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COMMUNITY STRUCTURE: Larval Trematodes in Snail Hosts

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Abstract

In species assemblages of larval trematodes in individual snail hosts, fewer multispecies infections are observed than might be expected by chance. Both interspecific competition and the isolating effect of heterogeneity in recruitment may explain this pattern of community structure. Here, we analyzed the expected and observed frequency of double infections, using data culled from 62 studies. Our analysis included 296,180 host snails. Of these, 62,942 were infected with one or more species of trematode (23% pooled over all studies, 24% average across studies). By incorporating information from subsamples, we were able to estimate the proposed isolating effect of heterogeneity in recruitment. Surprisingly, spatial and temporal heterogeneity as well as differential prevalence among host size classes typically led to intensification of interactions (average increases in interactions by +19%, +19%, and +23%, respectively), while partitioning among host species usually led to isolation of potential competitors (a −1% average decrease in interactions). We calculated the expected number of interspecific double infections by applying rules of independent assortment to the frequency of trematode species. The majority of the 14,333 expected interactions did not persist; only 4,346 double infections were actually observed (a 69% decrease, 62% average). Competition, via a variety of interspecific competitive mechanisms by dominant species, is the structuring process most consistent with this paucity of observed multispecies interactions. How important is competition? Overall, we estimated that 13% (10% average) of the trematode infections were lost to interspecific interactions. Subordinate species in particular suffered very high losses.

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INTRODUCTION

In this review, we examine the efforts of ecologists and parasitologists to interpret structure in communities of larval trematodes. May (77) considered a group of species lacking statistical association to be "unstructured"; the more a community differs from a random association of species, the more "structured" it is. Likewise, forces "structure" a community if they cause an association of species to depart from a null model of species abundance and distribution. To determine if a given community is structured, it is necessary to test whether it is significantly different from a random assemblage of species. For example, certain species combinations may occur more or less frequently than expected by chance. A null model based on independent assortment can serve to construct "null communities" for comparison with observed communities. The degree to which a community departs from a null model represents a quantitative measure of community structure (42).

Despite this apparently straightforward analytical approach, considerable disagreement centers on whether certain communities are structured or just random assemblages of species (94, 98, 107). Although disturbance, physical stress, recruitment dynamics, predation, and competition all might alter the distribution and composition of species in a community, the role of interspecific competition is at the center of the community structure debate (15–17, 26, 43, 96). Recently, some ecologists, particularly those who work in marine systems, have found it useful to separate structuring forces that affect patterns of recruitment from those forces that occur after recruitment. Particularly interesting is how heterogeneity in recruitment can affect the importance of post-recruitment structuring forces (37, 47).

Larval trematodes in their first intermediate molluscan hosts provide useful systems to examine theories of community structure. Certain species of snails and small clams are host to a rather rich fauna (up to 20 species) of larval trematodes. As with all studies of parasite ecology, the hosts provide natural and discrete habitat units. These molluscs are also generally abundant and readily sampled in a blind fashion with respect to trematode infection status. Within each mollusc, the larval trematodes multiply asexually, often reaching about half the tissue weight of the parasitized snail. Trematodes usually castrate their snail hosts (50, 58, 59, 93, 116) by manipulating the endocrine control of the snail's reproductive system (55). Thus, with a few exceptions, larval trematodes treat their first intermediate hosts as a limiting resource; generally fully used by the asexual progeny of a single infecting parasite (usually a penetrating miracidium, sometimes an ingested egg).

A Brief History

Because of their obvious importance to medical and veterinary diseases, careful quantitative sampling of snail first intermediate hosts began in the early part

of the twentieth century and often included samples from tropical regions. Sewell (97) recognized that, even when trematode prevalence (percentage of hosts infected) was high and snails were parasitized by a species-rich assemblage of trematodes, he infrequently observed interspecific double infections. The careful quantitative study of Dubois (29) emphasizes this point. Sewell proposed that a parasitized snail either lost its chemical attractiveness to other searching parasites, or infection altered its physiology to impede or prevent development of a later infection. Sewell felt that rare double infections were likely due to roughly simultaneous infection by two trematode species. Dubois concurred, assuming the absence of subsequent infections to be related to changes in immunity. In modern terminology, this would represent a form of concomitant immunity in which the presence of a parasitic infection induces a host defensive response against subsequent challenges. Dubois noted that there was no direct evidence, nor known mechanism, for hypotheses requiring biological antagonism, immunity, or incompatibility between two trematodes in a snail host. His extensive survey of Indian cercariae enabled Sewell (97) to suggest that only certain combinations of trematode species could coexist as double infections and that these double infections generally involved certain cercarial groups (furcocercariae, xiphidiocercariae, and monostome cercariae).

In contrast to Dubois and Sewell, Cort et al (19) reported a high frequency of multiple species infections in *Lymnaea* (= *Stagnicola*) *emarginata* from Douglas L., Michigan. They provided the first use of probability theory to compare the number of observed multiple infections (f_o) with the expected frequency, f_e = (A X B)/N, where A and B are the number of observed infections of trematodes A and B, and N is the number of snails examined. If species A and B are not independent of each other, we should see a difference between the expected and observed numbers of double infections. Cort et al (19) noted that Dubois and Sewell collected their snails from many locations over a long time and suggested it was likely that prevalence was too low in most of their collections to produce multiple infections. They also strenuously rejected the postulated explanations (immunity, altered attractiveness, or interspecific trematode antagonism) due to lack of evidence and mechanisms. Cort et al (19) found many combinations to occur at frequencies similar to their random expectations but observed that several combinations occurred much less frequently than predicted (often not occurring at all). Although they rejected the hypothesis that certain types of trematodes were less likely to engage in multiple infections, they did not test the significance of differences between f_e and f_o.

Thus, work by the late 1930s had already framed the key issues in community ecology. Were communities of larval trematodes assembled at random? If not, what were the causes of nonrandom patterns of association?

The extensive experimental studies of Lie and colleagues revealed several

mechanisms for the lack of double infections of certain interspecific combinations (reviewed by 12, 58, 66, 103–105). Using trematodes from the Malaysian snails *Lymnaea rubiginosa* and *Indoplanorbis exustus,* and the host of a human schistosome, *Biomphalaria glabrata,* they revealed the regular occurrence of predation by dominant species (with mouthed redial larval stages) on subordinate species. They also showed that certain species with only sporocyst larval stages (mouthless) were able indirectly to suppress the development of other subordinate species. In still other combinations, prior occupancy determined interspecific dominance. They were able to array the interspecific competitive abilities of these species in a largely linear dominance hierarchy (reviewed by 61, 66) (in our review, we refer to all interactions where one species negatively affects another species as *competition*). These interactions are comparable to intraguild predation as reviewed by Polis et al (82a). Other studies by Lie, Heyneman and co-workers (44, 68) established that prior infections altered the susceptibility of such snails to subsequent parasitization by other trematode species. However, rather than decreasing the likelihood of a second infection (interspecific heterologous immunity), these changes in snail defensive capabilities increase the likelihood of subsequent infections (44). Indeed, *Austrobilharzia terrigalensis* is an obligate secondary invader (113).

