LETTER

Behavioural interactions between ecosystem engineers control community species richness

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Abstract

Behavioural interactions between ecosystem engineers may strongly influence community structure. We tested whether an invasive ecosystem engineer, the alga *Caulerpa taxifolia*, indirectly facilitated community diversity by modifying the behaviour of a native ecosystem engineer, the clam *Anadara trapezia*, in southeastern Australia. In this study, clams in *Caulerpa*-invaded sediments partially unburied themselves, extending >30% of their shell surface above the sediment, providing rare, hard substrata for colonization. Consequently, clams in *Caulerpa* had significantly higher diversity and abundance of epibiota compared with clams in unvegetated sediments. To isolate the role of clam burial depth from direct habitat influences or differential predation by habitat, we manipulated clam burial depth, predator exposure and habitat (*Caulerpa* or unvegetated) in an orthogonal experiment. Burial depth overwhelmingly influenced epibiont species richness and abundance, resulting in a behaviourally mediated facilitation cascade. That *Caulerpa* controls epibiont communities by altering *Anadara* burial depths illustrates that even subtle behavioural responses of one ecosystem engineer to another can drive extensive community-wide facilitation.

Keywords

Behaviour, bivalves, ecosystem engineer, epibiota, facilitation cascades, habitat-forming species, invasive species, recruitment, trait-mediated indirect effects.

Ecology Letters (2009) **12**: 1127–1136

INTRODUCTION

Species interactions often have important cascading effects on communities. There are numerous examples of cascades mediated by biotic interactions (e.g. via predation) (Carpenter *et al.* 1985; Pace *et al.* 1999; Post *et al.* 1999; Schmitz *et al.* 2000; Shurin *et al.* 2002; Paine 2003) but examples of cascades resulting from abiotic interactions between species are rare. Ecosystem engineers are by definition modifiers of abiotic change (Jones *et al.* 1994, 1997). Habitat-forming ecosystem engineers are generally facilitative, and form the

basis of communities that are considered hierarchically organized (spatially, structurally and temporally) through positive interactions (Bruno & Bertness 2001; Bruno *et al.* 2003). Facilitation of communities by ecosystem engineers is commonly observed when a single habitat-forming species adds structure to otherwise open unstructured substrata (Posey 1988; Crooks 1998; Badano *et al.* 2006; Wright *et al.* 2006). Because they extensively modify ecosystems, ecosystem engineers responding to one another also have the potential for large cascading effects on associated biota (Callaway 1995; Bruno & Bertness 2001; Bruno *et al.* 2003).

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Although a recent example demonstrated that positive density meditated interactions between ecosystem engineers can result in a facilitation cascade (Altieri *et al.* 2007), we know little about the community level consequences of interactions between engineers.

The magnitude of facilitation in response to the addition of structure is a trait-mediated function of the ecosystem engineer. The amount of space available for colonization, and the degree to which environmental stress and predation risk is reduced vary with traits such as the architectural complexity, density, size or age of the ecosystem engineer (Jones *et al.* 1997; Bruno & Bertness 2001; Gutierrez *et al.* 2003). In addition, changes in the abiotic environment can in turn influence the behavioural traits of many species, including those of ecosystem engineers themselves (Diaz & Rosenberg 1995; Tallqvist 2001; Decker *et al.* 2003). Thus, habitat-forming species may also have trait-mediated interactions (TMIIs) with co-occurring ecosystem engineers resulting in community-level consequences. In food-webs, behavioural TMIIs have important cascading effects often via predator induced habitat shifts (Schmitz *et al.* 1997, 2004; Trussell *et al.* 2004, 2006). However, the ramifications of behavioural interactions among structure-provisioning species for associated biota remain unexplored, despite their far-reaching implications for community structure.

Here, we investigate how the behavioural response of a native ecosystem engineer to an invasive ecosystem engineer influences community diversity and species abundances. Mollusc shells in soft-sediment marine environments provide a hard surface for colonization by epibiotic communities that otherwise do not settle on soft-sediments (Gutierrez *et al.* 2003). The degree to which these communities are facilitated is, however, dependent on how the substrate traits are expressed (e.g. shell surface area available for colonization) (Caceres-Martinez *et al.* 1999; Creed 2000; Mouritsen & Poulin 2005). In our study system, the native soft-sediment dwelling bivalve *Anadara trapezia* (hereafter *Anadara*) bury less deeply in sediments invaded by the green alga *Caulerpa taxifolia* (hereafter *Caulerpa*) due to hypoxic conditions in *Caulerpa* (Wright J.T., unpublished data). Thus, adult clams in invaded habitat offer a greater surface area for colonization by epibiotic communities. This may explain high recruitment of *Anadara* juveniles to adults in *Caulerpa* compared with adults in nearby unvegetated sediments, although facilitation of recruits was also linked to reduced predation in *Caulerpa* (Gribben & Wright 2006a).

