 m between blocks. All plots were parallel to the marsh edge at the same tidal elevation, within the mid-intertidal area where the species co-occur naturally. We added 24 mussels to each treatment with mussels, which was similar to the mean mussel abundance in patches of the same area from the previous field experiment. We also controlled mussel size distribution across plots to mimic that of naturally occurring mussel patches (Appendix S1: Table S3). We initiated the experiment in July 2014 and continued the treatments for seven weeks. Mussels that died within the first 24 h of the experiment, likely due to high temperatures during experiment setup, were replaced (123 out of the 960 total in the experiment).

To create the *Limonium* belowground treatment, we removed the leaves from the woody shoots and roots of the plants. The leaves did not regrow during the course of the experiment. We created the artificial plant canopy treatment using leaf mimics made from thin, flexible foam attached to metal garden staples using cable ties to create shading similar to leaves, without the mussel attachment substrate provided by Limonium root and shoot structure. The artificial canopy consisted of 3 bunches of 12 artificial leaves each. Each artificial leaf was approximately 8 cm long, equivalent to the average length of Limonium leaves. We created the nutrient addition treatment by adding the per plot equivalent of 100 g/m^2 pelletized fertilizer (Osmocote brand, 19, 6, 12, % NPK) to the elevated nutrient plots at the initiation of the experiment, as these levels have previously been shown to increase plant growth in salt marshes (Silliman & Zieman, 2001). We wrapped nutrient pellets in nylon fabric and added them to 15 mL plastic conical tubes drilled with 16 holes of 1.6-mm diameter, which we buried in the sediment, allowing for gradual release of nutrients over time (Silliman & Zieman, 2001). We placed empty tubes in plots without nutrients to account for any disturbance to the plots. To determine whether mussels benefit from temperature amelioration due to shading by plants, we created mussel-mimic loggers, by placing temperature loggers

(iButton, Maxim Integrated Products, Inc.) inside empty mussel shells filled with clear silicone caulking, to approximate temperature conditions as experienced by the organism (Helmuth & Hofmann, 2001; Jost & Helmuth, 2007). Mussel-mimic loggers were deployed across all treatments in a subset of blocks ($N = 8$–9 per treatment), partially buried at the sediment surface and attached to small metal posts with zip ties, such that the mimics were not directly touching the metal. We collected temperature data at 10-min intervals for 4 weeks. For each plot with a mussel-mimic temperature logger, we calculated the maximum temperature reached during each day and then calculated the average daily maximum for each plot across all days for which we collected data.

At the beginning and end of the experiment, we counted the number of *Limonium* leaves and measured leaf length, which we estimated from the base of the plant at three points across the canopy. At the end of the experiment, we measured and counted flowering stems produced during the experiment. We tagged all mussels in the experiment by writing labels in oil-based paint marker and then painted with clear permanent adhesive, so that we could follow individuals through time. At the beginning of the experiment, we measured shell length to ±0.01 mm using electronic calipers and controlled for size distribution across our plots (Appendix S1: Table S3); we then measured mussels again at the end of the experiment. We also measured the growth of mussels over the course of the experiment by filing a small (~1 mm) notch in the shells of 12 mussels per plot (2–4 per size class; Appendix S1: Table S3) and measuring shell length from apex to notch and from apex to growing edge at the experiment's end (Ekaratne & Crisp, 1982; McQuaid & Lindsay, 2000). At the end of the experiment, we removed all mussels and preserved them by freezing. We quantified the condition index of all mussels recovered from the experiment as: [dry tissue mass/(tot wet mass − shell mass)] × 1000, following previous work with ribbed mussels (Chintala et al., 2006; Crosby & Gale, 1990).

We analyzed the effects of experimental treatments on all continuous metrics, including growth and condition index, using LMMs with experimental block as a random variable, as described above for Experiment 1. We analyzed the effects of experimental treatments on mussel survival using GLMMs with a binomial distribution, including experimental block as a random variable. Mussel survival responses for Experiment 2 were summed by plot. Mussel regrowth for notched mussels and mussel condition index were averaged by plot for analysis. We analyzed mussel survival in response to experimental treatments using GLMM with a binomial distribution. p values for GLMM models were determined using the Anova function in the car package in R, which uses type II Wald chi-square tests. We made multiple comparisons for mixed models with Tukey's HSD tests, using the glht function in the multcomp package. During Experiment 2, no plants died and there was negligible recruitment by mussels ($n = 4$ individuals).

