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ORIGINAL ARTICLE

Scaling up from epidemiology to biogeography: local infection patterns predict geographical distribution in fish parasites

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ABSTRACT

Aim We investigated how the spatial distribution of parasites, measured as either their geographical range size or their frequency of occurrence among localities, relates to either their average local abundance or the variance in their abundance among localities where they occur.

Location We used data on the abundance of 46 metazoan parasite species in 66 populations of threespine sticklebacks, *Gasterosteus aculeatus*, from Europe and North America.

Methods For each parasite species, frequency of occurrence was calculated as the proportion of stickleback populations in which it occurred, and geographical range size as the area within the smallest possible polygon delimited using the coordinates of the localities where it occurred. Generalized linear models were used to assess how these two measures of spatial distribution were influenced by several predictor variables: geographical region (North America or Europe), life cycle (simple or complex), average local abundance, the coefficient of variation in abundance across localities, and median prevalence (proportion of infected hosts within a locality).

Results Our analyses uncovered four patterns. First, parasites in North America tend to have higher frequencies of occurrence among surveyed localities, but not broader geographical ranges, than those in Europe. Second, parasite species with simple life cycles have wider geographical ranges than those with complex cycles. Third, there was a positive relationship between average abundance of the different parasite species and their frequency of occurrence, but not between average abundance and geographical range size. Fourth, the coefficient of variation in abundance covaried positively with both the frequency of occurrence and geographical range size across the different parasite species. Thus, all else being equal, parasites showing greater site-to-site variability in abundance occur in a greater proportion of localities and over a broader geographical area than those with a more stable abundance among sites.

Main conclusions Local infection patterns are linked with large-scale distributional patterns in fish parasites, independently of host effects, such that local commonness translates into regional commonness. The mechanisms linking parasite success at both scales remain unclear, but may include those that maintain the continuum between specialist and generalist parasites. Regardless, the observed patterns have implications for the predicted changes in the geographical distributions of many parasites in response to climate change.

Keywords

Europe, *Gasterosteus aculeatus*, geographical range, life cycles, local abundance, metazoan parasites, North America.

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INTRODUCTION

The positive, interspecific relationship between local abundance and geographical distribution is one of the best-documented empirical patterns observed in nature (Brown, 1984; Gaston *et al.*, 1997). As a rule, whatever the higher taxon or habitat type considered, locally abundant species tend to be widespread on larger spatial scales, whereas locally rare species tend to be more narrowly distributed. Several mechanisms can singly or jointly produce this relationship. For instance, according to the resource breadth hypothesis, species capable of exploiting a broad spectrum of resources should not only reach high local densities, but should also be more likely to persist in a wider range of localities than more specialized species (Gaston *et al.*, 1997; Gaston & Blackburn, 2000).

For parasitic organisms, however, the relationship between local abundance and geographical distribution remains mostly untested. On the one hand, as in free-living organisms, some of the characteristics that allow a parasite species to achieve high local abundance may also enable it to successfully establish and persist in numerous other localities. Indeed, we might expect that local epidemiological processes translate into biogeographical patterns. On the other hand, the abundance and distribution of a parasite may be tightly constrained by the abundance and distribution of its hosts (Waltari & Perkins, 2010; Poulin *et al.*, 2011a). Locally, parasite transmission and population sizes are strongly linked to host density (Anderson & May, 1978; Arneberg *et al.*, 1998; Arneberg, 2001), with parasites attaining higher prevalence (proportion of host individuals infected) and abundance (mean number of parasites per host individual) in dense host populations. Also, across large spatial scales, parasites can only persist in localities where populations of their key hosts are established. Thus perhaps parasite abundance and spatial distribution are merely epiphenomena of host density and geographical range. Studies of fleas parasitic on mammals provided the first test of the abundance–distribution relationship in parasites, although only indirectly. Flea species with low host specificity occur over larger geographical areas than host-specific fleas (Krasnov *et al.*, 2005a), and flea species with low host specificity also achieved higher abundance on their hosts (Krasnov *et al.*, 2004). Therefore, fleas occurring at higher average abundance are also the ones with larger geographical ranges. However, these studies compared fleas parasitic on different host species, and do not allow one to determine whether the observed patterns result from intrinsic parasite properties or whether they are mere reflections of host patterns. The ideal test of the abundance–distribution relationship would involve numerous parasite species that share a single host species, sampled across many localities, in order to standardize host influences and detect true patterns generated by parasite properties. Szöllösi *et al.* (2011) have recently used this approach to show that among genetically distinct lineages of avian malaria parasites sampled in nine populations of a single host species, lineages with higher prevalence within host populations also occurred in more of these populations. Yet it remains to be seen whether the link between local abundance and geographical distribution applies more widely to other parasite taxa.

