

Interactions between species and the structure of helminth communities

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SUMMARY

The role of interspecific interactions in the structure of gastrointestinal helminth communities has been at the core of most research in parasite community ecology, yet there is no consensus regarding their general importance. There have been two different approaches to the study of species interactions in helminths. The first one consists of measuring the responses of helminth species in concomitant infections, preferably in laboratory experiments. Any change in numbers of parasite individuals or in their use of niche space, compared with what is observed in single infections, provides solid evidence that the species are interacting. The second approach can only provide indirect, circumstantial evidence. It consists in contrasting observed patterns either in the distribution of species richness of infracommunities from wild hosts, in their species composition, or in pairwise associations between helminth species among infracommunities, with the random patterns predicted by appropriate null models. In many cases, observed patterns do not depart from predicted ones; when they do, alternative explanations are usually as plausible as invoking the effect of interactions among helminth species. The present evidence suggests that the role of species interactions in helminth community structure is often negligible, but that it must always be evaluated on a case-by-case basis.

Key words: Competition, exclusion, nestedness, niche segregation, species richness, saturation.

INTRODUCTION

Our knowledge of the patterns and processes underlying the structure of parasite communities has grown immensely in the past two decades (see reviews by Holmes & Price, 1986; Esch, Bush & Aho, 1990; Sousa, 1994; Poulin, 1997; Simberloff & Moore, 1997). There is still no general consensus, however, regarding the importance of interspecific interactions among parasites in the structuring of helminth communities. Some studies have suggested that helminth communities are isolationist and that the presence of one species has no influence on other species; in contrast, other studies have shown that helminth communities can be highly interactive and that species influence each other's abundance and distribution. The only attempt at a broad generalisation has been the suggestion that species interactivity is somehow linked to species richness and the average abundance of parasite individuals in hosts, or to whether the host is endothermic or not (Holmes & Price, 1986; Kennedy, Bush & Aho, 1986; Simberloff & Moore, 1997). Here I will review evidence from two parallel lines of research: experimental evidence from concomitant infections of captive hosts under laboratory conditions, and field evidence on patterns of richness and co-occurrence of parasite species from wild-caught hosts.

The study of concomitant infections intersects with parasite community ecology at the level of the individual host, i.e. at the level of the infra-

community. An infracommunity is the assemblage of all parasite individuals of all species within a single host, or within one organ in that host. The infracommunity is thus made up of all the parasite infrapopulations in a single host (*sensu* Bush *et al.* 1997). It is the interactions between infrapopulations in individual hosts that determine how many parasite species can coexist within single hosts, and ultimately in the parasite component community (all parasite individuals of all species within the host population; Bush *et al.* 1997). Much progress in parasite community ecology has been made at the level of the infracommunity, because it is usually the only level at which experimental manipulations of entire infrapopulations are possible. It is also the only level at which different parasite populations actually meet and interact in nature.

This review begins with a look at the sort of responses one can expect from parasitic helminth species interacting in concomitant infections, both on short ecological time scales and over evolutionary time. The following two sections examine the impact of species interactions on the structure of infracommunities. More precisely, these sections discuss the ways in which one can infer the existence and strength of species interactions from patterns in infracommunity structure. The bulk of the research on helminth communities has focused on gastrointestinal helminths of vertebrates; the present review is therefore restricted to these types of parasite communities. The importance of species interactions and their influence on community structure are no doubt different in other types of helminth communities, such as the communities of

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ectoparasitic monogeneans on fish (see Rohde, 1991, 1994). Communities of larval helminths in intermediate hosts, however, do have an effect on communities of adult helminths in vertebrate definitive hosts because of the way in which helminth larvae are recruited into adult communities (Lotz, Bush & Font, 1995). Therefore, the last section of the review summarises the patterns and processes occurring in larval helminth species interacting in a shared invertebrate, intermediate host.

