Patterns and processes in communities of helminth parasites

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What processes account for the structure and dynamics of helminth parasite assemblages within vertebrate and invertebrate hosts? Attempts to answer this question form the basis for the emerging subdiscipline of parasite community ecology. Negative interspecific interactions strongly affect the distribution and abundance of parasites in some systems, but only intermittently, if ever, in others. Empirical results provide only mixed support for recent theories that attempt to explain this variation.

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Assemblages of animal parasites consist of varying numbers of potentially interacting species that inhabit a spatially subdivided environment comprising numerous similar patches of discretely bounded habitat. These characteristics should make them attractive systems for study by community ecologists, yet until recently they were appreciated only by a small, but dedicated, cadre of parasite ecologists. The birth of quantitative parasite community ecology was marked by Holmes'[1] elegant experimental investigations of interactions between cestode and acanthocephalan parasites of rats. Although this was not the first demonstration of negative interactions between different species of parasites infecting the same animal host[2], Holmes' results were the first of their kind to receive serious attention from investigators of free-living communities, and to be cited in support of predictions from general ecological theory[3]. In the 30 years since Holmes published his findings, there have been many studies quantifying the distribution and abundance of endo- and ectoparasitic helminths, as well as their patterns of interspecific association[4–9].

Studies of adult helminths, which infect vertebrate hosts, have provided the foundation for most current theory concerning the organization of parasite communities, notwithstanding Price's[10] more integrative and taxonomically broader treatment. Larval helminths and the processes structuring their assemblages within invertebrate intermediate hosts have not figured prominently in the development of theories concerning parasite community structure. This is despite the classic studies of Lie and co-workers in the 1960s, which unambiguously demonstrated strong interactions among larval trematodes co-infecting freshwater snails[11].

Here, I examine recent empirical and theoretical efforts to understand the structure and dynamics of assemblages of parasitic helminths. This search has been guided (or some might say misguided) by a variety of alternative hypotheses or paradigms, some of which are strikingly similar to those proposed to explain patterns in communities of free-living species.

Hierarchical structure: definition of terms

Hosts are the habitats of infective stages in the life cycles of parasitic helminths. These life cycles can be quite complex and varied[6,9]. In each, there is an obligate sequence of intermediate (larval) and definitive (adult) hosts; transmission between hosts is effected either by free-living motile larvae that penetrate the host, or by eggs or encysted larvae that are ingested by the host. Patterns in the distribution and abundance of these parasites, and the processes that generate them, occur at several hierarchical and discrete spatial scales. To help clarify discussions of pattern and process at different scales of host habitat, a set of terms has been adopted by workers in the field (Table 1). Most empirical and conceptual research on the organization of parasite communities has been done at the infra- and component community levels. This review addresses patterns and processes in parasite infracommunities, recognizing that they can be strongly influenced by phenomena operating at larger spatial scales.

Infracommunity structure: theories

Integrating the earlier hypotheses of Holmes[5], Rohde[12] and Price[10], Holmes and Price[13] proposed a dichotomous classification of parasite infracommunities: interactive versus isolationist (Table 2). Colonization rate is the primary defining variable in this scheme: when high, infracommunities are interactive; when low, they are isolationist in nature. All else being equal, hosts that acquire infective stages more readily are expected to harbor denser infrapopulations of a greater number of parasite species. Such dense, diverse assemblages will be characterized by frequent, largely negative, interspecific interactions that cause either reduced spatial overlap and more even distribution of species infrapopulations along resource gradients (e.g. along the small intestine) or complete exclusion of the competitively inferior species. The occurrence of host or infection site specificity in the absence of present-day antagonistic interaction is attributed to strong interspecific competition in the evolutionary past that has selected for genetically-based niche partitioning among co-occurring parasite species, i.e. the 'ghost of competition past'[14].

When average colonization rates are low, either because of poor transmission or immunological barriers imposed by the host, infracommunities are expected to be depauperate and biotic interactions chronically rare or only intermittently important. In such cases, host or infection-site specificity represents independent specialization that has evolved for reasons other than interspecific competition, including host–parasite coevolution, enhancement of mate-finding and avoidance of hybridization.

