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LETTER

Foundation species patch configuration mediates salt marsh biodiversity, stability and multifunctionality

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Abstract

Foundation species enhance biodiversity and multifunctionality across many systems; however, whether foundation species patch configuration mediates their ecological effects is unknown. In a 6-month field experiment, we test which attributes of foundation species patch configuration – i.e. patch size, total patch area, perimeter, area-perimeter ratio, or connectivity – control biodiversity, stability and multifunctionality by adding a standardised density of mussel foundation species in patches of 1, 5, 10, 30, 60, 90 or 180 individuals to a southeastern US salt marsh. Over 67% of response variables increased with clustering of mussels, responses that were driven by increases in area–perimeter ratio (33%), decreases in perimeter (29%), or increases in patch size (5%), suggesting sensitivity to external stressors and/or dependence on foundation species-derived niche availability and segregation. Thus, mussel configuration – by controlling the relative distribution of multidimensional patch interior and edge niche space – critically modulates this foundation species' effects on ecosystem structure, stability and function.

Keywords

Community stability, ecosystem engineer, *Geukensia demissa*, landscape ecology, mussel, niche, population stability, primary productivity, *Spartina alterniflora*.

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INTRODUCTION

Foundation species, such as seagrasses, oysters, wetland sedges and trees, create novel niche space that supports high levels of associated community biomass and biodiversity (Dayton 1972; Bruno & Bertness 2001; Ellison *et al*. 2005; Angelini *et al*. 2011). Both directly through their alteration of physical conditions and biogeochemical processing, and indirectly through the activities of the organisms they facilitate, foundation species also commonly stimulate multiple ecosystem functions and services (Jones *et al*. 1994; Angelini *et al*. 2015; Ramus *et al*. 2017). Given their profound ecological importance, significant effort has been made to integrate the positive effects of foundation species into ecological theory (Bruno & Bertness 2001; Bruno *et al*. 2003), and to conserve and restore these dominant habitat-formers in threatened or degraded ecosystems (e.g. Byers *et al*. 2006; Crain & Bertness 2006; Silliman *et al*. 2015).

In these theories and management prescriptions, foundation species are considered to create relatively contiguous and homogenous habitats, a perception reinforced by the numerous correlational and experimental studies that compare ecological communities in areas where foundation species are present to those where they are absent or have been experimentally removed (e.g. Altieri & Witman 2014; Crotty & Bertness 2015; Kikvidze *et al*. 2015). However, all foundation species are patchy when investigated at appropriate spatial scales, distributions that may importantly modulate their effects on other species and ecosystem functioning. Regardless of their size or shape – from a single 0.1 m^2 epiphytic Bird's-nest fern to a 10,000 m^2 stand of seagrass – all foundation species' patches have interiors and edges, components that are characterised by distinct abiotic and biotic conditions (Laurance & Yensen 1991; Ries *et al*. 2004; Scheffers *et al*. 2014). Within patch interiors, foundation species' density and biomass are typically high, resulting in relatively high amelioration of physical stress, obstruction of predator access to prey, and provisioning of detritus and other food resources (Bruno & Bertness 2001; Crotty & Bertness 2015). In contrast, foundation species' density and biomass are often low on patch edges, resulting in a reduced physical and biological stress amelioration and resource benefits (Lovejoy *et al*. 1986; Andrén & Angelstam 1988; Ewers & Didham 2007). While some species that are vulnerable to physical stress may be precluded from patch edges, others may capitalise on this niche space, which may provide refuge from competitors or predators, or access to prey occurring both within and outside of the patch (Fagan *et al*. 1999; Macreadie *et al*. 2009; Angelini *et al*. 2011). In general, smaller-bodied prey species may more often reside in the more complex, low stress interior of foundation species patches, while larger-bodied, higher trophic level species that require access to multiple habitats may be more likely to thrive on edges.

As a result of this heterogeneous niche provisioning, foundation species' effects on biodiversity, population and community stability, and ecosystem functioning may importantly be influenced by the size, perimeter and compactness (i.e. area–perimeter ratio) of individual patches and by patch connectivity at larger scales (Forman 1995; Bruno & Kennedy 2000). Theory predicts that as diversity increases, community stability and ecosystem functioning increase, while the stability of individual populations decreases due to functional complementarity and compensatory responses (e.g. competitive or consumptive interactions) increasing with species richness

(Tilman 1996; Lehman & Tilman 2000; Griffin *et al.* 2009; Cardinale *et al.* 2012; O'Connor & Byrnes 2014; Gamfeldt *et al.* 2015; Lefcheck *et al.* 2015; O'Connor *et al.* 2017). Based on this work, one might expect that foundation species' patch configurations that elevate biodiversity will elicit these same effects on stability and functioning. However, if the distinct niches created by foundation species patch interiors and edges enable coexistence of species that otherwise could not co-occur due to their competitive or consumptive interactions, then community stability, population stability and multifunctionality may all increase alongside increases in biodiversity (Bulleri *et al.* 2016). Despite its ubiquity, general predictions for how patchiness of foundation species may mediate their cascading effects on ecosystem biodiversity, stability, and functioning, and influence theoretical relationships among these factors have yet to be developed or tested (Didham *et al.* 1996; Bender *et al.* 1998).

Southeastern US salt marshes offer a useful test bed for examining the effects of foundation species patch configuration. In the region, the dominant foundation species is smooth cordgrass, *Spartina alterniflora* (hereafter cordgrass), a C4 grass that forms monocultures that structurally define intertidal marsh habitat (Schalles *et al.* 2013). By providing attachment substrate, detrital food resources, and physical stress amelioration, cordgrass facilitates the establishment and growth of a second foundation species, the ribbed mussel (*Geukensia demissa*, hereafter mussel; Bertness 1984; Altieri *et al.* 2007). Mussels embed themselves in the mud around the base of cordgrass stems as isolated individuals and in clumped aggregations of >200 individuals, forming patches that vary in size and coverage within and among sites (Bertness & Grosholz 1985; Fig. S1). In patch interiors, nutrient- and sediment-rich pseudofeces deposited by mussels accumulate in interstitial spaces between the mussels, locally stimulating cordgrass growth, colonisation of juvenile stage deposit-feeding fiddler crabs (*Uca pugnax*), and belowground communal burrowing by omnivorous marsh crabs (*Sesarma reticulatum*; Angelini *et al.* 2015). In contrast, mud crabs (*Eurytium limosum*, *Panopeus obesus*) – generalist predators that consume all resident marsh invertebrates, including conspecifics – burrow almost exclusively along mussel patch edges, and exert top down control within a ~12 cm radius of their burrows (Kneib & Weeks 1990; Davidson *et al.* 2015). Adult fiddler crabs and periwinkle snails (*Littoraria irrorata*), which graze on benthic algae, detritus and fungus, are also common, but have not been shown to be as strongly associated with mussels (Angelini *et al.* 2015).

