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Distance decay of similarity among parasite communities of three marine invertebrate hosts

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Abstract The similarity in species composition between two communities generally decays as a function of increasing distance between them. Parasite communities in vertebrate definitive hosts follow this pattern but the respective relationship in intermediate invertebrate hosts of parasites with complex life cycles is unknown. In intermediate hosts, parasite communities are affected not only by the varying vagility of their definitive hosts (dispersing infective propagules) but also by the necessary coincidence of all their hosts in environmentally suitable localities. As intermediate hosts often hardly move they do not contribute to parasite dispersal. Hence, their parasite assemblages may decrease faster in similarity with increasing distance than those in highly mobile vertebrate definitive hosts. We use published field survey data to investigate distance decay of similarity in trematode communities from three prominent coastal molluscs of the Eastern North-Atlantic: the gastropods *Littorina littorea* and *Hydrobia ulvae*, and the bivalve *Cerastoderma edule*. We found that the similarity of trematode communities in all three hosts decayed with distance, independently of local sampling effort, and whether or not the parasites used the mollusc as first or second intermediate host in their life cycle. In *H. ulvae*, the halving distance (i.e. the distance that halves the similarity from its initial similarity at 1 km distance) for the trematode species using birds as definitive hosts was approximately two to three times larger than for species using fish. The initial similarities (estimated at 1 km distance) among trematode communities were relatively higher, whereas mean halving distances were lower, compared to published values for parasite communities in vertebrate hosts. We conclude that the vagility of definitive hosts accounts for a high similarity at the local scale, while the strong decay of similarity across regions is a consequence of the low probability that all necessary hosts and suitable environmental conditions coincide on a large scale.

Keywords Faunal similarity · Geographical distance · Intermediate host · Parasite · Species richness

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Introduction

The similarity in species composition between two communities often decreases as the distance between them increases. While this phenomenon of distance decay of similarity is a common pattern in biogeography, the actual rate at which similarity decays with distance has only recently come into focus. In an initial study, Nekola and White (1999) determined distance decay relationships in plant communities of North American spruce–fir forests. Comparing the decay of similarity among various plant groups, they were able to show that distance decay resulted from either a decrease in environmental similarity with distance, or from limits to dispersal among plant groups. Since this early study, other studies have determined rates of distance decay of similarity in various assemblages of free-living organisms, and a recent meta-analysis found distance decay of similarity to be a universal phenomenon in various taxonomic groups and ecosystems (Soininen et al. 2007).

To compare the various studies in their meta-analysis, Soininen et al. (2007) applied two measures of effect size: (1) the similarity at 1 km distance (initial similarity), and (2) the distance that halves the similarity from the initial similarity at 1 km distance (halving distance). While the initial similarity reflects beta diversity (i.e. species composition turnover among local sites), with high initial similarities indicating low beta diversity, the halving distance reflects the scale-dependence of beta diversity, with short halving distances indicating strong scale-dependence of turnover in species composition (Soininen et al. 2007). Both initial similarity and halving distance can be expected to vary among the communities considered due to three, non-exclusive mechanisms underlying the phenomenon of distance decay in similarity. First, with increasing distance between communities, the similarity of environmental parameters is likely to decrease. As species differ in their environmental preferences, this leads to niche-based community processes following gradients in environmental variables with increasing distance (Nekola and White 1999; Tuomisto et al. 2003; Gilbert and Lechowicz 2004). Second, dispersal rates of organisms depend on the spatial matrix of the landscape in terms of dispersal barriers, with similarity of community composition decreasing more rapidly with distance in heterogeneous landscapes containing major dispersal barriers compared to homogeneous landscapes with no or low dispersal barriers (Garcillán and Ezcurra 2003). Third, even under totally homogeneous environmental conditions, distance decay may be observed as organisms have limited dispersal (neutral theory of biodiversity and biogeography; Hubbell 2001).

The phenomenon of distance decay of similarity is not confined to free-living species but also occurs in parasite assemblages. Distance decay in similarity has been observed in helminth communities of mammals (Poulin 2003; Brouat and Duplantier 2007) and fishes (Poulin 2003; Karvonen and Valtonen 2004; Fellis and Esch 2005; Oliva and González 2005) as well as in flea communities of small mammals (Krasnov et al. 2005). However, in some host species investigated, no distance decay could be observed (Poulin 2003; Oliva and González 2005; Brouat and Duplantier 2007). In general, vagile hosts, like marine fishes in open and continuous habitats, show a lower rate of decay and hence longer halving distances compared to hosts in fragmented habitats like freshwater fishes (Oliva and González 2005). As the latter are more limited in dispersal, this also limits the dispersal of their parasites. However, host vagility may not always explain rates of distance decay (Poulin 2003). Varying dispersal abilities of parasites themselves via the dispersal abilities of the other host species in their life cycle also explains differences in the rate of distance decay of similarity for autogenic (completing their life cycles wholly within the confines of an aquatic system) and allogenic (completing their life cycles outside their immediate habitat) parasites. As the dispersal ability of allogenic parasites is very high, distance decay relationships can be expected to be weaker than in autogenic parasites with low dispersal ability, though actual data sometimes suggest a more complex pattern (Karvonen and Valtonen 2004; Fellis and Esch 2005). As a general rule, distance decay of similarity occurs in most parasite communities studied so far and seems to depend mainly on host dispersal and, probably to a lesser extent, on environmental gradients.

