



## Range size patterns in European freshwater trematodes

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While patterns in geographic range sizes in free-living species have received much attention, little is known on the corresponding patterns in parasites. For the first time, we report on patterns in geographic range sizes and dimensions of endoparasites, using published species lists of freshwater trematodes in 25 biogeographical regions of Europe. In general, the range sizes of trematodes showed a typical hollow curve frequency distribution, with most species having small ranges. Contrary to expectations, there were no differences in range sizes among trematodes using hosts with high (birds) and limited dispersal capacity (e.g. fish). This suggests that the well known importance of host dispersal capacity for parasite dispersal at small spatial scales is overridden by other factors on larger scales. Regression analyses and Rohde plots showed that the relationship between the latitudinal centre and trematode range size was hump-shaped in all host groups except for reptiles, for which it was linear. Most of the variation fell within the expectations given by null models, suggesting that the patterns mainly result from the geographic properties of the European continent and the biogeographical regions. Finally, trematode ranges tended to stretch more in east-west than in north-south directions, indicating dispersal barrier effects for parasite faunas, probably resulting from the geographical idiosyncrasies of the European continent.

There is substantial variation in the size of the geographic ranges of species, spanning up to 12 orders of magnitude (Brown et al. 1996, Gaston 2003). Within any taxonomic group, this variation in the size of geographic ranges can be visualised with a frequency distribution of the species-specific range sizes, with most taxa showing a unimodal distribution of range sizes with a strong right skew, called the “hollow curve” (Willis 1922, MacDonald 2003). While the hollow curve distribution of geographic range sizes is a universal pattern, the mean size of geographic ranges differs among major phylogenetic lineages. Within the vertebrates, fish have the smallest range sizes, followed by, in increasing order, amphibians, reptiles, mammals and birds (Anderson 1977, 1984a, b, Anderson and Marcus 1992, Brooks et al. 2001). There are also geographic patterns in range size variation. For example, the range sizes of species tend to decrease from high to low latitudes (Rapoport’s rule; Stevens 1989, Rhode 1996). Geographic ranges may not only vary in size but also in shape, i.e. ranges do not necessarily have the same extent in all dimensions, and major biogeographical barriers or large-scale climatic zones can restrict the contours of species’ ranges (Brown and Maurer 1989). Finally, geographic patterns in range sizes may simply result from the geometric properties of the

study area. The so-called mid-domain effect predicts that species richness is highest in the centre of a study area simply because if ranges were distributed at random, the overlap of ranges would be highest in the centre (Colwell and Lees 2000).

Whereas patterns in geographic range sizes of free-living species have received much interest, little is known about the range sizes of parasites. Some studies have found a positive correlation between the range sizes of hosts and the numbers of parasites infecting them (Dritschilo et al. 1975, Gregory 1990, Brändle and Brandl 2001, Krasnov et al. 2004), but, to our knowledge, only two studies to date have investigated patterns in geographic range sizes of parasites themselves. The geographic ranges of ectoparasitic fleas (Siphonaptera) from small mammals show the same hollow curve distribution as seen in free-living species (Krasnov et al. 2005, 2008). The geographic range size of flea species was negatively correlated with their degree of host specificity, i.e. host specific flea species had smaller ranges than generalists that infect a wide range of host species (Krasnov et al. 2005). However, host specificity may not be the only determinant of geographic range sizes of parasites. As parasites depend on their hosts for dispersal, the dispersal capacity of their hosts should be a strong determinant of the

range size of parasites. In parasites with complex life cycles, e.g. digenean trematodes, definitive hosts should be most relevant in this respect because their intermediate hosts (first intermediate hosts: molluscs; second intermediate hosts: invertebrates, amphibians or fish) have limited dispersal capacities (planktonic larval stages are not infected). Definitive hosts of trematodes are always vertebrates, which carry the adult parasites and then disperse the latter's eggs in their faeces. In general, the dispersal capacity of parasites in bird definitive hosts is considered to be higher than that of parasites of fish and other less vagile definitive hosts (Esch et al. 1988), an assumption supported by population genetics (Criscione and Blouin 2004). Hence, within a regional assemblage of trematodes, we expect parasites using freshwater fish as definitive hosts to have, on average, the smallest range sizes, and parasites utilising birds to have the largest range sizes.

