RESEARCH PAPER

Host diversity and latitude drive trematode diversity patterns in the European freshwater fauna

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ABSTRACT

Aim We investigated the relationship between host and parasite diversity as well as latitudinal gradients in parasite diversity on a continental scale in European freshwater trematodes.

Location European freshwaters.

Methods We extracted distributional data for 564 freshwater trematodes across 25 biogeographical regions in Europe from the *Limnofauna Europaea* and used multiple regression analyses to test for correlations between the diversity of definitive (vertebrates) or first intermediate (gastropods) hosts and that of trematodes, and for latitudinal gradients in trematode diversity. In particular, we investigated patterns in beta diversity among latitudinal bands and between trematode species that parasitize host groups with low (autogenic) and high (allogenic) dispersal capacity. We also tested for a latitudinal gradient in the proportional representation of these two trematode groups within regional faunas.

Results Latitude or first intermediate host richness had no effect on trematode richness, but definitive host richness was a strong predictor of trematode richness, among both allogenic and autogenic parasites. We found that beta diversity of trematode faunas within latitudinal bands decreased to the north, with similar values for allogenic and autogenic trematodes. Finally, we observed an increasing proportion of autogenic species toward the north of Europe.

Main conclusions The richness of definitive hosts appears to be the driver of trematode diversity at a continental scale. The latitudinal gradient in beta diversity reflects patterns observed in free-living species and probably results from recolonization in the aftermath of the ice ages. The similar beta-diversity patterns of allogenic and autogenic trematodes and the increasing proportion of autogenic trematodes with increasing latitude are surprising. We suggest that the geographical scale of our analysis or confounding factors such as differences in habitat utilization and specialization may partly explain these patterns.

Keywords
Allogenic parasites, autogenic parasites, beta diversity, Europe, freshwater, latitudinal gradients, macroecology, parasitism, trematodes.

INTRODUCTION

Many correlates of species diversity underpin the spatial distribution of free-living species on earth, such as latitude, habitat heterogeneity and productivity (Ricklefs & Schluter, 1993; Rosenzweig, 1995; MacDonald, 2003). However, for parasites it is the spatial distribution of their host species that largely constrains their geographical distribution because parasites are intimately associated with their hosts. As parasites are usually host specific (Poulin, 2007; Poulin & Keeney, 2008), parasite diversity should be positively correlated with host diversity, i.e. we expect more parasite species in localities with more host species.

Although perfectly logical, there is surprisingly little empirical evidence for this relationship, particularly on large spatial scales. Hechinger & Lafferty (2005) found a positive relationship between bird species richness and trematode richness in an estuarine snail among six sites in a coastal wetland. Similarly, Watters (1992) reported a positive correlation between fish species richness and unionid bivalve richness, across several drainage systems in the USA. Apart from these studies on local or regional spatial scales, we are only aware of one investigation of the relationship between host and parasite diversity on a larger continental scale. Krasnov *et al.* (2004, 2007) described a positive relationship between local mammal diversity and the species richness of fleas that are ectoparasitic on those mammals, across distinct geographical areas from several continents. However, we do not know if the observed patterns hold true for other parasite–host systems on these very large spatial scales, e.g. entire biogeographical regions or continents.