Predation trial

We hypothesized that *Limonium* may protect mussels from predation by visually obscuring mussels under the plant canopy and/or by providing a secure attachment site. To test this hypothesis, we compared predation rates for mussels associated with a *Limonium* plant versus other ambient vegetation at the Wakulla Beach field site (*S. alterniflora*), so that the results could be compared with the other experiments at this site. We tested differences in predation using tethering to keep mussels in place unless removed by predators (e.g., Bertness et al., 2002). Mussels were tethered to small poles using a fishing line affixed to one shell valve with marine epoxy (Splash Zone 2 part epoxy A 2788). We collected and tethered individual mussels, which we partially buried either under a naturally occurring *Limonium* plant or in a paired plot with *S. alterniflora* at the same tidal height, at least 10 cm away from the nearest *Limonium* plant ($N = 7$ per treatment). We measured water depth in each plot at high tide. We examined the tethered mussels every 24 h for 7 days to determine survival. We considered mussels lost to predation if missing from the tether, or with part of a crushed shell still attached to the tether. We did not observe any mussel mortality due to physical stress during the predation trials.

We analyzed survival of tethered mussels in the field predation trial with and without *Limonium* plants using GLMM with a binomial distribution, including water depth at high tide as a random variable. We also used Kaplan–Meier curves to compare survival with and without *Limonium* plants using the survfit function in the Survival package in R.

RESULTS

Field survey

There was a significant relationship between mussel density and *Limonium* percent cover in the field, but the shape of this relationship varied across field sites (ANCOVA, *Limonium* cover × site interaction, $F_{3,51} = 3.103$, $p = 0.032$; Figure 1A,B; Appendix S1: Table S4). At three of the four sites, the number of mussels increased linearly with *Limonium* cover ($F_{1,58} = 5.65$, $p = 0.02$, $R^2 = 0.07$, $y = 1.17 + 0.02x$; Figure 1B), although this relationship

explained only a small portion of the variation in mussel abundance. The quadratic term was not significant ($p > 0.595$), so it was removed from the model. The fourth site (Wakulla Beach) had much higher mussel densities, and mussel numbers peaked at intermediate *Limonium* cover, with a significant quadratic effect, and a greater portion of the variation explained ($F_{1,17} = 9.1$, $p = 0.008$, $R^2 = 0.35$, $y = -4.20759 + -0.06420x^2$; Figure 1A).

The relationship between mussel density and SOM also varied by field site (site × mussels, $F_{3,72} = 2.86$, $p = 0.04$; Appendix S1: Figure S3). At Wakulla Beach, where mussel densities were higher, there was a positive linear relationship between mussel density and SOM ($F_{1,18} = 7.39$, $p = 0.01$, $R^2 = 0.25$, $y = 2.26 + 0.006x$; Appendix S1: Figure S3); however, mussels were not a significant predictor of SOM ($p > 0.27$) across the other three sites.

At the Wakulla Beach plots that we followed through time, larger *Limonium* patches initially had more associated mussels (Figure 1C; $F_{1,23} = 19.79$, $p = 0.0002$, $R^2 = 0.44$; Appendix S1: Table S4), and they retained higher mussel numbers over the one-year survey period ($F_{1,23} = 10.12$, $p = 0.004$, $R^2 = 0.28$). We found that a significant negative relationship between initial mussel density and plant growth (change in number of leaves) was driven by one outlier, a very large plant that had died. When we removed this point from the analysis, there was no relationship between change in number of leaves and initial mussel density ($p = 0.90$; Appendix S1: Figure S4).

Experiment 1: Partner presence/absence and mussel density manipulation

Plant responses

There was significant mortality of mussels in the first two months of the experiment (see *Methods*), so we used mussel densities at the month 2 (August 2012) sampling date as the predictor of plant responses, rather than initial mussel density (Appendix S1: Table S5; see Appendix S1: Table S6 for results relative to the initial treatments). There was a nonsignificant trend toward higher *Limonium* survival at the end of the experiment in plots with higher densities of mussels in month 2, both across all treatments ($\chi^2 = 3.43$, df = 1, $p = 0.06$; Figure 2A; Appendix S1: Table S5) and in the subset of treatments in which mussels were directly manipulated ($\chi^2 = 3.25$, df = 1, $p = 0.07$). We also analyzed the effects of mussel presence and density at the end of the experiment on flowering shoots, as this time point coincided with flowering time. *Limonium* plants across all treatments grew more flowering stems when mussels were still present at the time of flowering ($\chi^2 = 12.31$, df = 1, $p = 0.0004$; Figure 2B) and at higher mussel densities ($\chi^2 = 12.11$, df = 1, $p = 0.0005$) at the end of the experiment. In manipulated treatments, mussel presence ($\chi^2 = 10.669$, df = 1, $p = 0.001$), but not density, at the end of the experiment led to increased number of flowering stems. Mussels also had a positive effect on *Limonium* size at the end of the experiment: plants with higher mussel densities in month 2 retained or grew more leaves during the experiment across all treatments ($F_{1,51} = 4.65$, $p = 0.04$; Figure 3C; Appendix S1: Table S5), and particularly in manipulated treatments ($F_{1,33} = 14.54$, $p = 0.0006$). Neither mussel presence nor density in month 2 predicted *Limonium* flowering stem production (Appendix S1: Table S5).