Using *Caulerpa* and *Anadara* we tested the hypothesis that behavioural interactions between ecosystem engineers can facilitate community diversity and species abundances. We tested this hypothesis by determining patterns of clam burial depth, and epibiotic community structure on clams inside and outside areas invaded by *Caulerpa*. Second, we experimentally investigated mechanisms driving the observed patterns. We found that changes in the behaviour of clams in *Caulerpa* (i.e. shallow burial) independent of habitat and predation exposure facilitates diverse epibiont communities on clams compared with unvegetated sediments. Thus, we demonstrated that behavioural interactions between ecosystem engineers can result in a facilitation cascade and that invasive ecosystem engineers can have indirect positive community level effects by altering the engineering of a native species.

METHODS

Species and study location

All data were collected from Sponge Bay and Yooralla Bay, Lake Conjola (35°15′44.3″ S, 150°26′47.8″ E), a temporary barrier estuary *c.* 210 km south of Sydney, Australia. The most abundant macrophyte in Lake Conjola is *Caulerpa* which was introduced in 2000 (Creese *et al.* 2004). As for many other habitat-forming ecosystem engineers *Caulerpa* provides a surface for colonization (Gribben & Wright 2006a), but also negatively affects sediment quality (Chisholm & Moulin 2003; Gribben *et al.* 2009; McKinnon *et al.* 2009). The native seagrasses *Halophila ovalis* and *Zostera capricorni* are also present but they are sparse and restricted to shallow zones fringing the bay. At our study sites, extensive areas of the benthos were covered by thick beds of *Caulerpa* intermingled with patches of unvegetated sediment. In Lake Conjola and other estuaries in New South Wales, Australia, *Caulerpa* commonly invades bays which contain large populations of *Anadara* (Arcidae, Deshayes 1840). At both bays studied, *Anadara* occurs in both *Caulerpa* invaded and unvegetated sediments. Populations in both habitats are dominated by larger individuals (> 40 mm shell length) of an equivalent size range (Gribben & Wright 2006b; Wright *et al.* 2007). Apart from the presence of *Caulerpa*, the shells of live *Anadara* are the only substrata available for colonization by epibiont communities in soft-sediment subtidal areas of our study sites. In the absence of available shell, epibiont communities are also absent (P.E. Gribben and J. T. Wright, personal observation). Detailed descriptions of the study sites and organisms can be found in Gribben & Wright (2006a,b) and Wright *et al.* (2007).

Community composition of epibiota

Differences in the community composition and biomass of epibiota (both sessile and motile) on live adult *Anadara* from *Caulerpa* invaded sediments and unvegetated sediments at both bays (*n* = 40 clams; 10/habitat/site; size range 57–65 mm) were investigated during June 2006. We only considered live adults because the shells from dead adults are generally found buried in the sediments in both habitats.

All clams were collected haphazardly on SCUBA from intermingling patches of unvegetated and invaded sediments. Once collected, *Anadara* were placed into individually labeled snap-lock plastic bags and frozen until analysed.

The species richness and abundance of individual invertebrate species attached to adults were identified to the lowest taxonomic level under a dissecting microscope and counted. Percent cover of filamentous tufting algae on the periostracum[1] (tufting algae were not found on the shell where the periostracum was absent) was estimated by placing a transparent sheet with a grid of dots (1 cm apart) over the periostracum on both valves and noting the percentage of dots that occurred over tufting algae. The dry weight (g) of epibionts attached to shells of *Anadara* was determined by collecting more clams as described above (n = 30 clams/habitat/site; size range 55–65 mm). Biomass was determined by carefully removing all epibionts from the surface of individual adults with a razor blade. Epibionts from individual clams were dried for two days at 60 °C and then reweighed.

Two-factor Analysis of Variance (ANOVA) was used to test the effects of habitat (fixed) and site (random) on the species richness and abundance of invertebrates, percent cover of tufting algae and total biomass of epibionts. The assumptions of ANOVA for these and subsequent analyses described below were performed by examination of the distributions of residuals, and plots of residuals vs. means (Quinn & Keough 2002). Data were transformed where required. Non-significant interaction terms were removed if $P > 0.25$ (Quinn & Keough 2002). Differences in community associations between habitats were further explored using non-metric Multi-Dimensional Scaling (nMDS) ordination and Analysis of Similarities (ANOSIM), based on Bray-Curtis measure of similarity (Clarke 1993). The contribution of each fouling species to differences between communities was tested using Similarity Percentages analysis based on the Bray–Curtis measure of dissimilarity. Species richness and abundance of invertebrates and total biomass of epibionts on clams were compared by standardizing to their surface area. Surface area (SA) (cm^2) for each clam was determined from the equation, SA (cm^2) = 0.98 × Shell length (mm) (calculated over a restricted size range: 35–55 mm, R^2 = 86.3) (W. O'Connor, unpublished data).

