Additive and site-specific effects of two foundation species on invertebrate community structure

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ABSTRACT: Many aquatic and terrestrial ecosystems are comprised of assemblages of multiple foundation species. Despite the common occurrence of multiple foundation species, relatively few studies have examined the independent and combined effects of multiple co-occurring foundation species or investigated whether they facilitate similar or distinct associated communities. At 2 sites in a temperate Australian mangrove forest, we examined the independent and interactive effects of co-occurring intermediate foundation species (the macroalga *Hormosira banksii* and the oyster *Saccostrea glomerata*—each of which is facilitated by mangrove pneumatophores) on associated community structure. Because the identity of the associated species facilitated by these 2 foundation species can differ, we hypothesized that their combined effects on species richness would be independent and additive. We found that despite their mutual facilitation by mangrove pneumatophores, the 2 intermediate foundation species exhibited independent and positive effects on associated species abundance, richness, and composition. Associated species abundance and richness increased consistently with *S. glomerata* biomass. In contrast, associated species abundance and richness only responded to *H. banksii* presence (not biomass), and this response differed across sites. Our finding that functionally different species produce additive effects on biodiversity is consistent with predictions from other recent studies of facilitation cascades. Furthermore, the site-specific effects of foundation species in this study add to growing evidence that while foundation species can set the potential abundance and richness of associated communities, realized community structure is determined by processes operating at larger spatial and temporal scales.

KEY WORDS: Algae · Context dependency · Facilitation cascade · Foundation species · Mangrove · Oyster

INTRODUCTION

Foundation species provide habitat and/or refuge from abiotic or biotic stress, facilitating diverse communities (Dayton 1972, Bruno et al. 2003). Many aquatic and terrestrial ecosystems are comprised of assemblages of multiple foundation species, yet they are rarely examined as such (Thomsen et al. 2010, Angelini et al. 2011). In some cases, multiple foundation species overlap with one another and are hierarchically organized into a facilitation cascade whereby a basal foundation species facilitates an

intermediate foundation species, and this intermediate (often in combination with the basal species) in turn facilitates a community of associated organisms (Gribben et al. 2009, Hughes et al. 2009, Altieri et al. 2010, Thomsen et al. 2010, Angelini et al. 2011, Bishop et al. 2012). In other instances, multiple foundation species can overlap, without cascading effects, or co-exist in spatial mosaics of discrete patches (Angelini et al. 2011, Bishop et al. 2012). Despite the common occurrence of multiple foundation species, relatively few studies have examined the independent and combined effects of multiple co-occurring foundation species or investigated whether they facilitate similar or distinct ecological communities (but see Gribben et al. 2009, Altieri et al. 2010, Bishop et al. 2012, Dijkstra et al. 2012).

Facilitation of biotic communities is highly dependent on the functional identity of the foundation species involved (Bruno & Bertness 2001, Ellison et al. 2005, Irving & Bertness 2009, Bishop et al. 2013, Gribben et al. 2013). Within habitats, co-occurring foundation species may modify different biotic or abiotic factors and, hence, support different ecological communities (Dijkstra et al. 2012). Thus, just as the number and functional identity of species in a community determine ecosystem processes (Cardinale et al. 2012, Hooper et al. 2012, Naeem et al. 2012), the number and functional identity of co-occurring foundation species may determine the richness, composition, and abundance of the facilitated community (Angelini & Silliman 2014). If multiple foundation species vary substantially in functional traits, then there may be little overlap in the composition of species that associate with each foundation species (Thomsen et al. 2010), leading to additive effects on the diversity and abundance of the associated community. Alternatively, co-occurrence of foundation species may conceivably increase or decrease community richness and/or abundance because of non-additive synergisms or antagonisms among the foundation species or their associates.

The community-level effects of foundation species can also depend on the relative abundance and functional variation of a given foundation species and not simply on its presence or absence (Hughes & Stachowicz 2004, Kimbro & Grosholz 2006, Bishop et al. 2012, 2013, Gribben et al. 2013). In particular, foundation species density and/or biomass can have strong effects on the abundance and richness of associated species. Because these same traits are often highly variable across space and time, it is likely that foundation species effects on the community vary across different contexts (Agrawal et al. 2007). How-

ever, relatively few manipulations of foundation species have included multiple levels of biomass or been replicated across different sites, limiting our understanding of context dependency in the strength of facilitation by foundation species.

