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Density-dependent facilitation cascades determine epifaunal community structure in temperate Australian mangroves

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Abstract. Co-occurring foundation species can determine biological community structure via facilitation cascades. We examined the density dependencies of facilitation cascades, including how the density of a basal foundation species influences the density of secondary foundation species, and how the density of secondary foundation species influences community structure. The system in which we assessed density dependencies was a temperate mangrove forest in which pneumatophores trap the fucoid alga *Hormosira banksii* and provide substrate for the oyster, *Saccostrea glomerata*. The alga and oyster in turn determine benthic community structure. In the field, algal biomass was positively correlated with pneumatophore density. Oysters, by contrast, were highly over-dispersed and correlated with the presence/absence of pneumatophores. Epifaunal abundance and species richness were positively correlated with algal and oyster abundance, but their effects were independent. The positive effect of pneumatophore density on epifauna was primarily an indirect effect of trapping more algae. Pneumatophores did not directly influence invertebrate communities. Experiments revealed that, at very low pneumatophore densities, algal retention was insufficient to facilitate epifauna above that found on pneumatophores alone. At higher densities, however, increasing the density of pneumatophores increased algal retention, and the density and diversity of associated invertebrates. Shading by the mangrove canopy reduced algal biomass but did not modify the density-dependent nature of the cascade. Our results extend facilitation theory by showing that the density of both basal and secondary foundation species can be critical in triggering facilitation cascades. Our study also reveals that, where foundation species co-occur, multiple, independent cascades may arise from a single basal facilitator. These findings enhance our understanding of the role of density-dependent facilitation cascades in community assembly.

Key words: Australian mangrove; Avicennia marina; *density dependence; ecosystem engineers; facilitation; foundation or habitat-forming species; hierarchical facilitation;* Hormosira banksii; *oysters; pneumatophores; positive interactions; trait mediation.*

Introduction

Foundation, or habitat-forming, species are important determinants of community structure (Dayton 1972, Bruno and Bertness 2001). They produce changes in environmental conditions that can be positive, negative, or neutral to individual species, but that typically lead to a net enhancement of diversity and abundance (Dayton 1972, Jones et al. 1994, Bruno et al. 2003). Over the past few decades, many examples of facilitative, foundation species have emerged from terrestrial and aquatic ecosystems (e.g., Callaway 1995, Bruno 2000). In many instances, foundation species can co-occur and are likely to interact to produce positive effects (Bruno and Bertness 2001), yet most studies have considered facilitation by individual foundation species in isolation (Wright and Jones 2006).

Foundation species might co-exist in adjacent or nested assemblages that cumulatively facilitate communities in one of several ways (Angelini et al. 2011). First, foundation species may form mosaics of monospecific patches among which segregation is maintained by competition or divergent environmental tolerances (Crain and Bertness 2006). Where these patches support different assemblages of dependent taxa, they add to give higher diversity at a larger scale (Yakovis et al. 2008). Second, the foundation species may co-occur, but not obligately, with the presence of one species modifying the way in which others influence the abiotic environment (Gribben et al. 2009). Third, two foundation species may form one-way nested facilitation cascades (analogous to predation-driven trophic cas-

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cades; see Pace et al. 1999) in which the abiotic environment provided by the basal foundation species is a precondition for colonization of a second, which in turn facilitates the focal community (Bruno and Bertness 2001, Altieri et al. 2007).

Previous research on facilitation cascades has been based on presence/absence manipulations of the foundation species and/or their simulated impacts (Altieri et al. 2007). Effects of foundation species are, however, often density dependent (van Hulzen et al. 2007, Irving and Bertness 2009, Harley and O'Riley 2011). Consequently, manipulation of only the presence or absence of foundation species is likely to tell us very little about their cumulative, realized role (Bruno and Bertness 2001). Relationships are likely to be complex because not only may the density of basal foundation species influence the density of secondary foundation species in linear or nonlinear ways, but also the density of the secondary foundation species may, in turn, produce density-dependent effects on associated communities. Empirical studies are needed to disentangle how multiple foundation species cumulatively determine community structure across the full range of their densities.

In many coastal ecosystems, mangroves are one of the most extensive foundation species, facilitating biodiversity at all trophic levels (reviewed by Nagelkerken et al. 2008). Similar to other foundation species, facilitation by mangroves occurs via multiple mechanisms such as the reduction of desiccation stress (e.g., canopy shading) and predation pressure (e.g., increasing habitat complexity), and by providing a surface for colonization by invertebrates (e.g., oysters) that otherwise would not settle on barren soft sediments (Morrisey et al. 2010). In southeastern Australia, the dominant species of mangrove, *Avicennia marina*, produces pneumatophores (aerial roots) that facilitate many species of mollusks and crustaceans by providing structure, shelter, trapping detrital material, and supporting growth of epiphytic algae (Beck 1998, Skilleter and Warren 2000, Ross 2006). Among the species facilitated by *A. marina* is the fucalean macroalga, *Hormosira banksii* (King 1981, King and Wheeler 1985), which is itself an important foundation species (e.g., Bishop et al. 2009).

H. banksii occurs among pneumatophores, under the mangrove canopy, either as persistent free-living populations, or attached to hard structure (King 1981, King and Wheeler 1985, McKenzie and Bellgrove 2008). The alga's distinctive fronds of spherical vesicles provide a hard substrate for attachment of invertebrates and the biofilms on which they feed, and might also offer refuge from predation (Bishop et al. 2009). *H. banksii* colonizes mangroves when fronds of the alga detach from the species' primary rocky shore habitat (King 1981, King and Wheeler 1985), wash ashore, and reproduce (McKenzie and Bellgrove 2009). Pneumatophores, in combination with natural topographic features, are likely to play a role in trapping the algae (King 1981). Once established, however, *H. banksii* can inhibit germination of *A. marina* propagules (Clarke and Myerscough 1993), although established *A. marina* continue to support *H. banksii* over ecologically relevant timescales (M. J. Bishop, *personal observation*). It is unclear whether the accumulation of *H. banksii* in mangroves requires a minimum pneumatophore density, whether a certain biomass of *H. banksii* is required to facilitate invertebrates, or how shading by the mangrove canopy may, through interfering with photosynthesis, modify these relationships. Furthermore, it is unknown whether a high biomass of *H. banksii* interferes with or complements the facilitation of other invertebrates by other co-occurring foundation species, such as *Saccostrea glomerata* oysters. Oysters attach to the trunks and pneumatophores of *A. marina* and facilitate invertebrate assemblages by providing habitat, a substrate for algal growth, and protection from predators (Branch and Branch 1980, Underwood and Barrett 1990, Minchinton and Ross 1999). Although the gregariously settling *S. glomerata* are highly over-dispersed, and respond generally to the presence or absence of pneumatophores rather than their density (Krassoi 2001), aggregations of oysters vary in their density and epifauna may respond to this variation.

Here, we determine the density dependencies of, and the relationships between, two co-occurring facilitation cascades of mangrove forests. Both cascades arise from *A. marina* pneumatophores, but the first involves *H. banksii* as the secondary foundation species and the second involves *S. glomerata* oysters. First, using mensurative field surveys, we test for spatially general relationships between densities of the basal facilitator, pneumatophores, the two secondary facilitators, *H. banksii* and *S. glomerata*, and epifauna. Second, to partition the density dependence of epifauna on pneumatophores into direct effects of the pneumatophores and indirect effects arising from their facilitation of *H. banksii*, we conduct manipulative experiments. For the cascade with *H. banksii*, we additionally determine how shading modifies relationships by partially or wholly offsetting the positive effects of mangroves that arise through pneumatophores retaining algae. We hypothesize that, irrespective of pneumatophore density, negative effects of shading on *H. banksii* biomass will be insufficient to offset positive effects of pneumatophores on algal retention. Our experiments do not manipulate oysters because previous experiments have demonstrated facilitative relationships between pneumatophores and oysters (Krassoi 2001), and oysters and invertebrates (e.g., Summerhayes et al. 2009). Our study provides the first assessment of how, within facilitation cascades, the density of a basal facilitator can influence the density of a secondary foundation species, and how the density of the secondary foundation species in turn shapes communities.