Burial depth of clams

The *in situ* burial depth of live *Anadara* in *Caulerpa* invaded sediments and unvegetated sediments were compared at both sites. Clams were haphazardly selected in both habitats

(n = 15 clams/habitat; size range 35–65 mm) and a line marked with a pencil on the shell *in situ* denoting the sediment surface/water interface. Once marked, clams were removed from the sediment and the distance perpendicular from the line to the bottom of the shell (the umbo) was measured to obtain burial depth. Total shell length was then measured along the same axis from the umbo to the posterior margin and percent burial depth for each individual determined. Two-factor ANOVA was used to explore the effects of habitat (fixed) and site (random) on clam burial depth.

Experiment to isolate responsible mechanism(s)

To examine the interaction of predation, habitat, and burial depth on the epibiont communities living on *Anadara* we conducted an orthogonal experiment over 12 weeks in summer 2007/8 (11 October to 5 January). Buried *Anadara* were collected from unvegetated areas from an adjacent estuary (St George's Basin). These clams were allowed to acclimate in Sponge Bay while buried for 1 month in an unvegetated area hand cleared of *Caulerpa*. The day before the experiment was established, the clams were retrieved, their shells scoured with a scrub pad, and then submerged rapidly in fresh water to remove any epibionts. Care was taken not to remove the periostracum. Clams were then placed in unfiltered seawater overnight to ensure that all clams survived cleaning; no mortality was observed.

Anadara were selected haphazardly and placed into plastic tubs (n = 10 clams/tub) (dimensions 10 × 10 × 25 cm) that were filled with sediment from an unvegetated area. Sediment from an unvegetated area was used to eliminate any effects of *Caulerpa*-associated substances or conditions (e.g. phytotoxins, associated bacteria, anoxia) that might affect infauna, such as *Anadara*. To manipulate burial depth, both shallow (2 cm depth) and deep (10 cm depth) tubs were used. In the shallow tubs, clams were inserted to the full depth of the tub and thus remained with approximately half their shell exposed aboveground; in deep tubs, clams were pushed to their full burial depth. Predator exposure was manipulated by completely covering half of the tubs with wire mesh (10 mm) that extended 5 cm over the tubs. These two treatments were further crossed with habitat by burying tubs of all treatments inside unvegetated and *Caulerpa* plots. Tubs were buried flush with the surrounding sediment and care was taken not to displace the canopy of *Caulerpa* when adding the tubs to this habitat.

We used a systematic split plot design with four blocks. Each block consisted of one plot of *Caulerpa* and one unvegetated plot where *Caulerpa* was removed by hand 2 months prior to the beginning of the experiment as bare unvegetated sediment present during community

[1]The periostracum is an organic layer, secreted as the outermost layer of most mollusk shells that protects the underlying shell from erosion.

composition study above was being invaded by *Caulerpa*, and to minimize any potential residual negative effects of *Caulerpa* on sediments. All plots were 2 × 2 m. Plots within blocks were separated by at least 2 m, blocks were > 10 m apart. Each treatment was replicated twice in each of four habitat blocks (total of eight replicates). Throughout the course of the experiment, unvegetated plots were maintained to ensure no encroachment of *Caulerpa* occurred.

At the end of the 3-month experiment, tubs were removed and we noted the percentage of each valve from all surviving clams that was extended above the sediment before individually bagging them. These clams were frozen and kept in the lab until analysis. Because of high loss of clams to predation in some predator-exposed tubs in both *Caulerpa* and unvegetated plots (survivorship of clams was similar between habitats, 27% and 21% for *Caulerpa* and unvegetated habitats, respectively), data were analysed as the mean values from two clams randomly selected from each tub. These clams were measured and examined under a dissecting microscope and all algae and invertebrates were removed, identified and weighed. As opposed to the *in situ* surveys, for filamentous alga instead of percent cover data of broad groups, we identified species to quantify diversity trends with more resolution.

A factorial ANOVA was used to test the effects of habitat, burial depth, and predator exposure (all fixed factors) and block and block × habitat (random factors) on total species richness, total abundance and species richness of invertebrates, species richness of filamentous algae and total biomass of epibiota.

Although the orthogonal design allowed us to test burial depth independent of habitat and predation, we further investigated the mechanism of burial depth by conducting four-factor Analyses of Covariance (ANCOVAS) using final colonizable shell area (i.e. area of shell above the sediment surface) as the covariate, because clams varied in burial depth within some treatments. This allowed us to investigate how the significance of the factor burial depth was affected once area was accounted for explicitly. Final colonizable area was determined by multiplying the total surface area of the clam (calculated using clam length in the equation above) by the percent of shell above the surface. Homogeneity of slopes was tested as described in Quinn & Keough (2002) for factorial designs. Non-significant interactions with the covariate were omitted and the models refitted (Quinn & Keough 2002).

To help visualize the highly significant effects of the covariate area and the factor burial depth in our analyses (see Results), we also conducted regression analyses on the relationship between final colonizable area vs. total species richness, abundance of invertebrates, species richness of invertebrates, algal species richness and total biomass.

