



Interactive effects of losing key grazers and ecosystem engineers vary with environmental context

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ABSTRACT: Loss of biodiversity may cause significant changes to ecosystem structure and functioning. Evidence from long-term *in situ* removal experiments is rare but important in determining the effects of biodiversity loss against a background of environmental variation. Limpets and mussels are thought to be important in controlling community structure on wave-exposed shores in the UK: limpets as key grazers, mussels as ecosystem engineers. A long-term factorial removal experiment revealed interactive effects that varied between 2 shores in SW England. At one site (Harlyn), removing limpets caused a significant shift in community structure, but where limpets were lost, the presence or absence of mussels made little difference. Where limpets were present, however, the removal of mussels changed the structure and variability of the community. At the other site (Polzeath), the loss of mussels caused significant changes in community structure, and limpets played a less important role. At Harlyn, furoid algae were abundant throughout the year. There were fewer algae at Polzeath, and cover was dominated by the summer bloom of ephemerals. At Harlyn, the limpets played a major role in controlling algae, but their effects were mediated by the presence of mussels. Other grazers were not able to fulfil their role. At Polzeath, mussels were far more important, and ephemeral algae grew on them regardless of the presence or loss of limpets. These findings emphasise the need to assess spatial and temporal variation in the effects of biodiversity loss and the importance of interactive effects of loss of multiple species from different functional groups.

KEY WORDS: Biodiversity · Functional groups · Spatial variation · Long term · Removal experiment · Limpets · Mussels · Interactive effects

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INTRODUCTION

Extensive changes in biodiversity have been widely documented (Millennium Ecosystem Assessment 2005). The effects of changing biodiversity on ecosystems remain unclear despite extensive research into biodiversity–ecosystem functioning (BEF) relationships (Millennium Ecosystem Assessment 2005, Naeem et al. 2009). Concerns have recently been raised that many BEF experiments to date have been too short to properly characterise the effects of diversity loss, particularly in marine ecosystems (Stachowicz et al. 2008a,b). Laboratory- or mesocosm-based manipulations need to

be supplemented by field-based removal experiments to ensure that general models derived from such studies are realistic (Díaz et al. 2003, Stachowicz et al. 2008a,b, Crowe & Russell 2009). The extent of spatial and temporal variation in consequences of biodiversity loss is also unclear and must be more fully characterised if an effective predictive framework is to be developed (Cardinale et al. 2000).

In seeking to improve prediction of effects of diversity loss, there has been a recent shift in emphasis from species-level diversity to functional diversity (Crowe & Russell 2009), such that the functional traits of taxa (e.g. feeding modes, habitat provision) are explicitly taken

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into account when considering impacts of their loss (Stachowicz et al. 2007, Mouchet et al. 2008, Griffin et al. 2009, O’Gorman et al. 2010). The loss of key taxa or strong interactors (Hurlbert 1997) within functional groups is likely to have a disproportionate effect on ecosystem structure and functioning. Although the functional role of key taxa can sometimes be replaced by other members of the group, longer-term studies have demonstrated their importance in the face of changing environmental circumstances (O’Connor & Crowe 2005). Combined effects of losing multiple key taxa from different functional groups are likely to be substantial and also interactive, such that the effects of losing 1 species depend on the presence or absence of others. BEF experiments have rarely been designed to test for the presence of such interactions. The widespread occurrence of interactive effects would have significant consequences for the predictability of effects of loss of diversity on ecosystem function, particularly if the nature of interactions varies with spatial and temporal environmental heterogeneity (Stachowicz et al. 2008a).

Although documented global extinctions are rare in the marine environment, local extinctions and dramatic changes in abundance are widespread (e.g. Airoldi & Beck 2007, Stachowicz et al. 2007). Rocky shore ecosystems are highly productive and can be a significant source of detrital material underpinning coastal food webs (Whittaker 1975, Raffaelli & Hawkins 1996). Many are characterised by the presence of strongly interacting species (Allison et al. 1996; sensu Hurlbert 1997). They also lend themselves to long-term experimental manipulation (Connell 1974, Paine 1977), particularly removal experiments (Díaz et al. 2003), and have already contributed significantly to the BEF debate (Allison et al. 1996, Stachowicz et al. 2007). On rocky shores in the Northeast Atlantic, both limpets (Southward 1964, Hawkins 1981, Hawkins & Hartnoll 1983, Jenkins et al. 1999a, 2008, Coleman et al. 2006) and mussels (Seed 1996) are thought to have key roles in driving ecosystem structure and functioning, although the relative importance of their respective roles is yet to be established (Hawkins et al. 1992).

Limpets regulate algal recruitment by grazing the early stages of macroalgae contained within epilithic microbial films (Hill & Hawkins 1991) and in some cases direct consumption of mature algae (Davies et al. 2007). This has been demonstrated by the establishment of opportunistic and furoid algae where limpets have been removed or excluded (Jones 1948, Southward 1964, Hawkins 1981, Jenkins et al. 1999a, 2008). In the absence of key species, availability of food for other grazers (such as littorinids and trochids) may increase (Cubit 1984, Dye & White 1991, Mak & Williams 1999), perhaps leading to increases in their abundance. Even if their numbers increase, however, they may or

may not be capable of controlling algal growth as effectively as limpets (O’Connor & Crowe 2005). The effect of herbivory on diversity of primary producers remains controversial (Olf & Ritchie 1998). High grazing pressure seems to reduce algal diversity while moderate grazing pressure can increase it (Paine & Vadas 1969, Lubchenco 1978, Anderson & Underwood 1997, Aguilera & Navarrete 2007). There is also evidence that plant diversity may depend more on spatial heterogeneity and variance in grazing pressure than its mean intensity (Olf & Ritchie 1998, Benedetti-Cecchi 2000, Sommer 2000).

Mussels have been described as foundation species or ecosystem engineers (Jones et al. 1994, Lawton 1994) because they modify their environment, changing its suitability for other organisms. Intertidal mussel populations provide a biogenic structure for a diverse array of species including annelids, crustacea and other molluscs (Lohse 1993, Seed 1996, Crowe et al. 2004). The architectural complexity of mussel shells decreases the influence of wave action, temperature and sunlight while increasing relative humidity and sedimentation (Sebens 1991). The biological activities of living mussels, such as filter feeding and biodeposition, can also affect biota (Crooks & Khim 1999).

