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A general test of the interactive-isolationist continuum in gastrointestinal parasite communities of fish

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Abstract

Parasite communities are generally believed to lie somewhere along the interactive-to-isolationist continuum, i.e. from rich assemblages of species with high colonisation rates in which interspecific interactions play an important structuring role, to species-poor assemblages where interactions are unlikely. This framework has become one of the paradigms of parasite community ecology. There is, however, no objective way of ranking a set of parasite communities in terms of the extent of interactivity among their constituent species. Here, we propose a simple index of interactivity based on the general likelihood of species co-occurrence, and thus on the potential for interactions, and we apply it to component communities of gastrointestinal helminth parasites from 37 species of marine fish hosts. The index essentially collapses several features of parasite communities thought to influence the degree of interactivity into a single number independent of the number of hosts examined or the total number of species in a component community. The range of values obtained here suggests that the potential interactivity in helminth communities of fish covers almost the full spectrum of possibilities, i.e. from isolationist to highly interactive communities. Although derived from presence/absence data only, the index correlates relatively strongly with the total parasite abundance per host, as well as the total prevalence of infection and the mean infracommunity richness. In other words, it captures properties of the community that influence interactivity. The use of the index in comparative studies may help in determining whether interactive helminth communities are, as widely believed, more common in endothermic vertebrate hosts than in fish hosts.

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1. Introduction

The search for the determinants of parasite community structure has long been, and still remains, at the core of ecological parasitology (see [Holmes, 1987](#); [Esch et al., 1990](#); [Simberloff and Moore, 1997](#); [Poulin, 2001](#)). Numerous early studies focused on niche overlap between co-existing parasite species as a way to evaluate the role of interspecific interactions in the structure of parasite communities (e.g. [Holmes, 1973](#); [Stock and Holmes, 1988](#); [Patrick, 1991](#)). Recently, several studies have looked instead at either the patterns of parasite species associations among host individuals and whether they depart from null models (e.g. [Poulin and Valtonen, 2001](#); [Gotelli and Rohde, 2002](#); [Morand et al., 2002](#)), or the repeatability or predictability

of parasite community structure among different populations of the same host species (e.g. [Carney and Dick, 2000](#); [Poulin and Valtonen, 2002](#)). One theoretical framework has influenced much of the research on parasite community ecology, underpinning many of the empirical studies mentioned above: the interactive versus isolationist classification of parasite communities ([Holmes and Price, 1986](#); [Esch et al., 1990](#); [Sousa, 1994](#)). Now viewed as extremes of a continuum rather than a dichotomy, the interactive-versus-isolationist view of parasite communities remains the only conceptual template available to interpret the huge variability observed in natural assemblages of parasites.

[Holmes and Price \(1986\)](#) characterised interactive parasite communities as consisting of many species, most with high host colonisation rates. These features result in infracommunities (sensu [Bush et al., 1997](#)) with many co-occurring parasite species, several having large intra-population sizes, and thus niche overlap and interspecific

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interactions are potentially extensive. In contrast, isolationist communities consist of fewer species, most with limited colonisation abilities; their infrapopulations are generally small and only rarely co-occur with those of other species in the same host at intensities high enough to result in significant interactions (Holmes and Price, 1986). Most parasite communities fall somewhere between these two extremes of a continuum. Although useful in principle, this conceptual framework has one major drawback: when applied to real data, the classification of parasite communities along the continuum has been the matter of subjective judgement. There is no single measure of the general degree of interactivity in parasite communities that can be used to classify or compare communities in a more objective manner. If such an index were available, it could be applied to large data sets in order to identify key parameters associated with different types of parasite communities.

Here, we develop such an index and apply it to a large data set on the gastrointestinal helminth communities of several species of marine fish from coastal Brazil. The index we propose is derived from an earlier one put forward by Dove (1999) and is based on a similar reasoning. If we accept that certain properties of parasite communities are very likely associated with the probability that different helminth species will co-occur and interact inside the same host individual (i.e. the same infracommunity), we can collapse these features of parasite communities into a single number. This number essentially measures the overall likelihood of many species co-occurring in the same host, across the entire community. In other words, it measures the potential for interactions, rather than interactivity per se.

Our objectives here are twofold. First, we describe the index of interactivity and its computation, and present the logic behind it. Second, we use it to quantify the degree of interactivity in the helminth communities of several species of marine fish, and we then determine whether two key descriptors of parasite communities, species richness and total abundance, correlate with the index. Our analysis provides the first quantitative test of the interactive-isolationist community continuum across a large sample of component communities, as well as providing a tool for further analyses of this kind.