Mussel responses

For consistency, we used *Limonium* presence in month 2 (August 2012) as our predictor of mussel responses, which reflects loss of some *Limonium* plants during the storm disturbance early in the experiment (Appendix S1: Table S2). Mussel densities remained higher over the course of the experiment in plots with *Limonium* present in month 2; both across manipulated treatments only ($F_{1,33} = 7.24$, $p = 0.011$) and across treatments including unmanipulated controls ($F_{1,50} = 22.45$, $p < 0.001$; Figure 2C; Appendix S1: Table S7). Plots with *Limonium* present in month 2 had higher recruitment of juvenile mussels ($\chi^2 = 22.41$, df = 1, $p < 0.001$; Figure 2D). Larger *Limonium* (i.e., plants with more leaves at the end of the experiment) had a greater proportion of mussels remaining per plot ($F_{1,51} = 54.98$, $p < 0.001$; Figure 3A; Appendix S1: Table S7) and more mussel recruits ($\chi^2 = 80.469$, df = 1, $p < 0.001$, $y = -0.37 + 0.03x$; Figure 3B; Appendix S1: Table S7). We used the final number of leaves per plant as the metric of *Limonium* size, since initial size was not significantly related to final size and we only have size data for those time points.

Sediment organic matter

SOM in month 2 of the experiment was significantly higher in plots where mussels were present (Welch two-sample test, $t = -3.32$, df = 57.50, $p = 0.002$; absent = 6.104 ± 0.263, present = 7.323 ± 0.256; Appendix S1: Figure S5A). There was also a nonsignificant trend toward increased SOM with higher mussel density in month 2 ($F_{1,69} = 3.216$, $p = 0.08$; Appendix S1: Figure S5B).