The average abundance or the typical prevalence achieved locally by a parasite may not be the only important aspects of its local success influencing its probability of occupying a broad geographical range. Parasite species displaying very little spatial variation in abundance may have lower rates of local extinction and a greater probability of colonizing new localities than parasites with highly variable abundances at the mercy of local conditions. Indeed, both theory and empirical data support a link between spatial variance in abundance and frequency of occurrence across localities (He & Gaston, 2003; Picard & Favier, 2011), and stochasticity in population abundance is also a key determinant of parasite extinction in host populations (Rohani *et al.*, 2002; Read & Keeling, 2007). Prevalence and abundance values vary in geographical space among conspecific parasite populations (Poulin & Dick, 2007), but generally show significantly lower variation among populations of the same parasite species than among populations of different parasite species (Arneberg *et al.*, 1997; Krasnov *et al.*, 2006; Poulin, 2006). Therefore prevalence and abundance can be seen as parasite species traits, in a loose sense. Nevertheless, these parameters still vary considerably among conspecific parasite populations, no doubt due to the influence of local conditions on transmission and infection. For instance, the free-living infective stages of helminth parasites are known to be susceptible to local abiotic conditions (Pietrock & Marcogliese, 2003) and to the presence of other organisms interfering with their transmission (Thieltges *et al.*, 2008). In addition, the type of life cycle used by a parasite may not only influence how variable its abundance is among localities, but also directly affect its geographical range. All else being equal, parasites requiring multiple hosts to complete their life cycle should inevitably be more susceptible to stochastic changes in local host availability, and thus more prone to local fluctuations in abundance or to extinction, than parasites with one-host life cycles. We predict (1) that parasite species displaying limited variation in abundance across the localities where they occur, and thus apparently better able to buffer against local conditions, will achieve a broader geographical distribution than species showing more pronounced variability in abundance, and (2) that parasite species with a simple life cycle will achieve a broader geographical distribution than species with complex life cycles.

Here, we use a large database on the metazoan parasites of threespine sticklebacks, *Gasterosteus aculeatus* L., to test the abundance–distribution relationship among parasite species, while controlling for the identity of the host species. Threespine sticklebacks are common fish found in a wide range of freshwater, estuarine and coastal habitats throughout the Northern Hemisphere above 35° N (Wootton, 1984); they have also been extensively sampled for parasites (see Poulin *et al.*, 2011b). Specifically, we address the following questions. (1) Does the average local abundance and/or median local prevalence of parasite species correlate positively with their wider distribution, here measured as their frequency of occurrence among localities and as their geographical range size? (2) Are parasite species with lower spatial variability in abundance achieving a wider geographical distribution than those with highly variable abundance? (3) Are parasite species with simple life cycles achieving a wider geographical distribution than those with complex cycles? Our study is one of the first attempts to link local infection patterns with global distributional patterns, scaling up from epidemiology to biogeography to determine whether local commonness translates into regional commonness.

MATERIALS AND METHODS

Dataset and variables

Data were obtained from a database of local parasite surveys from threespine stickleback populations scattered across the host's range in north-eastern North America and northern Europe; see Poulin *et al.* (2011b) for list of localities, matrices of parasite species by localities, and list of sources. Only surveys providing data on metazoan parasite abundance were retained, comprising 28 localities in north-eastern North America separated by an average ± SD distance of 439 ± 273 km and having 1–12 parasite species per locality, and 38 localities in northern Europe separated by 1277 ± 813 km and with 1–19 parasite species per locality (Fig. 1).

Some parasite taxa were only identified to the genus level in the original surveys. In the total species lists for each geographical region (north-eastern North America and northern Europe), when there were separate entries for both one or more named species of a particular genus and an unnamed generic entry, we included only the named species. However, if there was only an unnamed generic entry for a particular genus, it was retained as a parasite species in our analyses. Also, some parasite species occurred in both north-eastern North America and northern Europe. They were treated as statistically independent entries, i.e. essentially as different species. This is justifiable because (1) in parallel with the genetic isolation of their stickleback hosts between those regions (Colosimo *et al.*, 2005; Mäkinen & Merilä, 2008), parasites found on both continents may well represent distinct genetic lineages, as seen in the cestode *Schistocephalus solidus* (Nishimura *et al.*, 2011); and (2) the local epidemiological processes acting on these 'single' species and the resulting biogeographical patterns are likely to differ greatly between the two geographical regions.