2. Methods

2.1. The index of interactivity

The index of interactivity, CC_{50} , is derived from that proposed by Dove (1999) and is based on a similar set of arguments. It measures what percentage of the infracomunities (host individuals) in a sample must be examined for 50% of the parasite species in the component community to be found, when the infracomunities are ranked from most species-poor to most species-rich. In cases of ties (i.e. two or more infracomunities with equal species richness),

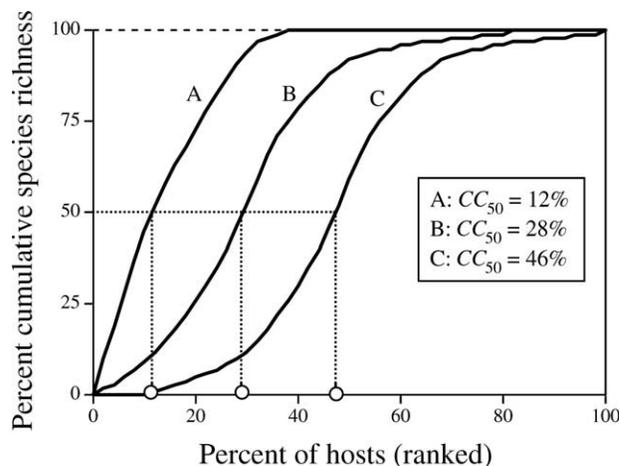


Fig. 1. Hypothetical species accumulation curves as a function of the number of hosts examined, for three parasite component communities (A, B and C), illustrating how to compute the index of interactivity, CC_{50} . Both the component community richness and the number of hosts examined are expressed as percentages; hosts, or infracomunities, are ranked from most species-poor to most species-rich (see text). The index CC_{50} is simply the percentage of hosts that need to be examined for 50% of the parasite species in a sample to be found.

the ones including species already found are ranked before the ones with new species. In other words, the ranking serves to delay the finding of rare species for as long as possible. Uninfected hosts (infracommunity species richness = zero) are also included, and have thus the highest ranks. Graphically, the ranks are represented as percentages of the total number of infracomunities (Fig. 1). The index CC_{50} therefore allows comparisons between component communities that differ widely with respect to either or both component community richness and number of infracomunities (host individuals) sampled, because the latter two variables are expressed as relative (percentage) and not absolute values. Note that the independence of CC_{50} from host sample size can break down if very small samples are used to compute the index; we recommend that the index CC_{50} should only be applied to samples including at least 30 hosts, i.e. 30 infracomunities.

The index actually measures the overall tendency of the different species in a component community to co-occur in the same infracomunities. Low values of CC_{50} are indicative of interactive parasite communities, whereas high values of CC_{50} are to be expected in isolationist communities. When component community richness is plotted as a cumulative function of the percentage of hosts (or infracomunities) examined, the curve can take a range of shapes but will eventually reach an asymptote representing the total parasite species richness of the component community (Fig. 1). The gradient of the curve is related to mean infracommunity richness: curves with steeper slopes (e.g. curve A in Fig. 1) generally indicate that the average richness of infracomunities is high, as one does not need to examine many hosts to find most parasite species in

the component community; in contrast, curves with gentler slopes (curve C in Fig. 1) are typical of lower mean infracommunity richness. As argued by Dove (1999), mean infracommunity richness is, to some extent, a reflection of the degree of niche overlap between parasite species in a community. Of course, the realised overlap between different parasite species depends on the ability of parasites to restrict their niche when co-occurring with other species, but all else being equal richer infracommunities should have a greater degree of niche overlap than poor infracommunities. Thus, steeper slopes and lower values of CC_{50} are indicative of the potential for species interactivity. The average prevalence of infection of the different parasite species in a component community is also accounted for by the index. For instance, in Fig. 1, curves B and C have identical shapes, but curve C is shifted to the right because about 10% of hosts in this component community are uninfected. Uninfected hosts are included in the computation of the index because they represent unused resource patches, and the latter are not expected to be as common in interactive communities as in isolationist communities. Component communities dominated by common (high-prevalence) species, that co-occur frequently in the same host individuals, are more likely to be interactive than those in which rare species, with low prevalences, form a greater proportion of total richness. Thus, values of CC_{50} are lower when parasite prevalences are higher (Fig. 1). In essence, the index CC_{50} collapses several properties thought to be associated with the degree of interspecific interactions in parasite communities into a single number that can be used for comparative purposes.

