

# Coral interactions and community structure: an analysis of spatial pattern

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**ABSTRACT:** The spatial patterns of the coral community along a reef flat transect at Heron Island, Great Barrier Reef, were studied at 2 scales to investigate the possible effects of coral interactions on community structure. The dominant aspect of spatial pattern at the small scale was a random mingling of the species. A minor aspect was that a few species pairs were not randomly mingled but were significantly less common as neighbours than could be expected by chance. The large-scale spatial pattern, itself decomposable into several components, was a zonation of species over the transect. None of the components of small-scale spatial pattern was strongly coupled with any components of the large-scale pattern. Only the minor nonrandom component of small-scale pattern could reasonably be the result of coral interactions. We conclude that coral interactions can play only a minor role in structuring this community.

## INTRODUCTION

Since their discovery by Lang (1971, 1973), aggressive interactions between neighbouring corals have been widely reported. Several different mechanisms are now known (e.g. Potts, 1976; Richardson et al., 1979), and a large number of species have been implicated (Sheppard, 1979). However, the ecological significance of the phenomenon remains unclear, despite the assertions of the above workers that these aggressive interactions are important structuring forces for coral reef communities. Sheppard (1979), for example, has argued that interspecific aggression is related to coral zonation, with the most aggressive species forming clearly defined, nearly monospecific zones.

The problem, in essence, is to demonstrate rather than assert the extent of the link between coral interactions and community structure. None of the studies above has demonstrated that link to our satisfaction. We address the problem directly as follows. Any ecological consequences of coral interactions must be manifested, in principle, as changes in the distribution and abundance of the corals concerned. Because they are sessile epibenthic organisms, these changes must be reflected, again in principle, in changes in their spatial patterns. Community structure may also be observed (once more, at least in principle) as spatial

pattern in benthic organisms. Therefore the putative effects of coral interactions on community structure may be counted in the common currency of spatial pattern.

The impediment to this strategy is the disparity in the characteristic scale of the 2 phenomena. Coral interactions are a small-scale phenomenon concerned with the immediate neighbourhood of a coral colony, while community structure is usually thought of as a large-scale phenomenon such as reef zonation. Our solution is to allow community structure to embrace both scales: the usual large-scale aspect and a small-scale aspect which may or may not be coupled together. Now we may investigate the supposed effects of coral interactions at the scale at which they occur and then track them if they propagate to larger scales.

This dissection emphasizes an important point. In principle, it is possible for coral interactions to affect community structure in terms of small-scale spatial pattern, but if the scales are not coupled, large-scale spatial patterns (the usual descriptors of community structure) need not be affected. Two distinct links are needed, and our analysis should isolate both. Therefore, in what follows, we first describe the spatial patterns of the coral community independently at both the large and small scales. Then we describe the coupling between the scales which could allow the propa-

gation of effects from one scale to the other. Finally we assess the possibilities for coral interactions to affect small-scale structure and for these effects to be propagated to large-scale structure.

The present study is the second of a series analysing the general problem. Preliminary results were reported at the International Coral Reef Symposium in Manila (Bradbury and Young, in press), while the third study, in preparation, will report analyses of coral reefs in 3 oceans.

### Data set

We collected information on the distribution and abundance of corals at Heron Island Reef (23°27' S, 151°55' E), a coral cay at the southern end of the Great Barrier Reef. Our survey involved 45 sites located at 50 m intervals along a 2.3 km north-south transect laid from crest to crest across the reef (Fig. 1). A total of 39 species was recorded across the transect. A description of the study area in general, the transect in particular and the species found there is given in Bradbury and Young (1981).

