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Biodiversity-productivity relations: an experimental evaluation of mechanisms

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Abstract To examine the mechanisms underlying productivity-diversity relationships, we manipulated nutrient levels in replicate small-scale artificial habitat units in the marine subtidal zone and followed the process of community assembly. In contrast to most enrichment studies, algal diversity increased in enriched habitats relative to controls along with biomass – a result that may be explained by the low nutrient status of the region. Both the total number of faunal species and the total number of individuals were also significantly greater in enriched habitats, but the relationship between algal resources and faunal diversity did not support the resource heterogeneity hypothesis.

Key words Resource heterogeneity · Nutrient enrichment · Community assembly · Marine benthos

Introduction

Perhaps the most fundamental structural attribute of any community or ecosystem is the number of species it can support. While many factors undoubtedly affect species richness, the supply of usable energy appears to be emerging as a preeminent explanation for observed variation (Wright et al. 1993). The energy-richness relationship is, however, scale dependent – on a global scale, richness increases monotonically with energy (Currie 1991), whereas at regional scales (100s of km), there appears to be a hump-shaped relationship between diversity and productivity, with greatest diversity at intermediate productivity levels (Grime 1973; Rosenzweig and Abramsky 1993). At local scales (metres to a few kilometres), most (but not all) of the observations and experimental work indicate that increases in productivity through the addition of nutrients reduce species diversity (e.g. DiTommaso and Aarsen 1989; Schindler 1990; Gough et al., in press). In the literature pertaining to marine soft sediments, the reductions in diversity with local enrichment (pollution) and the importance of algal and detrital food supply as a structuring force at regional scales are particularly well established (e.g. Pearson and Rosenberg 1987).

One mechanistic hypothesis that might explain species diversity patterns at the regional and local scales is the resource heterogeneity hypothesis (RHH) (Tilman 1987; Rosenzweig and Abramsky 1993). The RHH states that when the landscape is uniformly barren with respect to resource availability, the average location will not sustain many species and productivity will be very low. As the mean quality of the habitat increases, it is assumed that the spatial variability and diversity of resources also increases, thereby allowing both productivity and diversity to increase. Past a certain point, however, the opposite occurs and there is a reduction in resource heterogeneity and hence diversity. This reduction occurs because the species that are competitively superior under such conditions are favoured when everywhere is always a good site.

Results from nutrient enrichment studies in terrestrial plant communities are often interpreted in the light of the hump-shaped relationship between productivity and diversity (Gough et al., in press). Moreover, it has been predicted that nutrient enrichment may lead to effects consistent with the RHH by making plots more spatially homogeneous and removing poorer microenvironments upon which inferior competitors depend (Tilman 1987; Rosenzweig 1995). The RHH predicts, therefore, that increasing nutrient supplies will lead to increases in species richness at sites with low initial productivity, and decreases in species richness where resources are already abundant, and that these changes should be correlated with the heterogeneity of resources, expressed either in terms of the types of resources, or their temporal or spatial distribution. As noted above, however, most experiments conducted at local scales tend to show declines in

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diversity with enrichment. Thus, if the RHH is an adequate explanation of this response communities it implies that most studies have been undertaken against relatively rich background nutrient levels. Although most of the discussion of the RHH has focussed on plants, the hypotheses can of course apply equally to animals. In the context of this study, a corollary of the RHH would be that the diversity of fauna would show a similar response to that of the algae, owing to the greater diversity of resources and habitat architecture that a more diverse algal community would provide.

The most fundamental prediction of the RHH is that plant community structure and distribution should differ between enriched and control habitats and this will have consequent effects on the faunal community that can be supported. To test this prediction, we manipulated nutrient levels (and hence primary production) in replicate small-scale artificial habitat units placed near the sediment surface in a shallow subtidal seagrass bed. Although there have been many studies of enrichment effects in aquatic systems, none has specifically examined whether the diversity of algal resources and/or their spatial distribution changes as nutrient supplies increase and whether this could explain the diversity response of the rest of the community.

Materials and methods

Commercial pan scourers were used to construct small replicated habitat units (HUs) into which the plant and animal community could assemble. Each scourer was a 150×150 mm sheet of nylon netting material (5-mm mesh) which was tied into a three-dimensional structure to provide an open-mesh habitat. HUs were readily colonised by a rich and diverse fauna, particularly of directly developing crustacean species, which may be expected to reproduce within the habitat.

Previous workers have successfully used this technique to evaluate geographic patterns of biodiversity (e.g. Schoener 1974) and species turnover (Costello and Myers 1996). Perhaps the closest analogues of a natural community would be that associated with a kelp holdfast or the short turfing algae found on subtidal rock surfaces.

Nutrient levels were manipulated by placing commercial (Osmocote$^{(TM)}$) slow-release fertiliser (nitrate and phosphate) in a perforated vial at the centre of each HU. Osmocote technical specifications supplied by the manufacturer show that nutrient release rates from the fertiliser pellets are linear for about 120 days. A replacement schedule of 2 months ensured, therefore, that differences between treatments were maintained. For an indication of the nutrient levels obtained with the above manipulation, we analysed water sampled from within three enriched and three control HUs after leaving them at the study site for 48 h (Table 1). One-tailed *t*-tests on log-transformed data for elevated levels in HUs with fertliser showed statistically significant effects for ammonia (t=–2.37, P<0.05), nitrate (t=–3.32, P<0.05) and phosphate (t=–2.56, P<0.05), with nutrient levels generally between two and four times higher in enriched HUs. Clearly, differences in nutrient concentrations between treatments are likely to fluctuate somewhat with changes in tidal currents, but this analysis was undertaken simply to provide background nutrient levels to help put the manipulation in context.