Holmes and Price[13] admitted that their dichotomous construct was oversimplified, and shortly thereafter Goater *et al.*[15] interpreted isolationist and interactive infracommunities as extremes of a continuum. There has been a variety of elaborations on this basic scheme. For example, Bush and Holmes[16,17] predicted that within interactive communities it is the 'core'[18,19] species, i.e. those that are regionally common, locally numerous and often specialists in the particular host, that are most likely to interact and be negatively associated within infracommunities, as compared to less abundant 'secondary'[16,17] or even rarer 'satellite'[19] species that often exploit a variety of definitive hosts.

Table 1. Terms used to describe the hierarchical nature of parasite populations and communities[13,16,29,41,42]

All individuals of:	**Infecting:** A single individual of host species X	A population of host species X	Populations of all host species in an ecosystem
One parasite species	infrapopulation[a]	metapopulation[a]	suprapopulation[b]
All parasite species	infracommunity or infraguild	component community or component guild	compound community

[a]Generally comprised of one developmental stage in the life cycle of the parasite species.
[b]Includes all stages in the parasite's life cycle.

Table 2. Characteristics of interactive versus isolationist parasite infracommunities according to Holmes and Price[13]

	Type of infracommunity structure	
Characteristic	Interactive	Isolationist
Rate at which host is colonized by parasites	High	Low
Average density of parasite infrapopulations	High	Low
Frequency of interspecific interaction	High	Low
Species distributions in resource space	Evenly distributed; responsive to presence of other species	Individualistic; insensitive to the presence of other species
Species diversity	High; community saturated with species	Low; community unsaturated with species; some niches empty
General nature of the infracommunity	Non-equilibrial; stochastic factors important	Equilibrial and evolutionarily 'mature'

Infracommunity structure: empirical patterns and processes

Kinds and quality of evidence

Published evidence concerning the processes that structure assemblages of helminth parasites is largely circumstantial and, in most cases, is derived from the 'natural experiments'[20] afforded by the particular collection of hosts (Box 1). Such comparisons are not without their pitfalls[21,22]: unambiguous control treatments are lacking, and individual hosts are assumed (often without direct and independent corroborating evidence) to be good replicates of each other. The potentially confounding influences of variation in host size, age, sex or site of collection must be minimized either in the initial sampling procedure or by stratifying the subsequent analysis according to these host characteristics. Samples of field-collected hosts cannot be stratified with respect to some important but subtle characteristics such as their innate resistance to infection. Further, the construction of appropriate null models can be tricky.

Where logistically and ethically feasible, controlled manipulation of parasite populations under field conditions would be a better method of determining the existence and strength of hypothesized biotic interactions operating at relatively small spatial scales. However, the technical barriers to manipulating parasite community structure in a controlled fashion under field conditions are formidable. In fact, Esch and Fernandez[9] recently concluded that '[experimental] manipulation of most parasite infracommunities is virtually impossible' (also see Ref. 22). Establishing a predetermined level of infection, particularly by the exclusion or introduction of numerous, very small, free-living infective stages, is no doubt the greatest hurdle. To date, the few such experiments that exist have been conducted almost exclusively in the laboratory. To my knowledge, the only published 'field' experiments in which parasite communities were directly manipulated are those of Lie and co-workers conducted in artificial outdoor ponds[23]. Laboratory-reared eggs of freshwater echinostome trematodes were introduced into the ponds which contained snails naturally infected by larval schistosomes. The aim was to determine whether newly acquired echinostome infections would exclude established schistosome infections, as had been previously demonstrated in laboratory studies. In two of three trials, the echinostomes appeared to have excluded most or all schistosome infections from the pond.

The bottom line is that current assessments of the processes that structure parasite communities, particularly in vertebrate hosts, are based largely on inferences drawn from comparative analyses of patterns of distribution and abundance. As was true in the debate over the role of interspecific competition in free-living communities, advances in the field of parasite community ecology will require that ways be found to confirm the operation of hypothesized processes with direct observation or manipulative experiments.

An additional constraint on the development of general theory in this area is that few studies identify the precise mechanisms by which inferred interactions are occurring. Helminth parasites can potentially interact in a variety of ways, both negative and positive. Adult stages that inhabit vertebrate guts may compete exploitatively for nutrients, especially carbohydrates[24], or for space via direct or indirect forms of interference. An infrapopulation of one species of parasite may exclude and/or reduce the density of another species' infrapopulation by direct mechanical or chemical interference between individuals, or indirectly, by redirecting the host's immune reactions against its competitor[25,26], or by making the local tissue environment inhospitable to the second species[27]. In many cases, it may be difficult to distinguish whether helminths are competing for food or for space since characteristics of both resources are intimately linked to the specific site of infection[24].