CONSEQUENCES OF INTERACTIONS BETWEEN HELMINTH SPECIES

There are two types of immediate consequences of species interactions that are observable in concomitant infections. These are responses occurring on short ecological time scales and best measured in experimental studies, although they can also be documented from natural infections. First, a change in the infrapopulation size of one parasite species in response to the presence of another species is a sure sign that the two species are somehow interacting, and that their numbers are not independent of one another. Second, resource use by one parasite species may change when another species is present, also an indication that they are interacting. Ecologists often give more weight to the former phenomenon, a numerical response, than to the latter one, a functional response, when assessing whether species interactions occur (Thomson, 1980). Generally, in studies of helminth parasites, either or both numerical and functional responses are taken as evidence of interaction (Poulin, 1998). The possible scenarios are illustrated in Fig. 1.

Numerical responses are not only quite common in mixed infections of gastrointestinal helminths, but also often very substantial, with infrapopulations of one species reduced by as much as half the size they achieve when not sharing the host with another species (compare Fig. 1A and B; see examples in Dobson, 1985; Poulin, 1998). Note that numerical responses need not be negative; however, competitive interactions appear more common among helminths than positive interactions. When they are extremely strong, competitive interactions can lead to the exclusion of one species by the other, the most extreme numerical effect possible. An interesting feature of these numerical responses is their asymmetrical nature. Typically, one helminth species incurs severe reductions in numbers whereas the other is almost unaffected (e.g. Dash, 1981; Holland, 1984). A similar pattern emerges when it is reductions in average worm fecundity rather than reductions in infrapopulation sizes that are the numerical responses measured (e.g. Silver, Dick & Welch, 1980; Holland, 1984). Thus there is often a winner and a loser, an outcome that has at least two possible explanations. First, the interactions may be

closer to one-sided interference competition than classical exploitative competition, with one species intrinsically favoured when interacting with the other one. Second, there may be a priority effect, with the outcome of the interaction being dependent on which species first becomes established in the host; in this situation, neither species is intrinsically a winner, and all depends on which species gets a head start.

These types of large numerical responses are frequently observed in experimental infections, but the significance of the interspecific interactions uncovered in the laboratory for the structuring of helminth communities in nature may be much lower. The typical distribution of helminth numbers among host individuals follows an aggregated pattern (Shaw & Dobson, 1995), in which most hosts harbour few or no parasites and only few hosts harbour large infrapopulations. Assuming that the aggregated distributions of different parasite species are independent of one another, there may be few opportunities for two or more species of parasites to co-occur in the same host individual in sufficient numbers for competition and numerical responses to take place. Indeed, mathematical models (Dobson, 1985; Dobson & Roberts, 1994) and empirical studies (Morand *et al.* 1999) indicate that parasite aggregation may dampen the effects of interspecific competition. The possibility that parasites alter their use of resources when co-occurring with potential competitors also renders numerical responses less likely.

Like numerical responses, functional responses are best studied experimentally, although they can be inferred from natural infections. The evidence of antagonistic interactions provided by functional responses is not as solid as that from numerical responses (Thomson, 1980), but it can be very suggestive. In studies of gastrointestinal helminth parasites, the most widely studied type of functional response is a shift in the site of attachment of helminths in the host gut. This is viewed as a simplified measure of the niche of the parasite, focusing only on the spatial dimension of the niche because it is simpler to quantify. It then becomes possible to define the fundamental niche of a parasite species as the precise region of the gut it inhabits when in single infections, i.e. when not sharing the host with other parasite species. The fundamental niche represents the preferred range of infection sites among those where the parasite can develop successfully. When the parasite co-occurs with a competing species, it may alter its distribution in the host gut in order to minimise its spatial overlap with the competitor. The niche it then occupies is called its realised niche; it is often the portion of the fundamental niche that is competitor-free. The shift from the fundamental to the realised niche is the basic functional response to competition (compare

