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# Optimizing coastal restoration with the stress gradient hypothesis

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Restoration efforts have been escalating worldwide in response to widespread habitat degradation. However, coastal restoration attempts notoriously vary in their ability to establish resilient, high-functioning ecosystems. Conventional restoration attempts disperse transplants in competition-minimizing arrays, yet recent studies suggest that clumping transplants to maximize facilitative interactions may improve restoration success. Here, we modify the stress gradient hypothesis to generate predictions about where each restoration design will perform best across environmental stress gradients. We then test this conceptual model with field experiments manipulating transplant density and configuration across dune elevations and latitudes. In hurricane-damaged Georgia (USA) dunes, grass transplanted in competition-minimizing (low-density, dispersed) arrays exhibited the highest growth, resilience to disturbance and dune formation in low-stress conditions. In contrast, transplants survived best in facilitation-maximizing (high-density, clumped) arrays in high-stress conditions, but these benefits did not translate to higher transplant growth or resilience. In a parallel experiment in Massachusetts where dune grasses experience frequent saltwater inundation, fewer transplants survived, suggesting that there are thresholds above which intraspecific facilitation cannot overcome local stressors. These results suggest that ecological theory can be used to guide restoration strategies based on local stress regimes, maximizing potential restoration success and return-on-investment of future efforts.

## 1. Introduction

Coastal habitats make up only 2% of the world's surface, but protect 10% of the global population and the majority of the world's largest cities from severe storms, flooding and sea-level rise [1,2]. However, development, eutrophication, storms, overfishing and other stressors are causing large-scale destruction of coastal ecosystems [3,4]. Degradation of coastal systems has been reported across latitudes and ecosystems, including sand dunes, salt marshes, mangrove forests, seagrass meadows, and both oyster and coral reefs [5]. As stressors increase in frequency and intensity, the ability of coastal ecosystems to rebuild naturally between disturbances is compromised [1,6]. This seemingly runaway coastal destruction is expected to cost the United States $200 billion in repairs and lost ecosystem services by 2100 [7]. As such, investment in restoring coastal wetlands, reefs and dunes has escalated substantially in recent years [8–11]. These efforts, which include both the revitalization of degraded coastal systems and the strategic creation of new habitats, are aimed at addressing the global decline of coastal ecosystems and cultivating the valuable ecosystem services they provide [10,12].

In both coastal [10,13] and terrestrial ecosystems [14,15], habitat-forming foundation species (e.g. reef-building corals and bivalves, marine and terrestrial grasses, shrubs, and trees) are often transplanted to restore degraded habitats and jumpstart ecosystem recovery. In coastal ecosystems, this restoration strategy is gaining popularity, inspired in part by recent work suggesting that natural