As an alternative to the interactive (competitive) hypothesis, Cort et al (19) noted that spatial and temporal factors certainly influenced the behavior of definitive hosts (vertebrates that harbor adult worms). They suggested this environmental heterogeneity would affect recruitment of trematodes to snail first intermediate hosts and would isolate trematodes from encounters as multiple infections. Others have supported (5, 54) or recently espoused this view (32, 34, 35, 99, 102, 104, 105).

Following the Cort's work with several freshwater snail-trematode systems in Michigan (19–21), reports of multiple infections from several hosts were reported over the next 50 years. Most studies concluded that double infections were rarer than expected in at least some pairs of species (5, 13, 18, 45, 56, 61, 64, 72, 74, 83, 85, 88, 102, 104, 111, 117). A few studies claimed the frequency of double infections to be similar to random expectations (23, 46, 54, 89, 99).

Sousa (102) reinvigorated the issue of community structure by acknowledging (with Kuris—61) that interspecific competition determined the outcome within the snail (infracommunity level). However, Sousa questioned whether this led to a significant impact on community structure at the snail population level (component community). By expanding the paradigm of intermediate disturbance developed to explain patterns of high diversity in communities of corals, tropical trees (14) and marine algae (100), Sousa predicted that if competition was important, maximum trematode diversity should occur at

intermediate snail sizes. He recognized that, as a cohort of snails aged, the accumulating trematode infections would cause trematode species diversity to increase initially, and then interactions would cause the loss of subordinate species from older, larger snails with double infections. However, in the large majority of samples, in a system that is highly interactive within individual snails (*Cerithidea californica*), diversity did not significantly decline in large snails. Sousa (104) concluded that competition was not important for these assemblages and proposed that spatial (and temporal) heterogeneity of recruitment of trematodes to the snail population was the likely structuring force. Fernández & Esch (34, 35), Snyder & Esch (99), and Curtis & Hubbard (23) embraced Sousa's test; they also found no significant decline in trematode species diversity or richness in the largest size classes of snails. The most recent texts (32, 90) incorporate the paradigm that spatial and temporal heterogeneity in trematode recruitment to snails is a hypothesis, mutually exclusive to competition, that effectively accounts for the lack of observed multiple infections.

Recalling Robson & Williams' (88) discussion of the focal nature of transmission to snails, the structuring effect of heterogeneity results from the interplay of two independent and opposing factors. The first, isolation of species, occurs when the relative prevalence of each trematode species varies among subsamples. On the other hand, variation in the absolute total prevalence (all species combined) among subsamples intensifies the likelihood of double infections. Both factors act independently to determine whether species will interact more or less frequently than expected. If several species of vertebrate final hosts use the same site, or if one species of vertebrate acts as the final host for several species of trematodes, or if migratory behaviors of final hosts show similar patterns of seasonality, spatial and temporal heterogeneity may well concentrate trematode eggs at specific locations and times (38, 51, 74, 76, 82, 88, 119). These likely natural history patterns will intensify opportunities for multiple infections within snail first intermediate hosts (61, 64). Further, as discussed below, Sousa's (102) hyperbolic prediction will detect only competitive interactions so severe that they exclude subordinate species of trematodes from snail populations (61). It is a notably insensitive test for competition. The solution to these problems requires a method that analyzes effects of spatial and temporal (and other) sources of heterogeneity in conjunction with the competitive hypothesis. In other words, because heterogeneity in recruitment may *either* intensify *or* ameliorate competition, it is necessary to apportion the variance among recruitment and competition.

Recognizing that factors influencing recruitment of trematodes to snails must temporally precede interactions within the snails (47), Lafferty et al (64) developed methods to calculate preinteractive distributions of parasites among snails and to analyze available information on heterogeneous recruitment. They

then assessed the impact of competition (or facilitation) and quantified the interaction between environmental heterogeneity and worm competition with respect to both magnitude and direction (isolation vs intensification for environmental heterogeneity, competition vs facilitation for worm interactions). In this review, we assume that no heterogeneity exists within a subsample. As we argue below, this is likely to offer a conservative estimate of the magnitude of competition.

In addition to the problem that interpretations of observed structure have floundered because they could not account for the effects of spatial and temporal heterogeneity in parasite recruitment. Researchers have often underreported structure itself for two reasons (64). First, all previous studies that used null models of independent assortment to calculate the expected frequency of double infections used observed frequencies to parameterize their null models (except 64). As is explained in more detail later, such an approach usually leads to an underestimation of the expected frequency of double infections. Second, statistical tests used to compare observed and expected values were often performed on data that were too finely subdivided to have sufficient statistical power to reject the null hypothesis of no structure.

Here, we apply the approach of Lafferty et al (64) to 62 data sets, compare the outcomes with other methods of analysis (generally published with particular data sets) and perform a meta-analysis to gauge the global importance of competition, facilitation and four sources of environmental heterogeneity (spatial, temporal, snail size, snail species) on community structure of larval trematodes in their first intermediate snail hosts. This approach yields results that, in several cases, differ from the interpretations of the original authors.

OUR APPROACH

We searched the larval trematode literature extensively for data sets suited for analysis, and we chose studies of natural, identified host populations that reported the total number of host snails dissected, the frequency of each trematode species, and the number of double, triple, and quadruple infections observed. Some data sets provided pooled data on multiple species infections but did not stratify them by potential sources of heterogeneity. In such cases, we used a weighted randomization procedure to distribute the multiple infections among subsamples. This approach was conservative with respect to both the competition and heterogeneity hypotheses, because we have defined community structure as the extent to which the distribution of species varies from a random assemblage. Multiple infections were usually so infrequent that we could assign them to any subsample without significantly affecting the outcome. Trematodes were often only partially identified (often to cercarial groups, e.g. echinostome, xiphidiocercariae, etc), and we included such studies

treating the incomplete identifications as operational taxonomic units. This approach provided a conservative assessment of competitive interactions; the broader operational taxonomic units masked some potential interactions.