While parasite communities in vertebrates, serving mainly as definitive hosts for the parasites, have recently received interest concerning distance decay in similarity, nothing is known about distance decay in invertebrate intermediate hosts. In intertidal ecosystems, molluscs are important invertebrate hosts that serve as first intermediate hosts for trematodes (Mouritsen and Poulin 2002). Gastropods frequently function as first intermediate hosts, but many species of bivalve may also host trematodes. In the mollusc first intermediate host, the parasites develop freeliving infective stages—the cercariae. After being released into the environment, the cercariae infect a second intermediate host that, depending upon the trematode species, may be bivalves, gastropods, fishes, annelids, arthropods, or other aquatic organisms. As gastropods and bivalves hardly move, they are incapable of contributing to the dispersal of parasites on a geographic scale, and their larval stages do not harbour infections. Hence, the local composition of trematode communities depends on the influx of infective propagules from the definitive hosts. This is indicated by studies reporting strong correlations between bird definitive host diversity and parasite diversity in gastropod first intermediate hosts on small spatial scales (Hechinger and Lafferty 2005; Fredensborg et al. 2006; Byers et al. 2008). However, for parasites with complex life cycles, the coincidence of all their hosts in environmentally suitable locations is also important to maintain local populations. Especially at larger spatial scales, differences in the composition of local intermediate and definitive host communities and the general suitability of environmental conditions will lead to differences in the parasite faunas, as parasite communities reflect local diversity of free living animals (Hechinger and Lafferty 2005; Hechinger et al. 2007). Hence, distance decay in intertidal intermediate hosts may actually be stronger than expected from the fact that marine systems are an open and continuous habitat, and that all trematodes of molluscs are allogenic parasites that complete their life cycle in vagile hosts. Accordingly, distance decay in more or less sessile intermediate hosts may be stronger than in vagile definitive hosts that sample parasites over a much larger spatial scale. Considering the importance of vagility of definitive hosts for parasite dispersal, we should expect distance decay relationships to differ among trematodes using different types of definitive hosts. Trematodes using highly vagile migrating birds as definitive hosts should have greater halving distances compared to trematodes using less vagile fishes as definitive hosts. Likewise, distance decay may also vary between trematodes utilizing molluscs as first or second host. The former depend only on definitive hosts for dispersal while the latter depend also on large-scale distributions of their first intermediate hosts.

In this study, we investigate these predictions for trematode communities in intermediate invertebrate hosts by using published trematode inventories of three prominent molluscs of the eastern north-Atlantic. The gastropods *Littorina littorea* and *Hydrobia ulvae* are infected by trematodes utilizing these snails as first intermediate hosts (James 1968; Deblock 1980; Lauckner 1980), while the bivalve *Cerastoderma edule* serves as both first and second intermediate host for trematodes. We use a database compiled from the inventories to (1) determine the rate of distance decay in parasite communities of these intermediate invertebrate hosts, (2) investigate whether distance decay in similarity differs between parasites using birds or fishes as definitive hosts, (3) observe whether distance decay in similarity differs between trematodes using molluscs as first or second intermediate host, and (4) compare the rates of distance decay in invertebrate intermediate hosts with those previously published on parasite communities in vertebrate definitive hosts.

Materials and methods

We obtained data on the composition of parasite communities in *L. littorea*, *H. ulvae,* and *C. edule* from sites in the north-east Atlantic from the literature. Only studies that investigated the entire trematode community and that reported the sampling effort, i.e. the numbers of snails dissected per locality, were included. To reduce bias due to low sample sizes we included only those studies that investigated at least 30 individual bivalve and 80 individual snail hosts per sampling locality. All parasite species names were carefully matched with their known synonyms (e.g. James 1968; Lauckner 1971; Deblock 1980; Lauckner 1980, 1983), to avoid bias in faunal comparisons between sites resulting from differences in nomenclature.

The database consisted of three matrices (one per mollusc host species), with one row assigned to each parasite species, and one column to each sampling site (see Table 1 for a summary of the parasite community data and the literature sources used to compile the database). The whole database is available upon request from D.W.T. Presence/absence of each parasite species was noted for each site as well as sampling effort. For sites where data were available we also noted the prevalence (proportion of hosts infected) of each parasite species, as this was the only measure of infection level available for all three host species. In cases where the same site was sampled at different times, we used the total parasite inventory obtained, mean prevalence per species, and the total number of snails dissected during all sampling events. Coordinates from each site were obtained from the references or by using site descriptions from the literature and Google Earth (http://earth.google.com). If literature sources reported the mean of several sub-sites within a range of a few kilometres, we determined the coordinates of the centre of the sampling area. Using the coordinates, we then calculated the shortest linear distance ("as the crow flies") between all pairs of sites using great circle calculations (http://gc.kls2.com). For sites <20 km apart we used the lineal function in Google Earth. Taking potential inaccuracies in determining coordinates and minor deviations from the calculation procedures into account, a conservative estimate of the accuracy of distance values is 500 m for sites <20 km and 10 km for sites >20 km apart. Considering that most distances were in the range of hundreds to thousands of kilometres, these potential inaccuracies should

