

Relative influence of resident species and environmental variation on community assembly

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ABSTRACT: Prior residence by a species can affect subsequent community assembly. However, previous studies insulated their focal communities from additional sources of variation, and the role of resident species in the context of environmental heterogeneity is rarely considered. If environmental and resident species effects act independently, then each should be broadly predictable, and their contribution to community assembly should be quantifiable in relation to each other. Alternatively, if effects interact, their combination may explain more of the differences in communities than the additive influence of each alone. We estimated the effects of a common, early-colonising resident (the encrusting bryozoan *Hippopodina iririkiensis*) on community assembly relative to substrate orientation. Some species showed complex responses in association with orientation, with positive responses in one orientation, negative in the other. Variation in orientation explained the majority of variation in overall community assembly. Variation among the panels holding replicates of our resident species, a blocking factor in the analysis, permitted us to consider small-scale spatial variation. Abundances responded to resident species effects but interacted with spatial variation: the impact of the resident species on community assembly varied with orientation and space. Functional groups showed similarly idiosyncratic responses to the prior resident. Overall, we found that resident species effects were weak relative to the effects of environmental variation on community assembly. Furthermore, those resident species effects that we did detect were inconsistent across environments, suggesting that this species has little predictable influence on community assembly. Environmental variation may be an important contributor and requires more widespread consideration to better understand how resident species effects act in nature.

KEY WORDS: Recruitment · Sessile invertebrate · *Hippopodina iririkiensis*

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INTRODUCTION

A fundamental goal of community ecology is to explain variation in the structure and dynamics of communities. In marine communities, interactions between residents and potential members of the community during settlement and recruitment (Osman & Whitlatch 1995, Fukami & Morin 2003) can influence how communities assemble. Typically, the effects of resident species on assembly manifest in the suppression of later recruitment (Sutherland & Karl-

son 1977). Variation in the early sequence in which species settle may influence later community structure and properties through alterations to the patterns of interactions among species (Sutherland 1974, Connell & Slatyer 1977). The effects of prior residence of a species may occur because individuals arriving first can sequester important resources and deny opportunity to later arrivals (Urban & De Meester 2009), creating a number of stable community compositions at larger scales (Sutherland 1974). Facilitative interactions among species, where the presence of one spe-

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cies enhances the settlement of another, also occur (Dean & Hurd 1980, Sellheim et al. 2010, Nelson & Craig 2011). In this way, species interactions (competition and predation) can be powerful biotic factors in the structuring of communities (Grosberg 1981, De Meester et al. 2007, Nydam & Stachowicz 2007). However, effects are not predictable to a certainty, dependent as they are on species identity, successional state of the community and spatial variation (Sams & Keough 2012a), and are further mediated by variation in recruitment rate (Sams & Keough 2012b) and density (Sams & Keough 2013b).

Pre-settlement effects that shape the assembly of communities may include the direct predation of immigrant larvae (Nydam & Stachowicz 2007), although such effects may often be indirect, mediated by allelopathic chemical interactions between residents and immigrants (Jackson & Buss 1975, Thacker et al. 1998, Koh & Sweatman 2000). Post-settlement effects of a resident may also influence the abundances of sessile neighbours, by constraining their growth or eradicating them with overgrowth (Buss 1979, Russ 1982, Osman & Whitlatch 1995). Larger individuals are competitively superior in agonistic encounters (Buss 1979), but networks, rather than hierarchies, of competitive effects may exist, where no one species can dominate all others (Buss & Jackson 1979). Only recently appreciated, non-contact competition for oxygen in this system may also influence species distributions and abundances (Ferguson et al. 2013). Facilitative effects may also act before or after settlement. Chemical effects on larvae can lead to increased abundances of some species in the presence of others (Wieczorek & Todd 1997, 1998), but are particularly important in their aid of gregarious settlement of conspecifics (Scheltema et al. 1981, Burke 1986). Post-settlement, recruits of one species may be positively affected by another species that modifies the environment and mediates ecological adversity (Bertness & Callaway 1994).

Although residents can influence the assembly of marine communities through these pre- and post-settlement processes, the magnitude of these effects as they interact with other sources of variation is less clearly understood (Glasby 2000, Kardol et al. 2013). To date, numerous studies have controlled experimental conditions to minimize environmental variation that may impact on specific effects, suggesting that the occurrence of resident species effects may be widespread and fundamental to community assembly. However, in natural contexts, communities do not assemble in isolation from environmental effects. Determining the importance of resident species

effects on community assembly therefore requires estimation of the strength and consistency of these effects relative to other sources of relevant ecological variability in a multifactorial experimental context (Glasby 2000).

