COMMUNITY IMPACTS OF A TUSSOCK SEDGE: IS ECOSYSTEM ENGINEERING IMPORTANT IN BENIGN HABITATS?

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Abstract. Ecosystem engineers impact other organisms through environmentally mediated indirect interactions, but the potential for the mechanisms and importance of engineering to vary predictably across environmental gradients has not been investigated. Previously, we investigated how hummock formation by *Triglochin maritimum* in physically stressful salt marsh pannes influences the plant community that grows only on hummock tops and found that species diversity was dependent on indirect positive effects of *T. maritimum* engineering. Here we examined how *Carex stricta*, the tussock sedge, drives superficially similar spatial patterning of plants in relatively benign tidal freshwater marshes at the opposite extreme of an estuarine salinity gradient. In *C. stricta* marshes, the entire vegetative community is located almost exclusively on top of tussocks while inter-tussock spaces are bare mud buried in *C. stricta* wrack. We manipulated tussock height, belowground substrate, and aboveground competition for light to investigate the mechanisms by which *C. stricta* influences the wetland plant community. We also conducted wrack-removal experiments and phytometer assays to examine the importance of wrack deposition in this community and to investigate the spatial distribution of herbivore pressure, respectively. Transplants of four common species performed well in all treatments, except natural inter-tussock spaces buried in wrack. Removal of wrack from inter-tussock spaces enabled substantial seedling emergence and vegetative cover within one growing season. *C. stricta* therefore drives plant distribution primarily through indirect negative impacts of wrack accumulation in inter-tussock spaces. Once tussocks are established, plants obtain a secondary benefit when growing on tussocks, as the inter-tussock spaces become runways for small mammalian herbivores that concentrate feeding in low protected areas. These results differ dramatically from nearby salt marshes where *T. maritimum* facilitates community diversity by alleviating physical stresses. The mechanisms and outcomes of hummock-forming engineers may thus vary predictably across estuarine salinity gradients where hummock formation has facilitative and important impacts in physically stressful environments, but negative and less essential impacts in physically benign environments.

Key words: abiotic gradients; Carex stricta; *coastal marshes; ecosystem engineer; salinity gradient; tidal freshwater marsh.*

INTRODUCTION

Ecosystem engineers are organisms that, through their presence or activities, modify their surroundings and thereby indirectly impact other organisms (Jones et al.1994). In recent years, interest in the ecosystem-engineering concept has stimulated researchers to investigate both the mechanisms and outcomes of engineering on natural communities (e.g., Gutierrez et al. 2003, Lill and Marquis 2003, Fogel et al. 2004) and has focused interest on how organisms can influence the abiotic conditions that drive community patterns (Cardinale et al. 2004). Despite this interest, the relative role and importance of ecosystem engineering across abiotic gradients has received little attention.

Investigations into direct species interactions have demonstrated that, in general, organisms tend to have positive associations in more stressful environments and negative interactions in more benign physical environments (Bertness and Callaway 1994, Brooker and Callaghan 1998, Bruno et al. 2003). Because engineers impact other organisms through environmentally mediated indirect interactions, their impact or importance in communities may also vary predictably with background environmental conditions. Jones and colleagues (1997) suggested that engineers may be more important in harsh physical environments, but this hypothesis has not been investigated. Developing a predictive understanding of where and when engineers will have large community impacts is essential for developing the engineering concept, incorporating ecosystem engineering into ecological theory, and applying ecosystem engineering to conservation (Jones et al. 1997, Reichman and Seabloom 2002, Wilby 2002).

In wetland communities, the presence of hummocks created by wetland plants is a common engineering feature. Waterlogged soils have low oxygen content and generally reduced sediments (Mendelssohn et al. 1981,

Howes et al. 1986, Mitsch and Gosselink 2000), which pose a major physiological stress on terrestrially derived macrophytes (Cronk and Fennessy 2001). Wetland plants have both biochemical and structural adaptations to deal with anoxic sediments. Biochemical responses enable plants to respond quickly to anoxic conditions by converting to anaerobic metabolism (Mendelsohn et al. 1981, King et al. 1982), while structural adaptations are a longer term strategy. A particularly common structural adaptation is the formation of aerenchyma tissue, a system of hollow tubules that enables passive diffusion of oxygen from plant leaves to their roots (Armstrong 1978). Other structural adaptations include gas transport mechanisms such as pressurized ventilation (Dacey 1981) or venturi-induced convection (Armstrong et al. 1992), as well as stem and root adaptations. Hummock formation in wetlands is a relatively less-studied response to waterlogged soils and is the result of shallow rooting by plants that position their roots above the soil or in the thin oxygenated subsurface soil layer. Shallow roots subsequently capture and retain sediments on which roots continue to grow and build hummocks (Fogel et al. 2004). While an elevated root mass generally occurs in response to exposure to waterlogged soil conditions (Bertness et al. 1992, Fogel et al. 2004), and benefits the hummock-forming species, the community-level impacts of root mound formation are largely unknown. However, studies have shown that microtopographic heterogeneity in wetlands increases species diversity (Vivan-Smith 1997) and that, in freshwater wetlands, conversion from tussocked marshes to homogeneous topography is accompanied by a loss of species diversity (Werner and Zedler 2002). Therefore, plant hummocking may have large community-level impacts in wetlands.