Although current large-scale patterns of host and parasite diversity are linked with various environmental and geographical correlates, they have a historical component, too (Mac-Donald, 2003; Cox & Moore, 2005; Lomolino *et al.*, 2006). For example, seabirds and pinnipeds in the Holarctic have frequently been isolated into refugial zones during glaciation events in the late Pliocene and Pleistocene epochs, which also isolated their cestode faunas and led to an extensive radiation of cestode species (Hoberg, 1992). Such recolonization of habitats after glaciation events should be biased towards species with high dispersal capacity. For example, Hof *et al.* (2006, 2008) showed that in the European free-living freshwater fauna, the proportion of lentic (standing water) to lotic (running water) species increases with latitude. This is probably due to a faster recolonization of northern Europe by lentic species, with supposedly higher dispersal capacity (Ribera & Vogler, 2000; Ribera *et al.*, 2003; Marten *et al.*, 2006), than lotic species after the Last Glacial Maximum. Moreover, this study showed that beta diversity, which is expected to decrease with increasing dispersal capacities of organisms (Soininen *et al.*, 2007a,b), is lower in lentic species than in lotic species and generally decreases with latitude (Hof *et al.*, 2008). This probably reflects general postglacial recolonization events of the European fauna (Griffiths, 2006; for terrestrial examples see also Hewitt, 1999, 2000): recolonization was slow and dominated by highly dispersive species which distributed over large areas, resulting in the low beta diversity among northern regions (Hof *et al.*, 2008). As parasites depend on their hosts, we would expect the dispersal capacity of their hosts to be crucial in recolonizing habitats. However, little is known regarding the effects of host dispersal capacity on parasite dispersal on large spatial scales. Furthermore, to the best of our knowledge, no studies have so far investigated patterns in the beta diversity of entire parasite faunas.

Here, we investigate diversity patterns in the European freshwater trematode parasite fauna, expanding on studies of free-living species (e.g. Hof *et al.*, 2008; Dehling *et al.*, 2010; and references therein). Digenean trematodes typically have complex life cycles, including three hosts. The adult stages utilize vertebrates as definitive hosts, usually with high host specificity (i.e. they infect a small subset of potential hosts). Eggs shed with the host's faeces infect the first intermediate host, which always is a gastropod (and very rarely a bivalve). Host specificity is very high in the first intermediate host, and another free-living stage, the cercaria, develops within this first host and then infects a second intermediate host, which may be an invertebrate, amphibian or fish, depending on the trematode species (here host specificity is usually very low). When the second intermediate host is consumed by a definitive host, the cycle is completed. Given the host specificity in first and definitive hosts, we would expect these two host types to drive parasite diversity. However, the dispersal capacity of parasites will be different at different stages in the life cycle, with definitive hosts contributing most to the dispersal of parasites as the dispersal capacity of first and second intermediate hosts is usually limited. Trematode parasite species can be broadly grouped into two categories, depending on where they complete their complex life cycles and on their dispersal strategy (Esch *et al.*, 1988): autogenic parasites (parasites utilizing fish as definitive hosts and completing their entire life cycle in freshwater habitats) and allogenic parasites (parasites utilizing birds, mammals or reptiles as definitive hosts and completing their life cycles mainly outside freshwater bodies). In general, the dispersal capacity of allogenic parasites is considered to be higher than that of autogenic parasites (Esch *et al.*, 1988), an assumption supported by data on population genetics (Criscione & Blouin, 2004).

Using a large data base (Illies, 1978), we tackle several questions regarding diversity patterns in the European freshwater trematode parasite fauna: (1) does trematode species richness decrease with latitude; (2) does the diversity of either or both first intermediate or definitive hosts drive parasite diversity; (3) does the beta diversity of the regional trematode parasite faunas decline with latitude; and (4) does the proportion of parasite species with high dispersal capacity (allogenic parasite species) increase towards high latitudes?

MATERIALS AND METHODS

The data set used for the analyses was extracted from the *Limnofauna Europaea* (Illies, 1978) which has been used as a data source for biogeographical analyses in the past (Griffiths, 2006; Hof *et al.*, 2008; Dehling *et al.*, 2010). Compiled by leading experts in their fields, this book includes tables of the distribution of about 14,500 freshwater species within 25 biogeographical regions as defined by Illies (1978) (see also Hof *et al.*, 2008, for a map). We determined the northern and southern boundary of each biogeographical region using Google Earth (http://earth.google.com/) and calculated the latitudinal centre from these data (Table 1). For each biogeographical region, we recorded the presence or absence of all parasite and vertebrate (definitive) and gastropod (first intermediate) host species. As no quantitative measures of sampling effort are provided in the data set, we were unable to control for it. However, the parasite and vertebrate fauna of Europe are among the best known in the world, and the species lists were prepared by experts in their

Table 1 The 25 biogeographical regions as used in Illies (1978), their latitudinal centre (° N) and definitive (vertebrate) and first intermediate (gastropod) host species richness as well as trematode parasite species richness.