Materials and Methods

Study sites

To test whether there are spatially general patterns of association between the basal foundation species, *Avicennia marina* pneumatophores, and the two secondary facilitators, *Hormosira banksii*, and *Saccostrea glomerata* oysters, that determine epifaunal community structure, mensurative sampling was conducted within three mangrove forests of New South Wales (NSW), Australia, that were known to contain *H. banksii* and *S. glomerata*. These were: Quibray Bay, within Botany Bay (34°01′29″ S, 151°10′45″ E); Pretty Beach, Brisbane Waters (33°31′36″ S, 151°20′42″ E); and Salamander Bay, Port Stephens (32°43′43″ S, 152°05′53″ E). The manipulative experiments were conducted at Quibray Bay. At each of the sites, dense stands of the gray mangrove *A. marina* dominated the upper- to mid-intertidal elevations of the sedimentary intertidal shore. The sites were largely protected from wave action, but experienced seasonal winds that transported significant algal biomass from nearby rocky shores into the mangrove forest. Although most of the algae that washed into the mangrove forests were ephemeral, in contrast, free-living, reproductively viable populations of *H. banksii* were found year-round. *H. banksii* formed patches up to tens of meters long and of up to 90–100% cover under the mangrove canopy, at a tidal elevation where other facilitators, such as mangrove seedlings and dense epiphytic growth on pneumatophores, were uncommon. Mats formed by accumulations of the highly branched algae were typically 5–10 cm thick. At each of the study sites, benthic communities did not display strong seasonality (see Bishop et al. 2007), allowing us to conduct experiments year-round.

Spatial relationships among facilitators of epifaunal communities of mangroves

We conducted mensurative sampling to establish relationships between epifauna and the three facilitators, *A. marina* pneumatophores, *H. banksii*, and *S. glomerata*, in autumn (March–April) 2008. At each of the three study sites, we quantified the structural habitat and benthic community structure within 60 quadrats (0.5×0.5 m) randomly positioned on the mid-shore (mean low water [MLW] + 0.6–1.0 m), where *H. banksii* accumulates. Within our quadrats, pneumatophores were the only substrate to which oysters were attached. To ensure that our sampling encompassed the full range of pneumatophore densities, we stratified our sampling, positioning at least 10 quadrats randomly within each of six pneumatophore density strata: 0–30, 31–60, 61–90, 91–120, 121–150, and 151–180 pneumatophores per 0.25-m^2 quadrat. Within each quadrat we quantified (1) the density of pneumatophores, (2) the wet mass of towel-dried and defaunated *H. banksii*, (3) the abundance of *S. glomerata* oysters, and (4) the abundance of other epifaunal species (>5 mm diameter), which in mangroves are predominantly mollusks, noting their specific location (i.e., attached to pneumatophores, oysters, *H. banksii* itself, or on the sediment surface). To identify and enumerate fauna by substrate of attachment, we initially searched any *H. banksii* present within each quadrat for invertebrates. We then moved the algae aside, taking care not to dislodge invertebrates from pneumatophores, and identified and counted invertebrates on the pneumatophores and sediment surface below. To enumerate oysters and their associated fauna, it was necessary to remove them from pneumatophores. These were carefully bagged; back at the laboratory, oysters were separated and all epifauna that were retained on a sieve of 5 mm diameter were identified and enumerated. Because our sampling did not consider smaller organisms or infaunal taxa, and was conducted only at low tide, our study addressed larger, intertidal organisms only.

We used partial correlations to examine relationships between the sets of variables: (1) pneumatophore density, *H. banksii* biomass, and total epifaunal abundance and species richness; and (2) pneumatophore density, *S. glomerata* abundance, and the abundance and species richness of epifauna attached to oysters (hereafter oyster-dwelling epifauna). These calculate correlation coefficients between pairs of variables, removing the influence of the third. Additionally, Pearson's correlations tested for a relationship between *H. banksii* biomass and oyster density.

Density-dependent effects of mangroves on Hormosira banksii *that cascade to epifauna*

To ascertain how effects of *H. banksii* on epifauna are hierarchically controlled by the density of *A. marina* pneumatophores, we conducted a manipulative field experiment on the unvegetated Quibray Bay mudflat, below the seaward extent of the pneumatophore zone of the mangrove forest (MLW spring + 0.6 m). We manipulated the structure of pneumatophores using structural mimics, hypothesizing that a minimum density would be required for retention of the alga, and hence its facilitation of other species. Shading was simultaneously manipulated to examine the extent to which the mangrove canopy would reduce the biomass of the alga and its facilitation. Density of pneumatophore mimics had four levels (0, 50, 100, and 150 pneumatophores/0.25 m^2) and shading had two (shaded and exposed), which were manipulated in a crossed design. Densities of mimics were based upon the natural range of pneumatophore densities in NSW mangrove forests (see *Results*).

We conducted the experiment just outside of the mangrove forest so that we could manipulate shading by exposing some plots to direct sunlight. This setting was not unrealistic because, within many mangrove forests, the pneumatophore zone extends seaward of the mangrove canopy and retains persistent *H. banksii* (M. J. Bishop, *personal observation*). We deliberately

chose to focus on retention of algae rather than accumulation in plots, because the latter would require detailed knowledge of the hydrodynamics of Botany Bay and the factors that lead to dislodgement of *H. banksii*. Furthermore, our interest was in patch-scale effects of pneumatophore density rather than large-scale differences in *H. banksii* accumulation among mangrove forests.

In winter (July) 2009, we established 54 0.25-m^2 plots, each separated by 2–3 m, that were randomly allocated to the eight experimental and one control treatments ($n = 6$). This plot size was chosen based on the scale of natural spatial variation in pneumatophore density and *H. banksii* biomass. Pneumatophore mimics were established at the required density by inserting 230-mm lengths of 6-mm diameter dowel rods 100 mm into the sediment. We shaded plots by stretching a 1-m^2 piece of green 70% monofilament shade cloth between four 300-mm high wooden garden stakes arranged at the vertices of a 1×1 m square. The cloth, centered over the 0.25-m^2 area, continually shaded plots irrespective of time of day. The shade cloth produced a more severe reduction in light than the mangrove canopy and the results of our experiment were therefore interpreted as an extreme scenario. Four 300-mm wooden stakes, each separated by 1 m, were positioned around unshaded plots. To test for artifacts of the shade cloth, we established a control treatment at the pneumatophore mimic density of 100 per m^2. The control plots ($n = 6$) had 50×50 mm green polypropylene mesh stretched between the stakes; due to its large mesh size, this provided structure without shading.

Each of the 48 experimental plots was initially supplied with 2 kg wet mass of defaunated free-living *H. banksii* from the Quibray Bay mangrove forest. This algal biomass was based upon the average amount of algae present within 0.25-m^2 quadrats randomly placed in dense patches of *H. banksii* in the adjacent mangal. At low tide, when the plots were exposed, the *H. banksii* was spread evenly across the 0.25-m^2 area of each experimental plot. *H. banksii* was not fenced in quadrats, thus allowing for its biomass to adjust due to natural processes. A pilot study in which we investigated the ability of *H. banksii*-free plots to acquire the alga from adjacent plots indicated that plots were sufficiently far apart to be considered independent.