Among assemblages common to inshore man-made structures, variation in the orientation of substrates can profoundly influence the abundances and diversity of species (Pomerat & Reiner 1942, Young & Chia 1981, Connell 1999, Knott et al. 2004). Vertical substrates, compared to downward-facing horizontal surfaces, are challenging settings for many sessile organisms (Hart & Marshall 2013), as the greater exposure to siltation can block feeding and reproductive organs (Ryland 1977, Wendt et al. 1989). Man-made structures offer a complex matrix of vertical and horizontal surfaces for settlement, and interactive effects of orientation and other environmental factors generate complex variation in community properties (Glasby 2000, Glasby & Connell 2001). It is likely in many marine systems that there will be widespread variation in the identity of initial occupants that also coincides with variation in orientation. In spite of this, little is understood of how these 2 factors may act in concert, as most studies have minimized sources of variation that are extraneous to the focal effects of resident species. If the effect of resident species in the community interacts with variation in orientation, both of these effects in combination may explain more of the differences found among natural communities than the additive influence of each alone. If these effects act independently, however, then each should be broadly predictable, and the contribution of each to community assembly should be quantifiable in relation to the contribution of the other (Underwood 1997). In a first possible outcome, if community assembly is less influenced by orientation than by the effects of prior residence, we may expect broad similarity in properties and structure within and among communities regardless of orientation, i.e. resident effects would override environmental effects, and communities would be predictable according to the identity of the initial occupants. Alternatively, if differences among communities are predominantly driven by differences associated with substrate orientation, resident effects may act only subordinately, and communities will be principally defined by their orientation. A third possibility is that effects would interact: the community effects created by a resident species may differ according to the orientation they act in—resident effects exerted in one orientation may be quite different to those seen in another. A variation of this sce-

nario would be that responses differ in strength; the presence of a species in one orientation may have profound impacts on communities, but may be minimally influential in another orientation. Lastly, there is no reason to expect that effects among species would act uniformly among orientations, so that different species may respond in different orientations, creating a complex mosaic of effects across different orientations.

Here we used a factorial experiment to explore the simultaneous effects on communities of prior residence by a species and variation in substrate orientation in a marine system. We considered the effect of a single resident species, the encrusting bryozoan *Hippopodina iririkiensis*, on an assembly of a marine epibenthic community in the field using horizontal and downward-facing vertical substrates.

MATERIALS AND METHODS

Study system and species

To investigate the effects of prior occupancy by a species, we used *Hippopodina iririkiensis* (Tilbrook 1999; hereafter referred to only by genus), a lightly calcified species of encrusting bryozoan with a wide tropical and sub-tropical distribution. *Hippopodina* colonises available space early in the summer season in marinas of Moreton Bay, Queensland, Australia, when settlement and growth of these communities increase. It is a regular and persistent species, although it rarely dominates communities, and co-exists naturally with all of the sessile species found in this system, on all substrates regardless of orientation. *Hippopodina* therefore makes an ideal candidate with which to examine the effects of a resident species on assembly.

Cultivation of resident species

We arranged sanded A4 acetate sheets onto 21 PVC panels (500 × 500 × 5 mm) and suspended these ~1 m below the water line across 4 pontoons at Manly Harbour, that opens on to Moreton Bay. The depth of panels was constant, as all pontoons at Manly are floating pontoons. Marine invertebrate larvae were allowed to settle for 18 d and then brought to the laboratory in insulated aquaria. Ancestrulae and newly formed colonies of *Hippopodina* were identified and removed from the original settlement sheets, then transplanted onto clean sanded sheets for return to

the site within 48 h. *Hippopodina* recruits were reattached on their sheets to PVC panels and were cultivated for 5 wk into mature colonies ~80 mm in diameter. To maximize even, encrusting growth of sample colonies, unwanted detritus and other settlers were removed twice weekly.

Experimental design

Mature colonies were subdivided into fragments of uniform size (~178 mm², SD = 4.68) using wedge shaped leather-working clippers to cut the colonies and the backing together. These fragments were glued to 232 PVC settlement plates (110 × 110 × 5 mm), using a minimal quantity of cyanoacrylate glue (which cures and sets on contact with water) on the underside of the acetate backing. A further 232 plates were left unoccupied by a resident species (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m499p103_supp.pdf). We used an orthogonal design for the experiment: on each of 58 panels there were 2 orientations, vertical and downward-facing horizontal, and for each orientation there were 2 plates occupied by fragments of *Hippopodina* and 2 unoccupied, totaling 464 plates. Panels were again suspended underwater, distributed on a single floating pontoon (~30 m long) for the duration of the experiment. Panels were treated as a blocking factor (i.e. random) that permitted us to consider how spatial variation interacted with the 2 main treatment effects. Four settlement plates were lost during the experiment, all from vertically oriented environments: 3 occupied by a resident species fragment, 1 unoccupied.

Data collection

The experiment lasted for 3 wk, when plates were removed to the laboratory to photograph and dry the communities. On each of 460 plates, we assessed the composition and abundance of 12 species, and from these assays, we composed a number of data sets. To assess the ecological properties of communities in response to the 2 treatments (orientation and prior residence), we calculated 2 commonly used metrics in community ecology: overall abundance and Shannon-Wiener diversity (H'). H' was calculated as:

$$H' = -\sum_{i=1}^S (p_i \ln p_i) \quad (1)$$

where S is the total number of species in a community, and p_i is the relative density of species i (calcu-

lated as n_i/N , where n_i is the occupancy of each species i , and N is the abundance of the whole community on each settlement plate).