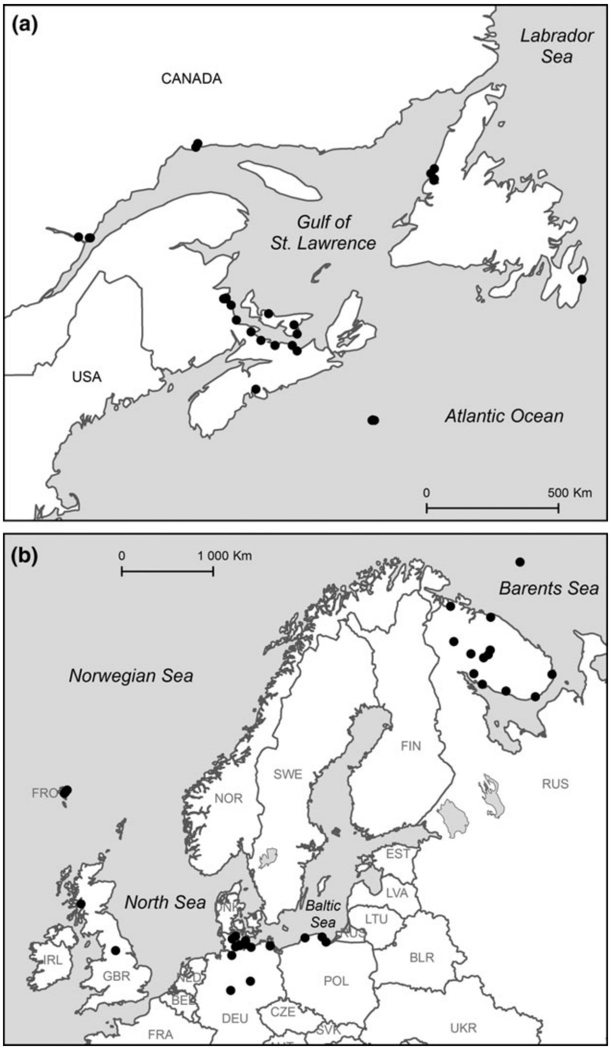

Figure 1 Maps showing (a) the location of the 28 localities from north-eastern North America and (b) the 38 localities from northern Europe from which parasite communities of threespine sticklebacks (*Gasterosteus aculeatus*) were sampled.

For each parasite species retained in each geographical region (see Appendix S1 in Supporting Information), we recorded its higher taxon (i.e. Digenea, Monogenea, Cestoda, Nematoda, Acanthocephala or Crustacea), whether its life cycle was simple or complex (i.e. requiring host species other than sticklebacks), and the type of definitive host it used (fish or bird/mammal). In addition, for each parasite species we calculated: (1) its frequency of occurrence among all surveyed localities in the region, expressed as a proportion; (2) its median prevalence across localities in the region where it occurred, with prevalence corresponding to the proportion of individual hosts infected by the parasite in one locality; (3) its average abundance, i.e. the mean number of individual parasites per individual host including uninfected hosts, calculated by averaging the mean abundance values from all localities within a region where the parasite occurred; (4) the coefficient of variation in average abundance, i.e. the standard deviation divided by the mean, used here as a measure of the spatial stability of parasite abundance across localities; and (5) its geographical range size, calculated using Google Earth Pro$^{\circledR}$ as the area within the smallest possible polygon delimited using the latitudes and longitudes of the localities where it occurred within a region. For marine or brackish water parasites restricted to coastal stickleback populations, a linear range computed as the length of coastline linking the two most distant localities where they occurred would be an alternative measure of geographical range; however, the elongated two-dimensional polygons captured well the range shape of those parasites. Median prevalence was available for most but not all species; in addition, the coefficient of variation in average abundance was only computed for parasite species occurring in at least two localities, and the geographical range size was calculated only for parasites occurring in at least three localities.

As indicated above, the dataset included freshwater, brackish and marine parasites. Prior to pooling them for our main analyses, we compared the geographical range sizes of these species to confirm that their salinity preferences and habitat restrictions did not impose constraints on their distributions (Appendix S2).

The data are based only on surveys of entire parasite communities in given stickleback populations, and exclude studies targeted at single parasite species for three reasons. First, including single-species studies would create asymmetry among parasite species in the number of localities on which estimates of occurrence and abundance are based, as some parasite species have received much more attention than others. By restricting inclusion to community-wide surveys only, estimates of occurrence and abundance are based on a standard set of localities in each geographical region (28 in north-eastern North America and 38 in northern Europe; Fig. 1). Second, including single-species studies would inevitably inflate estimates of frequency of occurrence for those well-studied parasite species, because single-species studies are almost invariably focused on selected localities where, obviously, the target species occurs. Third, including single-species studies would also bias estimates of average abundance, as targeted studies tend to select sites where the parasite is relatively abundant. Nevertheless, to evaluate how excluding these additional surveys may have affected our measures of geographical range size, we searched the Web of Science (using species names) for single-species studies on the most frequently studied stickleback metazoan parasites: *Schistocephalus solidus*, *Diphyllobothrium dendriticum*, *Diplostomum* spp., *Gyrodactylus* spp. and *Thersitina gasterostei*. We then re-calculated geographical range sizes for those species using localities from both single-species and community-wide surveys, tested for a correlation between those measures of range size and the ones based exclusively on community-wide surveys, and determined the relative difference between the two sets of range sizes.