Estimating Prevalence

The application of the null model, $f_e = (A \times B)/N$, to the distribution of larval trematodes among snails is inadequate because individuals that infected a host but that competition later eliminated do not show up in samples and, therefore, are not entered into the model (64). This leads to an underestimate of the expected number of double infections. The magnitude of this error increases with the prevalence of dominant species in the assemblage. Correcting for this error requires parameterizing the null model with the prevalence of each species expected to have recruited before any interactions. Lafferty et al (64) provided the details of estimating the "pre-interactive" prevalence of all the species in an assemblage. In general, the prevalence of a species of parasite recruiting to a host population will be equal to the prevalence of that species observed among those hosts where no dominant parasite species are present. (See *Note Added in Proof A.*)

To generate the preinteractive prevalences of a trematode community, we postulated a dominance hierarchy based on evidence available for each host-parasite system, according to set rules. For well-studied systems (e.g. trematodes from *Cerithidea* spp., *Ilyanassa obsoleta, Helisoma anceps,* or *Lymnaea rubiginosa),* we made use of published dominance relationships based on laboratory experimentation, field mark recapture studies, or histological observations (25, 34, 61, 104). For more poorly known systems, we used taxonomic relationships and other more indirect assays to postulate dominance (61). Compared with a dominance hierarchy proposed by Fernández and Esch (34) based on experimental evidence for the trematodes of *Helisoma anceps,* a postulated dominance hierarchy based on the indirect rules of Kuris (61) for that system proved conservative, detecting a smaller competitive effect. We developed a conservative algorithm to construct dominance hierarchies in little-studied systems by postulating a dominance-subordinance relationship only for taxa with a consistent history of strong dominance (e.g. echinostomes, philophthalmids, heterophyids), weak dominance (e.g. notocotylids, schistosomes), or subordinance (e.g. xiphidiocercariae, strigeids). In the large majority of data sets, researchers determined the presence of trematode infections by crushing the snail hosts rather than merely observing shedding of cercariae into the water. Thus, most studies did not suffer from underestimation of prevalence due to reluctant shedding as demonstrated by Curtis & Hubbard (23). When several different studies of a host were available, we carefully reviewed the taxonomic literature to ensure that we consistently assigned species to the appropriate operational taxonomic units.

Structure

We could examine the effect of various potential sources of heterogeneity for a number of studies. Two studies reported subsamples by host sex, 9 by host size classes, 8 by host species, 31 by geographic locations (over a wide range of scales), and 19 by temporal variation (usually monthly, sometimes annually). To see whether the distribution of different trematode species among these subsamples affected the expected number of interactions (isolation of species or intensification of interactions), we used methods developed by Lafferty et al (64) to quantify the effects of spatial heterogeneity in recruitment. This required two steps: (i) applying the null model to the pooled subsamples yielded the expected number of double infections that would occur if recruitment was homogenous; (ii) applying the null model to each subsample separately and then summing the expected number of double infections across all subsamples yielded the expected number of double infections that occurred as a result of heterogeneity among subsamples. By comparing the expected number of double infections from steps 1 and 2, we estimated the effect of heterogeneity in recruitment on interactions. To make relative comparisons among studies, we then standardized this effect according to the equation (pooled – summed) / pooled. An alternative statistical analysis to ours would require (i) a heterogeneity chi-square of species by subsample (that omitted the number of uninfected hosts) to indicate the significance of isolation, and (ii) a heterogeneity chi-square of prevalence (of all species combined) by subsample. The drawback is that this alternative would not quantify the net effect of heterogeneity on the expected frequency of double infections.

For the 15 studies that reported more than one category of heterogeneity (e.g. both site and time), we assessed the effect of each type of heterogeneity independently from the other. As an example, for a study subdivided by site and date, we first calculated the expected prevalence of recruitment for each species. Then, to determine the effect of spatial heterogeneity, we pooled these values over all sites within each date. Next, we calculated the expected number of double infections for each date. Summing these values over all dates gave the expected number of double infections without spatial heterogeneity. Likewise, we determined the independent effect of temporal heterogeneity by pooling the expected prevalence of each species over all dates within a site, calculating the expected number of double infections for each site and then summing over all sites.

To quantify the effect of interspecific competition on the persistence of multispecies infections, we compared the expected number of double infections summed across subsamples with the number of double infections observed in nature. Because our null model predicted only double infections, we counted the few observed triple infections as three observed double infections

(we counted a single quadruple infection as six observed double infections). Again, to make relative comparisons among studies, we standardized this effect according to the equation (observed − summed) / summed.

To quantify the importance of interspecific interactions for the entire assemblage, we estimated the proportion of the trematode individuals that were lost to competition. Clearly, if only a tiny fraction of the community interacts, effects of competition, though significant for interacting individuals, will have little consequence for the trematode community as a whole. Because interactions are more likely to negatively affect subordinate species, we made a more detailed assessment of the 25 studies that used littorine snails as hosts. Here, we classified species according to four levels of dominance. We then quantified, according to the level of dominance, the proportion of individuals lost from each species in each study.

Statistics

We statistically evaluated whether interactions or heterogeneity significantly structured a trematode assemblage in each study by calculating the confidence limits around the proportion of trematodes that were expected or observed to interact with another species (64). Specifically, we compared the proportion of interacting trematodes before (2 × pooled / number of trematodes) and after (2 × summed / number of trematodes) the effects of heterogeneity in recruitment. To assess the statistical significance of competition, we compared the expected (2 × summed / number of trematodes) and observed (2 × observed / number of trematodes) proportions of interacting trematodes. These statistics are conservative as they are not sensitive to structuring forces in a community that might act in opposite directions on different species (64). We excluded several data sets because they suffered from a combination of low sample size, low prevalence, or low species evenness in such a way that our statistical tests lacked the power to determine whether they were structured. As a rule of thumb, we required that studies have a sum of at least three expected double infections. A power analysis indicated that our statistical approach could always distinguish whether competition eliminated all double infections (64). We analyzed studies with fewer than three double infections separately to determine whether they were qualitatively different from the studies we included in our analysis.

We used meta-analyses (e.g. 43) with studies as independent replicates in a chi-square test to determine whether interactions and heterogeneity had significant effects on the structure of trematode communities. Since meta-analysis specifically includes studies that, by themselves, have low statistical power, we included the 15 studies that we excluded from our other analyses. However, it was necessary to pool information from these studies to accommodate the conditions for the chi-square analysis (>5 expected value). To test

for an effect of interactions, we calculated the squared deviation from the expected value for each study as (observed – summed)2 / summed. We carried out an analogous approach for each of the four forms of heterogeneity except that here the squared deviation from the expected value was (summed – pooled)^2 / pooled.

RESULTS

We entered more than 300,000 snails, collected over eight decades, into our analysis. Considering that each host is a potential habitat for a trematode infra-community, this may be the most extensive community analysis for any system. We derived summary statistics (Table 1) by pooling the information from all studies as well as by averaging across studies. The Appendix presents

Table 1 Summary statistics for all studies combined[a].