The experiment was conducted in a shallow subtidal habitat in Boston Bay, South Australia between September 1997 and March 1998. Water depth was approximately 3 m and our study site was on the margins of a seagrass bed, 2 m from a gently sloping rock platform that supports a diverse assemblage of turf algae. A total of 40 HUs were attached to five mounting frames (0.5×1.5 m) placed haphazardly (approx. 5 m apart) within the study site (Fig. 1). Each of the eight HUs on a frame was separated from its nearest neighbour by 0.5 m. The main experiment comprised two treatment levels – continuous enrichment with 10 g of Osmocote and non-enriched (ambient) controls. Five replicates of each treatment level were sampled at 2, 4 and 6 months, giving 30 HUs in total. A single replicate from each time×treatment combination was placed on each mounting frame, allocated randomly to one of the eight available positions. Two crossover treatments were also set up with one set of five replicates (low/high) left unenriched for 2 months and then subjected to the enrichment for a further 2 before sampling, while another set (high/low) was subjected to the opposite procedure. The remaining two positions on each mounting frame were occupied by one replicate from each of these two treatments. The crossover treatment was included to test whether enrichment led to simple additive effects that were only a function of the length of exposure to higher nutrient levels, or whether it led to priority effects. One might imagine, for example, that enrichment early in the colonisation process could allow particular algal forms to establish that would otherwise be excluded. Once established, such forms may continue to persist even after nutrient levels fall. Such an effect would be similar to the facilitation sce-

Table 1 Summary of preliminary nutrient analysis of water in enriched and non-enriched habitat units after 48 h in the subtidal zone. Data are the mean±1 SE

	Ammonia (μg l^{-1})	Nitrate (μg l^{-1})	Nitrite (μg l^{-1})	Phosphorus (μg l^{-1})
Control	14.26±0.80	0.60±0.01	9.53±2.65	2.50±0.95
Nutrient	42.73±31.2	3.37±5.05	42.10±28.84	4.83±1.29

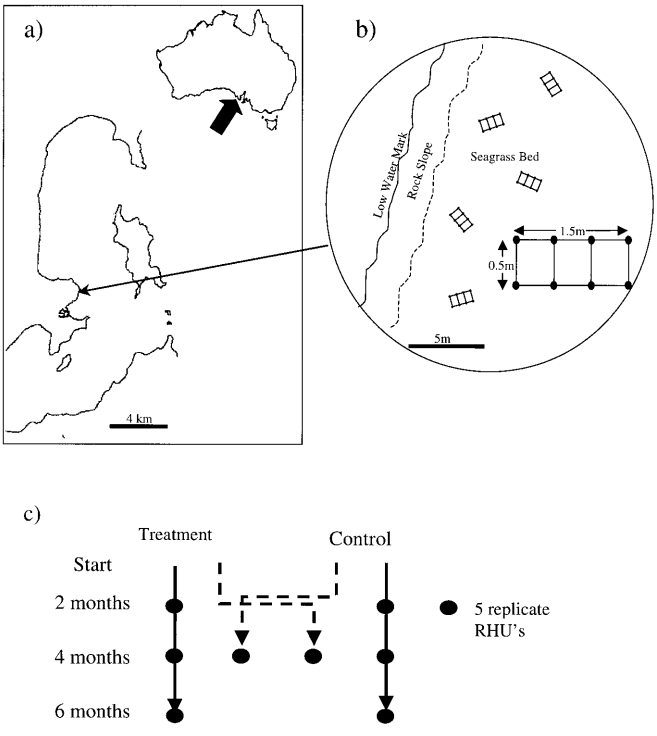

Fig. 1 **a** Location of the study site. **b** Spatial layout of frames and frame dimensions. Each frame supported eight habitat units (HUs). **c** Schematic showing the sampling schedule and experimental design

nario proposed by Connell and Slatyer (1977), except that facilitation would not be by another species, but by a fortuitous timing of favourable nutrient conditions.

At the appropriate time, each HU was removed from its mounting frame by a diver and placed immediately into an individual sample jar. One HU was, however, lost during sampling. On return to the laboratory, each HU was laid out flat in a tray and a strip of mesh (1×5 cm) was removed, placed in seawater and preserved with Lugol's iodine. This sample was used to enumerate the single-celled algae living on the surface of the mesh. The HU was then soaked in $MgCl_2$ solution for 30 min to anaesthetise any epifauna that were clinging to the mesh. The sample was then shaken and the supernatant passed through a 0.5-mm sieve along with the original water from the sample jar. The macrofaunal fractions retained were preserved in formaldehyde. HUs were also inspected visually, before preserving the mesh in formalin along with the foliose and encrusting algae attached to it.

Sample analysis

To enumerate attached macroalgae, the mesh was laid flat and the taxa occupying each intersection (node) of the mesh were identified. This approach gave approximately 1000 observations per HU. Although the three-dimensional relationship between nodes was lost when the mesh was laid flat, the method gave a good indication of the percentage cover of the various algal taxa, and the spatial pattern of algae on the mesh indicated the spatial heterogeneity of resources within and between HUs. Owing to the lack of good taxonomic keys and the difficult and time-consuming nature of algal identification, attached macroalgae could only be classified into six morphospecies categories. Percentage cover data was used to calculate conventional diversity indices (Hill's N1 and N2; Krebs 1989) while the spatial heterogeneity of algal resources was estimated by calculating for each node the number of neighbouring nodes that was occupied by a different algal taxon (hereafter denoted as Δ). Because more than one species could occupy a single node, we could find no alternative published index that provided a more suitable measure of spatial heterogeneity. In the literature dealing with landscape ecology, a number of fragmentation indices have been developed (Gustafson 1998), but in all cases indices require that sites in a landscape are only occupied by a single species or community.

The total biomass of foliaceous algae was determined by removing material from the mesh with forceps, drying and weighing. Epipsammic single-celled algae from the samples preserved in Lugol's iodine (see above) were enumerated by standard microscope counting and classified into 1 of 60 morphospecies.

Each macrofaunal sample was enumerated to species level where possible, but where the taxonomic status was uncertain, morphospecies were used. Species were also classified into functional feeding groups, based on morphology, consultation with taxonomic experts and descriptions of feeding habits available in the literature.

Statistical analysis

The effects of time and nutrient status were analysed by two-way ANOVA for the majority of response variables. Both treatment and time were treated as fixed factors. The validity of the assumptions underlying ANOVA were examined in all cases and appropriate data transformations undertaken where necessary. Where data were shown to be non-homogeneous, and data transformation failed to rectify the problem, ANOVA was still performed, recognising that only non-significant results could be clearly interpreted.

In addition to the above univariate analyses, non-metric multidimensional scaling (MDS) was used to examine community change from a multivariate perspective. An approximate test of significance for MDS was obtained using the ANOSIM randomisation routine described by Clarke (1993). Bray-Curtis dissimilarity matrices were calculated using both raw data values and fourth-root transformed data to examine the robustness of the conclusions that could be drawn.