Region code	Region	Latitudinal centre (° N)	Definitive host richness	First intermediate host richness	Parasite richness
IBE	Ibero-Macaronesian region	38.23	164	67	41
PYR	Pyrenees	42.53	100	48	43
ITA	Italy, Corsica and Malta	40.98	175	98	75
ALP	Alps	45.81	174	93	138
DIN	Dinaric western Balkans	44.37	178	210	78
HEL	Hellenic western Balkans	39.13	191	157	25
EAB	Eastern Balkans	41.73	199	70	120
WEH	Western Highlands	47.36	139	60	27
CEH	Central Highlands	49.74	162	52	193
CAR	The Carpathians	47.15	162	50	180
HUN	Hungarian Lowlands	46.48	167	51	203
PON	Pontic Province	45.83	228	52	287
WEP	Western Plains	46.90	189	63	123
CEP	Central Plains	55.17	189	43	226
BAP	Baltic Province	56.93	162	42	227
EAP	Eastern Plains	53.48	183	52	322
IRE	Ireland and Northern Ireland	53.39	113	31	16
GBR	Great Britain	56.16	153	37	110
ICE	Iceland	64.91	55	7	9
BOR	Borealic Uplands	64.13	120	28	12
TUN	Tundra	71.53	100	12	25
NSW	Northern Sweden	64.60	118	32	20
TAI	Taiga	63.03	149	35	123
CAU	The Caucasus	42.12	194	51	201
CAS	Caspic Depression	48.08	214	35	205

respective fields, allowing for as much accuracy as possible. In addition, the proportion of singletons (species present in a single region only) per bioregion was not related to trematode richness (see Appendix S1 in Supporting Information). One would expect bioregions with many trematode species to have a higher proportion of singletons than bioregions with low trematode richness if sampling effort was proportionally higher in these regions (the greater the sampling effort, the higher the chances of recording rare species).

We also extracted information on the type of definitive host used by each trematode species, as given in the database: (1) fish, (2) amphibians, (3) reptiles, (4) mammals, (5) birds and mammals (in the case of trematode species that can use either), and (6) birds. Species with unknown definitive hosts were excluded from the analyses. For some further analyses we grouped parasite species into two categories, depending on where they complete their life cycles and on their dispersal strategy (Esch *et al.*, 1988; see Introduction): autogenic parasites (parasites utilizing fish as definitive hosts) and allogenic parasites (parasites utilizing birds, mammals or reptiles). Parasite species that use amphibians as definitive hosts were not included in either category as their status is probably intermediate due to the strong dependence of amphibians on water bodies. For vertebrates and gastropods, we extracted the full list of species from the respective tables in the *Limnofauna*. These lists include those species in the respective groups that have an affinity to freshwater either by living in water or at the water's edge and by exclu-

sively or regularly feeding in water bodies. These species should constitute the majority of hosts for freshwater trematodes as gastropods serve as first intermediate hosts and because definitive hosts generally acquire parasites via predation on intermediate hosts. However, irregular visitors to water bodies, which are not included in the *Limnofauna*, might also acquire some of the parasites, and thus the total host richness used here for each bioregion is probably a conservative estimate.

In a first step, we investigated whether trematode or host richness (number of species per bioregion) correlated with latitude, using separate linear regressions. We then investigated whether trematode richness correlated with host richness, using multiple regressions with latitude, intermediate host richness and definitive host richness as predictors. As statistical tests with geographical data may be biased because of spatial autocorrelation, we tested all our models for spatial autocorrelation of residuals. These tests did not find evidence for spatial autocorrelation. First, the richness of trematodes showed little spatial autocorrelation. Second, we did not find strong indications of spatial autocorrelation of residuals in any of our models (see Appendix S2). Therefore we used ordinary linear models for our statistical tests throughout the paper.

