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Biogeography of parasitism in freshwater fish: spatial patterns in hot spots of infection

Isabel Blasco-Costa, Carlos Rouco and Robert Poulin

I. Blasco-Costa (isa.blasco.costa@gmail.com) and R. Poulin, Dept of Zoology, Univ. of Otago, PO Box 56, Dunedin 9054, New Zealand. – C. Rouco, Landcare Research, PO Box 1930, Dunedin 9054, New Zealand.

Contrary to species occurrence, little is known about the determinants of spatial patterns of intraspecific variation in abundance, particularly for parasitic organisms. In this study, we provide a multi-faceted overview of spatial patterns in parasite abundance and examine several potential underlying processes. We first tested for a latitudinal gradient in local abundance of the regionally most common parasite species and whether these species achieve higher abundances at the same localities (shared hot spots of infection). Secondly, we tested whether intraspecific similarity in local abundance between sites follows a spatial distance decay pattern or is better explained by variation in extrinsic biotic and abiotic factors between localities related to local parasite transmission success. We examined the infection landscape of a model fish host system (common and upland bullies, genus *Gobiomorphus*: Eleotridae) across its entire distributional range. We applied general linear models to test the effect of latitude on each species local abundance independently, including the abundance of each co-infecting species as another predictor. We computed multiple regressions on distance matrices among localities based on abundance of each of the four most common trematode species, as well as for geographic distance, biotic and abiotic distinctness of the localities. Our results showed that the most widely distributed parasites of bullies also achieve the highest mean local abundances, following the abundance – occupancy relationship. Variation in local abundance of any focal parasite species was independent of latitude, the abundance of co-occurring species and spatial distance or disparity in biotic attributes between localities. For only one parasite species, similarity of abundance between sites covaried with the extent of abiotic differences between sites. The lack of association between hot spots of infection for co-occurring species reinforces the geographic mosaic scenario in which hosts and parasites coevolve by suggesting non-deterministic, species-specific variation in parasite abundance across space.

Understanding the processes shaping the spatial distribution of parasitism is central in current scenarios of environmental change, biological invasions and emerging diseases (Rohde 2002, Poulin and Morand 2004, Harvell et al. 2009, Lafferty 2009, Morand and Krasnov 2010, Perkins et al. 2010, MacLeod and Poulin 2012, Altizer et al. 2013). Most research has focused on spatial variation in the composition of parasite communities, which can differ widely across host populations; typically, some parasite species occur over most of their host's geographical range whereas others are restricted to a few populations (Nelson and Dick 2002, Poulin et al. 2011). The distance decay in similarity among communities has emerged as a universal pattern in biogeography (Soininen et al. 2007). Not surprisingly, similarity in parasite community composition also decreases with increasing geographic distance between them (Poulin and Morand 1999), a phenomenon now documented among parasite communities of hosts inhabiting both fragmented and continuous habitats (Poulin 2003, Krasnov et al. 2005, Seifertová et al. 2008, Pérez-Del-Olmo et al. 2009, Thieltges et al. 2009b, 2010, Poulin et al. 2011). Distance decay in similarity can result from three non-exclusive types of processes: species-sorting along environmental gradients, dispersal constraints imposed by topography, and intrinsic species differences in dispersal abilities (Soininen et al. 2007). The limited evidence available to date suggests that environmental gradients are more important drivers of the distance decay in parasite community composition than spatial distance per se (Krasnov et al. 2005, Vinarski et al. 2007, Thieltges et al. 2010, Poulin et al. 2011).

Whereas much effort has gone toward elucidating the determinants of the spatial occurrence of parasite species, a single study has applied the distance decay model to intraspecific variation in parasite abundance across a geographical scale (Poulin et al. 2011). Abundance and occurrence are not independent: one of the first documented macroecological patterns is that species occurring in many localities on a regional scale also tend to be abundant locally (Brown 1984). Nevertheless, abundance of given parasite species can vary by more than one order of magnitude across their range (Poulin 2006). Thus, uncovering spatial patterns of parasite population parameters is crucial for epidemiology, veterinary medicine and wildlife management. Local parasite abundance is influenced by the interaction of both intrinsic properties of the species itself and extrinsic properties of the local environment (Arneberg et al. 1997, Krasnov et al. 2006, Poulin 2006, Vignon and Sasal 2010, Pérez-del-Olmo et al. 2011, Kubová et al. 2013). Local biotic and abiotic factors are often responsible for the high intraspecific variation in the population parameters (i.e. prevalence and abundance of infection) of parasites. For instance, the abundance of parasites is strongly dependent on the density of their hosts (Anderson and May 1978, Arneberg et al. 1998). In the case of parasites with complex life-cycles, the abundance of all hosts, overlapping in time and space, should be relevant (Waltari and Perkins 2010). Indeed, intermediate host densities correlate with the abundance of parasites in their final hosts (Hansen and Poulin 2006, de Montaudouin and Lanceleur 2011). Physical location (e.g. latitude, altitude, or distance downstream in river habitats) determines local abiotic factors that can also influence the population parameters of parasites (Koprivnikar et al. 2006, Poulin and Dick 2007, Thieltges et al. 2009a, Blasco-Costa et al. 2013). Whereas parasite and host dispersal abilities are key determinants of the regional distribution of a species (Thieltges et al. 2009b, 2013a, Poulin et al. 2011) and the differentiation among subpopulations (Blasco-Costa and Poulin 2013), processes influencing parasite transmission and the availability of suitable hosts are expected to determine the species abundance at a local scale. The fact that two nearby localities share a geological history and many biotic and abiotic features, whereas distant ones are more likely to differ, should influence the similarity in local abundance of particular parasite species between two host populations (Poulin and Dick 2007). Here, we test this central prediction while also accounting for spatial variation in selected extrinsic factors associated with local transmission success.