2.2. Data on fish parasite communities

All fish were collected by local fishermen from the coastal waters off the state of Rio de Janeiro, Brazil (latitude 21–23°S), during the period 1991–2002. Fish identification and taxonomy follow Figueiredo and Menezes (1978, 1980, 2000) and Menezes and Figueiredo (1980, 1985). Each individual fish was measured (total length) and examined for gastrointestinal helminth parasites, using standard parasitological methods. Washings from the lumen of the gut were passed through a sieve (154 μm mesh size) to recover even the smallest parasites. The helminths recovered consisted of trematodes, cestodes, nematodes, and acanthocephalans. All fish dissections and collection of the parasites were made using the same methods, and all parasite identifications were carried out or confirmed by the same person (J.L.L.). Thus, the data do not suffer from the problems associated with data sets compiled from different sources and based on different methods. The entire data set is shown in Table 1.

For each host species, we recorded the following variables: (1) the total number of fish examined; (2) the proportion of fish infected by at least one parasite species; (3) the mean length of the fish examined; (4) the total

number of parasite species, or component community species richness; (5) the proportion of core species in the component community, i.e. helminth species with a prevalence of 60% or more in the sample; (6) the mean number of parasite species per host individual, or mean infracommunity richness; (7) the mean number of parasites of all species combined per host individual, or mean total abundance; and (8) the index CC_{50} , computed as described above for each host species. Only component communities including at least four species of gastrointestinal helminths were included in the analyses.

Except for mean infracommunity richness and values of the CC_{50} index, all variables required transformation to meet the criteria for parametric tests. The total number of fish examined, the mean length of the host fish species, the component community richness, and the mean total parasite abundance were log-transformed, whereas the proportion of fish infected by at least one parasite species and the proportion of core species in the component community were arcsin-transformed.

3. Results

Our analysis included data from 37 fish species, representing 22 different families (Table 1). Among these 37 different parasite component communities, component community richness ranged from four to 13 helminth species, and values of the index CC_{50} ranged across most of the spectrum of possible values, from 3.6 to 86.7%. The frequency distribution of CC_{50} values provides a hint of bimodality (Fig. 2); however, this should be interpreted as a lack of sufficient data rather than as evidence of discrete categories of interactive and isolationist communities. Because the index is based on percentages and not on actual numbers of host individuals examined, CC_{50} values did not correlate with the number of fish examined ($r = 0.025$, $P = 0.885$) across the 37 fish species, nor did they correlate with mean fish length ($r = -0.026$, $P = 0.878$).

Because the index is also based on the cumulative percentage of parasite species and not on cumulative numbers, it should distinguish between potential interactivity and component community richness per se, the latter often thought to be a feature of interactive communities. In this study, component communities with few helminth species could generate both low and high index values (Fig. 3A), as did richer component communities (Fig. 3B). The figure shows that similar CC_{50} values can be obtained regardless of the size of the total pool of helminth species from which infracommunities are formed. Nevertheless, CC_{50} values were still correlated with component community richness, although not very strongly (Fig. 4A). The positive relationship between these two variables means that CC_{50} values tend to be high in species-rich component communities,

Table 1

Summary of the key descriptors of the gastrointestinal helminth component communities from the 37 fish species included in the analyses