The effects of nutrient treatments on species richness (S) was also analysed after accounting for differences in the number of individuals (N) found in each HU. This was achieved using the following analytic expression, derived by Hurlbert (1971), for the expected number of species [$E(S)$] that would be obtained if a given number of individuals (I) was drawn from a larger collection of individuals:

$$E(S) = S - \binom{I_c}{I}^{-1} \sum_{j=1}^{S} \binom{I_c I_j}{I}$$

where S=total number of species in the collection, I_c=total number of individuals in the collection, I_j=number of individuals of species j in the collection. We used this equation to rarify the data for each HU to calculate the number of species we would expect for a fixed number of individuals. Each HU was used as its own species pool, with 27 individuals drawn for all samples collected at month 4 and 122 individuals for month 6. These values corresponded to the minimum number of individuals found on a single HU at these time points. Analysis of these rarified estimates was then undertaken using ANOVA.

Results

Algal responses to enrichment

Algal biomass showed a significant response to nutrient enrichment with greater average standing stocks occurring in enriched habitat units (Table 2, Fig. 2a). In the enriched replicates, algal biomass reached its maximum at or before the first sample was taken at 2 months and appeared to decline slightly thereafter. In contrast, biomass in the control plots continued to increase until 4 months and then showed a larger decline with median

Table 2 Univariate ANOVA results for algal biomass, algal diversity and Δ (see text for explanation) (*NS* non-significant)

	df	SS	MS	*F*	*P*
Algal biomass					
Nutrient	1	0.678	0.678	9.547	<0.01
Time	2	0.126	0.063	0.888	NS
Nutrient×time	2	0.155	0.077	1.090	NS
Residual	23	1.633	0.071		
Hill's N1					
Nutrient	1	2.440	2.440	7.671	<0.05
Time	2	0.474	0.237	0.745	NS
Nutrient×time	2	0.651	0.326	1.024	NS
Residual	23	7.316	0.318		
Hill's N2					
Nutrient	1	1.250	1.250	3.979	NS
Time	2	0.332	0.166	0.529	NS
Nutrient×time	2	0.339	0.170	0.540	NS
Residual	23	7.224	0.314		
Δ					
Nutrient	1	69,974.5	69,974.5	15.067	<0.01
Time	2	22,139.5	11,069.7	2.384	NS
Nutrient×time	2	37,119.6	18,559.8	3.996	<0.05
Residual	23	106,817.2	4,644.2		

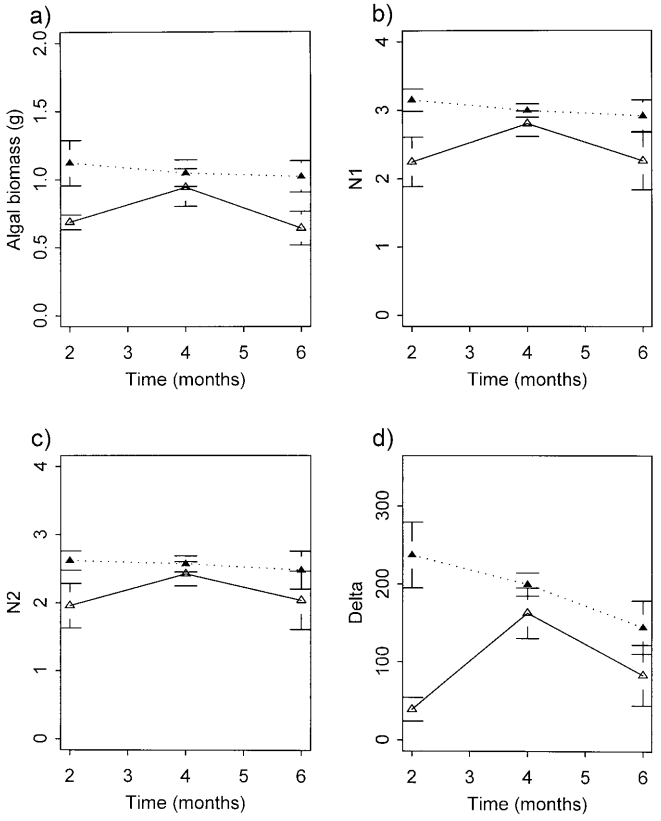

Fig. 2 Macroalgal biomass, diversity and heterogeneity in treatment and control HUs after 2, 4 and 6 months. *Filled symbols* and *dotted lines* indicate nutrient-enriched treatment (all data are the mean±1 SE).**a** Biomass. *b* Hill's N1. **c** Hill's N2. **d** Δ, the total number of neighbouring mesh nodes occupied by dissimilar algal taxa

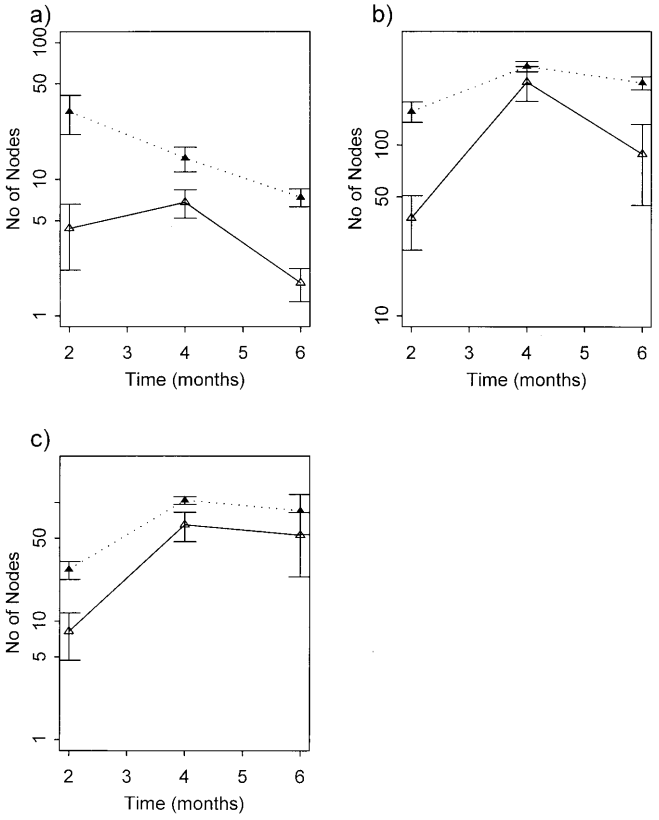

Fig. 3 Responses over time for macroalgal forms which showed a statistically significant treatment response, measured in terms of the total number of mesh nodes occupied. *Filled symbols* and *dotted lines* indicate nutrient enriched treatment (all data are the mean±1 SE). **a** Green foliose. **b** Red filamentous. **c** Red encrusting

