Habitat identity influences species–area relationships in heterogeneous habitats

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ABSTRACT: Loss of habitat is commonly identified as a reduction in area (or patch size) and its effects are often investigated using species–area relationships to evaluate loss of biodiversity. In many habitats, however, area alone is not sufficient to explain the decline of populations because natural habitats are rarely homogeneous. In fact, reductions in the diversity of habitats (e.g. destruction of microhabitats) might have even greater effects on the diversity of assemblages. Although these are 2 well-known attributes of habitats (i.e. area and diversity), there have been few empirical studies that have attempted to separate their effects by experimental manipulation. Experiments were carried out to separate the effects of number, relative proportion and identity of patches of habitat using additive designs. Predictions were tested using assemblages of marine molluscs colonizing artificial mimics of macroalgal habitats on rocky intertidal platforms. Our experiments to disentangle different attributes of habitat heterogeneity showed that these are complex and highly interactive. In particular, not all heterogeneous habitats had the numbers of species expected from a simple species–area relationship. Instead, the presence of more species in heterogeneous habitats could, to a great extent, be explained by the presence or absence of particular types of sub-habitats and not just by patch size. The complexity we found in responses of assemblages to composition of heterogeneous habitats was not predicted and could not have been observed without appropriate manipulations of habitat composition. A mechanistic understanding of the associations between species and particular types of habitats is essential for better predictions of species' responses to loss of natural habitats.

KEY WORDS: Additive design · Heterogeneity · Habitat structure · Mollusc · Species–area relationship

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INTRODUCTION

Natural and anthropogenic loss of habitat occurs when habitats are destroyed and organisms are subsequently displaced, resulting in declines in diversity of assemblages and abundance of populations (e.g. Bender et al. 1998, Hanski 2005). These modifications to natural habitats have negative effects on a range of organisms including birds and mammals (e.g. Andren 1994), reptiles (e.g. Gibbon et al. 2000), amphibians (e.g. Stuart et al. 2004), fish (e.g. Johnson & Heck 2006) and plants (e.g. Hobbs & Yates 2003). Although natural loss of habitat is mostly associated with unpredictable catastrophic events (e.g. landslides, storms, floods), the loss and degradation of natural habitats as a result of human activities has been linked to the growth of the human population and expansion of human activities (Sisk et al. 1994),

such as changes in landuse, introduction of alien species, over-exploitation of natural resources and pollution (reviewed by Sala et al. 2000).

Loss of habitat is commonly identified as a reduction in area (or patch size) or number of patches of habitat (Fahrig 2001) and its effects are often investigated using species–area relationships to evaluate loss of biodiversity (e.g. Ney-Nifle & Mangel 2000). In many habitats, however, area alone is not sufficient to explain the decline of populations (see review by Fahrig 2001) because natural habitats are rarely homogeneous — they are variable across a hierarchy of scales (Allen & Starr 1982). Their structural variability can be an important modifier of the environment and availability of resources, which, in turn, affect the spatial distribution of many species (e.g. Therriault & Kolasa 2000, Johnson et al. 2003, Lassau & Hochuli 2004, Tews et al. 2004). Thus, the reduction of the diversity of habitats (e.g. destruction of microhabitats; Hanski 2005) is likely to have negative impacts on the diversity of assemblages (e.g. Mckinney 1998), such as decreases in the diversity of fish assemblages as a result of region-wide reductions of rugosity on coral reefs (Alvarez-Filip et al. 2009).

Man-made coastal structures, such as seawalls or piers, remove the variety of habitats and microhabitats provided by rocky platforms, replacing them with homogeneous and regular structures. Such changes cause major shifts in local assemblages (Chapman & Bulleri 2003). Similarly, in terrestrial habitats, intensive farming often results in homogenization of landscapes, causing dramatic losses of local and regional diversity (Holzschuh et al. 2007). Finally, replacement of local biota by non-indigenous species has also been shown to result in homogenization of the local biota (Mckinney 1998), which can reduce the diversity of niches available to organisms living in these habitats. These examples, covering several types of habitats and ecological processes, emphasize the need for a collective understanding of the roles of area and composition of habitats in creating and maintaining the diversity of associated assemblages to be able to predict species' responses to loss or modification of their natural habitats.

Most studies on the composition of habitats have focused on number of types (i.e. structural diversity) and relative proportion of patches within landscapes (e.g. Li & Reynolds 1993). Any measure of habitat diversity that is based on the numbers of different of habitats (e.g. Tews et al. 2004) is intrinsically confounded with the relative proportion and identity of patches present in a habitat (Matias et al. 2007); habitats might differ in the diversity of patches present