Observed	pooled[b]	average[c]
Snails	296180	4356
Single infections	62942	926
Double infections	3871	57
Triple infections	155	2
Quadruple infections	1	0
Double interactions	4346	64
Prevalence	23%	24%
Number of trematodes	71153	1046
Trematodes interacting	12%	11%
Expected		
Summed double infections	14333	211
Number of trematodes	81621	1200
Trematodes interacting	35%	28%
Structuring changes		
Heterogeneity (net change in double infections)		
Spatial heterogeneity	+13%	+19%
Host size structure	+10%	+23%
Temporal heterogeneity	+10%	+19%
Host specificity	+2%	–1%
Change in interactions		
Double infections	–69%	–62%
Trematode abundance	–13%	–10%
Low power studies		
Change in double infections	–70%	–25%

[a] Unless noted, >3 expected double infections.
[b] Calculated by pooling values over all studies.
[c] Averaged across studies.

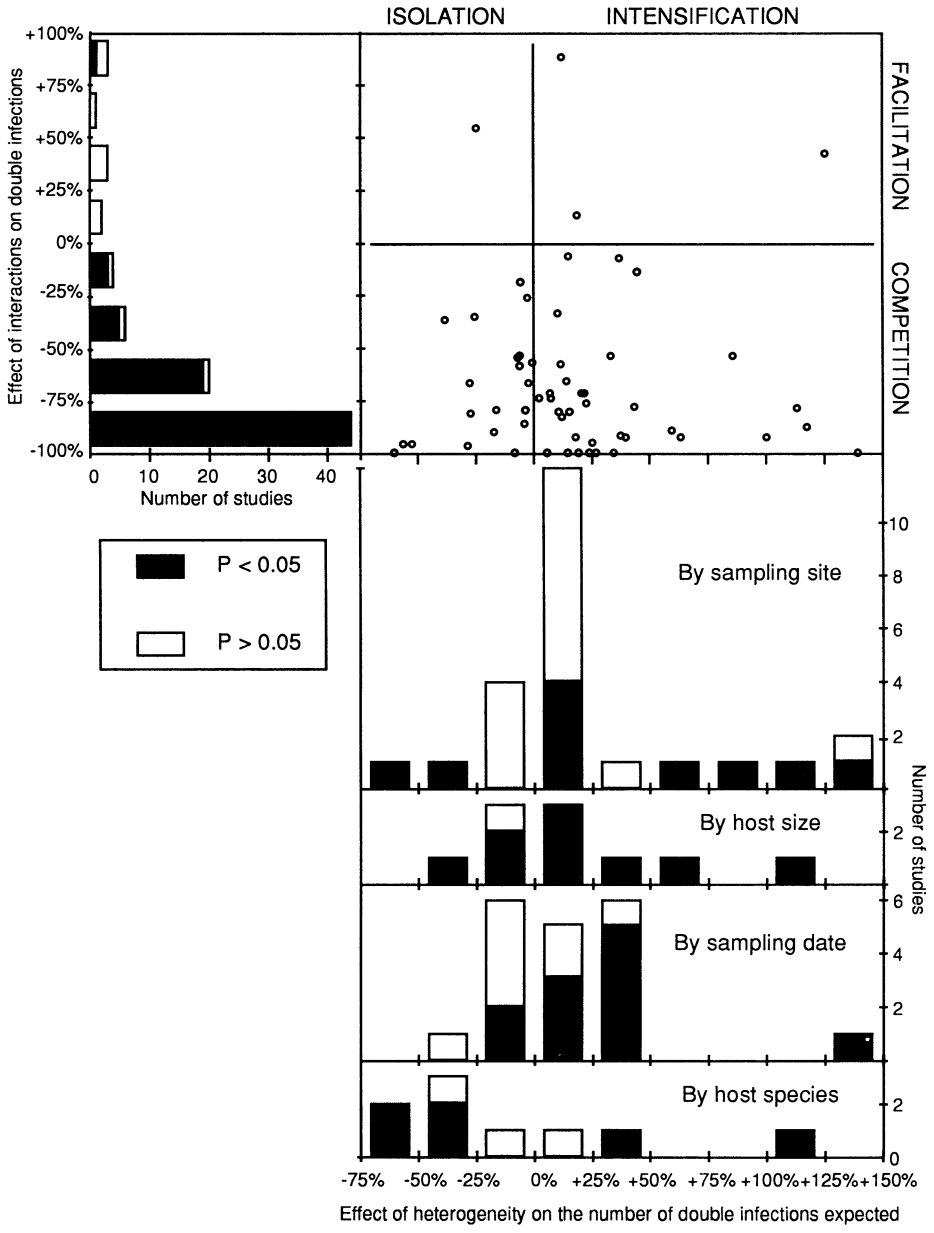

Figure 1 Effects of competition and heterogeneity on double infections. Scatter plot and histograms of the effects of heterogeneity and interactions on the expected and observed frequency of double infections. Each point represents a separate study. The effect of interactions on the number of double infections was calculated as (observed – sum of expected) / (sum of expected) while the effect of heterogeneity on the number of double infections was calculated as (sum of expected – expected of pooled) / (expected of pooled). A value of zero indicates no effect; −1 a complete loss of double infections. Filled bars represent studies in which a significant effect was detected; open bars represent studies where the effect was not significantly different from zero. Several studies were subdivided according to categories of sampling site, host size, sampling date and host species.

Table 2 Results from meta-analyses of the effect of heterogeneity and competition on the structure of trematode guilds.

Mechanism	chi-square	df[a]	p
Heterogeneity			
Sample site	617	23	<.001
Host size	184	8	<.001
Host species	241	8	<.001
Sample date	248	14	<.001
Competition	7,322	59	<.001

[a] The unit of replication is a study.

data from each study. Statistically significant instances of isolation and intensification occurred in all four types of subsamples (Figure 1). A meta-analysis for each type of heterogeneity resulted in strongly significant chi-square values (Table 2). Neither of the studies that investigated heterogeneity between host sexes (not shown in Figure 1) indicated an effect on the probability of interspecific interactions. Although differential use of host species had no consistent effect, spatial and temporal heterogeneity as well as differential prevalence among host size classes typically intensified the likelihood of interactions (Table 1).

Most expected interactions did not persist (Figure 1, Table 1). The studies that were not included in our analysis due to a lack of power (fewer than 3 expected double infections) indicated a similar effect (Table 1). In general,

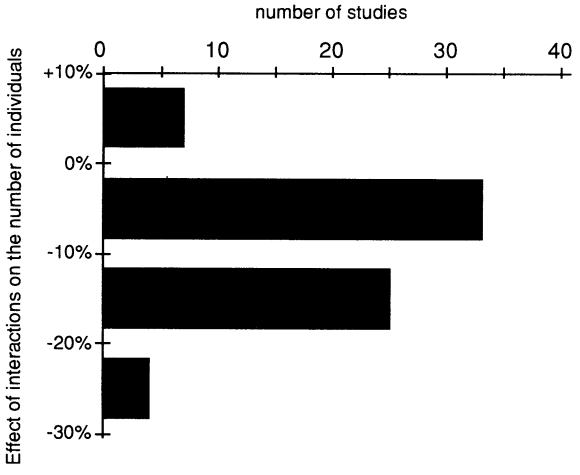

Figure 2 Effects of interactions on total trematode abundance for all studies.