biomass falling from 1 to 0.5 g dry weight. Despite an indication of a difference in the time course of the response between treatments, we found no statistically significant treatment×time interaction. Standard univariate measures of morphospecies diversity showed very little temporal change from 2 months to the end of the experiment (Fig. 2b,c). For both measures, mean values for controls were consistently lower than for enriched habitat units, but a statistically significant treatment effect was only detected for Hill's N1 (Table 2). This result is, perhaps, a reflection of the fact that only six morphospecies could be distinguished. Using Δ, the total number of neighbouring mesh nodes occupied by a different species as a measure of algal heterogeneity, we found a statistically significant treatment effect and a significant time×treatment interaction (Table 2, Fig. 2d).

Data for individual morphospecies of algae showed contrasting patterns (Table 3). For three morphospecies, red and brown tubular algae and brown filamentous algae, no statistically significant effects of treatments were detected. Tubular forms were uncommon on all replicates making it unlikely that we would detect a significant response. Brown filamentous algae, however, were the second most common group on average after red encrusting forms. The absence of a treatment effect in this group is unlikely, therefore, to be a consequence of lack of experimental power, but a true indication that they did not respond to enrichment. Green foliose algae were the only morphospecies to show both statistically significant time and treatment effects and a significant time×treatment interaction (Table 3, Fig. 3a), although it should be noted that variances were not homogeneous. The form of the interaction was similar to that shown for total algal biomass (compare Figs. 2a and 3a), although coverage of the green foliose form declined more steeply than biomass from 2 to 6 months. The two red algal forms that showed significant time and treatment effects (filamentous and encrusting) both showed a similar temporal response that was generally consistent between treatments, with an increase in the number of mesh nodes occupied to 4 months (Fig. 3b,c). Although variances were again non-homogenenous, in contrast to the green algae where no pattern was apparent, both red forms showed lower variability among the enriched replicates than among the controls.

Univariate measures of community response by epipsammic algae failed to reveal any statistically significant effects of enrichment or significant treatment×time

Table 3 Univariate ANOVA results for each macroalgal morphotype (*NS* non-significant)

	df	SS	MS	*F*	*P*
Red filamentous[a,b]					
Nutrient	1	52.87	52.87	6.539	<0.05
Time	2	142.19	71.09	8.793	<0.001
Nutrient×time	2	0.06	0.03	0.004	NS
Residual	23	185.96	8.09		
Red encrusting[a,b]					
Nutrient	1	207.82	207.82	18.618	<0.001
Time	2	233.17	116.59	10.445	<0.001
Nutrient×time	2	48.86	24.43	2.189	NS
Residual	23	256.73	11.16		
Red tubular[a]					
Nutrient	1	1.811	1.811	1.460	NS
Time	2	3.435	1.717	1.384	NS
Nutrient×time	2	0.416	0.208	0.168	NS
Residual	23	28.537	1.241		
Brown filamentous					
Nutrient	1	380.19	380.19	0.111	NS
Time	2	15,951.82	7,975.91	2.331	NS
Nutrient×time	2	911.14	455.57	0.133	NS
Residual	23	78,708.40	3,422.10		
Brown tubular[a,b]					
Nutrient	1	2.342	2.342	1.564	NS
Time	2	0.203	0.101	0.068	NS
Nutrient×time	2	6.885	3.442	2.299	NS
Residual	23	34.433	1.497		
Green leafy[a,b]					
Nutrient	1	41.220	41.220	27.337	<0.001
Time	2	14.207	7.104	4.711	NS
Nutrient×time	2	10.708	5.354	3.551	<0.05
Residual	23	34.681	1.508		

[a] Data were square root transformed
[b] Variances were heterogeneous by Levene's test ($P<0.05$, red encrusting and red filamentous; $P<0.01$, green leafy)

interactions. The only significant effect observed was for the total number of cells, which declined over time (data not shown). Because a large number of morphospecies were identified (in contrast to the macroalgae), we also examined the community response from a multivariate perspective using non-metric MDS and the randomisation test ANOSIM. This analysis revealed statistically significant differences between times (averaged across treatments, global $R=0.404$ for root-root transformed data, $P<0.001$) and between treatment groups (averaged across times, global $R=0.214$ $P<0.05$).

Faunal responses

Both the total number of faunal species and the total number of individuals were significantly greater in enriched than in control habitats (Table 4, Fig. 4a,b). For species richness, there was also a statistically significant time×treatment interaction. This interaction arose because the number species in enriched plots was almost constant between 4 and 6 months, while those in controls continued to increase throughout the experimental period. Unfortunately, however, data were non-homogeneous for species richness, making interpretation of statistical significance difficult. There was also no systematic pattern to the variability. Data for Hill's N1 also showed a significant treatment effect (Table 4, Fig. 4c), but N2 did not. For both these measures, the time course suggests a plateau, or possibly a decline between 4 and 6 months.

Only one of the five numerically dominant species, the polychaete *Metalaeospira tenuis*, showed a statistically significant response to nutrient enrichment (Table 5), with significantly higher numbers in the enriched habitats at 4 and 6 months (none were present in either treatment at 2 months). Although mean values for the most abundant taxon, a terebellid, were also consistently higher in the enriched habitats, and the ANOVA suggested a significant treatment effect, data were not homogeneous.

Examining the faunal response from a multivariate perspective using non-metric MDS and the randomisation test ANOSIM, we found statistically significant differences between times (averaged across treatments) for both root-root-transformed and untransformed data (global $R=0.602$, $P<0.001$, for transformed data). However, the test for a between-treatment group effect, averaged across times, was only significant for untransformed data (global $R=0.284$, $P<0.01$).