There is also considerable potential for mussels and limpets to interact in their effects on community structure, but the nature of such interactions may not be easy to predict. By providing habitat for other grazing gastropods (Lohse 1993), mussels could reduce the effects of loss of limpets by increasing the likelihood that other grazers will colonise the area. On the other hand, by providing refuges for algal propagules from both physical stress (Hruby & Norton 1979, Vadas et al. 1990, Brawley & Johnson 1991) and grazing pressure, they could enhance algal cover and reduce the effects of gastropod grazing (Hawkins & Hartnoll 1982, Lubchenco 1983, Witman 1985, Chapman 2000, Wahl & Hoppe 2002). Nevertheless, grazing marks found on and amongst mussels imply that at least some grazing does occur on this substratum (Lohse 1993, O’Connor & Crowe 2008).

Here we report a long-term field-based removal experiment designed to test the following hypotheses:

(1) Losses of key species from different functional groups (limpets as key grazers, mussels as ecosystem engineers) will each cause changes in ecosystem structure. Effects of loss of combinations of these species may be interactive. In particular:

(a) Other grazers will increase in abundance in response to loss of limpets, an effect which may be mediated by changes in habitat availability caused by loss of mussels.

(b) Cover and composition of macroalgal assemblages will change in response to changes in grazing

pressure and availability of refuges provided by mussels.

(2) Individual and interactive effects of loss of key species will vary spatially and through time.

MATERIALS AND METHODS

Study sites. The research was done at Harlyn Bay and Polzeath, 2 sites on the north coast of Cornwall in SW England separated by 6.5 km (50° 34' 50" N, 4° 55' 28" W and 50° 32' 36" N, 4° 59' 33" W, respectively). They are typical of the wave-exposed rocky shores on this coast. The shore at Polzeath consists mostly of gently sloping, slate bedrock platforms with only a few boulders and loose rocks. Despite the exposure of this site, its shallow gradient causes a reduction in wave energy. Harlyn Bay has a similar bedrock to that of Polzeath, with a higher degree of wave exposure. At each site, mid-tidal levels were covered by a mosaic of mussels, fucoid algae and barnacles. In the experimental area, mussels (a mixture of *Mytilus edulis*, *M. galloprovincialis* and hybrids) dominated the primary space, covering on average $79 \pm 1.98\%$ (SE, $n = 24$) and $64 \pm 2.0\%$ ($n = 24$) of plots at Polzeath and Harlyn, respectively. Overall cover of algae was greater on average at Harlyn than at Polzeath ($38 \pm 4.2\%$, $n = 24$ versus $18 \pm 4.5\%$, $n = 24$) at the start of the experiment (Fig. 1). The main foliose algae were *Fucus vesiculosus* var. *linearis*, *F. spiralis*, *F. serratus*, *Porphyra* spp., *Ulva lactuca* and *U.* (formerly *Enteromorpha*) *intestinalis*, and there were also some turf-forming and encrusting species, such as *Corallina officinalis*, *Gelidium* spp., *Lithothamnion* spp. and *Ralfsia* spp. A similar suite of algal species occurred at each site, but their relative proportions varied (see 'Results'). Densities of grazing gastropods were similar at each shore. The assemblage included limpets (*Patella vulgata*, *P. depressa* and *P. ulysiponensis*), littorinids (*Littorina littorea*, *L. mariae*, *L. obtusata*, *L. saxatilis*) and trochids (particularly *Gibbula umbilicalis* and some *Osilinus lineatus*).

Experimental design. To investigate the individual and combined effects of losing limpets and mussels, a factorial design was used. The treatments were as follows: + limpets, + mussels (+L+M); + limpets, - mussels (+L-M); - limpets, + mussels (-L+M); - limpets, - mussels (-L-M). There were 4 replicate plots per treatment. As part of a complementary study, 4 additional plots were initially set up for each treatment. These were destructively sampled after 11 mo. Eight replicate plots were therefore available for the first 11 mo of the experiment and 4 were available thereafter.

Procedures. In October 1998, plots measuring 0.5 × 0.5 m were chosen at each site, marked and randomly assigned to each of the 4 treatments. All but 5 of the

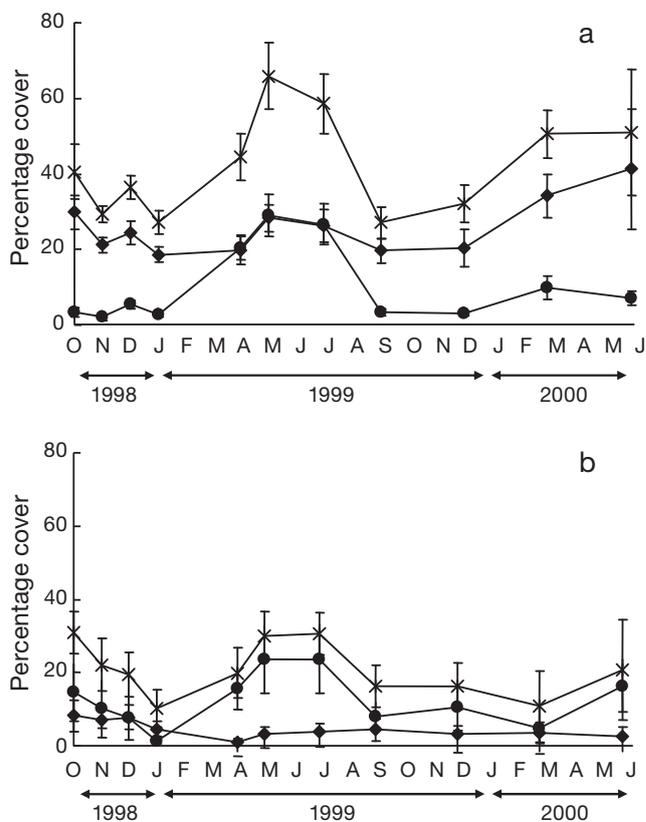


Fig. 1. Percentage cover of fucoid algae (◆), ephemeral algae (●) and all algae combined (×) in control plots (+ limpets, - mussels) throughout the experiment at (a) Harlyn and (b) Polzeath. (shown are means ± SE; $n = 8$ until September 1999, $n = 4$ thereafter)

plots had >60% cover of mussels, and all were separated from each other by a minimum of 1.5 m. Mussels were removed from the appropriate plots by chiselling. Care was taken to avoid damage to other organisms attached to the rock surface itself. Limpets were removed manually from the relevant plots and from a surrounding buffer zone 0.25 m wide to reduce re-invasion. They were prised from the substratum using screwdrivers every month for the duration of the experiment. Any mussels reinvading plots were also removed, but such reinvasions were rare.