Statistical analyses

Our analysis does not explicitly control for phylogenetic relationships among parasite species, a potentially confounding variable in comparative analyses (Harvey & Pagel, 1991). The parasite species we compare belong to vastly different taxa, representing different phyla, and there is insufficient available information to reconstruct a tree with branch lengths for all these species. However, the identity of the higher taxon to which the parasites belong was initially included in the models (see below), and emerged as the least important of all factors considered. Therefore, it is unlikely that the patterns we uncovered are phylogenetic artefacts.

We used generalized linear models (GLMs) implemented with the statistical software JMP 7.0 (SAS Institute Inc., Cary, NC, USA) to assess the influence of predictor variables on frequency of occurrence across localities and geographical range size, with those two response variables analysed separately. Only parasite species occurring in at least three localities per geographical region were included in these analyses because this is the minimum number of localities required to calculate the geographical range size. Variables were transformed when necessary, to normalize their distribution. Two nominal variables, the higher taxon to which a parasite belongs (Digenea, Monogenea, Cestoda, Nematoda, Acanthocephala, Crustacea) and the type of life cycle, are not independent of each other (all digeneans have multi-host life cycles, all monogeneans have one-host cycles, etc.); a preliminary analysis indicated that the type of life cycle had a stronger influence on both response variables, and parasite higher taxon was therefore excluded from the models. Another pair of nominal variables, the type of life cycle and the type of definitive host, are also non-independent (all parasites with simple life cycles inevitably use fish as definitive hosts); based on preliminary analyses, the type of definitive host had no influence on both response variables (Appendix S2), and it was excluded from the models. In each GLM, the set of explanatory variables included geographical region (north-eastern North America or northern Europe), life cycle (simple or complex), log-transformed average abundance, the coefficient of variation in abundance, and median prevalence; the significance of each factor's influence on the response variable was assessed based on the chi-square statistic. Both response variables, frequency of occurrence across localities and geographical range size, were log-transformed, and both models had a normal error structure and identity link function. Given the exclusion of species occurring in only one or two localities, there were no very low values of frequency of occurrence, and these data (proportions) were better normalized by a logarithmic transformation than by an arcsine transformation. No interaction terms were included in the models as we did not hypothesize strong interactions between any of the explanatory factors, and no significant interactions emerged from exploratory analyses. In all figures, the variables shown are uncorrected, i.e. they have not been adjusted for the influence of other variables.

RESULTS

In total, the dataset included 88 metazoan parasite species, consisting of 36 species from north-eastern North America and 52 from northern Europe (see Appendix S1). These parasites varied greatly in their spatial distribution, ranging from 0.026 to 0.786 in frequency of occurrence, and over more than six orders of magnitude in geographical range size. Of the 88 parasite species, 61 occurred in two or more sites, and 46 in three or more sites; only the latter were included in the GLMs.

We checked for issues of collinearity or associations among the predictor variables. Average abundance, its coefficient of variation, and median prevalence did not differ between parasites from North America and Europe (one-way ANOVAs, all $P > 0.167$) and between those with simple and complex life cycles (all $P > 0.092$). We found no significant correlation between average abundance and its coefficient of variation ($r = 0.017$, $N = 61$, $P = 0.8987$; including only parasite species that occurred at ≥ 3 sites: $r = -0.205$, $N = 46$, $P = 0.3931$), and between the coefficient of variation in abundance and median prevalence ($r = -0.227$, $N = 46$, $P = 0.1383$). However, average abundance and median prevalence were strongly positively correlated ($r = 0.736$, $N = 46$, $P < 0.0001$). To avoid collinear predictors, and because abundance already incorporates prevalence (abundance = prevalence*mean number of parasites per infected host), only average abundance was included in the GLMs.