Table 1 Summary of parasite community data compiled for the three mollusc host species in the data base and used to analyse distance decay in similarity

Host species	No. of host populations	Parasite richness (range)	Total parasite species richness	Latitude (range)	Longitude (range)	Sources[a]
Cerastoderma edule	19	2–12	15	34′52°N–67′17°N	8′43°W–9′59°E	1–6
Hydrobia ulvae	36	2–20	44	43′40°N–57′20°N	4′21°W–9′59°E	4, 7–12
Littorina littorea	35	1–6	10	44′39°N–58′52°N	8′08°W–11′26°E	5, 13–27

[a] *1* Krakau (2008), *2* Gam et al. (2008), *3* Russell-Pinto et al. (2006), *4* Kesting et al. (1996), *5* Desclaux (2003), *6* Thieltges and Reise (2006), *7* Deblock (1978), *8* Field and Irwin (1999), *9* Zander et al. (2000), *10* Zander et al. (2002), *11* Wiemerslage (1998), *12* Ferguson (2008), *13* Werding (1969), *14* Robson and Williams (1970), *15* Matthews et al. (1985), *16* James (1968), *17* Huxham et al. (1993), *18* Granovitch and Johannesson (2000), *19* Granovitch and Mikhailova (2004), *20* Rees (1936), *21* Lauckner (1986), *22* Lauckner (1984), *23* Lauckner (1993/1994), *24* Hughes and Answer (1982), *25* Reimer (1995), *26* Thieltges et al. (2006), *27* Dietvorst (1972)

be insignificant. In addition, we calculated the similarity in species composition for all pairs of sites using the programme Estimates (Colwell 2005). We computed three different similarity indices: we first used the Jaccard similarity index based on presence/absence of data because of its simplicity and widespread use in similar analyses. Its value ranges from 0 when two sites have no species in common, to 1 when the two sites have exactly the same parasite species. In addition, we computed the Morisita-Horn and Bray-Curtis similarity indices based on prevalence data. Like the Jaccard index, both vary from 0 (no similarity) to 1 (complete similarity). For the latter two indices, only a reduced subset of the database could be used as prevalence data were not available for all sites.

To determine the rate of distance decay, we performed linear regressions using $\ln(x + 1)$-transformed similarity index data as those gave the best fits. As the data points in the regressions are not strictly independent from each other (each community is used in more than one comparison), we tested the significance of each regression model using a randomisation approach. We used the programme Resampling (Howell 2000) to determine the regression probabilities based on 10,000 permutations. Using the regressions, we calculated initial similarity and halving distance following Soininen et al. (2007). We also calculated initial similarity and halving distance for other parasite communities from the literature using studies on helminth parasites and ranging over a similar distance (Poulin 2003; Fellis and Esch 2005; Oliva and González 2005). We did not include the recent analysis of Brouat and Duplantier (2007) as their analysis was on a much smaller scale (<100 km). As different similarity indices were used in the above published studies, we standardised all similarity values to the Sorensen index using the conversion provided by Soininen et al. (2007).

Results

The similarity of trematode communities in all three host species decayed with distance when using the total data set, no matter which similarity index was used (Table 2, Fig. 1). Initial similarity was relatively low in *H. ulvae* (0.364–0.504, depending on the type of similarity index used), and higher in *C. edule* (0.507–0.637) and *L. littorea* (0.510–0.721) (Table 2). Halving distance of trematode communities in the bivalve *C. edule* was about two times higher than for the trematode communities in the two snails, with similar values among the different similarity indices (Table 2).

In all three host species, the number of species recorded per site correlated positively with sampling effort (ln-transformed) (*C. edule*: $r^2 = 0.452$, $P = 0.002$; *H. ulvae*: $r^2 = 0.394$, $P < 0.001$; *L. littorea*: $r^2 = 0.128$, $P = 0.035$). Thus, we also restricted our analysis to include only sites with sufficient sampling effort such that there was no significant relationship between species richness and sampling effort (ln-transformed) (*C. edule*: $n > 80$ ind., $P = 0.129$; *H. ulvae*: $n \geq 1222$, $P = 0.655$; *L. littorea*: $n \geq 289$ ind., $P = 0.063$) (Table 3). For these restricted datasets, the observed distance decay relationships remained but initial similarities and halving distances differed between total and reduced datasets although, in most cases, the differences

Table 2 Regression statistics for the distance decay of similarity in trematode communities of the three host species using different similarity indices: Jaccard index based on presence/absence data and Morisita-Horn and Bray-Curtis indices based on prevalence (% infected individuals) data

