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Effects of structural diversity and identity of patches of habitat on diversity of benthic assemblages

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Abstract A fundamental problem in ecology, regardless of habitat or system, is understanding the relationship between habitats and assemblage of organisms. It is commonly accepted that differences in composition and surrounding landscape of habitats affect the diversity of assemblages, although there is not much empirical evidence because of difficulties of manipulating structure in many habitats. These relationships were examined experimentally, using habitats of artificial turfs that are colonized by diverse assemblages of gastropods. Each habitat was made of nine sub-habitats, which were sampled individually to allow tests of hypotheses about the effect of type of habitat and the influence of other adjacent sub-habitats on the colonizing assemblage. Turf habitats were deployed for 8 weeks on a rocky shore after which they were collected and the colonizing assemblages of gastropods sampled. Independently of the types of turfs combined to form different habitats, there were more species where there was more than one type of component in a habitat (i.e. structural diversity). The type of habitat (i.e. structural identity) itself had little or no influence on the colonizing assemblage. The number of species colonizing short-sparse and short-dense turfs was influenced by which type of habitat was adjacent. Thus, when units of one type (e.g. short-sparse turf) were added to a patch of habitat of long-sparse turfs, the number of species in short-sparse turfs was greater than in patches of the same type. This also increased total number of taxa in the whole patch of habitat. These results show how diversity of gastropods colonizing heterogeneous patches of habitat is influenced not only by the number of types of sub-habitats, but also by interactions with surrounding sub-habitats. These findings reiterate the importance of investigating the role of structure of habitats and of their surrounding landscapes across different systems, irrespective of their size or associated assemblages of organisms.

Key words: artificial habitat, composition, diversity, landscape, microgastropod.

INTRODUCTION

The role of structure of habitats in determining patterns of abundance and distribution of organisms has been examined in many habitats (see Simpson 1949; MacArthur & Wilson 1967; Lawton 1983; McCoy & Bell 1991). Generally, however, it has been difficult to identify mechanisms underlying the relationships between organisms and structure or which measures are relevant to describe the structure of habitats. Identifying and measuring the key structural elements or features which determine diversity and abundances of organisms has profound implications for the conservation of threatened habitats and for management of biodiversity (Tews *et al.* 2004).

Research on structure of habitat using natural or artificial plants has measured effects on many properties including diversity (Southwood 1961), density (Pearman 2002) and biomass (Stoner & Lewis 1985) of vegetation; surface area (Nilsson 1979; Attrill *et al.* 2000), volume and ratio of surface to volume (Coull & Wells 1983), height (MacDonald & Johnson 1995) and degree of branching of plants (Edgar 1983), canopy volume and interstitial volume (Hacker & Steneck 1990) or fractal dimension (Gee & Warwick 1994). This variety of variables makes it problematic to compare across habitats. Recent studies have argued that widely used frameworks of structure of habitat (e.g. McCoy & Bell 1991) are often difficult to be tested empirically because variable attributes of habitat cannot be separated from each other in field experiments (see discussion in Matias *et al.* 2007).

One of the issues in understanding relationships between organisms and habitat is that each habitat is rarely uniform, but is, instead, a mosaic of different resources of shelter, food and other requirements. Such mosaics are the substance of landscape ecology (Wiens *et al.* 1993). Most studies of landscapes have been in terrestrial environments (Turner *et al.* 1989), although they are becoming more common in aquatic and marine studies (e.g. Irlandi & Crawford 1997;

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Bell *et al.* 1999; Ward *et al.* 2001; Goodsell *et al.* 2004; Healey & Hovel 2004; Jackson *et al.* 2006). Dunning *et al.* (1992) highlighted the roles of spatial arrangement and characteristics of patches as essential components of any description of a landscape. Taylor *et al.* (1993) later argued that connectivity between patches is also essential and should be considered when studying landscapes. The response of a species to a mosaic of patches may depend on the scale of observations at which spatial pattern is perceived (Chust *et al.* 2003). For organisms in a patch, it is important that measures of habitat structure are relevant to the scale of organisms being studied. Thus, habitats are in a hierarchy of different scales, so that a landscape for some studies may be a patch for larger-scale investigations, or a patch may be a landscape for studies of a smaller scale (see particularly Allen & Starr 1982). Furthermore, the properties of a landscape should be observed at any scale that is relevant to the organisms or processes being studied.

