Journal of Animal Ecology 2007
76, 986–994

Interactions of components of habitats alter composition and variability of assemblages

MIGUEL G. MATIAS*†, A. J. UNDERWOOD† and ROSS A. COLEMAN†

**Marine Biology and Ecology Research Centre, School of Biological Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK; and †Centre for Research on Ecological Impacts of Coastal Cities, Marine Ecology Laboratories A11, University of Sydney, NSW 2006, Australia*

Summary

1. The nature and resources supplied by different components of habitats influence species, creating variability from place to place within a habitat.

2. Experiments were done to investigate the effects of altering components of habitats on the variability of assemblages of numerous species of intertidal gastropods.

3. Artificial habitats with three levels of structure, combining different types of turf (i.e. different densities and height of fronds) were sampled 8 weeks after deployment in the intertidal. They were rapidly colonized by up to 66 species of gastropods.

4. Independently of the types of turf combined to form different habitats, there were differences in assemblages where there was more than one type of component present. Multivariate dissimilarities among units making up each habitat were also greater where there were more than one type of unit, but there was no such difference in the variance of numbers of species per unit.

5. Altering the relative abundances of different types of components made little change to the assemblages, nor their multivariate variability among units of habitat and the variance in number of species per unit in each habitat.

6. Differences in assemblages due to the different structure of habitat are complex to interpret and simple characterizations of structure of habitat are inadequate. Comparing different habitats requires appropriate experimentation to ensure that variability within habitats is also investigated.

Key-words: artificial habitats, complexity, diversity; microgastropods, structure.

Journal of Animal Ecology (2007) **76**, 986–994
doi: 10.1111/j.1365-2656.2007.01277.x

Introduction

A fundamental goal of ecology is to quantify and understand the processes controlling the abundance and diversity of organisms in different habitats. Recent discussions around neutral models of biodiversity (e.g. Chase 2005), and ecosystem function (e.g. Petchey & Gaston 2006) have drawn attention to the fact that we do not yet understand the causal basis of patterns of distribution and diversity of animals on plants.

In many habitats, plants determine physical structure and influence the distributions and interactions of organisms (Southwood 1961; Lawton 1983; McCoy & Bell 1991). Research on the structure of habitats has been focused on physical dimensions of particular features of the habitat (e.g. leaf-length), often called structural components (McCoy & Bell 1991). The ecological meaning of structure of habitat is closely linked to the variety of structural components that make up the habitat.

Structurally complex habitats may provide more niches and diverse ways of exploiting resources and thus increase number of species (Bazzaz 1975; Lawton 1983). This has been called the 'habitat heterogeneity' model and is a well-established ecological theory (Simpson 1949; MacArthur & Wilson 1967). For example, MacArthur & MacArthur (1961) suggested that the physical structure of plants, i.e. how foliage is distributed vertically, may be more important for the diversity of birds than the actual composition of plant species. It has also been suggested (e.g. Attrill, Strong &

Correspondence: Ross A. Coleman, Centre for Research on Ecological Impacts of Coastal Cities, Marine Ecology Laboratories, A11, The University of Sydney, NSW 2006, Australia. Tel.: +61 29351 2039. Fax: +61 29351 6713. E-mail: ross.coleman@bio.usyd.edu.au

Rowden 2000) that the amount (e.g. surface area) of habitat increases with increasing complexity, but recent experimental evidence does not support this (M.G. Matias, A.J. Underwood & R.A. Coleman, unpublished data).

Effects of diversity of structural components (e.g. microhabitats) on the number of species colonizing habitats have been studied extensively (MacArthur & MacArthur 1961; Pianka 1966; Cody 1968; Murdoch, Peterson & Evans 1972; Abele 1974; Schoener 1974; Menge & Sutherland 1976; Connor & McCoy 1979; McGuinness & Underwood 1986; Jenkins, Walker-Smith & Hamer 2002; Healey & Hovel 2004). McGuinness & Underwood (1986) showed that the diversity of structural components did not always increase the diversity of organisms colonizing intertidal boulders.

McCoy & Bell (1991) provided a model of the two major components of habitat structure, in an attempt to clarify differences between the effects of different structural characteristics of habitat (Downes *et al.* 1998). The two major factors are complexity and heterogeneity, the influences of which depend on the scale at which they are measured (McCoy & Bell 1991). Complexity is measured as the total amount of some structural component in a habitat. Thus, patches of long grass would be more complex than those with short grass. Heterogeneity encompasses differences in structure attributable to differences in the relative abundance of different structural components (McCoy & Bell 1991; Downes *et al.* 1998). Thus, habitats differ in heterogeneity because they contain different relative amounts of various components. According to these definitions, some studies investigating ‘complexity’, in terms of species composition of plant assemblages (Dean & Connell 1987; Russo 1991), were actually studying the effects of heterogeneity, because they manipulated the relative abundances of different structural components (i.e. species of plants). There is the further complication that Downes *et al.* (1998), in clever experiments to unravel the two components of differences between habitats, stated that heterogeneity, as defined by McCoy & Bell (1991) referred to the addition of different types of structural elements. This was not the definition proposed by McCoy & Bell (1991).