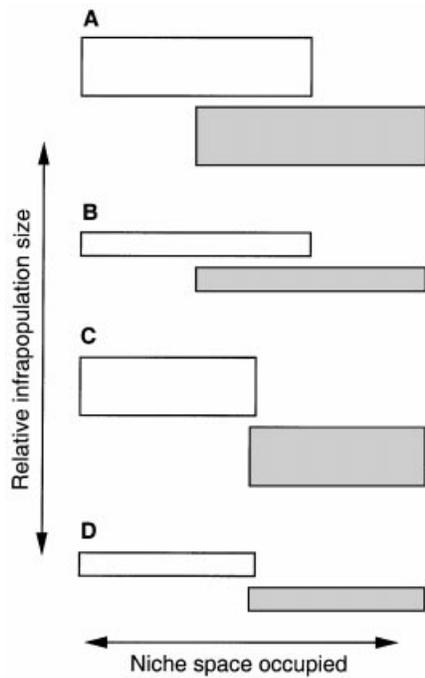


Fig. 1. Schematic representation of the possible effects of concomitant infections on the infrapopulations of two parasite species. Hypothetical infection doses, i.e. the number of parasite larvae of each species administered to hosts, are kept constant in all cases. The vertical dimension of the rectangles illustrates the relative size of each infrapopulation, while the horizontal dimension indicates the use of niche space by each infrapopulation. A, the infrapopulation sizes and fundamental niches of the two species when in single infections; B, a numerical response to concomitant infection, in which infrapopulation sizes are reduced; C, a functional response to concomitant infection, in which the realised niches of both parasites are adjusted to reduce niche overlap; and D, a joint numerical and functional response.

Fig. 1A and C), which Holmes (1973) called interactive site segregation. It has been beautifully illustrated in classical experimental studies of single-species and mixed-species infections (Holmes, 1961; Patrick, 1991). Functional responses can also be investigated by studying the niches of intestinal helminths in naturally infected hosts (e.g. Bush & Holmes, 1986*b*; Haukisalmi & Henttonen, 1993*b*; Ellis, Pung & Richardson, 1999). Competing parasite species may display either numerical or functional responses as a consequence of their interaction, or both responses simultaneously (compare Fig. 1A and D).

The realised niche of a parasite species co-occurring with competing species may not coincide with its preferred or optimal part of the fundamental niche. If the nutrient supply or other conditions are of lower quality in the realised niche than in the preferred portion of the fundamental niche, there will be a cost associated with the functional response. For the response to be favoured, this cost must be

lower than that associated with staying in place and competing with other parasite species. Evidence from species-rich intestinal helminth communities of birds suggests that a functional response is usually the best strategy, since realised niches of helminths are almost always more restricted than their fundamental niches (Bush & Holmes, 1986*b*; Stock & Holmes, 1988). However, other studies on gastrointestinal helminths with overlapping fundamental niches have not systematically found functional responses in competitive situations, whether or not numerical responses were observed (Moore & Simberloff, 1990; Ellis *et al.* 1999).

Finally, it is also possible that co-occurring species do not interact, either because they are not abundant enough to exert mutual pressures on one another, or because they differ in resource use and their fundamental niches do not overlap. There are many reasons for such differences in realised niches between species, many of which have nothing to do with species interactions. For instance, the reproductive success of helminths may vary as a function of each worm's position in the gut (Sukhdeo, 1991), and selection may have favoured a narrowing of the niche around sites where fitness is maximised. This could produce isolationist parasite communities, in which functional responses do not occur and the breadth and location of the niche of one species is independent of the presence of other species. However, the difference in resource use can be the product of an evolutionary niche shift that was selected as a result of intense competition in the past (Holmes, 1973). In other words, intense competition between common and abundant species will favour the evolutionary divergence of their fundamental niches, leaving only the ghost of competition past (*sensu* Connell, 1980). In all such scenarios, present-day interactions between helminth species would not be detectable and would play no role in structuring the parasite community.

SPECIES RICHNESS IN HELMINTH INFRACOMMUNITIES

If there are interactions between helminth species, we should expect that they would impact on the number of species in helminth communities and on their distribution among host individuals. The effect of interactions should be to push the observed patterns away from those expected from random, non-interactive assembly rules. In this section, I will review how the existence of species interactions can be inferred from patterns in the richness of infracommunities in natural systems; in the following section, I will discuss what the observed patterns in species composition and associations in infracommunities can tell us about the action of species interactions.