In New England estuaries, plant hummocking can be found in both salt and tidal freshwater marshes. These marshes experience predictable tidal inundation twice daily and thus experience similar waterlogging regimes. However, edaphic stress varies dramatically between these marshes due to variation in marine influence (Crain et al. 2004). Anoxic salt marsh sediments have high levels of salt and sulfide, both major physiological stressors for marsh macrophytes (Queen 1974, Koch et al. 1990), and are effectively absent in tidal freshwater marshes (Odum 1988). This shift in abiotic conditions correlates with shifts in marsh productivity (Odum 1988, Crain et al. 2004), confirming a gradient in stress for marsh plants. The estuarine gradient thus provides an ideal physical gradient to test whether the mechanisms and outcomes of ecosystem engineering by hummocking wetland plants shifts with environmental stress.

Recently, we investigated the mechanisms and consequences of mound engineering by *Triglochin maritimum* L. on plant communities in waterlogged forb pannes of northern New England salt marshes (Fogel et al. 2004). We found that by forming rings elevated 5–10 cm above the marsh surface, *T. maritimum* created drained sediments that were less reduced and saline than the background marsh and thereby promoted a greater diversity and abundance of other salt marsh species. At the opposite extreme of the estuarine salinity gradient, *Carex stricta* Lam., the tussock sedge, creates raised tussocks in tidal freshwater marshes. *Carex stricta* tussocks are large mounds of old culms and roots that bind sediment and can be >50 years old (Costello 1936). As in the *T. maritimum* marsh, the entire vegetative community in the *C. stricta* marsh grows almost exclusively on top of the tussocks and rarely in the background marsh. We conducted a series of experiments to determine how *C. stricta* drives this distinct spatial patterning and then compared our results to engineering by *T. maritimum* in stressful salt marsh pannes. Specifically, we addressed the following hypotheses: *C. stricta* tussocks drive plant distribution patterns through (1) positive feedbacks due to tussock height, (2) negative impacts of wrack deposition, (3) modification of herbivory patterns, or (4) differential seed dispersal. We tested these hypotheses by using experimentally manipulated tussocks to examine differences in plant performance due to above- and belowground competition and engineering effects of raised height and wrack deposition. Through these manipulations we were also able to compare the relative importance of engineering effects (raised height and wrack accumulation) vs. the direct competitive effects of *C. stricta* on the plant community.

Our results reveal that, while hummocks in freshwater and salt marsh habitats superficially appear to be similar and may be initiated by similar mechanisms, the community consequences and dynamics of freshwater marsh and salt marsh hummocks differ markedly as a function of the level of physical stress in these habitats.

METHODS

Fieldwork was conducted in tidal freshwater marshes on the Branch Brook fork of the Little River in the Wells National Estuarine Research Reserve/Rachel Carson National Wildlife Refuge in southern Maine, USA. Within the low-salinity marshes (0–3 ppt) in the upper reaches of the estuary, the tussock sedge, *Carex stricta*, grows in large mounds in the low intertidal, particularly on the inside banks of oxbow turns in the river channel. A high diversity of marsh macrophytes (over 20 species) live in these marshes and grow almost exclusively on top of tussocks. Inter-tussock spaces are buried in accumulated *C. stricta* wrack. *Carex stricta* zones generally occupy areas between 50 m^2 to 450 m^2 in area. The marshes are covered twice daily by the tide, which has a tidal amplitude of >3 m.

Tussock marsh description

Surveys were conducted to document vegetation patterns within a typical tidal freshwater tussock marsh.

In July 2002, 10 randomly selected tussocks and inter-tussock areas were characterized. Percent cover of dominant species (>3% cover) on tussocks and inter-tussock spaces was quantified and total aboveground biomass was harvested, sorted to species, dried, and weighed. To quantify differences in soil properties, we measured soil water content and percentage of organic matter. Cores ($5 \times 5 \times 10$ cm) were taken from each of the 10 tussock and inter-tussock areas to measure soil water content and percentage of organic content. Cores were weighed wet and dry, then homogenized, and a 5-g subsample was burned for 4 h at 550°C and weighed again. Tussock and inter-tussock diameters were recorded and height above mean sea level (MSL) was quantified with a Trimble 4800 global positioning system (Trimble, Sunnyvale, California, USA) in static download at a local marker, post-processed using On-line Positioning User Service (OPUS, system accurate to within 2 cm using the projection model of earth's gravity, Geoid99, corrected to the North American Vertical Datum from 1988 [NAVD88]; *available online*)[2] and visual survey equipment to integrate individual points.

Community impacts of ecosystem engineering

To examine the effects of the tussock-forming species on the vegetative community, we created eight experimental treatments to look at the main and inter-active effects of belowground competition (mud or tussock), height (up or down), and aboveground competition for light (with or without) on plant performance and community composition. Ten replicates of the eight following treatments were created: (1) control tussock (unmanipulated tussock), (2) tussock with *C. stricta* tillers removed (tussock with reduced aboveground competition), (3) tussock lowered to the height of the background mud (aboveground competition without tussock elevation), (4) lowered tussock with *C. stricta* tillers removed (reduced aboveground competition without tussock elevation), (5) artificial tussock with vexar shading to mimic aboveground competition for light (tussock mimic), (6) artificial tussock without shading (tussock mimic with reduced aboveground competition), (7) background inter-tussock mud with wrack (control inter-tussock), and (8) inter-tussock mud with wrack removed. While competition from aboveground plants or plant mimics (shade) differ from light reduction by wrack deposition, which additionally engineers the inter-tussock environment, we analyzed all of these treatments as aboveground competition to keep a balanced design examining the competitive factors naturally present in the various treatment types, and so we could examine relative plant performance across manipulations.