and in their sizes (amounts, densities). This sort of problem is analogous to the ongoing discussion about identity, as opposed to number, of species in investigations of biodiversity and its relationships to ecosystem function (biodiversity and ecosystem functioning [BEF]; e.g. Huston 1997, Benedetti-Cecchi 2004, Bruno et al. 2005). In BEF studies, adding species is generally considered to add positive effects to an assemblage (the so-called 'complementary effect'). Increasing the number of species can add some species with complementary traits to those in the existing assemblage. Alternatively, any positive effects of increased number of species may be due to the addition of particular species that have complementary traits, rather than being a consequence of adding more species per se (Huston 1997). Treatments with greater diversity in BEF experiments often include species with the greatest contributions for the variables analysed in the experiment. For example, there can be increased productivity in assemblages of plants if the added species are particularly weighty, simply as the result of greater plant biomass, rather than greater species diversity (i.e. the 'selection probability effect'; Huston 1997). Such 'identity effects' are an important issue when a particular species has disproportionate effects on the variables measured (Crawley et al. 1999, Bruno et al. 2005). Generally, it is thought that both mechanisms operate simultaneously (e.g. Leps et al. 2001). Here, we consider that these mechanisms are analogous to those controlling the diversity of organisms colonizing heterogeneous habitats, namely the importance of the identity of particular habitats (or 'keystone structures'; sensu Tews et al. 2004), as opposed to the diversity of habitats per se. We use the term 'identity' of habitats as an analogy to the use of the term 'identity' of species in BEF experiments to refer to disproportionate effects on responses as a result of species-specific traits of individual species (sensu Benedetti-Cecchi 2004). Thus, we considered habitat identity as the contribution of different types of habitats (i.e. different structural complexity) to explain the variability in numbers of species of macroinvertebrates in heterogeneous habitats.

The first aim of this study was to understand the importance of diversity and identity of habitats in explaining the diversity of assemblages in relation to the species–area relationship. Early explanations of species–area relationships (i.e. MacArthur & Wilson 1963, 1967) completely disregarded the diversity of habitats. Thus, greater numbers of species in larger and heterogeneous habitats could be expected solely as a result the increase in area (i.e. passive sampling

hypothesis; Simberloff 1976, Connor & McCoy 1979, Matias et al. 2010b). Habitat diversity — the number of different types of habitats in an area — has often been proposed as an alternative explanation for a species–area relationship (e.g. Ricklefs & Lovette 1999, Triantis et al. 2008) because changes in the area of habitats are often correlated with changes in the composition of habitats (Tews et al. 2004). In the present study, we assessed the numbers of species in heterogeneous habitats by measuring the ratio of the numbers of species in heterogeneous habitats to the numbers in monotypic habitats of similar size, thus measuring the divergence from the expected species–area relationship as a result of increased habitat diversity. A positive divergence from the null expectation indicates more species in heterogeneous habitats than would be expected from a simple increase in area of a monotypic habitat. Alternatively, a negative departure indicates that there were fewer species than expected from monotypic habitats of the same area. Any departure from this expectation can therefore be interpreted as the effect of 'addition' or 'modification' of the habitat because of increased heterogeneity. Hence, the effect of habitat diversity can be investigated independently of the area of the habitat.

The second aim of this study was to separate the effects of numbers of types of patches of different kinds in a habitat (i.e. habitat diversity) and which types were present (i.e. habitat identity). Experiments were carried out to separate the effects of number, relative proportion and identity of patches of habitat using additive designs (Underwood 1986). Four main models are proposed to explain different numbers of species in different habitats: (1) habitats have different types of patches; (2) habitats have similar types of patches, but in different relative proportions; (3) habitats have different types of patches and, therefore, different numbers of species, depending on which types of patches are present (i.e. an 'identity effect') and (4) differences in numbers of species are the result of an interaction between type, extent and identity of patches within habitats. Predictions from these models were tested using assemblages of marine molluscs colonizing artificial mimics of macro-algal habitats on rocky intertidal platforms. These assemblages consist of families of molluscs with different life histories, i.e. characteristics of feeding, reproduction, development, mobility and dispersal (Beesley et al. 1998, Kelaher 2000). In a previous study, we have shown that patch size and structural complexity have independent effects on assemblages of macroinvertebrates and that, regardless of their structural complexity, larger habitats were colonized by more species (Matias et al. 2010b). Furthermore, the greater number of species in larger habitats was not simply a result of random placement (e.g. Coleman 1981) associated with sampling an increased number of individuals. These studies provide the solid background information necessary to use these experimental habitats to test models about habitat composition (Matias et al. 2010b).

MATERIALS AND METHODS

Artificial habitats

Artificial turfs have been shown to be good mimics of algal turfs dominated by *Corallina officinalis* L. and useful to investigate the effects of habitat structure on benthic assemblages (e.g. Kelaher 2003, Matias et al. 2007). Three types of artificial turfs were selected (A, B, C in Table 1; Grassman). These artificial turfs were chosen because they differ in length (A < B < C) and also in density of fronds (A > B > C), which maximized the structural differences needed to test our hypotheses about different types of habitats (Matias et al. 2010a). Previous studies have

Table 1. Dimensions of artificial habitats with different area and composition of sub-habitats (A, B, or C). Number of sub-habitats (N), area (cm^2), density (fronds cm^{-2}), mean length of fronds (cm) and surface area (SA) of fronds per habitat (cm^2). Relative proportion of each type of sub-habitat is indicated by capital letters in the first column of the table (e.g. AB indicates 4 sub-habitats of type A and 4 sub-habitats of type B)