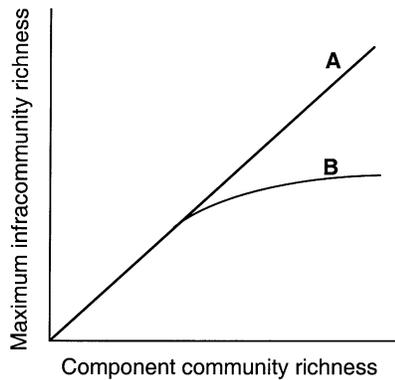


Fig. 2. Two possible relationships between the maximum (or mean) infracommunity species richness and the richness of the component community, across host populations or related host species. A, a linear relationship indicates that infracommunity richness increases proportionately with the richness of the component community, possibly because infracommunities are non-interactive; B, a saturation curve indicates that infracommunity richness reaches a limit and becomes independent of component community richness, perhaps as a result of species saturation and strong interspecific interactions.

Individual hosts from the same population do not all harbour the same number of parasite species. Some hosts may harbour most of the parasite species included in the component parasite community, others only one or two species. Characteristics of these hosts, such as age, size or preferred foraging site, may account for the variation among them in helminth species richness, by influencing their likelihood of acquiring certain parasite species. Among a random sample of hosts, however, and if hosts are random samplers of the parasites available in their habitat, one would generally expect the frequency distribution of parasite species richness values among hosts (i.e. among infracommunities) to follow a null model if species interactions are not important. If mechanisms such as competitive exclusion are acting, though, one would expect the distribution of richness values to depart from that expected by chance. Null models can be constructed for any particular system according to the total number of parasite species in the component community and their respective prevalences (Janovy *et al.* 1995). Comparisons of observed frequency distributions of helminth species richness among vertebrate hosts with those predicted by a null model indicate that the null model accounts for observed data in well over half of published studies (Poulin, 1996, 1997). Thus in the majority of cases, there is no evidence of interactions between helminth species in natural assemblages. Where departures from the null expectations do occur, species interactions are only one of many possible causes.

Recently, Dove (1999) proposed an index of interactivity based on the non-linear relationship between the number of hosts examined and the

estimated component community richness. In a sample of hosts, the number of recorded parasite species increases with the number of hosts examined until it reaches an asymptote corresponding to the true component community richness. Fitting a growth curve to observed data creates two key parameters, the asymptote and the gradient of the curve before the asymptote is reached. This gradient is related to the mean infracommunity richness: as the mean infracommunity richness increases and approaches the actual component community richness, the gradient of the slope becomes steeper. Dove (1999) suggests that the product of the two terms provides a measure of the degree of interactivity in a parasite community. High values of this index would indeed characterize communities traditionally viewed as interactive, i.e. those with many species with high prevalences (Holmes & Price, 1986). This provides another example of how patterns in infracommunity richness can be used to assess the role of species interactions in structuring parasite communities. Dove's (1999) index, however, will require some testing before its wide acceptance; it may reflect species saturation in infracommunities more than species interactions.

An investigation of species saturation itself can reveal the existence of species interactions if these are strong enough to lead to competitive species exclusion. The relationship between infracommunity richness and component community richness can be viewed as that between local and regional species richness in free-living communities (Cornell & Lawton, 1992; Srivastava, 1999). Two extreme scenarios are possible (Fig. 2). First, the relationship may be linear, suggesting that the number of species in an infracommunity is generally proportional to the number available in the component community, and that species interactions are negligible. Second, a curvilinear relationship would indicate that infracommunity richness becomes increasingly independent of component community richness as the latter increases, a phenomenon that may be due to interspecific interactions and the species saturation of infracommunities. The maximum number of species that can occur in an infracommunity is equal to the number of species in the component community. Typically, in species-rich component communities, no single infracommunity includes all available parasite species. On its own, however, a curvilinear relationship between local (infracommunity) and regional (component community) species richness is not sufficient to conclude that interspecific interactions lead to species saturation (Srivastava, 1999). Other lines of evidence, such as an experimental demonstration of competitive effects, are required to support any pattern in local and regional species richness.

This approach has been applied to parasite communities recently. In comparative studies of

gastrointestinal communities in different species of birds and mammals, the relationship between maximum infracommunity richness and component community richness came out as clearly linear (Poulin, 1998). In a study of 64 component communities of intestinal helminths from the same host fish species, however, the relationship proved to be curvilinear (Kennedy & Guégan, 1996). Here infracommunity saturation is a possible explanation because previous studies have demonstrated the existence of competitive interactions between pairs of parasite species (Kennedy & Guégan, 1996). Rohde (1998) suggests that this and other curvilinear relationships can also result from processes that have nothing to do with either interspecific interactions or saturation, and that no strong conclusions can be drawn from these results until null expectations can be generated that will take other processes into account. Rohde's (1998) views are based on computer simulations that are maybe a bit simplistic; nevertheless, caution is required in the interpretation of saturation curves.

