

REPORT

Co-occurrence of ectoparasites of marine fishes: a null model analysis

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Abstract

We used null model analysis to test for nonrandomness in the structure of metazoan ectoparasite communities of 45 species of marine fish. Host species consistently supported fewer parasite species combinations than expected by chance, even in analyses that incorporated empty sites. However, for most analyses, the null hypothesis was not rejected, and co-occurrence patterns could not be distinguished from those that might arise by random colonization and extinction. We compared our results to analyses of presence–absence matrices for vertebrate taxa, and found support for the hypothesis that there is an ecological continuum of community organization. Presence–absence matrices for small-bodied taxa with low vagility and/or small populations (marine ectoparasites, herps) were mostly random, whereas presence–absence matrices for large-bodied taxa with high vagility and/or large populations (birds, mammals) were highly structured. Metazoan ectoparasites of marine fishes fall near the low end of this continuum, with little evidence for nonrandom species co-occurrence patterns.

Keywords

Species co-occurrence, ectoparasite communities, niche saturation, competitive interactions, null model analysis, presence–absence matrix

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INTRODUCTION

Parasite communities are model systems for tests of community structure because community boundaries are discrete and replicate communities of the same host species can be collected (Holmes & Price 1986). Holmes & Price (1986) suggested that parasite communities fall between extremes of interactive and isolationist communities. Interactive communities are characterized by dense populations, frequent colonization and strong species interactions, whereas isolationist communities are characterized by low population densities and weak species interactions. Kennedy *et al.* (1986) hypothesized that helminth communities associated with endotherms are more highly structured than those associated with ectotherms.

However, it is difficult to test such generalizations because there are few taxa for which comprehensive data sets are available that can be compared with standardized analysis. Metazoan ectoparasites of marine fishes are one of these groups (Rohde *et al.* 1995). In this study, we analysed with null models (Gotelli & Graves 1996) a set of presence–absence matrices for ectoparasites of 45 marine fish host species. These analyses revealed little evidence for nonrandom

community patterns, reinforcing previous conclusions that these parasites live in largely unstructured assemblages (Rohde 1979, 1989, 1992, 1993, 1994, 1998a,b, 1999; Rohde *et al.* 1998; Morand *et al.* 1999). We compared our results to null model analyses of other taxa (Gotelli & McCabe, in press) and found that co-occurrence patterns of marine fish ectoparasites were more random and unstructured than co-occurrence patterns of birds and of mammals. These comparisons suggest that patterns of animal community structure reflect an ecological continuum: animals with little vagility and/or small individual or population size live in largely empty niche space and are less subject to structuring mechanisms (competition, facilitation, heterogeneity in infection) than animals that are large or live in large populations with much vagility and are closer to saturation (Rohde 1980).

METHODS

Parasite sampling

Parasite occurrence data from the head and gills of 45 fish species were used for this study (Table 1; for details see Rohde *et al.* 1995; Kleeman 1996). Almost all

Table 1 Significance test results for fish parasite presence–absence matrices.