Spatial modelling is a standard tool for assessing ecological responses of species to environmental conditions and predicting changes in their geographical distributions (Elith and Leathwick 2009). Large-scale databases of environmental and biotic variables are now publicly available, providing an invaluable source of information for spatial analysis. Recently, Real et al. (2006) proposed the notion of analysing the general favourability for the occurrence of a species through a mathematical function. The favourability function assesses the variation in the probability of species occurrence in certain conditions with respect to the overall frequency of occurrence across a geographical region. Consequently, it can be applied to compute the probability of local occurrence of a species, based on local conditions, in order to test how it relates to the local abundance of that species across multiple sites. The favourability concept has been used for species distribution modelling and habitat selection analysis (Real et al. 2009, Amici et al. 2010) among others. Despite its potential for epidemiology (Acevedo and Real 2012), it has just recently been applied for the first time in this context (Boadella et al. 2012). Here we investigate differences in parasite favourability between sites based on the probability of occurrence of the hosts and on local abiotic features that affect parasite transmission, to investigate its effect on the spatial decay model of intraspecific variation in parasite abundance across multiple parasite species and a large geographical scale.

Our host–parasite model system consists of two native, widely distributed freshwater fish species (the common bully *Gobiomorphus cotidianus* and the upland bully *G. breviceps*) that share the same parasite fauna throughout their distributional range in New Zealand (Hine et al. 2000). Both bully species are benthic and mostly territorial, such that their infection levels reflect local processes. Their most common parasites are trematodes that require three hosts to complete their life cycles. All of these use the same snail, *Potamopyrgus antipodarum*, as first intermediate host. Thereafter they follow different life cycle pathways. One trematode uses an invertebrate as second intermediate host and bullies as definitive hosts. Two other species share the same second intermediate and definitive hosts, the bullies used in this study and two native eel species respectively, whereas another species uses bullies as second intermediate host and birds as definitive hosts. Such differences among parasite species in host mobility provide an ideal situation to test the generality of any spatial patterns of abundance in the face of variation in life cycle characteristics.

The specific objectives of the study are three-fold. First, we test whether regionally common parasite species achieve higher abundances locally. Second, we assess whether 1) there is a latitudinal gradient in the abundance of parasite species, and 2) there are common hot spots of infection, i.e. whether the most widespread parasite species achieve their highest abundances in the same localities. Third, we evaluate whether intraspecific similarity in local abundance of the most common parasites between host populations 1) follows a distance decay pattern or 2) is better explained by dissimilarities in biotic or abiotic conditions among localities. Our findings provide a multi-faceted overview of spatial patterns in parasite abundance across several parasite species, and a test of several potential underlying processes.

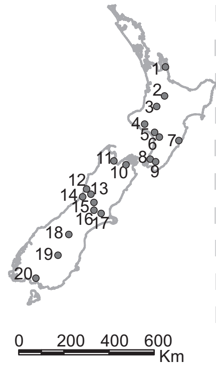
Material and methods

Collection of samples

Fish specimens (192 in total, 5 to 13 individuals per locality see Supplementary material Appendix 1, Table A1) of either or both *Gobiomorphus cotidianus* (common bully) and *G. breviceps* (upland bully) were sampled from 20 streams across New Zealand (Fig. 1) by using either electrofishing (small, shallow streams or rivers) or minnow traps (deep rivers). Fish were euthanised by spinal cord severing, and frozen at − 20°C. In the laboratory fish were subsequently thawed, measured (standard length) and dissected for parasite recovery following a standardized protocol. In brief, the digestive tract, liver, gall bladder, spleen, kidney, mesenteric tissue, gonads and muscle tissue were examined under a stereomicroscope for parasites; individuals of each parasite species were identified and counted.