This study investigates influences of heterogeneity of patches (i.e. number of types of different sub-habitats) and the influences of the 'landscape' in each patch (i.e. the surrounding sub-habitats) on the diversity of assemblages of gastropods. Artificial habitats (AHs) were designed to manipulate sub-habitats in monotypic and heterotypic mixtures, to investigate three general models that can account for differences in numbers of species in habitats with different structure:

1. Numbers of species are regulated by the *number* of sub-habitats that make up a habitat, regardless of the type of component. Assemblages in habitats with two or three different types of component are predicted to have more species than in habitats with only one type of component (Hypothesis 1).
2. Numbers of species are a result of the *type* of sub-habitats making up a habitat; as a consequence, any effects of increasing structural diversity should be dependent on which sub-habitats make up the habitat. If this were true, there should be more taxa in heterotypic habitats, but numbers will vary depending on which sub-habitats are present (Hypothesis 2, in contrast to Hypothesis 1).
3. Differences in numbers of species are caused by interactions between different types of sub-habitats. The combination of different sub-habitats in mixtures leads to the sub-assemblages associated with each type of component being altered by other types of sub-habitats that make up the whole habitat (i.e. the surrounding matrix). If this model were true, assemblages in sub-habitat Type A should have a different number of species when surrounded by Types B or C, than when surrounded by (i.e. in homogeneous patches of) Type A (Hypothesis 3a). Similarly, numbers of species should differ in units of Type B or C when different sub-habitats (A, C or A, B, respectively) are present in the surrounding patch of habitat (Hypotheses 3b and 3c).

These hypotheses were tested using assemblages of intertidal gastropods colonizing experimental patches of AHs constructed of different types of sub-habitats in different mixtures. These organisms are quite small, ranging from 0.5 to 3 mm in size. When studied at an appropriate scale, they are known to respond consistently in accordance with predictions based on models usually tested at larger scales (Matias *et al.* 2007). Note, however, that the width of experimental sub-habitats is 17–100 times their body lengths (see methods section). The 150 × 150 mm experimental habitats used here are 50–300 times larger than the snails. For small snails studied here, a patch of heterogeneous habitat of 150 × 150 mm could be considered a landscape (Fahrig & Merriam 1985; Steffan-Dewenter *et al.* 2002). Variability within heterogeneous patches of habitat could only realistically be interpreted when the landscape of components of habitat was also investigated (Addicott *et al.* 1987).

Gastropods were chosen because they are a diverse component of all the intertidal fauna; they are relatively easy to sort, identify and count. They are a good representative group for ecological processes affecting coralline algal turf assemblages (Kelaher *et al.* 2001) in that they show consistent patterns under different ecological conditions and their spatial and temporal patterns of variability reflect those of the whole assemblage (Underwood & Chapman 2006). It is worth noting that most studies of relationships between habitats and diversity also use a taxocene, rather than the whole assemblage (e.g. MacArthur & MacArthur 1961; Southwood 1961; Hacker & Steneck 1990; Downes *et al.* 1998).

As is common in terrestrial studies of terrestrial organisms (e.g. Southwood 1961; Pearman 2002), artificial plants have been widely utilized in experiments to study marine fauna associated with algae (Christie *et al.* 2003; Kelaher 2003; Schreider *et al.* 2003), because it is possible to create 'complex' and 'simple' artificial plants to examine independently the effects of varying structural features without any confounding influence of individual/biological characteristics of algae. Artificial turfs, rather than natural algal turf, were used to allow the necessary manipulations and, more importantly, to disentangle the biological properties of the different algae that make up turf from the physical properties of structure (Kelaher 2003; Matias *et al.* 2007). Artificial turfs made of synthetic grass have been shown to be excellent mimics for coralline turf because of their mat-like structure, which traps sediment and is quickly colonized by fauna (Kelaher 2003). Most species of gastropods found in natural turfs readily colonize artificial turfs.