Table 4 Univariate ANOVA results for the faunal community (*NS* non-significant)

	df	SS	MS	*F*	*P*
Total number of species[a,c]					
Nutrient	1	2.915	2.915	30.425	<0.001
Time	2	47.065	23.533	245.632	<0.001
Nutrient×time	2	1.120	0.560	5.845	<0.01
Residual	23	2.203	0.096		
Total number of individuals[b]					
Nutrient	1	1.487	1.487	19.119	<0.001
Time	2	34.324	17.162	220.688	<0.001
Nutrient×time	2	0.492	0.246	3.164	NS
Residual	23	1.789	0.078		
Hill's N1[b]					
Nutrient	1	0.172	0.172	5.878	<0.05
Time	2	6.173	3.086	105.272	<0.001
Nutrient×time	2	0.029	0.014	0.493	NS
Residual	23	0.674	0.029		
Hill's N2[b]					
Nutrient	1	0.018	0.018	0.430	NS
Time	2	3.664	1.832	44.302	<0.001
Nutrient×time	2	0.009	0.004	0.104	NS
Residual	23	0.951	0.041		

[a] Data were square root transformed
[b] Data were transformed to log(x+1)
[c] Variances were heterogenious by Levene's test (P<0.05)

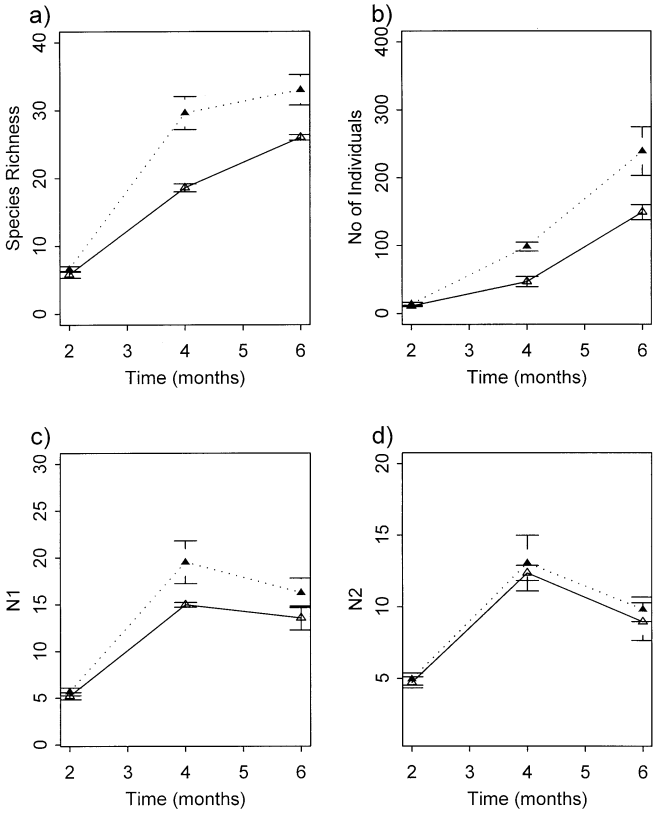

Fig. 4 The responses of the faunal community in treatment and control HUs after 2, 4 and 6 months. *Filled symbols* and *dotted lines* indicate nutrient-enriched treatment (all data are the mean±1 SE). **a** Species richness. **b** Total number of individuals. **c** Hill's N1. **d** Hill's N2

Table 5 Summary of results of univariate ANOVA for the five numerically dominant taxa in the experiment. All data were transformed to log(x+1)

Taxon	Time	Nutrient treatment	Time× treatment
Terebellid sp.[a]	***	**	NS
Metalaeospira tenuis[b]	*** (***)	** (*)	* (NS)
Ceradocus rubromaculatus[a]	*	NS	NS
Ceretonereis mirabilis[a]	***	NS	NS
Armandia maculata[a]	*	NS	NS

NS P>0.05; *P<0.05; **P<0.01; ***P<0.001
[a] Variances were heterogenous by Levene's test (Terebellid, P<0.001; *Ceradocus*, P<0.01; *Armandia* P<0.05)
[b] Variances were heterogeneous by Levene's test (P<0.001) when all times were included but were non-significant when only months 4 and 6 were used. The results for the truncated dataset are shown in parentheses

With respect to trophic groups, three of the six categories (detritivores, filter feeders and grazers) showed a statistically significant response to enrichment, each with greater numbers of individuals in enriched habitat units (Table 6, Fig. 5). Filter feeders also showed a statistically significant time×treatment interaction and they were the only group to show almost no colonisation in the first 2 months. With the possible exception of the scavenger category, the colonisation trajectory for the other groups could be most simply described as exponential, with no sign of a saturating response by the end of the experiment.

Species turnover

Turnover of fauna between time periods was determined by combining data for replicates within treatments and

Table 6 Summary of results of univariate ANOVA for each faunal functional group

Macroalgal morphotype	Time	Nutrient treatment	Time×treatment
Total number of species			
Detritivores	***	**	***
Filter feeders[a]	*** (*)	** (**)	NS (NS)
Grazers[b]	NS	NS	NS
Omnivores	***	**	NS
Predators[b]	***	*	NS
Scavengers	***	NS	NS
Total number of individuals			
Detritivores[b]	***	*	NS
Filter feeders[a,b]	*** (***)	***(**)	** (NS)
Grazers[b]	NS	*	NS
Omnivores[b]	***	NS	NS
Predators[b]	***	NS	NS
Scavengers[b]	***	NS	NS *

NS $P>0.05$; *$P<0.05$; **$P<0.01$; ***$P<0.001$

[a] Variances were heterogeneous by Levene's test ($P<0.001$) when all times were included but were non-significant when only months 4 and 6 were used. The results for the truncated data set are shown in parentheses