Here, we examine the independent and interactive effects of 2 co-occurring intermediate foundation species of temperate Australian mangrove forests, the macroalga *Hormosira banksii* and the oyster *Saccostrea glomerata*, on the richness and abundance of their associated communities. These intermediate foundation species are independently facilitated by pneumatophores of *Avicennia marina* mangroves, the alga responding to pneumatophore density, and the oyster responding to pneumatophore presence or absence (Bishop et al. 2012). Both intermediate species are found at different abundances across a range of microhabitats; when on their own, the density of each has been shown to influence the richness and abundance of the associated community they support (Bishop et al. 2012). In previous studies, we found that some invertebrate species are facilitated by each of these foundation species, but others are facilitated only by oysters (Bishop et al. 2012). Hence, it is possible that the effect of the 2 foundation species on invertebrate richness is independent and additive but that one foundation species alters the density-dependent effects of the other on the abundance of invertebrates. We conducted a factorial manipulation of foundation species presence-absence and density to examine how variation within each species influences the facilitative effects of the other. In addition, we tested the consistency of their effects on the associated community at 2 sites.

MATERIALS AND METHODS

Study system

Within temperate Australian mangrove forests, the macroalga *Hormosira banksii* and the oyster *Saccostrea glomerata* co-exist at mid-intertidal elevations among the pneumatophores of the mangrove *Avicennia marina* (Bishop et al. 2012). In mangroves, the alga is free living, retained in place by the entanglement of its long thalli of branched chains of vesicles among the pneumatophores (Bishop et al. 2012, 2013). Consequently, its density displays a positive relationship with the density and height of pneumatophores (Bishop et al. 2012, 2013). Despite this reliance of the alga on the pneumatophores, previous studies independently manipulating the density of

the alga and the pneumatophores have shown that the effect of the alga on invertebrates overwhelms the direct effects of the pneumatophores on invertebrates (Bishop et al. 2012). The oyster, although also exhibiting some dependency on pneumatophores as a substrate for attachment (Bishop et al. 2012), also forms small aggregations, typically 15 to 25 cm in diameter, around shell fragments found on the sediment surface (M. J. Bishop pers. obs.). Thus, in contrast to the alga, the small-scale distribution of oysters is independent of pneumatophore density (Bishop et al. 2012). By providing complex habitat, a hard substratum for the growth of biofilms, and protection from predators, both the oyster and alga substantially enhance the abundance and diversity of epifaunal invertebrates within mangrove forests (Branch & Branch 1980, Underwood & Barrett 1990, Bishop et al. 2009).

Field experiment

On January 12, 2012, we established a factorial field manipulation of *Saccostrea glomerata* and *Hormosira banksii* biomass at 2 sites separated by ~100 m in Quibray Bay (34° 01′ 29″ S, 151° 10′ 45″ E) within the Towra Point Aquatic Reserve, Botany Bay, New South Wales, Australia. The 2 sites were located at similar tidal heights of ~0.8 m above mean low water, yet they differed in pneumatophore density and intermediate foundation species dominance. One site (S1) had a pneumatophore density of 137.0 ± 5.0 (mean ± SE) per 0.25 m^2 plot and was dominated by *H. banksii* (1.39 ± 0.17 kg wet wt *H. banksii* per 0.25 m^2 plot, 0.70 ± 0.30 oyster clumps per 0.25 m^2 plot, n = 20). The other site (S2) had a pneumatophore density of 35.0 ± 5.0 per 0.25 m^2 and was dominated by clusters of *S. glomerata* (0.40 ± 0.15 kg wet wt *H. banksii* per 0.25 m^2 plot, 1.70 ± 0.60 oyster clumps per 0.25 m^2 plot, n = 20). By conducting our manipulation at these 2 sites, we assessed the context dependency of the facilitation cascades.

At each site, we established 54 experimental plots separated by 1 to 2 m by first clearing randomly selected circular habitat patches, 0.25 m^2 in area, of all *S. glomerata*, *H. banksii*, and associated benthic organisms, leaving bare sediment and pneumatophores. The plots were then randomly assigned to one of 9 experimental treatments with varying biomasses of the 2 foundation species (n = 6 per treatment): (1) no *S. glomerata*, no *H. banksii*; (2) no *S. glomerata*, low *H. banksii* biomass; (3) no *S. glomerata*, high *H. banksii* biomass; (4) low *S. glomerata*

biomass, no *H. banksii*; (5) low *S. glomerata* biomass, low *H. banksii* biomass; (6) low *S. glomerata* biomass, high *H. banksii* biomass; (7) high *S. glomerata* biomass, no *H. banksii*; (8) high *S. glomerata* biomass, low *H. banksii* biomass; and (9) high *S. glomerata* biomass, high *H. banksii* biomass. The range of biomass treatments for each of the foundation species was based on the range of variation in their abundance observed in this system (Bishop et al. 2012). For *S. glomerata*, we used naturally occurring oyster clusters (biomass per cluster = 0.20 ± 0.02 kg) to create plots of no (0 clusters), low (2 clusters), or high (4 clusters) biomass. Each cluster had an average of 7.56 ± 0.16 live oysters. For *H. banksii*, we manipulated the wet mass of algae present in the plots to create no (0 kg), low (1.25 kg), or high (2.5 kg) biomass treatments. All associated invertebrates were removed from oysters and algae by hand prior to their introduction to the experimental plots.