Inferring processes, such as interspecific interactions between helminth species, from patterns in community parameters is not without difficulties. The attempts at doing so have not produced any compelling evidence for a generally important role for these interactions in determining infracommunity richness in natural assemblages. The next section will summarise attempts at inferring the action of species interactions from the composition and structure of infracommunities.

STRUCTURE OF HELMINTH INFRACOMMUNITIES

When the helminth species forming each infracommunity are random subsets of the ones available in the component community, the obvious conclusion is that there are no forces acting to structure infracommunities. However, evidence that the composition of infracommunities is not random would suggest that structuring processes, one of which may be interactions among helminth species, are at work. As in the previous section, the main approach used to detect species interactions or other structuring forces consist of comparisons between observed patterns in natural assemblages and those expected from null models of species associations. Null models are useful because they provide a baseline for such comparisons; however, they must be chosen with great care so that they generate realistic and appropriate null patterns (Gotelli & Graves, 1996).

Nestedness in species composition is a common departure from randomness in free-living assemblages occupying insular or fragmented habitats (Patterson & Atmar, 1986; Worthen, 1996; Wright *et al.* 1998). In a parasite component community, a nested pattern would mean that the species forming a species-poor infracommunity are distinct subsets

of progressively richer infracommunities (Fig. 3). In other words, parasite species with high prevalences would be found in all sorts of infracommunities, whereas rare parasite species would only occur in species-rich infracommunities. Nestedness is a departure from a random assembly of species, and is tested against the expectations derived from a null model based on each species' prevalence (Patterson & Atmar, 1986). Of course, all kinds of structuring processes can generate nested patterns; in the context of interspecific interactions, finding a nested pattern would only indicate that structuring of the infracommunities is taking place, nothing more. Nestedness has been investigated in communities of fish ectoparasites (Guégan & Huguény, 1994; Worthen & Rohde, 1996), but the only nestedness analyses of gastrointestinal helminth communities of vertebrates were done on 2 mammal species and 8 marine fish species (Poulin, 1996; Rohde *et al.* 1998). Of the 10 component communities tested, significant nestedness was only observed in 2 communities of marine fish. Similarly, nestedness does not appear to be common among communities of metazoan ectoparasites of fish (Worthen & Rohde, 1996; Rohde *et al.* 1998). Thus to date these analyses tend to indicate that the composition of infracommunities does not usually follow a nested pattern, which could mean that the actions of interspecific interactions or other structuring processes are not apparent. However, a considerable number of the parasite communities investigated by Rohde *et al.* (1998) suggest (based on the *P* values and how they were derived) that another non-random pattern is common, one that may be best referred to as anti-nestedness (R. Poulin & J.-F. Guégan in press); this strange pattern will require further study, but it may yet serve to highlight the existence of interactions or other structuring forces.

The associations between different pairs of helminth species among infracommunities is by far the aspect of parasite community structure that has received the most attention to date (e.g. Andersen & Valtonen, 1990; Moore & Simberloff, 1990; Lotz & Font, 1991, 1994; Haukisalmi & Henttonen, 1993 *a*). Positive and negative associations between helminth species, that is co-occurrences of pairs of species that are more or less frequent than expected by chance, respectively, can provide strong evidence that species interactions exist and act on community structure. These associations can be computed using presence/absence data, or preferably using actual parasite numbers or biomass. A common assumption (the null model) in tests of pairwise associations among species is that the number of positive covariances should equal the number of negative ones if infracommunities are assembled randomly. In many systems, the number of positive associations among helminths in infracommunities exceeds the number of negative ones, suggesting that positive interactions