Box 1. Types of circumstantial evidence of interspecific interaction in helminth infracommunities

The following associational and distributional patterns have been interpreted as evidence that competition is responsible for structuring assemblages of helminth parasites in the gastrointestinal tracts (GIT) of vertebrate hosts:

Comparisons between host individuals

1. A shift in the mean or median of a parasite's GIT distribution in a mixed-species infection as compared to an infection in which a putative competitor is less dense or absent; in some cases, one species completely displaces another (Type 3, below).
2. A reduction in the density or biomass of a parasite infrapopulation in mixed- versus single-species infections (or as the density or biomass of putative competitors in mixed-species infections goes up).
3. Species of parasites are negatively associated among host individuals.

Patterns within individual hosts

4. Overlap in the 'realized distributions' of different parasite species within individual hosts is less than the overlap in their 'fundamental distributions' (i.e. their summed distributions across all hosts in the sample).
5. The distributional range of a parasite species within the GIT increases with infrapopulation density, but the overlap of its distribution with those of other species in a mixed-species infection does not.
6. Negative association in the linear distributions and/or abundances of species along the GIT; complementary or disjunct distributions.
7. In mixed-species infections, the means or medians of the species' distributions are evenly spaced.

Different species of larval helminths co-inhabiting the same intermediate invertebrate or vertebrate host may also negatively interact by a variety of mechanisms, some very similar to those hypothesized for adult stages, and some apparently unique to the larval stages of particular taxa. Exploitative competition for nutrients or oxygen, chemical interference or defensive cellular reactions in the host induced by the presence of one parasite species that differentially harm a second, have all been invoked to explain cases of abnormal or slowed larval development in mixed-species versus single-species infections, or negative spatial associations within or among individual hosts. In most cases, as for assemblages of adult helminths, the precise mechanism is poorly known[11]. The best documented mechanism of interspecific antagonism between larval helminths is predation by redial larvae of particular species of trematodes on the larval stages of other trematode species within intermediate snail hosts[11,28–31].

The emphasis of the research discussed thus far has been on negative associations among parasite species, but positive associations are not uncommon. Helminths that exploit the same species of intermediate host will often co-occur within individual vertebrate hosts which acquire infections by feeding on that intermediate host[16,32]. Similarly, if adult worms of two or more species co-infect a given vertebrate host, their larval stages are more likely to occur in mixed-species infections within intermediate hosts[33]. Other mechanisms that promote positive associations include suppression of the host's immune response by an initial infection that facilitates establishment of another[26,34], or any positively correlated response by different parasite species to heterogeneity in the qualities of individual hosts, e.g. their age, size, sex, location, etc. An important caveat is that, while such positive associations can be mutualistic[35], often they are not; the growth and development of one species suffers and in time it may be excluded altogether[28,31,32].

Infracommunities of adult helminths

Given the limitations of the data discussed above, can the infracommunities of adult helminths in vertebrate hosts be unambiguously arrayed along a one-dimensional continuum from isolationist to interactive (Table 2)? Kennedy *et al.*[36] summarized their own data on infracommunities of alimentary tract helminths in five species of birds, nine species of freshwater fishes and one species of small mammal, the rice rat. They compared the mean intensity of infection, mean species richness and the mean diversity of the assemblages. The distributions of all three community characteristics were fairly continuous: birds (with one exception) and the rice rat had, on average, denser infracommunities than any of the freshwater fishes, and without exception, their infracommunities were more species-rich and diverse than any of the latter.

Kennedy *et al.*[36] attributed the generally denser, more diverse infracommunities of endothermic versus ectothermic vertebrate hosts to: (1) the more differentiated intestinal tracts of endotherms, which afford a greater number of infection sites; (2) the higher rate of food consumption; (3) the vagility of endotherms [both (2) and (3) increasing their rate of exposure to parasites]; and (4) the broader diet of many endotherms, which enhances the diversity of larval parasites that they consume. They acknowledged exceptions to this pattern, including endothermic host species (or populations thereof) that specialize on a few prey items, or are relatively sedentary. Kennedy *et al.*[36] also hypothesized that interspecific interactions should be relatively more important in structuring the dense, diverse assemblages in endothermic definitive hosts than the more depauperate infracommunities of ectothermic hosts.

