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ORIGINAL PAPER

Spatial covariation of local abundance among different parasite species: the effect of shared hosts

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Abstract Within any parasite species, abundance varies spatially, reaching higher values in certain localities than in others, presumably reflecting the local availability of host resources or the local suitability of habitat characteristics for free-living stages. In the absence of strong interactions between two species of helminths with complex life cycles, we might predict that the degree to which their abundances covary spatially is determined by their common resource requirements, i.e. how many host species they share throughout their life cycles. We test this prediction using five trematode species, all with a typical three-host cycle, from multiple lake sampling sites in New Zealand's South Island: *Stegodexamene anguillae*, *Telogaster opisthorchis*, *Coitocaecum parvum*, *Maritrema poulini*, and an *Apatemon* sp. Pairs of species from this set of five share the same host species at either one, two, or all three life cycle stages. Our results show that when two trematode species share the same host species at all three life stages, they show positive spatial covariation in abundance (of metacercarial and adult stages) across localities. When they share hosts at two life stages, they show positive spatial covariation in abundance in some cases but not others. Finally, if two trematode species share only one host species, at a single life stage, their abundances do not covary spatially. These findings indicate that the extent of resource sharing between parasite species can drive the spatial match-mismatch between their abundances, and thus influence their coevolutionary dynamics and the degree to which host populations suffer from additive or synergistic effects of multiple infections.

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Introduction

The abundance of any parasite species varies spatially, reaching higher values in some parts of their geographical range than in others (Poulin 2006; Poulin and Dick 2007; Perez-del-Olmo et al. 2011). Presumably, higher abundance is achieved in localities where resources (i.e. hosts) are plentiful and other conditions are well-suited to transmission and the survival of free-living stages. Both epidemiological theory (Anderson and May 1978, 1979; May and Anderson 1979; Diekmann and Heesterbeek 2000) and empirical evidence (Arneberg 2001; Arneberg et al. 1998; Lagrue and Poulin 2015) indeed show that parasites generally achieve their highest abundance where suitable hosts occur at high densities. What is less clear, however, is the extent to which different parasite species using the same hosts have matching patterns of spatial variation in abundance. Are the hotspots of abundance for parasite A the same as those for parasite B if the two share the same hosts and have similar geographical ranges? Spatial covariation in abundance has been reported for free-living organisms. For example, based on census data from multiple sites across the North American continent, hotspots of abundance for several different passerine birds are significantly positively associated, i.e. the abundance distributions of different species are not independent but instead peak in the same places (Brown et al. 1995). We currently lack solid evidence of spatial covariation in abundance for parasites, and the extent to which it is determined by the level of host sharing.

On very small scales, i.e. when comparing individual hosts within a population, both positive and negative associations

between infection intensities of pairs of parasite species are commonly reported (Bush and Holmes 1986; Lotz and Font 1991; Haukisalmi and Henttonen 1993; Holmstad and Skorping 1998; Dezfuli et al. 2001). Negative associations are generally interpreted as evidence of competition or other form of antagonistic interactions, whereas positive associations may arise from facilitation via immunosuppression or through concomitant transmission (Poulin 2001). On larger spatial scales, i.e. when comparing distinct geographical localities, associations between the local abundances of pairs of parasite species are more likely to reflect co-dependency on host resources. This is because within-host interactions such as competition are unlikely to be strong enough to impact the size of a local parasite population, given that competing parasite species may be distributed differently among individual hosts (Dobson 1985; Dobson and Roberts 1994). Therefore, in the context of helminths with complex life cycles, a simple prediction is that the degree to which the abundances of two species covary spatially should be determined by how many hosts they share throughout their life cycles. Two species with identical life cycles, i.e. using the same intermediate and definitive host species, have matching resource requirements: wherever the conditions are ideal for one species to achieve high abundance, they should be equally good for the other species. In contrast, two parasite species having a single host in common at one life stage would be more likely to have independent spatial variation in abundance, as the other resources (i.e. the other hosts) they require are not shared and their local availability may not coincide across localities.