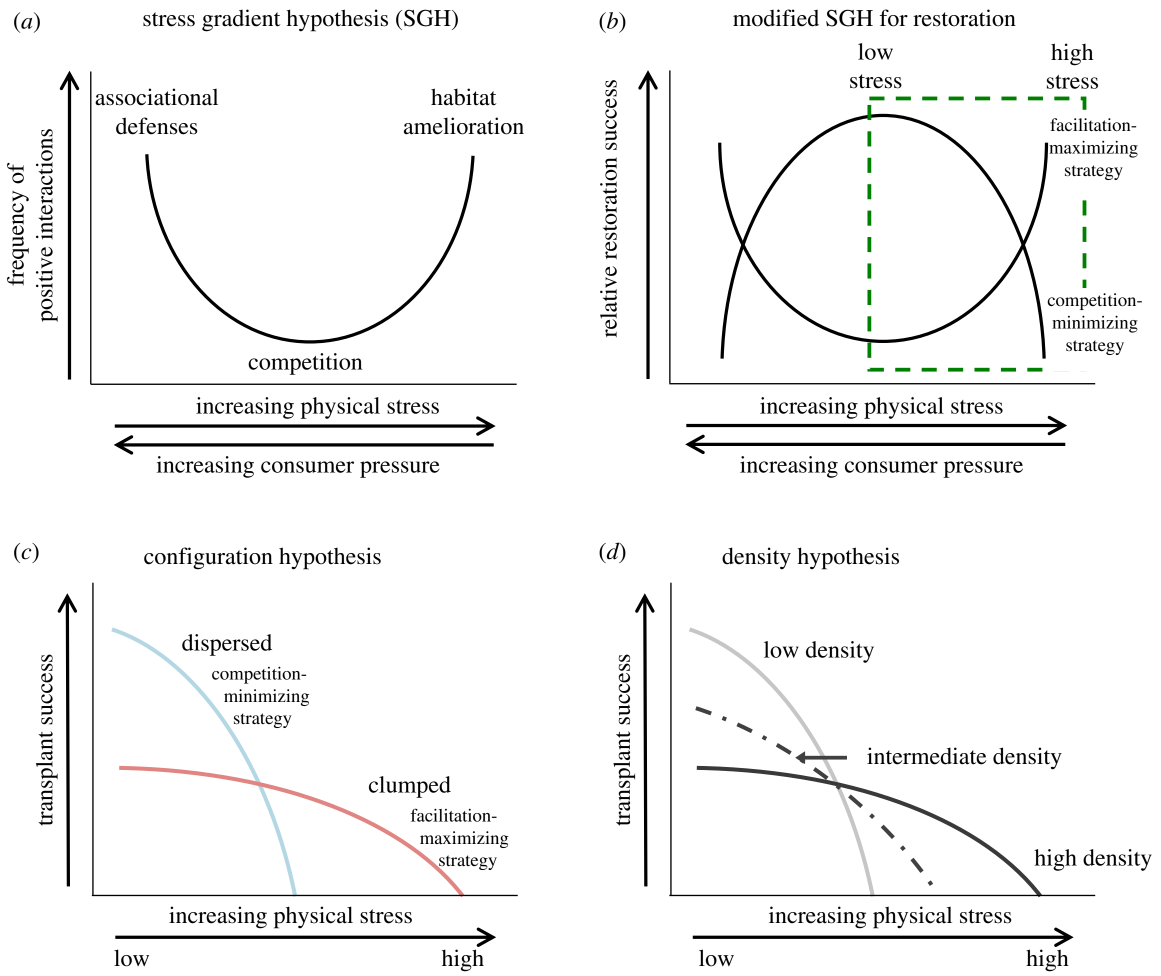

**Figure 1.** (*a*) The original SGH predicts an increase in positive interactions with increasing physical and biological stresses. (*b*) The SGH for restoration predicts which transplant configurations (i.e. facilitation-maximizing or competition-minimizing) will show higher performance across a physical and biological stress gradient. The dashed box represents the physical stress gradient analysed in this study. (*c*,*d*) The SGH for restoration modified to predict transplant success in different (*c*) configurations and (*d*) densities across a physical stress gradient. (Online version in colour.)

ecosystems are more resilient to storms and better protect against flooding than built infrastructure (i.e. sea walls, levees, etc.) [9,10]. Yet there exists a conceptual disconnect between traditional foundation species deployment, which focuses on minimizing competition between transplants, and ecological theory, which proposes that positive interactions can be essential for species' survival in high-stress conditions [16,17], including those that often typify restoration sites. Conventionally, foundation species transplants are deployed in uniformly spaced arrays with the expectation that such dispersed distributions minimize intraspecific competition [16,18–20]. However, recent theoretical and perspective studies [13,17,18,21] and follow-up experimental work [16,22–25] across a variety of ecosystems have shown that harnessing positive interactions by clustering transplants and/or co-transplanting foundation species with their mutualistic partners, can significantly enhance restoration success. For example, planting salt marsh grasses in high-density arrays increased biomass by nearly 200% [16] and deploying seeds under preestablished nurse shrubs in Mediterranean mountains increased seedling establishment and survival [21]. Introducing facilitation theory to restoration is particularly important as restoration attempts in coastal ecosystems are notorious for their high cost and low success rate, which is less than 40% in some ecosystems [11]. Despite this need, ecologists have yet to build and test a predictive model for where facilitation-maximizing plantings should prevail over more traditional competition-minimizing arrays.

The stress gradient hypothesis (SGH) [26,27] predicts that positive interactions are relatively more important in structuring communities at physical and biological stress extremes, while competition is the principle driver at intermediate stress levels (figure 1*a*). The SGH may provide a useful framework for resolving the disconnect between experimental research and application by informing how practitioners may adapt restoration strategies to local stress and resource gradients. Here, we modify the SGH to improve its application to restoration (figure 1*b*) by suggesting that, in low-stress areas, planting designs should minimize competition to enhance transplant success (i.e. survival, growth, resilience), given the predicted importance of this interaction in benign conditions. As either physical or biotic stress levels increase, planting designs should instead promote positive interactions. For simplicity in presentation and direct application to our study system, we focus on low to high physical stress gradients, although this theoretical framework additionally extends to biotic stress gradients. Competitive and facilitative interactions can increase in strength when plants are clumped together [28] or at high densities [29]. Accordingly, we further modify the SGH to predict that dispersed and low-density arrays will outperform clumped and high-density arrays under low physical stress conditions,