The two different measures of parasite spatial distribution, i.e. frequency of occurrence and geographical range size, were correlated positively, although not very strongly ($r = 0.442$, $N = 46$, $P = 0.0021$). Nevertheless, the two measures capture different aspects of parasite distribution. Indeed, the scatter of points indicates that species occurring in a high proportion of local stickleback populations almost invariably have a large geographical range, whereas those occurring in few localities have range sizes that may vary from small to large (Fig. 2). The range size estimates we use here, which are based on community-wide surveys only, are considerably smaller than those based on the combination of community-wide and all single-species surveys found in a literature search; however, the two sets of estimates tend to covary positively (Appendix S2). Therefore, our range size estimates, although lower than the 'true' range sizes, are still suitable for our comparative purposes.

The results of the GLMs reveal four distinct patterns (Table 1). Firstly, parasite species in north-eastern North America tend to have slightly higher frequencies of occurrence among surveyed localities (mean and range: 0.13, 0.04–0.79 vs. 0.11, 0.03–0.47), but not broader geographical ranges (mean ± SD: 162,269 ± 152,720 vs. 197,866 ± 422,815 km^2), than their counterparts in northern Europe. Secondly, parasite species with simple life cycles have wider geographical ranges (Fig. 3), but similar frequency of occurrence (mean and range: 0.15, 0.03–0.29 vs. 0.11, 0.03–0.79), compared to those with complex life cycles. Thirdly, there was a slight positive relationship between average abundance of the different parasite species and their frequency of occurrence (Fig. 4), but not between average abundance and geographical range size. The relationship between average abundance and frequency of occurrence, however, was mainly due to a few species either rare locally and geographically, or common at both scales, with other species showing no clear pattern (Fig. 4). Fourthly, the coefficient of variation in abundance covaried positively with both the frequency of occurrence and geographical range size across the different parasite species (Table 1). The pattern, which is clearer for geographical range size (Fig. 5), means that all else being equal, parasite species showing greater site-to-site variability in abundance tend to occur in a greater proportion of localities, and over a broader geographical area, than parasite species with a more stable abundance among sites.

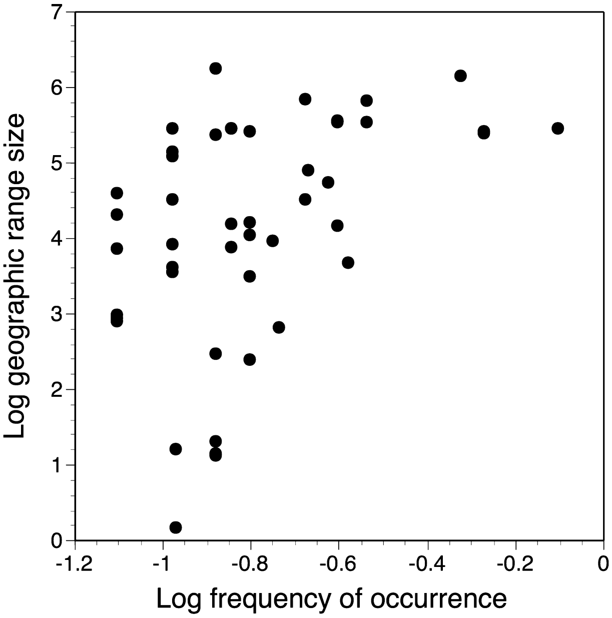

Figure 2 Geographical range size (km^2) as a function of the frequency of occurrence across all surveyed localities in a region, among 46 metazoan parasite species of threespine sticklebacks (*Gasterosteus aculeatus*).

DISCUSSION

This study provides a test of the general hypothesis that local parasite abundance predicts geographical distribution, by making comparisons among parasite species all sharing one host species in an attempt to minimize any host effects on both

Table 1 Results of generalized linear models of the factors influencing either the frequency of occurrence of a parasite in localities sampled across a region or its geographical range size, among metazoan parasite species of the threespine stickleback (*Gasterosteus aculeatus*). The chi-square tests assess the significance of the deviance explained by each factor.

Response variable	Factor	d.f.	χ^2	*P*-value
Frequency of occurrence ($n = 46$ species)	Geographical region	1	8.794	0.0030
	Life cycle	1	0.585	0.4443
	Average abundance	1	4.034	0.0446
	CV abundance	1	4.388	0.0362
Geographical range size ($n = 46$ species)	Geographical region	1	0.539	0.4628
	Life cycle	1	4.123	0.0423
	Average abundance	1	0.301	0.5835
	CV abundance	1	5.117	0.0237

CV, coefficient of variation.