We allocated species to 1 of 3 groupings defined *a priori* by morphological and functional similarity. (1) We measured the surface coverage of the 5 encrusting organisms (all of them bryozoans in this instance: new recruits of *Hippopodina iririkiensis*, all of which were readily distinguishable from the original residents, as well as *Celleporaria* sp., *Schizoporella* sp., *Hippoporina indica*, *Watersipora subtorquata*) that are 1 to 2 mm thick and occupy the boundary layer, hereafter called the encrusting group. (2) We identified a second functional group of 4 species of intermediate height (2 to 6 mm) that are sited in close proximity to the substrate, namely the common barnacle (*Balanus balanoides*) and erect sponges (*Sycon* spp.), and used 3 sub-samples of 100 mm² to estimate the number of calcifying worms (*Hydroides diramphus* and *Janua pagenstecheri*). (3) As a third functional group, we counted the numbers of 3 weedy and arborescent bryozoan species (*Bugula neritina*, *B. stolonifera* and *Savignyella lafontii*), typically 30 to 60 mm long that grow perpendicular to the substrate, hereafter the arborescent group. Finally, we pooled the abundances for each of the 3 functional groups to assess treatment effects at this level.

Data analysis

We used the multivariate non-metric multidimensional scaling (NMDS) routine in PRIMER 6 (Clarke & Warwick 2001) to distinguish and graphically represent the similarities among communities between the 2 crossed treatments. We used untransformed data to avoid creating negative, and therefore nonsensical, abundance values for the Bray-Curtis similarity matrix we composed (Quinn & Keough 2002). We also used the PERMDISP statistical test in the PERMANOVA routine of PRIMER 6 to assess whether treatment factors affected the dispersion, as opposed to just the location, of community similarities. As our data were composed of different scales (counts and surface areas), for the further analyses in a mixed-model framework, all done in SAS 9.3 using Proc Mixed, values within each variable were standardized to unit variance.

First, to partition and compare the magnitude of environmental, spatial and ecological variables, we applied univariate random effect models first to each of the 2 community metrics, and second to the overall abundances in each of the 3 functional groups. The

model comprised terms for orientation (horizontal versus vertical plates), resident species effect (presence versus absence of the resident species, *Hippopodina*), and block (variation among backing panels) as well as their interactions. The major effect terms were modelled with no diagonal D matrix in the covariance matrix to accommodate the single degree of freedom available in each (i.e. type = FA0[1]); for the blocking terms (panel), we used an unstructured covariance matrix (i.e. type = UN).

Next, to examine the effect of orientation and prior residence of a species on communities, conditional on random panel effects and associated interactions, we applied a multivariate mixed model. We used log likelihood ratio tests to assess whether removal of terms significantly reduced model fit. This model enabled us to consider more fully the role of orientation effects as they interacted with the potential ecological effects created by prior residence by *Hippopodina*. Last, where significant effects of prior residence were found in a functional group, we applied a multivariate mixed model to examine treatment effects at the level of individual species. (Analyses of individual community metrics and of additional species-level responses to treatment are reported in Tables S2 & S3 in the Supplement).

RESULTS

Variation in substrate orientation had a profound effect on community assembly: all but 1 species were considerably more abundant in the horizontal orientation than in the vertical, though in neither orientation did communities completely occupy the available space on settlement plates (Fig. 1). *Hippopodina* and *Celleporaria* were the most extensive species in terms of surface coverage in both orientations; the most abundant taxa on both horizontal and vertical plates were *Sycon* and *Bugula stolonifera*. The only species to show uniformly higher abundance in the vertical environment was *Janua* sp., a spirorbid tube-worm. Responses in mean recruitment of individual species to the presence or absence of the focal species were variable, with some showing higher abundances in sites unoccupied by *Hippopodina* (e.g. *Celleporaria*, *Schizoporella*, *B. neritina*), while others were more abundant on plates associated with prior residence by *Hippopodina* (e.g. *Hippoporina*, *Sycon*, *Savignyella*). Several species showed different mean responses to a species with prior residence in different orientations: for instance, *Watersipora* was on average more abundant in horizontal communities