[b] Data were transformed to $\log(x+1)$

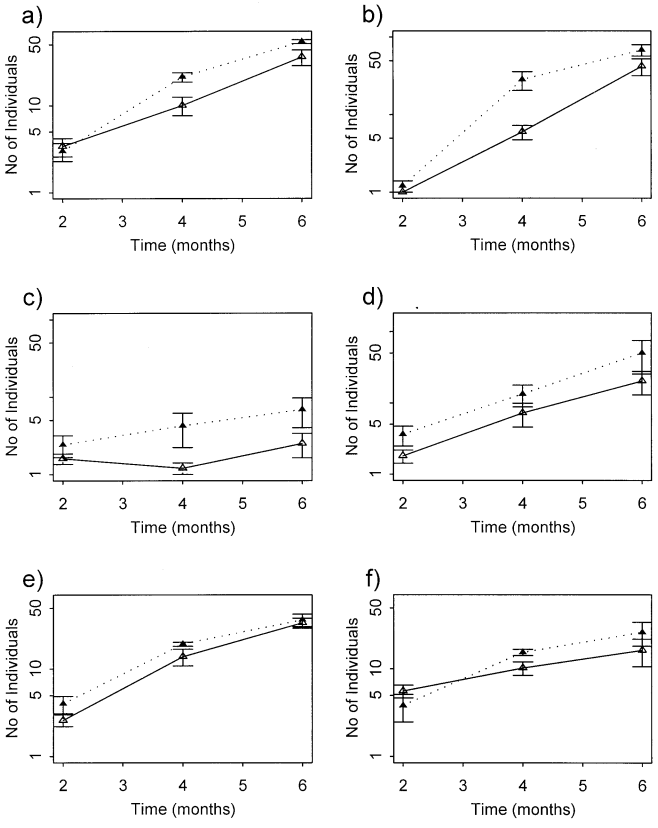

Fig. 5 The responses of faunal functional groups in treatment and control HUs after 2, 4 and 6 months. *Filled symbols* and *dotted lines* indicate nutrient-enriched treatment (all data are the mean±1 SE). **a** Detrivores. **b** Filter feeders. **c** Grazers. **d** Omnivores. **e** Predators. **f** Scavengers

calculating the number of species that occurred at both month 4 and 6, the number that were gained between months 4 and 6 and the number that were lost (Table 7). Owing to the loss of the fifth replicate for the control HUs at 6 months, only the first four replicates from the other treatment time combinations were used to calculate species turnover. Although absolute turnover was higher in enriched HUs, when these data were normalised by the total number of species found in each treatment (combined over both times), the resulting turnover percentages were remarkably similar. This result suggests that turnover rates may be related to species richness rather than productivity per se (see Discussion).

Table 7 Species turnover in enriched and non-enriched treatments between 4 and 6 months (*Both* the number of species that occurred in both time periods, *Lost* the species present at 4 months, but absent at 6 months, *Gained* species absent at 4 months, but present at 6 months). Values in parentheses are the percentage of the total number of species found in that treatment. Data were summed for the first four replicates only, to maintain equal sample sizes

Treatment	Both	Lost	Gained
Control	36 (37.1)	26 (26.8)	31 (31.9)
Nutrient	27 (39.1)	17 (24.6)	25 (36.2)

Rarefaction analysis

Perhaps the most parsimonious explanation for the difference in species richness among HUs is that it was a passive consequence of differences in the number of individuals. Trends in the expected mean number of species for enriched and non-enriched plots support this explanation. At month 4, enriched plots show identical expected means for each treatment (Table 8). Although the mean value for month 6 was higher in the enriched plot, no statistically significant differences between treatments were detected by ANOVA.

Treatment switching.

The objective of the treatment switch was to test whether the assembly process was affected by the temporal sequence of enrichment. To examine this proposition, we tested for differences between treatments for all samples taken at 4 months. Thus, we have four treatments, two with continuous supply rates (the treatment and controls analysed above) and two treatments where the levels

were switched after 2 months (enriched to control and vice versa).

With respect to macroalgae, we found no statistically significant differences between treatments for biomass, or the Hill's diversity indices (Table 9). Results for Δ, the total number of shared mesh nodes were almost significant (P=0.051), but variances were heterogeneous (P<0.05). For Biomass and Hill's N1, the results are somewhat at odds with our previous analysis, where a significant difference between continuously enriched and non-enriched treatments occurred. Our failure to detect a difference in this case, however, may reflect the lower statistical power when data for only one time point were used. For the individual morphospecies, the only statistically significant difference between treatments occurred for red filamentous algae (Table 9). A post hoc multiple-comparison test and examination of treatment means indicated that the control and high/low treatment were significantly lower in abundance than the nutrient and low/high treatment, suggesting that it is higher levels of nutrients in the later stages of the colonisation process that are most important for this taxon. For the epipsammic algae, the only statistically significant effect of the switching occurred for Hill's N1 ($F_{3,16}$=3.46, P<0.05, data not shown). In this case, however, control and high/low treatment had significantly higher values than the nutrient and low/high treatment, suggesting that higher levels of nutrients in the later stages of the colonisation process led to an increase in dominance by a few taxa.

For the fauna, only data for total number of species and individuals revealed a statistically significant difference between treatments (Table 9). In both cases, the source of significance was a difference between the permanently enriched treatment and the other three, with the order of mean values as control<high/low<low/high<nutrient.

Table 8 The expected number of species (calculated by rarefaction analysis) for the enriched and non-enriched treatments at months 4 and 6. Each HU sample was used as its own species pool from which the expected number of species was calculated assuming the number of individuals drawn for each HU was equivalent to the lowest abundance found in that month (i.e. 27 individuals for month 4 and 122 for month 6)

Treatment	Month 4	Month 6
Control	15.4±0.6	24.3±0.9
Nutrient	15.4±0.9	28.0±2.0

Relationships between algal and faunal community structure

The RHH hypothesis is predicated on the idea that species diversity is determined by the heterogeneity of re-

Table 9 Univariate ANOVA results for the treatment-switching experiment. Degrees of freedom are 3 and 16 in all cases (*NS* non-significant)

		SS	MS	F	P
Macroalgal community measures					
Algal biomass	Nutrient	0.075	0.025	0.237	NS
	Residual	1.681	0.105		
Algal NI	Nutrient	0.198	0.066	0.378	NS
	Residual	2.784	0.174		
Algal N2	Nutrient	0.235	0.078	0.541	NS
	Residual	2.313	0.145		
Algal Δ[a,b]	Nutrient	122.160	40.720	3.224	0.051
	Residual	202.099	12.631		
Abundances of individual macroalgal forms					
Red filamentous	Nutrient	17,845.75	5,948.58	4.364	<0.05
	Residual	21,808.80	1,363.05		
Red encrusting	Nutrient	68,389.8	22,796.6	2.749	NS
	Residual	132,682.4	8,292.6		
Red tubular	Nutrient	8.950	2.983	0.645	NS
	Residual	74.000	4.625		
Brown filamentous	Nutrient	3007.0	1,002.3	0.286	NS
	Residual	56,146.0	3,509.1		
Brown tubular[a]	Nutrient	2.374	0.791	0.620	NS
	Residual	20.404	1.275		
Green leafy[a]	Nutrient	4.968	1.656	0.606	NS
	Residual	43.740	2.734		
Faunal community measures					
Total number of species	Nutrient	351.400	117.133	7.732	<0.01
	Residual	242.400	15.150		
Total number of individuals	Nutrient	7,050.2	2,350.1	5.504	<0.01
	Residual	6,832.0	427.0		
Faunal N1[b,c]	Nutrient	0.164	0.055	1.408	NS
	Residual	0.622	0.039		
Faunal N2[c]	Nutrient	0.017	0.006	0.087	NS
	Residual	1.043	0.065		