Composition	N	Area	Density	Length	SA
A	4	100	66.2	1.0	26.5
AA	8	200	66.2	1.0	53.0
AB	8	200	44.4	1.5	45.0
AC	8	200	41.2	2.5	52.4
AAA	12	300	66.2	1.0	79.5
ABB	12	300	55.7	2.5	63.5
ACC	12	300	49.3	4.5	78.3
B	4	100	22.6	2.0	18.5
BB	8	200	22.6	2.0	36.1
BA	8	200	44.4	1.5	45.0
BC	8	200	19.4	3.0	44.4
BBB	12	300	22.6	2.0	54.1
BAA	12	300	51.7	1.3	71.5
BCC	12	300	18.3	3.3	70.3
C	4	100	16.2	4.0	25.9
CC	8	200	16.2	4.0	51.8
CA	8	200	41.2	2.5	52.4
CB	8	200	19.4	3.0	44.4
CCC	12	300	16.2	4.0	77.8
CAA	12	300	49.5	2.0	78.9

shown that assemblages of molluscs colonizing artificial habitats respond negatively to greater densities of fronds (Kelaher 2003) and positively to longer fronds (Kelaher 2002). Therefore, the assemblages that colonize our artificial habitats were affected by the combined effect of density and length of fronds (see Table 1 for details on the physical dimension of habitats). These habitats modify the environment and provide different resources that will support different numbers of species (e.g. Matias et al. 2010b). Sub-habitats were squares of turf (5 × 5 cm), cut as described in previous experiments (Matias et al. 2007). Each sub-habitat was glued to square pieces of rubber and attached to wire mesh in such a way as to minimize the distance between sub-habitats (see detailed design in Matias et al. 2007).

Artificial habitats were of 3 sizes: small (made up of 4 sub-habitats); intermediate (8 sub-habitats) and large (12 sub-habitats) with areas of 100, 200 and 300 cm^2, respectively. Previous experiments showed that artificial habitats of these sizes are appropriate to test these hypotheses about patch size (Matias et al. 2010b). There were 7 different combinations for each type of habitat. Six were constructed according to 3 levels of identity (+A, +B or +C) orthogonal to 2 levels of extent (i.e. 8 or 12 sub-habitats). In total, there were 21 different habitats of different compositions (Fig. 1). The effect of habitat identity was examined by comparing treatments that only differed by the addition of a particular type of habitat. The effect of habitat extent was examined by comparing treatments that differed in the size of the habitat that was added. Our 'control' treatments were all small monotypic habitats (i.e. 4A, 4B or 4C; Fig. 1). These controls are analogous to those in other experiments that have manipulated diversity, identity or densities of species (e.g. competition experiments and BEF; Creese & Underwood 1982, Underwood 1986, Benedetti-Cecchi 2004). In competition experiments, for example, controls consist of treatments with a single species at small (or natural) densities whereas in BEF experiments, controls are often monocultures of single species at small densities. Furthermore, in all additive designs, controls are essential to provide the contrast required by the hypotheses for comparisons with the other heterogeneous treatments; this must be by an asymmetrical contrast in an ANOVA (controls vs. others). Treatments with all 3 types of turfs were not included because the experiment was already very complicated. Furthermore, for the tests of the hypotheses presented here, a treatment would not be strictly necessary (see comparisons between habitats with 1, 2 and 3 types of sub-habitats in Matias et al. 2007, 2010a).
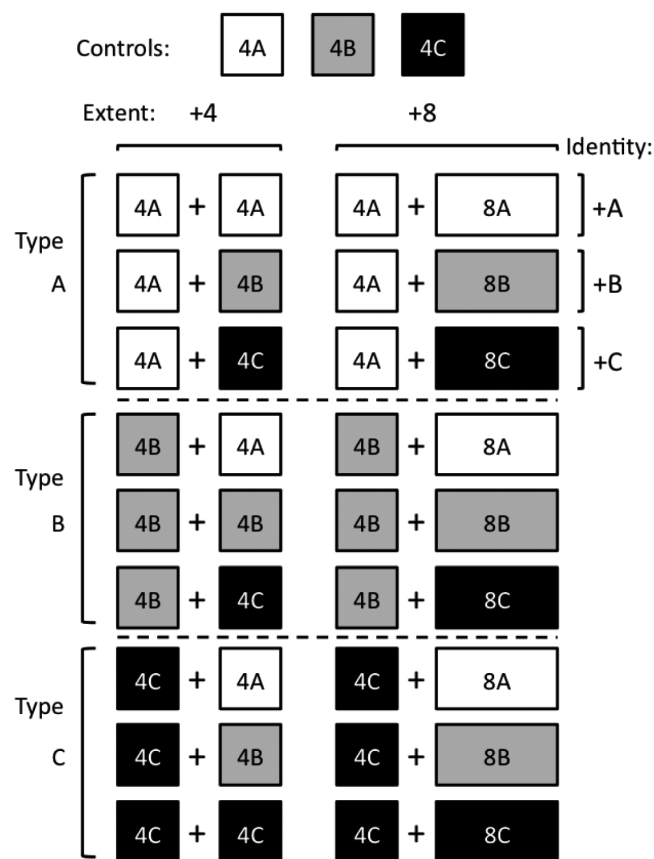