Patterns of beta diversity in the trematode fauna were studied by grouping the 25 bioregions into four latitudinal bands, as determined by their latitudinal centres: < 45° N, 45–50° N, 50–60° N, > 60° N (following Hof *et al.*, 2008). We then used two different methods to calculate beta diversity for each of the
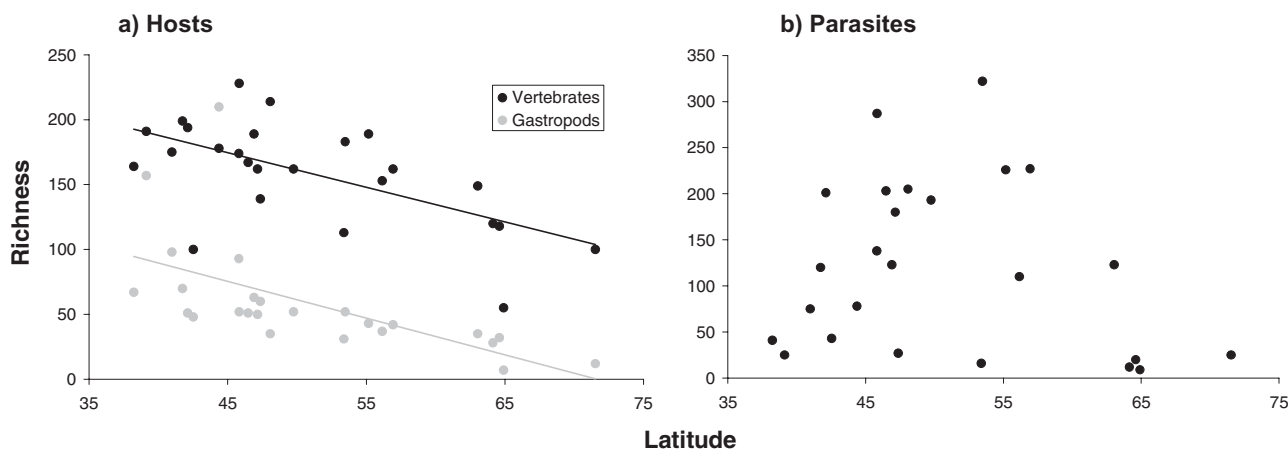
Figure 1 Relationship between latitude and species richness for (a) host species (number of vertebrate (definitive hosts) or gastropod (first intermediate hosts) species per region) and (b) parasite species (number of trematode species per region) across 25 biogeographical regions. The lines indicate the best fit of significant linear regressions (vertebrates: $y = -2.6689x + 294.67$; gastropods: $y = -2.831x + 202.83$).

two life-cycle/dispersal categories (allogenic and autogenic) and for each of the four bands. First, we used additive partitioning of species diversity (Crist *et al.*, 2003; Hof *et al.*, 2008). Underlying the additive partitioning of species diversity is the idea that alpha and beta diversity sum up to the total diversity (gamma) and that the total species richness can thus be partitioned into alpha and beta diversity components. The resulting values indicate the degree of beta diversity: the value is 1 if all species occur only in a single region within a band, and it is 0 if all species occur in all regions within a band. We used the area of regions, as determined by GIS, as weights for the analyses (see Hof *et al.*, 2008). Second, we used a multi-site similarity index, which accounts for differences in the number of regions within latitudinal bands (Baselga *et al.*, 2007). Values were calculated as $1 - M_{Sim}$ (where M_{Sim} is the multi-site similarity index) to compare them with the values obtained from additive partitioning.