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MATERIALS AND METHODS

Study site

Experiments were carried out in Chowder Bay, Sydney Harbour (NSW, Australia 33°50.83′S, 151°25.08′E), between May and June 2005. To replicate the experiment to assess how general the results may be, experimental treatments were all established in each of three sites, 10–20 m apart. Sites this far apart were considered to be independent of one another for the purposes of these experiments as it has been previously shown that assemblages in these habitats vary at a scale of <1 m (Olabarria & Chapman 2001). All experimental sites had extensive covers of algal turf dominated by *Corallina officinalis* L. Sites were gently sloping low-shore rock platforms or large boulders, with similar orientation and exposure to waves. The numbers and varieties of gastropods colonizing experimental habitats were sampled; gastropods were all <3 mm and comprised small species and some juveniles of larger species.

AHs

From pilot studies, three types of artificial, plastic turf (Team Sports Pty Ltd, Sydney) were selected with different densities and length of fronds. These were chosen to allow construction of different types of habitats, so that hypotheses could be tested. Particular turfs were quickly colonized by numerous species of invertebrates from the entire range of those colonizing natural turfs (Kelaher *et al.* 2001; Matias *et al.* 2007). Kelaher (2002) showed no differences between artificial turfs and natural turfs at 2, and 4, months after colonization.

Note that artificial turfs were not real turfs, but provide shelter and resources, allowing control of the structure of the habitats. They achieved this because they are colonized by species that occupy natural turfs. Turf A had short (9–10 mm) and sparse (64 fronds cm^{-2}) fronds, turf B had long (19–20 mm) and equally sparse fronds; turf C had short and dense (102 fronds cm^{-2}) fronds. Each AH, of 150 × 150 mm, was made of nine 50 × 50 mm units arranged in three rows of three units. Note that these small units are large enough to provide meaningful information – they were colonized by an average of 16 species. Each unit was glued to individual pieces of rubber and attached to wire mesh to maintain a contiguous structure. The surface-area of fronds ranged between 608 and 1140 cm^2. No linear relationship has been found between the surface-area of fronds and numbers of taxa present ($r^2 < 0.01$, $F_{(1,71)} = 0.03$ $P > 0.86$, M. G. Matias, unpublished data, 2007).

Field and laboratory work

Previous studies suggested that rates at which organisms arrive at patches may depend on the characteristics of surrounding habitat. Nevertheless, there was no consistent relationship between numbers of species colonizing a patch of artificial turf and its distance from the nearest natural turf (M. G. Matias, unpubl. data, 2007). Regardless, for the present experiments, the gap was standardized to be <1 cm by making clearings approximately 0.15 × 0.15 m in areas of natural turfs. AHs were attached to cleared areas by four masonry nails and rubber washers at 0.45–0.55 m above Mean Low Water (MLW) to minimize any variability because of height on shore.

The AHs were retrieved after 48–53 days; this period is sufficient for colonization by many organisms. All AHs were deployed at the same time but there were a few days difference in the day they were collected, because of logistical constraints. These differences were randomized across treatments. AHs are rapidly colonized (Olabarria 2002; Kelaher 2003) and it has also been reported that were no differences in diversity and abundance between natural and artificial turfs after 2, 4 and 12 months (Matias *et al.* 2007). Additionally, Matias *et al.* (2007) demonstrated that assemblages colonizing artificial turfs can show significant differences between patches with different structural diversity. From these considerations, the time allowed for colonization was considered appropriate to test models about colonization of patches of habitat.