In this study, we investigate for the first time patterns in the size and shape of ranges of the entire European freshwater trematode fauna. Besides determining the frequency distributions of range sizes, we also investigate whether the range sizes are determined by the dispersal capacity of the definitive hosts. Based on the distributions of trematodes in 25 biogeographical regions of Europe, we ask the following questions: 1) do the range sizes of trematodes exhibit the typical hollow curve distribution known from free-living species? 2) Do the mean range sizes of trematodes differ depending on the type of definitive host they use? 3) Do the range sizes of trematodes increase with latitude (Rapoport's rule)? 4) Are the shapes of the ranges of trematodes in Europe constrained by major topographic features such as mountain ranges?

## Materials and methods

We used presence/absence data on digenean trematodes in each of 25 bioregions published in the Limnofauna Europaea (Illies 1978). All trematode species included in these tables spend at least the first part of their life cycle in freshwater habitats, i.e. the first intermediate host is always a freshwater mollusc. For each trematode species, Illies (1978) also lists the type of definitive hosts: 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. Our data set included 564 freshwater trematode species (see Fig. 1 for numbers per definitive host group). For each biogeographical region, as defined in the book, we determined the northern, southern, eastern and western boundaries using <http://earth.google.com/> and calculated the area using GIS (Table 1; see Hof et al. 2008 for a map). For each trematode species, we calculated four parameters: 1) number of biogeographical regions occupied; 2) total area occupied; 3) latitudinal centre of a species' range and 4) shape of the range (maximum north-south and east-west extent in km). For the latter we used the northern, southern, eastern and western boundaries of a parasite's total range and great circle calculations. The east-west extent was calculated at the mean latitude of a species' range.

When plotting the frequency distribution of range sizes, we used the total number of regions occupied by a species as this measure is least biased in respect to area overestimation (see Discussion). We tested for differences in the mean range size of trematode species utilising different definitive host groups with one-way ANOVAs (type 3 SS), using log-transformed data of 1) number regions occupied by each species and the 2) total area occupied. For post-hoc comparisons we used Tukey's HSD tests (for unequal  $n$ ).

To investigate the relationships between the latitudinal centres of each species' range and the total area occupied by the species (log-transformed), we used regression analyses and Rohde plots (named after Rohde et al. 1993, although this type of plot was originally introduced by Graves 1985). For the regression analyses, we included simple and squared latitudinal centre as independent variables since the plots of  $\log(\text{area})$  vs latitudinal centre suggested a hump-shaped relationship in most cases. For the Rohde plots, we divided the geographic domain into latitudinal bands of  $3^\circ$  width. Within each of these bands, we calculated the mean  $\log(\text{area})$  of all species whose latitudinal centre fell within the band (for details, see Rohde et al. 1993).

Because the shape of Europe constrains the possible locations and shapes of geographic ranges, a hump-shaped relationship between latitude and range size is expected even in the absence of ecological processes (Colwell and Hurtt 1994). We compared the observed patterns to null models. For each host group, we used a modification of the "spreading dye" algorithm (Jetz and Rahbek 2001) to generate a set of random cohesive ranges. This algorithm keeps the range size distribution constant (in this case the number of occupied regions), while randomizing the geographic location of each range. We then used the generated ranges to calculate slopes and intercepts for regressions of  $\log(\text{area})$  vs latitudinal centre (including both the linear and quadratic term of the latter). This procedure was repeated 1000 times, and the coefficients were averaged to generate composite models for the null expectation of area-latitude plots. We also added 95% confidence intervals of the null model to all Rohde plots, based on the 2.5 and 97.5 quantile values from the 1000 sets of simulated ranges.

We plotted the east-west extent of ranges versus their north-south extent (km). If all species exhibited equal dimensions in each direction, we would expect these values to cluster around a diagonal line with slope = 1 (Brown and Maurer 1989). To account for the shape of the European continent and the location of biogeographical regions, we also added a line indicating the orientations of the null model ranges generated above.