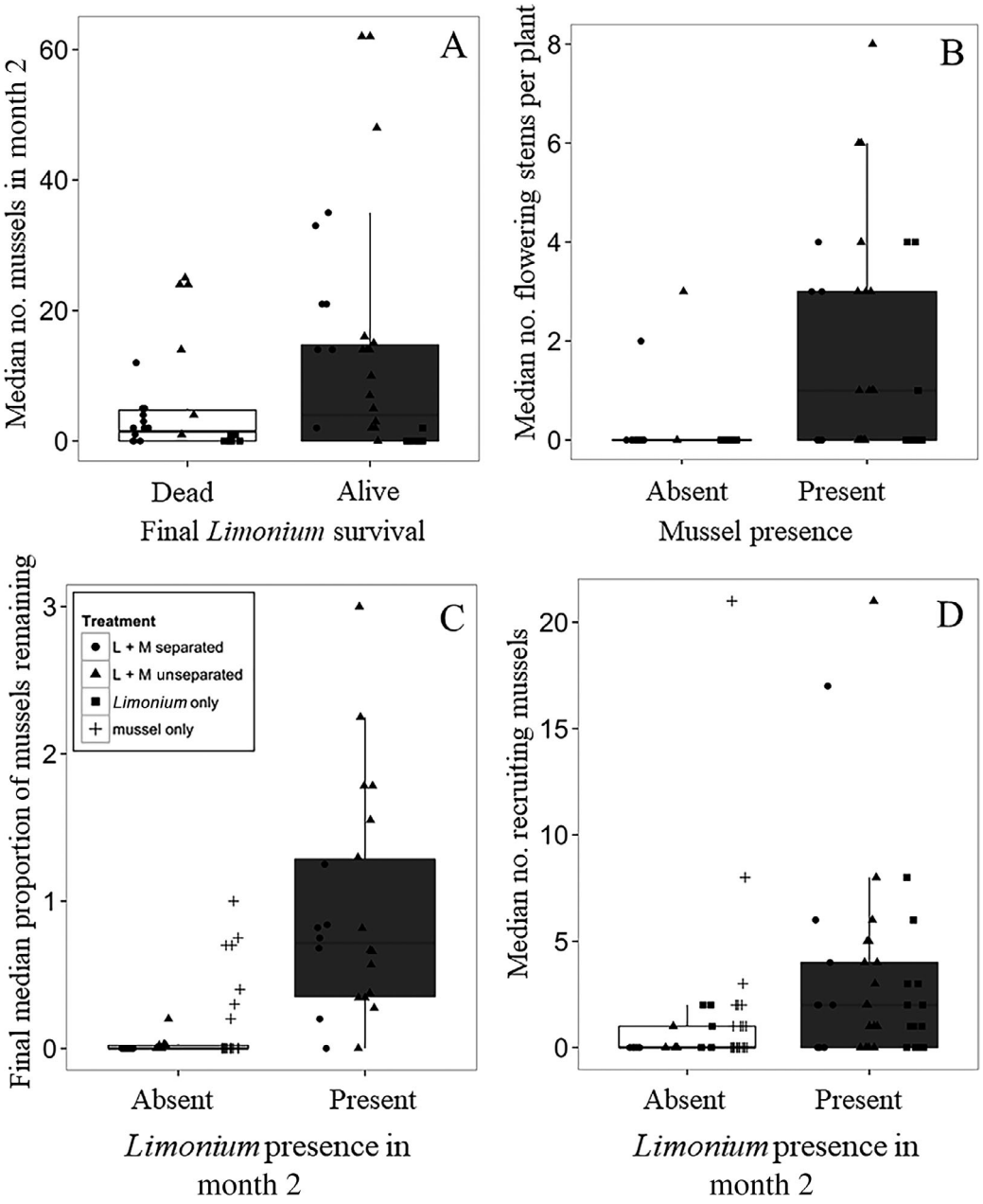
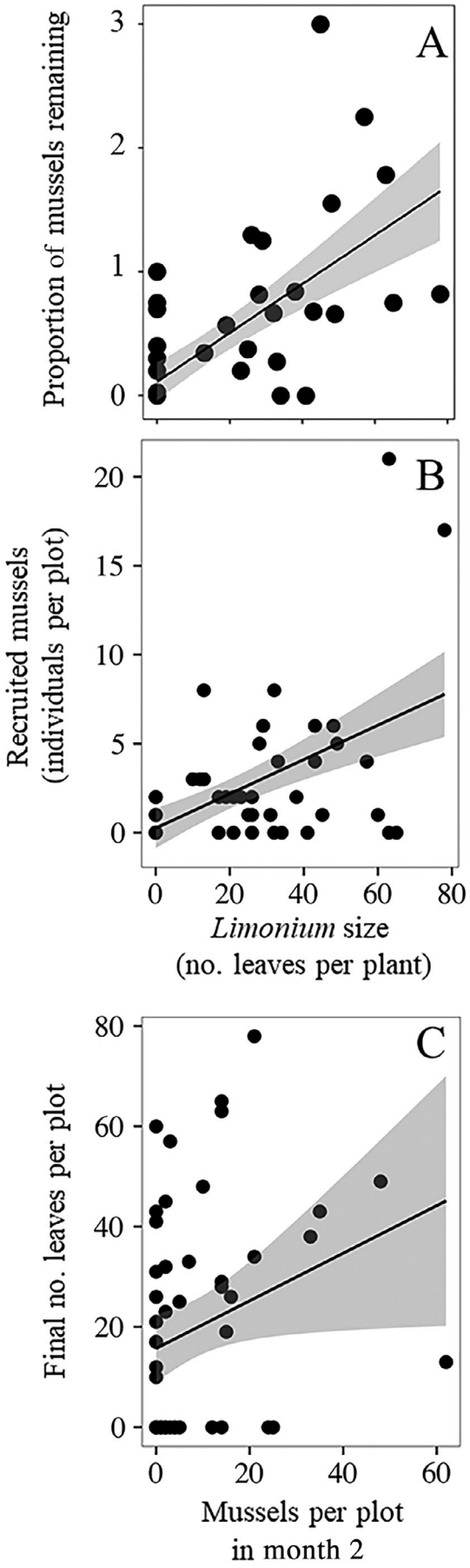


FIGURE 2 Plant and mussel responses in Experiment 1. All panels are box and whisker plots, with individual datapoints overlayed. The center line is median, the outer box edges are the upper and lower quartiles (25th and 75th percentiles), and whisker lines are the upper and lower quartiles ±1.5 × interquartile range, respectively. Plant responses: (A) *Limonium* (L) survival to the end of the experiment by mussel (M) density in month 2, across all treatments with *Limonium* and (B) number of flowering stems per plant in plots with and without mussels remaining at the time of flowering. Mussel responses: (C) proportion of initial mussels remaining at end of experiment (initial number of mussels/final number of mussels), and (D) number of juvenile mussels that were recruited per plot, in plots with and without *Limonium* present at month 2. Note that because the proportion of mussels remaining (C) does not distinguish between survival and recruitment here, some plots gained mussels and have a proportion >1.