Host species	Number of parasite species	Number of hosts	Number of occupied hosts	Checker fixed–fixed	Checker fixed–eq	C-score fixed–fixed	C-score fixed–eq	Combo fixed–fixed	Combo fixed–eq	V-ratio fixed–eq
<i>Zeus faber</i>	3	22	13	ns	ns	ns	ns	ns	ns	ns
<i>Trigla lucerna</i>	4	28	25	ns	ns	ns	ns	ns	ns	ns
<i>Trichiurus lepturus</i>	4	60	46	ns	ns	ns	ns	ns	ns	ns
<i>Syngnathus griseolineatus</i>	4	103	61	ns	ns	ns	ns	ns	ns	ns
<i>Siganus lineatus</i>	14	16	16	ns	ns	ns	ns	ns	ns	ns
<i>Seriola lalandi</i>	4	21	21	ns	ns	S	A	ns	ns	A
<i>Sebastes pinniger</i>	4	24	22	ns	ns	ns	ns	SS	S	ns
<i>Sebastes maliger</i>	4	28	28	ns	ns	ns	ns	ns	ns	ns
<i>Sebastes flavidus</i>	3	22	8	ns	ns	ns	ns	ns	ns	ns
<i>Sebastes brevispinnis</i>	3	24	24	ns	ns	ns	ns	ns	ns	ns
<i>Sebastes alutus</i>	4	32	32	ns	ns	ns	ns	ns	ns	ns
<i>Scomberoides tol</i>	6	23	23	ns	ns	ns	ns	ns	ns	ns
<i>Scomber scombrus</i>	3	83	62	ns	ns	ns	ns	ns	ns	A
<i>Scomber japonicus</i>	6	98	55	ns	ns	ns	AA	ns	ns	A
<i>Rhabdosargus sarba</i>	5	77	52	ns	ns	ns	AA	ns	ns	AA
<i>Prionotus nudigula</i>	4	66	45	ns	ns	ns	ns	ns	ns	ns
<i>Platichthys stellatus</i>	6	23	23	ns	ns	S	ns	AA	AA	ns
<i>Nemadactylus macropterus</i>	6	25	25	ns	ns	ns	ns	ns	ns	ns
<i>Mugil cephalus</i>	4	59	47	ns	ns	ns	SS	ns	ns	SS
<i>Monodactylus argenteus</i>	3	35	34	ns	ns	ns	ns	ns	ns	ns
<i>Micropogon furnieri</i>	5	31	24	ns	ns	ns	AA	ns	ns	AA
<i>Megalaspis cordyla</i>	5	13	13	ns	ns	ns	ns	ns	ns	ns
<i>Macrourus holotrachys</i>	3	20	13	ns	ns	ns	ns	ns	ns	ns
<i>Lethrinus nebulosus</i>	15	14	14	ns	ns	ns	ns	ns	ns	ns
<i>Lepidotrigla argus</i>	2	44	3	ns	ns	ns	ns	ns	ns	ns
<i>Lepidopsetta bilineata</i>	6	38	27	ns	ns	ns	ns	ns	ns	ns
<i>Hoplichthys haswelli</i>	4	26	23	ns	ns	ns	ns	ns	S	ns
<i>Hippoglossoides elassodon</i>	4	47	25	ns	ns	ns	ns	ns	ns	ns
<i>Herklotsichthys castelnaui</i>	4	118	37	ns	ns	SS	ns	ns	ns	ns
<i>Helicolenus papillosus</i>	4	29	17	ns	ns	ns	ns	ns	ns	ns
<i>Girella tricuspidata</i>	6	44	22	ns	ns	ns	ns	ns	ns	ns
<i>Genypterus blacodes</i>	3	25	20	ns	ns	ns	A	ns	ns	A
<i>Gasterosteus aculeatus</i>	5	20	18	ns	ns	ns	ns	ns	ns	ns
<i>Gadus morhua</i>	3	44	34	ns	ns	ns	ns	ns	ns	ns
<i>Gadus macrocephalus</i>	4	20	16	ns	ns	ns	A	ns	ns	ns
<i>Damalichthys vacca</i>	5	21	20	ns	ns	ns	ns	ns	ns	ns
<i>Cymatogaster aggregata</i>	4	40	39	ns	ns	ns	A	ns	ns	ns
<i>Chlorophthalmus nigripinnis</i>	5	34	14	ns	ns	ns	A	ns	ns	A

Table 1 (continued)