To assess retention of *H. banksii*, we measured the wet mass of *H. banksii* remaining in each experimental plot two weeks, four weeks, six weeks, and six months after experimental addition. All *H. banksii* present within each 0.25-m^2 plot was removed for weighing with a spring balance and then returned to its respective plot immediately afterward. Six weeks and six months after algal addition, we also assessed colonization of the plots by epifaunal assemblages. Sampling of epifauna was done within a 0.2×0.2 m quadrat placed in the center of each plot, so as to minimize edge effects. Within each quadrat, we recorded the number of epifauna present by species, noting also the substrate to which they were attached (see mensurative experiment). Following enumeration, epifauna were returned to the plot from which they had come.

Data were analyzed using multivariate (epifaunal community structure) and univariate (algal biomass, epifaunal abundance) PERMANOVA analyses (Anderson 2001). We used PERMANOVAs throughout this study because, unlike ANOVAs or MANOVAs, they do not assume normal distributions and can work with any distance measure that is appropriate to the data. First, we used one-way PERMANOVA to test for experimental artifacts associated with the shading treatment. Across plots with 100 pneumatophores, we compared the biomass of *H. banksii* and the abundance and species richness of epifauna among shading control, unshaded, and shaded treatments. Second, we used two-way PERMANOVAs to test for interacting effects of pneumatophore density and shading on: (1) algal biomass; (2) epifaunal community structure; and (3) total epifaunal abundance, at each sampling time. The shading control was omitted from two-way PERMANOVAs because its *H. banksii* biomass and invertebrate communities were similar to those of the unshaded plots (see *Results*). A separate PERMANOVA was run for each sampling time because these were nonindependent and we expected time $\times$ plot interactions, which would prevent the calculation of independent measures of residual variation by repeated-measures designs (see Underwood 1997). PERMANOVAs used zero-adjusted Bray-Curtis dissimilarities among samples (see Clarke et al. 2006), calculated from untransformed data.

Pearson's correlations tested for relationships between *H. banksii* biomass and invertebrate abundance within experimental plots.

Direct effects of pneumatophore density and Hormosira banksii *biomass on epifaunal communities*

To parse the effects of pneumatophore density and *Hormosira banksii* biomass on epifaunal colonization, we conducted a second experiment in which the two factors were manipulated independently in a crossed design. The levels of the two factors were chosen to encompass the range of variation in the two factors evident from our mensurative sampling. Pneumatophore density had three levels (50, 100, and 150 pneumatophores/m^2) and biomass of *H. banksii* had six levels (0, 0.5, 1, 1.5, 2, and 2.5 kg wet mass/0.25 m^2).

In late winter (August) 2008, we established 108 circular 0.25-m^2 plots on the mid-shore ($\sim$MLW + 0.8 m) of the Quibray Bay mangrove forest, in areas where the pneumatophore density exceeds 600/m^2 and *H. bansksii* is naturally present. Oysters were either absent from plots or were manually removed to eliminate their influence. Each plot was randomly assigned to one of the 18 experimental treatments ($n = 6$ plots per treatment) and all algae and mollusks (including oysters) that were >5 mm in diameter were removed from each. We

TABLE 1. Partial correlations between pairs of variables, controlling for effect of the third: (A) mangrove (*Avicennia marina*) pneumatophore density, fucoid alga (*Hormosira banksii*) biomass, and abundances of all invertebrates; (B) the oyster *Saccostrea glomerata* and oyster-dwelling invertebrates at three sites in New South Wales, Australia.

Pairwise comparison	Quibray Bay		Pretty Beach		Salamander Bay	
	r	*P*	*r*	*P*	*r*	*P*
A) Relationships with *H. banksii*						
Pneumatophores and *H. banksii*	0.335	**0.010**	0.629	**<0.001**	0.343	**<0.001**
H. banksii and invertebrates	0.439	**<0.001**	0.123	0.346	0.284	**0.024**
Pneumatophores and invertebrates	0.183	0.164	0.193	0.136	0.236	0.064
B) Relationships with *S. glomerata*						
Pneumatophores and *S. glomerata*	−0.037	0.781	0.342	**0.008**	0.084	0.512
S. glomerata and oyster invertebrates	0.654	**<0.001**	0.652	**<0.001**	0.944	**<0.001**
Pneumatophores and oyster invertebrates	−0.093	0.487	−0.031	0.819	0.031	0.803

Notes: For each correlation between a pair of variables, the influence of the third in the group was removed. Correlations significant at $\alpha = 0.05$ are highlighted in bold.