To investigate latitudinal trends in the proportion of the two life-cycle/dispersal categories across the bioregions, we plotted the proportion of allogenic and autogenic trematodes against latitude, for both species and genera. Genera plotting was used as a measure to test whether potential radiation within genera, once they had colonized an area, could have caused any observed pattern. Although phylogeny may confound comparisons like this, we could not conduct comparative analyses because species within trematode families usually share the same type of definitive host (e.g. birds). Hence, there are only a few or no cases where two or more types of definitive host occur within the same lineage that we could use for a comparative analysis. Due to the bounded nature of proportional data we performed logistic regressions, using the proportions of allogenic and autogenic species per bioregion. Significance was tested by calculating a likelihood-ratio chi-square.

RESULTS

The analyses included a total of 564 trematode species (447 allogenic, 67 autogenic, 50 in amphibians), 466 vertebrate

Table 2 Standardized coefficients (*b*), standard error (SE) and associated *t*-tests of multiple correlations of parasite species richness within 25 European biogeographical regions versus latitude and first intermediate host (gastropod) and definitive host (vertebrate) species richness, for allogenic (parasites utilizing birds, mammals or reptiles as definitive hosts and completing their life cycles mainly outside freshwater bodies) and autogenic (parasites utilizing fish as definitive hosts and completing their entire life cycle in freshwater habitats) parasites.

	b	SE	*t*	*P*
Allogenic parasites				
Latitude	0.207	0.204	1.014	0.322
Richness first intermediate hosts	−0.314	0.171	−1.839	0.080
Richness definitive hosts	0.909	0.175	5.191	< 0.001
Autogenic parasites				
Latitude	0.294	0.219	1.339	0.195
Richness first intermediate hosts	−0.082	0.213	−0.384	0.705
Richness definitive hosts	0.713	0.190	3.755	0.001

species (definitive hosts) and 553 gastropod species (first intermediate hosts), though the numbers per region varied widely (see Table 1). While trematode richness was not correlated with latitude ($P = 0.38$), host richness significantly decreased with increasing latitude (definitive hosts: $r^2 = 0.37$, $P = 0.001$; gastropod hosts: $r^2 = 0.36$, $P = 0.002$; Fig. 1). The pattern was similar when allogenic (definitive hosts: $r^2 = 0.39$, $P = 0.001$; trematodes: $P = 0.41$) and autogenic (definitive hosts: $r^2 = 0.19$, $P = 0.03$; trematodes: $P = 0.88$) host and parasites species were analysed separately. In subsequent analyses we investigated the relationship between latitude and definitive and first intermediate host richness, and allogenic and autogenic parasite species richness, using multiple regressions. In both cases, definitive host richness significantly affected parasite richness, while latitude and first intermediate host richness did not show any effect (Table 2, Fig. 2). However, in allogenic parasites the effect of the richness
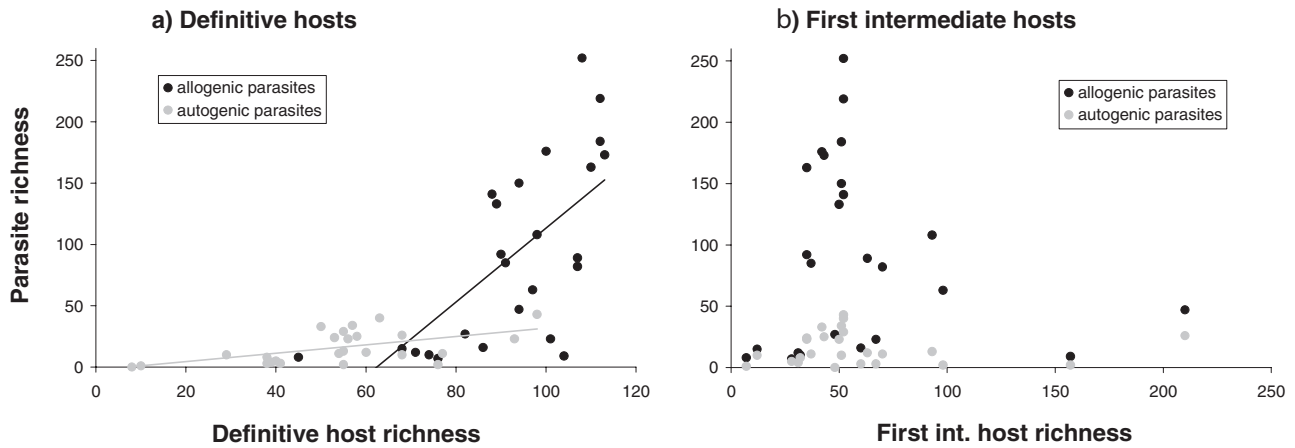
a) Definitive hosts