Host species	Number of parasite species	Number of hosts	Number of occupied hosts	Checker		C-score		Combo		V-ratio
				fixed–fixed	fixed–eq	fixed–fixed	fixed–eq	fixed–fixed	fixed–eq	
<i>Centroberyx affinis</i>	3	37	19	ns	ns	ns	ns	ns	ns	ns
<i>Bodianus vulpinus</i>	6	31	31	ns	ns	ns	ns	ns	ns	ns
<i>Atractoscion aequidens</i>	5	26	16	ns	A	S	ns	SS	ns	ns
<i>Sillago flindersi</i>	4	40	40	ns	ns	ns	ns	ns	ns	ns
<i>Sillago ciliata</i>	5	40	18	ns	ns	ns	ns	ns	ns	ns
<i>Leihrinus miniatus</i>	22	41	41	ns	SSS	ns	ns	ns	ns	ns
<i>Leihrinus seminatus</i>	15	14	14	ns	ns	ns	ns	ns	ns	ns

Each row represents a different host species sampled. The first three columns give the number of parasite species recorded, the number of host individuals examined, and the number of host individuals occupied by one or more parasite species. The remaining columns give the co-occurrence index used and the null model used for analysis (see text for details). The entries represent significant deviations from the null hypothesis. “S” indicates cases in which the pattern was significant segregation and less co-occurrence than expected by chance (one-tailed test). “A” indicates cases in which the pattern was significant aggregation and more co-occurrence than expected. S or A = $P < 0.05$; SS or AA = $P < 0.01$; SSS or AAA = $P < 0.001$; ns = not significant ($P > 0.05$).

specimens of each host species were collected from a well-defined locality at one time. Only freshly caught fish were used and were placed immediately after capture in plastic bags containing 10% formalin. The few parasites that dropped off the hosts were collected from the sediment in bags (see Table 2 in Rohde *et al.* 1995). Therefore, any significant error due to loss of parasites is unlikely. Fish were brought back to the laboratory, dissected and their gills and head examined for parasites under a dissecting microscope. Parasites were stained, mounted and identified (for details see Rohde *et al.* 1995). All metazoan parasite taxa were recorded, including Copepoda, Monogenea Polyopisthocotylea, Monogenea Monopisthocotylea, Trematoda, larval Cestoda, Isopoda and Branchiura. Specimens were identified by KR and various experts.

Data organization

For each host species, we organized the data as a presence–absence matrix, a fundamental unit of study in community ecology and biogeography (McCoy & Heck 1987). In such a matrix, each row represents a different parasite species and each column represents a different individual host. The entries in the matrix represent the absence (0) or presence (1) of a particular parasite species in a particular host (Simberloff & Connor 1979). We chose to analyse presence–absence data, rather than abundance data, because there is less uncertainty in measuring occurrence than in measuring abundance, and because we wanted to compare our results quantitatively to analyses of presence–absence matrices for other taxa (Gotelli & McCabe, in press). Haukialmi & Henttonen (1993) analysed coexistence patterns of helminth parasites of bank voles (*Clethrionomys glareolus*), using both presence–absence data and abundance data. They obtained similar results with both sets of analyses, suggesting that the use of presence–absence data will not necessarily mask nonrandom community patterns.

Measuring community structure

We used four indices to quantify patterns of parasite community structure: the number of species combinations, the number of checkerboard species pairs, the C-score and the variance ratio. Each index is a single number that measures pattern for an entire presence–absence matrix. Gotelli (2000) describes the statistical properties of these indices and their performance in null model tests. Here we describe how each index is calculated and what the expected value of the index is in a competitively structured community.

Table 2 Summary of null model tests for deviations of fish parasite presence–absence matrices from randomness.

Index	Null Model	Average SES	<i>P</i>	Adjusted <i>P</i>
Checker	Fixed–fixed	–0.007 (A)	0.946	1.000
Checker	Fixed-	–0.117 (A)	0.357	1.000
C-score	Fixed–fixed	0.351 (S)	0.034	0.236
C-score	Fixed-	–0.438 (A)	0.024	0.167
Combo	Fixed–fixed	–0.563 (S)	0.001	0.004
Combo	Fixed-	–0.646 (S)	0.0005	0.001
V-ratio	Fixed-	0.414 (A)	0.021	0.146

The first column gives the index used, the second column the null model algorithm, and the third column the average SES for the 45 presence–absence matrices. “S” indicates a deviation in the direction of segregation (less species co-occurrence) and “A” indicates a deviation in the direction of aggregation (more species co-occurrence). The *P*-value is the significance level for the test of the null hypothesis that the SES = 0.0, and the adjusted *P* is the value after the Bonferonni correction for multiple tests. Checker = number of species pairs with exclusive checkerboard distributions; Combo = number of distinct species combinations. Fixed–fixed = null model in which matrix row and column sums are preserved; Fixed = null model in which column totals of the matrix are allowed to vary freely. See text for description of indices and null model algorithms.