Host species	No. of hosts examined	No. of hosts infected	Component community richness	No. of core species	Mean infracommunity richness	Mean total abundance	CC ₅₀
<i>Aluterus monoceros</i>	39	38	5	3	2.87	28.2	25.6
<i>Archosargus rhomboidalis</i>	29	21	5	1	1.41	9.5	58.6
<i>Balistes capriscus</i>	66	64	11	1	1.56	15.6	72.7
<i>Balistes vetula</i>	30	26	7	0	1.57	9.8	60.0
<i>Caranx hippos</i>	60	44	6	0	1.07	12.1	63.3
<i>Caranx latus</i>	55	44	7	0	1.15	7.2	72.7
<i>Chaetodipterus faber</i>	110	56	4	0	0.87	5.0	58.2
<i>Cynoscion guatucupa</i>	69	60	7	0	1.35	8.9	60.9
<i>Dactylopterus volitans</i>	30	29	13	0	2.47	9.0	53.3
<i>Euthynnus alleteratus</i>	46	46	6	1	2.15	59.5	39.1
<i>Genypterus brasiliensis</i>	55	55	4	3	2.86	62.9	3.6
<i>Gymnothorax moringa</i>	30	30	5	4	3.33	30.5	13.3
<i>Haemulon steindachneri</i>	80	61	8	0	1.35	5.1	60.0
<i>Macrodon ancylodon</i>	31	22	6	0	0.97	4.5	71.0
<i>Menticirrhus americanus</i>	115	86	9	0	1.24	7.1	61.7
<i>Micropogonias furnieri</i>	100	80	10	1	1.29	7.4	64.0
<i>Mugil platanus</i>	150	127	12	0	1.89	17.5	42.0
<i>Mullus argentinae</i>	100	89	5	0	1.74	6.4	30.0
<i>Netuma barba</i>	63	37	5	0	0.81	5.5	71.4
<i>Oligoplites palometa</i>	84	82	6	1	1.94	75.4	59.5
<i>Oligoplites saliens</i>	36	35	5	2	1.72	24.7	83.3
<i>Oligoplites saurus</i>	37	36	6	2	2.11	21.5	24.3
<i>Orthopristis ruber</i>	162	148	9	0	2.09	37.4	34.6
<i>Paralichthys isosceles</i>	36	36	5	2	2.08	7.0	36.1
<i>Paralichthys brasiliensis</i>	93	74	6	0	0.96	4.1	77.4
<i>Peprilus paru</i>	30	29	4	2	1.83	34.9	30.0
<i>Pomatomus saltator</i>	55	47	4	2	2.31	23.0	20.0
<i>Priacanthus arenatus</i>	58	57	4	3	2.48	20.2	10.3
<i>Prionotus punctatus</i>	47	39	6	0	1.47	4.4	51.1
<i>Sciadeichthys luniscutis</i>	30	12	6	0	0.47	0.6	86.7
<i>Scomber japonicus</i>	100	97	4	2	2.02	49.0	12.0
<i>Selene setapinnis</i>	89	60	8	0	1.43	4.6	61.8
<i>Trichiurus lepturus</i>	55	55	7	2	2.29	1067.5	74.5
<i>Tylosurus acus</i>	31	29	5	4	2.94	16.1	19.4
<i>Umbrina canosai</i>	58	47	7	2	2.00	17.7	60.3
<i>Urophycis brasiliensis</i>	75	71	9	0	2.75	24.3	20.0
<i>Urophycis mystaceus</i>	55	51	6	1	1.71	4.3	30.9

indicating that the potential for interactivity among helminth species is lower in rich component communities than in species-poor ones. This appears to be a result of the greater proportion of rare species in some species-rich component communities, which decreases the overall likelihood of interactions among species. Indeed, the proportion of core species in the component communities correlated strongly with the CC₅₀ index ($r = -0.657$, $P = 0.0001$), indicating that abundant species increase the potential for interactivity.

Mean infracommunity richness was not correlated with component community richness ($r = -0.126$, $P = 0.457$), and is thus an independent measure of species richness. It correlated strongly and negatively with the index CC₅₀ (Fig. 4B): the higher the mean infracommunity richness, the lower the CC₅₀ value, and thus the more likely it is that

interactions play a role in structuring the community. This relationship remains if we use the mean infracommunity richness expressed as a percentage of component community richness instead of the raw value ($r = -0.807$, $P = 0.0001$).

Component community richness did not correlate with either the proportion of fish infected by at least one helminth species or the mean total abundance of all helminth species combined (both $P > 0.52$). However, mean infracommunity richness correlated positively with both the proportion of infected fish ($r = 0.807$, $P = 0.0001$) and mean total abundance ($r = 0.638$, $P = 0.0001$), and the latter two variables also correlated with one another ($r = 0.736$, $P = 0.0001$). These three variables are therefore not mutually independent. It is still interesting that CC₅₀ values correlated negatively with both the proportion of infected

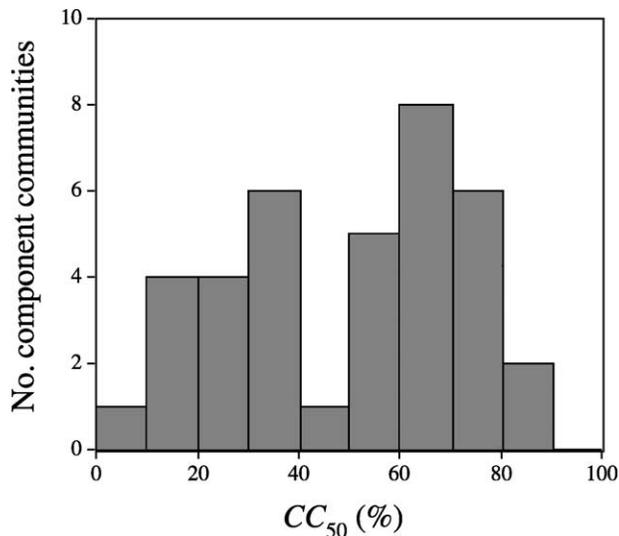


Fig. 2. Frequency distribution of CC_{50} values among the helminth component communities of 37 species of marine fish. The index CC_{50} is the percentage of hosts that need to be examined for 50% of the parasite species in a sample to be found.