The experiment was monitored monthly for the first 3 mo after initiation and every 3 mo after that for a total duration of 20 mo. Plots were monitored using a 0.5 × 0.5 m quadrat, strung to provide 49 intersection points for estimates of percentage cover. The following variables were recorded: (1) overall percentage cover of fucoid algae, (2) after moving fucoids aside, percentage cover of sessile organisms (particularly mussels and barnacles), other algal species and *Fucus* germlings (defined as *Fucus* plants <2 cm long). The point of attachment (barnacle/rock or mussel shell) of algae and sessile fauna was noted in each case. Sessile spe-

cies that did not occur under an intersection were recorded as present and assigned 0.5% cover in the analyses; (3) abundances of mobile species (mainly gastropods). Again, associations with mussels or bare rock were noted. Individuals within 0.5 cm of a mussel shell were considered to be associated with mussels. Littorinids on algae were considered associated with mussels if the alga they were on was attached to a mussel shell. Limpets <1.5 cm long were recorded as 'juvenile limpets'. In October 1999, to provide a more detailed analysis of the role of mussels as a refuge for *Fucus* germlings, the numbers of germlings growing on mussels and on bare rock in each plot were counted.

Analyses. To guide formal analyses, changes in algal cover in unmanipulated controls (+L+M) were examined over the 20 mo duration of the experiment. There was a distinct summer peak in total algal cover at each of the sites (Fig. 1). This was driven largely by variations in cover of ephemeral/green algae (*Porphyra* spp., *Ulva lactuca* and *U. intestinalis*). At each site, cover of ephemeral algae rose from <10% in winter and spring to >20% in summer (May to July). At Harlyn, there was also a moderate cover (~30%) of fucoid algae (*Fucus vesiculosus vesiculosus* and *F. spiralis*) throughout the year (Fig. 1). At Polzeath, there was very little fucoid algal cover (mean <10%) at any time (Fig. 1). Any influence of treatments on algal cover during the summer peak was therefore most likely to exert a strong influence over the export of macroalgal detritus from the shores. Therefore, the main analyses focussed on representative times from the summer peak in each of July 1999 and June 2000.

Non-metric multidimensional scaling (nMDS) was used to assess the impact of the treatments on overall community structure (excluding limpets and mussels). nMDS is an ordination technique based on rank dissimilarity, in this case measured with the Bray-Curtis index on square-root transformed data (Clarke 1993). SIMPER analysis in the PRIMER package was used to assess which species were most influential in causing similarity among plots within treatments and dissimilarity among different treatments (Clarke & Warwick 1994). Permutational multivariate analysis of variance (PERMANOVA, McArdle & Anderson 2001, Anderson 2005) was used to test hypotheses of differences in community structure. Analyses of data from each of the 2 selected dates were based on Bray-Curtis similarities of square-root transformed data. Factors were Site (2 levels, random), Limpet (2 levels, fixed, orthogonal) and Mussel (2 levels, fixed, orthogonal). Separate analyses were done for each sampling occasion.

To test hypotheses about the responses of grazers other than limpets to the experimental removals, a series of analyses of variance were done on data

derived by combining abundance of all grazers other than limpets (*Littorina littorea*, *L. saxatilis*, *L. nigrolineata*, *L. obtusata/mariae*, *Gibbula umbilicalis*, *Osilius lineatus*, *Melaraphe neritoides*). The count data were $\ln(x+1)$ transformed prior to analysis. Factors were Site (2 levels, random), Limpet (2 levels, fixed, orthogonal) and Mussel (2 levels, fixed, orthogonal). Separate analyses were done for each of the 10 sampling occasions after manipulation to avoid non-independence. Homogeneity of variance was tested with Cochran's test. Post-hoc pooling was used as appropriate to maximise the power of tests of relevant terms (Underwood 1997). The Student-Newman-Keuls (SNK) procedure was used for post hoc multiple comparisons (Underwood 1997).

Analysis of variance was used to test effects of the treatments on cover of fucoid algae (*Fucus vesiculosus vesiculosus*, *F. spiralis* and *F. serratus*), cover of ephemeral algae (*Porphyra* spp., *Ulva lactuca* and *U. intestinalis*) and total algal cover (including turf-forming and encrusting species). The model and procedures used were the same as those used for grazers (described above). The same analysis was applied to counts of *Fucus* germlings made in October 1999.

Associations of *Fucus* germlings with mussels and bare rock in the presence and loss of limpets were tested using chi-squared analysis based on counts made in October 1999. For each plot, the number of germlings on mussels and the number of germlings on bare rock were counted. Percentage covers of these substrata were used to generate expected distributions based on random chance. Separate analyses of observed versus expected frequencies were completed for combined data from all plots assigned to (1) +L+M and (2) -L+M.

RESULTS

Manual removals of limpets were effective in maintaining considerably reduced densities and hence grazing pressure. Averaged across the experiment as a whole, sampled 10 times, limpet removals at Harlyn reduced limpet density from $34.0 \pm 1.40 \text{ m}^{-2}$ (SE, $n = 165$) to $7.6 \pm 0.65 \text{ m}^{-2}$, and at Polzeath, the reduction was from $43.7 \pm 2.20 \text{ m}^{-2}$ to $9.0 \pm 0.98 \text{ m}^{-2}$. At each site, densities were reduced by approximately 80%.