Experiment 2: Partner presence/absence, plant structure, and nutrient manipulations

Plant responses

Leaf length and flowering stem length, but not the final number of leaves or flowering stems (Appendix S1: Figure S6A,C and Table S8), varied across treatments (leaf length: $F_{2,27} = 3.26$, $p = 0.05$; flowering stem length: $F_{2,18} = 4.44$, $p = 0.02$; number of leaves: $F_{1,25} = 0.42$, $p = 0.66$; number of flowering stems: $F_{2,18} = 1.83$, $p = 0.19$). The initial number of leaves was a strong predictor of the final number ($p < 0.001$; Appendix S1: Table S8) and was included as a covariate in all analyses. Leaves were significantly longer in the nutrient addition treatment (mean = 8.52 ± 0.58)



compared with *Limonium* alone (mean = 6.98 ± 0.30), but neither of those treatments was different from *Limonium* with mussels (mean = 7.63 ± 0.33; Appendix S1: Figure S6B). Flowering stems in the nutrient addition treatment (mean = 16.67 ± 2.14) were significantly longer than those in treatments with *Limonium* alone (mean = 10.46 ± 1.78) and *Limonium* with mussels (mean = 10.97 ± 1.10; Appendix S1: Figure S5C).

Mussel responses

Mussels were more likely to survive in treatments with a natural or artificial canopy ($\chi^2 = 21.88$, df = 1, $p < 0.001$; Figure 4A; Appendix S1: Table S8). Mussels also grew more in treatments with canopies ($F_{3,23.9} = 6.67$, $p = 0.002$; Figure 4B). However, initial plant size did not influence mussel survival ($p = 0.835$) or growth ($p = 0.883$). The average mussel condition index did not vary by treatment ($p > 0.21$). Mussel recruitment during this experiment was negligible ($n = 4$ individuals). See Appendix S1: Table S9 for a comparison of Experiment 1 and 2 results for plant and mussel responses.

Temperature

The average daily maximum temperature differed significantly by treatment ($F_{5,35} = 14.00$, $p < 0.001$; Figure 5A). Treatments with a real or artificial plant canopy maintained lower daily maximum temperatures compared with those lacking a canopy (Figure 5A), mirroring patterns of mussel survival (Figures 4A and 5B).

Predation trial

Tethered mussels were more likely to survive under *Limonium* plants than in adjacent *S. alterniflora* ($\chi^2_1 = 3.7957$, $p = 0.05$; Appendix S1: Figure S7). Kaplan–Meier cumulative hazard curves were not significantly different between the two groups ($\chi^2 = 0.9$, df = 1, $p = 0.35$).

FIGURE 3 Scatterplots with fitted line and 95% CIs (gray shading) showing that *Limonium* size in Experiment 1 had positive effects on (A) the proportion of initially planted mussels still remaining at the end of the experiment (initial number of mussels/final number of mussels), and (B) the number of juvenile mussels recruiting to plots. Mussel density in month 2 (C) was positively associated with final *Limonium* size (number of leaves). Note that because the proportion of mussels remaining (A) does not distinguish between survival and recruitment here, some plots gained mussels and have a proportion >1.

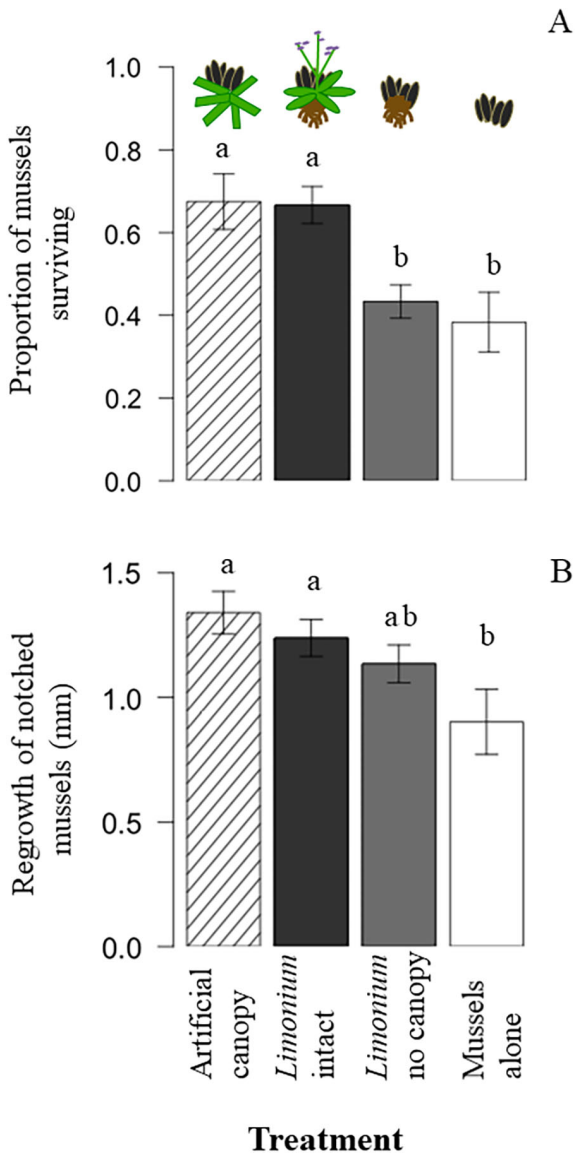


FIGURE 4 Mussel responses in Experiment 2. (A) Proportion of mussels surviving per plot and (B) mussel growth (regrowth of notched shells; mean ± SE) as a function of *Limonium* treatments: artificial canopy, intact *Limonium* plants, *Limonium* roots with no canopy, and mussels alone. Symbols above bars indicate *Limonium* treatments. Different letters above bars indicate significant differences between treatments (Tukey's honestly significant difference test, $p < 0.05$).