b) First intermediate hosts

Figure 2 Relationship between parasite species richness and (a) definitive host species richness (vertebrates) and (b) first intermediate host species richness (gastropods), in both autogenic (parasites utilizing fish as definitive hosts and completing their entire life cycle in freshwater habitats) and allogenic (parasites utilizing birds, mammals or reptiles as definitive hosts and completing their life cycles mainly outside freshwater bodies) trematode species. The lines indicate the best fit of significant linear regressions (allogenic parasites: $y = 3.0159x - 188.15$; autogenic parasites: $y = 0.3419x - 2.51$).

of first intermediate hosts was marginally significant ($P = 0.08$; Table 2).

Beta diversity of trematodes within the four latitudinal bands generally decreased with increasing latitude, for both autogenic and for allogenic species. The values for autogenic and allogenic trematode species were extremely similar within all four latitudinal bands when using additive partitioning (Fig. 3). However, when using the multiple-site similarity index, beta diversity values for allogenic parasite species were always marginally higher than those for autogenic species, particularly in the northernmost latitudinal band (Fig. 3).

The proportion of allogenic species within a biogeographical region decreased with increasing latitude, while the proportion of autogenic species increased (logistic regression; chi-square = 17.6, $P < 0.001$; Fig. 4a). This trend held true when the analysis was repeated at the genus level (logistic regression; chi-square = 7.2, $P = 0.007$; Fig. 4b), which indicates that any species radiations within genera are not responsible for the observed patterns.

DISCUSSION

The data extracted from the *Limnofauna Europaea* offer a rare chance to investigate diversity patterns of entire parasite faunas on large spatial scales. An increase in species richness with decreasing latitude seems to be an almost universal pattern in free-living species (Rohde, 1992, 2005; Willig *et al.*, 2003; Hillebrand, 2004), and was also observed in definitive and first intermediate hosts in our analyses. In contrast, there was no such gradient in freshwater trematodes (Fig. 1 rather suggests a hump-shaped relationship), which is contrary to previous studies on marine and freshwater fish parasites (Rohde, 1982; Rohde & Heap, 1998; Choudhury & Dick, 2000; Poulin, 2001). The relationship between latitude and host richness explained only 19–39% of the variance in the data, and it may be that the

residual host richness is a stronger driver of parasite site richness than latitude (see below). This residual host richness might also underlie the hump-shaped pattern.