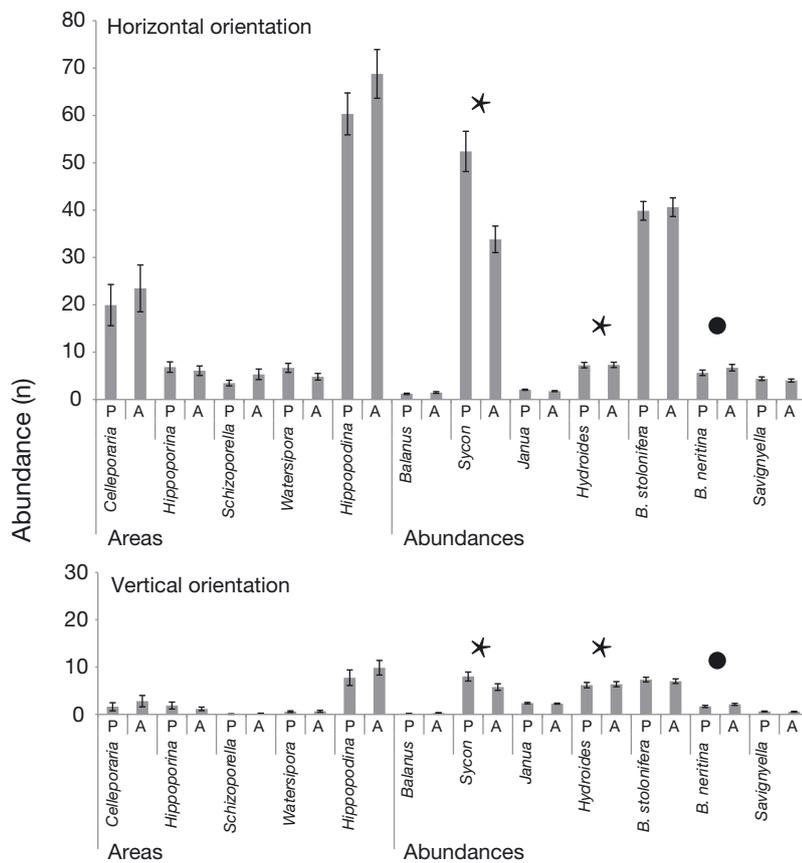


Fig. 1. Mean (\pm SE) abundances of 12 species present in 2 orientations (horizontal and vertical) in response to the presence (P) or absence (A) of *Hippopodina*. \star : significant Orientation \times Resident effect, \bullet : significant Resident effect ($p \leq 0.05$)

where *Hippopodina* was present, but less abundant in its presence in vertical communities.

Vertical communities showed less clustering than horizontal communities in the 2-dimensional space modelled, indicating that similarity among horizontal communities was greater than that among vertical communities (Fig. 2). There was no obvious indication of similarities created by prior residence of a species in either single orientation or among orientations. Community similarities were found to differ in dispersion among the 4 effects of the 2 crossed treatment factors ($F_{3, 435}$, p [perm] = 0.001). Thus there was significant variation in the similarities of communities among treatment combinations.

Variation in abundances within communities was affected by interactions of the resident species effect with small-scale spatial variation among panels (Table 1). Therefore, in terms of abundances, community responses to the presence of a resident species differed according to the panel on which the communities assembled. For community diversity (Table 1), a

more complex pattern of spatial variation in resident effect existed, as variation in resident effects among panels also varied across orientations: communities in one orientation on one panel differed significantly in diversity from communities in another orientation on the same panel in response to resident effects. Differences in orientation accounted for the sizeable majority of variation, more than any other term in either univariate model of overall abundance or diversity in experimental communities (Table 1 and Fig. 3A). Prior residence by *Hippopodina* had no detectable impact on abundances within communities, where orientation explained 75% of the variation. Effects generated by the presence of a resident species explained only a small proportion of variation in diversity.

Variance partitioning for abundances within each of the 3 functional groups showed uniform dominance by variation between horizontal and vertical communities (45 to 70%) over all other terms (Table 2 and Fig. 3B). The main effect of prior residence by *Hippopodina* varied between the functional groups, describing at most 7% of the variation among encrusting and arborescent communities, but could not be discerned at all among the intermediate taxa. In the intermediate group (Table 2), significant 3-way interactions between orientation, resident effect and panel suggested that both spatial and environmental varia-

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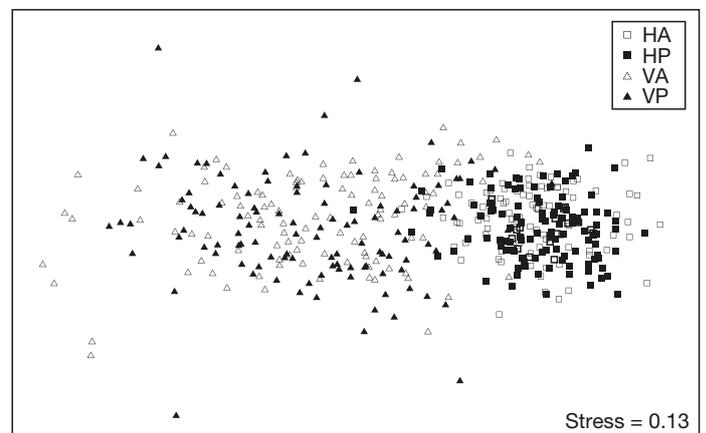


Fig. 2. NMDS ordination representing community responses to crossed factorial treatments of orientation (horizontal and vertical, H and V) and presence (P) or absence (A) of a species with prior residence, viz. *Hippopodina*

Table 1. Variance estimates for 2 common metrics of communities (overall abundance and species diversity) associated with resident *Hippopodina*, and the proportions of overall variance explained by each source of variation modelled. **Bold:** significant ($p \leq 0.05$)

Source	Estimate	Proportion of total variance
Abundance		
Orientation	1.1214	0.7515
Resident effect	0	0
Orientation × Resident effect	0	0
Panel	0.0342	0.0229
Orientation × Panel	0.1863	0.1248
Resident effect × Panel	0.0207	0.0139
Orientation × Resident effect × Panel	0.0088	0.0059
Residual	0.1208	0.081
Diversity		
Orientation	0.6348	0.423
Resident effect	0.0699	0.0466
Orientation × Resident effect	0	0
Panel	0.0813	0.0542
Orientation × Panel	0.053	0.0353
Resident effect × Panel	0	0
Orientation × Resident effect × Panel	0.0881	0.0587
Residual	0.5736	0.3822