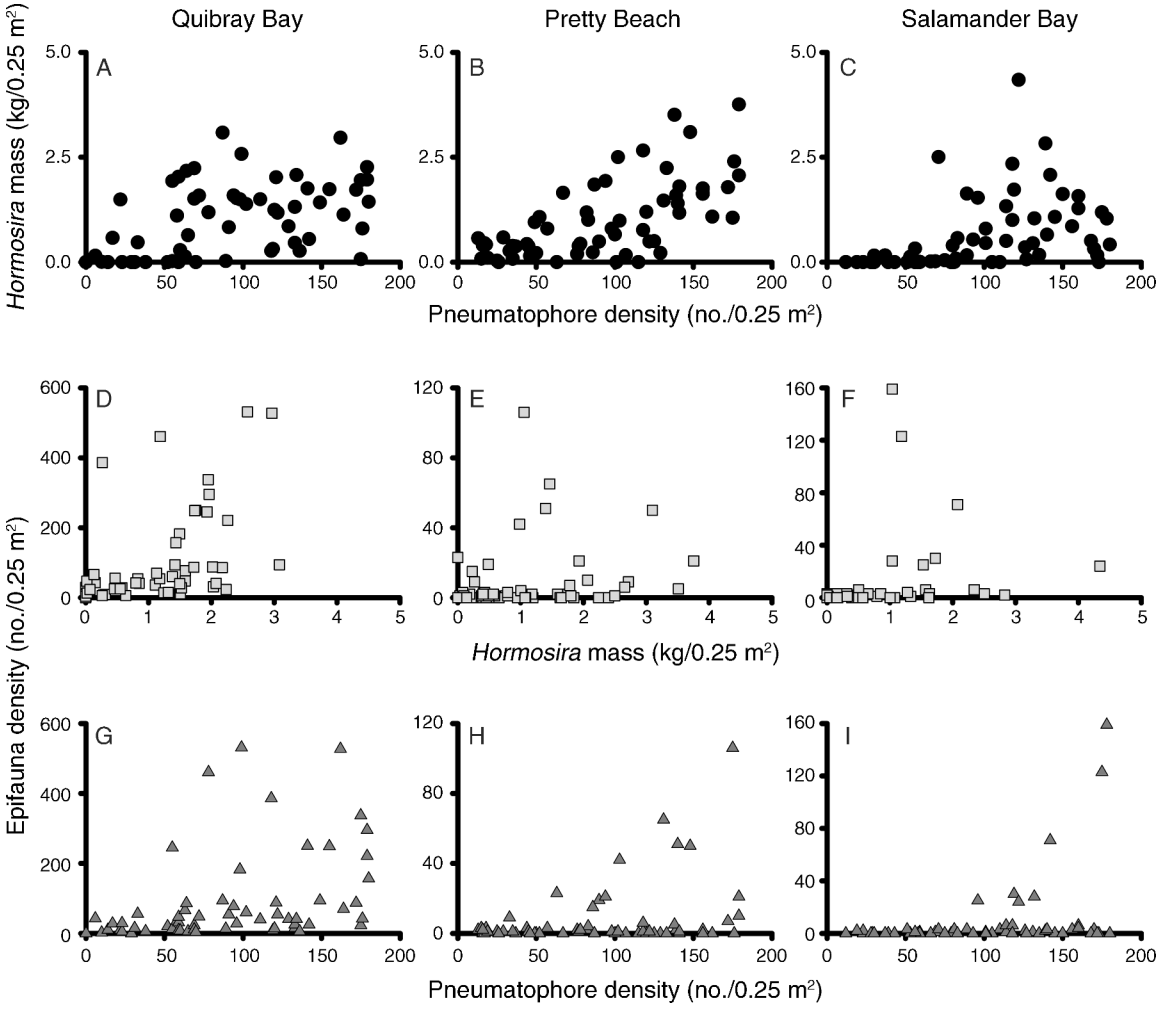

FIG. 1. The relationships between (A–C) mangrove (*Avicennia marina*) pneumatophore density and wet biomass of the fucoid alga *Hormosira. banksii*; (D–F) *H. banksii* wet biomass and abundance of total epifauna; and (G–I) pneumatophore density and abundance of total epifauna at three sites in New South Wales, Australia.

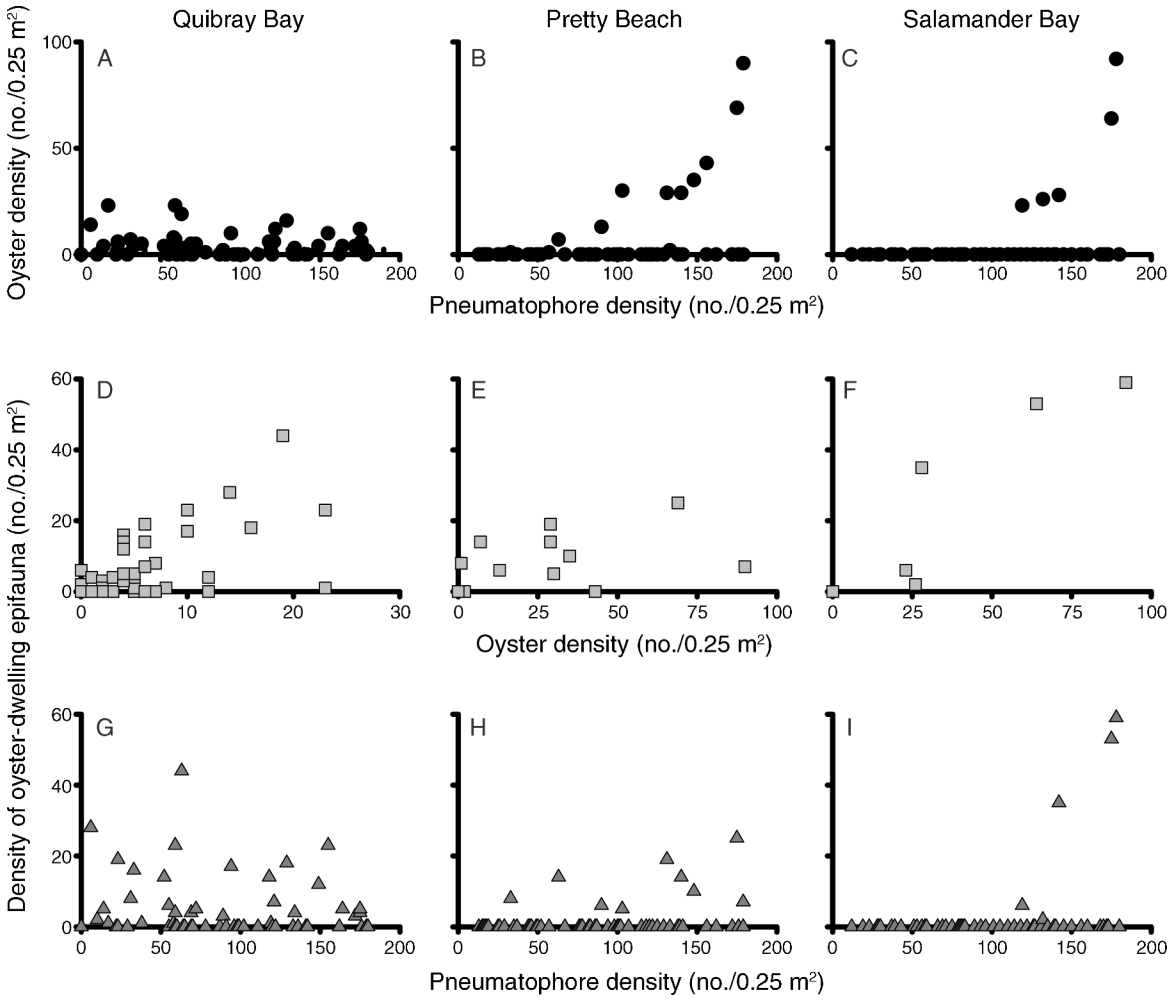

FIG. 2. The relationship between (A–C) the density of pneumatophores and oysters; (D–F) the density of oysters and oyster-dwelling epifauna; and (G–I) the density of pneumatophores and oyster-dwelling epifauna.

manipulated the aboveground density of pneumatophores in the plots by haphazardly pruning pneumatophores at the soil line until the desired density was attained. A pilot study indicated that the injury inflicted to pneumatophores by cutting did not release compounds that confounded effects of pneumatophore removal on invertebrate communities. The *H. banksii* used for experimental manipulations was from the surrounding mangrove forest and was defaunated by hand prior to reintroduction to plots at appropriate experimental biomasses. To ensure that *H. banksii* was retained at the experimental density, but that epifauna could still colonize, we erected a galvanized mesh fence around each plot with a 50-mm gap at the base (see Bishop et al. 2009). The fences were 200 mm high and were constructed of 5-mm galvanized mesh held in place by three plastic stakes 450 mm long. The tops of the fences were open to predators. The fences were sufficiently high to prevent *H. banksii* from floating out the top at high tide.

After 2, 6, and 12 weeks, we assessed the colonization of experimental plots by epifauna within a single 0.2 × 0.2 m quadrat using the methods previously described. We tested for interacting effects of pneumatophore density and *H. banksii* biomass on epifaunal community structure, and the total abundance and species richness of epifauna per plot using two-way PERMANOVAs of Bray-Curtis dissimilarities among samples, calculated from untransformed data. A separate analysis was conducted for each of the nonindependent sampling times. Where significant treatment effects were detected, PERMANOVAs were followed with post hoc tests.

RESULTS

Spatial relationships among facilitators of epifaunal communities of mangroves

Fourteen species of epifauna were identified in the mangroves, of which all but one (the cushion star *Parvulastra exigua*) were mollusks. Five species (the oyster drill *Bedeva hanleyi*, the mussels *Limnoperna*

TABLE 2. Results of two-way PERMANOVAs testing for spatial variation in the wet mass of *Hormosira banksii* retained by experimental plots.