Tussock manipulations were created by digging around the base of the tussock to >60 cm depth in

order to keep the roots intact. Tussocks were then either replaced as controls, or soil was excavated from below the roots and the tussock was then sunk to be flush with the background mud. For *C. stricta* removals, shoots were pulled gently from their belowground roots and repeatedly weeded weekly throughout the growing season; however, regrowth was minimal after the first month of weeding.

Artificial tussocks (tussock mimics) were constructed by creating cylinders of 0.5 cm black plastic mesh (Vexar) closed with cable ties and filled with mud excavated from lowered tussock treatments. The tussock mimics were stabilized on the marsh surface by sinking two 60 cm lengths of rebar (metal reinforcement rod) through the artificial tussock and into the substrate as anchors. Artificial tussocks were constructed to be the average size of natural tussocks and were ~25 cm tall and 30 cm in diameter. Artificial tussocks were shaded to mimic aboveground competition for light by stapling a double layer of 0.5-cm black plastic mesh (Vexar) to four 2 m tall wooden stakes placed around the artificial tussock. Finally, low mud treatments were selected by demarcating inter-tussock spaces and either leaving standing dead wrack intact or removing the wrack and pinning back overhanging tussock vegetation with garden staples.

In May 2002, size-standardized transplant units of four species common to the tussock marsh were transplanted into each of the tussock treatments to examine plant performance. Individual ramets of the perennials *Calamagrostis canadensis* Michx., and *Carex stricta* Lam., three ramets of the perennial *Juncus balticus* Willd., and individual seedlings of the perennial *Aster novi-belgii* L. were harvested and transplanted onto each of the experimental tussock treatments (80 transplants/species) and marked at the base with twist-ties. Aboveground biomass of all transplants was harvested in mid-August, dried, and weighed. Naturally occurring *Aster novi-belgii* seedlings on half of the treatment tussocks ($N = 5$) were also marked in May 2003 with colored toothpicks and followed until the end of August to monitor the success of naturally dispersing seedlings in different treatment types.

Within each experimental tussock treatment, edaphic factors were measured over the growing season. Salinity was recorded weekly throughout 2002 and monthly in 2003 by squeezing small sediment cores ($2 \times 2 \times 2$ cm) onto a hand-held NaCl refractometer ($\pm$ 2 ppt; Extech Instruments, Waltham, Massachusetts, USA). Light levels (photosynthetically active radiation [PAR] in μmol·m^{-2}·s^{-1}) at the base of the treatment were measured with a Quantum Meter (Apogee Instruments, Logan, Utah, USA) wand integrating over 0.5 m on a cloudless day in July. To specifically address the impact of height and cover on temperature, data loggers (Onset Corporation, Bourne, Massachusetts, USA) were deployed in raised artificial and natural tussocks and in inter-tussock spaces with and without natural wrack

deposition for the month of May 2004, recording ambient air temperature at the treatment surface every 15 min.

Plant community characteristics on the experimental tussocks themselves were monitored by quantifying percent cover of vegetation on the tussocks in May, July, and August of 2002 and 2003. In August 2003, total aboveground vegetation in a central 10 × 10 cm quadrat of each experimental treatment was harvested, sorted to species, dried, and weighed. To assess longer term effects of tussock height on the plant community, total aboveground biomass on all raised and lowered tussocks with *C. stricta* intact was harvested in August 2004, sorted to species, dried, and weighed, and data was used to calculate Shannon-Weiner diversity indices for each treatment.

Seed dispersal

To address an alternative hypothesis that seed dispersal drives spatial patterns of the vegetation, we quantified seed dispersal throughout the tussock marsh. In September 2002, seed traps were deployed on raised control tussocks with vegetation intact, raised artificial tussocks, natural inter-tussock spaces buried in wrack, and natural inter-tussock spaces with wrack removed (N = 30 per treatment). This array allowed us to test the effects of height and cover (tussock vegetation in raised treatments and *C. stricta* wrack in inter-tussock spaces) on seed delivery. Seed traps were constructed by cutting Styrofoam plates into 6 cm diameter circles onto which a thick coat of Tanglefoot insect trap was smeared (Tanglefoot, Grand Rapids, Michigan, USA). Plates were then deployed into the four tussock treatments and secured with a garden staple. Plates were collected in mid-November and the identity and number of seeds on each plate was counted under a magnifying lamp.