Table 2. Variance estimates of abundances of 3 functional groups within communities associated with resident *Hippopodina*, and the proportions of overall variance explained by each source of variation modelled. **Bold:** significant ($p \leq 0.05$)

Source	Estimate	Proportion of total variance
Encrusting species		
Orientation	0.8774	0.5538
Resident effect	0.0539	0.034
Orientation × Resident effect	0.0385	0.0243
Panel	0.0443	0.0279
Orientation × Panel	0.2977	0.1879
Resident effect × Panel	0.0376	0.0237
Orientation × Resident effect × Panel	0	0
Residual	0.2349	0.1483
Intermediate species		
Orientation	0.8969	0.4997
Resident effect	0.126	0.0702
Orientation × Resident effect	0.2203	0.1227
Panel	0.0826	0.046
Orientation × Panel	0.2938	0.1637
Resident effect × Panel	0.0047	0.0026
Orientation × Resident effect × Panel	0.0799	0.0445
Residual	0.0906	0.0505
Arborescent species		
Orientation	1.1049	0.7438
Resident effect	0	0
Orientation × Resident effect	0	0
Panel	0.0752	0.0504
Orientation × Panel	0.1929	0.1293
Resident effect × Panel	0.0041	0.0028
Orientation × Resident effect × Panel	0.0082	0.0055
Residual	0.1017	0.0682

tion mediated the effect of prior residence on community assembly. Interactions between resident effects and orientation explained a further 12% of variation, indicating that effects were different in each orientation. The main treatment effect of resident effect showed inconsequential variances in the encrusting and arborescent functional groups, and did not interact with any other term modelled.

Mixed-model analyses highlighted that the properties of communities were strongly influenced by variation in several factors. We found for all of these models that removal of the 3-way interaction term (Orientation × Resident effect × Panel) within the random effects significantly reduced model fit (see Table S1 in the Supplement) and consequently the term was retained in further analyses. The required retention of the higher-order interaction term underlines the importance of small-scale spatial variation on effects of difference in substrate orientation and prior occupancy by a resident species. In other words, we found that different community responses to each of the 2 orientations also varied among panels, to an extent that significantly contributed to the partitioning of variation among communities.

No functional group showed significant responses to the presence of a resident species in terms of overall abundance (Table 3). Within the arborescent group, individual species responded differently to resident effects (Table 3). In the intermediate group, variation among species in response to resident effects also acted differently between different substrate orientations (Table 3). For the arborescent and intermediate taxa, we therefore pursued analysis of treatment effects among the individual species within each group. (in Table S3, we include a species-level analysis of abundances in relation to the 2 treatment effects within the encrusting group alone).

Abundances of the 3 taxa within the arborescent group all showed responses to the orientation of plates with reduced numbers in vertically oriented plates, but only *Bugula neritina* showed greater numbers on plates unoccupied by *Hippopodina* regardless of substrate orientation (Table 4). Species

within the intermediate functional group showed a slightly more complex picture (Table 5): 2 species (*Balanus* and *Janua*, Table 5) responded only to differences in orientation (increased abundances in vertical plates in the case of *Balanus*, reduced in the same orientation for *Janua*). However, the other 2 taxa in the same group (*Hydroïdes* and *Sycon*, Table 5) responded to the prior residence of *Hippopodina* but this differed according to orientation. *Hydroïdes* showed higher abundances on plates unoccupied by *Hippopodina*, but this signal was stronger among vertical than horizontal plates. *Sycon* showed a contrary set of responses, being more abundant on plates that were already occupied by *Hippopodina*, and showing a more pronounced trend in the vertical orientation than on horizontal plates.

Table 3. Estimates of fixed effects, over conditional mean in a mixed-model analysis, for abundances of individual species in 3 functional groups of communities associated with the presence or absence of *Hippopodina*. **Bold:** significant ($p \leq 0.05$)

Source	df	F	p
Encrusting functional group			
Species	4,53.2	139176	<0.0001
Resident effect	1,37.7	0.36	0.5548
Resident effect × Species	4,42.1	1.84	0.1386
Orientation	1,56.5	150.54	<0.0001
Orientation × Species	4,53.2	12.06	<0.0001
Orientation × Resident effect	1,66.1	0.26	0.6146
Orientation × Resident effect × Species	4,30.6	1.04	0.4028
Intermediate functional group			
Species	3,53.7	28848.8	<0.0001
Resident effect	1,45	1.51	0.2256
Resident effect × Species	3,39.5	10.61	<0.0001
Orientation	1,55.5	560.69	<0.0001
Orientation × Species	3,58.4	82.89	<0.0001
Orientation × Resident effect	1,22.1	3.33	0.0817
Orientation × Resident effect × Species	3,23.5	5.17	0.0069
Arborescent functional group			
Species	2,56	22877.4	<0.0001
Resident effect	1,70.1	0.69	0.4098
Resident effect × Species	2,67.6	3.44	0.0378
Orientation	1,57	271.48	<0.0001
Orientation × Species	2,56	8.64	0.0005
Orientation × Resident effect	1,66.2	0.26	0.6126
Orientation × Resident effect × Species	2,70.5	1.19	0.31

Table 4. Estimates of fixed effects, over conditional mean in a mixed-model analysis, for abundances of 3 species in the arborescent functional group in association with the presence or absence of *Hippopodina*. **Bold:** significant ($p \leq 0.05$)