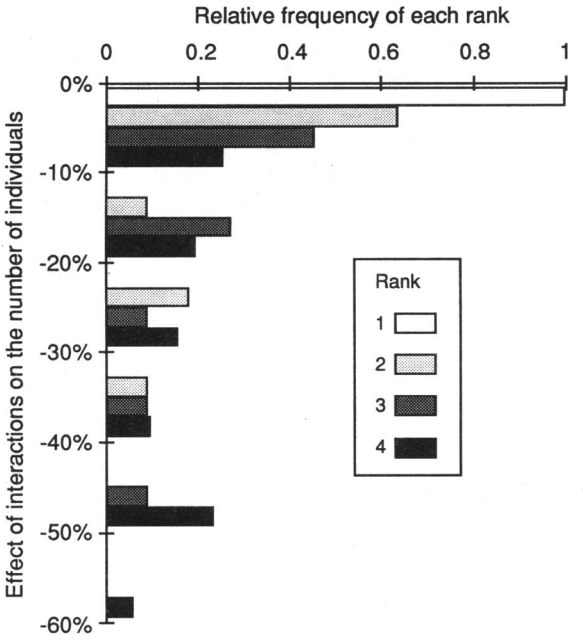

Figure 3 **Effects of competition on species abundances in littorine hosts. The change in abundance (as a percentage) was calculated for each species in each study. Species were then grouped according to four ranks of competitive dominance (1 being most dominant). Each bar indicates the proportion of species (not pooled over studies) in a rank that suffer a certain percent loss to competition (e.g. the results show a higher proportion of subordinant than dominant ranking species suffer high losses).**

interactions led to a dramatic decrease in the number of double infections. One significant case of facilitation (more double infections than expected) was evident. The meta-analysis for interaction also resulted in a strongly significant chi-square value (Table 2). There was no significant variation in the strength of competition among host species (ANOVA, $F = .987$, $df = 7, 47$, $p = .452$). The structuring effects of heterogeneity and competition were not associated (Figure 1, $r = 0.15$, $N = 59$, $p > 0.05$).

By comparing the total number of expected and observed trematodes, we estimated that competition eliminated 13% (pooled) or 10% (mean of studies) of the trematode individuals. Figure 2 indicates how this loss was distributed among the studies (several studies indicated a minor gain in individuals due to facilitation). Similarly, Figure 3 illustrates how, for the littorine studies, subordinate species suffered relatively high losses.

DISCUSSION

Our results did not support the recent paradigm for trematode communities. Isolation of species due to spatial and temporal heterogeneity does not explain the rarity of multispecies infections. The most frequent structuring forces in trematode communities involve a combination of intensification of interspecific interactions due to heterogeneity in recruitment followed by competitive interactions that greatly reduce the abundance of subordinate species.

Heterogeneity

Of greatest interest were those studies that discussed effects of heterogeneity and competition. Our study confirmed interpretations of researchers who found that size classes did not significantly structure recruitment and that competition significantly reduced negative interspecific interactions (40), differences in sites isolated potentially interacting species (76), and heterogeneity of recruitment over time and sites intensified the significant competitive interactions between larval trematodes (18, 82). Sousa (104, 105) characterized temporal and spatial heterogeneity exclusively as isolating forces, reducing the impact of competition between trematodes within snail hosts. Prevalences at his sites were significantly different (22% to 14%) and varied greatly between years (12% to 54% at one site, 5% to 26% at the other site; trends over time changing in opposite directions at the two sites). However, our analyses of these studies indicate that heterogeneity actually intensifies competition, because there were only minor variations in relative worm species abundance over space and time. Three studies by Esch and colleagues (34, 35, 118) all claimed (without providing analyses) marked isolating heterogeneity with respect to either or both space and time. Our statistical analyses detected no significant spatial or temporal heterogeneity in their data sets. These studies also argued that the great majority of pairs of trematodes did not significantly interact. In fact, although we find a strong net competitive effect in their studies, their analyses broke down the many sites and times so finely that they could not detect competition in their system. Thus, we reject their conclusions that the trematodes in *Helisoma anceps* host system are noninteractive and structured by spatial and temporal heterogeneity. We maintain the perspective that this system is highly interactive (competitive) and that variation in space and time neither isolates potential competitors nor intensifies their likely interactions.

Spatial heterogeneity is the form of variation in recruitment that we can most readily interpret. A higher proportion of trematodes will potentially experience interspecific interactions if heterogeneity concentrates their recruitment within a small region (e.g. 88), as opposed to being evenly spread over the host's distribution. An overlap in the habitat preferences of definitive hosts

or spatial variation in transmission efficiency could produce such a pattern. Conversely, isolation in space will occur when vertebrate final hosts exhibit different habitat specificity.

Several mechanisms could foster intensification by host size class. Variation in parasite resistance with host age might produce intensification in certain snail size-classes. Increased resistance to larval trematode infections with increasing snail size has been well documented (reviewed by 70), and its genetic basis in *Biomphalaria glabrata* carefully described (71, 87). Ontogenetic changes in habitat use or behavior might also affect infection rates. The instantaneous risk of infection will likely be higher for large than for small snails if transmission occurs by way of the ingestion of trematode eggs (assuming large snails eat more) or because large snails present a large target for infective miracidial stages because these use a combination of random and chemosensory searching behavior (e.g. 75). In any case, if larger hosts are older, they will have been exposed to a greater cumulative risk of infection by several species, and nearly all studies show a monotonic increase in overall parasitic prevalence with increasing size of snails. We note that the relationship between age and growth in parasitized snails is complex and system specific. Some studies have experimentally shown that parasitized snails can grow faster than uninfected counterparts (81, 93, 116,), sometimes exhibiting gigantism (91). In other systems, trematodes strongly reduce the growth of parasitized snails (50, 60, 62, 101, 108). There have also been reports of high snail mortality rates associated with parasitism by larval trematodes (e.g. 19, 50, 54, 62, 92), and this may skew the size-prevalence relationship. Unless the sizes of the sexes are quite different, one would predict little effect of host sex as a source of heterogeneity, and our analysis revealed none for the two studies that reported infections by host sex.