RESULTS

Community composition of epibiota

A total of 11 species of epibionts were found on *Anadara* in *Caulerpa* invaded habitat and only three species were found on *Anadara* in unvegetated habitats (Table 1). Species richness ($F_{1,37} = 62.712$, $P < 0.001$), total abundance ($F_{1,37} = 44.406$, $P < 0.001$) and the biomass of epibionts ($F_{1,117} = 12.1391$, $P < 0.001$), were significantly higher on clams collected from *Caulerpa* compared with unvegetated habitat (Fig. 1a–c). There were also significant differences in community structure between habitats (nMDS Stress = 0.12; ANOSIM: $R = 0.69$, $P < 0.001$). Communities were 50% dissimilar between habitats, mostly due to the tubeworm *Spirorbis* sp. which accounted for 38.09% of dissimilarity. The difference in total abundance between habitats was mainly driven by the high abundance of spirorbids in *Caulerpa* ($F_{1,37} = 33.389$, $P < 0.001$), although spirorbids were numerically dominant in both habitats – spirobids accounted for *c.* 75% and *c.* 98% of invertebrates in *Caulerpa* and unvegetated sediments, respectively (Table 1). Both total abundance of other invertebrates (i.e. not including spirorbids) and percent tufting algae were significantly higher on clams in *Caulerpa* compared with unvegetated sediments (all Tukey's tests $P < 0.05$) (Fig. 1b), although the strength of the relationship varied with site (habitat × site interactions for total abundance of other invertebrates pooled within habitats because of low numbers of individual species, $F_{1,36} = 8.272$, $P = 0.007$, and percent tufting algae on the periostracum, $F_{1,36} = 7.393$, $P = 0.010$; both square root-transformed).

Burial depth of clams

Anadara were buried significantly more deeply in unvegetated sediment compared with *Caulerpa* invaded sediments ($F_{1,57} = 20.009$, $P < 0.001$) (Fig. 2). There was no effect of site ($F_{1,57} = 0.036$, $P = 0.851$) and the interaction was non-significant and removed from the analysis ($F_{1,56} = 0.105$, $P = 0.747$).

Experiment to isolate responsible mechanism(s)

Total species richness, invertebrate richness, invertebrate abundance and algal richness were all significantly higher on shallow buried clams (Fig. 3a–d, Table 2). There was no effect of burial depth on biomass (Fig. 3e). Total species richness, invertebrate richness, invertebrate abundance and biomass but not algal richness were all significantly higher in caged treatments (Fig. 3a–e, Table 2). There was no effect of habitat for all response variables. There were significant effects of block for all variables except biomass.

Table 1 Mean abundance (± SE) of epibionts/cm^2 on *Anadara* collected from *Caulerpa* and unvegetated habitats, in Yooralla and Sponge Bay (data pooled across sites), in June 2006

	Species	Clams in unvegetated areas	Clams in *Caulerpa* invaded areas
Cnidarians	Unidentified anemone		0.010 (0.001)
Polychaetes	Spirorbis sp.	0.011 (0.006)	0.760 (0.201)
	Hydroides sp.	0.014 (0.006)	0.131 (0.029)
Bivalves	*Chama fibula*		0.014 (0.005)
	Musculus varicosus		0.005 (0.002)
	Anadara trapezia		0.002 (0.001)
Gastropod	*Calthalotia fragum*		0.014 (0.005)
Amphipods	*Cymadusa setosa*		0.002 (0.001)
Algae	*Caulerpa taxifolia*		0.046 (0.008)
	Codium fragile		0.014 (0.005)
	Percent cover tufting algae	15.25 (2.10)	63.75 (5.15)

Importantly, all interaction terms were non-significant and were dropped from the models for $P > 0.250$. Thus, although there were effects of predator exposure, the absence of significant habitat × predator exposure interactions indicated predation pressure was consistent between habitats (Fig. 3a–e, Table 2).

There was still a significant effect of burial depth on total richness and algal richness once area was explicitly accounted for (Table 3). In all analyses F-values for the factor burial depth were greatly reduced once area was accounted for explicitly; indicating area exposed is the main reason driving burial depth's importance in the earlier models (Table 3).

Final colonizable area was positively associated with all variables although the R^2-values were low in some instances (Fig. 3f–j): total species richness ($F_{1,100} = 45.461$, $P < 0.001$; $R^2 = 0.313$), invertebrate richness ($F_{1,100} = 38.166$, $P > 0.001$; $R^2 = 0.273$), invertebrate abundance ($F_{1,100} = 52.470$, $P < 0.001$; $R^2 = 0.344$), algal richness ($F_{1,100} = 19.654$, $P < 0.001$; $R^2 = 0.164$) and biomass ($F_{1,102} = 9.383$, $P < 0.003$; $R^2 = 0.081$).