Host species	Slope	Intercept	Initial similarity	Halving distance (km)	*n*	r^2	*P*
Cerastoderma edule Jaccard	−0.000083	0.4658	0.594	2,805	171	0.247	<0.001
Cerastoderma edule Morisita–Horn	−0.000091	0.4926	0.637	2,704	171	0.245	<0.001
Cerastoderma edule Bray–Curtis	−0.000074	0.4104	0.507	2,776	171	0.168	<0.001
Hydrobia ulvae Jaccard	−0.000140	0.3189	0.376	1,139	630	0.164	<0.001
Hydrobia ulvae Jaccard 2[a]	−0.000132	0.3097	0.363	1,172	561	0.154	<0.001
Hydrobia ulvae Morisita–Horn	−0.000170	0.4077	0.504	1,198	561	0.14	<0.001
Hydrobia ulvae Bray–Curtis	−0.000123	0.3333	0.395	1,356	561	0.123	<0.001
Littorina littorea Jaccard	−0.000192	0.5219	0.685	1,359	595	0.248	<0.001
Littorina littorea Jaccard 2	−0.000247	0.5406	0.716	1,096	435	0.388	<0.001
Littorina littorea Morisita–Horn	−0.000180	0.5435	0.721	1,511	435	0.199	<0.001
Littorina littorea Bray–Curtis	−0.000183	0.4126	0.510	1,129	435	0.248	<0.001

Slope and intercept of each regression are based on $\ln(x + 1)$-transformed similarity values. Initial similarity (back-transformed Jaccard, Morisita-Horn and Bray-Curtis indices) and halving distance (km) were calculated following Soininen et al. (2007)

n number of pair-wise comparisons

r^2 and *P*-values were determined using randomisation procedures; all regression probabilities are based on 10,000 permutations

[a] As prevalence data were not available for all sampling sites, a second Jaccard index (Jaccard 2) was computed for the reduced datasets

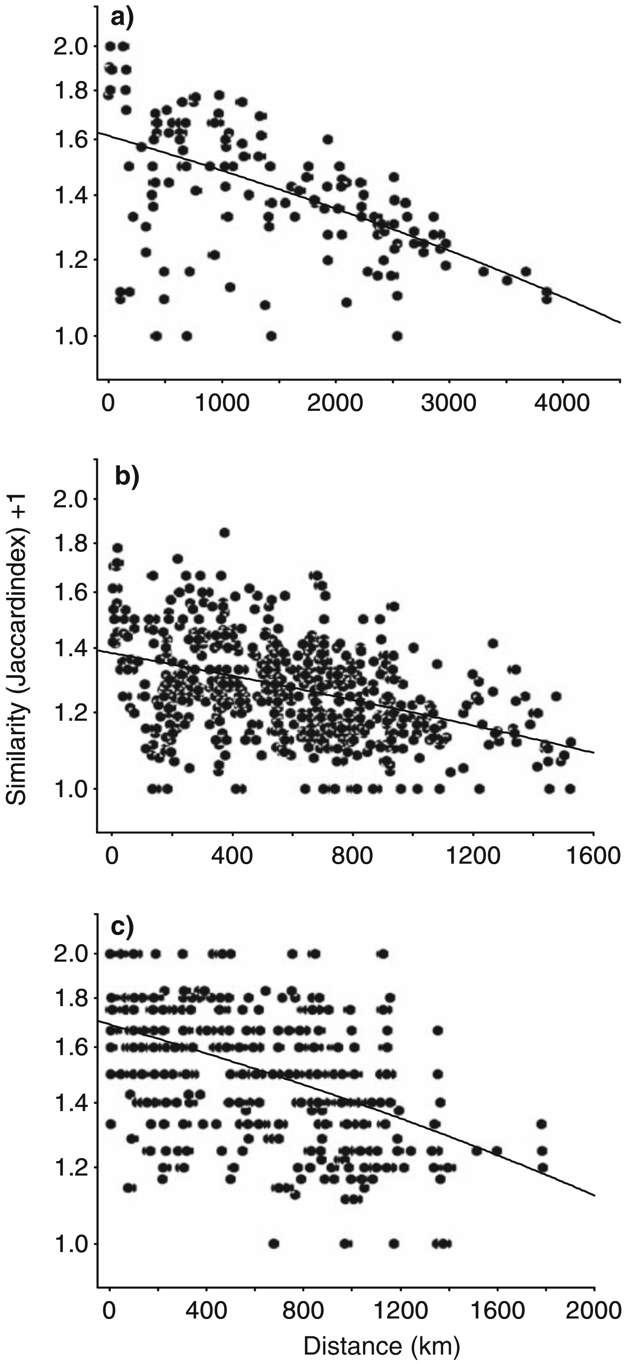

Fig. 1 Similarity (Jaccard index) of trematode communities plotted against distance (km) for all pair-wise comparisons in the total datasets of the three host species. *Lines* Best linear fits. For intercepts and slopes as well as significance values see Table 2. While only the Jaccard index is displayed, the other indices gave similar results. Note the log scale for similarity values. **a** *Cerastoderma edule*, **b** *Hydrobia ulvae*, and **c** *Littorina littorea*

were small (Table 3). This suggests that the analyses are relatively robust against differences in sampling effort. In most cases, the amount of variance explained by the regression was not substantial, though far from trivial (r^2 values between 0.100 and 0.400) (Table 3).