fish and the mean total abundance (Fig. 5). The correlation with mean total abundance was not very strong, in large part due to a single point (in the upper right corner of Fig. 5B). This point corresponds to the fish *Trichiurus lepturus*, which has a mean total abundance of more than 1000 parasites per host. All other fish species in our data set had total abundances of 75 or less (see Table 1). The component community of *T. lepturus* consists of seven helminth species, including two hugely abundant species found in almost all fish, and four rare species each found in only one or two of the 55 hosts examined. Excluding this unusual community from the analysis greatly strengthened the relationship between CC_{50} values and mean total abundance ($r = -0.589$, $P = 0.0002$). However, if we corrected for the positive association between the proportion of infected fish and mean total abundance by using partial correlations, the association between total abundance and CC_{50} disappeared, whether *T. lepturus* is included or not ($P > 0.28$).

Finally, it is possible that the ranking procedure used to sort the host individuals (or infracommunities) from most species-poor to most species-rich corresponds simply to ranking the hosts by body size, since larger host individuals often harbour more parasites than their smaller conspecifics. In each of the 37 fish species, we checked for a potential relationship between the rank of a fish and its body length. We found significant, positive correlations (Spearman rank correlations, $P < 0.05$) in 10 of the 27 fish species. However, there was no significant difference in CC_{50} values between these 10 fish species and the 27 others for which fish rank and body length were not correlated (two-tailed t -test: $t = 0.195$, d.f. = 35, $P = 0.846$). Therefore, any structuring effect that host body size may have on helminth communities is unlikely to have influenced our results.

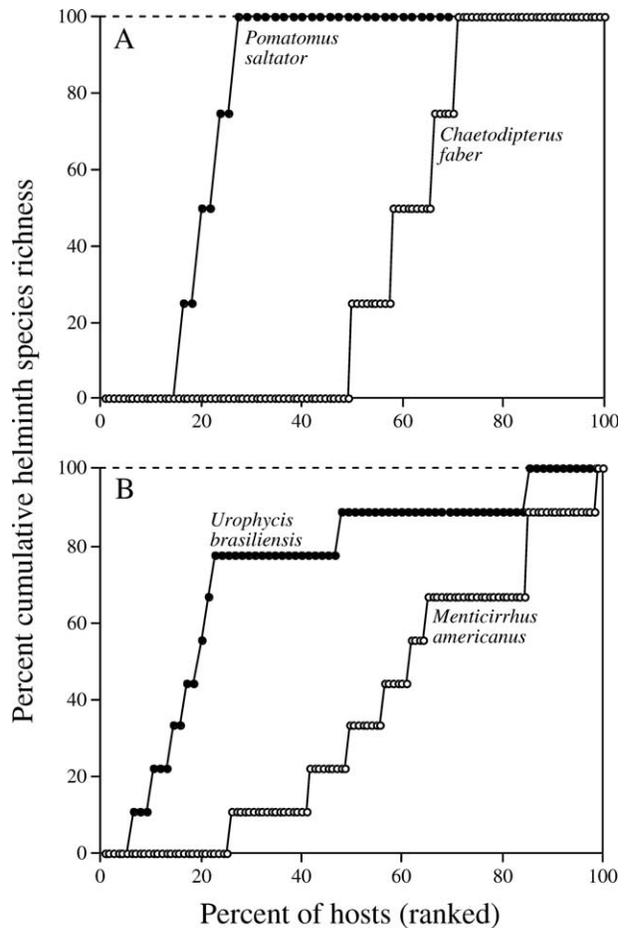


Fig. 3. Examples of species accumulation curves as a function of the percent of hosts examined for the helminth component communities of four species of marine fish. (A) Two component communities each consisting of four helminth species. (B) Two component communities each comprising nine helminth species. Note that although the species richness of their component communities differs, *Chaetodipterus faber* and *Menticirrhus americanus* have very similar CC_{50} values (58.2 and 61.7%, respectively); the same is true of *Pomatomus saltator* and *Urophycis brasiliensis* (both exactly 20%).