How well have the expectations of Holmes and Price[13] and Kennedy *et al.*[36] held up? Table 3 summarizes the findings of studies that (1) provide quantitative information on the structure of fully censused infracommunities, and (2) statistically examine such data for evidence of interspecific interaction among parasites. Most of them were published after 1986, the year that Kennedy *et al.*[36] appeared. Even a cursory scan of the abridged results in Table 3 reveals that neither the Holmes and Price[13] nor Kennedy *et al.*[36] scenarios reliably predicts the degree to which parasite infracommunities of vertebrate hosts are structured by interspecific interactions. While some host species and their associated parasite assemblages fit the predictions reasonably well [e.g. salamanders; lesser scaup, *Aythya affinis* (data included in Kennedy *et al.*'s analysis); grebes, *Aechmophorus occidentalis* and *Podiceps* spp.], clearly, neither a host's mode of thermoregulation nor infracommunity diversity exclusively define the interactive nature of a host's parasite fauna. There are assemblages of low diversity and modest densities in either ectothermic (e.g. three-spined stickleback, *Gasterosteus aculeatus*) or endothermic hosts (e.g. bobwhite quail, *Colinus virginianus*; fulmar, *Fulmarus glacialis*; and long-billed curlew, *Numenius americanus*) that are interactive. There are other endothermic hosts whose infracommunities have similar characteristics but are noninteractive (e.g. bats; wood mice, *Apodemus sylvaticus*; black bear, *Ursus americana*). Host characteristics that co-vary with mode of thermoregulation, such as host gut morphology, diet and vagility, are also not particularly successful predictors of either infracommunity structure or levels of interspecific interaction. For example, both sticklebacks and salamanders have relatively simple enteric systems, are fairly sedentary and possess simple infracommunities, yet parasites are interactive in the former, but not the latter. Bobwhite quail and long-billed curlew have relatively complex enteric systems, diverse diets and are vagile, yet

Table 3. Patterns and processes in helminth infracommunities of vertebrate definitive hosts

Host species	Sample size[a] (N)	Mean number of parasite species per (range) host	Mean total parasites per host	Component community species richness	Author(s)' classification of infracommunity	Supporting evidence[b]	Refs
Ectothermic hosts							
Fishes							
Gasterosteus aculeatus	601	0.5 (0–2)	0.9	2	Interactive	Type 1 Tested for, not found: Types 2, 3	43
Salamanders							
Leurognathus marmorata	50	0.7 (0–3)	1.1	4	Isolationist	PD	15
Desmognathus monticola	125	1.9 (0–6)	5.3	8	Isolationist	PD	15
D. ochrophaeus	107	1.1 (0–4)	2.2	7	Isolationist	PD	15
D. quadramaculatus	115	2.0 (0–7)	6.4	8	Isolationist	PD, except too few uninfected hosts	15
Endothermic hosts							
Birds							
Aythya affinis	45	14.0 (8–26)	22 163	52	Interactive	Types 4, 5, 6, 7 Tested for, not found: Type 3	16,17
Aechmophorus occidentalis	20	6.4 (4–10)	360	16	Interactive	Types 4, 5, 6 Tested for, not found: Types 3, 7	44,45
Podiceps grisegena	33	10.7 (4–14)	1808	23	Interactive	Types 1, 4, 5, 6 Tested for, not found: Types 3, 7	27,44,45
P. nigricollis	31	9.1 (2–15)	3640	26	Interactive	Types 4, 5, 6 Tested for, not found: Types 3, 7	44,45
P. auritus	7	6.7 (4–8)	1808	14	Interactive	Types 4, 5, 6 Tested for, not found: Type 3, 7	44,45
Numenius americanus	18	4.2 (2–7)	317.6	9	Interactive	Types 4, 5, 6 Type 7: test result equivocal Tested for, not found: Type 3	46
Recurvirostra americana	5	7.0 (?)	133	14	Isolationist	For pooled sample of 22 birds: Types 4, 5; but detected fewer negative relationships and more vacant infection sites in isolationist assemblages Tested for, not found: Types 1, 2, 3	37
	5	7.0 (?)	496	16	Isolationist		
	6	13.5 (?)	3709	26	Interactive		
	6	11.0 (?)	9419	18	Interactive		
Colinus virginianus	158	4.0 (?)	98.1	12	Interactive	Types 3, 6	47
Fulmarus glacialis	30	2.7 (2–3)	164.2	3	Interactive	Type 1	48
Mammals							
Eptesicus fuscus	26	0.1 (0–1)	0.1	2	Isolationist	RID	32
	47	2.9 (1–7)	95.2	12	Isolationist	RID	
	83	4.3 (0–9)	70.3	29	Isolationist	PA	
Myotis lucifugus	22	4.9 (1–10)	326.8	12	Isolationist	PA	32
	32	6.6 (1–12)	326.5	16	Isolationist	PA	
M. austroriparius	255	2.5 (0–6)	69	11	Isolationist	PA	32
Nycticeius humeralis	18	3.4 (0–6)	38.9	10	Isolationist	PA	32
	22	3.8 (1–7)	40.1	10	Isolationist	PA	
	42	2.8 (1–6)	37.0	9	Isolationist	RID	
Pipistrellus subflavus	52	1.4 (0–4)	39.4	8	Isolationist	RID	32
Tadarida brasiliensis	27	0.9 (0–3)	2.1	5	Isolationist	RID	32
	32	0.7 (0–3)	1.6	3	Isolationist	RID	
Apodemus sylvaticus	4–126[c]	0–4 (?)[c]	0–89.6[c]	9	Isolationist	Type 3, but for only 6 of 36 pairwise tests Tested for, not found: Type 2	38
Odocoileus virginianus	10	2.5 (1–4)	2615	5	Isolationist	PD	49
	11	3.4 (2–5)	1588	6	Isolationist	PD	
Ursus americana	14–54	2.4–3.1 (?)	11.8–300.9	8–11	Isolationist	For pooled sample of 104 bears from 4 localities: PD	49
Canis latrans	177	4.7(?)	317.9	16	?	PD, but author believes recurrent group of common spp. likely to interact	49