DISCUSSION

Incorporating facilitation into models of community structure requires a mechanistic understanding of how facilitation occurs and, where the facilitator is an invasive species, provides valuable information on the mechanisms of impact of invasive species. Here, we have experimentally demonstrated that modification of the behavioural traits of one ecosystem engineer by another ecosystem engineer results in community wide facilitation. The invasive green alga, *Caulerpa taxifolia*, facilitated epibiotic communities on the native bivalve, *Anadara trapezia*, via modification of the burial depth of *Anadara*. *Anadara* burial depth is also significantly reduced in *Caulerpa* compared with clams in unvegetated sediments and seagrass in several estuaries in this region (Wright *et al.* in review). Thus, facilitation of epibiont communities on clams in *Caulerpa* is likely a large scale phenomenon. In addition, although our study sought to compare community diversity on a standardized substrate (clam shell) in unvegetated and *Caulerpa* invaded areas, the novel habitat structure provided by *Caulerpa* also facilitates sediment surface dwelling epibionts (McKinnon *et al.* 2009) and different epibionts on *Caulerpa* itself to those on clams (Gribben P.E. & Wright J.T., unpublished data). Thus, the *Caulerpa* epibiont community is potentially even more diverse than described here. This overall positive influence on epibiont communities contrasts to the negative influence *Caulerpa* has on some infaunal taxa (e.g. suspension feeders) (McKinnon *et al.* 2009).

Habitat-forming ecosystem engineers commonly facilitate biodiversity via direct effects on the density of resident species, such as increasing propagule supply or retention through baffling, decreasing abiotic stress or reducing predation pressure (Day & Wright 1989; Bertness & Hacker 1994; Callaway 1995; Crooks 2002; Gribben & Wright 2006a). However, in this study, there were limited effects of habitat or its interactions with predation and burial depth. This finding indicates that the higher diversity and abundance of epibionts (on *Anadara*) in *Caulerpa* were driven predominantly by changes in burial depth of clams, which determines the surface area available for colonization, and not via differences in density mediated interactions between habitats.

Altered abiotic conditions caused by introduced ecosystem engineers often exert concomitant negative impacts on associated biota (Melgoza *et al.* 1990; D'Antonio & Mahall 1991; Hacker & Dethier 2006; Neira *et al.* 2006). However, altered abiotic conditions can also have positive effects on biota often via changing predator behaviour. For example, in terrestrial systems, harsh abiotic conditions associated with increases in altitude reduce herbivory on mountain vegetation (Louda & Rodman 1983). Similarly, Altieri (2008) demonstrated that seasonal hypoxia reduces the foraging behaviour of key marine predators that cannot tolerate such
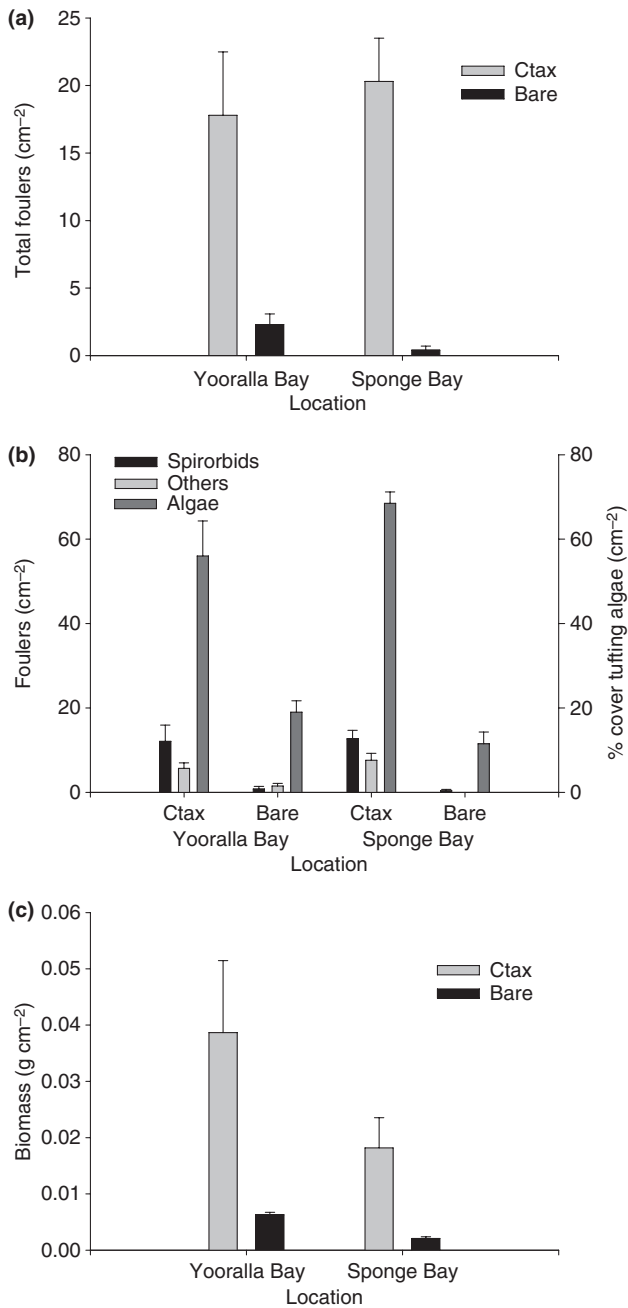
Figure 1 Mean (± SE) of (a) total no. of epibionts, (b) spirorbids, other epibionts and percent cover tufting algae and (c) biomass of epibionts (grams) on *Anadara* collected from unvegetated (Bare) and *Caulerpa* (Ctax) invaded sediment in Yooralla Bay and Sponge Bay, Lake Conjola [*n* = 15 clams/habitat/site for (a) and (b); *n* = 30 clams/habitat/site for (c)].
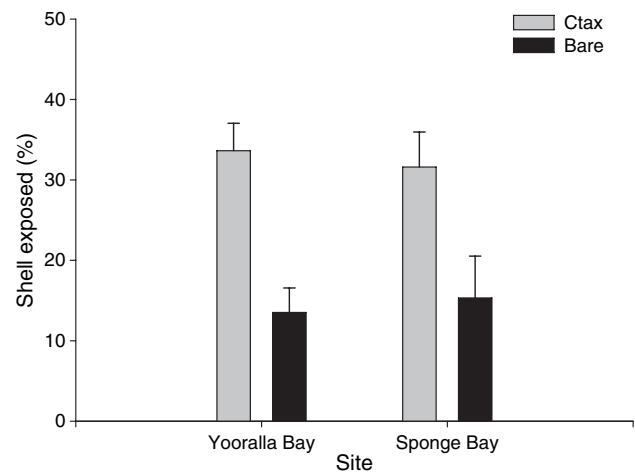
Figure 2 Mean per cent (± SE) shell length of *Anadara* exposed in *Caulerpa* invaded (Ctax) and unvegetated (Bare) sediments in Yooralla Bay and Sponge Bay (*n* = 15/habitat).