Multivariate community structure

At Harlyn, the loss of mussels and the loss of limpets had significant effects on community structure on both sampling occasions (Fig. 2, Tables 1 & 2). The effect of limpets was more marked than that of mussels, partic-

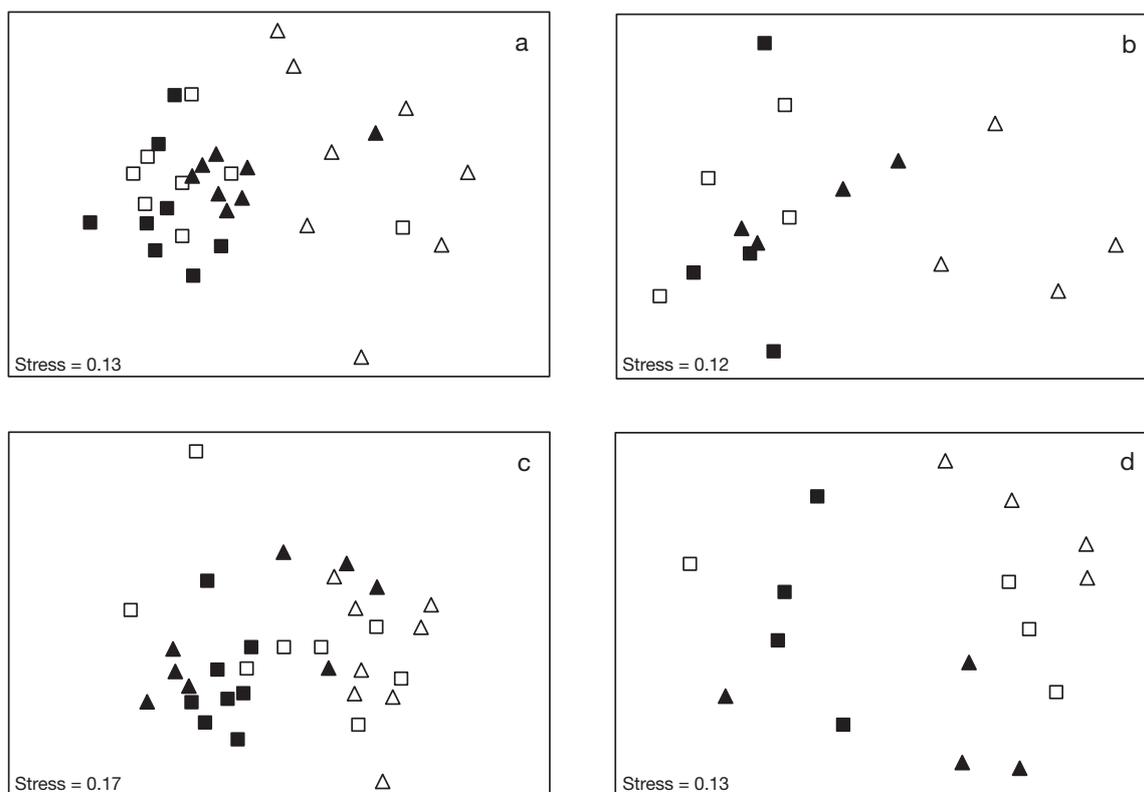


Fig. 2. Non-metric multi-dimensional scaling (nMDS) representations of community compositions in the experimental plots in (a) July 1999 at Harlyn, (b) June 2000 at Harlyn, (c) July 1999 at Polzeath and (d) June 2000 at Polzeath. ▲: + limpets, + mussels; △: + limpets, - mussels; ■: - limpets, + mussels; □: - limpets, - mussels. For (a) and (c), $n = 8$, for (b) and (d), $n = 4$

ularly in July 1999, after 9 mo, but also in June 2000, after 20 mo (Fig. 2). The most dramatic shift in community structure was caused by the removal of mussels from plots at which limpets were left in place (Fig. 2a). These plots also became considerably more variable than those in other treatments (see widely spread points, Fig. 2a). Mussels and limpets did not have interactive effects on community structure (Table 1). At the end of the experiment, plots without limpets were distinct from plots with limpets due to increases in furoid algae and *Ulva intestinalis* and reductions in barnacle cover (Table 2). Those species also contributed most to the dissimilarity of plots with and without mussels, with presence of mussels causing increased cover of algae and reduced cover of barnacles (Table 2).

At Polzeath, the loss of mussels had a more consistent effect on community structure than did the loss of limpets (Fig. 2, Tables 1 & 2). In June 2000, the presence or loss of limpets had no discernible effect (Fig. 2d, Table 1, pairwise post hoc comparisons). As at Harlyn, barnacles were again important in contributing to dissimilarity among treatments and again tended to have greater cover where limpets were absent or mussels were present (Table 2). Other taxa

influencing multivariate patterns included *Ulva intestinalis* and *Fucus vesiculosus* var. *linearis*, which, although rare, were strongly associated with mussels and the loss of limpets and *Porphyra*, which was exclusively associated with mussels (Table 2).

Table 1. Results of PERMANOVA analyses for July 1999 and June 2000. Analyses were based on Bray-Curtis similarities of square-root transformed data. * $p < 0.05$, ** $p < 0.01$ (based on Monte Carlo simulations)

Source	df	July 1999		June 2000	
		MS	Pseudo-F	MS	Pseudo-F
Site (S)	1	16977.0	13.41**	9450.7	8.58**
Limpet (L)	1	10992.0	7.02*	4809.9	1.85
Mussel (M)	1	9678.8	2.08	6823.4	6.14*
S × L	1	1566.9	1.24	2593	2.35*
S × M	1	4651.4	3.68**	1110.7	1.01
L × M	1	2335.4	1.41	2042.2	0.92
S × L × M	1	1658.2	1.31	2213.9	2.01
Residual	56/24 ^a	1265.5			

^aThere were 56 df for the residual in July 1999 and 24 in June 2000 (see 'Materials and methods: Experimental design')

Table 2. SIMPER analyses for June 2000 corresponding to significant PERMANOVA results. Listed are the 5 species in each case that contributed most to dissimilarity between groups of treatments. Abundance data shown were untransformed so that abundances/percentage covers were interpretable. The SIMPER analyses presented were based on square-root transformed data to correspond with the PERMANOVA presented in Table 1. Avg. abund: average abundance or cover (untransformed); Avg. diss: average dissimilarity among pairs of samples in terms of the species in question; Diss/SD: a measure of variation in the contribution of the species to dissimilarities between pairs of samples; Contrib%: percentage contribution of the species to the average overall dissimilarity between groups of treatments; Cum. %: cumulative contribution of the listed species