Communities of trematodes using *C. edule* as second intermediate host showed a high (0.513–0.689, depending on the type of similarity index used) initial similarity and a significant decay of similarity with distance when using the total datasets (Table 4). In contrast, distance decay was absent in communities of trematodes using the bivalve as first intermediate hosts (Table 3). This pattern remained when using the reduced datasets and Jaccard or Bray–Curtis indices (Table 5). However, when using the Morisita–Horn index, trematodes using cockles as first intermediate host showed a significant distance decay of similarity in the reduced dataset (Table 5).

In *H. ulvae*, trematode communities of species using birds as definitive hosts showed a higher initial similarity compared to communities using fishes as definitive hosts (Table 4). However, this pattern disappeared when using the reduced datasets (Table 5). Halving distance in trematode communities using birds as definitive hosts was over 2–3 times higher than that of trematodes using fish in both the total and reduced datasets (Tables 4, 5). These comparisons could not be performed for trematodes in *L. littorea*, as only one species in this snail uses fishes as definitive hosts.

Compared to communities of parasites in other host groups, initial similarities of trematode communities in molluscs were relatively high (Fig. 2). Mean halving distance in trematode communities of molluscs was lower compared to parasite communities in other groups (Fig. 2), and single values were even lower in the communities of the two snail hosts (Table 2). The regression models of distance decay among the molluscan parasites explained only a small proportion of the variance in the datasets, with values generally lower than those observed in all other host systems (Fig. 2). However, these data are based on very low sample sizes (2–3) and probably represent only rough estimates of the actual values. Hence, we refrained from a statistical analysis.

Discussion

Distance decay of similarity occurred in the trematode communities of all three host species, regardless of whether similarity was measured based on presence/absence data only or using prevalence; thus, distance decay of similarity seems to be a universal phenomenon not only in parasite communities of definitive vertebrate hosts but also of intermediate invertebrate hosts. The dispersal capacity of the parasites' propagules and that of their first intermediate hosts is limited. Miracidia (hatching from eggs released from the definitive hosts' faeces) and cercariae (shed by infected first intermediate host snails) both have short lifespans, which limit their dispersal (Galaktionov and Dobrovolskij 2003). Gastropods and bivalves hardly move and

Table 3 Regression statistics for the distance decay of similarity in trematode communities of the three host species comparing total with reduced data sets

Host species	Similarity index	Slope	Intercept	Initial similarity	Halving distance (km)	*n*	r^2	*P*
Cerastoderma edule	Jaccard	−0.000083	0.4658	0.594	2,805	171	0.247	<0.001
Cerastoderma edule ≥ 80 ind.	Jaccard	−0.000096	0.4994	0.647	2,601	45	0.214	0.001
Cerastoderma edule	Morisita–Horn	−0.000091	0.4926	0.637	2,704	171	0.245	<0.001
Cerastoderma edule ≥ 80 ind.	Morisita–Horn	−0.000185	0.5462	0.726	1,476	45	0.642	<0.001
Cerastoderma edule	Bray–Curtis	−0.000074	0.4104	0.507	2,776	171	0.168	<0.001
Cerastoderma edule ≥ 80 ind.	Bray–Curtis	−0.000144	0.4365	0.547	1,517	45	0.626	<0.001
Hydrobia ulvae	Jaccard	−0.000140	0.3189	0.376	1,139	630	0.164	<0.001
Hydrobia ulvae ≥ 1,222 ind.	Jaccard	−0.000219	0.4348	0.545	992	45	0.333	<0.001
Hydrobia ulvae	Morisita–Horn	−0.000170	0.4077	0.504	1,198	561	0.14	<0.001
Hydrobia ulvae ≥ 1,222 ind.	Morisita–Horn	−0.000183	0.5160	0.675	1,338	28	0.536	0.001
Hydrobia ulvae	Bray–Curtis	−0.000123	0.3333	0.395	1,356	561	0.123	<0.001
Hydrobia ulvae ≥ 1,222 ind.	Bray–Curtis	−0.000175	0.4724	0.603	1,351	28	0.508	0.009
Littorina littorea	Jaccard	−0.000192	0.5219	0.685	1,359	595	0.248	<0.001
Littorina littorea ≥ 300 ind.	Jaccard	−0.000200	0.5129	0.670	1,282	325	0.228	<0.001
Littorina littorea	Morisita–Horn	−0.000180	0.5435	0.721	1,511	435	0.199	<0.001
Littorina littorea ≥ 300 ind.	Morisita–Horn	−0.000113	0.5097	0.665	2,254	231	0.265	<0.001
Littorina littorea	Bray–Curtis	−0.000183	0.4126	0.510	1,129	435	0.248	<0.001
Littorina littorea ≥ 300 ind.	Bray–Curtis	−0.000161	0.3894	0.476	1,210	231	0.395	<0.001

For details see Table 2

Table 4 Regression statistics for the distance decay of similarity, using the total datasets, in trematode communities utilising *Cerastoderma edule* as first or second intermediate host and in communities in *Hydrobia ulvae* using birds or fishes as final hosts