Despite significant understanding about how individual mussel patches mediate salt marsh structure and function, the effects of mussel patch configuration are unknown. We therefore transplanted a standardised density of mussels (180) in patches of 1, 5, 10, 30, 60, 90 and 180 individuals into 4 m^2 experimental plots on a high marsh platform and analysed which metrics of their resulting configurations – patch size (i.e. experimental treatment), total patch area (which accounts for the area occupied by the mussels themselves and area of interstitial spaces between them; Fig. 1a), total patch perimeter (Fig. 1b), patch area–perimeter ratio (Fig. 1c) and connectivity (Fig. 1d) – controlled invertebrate biomass, diversity, population and community stability, and several ecosystem function response variables over a 6-month growing season. Given that mussel patches function as a hot spots for resident predator–prey interactions (Angelini *et al.* 2015), we hypothesized that: (1) prey biomass and population stability, as well as total community biomass, biodiversity and stability would increase with area–perimeter ratio, as this metric is maximised on patches with the highest availability of low stress interior habitat relative to stressful edge habitat (i.e. highest niche availability and segregation); whereas (2) mud crab predator biomass and population stability would increase with perimeter, given the affinity of this functional group for edge niche space. Finally, we hypothesized that (3) multifunctionality and most ecosystem functions – including cordgrass and benthic algae productivity, sediment accretion and mussel growth – would increase with total patch area since these metrics are strongly modulated by direct mussel activity, rather than indirectly through the invertebrate communities facilitated by mussels.

MATERIALS AND METHODS

This study was conducted on Sapelo Island, Georgia, USA (31°25′19″N, 81°17′27″W). In March 2015, we marked and removed all mussels from 40, 4 m^2 marsh platform plots that were positioned ~70 m from the nearest tidal creek, inundated for a total of ~0.5–5 hours per day by semi-diurnal tides, and spaced >3 m apart. This area is dominated by short-form cordgrass, which reaches ~50 cm at the end of the growing season and is interspersed with single mussels and mussel patches that occupy about 4% of the marsh surface. Plots were randomly assigned to one of eight treatments: no-mussel controls, or 180 mussels added as isolated individuals or in patches of 5, 10, 30, 60, 90 or 180 individuals ($N = 5$ replicates per treatment). Mussels were collected at the experimental site and sorted into size classes by shell length: small (40–60 mm), medium (60–80 mm) and large (80–100 mm). To standardise mussel biomass, 60 mussels from each size class were assigned to each plot, 30 of which were labeled using 8 × 4 mm glue-on shellfish tags (Hallprint; Hindmarsh Valley, Australia) and measured for initial length. Mussels were inserted so that ~30% of their shell protruded above the marsh surface in configurations within plots corresponding to the assigned treatment. Dead mussels observed after 1 week (3 of 6300 transplanted) were replaced. The experiment ran from 28 March to 10 October 2015.

Invertebrate density and diversity

In each of five permanently marked 0.5 × 0.5 m quadrats positioned 0.5 m from the plot boundary on each side and in the centre of each plot, we counted the number of resident (non-tidally migrating) macro-invertebrates, including predatory mud crabs (*E. limosum* and *P. obesus*), omnivorous marsh crabs (*S. reticulatum*), juvenile and adult deposit-feeding fiddler crabs (*U. pugnax*), and fungal-farming and detritivorous periwinkle snails (*L. irrorata*). Quadrats were positioned on and off mussel aggregations in larger patch treatments and in areas that varied in mussel density in singleton and small patch treatments to capture the plot-scale effects of each

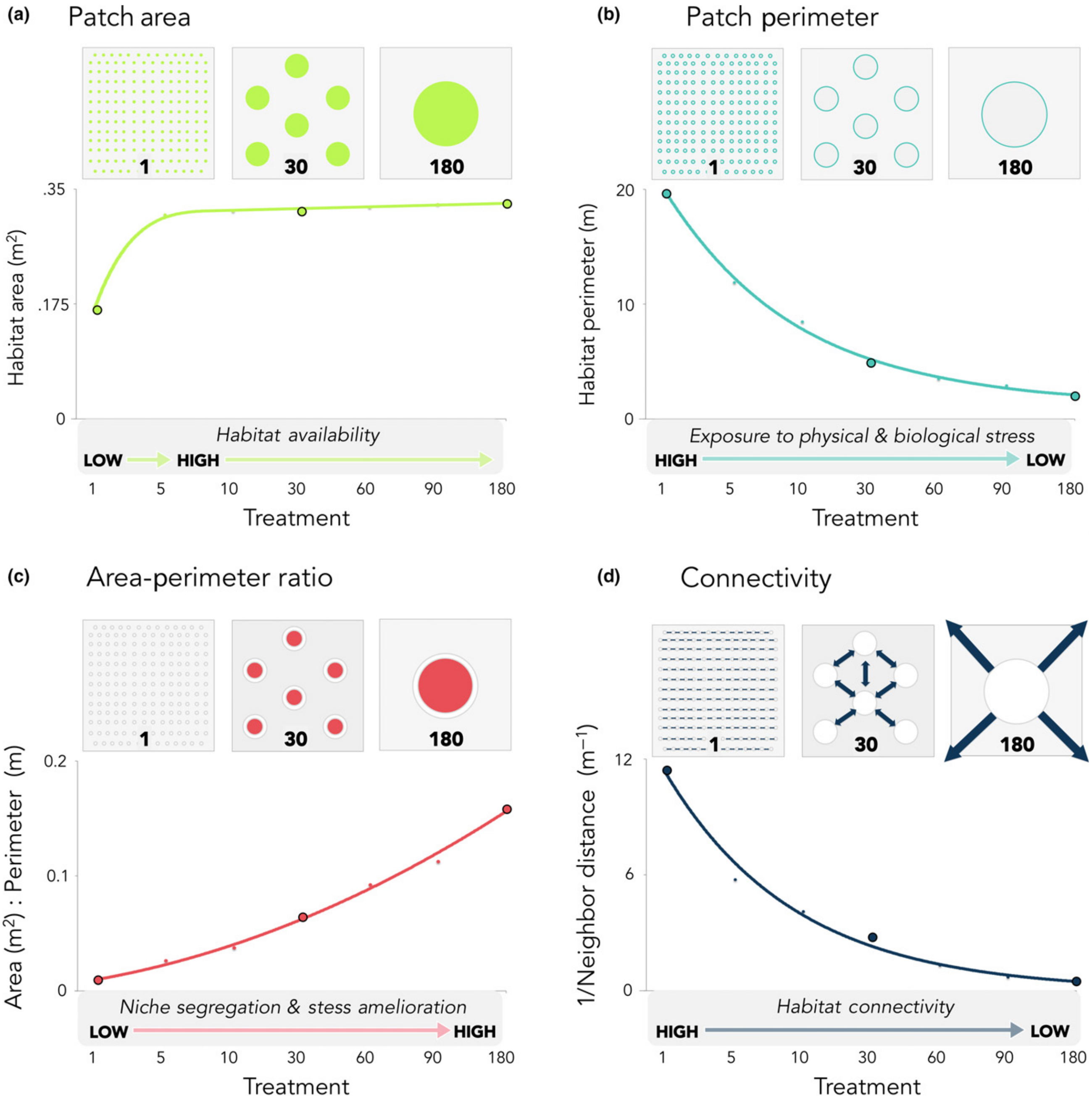

Figure 1 Functional relationships between experimental treatment (i.e. mussel patch size) and patch configuration metrics measured in the field (see Supplemental Methods) including (a) total mussel patch area, (b) total mussel patch perimeter, (c) area–perimeter ratio and (d) connectivity (i.e. 1/distance to nearest neighbouring mussel patch). In all panels, experimental treatments are presented at regularly spaced intervals along the *x*-axis, rather than on a continuous scale. In each panel, the diagrams depict an aerial view of experimental plots with patches of 1, 30 and 180 mussels and highlight how each metric was calculated: green circles denote mussel patch area which was summed across all patches in each plot in (a), blue rings denote mussel patch perimeter which was summed across all patches in each plot in (b), red circles outlined in white denote area–perimeter ratio (summed patch area divided by summed patch perimeter in each plot) (c), and the blue arrows denote how connectivity between patches was measured in each plot (d).