The number of checkerboard species pairs

Diamond (1975) introduced the idea of “checkerboard distributions” of species pairs that never co-occur because of competitive interactions. We counted the number of such unique checkerboard pairs in each matrix. In a competitively structured community, there should be more such checkerboard pairs than expected by chance (Gotelli 2000; Gotelli & McCabe, in press).

The C-score

Stone & Roberts (1990) introduced the C-score as an index that quantifies the degree of species co-occurrence. The index quantifies the number of “checkerboard units” that can be found for each species pair. A checkerboard unit is a 2×2 submatrix of the form 01/10 or 10/01. For each species pair, this number is $(R_i - S)(R_j - S)$, where R_i is the number of occurrences (= row total) for species i , R_j is the number of occurrences for species j , and S is the number of sites in which both species occur. The C-score is the average number of checkerboard units for each unique species pair. The larger this index, the less co-occurrence of species pairs (Haukialmi & Henttonen 1998; Gotelli & Arnett 2000). The C-score measures the extent to which species pairs are segregated across a set of sites, but it does not require complete segregation, as in the more stringent checkerboard pattern.

The number of species combinations

In a community of n species, there are 2^n possible species combinations, including the combination in which none of

the species are present. We counted the number of species combinations by scanning the columns of each matrix for distinct arrangements. In a competitively structured community, not all species combinations will be represented (Diamond 1975), although differences in site quality will also cause some combinations to be missing (Pielou & Pielou 1968).

The V-ratio

Schluter (1984) popularized the variance ratio (*V*-ratio) as a measure of community structure. This ratio is the variance of the column sums to the sum of the row variances. If the average covariance between species pairs is 0.0, the ratio will equal 1.0. Strong positive covariance will increase the ratio above 1.0, and strong negative covariance will generate values less than 1.0. Alternatively, if the variance in the number of species per site (= column sum) is small, the variance ratio will be small (Dobson & Pacala 1992; Haukialmi & Henttonen 1993; Forbes *et al.* 1994). Unlike the other three indices, the variance ratio does not measure patterns of co-occurrence within the matrix, but is instead determined exclusively by the row and column sums of the matrix (Gotelli 2000). Consequently, the fixed–fixed null model (described below) is not meaningful for this index because it does not vary the row and column totals of the matrix.

Null models

For each matrix, we calculated the observed index, and then compared it with the index for 5000 randomly assembled null communities; results were similar with as few as 1000

and as many as 10 000 replications. We used two null algorithms for each comparison:

Fixed–fixed (ff)

In this algorithm, both the row and column sums of the original matrix are fixed, so that differences in the frequency of occurrence of each parasite species (row sums) and differences in the number of parasite species per host (column sums) are preserved (Connor & Simberloff 1979).

We created null matrices with a sequential swap algorithm by repeatedly swapping randomly selected submatrices of the form 01/10 (Stone & Roberts 1990; Manly 1995). Each swap generates a new matrix, but preserves the row and column totals of the matrix. For each analysis, we used 30 000 initial random transpositions, then retained each matrix created by the next 5000 transpositions. Gotelli (2000) compared the results of the sequential swap algorithm to other algorithms and found that this null model had good statistical properties. It was not prone to Type I errors (falsely rejecting the null hypothesis), but had good power for detecting nonrandomness. Sanderson *et al.* (1998) criticized some aspects of this algorithm, but a careful re-analysis confirms that it is statistically well behaved (Gotelli & Entsminger, in press).