Host species	Similarity index	Slope	Intercept	Initial similarity	Halving distance (km)	*n*	r^2	*P*
Cerastoderma edule second int host	Jaccard	−0.000100	0.5237	0.689	2,617	171	0.312	<0.001
Cerastoderma edule first int host	Jaccard	−0.000019	0.2118	0.236	5,568	156	NS	0.385
Cerastoderma edule second int host	Morisita–Horn	−0.000091	0.4930	0.637	2,697	171	0.245	<0.001
Cerastoderma edule first int host	Morisita–Horn	−0.000060	0.4648	0.592	3,852	78	NS	0.064
Cerastoderma edule second int host	Bray–Curtis	−0.000075	0.4137	0.513	2,767	171	0.167	<0.001
Cerastoderma edule first int host	Bray–Curtis	−0.000031	0.1866	0.206	2,994	156	NS	0.079
Hydrobia ulvae fish	Jaccard	−0.000108	0.1443	0.155	669	585	0.051	<0.001
Hydrobia ulvae birds	Jaccard	−0.000126	0.3415	0.406	1,357	630	0.108	<0.001
Hydrobia ulvae fish	Morisita–Horn	−0.000126	0.1560	0.169	619	561	0.057	<0.001
Hydrobia ulvae birds	Morisita–Horn	−0.000131	0.4263	0.531	1,628	561	0.081	<0.001
Hydrobia ulvae fish	Bray–Curtis	−0.000107	0.1345	0.143	631	561	0.053	<0.001
Hydrobia ulvae birds	Bray–Curtis	−0.000101	0.3460	0.413	1,713	561	0.077	<0.001

For details see Table 2

int Intermediate

the larval stages of molluscs do not harbour infections; thus they cannot contribute to the large-scale dispersal of parasites. Hence, the input of parasite propagules to local parasite communities in the first intermediate mollusc hosts depends on the dispersal by the parasites' definitive hosts (birds and fishes). In general, birds and fishes are vagile and their local movements can be expected to lead to a more or less homogenous dispersal of parasites at small spatial scales. This explains the relatively low beta diversity of the trematode communities in our data as indicated by the relatively high initial similarities. However, at larger spatial scales, general environmental conditions are likely to change. This affects the presence of suitable habitats for definitive hosts but also for other intermediate hosts in the

Table 5 Regression statistics for the distance decay of similarity, using the reduced data sets, in trematode communities utilising *Cerastoderma edule* as first or second intermediate host and in communities in *Hydrobia ulvae* using birds or fishes as final hosts

Host species	Similarity index	Slope	Intercept	Initial similarity	Halving distance (km)	*n*	r^2	*P*
Cerastoderma edule second int host	Jaccard	−0.000117	0.5370	0.711	2,295	45	0.301	<0.001
Cerastoderma edule first int host	Jaccard	−0.000011	0.3291	0.390	14,964	45	NS	0.819
Cerastoderma edule second int host	Morisita–Horn	−0.000186	0.5467	0.728	1,469	45	0.645	<0.001
Cerastoderma edule first int host	Morisita–Horn	−0.000116	0.6560	0.927	2,828	28	0.285	0.002
Cerastoderma edule second int host	Bray–Curtis	−0.000146	0.4375	0.548	1,500	45	0.397	<0.001
Cerastoderma edule first int host	Bray–Curtis	−0.000281	0.3025	0.353	539	45	NS	0.475
Hydrobia ulvae fish	Jaccard	−0.000341	0.4197	0.520	616	45	0.336	<0.001
Hydrobia ulvae birds	Jaccard	−0.000162	0.4196	0.520	1,297	45	0.190	0.003
Hydrobia ulvae fish	Morisita–Horn	−0.000394	0.4783	0.613	607	28	0.360	<0.001
Hydrobia ulvae birds	Morisita–Horn	−0.000134	0.5149	0.674	1,921	28	0.214	0.022
Hydrobia ulvae fish	Bray–Curtis	−0.00038	0.4655	0.592	613	28	0.358	0.001
Hydrobia ulvae birds	Bray–Curtis	−0.00012	0.4620	0.587	1,925	28	0.171	0.021

For details see Table 2

int Intermediate

complex life cycles of the trematodes. As a result, at large distances, differences in environmental conditions and the composition of local intermediate and definitive host communities will lead to differences in the parasite faunas, as parasite communities reflect local diversity of free-living animals (Hechinger and Lafferty 2005; Hechinger et al. 2007). Hence, while vagility of definitive hosts accounts for a high similarity at a local scale, the decay of similarity across regions is a consequence of the low probability that all necessary hosts and suitable environmental conditions for a certain parasite species coincide on a large spatial scale.

Besides this necessary coincidence, differences in definitive host vagility are likely to modify distance decay patterns. This is indicated by the differences in halving distances of parasite communities in *H. ulvae* using different types of definitive hosts. Halving distance in parasite communities using birds as definitive hosts was 2–3 times longer than in parasite communities using fishes as definitive hosts. The tidal flats of the Eastern North-Atlantic are used by millions of migrating waders and other birds as a migration stop along the East Atlantic flyway (Smit and Piersma 1989). Hence, we can expect that parasites are dispersed together with their bird hosts over large distances. In contrast, dispersal of intertidal fish species is usually more limited, with many species being local residents (Horn et al. 1999). Although fishes may disperse their parasites over small to medium scales, dispersal over large spatial scales is probably less common compared to birds. Accordingly, the halving distances between the two groups vary, with parasite communities utilising birds as definitive hosts exhibiting longer halving distances. The differing vagility of the two host groups might also be relevant on a smaller scale, as trematode communities of species using birds as definitive hosts showed a higher initial similarity (suggesting higher dispersal rates) compared to communities using fishes as definitive hosts. However, this pattern disappeared in the reduced datasets, casting doubt over the generality of this pattern. Studies on parasite communities in definitive hosts have found a similar relationship between host vagility and the strength of the distance decay of similarity (Poulin 2003; Oliva and González 2005). In general, more vagile hosts show longer halving distances than less vagile hosts. For example, while distance decay occurred in vagile pelagic or demersal marine fishes, it was not observed in a benthic non-vagile species (Oliva and González 2005). However, the pattern does not seem to be universal as there are exceptions to this rule (Poulin 2003).