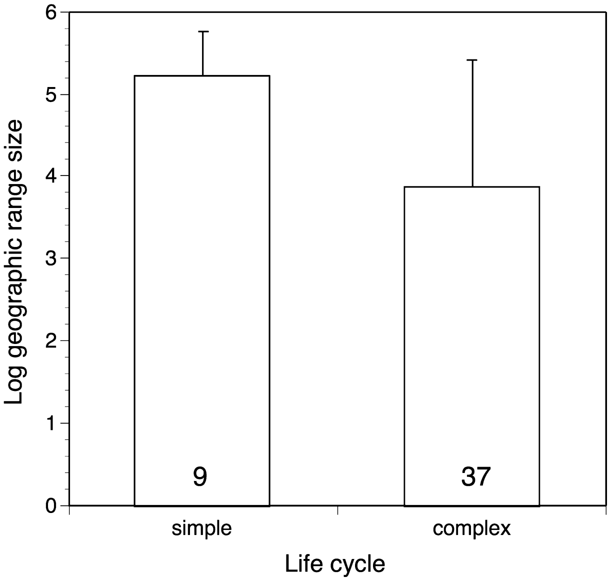

Figure 3 Mean (± SD) geographical range size (in km^2) of parasite species with either simple life cycles, i.e. involving only threespine sticklebacks (*Gasterosteus aculeatus*) as hosts, or complex life cycles involving additional host species. The numbers of parasite species of each type are indicated on the bars.

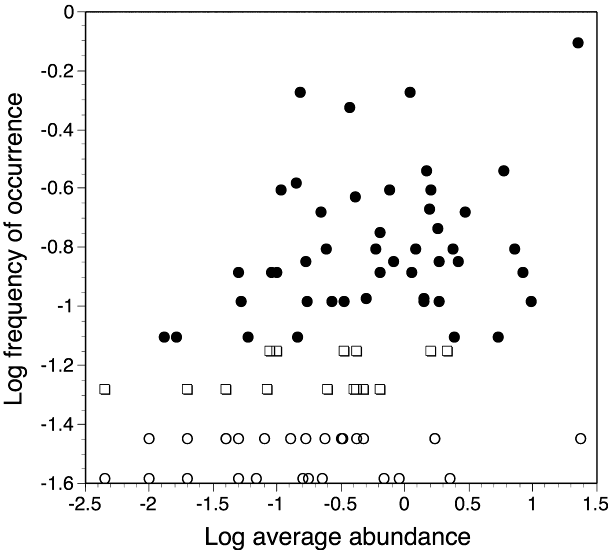

Figure 4 Frequency of occurrence across all surveyed localities in a region as a function of average abundance, among 88 metazoan parasite species of threespine sticklebacks (*Gasterosteus aculeatus*). Different symbols represent species occurring in only one locality (open circles), in only two localities (open squares), and in three or more localities (filled circles) out of either 28 localities in north-eastern North America or 38 in northern Europe. Only species occurring in three or more localities were included in the GLMs.

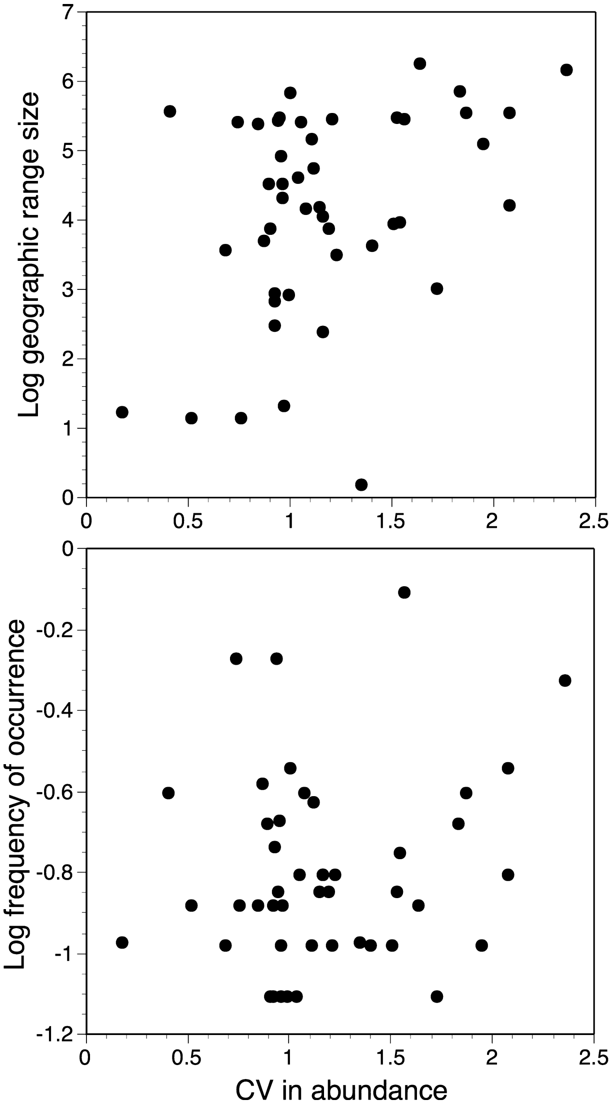

Figure 5 Geographical range size (in km^2; top) and frequency of occurrence across all surveyed localities in a region (bottom), as a function of the coefficient of variation (CV) in local abundance, among 46 metazoan parasite species of threespine sticklebacks (*Gasterosteus aculeatus*).