Fig. 1. Experimental treatments. Habitats with different types of sub-habitats are grouped in 3 levels of the factor type (A, B or C); habitats with different sizes (8 or 12 sub-habitats) are grouped in 2 levels of the factor extent. Identity is a factor that groups all habitats to which particular types of sub-habitats were added (i.e. +A, +B or +C). Controls are monotypic habitats with 4 sub-habitats (i.e. one type of sub-habitat); squares with different colours indicate 3 types of turfs: type A (white), type B (grey) and type C (black)

Study site

This experiment was carried out on intertidal rock platforms at the Cape Banks Scientific Marine Research Area, NSW, Australia (34° 00′ S, 150° 15′ E) in July–September 2007. Assemblages associated with coralline turfs vary with slope (Akioka et al. 1999) and height on the shore (Kelaher 2003), and show small-scale patchiness (Olabarria & Chapman 2001). For these reasons, 2 locations tens of metres apart were chosen, each large enough to attach experimental habitats amongst meadows of algal turf dominated by *Corallina officinalis*. The locations had similar orientations and exposure to waves. Artificial habitats were interspersed on rock platforms or large boulders, between 0.3 and 0.6 above mean low water,

in between natural patches of coralline turfs, and attached to shore using stainless steel screws and rubber washers. The artificial habitats were retrieved 60 to 65 d after being deployed; this period is appropriate for colonization by a representative assemblage (Kelaher 2003, Matias et al. 2007, 2010b).

Fauna and epiphytes can be easily dislodged from the artificial turfs when habitats are removed from the shore. To avoid this problem, a grid of 50 × 50 mm square plastic corers was used, which isolated each sub-habitat 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 each sub-habitat in a corer. The screws were then undone and each corer was emptied into a separate plastic bag, guaranteeing that epiphytes and fauna associated with each sub-habitat in the habitat were completely sampled. All sub-habitats were labelled and preserved in 7% formalin. Three sub-habitats were randomly selected from each habitat; each sub-habitat was washed in a 500 µm sieve and all invertebrates sorted and counted under a binocular microscope at ×16 magnification. All molluscs were identified to either species or morphospecies (Underwood & Chapman 2006).

Data analyses

Numbers of species observed in heterogeneous habitats were compared with numbers of species in monotypic habitats of similar size. For example, habitat AB (A+B) was compared with habitat AA, and habitat ABB (A+BB) was compared with habitat AAA. The ratio was calculated for every heterogeneous habitat as $S = \log(N_H/N_M)$, where N_H is the number of species in the heterogeneous habitat and N_M is the number of species in the monotypic habitat of the same size and type of sub-habitat. Ratios were transformed to logarithms to help normalize the data and to homogenize their variances. Different null expectations were calculated based on the numbers of species in each of type of monotypic habitats of 200 or 300 cm^2. Positive values of S indicate greater numbers of species in heterogeneous habitats than would be expected simply from an increase in area of a monotypic habitat. Negative values of S indicate numbers of species smaller than would be expected solely due to an increase in area. The null hypothesis of no differences in ratios was tested using a 3-way ANOVA with extent as the comparison between habitats with different sizes (8 or 12 sub-habitats) to which sub-habitats with different identity (+A, +B or

+C) are added; location was a random factor with 2 levels (n = 6).

The effects of composition on number of species were tested using an asymmetrical ANOVA with 4 factors: type is a comparison between habitats with sub-habitats A, B or C and Composition; extent and identity are as in the previous analysis (above). Type, extent and identity are fixed factors. Composition is the comparison among all 7 combinations; 'controls vs among others' is an asymmetrical contrast comparing controls with all other types of habitats. The responses to changes in composition were analysed by estimating the numbers of species in each whole habitat, i.e. the number of different species summed over all types of sub-habitats making up a habitat. Preliminary analyses showed that the effects of composition interacted with those of location; analyses were therefore performed separately for each location. All analyses were performed on untransformed data following non-significant Cochran's tests for heterogeneity of variances.

Species abundance distributions (SADs) were calculated to examine the occurrence of rare species in 3 types of habitats. SADs were calculated following the modified Preston method (Williams 1964, McGill 2003), which has been widely used to investigate the shape of the species abundance distribution (e.g. Gray et al. 2006). Data from all 106 habitats were used in this analysis.

RESULTS

In total, we counted 28 816 ind. of 117 different species. The mean (±SD) number of species per sub-habitat in controls (i.e. small monotypic habitats of size 5 × 5 cm) was 9.3 ± 0.5 (n = 6) in A, 8.9 ± 0.8 in B and 12.5 ± 1.7 in C. The numbers of species in monotypic habitats were consistently greater in larger habitats, whereas numbers of species in heterogeneous habitats showed complex responses depending on the location and composition of habitats (i.e. the component sub-habitats).