Statistical analyses

Data on abundance (number of parasite individuals per individual host) for all parasite species recovered were log $(x + 0.1)$ transformed to meet the requirements of



Site	Location	Latitude	Longitude
1	Taiura River	37º 4.05S	175º 46.83E
2	Waipapa River	38º 17.51S	175º 40.68E
3	Opotiki Stream	38º 47.96S	175º 12.10E
4	Patea River	39º 33.87S	174º 33.87E
5	Tuaraki River	39º 56.99S	175º 19.77E
6	Rangitawa Stream	40º 7.55S	175º 26.88E
7	Porangahau River	40º 16.82S	176º 34.11E
8	Silverstream Creek	41º 8.70S	175º 0.25E
9	Bocketts Stream	41º 12.49S	175º 11.68E
10	Moutere River	41º 10.34S	173º 59.49E
11	Rai River	41º 19.93S	172º 34.45E
12	Grey River	42º 26.50S	171º 18.74E
13	Bruce Creek	42º 40.12S	171º 26.86E
14	Hotikiti River	42º 44.01S	170º 59.03E
15	Cass Creek	43º 1.52S	171º 44.73E
16	Acheron River	43º 17.81S	171º 42.33E
17	Hawkins River	43º 24.59S	172º 1.90E
18	Ohau River	44º 19.92S	170º 11.27E
19	Manuherikia River	45º 11.52S	169º 27.34E
20	Aparima River	46º 7.95S	168º 0.14E

Figure 1. Location of the 20 sampling sites and their geographical co-ordinates in New Zealand.

parametric tests. Two accidental species (an unknown nematode and trematode larvae) found infecting a single fish each were excluded from the analyses. In order to investigate the abundance–occupancy relationship among the parasites of bullies, we tested for a correlation between the log $(x + 0.1)$-transformed average local abundance of each parasite species across the sites where it occurred, and the log-transformed number of sites occupied by that species.

Hereafter we focused our analyses on the four most common parasite species (those present in more than half of the localities), all of which were trematodes: *Coitocaecum parvum* (Opecoelidae), *Apatemon* sp. (Strigeidae), *Stegodexamene anguillae* (Lepocreadiidae) and *Telogaster opisthorchis* (Cryptogonimidae). There was no correlation across sites between mean fish standard length and local mean abundance nor between fish sample size and local mean abundance, in any of the four species (all $p > 0.149$ and $p > 0.161$ respectively); for this reason, and because fish length did not emerge as a significant factor in any preliminary analysis, they were not considered in subsequent analyses. Further, no difference in mean local abundance was detected between sites with only common bullies, upland bullies or both (all $p > 0.387$). Thus, host species was not included as a factor in later analyses.

The effect of latitude on mean local abundance was assessed separately for each of the four parasite species, using general linear models (with a Gaussian error structure). In each case, in addition to latitude, the local mean abundances of the other three common species were also included as predictor variables, to account for any effect of competition or facilitation between parasite species.

We evaluated the contribution of geographic, biotic and abiotic distances (i.e. differences) between localities on the dissimilarity in parasite abundance among localities, separately for each of the four common trematode species, using multiple regressions on distance matrices ((MRM) see Manly 1986, Legendre and Legendre 1998, Lichstein 2007, for details). MRM is an extension of partial Mantel analysis that is used to investigate relationships between a multivariate response distance matrix (in our case, pairwise differences in mean parasite abundance between localities) and any number of explanatory distance matrices (Lichstein 2007). Biotic and abiotic attributes for each sampling site were obtained from its unique segment (river or stream section between adjacent confluences in which our sampling site was located) from the Freshwater Ecosystems of New Zealand geodatabase ver. 1 (see also Leathwick et al. 2008, 2009, Dept of Conservation 2010). Biotic factors considered for the dissimilarity analysis were integrated as 'Parasite Favourability' (see below), a proxy for relative host abundance (we assumed a positive correlation between abundance and the favourability of the species). From the database, we obtained data on occurrence probability for the snail *Potamopyrgus antipodarum*, first intermediate host of the four trematode species, as well as for the common and upland bullies (second intermediate hosts of *Apatemon* sp., *S. anguillae* and *T. opisthorchis* and definitive hosts of *C. parvum*). Data for *Paracalliope fluviatilis*, second intermediate host of *C. parvum*, and *Anguilla australis* and *A. dieffenbachii*, definitive hosts of *S. anguillae* and *T. opisthorchis,* were also included. Because the definitive host of *Apatemon* sp. is an unknown bird, we could not take it into account. Despite other fish species (e.g. galaxiids) also serving as hosts (either intermediate or definitive) of these trematode species, common and upland bullies are typically much more numerous. Thus, bullies are the most important hosts for the maintenance of the parasite populations.

The predicted favourability (F) values are a measure of the degree to which local conditions lead to a local probability of occurrence higher or lower than that expected at random (F ranges from 0–1, with $F = 0.5$ being neutral), with the random probability being defined by the overall prevalence of the event (Boadella et al. 2012). Although not as direct a measure as host abundance itself, this approach is nevertheless proving very promising for predictive modelling (Real et al. 2006, Boadella et al. 2012). Thus, F can be used to identify localities at which the presence of a given host is actually favoured (i.e. $F > 0.5$). We calculated 'Parasite Favourability' (F_p) in two steps. First we calculated Favourability (F) for each of the required hosts of a given parasite according to the following equation (Real et al. 2006):

$$F = \frac{\frac{P}{(1-P)}}{\frac{n_1}{n_0} + \frac{P}{(1-P)}}$$

where P is the probability of occurrence of a given host species in a given site, n_1 is the number of sites where a given host was observed and n_0 is the number of sites where it was not observed (information obtained from Leathwick et al. 2008, 2009). Secondly, 'Parasite Favourability' (F_p) was considered as the minimum F value obtained across the different hosts for a given parasite. Therefore, F_p is the minimum favourability that all required hosts of a given parasite occur in a given site (see F_p values at each locality in Supplementary material Appendix 1, Table A1).