The seasonal behavior of definitive hosts is the most likely factor responsible for temporal heterogeneity. When seasonality correlates positively among definitive hosts (e.g. migratory shore birds), recruitment will come in pulses and intensify interactions. Only when definitive hosts have opposing chronological patterns of activity will temporal heterogeneity act to isolate species. Such heterogeneity may not strongly alter the frequency of interactions because experimental studies have shown trematodes do not necessarily have to recruit at the same time to interact. Temporal heterogeneity may have subtler effects on structure, however. Prior residency is an important factor that determines dominance for some interactive pairs of trematodes (61, 69). Here, species that recruit early will have an advantage. Also, sampling during a period of pulsed recruitment (e.g. 46) should yield many double infections undergoing the process of competitive exclusion. Such communities may be highly interactive, yet yield a ratio of expected to observed double infections similar to less interactive systems. This was achieved experimentally by Heyneman & Um-

athevy (45) who added echinostome eggs to a pond where they had established a high prevalence of a subordinate species, *Schistosoma bovis* (46).

Long-lived snail hosts effectively integrate temporal variation in transmission. Thus, inter-trematode antagonisms will eventually happen. In contrast, short-lived hosts may either "miss" certain episodes of transmission, or experience relatively regular seasonal patterns of infection depending on the frequency, periodicity, and amplitude of trematode transmission and the strength of seasonality of snail population dynamics. Among the well-studied long-lived hosts that slowly accumulate parasites are *Cerithidea californica,* the littorines and *Ilyanassa obsoleta.* Here, in the largest size classes, prevalence often approaches 100% (13, 51, 61, 73, 76, 88, 102, 104, 115). Many freshwater species live only a few months and have strongly seasonal patterns of transmission (19, 34, 35, 99). It would be of interest to compare the temporal patterns and community structure of the larval trematodes of *Cerithidea californica* with *C. scalariformis* of the Atlantic coast of Florida as the latter lives one to two years (48) whereas the former lives at least 6–10 years (48, 84; AM Kuris, personal observation).

The trade-off between variation in host species suitability (how susceptible it is to infection) and specificity (the extent to which trematodes use it as an exclusive host) will modulate the effect of heterogeneity in recruitment among host species. The specificity of larval trematodes for certain snail hosts will cause heterogeneity in recruitment among snail species. Where some snail species serve a disproportionate role as hosts to several species, trematode species will interact more strongly. When each host species has its own unique assemblage of trematode species, isolation will occur.

Although a number of studies provide samples from different snail species, the definitive survey to analyze the effect of host specificity on larval trematode community structure has not yet been conducted. Sampling is very uneven, and well-known, heavily parasitized species, such as the littorines, attract repeated studies. Ecologists have tended to ignore species with few parasites, thus minimizing the impact of the isolation of highly host-specific species on community structure. Samples from taxonomic studies exhibit the reverse bias. Rare parasites often parasitize poorly studied host species and these can be over-represented in some surveys. We advocate a sampling procedure developed by Lafferty et al (64), who sampled snails at random until a previously specified number of *infected* snails were detected. This permits an analysis of community structure with sufficient statistical power to detect effects even when prevalence is uneven or low.

Despite sampling problems with surveys across host taxa, we can discuss at least the best studied marine systems involving mostly trematode parasites of shorebird hosts. First, a few species of generally abundant snails seem to channel a relatively large proportion of the available parasite species. These

include *Ilyanassa obsoleta* on mud flats, *Cerithidea* spp. in salt marshes and mangroves, and *Littorina* spp. in rocky intertidal habitats. Second, a taxonomically very similar assemblage of larval trematodes occurs over great distances, and sometimes over related host species. For 15 studies of *Littorina* spp., at least 10 included *Cryptocolyle lingua, Renicola roscovita, cercaria lebouri* and a species of *Himasthla.* Four species of *Cerithidea* occur along the Atlantic coast of the United States, the Gulf of Mexico, the Pacific coast of the United States, and the Sea of Cortez. Yet all report *Parorchis acanthus,* three similar species of renicolids, a species of *Himasthla,* a species of *Austrobilharzia,* and three similar species of heterophyids (see also 7). This suggests a strongly historic component to these communities, perhaps involving co-accommodation and co-speciation. Third, the geographically widespread distribution of these assemblages suggests that a common system of dispersal and recruitment operates for each host-parasite system. Because the parasites often span several biotic provinces (defined by free-living animals), it suggests that, at least for marine species, vertebrate host behavior is a more powerful integrator of the parasite biotic provinces than are the ocean currents for their host snails.

Although heterogeneity in recruitment was shown here usually to be a weak structuring force relative to competitive interactions, several sources of heterogeneity could act in concert to alter the overall expected frequency of interactions. However, since heterogeneity generally intensified interactions, it is unlikely that unstudied aspects of heterogeneity in recruitment could provide a general alternative to competitive exclusion as an explanation for the low number of observed double infections. Further, one form of heterogeneity that we have not been able to assess is the repeatedly documented differential high susceptibility of previously infected snails (e.g. 44, 69). This source of heterogeneity could greatly intensify the expected frequency of multiple infections.

Competition

A few studies indicate facilitation, in which the presence of trematode infections increases the abundance of other species of trematodes. Most of these involve the only described obligate secondary invader, *Austrobilharzia terrigalensis* (113), which appears to use prior infections of other species in proportion to their availability (3). Our analysis provides an alternative conclusion for a number of studies. Several original studies reported a combination of negative, positive, or neutral associations between pairs of trematodes (5, 19, 21, 65, 88, 111, 115, 119). In all of these cases, the net effect of interactions significantly decreased the number of double infections. It was also common to find interactions reported as unimportant when, in fact, our analysis revealed significant negative associations. Some of these were due to problems with probability theory (35, 36, 54, 89); others occurred because double infections were numerous and the authors made no direct statistical comparison (20, 24,

109). Two studies (80, 112) claimed a significant effect, but our approach indicated that interspecific interactions did not significantly structure those communities. Both anomalies result from a lack of sufficient statistical power due to low prevalence or sample size. One study (51) emphasized the phenomenon of a priori infection increasing the susceptibility to a second infection, although our analysis indicated a net effect of competitive interactions rather than facilitation.

Four factors increase the frequency of competitive events: high species evenness, high prevalences of infection, intensification of interactions due to heterogeneity in recruitment, and dominance hierarchies. Clearly, competition eliminates the majority of interspecific interactions. How can such strong competition persist? Standard predictions made for competing populations in closed recruitment systems do not apply to larval trematodes; in the same way they fail to predict interactions in marine systems with open recruitment (37). Complex trematode life-cycles, when coupled with the dispersal capabilities of their definitive hosts, open the nature of trematode recruitment and make it possible for a number of fierce competitors to coexist in a rich, yet interactive assemblage.