At each site, we recorded the occurrence of corals at

a series of equidistant points 20 cm apart along a 60 m line normal to the transect. Each of the 300 records at a site consisted of the major (in most cases, the only)

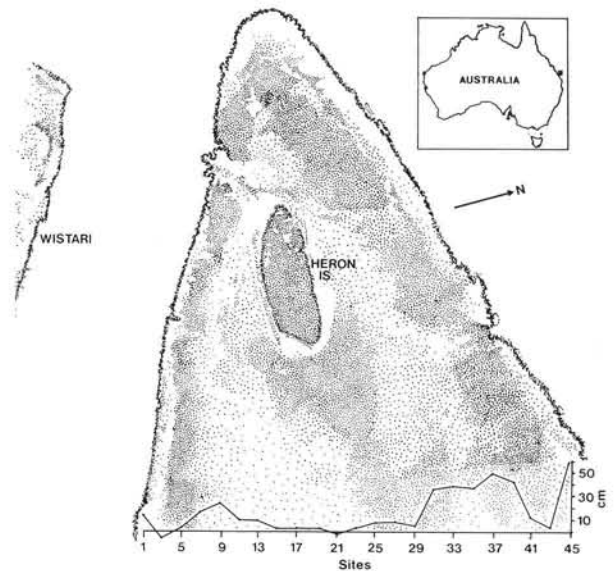


Fig. 1. Heron Island Reef. Transects, sites and relative levels. (After Bradbury and Young, 1981).

Table 1. Distribution and abundance of corals on the transect

Site	Reef zone	No. of species	No. of corals	No. of coral-coral events	Site	Reef zone	No. of species	No. of corals	No. of coral-coral events*
1	SC	17	160	91	24	L	6	28	9
2	SORF	16	81	38	25	L	6	77	41
3	SORF	23	96	50	26	PZ	7	93	58
4	SORF	24	126	71	27	PZ	6	72	42
5	SORF	17	83	31	28	PZ	6	83	49
6	SORF	14	96	53	29	PZ	10	118	78
7	SIRF	9	43	18	30	PZ	8	110	75
8	SIRF	5	19	4	31	NIRF	6	90	47
9	SIRF	6	20	8	32	NIRF	8	89	39
10	SIRF	4	5	1	33	NIRF	6	64	22
11	SIRF	3	12	4	34	NIRF	6	72	35
12	SIRF	2	7	5	35	NIRF	7	74	35
13	L	0	0	0	36	NIRF	5	62	25
14	L	1	2	1	37	NIRF	8	27	10
15	L	1	2	1	38	NIRF	7	31	13
16	L	1	1	0	39	NORF	8	34	10
17	L	2	2	0	40	NORF	10	68	38
18	L	3	3	0	41	NORF	13	84	53
19	L	0	0	0	42	NORF	17	103	75
20	L	0	0	0	43	NORF	15	118	80
21	L	4	7	1	44	NC	9	29	16
22	L	2	2	0	45	NC	2	5	1
23	L	4	9	3					

Total no. of species = 39

Total no. of records = 2,307

Total no. of coral-coral events = 1,231

SC = south crest; SORF = south outer reef flat; SIRF = south inner reef flat; L = lagoon; PZ = *Pocillopora* zone; NIRF = north inner reef flat; NORF = north outer reef flat; NC = north crest

species under a circle 10 cm in diameter centred on that point. This method, commonly used in plant ecology, prevents minor details of the spatial pattern from obscuring its major features (Pielou, 1979, p. 193). The interval chosen approximated the average colony size for the study area. When no macroscopic species occupied the circle, a bare space was recorded. We established the adequacy of the sample size in our earlier study (Bradbury and Young, 1981) by using the test of Sandland and Young (1979a, b) to show statistically significant ( $p < 0.05$ ) within-site homogeneity.

Each list of 300 records gave a list of 299 transitions between adjacent records which we have called neighbour events. Neighbour events could be of 3 types: transitions between adjacent coral records (here called coral-coral events); transitions between adjacent space records (space-space events); and transitions between a coral record and a space record in whatever order (coral-space events). Every record in the list, except the first and last, has the opportunity of being involved independently in 2 events. Thus analyses of the distribution and abundance of the events taken together with the distribution and abundance of the records have the potential to tell us much about the distribution and abundance of the corals. Table 1 summarizes the distribution of both coral records and coral-coral events across the transect, while Table 2 gives the ranked abundances of the 39 species.