[a] Data were square root transformed
[b] Variances were heterogeneous by Levene's test (P<0.05)
[c] Data were transformed to log(x+1)

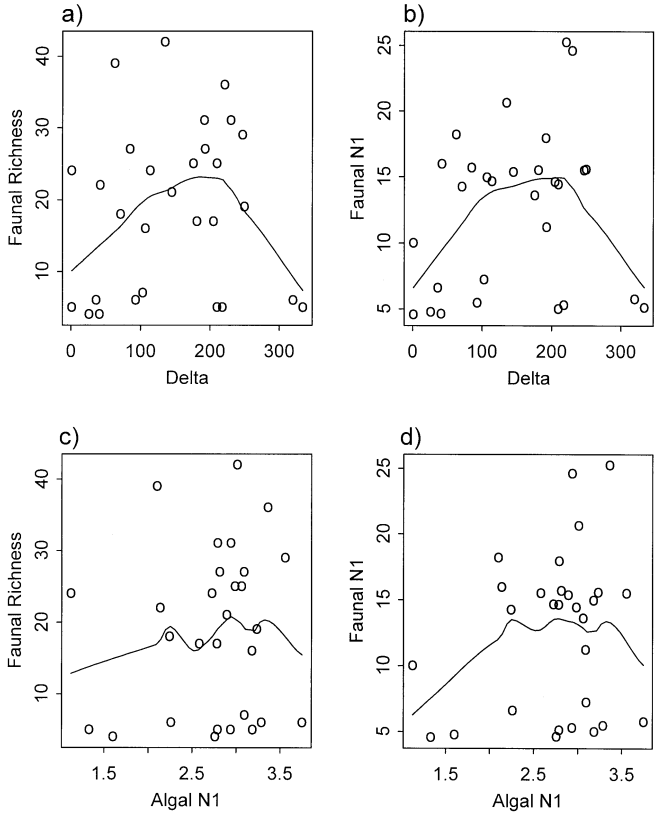

Fig. 6a–d The relationship between the diversity of the faunal community (species richness and Hill's N1) and the macroalgal community (Δ, and Hill's N1) for all HUs from the main experiment combined. Trend lines fitted by locally weighted (loess) regression, using identical smoothing parameters for each plot

sources. Since the algal community can be viewed as a resource for the fauna that inhabits HUs, it is legitimate to ask, therefore, whether the diversity of the fauna is related to the heterogeneity of the algal community. We examined this graphically by plotting measures of these two properties against one another and fitting a locally weighted (loess) smoothed trend line (Fig. 6). Our a priori expectation was that there should be a monotonic increasing trend for these plots, but two HUs with the highest algal heterogeneity had low faunal diversity, which led to a hump-shaped curve when Δ was used on the ordinate. Other measures of diversity showed similar patterns to the plots shown in the figure.

Discussion

The primary objective of this experiment was to determine whether manipulating rates of nutrient supply led to differences in the pattern of assembly for the algal community and whether this in turn led to differences in the animal community that was supported. With respect to the algal response, previous nutrient manipulation experiments in both terrestrial and aquatic systems have been rather consistent: primary productivity usually increases, but species diversity declines (Wright et al. 1993). For terrestrial systems, this pattern even seems to hold for various stages in the assembly process from new fields to woodland. For the macroalgae in this study, however, we did not observe the usual pattern, since nutrient enrichment was consistently associated with a higher mean morphospecies diversity (Fig. 2). This effect was confirmed by some (but not all) of our statistical analyses, with a significant enrichment effect for one of the standard univariate diversity measure (Hill's N1) and for our Δ measure of heterogeneity. Interestingly, this pattern in diversity was not observed with the epipsammic algae for which there was no significant effect on overall diversity, despite significantly greater numbers of cells in enriched replicates. We did, however, observe differences in community structure between treatments when multivariate statistical analysis was used.

While a decline in algal diversity with enrichment is usually observed, a few other studies have also found increases. The most notable in the present context is Pringle (1990) who, in a study of a freshwater stream system, found that the taxon diversity of algae was greater in all nutrient treatments relative to controls. The author also found that diversity was highest on enriched substrata exposed to low ambient nutrient levels. Although the RHH predicts that manipulation of productivity will lead to a change in diversity, with a hump-shaped curve, the direction of change cannot be predicted without knowing the starting point on the productivity gradient. In common with Pringle (1990), the increase in diversity we observed with enrichment, perhaps implies that ambient nutrient levels are low at our study site which is located in a region that receives minimal fresh water input (Spencer Gulf is an inverse estuary, with no major river system), and is generally considered to be an area of low productivity. Out of 13 ecosystems reviewed by Smith (1991), Spencer Gulf had the lowest total primary productivity, with a value approximately half that of the median.

For the fauna, we observed results that were broadly similar to those for algae, with overall numbers of individuals significantly higher in enriched HUs. This numerical response was mainly due to statistically significant increases in detrivores and grazers, which we would perhaps expect to be most responsive to changes in algae. However, we also observed a significant increase in filter feeders, which is less easily explained as a response to the rise in algae. With respect to faunal diversity, there were consistently higher mean levels in enriched HUs than in control plots. With one exception, however, these were not statistically significant, or were difficult to interpret due to non-homogeneous variances. Given the trends in mean values and the result from treatment switching (see below), we suspect that greater levels of replication (and hence statistical power) may have given statistically significant responses for faunal species diversity, but this awaits further experimentation. Since faunal responses will probably lag those of algae, more marked contrasts may have developed if the experiment had run for longer.