As we mentioned previously, Sousa (102) predicted that if competition is an important structuring force at the component community level, the highest trematode diversity should occur in medium-sized snails (or populations with intermediate prevalence) because competitive exclusion will eliminate subordinate species from older (larger) snails (or from areas of high prevalence). Unfortunately, this prediction has limited generality. For any community, when *subordinate* individuals are common, their competitive exclusion will generate the pattern opposite to Sousa's prediction; diversity will increase. Therefore, a negative association between prevalence and diversity is likely to hold only in the limiting case in which competition leads to the total exclusion of some species (61). Such in fact occurred at 2 of Sousa's 38 sites. The hyperbolic association of worm diversity and snail size depends on simplifying assumptions that may be difficult to meet in snail-trematode systems. Variation in snail growth rates among populations (62, 102) or between infected and uninfected snails (60, 62, 81, 101, 102) may make size a poor indicator for the age of an infected snail. Hence, associations between trematode diversity and snail size are difficult to interpret. Sousa's hypothesis also predicts that in host populations with high prevalence, competition should be more intense and diversity should be low. This is difficult to assess because the opposing pattern, high diversity in areas of high prevalence, should occur if there is a positive association between the density of definitive hosts and the diversity of trematodes inhabiting those hosts. Even when the predicted hyperbolic diversity curve occurs, Fernández & Esch (35) pointed out that alternative explanations such as parasite-induced host mortality may obscure analyses of competitive

effects. Finally, a general problem with predictions involving community diversity indices is that differences are difficult to detect (6). Therefore, absence of statistically significant changes in diversity indices may simply reflect the lack of power of this approach.

Although it is clear that interspecific competition reduces the number of interspecific interactions that can persist within a host (the infracommunity), does it affect the overall composition of the trematode assemblage that parasitizes a host population (the component community)? An interesting theoretical issue was raised by the claim that competition could be the predominant structuring force within the individual snails but not among the snails in a population (32, 35, 90, 102, 104). Is the system not additive? Can the extrinsic spatial and temporal heterogeneity effects be so large that they render intrinsic competitive effects unimportant at the level of the host population? Overall, our analysis indicates that infracommunity interactions are additive at the component community level because they must operate after potential isolating mechanisms occur at recruitment. "Important" is a loaded word, defined by the beholder. Our results show that competition significantly shapes the community beyond a simple reflection of recruitment. Its impact is most clearly important for subordinate species as their abundance is generally very much reduced by the impact of competitive dominants (Figure 3).

FUTURE WORK

Trematode Community Studies

Improved methods of analysis (64) have clearly altered the interpretation of past studies. Unfortunately, researchers usually did not design the stratification of samples to analyze heterogeneity in recruitment. Thus, the quality of our analysis reflects the quality of data that, often times, were not collected explicitly for our purpose. We hope that future studies will incorporate stratified sampling designs that balance the number of trematodes in each subsample. Also, it would be very instructive to investigate several levels of heterogeneity simultaneously to see how they interact to shape the number of expected interactions. Investigations into the effects of transmission to second intermediate and definitive hosts would also help determine whether heterogeneity transfers along the trematode life-cycle. Such hosts are often more vagile than snails and might act to homogenize effects of heterogeneity experienced by snails. (See *Note Added in Proof B.*) Finally, descriptive studies of larval trematode assemblages will continue to benefit from insights gained from experimental studies such as those pioneered by Sousa (102, 104), and there continues to be room for improved means of analysis.

Trematode Communities as Biomonitoring Tools

Gardner & Campbell (39) recently argued that parasites can act as probes for biodiversity because they track host food webs so broadly. A further use of parasites in biomonitoring studies stems from the similar hypothesis that parasites provide a representation of environmental quality and complexity. This is especially true for trematodes that usually have complex life-cycles involving trophic transmission. In a sense, trematode communities in snail hosts record the presence of definitive hosts and the abiotic conditions required for transmission in a particular wetland system. They also may indirectly represent the presence of second intermediate hosts. For example, Lafferty (63) noted fine-scale variation in prevalence between a population of snails from an undisturbed (25%) and a highly disturbed adjacent section (1%) of a salt marsh. Although some comparisons among sites could prove difficult to interpret, comparing changes in a location over time might be very instructive. Cort et al (18) did just this when they compared the larval trematodes from Douglas Lake in Michigan. Over a 20-year period, both prevalence and species diversity were greatly reduced (prevalence changed from 38–77% to 12–15%; species richness declined from 12–15 spp. to 3–4 spp.). They suggested that the increased number of summer cottages had led to a reduction in the number of vertebrates, especially shore birds, that visited the beaches. It would be interesting to see if this trend has continued over the past four decades. The considerable historical information that exists for trematode assemblages in several geographic areas provides ample opportunity for parallel comparisons.

Biological Control

Our findings that researchers have generally substantially underestimated competitive interactions in snail trematode systems, coupled with the demonstration that the most damaging human parasites (schistosomes) are largely competitive subordinates, should renew interest in the use of competitive dominants (notably echinostomes and cathaemasiids) as biological control agents. Many have suggested this approach (4, 10, 58, 66, 72, 80) and pilot studies have achieved success (reviewed by 12, 58, 66). However, biological control, along with other approaches to control of schistosomes by altering risk of transmission to humans, has lost favor largely because transmission models incorporate a low global prevalence of 1–2% (1). Our analysis shows that factors producing significant spatial and temporal heterogeneity can greatly elevate numbers of infected snails in likely foci of transmission. Thus, efforts at bio-control using trematode competitors should be explored, along with other efforts at local control of transmission to humans.

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NOTES ADDED IN PROOF

Despite the large number of studies encompassed in our analysis, we feel that the definitive study of trematode communities has yet to be done. Future analyses of the effects of recruitment and post-recruitment contributions to community structure should include evaluation of the impact of heterogeneity in snail densities at different sites. This can be incorporated by weighting samples proportional to density. We did not weight observed values according to sample size as in Lafferty et al. (64) because no other studies explicitly increased sample sizes from sites where prevalence was low. In data sets with multiple samples, large sample sizes contribute disproportionately to the pooled analysis. However, there was no discernible bias towards sites with either high or low prevalence. In some cases, the sample sizes may reflect abundance of snails. In a definitive study of community structure, this would be most appropriate. Analytical refinements are also needed to investigate the nature of changes in species composition over time. Changes as snails grow and as time passes may be due to either post-recruitment processes or to pulses in recruitment. The use of sentinel snail experiments would be very helpful to sort out these components. There is still much to learn.