These defined terms are, however, more useful when comparing among habitats where different components within each habitat are not considered. Thus, fauna in patches of seagrass can be compared with fauna in patches of subtidal algae (e.g. Stoner & Lewis 1985). Where complexity is measured as total surface area of plants per unit area of space, the two habitats may have the same complexity. They differ in heterogeneity because they are made from different types of plants (i.e. the relative abundances of seagrass and algae are completely different).

It is, however, often difficult and frequently impossible to manipulate these two components of structure independently to test hypotheses about their effects. Thus, creating habitats with different relative abundances of two elements, A and B, can manipulate heterogeneity, but the absolute abundances of each will also be altered in patches of habitat of the same size. As an example, Beck (2000) attempted to alter complexity of patches simulating pieces of rocky shore by adding pits of different diameters and depths. The pits are, however, different components of habitat, to which species of intertidal gastropods respond very differently (Underwood 2004). Thus, any alteration to surface area (complexity) was confounded with altered heterogeneity in Beck’s (2000) experiments because it also altered the relative abundances of different types of pits.

This suggests that altering components of habitat to test hypotheses about responses by assemblages of animals will be fraught with difficulties where insufficient is known about the resources needed by the animals and the resources supplied by different components of habitat.

So, rather than hypothesize about complexity vs. heterogeneity, it seemed better to manipulate components of habitat in monotypic and mixed patches, to investigate several models for causes of differences among assemblages of animals in different habitats.

Three general models can account for the differences among assemblages in habitats of different structure:

1. Differences are caused by the variability in numbers of components that make up a habitat, regardless of the type of component. This leads to the prediction (Hypothesis 1a) that assemblages in habitats of only one type of component will vary from those in habitats with two or three different types of component. Further, variation among subassemblages associated with different structural components in a habitat will alter according to how many types of components are in the habitat (Hypothesis 1b).

2. Differences are caused by the variability in relative abundances (i.e. heterogeneity) of structural components, regardless of their type(s). So (Hypothesis 2a) assemblages will vary among habitats of different mixtures of the same number of types of components. Additionally, variation in assemblages from one part of a habitat to another will differ with differences in relative abundances of components (Hypothesis 2b).

3. Differences in assemblages are caused by some combination or interaction of numbers of types of components and their relative abundances, so that the differences cannot be associated with differences due solely to one or other of these. From this, the combination of different components in different mixtures may lead to the subassemblages associated with each type of component being altered by other types of components that make up the whole habitat. Thus, assemblages in units of type A will differ from each other (Hypothesis 3a) and will be more variable (Hypothesis 3b) when they are surrounded by units of types B or C than when in homogeneous patches only of A. Similarly, assemblages should differ and variability among units of B or C should be changed when different components (A, C or A, B, respectively) are present in a patch of habitat.

These predictions were tested using assemblages of intertidal gastropods colonizing experimental patches of habitat constructed of different types of components in different mixtures. We used artificial habitats (AHs) rather than natural algal turf because of the intractability of the habitat manipulations required and, more importantly, to unconfound the biological properties of the algal turf from the physical properties of structure. Differences among habitat types were examined by multivariate analyses of differences among assemblages in different habitats. Variability in assemblages was examined by multivariate measures of dissimilarity among units within habitats and by examination of the variances of numbers of species in different habitats. Interactions among difference components of habitats were examined by analyses of units of a particular type of habitat when in habitats of different complexity of heterogeneity.

Materials and methods

STUDY SITE

Experiments were done in Chowder Bay, Sydney Harbour (NSW, Australia 33°50·83′S 151 °25·08′E), between May and June 2005. Assemblages associated with coralline habitats vary with slope (Akioka *et al.* 1999), height on the shore (Kelaher, Chapman & Underwood 2001) and show small-scale patchiness (Olabarria & Chapman 2001). Sites were chosen to have consistent areas of natural rocky shore available for the deployment of the experimental treatments among meadows of algal turf dominated by *Corallina officinalis* L. on gently sloping low-shore rock platforms or large boulders, with similar orientation and exposure to waves. The numbers and varieties of micro-gastropods (< 3 mm) colonizing experimental habitats were sampled. Gastropods were chosen because they are a diverse component of all the intertidal fauna; they are relatively easy to sort and count and they show consistent patterns under different ecological conditions (Underwood & Chapman 2006).

ARTIFICIAL HABITATS

From pilot studies, three types of artificial, plastic turf (Team Sports Pty Ltd, Sydney, NSW, Australia) were selected with different densities and length of fronds. 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. Each unit was glued to individual pieces of rubber and attached to wire mesh to maintain a contiguous structure.

FIELD AND LABORATORY WORK

At 0·45–0·55 m above mean low water (MLW), squared clearings (*c.* 500 × 500 mm) were made in natural coralline turf, to minimize the gap between the edge of the artificial turf and the surrounding coralline algae. AHs were attached to cleared areas by four masonry nails and rubber washers.

AHs were retrieved after 48–53 days; this period is sufficient for colonization by many organisms (Kelaher *et al.* 2001). Preliminary work showed that fauna and epiphytes 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^2 stainless steel corers (similar to an ice-cube tray), which isolated the units so that they could be sampled separately, but simultaneously. The grid of corers was carefully placed over the habitat and then pressed firmly down to enclose the nine units. Each corer was then emptied into a separate plastic bag, guaranteeing that the epiphytes and fauna 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.