Seedling emergence

A wrack removal experiment was conducted in *C. stricta* tussocks along a nearby tributary to examine the potential for vegetation to colonize inter-tussock spaces when wrack was experimentally removed. Tussocks along a 0.4-km section of the creek bank were used in this experiment. Within this region, sixteen inter-tussock spaces were randomly selected and, in late March 2003, all wrack was raked and removed from the area while another 16 inter-tussock spaces were left with wrack intact. Percent cover of total vegetation in inter-tussock areas was recorded in May, July, and August. In addition, a 10 × 10 cm area within each inter-tussock space was demarcated and individual grass and forb seedlings within the area were counted and monitored in June, July, and August to calculate seedling mortality rates.

Herbivory

The presence of mammalian herbivores, particularly muskrat, groundhog, and deer, was apparent within the tussock marsh, especially in inter-tussock habitats. We hypothesized that these herbivores could play a role in tussock maintenance by focusing their herbivory in inter-tussock habitats. In spring 2003, we quantified herbivory in this system by recording evidence of herbivory within experimental tussocks. Plants clipped at their base or abandoned green leaves with gnaw marks were scored as evidence of herbivory, and each experimental tussock was scored as having either presence or absence of herbivore evidence.

In addition, a plant tethering experiment was conducted to examine the spatial dynamics of herbivore pressure. In June 2003, centrifuge tubes filled with sugar water were sunk flush with the substrate of vegetated and non-vegetated raised tussocks and low inter-tussock spaces with and without wrack (N = 10). In the late afternoon of June 26, healthy green shoots of *Carex stricta* and *Aster novi-belgii* were clipped at their base and one shoot of each species was placed within each centrifuge tube. On the morning of June 27, plants were collected and scored as eaten or not. This experiment was replicated on two more consecutive nights.

Statistical analysis

Data were analyzed with JMP statistical software (SAS Institute 2001). Biomass data were log(x + 1)-transformed when necessary to improve homogeneity of variances. Transplant biomass and seedling survival were analyzed as fully factorial experiments testing substrate, height and competition and all of the interactions. Because tussock and mud treatments began at such different starting points, *C. stricta* biomass and dead material after two growing seasons were analyzed by height and competition only in tussock treatments. Height effects on species diversity (Shannon-Wiener diversity index, H') was analyzed after three growing seasons for raised and lowered tussocks with *C. stricta* intact.

RESULTS

Tidal freshwater tussock marshes are characterized by a highly productive and diverse plant community growing exclusively on the tops of tussocks surrounded by inter-tussock areas that are bare mud and buried in *C. stricta* wrack. Tussocks were raised ~25 cm above the background mud (tussock = 1.55 ± 0.0084 m above MSL; mud = 1.3 ± 0.011 m above MSL). Dominant plant species growing on the tussocks were somewhat patchy and varied temporally throughout the growing season with *C. stricta* growing and flowering first in June, followed by *Spartina pectinata* Bosc ex Link and *Calamagrostis canadensis* in late July, and finally in fall by *Aster novi-belgii*. Aboveground biomass growing on raised tussocks averaged close to 800 g/m², while in inter-tussock spaces biomass was essentially 0 g/m². Soil water content was not significantly different in inter-tussock vs. tussock cores (61.1% ± 1.03% vs. 58.2% ± 1.7%, respectively; $F_{1,19}$ = 2.05,
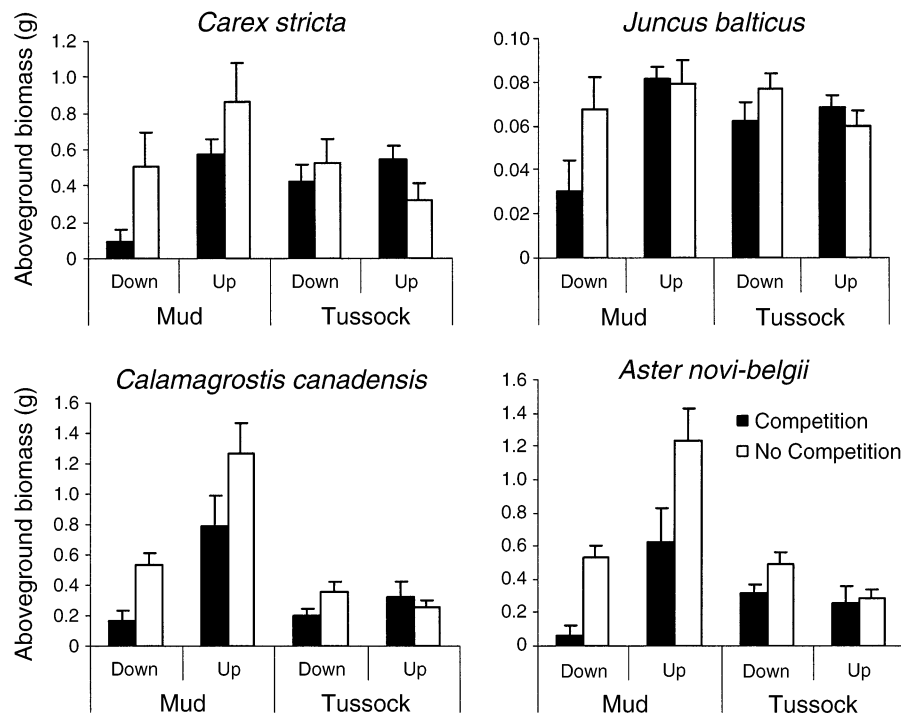
FIG. 1. Aboveground biomass (g) of four common tussock marsh species transplanted to manipulated tussocks that vary in substrate (mud or tussock), height (up or down), and aboveground competition (with or without). Columns are means + SE for 10 individuals per treatment. In the tussock treatment, up and down refer to naturally raised or artificially lowered tussocks, and competition and no competition refer to with or without aboveground *C. stricta* shoots. In mud treatments, up and down refer to artificially raised or naturally low mud, and competition and no competition on raised mud refer to with or without artificial vexar shades, while in low mud they refer to with or without natural *C. stricta* wrack.