4. Discussion

The isolationist-versus-interactive view of parasite communities has provided a useful perspective on the variability in helminth community structure observed among different host species (Holmes and Price, 1986; Esch et al., 1990; Sousa, 1994). However, its use for comparative purposes has been hampered by the lack of a simple quantitative measure that could provide an estimate of the likelihood or importance of species interactions in a parasite community. Here, we propose such an index of interactivity, which collapses several features of a parasite community (species richness, overall prevalence and abundance) into a single number. Using this index, we showed that helminth communities in marine fish hosts potentially span the whole spectrum from isolationist to interactive, and that

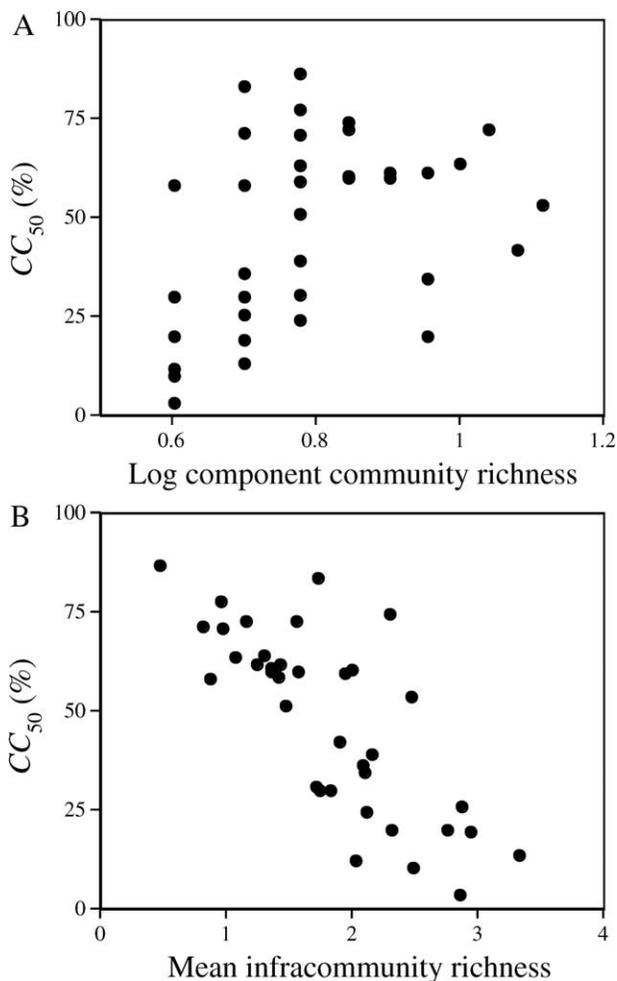


Fig. 4. Relationship between the index CC_{50} and two measures of helminth species richness across 37 species of marine fish. (A) Component community richness ($r = 0.390$, $P = 0.017$). (B) Mean infracommunity richness ($r = -0.773$, $P = 0.0001$). The index CC_{50} is the percentage of hosts that need to be examined for 50% of the parasite species in a sample to be found.

the potential extent of interactivity correlates with some key features of the communities.

The index of interactivity, CC_{50} , is derived from that proposed by Dove (1999) but with some important modifications. We believe that the present index presents some advantages over that of Dove (1999). First, CC_{50} has a fixed range of values that are simple to interpret biologically, whereas Dove's (1999) index is a number with no units and no clear upper bound. Second, CC_{50} does not require a complex algorithm that may be sensitive to sample size or the distribution of infracommunity richness values. Third, the index CC_{50} assumes a worst-case scenario in its evaluation of what percentage of hosts must be examined to find half of the species in a component community: by ranking the hosts (infracommunities), the procedure ensures that rare species are always found after the common ones. Dove's (1999) procedure is less