EXPERIMENTAL DESIGN

Three types of habitats were designed: monotypic habitats (nine units of the same turf); habitats with two structural components (six units of one turf and three units of a different one); and habitats with three structural components (three units of each of the turf). To ensure independent tests for each hypothesis (Underwood 1997), but to avoid confounding differences among AHs with any differences due to units being on edges or corners of each AH, units of each type of turf were allocated equally to centres, edges and corners across the replicate habitats of the same type. Following these rules, three monotypic (i.e. 9A, 9B, 9C) and five non-monotypic (i.e. AB: 6A + 3C; BA: 6B + 3A; CA: 6C + 3A; ABC: 3A + 3B + 3C) were constructed (Table 1). 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; thus 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).

Multivariate data consisted of abundances of 66 species of gastropods found in the 71 AHs recovered. All multivariate analyses used Bray–Curtis measures of dissimilarity (Bray & Curtis 1957) using untransformed data. This summarizes all differences between

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

	Component of habitat	No. of types of component	No. of units 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

Table 2. Multivariate analyses (np-manova) of Bray–Curtis dissimilarities between assemblages in artificial habitats (AHs) of different number of types of components. There was no significant interaction ($P > 0{\cdot}30$ with 4, 27 d.f.). There were significant differences among AHs with different numbers of types ($P < 0{\cdot}01$ with 2, 31 d.f.), Sites were significant ($P < 0{\cdot}012$, 31 d.f.; $P < 0{\cdot}01$); there was no significant interaction ($P > 0{\cdot}30$). Diagonal data are mean Bray–Curtis dissimilarities within each number of types; other entries are between pairs of different numbers of types

No. of types	1	2	3
1	35	–	–
2	40*	40	–
3	43*	38	36

*$P < 0{\cdot}05$.

abundances of taxa between samples and was chosen because it has advantages over some alternatives (Clarke *et al.* 2006).

To test Hypotheses 1 and 3, assemblages (i.e. averaged over all units in each AH) were compared among treatments and between sites, using a two-factor np-manova (Anderson 2001); one factor (habitat) is the fixed of different types of AHs (see above); the other factor (site) is a random comparison with three levels.

To test Hypotheses 3a and 3b about variability among units in habitats of different numbers or mixtures of types of components, the mean Bray–Curtis dissimilarity was calculated over every pair of units of the same type of turf in each replicate AH of each type of habitat. These were then compared (by two-factor analyses of variance), using the values from each AH as replicates, in separate analyses for each type of turf. Habitats were fixed comparisons of units of Type A (six levels: A, AB, AC, BA, CA, ABC), Type B (four levels: B, AB, BA, ABC) and Type C (four levels: C, AC, CA, ABC). For each analysis, the second factor, Sites, was random with three levels.

Similar analyses were done using randomly selected AHs made up of one, two or three types of components, regardless of the mixtures of components in each. Significant means were separated by SNK tests, the sequential nature of these tests means the experiment-wise error rate is reduced (Underwood 1997; Zar 1999).

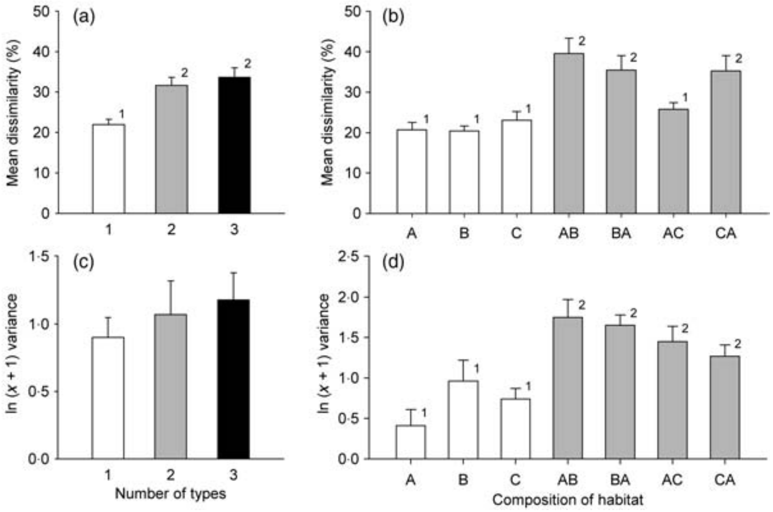

Fig. 1. Variation in assemblages in different habitats. (a) Mean (+SE) Bray–Curtis dissimilarity among units in four replicate artificial habitats (AHs) from each of three sites (i.e. $n = 12$); Number of Types 1 is AHs of Types A, B and C; 2 is AB, AC, BA, CA; 3 is ABC; (b) mean (+SE) of ln(variance + 1) of number of species per unit among units in AHs as in (a); (c) mean (+SE) Bray–Curtis dissimilarity among units in AHs of different compositions, using three replicate AHs of each composition from each of three sites (i.e. $n = 9$); (d) mean (+SE) of ln(variance + 1) of number of species per unit among units of different composition as in (a). White are monotypic; grey are habitats of two types of units; black have three types, numbers over bars are represent results of SNK tests such that where the numbers are the same, there were no significant differences between treatment means.

Results

MODEL 1: DIFFERENCES AMONG ASSEMBLAGES ARE ASSOCIATED WITH DIFFERENT NUMBERS OF TYPES OF COMPONENTS OF HABITAT

The assemblages colonizing AHs with different numbers of components were significantly different (Table 2), providing support for Hypothesis 1a. Assemblages where there was only one component (A or B or C) differed from those with two (AB, BA, AC, CA), but these were not different from assemblages in AHs with three components (ABC).