Preliminary work showed that fauna were easily dislodged from the units of turf when habitats are sampled. To avoid this, AHs were retrieved using a 3 × 3 grid of 50 × 50 mm squared stainless steel corers (similar to an ice cube tray) which isolated the units so that they could be sampled separately, but simultaneously (see also Kelaher 2000). The grid of corers was carefully placed over the habitat and then pressed firmly down to enclose each of the nine units in a separate corer, with a plastic bag fixed to the end of each corer. No animals could leave or be dislodged from the unit of turf held in each of the corers. The backing mesh was then detached from the rock, the assembly inverted and each habitat type pushed into the corer. The contents of each corer were then emptied into the plastic bag at its end, guaranteeing that the animals associated with each unit were completely sampled. Each unit was labelled, preserved in 7 % formalin and was washed in a 63 μm sieve. Gastropods were sorted and counted under a binocular microscope (×16 magnification). Taxa were identified to different levels of taxonomic resolution according to available taxonomic expertise; most were identified to species, but, for some, this was not possible. These were consistently identifying as morphospecies.

The number of species in each AH was estimated from an actual patch area of 0.0075 m^2 (i.e. three units of 50 × 50 mm) which is 50% greater than the area suggested by Kelaher (2000) as appropriate to provide a good compromise between precise estimates of the richness and abundance of gastropods in natural turfs and the time necessary for processing a sample (i.e. 0.005 m^2, Kelaher 2000).

Experimental design

Three types of habitats were designed: monotypic habitats; habitats with two sub-habitats; and habitats with three sub-habitats (see Table 1 for details). To ensure independent tests for each hypothesis (Underwood 1997), but to avoid confounding differences among AHs with any differences because of units being on edges or corners of each AH, units

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of each type of turf were allocated equally to centres, edges and corners across the replicate habitats of the same type. Treatments with different relative abundance of similar types of sub-habitats (e.g. 6A + 3B and 6B + 3A) were used to examine potential effects of differences relative density of sub-habitats in habitats with the same structural diversity. In a previous study on this system, the AB treatment is incorrectly referred to as 6A + 3C (Matias *et al.* 2007), this treatment, as in the work described here was 6A+3B. Two treatment combinations (BC and CB) were not used because there were already enough comparisons to test the proposed models and these other combinations would have generated considerably more work for little gain in information. The last design has only one configuration because it was the only possible combination of equal numbers of the three types of turf. Originally, four replicate AHs of each of the eight types were deployed in each of three sites, but bad weather caused the loss of some experimental AHs. Only $n = 3$ replicate AHs were available from every combination of site and configuration. So, three AHs were chosen at random from those available, except for Site 1, where only two replicates of habitat AC were retrieved; a third 'replicate' was created by averaging the other two replicates and reducing the number of degrees of freedom of residuals in analyses (Underwood 1997).

The number of taxa sampled is often dependent on the size of sample. Species accumulation curves (plotting number of species *vs.* numbers of samples) were therefore calculated from averages of units for each habitat using PRIMER 5 (Primer-E, Plymouth) to check that effects of habitat structure on number of taxa were not confounded by different accumulation curves.

Hypotheses 1 and 2 were tested using assemblages from habitat patches; Hypothesis 3 was tested using assemblages from a single type of sub-habitat within habitat patches. The numbers of taxa in different types of habitats were compared using ANOVA, with Habitat as a fixed factor (habitats A, B, C, AB, AC, BA, CA); site is a random factor with three levels. Interactions among different sub-habitats were examined using units of a particular type of habitat when in habitats of different levels of heterogeneity. ANOVAs were preceded by Cochran's tests to check for homogeneity of variances between treatments. Multiple comparisons of significant terms were examined by Student-Newman-Keuls (SNK) tests (Underwood 1997).

RESULTS

Hypothesis 1 was that assemblages in habitats with two or three different types of sub-habitats should have more taxa than those in monotypic habitats. The number of taxa was greatest in AHs with three sub-habitats (Fig. 1a), supporting hypothesis 1. Increased number of taxa was consistent among the three sites (Table 2).