$P = 0.1692$) and organic content was significantly greater on tussocks than between tussocks (40.3% ± 2.4% vs. 27.3% ± 1.8%, respectively; $F_{1,19} = 18.55$, $P = 0.0004$). Tussocks had consistent size and spatial distribution; tussock diameter averaged 40.05 ± 1.67 cm and inter-tussock space averaged 22.01 ± 0.99 cm across.

Community impacts of ecosystem engineering

In general, plant performance for the four transplanted species was consistent across experimental tussocks with two exceptions (Fig. 1, Table 1). Most importantly, all transplants performed the worst and were effectively unable to survive in inter-tussock spaces buried in wrack (Fig. 1; mud, down, competition). When wrack was removed from inter-tussock mud, transplants performed as well as they did on tussocks, indicating that wrack burial, not height, limited plant performance in inter-tussock spaces. Lowering the tussocks themselves had little impact on transplant biomass, and removing *C. stricta* shoots on raised and lowered treatments had no consistent effect on transplant success. The only treatment where transplants consistently performed better was on artificial tussocks with no shade. This treatment had the benefit of being raised with no belowground competition from roots or aboveground re-

TABLE 1. Performance of four common species transplanted to tussocks, where substrate (S), height (H), and competition (C) were experimentally manipulated.

Variable	Carex stricta		Juncus balticus		Calamagrostis canadensis		Aster novi-belgii	
	F	P	F	P	F	P	F	P
Substrate	0.011	0.918	0.107	0.745	18.734	**<0.0001**	8.377	**0.005**
Height	5.668	**0.020**	3.321	**0.074**	12.012	**0.001**	8.502	**0.005**
Competition	1.449	0.233	2.061	0.157	8.173	**0.006**	13.881	**<0.0001**
S × H	7.338	**0.009**	6.496	**0.014**	11.444	**0.001**	18.743	**<0.0001**
H × C	2.524	0.117	4.720	**0.034**	0.673	0.415	0.203	0.654
C × S	4.894	**0.030**	1.063	0.307	4.530	**0.037**	7.512	**0.008**
S × H × C	0.142	0.708	0.299	0.587	0.524	0.472	0.002	0.961

Notes: Degrees of freedom for all tests were 1, 54. Significant effects ($P < 0.05$) are in boldface.
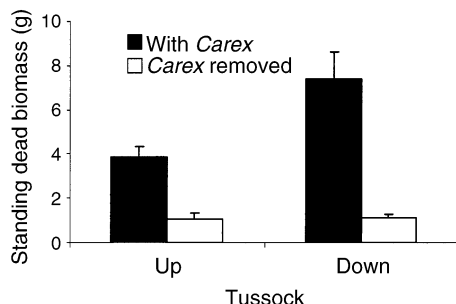
FIG. 2. Standing dead biomass in 100 cm^2 from natural tussocks after two growing seasons of experimental manipulation. Up and down refer to naturally raised and artificially lowered tussocks. Columns are means + SE for 10 independent tussocks.

duction in light, indicating that the tussock marsh is a highly competitive environment and only removal of all sources of competition allows a competitive release for transplanted plants.

Survival of naturally occurring seedlings again was highest in artificial tussocks with no shade and lowest in low mud buried in wrack (80.835% ± 9.82% and 5% ± 5%, respectively). Only the main effects of height and competition were significant in driving seedling mortality. Seedling mortality was consistently higher in low treatments ($F_{1,31} = 8.14$, $P = 0.0076$) and with competition (and $F_{1,31} = 12.7$, $P = 0.0012$).

In natural tussock manipulations, treatment height had a substantial impact on the plant community. Raised tussocks were significantly more diverse than lowered tussocks (raised tussock $H' = 0.52 ± 0.036$, lowered tussock $H' = 0.35 ± 0.053$; $F_{1,18} = 7.18$, $P = 0.0158$) primarily due to higher species evenness. Lowering the tussocks caused C. stricta biomass to more than double (lowered = 1079.6 ± 193.2 g/m^2 vs. raised = 496.0 ± 112.7 g/m^2; $F_{1,17} = 4.96$, $P = 0.04$) due to trends both to increase biomass per stem and increase stem density in lowered tussocks (C. M. Crain and M. D. Bertness, unpublished data). Standing dead production was much higher in lowered plots and those with C. stricta intact (Fig. 2), indicating both that C. stricta is the species responsible for standing dead production and that C. stricta increased production when lowered. Conversely, direct aboveground competition by the engineer had little effect on the remaining community. Removal of C. stricta shoots had no significant effect on other species, suggesting that belowground resources within tussocks are equally limiting, so that plants could not take advantage of reduced aboveground competition.