Mean Bray–Curtis dissimilarity was greater among units with two different components (Fig. 1a, Table 3a), supporting Hypothesis 1b. Habitats with three components were, however, no more variable than those with two. Increased multivariate dissimilarity from one to two or three components was consistent among the three sites (note the lack of statistical interaction in Table 2).

Variances of numbers of species among units in the AHs showed no evidence for (and no significant) differences in habitats of different heterogeneity (Fig. 1b, Table 2b), although the trend was for greater variance where two components of habitat were present.

Table 3. Analyses of (a) mean Bray–Curtis dissimilarity among units in randomly chosen habitats with different numbers of types of components. 'Number of types' is a fixed comparison of artificial habitats (AHs) with one (A, B or C), two (AB, BA, AC, CA) or three (ABC) types of turf. $n = 4$ replicate AHs were chosen at random from those available for each number in each site; (b) mean variance of numbers of species among units in AHs of each number of types, with variances transformed to $\ln(x + 1)$. Mean values are in Fig. 1a,b

		(a)			(b)		
Source	d.f.	MS	*F*	*P*	MS	*F*	*P*
Number of types C	2	470·9	10·9	< 0·001	0·24	0·6	> 0·30
Sites S	2	50·3	1·2	> 0·300	0·50	1·0	> 0·50
C × S	4	–			–		
Residual	27	40·8			0·48		
Pooled C × S + residual*	31	43·6			0·47		
No. of types:	1	2	3		3		
Mean (+SE)	22 (1·3)	< 32 (2·0)	34 (2·3)				

*Pooled because C × S was not significant at $P > 0{\cdot}25$.

MODEL 2: DIFFERENCES ARE ASSOCIATED WITH DIFFERENT MIXTURES OF THE SAME NUMBER OF COMPONENTS OF HABITAT

Assemblages in different types of habitat (A, B, C, AB, AC, BA, CA) showed confusing patterns because the overall analysis indicated that differences among habitats were not the same from one site to another (see Fig. 2; NP-MANOVA, habitat × site interaction, 14, 47 d.f., $P < 0{\cdot}001$). Comparisons of the habitats separately for each site demonstrated no pair-wise differences (all comparisons, $P > 0{\cdot}05$ in each site). Although there are some apparent differences (e.g. habitats C vs. AC) none was significant. Thus, there were no patterns relating to different relative abundances of types of components (i.e. different heterogeneities), and thus no support for Hypothesis 2a. A more specific analysis (not presented here) compared the four habitats with two types of components, but in different relative abundances (i.e. AB, AC, BA, CA), but, again, there were no pair-wise differences in any site.

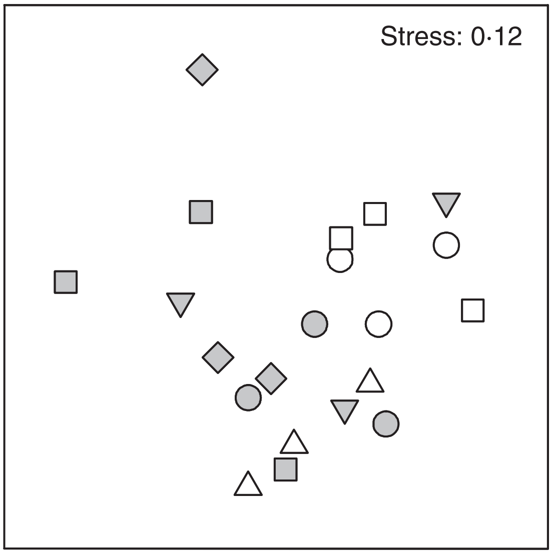

Fig. 2. nMDS ordination of centroids of assemblages in habitats of different composition, using $n = 3$ artificial habitats of each type from each of three sites. White symbols are monotypic: A (○), B (△), C (□); grey symbols are habitats with two types of unit: AB (●), BA (■), AC (▽), CA (◇).

AHs from the different types of habitat differed in their Bray–Curtis dissimilarities among component units (Table 4a) and differences were similar in each site. There was a clear-cut difference in that habitats A, B, C and AC all had smaller dissimilarity among the assemblages in the units making up each AH than was the case for habitats AB, BA and CA (Fig. 1c; SNK tests, $P < 0{\cdot}05$). Thus, the major influence was the difference due to different numbers of types of components described previously (i.e. one type, A, B, C vs. two types AB, BA, CA). AC showed the only evidence for an effect of different mixtures of components; AC differed from the other habitats with two types of components.

The variances in numbers of species from unit to unit in the AHs also varied among different habitats. The differences were similar in the three sites (Table 4b). The data were consistent with the model that numbers of types of components, not their relative abundances, influenced the variance in numbers of species. The only significant pattern found in SNK multiple comparisons (at $P = 0{\cdot}05$) was that all habitats of one type of unit (A, B, C) had smaller variances than habitats with two types (AB, BA, AC, CA; see Fig. 1d). There were no differences attributable to different mixtures of two types.