To ensure that the biomass treatments of the negatively buoyant *H. banksii* were maintained, each plot was surrounded by a 200 mm high, 0.25 m^2 circular fence constructed of 5 mm galvanized mesh and raised 2 cm off the sediment surface. The fences had open tops to allow predator access. In previous studies, this fence design prevented the loss or gain of *H. banksii* biomass through lateral transport and did not modify the process of invertebrate community establishment when compared to unfenced control plots (Bishop et al. 2009, 2012). At our study sites, the invertebrate community is dominated by littorinid, batillariid, and trochid gastropods that are, on average, <2 cm in diameter and that can crawl under or over the fences (Bishop et al. 2009, 2012). Crabs and larger gastropods, such as *Pyrazus ebeninus* and *Polinices* spp., can partially or fully bury in the sediment and so are also unimpeded by the fences (Bishop et al. 2009, 2012). Given our previous demonstration of no significant fencing artifacts at the study sites (Bishop et al. 2009) and the consistent application of fencing to all experimental treatments in the present study, a control for fencing was not repeated here.

On April 2, 2012, we quantified *in situ* the identity and abundance of all epifauna >2 mm in diameter found in 0.2 × 0.2 m quadrats placed in the center of the plots (to minimize edge effects). A 3 mo experimental duration was chosen because (1) our previous research at this study site demonstrated that the invertebrate community recolonization in defaunated plots becomes indistinguishable from the recolonization in undisturbed plots 3 mo after experimental intervention (Bishop et al. 2009) and (2) there is little

seasonality in the ecology of this system (Bishop et al. 2007). First, we thoroughly searched the *H. banksii* present within each quadrat for invertebrates. We then moved the alga aside and identified and counted invertebrates on the pneumatophores, oysters, and the sediment surface below (Table 1). *In situ* sampling was necessary because our study site was designated as a no-take aquatic reserve from which we were not permitted to remove specimens. Species were pooled at the plot level across all substrates (e.g. S. *glomerata* cluster, *H. banksii* canopy, pneumatophore, sediment surface).

Table 1. Taxa observed, feeding guilds, and substrates for attachment ('–' = absent from substrate; '+' = present on substrate; Pneum. = pneumatophore; Alga = *Hormosira banksii*; Oyster = *Saccostrea glomerata*; Mud = substratum)

Taxon	Feeding guild	Pneum.	Alga	Oyster	Mud
ARTHROPODA					
Varunidae					
Paragrapsus laevis	Detritivore	–	+	+	–
ECHINODERMATA					
Asterinidae					
Parvulastra exigua	Grazer	–	+	+	+
MOLLUSCA					
Polyplacophora					
Chitonidae					
Juvenile chiton	Grazer	–	–	+	–
Gastropoda					
Amphibolidae					
Salinator fragilis	Grazer	–	+	+	–
Batillaridae					
Batillaria australis	Detritivore	+	+	+	+
Ellobiidae					
Pleuroloba quoyi	Grazer	–	–	+	–
Littorinidae					
Bembicium auratum	Grazer	+	+	+	+
Lottiidae					
Patelloida mimula	Grazer	–	–	+	–
Muricidae					
Bedeva paivae	Predator	–	–	+	+
Naticidae					
Conuber sordidum	Predator	–	–	–	+
Nassariidae					
Nassarius burchardi	Scavenger	–	–	+	+
Neritidae					
Nerita atramentosa	Grazer	–	–	+	–
Onchidiidae					
Onchidella nigricans	Detritivore	–	–	+	+
Potamididae					
Pyrazus ebeninus	Detritivore	–	–	–	+
Trochidae					
Austrocochlea porcata	Grazer	–	+	+	+
Bivalvia					
Mytilidae					
Xenostrobus securis	Suspension feeder	–	–	+	–
Lasaeidae					
Lasaea australis	Suspension feeder	–	–	+	–
PLATYHELMINTHES					
Stylochidae					
Stylochus (*Imogine*) sp.	Predator	–	–	+	–

Statistical analyses

We analyzed the abundance and species richness of the associated community using separate factorial ANOVAs, with *Hormosira banksii* biomass (none, low, or high) and *Saccostrea glomerata* biomass (none, low, or high) as categorical, fixed factors and site as a random factor. We used post hoc Tukey's tests to differentiate among means. ANOVAs were run in R software (ver. 2.15.0).

In our study, observed species richness was positively correlated with associated community abundance (richness = $0.05 \times$ abundance + 1.94; $R^2 = 0.52$), as is commonly the case (Rossi 2011). Thus, we used the 'rich' package in R to compare rarefied species richness across different levels of *H. banksii* and *S. glomerata* biomass at each site. This comparison allowed us to control for differences in associated species abundance in these treatments (Rossi 2011). We calculated the bootstrap mean and SD of species richness for each level of foundation species biomass at each site using a standard density of 200 individuals.