We also included local abiotic attributes that may have an effect either directly on the transmission of the parasites or indirectly on the stability of the host populations (particularly the invertebrate hosts (Townsend and Hildrew 1994)). Seven variables were considered: 1) segment flow stability (a ratio between the mean annual low flow and the mean average flow, with high values indicating stability and low values average variations in flow); 2) average downstream slope (elevation at the mid point of the river segment and the distance to the coast); 3) days of rain (frequency of days of significant rainfall (> 25 mm) in the upstream catchment which indicates the likely frequency of elevated flows); 4) seasonal temperature range (deviation in winter temperature from that expected given the summer temperature, indicating seasonal climates); 5) distance to the coast (downstream distance from the mid-point of the segment to the coast); 6) stream nitrogen load; 7) latitude of the sampling site. Variables 1–3 affect the frequency of disturbance events that could disrupt transmission in different ways (e.g. changing the distribution of the host populations during a flood, increasing flow velocity that might hamper host-finding by the free living stages of the parasites, etc.); variables 4 and 7 capture the extent of warmer periods during which transmission is typically enhanced; variable 5 may favour higher abundance of parasites as it affects the composition of freshwater communities; and variable 6 may favour higher productivity and higher density of grazers such as snail hosts.

Biotic and abiotic variables were considered separately. Principal component analysis (PCA) was used to reduce the abiotic attributes to two factors, derived from the first and second components of the PCA (comprising 54% of the explained variance in the PCA). Geographical distances between localities were calculated as great circle distances using the R library fields (Fields Development Team 2006). We computed dissimilarity matrices of geographic distance and abiotic attributes (based on the scores of the PCA) among all pairs of localities based on Euclidian distances. Dissimilarity matrices on biotic attributes (one for each of the four trematode species) were calculated as absolute difference in F_p among localities. These distance matrices were used as independent matrices in a MRM. The dependent matrices (one for each of the four trematode species) were calculated as absolute difference in abundance among localities. In one case, *C. parvum*, four localities with zero mean abundance were excluded prior to analysis. Because pairwise comparisons among localities are not truly independent, the significance of the regression coefficients and the r^2 were tested using 9999 permutations. All analyses were carried out in R (ver. 3.0.2, R Development Core Team) using the libraries vegan and ecodist (Goslee and Urban 2007, Oksanen et al. 2013).

Results

General patterns

A total of eight parasite species belonging to four major taxa (Trematoda, Cestoda, Nematoda, Mollusca; Table 1) were detected infecting bullies across our samples. *Nippotaenia* cf. *contorta* represents a new parasite record for upland bully, whereas the mussel larvae (glochidia) of *Echiridella* sp. (formerly *Hyridella*) and the nematode *Eustrongylides* cf. *ignotus* represent new parasite records for common bully.

Among those 8 parasite species in bullies, mean abundance showed a strong abundance – occupancy correlation ($r^2 = 0.71$, $p = 0.008$; Fig. 2); in other words, locally abundant parasite species are also those occurring in a high proportion of localities. The most widely distributed and abundant parasites were four trematode species, *Coitocaecum parvum*, *Apatemon* sp., *Stegodexamene anguillae* and *Telogaster opisthorchis*. These showed generally high prevalence of infection (proportion of individual hosts infected per locality), and abundances of tens or hundreds of individuals per fish (Table 1); they also each occurred in at least 16 of the 20 studied localities.

Table 1. Summary data for each parasite species. Prevalence indicates the proportion of infected hosts out of the total number of hosts examined at each locality. Mean abundance indicates the average number of individual parasites per individual host at each locality.

	No. of localities	Prevalence Range (mean)	Mean abundance Range (mean)
Trematoda			
Coitocaecum parvum	16	0.2–1.0 (0.6)	0–72.9 (7.6)
Apatemon sp.	20	0.2–1.0 (0.9)	0.8–152.2 (52.6)
Telogaster opisthorchis	19	0.2–1.0 (0.8)	0–580.7 (46.5)
Stegodexamene anguillae	20	0.3–1.0 (0.9)	0.3–80.1 (19.5)
Cestoda			
Nippotaenia cf. *contorta*	1	0.3	0–0.3
Paradilepis sp.	3	0.1–0.2 (0.1)	0–0.4 (0.2)
Nematoda			
Eustrongyloides cf. *ignotus*	4	0.1–0.3 (0.2)	0–0.4 (0.2)
Mollusca			
Glochidia of *Echiridella* sp.	3	0.1–0.8 (0.3)	0–5.2 (1.9)

Spatial patterns in local abundance

Mean local abundance did not covary significantly with latitude in any of the four common trematode species. Neither latitude, the mean abundance of co-occurring species, or the interaction of co-occurring species abundance with latitude had an effect on the mean abundance of each focal parasite species (Table 2). Although non-significant, mean abundance of *S. anguillae* appeared to be influenced negatively by the interaction of *T. opisthorchis* mean abundance and latitude (Table 2). From a spatial perspective,

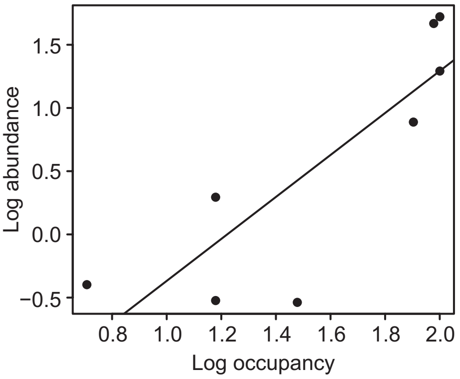


Figure 2. Interspecific correlation of average local abundance against the proportion of sites occupied across eight parasite species of bullies, *Gobiomorphus cotidianus* and *G. breviceps*.