Species turnover was generally higher in enriched HUs, but this difference disappeared when data were normalised by the number of individuals present. Similarly, our rarefaction analysis suggested that any differences in species richness between treatments are likely to be directly related to the number of individuals supported by an HU. Perhaps the most parsimonious interpretation of this pattern is one in which species are sampled randomly from the species pool, with sample size (number of individuals) determined by the level of productivity.

The crossover treatment was included to test whether enrichment led to simple additive effects that were only a function of the length of exposure to higher nutrient levels, or whether it led to priority effects. Only the results for red filamentous algae showed any sign of such an effect, with higher levels of enrichment in the later half of the experiment leading to greater abundance. One possible explanation for this result is that colonisation by this algal form was largely restricted to the latter part of the experiment so that only enrichment in the latter stages could enhance abundance. Interestingly, we also observed a priority effect for the epipsammic algae, when diversity was expressed as Hill's N1. In this case, however, higher levels of nutrients in the latter stages led to a decrease in diversity rather than an increase. While this result suggests that higher levels of nutrients later in the successional sequence led to increased dominance by a few epipsammic taxa, perhaps through some form of competitive exclusion process, it may be spurious because we did not observe a nutrient response in our main experiment. For the fauna, we did not observe any priority effects, but species richness was significantly greater in the permanently enriched plot.

An interesting feature of our main experiment that may in part explain the absence of priority effects in our crossover experiment is the frequency of time and treatment effects, but the absence of statistically significant interactions in most cases. This pattern indicates that, for the most part, a relative difference between enriched and control community structure was established between 0 and 2 months, and was maintained thereafter. In other words, after 2 months, enriched and control communities followed different but "parallel" trajectories. Our crossover treatment was only implemented at 2 months, which may have been too late in the assembly process to influence the outcome. These results suggest that greater attention needs to be paid to the effects of enrichment on recruitment and early survival of algae, and imply that the magnitude of any difference established in the early stages of community assembly is preserved thereafter.

We have shown that enrichment does lead to differences in the diversity of both plants and animals in this system and that the direction of change is contrary to most studies undertaken thus far. However, it is important to recognise the short-term and small-scale nature of our experiment. As DiTommaso and Aarsen (1989) point out, effects of processes that may present themselves over longer periods of time may not occur on shorter experimental time scales. Although there was no indication that enriched and non-enriched plots were converging upon one another, the assembly process was clearly not complete by the end of the experiment; for the fauna in particular, some functional groups showed no sign of a decline in colonisation rate. One must recognise, therefore, that the longer-term temporal dynamics, including any seasonal and population dynamical effects remain unexplored. Experiments are now underway to examine these longer-term dynamics. The necessarily small spatial scale of our manipulation and the consequent caveats to interpreting the results must also be taken into account. However, although links to regional-scale phenomena are not certain, we would argue that one should give more credence to mechanistic hypotheses that are supported by small-scale experiments than those that are not.

The most fundamental prediction of the RHH – a change in diversity with enrichment – was upheld. At best, however, this is an extremely weak support of the hypothesis, and other hypotheses incorporating factors such as environmental stress (Grime 1973, 1979) or predation (Leibold 1996) could also be invoked to explain our observations. Experiments are now underway which explicitly manipulate the spatial distribution of nutrient supply on HUs. A more critical test of the RHH for the fauna is afforded by the prediction of a monotonic increasing relationship between the heterogeneity or diversity of algal resources and the diversity of the animal community. Our data do not support this prediction – instead we observed a hump-shaped relationship. Although this hump-shaped pattern was rather weak for some diversity measures and there were few observations at the upper end of the algal diversity spectrum, it would be difficult to argue from our data that algal resource heterogeneity could explain faunal responses in a manner consistent with the RHH.

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References

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143

Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. Am Nat 111:1119–1144

Costello MJ, Myers AA (1996) Turnover of transient species as a contributor to the richness of a stable amphipod (Crustacea) fauna in a sea inlet. J Exp Mar Biol Ecol 202:49–62

Currie DJ (1991) Energy and large-scale patterns of animal- and plant-species richness. Am Nat 137:27–49

DiTommaso A, Aarsen LW (1989) Resource manipulations in natural vegetation: a review. Vegetatio 84: 9–29

Gough L, Osenberg CW, Gross KL, Collins SL (in press) Fertilization effects on species density and primary productivity in herbaceous plant communities. Oikos
Grime JP (1973) Control of species density in herbaceous vegetation. J Environ Manage 1:151–167
Grime JP (1979) Plant strategies and vegetation processes. Wiley, New York
Gustafson EJ (1998) Quantifying landscape spatial pattern: what is the state of the art? Ecosystems 1:143–156
Hurlbert SH (1971) The nonconcept of diversity: a critique and alternative parameters. Ecology 52:577–586
Krebs CJ (1989) Ecological methodology. Harper and Row, New York
Leibold MA (1996) A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. Am Nat 147:784–812
Pearson TH, Rosenberg R (1987) Feast and famine: structuring factors in marine benthic communities. In: Gee JHR, Giller PS (eds) Organization of communities past and present. Blackwell, Oxford, pp 373–395
Pringle CM (1990) Nutrient spatial heterogeneity: effects on community structure, physiognomy, and diversity of stream algae. Ecology 71:905–920
Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge, UK
Rosenzweig ML, Abramsky Z (1993) How are diversity and productivity related. In: Ricklefs RE, Schluter D (eds) Species diversity in ecological communities: historical and geographic perspectives. University of Chicago Press, Chicago, pp 52–65
Schindler DW (1990) Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. Oikos 57:25–41
Schoener A (1974) Experimental zoogeography: colonization of marine mini-islands. Am Nat 108: 715–738
Smith SV (1991) Stoichiometry of C:N:P fluxes in shallow-water marine ecosystems. In: Heal OW, Grime JP (eds) Comparative analysis of ecosystems: past lessons & future directions. Springer, Berlin Heidelberg New York, pp 259–286
Tilman D (1987) Secondary succession and the pattern of plant dominance along experimental nitrogen gradients Ecol Monogr 57:189–214
Wright DH, Currie DJ, Maurer BA (1993) Energy supply and patterns of species richness on local and regional scales. In: Ricklefs RE, Schluter D (eds) Species diversity in ecological communities. Chicago University Press, Chicago, pp 66–74