While salinity did not differ across tussock treatments ($P > 0.24$, all tests), light and temperature varied significantly across treatment tussocks. Measurements of PAR in experimental tussocks showed that both lower treatments and treatments with competition intact had reduced light penetration (Fig. 3). In lowered tus-

socks with C. stricta removed, light penetration was as low as raised tussocks in full competition. As suspected, light penetration was severely reduced in lowered mud treatments with wrack intact. PAR measurements confirmed that, for artificial tussock treatments, shade mimics (Vexar) effectively replicated aboveground light reduction from C. stricta shoots. Temperature also varied substantially across tussock treatment. Mean base temperatures were significantly lower in low and vegetatively covered (by plants on tussocks or wrack in inter-tussock spaces) treatments, and there was no significant interaction ($F_{1,8} = 35.05$, $P = 0.002$ and $F_{1,8} = 9.12$, $P = 0.0295$ main effects of vegetative cover and height, respectively). Vegetative cover significantly reduced the extremes of temperature variability, while height and the interaction had no effect. Maximum temperature in non-vegetated treatments was 42.7° ± 1.53°C vs. 25.9° ± 1.4°C with vegetation and minimum temperatures were 0.82° ± 0.6°C and 3.0° ± 0.55°C in non- and vegetated treatments, respectively.

Seed delivery and seedling emergence

Seed delivery varied substantially for the two species captured in great enough abundance to analyze. More Aster seeds were trapped on raised treatments ($F_{1, 117} = 3.75$, $P = 0.055$) and uncovered plots ($F_{1, 117} = 3.27$, $P = 0.073$). Height and vegetative cover interactively influenced C. stricta seed supply with cover increasing delivery much more on raised tussocks than in lowered tussocks. Total seed delivery was only influenced significantly by height ($F_{1, 117} = 8.76$, $P = 0.0037$), with higher delivery in raised plots (Fig. 4). Regardless, seeds were trapped in all sites tested, and thus, seed dispersal is not limiting the spatial distribution of the vegetation.

When wrack was experimentally removed, significantly more seedlings emerged in the spring ($F_{1,31} = 21.93$, $P < 0.0001$). Although seedling mortality was high in inter-tussock spaces with wrack removed, vegetative cover at the end of the growing season was significantly greater in the wrack-removal than in the wrack-intact inter-tussock spaces (Fig. 5).
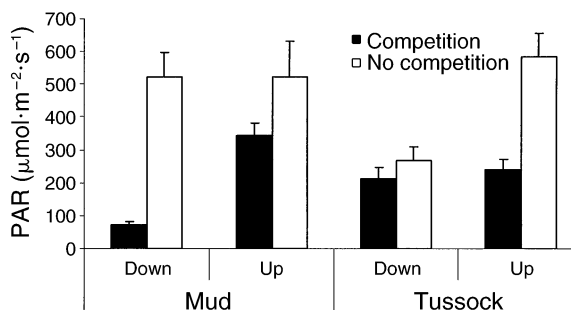

FIG. 3. Photosynthetically active radiation (PAR in μmol·m^{-2}·s^{-1}) at the base of experimental tussocks ($N = 10$). See Fig. 1 for treatment descriptions.
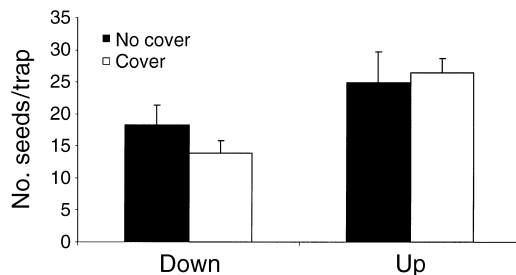
FIG. 4. Total seeds captured on 10 cm diameter sticky traps placed on natural and artificial tussocks (''Up'': cover and no cover, respectively) and inter-tussock mud with and without wrack (''Down'': cover and no cover, respectively). Data are means + SE for 30 replicate seed traps.

Herbivory

Evidence of herbivory in experimental tussock treatments was substantially higher in all mud treatments (full model ordinal logistic fit $\chi^2 = 42.85$, df = 7, N = 80, $P < 0.0001$; post hoc Pearson's chi square testing the main effects of and cover and height $P > 0.15$, but substrate $\chi^2 = 31.6$, df = 1, $N = 80$, $P < 0.0001$). In inter-tussock mud areas, herbivory was present in 80% of both wrack-removal and wrack-intact sites. In artificial tussocks, herbivore evidence was present in 50% of shaded and 50% of open treatments. Herbivore evidence was much lower in natural tussocks regardless of height or *C. stricta* removal. Only 5% of the raised tussocks and 5% of the lowered tussocks had evidence of herbivory.

When *Aster* and *C. stricta* were distributed in centrifuge tubes, substantial herbivory was seen, mostly in inter-tussock areas (Fig. 6). For *Aster*, ~40% of the transplants were consumed in inter-tussock areas, both with and without wrack burial, while only 5% were consumed on raised mud or artificial tussocks. Only the effect of height was significant on *Aster* consumption ($F_{1,8} = 30.08$, $P < 0.0006$). For *C. stricta*, herbivores solely ate stems placed in low areas.