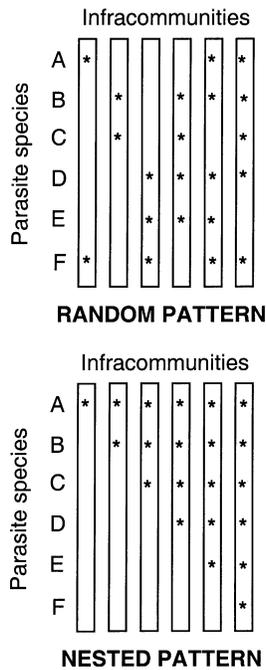


Fig. 3. Two hypothetical distributions of parasite species among infracommunities (i.e. among host individuals) in a component community. Each rectangle represents a different infracommunity, and infracommunities are arranged from least (at left) to most (at right) species-rich. The average infracommunity richness and the average prevalence of the six parasite species are the same in the two examples of presence/absence matrices. In a perfectly nested design, a parasite species occurring in a host individual with n parasite species will be found in all host individuals with at least $n + 1$ species (adapted from Poulin, 1998).

among species structure the community (e.g. Bush & Holmes, 1986a; Lotz & Font, 1991). However, several factors can generate spurious covariances and bias the sign of associations, and a precise null model must be used to assess whether positive or negative interactions are predominant. Lotz & Font (1994) showed that a high proportion of rare parasite species, with low prevalence in the component community, can produce an excess of spurious negative associations, whereas a high proportion of common species with high prevalence can lead to an excess of positive associations. In addition, they showed that the number of hosts (infracommunities) sampled also influences the likelihood of obtaining false pairwise associations between species. Using randomisation procedures to generate a more precise null model, Lotz & Font (1994) showed that the excess in positive associations that they had observed in an earlier study of helminths parasitic in bats (Lotz & Font, 1991), were unlikely to reflect a predominance of positive interactions between species.

Even if positive or negative associations are more numerous than predicted by a refined null model, they may have several explanations. First, they may

indeed reflect the action of interspecific interactions on community structure. Negative associations could result from strong interspecific competition which can lead to the exclusion of one species by another; positive associations could result from facilitation processes, such as immunosuppression induced by one species and benefiting other species. Second, most statistical methods used to detect species covariances are more sensitive to positive associations than to negative ones, which can bias any analysis of pairwise associations (Haukisalmi & Henttonen, 1998). Third, heterogeneity among host individuals can lead to certain hosts acquiring certain sets of parasite species and other hosts acquiring others, without species interactions among parasites being necessary. Fourth, similarity between helminth species with respect to the time of year at which they are acquired by vertebrates, combined with long durations of infection, can generate positive associations between species (Forbes *et al.* 1999).

One other process can generate patterns of species associations among species of gastrointestinal helminths in vertebrate hosts. With rare exceptions, helminths join an infracommunity when their larvae are ingested by the host. Larvae of acanthocephalans, cestodes, digeneans and many nematodes are acquired when the definitive host preys on an intermediate host which may contain larvae of more than one helminth species. Thus larvae arrive in packets, not singly (Bush, Heard & Overstreet, 1993). The recruitment of one species may not be independent of other species, if larvae are positively or negatively associated in intermediate hosts. The structure of larval helminth communities can be transferred to adult helminth communities in vertebrates. Using computer simulations, Lotz *et al.* (1995) found that pairwise associations in intermediate hosts can be transferred to definitive hosts, especially positive ones. Therefore observed species associations among gastrointestinal helminths in definitive hosts may have nothing to do with species interactions or other processes operating in definitive hosts. They may, however, reflect interactions among larval helminths in intermediate hosts. It is thus time to look briefly at what is known of species interactions among larval helminths in their intermediate, invertebrate hosts.

HELMINTH COMMUNITIES IN INTERMEDIATE HOSTS

There are basic differences between larval helminth communities in intermediate hosts and adult helminth communities in definitive hosts. First, communities in intermediate hosts usually comprise much fewer species than those in definitive hosts. Second, the prevalences of helminth species in their intermediate hosts are typically very low (often

< 1%; see review in Marcogliese, 1995). Third, many helminth larval stages, such as the metacercariae of digeneans (but not the sporocysts or rediae), the cystacanths of acanthocephalans, or the cysticercoids of cestodes, consume few host resources and are mostly inactive. These differences might suggest that competition or other types of species interactions are unlikely to be important in invertebrate intermediate hosts.