Hypothesis 2 was that assemblages in non-monotypic habitats should have different numbers of taxa depending on which sub-habitats are present in the habitat (i.e. A and B or A and C). There were no significant differences in number of taxa found in AHs AB *versus* AC ($F_{(1,42)} = 0.93$, $P > 0.3$), nor in BA *versus* CA ($F_{(1,42)} = 1.39$, $P > 0.2$). Although there were more taxa in AHs with A and B units (i.e. AB and BA) than in monotypic A or B units (Fig. 1b), differences between means were not significant (SNK tests in Table 2b). Similarly, the mean number of taxa in AHs with A and C units (i.e. AC and CA) was greater than that in monotypic A or C units (Fig. 1b), although these differences were not significant (SNK tests in Table 2b). There were no significant patterns relating identity of sub-habitats in the habitat (e.g. AB or AC) with the diversity of gastropods and thus no support for Hypothesis 2.

As predicted (Hypothesis 3a), the number of taxa in units of Type A differed depending on whether they were in homogeneous AHs (A) or surrounded by units of B or C (Table 3a). Despite a significant effect of composition of habitat, SNK tests could not separate means (Table 3a), so it is not possible to say which AHs differed (Fig. 2a). Similarly, for units of Type C (Hypothesis 3c), there were fewer taxa in A, AC and CA than in ABC (Table 3c, SNK tests at $P < 0.05$ of the means shown in Fig. 2c). In contrast to what was predicted for units of Type B (Hypothesis 3b), there were no significant differences in number of taxa among units of Type B according to whether they were in B, AB, BA, or ABC (Fig. 2b).

Table 1. Numbers of units of different turfs in experimental artificial habitats

Composition of habitat		No. of types	No. of units of each type		
			A	B	C
Monotypic	A	1	9		
	B	1		9	
	C	1			9
Mixed	AB	2	6	3	
	AC	2	6		3
	BA	2	3	6	
	CA	2	3		6
	ABC	3	3	3	3

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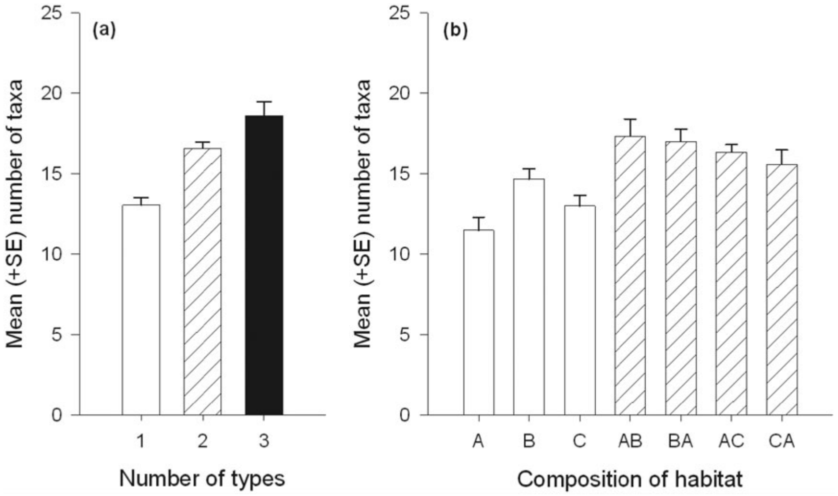

Fig. 1. Diversity of assemblages in habitats with different composition. (a) Mean (+SE) number of species of assemblages in artificial habitats (AHs) with different number of types of sub-habitats (i.e. 1, 2 and 3); Number of Types 1 is AHs of types A, B and C; 2 is AB, AC, BA, CA; 3 is ABC; $n = 4$ replicate AHs were chosen at random from those available for each number in each site. (b) mean (+ SE) number of species per unit among units in AHs as in (a); White are monotypic; hatched bars are habitats of two types of units; black have three types. In (a), all three means differed in SNK tests ($P < 0.05$).