[a] Sample size; multiple entries or range given when more than one host population sampled.
[b] Types of evidence for interactive infracommunity numbered and described in Box 1. Types of evidence for isolationist infracommunity: PD – frequency distribution of parasite species per host did not differ from Poisson. RID – Randomization test showed parasites to be randomly and independently distributed among hosts. PA – Randomization test showed parasites to be positively associated among hosts.
[c] Ranges for 76 monthly samples collected from 12 populations.

their parasite infracommunities are neither diverse nor particularly dense. Contrary to theoretical expectations, interspecific interactions apparently do occur among their parasites.

Obviously, many details of the natural history and life cycles of both host and parasites must be stipulated before one can accurately predict how interactive the infracommunity in a particular host will be. Salamanders, for example, being generalist insectivores, have a broad diet that one might expect would generate a diverse infracommunity of parasites. It just so happens that few of the insect species they prey upon serve as intermediate hosts for helminths such as trematodes or cestodes; instead, their infracommunities are dominated by a few species of nematodes with simple, direct life cycles[15]. Further complicating any search for general patterns is the fact that the structure of the infracommunities in a particular host species, as well as the degree of interspecific interaction within them, can vary among host populations and in time[37–39]. Kennedy *et al.*[36] fully recognized such complexities (see their discussion), but chose to emphasize what appeared to be a strikingly consistent relationship between the mode of host thermoregulation (and associated life history features) and parasite infracommunity structure. With the 20:20 hindsight afforded by the data that have accumulated since their paper appeared, it is easy to see that they either underemphasized or underestimated the complexity and variability of processes that determine the structure of parasite infracommunities within vertebrate hosts.

Infracommunities of larval helminths

As noted earlier, assemblages of larval helminths within invertebrate or vertebrate intermediate hosts have been largely ignored in past discussions of parasite infracommunity structure which focused almost exclusively on the adult phase of the life cycle. To a large extent, this benign neglect reflects the historical accident that most of the early contributors to the discipline were working at the time primarily with gastrointestinal parasites of vertebrates.