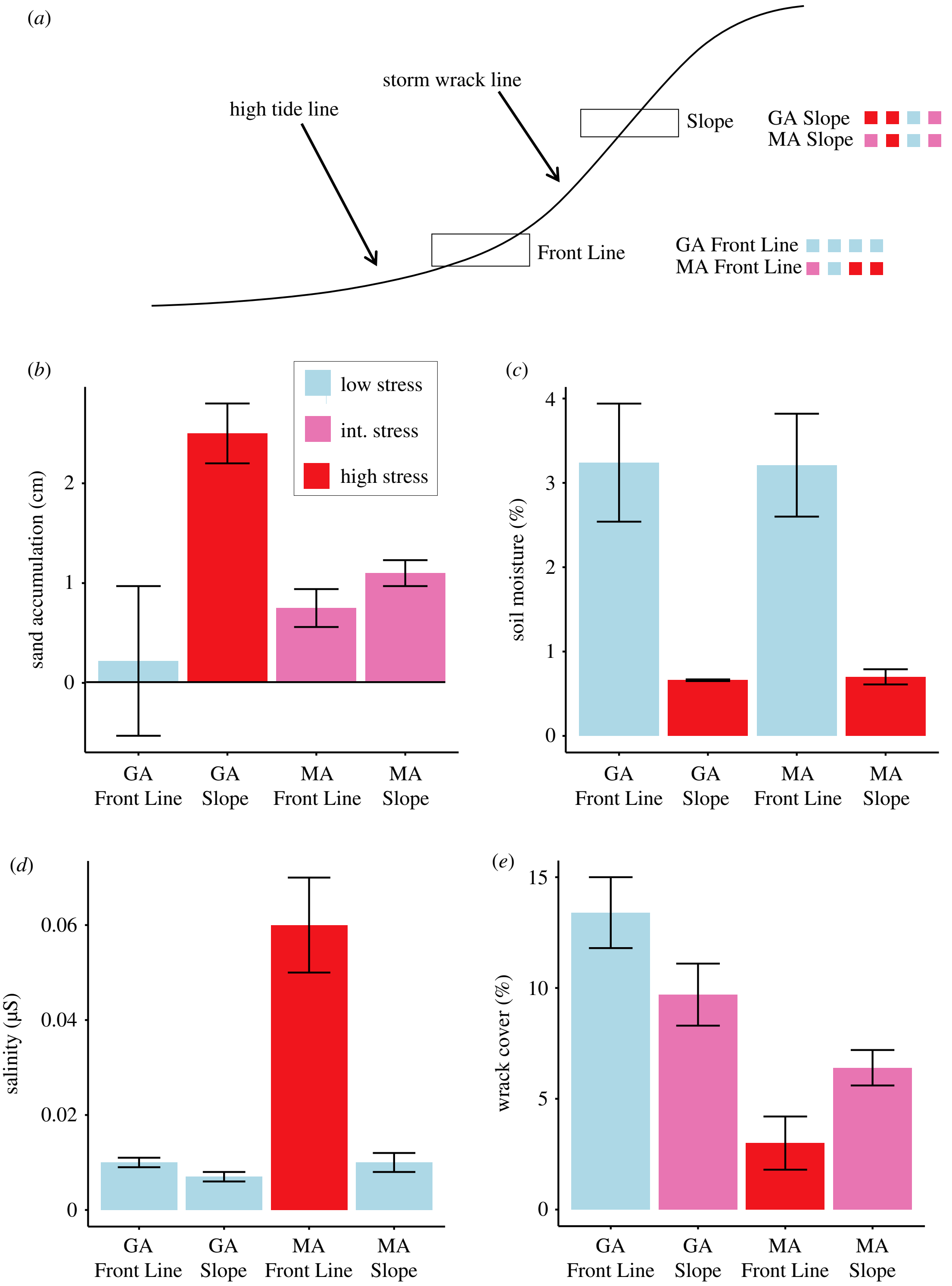

**Figure 2.** (*a*) Planting zones along a hypothetical dune delineated by the high tide and wrack lines. (*b*) Sand mobility, (*c*) soil moisture, (*d*) salinity and (*e*) wrack cover of Front Line and Slope zones in Georgia (GA) and Massachusetts (MA). In *b–e*, colours denote the relative stress level experienced by each zone (low, intermediate or high stress). These stress levels are also summarized in the small squares next to each zone in (*a*). Justifications for the stress level designations are presented in electronic supplementary material, table S1. Error bars are mean ± s.e. (Online version in colour.)

while the reverse pattern will arise under high physical stress conditions (figure 1*c*,*d*).

To test if the modified SGH can be used to optimize restoration success, we conducted a field experiment along a hurricane-damaged coastal dune system in Georgia (GA), USA and a high-energy beach in Massachusetts (MA). Across physical stress and nutrient gradients, we manipulated the transplant configuration and planting density of the dominant dune grass. We then tracked transplant growth, resilience to a standardized disturbance (GA only), dune formation and transplant survivorship. At the Georgia site, we hypothesized that high-density, clumped configurations promoting facilitative interactions would have the highest restoration success on the more physically stressful dune slope (hereafter 'Slope', figure 2*a*). In contrast, on the high nutrient Georgia Front Line (lower elevation than the Slope), low-density, dispersed arrays that minimize competition would outperform high density and clumped configurations. We additionally predicted that facilitation would be critical for transplant survival and growth at the Massachusetts site, which exhibits higher stress levels, resulting in facilitation-maximizing transplants outperforming low-density, dispersed transplants across zones.

## 2. Methods

The primary experiment was performed from March through November 2018 on Sapelo Island, Georgia (31.409, −81.256). In September 2017, five months prior to the experiment's deployment, Hurricane Irma hit the region, removing 10–25 m of dune along the island's eastern side. Following Irma, dead plants and algae from the hurricane surge, material known as wrack, remained at the base of the surviving dunes and was used to define the two zones of interest in the experiment: the Slope was defined as the landward margin of the storm wrack line while the Front Line was defined as the area between the mean high tide line and storm wrack line (figure 2*a*).

A parallel experiment was deployed in Wellfleet, Massachusetts (41.916, −70.071) from May through October 2018 to evaluate the relative success of the restoration treatments across a broader stress gradient. Wrack lines from winter storms were used to delineate the Slope and Front Line zones. Due to a shift in species composition and local restoration approaches, *Uniola paniculata* (hereafter sea oats) was planted in Georgia and *Ammophila breviligulata* (hereafter American beachgrass) was planted in Massachusetts. Both grass species dominate the foredune of their respective latitudes [19,20] and display vegetative growth strategies that provoke the formation of embryo dune [30]. Because the two species' ranges overlap in the Mid-Atlantic [31] and sea oats show an increased growth at temperatures above 27° while the growth of American beachgrass decreases above this threshold [32,33], it is likely that temperature tolerances set the range limits of the two species. Importantly, the two plant species show near-identical sensitivity to soil moisture [34,35] and salinity [32,33] stress.

In each latitude, we deployed five experimental 'blocks' (i.e. approx. 120 m long sections of dune) located along a 2 km stretch of shoreline that exhibited a similar per cent cover of wrack, beach width, foredune slant and elevation. In each block, we marked 8 plots in both the Front Line and Slope zones, and randomly assigned one of four planting configurations (no plant, single plant, clumped or dispersed) and one of five planting densities (0, 1, 4, 9 or 16 transplants) to each plot ($n = 5$ replicate plots of each treatment, 8 treatment types, 40 plots per zone). Each plot was 4 $\text{ft}^2$ (0.37 $\text{m}^2$), a size chosen based on standard restoration practices calling for the planting of dune grasses at 1 ft (0.30 m) centres [19,20], which we mirrored the nine-plant dispersed treatment. Transplants were purchased from wholesale suppliers (Aquatic Plants of Florida, Sarasota FL and Cape Coastal Nursery, Orleans MA) and planted into 15 cm deep holes.

To evaluate stresses experienced by dune-building grasses, we measured four physical variables known to limit dune plant survival [33,35–37]: sand mobility, water limitation, soil salinity and wrack cover in July 2018. Sand mobility was quantified by hammering 3 cm diameter posts to refusal and then trimming them to 20 cm above surface level ($n = 15$ posts per zone, see electronic supplementary material, figure S1 for details). Posts were spaced within and between replicate blocks, greater than 2 m away from any plants, to capture sand mobility levels of each zone at both sites. Sand mobility was reported as the cm of sand accreted or eroded after 30 days. Soil moisture was quantified using a TH150 ThetaProbe (Dynamax, Huston TX) inserted to 15 cm depth in each plots ($n = 2$ measurements per plot). Salinity was measured using a HI98331 Direct Soil Conductivity Tester (Hanna Instruments, Woonsocket RI) by collecting 10 replicate 0.5 g samples of sand per zone and suspending each in 3 ml of deionized water. The percentage cover of wrack, which functions as a major source of carbon and nutrients along the dune face [36,38], was estimated in each plot.