Table 2. Analyses of (a) mean number of taxa in randomly chosen habitats with numbers of types of sub-habitats (i.e. 1, 2 or 3). 'Number of types' is a fixed comparison of artificial habitats (AHs) with one (A, B or C), two (AB, BA, AC or CA) or three (ABC) types of turf

	(a)			(b)			
Source	d.f.	MS	*F*	Source	d.f.	MS	*F*
Number of Types C	2	81.37	115.63***	Habitat H	7	37.76	3.80***†
Sites S	2	1.03	0.08 ns	Sites S	2	5.05	0.59 ns
S × C	4	0.70	0.05 ns	H × S	–	–	–
Residual	18	13.44		Residual	47	8.55	
Cochran's test, *C* = 0.28 ns					Cochran's test, *C* = 0.14 ns		
SNK		1 < 2 < 3			A = C = B = CA = AC = BA = AB		

N = 4 replicate AHs were chosen at random from those available in each number in each site; (b) mean number of species in AHs with different composition. Habitat (H) is a fixed factor comparison among habitats (A, B, C, AB, AC, BA, CA) and Sites (S) is the random comparison among three sites; SNK tests on differences among means at $P < 0.05$. ***$P < 0.001$; **$P < 0.01$, *$P < 0.05$; ns, $P > 0.05$. †H was tested against the residual because H×S was eliminated from the analysis (see procedures in Underwood 1997).

DISCUSSION

There have been numerous examples of effects of diversity of sub-habitats on diversity of animals, e.g. web-spiders (Pianka 1967), desert reptiles (Atauri & de Lucio 2001), amphibians (McGuinness & Underwood 1986), intertidal gastropods (Matias *et al.* 2007) and freshwater macroinvertebrates (Downes *et al.* 1998), structural diversity has often been studied or manipulated, but the lack of a general definition of habitat often makes it difficult, if not impossible, to compare among studies (see discussion in Matias *et al.* 2007).

Here, the number of types of sub-habitats (i.e. structural diversity) making up a habitat (to two or three from one) increased the number of taxa in AHs. By contrast, the composition of habitat (i.e. which types were present) did not influence the number of taxa present in AHs. Where B or C were added to AHs with A sub-habitats, there were no significant differences in numbers of taxa that could be explained by the presence of particular types of sub-habitats. Previous studies have shown that variability of assemblages is influenced by particular sub-habitats within habitats (Irlandi & Crawford 1997), even though, here, the composition of habitat did not influence the number of

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Table 3. Analyses of mean number of taxa; Habitat (H) among all habitats containing (a) units A (A, AB, BA, AC, CA, ABC) (b) units B (B, AB, BA, ABC) (c) units C (C, AC, CA, ABC); S is the random comparison among three sites and $n = 3$

	(a) Units A			(b) Units B			(c) Units C		
Source	df	MS	F	df	MS	F	df	MS	F
Habitats H	5	36.61	3.92**	3	23.00	1.35	3	18.55	7.03*
Sites S	2	47.17	9.43***	2	79.08	29.05***	2	40.78	15.45***
H × S	10	9.34	1.87†	6	17.08	6.28***	6	3.51	1.33†
Residual	36	5.00		24	2.72		24	2.64	
Cochran's test		$C = 0.23$ ns			$C = 0.21$ ns			$C = 0.39$ ns	
SNK		ns			ns			C = AC = CA < ABC	

SNK tests differences between means at $P < 0.05$. ***$P < 0.001$; **$P < 0.01$, *$P < 0.05$; ns, $P > 0.05$. †Pooling procedures did not identify any further effects of Habitat, so pooled analyses are not shown.

species. These patterns are generally consistent with responses of entire assemblages to similar manipulation of habitat. Matias *et al.* (2007) reported that the addition of different components altered the constituent sub-assemblages in different sub-habitats. Similarly, they showed no major effects of composition on the variability of number of species (Matias *et al.* 2007).