Species	Avg. abund With	Avg. abund Without	Avg. diss	Diss/SD	Contrib%	Cum%
With versus without limpets at Harlyn (average dissimilarity 65.73)						
<i>Fucus vesiculosus</i> var. <i>linearis</i>	11.73	41.58	12.52	1.22	23.47	23.47
<i>Fucus spiralis</i>	10.20	26.02	12.03	1.34	22.56	46.03
Barnacles	21.43	7.53	5.74	1.11	10.77	56.80
<i>Ulva intestinalis</i>	3.57	7.78	5.69	1.05	10.66	67.46
<i>Gibbula</i>	1.88	1.50	3.02	1.25	5.65	73.11
With versus without limpets at Polzeath (average dissimilarity 63.51)						
Barnacles	34.18	20.15	30.23	1.27	47.59	47.59
<i>Ulva intestinalis</i>	2.42	8.04	10.02	1.11	15.77	63.36
Unidentified alga	3.06	0.64	5.33	0.67	8.39	71.76
<i>Fucus vesiculosus</i> var. <i>linearis</i>	1.28	4.34	5.17	0.80	8.14	79.90
<i>Porphyra</i> spp.	2.81	2.04	4.67	0.78	7.35	87.25
With versus without mussels, both sites combined (average dissimilarity 60.73)						
<i>Fucus vesiculosus</i> var. <i>linearis</i>	16.96	12.50	11.40	1.40	18.76	18.76
Barnacles	10.91	30.74	9.64	1.16	15.88	34.64
<i>Ulva intestinalis</i>	9.63	1.28	8.13	1.30	13.38	48.02
<i>Fucus spiralis</i>	11.86	6.25	7.63	0.75	12.56	60.58
<i>Porphyra</i> spp.	3.25	0.00	4.27	0.77	7.04	67.62

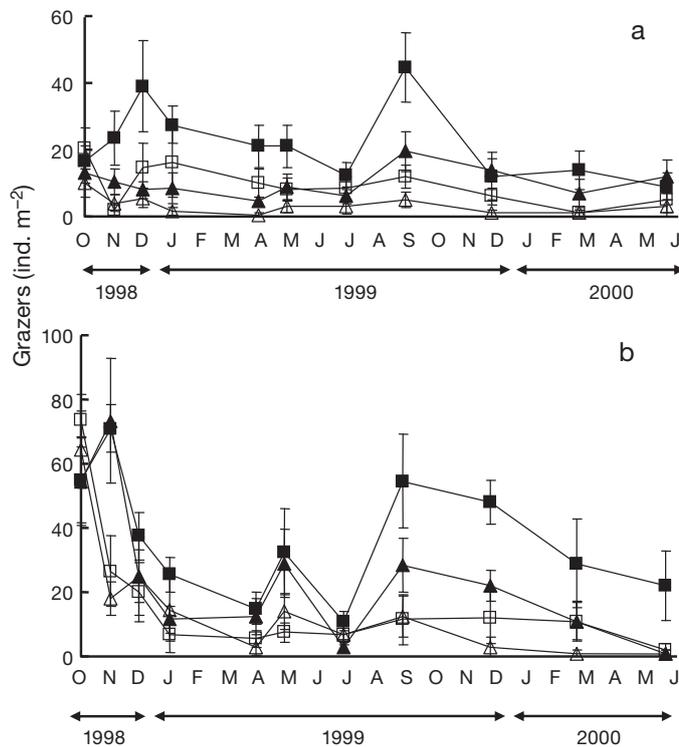


Fig. 3. Number of grazers other than limpets in plots throughout the experiment at (a) Harlyn and (b) Polzeath. ▲: + limpets, + mussels; △: + limpets, - mussels; ■: - limpets, + mussels; □: - limpets, - mussels; shown are means + SE; n = 8 until September 1999, n = 4 thereafter

Other grazers

Over the course of the experiment, more than 90% of the grazers other than limpets were topshells *Gibbula umbilicalis*, but littorinids, such as *Littorina littorea*, *L. obtusata* and *L. mariae*, were also found. Their combined numbers varied considerably through time (Fig. 3). Nevertheless, they were consistently more abundant when mussels were present than when they were absent (Table 3). On several occasions, there were trends for increases in abundance of other grazers in response to loss of limpets (Fig. 3). July 1999 was the only occasion, however, on which loss of limpets caused detectable increases in abundance of other grazers (Table 3).

Macroalgae

At each of the sites, there were no clear differences in total algal cover in the different treatments for the first few months of the experiment (Fig. 4). The treatments began to diverge in spring 1999, about 6 to 7 mo after initiation. After that time, cover at Harlyn ranked consistently greatest in plots from which limpets had been removed, i.e. greatest in -L+M plots, second greatest in -L-M plots, third greatest in +L+M plots and least in +L-M plots (Fig. 4a). At Polzeath, cover tended to be greater in treatments with mussels than in treatments without mussels; the influence of limpets was secondary (Fig. 4b). The greatest separation between treatments corresponded to the summer peak of algal cover, particularly at Polzeath (Fig. 4).

In July 1999, the removal of mussels and of limpets had significant effects on cover of fucoids at Harlyn, but not at Polzeath (Table 4a.i: S × M); at Harlyn, cover of fucoids was greater in the presence of mussels and where limpets had been lost (Fig. 5a; SNK procedure, $p < 0.01$). There were very few fucoids at Polzeath, and cover was not affected by the treatments (Fig. 5c; SNK procedure, $p > 0.05$). Mussels and limpets had interactive effects on ephemeral algae that varied from site to site (Table 4a.ii:

Table 3. Analyses of variance of abundance of grazers other than limpets in December 1998, January 1999, April 1999, May 1999, July 1999, September 1999. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Source	df	Dec 1998		Jan 1999		Apr 1999		May 1999		July 1999		Sept 1999	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Site (S)	1	5.14	6.12*	0.35	0.44	0.00	0.00	2.47	3.17	0.10	0.20	0.32	0.35
Limpet (L)	1	3.12	3.72	4.51	2.64	5.04	3.47	0.62	0.30	1.27	637.78*	1.56	1.70
Mussel (M)	1	6.70	8.18**	9.39	11.82**	6.58	12.14***	7.19	9.24**	0.41	203.19*	16.94	18.42***
S × L	1	0.62	0.74	1.71	2.15	1.45	2.68	2.10	2.70	0.00	0.00	0.59	0.64
S × M	1	0.04	0.05	0.00	0.00	0.02	0.04	0.00	0.00	0.00	0.00	0.29	0.31
L × M	1	1.66	1.98	2.66	3.34	0.00	0.00	0.36	0.46	0.93	0.87	0.25	0.28
S × L × M	1	0.03	0.04	0.45	0.56	0.03	0.05	0.01	0.02	1.07	2.09	0.44	0.48
Residual	56	0.87		0.81		0.56		0.81		0.15		0.95	

S × L × M): at Harlyn, ephemerals grew wherever mussels were present or limpets were absent, but did not grow where mussels had been removed and limpets left in place (Fig. 5a, SNK procedure, $p < 0.01$). Ephemerals grew most prolifically (mean cover 81%) where mussels were present and limpets had been removed (Fig. 5a); at Polzeath, ephemerals only grew abundantly where mussels were present, and were more abundant on mussels when limpets had been removed than when limpets had been left in place (Fig. 5c, SNK procedure, $p < 0.01$). The total cover of algae was affected by loss of limpets and by loss of mussels at each site (Table 4a.iii: S × L, M). The effect of loss of limpets was more pronounced at Harlyn (S × L, SNK procedure, $p < 0.01$) than at Polzeath (S × L, SNK procedure, $p < 0.05$).