MODEL 3: DIFFERENCES AMONG ASSEMBLAGES ARE INFLUENCED BY INTERACTIONS AMONG DIFFERENT COMPONENTS OF HABITAT

If components of habitat interact (i.e. assemblages developing in units of a particular type are influenced by the 'landscape' of surrounding units in a habitat), assemblages in a particular type of unit should differ among habitats of different composition. There were differences in mean Bray–Curtis dissimilarities among

Table 4. Analyses of (a) mean Bray–Curtis dissimilarities among units in randomly chosen habitats of different composition. Habitat (H) is a fixed factor comparing seven habitats (A, B, C, AB, AC, BA, CA) in each of three sites (S) (a random factor). $n = 3$ replicate artificial habitats were chosen at random from those available in each site (more were not available for a balanced analysis); units were used as in Table 1; (b) mean variance of numbers of species among units in AHs of each structure as in (a), with variances transformed to $\ln(x + 1)$. Mean values are in Fig. 1c,d

		(a)			(b)		
Source	d.f.	MS	*F*	*P*	MS	*F*	*P*
H	6	512·0	11·3	< 0·0001	2·2	4·4	< 0·01
S	2	108·8	2·4	> 0·1000		1·7	> 0·15
H × S	12				0·4	2·0	> 0·05
Residual	42	44·1			0·5		
Pooled H × S + residual*	54	45·2			0·3		

*Pooled because H × S was not significant at $P > 0{\cdot}25$.

Table 5. Analyses of mean Bray–Curtis dissimilarities among units of the same type in randomly chosen artificial habitats (AHs) of different compositions. Bray–Curtis dissimilarities were calculated for all pairings of three units of a given type, for each of $n = 3$ AHs in each of three sites. (a) Units of Type A in six habitats: A, AB, AC, BA, CA, ABC; (b) units of Type B in four habitats: B, AB, BA, ABC; (c) units of Type C in four habitats: C, AC, CA, ABC. In each analysis, habitats (H) is fixed; sites (S) is random

	(a)				(b)				(c)			
Source	d.f.	MS	*F*	*P*	d.f.	MS	*F*	*P*	d.f.	MS	*F*	*P*
H	5	316	7·4	< 0·001	3	777	6·0	< 0·05	3	290	4·0	< 0·02
S	2	164	3·8		2	204	3·6	< 0·05	2	28	0·4	> 0·65
H × S	10				6	129	2·3	> 0·05	6			
Residual	35	47			24	57			23	86		
Pooled H × S + residual*	45				30	–			29	73		

units of Type A according to whether they were in A, AB, BA, AC, CA or ABC habitats (Table 5a). The habitats were in two groups; A, ABC, AB and BA were similar and all had smaller dissimilarities among units than was found for AC and CA, which did not differ (SNK tests at $P = 0{\cdot}05$ of the means shown in Fig. 3a).

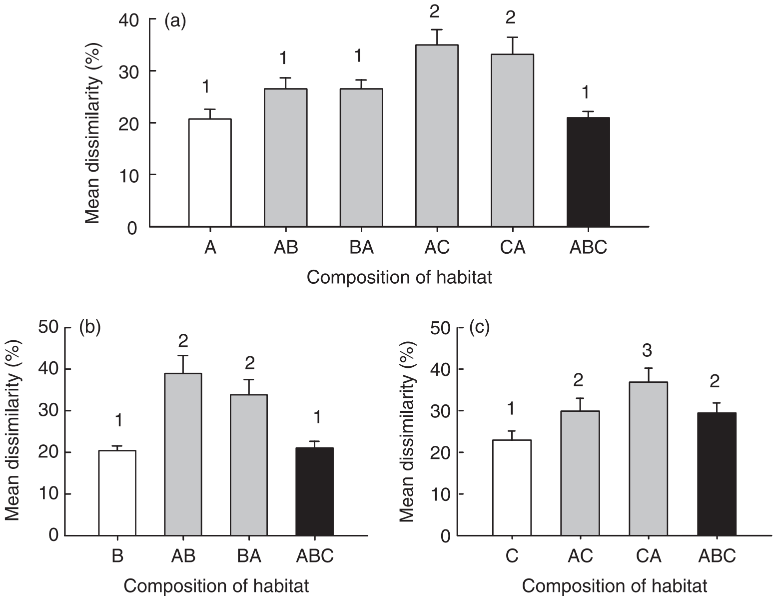

Fig. 3. Mean (+SE) Bray–Curtis dissimilarity among units of the same type from $n = 3$ replicate artificial habitats from each of three sites; (a) units of Type A (short, sparse); (b) Type B (long, sparse); (c) Type C (short, dense).

For units of Type B, there were, again, significant differences (Table 5b). Dissimilarities in AHs of B and ABC were smaller than those in BA and AB (SNK tests of the means shown in Fig. 3b).

Finally, units of Type C also differed (Table 4c); habitat C had smaller dissimilarity than ABC and AC (which did not differ), which were smaller than CA (SNK tests of the means shown in Fig. 3c).

Assemblages in units of Type A differed when these were on their own (A habitat) from those where units of Type A were in combinations (AB, BA, AC, CA, ABC habitats; NP-MANOVA, $P < 0{\cdot}01$ for all comparisons; see Fig. 4a). None of these combinations differed. These results support Hypothesis 3a. Units of type C showed exactly the same pattern (assemblages in C differed from all combinations; Fig. 4c)

Assemblages in units of Type B in habitats B and ABC were similar, but differed (NP-MANOVA, $P < 0{\cdot}01$) from those in habitats AB and BA. The latter two did not differ significantly (Fig. 4b). Again, results support Hypothesis 3a.