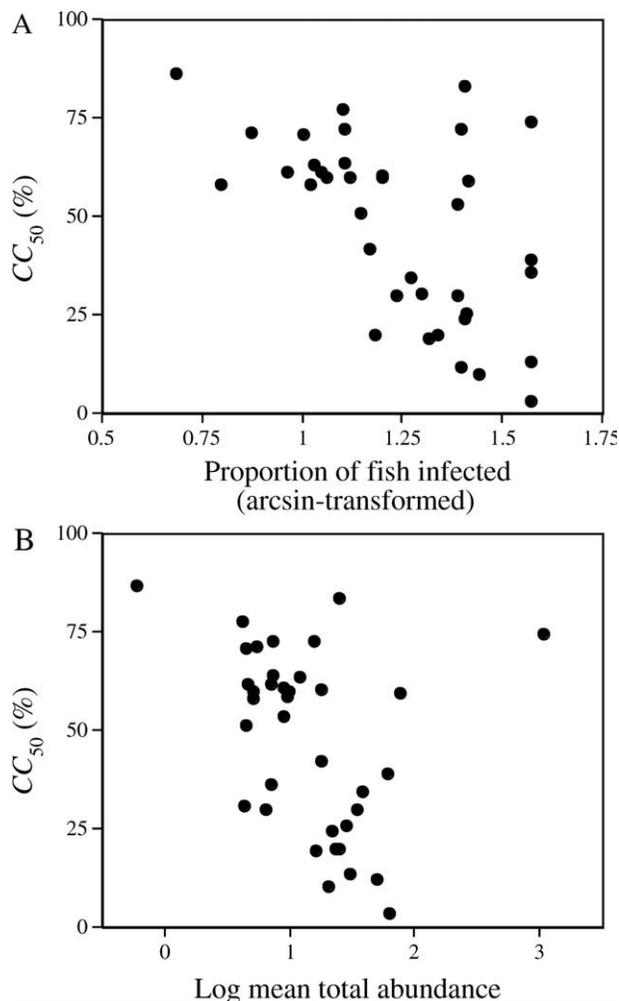


Fig. 5. Relationship between the index CC_{50} and two measures of helminth infection level across 37 species of marine fish. (A) Proportion of fish infected by at least one parasite species ($r = -0.564$, $P = 0.0003$). (B) Mean total abundance, all helminth species combined ($r = -0.348$, $P = 0.0349$). The index CC_{50} is the percentage of hosts that need to be examined for 50% of the parasite species in a sample to be found.

conservative, using a randomisation procedure that creates an average curve instead of our worst-case one. Fourth, and perhaps most important, it is independent of both host sample size (or the number of infracommunities sampled) and component community richness, making it perfectly suited for comparisons among parasite communities.

The main weakness of the new index is that it does not directly measure the extent of interactivity in the parasite community. Instead, it captures many properties of parasite communities thought to correlate with interactivity, and collapses them into a single number. These properties are the mean number of species per infracommunity and the relative number of highly prevalent species, or the proportion of core species in the component community. For these variables, the index uses presence-absence data that are easily obtained from several component communities. High numbers of parasite individuals per host is

another feature of parasite communities also associated with interactivity. Our index generally covaries with mean total numbers of parasites per host, again suggesting that it reflects the potential for interspecific interactions to occur. Still, it must be taken as a first approximation, and can in certain circumstances generate paradoxical results. For example, in a component community consisting of a few very abundant species and a few extremely rare ones, the index can reach relatively high values despite the potential interactions among the abundant species. Such instances might be rare: in our data set, only one of 37 host species, *T. lepturus*, harbours such a community. Direct measurements of species interactions, involving either or both functional (niche shifts) and numerical (changes in abundance) responses, remain the only way to assess whether interactions take place between pairs of parasite species, and how important they are (Poulin, 2001). Given the near impossibility of obtaining such data under controlled conditions for many host species, the present index presents a simple alternative that captures several factors likely to determine the level of interactivity in parasite communities.

Accepting that the index does indeed measure the degree of interactivity in parasite communities, what did it tell us about the helminth communities of the 37 fish species investigated here? Two results stand out. First, infracommunity species richness appears much more important as a determinant of potential interactivity than the overall species richness of the component community. In fact, among the fish species in our data set, the two measures of richness were entirely independent of one another, and infracommunity richness on its own could explain almost 60% of the variance in values of the CC_{50} index. Thus, even in species-poor component communities, it is possible for sufficient species to co-occur in infracommunities often enough to allow for interactions to take place. Second, although the index CC_{50} is computed solely based on presence-absence data, it still provides information on numbers of parasite individuals per host. The index thus indirectly captures a key feature of the parasite community, without requiring it for its computation. Despite relying on species presence-absence data, the index encapsulates two other properties of parasites, their prevalence and abundance, making it a useful snapshot of the status of the community and the likelihood of interactions.

Several authors have suggested that helminth communities are more likely to be interactive in endothermic vertebrate hosts than in fish hosts (see Kennedy et al., 1986; Bush, 1990). We might thus expect CC_{50} values to be generally lower for helminth communities in bird or mammal hosts than in the fish hosts studied here. Nevertheless, the values we obtained for 37 fish species cover almost the full spectrum of the index from isolationist to interactive, and interspecific interactions can thus be important structuring forces in some parasite communities

in fish. Previous studies have indeed documented competitive interactions among helminth species in fish hosts (e.g. Bates and Kennedy, 1990; Vidal-Martinez and Kennedy, 2000). Our results indicate that the full range of community types might be found in fish hosts. We have also demonstrated that the index CC_{50} captures the essential features of parasite communities (prevalence, abundance, species richness) that determine the extent of species interactions, and renders them as a single number. Its application to helminth communities in birds and mammals should provide us with a useful first approximation when determining what impact different types of hosts have on the nature of parasite communities.