Independent of latitude, trematode diversity was closely linked to definitive but not first intermediate host richness. The strong effect of definitive hosts is not surprising, given that hosts are, by definition, crucial resources for parasites, and thus bioregions inhabited by more potential definitive host species allow more trematode species to occur. The steeper relationship in allogenic compared with autogenic parasites probably results from the fact that fish (constituting all autogenic hosts) harbour, on average, much fewer parasite species than other vertebrate hosts, in particular birds (Poulin & Morand, 2004; with the latter constituting almost 70% of the allogenic host group). The observed lack of correlation between trematode and first intermediate host richness can probably be attributed to the fact that only a few gastropod species out of a large pool of potential hosts seem to serve as first intermediate hosts (Pechenik *et al.*, 2001), while probably all bird species are infected with several parasite species (Atkinson *et al.*, 2008). It would require detailed information on the host specificity of each parasite species to further investigate these matters, but unfortunately these data are not available. It would also be interesting to test whether the pattern holds true if other environmental gradients like temperature or productivity are included (but it might be questionable whether values estimated over large bioregions with very diverse habitats and altitudes provide a meaningful variable). The general pattern of host diversity driving parasite diversity reflects the results of previous studies (Watters, 1992; Krasnov *et al.*, 2004, 2007; Hechinger & Lafferty, 2005). However, more studies on different spatial scales and on different host and parasite groups, ideally integrating detailed information on host specificity and other environmental factors, are needed to validate the universality of the pattern.
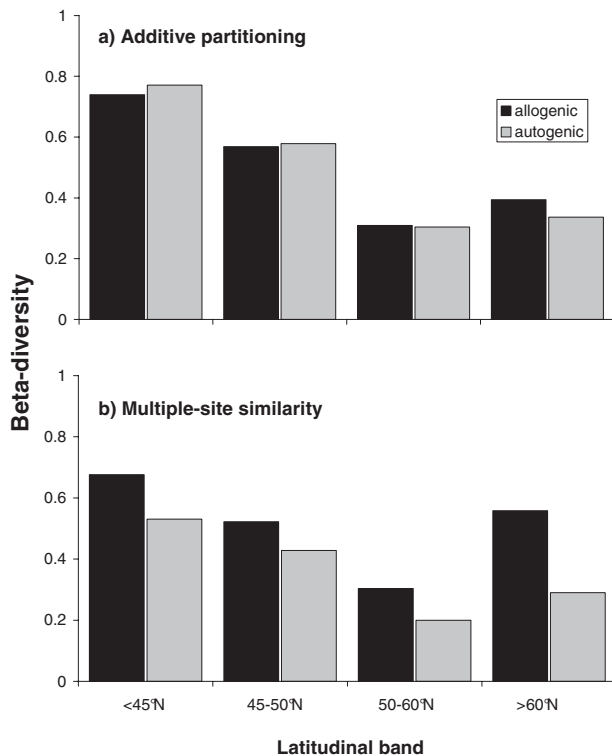
Figure 3 Beta diversity of allogenic and autogenic parasites within four latitudinal bands (< 45° N, 45–50° N, 50–60° N, > 60° N) in European freshwaters. Values of beta diversity were calculated by two different methods. (1) For the upper graph, we used additive partitioning of species diversity (Crist *et al.*, 2003; Hof *et al.*, 2008). A value of 0 indicates that all parasite species occur in all regions within a band, while a value of 1 indicates that all species only occur in a single region within a latitudinal band. (2) For the lower graph, we used the multi-site similarity index, M_{Sim} (Baselga *et al.*, 2007). Values are calculated as $1 - M_{Sim}$ to compare them with the values obtained from additive partitioning.