We also conducted multivariate analyses to examine variation in community composition. First, we conducted a permutational multivariate analysis of variance (PERMANOVA) on untransformed data. This analysis is not only influenced by community composition but also strongly affected by the abundance of dominant taxa. Hence, to disentangle the effects of the identity of taxa versus their abundance, we ran a second PERMANOVA on presence-absence transformed data. Differences in the 2

analyses suggest that the abundances of taxa are more important than their identities in contributing to dissimilarity among treatments. Each of the PERMANOVAs had the same 3 factors as the ANOVAs and used Bray-Curtis dissimilarities. PERMANOVAs were followed by similarity percentages (SIMPER; Clarke 1993) analyses to identify the taxa that were good discriminators among treatments. A good discriminating species contributes heavily to inter-treatment dissimilarity and has a small SD; here, we defined good discriminators as species with a Bray-Curtis dissimilarity:SD (diss:SD) ratio >1. We ran separate univariate ANOVAs on these individual taxa contributing most to dissimilarity. Non-metric multidimensional scaling plots, using individual plots as points, were used to visualize sources of dissimilarity in the (1) untransformed and (2) presence-absence transformed data.

RESULTS

Over the 3 mo experiment, 18 invertebrate taxa colonized our experimental plots (Table 1). Of these, 5 taxa were found exclusively on oysters, and an additional 3 taxa were found on *Saccostrea glomerata* or on the sediment surface below. Six taxa were observed on *Hormosira banksii*, all of which were also observed on oysters (Table 1) and many of which were also found on the sediment surface or on pneumatophores. Two taxa were found exclusively on the sediment surface (Table 1).

At the end of the 3 mo experiment, there was no interactive effect of *S. glomerata* and *H. banksii* biomass on either the abundance or the species richness of invertebrates at either site (p > 0.05, oyster × alga × site and oyster × alga; see Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m508p129_supp.pdf for complete ANOVA results). Hence, the effects of *S. glomerata* and *H. banksii* on these variables could be interpreted independently. The abundance of associated invertebrates increased with *S. glomerata* biomass at both sites (oyster $F_{2,90}$ = 67.83, p < 0.001; Fig. 1A, Fig. S1 in the Supplement). *H. banksii* presence had similar positive effects on invertebrate abundance at S1 but not at S2 (site × alga $F_{2,90}$ = 7.45, p < 0.01; Fig. 1B, Fig. S1 in the Supplement), and where this facilitation occurred, it depended on the presence of algae rather than its biomass. The species richness of the associated community also responded to both foundation species, increasing with *S. glomerata* biomass (oyster $F_{2,90}$ = 76.09, p < 0.001; Fig. 2A, Fig. S2 in the Supplement)
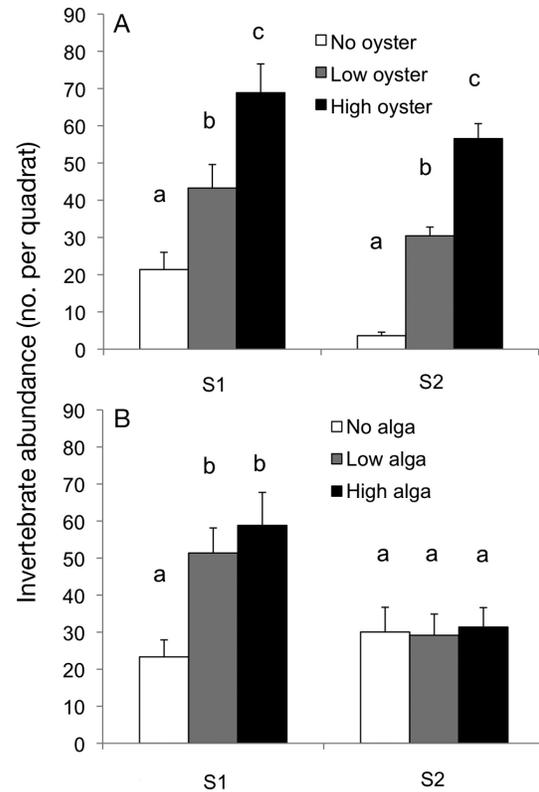

Fig. 1. (A) Abundance of epifaunal invertebrates increased with *Saccostrea glomerata* biomass in both experimental sites (S1, S2). (B) *Hormosira banksii* presence, but not biomass, facilitated greater abundances of associated invertebrates only in S1. Error bars: +1 SE. Different lower-case letters indicate significant differences at p < 0.05. Because there were no site-specific differences in (A), mean comparisons were only conducted across levels of oyster biomass

and *H. banksii* presence (alga $F_{2,90}$ = 8.10, p < 0.001; Fig. 2C, Fig. S2 in the Supplement). This response was consistent across sites, despite higher overall associated community species richness at one site (S1; Fig. 2A,C). Estimates of rarefied species richness that controlled for variation in associated species abundance did not differ substantially from observed richness, other than an increase in species richness in the absence of oysters or algae, particularly at S2 (Fig. 2B,D).