The sampling method was chosen for its rapidity as well as its efficiency as described above. However it had the drawback that a set of adjacent records of the same coral species could not discriminate between one large colony and several small adjacent colonies of that species. Coincidentally, in the field, it is often hard to estimate whether or not one is observing a single colony or several colonies of the one species. Thus the sampling problem mimics a real world problem. In any case our concern is mainly focussed on the problems of the adjacency of different species where this drawback does not arise.

### Large-scale pattern of coral zonation

In our earlier study (Bradbury and Young, 1981), it seemed that the transect crossed a series of reef zones, which we had subjectively delineated (Table 1). The existence of these zones was broadly confirmed in that study by a set of multivariate analyses of the between-site patterns of coral distributions. The analyses consisted of a classification and an ordination of the 45 sites, and a diagnostic analysis of the contribution of the 39 coral species to the ordination. They revealed a series of well defined reef zones characterized by coral species groups.

Table 2. Ranked abundance of coral species

Species	Total no. of records
<i>Pocillopora damicornis</i> (Linnaeus)	750
<i>Acropora cuneata</i> (Dana)	489
<i>Porites lichen</i> (Dana)	245
<i>Acropora tubicinaria</i> (Dana)	122
<i>Seriatopora hystrix</i> Dana	108
<i>Acropora aspera</i> (Dana)	101
<i>Acropora millepora</i> (Ehrenberg)	59
<i>Acropora palifera</i> (Lamarck)	56
<i>Porites cf. annae</i> Crossland	36
<i>Goniopora tenuidens</i> (Quelch)	33
<i>Stylophora pistillata</i> Esper	32
<i>Goniastrea cf. favulus</i> (Dana)	32
<i>Favites abdita</i> (Ellis & Solander)	31
<i>Porites lutea</i> (Edwards & Haime)	29
<i>Acropora humilis</i> (Dana)	25
<i>Platygyra sinensis</i> (Edwards & Haime)	21
<i>Montipora informis</i> Bernard (rough form)	18
<i>Favia pallida</i> (Dana)	18
<i>Porites andrewsi</i> Vaughan	14
<i>Acropora hyacinthus</i> (Dana)	11
<i>Goniastrea retiformis</i> (Lamarck)	10
<i>Lobophyllia hemprichii</i> (Ehrenberg)	9
<i>Acrhelia horrescens</i> (Dana)	9
<i>Acropora austera</i> (Dana)	7
<i>Montipora informis</i> Bernard (smooth form)	6
<i>Leptastrea purpurea</i> (Dana)	5
<i>Leptoria phrygia</i> (Ellis & Solander)	5
<i>Montastrea curta</i> (Dana)	4
<i>Hydnophora microconos</i> (Lamarck)	3
<i>Plesiastrea versipora</i> (Lamarck)	3
<i>Merulina ampliata</i> (Ellis & Solander)	3
<i>Astreopora myriophthalma</i> (Lamarck)	2
<i>Symphyllia radians</i> Edwards & Haime	2
<i>Psammocora haimeana</i> Edwards & Haime	2
<i>Fungia fungites</i> (Linnaeus)	2
<i>Echinopora lamellosa</i> (Esper)	2
<i>Pavona decussata</i> (Dana)	1
<i>Acropora cerealis</i> (Dana)	1
<i>Turbinaria heronensis</i> Wells	1

The results showed that there were two major independent components of the zonation, each of which revealed different relationships with wave energy, a major forcing function on the community. One component reflected the attenuation of wave energy from reef crest to lagoon. The other reflected the different wave energy regimes on the north and the south sides of the reef – cyclones and trade winds respectively. The effect on the south or trade wind side of the reef was a rich, non-linear one. The diagnostic analysis isolated the suites of species which characterized these components.

The simple distribution data of Table 1 show that the abundance and species richness of corals reflect, as large-scale zonation patterns, the combined components just described. They are both lowest in the

lagoon and highest towards the reef crests and *Pocillopora* zone. Therefore these data may be used as simple descriptors of community structure, in contrast to the more subtle descriptors extracted by the multivariate analyses.

We will invoke both classes of descriptors in our analysis of the coupling between scales.