Statistics, by period	Source of variation: Pneum (df = 3)	Shade (df = 1)	Pneum × Shade (df = 3)	Residual (df = 40)	Tests, a posteriori, by period
2 weeks					**Pneum × Shade**:
MS	4980	220	252	52	[N, S]: 0 < 50 < (100 = 150);
Pseudo *F*	96.1	4.2	4.9		[0, 50]: N = S;
P	**<0.001**	**0.027**	**0.002**		[100, 150]: N > S
4 weeks					
MS	6214	361	65	42	**Pneum**: 0 < 50 < (100 = 150)
Pseudo *F*	149.2	8.7	1.6		**Shade**: N > S
P	**<0.001**	**<0.001**	0.220		
6 weeks					**Pneum**: 0 < (50 = 100 = 150)
MS	5775	462	76	47	**Shade**: N > S
Pseudo *F*	123.4	9.9	1.6		
P	**<0.001**	**0.002**	0.191		
6 months					**Pneum × Shade**:
MS	1835	1607	274	84	[N, S]: 0 < 50 < (100 = 150);
Pseudo *F*	21.7	19	3.2		[0]: N = S;
P	**<0.001**	**<0.001**	**0.026**		[50, 100, 150]: N > S

Notes: Treatments were: Pneum, density of pneumatophore mimics (four levels: 0, 50, 100, 150 dowels/0.25-m^2 plot), and Shade (two levels: not shaded [N], shaded [S]), and their interaction; $n = 6$ plots/treatment, 48 plots in total. Terms significant at $\alpha = 0.05$ are highlighted in bold. In PERMANOVAs with a semi-metric distance measure (such as Bray-Curtis used here), the pseudo *F* statistic is not identical to Fisher's *F*. For significant interactions, a posteriori tests were used to identify significant differences among levels of one factor (at $\alpha = 0.05$; denoted by < or > symbols for univariate tests and ≠ for multivariate tests) within levels of the other (indicated in parentheses). Where interactions were not significant, a posteriori tests examined sources of differences (<, >, ≠) for significant main effects. For example, [N, S]: 0 < 50 < (100 = 150) means that despite the significant interaction, both shaded and unshaded treatments displayed the same pattern of significantly less *H. banksii* in plots with 0 pneumatophores than all other treatments, and significantly less *H. banksii* in plots with 50 pneumatophores than those with 100 or 150 pneumatophores (which in turn were not statistically distinguishable).

securis and *Trichomya hirsuta*, the limpet *Patelloida mimula*, and the gastropod *Ascorhis tasmanica*) were only found on oysters. The moon snail *Polinices sordidus* and the sea slug *Haminoea* sp. were exclusively found on the sediment surface, and the whelks *Pyrazus ebeninus* and *Batillaria australis* were almost always found on the sedimentary bottom. Not one species was limited to either *H. banksii* or pneumatophore substrates, but the trochid gastropod *Calthalotia fragum* was only found off the sediment and the gastropods *Bembicium auratum* and *Austrocochlea porcata* were more numerous on substrata above the sediment surface at two of the three sites (Pretty Beach, Salamander Bay). *Onchidum* sp. and *P. exigua* did not display strong associations with particular microhabitats.

At each of the three sites, the wet mass of *H. banksii* was positively correlated with the density of pneumatophores (Table 1A, Fig. 1A–C). At two of the sites (Quibray Bay, Salamander Bay) there was also a positive correlation between the abundance of invertebrates and *H. banksii* biomass (Table 1A, Fig. 1D, F), but invertebrate abundance and pneumatophore density were not correlated with one another when the effect of *H. banksii* was removed (Table 1A, Fig. 1G–I). Invertebrate richness displayed relationships to pneumatophore density and *H. biomass* similar to those of invertebrate abundance, so these data are not presented.

Unlike *H. banksii* biomass, oyster density was only correlated with pneumatophore density at one of the three sites (Pretty Beach; Table 1B, Fig. 2B). Oyster density and the abundance of oyster-dwelling mollusks were, by contrast, strongly correlated (Table 1B, Fig. 2D–F). There was no density-dependent effect of pneumatophores on oyster-dwelling epifauna at any of the three sites (Table 1B, Fig. 2G–I). Patterns of species richness in oyster-dwelling invertebrates were similar to patterns of abundance. The biomass of *H. banksii* had no influence on oyster abundance in any of the mangroves (Pearson's correlations, $P > 0.05$).

Density-dependent effects of mangroves on Hormosira banksii *that cascade to epifauna*

Following addition of *H. banksii*, the alga was rapidly lost from plots without pneumatophore mimics, and was gradually lost from plots with the low density of 50 mimics (Table 2, Fig. 3A, B). Plots with greater densities of mimics retained most of their algae throughout the early weeks of the study, but had lost 50–75% by 6 months (Fig. 3A, B). Nevertheless, across each of the four timescales (2, 4, 6 weeks and 6 months), both the density of pneumatophore mimics and shading influenced the biomass of *H. banksii* in experimental plots (Table 2). Plots with no pneumatophore mimics contained a significantly lower algal biomass than any of the three treatments with mimics (Table 2, Fig.

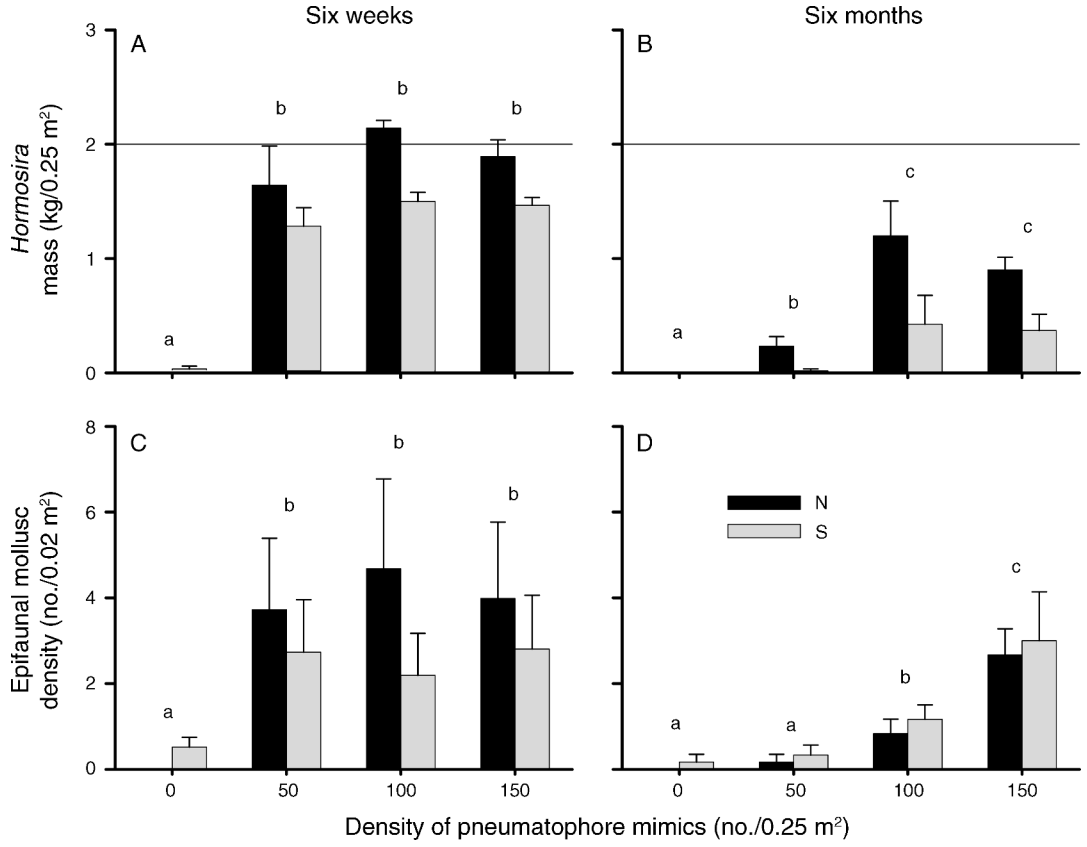

FIG. 3. (A, B) Wet mass (mean + SE) of *H. banksii* and (C, D) density of all epifauna across sediment and pneumatophore mimics in 0.25-m^2 experimental plots receiving 0, 50, 100, or 150 dowel rods that mimicked the structure of pneumatophores, six weeks and six months after addition of 2 kg of *H. banksii* to each. To ascertain how shading by the mangrove canopy might modify relationships, six replicate plots per pneumatophore treatment were shaded with cloth (S) while six per pneumatophore treatment received full sunlight (N, no shade). Horizontal black lines show the starting *H. banksii* biomass of 2 kg/plot. N indicates plots with no shade (in full sunlight); S indicates shaded plots. Different lowercase letters denote significant differences among mimic densities (PERMANOVA, $P < 0.05$). Shaded plots contained a smaller biomass of *H. banksii* than did those receiving full sunlight (PERMANOVA, $P < 0.05$).