Every four weeks, we assessed growth by counting the total number of fully emergent stems per plot, the average and maximum height of leaves in each plot, and the number of expansion tillers, which we defined as stems emerging from the initial transplant (electronic supplementary material, figure S2). Additionally, we quantified both transplant stem production (the number of stems produced by individual transplants) and whole plot production (the number of stems per a plot) to assess plant growth at two spatial scales. As every Massachusetts plot lost leaves over the course of the experiment, we just report the results from Georgia.

Given both the vulnerability of coastal dune environments to disturbances and the interest of practitioners in establishing habitats capable of recovering from episodic disturbances [22], we trimmed all Georgia transplants to surface level five months into the experiment. Plant growth was then monitored for an additional three months. Percentage change in stem counts were calculated at one and three months post-disturbance. At the end of the growing season in November 2018, we measured the dimensions of sand mounds, known as embryo dunes, that had accreted in each plot and calculated their volume. As transplant survival was low and no measurable dunes had formed around the transplants in Massachusetts, these measurements were only completed in Georgia. Across both latitudes, transplant survival was assessed at the experiment's conclusion. As the growing season length differs with latitude (five months in Massachusetts versus eight months in Georgia), plant survival after one growing season, rather than a standardized length of time, was compared. We did not harvest final plant biomass due to permitting constraints.

All statistics were performed in R (v. 3.3.3). Due to differences in the transplanted species' identity, experiment duration and local weather, we do not directly compare physical stress variables or transplant performance metrics across the two sites. Using separate tests for each latitude, we evaluated the main effect of zone on sand mobility, salinity and wrack using one-way ANOVAs. Soil moisture was analysed using a mixed effects nested ANOVA where configuration, density and their interaction were nested within zone (fixed effects), and block was treated as a random effect. Stem counts were analysed at the transplant and plot scale with a mixed effects four-way repeated-measures date × zone × density × configuration ANOVA, where date was used to indicate repeated measurements. We then evaluated final stem counts, transplant height, number of expansion tillers and embryo dune volume with a nested ANOVA where configuration, density and their interaction were nested within zone, and block was treated as a random effect. We used a linear regression to assess the relationship between stem counts and embryo dune volume. Nested ANOVAs (transplant configuration or density nested within zone) was used to evaluate treatment effects on transplant survival in both Georgia and Massachusetts. All ANOVAs were followed by Tukey's HSD tests with adjusted *p*-values of $p < 0.01$. Tables summarizing all ANOVA tests are presented in the electronic supplementary material (electronic supplementary material, tables S2–S10). One Georgia plot was lost shortly after deployment due to sand burial and was dropped from all analyses. All values are presented as means ± s.e.m.

## 3. Results

### (a) Physical stress and nutrient gradients

Measurements of physical stressors and nutrient levels revealed differences between zones at both sites. In Georgia, sediment mobility posts (figure 2*b*) showed that background sand accretion is 11 times higher on the Slope than Front Line ($F_{1,28} = 7.8$, $p = 0.009$). On the Georgia Front Line, 33% of the posts eroded while all posts on the Slope accumulated sand.

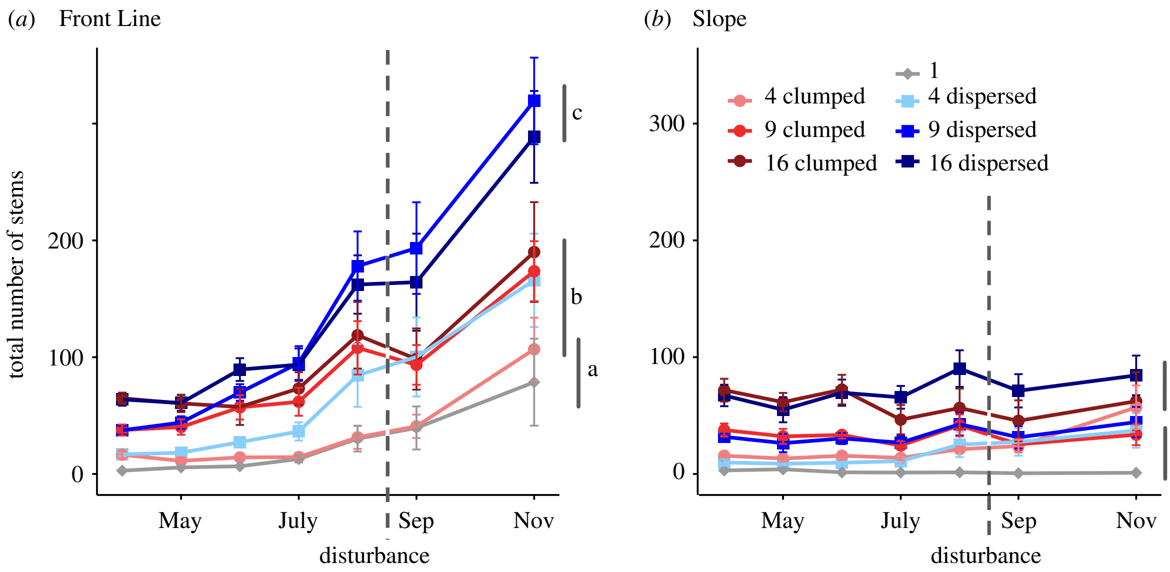

**Figure 3.** Total number of stems counted at 7 time points over the eight-month study in both the Georgia (*a*) Front Line and (*b*) Slope. Numbers in legend are transplant density. Vertical line indicates disturbance when all plants were trimmed to surface level and points to the right of that line depict plant regrowth. Tukey's HSD $p < 0.001$, error bars are mean stem count ± s.e. (Online version in colour.)