Our multivariate analyses confirmed the independent effects of *S. glomerata* and *H. banksii* on community composition (Fig. 3). The analysis of untransformed data, which is strongly influenced by the most abundant taxa, revealed interactions between site and *S. glomerata* (pseudo-$F_{2,90}$ = 5.13, p < 0.001) and site and *H. banksii* (pseudo-$F_{2,90}$ = 2.69, p < 0.01). The effects of *S. glomerata* biomass on the associated
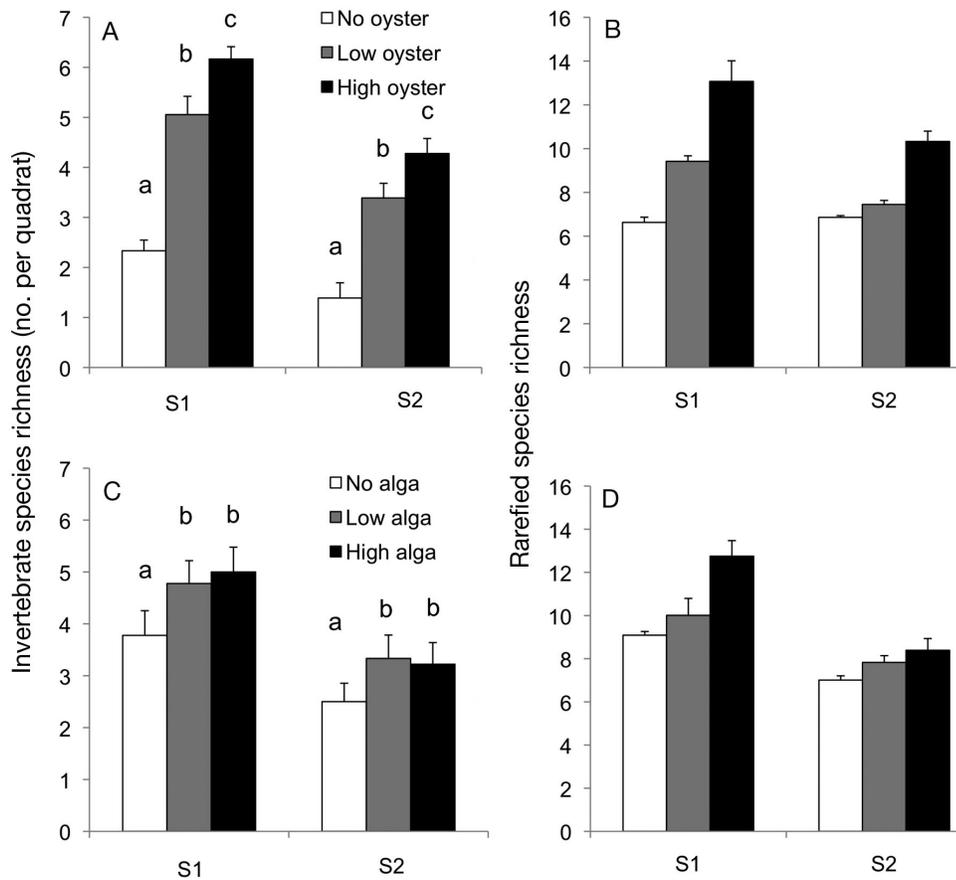
Fig. 2. (A) Epifaunal species richness increased significantly with *Saccostrea glomerata* biomass in both sites (S1, S2). (B) Patterns of rarefied richness were similar to measured richness, although the differences between no *S. glomerata* and low *S. glomerata* biomass were not as great. (C) *Hormosira banksii* presence, but not biomass, caused increases in epifaunal species richness in both sites. (D) Rarefied richness showed a similar pattern across *H. banksii* biomass. Overall, observed and rarefied species richness values were greater in S1 than in S2. Error bars: +1 SE in (A) and (C) and +1 SD in (B) and (D). Different lower-case letters indicate significant differences at p < 0.05. Because there were no site-specific differences, mean comparisons were only conducted across levels of oyster and algal biomass
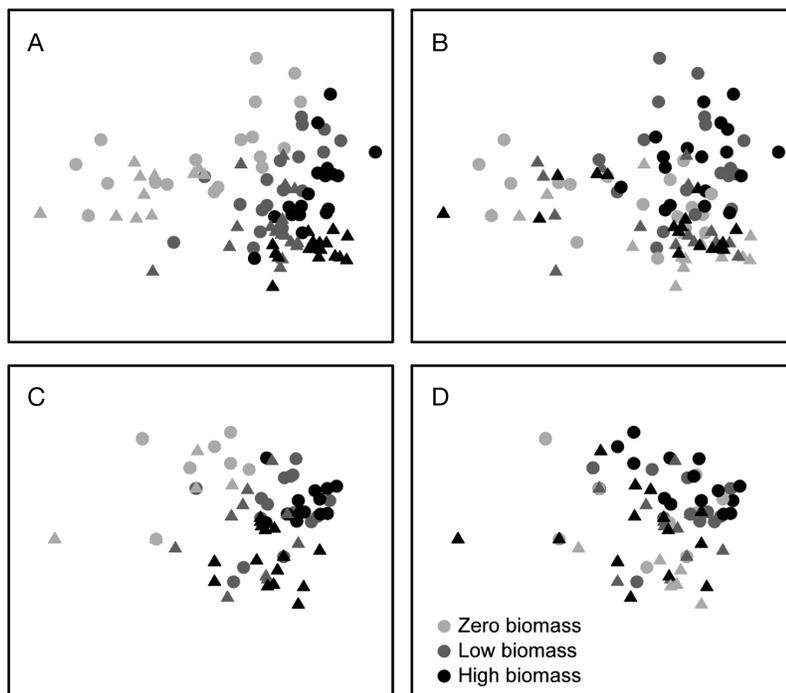