Fixed–equiprobable (fe)

In this algorithm, the elements in each row of the matrix are reshuffled, with no constraints on the column totals. The occurrences of each parasite species are randomly distributed among hosts, and there are no limits to the number of parasite species that can be supported by a single host. This null model assumes that all hosts are equivalent, whereas the fixed–fixed model preserved differences among hosts in the number of parasites species they contained. Like the fixed–fixed algorithm, the fixed–equiprobable model also has good statistical properties (Haukisalmi & Henttonen 1998; Gotelli 2000).

Once each set of null communities was created, we measured the co-occurrence index for each of the 5000 null communities and created a histogram of the index values. This histogram represents the distribution of the index under the null hypothesis. We then measured the tail probability for obtaining the observed index or a more extreme value, a standard procedure for Monte Carlo analysis (Manly 1991). We used a new set of random matrices for each test we conducted. Analyses were conducted with EcoSim 6.10 software (Gotelli & Entsminger 2001).

Empty sites

“Empty” sites are records in which no parasites were found in a host. Such empty sites can be potentially important in null model analysis (Reddingius 1983), but they are rarely

recorded in presence–absence matrices (Gotelli & Graves 1996). This study provides an opportunity to examine their effect on null model analysis. Empty sites may be interpreted in two ways: as hosts that are not suitable for colonization, or as hosts that could be used, but, by chance, were not colonized. The fixed–fixed null model treats the empty sites as unusable, whereas the fixed–equiprobable null model treats the empty sites as random absences. In the fixed–equiprobable null model, empty sites in the real data sets may be occupied in the null communities, whereas in the fixed–fixed null model, empty sites in the real data sets remain empty in the null communities.

Meta-analyses

To compare results across studies, we calculated a standardized effect size (SES) for each matrix. The SES measures the number of standard deviations that the observed index is above or below the mean index of the simulated communities. The null hypothesis is that the average SES measured for the set of 45 presence–absence matrices is zero.

In meta-analysis, an “effect size” is calculated by standardizing the difference between “control” and “treatment” groups (Gurevitch *et al.* 1992). In our analysis, the observed index (I_{obs}) corresponds to the “treatment” group. The mean of the 1000 indices from the simulated communities (I_{sim}) corresponds to the “control” group, because it reflects the pattern expected in the absence of species interactions. We used the standard deviation of the 5000 indices from the simulated communities (s_{sim}) to calculate the SES as:

$$\text{SES} = (I_{\text{obs}} - I_{\text{sim}}) / s_{\text{sim}}$$

We used a one-sample *t*-test to test the null hypothesis that the SES for each index did not differ from 0.0. Assuming a normal distribution of deviations, approximately 95% of the SES values should fall between –2.0 and 2.0. With four indices and two null models, there were seven such tests (the *V*-ratio cannot be tested with the fixed–fixed null model), so we used the Bonferonni procedure to correct the individual tail probabilities of these tests.

Sample size effects

Although the SES should, in theory, control for differences in matrix size, we wanted to ensure that the patterns did not merely reflect variation in the number of hosts examined or the number of parasite species collected. For each analysis, we tested for correlations between SES and the number of rows (= parasite species) and number of columns (= individual hosts) in the matrices. With seven null model tests, there were 14 regression analyses. Of these, only one

significant result emerged: a positive correlation between SES and the number of parasite species for the C-score using the fixed–fixed model ($r = 0.358$, $P = 0.016$). However, even this pattern was due entirely to a single outlier with high species richness, the host species *Letbrinus miniatus* (22 species, $SES = 3.408$). With this single datum removed, there was no relationship between species number and SES ($r = 0.101$, $P = 0.513$). We conclude that patterns in our data do not merely reflect variation in the dimensions of the data matrices.

RESULTS

Number of checkerboard species pairs

The number of checkerboard pairs did not differ significantly from the null expectation for either of the two null models (Fig. 1, Table 2), and the null hypothesis was never rejected for any of the host species (Table 1).