In Massachusetts, sand accumulation did not differ between zones ($p = 0.42$). In both Georgia and Massachusetts, soil moisture (figure 2*c*) was elevated in the Front Line, especially in clumped and high-density plantings relative to dispersed or low-density plantings, but did not vary between treatments in the Slope zone at either site (GA: zone [density × configuration]: $F_{4,122} = 6.9$, $p < 0.001$; MA: zone [density × configuration]: $F_{4,129} = 13.4$, $p < 0.001$). Soil moisture was three times higher in clumped relative to dispersed plots, and plots with 4, 9 or 16 plants had approximately two times higher soil moisture levels than single plant or bare plots in both Front Lines (Tukey's HSD $p < 0.01$). Soil salinity (figure 2*d*) in the Massachusetts Front Line was six times higher than the Massachusetts Slope ($F_{1,18} = 19.1$, $p < 0.001$). In Georgia, soil salinity was far lower and did not vary with zone ($p = 0.20$). The per cent cover of wrack (figure 2*e*) was 1.5 times higher on the Georgia Front Line than Slope ($F_{1,78} = 14.9$, $p < 0.001$), while the reverse trend occurred in Massachusetts where wrack was higher on the Slope than the more tidally exposed Front Line ($F_{1,78} = 13.4$, $p < 0.001$). Based on this compilation of measurements and prior research evaluating the sensitivity of sea oats and American beachgrass [32–35], we consider the Georgia Front Line to be the lowest-stress zone, the Georgia and Massachusetts Slopes to be intermediate-stress zones and the Massachusetts Front Line to be the highest-stress zone (see electronic supplementary material, table S1 for more information on stress levels across latitudes).

## (b) Transplant growth

By tracking the number of stems produced per an initial transplant in Georgia, we discovered that stem counts varied over time, across zones and with transplant density and configuration (date × zone × configuration × density: $F_{12,317} = 4.4$, $p < 0.001$; electronic supplementary material, figure S3). After eight months, transplants on the Front Line (33 ± 6 stems) produced more stems per an initial transplant than those on the Slope (6 ± 1 stems), and single transplants located on the Front Line (78 ± 37 stems) produced two to five times more stems than all other plantings (zone [configuration]: $F_{4,51} = 6.3$, $p < 0.001$). Transplant stem production did not differ for any other intra-zone pairwise comparisons (all Tukey's HSD $p > 0.01$).

Whole-plot stem production also varied across time, zones, transplant densities and transplant configurations in Georgia (date × zone × configuration × density: $F_{12,317} = 12.7$, $p < 0.001$; figure 3). After eight months, whole-plot stem production was four times higher on the less stressful Front Line (189 ± 19 stems) than the Slope (45 ± 7 stems). Dispersed configurations in the Front Line (258 ± 27 stems) produced 150% more stems than clumped configurations (157 ± 20 stems; zone [configuration]: $F_{4,51} = 14.7$, $p < 0.001$), and high-density plantings (9 and 16 transplants per plot; 243 ± 22 stems) produced twice as many stems as low density plantings (1 and 4 transplants; 117 ± 21 stems; zone [density]: $F_{4,51} = 7.5$, $p < 0.001$). On the less productive Slope, neither transplant configuration nor density influenced whole plot stem production (Tukey's HSD $p > 0.01$). Importantly, high density plantings had 2–16 times more stems per plot than low density plantings at the start of the experiment, meaning high density transplants underperformed relative to low density plantings in the Front Line, despite producing more leaves at the plot scale. The results collectively suggest that low density, dispersed plantings are optimal in the Front Line while neither configuration nor density impacted plant production in the Slope zone.

## (c) Transplant resilience to disturbance

In Georgia, short-term resilience, the per cent change in stem counts one month after the standardized disturbance, was 110 ± 6% on the Front Line but only 71 ± 8% on the Slope (figure 3), indicating that transplants on the Front Line more than fully re-sprouted while those on the Slope did not. Regardless of zone and transplant configuration, four-plant treatments exhibited higher short-term resilience compared to all other planting densities (zone [density]: $F_{4,51} = 7.0$, $p < 0.001$). Single plant treatments on the Slope displayed the lowest short-term resilience (zone [configuration]: $F_{4,51} = 6.5$, $p < 0.001$). Similarly, long-term resilience, the percentage change in stem counts three months after the standardized

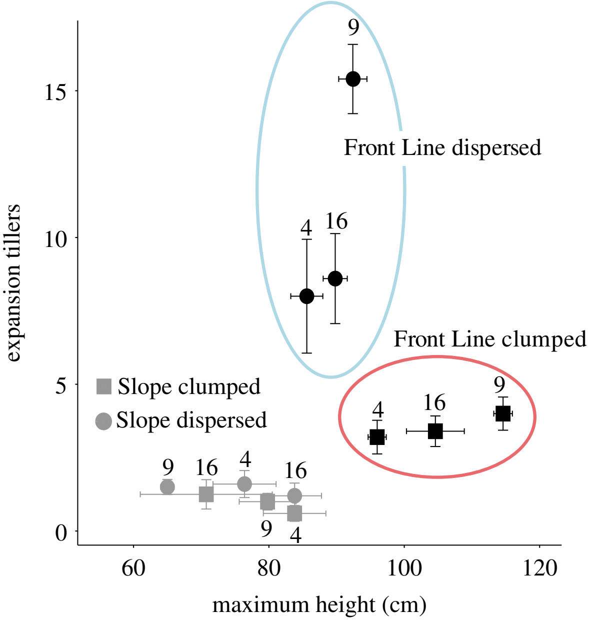

**Figure 4.** Trade-off between height and vertical expansion in Georgia. Spatial configuration of plants on the Front Line led to an increased investment in either vertical growth (clumped arrays) or horizontal expansion (dispersed arrays). Plants on the Slope did not display this same trade-off. Error bars are mean ± s.e. (Online version in colour.)

disturbance, was two times higher on the Front Line (226 ± 18%) than on the Slope (112 ± 17%). The four-plant density plots continued to outperform all other density treatments, and single plantings on the Slope again showed the lowest resilience (zone [configuration × density]: $F_{4,51} = 4.12$, $p = 0.005$; Tukey's HSD $p < 0.01$).