Fig. 3. Non-metric multidimensional scaling plots showing dissimilarity in invertebrate communities among plots. Two ordinations are presented, based on (A,B) untransformed data and (C,D) presence-absence transformed data. For each ordination, we separately show effects of (A,C) *Saccostrea glomerata* oyster biomass and (B,D) *Hormosira banksii* algal biomass across the 2 sites, as the 2 foundation species had independent effects. Circles = Site 1 (S1); triangles = Site 2 (S2); light grey symbols = no foundation species; dark grey species = low biomass of the foundation species; black symbols = high density of the foundation species

community were strong at both sites (*a posteriori* differences among oyster biomass levels significant in both sites with p < 0.01). However, the effects of *H. banksii* were only evident at S1, and they resulted from *H. banksii* presence rather than biomass (*a posteriori* differences of low and high algal biomass from no algal biomass significant with p < 0.001). The analysis of presence-absence data, which removes the influence of dominant species and hence disentangles the effect of the identity of species present, indicated that oyster biomass (pseudo-$F_{2,90} = 78.28$, p < 0.05) and site (pseudo-$F_{1,90} = 27.18$, p < 0.001) affected the constituent species of the associated community independently (i.e. there were no significant interactions among factors; pseudo-$F < 1.18$, p > 0.30). The effect of *H. banksii* was not significant (pseudo-$F_{2,90} = 2.85$, p > 0.15) in this analysis.

SIMPER analyses indicated that the littorinid gastropod *Bembicium auratum*, the batillariid gastropod *Batillaria australis* (= *Velacumantus australis*), and the lottiid limpet *Patelloida mimula* were the key taxa contributing to multivariate differences in communities (diss:SD ratio consistently >1). *B. auratum* and *P. mimula* abundances were interactively affected by *S. glomerata* biomass and site (*B. auratum* site × oyster $F_{2,90} = 5.12$, p < 0.01; *P. mimula* site × oyster $F_{2,90} = 9.94$, p < 0.001); in both cases, their abundances showed a greater increase in S2 than in S1 (Fig. 4A,C). *B. auratum* abundance also increased with *H. banksii* presence, regardless of site (alga $F_{2,90} = 8.01$, p < 0.001; Fig. 4B), but *P. mimula* did not (alga $F_{2,90} = 0.43$, p > 0.65). *B. australis* also responded to *H. banksii* presence but only at S1 (site × alga $F_{2,90} = 5.69$, p < 0.01; Fig. 4D); it did not respond to *S. glomerata* biomass in either site (oyster $F_{2,90} = 0.98$, p > 0.05; site × oyster $F_{2,90} = 1.26$, p > 0.05).