treatment. Invertebrates were monitored every 5–7 weeks on 23 April, 9 June, 15 July, 5 September and 8 October, 2015. Invertebrates were categorised by functional group rather than taxonomic species to account for differences in ecological function between life stages of the same species (juvenile and adult fiddler crabs excavate short, narrow and deeper, wider burrows respectively) and functional similarities among species (both mud crab species create similar sized burrows, demonstrate an affinity for mussel patch edges and consume the same prey). Snails were counted on the marsh surface and on cordgrass stems, while crabs were counted using non-destructive burrow counts. The burrows of each crab functional group exhibit unique, readily identifiable characteristics and are a close proxy for crab density (Angelini *et al.* 2015).

To standardise plot-scale responses on each date, we summed invertebrate counts across the five quadrats per plot and converted these data to dry biomass estimates by multiplying the number of individuals recorded on each date by the mean dry biomass of 10 individuals per functional group. In each plot at each date, we summed all functional group biomass measures to estimate invertebrate community biomass and recorded functional group richness as the number of functional groups present. We also calculated the exponential Shannon diversity index (Jost 2006), using eqn 1:

$$e^{H} = e^{-\sum_{i=1}^{s} p_i \ln p_i} \tag{1}$$

where p is the proportion of the population belonging to functional group i and S is the total pool of functional groups. Functional group evenness was calculated as exponential Shannon diversity (e^{H}) divided by functional group richness in each plot.

Population and community stability

To quantify the population stability, S_T, of each functional group, we used the following equation:

$$S_T = \frac{\mu_T}{\sigma_T} \tag{2}$$

where mean biomass, $\mu_{T,}$ is the mean biomass of each functional group recorded in each plot across all five dates and σ_T is the standard deviation of the mean biomass over the same dates (Lehman & Tilman 2000). We use temporal stability, rather than the temporal coefficient of variation (σ/μ), so that decreases in σ relative to μ would more intuitively be reflected as increases in the metric of stability.

To calculate invertebrate community stability, we used eqn 2; however, in this iteration, mean abundance, $\mu_{T,}$ is defined as the sum of the mean biomass of each functional group recorded over the five monitoring dates and standard deviation, $\sigma_{T,}$ is defined as the square root of the summed variance of individual functional group biomass measures plus the summed covariance of every possible pair of two functional groups' biomass over the same dates (Long *et al.* 2011).

Ecosystem functions

To quantify how mussel addition and configuration affect ecosystem functioning, we scored the following five functions in each plot as well as mussel survival and growth in mussel addition plots.

Aboveground cordgrass biomass

To quantify cordgrass biomass, all stems were harvested from each plot in October and measured for fresh, wet weight. From each plot, three 40–60 g cordgrass subsamples were measured for both fresh and oven-dried weights. The average fresh:dry weight ratio was then used to calculate aboveground cordgrass biomass for each plot.

Diatom and cyanobacteria biomass

To quantify benthic algae production, a key resource supporting salt marsh food webs, we measured diatom and cyanobacteria biomass on each monitoring date using a handheld fluorometer (BenthoTorch, bbe Moldaenke GmbH, Germany) placed in three randomly chosen locations within each quadrat (N = 15 measurements/plot/date). We report the average biomass per plot (μg^{cm-2}) of each algae class in October because values and trends did not vary significantly over the course of the experiment.

Secondary production

To estimate invertebrate biomass as a measure of secondary production, community biomass was calculated for each plot by multiplying the plot-scale density values recorded in October by the average biomass per individual of each functional group and summing all functional group values. Mussels were not included in this calculation.

Sediment accretion

To quantify variation in sediment accretion, we measured the depth of fine-grained, loose sediment on the marsh surface – i.e. that which was recently deposited either by mussels as pseudofeces or by cordgrass through its baffling of water flow at high tide and not yet bound in plant roots. Sediment accretion was recorded on each monitoring date in three randomly chosen locations in each quadrat using a 0.2 cm diameter dowel inserted vertically through the soft surface layer of sediment until resistance produced by the cordgrass root mat was reached (Angelini *et al.* 2015). We calculated the mean sediment depth in the five quadrats per plot in October as a final measure of sediment accretion.

Mussel survivorship and growth

In October, all mussels were harvested and scored as alive or dead. We re-measured each labeled, live mussel for final length using a digital caliper. To quantify size-standardised mussel growth rate, we used the von Bertalanffy growth curve (von Bertalanffy 1938) where growth rate decreases with increasing mussel size:

$$k = (\ln((\mathrm{L}_{t2} - \mathrm{L}_{\infty})/(-\mathrm{L}_{\infty} + \mathrm{L}_{t1})))/(\mathrm{t}_1 - \mathrm{t}_2) \tag{3}$$

where k is the growth constant (year^{-1}), L_{t1} is mussel shell length (mm) in March, L_{t2} is mussel shell length (mm) in October, L_{∞} is the maximum length mussels can attain in this system (100 mm), $t_1 = 0$ and $t_2 = 0.50$ year (Derksen-Hooijberg *et al.* 2017).

Multifunctionality

To test the effects of mussel configuration on the simultaneous performance of multiple ecosystem functions, we calculated mean multifunctionality (Byrnes *et al.* 2014). We first standardised the five ecosystem functions quantified in all plots to be a percent of maximum functioning by dividing raw values of each function in each plot by the mean of the three highest values of that function recorded across all plots. Maximum functioning was determined to be the highest values of each response variable as an increase in each implies the addition of biomass or other physical material into the system. We then averaged the five standardized ecosystem function values measured in each plot to calculate mean multifunctionality.

Statistical analyses

We analysed the effects of mussel treatment and date on invertebrate functional group and community biomass metrics, as well as the three diversity indices with repeated measures analysis of variance (RM-ANOVA; Stata SE v 13.1). To quantify the effects of treatment on mussel mortality, we ran a one-way ANOVA, with treatment as the factor. All *post hoc* analyses were completed using Tukey HSD tests. To test which mussel patch configuration metric explained the most variation in each response variable, we fit null ($Y = a$) and linear ($Y = a + bX$) functions using each configuration metric (patch size, total patch area, total patch perimeter, area–perimeter ratio and connectivity) as the independent variable and each biomass, biodiversity, stability and function response variable as the dependent variable. We fit six models for each of our 21 response variables and used Bonferroni-corrected P values to assess model significance. We analysed invertebrate biomass and diversity responses recorded in October given that they provided a representative and integrated measure of these metrics. For each response variable, we selected the best-fitting model using Akaike's information criterion corrected for low sample size, AICc (AICcmodavg package; R v. 3.0.2). Specifically, to select the best-fitting model, we calculated all delta AICc values, as well as the relative likelihood and Akaike weights for each model. For all models within a delta AICc of 2 of the best-fitting model (AICc_{min}), we present all statistically significant models and associated Akaike weights in Table S1 (Burnham & Anderson 2002; Burnham *et al.* 2011).