The pattern of results was similar in June 2000, although cover of furoids at Harlyn appeared greater than in 1999 and cover of ephemerals was reduced relative to the previous year at each site (Fig. 5). Again, furoid algae were rare at Polzeath and unaffected by the treatments (Fig. 5d, Table 4b.i: S × L; SNK procedure, $p > 0.05$). At Harlyn, furoids were affected by limpets, regardless of the presence of mussels (Fig. 5b, Table 4b.i: S × L; SNK procedure, $p < 0.01$). Cover of ephemerals depended entirely on the presence or absence of mussels at each site (Fig. 5b,d, Table 4b.ii: M). Total cover of algae at Harlyn depended on the combination of limpets and mussels present (Table 4b.iii: M, S × L; SNK procedure, $p < 0.01$). At Polzeath, which was dominated by ephemerals, only the loss of mussels had a significant effect on total algal cover (Table 4b.iii: M, S × L; SNK procedure, $p > 0.05$).

Role of mussels as refuges for *Fucus* germlings

Limpets and mussels had a strongly interactive effect on recruitment of *Fucus* germlings. In

samples taken in October 1999, after 12 mo, germlings only occurred in plots with limpets when mussels were present, but were also found in plots from which mussels had been removed if limpets were absent (Fig. 6, Table 5). When limpets were present at Harlyn, disproportionately larger numbers of germlings were found on mussels within each plot than on bare rock ($\chi^2 = 140.4$, $p < 0.01$). Where limpets had been lost, however, patterns were more variable among plots, but a disproportionate number of germlings were generally found on rock ($\chi^2 = 46.9$, $p < 0.01$). At Polzeath, there were too few germlings for chi-squared analysis (Fig. 6).

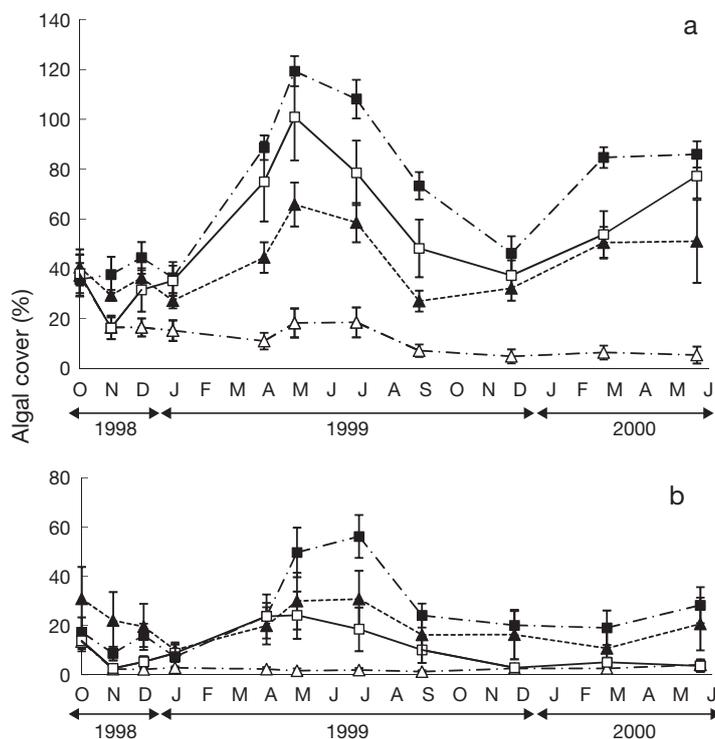


Fig. 4. Total percentage cover of algae in each treatment throughout the experiment at (a) Harlyn and (b) Polzeath. \blacktriangle : + limpets, + mussels; \triangle : + limpets, - mussels; \blacksquare : - limpets, + mussels; \square : - limpets, - mussels; shown are means + SE; $n = 8$ until September 1999, $n = 4$ thereafter

Table 4. Analyses of variance of algal cover in July 1999 and June 2000 for fucoid algae, ephemeral algae and all algae combined. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Source	df	(i) Fucoid algae		(ii) Ephemeral algae		(iii) All algae combined	
		MS	F	MS	F	MS	F
(a) July 1999							
Site (S)	1	11180.95	89.83***	5646.34	11.28**	24454.70	39.76***
Limpets (L)	1	1697.44	1.40	12559.09	14.0	23038.69	5.04
Mussels (M)	1	1914.28	2.09	34447.38	123.6	18557.93	1981.92*
S × L	1	1212.61	9.74**	896.91	1.79	4569.42	7.43**
S × M	1	913.85	7.34**	278.71	0.56	9.36	0.02
L × M	1	134.68	1.05	349.69	0.14	2.34	0.01
S × L × M	1	128.77	1.03	2414.07	4.82*	376.26	0.61
Residual	56	124.46		500.57		615.05	
Cochran		C = 0.2790		C = 0.2981		C = 0.2729	
(b) June 2000							
S	1	14087.23	50.18***	65.90	0.71	13286.95	46.14***
L	1	4748.01	16.91***	137.53	1.48	6501.42	22.58***
M	1	812.15	2.89	1394.18	15.02***	4575.90	15.89***
S × L	1	3629.73	12.93**	31.28	0.34	4974.53	17.28***
S × M	1	287.46	1.02	84.63	0.91	84.63	0.29
L × M	1	896.66	3.19	39.92	0.43	415.44	1.44
S × L × M	1	1174.79	4.18	9.42	0.10	1019.26	3.54
Residual	24	280.72		92.82		287.95	
Cochran		C = 0.4517*		C = 0.5987**		C = 0.4824*	