Another distinct pattern observed in the data set was the decrease in beta diversity of the trematode fauna towards the north. This pattern strongly resembles the one observed in a previous study based on data from the *Limnofauna Europaea*, which focused on various groups of free-living species (Hof *et al.*, 2008). This suggests that this pattern is not unique to parasites but is shared by the European freshwater fauna in general. It probably results from the geographical distribution of landmasses in Europe as well as from recent biogeographical events in the aftermath of the ice ages. The fragmentation of landmasses in the south of Europe by the Mediterranean Sea has led to distinct regional faunas and local endemism, resulting in high beta diversity. In contrast, in the north the more continuous distribution of landmasses and recolonization processes from southern and eastern refugia after the ice ages probably resulted in a more homogeneous distribution of species (Hewitt, 1999, 2000; Griffiths, 2006). During these processes, parasites probably followed their hosts, resulting in similar patterns of beta diversity.
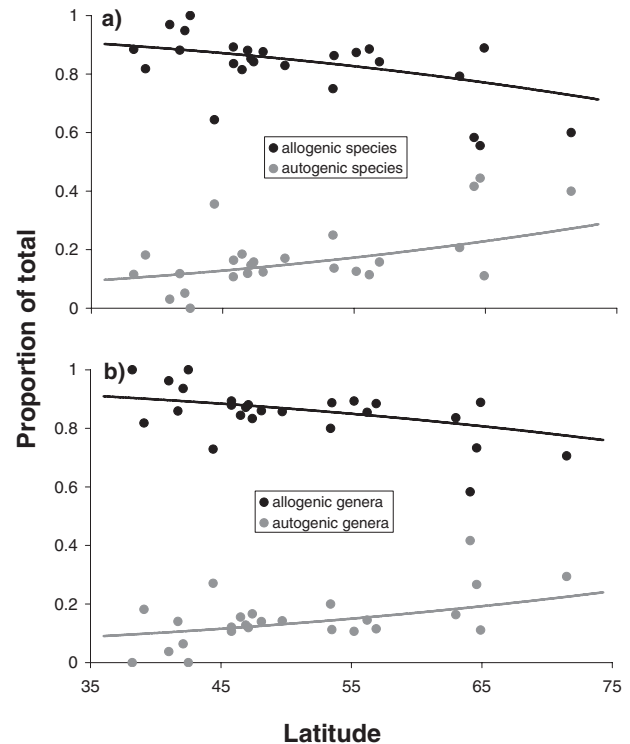

Figure 4 Proportion (%) of allogenic and autogenic trematode species (a) and trematode genera (b) in relation to latitude (latitudinal centre of each biogeographical region). The lines indicate the best fit of logistic regressions.

During the recolonization events after the ice ages, one would expect species with high dispersal capacity to dominate over species with low dispersal capacity. While this seems to be true for free-living freshwater species (e.g. Hof *et al.*, 2006, 2008), trematodes showed the opposite trend, as the proportion of allogenic species (with highly vagile bird definitive hosts) decreased toward the north. This contradicts studies on fish parasite communities which suggest a crucial role for the dispersal capacity of definitive hosts in determining parasite dispersal (Esch *et al.*, 1988), and also phylogeographical evidence that indicates pronounced genetic structure among autogenic parasite populations but not among allogenic parasite populations in freshwaters (Criscione & Blouin, 2004). Why do our results differ from previous studies? It may have to do with the spatial scale of the respective studies. The structuring mechanisms acting on local spatial scales may be overcome by other forces on regional to continental scales (those used in our analysis). It may also be that there are confounding factors at work. For example, habitat utilization certainly differs among hosts. Although fish parasites are all autogenic, their hosts may preferentially utilize lentic or lotic habitats. Considering the varying latitudinal patterns in beta diversity of free-living species utilizing lentic and lotic habitats (Hof *et al.*, 2008), differences in habitat use could confound the pattern expected from the dispersal capacity of the hosts. Unfortunately, the data on habitat use of vertebrates given in the *Limnofauna Europaea* are too

coarse to test this hypothesis, as almost all vertebrate species appear to be generalists. Another confounding mechanism may be that the proportion of specialists (i.e. highly host-specific parasites) is higher in allogenic than in autogenic parasites. Such specialist parasites would be confined to the dispersal ranges of their few definitive hosts, and this may offset any advantage associated with the high dispersal capacity of the host group in general. However, consistent comparative data are not available to test these ideas.

In summary, our analyses suggest that definitive host diversity is a strong driver of trematode diversity in European freshwater systems. They also suggest that the exchange of trematode species among biogeographical regions was shaped by the geographical distribution of landmasses in Europe and historical recolonization events in the aftermath of the last ice age, resulting in a decrease in beta diversity with increasing latitude. Overall, this rare study of diversity patterns across entire parasite faunas improves our understanding of the processes shaping the geography of parasitism.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

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

Appendix S1 Trematode singletons per bioregion.
Appendix S2 Spatial autocorrelation profile of trematode richness.

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Editor: Sean Connolly