Here, we test this general prediction with data on the abundances of five trematode species from multiple localities in New Zealand's South Island. All trematodes considered here have a typical three-host life cycle, with a snail as the first intermediate host, a second intermediate host in which the parasites encyst as metacercariae, and a vertebrate definitive host in which adult worms live and reproduce. Various pairs of species from this set of five trematodes share either one, two, or all three hosts at different life cycle stages. Previously, spatial covariation in abundance has been investigated by Blasco-Costa et al. (2015) in four of these five species; it was found that even pairs of species with identical life cycles and sharing all their hosts had completely independent patterns of abundance hotspots throughout their range. However, this earlier study focused on abundance of a single life stage, used a host-centric measure of abundance, and was performed on a very large scale (all of New Zealand) involving a broad range of environmental conditions (Blasco-Costa et al. 2015). Here, using a completely different data set, we focus on a much smaller scale where conditions are likely less heterogeneous, we investigate abundance of two life stages (metacercariae and adults) and we use a measure of abundance that captures the parasite population size rather than the severity of infections incurred by hosts.

We test the general prediction that the more hosts are shared by two parasite species at different life stages, the more likely their abundances are to covary positively across localities. Our results shed new light on whether, and in what circumstances, different parasites have common hotspots of high abundances, and thus the extent to which different parasites can have additive effects on host population dynamics.

Methods

Study species

The five trematode species considered here belong to different families (Table 1) and are all common in New Zealand freshwater ecosystems. All five species use the freshwater snail *Potamopyrgus antipodarum* as the first intermediate host; this is the only host shared by all species. Two trematodes, *Stegodexamene anguillae* and *Telogaster opisthorchis*, share all their hosts and have essentially identical life cycles; any other pair of species share hosts at either a single or at most two life cycle stages (Table 1). Two species, *Maritrema poulini* and *Apatemon* sp., have avian definitive hosts; birds were not sampled in this study, and therefore no data are available on adult abundance for those two trematodes.

We focused on the abundance of these parasites in their crustacean and fish hosts. We did not analyse spatial variation in the abundance of parasites in their first intermediate host, the snail *P. antipodarum*, because prevalence of infection in snail populations was rather low. Also, the relative use of different host species at a particular life stage by any two parasites sharing these hosts is always the same. For example, *S. anguillae* and *T. opisthorchis* both use two fish species as their second intermediate host (Table 1); however, for both species, ⩾95 % of the population is found in only one of these fish, the same for both trematodes, i.e. the bully *Gobiomorphus cotidianus*. The same pattern of roughly identical usage of different hosts applies to all cases, and therefore, we used a simple classification: pairs of trematodes share hosts at either one, two, or three life stages.

Field sampling and laboratory processing

We sampled the fish and crustacean hosts of these five trematodes in the littoral zone of four lakes within the Otago region of the South Island of New Zealand: Lake Waihola, Lake Tuakitoto, Tomahawk Lagoon, and Lake Hayes. These are small- to medium-sized lakes, mostly shallow, and at different altitudes and distances from the coast; for their exact location and characteristics, see Lagrue and Poulin (2015). In each lake, we sampled four sites consisting of square areas (15 m×15 m) with one side of the square along the shore, distant by 123 to 2250 m from each other and selected to

Table 1 Trematode species included in the present analysis and the hosts used in their life cycles

Trematode species	Family	First intermediate host	Second intermediate host	Definitive host	Number of sites
Maritrema poulini	Microphallidae	Snail[a]	Amphipods[b,c,d], Isopods[e]	Unknown birds	8
Coitocaecum parvum	Opecoelidae	Snail[a]	Amphipod[b,c]	Fish[f,h,i,j,k,l]	12
Apatemon sp.	Strigeidae	Snail[a]	Fish[f]	Unknown birds	16
Stegodexamene anguillae	Lepocreadiidae	Snail[a]	Fish[f,g]	Fish[l,m]	16
Telogaster opisthorchis	Heterophyidae	Snail[a]	Fish[f,g]	Fish[l,m]	16