### Small-scale pattern of coral neighbours

The distribution of specific types of coral-coral events is embedded within the distribution of coral-coral events in general. Coral-coral events are one of the 3 classes of neighbour events that together define the distribution of corals and space. Thus the general distribution of corals and space needs to be established before the distribution of specific coral-coral events is tackled. We established it separately at each site since the abundance of corals varies greatly between sites (Table 1). Thirty-one of the sites had at least 10 coral records. In these sites, the type of intermingling of corals and space was statistically inferred from the observed distributions of runs of each of these 2 states by using a test of Pielou (1962). This makes use of the fact that clumped or aggregated corals will have longer runs than randomly mingled corals which will, in turn, have longer runs than regularly spaced corals. Twenty-nine of the 31 sites showed significantly ( $p < 0.05$ ) clumped coral distributions. Two sites (1 and 8) were random. Other studies have shown similar clumped distributions of corals (Lewis, 1970; Maragos, 1974).

We analysed the distribution of specific types of coral-coral events differently from earlier workers (Lang, 1973; Richardson et al., 1979; Sheppard, 1979), who observed only the frequency with which particular species pairs were neighbours. This observation, taken alone, is of little use since, for either species of the pair, it contains no information about that species distribution when it was not a neighbour of the other species. To allow for this, we placed this observation in the context of which species in the neighbourhood could possibly have been neighbours. Thus, we cast our observations into a contingency table of which the above observation is only 1 cell (Table 3).

Table 3 confirms that the observed frequency with which species *i* is a neighbour of species *j* at a site is only 1 of 4 classes of data needed to establish whether or not species *i* is a neighbour of species *j* more (or less) often than one would expect by chance alone. We need also to know the observed frequencies with which species *i* and *j* are neighbours of all other species in the neighbourhood except species *j* and *i* respectively, and the frequency with which all species in the neighbour-

hood except species *i* and *j* are neighbours. These 4 classes of data together exhaust the types of coral-coral events.

We then used the Fisher exact probability test (Kendall and Stuart, 1979) with the coral-coral event frequencies cast into the above contingency table to evaluate the probability of the occurrence of the

Table 3. Contingency table of coral neighbours. Note: If the *i/i* case were to be considered, *N* would need to be augmented by adding *b* (= *c* in this case) to offset the double counting problem

		Species <i>j</i>	
		+	-
Species <i>i</i>	+	a	b
	-	c	d
		N	

*a* = Number of times species *i* is a neighbour of species *j* at the site  
*b* = Number of times species *i* is a neighbour of all other species at the site except species *j*  
*c* = Number of times species *j* is a neighbour of all other species at the site except species *i*  
*d* = Number of times all species at the site except species *i* and *j* are neighbours  
*N* = Total number of neighbours at the site  
= *a* + *b* + *c* + *d*

observed frequency of species *i* as a neighbour of species *j* at a site under the null hypothesis that the species were randomly mingled. We calculated this probability value for each of a series of species pairs within each of a series of sites. Only the 27 sites with 10 or greater coral-coral events were used. These dense sites contained 1193 or 97 % of the observed coral-coral events. The sites with fewer than 10 coral-coral events were omitted because it was felt that, in these sparse sites, random mingling of species would have little biological meaning. Conspecific species pairs (i.e. *i/i* pairs) were not used in this analysis, although the test was applicable, since our sampling strategy could not distinguish between adjacent colonies of the same species and 1 large colony repeatedly sampled. Species pairs were also omitted at a site if each of the species did not have at least 1 coral neighbour. Otherwise this would have given an all-zero row or column and an indeterminate test.

A total of 545 types of *i/j* coral-coral events meeting our requirements were observed over the study area. None of these was found only in the sparse sites excluded from the analysis. The Fisher's test found 24 of these types to depart significantly ( $p < 0.05$ ) from the

null hypothesis of random mingling in at least 1 of the sites in which they were found.

Given the large numbers of Fisher's tests performed, some of these types could have achieved significance by chance alone. To test this, for each of the 24 significant types of coral-coral event, we compared the number of sites where the particular type of event was significant against the number of sites where it was not significant by using the binomial test (Kendall and Stuart, 1979). In this way, the 24 event types generated a total of 239 Fisher's tests of which 47 were significant. Of these, only 5 event types, the result of 22 Fisher's tests, had a probability ( $p < 0.05$ ) under the binomial distribution that they could have achieved significance by other than chance alone. It is clear that very few types of coral-coral event, 5 out of an observed 545, consist of other than randomly mingled species. These species pairs are given in Table 4.