in review). Accordingly, in our system, the altered abiotic conditions elicited by one ecosystem engineer changed the behaviour of another ecosystem engineer (*Anadara* burial depth) which resulted in additional abiotic change (increased shell surface area for colonization) subsequently resulting in community wide-facilitation – all components of this facilitation cascade are explicitly abiotic and non-trophic. This mechanism of facilitation has not previously been described and may be particularly important where habitat-forming species strongly modify the abiotic environment, provide novel abiotic interactions (in particular invasive species) and where availability of substrata for recruitment may be limiting for many species.

Area has a well-known positive influence on species diversity. Epibiont diversity and abundance on clams was driven primarily by the influence of burial depth on exposed colonizable shell area. However, in several of the ANCOVA analyses (algal richness and total richness) burial depth is still a significant factor even after accounting for exposed shell area. The remaining influence of burial depth underscores that the facilitated epibiont community is not exclusively through enlarged colonizable surface area. Because surface topography also influences epibiont colonization (Kohler *et al.* 1999; Berntsson *et al.* 2000; Scardino & de Nys 2004), an additional effect of reduced burial depth may be an increase in microhabitat heterogeneity on the rugose shell surface as the shell becomes increasingly exposed. Additionally, interactions of exposed shell with water currents may vary as a function of height off of the bottom, thus creating a variety of micro-environments, independent in some cases of the species-area effect.

Despite indirect positive effects on epibionts, *Caulerpa* could actually have a net negative effect on epibiont

conditions thus facilitating invertebrate prey species that apparently thrive in the hypoxic environment. Recent evidence shows that *Anadara* bury shallowly in response to changes in concentrations of dissolved oxygen (Wright *et al.*

Table 2 Summary of results of four factor ANOVAs examining the effects of block, habitat, burial depth and predator exposure on total species richness, abundance of invertebrates (square root-transformed transformed), species richness of invertebrates, algal species richness ($\log_x$ transformed) and biomass (g) ($\log_{x+0.001}$ transformed) on *Anadara trapezia* in Sponge Bay Lake Conjola