C-score

With the fixed–fixed null model algorithm, the SES of the C-score was significantly larger than expected ($P = 0.034$), whereas with the fixed–equiprobable null model the SES of the C-score was significantly smaller than expected ($P = 0.024$; Fig. 2). Neither effect was significant after using the Bonferonni correction (Table 2). For the fixed–fixed model, there were five host species in which the null hypothesis was rejected ($P < 0.05$; one-tailed test), and there were nine host species for the fixed–equiprobable null model (Table 1).

Number of species combinations

For both null models, the SES of the number of species combinations was significantly less than expected by chance, even after the Bonferonni correction (Fig. 3, Table 2). The null hypothesis was rejected for three host species in the fixed–fixed model and four host species in the fixed–equiprobable model (Table 1).

V-ratio

The SES of the variance ratio was significantly larger than expected ($P = 0.021$; Fig. 4), although the effect was not significant after the Bonferonni correction (Table 2). The null hypothesis was rejected for eight host species (Table 1).

DISCUSSION

Overall, we did not find that communities of fish parasites were highly structured in a consistent fashion. In the

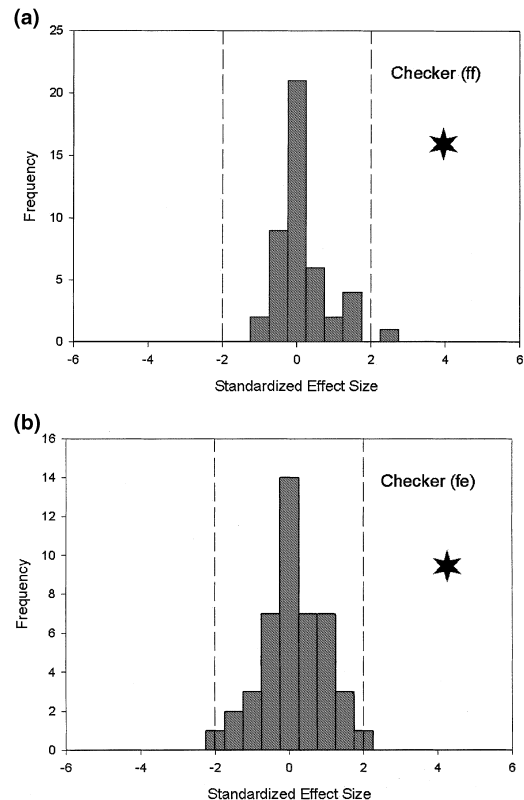


Figure 1 Histogram of SES of the number of species pairs forming checkerboard distributions. Each observation is an SES for a different host-parasite presence–absence matrix (host species list in Table 1). The dashed vertical lines indicate ± 2 standard deviations, the approximate boundaries for statistically significant patterns. The null hypothesis is that the observed distribution does not differ significantly from a mean of 0.0. In all figures, the asterisk indicates the tail of the distribution for which species co-occurrence would be less than expected by chance, indicating competitive structuring. See Table 2 for observed means and Table 1 for a list of host taxa. (a) Fixed–fixed null model algorithm; (b) fixed–equiprobable null model algorithm. See text for a description of indices and algorithms.

fixed–fixed model, the C-score was statistically greater than zero (Fig. 2a), which is consistent with the predictions of Diamond's (1975) model. However, the pattern is significant in the opposite direction when empty hosts are included in the analysis (Fig. 2b). There was no evidence that species are unusually segregated into perfect checkerboard distributions (Fig. 1). The variance ratio test also gave a result indicating aggregation, not segregation, of parasite species in hosts (Fig. 4). This result is consistent with positive pairwise associations reported in earlier studies (Rohde *et al.* 1994, 1995). None of the patterns in our study were especially strong, and the significance values were not maintained after correction for multiple testing (Table 2). Although