Table 2. Results of the general linear models testing the relationship between each trematode species abundance and latitude, the co-occurring species abundance and the interaction of co-occurring species abundance with latitude. None of the predictor variables emerged as significant.

Response	Parameters	Estimates	SE	p-values	r^2	p-value
C. parvum					0.591	0.248
	Intercept	0.408	0.152	0.028		
	Latitude	−0.085	0.076	0.301		
	Apatemon sp. abundance	0.453	0.277	0.140		
	S. anguillae abundance	0.596	0.583	0.336		
	T. opisthorchis abundance	−0.012	0.235	0.960		
	Latitude × *Apatemon* sp. abundance	−0.083	0.186	0.668		
	Latitude × *S. anguillae* abundance	0.040	0.157	0.804		
	Latitude × *T. opisthorchis* abundance	−0.047	0.252	0.858		
Apatemon sp.					0.494	0.206
	Intercept	1.197	0.172	0.000		
	Latitude	−0.033	0.088	0.714		
	C. parvum abundance	0.537	0.261	0.062		
	S. anguillae abundance	0.031	0.417	0.943		
	T. opisthorchis abundance	0.113	0.242	0.649		
	Latitude × *C. parvum* abundance	0.029	0.103	0.781		
	Latitude × *S. anguillae* abundance	−0.096	0.138	0.502		
	Latitude × *T. opisthorchis* abundance	0.354	0.179	0.073		
S. anguillae					0.627	0.052
	Intercept	1.156	0.129	0.000		
	Latitude	0.060	0.058	0.317		
	C. parvum abundance	0.168	0.202	0.422		
	Apatemon sp. abundance	0.028	0.197	0.888		
	T. opisthorchis abundance	0.086	0.163	0.606		
	Latitude × *C. parvum* abundance	0.023	0.073	0.759		
	Latitude × *Apatemon* sp. abundance	0.059	0.119	0.627		
	Latitude × *T. opisthorchis* abundance	−0.203	0.119	0.112		
T. opisthorchis					0.604	0.069
	Intercept	0.911	0.176	0.000		
	Latitude	0.111	0.093	0.257		
	C. parvum abundance	0.147	0.302	0.636		
	Apatemon sp. abundance	0.239	0.270	0.393		
	S. anguillae abundance	0.167	0.428	0.702		
	Latitude × *C. parvum* abundance	−0.169	0.105	0.134		
	Latitude × *Apatemon* sp. abundance	0.260	0.174	0.160		
	Latitude × *S. anguillae* abundance	−0.197	0.130	0.154		

the four parasite species showed independent and non-overlapping abundance hot spots (Fig. 3). In other words, the abundance of each species peaked in different geographic areas, even in the case of *S. anguillae* and *T. opisthorchis*, which have identical life cycles and host requirements.

The multiple regressions of matrices of geographic, biotic and abiotic dissimilarities showed no correlation with differences in mean abundance between localities except for *C. parvum* (Table 3). *Coitocaecum parvum* was the only species to show the expected positive relationship between difference in mean abundance and environmental dissimilarity between localities (Fig. 4), but its abundance did not covary with the biotic and geographic distance measures.

Discussion

The present study investigated spatial patterns of abundance using original data on multiple parasite species in freshwater hosts throughout their entire distribution range, and yielded three main findings. First, parasite species infecting common and upland bullies (*Gobiomorphus cotidianus* and *G. breviceps*, respectively) exhibit a positive correlation between their mean local abundance and their frequency of occurrence among localities, following the well-documented abundance–occupancy relationship (Brown 1984, Gaston and Blackburn 2000). Second, and most intriguingly, hot spots of infection by different parasite species are independent of each other. Even two trematode species with identical life cycles (i.e. requiring exactly the same combination of host species) attain their maximal abundances in different geographical regions. Third, variation in local abundance of any focal parasite species proved to be independent of latitude, of the abundance of other co-infecting species, and of spatial distance or disparity in biotic attributes among sites. However, for one trematode species, similarity of abundance achieved at different sites was related to the extent of abiotic differences between sites.

Abundance–distribution relationships have become established as a macroecological 'rule' (Gaston and Blackburn 2000, 2003). Typically, species with high local abundance are more widely distributed across localities in any environment.