These findings are related to some of the current discussion about identity as opposed to number of species in investigations of biodiversity and its relationships to ecosystem function (e.g. Naeem *et al.* 1995; Tilman 1997). As discussed by Matias *et al.* (2007), sampling habitats with different numbers of types of sub-habitats could create differences in numbers of species because more diverse habitats include types of sub-habitats that are particularly good habitat for a broad variety of species, rather than because they contain more types of sub-habitats. This is an important issue because measures of structural diversity based on number of types of patches are widely used across many ecological systems as a measure of loss or degradation of natural habitats (e.g. Tews *et al.* 2004). For example, in terrestrial habitats, intensive farming often results in homogenization of landscapes, causing dramatic losses of local and regional diversity (Holzschuh *et al.* 2007). A decrease in diversity of habitats in these landscapes might explain the decline of numbers of species but provide no information about which types of habitat sustained large numbers of species. A better understanding of such impacts may require approaches that focus on which types of habitats better explain the decline of species as a result of loss of diversity, as opposed to simply measuring the number of types of sub habitats.

The number of species were clearly influenced by interactions between different sub-habitats and responded to the juxtapositions of sub-habitats of different types. The addition of different sub-habitats also altered the number of species of constituent sub-assemblages in different sub-habitats. Thus, different numbers of species were found in units surrounded by units of different types. When units of A were surrounded by other A (in A habitats), they had fewer species than those in A units surrounded by B or C (in AB or AC habitats). Similarly, units of C surrounded by other C (in C habitats) had fewer species than those in C units surrounded by A or B (in AC, CA, ABC habitats).

The number of species in B units was not significantly altered by its surroundings. This may have been because B units are colonized by more species. Hence, when surrounded by sub-habitats with fewer species (i.e. A), there is no alteration of the number of species when compared with B units surrounded by B units in monotypic habitats. These results are consistent with previous studies that have shown that not all types of sub-habitats were modified by surrounding sub-habitats (Matias *et al.* 2007). This is further evidence that the arrangement of sub-habitats in a landscape of different types of sub-habitats may generate variability among assemblages because of differential influence of the surrounding sub-habitats.

The magnitude of interactions between sub-habitats may be related to how different the sub-habitats are in terms of the resources they provide (Wiens & Milne 1989). The magnitude of these differences may be more important in explaining the responses of assemblages to different properties of habitat structure than are the density or diversity of sub-habitats themselves. For example, similar sub-habitats will probably provide similar resources and be colonized by similar species. Interactions between these sub-habitats would then only add few new species to the overall assemblage. If, on the other hand, differences between sub-habitats are greater in terms of the resources they provide, many species will probably occur in some particular sub-habitats. Mixtures that include such sub-habitats will then house more diverse assemblages. These interactions could potentially be explained by source-sink dynamics between assemblages colonizing different sub-habitats within each