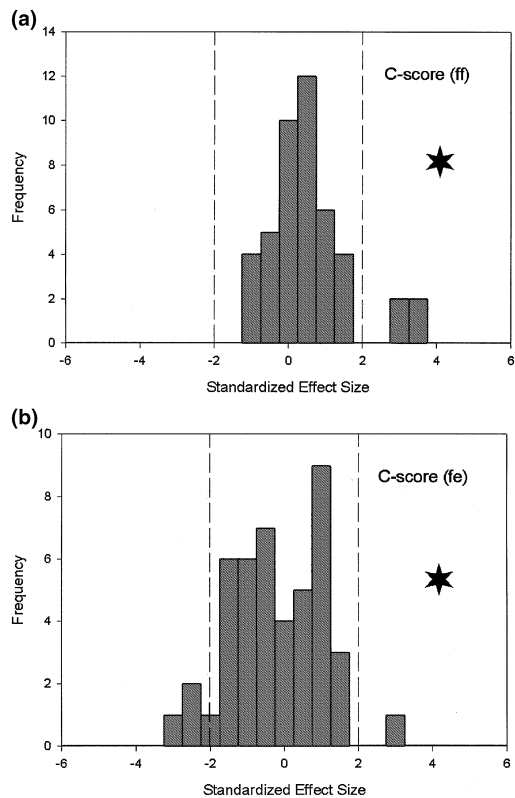


Figure 2 Histogram of SES of C-score. (a) Fixed–fixed null model algorithm; (b) fixed–equiprobable null model algorithm. See Fig. 1 legend for details.

presence–absence matrices for some host species do show strong patterns of nonrandomness (in both positive and negative directions; Table 1), the null hypothesis cannot be rejected for the majority of host species tested.

The one strong pattern that emerged with both null models is that there are fewer parasite species combinations represented in these data than expected by chance (Fig. 3). Diamond (1975) argued that such a pattern reflects competitive structuring, although Pielou & Pielou (1968) cautioned that a similar pattern can arise if there are differences in the suitability of sites (= hosts) for colonizing species. Because it is difficult to distinguish between these alternative hypotheses, we cannot determine the extent to which this negative association is due to competitive interactions among species or to isolation of parasite species. Both isolation and intensification of parasites among hosts are possible since it is highly unlikely that all hosts will have identical patterns of feeding or habitat use, thus ensuring infection with exactly the same parasites.

Overall, our results reinforce other evidence that parasites of marine fishes live in assemblages largely unstructured by interspecific competition: prevalence and intensity of infections are low (Rohde 1979); many species are unaffected

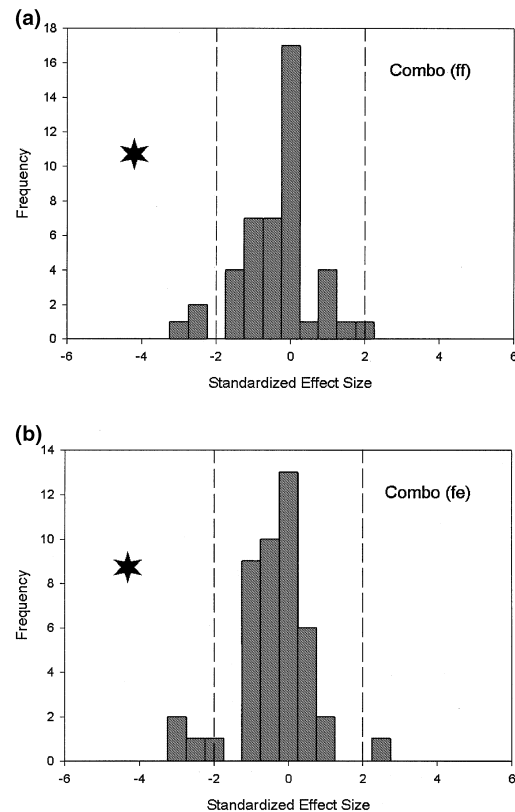


Figure 3 Histogram of SES of number of species combinations. (a) Fixed–fixed null model algorithm; (b) fixed–equiprobable null model algorithm. See Fig. 1 legend for details.