RESULTS

Patch treatment effects over time on invertebrate communities

While snail and adult fiddler crab biomass were similar, regardless of treatment (Fig. 2a, b; $P > 0.08$), juvenile fiddler, mud and marsh crab biomass were all elevated in mussel addition relative to no-mussel control plots and increased significantly with patch size over time (Fig. 2c–e, see figure for statistics summary here and below). Invertebrate functional groups differed in their temporal dynamics over the 6-month experiment; while fiddler and mud crab densities peaked in mid-summer and tapered off in all treatments, marsh crab density tended to increase through October, while snail densities, in contrast, decreased over time in all treatments.

As a result of natural pulses in recruitment and individual functional group responses to mussel addition and configuration, response variables including total community biomass, functional group richness, evenness and invertebrate diversity – measured as the exponential Shannon diversity index – all increased over time from April 2015. Furthermore, all treatments with patches of ≥30 mussels supported significantly higher invertebrate biomass, richness, evenness and diversity than no-mussel controls by October 2015, with the largest patches supporting even higher diversity than small patches or singleton mussels (Tukey HSD, $P < 0.05$; Fig. 2f–i; Fig. S2).

Patch configuration effects

Biodiversity

While snail biomass did not vary significantly with any mussel patch configuration attribute (Fig. 3a), adult fiddler crab biomass increased linearly with patch size (i.e. treatment), and juvenile fiddler, mud and marsh crab biomass, as well as invertebrate community biomass, increased linearly with area–perimeter ratio (Fig. 3b–f). Functional group richness, evenness and exponential Shannon diversity all decreased linearly with increasing mussel patch perimeter (Fig. 2g–i).

Population and community stability

While snail and adult fiddler crab population stabilities were not affected by mussel configuration (Fig. 4a, b), juvenile fiddler crab and marsh crab stability decreased linearly with increasing patch perimeter, and predatory mud crab population stability increased with area–perimeter ratio (Fig. 4c–e, see figure for statistics summary here and below). Invertebrate community stability did not vary with mussel treatment or any patch configuration metric (Fig. 4f).

Ecosystem functions and multifunctionality

Primary productivity functions (i.e. cordgrass, diatom and cyanobacteria biomass) did not vary significantly with mussel patch configuration (Fig. 5a–c). However, mussel addition increased aboveground cordgrass biomass (+23 ± 9%; mean ± SE) and diatom biomass (+8 ± 4%), and decreased cyanobacteria biomass (−17 ± 4%) relative to no-mussel controls. In contrast, sediment accretion increased linearly with area–perimeter ratio (Fig. 4d). Mussel growth, however, decreased linearly with patch perimeter (Fig. 4e), suggesting that physical stress rather than competition within patches limits the growth of this foundation species. Mussel mortality was >3× higher when mussels were deployed as singletons (14.0 ± 1.6%) than in any aggregated patch treatment, which did not differ from one another (3.5 ± 0.6%; $F_{7,30} = 9.2$, $P < 0.0001$; Tukey HSD, $P < 0.01$). Driven largely by increases in invertebrate community biomass (Fig. 3f) and sediment accretion (Fig. 5d) with area–perimeter ratio, and mussel growth (Fig. 5e) with decreasing patch perimeter, mean multifunctionality increased linearly with area–perimeter ratio (Fig. 5f).

DISCUSSION

These experimental results reveal that mussel patch presence and configuration can importantly control patterns in salt marsh biodiversity, population stability and multifunctionality. Among landscapes with a standardised density of mussels, those containing particularly large patches with high area–perimeter ratios and limited patch perimeters enhanced the biomass of most invertebrates and elevated biodiversity respectively (Fig. 3). Coincident with these biodiversity enhancements, we also observed an increase in the population stability of predatory mud crabs as a function of increasing area–perimeter ratio, and in the population stability of three of the four prey functional groups as a function of decreasing mussel patch perimeter (Fig. 4a–e). Contrary to our hypotheses, neither mussel presence nor configuration affected