[a] *Potamopyrgus antipodarum*
[b] *Paracalliope fluviatilis*
[c] *Paracorophium excavatum*
[d] *Orchestia* sp.
[e] *Austridotea annectens*
[f] *Gobiomorphus cotidianus*
[g] *Galaxias maculatus*
[h] *Perca fluviatilis*
[i] *Rhombosolea retiaria*
[j] *Salmo trutta*
[k] *Retropinna retropinna*
[l] *Anguilla dieffenbachii*
[m] *Anguilla australis*

represent all habitat types (substrate, macrophytes, riparian vegetation, etc.) present within each lake. This gave us 16 study sites (4 lakes×4 sampling sites per lake), with each site sampled in three seasons (September 2012 and January and May 2013).

Fish were sampled using a combination of gear types following a standardised protocol to achieve estimates that represented as accurately as possible actual fish diversity and density per site (see Lagrue and Poulin 2015; Lagrue et al. 2015). Two fyke nets were set overnight along the edges of the sampling area, perpendicular to the shore, and two 15-m-long multi-mesh gillnets were deployed in the same place during the day. These were used to capture all fish swimming in and out of the area, i.e. both residents and visitors to the area. In addition, a standard, fine-mesh purse seine net was dragged across the whole area to capture small and/or sedentary resident fish not captured by passive gear, like fyke nets or gillnets. All fish caught were identified to species, counted, and a subsample was returned to the laboratory for dissection. In each site and in each season, six samples of benthic invertebrates, distributed haphazardly across the sampling area, were taken using a standard Surber sampler net with a 0.1-m^2 horizontal metal frame fitted with a 250-μm-mesh collecting net. In addition, six samples of demersal invertebrates, living on or near the substrate but not captured in Surber nets, were sampled using a rectangular dip net (30 cm wide and 22 cm high opening) with a 250-μm-mesh net; each sample consisted of a fast, 2-m-long sweep of the net along the lake bottom without dredging the substrate. All invertebrate samples were preserved in ethanol for later identification, counting, and dissection.

In the laboratory, all individuals were identified to species and counted, after which a subsample of each species was dissected carefully following a standardised protocol for parasite recovery and identification (see Lagrue and Poulin 2015; Lagrue et al. 2015).

Data analysis

For each life stage (metacercariae in second intermediate hosts and adults in definitive hosts) of each trematode species in each site where they were found, we calculated density (individuals per m^2) as a measure of local 'population' size. Parasites are rarely quantified this way (but see Hechinger et al. 2008; Sonnenholzner et al. 2011); instead, parasite populations are usually quantified as individuals per host rather than per surface area. However, here, we want a measure that integrates parameters such as prevalence and intensity of infection across all host species used by a parasite at a particular life stage; density provides such a measure. In addition, as stated earlier, for any pair of parasite species, both achieve by far their highest abundance and prevalence in a single host species, the same for both parasites; thus, analyses using traditional measures of mean intensity or abundance of infection would yield very similar results to those of the present analysis. For each site and each sampling period, we first averaged the density values for each parasite life stage across all samples. Then, we calculated the mean density per site across all

three sampling periods. Averaging across seasons provides a better estimate of local density, especially given that there are no marked seasonal changes in the abundance and composition of freshwater communities in southern New Zealand.

Parasite density values were log-transformed prior to analysis. To test for spatial covariation in density among parasite species, we tested for a relationship between local densities for all pairs of trematode species, separately for each life stage (metacercariae or adults). These were tested using separate generalised linear models with Gaussian error structure implemented in JMP version 11.0 (SAS Institute Inc., Cary, NC, USA). A Gaussian error structure was chosen because our data are not counts but ratios (average no. of individuals per m^2). Our main goal was to test the relationship between the density of one species and density of another species. Therefore, density of one trematode species in a pair was included as a fixed factor in the models, and density of the other species was the response variable. Densities of parasites can vary widely among different lakes because variables affecting host abundance, such as primary productivity and abiotic conditions, vary among lakes. For that reason, lake identity was also included as a fixed factor in the models. This accounts for idiosyncrasies of particular lakes and allows a better estimate of the true spatial covariation in parasite densities independent of unknown lake effects.