DISCUSSION

Vegetation in tidal freshwater tussock marshes is almost exclusively located on the tops of regularly spaced tussocks created by *C. stricta*, the tussock sedge (see Plate 1). Inter-tussock spaces are inhospitable environments due to the growth morphology of *C. stricta*, whose roots and rhizomes build on top of each other to form large tussocks and which holds standing dead material that falls and accumulates in surrounding inter-tussock spaces.

Community impacts of ecosystem engineering

Plant performance of transplanted individuals of four species, as well as naturally occurring seedlings, revealed that plant survival in the tidal freshwater marsh was not dependent on *C. stricta* tussocks. In contrast, indirect negative effects of *C. stricta* tussocks limited

available space for vegetation and thereby created distinct spatial patterning of the marsh vegetation.

All transplants were able to persist in all treatments except inter-tussock spaces buried in *C. stricta* wrack. Transplant survival in inter-tussock spaces when wrack was removed showed that background environmental variables (low elevation and substrate type) were not responsible for limiting plant growth in these areas. Results from our study confirmed previous findings that inter-tussock spaces have lower temperatures (LaDeau and Ellison 1999), lower oxygen content (Costello 1936), and more waterlogged sediments than tussocks. Despite these differences, the physical environment in inter-tussock spaces was not stressful enough to limit growth of dominant vegetation. Instead, burial by wrack was the key feature driving plant performance in the tussock marsh. Wrack burial has previously been shown to drive plant mortality in marshes (Bertness and Ellison 1987, Valiela and Rietsma 1995), and in *C. stricta* marshes wrack deposition and retention in inter-tussock spaces make wrack burial a constant spatial feature. *Carex stricta* wrack in inter-tussock spaces severely reduced light penetration (Fig. 2), and though not directly tested, it is likely that *C. stricta* wrack additionally created a major physical barrier to seedling growth (sensu Bergelson 1990). Results of the wrack-removal experiment further confirmed that, without the indirect negative effects of *C. stricta* wrack, seedling colonization and vegetative cover increased in inter-tussock areas.

Ecosystem engineer mediates herbivore impacts

The spatial pattern of tussock marsh vegetation is thus driven primarily by the negative impacts of *C. stricta* wrack. Once the pattern is developed, however, positive feedbacks reinforce the spatial structure. Inter-tussock valleys are at a disadvantage for light capture, so that even when wrack is removed, succession in these areas is slow compared to raised mud (C. M. Crain and M. D. Bertness, *unpublished data*), despite substantial seed delivery and germination success.
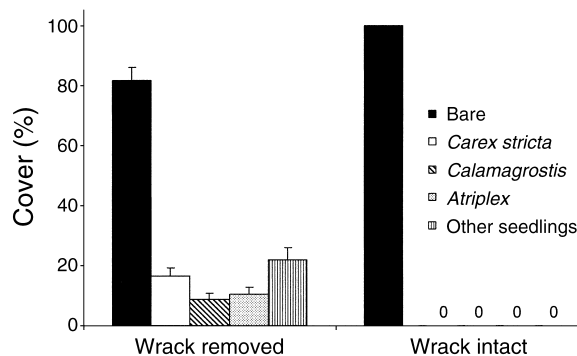

FIG. 5. Percent cover of bare space and colonizing seedlings and runners in wrack-intact and wrack-removed inter-tussock spaces ($N = 16$). Data are means + SE.
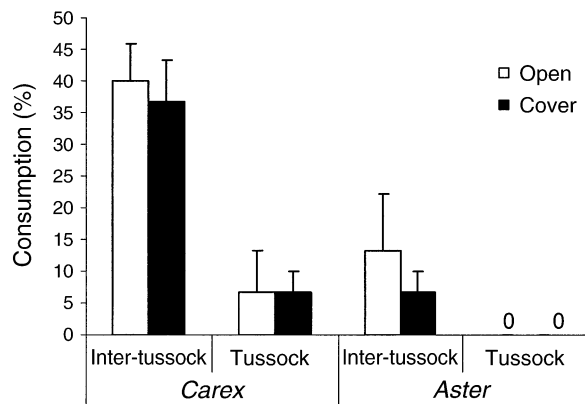
FIG. 6. Percentage of consumption of *Aster novi-belgii* and *Carex stricta* placed in inter-tussock spaces with and without wrack, and raised tussocks with and without vegetation. Data are mean percentage consumed + SE for three consecutive nights.

More importantly, inter-tussock spaces appear to serve as corridors for herbivore movement, which then concentrate herbivory in these areas. In the tethering experiment, shoots on raised tussocks had a large advantage over low areas in avoiding herbivory, due to both an advantage of raised height and vegetative cover. Associational defenses have been previously documented in *Carex* tussocks in streambed plant communities (Levine 2000). In light of this secondary structuring force, *C. stricta* engineering improves plant performance on raised tussocks, and thus reinforces spatial patterning. Therefore, the full community impacts of *C. stricta* are only apparent when this secondary process is considered. As in Levine 2000, these results emphasize the composite nature of plant interactions, in which both negative and positive effects contribute to ultimate distribution patterns. These results additionally highlight the importance of examining engineering over various scales of space and time to accurately capture engineering outcomes in light of other structuring forces such as predation and disturbance.