DISCUSSION

This study extends previous work on facilitation cascades by examining how 2 intermediate foundation species, *Saccostrea glomerata* and *Hormosira banksii*, each facilitated by the same basal foundation species (the mangrove *Avicennia marina*), interact to influence the associated community. We found that the 2 intermediate foundation species independently facilitated the abundance and richness of associated communities. Associated species abundance and richness increased consistently with *S. glomerata* biomass but only responded to *H. banksii* presence (not biomass). Faunal responses varied between our 2 sites, but in general, the effect of algal presence and
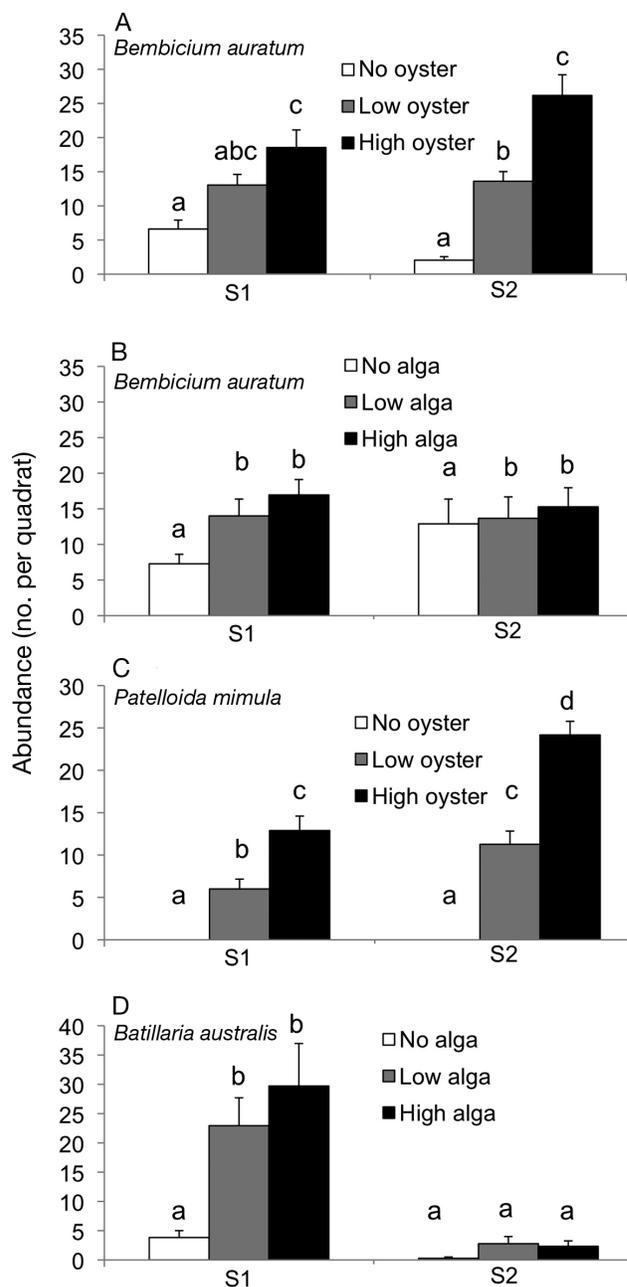

Fig. 4. (A) Abundance of the gastropod *Bembicium auratum* increased with *Saccostrea glomerata* biomass, but this relationship varied across sites (S1, S2). (B) *B. auratum* abundance also increased in the presence of *Hormosira banksii* in both sites. (C) Abundance of the limpet *Patelloida mimula* increased with oyster biomass, but the strength of this relationship varied across sites. (D) The gastropod *Batillaria australis* increased in abundance in response to *H. banksii* in S1 but was virtually absent in S2. Error bars: +1 SE. Different lower-case letters indicate significant differences at p < 0.05. Because there were no site-specific differences in (B), mean comparisons were only conducted across levels of algal biomass

oyster biomass was to increase both invertebrate richness and abundance. The additive effects of the 2 foundation species could in part be attributed to a number of taxa that were unique to oysters. This result, however, also indicates that the presence of one foundation species did not make the other foundation species more or less habitable by invertebrates.

The absence of interactive effects of *S. glomerata* and *H. banksii* on associated species richness, abundance, and identity supports predictions that foundation species with different functional traits will have independent and predictable effects on community structure (Thomsen et al. 2010, Angelini & Silliman 2014). Although we did not quantify the functional traits of the 2 foundation species in the present study, they each occupy different feeding guilds (the alga is an autotroph, and the oyster is a suspension feeder); they appear to differ in the structure they provide (*H. banksii* has long chains of vesicles, whereas oysters occur in clusters); their surface structure differs (the algal substrate is softer, and receptacles add fine-scale rugosity on its surface); and their different shapes result in the formation of different types of interstices for organisms. Whereas the matrix of oysters provides interstices in which small organisms could seek refuge from predators and desiccation stress, it provides little structural protection to organisms on the sediment surface. The additive effects of the 2 foundation species are likely to have resulted from (1) a subset of species that were unique to oysters responding to the manipulation of oyster biomass but not algal biomass; and (2) habitat generalists that require substrate for grazing or attachment, responding additively to increases in substrate availability.

We found that community structure responded not only to foundation species identity but also to the biomass of one of the foundation species, the oyster *S. glomerata*. Both invertebrate species abundance and richness increased with oyster biomass. The effect of oyster biomass is consistent with previous work demonstrating that the magnitude of facilitative interactions often varies with facilitator abundance or biomass (Bracken et al. 2007, Irving & Bertness 2009, Stier et al. 2012, Hughes et al. 2014). Interestingly, the effects of this within-species variation were comparable in magnitude to the effects of changing foundation species identity. Our findings reinforce the importance of intraspecific variation in individual- and population-level traits of foundation species in influencing community structure (Kimbro & Grosholz 2006, Bishop et al. 2012, 2013). However, additional manipulations of multiple foundation species are needed to determine the relative importance of trait variation within versus across foundation species for associated species richness and abundance.