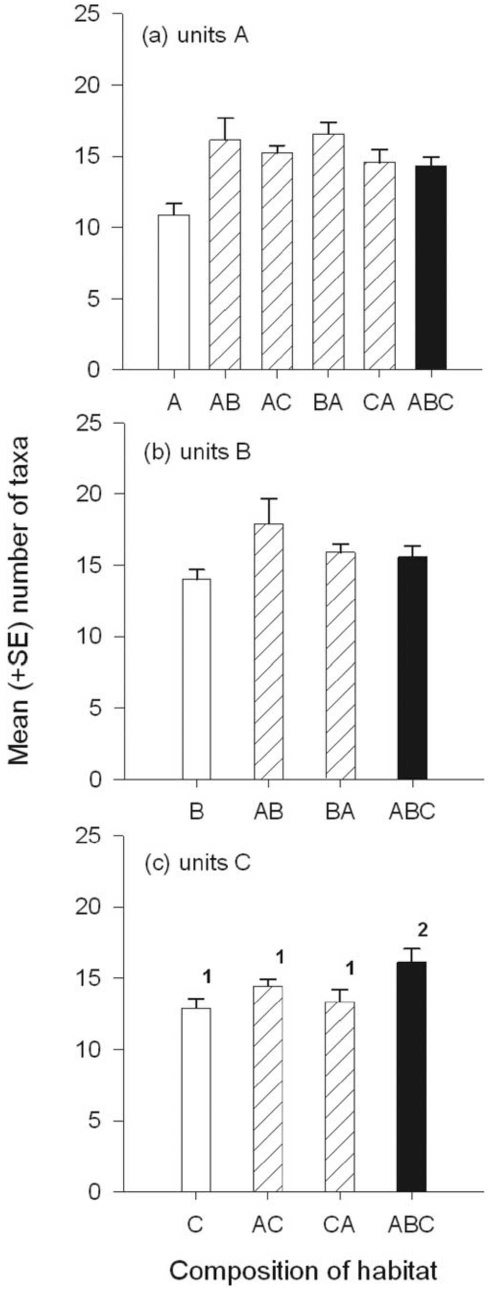

Fig. 2. Mean (+ SE; $n = 3$) number of species of assemblages in (a) units A (b) units B (c) units C; clear bars are monotypic (A, B or C); hatched bars are habitats of two types of units (AB, AC, BA or CA); black are AHs with three types (ABC). In (c), ABC was larger than C, AC and CA which did not differ (SNK test, $P < 0.05$, different numbers denote significant differences among means); in (a) and (b) SNK tests showed no difference.

habitat (*sensu* Holyoak *et al.* 2005). As suggested by our results, sub-habitats colonized by greater number of species (i.e. Type B) may be acting as 'sources' of individuals and species for assemblages colonizing other sub-habitats that would otherwise have lower number of species, therefore increasing the mean number of species. This explanation warrants further investigation but also highlights the usefulness of these artificial landscapes to understand the mechanisms that might explain the diversity and abundance of these assemblages.

Most gastropods colonizing patches of coralline turf are thought to disperse by crawling, passive advection or rafting on the surface of the water (Beesley *et al.* 1998). Previous studies on the colonization of these habitats have shown that most species quickly colonize patches of the turf habitat irrespective of the mode of dispersal, although the most likely mode of colonization is through settlement from the water column after advection (Kelaher 2005). It is likely that some of these gastropods move large distance across the shore before settling in a favourable habitat. It has been shown that gastropods have preference for particular types of habitat to which they move actively by crawling (Olabarria *et al.* 2002, choice experiments paper). This suggests that the differences between assemblages colonizing different sub-habitats might occur post-settlement. Furthermore, it has been shown in other habitats that gastropods can float back into the water column in response to unfavourable conditions (e.g. overcrowding or depleted resources, Levinton 1979). These differential mechanisms of dispersal highlight the importance of considering different hierarchies of scale of habitats to understand the patterns of diversity of these assemblages, and have implications for our understanding of the scales at which these assemblages respond to changes in their habitats. Before settlement, experimental patches of habitat (150 × 150 mm) are part of a landscape made of many patches. The spatial extent of this landscape is determined by hydrodynamic mechanisms that affect the duration and direction of passive dispersal through the water column (Roberts 1997). After settlement, most gastropods change their mode of dispersal to crawling, which necessarily increases the grain of their habitat (or landscape *sensu* Kotliar & Wiens 1990). Further research should investigate how different modes of dispersal may affect the responses of these assemblages to changes in structure of habitats.

From these considerations, it is clear that understanding relationships between structure of habitat and diversity of organisms living in patches can benefit enormously by including concepts from landscape ecology to interpret influences of different sub-habitats around each habitat in any patch. The patterns of mosaics of patches and their effects on assemblages should be studied at the scales appropriate to the organisms and processes being investigated (Wiens & Milne 1989), but also using experimental designs that separate the influences of the number of types of sub-habitats from the consequences of the identities of sub-habitats making up habitats.

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The hypotheses tested in this study are unlikely to be tested at larger spatial scales because of difficulties of manipulating structure or tractability of other habitats. These difficulties offer a greater relevance to these controlled manipulative studies, which advances our understanding of relationships between species and their habitats across different ecological systems.

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