DISCUSSION

We experimentally demonstrated that *Limonium* has strong positive effects on mussels that are mediated through plant canopy presence and structure, with weak positive or neutral feedbacks of mussels on *Limonium*. Mussels were more abundant in association with *Limonium* in the field, and our experiments demonstrated that a combination of increased mussel survival and recruitment contribute to this relationship. The plant canopy created a shaded microhabitat that ameliorated high summer temperatures, and it may also provide a refuge from predation. In addition, canopies benefited mussel recruitment, and this effect was stronger for plants with larger canopies. At the same time, higher mussel densities allowed *Limonium* plants to retain or grow more leaves, creating a positive feedback between mussel aggregation and canopy size. Mussels also increased *Limonium* production of flowering stems, and they had neutral or weakly positive effects on survival. The increase in above ground structures of *Limonium* was likely due in part to deposition of organic matter by mussels alleviating nutrient limitation, and less likely due to the structure of mussel shells themselves (Zhu et al., 2019). However, these effects were only evident in our yearlong experiment and not in the subsequent 7-week experiment, suggesting that any fertilization benefits to *Limonium* from mussels operate over longer timescales or different seasons. The effects of mussels on organic matter we report from Experiment 1 are from month 2 of the experiment and may be an underestimate of the total deposition over the course of the yearlong experiment. We did not identify any negative feedbacks of mussels on *Limonium*. Thus, the relationship appears to be asymmetrical, with mussels benefitting strongly on a short timescale, and *Limonium* benefitting less and on a longer timescale (Appendix S1: Table S9).

Positive interactions such as mutualism and facilitation can be considered along a continuum from more symmetrical benefits to one-sided benefits such as commensalism, depending on the balance of costs and benefits of the interaction (Bronstein, 2001; Vellend, 2008). Facilitators providing habitat amelioration can experience significant negative feedbacks and fitness costs from their beneficiaries (O'Connor et al., 2006; Schöb et al., 2014). However, facilitative plant–animal interactions may be less influenced by competition, making net positive outcomes more likely (Bulleri, 2009). The bidirectional benefits we observed between *Limonium* and mussels are consistent with this prediction. However, the pattern of highest *Limonium* percent cover at intermediate mussel abundance at one field site could be consistent with density-dependent costs of the association at very high mussel densities, which can occur in plant–mussel interactions (Reusch & Williams, 1999). In addition, the benefits of association seem to be asymmetrical: mussels consistently benefitted from *Limonium* in both experiments, but we only detected positive effects of mussels on *Limonium* in the longer term Experiment 1. This discrepancy may result from differences in either the timescale or seasonality of their effects; in particular, alleviation of plant nutrient limitation by mussels may operate on a longer timescale or at a time of year that the shorter