As the analyses of Rapoport's rule and of geographical orientation of ranges along the north-south and east-west axes combine data from various trematode lineages, we tested for potential phylogenetic effects. Unfortunately, no complete phylogeny of trematodes is currently available. Instead we used the latest taxonomy used in a current comprehensive revision of the Trematoda (Gibson et al. 2002, 2008, Jones et al. 2005) to test for effects of superfamily, family or genus on area, latitudinal centre, east-west and north-south extent of the parasite ranges used in the analyses. We tested each taxonomic level separately, using one-way ANOVAs, as nested designs combining all

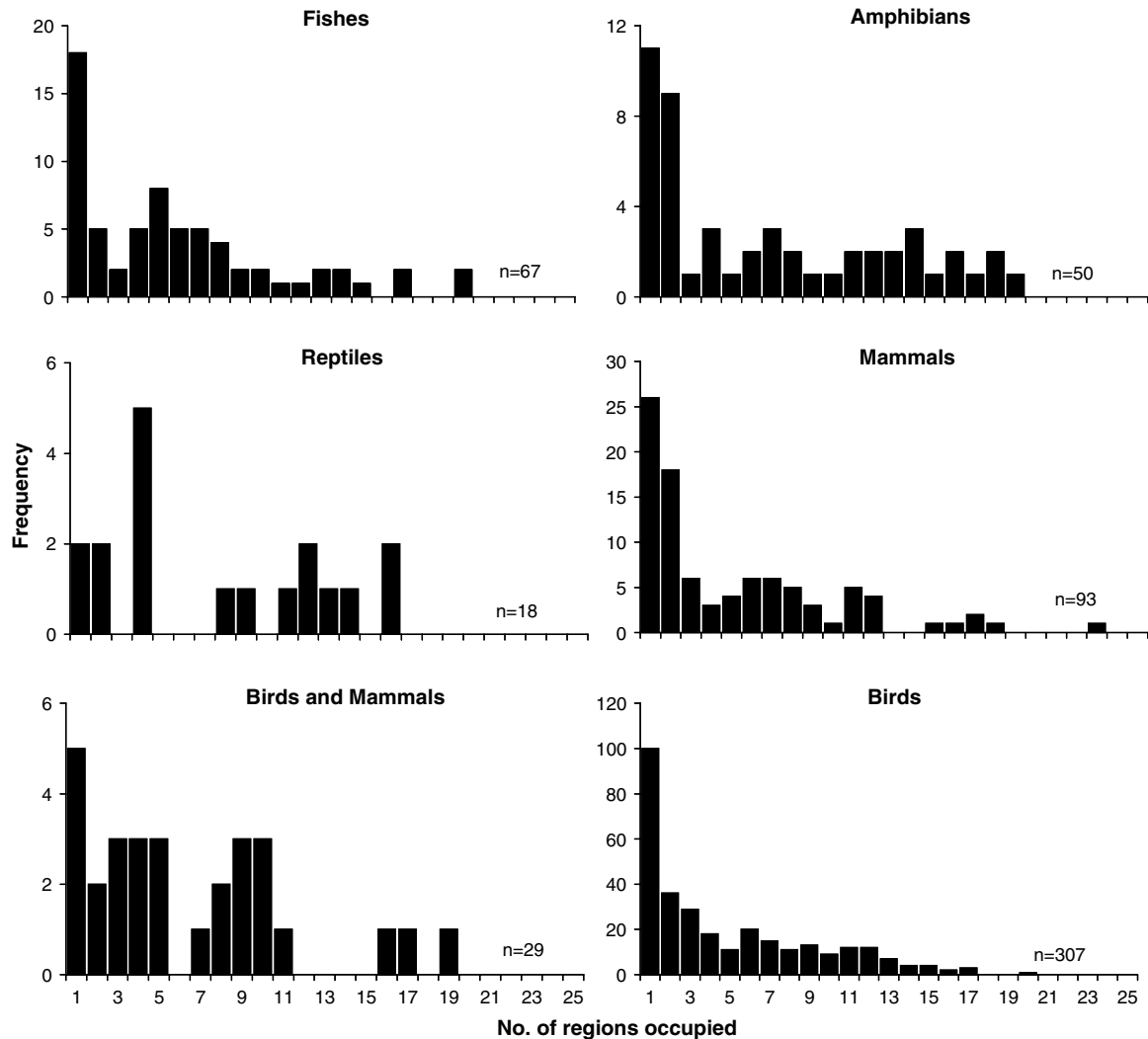


Figure 1. Frequency distribution of range sizes (no. of regions occupied) of European freshwater trematodes utilising different types of definitive hosts. Numbers of trematode species in each host group are shown.

taxonomic levels in a single analysis were not possible due to many missing cells resulting in incomplete designs.