Discussion

There were two consistent, striking influences of diversity of structure of habitats. First, the number of different types of components making up a habitat altered the assemblages and their variability among replicates. Where two different types of subhabitat were

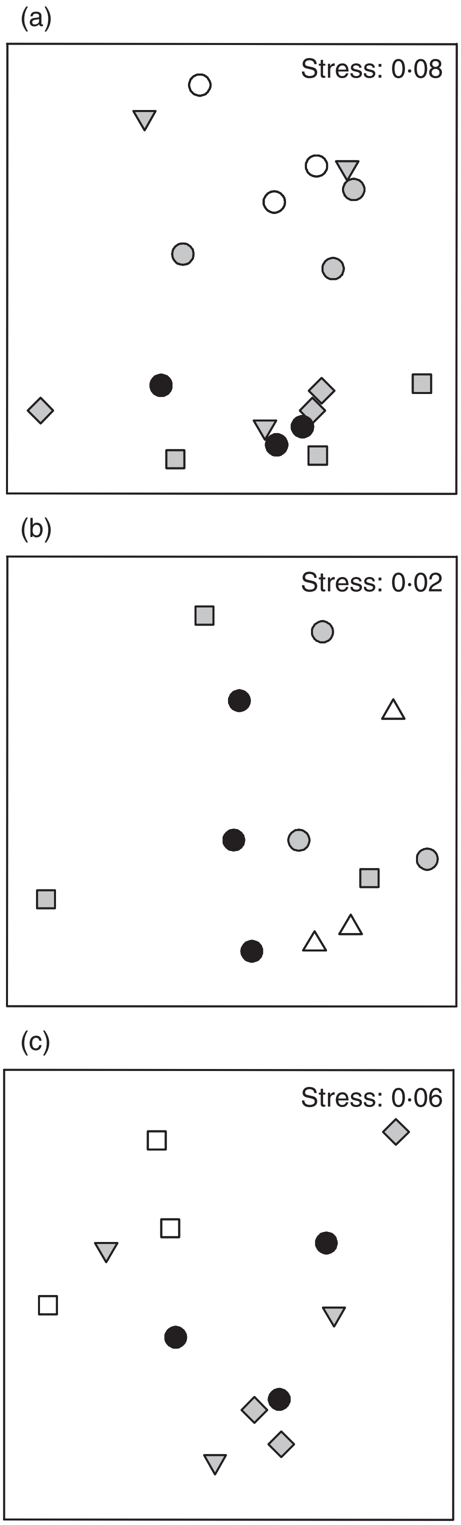

Fig. 4. nMDS ordination of centroids of assemblages in three units of a particular type in $n = 3$ replicate artificial habitats of each type from each of three sites: (a) Type A; (b) Type B; (c) Type C.

present, assemblages were different from those where there was one type. Multivariate dissimilarities among assemblages averaged for each habitat were greater where there were two types of component. In neither case was there any difference between assemblages where there were three, as opposed to two, types of component in a habitat.

Second, the addition of different components also altered the constituent subassemblages in different components of habitat. Thus, quite different assemblages developed in units of A-type habitat (short, sparse turf) from those in B (long, sparse) and C (short, dense). When units of A were surrounded by other A (in A habitats) they developed different assemblages of gastropods from those in A units surrounded by other types of units (e.g. AB, AC habitats). There were interactions due to the arrangement in a landscape of different types of components.

From these findings, issues arise that are related to quite distinct approaches to current ecological research into habitats. Obviously, there are issues about the structure of nonhomogeneous habitats. The insightful review by McCoy & Bell (1991) tried to identify a logical structure to analyses of habitat. By generating understanding and better definition of components of habitat, they hoped to reduce the confusion that occurs wherever different studies of the same habitat or studies of different habitats were compared. The subsequent literature has, however, not been particularly better structured (e.g. Beck 2000) because of persistent confusion over the definitions of terms and how they can be measured.

This study is no exception, in that altering the number of types of components in a habitat simulates a replacement series, as used in designs of experiments about interspecific competition (e.g. De Benedictus 1974; Trenbath 1974). It has long been recognized that such designs are confounded (reviewed by Underwood 1986, 1992). For example, comparing experimental treatments that contain 10 individuals of species A with treatments that have 5A + 5B (e.g. Gill & Hairston 1972; Haven 1973; Bertness 1981) prevents inferences about interspecific effects of B on A. Any differences are confounded with the simultaneous difference in density of A and any potential intraspecific competition of A on A. Yet, in constructed habitats of the sort used here, adding B to A to make AB and BA habitats also reduces the total amount of A in fixed-size patches of habitat.

Why this may matter is easily illustrated by the simple case of adding to units of type X, some units of type Y, which happens not to provide resources for some species. Patches of 6X and 3Y or 3X and 6Y have fewer X than in a patch of 9X. So, the combinations provide less resource for species using X. If they cannot use Y, they will be less abundant in the habitat as a whole.

Because of widespread species–area relationships (Arrhenius 1921; Coleman 1981; McCoy & Bell 1991), there will be a small probability of species finding units of X because there are fewer in mixtures. So, as with studies of competition, experiments on differently structured habitats need to be designed to hold constant the amounts of one type of unit in the absence or presence of other types.