By contrast, only the presence of *H. banksii*, and not its biomass, affected associated species richness and abundance in our study, suggesting that variation in biomass may be less important for some foundation species than for others. Theory (Bruno & Bertness 2001) and recent empirical research (Bishop et al. 2012) suggest that the benefits of facilitators on their associated community reach a threshold at some point of facilitator abundance. Given the different traits of the 2 intermediary facilitators, it is possible that our experimental treatments placed the foundation species on different parts of their threshold curve. For instance, our low algal biomass treatment may have already approached the asymptotic part of its functional relationship, whereas our low oyster biomass treatment may have been quite far from the asymptotic portion of its functional relationship.

The richness and identity of invertebrate species in our plots were comparable to the natural environment at our study site (Table 1; see Bishop et al. 2009, 2012). Of the 18 associated species, 3 mollusc species (2 grazers and 1 detritivore) were particularly important in driving differences in community structure among treatments. *Bembicium auratum*, a grazing gastropod that consumes microalgae on hard surfaces or on mud (Reid 1988), increased in abundance with the biomass of oysters and with the presence of *H. banksii*. This effect was evident across each of the 2 study sites. It is likely that the consistent response of *B. auratum* to each foundation species reflected an increase in the availability of substrate for grazing in food-limited mangrove systems (Branch & Branch 1980). Refuge from predation is less likely to have been the cause, as the gastropod has a thick shell and suffers relatively low rates of predation from crabs and fish, even away from foundation species (Reid 1988). The abundance of the small limpet grazer *Patelloida mimula* (Minchinton & Ross 1999) was higher at S2, the site with higher surrounding oyster densities. This species was completely absent in the no-oyster plots but increased significantly with increasing *S. glomerata* biomass (Fig. 4C). The density of *P. mimula* is typically limited to 1 individual per oyster (Minchinton & Ross 1999), and its linear increase in density with the abundance of oysters is consistent with the enhancement of substrate availability. The third taxon responding most strongly to our experimental manipulation was the detritivorous gastropod *Batillaria australis*, a species that is gener-

ally more abundant on sedimentary substrates than on hard substrates (Ewers 1967, Bishop et al. 2009). *B. australis* increased strongly in response to *H. banksii* presence (but not biomass) only in the site with higher pneumatophore densities and surrounding algal biomass (S1). The algal mats formed by *H. banksii* provide a greater cover of the sediment substratum than oyster clumps, potentially protecting the gastropod from predation (Bishop et al. 2009). Alternatively, the effect of *H. banksii* on *B. australis* may have arisen through direct and indirect enhancement of the organic matter on which the gastropod feeds. Additional experiments are needed to ascertain the specific mechanisms of facilitation.

Spatial variation in species interactions has long been appreciated by ecologists (Menge & Lubchenco 1981, Sanford 1999, Leonard 2000), yet relatively few studies of foundation species examine how their effects vary across multiple sites or environmental conditions (but see Altieri & Witman 2006, Gribben et al. 2009). The effects of *S. glomerata* and *H. banksii* in this study varied substantially across 2 sites close to each other, complicating our ability to predict the effects of changes in the presence or absence of intermediate foundation species in this system. The responses of individual taxa (e.g. habitat specialists such as *B. australis* and *P. mimula*) suggest that variation in background intermediate foundation species abundance across sites contributed to their differences, consistent with previous demonstrations of site- and habitat-specific differences in the community-level effects of key taxa (Beck 1998, Crowe et al. 2011). However, we are unable to ascribe differences between the sites to specific characteristics such as the dominant foundation species because we only tested 1 site for each habitat type. Future studies that replicate sites varying in foundation species dominance are needed to test the generality of the patterns suggested here.

Our study suggests that caution is warranted in the 'build it and they will come' approach to restoring foundation species. Community structure in our experiment depended strongly on foundation species biomass for one species (oysters) but on presence-absence for the other (algae). Furthermore, although our experimental sites were close to each other (<100 m), we found strong differences in the communities associated with each foundation species across sites. The timing and relatively short duration of our experiment may have contributed to these results; it is possible that seasonal recruitment events would have homogenized the associated communities across sites or that a longer duration would have allowed for colonization of additional species from the surrounding area. Despite these caveats, the site-specific effects of foundation species in this study add to growing evidence that while foundation species can set the potential abundance and richness of associated communities, realized community structure is determined by processes operating at larger spatial and temporal scales (Witman et al. 2004, Harrison & Cornell 2008, Bishop et al. 2013).

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