## (d) Transplant growth strategies

Sea oats transplants displayed plasticity in their growth strategies based on planting zone and configuration (figure 4). Dispersed transplants on the Front Line produced three times more expansion tillers than their clumped counterparts and clumped transplants grew an average of 16 cm taller than dispersed ones (zone [configuration]: $F_{4,51} = 14.1$, $p < 0.001$ (height); $F_{4,51} = 5.8$, $p < 0.001$ (expansion tillers)). Interestingly, this plasticity in growth allocation only occurred in the Front Line where plants were 45% taller and produced 6.5 times more expansion tillers than those on the Slope. On the Slope, configuration did not affect expansion tiller production or stem height and transplant density had no effect on plant growth strategy in either zone (Tukey's HSD $p > 0.01$). These findings indicate that sea oats are highly responsive to the configuration, but not density, of conspecifics in benign conditions.

## (e) Dune formation

By quantifying embryo dune volume in each Georgia plot, we discovered that embryo dune volume was positively related to whole plot stem production (adj. $R^2 = 0.93$, $p < 0.001$; figure 5*a*), indicating that planting arrays that produce the largest numbers of stems also build the largest embryo dunes. Additionally, dispersed transplants built embryo dunes six times larger than clumped transplants on the Front Line (zone [configuration]: $F_{4,51} = 6.2$, $p < 0.001$; figure 5*b*). Planting density did not influence embryo dune volume on the Slope (zone [density]: $p = 0.14$). Thus, dispersing transplants in the lower-stress Front Line supports high stem production and therefore increases dune formation.

## (f) Context dependency of transplant survivorship

On the Massachusetts Front Line, only 28% of plots contained at least one surviving transplant at the end of the experiment whereas 74%, 80% and 100% of plots contained living transplants in the Massachusetts Slope, Georgia Slope and Georgia Front Line, respectively (figure 6*a*). Due to the high mortality rates, there was no significant effect of density or configuration on transplant survival in the Massachusetts Front Line. In the moderately stressful Massachusetts Slope, survivorship of clumped transplants was 43% greater than that of dispersed transplants (zone [configuration]: $F_{2,12} = 6.9$, $p = 0.01$; figure 6*a*). Similarly, on the Georgia Slope, clumping resulted in a 15% increase in transplant survival (zone [configuration]: $F_{2,12} = 5.0$, $p = 0.03$). Survivorship by density followed similar patterns in the Massachusetts and Georgia Slopes (electronic supplementary material, figure S4). Intermediate and high density plantings (4, 9 or 16 plants per plot) survived 55–80% better in Massachusetts (zone [density]: $F_{4,20} = 5.8$, $p = 0.003$) and 65–70% better in Georgia (zone [density]: $F_{4,20} = 9.6$, $p < 0.001$). However, clumping or increasing density did not alter any other metric of plant success (i.e. tiller counts, transplant heights, numbers of expansion tillers) on the Slope at either site (all $p > 0.05$). These results predominantly align with the predictions of the configuration extension of the modified SGH (figure 6*b*).

# 4. Discussion

These experimental results indicate that competition-minimizing planting arrays are far superior to facilitation-maximizing ones for recreating resilient, high-functioning dunes in low-stress areas, supporting the low-stress portion of the modified SGH (figure 1*b*). In high-stress locations, survivorship was increased in clumped treatments relative to dispersed ones, but all other metrics of transplant performance were unaffected by transplant density and configuration.

## (a) Transplant growth and resilience

The results from the Georgia experiment indicate that dune grass performance is significantly higher within the less physically stressful Front Line at both the transplant and plot scale. These results align with findings from coral reef restoration experiments in which coral growth was fastest when fragments were deployed individually at sites exhibiting low transplant mortality [39]. However, contrary to the modified SGH predictions (figure 1*c*,*d*) and evidence from salt marshes where clumping grass transplants in high-stress zones increased stem densities by 80% [16], clustering transplants to enhance facilitation did not support higher transplant or whole plot stem production in the more physically stressful Slope. This result may have occurred due to the notoriously low levels of nutrients present in this zone [38], which can significantly stifle the potential growth of transplants.

Sea oats planted in the Front Line not only grew vigorously, but also rapidly re-sprouted post disturbance. Our finding that 4-density plantings exhibited the highest resilience suggests that low and intermediate planting densities allow transplants access to sufficient belowground resources due to reduced