Source	d.f.	MS	F-ratio	P
Total richness				
Block	3	50.338	9.467	**< 0.001**
Habitat	1	7.668	1.442	0.236
Predator exposure	1	37.306	7.016	**0.011**
Depth	1	68.133	12.814	**< 0.001**
Habitat × Predator exposure	1	11.012	2.071	0.157
Habitat × Depth	1	14.409	2.710	0.106
Error	49	5.317		
Invertebrate abundance				
Block	3	13.653	9.148	**< 0.001**
Habitat	1	2.988	2.002	0.163
Predator exposure	1	7.247	4.856	**0.032**
Depth	1	12.209	8.181	**0.006**
Error	49	1.492		
Invertebrate richness				
Block	3	19.395	7.139	**< 0.001**
Habitat	1	0.523	0.192	0.663
Predator exposure	1	45.243	16.653	**< 0.001**
Depth	1	22.573	8.309	**0.006**
Predator exposure × Habitat	1	4.231	1.558	0.218
Predator exposure × Depth	1	4.136	1.522	0.223
Error	49	2.717		
Algal richness				
Block	3	0.430	2.858	**0.047**
Habitat	1	0.350	2.324	0.134
Predator exposure	1	0.045	0.297	0.589
Depth	1	1.056	7.014	**0.011**
Predator exposure × Depth	1	0.287	1.909	0.173
Error	48			
Biomass				
Block	3	5.803	2.262	0.094
Habitat	1	0.017	0.003	0.957
Predator exposure	1	24.348	9.492	**0.003**
Depth	1	5.360	2.090	0.155
Block × Habitat	1	5.095	1.986	0.129
Error	46	2.565		

Table 3 Summary of results of four factor ANCOVAs examining the effects of block, habitat, burial depth and predator exposure with colonizable area as the co-variate on total species richness, abundance of invertebrates (square root-transformed transformed), species richness of invertebrates, algal species richness ($\log_x$ transformed) and biomass (g) ($\log_{x+0.001}$ transformed) on *Anadara trapezia* in Sponge Bay Lake Conjola

Source	d.f.	MS	F-ratio	P
Total richness				
Block	3	39.675	9.264	**< 0.001**
Habitat	1	2.359	0.551	0.462
Predator exposure	1	20.522	4.792	**0.034**
Depth	1	18.945	4.424	**0.041**
Area	1	63.023	14.717	**< 0.001**
Predator exposure × Habitat	1	13.597	3.175	0.081
Error	47	4.283		
Invertebrate abundance				
Block	3	9.783	8.241	**< 0.001**
Habitat	1	1.787	1.505	0.226
Predator exposure	1	3.305	2.784	0.102
Depth	1	2.457	2.070	0.157
Area	1	15.560	13.108	**< 0.001**
Predator exposure × Habitat	1	2.462	2.074	0.156
Error	47	1.187		
Invertebrate richness				
Block	3	15.321	6.476	**< 0.001**
Habitat	1	1.577	0.666	0.418
Predator exposure	1	31.091	13.141	**< 0.001**
Depth	1	5.343	2.258	0.140
Area	1	20.628	8.719	**0.004**
Predator exposure × Habitat	1	5.371	2.270	0.139
Error	47	2.366		
Algal richness				
Block	3	39.675	9.264	**< 0.001**
Habitat	1	2.359	0.551	0.462
Predator exposure	1	20.522	4.792	**0.034**
Depth	1	18.945	4.424	**0.041**
Area	1	63.029	14.717	**< 0.001**
Predator exposure × Habitat	1	13.597	3.175	0.081
Error	47	4.283		
Biomass				
Block	3	2.452	1.882	0.146
Habitat	1	0.017	0.007	0.936
Predator exposure	1	5.192	3.984	0.052
Depth	1	1.555	1.193	0.281
Area	1	59.353	45.547	**< 0.001**
Block × Habitat	1	2.273	1.744	0.172
Error	47	1.303		

communities by differentially affecting clam survivorship, e.g. via density mediated interactions. Over the time–course of our experiment there was no differential effect of *Caulerpa* on *Anadara* density – survivorship of *Anadara* was 27 and 21% in predator-exposed tubs in *Caulerpa* and unvegetated sediments, respectively (Byers *et al.* in review). Therefore, the only interactions that contributed to differences in shell surface area between habitats were positive behaviourally mediated ones, not density mediated effects on clams themselves. However, at larger temporal and