3A, B). Among plots with pneumatophore mimics, those with 50/0.25 m^2 contained significantly less algae than those with 100 or 150/0.25 m^2 at three of the four sampling times (Table 2, Fig. 3A, B). Algal biomass was generally greater in unshaded than shaded plots (Table 2, Fig. 3A, B), although there was no difference between shading treatments in plots with 0 or 50 mimics after two weeks, or in plots with no mimics after 6 months, which had lost all their algae. One-way PERMANOVAs did not detect a significant difference in the biomass of *H. banksii* or the density of epifaunal mollusks between controls for shading and open (no-shade) plots at any of the sampling times ($P > 0.05$).

At each time of sampling, we detected eight species of epifauna in experimental plots. Of these, *Bembicium auratum* and *Batillaria australis* were the most abundant, comprising 53% and 27%, respectively, of the total epifauna sampled across each of the two times. At the 6-week sampling, 47% of epifauna were on the *H. banksii*, 22% were on pneumatophore mimics, and 30% were on the sediment surface. By 6 months, numbers of epifauna were lower in all microhabitats, with 36% of epifauna on the alga, 44% on pneumatophore mimics, and 20% on the sediment surface.

Density of pneumatophore mimics influenced epifaunal community structure at six weeks and 6 months, but shading did not (Table 3, Fig. 3C, D). Six weeks after the start of the experiment, epifaunal abundance was positively correlated with *H. banksii* biomass ($r = 0.47$, $df = 46$, $P < 0.01$). Significantly fewer epifauna were found in the plots without pneumatophore mimics than in plots with 50, 100, or 150 mimics, driving the treatment effect on community structure (Table 3, Fig. 3C). No significant difference in epifaunal abundance was found between the shaded and unshaded treatments (Table 3, Fig. 3C). At six months, by which time *H. banksii* biomass, even in plots of high pneumatophore mimic density, had declined to <70% of the starting biomass, epifaunal abundance had decreased. At this time, epifaunal abundance was greatest in plots with 150 mimics, intermediate within plots with 100 mimics, and lowest in plots with 50 or 0 mimics (Table 3), following

TABLE 3. Results of two-way PERMANOVAs testing for spatial variation in the community structure and abundance of associated epifauna.

Statistics, by period	Source of variation: Pneum (df = 3)	Shade (df = 1)	Pneum × Shade (df = 3)	Residual (df = 40)	Tests, a posteriori, by period
A) Community structure					
6 weeks					**Pneum**:
MS	7773	965	462	1074	$0 \neq (50 = 100 = 150)$
Pseudo *F*	7.2	0.9	0.4		
P	**0.001**	0.445	0.936		
6 months					**Pneum**:
MS	8542	2681	1205	1377	$0 \neq (50 = 100) \neq 150$
Pseudo *F*	6.2	1.9	0.9		
P	**0.001**	0.085	0.601		
B) Epifaunal abundance					
6 weeks					**Pneum**:
MS	9636	382	134	592	$0 < (50 = 100 = 150)$
Pseudo *F*	16.3	0.6	0.2		
P	**0.001**	0.512	0.970		
6 months					**Pneum**:
MS	4813	43	293	423	$(0 = 50) < 100 < 150$
Pseudo *F*	11.4	0.1	0.7		
P	**0.001**	0.885	0.608		

Notes: Treatments were: Pneum, density of pneumatophore mimics (four levels: 0, 50, 100, 150 dowels/0.25-m^2 plot), and Shade (two levels: not shaded [N], shaded [S]), and their interaction; $n = 6$ plots/treatment, 48 plots in total. Terms significant at $\alpha = 0.05$ are highlighted in bold. See Table 2 for an explanation of the a posteriori tests.

patterns of *H. banksii* biomass at the patch scale (Pearson's correlation, $r = 0.35$, df = 46, $P < 0.01$). Epifaunal abundance remained similar between shaded and unshaded treatments (Table 3, Fig. 3D).

Direct effects of pneumatophore density and Hormosira banksii *biomass on epifaunal communities*

Over the 12 weeks of the experiment, nine species of mollusk and the cushion star, *Parvulastra exigua*, colonized experimental plots. *Batillaria australis*, *Bembicium auratum*, and *Salinator fragilis* were numerically dominant, respectively accounting for 50–76%, 15–17%, and 5–30% of total invertebrates counted at each sampling time.

Two weeks after the start of the experiment, epifaunal communities significantly differed between the plots without *H. banksii* and those with the alga (Table 4A). This pattern persisted until at least week six of the experiment (Table 4A). By week 12, however, the differences were not just based on presence/absence of *H. banksii*; rather, communities in plots with the greater biomasses of *H. banksii* also differed from those in plots with lower biomasses of the alga (Table 4A). At no point in the experiment did we detect a significant effect of pneumatophore density on epifaunal community structure, or an interaction between pneumatophore density and *H. banksii* biomass (Table 4A).

Multivariate differences in community structure between plots with and without the alga were largely driven by differences in the abundance of taxa between the treatments. At each time of sampling, we detected a greater total abundance of macroinvertebrates in plots containing *H. banksii* than in plots without the alga (Table 4B, Fig. 4), and by week six, differences between intermediate (0.5–1.5 kg) and high (2.0–2.5 kg) biomasses of *H. banksii* were also evident (Table 4B, Fig. 4B, C). The pattern of greater invertebrate abundance in plots with a larger *H. banksii* biomass strengthened over time (Table 4B, Fig. 4) and was attributed to both the habitat provided by the *H. banksii* itself and to greater abundances of invertebrates on the substrate below the algae (Fig. 4). Species richness was greater in plots with than without the alga at each time of sampling (Table 4C). Only at 6 weeks was a significant difference among nonzero algal treatments seen, with plots with 0.5 kg containing fewer species than those with 1.0–2.5 kg (Table 4C).

DISCUSSION

The important role of mangroves in maintaining diversity and abundance of gastropods in temperate mangrove forests has been highlighted by many studies (reviewed by Morrisey et al. 2010). It was not surprising, therefore, that we found that the abundance and species richness of epifaunal invertebrates increased with pneumatophore density at the patch scale. What was unexpected, however, was that pneumatophore density had little direct effect on invertebrates. The relationship between mangrove pneumatophore density and community assembly was, instead, an indirect effect of higher pneumatophore densities trapping more *H. banksii* and, to a lesser extent, providing substrate for

TABLE 4. Two-way PERMANOVAs testing for effects of *H. banksii* biomass (Horm) and pneumatophore density (Pneum) on epifaunal (A) community structure (density × shade effects), (B) abundance, and (C) richness.