Results

For all species and for both the metacercarial and adult life stages, densities varied across sites by a few to many orders of magnitude. There were differences among the four lakes in the densities of particular parasite species. Indeed, in most models testing the pairwise relationship between the densities of two trematode species, significant effects of lake identity were found. Typically, these involved within-lake relationships that differed among lakes (i.e. positive relationship between densities of both parasites among sites within one lake, but negative relationships in other lakes) or within-lake relationships that differed from the general across-lakes relationship.

Because two species use avian definitive hosts and birds were not sampled as part of this study, there were few possible tests of pairwise relationships between adult trematode densities (Table 2). Independently of any lake effect, there was a significant positive relationship between the local adult densities of the two species with fully identical life cycles, *S. anguillae* and *T. opisthorchis* (Table 2; Fig. 1). Neither of those species showed significant density covariation with adult populations of *Coitocaecum parvum*, with which they share hosts at only two life stages (Table 2).

For densities of metacercariae, there was surprisingly no significant covariation between *S. anguillae* and *T. opisthorchis* (Table 2). This may be due to a confounding lake effect, however: although the overall trend is generally positive, within-lake patterns are not clear in all cases (Fig. 1). Local metacercarial densities of both these trematodes covaried positively across sites with those of *Apatemon* sp., with whom both share hosts at two of the three stages in their life cycles (Table 2; Fig. 2). There were no other significant relationships between the pairwise metacercarial densities of any trematode species across sampling sites (Table 2).

Discussion

Our goal was to test the prediction that the more hosts two parasite species share at different life stages, the more likely their abundances will covary positively across localities. The prediction is founded on the assumption that similarity in resource requirements should, in the absence of strong interspecific interactions, lead to two species achieving their highest abundances in the same localities. Our results provide some support to this prediction, while also demonstrating that life cycle similarity is not in itself a guarantee that two parasite species will have similar hotspots of abundance.

In the case of the two species with identical life cycles, *S. anguillae* and *T. opisthorchis*, adult densities showed a clear interspecific positive association across localities sampled. Whatever factors and conditions culminated in one species reaching high abundance in one locality had similar effects on the other species. The positive covariation is visible both among sites within the same lake and across all lakes (Fig. 1). In contrast, there was no significant covariation between densities of these two species at the metacercarial life stage, once lake effects were taken into account. There is no convincing evidence of strong competition among metacercariae of those two species within fish second intermediate hosts (e.g. Herrmann and Poulin 2011) that could lead to one species achieving high abundance at the expense of the other. A more likely explanation is that a strong lake effect masked a tendency for metacercarial densities of *S. anguillae* and *T. opisthorchis* to covary. Indeed, as seen in Fig. 1, the overall trend and the separate trends in three of the four lakes indicate a general positive relationship between densities of the two species. Only in Lake Hayes was there no such pattern. It is probably safe to say that densities of *S. anguillae* and *T. opisthorchis* generally covary positively across localities, at both the metacercarial and adult stages. This clashes with the results reported for these two species on a much larger spatial scale, with the two species achieving their highest metacercarial abundances in completely different places across New Zealand (Blasco-Costa et al. 2015). Hotspots of infection for *S. anguillae* were found in the northern part of the North Island and in south-central South Island, whereas those for *T. opisthorchis* occurred toward the southern tip of the North Island and the west coast of the South Island. The

Table 2 Summary of results of generalised linear models testing for spatial covariation in local density among all pairs of trematode species, separately for each life stage; results for metacercariae are shown below the diagonal, those for adults above the diagonal