Other considerations, however, such as species–area relationships require that patches of habitat of different composition should be of the same size (as created here). Really, two different designs (additive and replacement to use the phraseology of studies of competition; reviewed by Underwood 1986, 1992) are needed for a better analysis.

There are also issues about relationships between habitats made up of different components and concepts of landscape ecology. Assemblages in units of a particular type in a habitat made up of several types were affected by the nature of the surrounding units. In landscape terms, the units surrounding a unit of, say, Type A, are the matrix (Fahrig & Merriam 1985). The present results therefore identify that the influences of a complex, nonmonotypic patch of habitat will only be interpretable when the landscape of the habitat is investigated (see Fahrig & Merriam 1985). Thus, a patch of ABC habitat consists of units of A, B and C and their interactions. Results from our experiment indicate further investigation involving analysis of the landscape issues – the connectivity and interactions of the different components.

Finally, there are issues for interpretation that link strongly to some of the current discussion about identity as opposed to number of species in investigations of biodiversity and its relationships to ecosystem function, or BEF, (Naeem *et al.* 1995; Tilman 1997). As pointed out by Huston (1997) among others, several experiments were difficult to interpret because assemblages with more species always have a greater chance of including functionally important species (see also Aarssen 1997). Consequently, this sampling artefact (Huston 1997) would create a difference in measures of function for assemblages with more species, but not *because* they contain more species.

The same issue may well be true for analyses using experimental habitats containing different numbers of types of unit. For example, suppose that units of type C are particularly good habitat for a broad variety of species, but A and B are good habitat for very few species. Any comparison of habitats A, B, C vs. AB, BA, AC, CA vs. ABC would be likely to show increasing numbers of species with increasing complexity, simply because C habitats are present in 1/3 of the monotypic habitats, 1/2 of the habitats with two components, and all of the most complex habitats. Experimental designs to separate the effects of identities and numbers of species have recently been proposed (Benedetti-Cecchi 2004, 2006).

This did not seem to be a confounding issue in interpretation of the present results because there were no patterns indicating major differences between units of Types A, B or C that could have caused problems for interpreting their combinations. Nevertheless, caution is needed in how to interpret experiments where such issues have not been resolved.

From these considerations, it is clear that the influence of complex as opposed to simple habitats is going to require more care in future experimental studies. Furthermore, comparisons of assemblages across different habitats will probably benefit from much better understanding of the variability in numbers and types of species from one component (or subhabitat) to another within each habitat.

Acknowledgements

This work was supported by funds from the Australian Research Council through the Special Research Centres Programme to A.J.U. and R.A.C. We thank Giordana Cocco, Mark Breckels and Tom Espinoza for assistance in the field; Basil Panayotakos gave valuable advice in the design of the AHs and sample collector. Kevin McCann and two anonymous referees are thanked for their helpful and insightful comments.

References

Aarssen, L.W. (1997) On the progress of ecology. *Oikos*, **80**, 177–178.

Abele, L.G. (1974) Species-diversity of decapod crustaceans in marine habitats. *Ecology*, **55**, 156–161.

Akioka, H., Baba, M., Masaki, T. & Johansen, H.W. (1999) Rocky shore turfs dominated by corallina (Corallinales, Rhodophyta) in northern Japan. *Phycology Research*, **47**, 199–206.

Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**, 32–46.

Arrhenius, O. (1921) Species and area. *Journal of Ecology*, **9**, 95–99.

Attrill, M.J., Strong, J.A. & Rowden, A.A. (2000) Are macroinvertebrate communities influenced by seagrass structural complexity? *Ecography*, **23**, 114–121.

Bazzaz, F.A. (1975) Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology*, **56**, 485–488.

Beck, M.W. (2000) Separating the elements of habitat structure: independent effects of habitat complexity and structural components on rocky intertidal gastropods. *Journal of Experimental Marine Biology and Ecology*, **249**, 29–49.

Benedetti-Cecchi, L. (2004) Increasing accuracy of causal inference in experimental analyses of biodiversity. *Functional Ecology*, **18**, 761–768.

Benedetti-Cecchi, L. (2006) Understanding the consequences of changing biodiversity on rocky shores: how much have we learned from past experiments? *Journal of Experimental Marine Biology and Ecology*, **338**, 193–204.

Bertness, M.D. (1981) Competitive dynamics of a tropical hermit crab assemblage. *Ecology*, **62**, 751–761.

Bray, J.R. & Curtis, J.T. (1957) An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs*, **27**, 326–349.

Chase, J.M. (2005) Towards a really unified theory for metacommunities. *Functional Ecology*, **19**, 182–186.

Clarke, K.R., Chapman, M.G., Somerfield, P.J. & Needham, H.R. (2006) Dispersion-based weighting of species counts in assemblage analyses. *Marine Ecology-Progress Series*, **320**, 11–27.

Cody, M.L. (1968) On methods of resource division in grassland bird communities. *American Naturalist*, **102**, 107–147.

Coleman, B.D. (1981) On random placement and species–area relations. *Mathematical Biosciences*, **54**, 191–215.

Connor, E.F. & McCoy, E.D. (1979) Statistics and biology of the species–area relationship. *American Naturalist*, **113**, 791–833.

De Benedictus, P.A. (1974) Interspecific competition between tadpoles of *Rana pipiens* and *Rana sylvatica*: experimental field study. *Ecological Monographs*, **44**, 129–151.