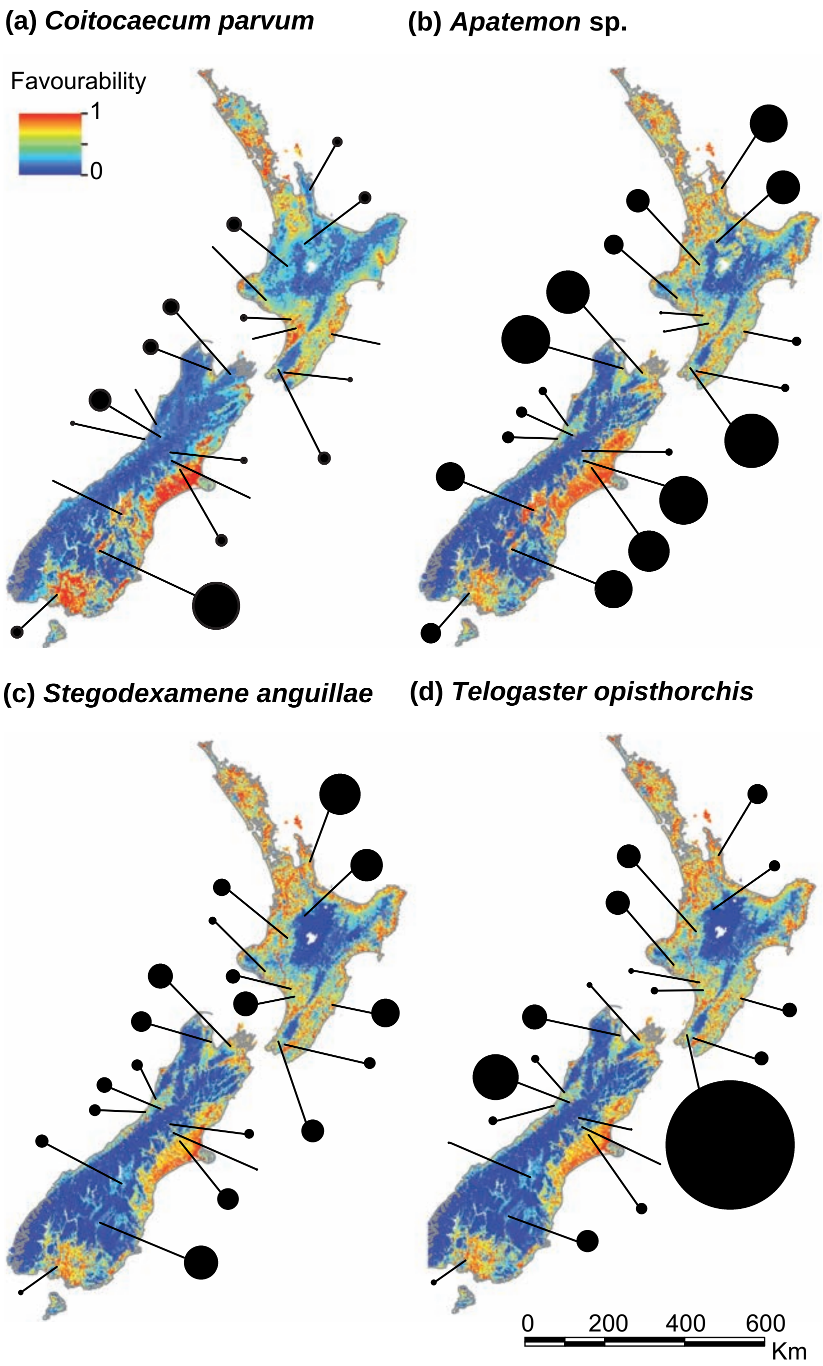


Figure 3. Distribution of the four most common parasite species. Relative diameter of black circles represents mean abundance at each site. Background colour in the maps indicate predicted Parasite Favourability (probability that all host species required by a parasite occur in an area) with F_p values above 0.5 being more favourable for parasite populations.

The same pattern applies to parasite communities investigated to date (Barker et al. 1996, Cone et al. 2004, Poulin et al. 2012, Thieltges et al. 2013a). Different causal pathways have been proposed to explain this common pattern. Structural causality in interspecific relationships may result from species differences in ecological attributes (e.g. dispersal) (Borregaard and Rahbek 2010). Given the tight association between parasites and their hosts and the limited mobility of free-living infective stages, parasite dispersal relies mostly on their host's ability to disperse. In general, parasites using birds or mammals as definitive hosts are capable to disperse further than those restricted to aquatic environments (fish definitive hosts), as documented molecularly and macroecologically (Criscione and Blouin 2004, Thieltges et al. 2009b, 2013a, Blasco-Costa and Poulin 2013). In our study system, all but two species (*Apatemon* sp. and *Paradilepis* sp.) complete their entire life cycle in the aquatic environment, as do three out of the four most abundant and widely distributed species investigated in more detail. Since river catchments are isolated ecosystems surrounded by land, the presence of

Table 3. Results for the multiple regressions of matrices of geographic, biotic (Parasite Favourability) and abiotic (environmental) dissimilarities with the differences in mean abundance between localities. Statistically significant results are shown in bold.