In fact, the available evidence suggests otherwise. There have been few experimental studies of species interactions between helminths in intermediate hosts. However, these few studies show strong effects of larvae of one species on the establishment or survival of larvae of a second species (Gordon & Whitfield, 1985; Barger & Nickol, 1999). Field studies examining patterns of mixed infections in wild intermediate hosts have all focused on larval digeneans in their gastropod intermediate hosts. In a comprehensive review of field surveys, Kuris & Lafferty (1994) found that strong asymmetrical numerical effects were the norm, with dominant larval digenean species typically causing substantial reductions in the abundance of subordinate species, if not causing their complete exclusion. They found that double or mixed infections of snails were much less frequent than expected based on the respective prevalences of digenean species in a community. Competition, and even predation, are common interspecific interactions within infracommunities of larval digeneans in their molluscan hosts (Sousa, 1992, 1993). It must be pointed out, though, that interspecific interactions between larval digeneans may be unimportant in systems where different species only co-occur infrequently (Curtis & Hubbard, 1993; Curtis, 1997), or in systems where infection of snails by the different parasite species is subject to extensive spatial or temporal heterogeneity (Esch *et al.* 1997).

We may also expect strong positive associations between larval helminths in systems where one larval helminth species is capable of manipulating the phenotype of the intermediate host to increase its probability of being ingested by a suitable definitive host. Host manipulation by parasites is a relatively common phenomenon that can greatly improve transmission rates of helminths with complex life cycles (Poulin, 1998). Parasite species sharing an intermediate host population with a manipulator species would benefit by associating with the manipulator, as they would obtain a cost-free ride to the definitive host, assuming they also share the latter with the manipulator (Thomas, Renaud & Poulin, 1998; Lafferty, 1999). The few tests of this idea have generally found the predicted positive association between the manipulator and the 'hitch-hiker' (Lafferty, Thomas & Poulin, 2000). Similarly, negative associations may be expected between larval parasites with conflicting interests, such as two

species capable of manipulating intermediate hosts but with different definitive host species. In these cases, larvae of one species would benefit by avoiding larvae of the other species because their destinations are different (Lafferty *et al.* 2000). Thus both negative and positive associations, resulting or not from species interactions, can occur in intermediate hosts and be transferred to definitive hosts, rendering more difficult the detection of interactions between adult helminths from non-random patterns in infracommunity structure.

CONCLUSIONS

In experimental studies, the importance of species interactions in concomitant infections can be demonstrated clearly in a straightforward manner: when two species co-occur, either there are numerical or functional effects, or there are not. Since effects have often been observed, it is natural to ask whether species interactions play a role in structuring natural parasite communities. This question lies on a grander scale than that of a two-species laboratory system, and cannot easily be addressed experimentally. Studies of natural patterns in parasite communities have been slowly accumulating, mainly following the application of concepts (e.g. the relationship between local and regional species richness, and nestedness) initially developed for communities of free-living organisms. When trying to infer the existence and importance of species interactions from patterns in the structure of natural parasite communities, however, two ubiquitous problems make all conclusions tentative. First, observed patterns must depart from randomness to be meaningful, and it has not always been possible to devise appropriate null models for comparisons with observed patterns. Second, several explanations other than the effect of species interactions can account for the discrepancies between observed and null patterns, making it impossible to determine whether there are any interactions. To be rigorous, one should always obtain a direct demonstration of species interactions to conclude that they exist and influence community structure. In other words, to use a metaphor, departures from random patterns of community structure are only circumstantial evidence, a controlled experiment is an eyewitness account, and an observed response during concomitant infection is a smoking gun.

Sousa (1994) reviewed quantitative studies of helminth infracommunity structure to see if they supported the general notion that interactions would be important in the dense, speciose infracommunities of endothermic vertebrates (Holmes & Price, 1986; Kennedy *et al.* 1986). He found that while some systems fit the predictions rather well, it was not possible to accurately predict whether a community would be interactive or isolationist based on its

species richness or the nature of its host. Broad generalisations are still impossible at this time, and a case-by-case approach remains the best way to assess the importance of species interactions in helminth communities.

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