Statistics, by period	Source of variation: Horm (df = 5)	Pneum (df = 2)	Horm × Pneum (df = 10)	Residual (df = 90)	Tests, a posteriori, by period
A) Community structure					
2 weeks					**Horm**:
MS	9223	2179	1967	3316	$0 \neq (0.5 = 1 = 1.5 = 2 = 2.5)$
Pseudo *F*	2.8	0.7	0.6		
P	**<0.001**	0.816	0.997		
6 weeks					**Horm**:
MS	10 047	3226	2719	3096	$0 \neq (0.5 = 1 = 1.5 = 2 = 2.5)$
Pseudo *F*	3.2	1.0	0.9		
P	**<0.001**	0.393	0.746		
12 weeks					**Horm**:
MS	6843	3027	2660	2266	$0 \neq (0.5 = 1 = 1.5) \neq 2 \neq 2.5$
Pseudo *F*	3.0	1.3	1.2		
P	**<0.001**	0.183	0.185		
B) Epifaunal abundance					
2 weeks					**Horm**:
MS	6031	1293	846	1517	$0 \neq (0.5 = 1 = 1.5 = 2 = 2.5)$
Pseudo *F*	3.9	0.9	0.6		
P	**0.001**	0.489	0.929		
6 weeks					**Horm**:
MS	11 677	1806	1219	1203	$0 \neq 0.5 \neq (1 = 1.5) \neq (2 = 2.5)$
Pseudo *F*	9.7	1.5	1.0		
P	**0.001**	0.180	0.439		
12 weeks					
MS	6014	1012	862	1221	**Horm**:
Pseudo *F*	4.9	0.8	0.7		$0 \neq (0.5 = 1 = 1.5) \neq (2 = 2.5)$
P	**0.001**	0.481	0.805		
C) Epifaunal richness					
2 weeks					
MS	1705	216	128	321	**Horm**:
Pseudo *F*	5.3	0.7	0.4		$0 \neq (0.5 = 1 = 1.5 = 2 = 2.5)$
P	**0.001**	0.555	0.985		
6 weeks					
MS	3636	362	263	195	**Horm**:
Pseudo *F*	18.7	1.9	1.3		$0 \neq 0.5 \neq (1 = 1.5 = 2 = 2.5)$
P	**0.001**	0.144	0.193		
12 weeks					
MS	1321	108	97	200	**Horm**:
Pseudo *F*	6.6	0.5	0.5		$0 \neq (0.5 = 1 = 1.5 = 2 = 2.5)$
P	**0.001**	0.642	0.952		

Notes: There were six levels of *H. banksii* biomass (Horm: 0, 0.5, 1, 1.5, 2, 2.5 kg per 0.25-m^2 plot) and three levels of pneumatophores density (Pneum: 50, 100, 150 per 0.25-m^2 plot). Terms significant at $\alpha = 0.05$ are highlighted in bold; $n = 6$ plots per treatment for 18 treatments (108 plots in total).

oysters, which each in turn directly influenced fauna. Although our study did not directly manipulate oysters, previous research in an adjacent mangrove forest has demonstrated a causative role for oysters in determining the distribution of snails (Underwood and Barrett 1990). Our mensurative sampling suggested that the effect of oysters on epifauna was independent of *H. banksii*, because the biomass of the two facilitators was not related and oysters supported different invertebrate species than did the alga. Consequently, the single basal foundation species, the mangrove, generated two independent facilitation pathways arising from pneumatophores (Fig. 5).

Of the two secondary foundation species, *H. banksii* and oysters, the alga was more influential on epifauna. In our experiments, loss of the alga was accompanied by loss of epifauna, even where pneumatophore density did not change. Facilitation of mollusks by *H. banksii* probably was due both to animals using *H. banksii* directly and *H. banksii* modifying the habitat value of the sediment below. *H. banksii* provides a surface to which gastropod grazers can attach, and the biofilms on

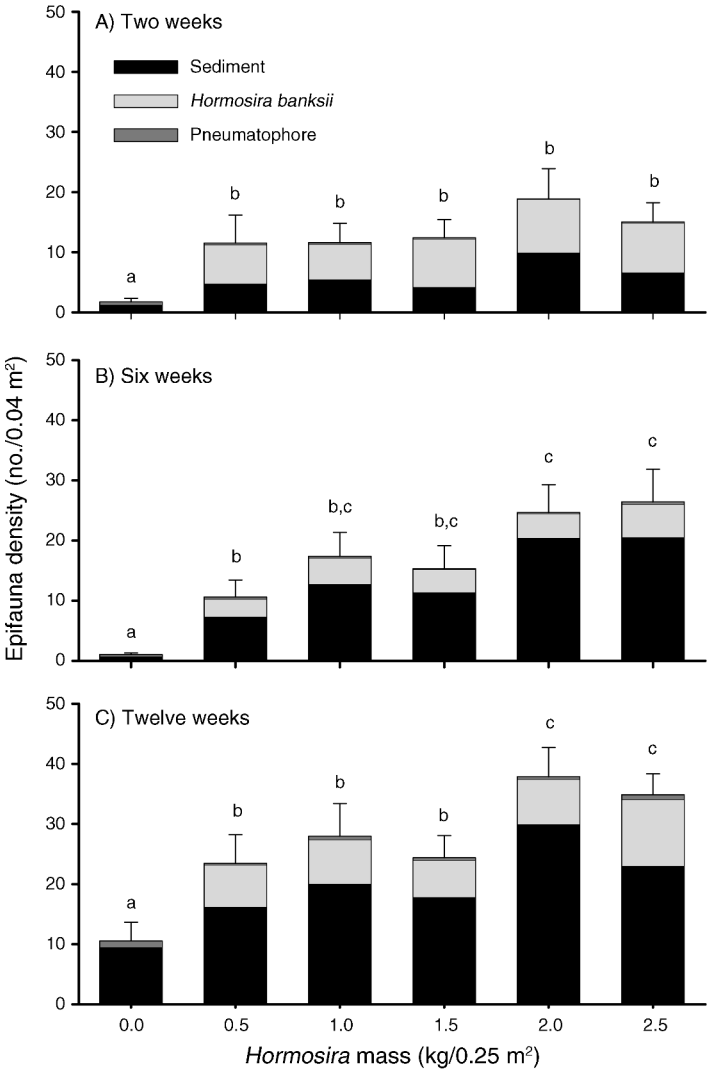

FIG. 4. Abundance (mean + SE) of epifauna per 0.25-m^2 plot following experimental manipulation of *H. banksii* biomass ($n = 18$ plots per treatment; 108 plots in total). Data were pooled across pneumatophore densities ($n = 3$), which did not significantly differ in their abundance of epifauna. Different lowercase letters denote treatments that differed significantly (PERMANOVA, $P < 0.05$). Abundance is partitioned according to the substrate to which epifauna were attached.

which they graze can grow (Bishop et al. 2009). It may, however, also reduce access by predators to sediments, and enhance organic matter accumulation or water retention at low tide (Bishop et al. 2009). We found that oysters were, nevertheless, important in providing a substrate for several species that were not found on any other microhabitat (see also Minchinton and Ross 1999).

Experiments revealed that the basal facilitator, mangrove pneumatophores, facilitated *H. banksii* in a density-dependent manner; in turn, facilitation of invertebrates by *H. banksii* was also density dependent (Figs. 3 and 4).The net effect of these two steps was a facilitation cascade in which facilitation of epifauna increased with pneumatophore density (Figs. 1 and 3). Mensurative sampling and manipulative experiments revealed that, at very low pneumatophore densities, algal retention was insufficient to facilitate epifauna above what would be found on pneumatophores alone.