Direct vs. indirect impacts

Since all organisms engineer their environment at some level, an important criterion for determining when engineering is a significant community-driving process is when the importance of an organism's indirect engineering effects outweigh its direct effects. Here we found that direct competition by *C. stricta* was far less important than indirect engineering effects in driving species distribution, despite the highly competitive nature of this relatively benign environment.

Experimental transplants indicated that below- and aboveground competition were equally limiting in the tussock marsh, so that release from one alone (*C. stricta* removal or artificial tussocks with shading) did not substantially alter transplant performance (Fig. 1). Additionally, the diversity of species living in these marshes guaranteed that even with removal of the dominant species, others opportunistically exploited available resources. Transplants only exhibited competitive release when all sources of competition were removed in artificial tussocks without shading. In this highly competitive environment, removal of the direct competitive effects of the engineer is relatively insignificant and instead, habitat modification by *C. stricta* has much higher community impact.

Lill and Marquis (2003) also found that indirect engineering effects of leaf-tying caterpillars that create shelter for herbivorous insects outweighed direct biotic interactions in importance. We suspect the balance between the direct and indirect impacts of engineers varies with species and environment. Further research may reveal where and when one outweighs another.

Species diversity

While transplanted individuals enabled us to assess short-term plant performance in experimental treatments, tussock manipulations themselves enabled us to follow longer term impacts on the whole plant community. When tussocks were lowered, *C. stricta* substantially increased biomass production, possibly a mechanism promoting tussock formation (Fig. 2). Robust aboveground biomass made *C. stricta* so competitively dominant that species diversity plummeted in lowered tussocks. *Carex stricta* is more competitively dominant in low elevations, making species diversity benefit in raised tussock environments. While established tussocks negatively drive spatial distribution of plants through wrack accumulation in inter-tussock spaces, the growth and aging of tussocks promotes species diversity that might otherwise be competitively excluded. Tussock-promoted environmental heterogeneity may thus protect species diversity in these relatively benign marsh systems that are particularly susceptible to invasion by monotypic dominants (Chambers et al. 2003, Silliman and Bertness 2005). The removal of topographic heterogeneity has been shown to reduce species diversity in other wetland systems (Vivan-Smith 1997, Werner and Zedler 2002).

Ecosystem engineers in benign physical environments

This study elucidated the mechanisms and impacts of a tussock-forming engineer in a tidal freshwater marsh. Spatial patterning of vegetation in this marsh is driven primarily by the indirect negative effect of wrack deposition. Environmental conditions in this marsh are such that all species tested would be able to persist in the absence of the engineer, so while the engineer drives spatial distribution, it does not facilitate the community.

We recently conducted a similar study of a mound-forming species at the opposite end of the estuarine salinity gradient in a nearby salt marsh on Drake's Island, Wells, Maine, USA (Fogel et al. 2004). *Triglochin*

PLATE 1. Vegetation in a typical *C. stricta* marsh grows almost exclusively on tops of tussocks which are elevated above the water line at high tide. *C. stricta* drops dead wrack from the base of the tussock which accumulates in the low inter-tussock areas, limiting plant growth. Small mammalian herbivores then forage preferentially in the inter-tussock mud areas protected by wrack cover and further limit vegetation. Photo credit: C. Crain.

maritimum, common arrow grass, creates raised rings in waterlogged salt marsh forb pannes. *T. maritimum* engineering increases soil drainage and thereby increases reduction potential of the soil, which enables an increased abundance and richness of panne species to live on top of the rings. Similar spatial patterns of plants in these two environments were thus driven by entirely different mechanisms; negative feedbacks in the fresh marsh limit plant cover in inter-tussock spaces, while positive feedbacks in salt marsh pannes enable species to persist on raised rings. Additionally, species diversity is promoted in the salt marsh by alleviating limiting environmental factors, while it is promoted in the fresh marsh by reducing competition. It is therefore essential to experimentally test mechanisms of species interactions before process is assumed.

These comparative studies show that the outcomes of engineering may follow the proposed theoretical model that species interactions tend to be positive in stressful and negative in benign physical environments (Bertness and Callaway 1994, Bruno et al. 2003). This comparison also suggests that the importance of ecosystem engineering to the community may vary across physical stress gradients. In the salt marsh, species would be unable to populate the marsh without *T. maritimum*, while in the fresh marsh spatial pattern would change without *C. stricta*, but plant species may not be lost. We suspect that this context dependency of ecosystem engineering impacts on communities is a common and currently underappreciated aspect of ecosystem engineers.

Conclusions

In this study, we investigated the outcomes and mechanisms of engineering by *C. stricta* and addressed some unresolved problems with the ecosystem engineering concept. Understanding the relative importance of engineering, the scale and context dependency of

engineering, and the potential for engineering impacts to vary predictably with environment will help to improve the general concept and identify when and where engineering should be a key community-driving process. Understanding where engineers have a large effect will not only improve our ecological understanding of various communities, but has promising conservation implications. Engineers are potential targets of conservation since they can have inordinately large effects on the community (Bruno et al. 2003), increase habitat heterogeneity and, therefore, species diversity at a landscape scale (Wright et al. 2002), and control many ecological processes and functions that humans depend on. Thus, developing a predictive understanding of when and where engineers are likely to have large community impacts is a crucial step in integrating ecosystem engineering into conservation biology.

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