Appendix Data compiled from studies used in our analyses

			Number of snails								
				Observed infections			Expected double		p value		
heterogeneity	Taxa[a]	S[b]	Total	Single	Double	Triple	Pool	Sum	Hetero.	Comp.	Reference
none	bi	2	2011	576	4	0	—	6	—	.250	80
none	bu	3	628	377	0	0	—	89	—	<.001	28
none	ce	17	12995	7153	646	23	—	3392	—	<.001	74
none	ce	10	2908	433	12	0	—	21	—	.009	119
none	ce	7	1652	838	34	1	—	256	—	<.001	79
none	ce	15	305	140	11	1	—	51	—	<.001	[d]
none	ce	5	191	108	4	0	—	30	—	<.001	33
none	he	6	2000	406	0	0	—	22	—	<.001	118 A
none	he	8	806	518	0	0	—	60	—	<.001	22
none	he	5	556	207	0	0	—	12	—	<.001	40
none	il	8	5025	326	14	0	—	9	—	.068	112
none	il	6	379	162	134	65	—	346	—	.001	23
none	li	7	6843	2798	110	4	—	393	—	<.001	54 A
none	li	6	2690	1244	22	0	—	29	—	.070	54 B
none	ly	2	6281	502	1	0	—	10	—	<.001	4
none	ly	5	425	425	0	0	—	69	—	<.001	67
none	ly	4	649	103	0	0	—	5	—	.003	2
none	ly	9	323	163	2	0	—	31	—	<.001	27
none	ot	7	3817	2476	364	9	—	1578	—	<.001	53
none	ot	12	1165	570	44	4	—	193	—	<.001	114
none	ot	4	650	246	51	0	—	53	—	.780	46
none	ph	5	104	30	2	0	—	5	—	.090	8
sex	li	3	3049	753	20	0	18	19	0.830	.830	73
sex	li	11	838	707	7	0	101	102	0.806	<.001	13
site	bi	2	2255	862	34	0	80	75	0.366	<.001	41 A
site	bu	2	765	144	8	0	7	5	0.330	.167	41 B

site	ce	15	24252	3626	74	1	342	395	<.001	<.001	104
site	ce	9	849	493	7	0	88	104	0.008	<.001	64
site	ce	6	416	64	10	2	5	11	0.002	.150	7
site	he	8	3963	1209	11	0	83	80	0.576	<.001	34/35
site	he	6	2007	321	0	0	14	16	0.490	<.001	118 B
site	he	9	1179	958	79	0	333	241	<.001	<.001	20
site	li	6	6169	960	29	0	62	70	.210	<.001	115
site	li	6	3586	236	0	0	6	7	.517	<.001	9
site	li	8	2831	1230	48	0	340	681	<.001	<.001	38
site	li	8	2785	673	71	3	94	175	<.001	<.001	82
site	li	8	600	338	3	0	184	80	<.001	<.001	76 C
site	li	2	520	181	4	0	10	12	.490	.001	109
site	li-ot	3	417	106	0	0	9	9	.791	<.001	30
site	li	5	335	203	21	0	62	74	.006	<.001	51
site	ly	16	4795	2593	256	10[c]	1055	1135	<.001	<.001	19
site	ot	3	8870	1024	155	1	75	84	.130	<.001	3
site	ot	5	4168	684	0	0	6	9	.232	<.001	52
site	ot	4	1700	193	8	0	7	9	.543	.790	57
site	ot	5	1244	803	237	0	310	293	.066	<.001	65
site	ph	7	5200	710	4	0	15	16	.866	<.001	95
site	ph	6	2491	762	9	0	77	126	<.001	<.001	21
size	bu	4	991	280	12	0	34	71	<.001	<.001	31
size	ce	9	970	320	7	0	41	66	<.001	<.001	[c]
size	he	8	4574	1374	11	0	65	54	.049	<.001	34/35
size	he	5	550	200	0	0	10	9	.683	<.001	40
size	li	4	5908	2194	145	0	516	634	<.001	<.001	88
size	li	6	1145	353	19	0	42	90	<.001	<.001	115
size	ot	6	3994	1656	192	1	266	294	.006	<.001	89
size	ot	5	1211	798	237	0	491	365	<.001	<.001	65
size	ph	6	2850	609	8	0	378	109	<.001	<.001	21
species	li-hy	10	4639	711	1	0	44	32	.004	<.001	86
species	li	8	2785	673	71	3	131	175	<.001	<.001	82
species	li	7	600	338	3	0	170	80	<.001	<.001	76 B

Appendix *(Continued)*

heterogeneity	Taxa[a]	S[b]	Number of snails: Total	Observed infections: Single	Double	Triple	Expected double: Pool	Sum	p value: Hetero.	Comp.	Reference
species	li	5	313	153	0	0	50	20	<.001	<.001	76 A
species	li-hy	24	42926	2561	25	0	64	40	<.001	<.001	11
species	ly-ot	41	2374	657	27	3	84	84	0.89	<.001	29
species	bi-bu	3	43526	2899	28	0	108	234	<.001	<.001	41 C
species	ot	4	248	57	11	0	8	10	.413	.640	36
time	bu	4	2045	437	3	0	22	16	.055	<.001	10
time	ce	15	24252	3626	74	1	356	395	<.001	<.001	104
time	he	8	4574	1374	11	0	56	54	.678	<.001	34/35
time	he	9	1179	958	79	0	247	241	.527	<.001	20
time	hy	13	15051	5249	428	7	1171	1100	<.001	<.001	111
time	il	6	14878	609	0	0	8	19	<.001	<.001	78
time	il	8	5677	1420	52	0	498	686	<.001	<.001	38
time	il	6	4314	254	0	0	5	6	.444	<.001	106
time	li	4	5876	2124	145	0	469	674	<.001	<.001	88
time	li	8	2785	673	71	3	186	175	.152	<.001	82
time	ly	16	4795	2593	256	10	1056	1135	<.001	<.001	19
time	ly	6	1639	571	195	15	199	288	<.001	<.001	5
time	ot	6	4920	2146	41	0	519	429	<.001	<.001	85
time	ot	7	1887	781	63	0	88	85	.678	.002	49
time	ot	9	304	94	0	0	11	14	.243	<.001	110
time	ph	6	1178	378	83	3	73	100	.001	.371	99
time	ph	6	697	356	5	0	83	104	<.001	<.001	21
time (mo)	ly	13	1697	678	53	2	171	209	<.001	<.001	18
time (yr)	ly	13	1697	678	53	2	195	209	.081	<.001	18

[a] Species codes are: bi = *Biomphalaria*, bu = *Bulinus*, ce = *Cerithidea*, he = *Helisoma*, hy = *Hydrobia*, il = *Illynassa*, li = *Littorina*, ly = *Lymnaea*, ot = other, ph = *Physa*.

[b] Species richness of larval trematodes.

[c] A quadruple infection was observed.

[d] Wardle, unpublished

[e] Kuris, unpublished

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