Source	df	F	p
<i>Bugula stolonifera</i>			
Resident effect	1,56.8	0.06	0.801
Orientation	1,57	209.84	<0.0001
Orientation × Resident effect	1,56.7	0.54	0.4674
<i>Bugula neritina</i>			
Resident effect	1,113	6.4	0.0128
Orientation	1,57	45.51	<0.0001
Orientation × Resident effect	1,113	1.41	0.2372
<i>Savignyella lafontii</i>			
Resident effect	1,56.8	1.87	0.1773
Orientation	1,57	75.59	<0.0001
Orientation × Resident effect	1,56.7	0.89	0.3507

DISCUSSION

Different communities formed on different substrate orientations, whereas the presence of a resident species had relatively minor effects on community assembly. Where resident species effects were detected, these varied significantly with both substrate orientation and among panels distributed in space. Abundances within communities were universally higher on horizontal than on vertical substrates. Summary metrics of communities were largely unaffected by the presence of a resident species, although among the 3 functional groups, 2 showed complex 2- and 3-way interaction effects involving small-scale spatial variation in resident effects. The majority of species abundances did not differ according to the presence or absence of *Hippopodina*. However, among those species that did respond to prior residence, 2 were found in higher densities on unoccupied plates, and 1 was higher on occupied plates. These results confirm that variation in substrate orientation can be a powerful predictor of community properties and structure,

Table 5. Estimates of fixed effects, over conditional mean in a mixed-model analysis, for abundances of 4 species in the intermediate functional group in association with the presence or absence of *Hippopodina*. **Bold**: significant

Source	df	F	p
Balanus			
Resident effect	1,56.9	2.75	0.1025
Orientation	1,56.8	28.26	<0.0001
Orientation × Resident effect	1,288	0.2	0.6586
Sycon			
Resident effect	1,56.8	35.17	<0.0001
Orientation	1,57	72.19	<0.0001
Orientation × Resident effect	1,56.8	23.12	<0.0001
Janua			
Resident effect	1,170	0.07	0.7859
Orientation	1,170	124.12	<0.0001
Orientation × Resident effect	1,170	0.04	0.8495
Hydroides			
Resident effect	1,113	11.53	0.0009
Orientation	1,57	1060.86	<0.0001
Orientation × Resident effect	1,113	5.88	0.0169

and that, by comparison, the presence of a resident species may elicit response in only a minority of species but show further complex interactions with orientation.

This study demonstrates fundamental differences in the properties and structure of communities according to whether they are vertically or horizontally orientated. In itself this is unremarkable, and accords with previous studies that quantified species abundances in similar settings, finding the same environmental variation to influence the density of communities (Connell 1999, Glasby 2000, Glasby & Connell 2001, Knott et al. 2004). A number of underlying factors have been proposed to explain the differences in communities associated with variation in orientation, principal among them

the sedimentation regime (Ryland 1977, Wendt et al. 1989). Variation in orientation is a typical component of environmental heterogeneity in these systems, composed as they are of a matrix of horizontal and vertical surfaces on boats, pontoons, piers and pilings. However, our focus was on the contribution to community assembly that species interactions make under these conditions of differing orientation.

Early assembly history can affect the later trajectory of communities and underlie variation in stable outcomes of community composition (Sutherland 1974). Resident effects may explain how apparently stochastic variation in larval density, behaviour and disturbance regime may resemble deterministic forces in shaping community outcomes (Hoverman & Relyea 2008, Chase & Myers 2011, Sams & Keough 2013a). Prior residence by a species may exclude potential immigrants pre-settlement, eradicate recruits post-settlement or facilitate the settlement of others, thereby influencing the composition of associated communities (Fukami & Morin 2003). Our results show how the ultimate effects of interactions with a resident species can also vary according to substrate orientation: we demonstrated that resident effects may be specific to different environments, such that predictions that hold in one orientation do not hold in