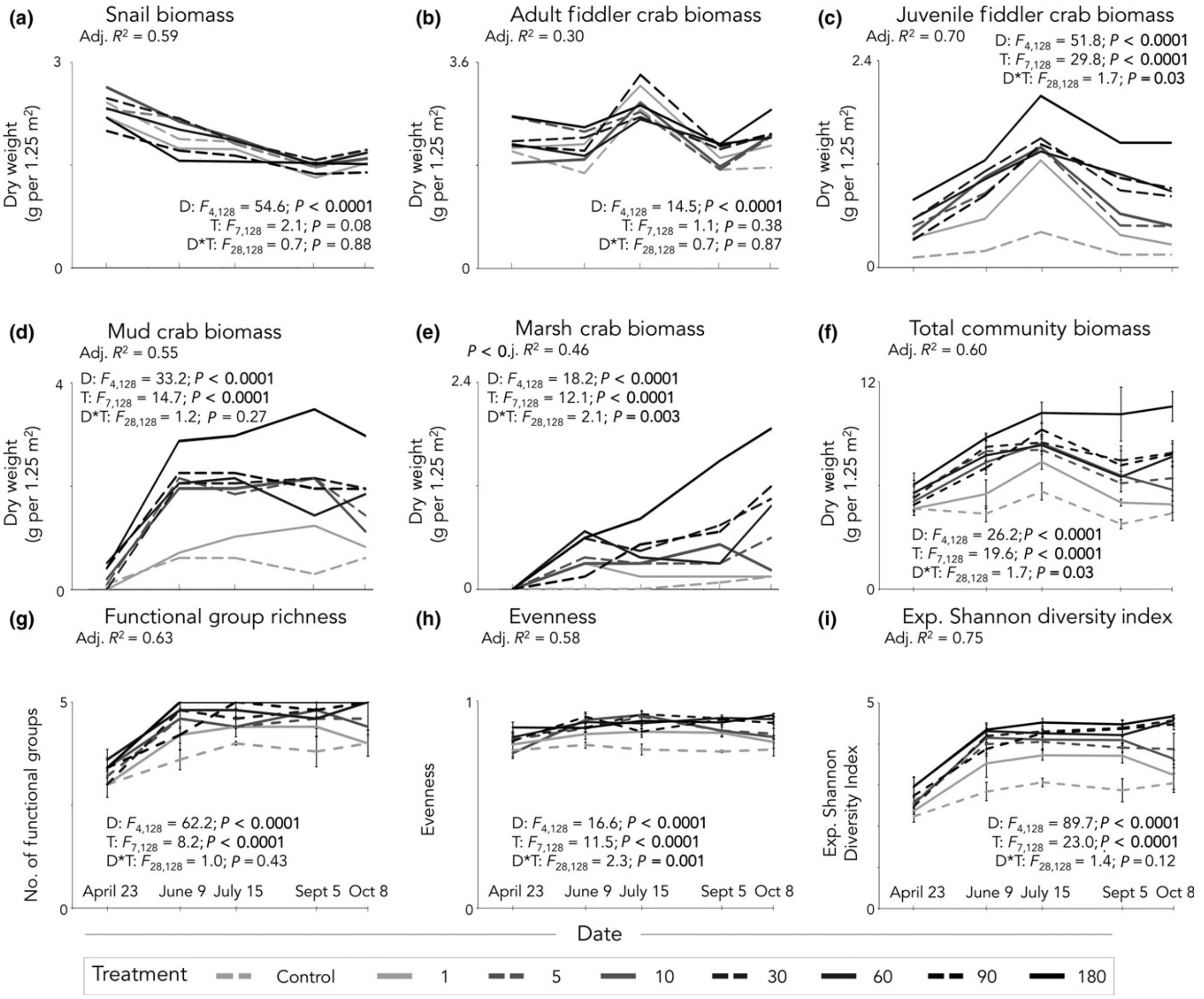

Figure 2 Invertebrate functional group biomass and diversity over time. Mean functional group biomass of (a) snails, (b) adult fiddler crabs, (c) juvenile fiddler crabs, (d) mud crabs, and (e) marsh crabs, as well as (f) total community biomass, (g) functional group richness, (h) evenness and (i) exponential Shannon Diversity Index measured over the 6-month experiment. Results of RM-ANOVAs assessing the effects of date, D, and mussel patch size treatment, T, are presented as an inset in each panel and significant *P* values are noted in bold text. Experimental treatments are differentiated by solid and dotted lines, with darker colours reflecting more clustered treatments (mean ± SE of five replicate plots per treatment for panels f–i). All *y*-axes are shown on a linear scale.

community stability (Fig. 4f) and only mussel presence, not configuration, altered primary production measures (cordgrass, diatom and cyanobacteria biomass) relative to no-mussel controls. However, resulting from increases in community biomass, sediment accretion and mussel growth functions, mean multifunctionality increased with patch area–perimeter ratio (Fig. 5). Together, these results indicate that the effects of this foundation species cannot be predicted based on its area or density on the landscape alone. Instead, how mussels are spatially arranged, and how this configuration then influences the relative availability of low-stress, high-resource interior relative to more exposed edge niche space, powerfully modulates this foundation species' facilitation of diverse, stable and high functioning communities.

Prior theoretical and experimental studies have proposed and demonstrated that foundation species enhance the fundamental niche of facilitated species through their creation of complex habitat (Bruno *et al.* 2003; Crotty & Bertness 2015). Our results expand on this work and indicate that mussels, a foundation species common to salt marshes across the eastern seaboard of the US (Bertness & Grosholz 1985), may have more dynamic effects on niche availability and diversity than is currently appreciated, especially when their landscape and regional patchiness are acknowledged. Within patch interiors, foundation species' density, biomass and ecological effects above- and belowground can be relatively high, enabling them to generate multiple, complex, three-dimensional niches (Bruno *et al.* 2003; Moore & Hovel 2010; Fig. 6). In the context of mussel patches, we observed that resident invertebrate prey species capitalise on these distinct niches in the patch interior; juvenile fiddler crabs burrow in and feed on pseudofeces trapped interstitially between mussels

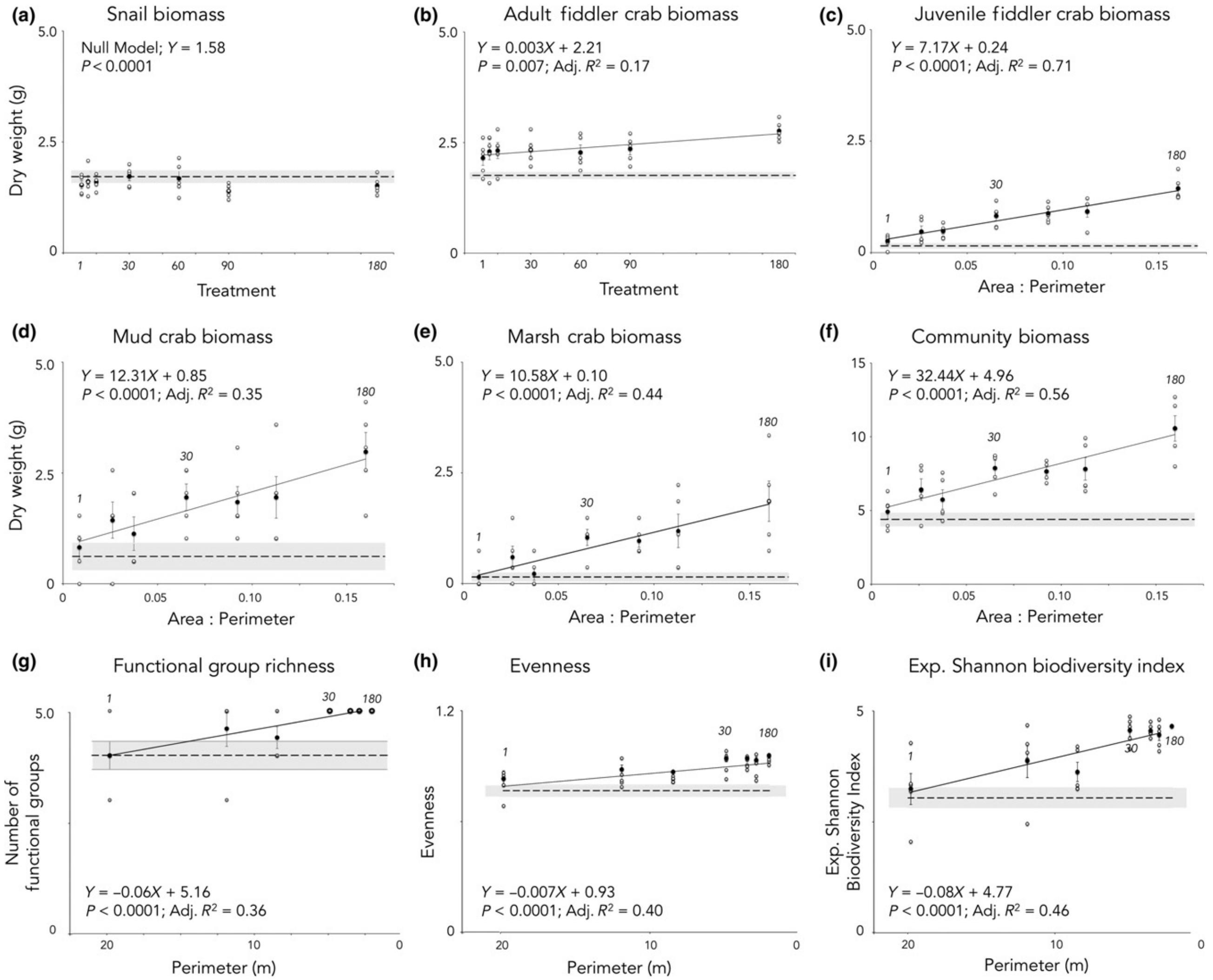

Figure 3 Mussel patch configuration effects on invertebrate biomass and diversity. Relationship between mussel patch configuration metric (best fitting model) and October mean functional group biomass of (a) snails, (b) adult fiddler crabs, (c) juvenile fiddler crabs, (d) mud crabs, and (e) marsh crabs, as well as (f) total community biomass, (g) functional group richness, (h) evenness and (i) exponential Shannon Diversity Index. The level of each response variable measured in no-mussel control plots is shown as a dotted black line within a shaded grey interval (mean ± SE) in each panel. Raw data are shown as non-shaded circles with mean ± SE shown in shaded black circles with error bars. Best-fitting model results, P value, and adjusted R^2 values are inset in each panel. Non-significant model results are denoted as NSD and plotted with treatment on the x-axis. Perimeter is plotted along an inverted x-axis, such that smaller patch treatments are on the left, and larger patch treatments are on the right of the panel. All y-axes are plotted on a linear scale.