Recently, there has been renewed ecological interest in natural larval trematode–snail associations, particularly with respect to the relative roles of interspecific antagonism and recruitment processes in determining patterns of interaction and coexistence within infracommunities. Several features of the biology of trematode larvae and their snail hosts enhance the likelihood of interspecific interaction, whether positive or negative. By asexual reproduction, a single, free-living miracidium larva that successfully infects a snail can rapidly give rise to hundreds, if not thousands, of parasitic redial or sporocyst larvae. Therefore, larval infrapopulations are almost always dense, and tissues of some target organs in the snail, e.g. the gonad, may be completely eliminated by their feeding activity. By contrast, infrapopulations of adult helminths increase in size only if the host is penetrated by, or consumes, additional infective larvae. One feature of invertebrate hosts that further enhances the opportunity for interaction among co-occurring larval parasites is that these hosts offer fewer, and more spatially homogeneous, target organs to parasites than do vertebrate hosts. Thus, parasite resources within invertebrate hosts can potentially be more easily monopolized by one or a few species than can the more complex enteric systems of vertebrates.

There is abundant circumstantial and direct evidence that interspecific interactions occur among different species of larval trematodes that naturally infect the same snail[11,28–31,33]. The most commonly cited circumstantial evidence is the observation that mixed-species infections are less frequent than would be expected under the null hypothesis of random and independent distribution of parasites among hosts. While a variety of mechanisms other than negative interspecific interactions might produce such negative associations, several studies have provided unambiguous evidence that direct interspecific antagonism prevents species coexistence within some infracommunities[11,28–31,33].

In field mark–recapture studies and laboratory challenge experiments, the larvae of particular species of trematodes invaded and excluded pre-existing infections of other species, while established infections of the former species effectively resisted invasion. In many cases, the dominant species in these interactions were those with the largest redial larvae; in dissections of snails carrying mixed-species infections these larvae were observed to actively prey on smaller redial or sporocyst larvae of other species[31]. Predation on conspecific larvae has seldom been observed. Rediae possess a mouth, muscular pharynx and gut with which they actively feed on host tissues (and subordinate competitors), whereas sporocysts, which lack these features, absorb nutrients through their body walls. While predation by rediae on other larvae has been observed in a number of trematode–snail associations, larval type (redia versus sporocyst) and size do not explain all observed outcomes of interactions among larval trematodes[30]. Priority effects are sometimes important, as are indirect mechanisms of interspecific antagonism and facilitation that operate even when larvae are not in direct contact.

Predation is not the only trophic interaction unique to parasite infracommunities of molluscan intermediate hosts. Lie *et al.*[40] observed that differential hyperparasitism by a microsporidian of the rediae of an antagonistically dominant echinostome trematode prolonged their coexistence with sporocysts of a subordinate schistosome trematode.

Clearly, infracommunities of larval trematodes have the potential to be strongly interactive. Since asexual propagation insures that infrapopulations of intramolluscan stages will be dense regardless of the number of miracidia that penetrate a snail, the occurrence of interspecific interaction and its impact on the structure of larval trematode infracommunities depends primarily on factors controlling the availability of infective eggs or miracidia and their transmission and establishment in snails. These factors include processes that affect the abundance and reproductive performance of adult stages in definitive vertebrate hosts. The limited long-term data now available indicate that rates of parasite transmission from definitive vertebrate hosts to first intermediate snail hosts are quite spatially and temporally variable, as are the rates of interspecific interaction among intramolluscan larval stages[31,33]. Given such variation, an infracommunity comprising a single species of larval trematode can represent either a case of antagonistic interspecific exclusion or the failure of more than one species to successfully colonize the host. Thus, the nature of parasite infracommunities within molluscan intermediate hosts, i.e. isolationist versus interactive, can vary markedly in space and time.

Final comments

We are now in a very exciting phase in the growth of the discipline of parasite community ecology. Data on the structure and dynamics of parasite infracommunities are being gathered more extensively and rigorously than ever before, allowing for more definitive tests of hypotheses. As Holmes and Price[13] hoped, their distinction between interactive and isolationist communities has proved a very useful first step; now it is time to consider the exceptional cases for what they might suggest in terms of a more precise and predictive framework. All the while, we should bear in mind that broad generalizations may prove elusive in such complex systems. Ultimately, differences in the structures of parasite infracommunities reflect variation in the actions of several screens (or filters) that determine what subset of the potential pool of parasites comprises a realized infracommunity[24]. These screens include (1) physical and biological processes that determine host exposure to parasites, (2) host and parasite factors that affect the establishment and viability of an infection, and (3) direct and indirect interspecific interactions within mixed-species infections.

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