local and global parasite parameters. Our results have answered the three questions posed in the Introduction. First, locally abundant parasite species tended to occur in a higher proportion of localities, i.e. a higher proportion of threespine stickleback populations, within their geographical range than locally rare species, although this pattern was not very strong. Second, contrary to our expectation, parasite species with higher spatial variability in abundance occupied a broader geographical range, and a higher proportion of localities within their range, than those with less variable abundance. Third, as predicted, parasite species with simple life cycles achieved a wider geographical range than those with complex cycles.

The different parasite species varied greatly in both frequency of occurrence and geographical range size. However, the relationship between these two measures of spatial distribution was not simply linear: the scatterplot (Fig. 2) shows that species occurring in a high proportion of localities almost invariably have a large range, whereas those occurring in few localities can have any range size. With the number and location of sampling sites predetermined by the surveys automatically setting a maximum geographical range, it is inevitable that species with a high frequency of occurrence approach this maximum range. Species occurring in few localities may be found in adjacent or distant places, therefore showing more variable range sizes. The two measures are thus not capturing the same elements of spatial distribution (Holt *et al.*, 2002). The frequency of occurrence estimates the probability of persistence across localities within the range, whereas the range itself quantifies the spatial extent across which a species can be found.

The positive relationship between local abundance and regional distribution, although weak, is in line with the well-documented interspecific relationship between local abundance and geographical distribution applying to plants and animals in general (Brown, 1984; Gaston *et al.*, 1997; Gaston & Blackburn, 2000). Our results mirror those of earlier studies on fish parasites performed on smaller spatial scales (Barker *et al.*, 1996; Cone *et al.*, 2004; Pérez-del-Olmo *et al.*, 2009) and of a study on avian malaria (Szöllösi *et al.*, 2011). These earlier studies used either mean or maximum prevalence instead of abundance as the local parameter related to regional distribution, but as shown here and elsewhere (Morand & Guégan, 2000), prevalence and abundance are strongly correlated. Thus, the characteristics that allow a parasite species to be locally successful may also enable it to successfully establish and persist in numerous other localities. For instance, parasites infecting a high percentage of host individuals in a fish population have a higher probability of being dispersed by avian predators feeding on the fish, or of joining small subsets of fish colonizing new areas, than locally rare parasites. Differences in mean abundance among parasite species in regional assemblages might be a driving force behind the nested distribution of parasite presences among localities observed for numerous host–parasite systems (e.g. Krasnov *et al.*, 2005b). In a process similar to propagule pressure in invasion ecology (Lockwood *et al.*, 2005; Colautti *et al.*, 2006), parasites common in one locality will reach adjacent localities more frequently and in greater total numbers than rare species, ensuring their spread to most host populations in a given geographical area. Nevertheless, the effect of local abundance on frequency of occurrence among localities remains statistically weak, probably because of the effect of local biotic and abiotic conditions on the transmission success of parasites colonizing new sites (Pietrock & Marcogliese, 2003; Thieltges *et al.*, 2008).

In contrast to our expectation, parasite species with a high coefficient of spatial variation in abundance occupied a larger geographical range, and more localities within their range, than those with more stable abundance values. This finding is independent from average abundance itself because the coefficient in variation in abundance and average abundance did not covary. It is also not a simple consequence of spatial autocorrelation in abundance, as we have earlier demonstrated that the similarity in abundance values between two localities is independent of the distance between those localities, for most of the parasites studied here (Poulin *et al.*, 2011b). We had hypothesized that parasite species better able to buffer against local conditions, and thus displaying little variation in abundance across localities, should achieve a broader geographical distribution than species showing pronounced variability in abundance. Instead, perhaps spatial variability in local abundance indicates the ability of a species to persist at very small population sizes under suboptimal conditions and at much larger population sizes under favourable conditions, a flexibility that should enhance the colonizing ability of parasites. Alternatively, perhaps parasite species with a high coefficient of spatial variation in abundance are generalists capable of using hosts other than threespine sticklebacks, and spatial variation in the relative abundance of these other hosts modulates the extent to which sticklebacks are used in any given locality.