Interestingly, there was no decay of similarity in the three trematode species utilising the bivalve *C. edule* as first intermediate host (although a single regression was significant in the reduced dataset, see Table 5). All three trematode species using the cockle as first intermediate host seem to have a uniform distribution over the geographic range of cockles (de Montaudouin et al. 2000; Thieltges and Reise 2006; Gam et al. 2008), probably because they use highly mobile definitive hosts. In addition, for two of the parasites, the bivalve serves both as first and second intermediate host, thus freeing the parasite from the necessity of the presence of a suitable second intermediate host. The remaining parasite species uses gobiid fishes as second intermediate host. Gobiids are typical intertidal fishes, usually present in high numbers in coastal ecosystems (Horn et al. 1999). Hence, the life cycles of the three parasite species make them less dependent on the coincidence of suitable species as discussed above, and this results in a large geographic distribution over Europe. However, despite their

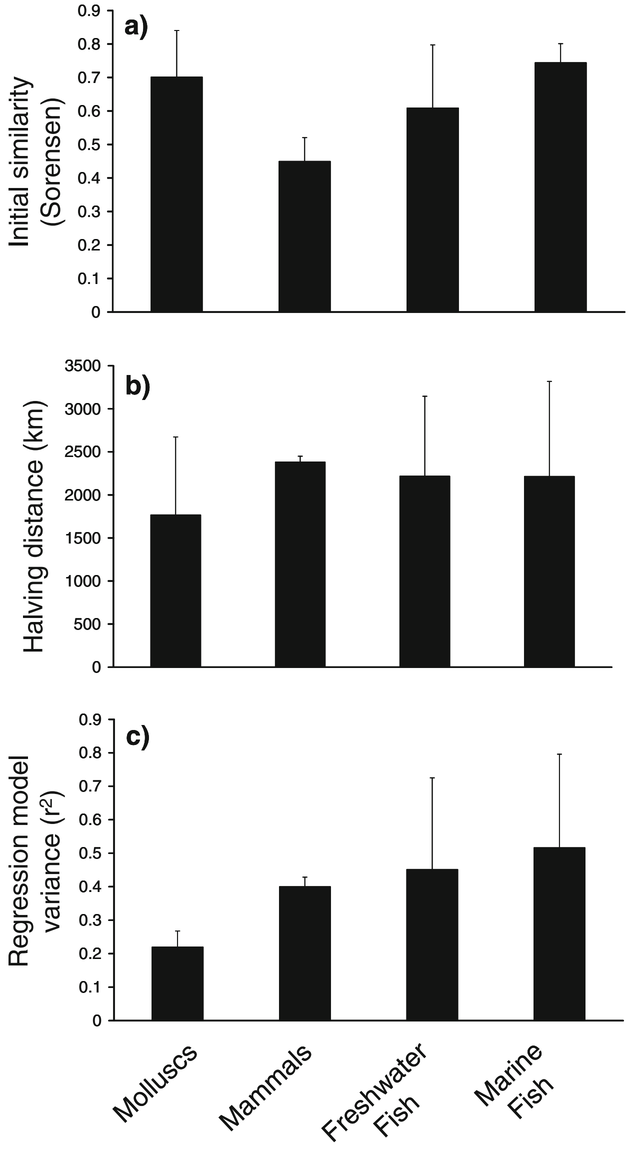

Fig. 2 **a** Initial similarity (Sorensen Index), **b** halving distance (km) and **c** variance explained (r^2) in regression models (means + SD) of helminth parasite communities in molluscs (this study, $n = 3$) and mammals, freshwater fish and marine fish (all from literature sources, $n = 2, 3, 3$, respectively)

large geographic distribution, the three parasites show strong spatial heterogeneity on small scales (de Montaudouin et al. 2000; Thieltges and Reise 2006; Gam et al. 2008). This may be attributed to local heterogeneities in environmental conditions resulting in local habitats of varying suitability for hosts and parasites. It may also be the result of stochastic processes, with definitive hosts more or less randomly visiting sites and distributing parasites. A combination of small- and large-scale factors may generate the very low decay of similarity observed in this case. This illustrates that patterns and mechanisms of distance decay of similarity in first intermediate hosts might actually be more complex than the parasite communities in the two gastropod species (all using the snails as first intermediate hosts) suggest.