The significant species pairs involved a total of 7 species. We compared the rank abundances over all sites of these species with those of nonsignificant species with a Mann-Whitney U test (Kendall and Stuart, 1979). It showed the abundances of the former to be significantly ( $p < 0.01$ ) greater than the latter. In fact, 5 of the 7 most abundant species (Table 2) in the study area were involved in significant events.

We conclude that the small scale-pattern has 3 components: (a) the corals are aggregated nearly everywhere; (b) the great majority (540 out of 545) of types of *i/j* coral-coral events are random with respect to species; (c) a small minority (5 out of 545) of types of *i/j* coral-coral events (involving some abundant species) are not random with respect to species.

### Coupling between scales

Each of the components of small scale structure is potentially the direct result of coral interactions, but for interactions to influence large-scale structure, each

affected component must be coupled with that structure. We will examine the components in turn.

The clumping effect, our first component of small-scale structure, occurred at 29 of the 31 sites tested. Thus the effect was more or less uniform over the sites containing 98% of the corals and 99% of the coral-coral events. This uniformity contrasts so strongly with the effects of all of the components of large-scale structure (any one of which displays graded or zoned changes across the sites) that statistical tests of relationship across the scales would be trivial. They are unrelated. Thus the clumping component of small-scale structure is not coupled with any of the components of large-scale structure.

Our second component of small-scale structure is the random pattern of within-site distribution of each of 540 observed types of coral-coral events. As before, since the patterns of large-scale structure are all graded or zoned, statistical tests of the relationship across scales would be trivial. None of the 540 random patterns at the small scale can be related to the observed graded patterns at the large scale.

The third component of small-scale structure – the 5 types of coral-coral events showing nonrandom patterns of within-site distributions – involves 7 species. Both the events and the species need investigation before a definitive statement of the coupling between the scales is made.

Since we had established earlier that those species were significantly more abundant than other species, we attempted to see if this significant between-species effect was translated into a between-sites effect. This would imply coupling between the scales. We examined the distribution of the 22 site occurrences of the 5 significant types of event taken together over groups of sites to see if they were differentially arrayed across the sites. We first compared the frequency of occurrence in the 10 sites with the highest coral abundance (50.8% of all corals) with the corresponding frequency in the remaining sites of lower abundance.

Table 4. Significant coral-coral neighbours found on the transect

Species x/Species y	Type of association <sup>1</sup>	No. of sites		Mann-Whitney U test <sup>2</sup>	
		significant	nonsignificant	species x	species y
<i>Acropora cuneata/Pocillopora damicornis</i>	negative	8	21	n. s.	n. s.
<i>Acropora cuneata/Symphyllia radians</i>	negative	1	0	no test	no test
<i>Pocillopora damicornis/Porites lichen</i>	negative	10	11	••	••
<i>Acropora aspera/Acropora millepora</i>	negative	10	11	n. s.	n. s.
<i>Acropora millepora/Porites lutea</i>	negative	1	0	no test	no test

<sup>1</sup> Negative = species less frequently neighbours than expected by chance  
<sup>2</sup> Test compares the abundance of a species of the pair in sites where the pair formed significant events to its abundance in sites where the pair formed nonsignificant events. See text for details  
n. s. = not significant,  $p > 0.05$ ; •• = significant,  $p < 0.01$

The frequencies did not differ significantly ( $p > 0.05$ ) by the  $\chi^2$  test (Kendall and Stuart, 1979) from the 50.8:49.2 ratio expected under the null hypothesis of random occurrence of significant types of events in sites. We then compared the frequencies of occurrence in 3 groups of zones: the southern reef crest and flat (Sites 1 to 12); the lagoon and *Pocillopora* zone (Sites 13 to 30); and the northern reef flat and crest (Sites 31 to 45). Again the frequencies did not differ significantly ( $p > 0.05$ ) by the  $\chi^2$  test from the frequencies expected under the null hypothesis of random occurrence. We did not classify the sites into more than 3 groups because, with the limited number of occurrences, we had reached the practical limits of the  $\chi^2$  test. We must conclude that the significant within-site spatial patterns of the 7 species taken as a whole are not translated into significant between-site differences.