	Stegodexamene anguillae	*Telogaster opisthorchis*	*Apatemon* sp.	*Coitocaecum parvum*	*Maritrema poulini*
S. anguillae	–	**0.998 (14)**	N/A	0.059 (12)	N/A
		***P*<0.0001**		*P*=0.8915	
T.opisthorchis	0.267 (16)	–	N/A	−0.057 (12)	N/A
	P=0.3789			*P*=0.8865	
Apatemon sp.	**0.580 (16)**	**0.833 (16)**	–	N/A	N/A
	***P*=0.0373**	***P*=0.0004**			
C. parvum	0.446 (11)	0.352 (11)	0.510 (11)	–	N/A
	P=0.1414	*P*=0.1854	*P*=0.0878		
M. poulini	−0.572 (8)	−0.228 (8)	−0.527 (8)	−0.633 (8)	–
	P=0.1798	*P*=0.6389	*P*=0.2775	*P*=0.2569	

For each pair, the species in the row served as predictor and that in the column as the response variable in the models. Shown are the coefficient estimates, the number of sites where both species co-occurred (in parentheses), and the *P* value; significant ones are shown in bold

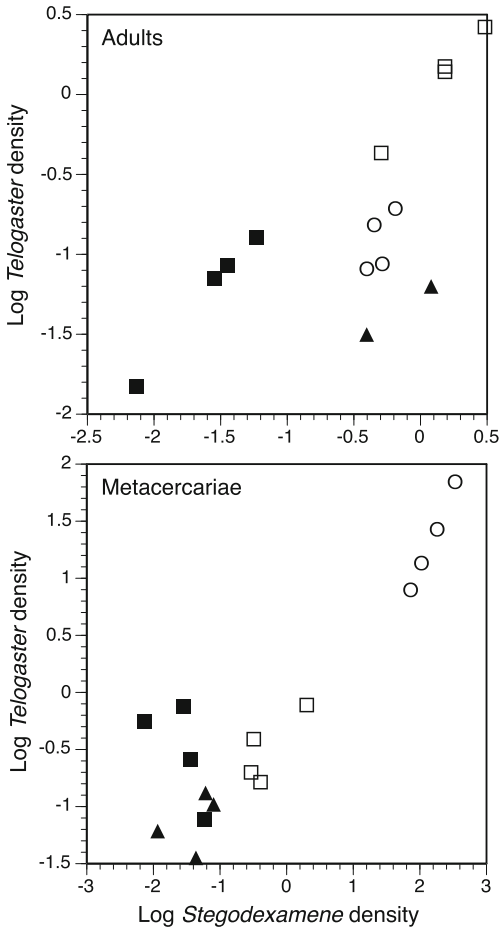

Fig. 1 Relationship between local densities (individuals m^{-2}, log-transformed) of the trematodes *Stegodexamene anguillae* and *Telogaster opisthorchis* across sampling sites in lakes from New Zealand's South Island. Data are shown separately for two different life stages, adults (*top*) and metacercariae (*bottom*). Sites from different lakes are shown by different symbols: *black squares*=Lake Hayes, *open circles*=Tomahawk Lagoon, *black triangles*=Lake Tuakitoto, *open squares*=Lake Waihola