Monotypic vs. heterogeneous habitats

The numbers of species in heterogeneous habitats were compared with the numbers in monotypic habitats of similar sizes. For heterogeneous habitats, sub-habitats of type C influenced the numbers of species significantly more than was the case for the other 2 sub-habitats (Fig. 2). The influences of types A and B
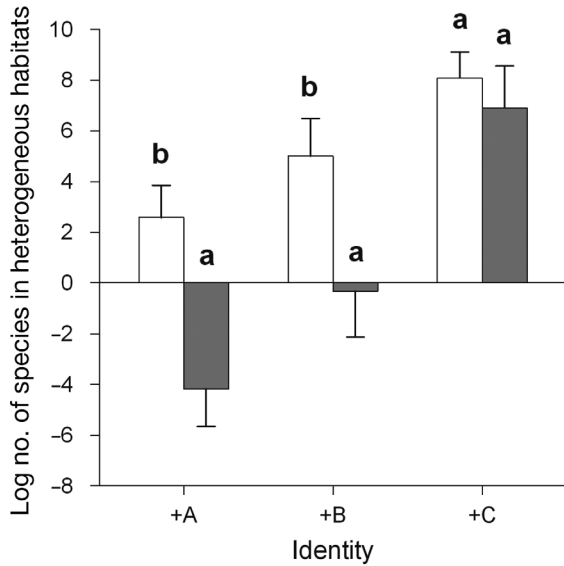
Fig. 2. Mean (±SE, n = 6) log number of species in heterogeneous habitats in relation to the number of species in monotypic habitats of the same size. Positive or negative values indicate greater or smaller numbers of species, respectively, in heterogeneous habitats than would be expected by an increase in area of a monotypic habitat. Identity has 3 levels: +A, +B and +C; extent is a comparison between habitats with different numbers of sub-habitats (8, white bars or 12, grey bars). Data are averaged across 2 random locations (n = 6). Letters indicate significant differences between levels of extent within each level of identity (SNK p < 0.05; Table 2)

Table 2. ANOVA and pair-wise comparisons of log number of species in heterogeneous habitats in relation to the number of species in monotypic habitats of the same size (see 'Materials and methods' for details). Type is a comparison between habitats with sub-habitats A, B and C; extent is a comparison between habitats with different numbers of sub-habitats (8 and 12 sub-habitats); identity has 3 levels: +A, +B and +C. Means and results of SNK tests are shown in Fig. 2. Numbers in bold indicate significant differences between means

Source	df	MS	F	p
Location	1	130.7	5.3[b]	<0.03
Identity	2	463.3	18.6[b]	<0.001
Extent	1	528.1	21.2[b]	<0.001
Location × Identity[a]	2	37.5	–	–
Location × Extent[a]	1	0.1	–	–
Identity × Extent	2	85.0	3.4[b]	<0.04
Location × Identity × Extent[a]	2	0.5		
Residual	60	25.6		

Pair–wise comparisons			
	Identity (Extent)	Extent (Identity)	
8 sub–habitats	A = B = C	A	**2 < 1**
12 sub–habitats	**A = B < C**	B	**2 < 1**
		C	2 = 1

[a]Pooled terms.
[b]Tested against pooled residual Location × Identity + Location × E + Location × Identity × E + Residual

depended on the amount of each sub-habitat added to a habitat (extent × identity, $F_{2,60}$ = 3.4, p < 0.04; Table 2). Across the 2 extents, there was a similar increase in numbers of species when sub-habitat C was added, although these differences were only significant in larger habitats (i.e. 12 sub-habitats, Fig. 1; results of Student-Newman-Keuls [SNK] tests in Table 2). When analysing the effects of extent, there were, on average, more species in smaller habitats in all comparisons, although means were not different in habitats C (SNK tests; Table 2).

Diversity, identity and relative proportions of habitats

In location 1, the numbers of species in heterogeneous habitats of type A (Fig. 3) and type B (Fig. 3) were greater when sub-habitats of type C were present. Numbers of species in heterogeneous habitats of type C were not greater than monotypic habitats, regardless of which sub-habitats were part of the heterogeneous habitat (Fig. 3). Asymmetrical ANOVA demonstrated that interactions among the 3 main fac-

tors (type, extent and identity) were associated with differences among the numbers of species colonizing habitats with different composition (location 1: type × extent × identity interaction; $F_{4,42}$ = 3.0, p < 0.035; Table 3). Pair-wise comparisons revealed greater mean numbers of species in habitats with greater extent (i.e. 7 of 9 comparisons, SNK p < 0.05; Table 3). Note that several comparisons were not significant, but the order of means was consistent. Furthermore, when analysing the effects of identity, there were consistently greater mean numbers of species when habitat type +C was added to the habitat (i.e. 5 of 6 comparisons, SNK p < 0.05; Table 3), whereas +B had the smallest mean numbers of species in 4 of 6 comparisons (Table 3).