Species	Estimates	p-values	r^2	p-value
C. parvum			**0.203**	**0.025**
intercept	0.185	0.950		
Geographic	−0.000	0.766		
Favourability	−0.116	0.360		
Environmental	**0.105**	**0.009**		
Apatemon sp.			0.017	0.716
intercept	0.417	0.281		
Geographic	0.000	0.167		
Favourability	0.014	0.927		
Environmental	0.002	0.931		
S. anguillae			0.627	0.052
intercept	0.282	0.759		
Geographic	0.000	0.105		
Favourability	0.167	0.126		
Environmental	−0.029	0.347		
T. opisthorchis			0.494	0.206
intercept	0.376	0.496		
Geographic	0.000	0.432		
Favourability	0.104	0.424		
Environmental	–0.002	0.957		

widely distributed water-bound parasites throughout the country requires that historical connections between isolated catchments once existed (or at least episodic flooding events) to allow dispersal of hosts and parasites together. Historical changes in the geology of rivers can account for the current distribution of fish species (see Waters et al. (2001) for an example in New Zealand) and also parasites (Criscione and Blouin 2007). In addition, long distance transport of invertebrates via water birds could also promote sporadic movement of parasites in their intermediate hosts across water bodies. Parasites constrained to freshwater habitats may then be subjected to sporadic dispersal in which locally abundant species have an advantage (Poulin et al. 2012) by having a higher chance of acting as source of colonisers to new localities in a metapopulation context. In addition, Poulin et al. (2012) found that species with high occupancy also have more variable local abundances, suggesting they can maintain populations through a larger range of different environments. After colonisation, the local abundance achieved by any species may depend on its intrinsic properties (e.g. survival, growth, fecundity, etc.) since mean local abundance is a species attribute (Arneberg et al. 1997, Krasnov et al. 2006, Poulin 2006, Pérez-del-Olmo et al. 2011).

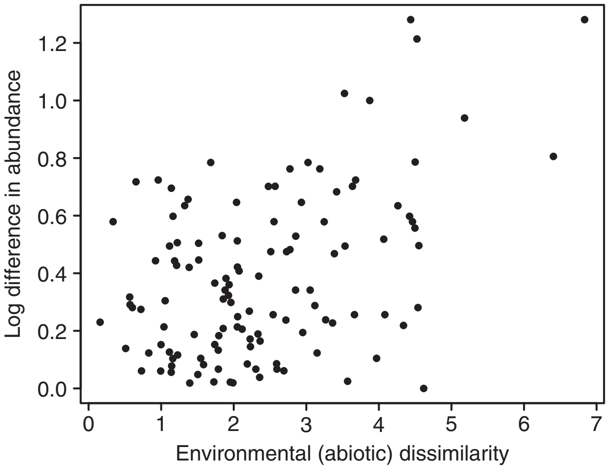


Figure 4. Difference in abundance of *Coitocaecum parvum* between pairs of localities sampled, as a function of pairwise environmental distance between sites.

Among parasite species completing their entire life cycle within freshwater habitats, those with a broad host range could achieve greater site occupancy, with host specificity driving the abundance – distribution relationship (Thieltges et al. 2013a). This would fit with the 'resource use' hypothesis (Brown 1984) that postulates an advantage for generalist species that have a larger breadth of resource usage (for an example on parasitic organisms see Krasnov et al. (2004)). However, specialization can lead to high local abundance and the relationship between resource breadth and local abundance is not always supported empirically in either free-living (Gregory and Gaston 2000, Köckemann et al. 2009) or parasitic species (Poulin 1998, Morand and Guégan 2000). In our system, the four most common parasite species are highly specific to the first intermediate host, but show low specificity to the second and definitive hosts. The second intermediate host of *S. anguillae* are at least six species of *Gobiomorphus* and *Galaxias*; *T. opisthorchis* uses 12 species belonging to *Gobiomorphus*, *Galaxias*, *Neochanna* and *Retropinna; Apatemon* sp. has been reported from a few *Gobiomorphus* spp. and *Galaxias* spp. (Hine et al. 2000, Kelly et al. 2009); and *C. parvum* uses either a mysid or an amphipod species (Manter 1954). The definitive hosts of *S. anguillae* and *T. opisthorchis* are two *Anguilla* spp., *C. parvum* infects *Galaxias* spp. and *Gobiomorphus* spp.; and although the definitive host of *Apatemon* sp. is still unkown, it is likely to infect more than one bird species as do other *Apatemon* spp. The extent to which resource breadth is an important factor shaping the abundance–distribution relationship of species will require further testing in both free-living and parasitic species.