However, our statistical tests are all essentially correlative analyses, and the arrow of causality could be turned the other way. Indeed, instead of local epidemiological processes influencing the large-scale distributional patterns of parasites, perhaps instead these biogeographical properties constrain the abundance that a parasite can achieve locally. In their synthesis of studies on the relationship between local abundance and geographical distribution, Gaston & Blackburn (2000, p. 153) note that when a causal link is identified, the predominant direction of causality seems likely to run from local abundance to range size, and not vice versa. Nevertheless, it also seems likely that environmental conditions covary more strongly across localities on small than on large spatial scales. Therefore, parasite species with large range sizes should experience very different environmental conditions, leading to large fluctuations in their local abundance. For example, the presence or abundance of other necessary hosts in their life cycles, as well as abiotic conditions like temperature, will vary more widely over large than short distances. Indeed, similarity in local parasite abundance decreases with increasing distance in other host–parasite systems (Poulin & Dick, 2007; Thieltges *et al.*, 2009; Locke *et al.*, 2011). In contrast, parasite species with small ranges are more likely to meet a similar array of host species and environmental conditions within this range. Hence, parasites occurring in a greater proportion of localities and over a broader geographical area should show greater site-to-site variability in abundance.

Another pattern that emerged from our analysis is that parasite species with simple life cycles requiring only threespine sticklebacks as hosts achieved a wider geographical range than those with complex cycles requiring additional host species. This is expected given the extra distributional constraints imposed by additional hosts, limiting parasites with complex cycles to the area where the distributions of their many required hosts overlap (Waltari & Perkins, 2010). Interestingly, parasites with complex life cycles using birds as definitive hosts, and therefore with greater dispersal potential, were not found in a higher proportion of localities or across a broader geographical range than those using fish (Appendix S2). This finding mirrors the results of a recent study performed on completely different data and at a different scale (Thieltges *et al.*, 2011). Finally, we also observed that parasite species in north-eastern North America had slightly higher frequencies of occurrence among surveyed localities, but not broader geographical ranges, than those in northern Europe. This may be explained simply by the fact that the average inter-locality distance in Europe was about three times larger (1277 vs. 439 km) than in North America, and by the more contiguous arrangement of localities surveyed in north-eastern North America (see Fig. 1). Alternatively, historical processes may also account for present-day differences between the continents. Indeed, the presence of refuges during ice ages in North America but not in northern Europe may account for the greater fish diversity in the former than in the latter (Tonn *et al.*, 1990; Rohde, 2005), just as it may partly explain the observed differences in parasite distributions.

Earlier we mentioned that some parasites may be capable of using hosts other than threespine sticklebacks, and this points to a caveat that applies to our results. Our data come strictly from stickleback hosts, although many of the parasite species are not host specific and would also occur in other fish species (see Margolis & Arthur, 1979). The local abundance of a given parasite species can vary substantially among its different fish hosts (Poulin, 2005). In addition, generalist parasites capable of exploiting many fish species tend to occur at lower average abundance in their different hosts than specialists, suggesting a possible trade-off between specialization and within-host performance (Poulin, 1998). Spatial stability in abundance, as measured by its coefficient of variation, may also be linked to host specificity (Morand & Krasnov, 2008). However, by using abundance in threespine stickleback as a yardstick and assuming that local abundance in sticklebacks reflects relative abundance in other local hosts, our comparisons among localities should still provide insights into local–global relationships.

Our findings have implications for the predictions that the geographical distributions of many parasites are likely to either shrink or expand, depending on the species, in response to climate change (Marcogliese, 2001; Harvell *et al.*, 2002; Brooks & Hoberg, 2007). The local epidemiological parameters that characterize a species may either facilitate or constrain its geographical expansion under changing climatic conditions beyond what is generally predicted based solely on altered abiotic variables. The next important step will be to identify the mechanism linking local parasite abundance with large-scale distribution. One possibility is that all else being equal, certain life history traits, such as fecundity, lifespan or survivorship of infective stages under varying conditions, are important determinants of both local transmission success and persistence as well as colonization success of new host populations.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Data on the local abundance and prevalence, and the regional distribution, of metazoan parasite species from stickleback populations in Europe and North America.

Appendix S2 Assessment of the effect of the parasite's habitat (marine, freshwater, euryhaline) and type of definitive host on their geographical distributions, and comparison of species range sizes based only on community-wide surveys (as used in the present analyses) with those based on all available studies, for the most widely studied stickleback parasite species.

BIOSKETCH

Robert Poulin is a professor at the University of Otago. His research covers most ecological aspects of host–parasite interactions, in particular patterns and processes underlying parasite biodiversity, and the impact of parasitism on communities and ecosystems.

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