The results for location 2 were similarly complex. There were generally more species in heterogeneous habitats of type A than in monotypic habitats, although the effect of identity of sub-habitats type C was not as clear (Fig. 3). In contrast to location 1, none of the heterogeneous habitats of type B were colonized by greater numbers of species than in monotypic habitats (Fig. 3). Heterogeneous habitats of type C did not have more species than monotypic
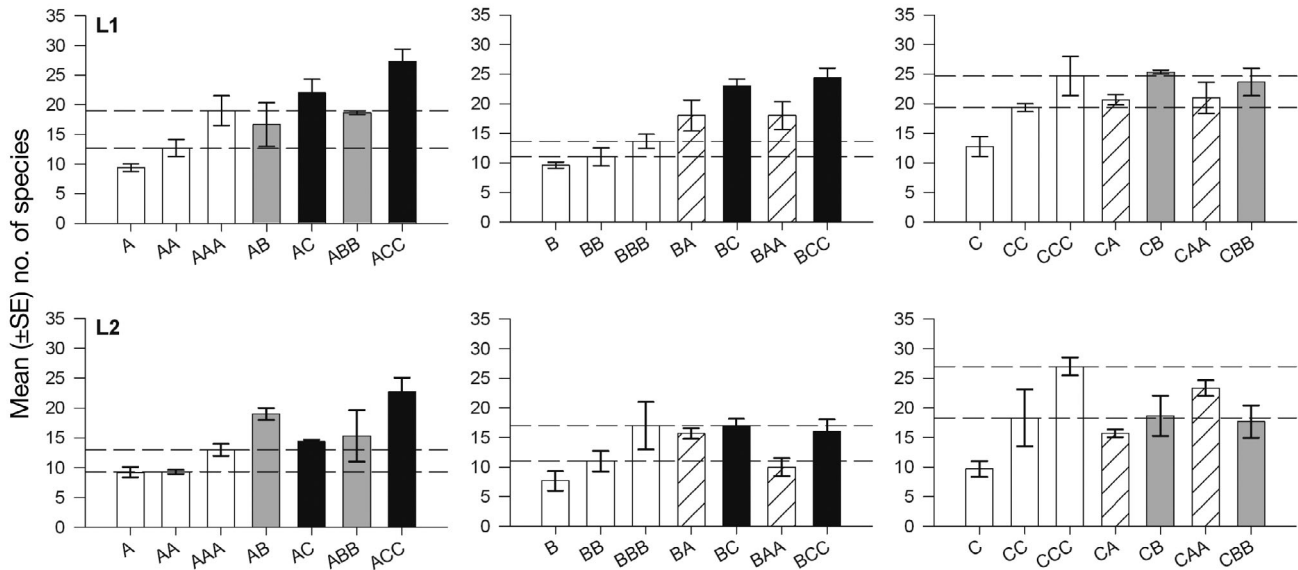
Fig. 3. Mean (±SE, n = 3) number of species in habitats with different composition across 2 locations (L1 and L2). Bars with different patterns and colours indicate the composition treatment identity: +A (dashed), +B (grey), +C (black) or monotypic (white). Dashed horizontal lines indicate the mean number of species in monotypic habitats with 8 (lower line) and 12 (higher line) sub-habitats

Table 3. ANOVA and pair-wise comparisons of number of species in habitats with different composition. Composition is a comparison between all 7 types of treatment; controls vs. among others is an asymmetrical contrast between controls (4A, 4B and 4C) and all other treatments; type is a comparison between habitats with sub-habitats A, B and C; extent is a comparison between habitats with different amounts of sub-habitats (8 and 12 sub-habitats); identity has 3 levels: +A, +B and +C. All factors are fixed and n = 3. Numbers in bold indicate significant differences between means.

Source	df	Location 1			Location 2		
		MS	F	p	MS	F	p
Composition	6	185.3	19.4	<0.001	158.3	10.4	<0.001
Controls vs. Among others	1	707.1	74.1	<0.001	486.9	31.8	<0.001
Among others							
Extent	1	104.2	10.9	<0.003	88.2	5.8	<0.022
Identity	2	130.1	13.6	<0.001	112.7	7.4	<0.003
Extent × Identity	2	20.1	2.1	>0.134	74.7	4.9	<0.013
Type	2	251.4	26.4	<0.001	124.2	8.1	<0.001
Type × Composition	12	33.2	3.5	<0.003	31.2	2.0	<0.046
Type × Controls vs. among others	2	9.9	1.0	>0.361	11.5	0.8	>0.458
Type × Among others							
Type × Extent	2	22.2	2.3	>0.113	11.6	0.8	>0.475
Type × Identity	4	55.2	1.9	>0.120	18.4	0.3	>0.882
Type × Extent x Identity	4	28.4	3.0	<0.035	63.6	4.2	<0.007
Residual	42	9.5	15.3				