Perhaps our most intriguing and important result is the observation that there is no correspondence between the spatial variation in abundance of one parasite species and that of another species. The locations of maximum abundance values, i.e. hot spots of infection, recorded for one species are independent of those for other species. This was true not just for any pair of parasite species using bullies, but even for the two with totally identical host requirements and life cycles. This result is not simply based on the visual interpretation of abundance maps (Fig. 3), but also on the fact that the general linear models of parasite abundance for each focal species revealed no significant effects of the abundance of co-infecting species (Table 2). Similar host requirements should promote positively covarying abundances across localities for different parasite species in the absence of significant competition between them (or negatively covarying abundances under strong competition). The reasons for the spatial mismatch between the peak abundances of different parasite species remain unclear, but possibly involve abiotic influences yet to be determined. However, the evolutionary implications are very deep in the context of coevolution and local adaptation (Kawecki and Ebert 2004). In host species with limited mobility, like bullies, the spatial mismatch between the abundance distributions of their parasites reinforces the mosaic nature of the biotic environment across their geographic range (Thompson 2005). Although most host populations encounter roughly the same parasite species, the abundance of each parasite species varies independently of that of other parasites and of most environmental variables (see below). Therefore, the numerically dominant enemy encountered differs almost stochastically from one locality to the next. This should promote strong local adaptation, even on small geographic scales, of immune or other defence mechanisms of the hosts (Kawecki and Ebert 2004, Richardson et al. 2014).

In addition to its independence from other parasite species, spatial variation in local abundance of any given parasite species was also unaffected by latitude. The lack of an effect of latitude on individual parasite infection levels in bullies is in agreement with many previous studies on snails (Poulin and Mouritsen 2003), cockles (Studer et al. 2013), marine fish (Rohde and Heap 1998) and freshwater fish (Poulin and Dick 2007), although latitudinal gradients have also been reported (ectoparasites of marine fish: Rohde and Heap 1998, trematodes in amphipods: Thieltges et al. 2009a). Our study, although restricted to a 10° latitudinal band, almost completely spans the distribution range for both host and parasite species studied here. It is likely that on that scale, differences in latitude do not capture variation in any of the environmental factors determining local parasite abundance.

Host populations that are close in space and/or occupying similar environments often share many parasite species in common (Poulin 2003, Krasnov et al. 2005), but much less is known of how spatial distances and biotic/abiotic similarity affect similarity in abundance of given parasite species between host populations. In our system, we found no evidence for a distance decay in similarity of parasite abundance. Similarly, Poulin et al. (2012) found that generally there was no decay of similarity in abundance with increasing distance in 8 out of 12 metazoan parasite species of stickleback fish. Our findings support their conclusion that the distance between localities may be crucial for reciprocal exchanges of parasites and to explain their presence in a particular locality, but the abundance that parasites achieve afterward in that locality depends on totally different factors. With this in mind, we included two more variables in our analyses, dissimilarity in Parasite Favourability (as a measure of relative probability of occurrence of all required hosts) and environmental dissimilarity (including primarily variables that could influence transmission). Although host population density can account for intraspecific variation in parasite population parameters (Poulin 2007), the difference in Parasite Favourability between populations had no significant effect on variability in abundance, for any of the four trematode species. A possible explanation for the lack of a relationship is that whereas abundance of directly transmitted species (such as nematodes parasitizing mammals or monogeneans parasitizing fish) correlates positively with host density (Arneberg et al. 1998), transmission through intermediate hosts may disconnect parasite abundance in one host species from the local density of other hosts. However, several studies have shown that intermediate host densities are in most cases correlated with the abundance of parasites in the final hosts (Hansen and Poulin 2006, de Montaudouin and Lanceleur 2011). Another non-exclusive explanation could be that the relationship between the favourability index and the abundance of a species may not be linear but triangular (VanDerWal et al. 2009). Thus, sites with low favourability for host species would always harbour low abundance of the parasite, whereas sites with high favourability may or may not support high abundance depending on other local factors. Yet another possibility is that dissimilarity in favourability (a measure of biotic habitat compatibility) is overshadowed by dissimilarity in the abiotic environment between localities. However, in three of the four trematode species tested here, the dissimilarity in abiotic environment between host populations had no significant effect on variability in parasite abundance. Interestingly, the one species in which dissimilarity in abiotic environment affected variability in abundance was *Coitocaecum parvum*, which uses two invertebrate and one vertebrate hosts, as opposed to the other three species which use one invertebrate and two vertebrate hosts. Invertebrates are more susceptible to environmental variation and disturbances (Townsend and Hildrew 1994), possibly making their parasites more responsive, indirectly, to environmental factors. A myriad abiotic and biotic factors can influence transmission success of aquatic parasites (Pietrock and Marcogliese 2003, Thieltges et al. 2008), and with the limited data available, our analysis may have missed important variables, ranging from water chemistry to the presence of non-host organisms that interfere with transmission (Thieltges et al. 2013b).

In conclusion, we found that widely distributed parasites of bullies achieve higher mean local abundances than parasite species with more restricted occurrences. However, within parasite species, it was not possible to explain which localities had the highest abundance based on their spatial separation or their dissimilarity in either biotic or abiotic variables. Finally, and most interestingly, each of the parasite species studied, even if sharing all their required hosts, displayed independent and non-matching distributions of abundance, with hot spots of infection by one species having no association with those of other species. This finding provides a more quantitative, abundance-based assessment, compared to many earlier ones based on presence–absence data, of the infection landscape of a model host taxon, across a broad spatial scale. It also reinforces the geographic mosaic scenario in which hosts and parasites coevolve by suggesting non-deterministic, species-specific variation in parasite abundance in space.

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Supplementary material (Appendix ECOG-01020 at <www.ecography.org/readers/appendix>). Appendix 1.