spatial scales, abundances of clams are lower in *Caulerpa* compared with unvegetated sediments in several estuaries in this region (Wright *et al.* 2007). Thus, it becomes increasingly important to account for *Caulerpa*'s density mediated effects on clams. Yet despite reduced abundances in
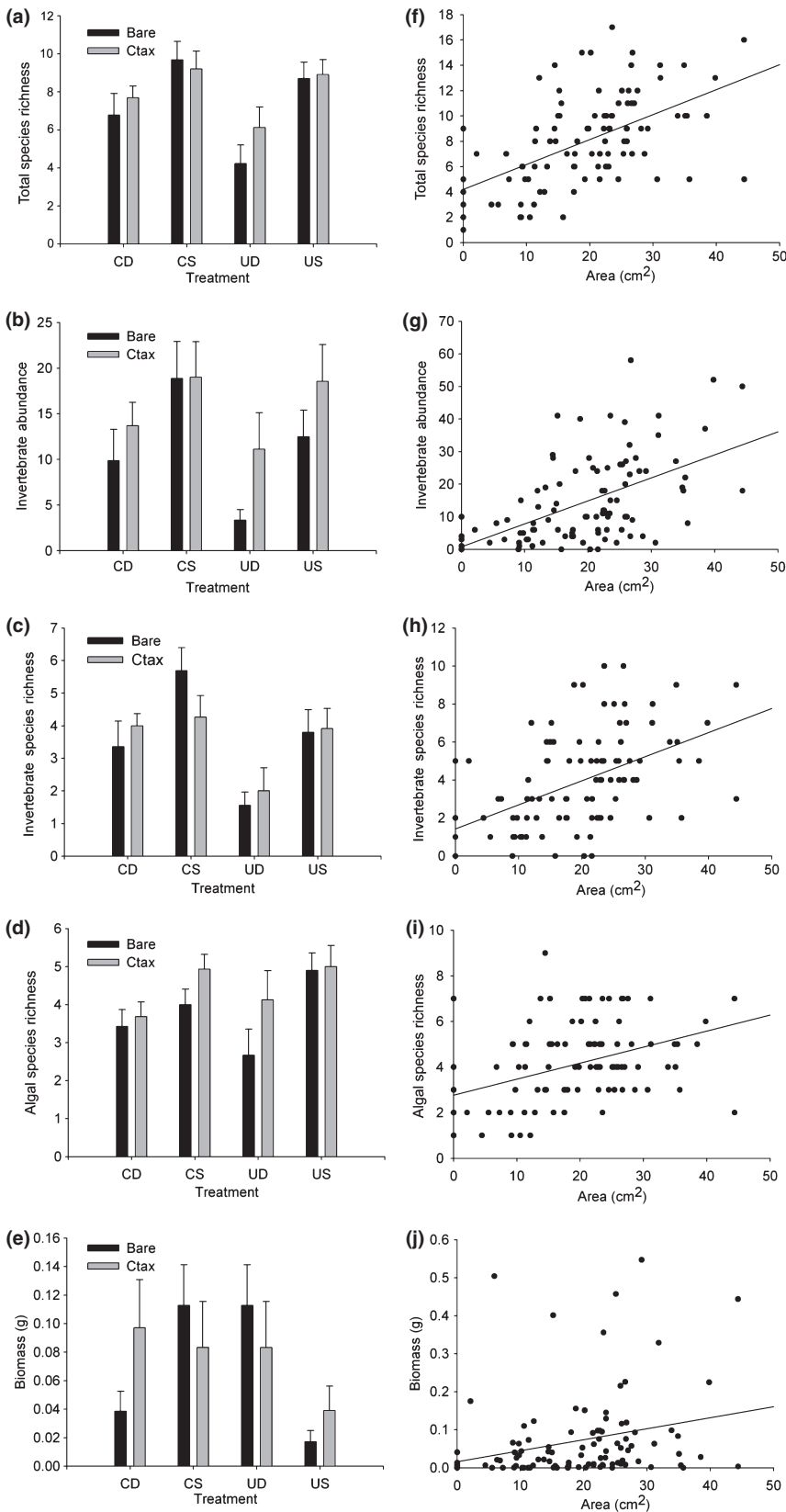
Figure 3 Mean (± SE) of (a) total species richness, (b) abundance of invertebrates, (c) species richness of invertebrates, (d) species richness of algae and (e) biomass of epibionts on *Anadara* on deep and shallow clams, in caged and uncageded treatments in *Caulerpa* invaded (Ctax) and unvegetated sediments (Bare, *n* = 8–15 clams/treatment). CD, caged deep trays; CS, caged shallow trays; UD, uncaged deep trays; US, uncaged shallow trays. Regressions between final colonizable area and (f) total species richness, (g) abundance of invertebrates, (h) species richness of invertebrates, (i) species richness of algae and (j) biomass of epibionts on *Anadara* (*n* = 102 for each analysis).These regression plots show all clams shown in the left graph (pooled across treatment) and only as a function of exposed clam surface area.

Caulerpa, in Lake Conjola high abundances of *Anadara* (> 10 m^{-2}) have persisted in *Caulerpa* since the estuary was invaded (i.e. for > 8 years) (Wright *et al.* 2007), indicating potentially long-term facilitation of epibiont communities by *Caulerpa*. Moreover, because of *Anadara*'s behavioural response, epibiont communities in *Caulerpa* will only experience a net loss once clam abundances are 50% lower compared with those in unvegetated sediments. Even if this occurs, the facilitation cascade will still act to mitigate *Caulerpa*'s negative density mediated effects on whole clams as the surface area available for colonization will still be twice that expected if behavioural modifications did not occur.

We have demonstrated that a habitat-forming ecosystem engineer can indirectly facilitate epibiotic community richness and abundance, and that the facilitation can occur via modification of the behavioural traits of another ecosystem engineer. Accordingly, incorporating mechanisms of facilitation into predictive models will need to also consider positive interactions between engineers. Moreover, to better understand the complex impacts of invasive habitat-forming engineers we need to determine the behavioural response of native habitat-forming species and impacts on associated species.

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