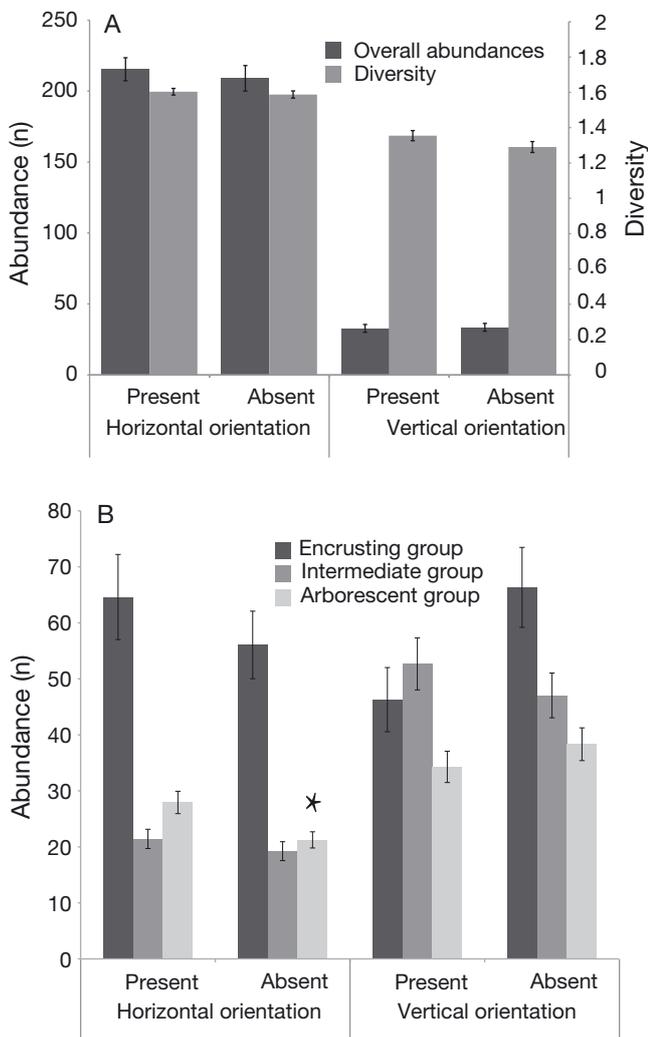


Fig. 3. (A) Mean (\pm SE) abundances and diversity present in 2 orientations (horizontal and vertical) in response to the presence or absence of *Hippopodina*. (B) Mean (\pm SE) abundances of 3 functional groups. * : Significant Orientation \times Resident effect ($p \leq 0.05$)

another. Where resident effects also differ across orientations, the variation visible in communities will depend not only on orientation but will also be contingent on assembly history (Chase & Myers 2011). This interaction suggests that a simple distinction among communities that diverge according to environmental variation (single equilibrium communities), in contrast to communities driven by assembly history (multiple state equilibria), may be overly simplistic in the face of actual variation in community assembly patterns and processes (Chase & Myers 2011). Although we have examined the resident effects generated by only 1 species, our study highlights that complex interactive effects, not the strength of the resident species or orientation effect per se, mean that neither effect can be assumed to act predictably.

In spite of the fact that environmental variation can alter the effects of resident species, ultimately these biotic effects on assembly may concern only a minority of species, with no apparent effect on the overall community properties. As demonstrated here, resident effects may play a comparatively small part in the dynamics of assembly, which in turn may explain why in contrast to theoretical expectations, variation in the stable states of communities is, in fact, limited (Belyea & Lancaster 1999). Our findings are in contrast to those of several others that have reported more pervasive resident effects on assembling populations and communities. For instance, *Diplosoma* and *Botryllus* both reduced overall recruitment to communities by overgrowing neighbours (Osman & Whitlatch 1995); further, general effects are seen in potential prey species that avoid sites previously occupied by their predators (Johnson & Strathmann 1989). However, the effects of prior residence are not invariable and are likely to be mediated by variation in supply-side factors. Variation in the identity of initial residents, as well as the rate of their recruitment, may significantly alter community composition (Sams & Keough 2012b). Similarly, variation in the identity of recruiting species alters the structure of communities but also the persistence of community outcomes (Sams & Keough 2012a). The effects of a resident species on communities may also be altered by the presence of a second resident species, generating complex patterns of contingent community assembly (Sams & Keough 2013a). Resident species effects that are comparatively limited and species-specific, however, such as those found here, are not unprecedented. For example, the arborescent bryozoan *Bugula neritina* facilitates the preferential settlement of *Hydroïdes* worms (Bryan et al. 1998); also, the gre-

gious settlement of individual species may lead some to be represented at higher densities in communities (Scheltema et al. 1981), and environmental differences have also been shown to influence these outcomes (Pawlik & Butman 1993).

In this study, we examined the relative influence of, and the interactions between, 2 qualitatively different factors that act on community assembly: the stochastic impact of resident effects and the deterministic shaping of the assembly by environmental variation in substrate orientation. If resident effects are modified by the specific identity of the taxa interacting, this adjustment by biotic interactions occurs within the limitations imposed by environmental constraints that fundamentally determine the potential spatial distributions of species (Belyea & Lancaster 1999). Interaction effects, whether positive or negative, modify these fundamental niche constraints; positive interactions, which are more rarely considered, effectively increase the realized niche space for species that benefit (Bruno et al. 2003). Although these findings bear out the general prediction that species interactions will be comparatively inconsequential under conditions of physical harshness (Connell 1975), they also accord with the expectation that species interactions will be decreasingly competitive under increasing stress (Bertness & Callaway 1994, but see Hart & Marshall 2013). The importance of these non-consumer interactions between 2 or more species in the structuring of communities remains contentious, but they may occur where one species modifies the environment advantageously for another, particularly under stressful conditions (Bertness & Callaway 1994). These positive interactions may be generally common, but here specifically, we found that only some interactions with *Hippopodina* in vertical orientations resulted in increased abundances of other species. Similar environmentally determined interactions occur where the presence of *Ascophyllum nodosum* can alleviate the effects of desiccation for recruits on the more stressful higher rocky shore, but on the lower shore effects of predation suppress many species abundances (Bertness et al. 1999).

We found that variation in substrate orientation had profound effects on community properties and structure. Resident effects generated by *Hippopodina* were comparatively minor, but did show that environmental variation modulates species' responses to the presence of a prior resident. Complex patterns of interactions among species, therefore, may interact with environmental variation, with both negative and positive effects on species abundances

depending on the identity of the species involved. Thus, it is likely that interactions of a suite of ecological factors may affect the composition and assembly trajectory of communities unpredictably across environmentally heterogeneous landscapes.