on the marsh surface; marsh crabs excavate expansive communal burrows underneath mussel patches where they find refuge from mud crabs and larger, roaming predators (e.g. birds, fish, raccoons) and have access to nutrient-enriched roots (Derksen-Hooijberg *et al.* 2017); and snails farm fungus and seek refuge from nektonic predators in the cordgrass canopy, which grows taller and exhibits higher nitrogen content on mussel patches (Silliman & Newell 2003; Davidson *et al.* 2015; Derksen-Hooijberg *et al.* 2017). Predatory mud crabs, in contrast, exhibit a strong affinity for mussel patch edges where they benefit from access to high prey availability within the mussel patch but also to adult fiddler crab prey in the less structurally complex areas outside of the patch (Fig. 6). Importantly, the relative availability of these distinct niches varies with mussel patch size. In small patches, for example, little pseudofeces accumulates (Angelini *et al.* 2015), resulting in limited access to this niche and, hence, a reduced ability of the patch to support high juvenile fiddler crab densities, with potentially cascading effects on the density and stability of higher trophic levels, such as mud crabs. Based on prior studies monitoring physical stress and/or predator–prey interactions along patch edges and interiors (e.g. Ewers & Didham 2007), we suspect that this multidimensional niche creation and the segregation of different niche types among patch edges and interiors may be fundamental mechanisms determining when and where foundation species have particularly powerful, positive effects on biodiversity.

Paralleling trends in biodiversity (Fig. 3f–i), and in disagreement with our initial hypothesis (1), we found that the population stability of prey species–including juvenile fiddler crabs and marsh crabs – increased with decreasing patch perimeter. This result likely reflects the sensitivity of these functional

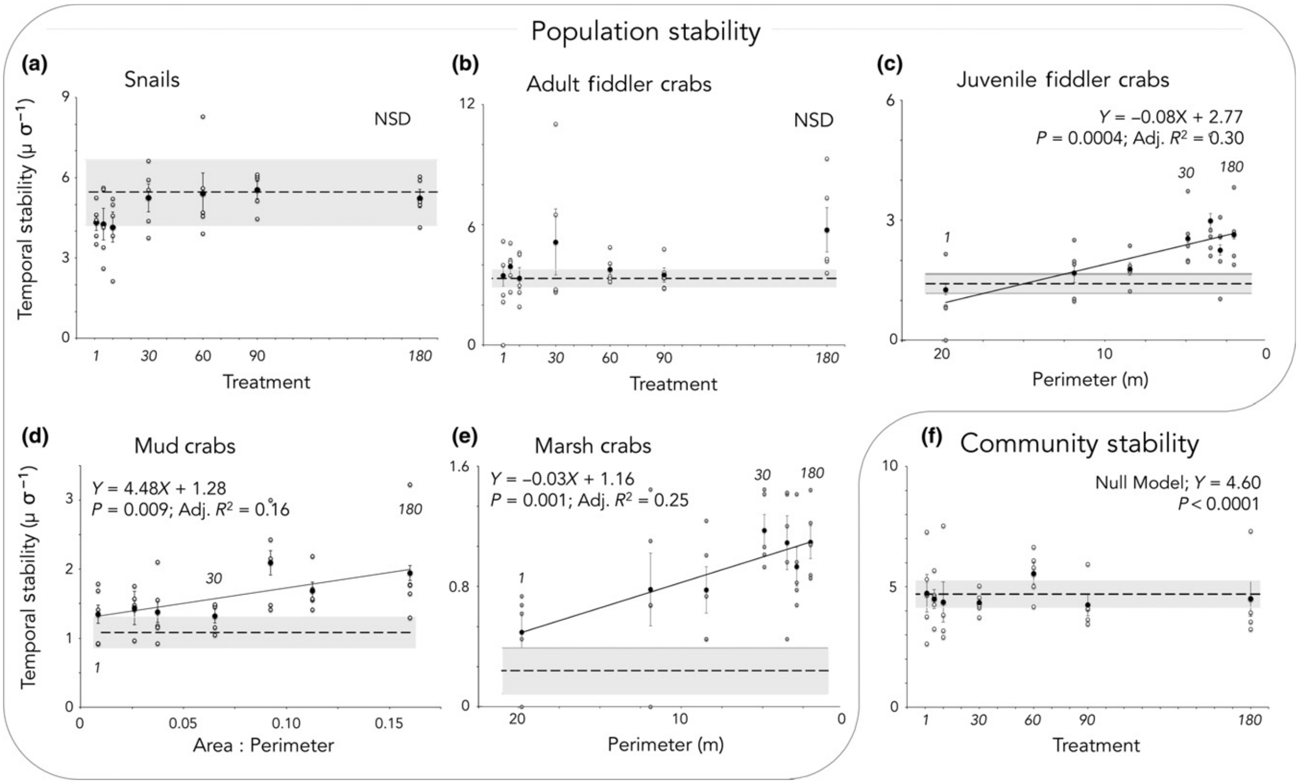

Figure 4 Mussel patch configuration effects on population and community stability. Relationship between spatial configuration metric (best fitting model) and population stability of (a) snails, (b) adult fiddler crabs, (c) juvenile fiddler crabs, (d) mud crabs, and (e) marsh crabs and (f) community stability. No-mussel control results are shown as a dotted black line within a shaded grey interval (mean ± SE). Raw data are shown as non-shaded circles and means ± SE are shown in shaded black circles with error bars. Best-fitting model results, P value, and adjusted R^2 values are inset in each panel. Non-significant model results denoted as NSD and plotted with treatment on the x-axis. Perimeter is plotted along an inverted x-axis, so that small patch treatments are on the left of the panel, and larger patch treatments are on the right.