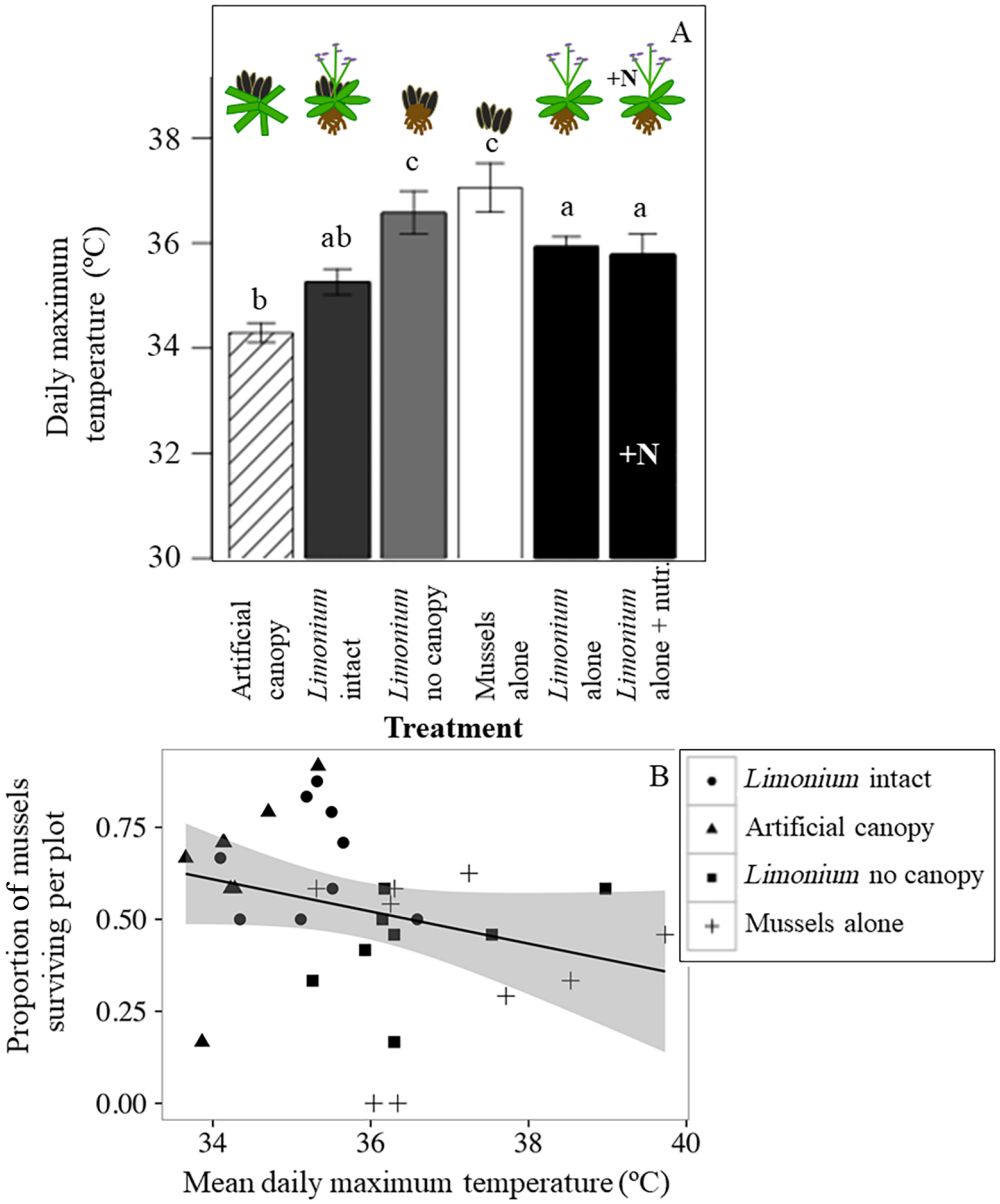


FIGURE 5 (A) Daily maximum temperature (mean ± SE) by treatment: artificial canopy, intact *Limonium* plants, *Limonium* roots with no canopy, and mussels alone, *Limonium* alone, and *Limonium* with nutrient addition. Symbols above bars indicate *Limonium* treatments. Different letters above bars indicate significant differences between treatments (Tukey's honestly significant difference test, $p < 0.05$). (B) Scatterplot with fitted line and 95% CIs (gray shading) showing proportion mussels surviving per plot as a function of mean daily maximum temperature per plot across treatments: artificial canopy, intact *Limonium* plants, *Limonium* roots with no canopy, and mussels alone.

second experiment did not capture. Benefits to mussels from temperature amelioration, on the other hand, are expected to occur during the summer months (Cartwright & Williams, 2014; Kawai & Tokeshi, 2004), which were included in both experiments. Species of different trophic levels may have different resource needs and perceive stress differently (Bulleri, 2009), and thus the costs and benefits of cross-trophic facilitation may depend on mechanisms for each species that operate on different timescales or under different conditions.

Both our focal species were common at our experimental field site, Wakulla Beach. Mussel densities were much higher at this site, compared with other local sites we surveyed. However, *Geukensia* mussels are generally common at varying densities across the Gulf of Mexico (Honig et al., 2015; Rietl et al., 2017). Many factors can influence site-level variation in mussel abundance, including larval supply (Franz, 2001), settlement on adult conspecifics (Nielsen & Franz, 1995), mortality rates (Bertness & Grosholz, 1985; Stiven & Gardner, 1992), and

abiotic factors (Honig et al., 2015). Although our study did not examine the factors influencing the high variability of mussel densities locally, the dynamics at our experiment site are of interest in part because of the high mussel densities relative to nearby sites, which could be consistent with a refuge or population source site. We examined the role of density variation by manipulating mussel density in Experiment 1 and found a positive feedback between mussel density and plant size, consistent with the positive association we observed in the field. Across the northern Gulf of Mexico, *Limonium* can have up to 72% percent cover, with an average of ~25% when present (R. Hughes, unpublished data). The abundance of *Limonium* is also variable locally, with high densities at some sites (20%–100% cover in 0.25-m^2 plots across large swaths of the intertidal) and near absence from others, across St. Joseph Bay (R. Hughes, unpublished data). It is possible that a combination of larval supply and temperature refuge from abundant *Limonium* facilitate high mussel abundance at this site, potentially making it important in maintaining local mussel populations. Further study of facilitation dynamics across sites varying in species abundances and conditions would provide better conclusions about how the association may vary across a larger geographic area.