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Relative influence of resident species and environmental variation on community assembly

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Supplement. Supporting data

Table S1. Model reduction results: effect of removing the random 3-way interaction term (Orientation × Panel × Resident effect) for each of the 3 data sets estimating effect of presence or absence of *Hippopodina* on community composition

	<i>Log-likelihood of each model</i>		X^2	df	p
	Full	Reduced			
Encrusting	5746.6331	5775.2197	28.5866	15	0.0182
Intermediate	4033.4227	4075.4196	41.997	10	<0.0001
Arborescent	2455.9889	2477.516	21.5271	6	0.0015

Table S2. Estimates of fixed effects, over conditional mean in a mixed-model analysis, for community metrics (abundances and diversity) of 13 species in association with the presence or absence of *Hippopodina*. Significant ($p < 0.05$) values are shown in **bold**

Source	df	F	p
Abundance			
Resident effect	1, 56.9	0.33	0.5673
Orientation	1, 57	330.02	< 0.0001
Orientation × Resident effect	1, 56.6	0.8	0.3745
Diversity			
Resident effect	1, 113	2.52	0.1151
Orientation	1, 56.9	97.65	< 0.0001
Orientation × Resident effect	1, 113	0.88	0.3508

Table S3. Estimates of fixed effects, over conditional mean in a mixed-model analysis, for abundances of 5 species in the encrusting functional group in association with the presence or absence of *Hippopodina*. Significant ($p < 0.05$) values are shown in **bold**

Source	df	F	p
<i>Celleporaria</i>			
Resident effect	1, 56.8	2.46	0.122
Orientation	1, 57	12.17	0.0009
Orientation \times Resident effect	1, 287	1	0.3188
<i>Hippopodina</i>			
Resident effect	1, 56.9	0.66	0.4195
Orientation	1, 344	35.93	<0.0001
Orientation \times Resident effect	1, 344	0.01	0.9329
<i>Schizoporella</i>			
Resident effect	1, 113	2.71	0.1024
Orientation	1, 56.9	30.22	<0.0001
Orientation \times Resident effect	1, 113	2.09	0.1512
<i>Watersipora</i>			
Resident effect	1, 344	1.88	0.1711
Orientation	1, 56.9	57.75	<0.0001
Orientation \times Resident effect	1, 344	2.24	0.1353
<i>Hippopodina</i>			
Resident effect	1, 56.9	2.77	0.1017
Orientation	1, 57	109.21	<0.0001
Orientation \times Resident effect	1, 56.8	1.25	0.2683

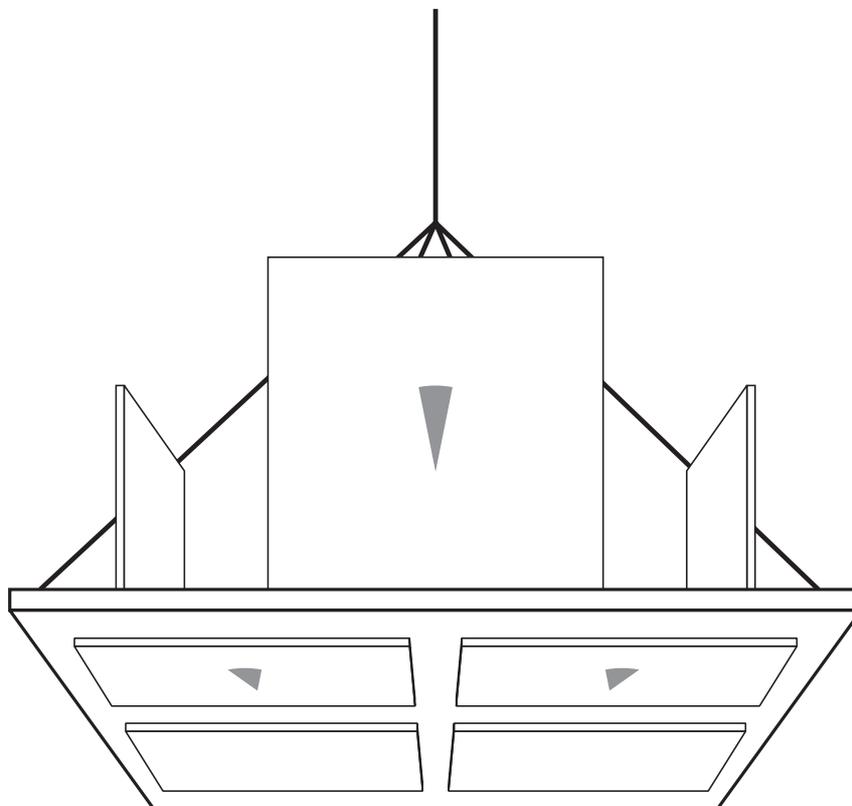


Fig. S1. Arrangement of settlement plates (110 \times 110 \times 5 mm) on backing panels (250 \times 450 \times 5 mm). The presence of the resident species, *Hippopodina*, is indicated by grey segments in the centre of the settlement plates