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References

- Bates, R.M., Kennedy, C.R., 1990. Interactions between the acanthocephalans *Pomphorhynchus laevis* and *Acanthocephalus anguillae* in rainbow trout: testing an exclusion hypothesis. *Parasitology* 100, 435–444.
- Bush, A.O., 1990. Helminth communities in avian hosts: determinants of pattern. In: Esch, G.W., Bush, A.O., Aho, J.M. (Eds.), *Parasite Communities: Patterns and Processes*, Chapman and Hall, London, pp. 197–232.
- Bush, A.O., Lafferty, K.D., Lotz, J.M., Shostak, A.W., 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *J. Parasitol.* 83, 575–583.
- Carney, J.P., Dick, T.A., 2000. Helminth communities of yellow perch (*Perca flavescens* (Mitchill)): determinants of pattern. *Can. J. Zool.* 78, 538–555.
- Dove, A.D.M., 1999. A new index of interactivity in parasite communities. *Int. J. Parasitol.* 29, 915–920.
- Esch, G.W., Bush, A.O., Aho, J.M., 1990. *Parasite Communities: Patterns and Processes*, Chapman and Hall, London.
- Figueiredo, J.L., Menezes, N.A., 1978. *Manual de Peixes Marinhos do Sudeste de Brasil II. Teleostei (1)*. Museu de Zoologia, Universidade de São Paulo, Brazil.
- Figueiredo, J.L., Menezes, N.A., 1980. *Manual de Peixes Marinhos do Sudeste de Brasil III. Teleostei (2)*. Museu de Zoologia, Universidade de São Paulo, Brazil.
- Figueiredo, J.L., Menezes, N.A., 2000. *Manual de Peixes Marinhos do Sudeste de Brasil VI. Teleostei (5)*. Museu de Zoologia, Universidade de São Paulo, Brazil.
- Gotelli, N.J., Rohde, K., 2002. Co-occurrence of ectoparasites of marine fishes: a null model analysis. *Ecol. Lett.* 5, 86–94.

- Holmes, J.C., 1973. Site segregation by parasitic helminths: interspecific interactions, site segregation, and their importance to the development of helminth communities. *Can. J. Zool.* 51, 333–347.
- Holmes, J.C., 1987. The structure of helminth communities. *Int. J. Parasitol.* 17, 203–208.
- Holmes, J.C., Price, P.W., 1986. Communities of parasites. In: Anderson, D.J., Kikkawa, J. (Eds.), *Community Ecology: Pattern and Process*, Blackwell Scientific, Oxford, pp. 187–213.
- Kennedy, C.R., Bush, A.O., Aho, J.M., 1986. Patterns in helminth communities: why are birds and fish so different? *Parasitology* 93, 205–215.
- Menezes, N.A., Figueiredo, J.L., 1980. Manual de Peixes Marinhos do Sudeste de Brasil IV. Teleostei (3). Museu de Zoologia, Universidade de São Paulo, Brazil.
- Menezes, N.A., Figueiredo, J.L., 1985. Manual de Peixes Marinhos do Sudeste de Brasil V. Teleostei (4). Museu de Zoologia, Universidade de São Paulo, Brazil.
- Morand, S., Rohde, K., Hayward, C., 2002. Order in ectoparasite communities of marine fish is explained by epidemiological processes. *Parasitology* 124, S57–S63.
- Patrick, M.J., 1991. Distribution of enteric helminths in *Glaucomys volans* L. (Sciuridae): a test for competition. *Ecology* 72, 755–758.
- Poulin, R., 2001. Interactions between species and the structure of helminth communities. *Parasitology* 122, S3–S11.
- Poulin, R., Valtonen, E.T., 2001. Nested assemblages resulting from host-size variation: the case of endoparasite communities in fish hosts. *Int. J. Parasitol.* 31, 1194–1204.
- Poulin, R., Valtonen, E.T., 2002. The predictability of helminth community structure in space: a comparison of fish populations from adjacent lakes. *Int. J. Parasitol.* 32, 1235–1243.
- Simberloff, D., Moore, J., 1997. Community ecology of parasites and free-living animals. In: Clayton, D.H., Moore, J. (Eds.), *Host-Parasite Evolution: General Principles and Avian Models*, Oxford University Press, Oxford, pp. 174–197.
- Sousa, W.P., 1994. Patterns and processes in communities of helminth parasites. *Trends Ecol. Evol.* 9, 52–57.
- Stock, T.M., Holmes, J.C., 1988. Functional relationships and microhabitat distributions of enteric helminths of grebes (Podicipedidae): the evidence for interactive communities. *J. Parasitol.* 74, 214–227.
- Vidal-Martinez, V.M., Kennedy, C.R., 2000. Potential interactions between the intestinal helminths of the cichlid fish *Cichlasoma synspilum* from southeastern Mexico. *J. Parasitol.* 86, 691–695.