Pair-wise comparisons:		Type			Type		
Extent (Type × Identity)		A	B	C	A	B	C
Identity	+A	**8 < 12**	8 = 12	**8 < 12**	8 = 12	12 = 8	**8 < 12**
	+B	12 = 8	8 = 12	8 = 12	**12 < 8**	8 = 12	12 = 8
	+C	12 = 8	8 = 12	**8 < 12**	**8 < 12**	8 = 12	**8 < 12**
Identity (Type × Extent)		A	B	C	A	B	C
Extent	8	A = B = C	**B < A = C**	C = A = B	A = C = B	B = A = C	A = C = B
	12	B = A = C	B = A = C	B = A = C	**B = A < C**	A = B = C	B = A = C

habitats, regardless of which sub-habitats were included (Fig. 3). Similarly to location 1, there was an interaction of type, extent and identity that influenced the numbers of species colonizing habitats

with different compositions (Location 2: type × extent × identity; $F_{4,42} = 4.2$, p < 0.007; Table 3). As in location 1, pair-wise comparisons revealed greater average numbers of species in habitats with greater
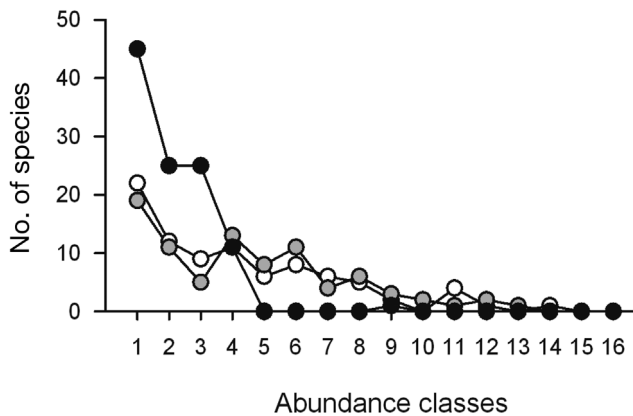
Fig. 4. Species abundance distributions in different different types of sub-habitats within habitats of different composition. Bins were calculated following the modified Preston method (Williams 1964, McGill 2003): bin 0 = half the number of species with one individual per species; bin 1 = half the number of species with one individual per species plus half the number of species with 2 individuals per species; bin 3 = half the number of species with 2 individuals per species, all the number of species with 3 individuals per species and half the number of species with 4 individuals per species, etc. White, grey and black circles indicate sub-habitats A, B and C, respectively

extent (i.e. 6 of 9 comparisons, SNK p < 0.05; Table 3) and greater mean numbers of species when +C was added to the habitat (i.e. 5 of 6 comparisons, SNK; Table 3). Also, +B had the smallest average numbers of species in 3 of 6 comparisons.

Species abundance

Distributions of individuals in different species were quite different between different types of sub-habitats. Sub-habitats of type C were mostly colonized by greater numbers of mostly rarer species and by few abundant species. Types A and B had considerably fewer rarer species and more of the abundant species (Fig. 4). The pool of species colonizing the artificial habitats differed between the 3 different types of sub-habitats. Sub-habitats of type C were colonized by a total of 95 species, whereas sub-habitats of type A and type B were colonized by 73 and 74 species, respectively. Of the 117 species found, 16 were only found in sub-habitats of type C. The pool of species colonizing artificial habitats differed between locations, mostly because fewer, i.e. 65, species colonized sub-habitats of type C at location 2, 23% fewer species than in the same sub-habitat at location 1 (84 species).

DISCUSSION

The key findings of this study were not that all heterogeneous habitats had the expected numbers of species predicted from a simple species–area relationship. The greater numbers of species in heterogeneous habitats could, to a great extent, be explained by the presence or absence of particular types of sub-habitats and not just patch size. These responses were, however, the result of the contributions of an interaction of 3 different factors: number, relative proportion and identity of patches of habitat. The complexity we found in such responses was not predicted and could not have been demonstrated without appropriate manipulations of composition of habitats. Such an approach allows separation of the effects of sub-habitat type and the effects of patch size in monotypic habitats. This helps in the development of hypotheses about the numbers of species in assemblages in heterogeneous habitats. It also identifies the responses of species to the identity of particular types of habitats. The numbers of species also respond to different sizes of habitat in addition to responses to different types of sub-habitat. Experiments are essential for separating the effects of patch size *per se*.

Nevertheless, the identity of habitats could not, itself, explain all the differences in numbers of species in habitats with different relative proportions of sub-habitats. Identity interacted with extent within each habitat patch. Sub-habitats of type A and B had relatively small effects on the number of species when they were in large proportions within habitats (e.g. in habitats CAA or CBB). These differences are quite striking when compared with what would have been expected by a simple increase in habitat area. In contrast, when sub-habitats of type C were part of heterogeneous habitats, their effect on the diversity of the overall habitat seemed to be independent of their relative proportion within the habitat. This demonstrates that the number of species in heterogeneous habitats depends on the relative proportions and the identity of the sub-habitat in any habitat.