Trematode communities utilising the bivalve *C. edule* as second intermediate host also showed a decay of similarity with distance. In the case of second intermediate hosts, distance decay is caused not only by the parasites' dispersal capabilities via their definitive hosts (in this case mainly birds), but also by the large-scale distributions of the appropriate first intermediate hosts. The distributions of the different first intermediate hosts are not completely overlapping and do not cover the full geographic range of cockles, and thus the parasite communities in the cockles change, too, over large spatial scales. In contrast, on small spatial scales, the local faunas of potential intermediate host species can be expected to be similar, and propagules dispersed by the definitive hosts are more likely to find suitable first intermediate hosts than on larger spatial scales. The observed relatively low beta-diversity values (high initial similarities) might be explained by a combination of local definitive host dispersal and similarity of the fauna in nearby localities. On larger spatial scales, changes in environmental conditions and the intermediate and final host fauna are again responsible for the observed distance decay patterns. With increasing distance, the actual local composition of intermediate hosts should become more important as it will be less likely that the parasites' propagules find a suitable first intermediate host, even if they have successfully been dispersed by their definitive hosts. Hence, when changes in the intermediate host community occur with increasing distance, we can expect the composition of the parasite community to change too. That this is actually the case in the bivalve *C. edule* is illustrated by the fact that some parasite species occur only at the northern or southern end of the cockle's North-Atlantic distribution, depending on the distribution of their first intermediate hosts (de Montaudouin et al. 2000; Thieltges and Reise 2006; Gam et al. 2008).

Although we observed various significant distance decay relationships, there was a high scatter in the data, especially on small-to-medium spatial scales (1 to several 100 km). This is reflected in the relatively low amount of variance explained by the various regression models, though these were far from trivial (most r^2 values between 0.100 and 0.400). Hence, distance matters for the composition of parasite communities in intermediate invertebrate hosts but it is not the only determinant. Small-to-medium scale heterogeneity in parasite community composition as well as in infection levels in intermediate hosts is well known for intermediate mollusc hosts in intertidal systems (Sousa 1990; Lafferty et al. 1994; Kuris and Lafferty 1994). For parasite communities in first intermediate hosts, the distribution and abundance of definitive hosts is a strong driver of this heterogeneity (Hechinger and Lafferty 2005;

Fredensborg et al. 2006; Byers et al. 2008). Similarly, the distribution and abundance of first intermediate hosts have strong effects on the composition and infection levels of parasite communities in second intermediate hosts (Thieltges and Reise 2007). Other explanations for the high scatter in the data may of course involve our methodology. The sample effort differed among the localities and showed positive relationships with local species richness in the total datasets. However, taking this into account in the reduced datasets gave similar results and there is no reason to believe that there is a consistent trend in the remaining data obscuring true patterns or generating spurious ones. Taxonomic synonymies and uncertainties may also affect the analysis. We have to trust the identification skills of the various original researchers as it is impossible for a single person to investigate all sites and species. However, for all three species, various taxonomic references (e.g. Lauckner 1971; James 1968; Deblock 1980; Lauckner 1980, 1983) have long been available to all researchers, and we also carefully checked them for known synonyms. Therefore, we are confident that the scatter is not an artefact but real, resulting from the biological phenomena discussed above.

Compared with data available for parasites in vertebrate definitive hosts, the scatter observed in the data is unusually high, as indicated by low r^2-values (Fig. 2). As discussed above, small to medium scale heterogeneity in parasite community composition is driven by heterogeneities in definitive host distribution and abundance (Hechinger and Lafferty 2005; Fredensborg et al. 2006; Thieltges and Reise 2007; Byers et al. 2008). In contrast, definitive hosts are vagile and may sample parasites from several regional localities, thus dampening the effects of stochastic events, something that should result in less scatter in the data. However, r^2-values for some distance decay relationships are lower than the mean values presented in Fig. 2 for some single host species (indicated by the large SDs), and the presence and magnitude of scatter might be more related to peculiarities of host-parasite systems and not associated with certain host groups. More studies on the decay of similarity in parasite communities are needed to investigate whether the differences between intermediate and definitive hosts hold true. The lower halving distances seen in the three intermediate hosts compared to vertebrate host groups probably result from the fact that the large-scale dispersal of parasite propagules by definitive hosts is efficient and that intermediate host faunas are similar on small-to-medium spatial scales. In contrast, definitive hosts can be expected to acquire parasites over a large geographical area and thus sample from distant parasite communities, a process that can result in longer halving distances. Again, high standard deviations cast doubt on whether this difference between intermediate and definitive hosts is real; more studies are needed to confirm this pattern. As discussed above, initial similarity of parasite communities in the three intermediate hosts was high. The values were similar to parasite communities in fishes but higher than in mammals. Potentially, the small-scale dispersal of parasites in mammals is limited due to host ranges and territories. Whatever the patterns and potential mechanism, as apparent from the legend in Fig. 2, numbers of available studies are low for all host groups, thus making generalisations of the observed patterns difficult. In addition to looking at large geographical distances (>1,000 km), some attempts have also been made to investigate distance decay relationships over small spatial scales (< 100 km) (Brouat and Duplantier 2007). More studies over several spatial scales are needed to understand the full biogeographical structuring of parasite communities.

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