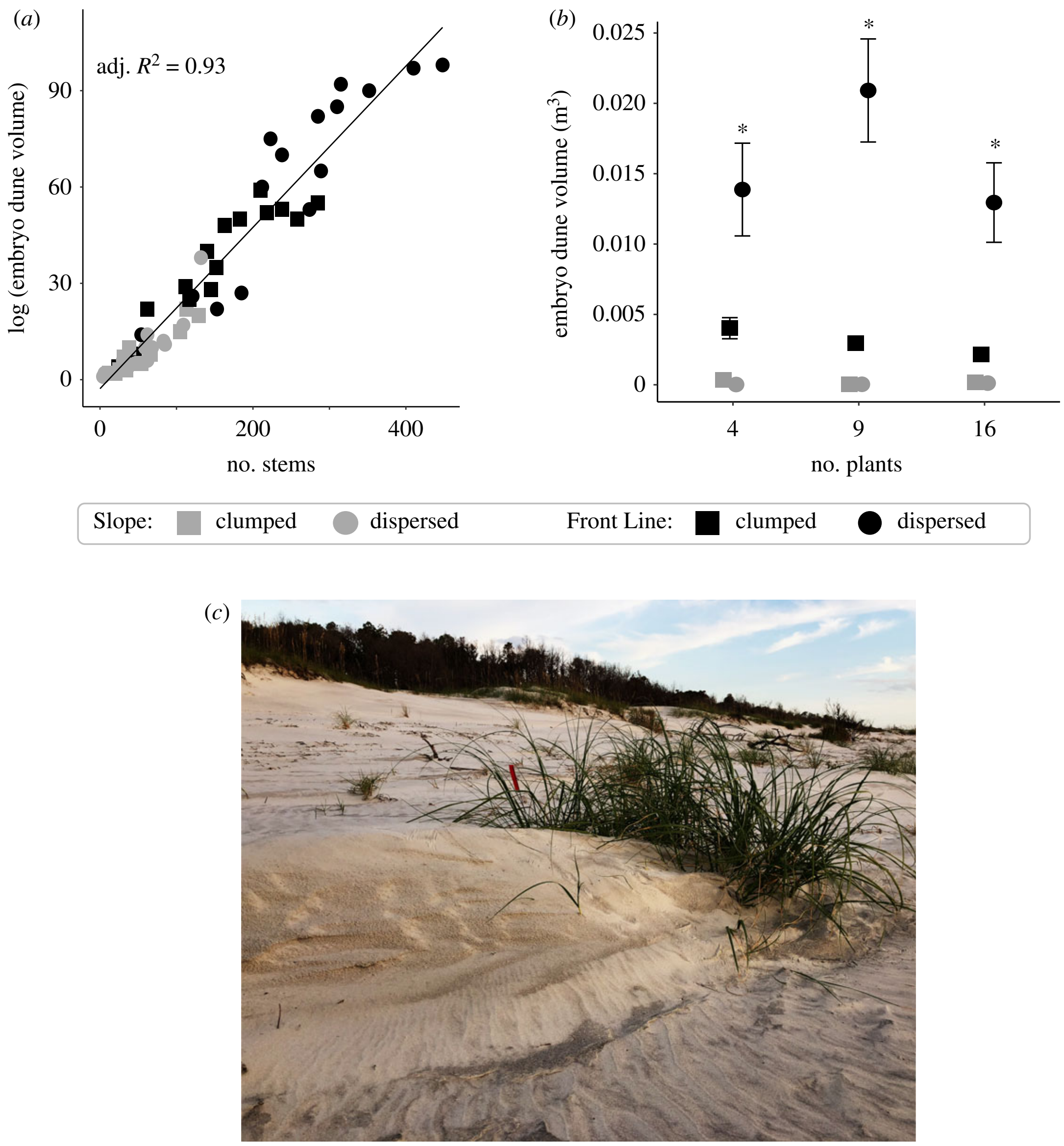

**Figure 5.** Embryo dune formation in Georgia. (*a*) Stem count is tightly linked to dune formation. (*b*) On the Front Line, dispersed arrays built significantly larger embryo dunes than clumped ones. (*c*) Photograph of embryo dune form in a nine-plant dispersed treatment on the Front Line. Error bars in (*b*) are mean dune volume ± s.e. Asterisk indicates significant differences between configurations (Tukey's HSD $p < 0.01$); density did not influence embryo dune volume. (Online version in colour.)

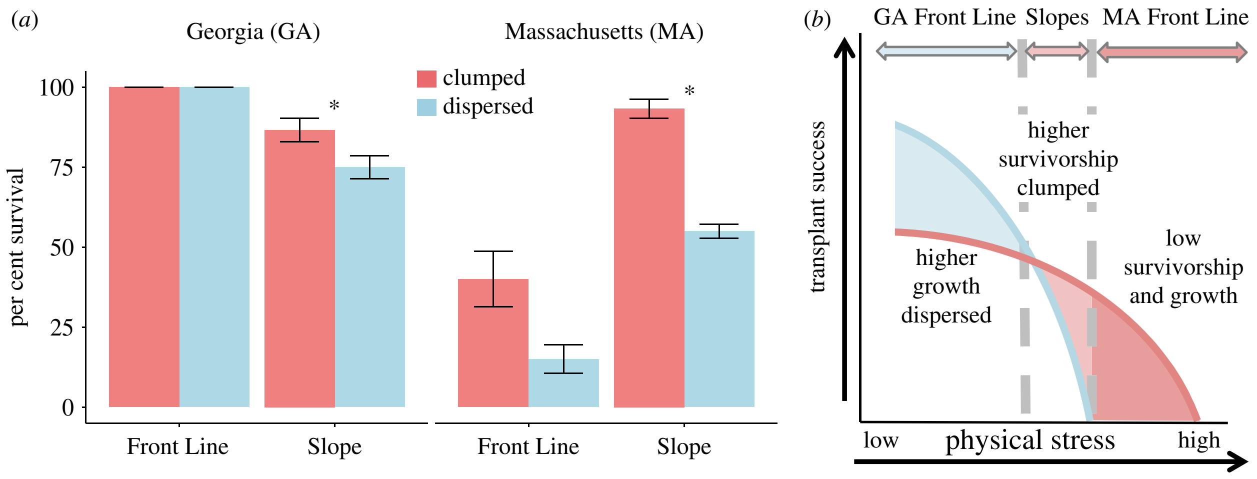

**Figure 6.** (*a*) Survival across experimental zones in Georgia (GA) and Massachusetts (MA) by planting configuration. (*b*) Zones marked along the modified SGH predicting optimal planting configuration across a physical stress gradient. Error bars are mean survival ± s.e. Asterisk indicates significant differences (Tukey's HSD $p < 0.01$) between clumped and dispersed arrays. (Online version in colour.)

intraspecific competition. Dispersed transplants on the Front Line also re-sprouted more tillers than those in clumped configurations post-disturbance (although the percentage increase in tiller counts were similar across these treatments), indicating configurations that promote growth also promote resilience. Research on dune resilience has thus far focused predominantly on large-scale sediment transport and dune migration processes [40,41], with little known about disturbance effects on individual dune plants. Here, we show that the resilience of dune plants to disturbance depends on their spatial configuration, both with regards to the number and proximity to neighbouring conspecifics. In short, both naturally occurring and restored dune plants are most likely display resilience when they occur in low-stress, high-nutrient areas and experience little competition from neighbours.