groups to top down control by mud crab predators and/or physical stress exposure on small mussel patches that are typified by relatively large perimeters. In contrast, and also in disagreement with our hypothesis (2), population stability of predatory mud crabs increased with area–perimeter ratio (Fig. 4a–e), potentially reflecting their dependence not only on perimeter edge habitat, but also on the consistent availability of prey supported and maintained within the mussel foundation species' patch. While contrary to theoretical predictions (Tilman 1996; Lehman & Tilman 2000), this positive association between biodiversity and population stability aligns with prior work from multi-trophic aquatic and terrestrial systems (Jiang & Pu 2009). Two potential mechanisms have previously been suggested as drivers of this positive association between biodiversity and population stability in multi-trophic communities. First, coupling of bioenergetic and complex food web models has suggested that increases in diversity can drive increases in population stability when predator-prey biomass ratios are within certain ranges (i.e. when predators are 10–100 times larger than their prey; Brose *et al.* 2006; Jiang & Pu 2009). Second, others have suggested a 'weak interaction effect' whereby diverse communities are more stable because weak trophic interactions are more common than strong trophic interactions in multi-trophic communities and serve to dampen the population-level effects of strong trophic interactions (McCann *et al.* 1998; McCann 2000; Jiang & Pu 2009; Jiang *et al.* 2009). Our results highlight a third currently unacknowledged mechanism. Specifically, foundation species can enhance both biodiversity and population stability through their spatial partitioning of patch interior and patch edge niches, which serves to dampen negative interactions (e.g. competition and predation) among species capitalising on each niche. This mechanism that acknowledges the role of foundation species in hierarchically controlling the distributions of associated species may be responsible for driving 'weak interaction effects' and allowing stable coexistence of multiple trophic levels and populations more generally across systems (Loreau & de Mazancourt 2013).

Ecological theory and experimental studies across ecosystems have additionally shown a positive relationship between biodiversity and community stability (Cottingham *et al.* 2001; Griffin *et al.* 2009). Our experiment, however, revealed no significant relationship between mussel patch addition or configuration – and, consequently, associated biodiversity – on community stability (Fig. 4f). This result likely arose because the organisms most strongly facilitated by mussels – mud, marsh and juvenile fiddler crabs – comprise a lower percent of the total community biomass and are thus less influential in the community stability calculation compared to snails and adult fiddler crabs, which generally occur at high densities independent of mussel presence or configuration (Figs. 2 and 3). However, if we were to annually census these communities

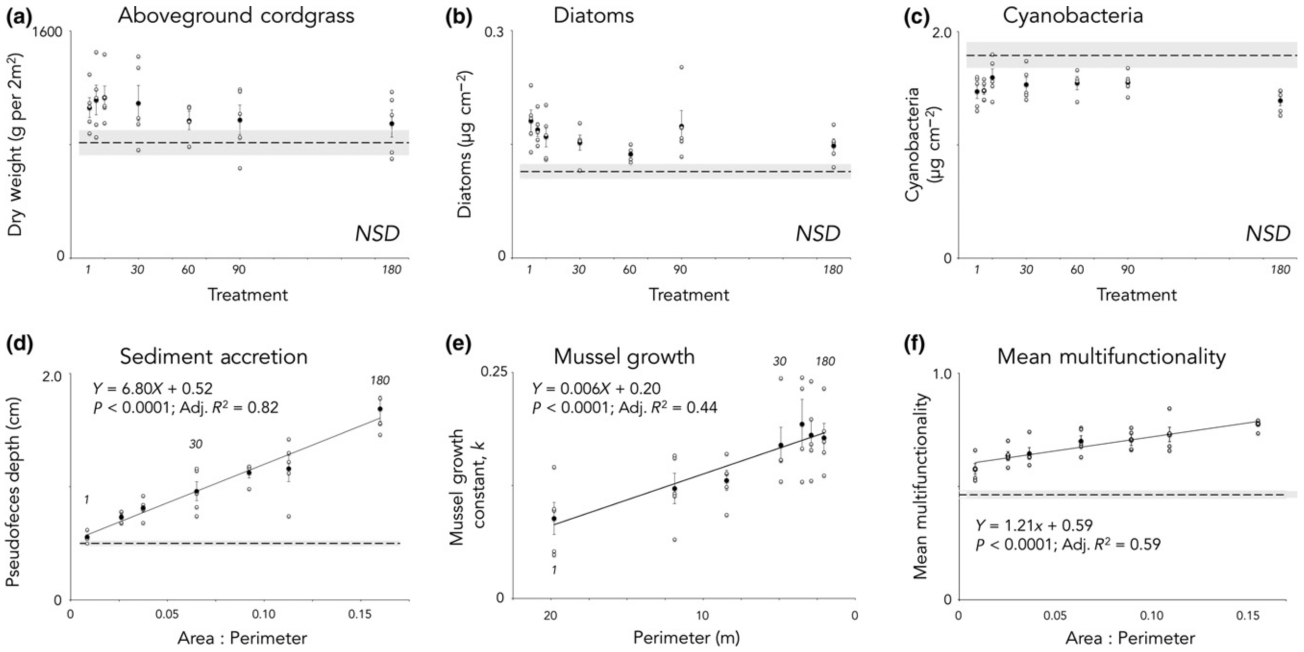

Figure 5 Foundation species patch configuration effects on ecosystem functions and mean multifunctionality. Relationship between the mussel patch configuration metric (best fitting model) and (a) aboveground cordgrass biomass, (b) diatom and (c) cyanobacteria benthic algae biomass, (d) sediment accretion, (e) mussel growth and (f) mean multifunctionality. No-mussel control results are shown as a dotted black line within a shaded grey interval (mean ± SE). Raw data are shown as non-shaded circles and the means ± SE are shown in shaded black circles with error bars. Best-fitting model results, P value, and adjusted R^2 values are inset in each panel. Non-significant model results denoted as NSD and plotted with treatment as the x-variable. Perimeter is plotted along an inverted x-axis, so that smaller patch treatments are on the left and larger patch treatments are on the right of the panel.

and calculate community stability over multiple years, we anticipate that it would be higher in mussel addition plots because mussels significantly enhance cordgrass resilience to drought, a primary manifestation of climate change in the region (Angelini *et al.* 2016). In following, by mitigating cordgrass die-off and enhancing the persistence of habitat that snails and fiddler crabs depend on (Bertness 1985; Silliman & Newell 2003), mussels likely support larger and more stable communities over longer timescales.

Despite many decades of work within the landscape ecology literature demonstrating the importance of habitat patch connectivity (e.g. Fahrig & Merriam 1985; Thompson *et al.* 2016), we found that connectivity among mussel patches, measured in this study as nearest neighbour distance, does not exert control on diversity, stability or ecosystem functioning within salt marshes. We suspect that this was due to the nature of dispersal in our system. Specifically, all macro-invertebrate functional groups considered in this study recruit into the marsh from planktonic larvae in the summer months and – with the exception of mussels which are sessile – are mobile post-settlement, and can move several meters or more per day (Kneib 1984). Therefore, organisms were likely mobile enough to disperse among mussel patches, as well as within and among experimental plots over the course of our experiment. We suggest that dispersal may be an important mediator of foundation species patch configuration effects in other systems, however (e.g. Cushman 2006); specifically, where facilitated species are less mobile or suitable foundation species' patches are further apart, connectivity among patches may control species colonisation and extinction dynamics, and ecosystem functioning. Experimental manipulations of foundation species cover and configuration in dispersal-limited systems will be necessary to quantify the relative importance of connectivity in this context.