DISCUSSION

Our study comprised a comparatively simple experiment, focussed on 2 taxa noted for their strong, but different roles in rocky shore ecosystems. Its factorial design, however, enabled characterisation of interactive effects. By replicating it in space and extending it through time, valuable insights were gained into variation in effects of loss of key species. The sites selected were very similar to one another in physical terms and were not far apart (only 6.5 km), yet the effects of species loss varied considerably between them. Harlyn had greater algal cover, particularly of fucoids, and was more strongly affected by loss of limpets, whose influence was substantially modified by the presence of mussels. Polzeath's algal assemblage was

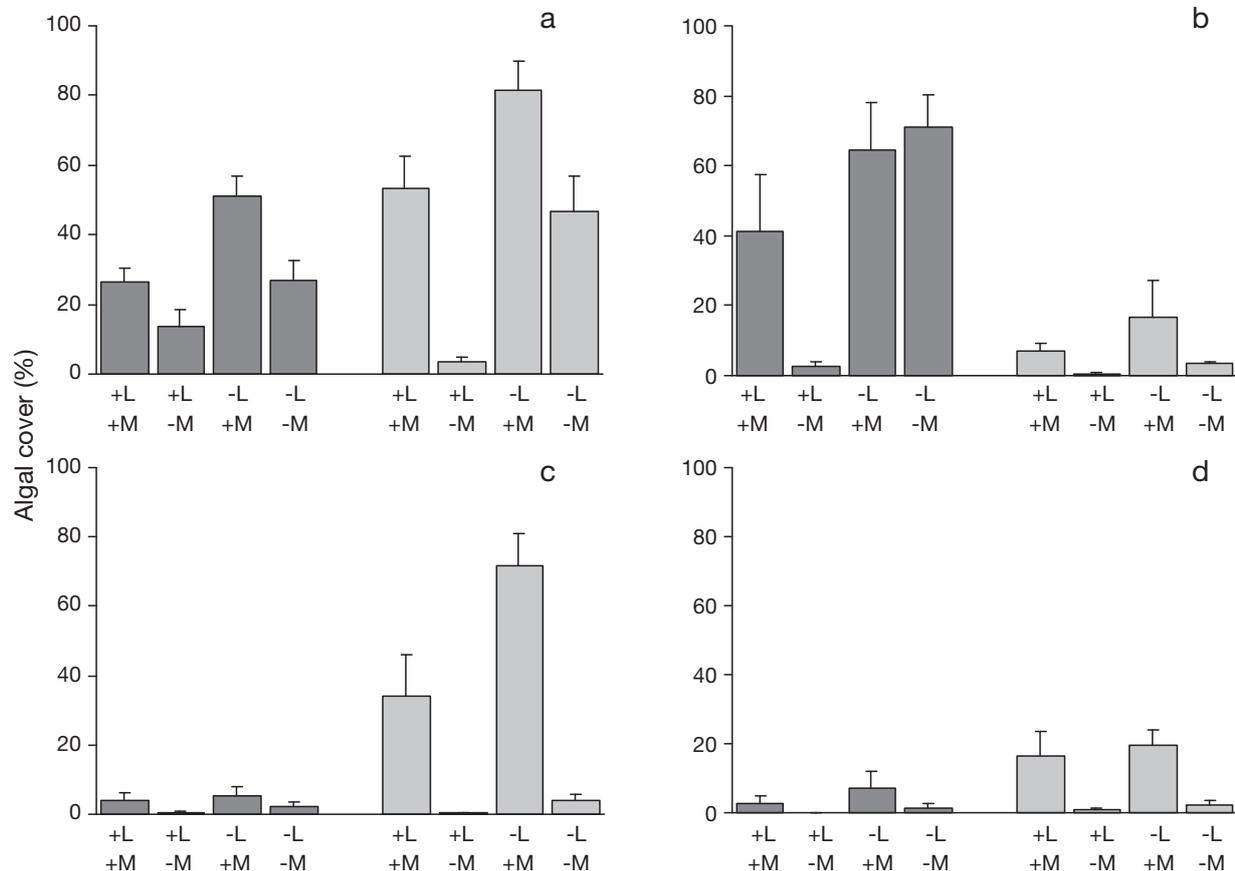


Fig. 5. Percentage cover of fucoid algae (dark shading) and ephemeral algae (pale shading) in plots at (a) Harlyn in July 1999, (b) Harlyn in June 2000, (c) Polzeath in July 1999 and (d) Polzeath in June 2000. Shown are means + SE. For (a) and (c), $n = 8$, for (b) and (d), $n = 4$. L: limpet; M: mussel; +: left in place; -: removed

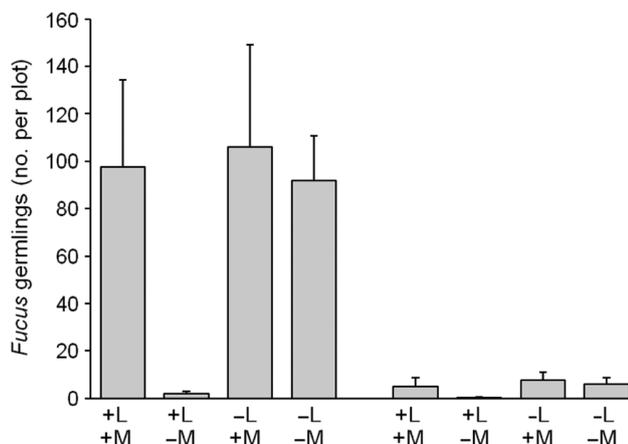


Fig. 6. *Fucus* spp. Abundance of germlings in plots at Harlyn and Polzeath in October 1999. Shown are means + SE; $n = 4$. L: limpets; M: mussels; +: left in place; -: removed

more dominated by ephemeral algae (particularly *Porphyra*) and was more strongly affected by loss of mussels than of limpets.

By sampling repeatedly over a 2 yr period, we were also able to recognise patterns of temporal variation in the natural and manipulated communities. Certainly, no effects of diversity loss were apparent during the first 6 to 7 mo of the experiment, and no significant effects would have been detected until 8 to 9 mo. This finding lends further weight to recent calls by Stachowicz et al. (2008a,b) for longer-term BEF experiments to accurately capture the responses of real ecosystems to changes in biodiversity. There was also some variation between Year 1 and Year 2, both in terms of natural algal cover and the influence of loss of limpets and mussels.