### (b) Transplant growth strategies

Similar to many foundation species in marshes, seagrass and other dune systems, sea oats and American beachgrass propagate via vegetative expansion and can exhibit trade-offs in lateral versus vertical growth [42]. We show such morphological plasticity can be sensitive to environmental settings and planting configurations. Specifically, sea oats were consistently taller and grew more stems on the low-stress Front Line (figures 3 and 4). Within this zone, transplants in clumped, facilitation-maximizing arrays increased their allocation to vertical growth, while the competition-minimizing plantings allocated more resources to rhizomatic growth. Similar intraspecific plasticity has been observed in seagrass meadows, where rhizome morphology varied based on position within a patch and number of competitors [43], and in grassland systems, where lateral expansion was reduced in the presence of competitors [44]. In both of these studies and in our experiment, plants in low-competition environments showed a greater tendency to colonize new areas, which is a critical dimension of transplant performance for restoration efforts focused on rehabilitating large habitats. Thus, our results can probably be expanded to other ecosystems, where varying transplant configuration can be used as a tool to maximize either plant vertical growth or lateral expansion to meet project-specific performance targets.

### (c) Dune formation

Embryo dune formation has been a key focus of dune restoration efforts as it is a crucial first step to establishing new habitat [30,45]. The formation of these structures depends on geo-physical factors such as beach width, sediment grain size, wind speed, storm frequency [45,46] and biological factors such as plant cover and species composition [30]. By allocating resources to lateral expansion, we discovered that dispersed plantings on the Front Line created biogenic conditions particularly conducive to dune building (figure 5). As such, transplant configuration and planting location appear to play important roles in mediating habitat formation rates. While embryo dune formation is unique to sand dunes, many coastal restoration projects rely on sediment capture by foundation species to expand the focal habitat and re-establish its ecological functionality [10,12]. Sediment instability often leads to failure in restoration efforts across coastal ecosystems including mangroves [47], marshes [48] and seagrass beds [49], and thus stabilizing sediment with dispersed plantings of clonally propagating species may be a broadly applicable mechanism for improving restoration outcomes.

### (d) Context dependency of transplant survivorship

Our results from Georgia clearly support the planting of low-density, dispersed treatments in areas of low physical stress. As stress increased, clumping transplants and increasing transplant density stimulated intraspecific facilitation and increased transplant survival at both sites. However, all other metrics of restoration success (stem production, resilience, dune formation) did not respond to planting configuration or density in high-stress areas. These findings align with other studies in sand dunes [50] and streamside plant communities [51], where, in highly stressful and nutrient poor conditions, facilitation increased plant survival but not growth. These results highlight that the predictions from the modified SGH hold as stress levels increase but that additional interventions, such as nutrient amendments via wrack addition or fertilization, may be needed to boost the growth of surviving plants in high stress locations. Finally, in the zone most influenced by saltwater inundation, the Massachusetts Front Line, we saw reduced growth and survival of all transplants, regardless of treatment. This suggests that investment in restoration may not be wise in such locations, as simple solutions such as clumping transplants are unable to ameliorate stressors. Alternatively, additional interventions may be needed to restore dune zones experiencing such high-stress regimes, such as the placement of offshore shoals to reduce wave stress. More broadly, this finding highlights that at levels of extreme physical or biological stress, facilitation benefits derived from re-configuring transplants can be exceeded and thus using the modified SGH alone may not be sufficient for developing successful restoration designs.

## 5. Conclusion

This study sheds light on how planting location, density and configuration affect restoration yields. We observed strong evidence for the use of competition-minimizing arrays in low-stress environments, and showed that facilitation-maximizing arrays can increase transplant survival as stressors increase, up to a certain threshold. As transplant success was highest in dispersed configurations on the Georgia Front Line but lowest in those same treatments on the Massachusetts Front Line, our study reveals that identifying the stress gradients of a system and assessing how those stressors act on the habitat-forming foundation species are crucial first steps in restoration design. Once such gradients are understood, practitioners can prioritize the restoration of relatively low-stress locations, where transplants are most likely to exhibit fast growth, high resilience and significant habitat formation, and use competition-minimizing planting strategies in these locations. With increasing stress, clustering plantings can increase survivorship, but additional interventions may be needed to increase growth. Additionally, as stressors such as storm frequency, heatwaves, rising sea levels and drought increase, novel restoration strategies may be needed given our finding that facilitation did not increase restoration outcomes in the highest-stress zone of our study.

Further work is now needed to evaluate if facilitation-maximizing arrays improve restoration success on the larger scales at which restoration typically takes place and over the longer time frames needed for transplants to converge and develop into contiguous habitats. While revegetation is the most common form of dune restoration globally, it is inherently limited in scale as transplants must be individually planted [52]. Our results and many other restoration studies focus on improving restoration strategies at this transplant scale. Additional research is now needed to assess the potential for competition-minimizing and facilitation-maximizing strategies to be integrated into restoration designs at larger 'patch' and ecosystem scales. Such optimization of patch-to-patch and cross-ecosystem facilitation benefits for foundation species may be vital for enhancing the pace and scales at which restoration is needed to regain degraded ecosystems.

Data accessibility. Data has been deposited to the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.v314nd6 [53].

Authors' contributions. H.S.F., S.M.C. and C.A. designed the study, H.S.F. and S.M.C. collected the data, H.S.F. analysed the data, H.S.F. and C.A. wrote the manuscript and all authors revised the manuscript.

Competing interests. We declare we have no competing interests.

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