There have not been many examples of this kind of experiment in marine systems, and it is therefore difficult to establish parallels. O'Connor & Crowe (2005) examined the effects of number and identity of species (grazing gastropods) by using an experimental design that separated the effects of number, identity and density of species of grazers. O'Connor & Crowe (2005) found that the identity of species of grazers was more important than their number in determining patterns of algal productivity, after controlling

for changes in density. Similarly, Maggi et al. (2009) performed a study on the effects of changes in composition of intertidal assemblages using an experimental design to separate the effects of species richness and identity, while controlling for variation in species abundance. Their results showed significant effects of changes in number and identity of habitat-forming species on other organisms, even though the magnitude and direction of these effects were determined by the abundance of manipulated species. In addition to the results of our study, these examples emphasize the importance of investigating the contribution of habitat number and identity in ecological experiments as they offer a different perspective on the investigation of the roles of habitat characteristics.

In addition to the parallels with BEF research, our results may also be analogous to the responses of natural populations to minimal thresholds or 'critical' patch sizes, which are necessary to support certain populations in heterogeneous landscapes (e.g. Thomas & Jones 1993, Fahrig 2001). If there is some minimal threshold, it could explain the fact that numbers of species in habitats with sub-habitats of type C did not differ, whatever the amount of sub-habitat C available. Thus, there were similar numbers of species in heterogeneous habitats with +4C and those with +8C. Presumably, 4 patches of C provide an appropriate amount of sub-habitat C for any species that might respond. No additional amount of C makes any further difference. This explanation is clearly not correct for the other 2 types of sub-habitat. Increasing the amounts of these in a habitat either caused only a small increase (adding B) or caused a decrease (adding A) in numbers of species. Increasing the relative proportions of A or B in a habitat of a given size necessarily decreases the relative amount of C present. This, in turn, would generally decrease the number of species in the whole habitat. It is, however, currently difficult to understand which processes are operating here, because there seemed to be a minimal amount of C necessary to attract or to maintain the species associated with this sub-habitat.

An alternative explanation for such differentiation can be drawn from concepts of source–sink dynamics in metapopulations (Hanski & Gilpin 1991) and meta-communities (Loreau & Mouquet 1999, Leibold et al. 2004). In a source–sink system, species are not excluded from areas where they are inferior competitors (i.e. sinks), because they can emigrate from other areas (i.e. sources), where they are good competitors (Loreau & Mouquet 1999). This could explain why there are generally more species in sub-habitats type A and type B in habitats where there are also sub-

habitats of type C. Of the 3 types of habitat, C had the greatest number of species and may function as a source of colonists of species that would not otherwise colonize sink sub-habitats (i.e. types A or B). Several species were found only in sub-habitats of type C and therefore do not occur in these artificial habitats unless sub-habitats of type C are present. This explanation is based on the assumption that there is dispersal between sub-habitats within the habitat (or metacommunity; *sensu* Loreau & Mouquet 1999). We could not examine this process in this study, although it has been posited that many species of molluscs colonize patches by passive advection through the water column (Beesley et al. 1998). Some of these small snails have been shown experimentally to move (by crawling) to their preferred types of habitats (Olabarria et al. 2002). Future studies should investigate the mechanisms underlying the observed patterns by quantifying dispersal of individuals within habitats of different composition.

We have reported differences in total number of species between locations and that particular types of sub-habitats were more affected than others by this reduction (i.e. type C). The effect of the most species-rich sub-habitat, type C, was greatly reduced at location 2 where there were fewer species. The species absent from location 2 were mostly singletons, i.e. species of which only one individual was found in all the samples, or were species of relatively small abundances. This is consistent with a number of studies showing that the number of species occurring locally is related to the number occurring regionally (reviewed by Lawton 1999). For example, it has been shown that numbers of species in coral reefs are correlated with the number of species occurring regionally, in addition to there being correlations with local measures of 'architectural complexity' (Cornell & Karlson 1996).

CONCLUSIONS

The complexity we found in the responses of assemblages to the composition of heterogeneous habitats was not predicted and could not have been observed without appropriate manipulations of composition of habitats. Such an approach allows separation of the effects of type of sub-habitat and the effects of patch size in monotypic habitats. This helps in the development of hypotheses about the numbers of species in assemblages in heterogeneous habitats. It also identifies the responses of species to the identity of particular types of habitats. The numbers of

species also respond to different sizes of habitat in addition to different types of sub-habitat. Experiments are essential for separating the effects of patch size *per se*.

Conserving biological diversity often relies on the protection or restoration of habitats and their associated microhabitats where endangered species occur (e.g. microhabitats in streams; Nislow et al. 1999). Some habitats have been shown to be 'hotspots' of biological diversity in their own right. For example, intertidal boulder fields are colonized by many rare species that do not exist elsewhere (Chapman 1999). Commonly used indices of habitat diversity provide useful information about the level of heterogeneity of habitats (see Tews et al. 2004 for review). Quite often, however, they do not offer any information about the relative contribution of each type of habitat to any overall effect of heterogeneity on the diversity of the associated assemblages (Matias et al. 2007). In particular, they disregard the importance of particular types of sub-habitats (e.g. MacDonald & Johnson 1995). A mechanistic understanding of the associations between species and particular types of habitats is therefore helpful and necessary for interpreting species' responses to loss of entire habitats.

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