Limpets have here been shown again to be a dominant force within the grazer functional group on rocky shores (Lodge 1948, Branch 1981, Hawkins 1981, Jenkins et al. 1999a, O'Connor & Crowe 2005, Coleman et al. 2006). By using well-replicated manual removals

Table 5. *Fucus* spp. Analysis of variance of abundance of germlings counted in October 1999. Data were square-root transformed. Cochran's $C = 0.33$ (not significant). * $p < 0.05$, ** $p < 0.01$

Source	df	MS	F
Site (S) ^a	1	142.63	12.55**
Limpet (L)	1	20.56	0.94
Mussel (M)	1	14.48	2.14
$S \times L^a$	1	21.98	1.93
$S \times M^a$	1	6.76	0.59
$L \times M^a$	1	61.48	5.41*
$S \times L \times M^b$	1	13.06	1.15
Residual ^c	56	11.30	

^aTested over pooled $MS_{b+c} = 11.36$, 25 df

in open plots and monitoring responses of all grazers, the current study was able to discriminate unequivocally between the roles of limpets and other grazers. Other grazers rarely increased in abundance in response to loss of limpets and were not able to compensate for their loss. It should be noted, however, that at Polzeath the influence of limpets was limited. Assemblages and cover of algae there were more strongly affected by the presence or absence of mussels. This may be explained in part by the low levels of natural cover of furoid algae at Polzeath and lack of recruitment of canopy species (see also Coleman et al. 2006).

Where mussels were removed, the cover of barnacles (mainly *Chthamalus* spp.) increased. However, these alternative ecosystem engineers were unable to compensate in functional terms for the absence of mussels as they failed to prevent changes in algal cover and assemblage structure, despite their documented capacity to do so in the NE Pacific (Farrell 1991 and see Maggi et al. 2009 for a Mediterranean example of variation in influence of ecosystem engineers). Our study has shown that mussels can indeed play a key role on NE Atlantic shores, apparently providing a specialised habitat for some species of algae (e.g. *Porphyra* only occurred on mussels regardless of the presence or loss of limpets) and offering a refuge for algae from limpet grazing, with a consistent trend for increased algal cover in the presence of mussels. Mussels also modify physical conditions and offer a large surface area for attachment, and the value of complex microhabitats for algal recruitment has been documented by a number of authors (e.g. Norton 1983, Brawley & Johnson 1991). It is notable, however, that even within plots containing mussels, there was a significant increase in algal cover when limpets were removed, suggesting that limpets do indeed graze among mussels to some extent on these shores (see also Witman 1985, Lohse 1993, O'Connor & Crowe 2008). Although recruitment of furoid germlings varied substantially between sites, the experiment provided clear evidence for the consistent roles of limpets in controlling their survival and mussels in providing a refuge for them. In the presence of limpets, germlings grew only on mussels (see also Jenkins et al. 1999a); in their absence, they were disproportionately abundant on rock. Changes in overall diversity and community structure caused by loss of mussels are underestimated in the current study because it did not include consideration of the interstitial fauna (Lohse 1993, Seed 1996).

It is not unusual to observe differences in interaction strength between species at different locations. Such discrepancies are a reflection of the differing abiotic and biotic conditions and the relative species abundances at each site (e.g. Farrell 1991, Kim 1997). In different habitats, grazers may have different effects

(Lubchenco 1983). Johnson et al. (1997) showed that limpets had an impact on algal recruitment at some sites on the Isle of Man but not all. Similarly, manipulations of grazer density and *Ascophyllum* on sheltered shores suggested that limpets played a very limited role in structuring the mid-shore community of sheltered shores (Jenkins et al. 1999b). This is in sharp contrast to the situation on more exposed barnacle-dominated shores of northwest Europe, where the ability of limpets to limit algal recruitment means that they are often the dominant structuring organism (Southward 1964, Southward & Southward 1978, Hawkins 1981, Hawkins et al. 1992).

While the interaction examined here was the role of limpet grazing and mussel refuges in determining algal abundance, on other coastlines, different interactions between grazers and refuges are apparent. On NW Atlantic coasts, where limpets are absent, mussels are thought to competitively exclude *Fucus* from mid-shore assemblages when biotic and physical disturbances are lacking (Menge & Sutherland 1976, Petraitis 1987, Chapman & Johnson 1990). In contrast, McCook & Chapman (1991) found that *Fucus* was competitively dominant to mussels on shores in Canada during primary succession after ice scour, when grazers were rare. The impact of grazing intensity on fucoids at the different locations may have caused the differences in these results (see also Jenkins et al. 2008). In the Mediterranean, Benedetti-Cecchi et al. (1996) found no evidence of interactions between limpets and mussels in determining algal abundance, and each species had independent effects that were consistent among locations.

The magnitude of change in algal cover caused by loss of grazers and/or mussels was substantial and would undoubtedly have a significant effect on ecosystem functions such as nutrient sequestration and export of detrital material from these shores to other coastal habitats. Although more sophisticated methodologies are now available for assessing ecosystem functioning *in situ* on rocky shores (e.g. Nielsen 2001, Martins et al. 2007, Noël et al. 2010), changes in macroalgal cover provide a meaningful indication of functional impacts with potential to affect provision of goods and services by the coastal environment. Sampling a range of functional variables, however, may yield different outcomes, which themselves vary in space and time (Duffy 2009).

Characterising species according to their functional roles and interaction strength has considerable potential to improve the generality of BEF models by accounting for apparently idiosyncratic variation due to so-called selection effects (Allison et al. 1996, Petchey 2004, Crowe & Russell 2009, O’Gorman & Emmerson 2009). Nevertheless, where combinations of strong interac-

tors are lost, comparatively unpredictable interactive effects many have a major influence, as in the current study. To improve prediction of the effects of biodiversity loss, it is also necessary to characterise the factors underpinning variation in its consequences. In this case, initial variation in algal cover and assemblage structure prior to treatment appears to have been important, but these patterns may themselves have been driven by variation in the physical environment. Although theoretical models are valuable in stimulating new research pathways and synthesising existing findings, long-term experiments replicated in a wide range of environmental contexts are needed as an empirical basis for them (Stachowicz et al. 2008a,b, Boyer et al. 2009, Duffy 2009, Naeem et al. 2009).

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