Finally, in agreement with earlier work showing that large individual mussel patches have particularly strong effects on salt marsh multifunctionality (Angelini *et al.* 2015), we found that mean marsh multifunctionality was enhanced where mussels were clustered in fewer, larger patches with the highest area-perimeter ratios (Fig. 5). These effects were likely caused by mechanisms promoted by the activities of the mussels themselves (e.g. via their depositing nutrient and sediment-rich pseudofeces on the marsh at the plot scale) and through their facilitation of other key autogenic and allogenic ecosystem engineers that further stimulate functions (Jones *et al.* 1994). Foundation species effects were function-specific, however. While all primary productivity functions were elevated or depressed at the landscape similarly, other functions were responsive to changes in the area–perimeter ratio (sediment accretion and secondary production) or perimeter extent (mussel growth). These results have two primary implications; first, since there exists considerable variation across marshes in the size distribution and density of mussels (Fig. S1; Angelini *et al.* 2015), it is likely that differences in mussel cover and configuration contribute to among-marsh variation in multifunctionality more broadly throughout the region. Second, if foundation species are to be deployed across landscapes to restore or enhance ecosystem functioning, the optimal spatial configuration depends on the relationships between the function of interest, the foundation species and the associated ecological community.

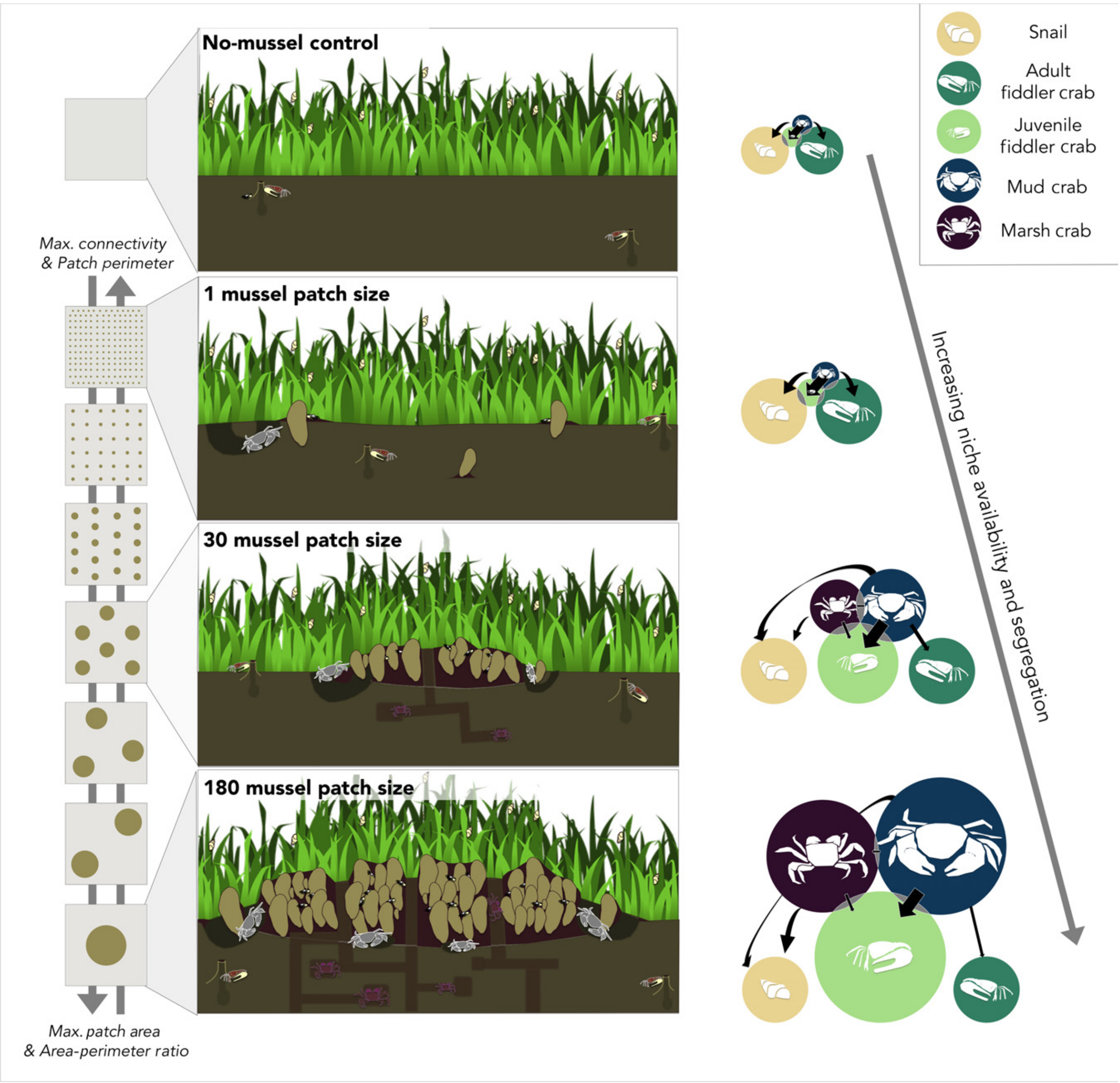

Figure 6 Conceptual depiction of mussel patch configuration effects on food web interactions, niche availability and niche segregation. Treatment diagrams (left) are shown along gradient of patch configuration metrics, including connectivity and patch perimeter (maximized where there are many, small mussel patches), and patch area and area–perimeter ratio (maximized where there are fewer, large mussel patches). Cross-sectional illustrations of no-mussel controls, 1-mussel, 30-mussel and 180-mussel patch size treatments demonstrate the multidimensional niche space provided by this foundation species with increasing patch size. For example, predatory mud crabs are limited to edge habitat, while juvenile fiddler crabs utilise the pseudofeces trapped in the interior of the mussel patch and marsh crabs utilize extensive belowground refuge from predators. Food web interactions (right) depict population size of each functional group (denoted by each circle's size), magnitude of direct, consumptive effects among functional groups (black arrows) and degree of niche overlap (overlap of functional group circles). As patch size increases, both niche availability and segregation increase for each functional group, thereby supporting the largest, most stable communities at the largest patch sizes.

CONCLUSIONS

Foundation species are globally experiencing habitat fragmentation and loss, both as direct and indirect results of anthropogenic stressors (Haddad *et al.* 2015). This fragmentation is occurring across spatial scales, ecosystem types, and latitudes and is importantly altering all metrics of foundation species spatial configuration, including patch area, perimeter, area–perimeter ratio and connectivity (Crooks *et al.* 2017). Understanding how foundation species patch size and configuration mediate the persistence and stability of ecological communities and provisioning of ecosystem functioning is therefore an important step towards future conservation planning, especially as climate change interacts with these landscape-scale processes (Opdam & Wascher 2004; Pressey *et al.* 2007). Our results suggest that the focus of conservation and restoration ecology on foundation species (Byers *et al.* 2006; Crain & Bertness 2006; Silliman *et al.* 2015) is warranted, but to be most effective, should utilise foundation species patch configurations that are optimal for facilitating the establishment and persistence of ecological communities and/or the resilient provisioning of ecosystem functions of interest.

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AUTHORSHIP

CA designed the study. All the authors performed the experiment and collected the data. SC & SS performed the statistical analyses. CA & SC wrote the manuscript and all the authors revised the manuscript.

DATA ACCESSIBILITY STATEMENT

All data are archived and freely available through the Figshare online data portal (https://doi.org/10.6084/m9.figshare.6930689.v1).

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