There remains the possibility that the distribution of particular species might be related to the occurrence of significant types of events. This could provide a large-scale consequence of coral interactions, albeit not a consequence in terms of community structure. Of the 5 significant species pairs, 3 were sufficiently common for analysis. These comprised 5 of the 7 species. For each species of a pair, we compared, using the Mann-Whitney U test, the abundance of the species in sites where the pair formed significant events to its abundance in sites where the pair formed nonsignificant events. The results (Table 4) showed that only 2 species, *Pocillopora damicornis* and *Porites lichen*, were found to significantly ( $p < 0.05$ ) differ in abundance between sites and then only in events with each other. Both species were significantly more abundant in sites where they formed significant coral-coral events.

Now we need to ask if this significant effect is translated into a significant community structure effect. That is to say, can any of the components of large scale community structure be related to the significant disjunct distributions of the 2 species apparent at both the small and large scales? Our earlier diagnostic analyses (Bradbury and Young, 1981; Table 5) quickly confirm that they cannot. These analyses reveal that each of the 2 species are well correlated with the first ordination vector (accounting for 53% of the variance). But they also reveal that the correlations with this vector are of the same sign (*Pocillopora* =  $-0.80$ , *Porites* =  $-0.55$ ) indicating that the 2 species tend to be found in the same areas on the large scale. That is, they tend to covary at this scale.

We conclude that of the 3 components of small-scale structure only 1 shows any evidence of large-scale consequences, and it is more easily interpreted as a species specific effect than a community structure effect.

### Potential effects of coral interactions on small-scale structure

Any of the spatial patterns of coral neighbours, our descriptors of small-scale community structure, could be the consequence of coral interactions. However there may be other more parsimonious possibilities. These need to be exhausted first.

The clumping component operates uniformly over the study area. Thus it cannot be correlated with a species specific neighbour effect. This is because the multivariate analyses of the large-scale structure clearly show that different parts of the transect are characterized by different suites of species. It seems more likely to us that the clumping is produced by something much less subtle than species specific coral interactions, perhaps by the physical imperatives of water flows.

The great majority of types of coral-coral events are random with respect to species. It is conceivable that this effect could be the direct result of coral interactions. But if this is so, then the consequences of coral interactions cannot be distinguished from the sum of random effects on the corals producing random neighbours. Thus, whether or not coral interactions produce random neighbours, the parsimonious explanation is that they do not. Again, it seems likely to us that, in fact, they do not, and that the random neighbours express the combined workings of many effects.

The small minority of types of non-random coral-coral events are likely candidates as consequences of coral interactions. They are all negative types of association (Table 4) in the sense that the species involved are found together significantly less often than one would expect by chance alone. It is quite plausible that the typically aggressive interactions between corals could have produced such a result. This explanation is strengthened by the fact that 2 of the species are significantly more abundant when they are not neighbours.

### CONCLUSION

It is clear from the analyses above that neither the link between coral interactions and small-scale structure nor the link between small- and large-scale structure is strong. This obviously implies that coral interactions are likely to play only a minor role in community structuring. Nor is this implication relieved by restricting our conception of community structure. If we ignore the large-scale spatial patterns and focus on small-scale spatial patterns as our major descriptors of community structure, we may ignore the weak coupling between scales but we are still confronted by the

weak possible effects of coral interactions at the small scale. Again, we may argue restrictively that community structure patterns are no more than the sum of species patterns, that there are no emergent community properties. This restriction still confronts us with the fact that the distribution of only 2 species could have been affected by coral interactions.

We conclude that, while there is a minor component of small-scale structure which is a likely effect of coral interactions, even this component is weakly coupled to large-scale structure. Thus it is unlikely that aggressive interactions between corals play more than a minor role in structuring this reef community.

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