Phenotypic traits of interactors, such as size and density of structures, can be key to determining which species benefit one another through facilitation (Bishop et al., 2013; Irving & Bertness, 2009; McAfee et al., 2018). The temperature amelioration provided by *Limonium* appears to be related to its particular canopy structure, which differs from other marsh plants at our field sites. In particular, the basal rosette of leaves near the sediment surface is very distinct from the upright growth form of the dominant marsh grass *S. alterniflora*, another known facilitator of mussels (Angelini et al., 2015; Bertness, 1984). The role of *Limonium* for mussels in our study region likely differs from parts of the Atlantic coast, where it can be quite rare (e.g., Hacker & Bertness, 1999) and where dense stands of *S. alterniflora* sometimes provide shading for mussels (Angelini et al., 2015). However, *S. alterniflora* may increase temperature stress for mussels under some conditions by buffering airflow and reducing convective cooling (Jost & Helmuth, 2007). Thus, *Limonium* may be a more effective facilitator of mussels than *S. alterniflora* at our field site where *S. alterniflora* density is relatively low, and summer temperatures in our mussel-mimic temperature loggers often exceeded the potentially lethal threshold of 45°C (Jost & Helmuth, 2007). The role of physical structures in broader scale habitat modification has been recognized in the context of ecosystem engineering (Jones et al., 1994) and foundation species (sensu Dayton, 1972). Our results highlight the importance of phenotypic traits and physical structure, rather than species specificity, in facultative interactions such as facilitation.

Although trait-dependent facilitation (i.e., the effect of traits on facilitation) is well documented, less attention has been paid to the ways the traits themselves may be influenced by feedbacks between partners (i.e., the effect of facilitation on traits) as well as the consequences such feedbacks on traits may have for an interaction. Reciprocal effects between interacting partners may influence the very traits that ameliorate stress for one another (Michalet et al., 2011). Positive feedbacks between the traits of interacting species that enhance benefits may serve to stabilize facilitative interactions over time (Bronstein, 2009). For example, nutrient enrichment from reef fish aggregations can maintain the highly productive seagrass patches that provide habitat for the fishes, leading to a positive feedback in facilitative effects of the vegetation (Peterson et al., 2013). Recent studies in terrestrial systems have focused on shifts in functional traits of beneficiary plants toward more resource-acquisitive states in response to facilitation (e.g., Doudová & Douda, 2020; van der Merwe et al., 2021). Yet, we have a limited understanding of how facilitation affects the traits of both partners simultaneously and how feedbacks on partner traits influence habitat amelioration. Both interacting species in our study had positive effects on traits that might serve to enhance the mutual facilitation. *Limonium* both benefitted from higher densities of mussels and increased mussel density over time, while mussels benefitted more under larger *Limonium* canopies, and their presence allowed *Limonium* to maintain canopies with more leaves. This positive feedback between partner traits may be important for maintaining the association. Further, an experimental approach that is bidirectional and connects traits with mechanisms, as we used in this study, can provide a foundation to explore the evolutionary importance of facilitation (Verdú et al., 2021) and enhance our understanding of the evolutionary stability of facilitation through time (Bronstein, 2009).

The amelioration of physical stress, such as that provided by *Limonium* for mussels, is a feature of many facilitative interactions in physically stressful environments, including intertidal and arid ecosystems (Brooker et al., 2008; He & Bertness, 2014). Positive interactions can allow associated species to persist in habitats that would otherwise be too stressful, thus expanding the realized niche of beneficiary species (Bruno et al., 2003; Crotty & Bertness, 2015). Niche expansion due to facilitative interactions may determine local persistence and even larger scale geographical ranges if stressful conditions intensify (Bulleri et al., 2015). We were able to demonstrate the ameliorating effects of *Limonium* canopies on temperature

and establish this as a mechanism of benefit for mussels. Although many studies of facilitation propose stress amelioration as a likely benefit, relatively few studies actually measure the physical stressors needed to confirm this as a mechanism (Bulleri, 2009). More studies connecting traits to specific mechanisms of facilitation will enhance our understanding of these interactions and their outcomes. The availability of facilitators and their functional traits (Stelling-Wood et al., 2020) may determine the response of many species to global change (Kearney et al., 2009; Sunday et al., 2014). Thus, a mechanistic, trait-based approach to facilitation is needed to predict outcomes for vulnerable species under climate change (Bulleri et al., 2018).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Moore & Hughes, 2023) are available from the Northeastern University Library Digital Repository Service: http://doi.org/10.17760/D20486980.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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