Whether there was a threshold density above which further increases in pneumatophore density did not increase algal biomass was less clear. In experiments, densities of 50, 100, and 150 pneumatophores/0.25-m^2 plot were equally effective at retaining algae over a six-week period, but over a six-month period, algal retention was greater at greater pneumatophore density. Furthermore, mensurative sampling suggested that although positive relationships of pneumatophore density on *Homorsira* exist at all sites, the strength of the relationship varies. Spatiotemporal variation in the transport of algae may contribute to larger-scale variation in these relationships. Trapping of algae by pneumatophores requires delivery, penetration, and, over longer timescales, retention. Penetration, in theory, may be impeded at very high pneumatophore density, although we found no evidence of this in our field surveys. Our manipulative experiments considered only effects of pneumatophore density on algal retention.

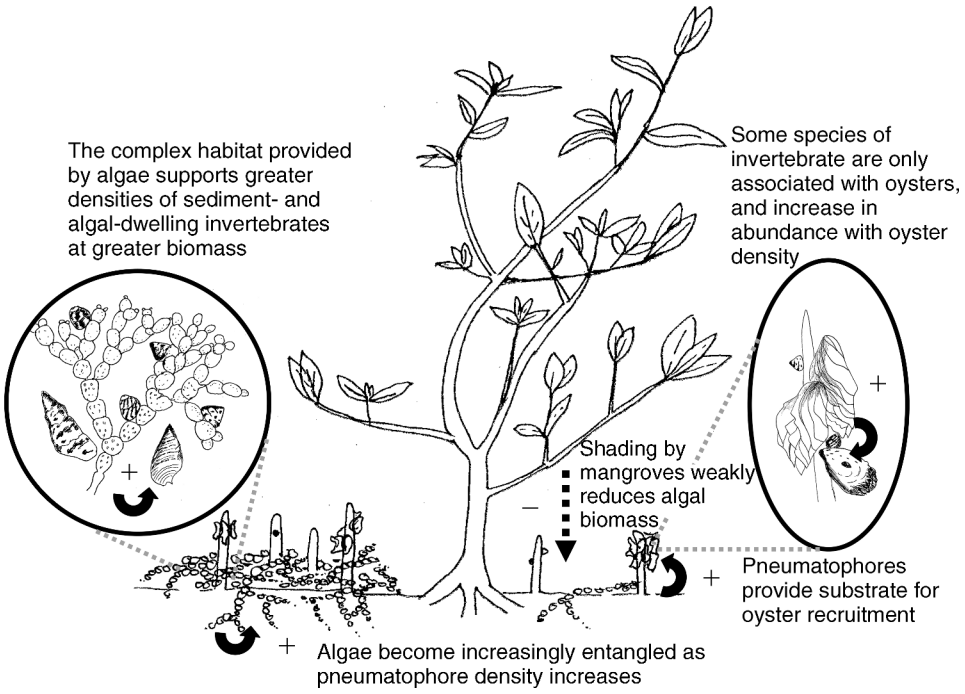

FIG. 5. Diagrammatic summary of interactions between the basal foundation species (the mangrove) and secondary foundation species (oysters and algae), which determine invertebrate communities in temperate Australian mangrove forests.

In addition to the primary effect of mangroves in trapping *H. banksii,* mangroves also had a secondary effect on *H. banksii* resulting from shading by the canopy (Fig. 5). In manipulative field experiments, comparisons among experimental plots of similar pneumatophore density revealed that shading of *H. banksii* reduced its biomass below that of unshaded plots. Although we did not specifically examine the mechanism/s for the biomass reduction in the shaded treatment, we suspect that reduced photosynthetic activity and, hence, reduced productivity was responsible. Despite the negative effect of shading on *H. banksii* biomass, the positive effect of roots retaining the alga was more important than the negative effect of canopy shade on the alga, and the density dependence of this relationship was robust to effects of shading (Fig. 5).

The facilitation cascade with oysters as the secondary foundation species was, by contrast to the *H. banksii* cascade, not fully density dependent. At several of our study sites, oysters did not follow the density of the basal facilitator, pneumatophores. The absence of a pervasive density-dependent relationship between the basal and intermediary habitat-formers implies that oysters are not substrate limited. Rather, recruitment processes may be responsible. Specifically, the gregarious settlement of oysters leads to highly over-dispersed distributions (Krassoi 2001). Oysters require hard substrate, such as mangrove pneumatophores and trunks, to start aggregations, but once adults are established, new recruits will settle on top of adults instead of on free substrate. Consequently, oysters may exhibit a stronger response to the presence or absence of pneumatophores than to their density. Additionally, larger scale processes may be limiting the delivery of oyster larvae to certain bays along the coast. Regardless, oysters are clearly important to biodiversity. Our mensurative sampling revealed a strong relationship between the density of oysters and epifauna and, although we did not directly manipulate oysters, previous studies indicate that increasing the area of substrate they provide increases the density of many associated species of mollusks (Summerhayes et al. 2009).

Despite the over-arching conclusions that could be drawn about the role of facilitation cascades in temperate Australian mangroves, mensurative sampling revealed considerable variation in the strength of relationships at both the patch and site scales. In particular, at certain sites, although there was a trend for increasing abundance and richness of epifauna with increasing densities of the respective secondary foundation species, there were also a large number of plots in which zero abundance of epifaunal taxa was recorded. We posit that, although facilitation cascades set the potential abundance of epifauna, the realized abundance depends on dispersal. Particularly where dispersal of basal facilitators, secondary facilitators, and focal communities operate at different spatiotemporal scales to one another, the full effects of facilitation cascades may not be realized. Additionally, variation in traits of the facilitators not quantified here (e.g., pneumatophore height, *H. banksii* vesicle size and chain length; e.g., Bayliss 1993, Bishop et al. 2009) and environmental

differences among sites (see Bertness and Callaway 1994) may contribute to spatial variation in relationships.

Our study moved beyond simple presence/absence manipulations of basal and secondary facilitators (Altieri et al. 2007, Gribben et al. 2009) to provide the first consideration of the sensitivity of facilitation cascades to changes in the density of basal and secondary foundation species. We have done so by successfully partitioning the density dependence of epifauna on pneumatophores into direct effects and indirect effects arising from their facilitation of the secondary foundation species, *H. banksii* and *S. glomerata*. We have shown that the density of both basal and secondary foundation species can affect the impact, and in some instances the occurrence, of facilitation cascades. First, the density of the secondary facilitator may be independent of, linearly, or nonlinearly related to the density of the basal species. Second, associated species may be independent of, linearly, or nonlinearly dependent on the density of the secondary facilitator. Where the density of the secondary facilitator responds only to the presence or absence of the basal habitat former (as in the pneumatophore–oyster–epifauna cascade here), the net effect is a facilitation cascade that is not fully density dependent across the full cascade. Where, however, density dependence is evident between the basal and secondary foundation species, the strength of facilitation cascades, and indeed their occurrence, will vary across the natural range of densities at which facilitators occur, according to density-dependent effects of both basal and secondary species. Given the density dependence of many individual facilitators (e.g., van Hulzen et al. 2007, Irving and Bertness 2009, Harley and O'Riley 2011), such complex relationships are likely to be seen in all ecosystems in which foundation species co-occur and interact.

Not only have we shown how the outcome of facilitation cascades may be modified by the density of basal and secondary foundation species, but also we have expanded the understanding of facilitation cascades by, for the first time, documenting a network of independent cascades in which two secondary foundation species are dependent on one basal foundation species (Fig. 5). These networks of cascades, which cumulatively determine biodiversity, are likely to be common. Overall, our study adds to the increasing evidence that facilitation cascades are found in a diversity of habitats and are of broad ecological significance in determining community structure and function (Altieri et al. 2007, Gribben et al. 2009). The exposure of density-dependent facilitation cascades greatly enhances our mechanistic understanding of community assembly.

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