by the presence (Rohde 1991) or morphology (Rohde & Hobbs 1986; Rohde 1989) of other potentially competing species; interspecific aggregation is reduced relative to intraspecific aggregation (Morand *et al.* 1999); there is little evidence for nestedness (Worthen & Rohde 1996; Rohde *et al.* 1998); positive species associations are much more frequent than negative associations (Rohde *et al.* 1995); hyperparasitism is rare (Rohde 1989); and these assemblages do not conform to the community “packing rules” of Ritchie & Olff (1999; Rohde 2001). The conclusions are well supported by various methods for marine ectoparasites, although some authors have interpreted findings on other parasite groups differently (references in Holmes & Price 1986).

Null model and randomization tests have revealed patterns of species association in other parasite assemblages (Lotz & Font 1985; Moore & Simberloff 1990; Sousa 1992, 1993; Lafferty *et al.* 1994; Haukisalmi & Henttonen 1998). Larval trematode parasites of marine snails exhibit strong evidence of species segregation (Sousa 1993; Lafferty *et al.* 1994), and multiple infections are usually less frequent than expected by chance (Kuris & Lafferty 1994). Intestinal

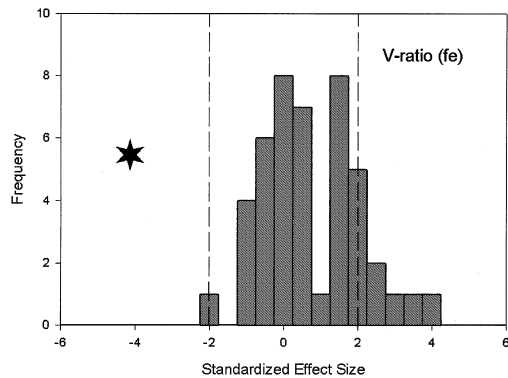


Figure 4 Histogram of SES of variance ratio, using fixed–fixed null model algorithm. See Fig. 1 legend for details.

helminths of bobwhite quail show evidence of both positive and negative species associations, but do not conform entirely to existing models of parasite community structure (Moore & Simberloff 1990). However, both the larval trematode and the intestinal helminth assemblages are characterized by much higher infection intensities and prevalences than are marine ectoparasites of fishes; our analyses using the SES give equal weight to high- and low-prevalence assemblages.

Using statistical methods similar to those in this study, Gotelli & McCabe (in press) analysed 96 published presence–absence matrices for free-living organisms and compared deviations from randomness among different taxonomic groups. Strong positive deviations characterized presence–absence matrices of birds and mammals, but weak (nonsignificant) positive deviations characterized presence–absence matrices of herps. The C-score SES for this large set of fish parasite presence–absence matrices is relatively small, closer to that of herps than to those of mammals and birds (Table 3).

Compared with birds and mammals, marine fish ectoparasites (and herps) have relatively small body size and poor vagility. As a consequence of these life history

Table 3 Null model comparisons of SES among taxa.

Taxon	SES	N
parasites of fish	0.35	45
herps	1.29	15
birds	3.65	25
mammals	3.10	16

The SES reported is for the C-score using the fixed–fixed model; N = number of presence–absence matrices analysed. The parasite data are from the current study. Other values are adapted from Gotelli & McCabe (in press). Effect sizes are lowest for small-bodied taxa with low vagility and/or small populations (parasites of marine fish, herps) and highest for large-bodied taxa with high vagility and/or large populations (birds, mammals).

characteristics, ecological niches are not saturated and population densities are chronically low, so that interspecific interactions are weak and do not have much influence on community structure (Rohde 1980, 1991). Although interspecific competition is important in some parasite assemblages (Sousa 1992, 1993; Lafferty *et al.* 1994), our null model analyses reinforce other evidence that assemblages of marine fish parasites are largely unstructured by species interactions (Rohde 1979, 2001; Morand *et al.* 1999).

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