Dean, R.L. & Connell, J.H. (1987) Marine invertebrates in an algal succession. III. Mechanisms linking habitat complexity with diversity. *Journal of Experimental Marine Biology and Ecology*, **109**, 249–273.

Downes, B.J., Lake, P.S., Schreiber, E.S.G. & Glaister, A. (1998) Habitat structure and regulation of local species diversity in a stony, upland stream. *Ecological Monographs*, **68**, 237–257.

Fahrig, L. & Merriam, G. (1985) Habitat patch connectivity and population survival. *Ecology*, **66**, 1762–1768.

Gill, D.E. & Hairston, N.G. (1972) Dynamics of a natural population of *Paramecium* and role of interspecific competition in community structure. *Journal of Animal Ecology*, **41**, 137–151.

Haven, S.B. (1973) Competition for food between intertidal gastropods *Acmaea scabra* and *Acmaea digitalis*. *Ecology*, **54**, 143–151.

Healey, D. & Hovel, K.A. (2004) Seagrass bed patchiness: effects on epifaunal communities in San Diego Bay, USA. *Journal of Experimental Marine Biology and Ecology*, **313**, 155–174.

Huston, M.A. (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, **110**, 449–460.

Jenkins, G.P., Walker-Smith, G.K. & Hamer, P.A. (2002) Elements of habitat complexity that influence harpacticoid copepods associated with seagrass beds in a temperate bay. *Oecologia*, **131**, 598–605.

Kelaher, B.P., Chapman, M.G. & Underwood, A.J. (2001) Spatial patterns of diverse macrofaunal assemblages in coralline turf and their association with environmental variables. *Journal of the Marine Biological Association of the United Kingdom*, **382**, 1–14.

Lawton, J.H. (1983) Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology*, **28**, 23–39.

MacArthur, R.H. & MacArthur, J.W. (1961) On bird species diversity. *Ecology*, **42**, 594–598.

MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.

McCoy, E.D. & Bell, S.S. (1991) Habitat structure: the evolution and diversification of a complex topic. *Habitat Structure: the Physical Arrangement of Objects in Space* (eds E.D. McCoy, S.S. Bell & H.R. Mushinsky), pp. 3–27. Chapman & Hall, London.

McGuinness, K.A. & Underwood, A.J. (1986) Habitat structure and the nature of communities on intertidal boulders. *Journal of Experimental Marine Biology and Ecology*, **104**, 97–123.

Menge, B.A. & Sutherland, J.P. (1976) Species-diversity gradients: synthesis of roles of predation, competition, and temporal heterogeneity. *American Naturalist*, **110**, 351–369.

Murdoch, W.W., Peterson, C.H. & Evans, F.C. (1972) Diversity and pattern in plants and insects. *Ecology*, **53**, 819–829.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1995) Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, **347**, 249–262.

Olabarria, C. & Chapman, M.G. (2001) Comparison of patterns of spatial variation of microgastropods between two contrasting intertidal habitats. *Marine Ecology Progress Series*, **220**, 201–211.

Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters*, **9**, 741–758.

Pianka, E.R. (1966) Convexity, desert lizards and spatial heterogeneity. *Ecology*, **47**, 1055–1059.

Russo, A.R. (1991) Do predatory fishes affect the structure of an epiphytal amphipod assemblage on a protected algal reef in Hawaii? *Hydrobiologia*, **224**, 185–192.

Schoener, T.W. (1974) Resource partitioning in ecological communities. *Science*, **185**, 27–39.

Simpson, E.H. (1949) Measurement of diversity. *Nature*, **163**, 688.

Southwood, T.R.E. (1961) The number of species of insect associated with various trees. *Journal of Animal Ecology*, **30**, 1–8.

Stoner, A.W. & Lewis, F.G. (1985) The influence of quantitative and qualitative aspects of habitat complexity in tropical seagrass meadows. *Journal of Experimental Marine Biology and Ecology*, **94**, 19–40.

Tilman, D. (1997) Distinguishing between the effects of species diversity and species composition. *Oikos*, **80**, 185–185.

Trenbath, B.R. (1974) Biomass productivity of mixtures. *Advances in Agronomy*, **26**, 177–210.

Underwood, A.J. (1986) The analysis of competition by field experiments. *Community Ecology: Pattern and Process* (eds J. Kikkawa & D.J. Andersom), pp. 240–268. Blackwell Scientific Press, Oxford.

Underwood, A.J. (1992) Competition in marine plant–animal interactions. *Plant–Animal Interactions in the Marine Benthos* (eds D.M. John, S.J. Hawkins & J.H. Price), pp. 443–475. Clarendon Press, Oxford.

Underwood, A.J. (1997) *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge University Press, Cambridge.

Underwood, A.J. (2004) Landing on one's foot: small-scale topographic features of habitat and the dispersion of juvenile intertidal gastropods. *Marine Ecology-Progress Series*, **268**, 173–182.

Underwood, A.J. & Chapman, M.G. (2006) Early development of subtidal macrofaunal assemblages: relationships to period and timing of colonization. *Journal of Experimental Marine Biology and Ecology*, **330**, 221–233.

Zar, J.H. (1999) *Biostatistical Analysis*, 4th edn. Prentice Hall, Princeton, NJ.

Received 19 December 2006; accepted 25 May 2007
Handling Editor: Guy Woodward