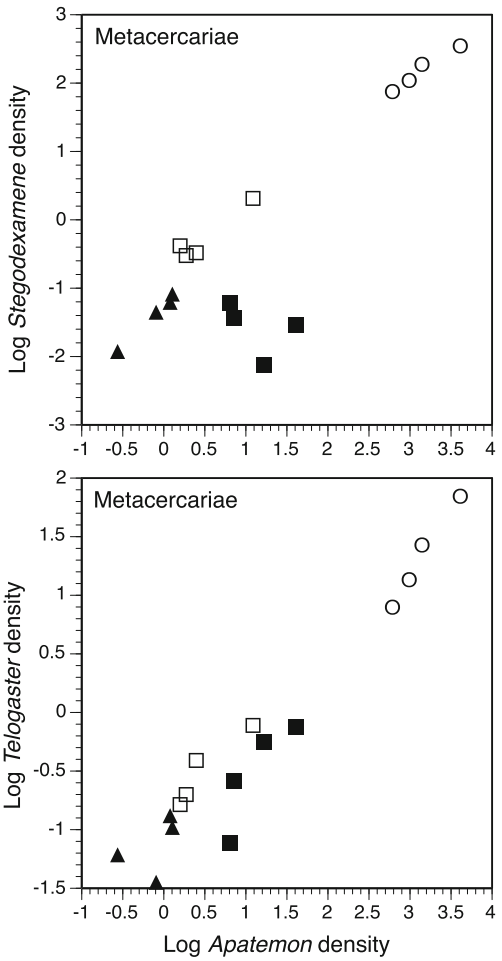

Fig. 2 Relationship between local densities (individuals m^{-2}, log-transformed) of the trematode *Apatemon* sp. and those of two other trematodes, *Stegodexamene anguillae* (*top*) and *Telogaster opisthorchis* (*bottom*) across sampling sites in lakes from New Zealand's South Island. Data are restricted to densities of metacercariae. Sites from different lakes are shown by different symbols (as in Fig. 1)

differences between the findings of the present study and those of Blasco-Costa et al. (2015) can be reconciled not only by the fact that the two studies used different measures of local parasite abundance but also by their very different spatial scales. The influence of shared host resources leading to common hotspots of population density matching local host availability may be eclipsed at larger scales by geographic differences in climate and other abiotic variables and their species-specific effects on the survival and performance of free-living infective stages, and thus on parasite transmission and population dynamics.

The set of five trematode species investigated here included both autogenic and allogenic species (*sensu* Esch et al. 1988). Autogenic parasites complete their entire life cycle in freshwater habitats, i.e. all their hosts are aquatic species, whereas allogenic parasites have one non-aquatic host capable of movement and dispersal across different freshwater ecosystems. In such cases, the mobile host is usually the definitive host, and is commonly a bird. The inclusion of a mobile host in the life cycle is thought to be responsible for profound differences between autogenic and allogenic parasites in terms of local infection levels (Kennedy et al. 1986; Esch et al. 1988), population genetic structure (Criscione and Blouin 2004; Blasco-Costa and Poulin 2013), and geographic distribution (Thieltges et al. 2011). The use of mobile versus water-bound definitive hosts may also uncouple patterns of spatial variation in local densities between autogenic and allogenic parasites that otherwise have shared intermediate hosts in their life cycles. Instead, we found clear, positive spatial covariation in densities of metacercariae across sites sampled between *Apatemon* sp., which use avian definitive hosts, and both *S. anguillae* and *T. opisthorchis* which have fish definitive hosts. Whatever differences may exist among these species in terms of local input of eggs from adult worms appear to be outweighed by the use of common resources (first and second intermediate hosts) in the early phases of the life cycle. One possibility is that strong processes occurring within snails (e.g. patterns of among-host resistance or susceptibility, intra-host parasite competition, etc.) regulate the production of cercariae of all species.

The results can be summarised as follows. When two trematode species share hosts at all three life stages (e.g. *S. anguillae* and *T. opisthorchis*), they show positive spatial covariation in density across localities. When two trematode species share hosts at two life stages, they either show positive spatial covariation in density (e.g. *Apatemon* sp. and *T. opisthorchis*) or they do not (e.g. *C. parvum* and *M. poulini*). Finally, if two trematode species share hosts at a single life stage (e.g. *S. anguillae* and *M. poulini*) then their densities do not covary spatially. The extent of resource sharing throughout ontogeny and adulthood determines whether or not the abundances of different parasite species are spatially coupled. It will be essential to determine how widely this pattern holds beyond the few species studied here. Not only are spatial patterns of matching and mismatching densities among parasite species important drivers of coevolutionary dynamics (see Thompson 2005), but they also determine the extent and frequency at which host populations suffer from additive or synergistic effects of multiple infections (e.g. Ferguson and Stiling 1996; Rauque et al. 2011). The findings of the present study suggest that a basic comparison of life cycle requirements may provide a simple predictive framework, an insight that will require further empirical validation from other systems.

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