## Results

The species-range size distributions based on the no. of regions occupied showed that most trematode species occupy only a few bioregions (Fig. 1). Overall, this pattern was less clear in trematodes of definitive host groups for which only limited numbers of parasite species were available (reptiles, birds and mammals, Fig. 1). The range size distributions were similar when based on the total area occupied (Supplementary material Fig. S1) and both measures of geographic range size were highly correlated ( $r^2=0.84$ ,  $p<0.001$ ). The fact that most trematodes occupy only a few bioregions was reflected in the mean geographic range sizes or dimensions of trematode species among the different types of definitive hosts. Although trematode species utilising mammals or birds as definitive hosts had the smallest geographic ranges (Fig. 2), statistical

differences were either absent or not particularly marked (ANOVAs: area:  $F_{5,558}=1.66$ ,  $p=0.14$ ; no. of regions:  $F_{5,558}=2.59$ ,  $p=0.02$ ). Subsequent post-hoc comparisons for the significant ANOVA showed no significant differences among any of the different pairwise comparisons (in all comparisons  $p\geq 0.53$ ).

The relationship between latitudinal centre and area was hump-shaped in all host groups except for reptiles, for which it was linear (Fig. 3, 4; Supplementary material Table S1). The linearity of the relationship for reptiles may arise because only a part of the latitudinal gradient is realised: no trematode species are associated with reptiles above  $55^\circ\text{N}$  (Fig. 3 upper left). Both the regression analyses and the Rohde plots showed that most of the variation fell within the expectations due to geometric constraints. However, when comparing observed and simulated values, most observed relationships were steeper than expected from the null model simulations. This is also indicated by the differences in the slopes and intercepts between observed and simulated relationships (Supplementary material Table S1).

Table 1. Names and areas of the 25 different biogeographical regions defined by Illies (1978).

No.	Region	Area (km <sup>2</sup> )
1	Ibero-Macaronesian region	623512
2	Pyrenees	47177
3	Italy, Corsica and Malta	259796
4	Alps	230555
5	Dinaric western Balkan	169565
6	Hellenic western Balkan	148864
7	Eastern Balkan	166136
8	Western highlands	163624
9	Central highlands	265879
10	The Carpathians	187997
11	Hungarian lowlands	171969
12	Pontic province	245422
13	Western plains	403351
14	Central plains	551551
15	Baltic province	205697
16	Eastern plains	2320724
17	Ireland and Northern Ireland	91572
18	Great Britain	246186
19	Iceland	110541
20	Borealic uplands	321639
21	Tundra	415856
22	Northern Sweden	258423
23	Taiga	1647955
24	The Caucasus	379397
25	Caspic depression	780402

Trematodes in all six types of definitive hosts showed similar trends in the shape of their ranges. All ranges tended to stretch more in east-west than in north-south direction: the vast majority of points fell below the diagonal line that indicates equal north-south and east-west extents (Fig. 5). Furthermore, most of the points also fell below the lines that mark the patterns expected from the null models – most species have range shapes that stretch even more towards east-west vs north-south than expected given the geographic extent and shape of the European continent and its biogeographical regions (Fig. 5, Supplementary material Fig. S2).

Tests for potential phylogenetic effects in the latter two analyses (results in Fig. 3–5) showed significant overall ANOVAs in only a few cases. However, post-hoc tests did not reveal significant differences among particular taxonomic

groups, which suggests that potential differences among groups were too small to be detectable. While this does not completely rule out any differences among groups, it indicates that potential differences are very small and that phylogenetic effects should not confound the analyses. The only significant tests occurred in trematodes of the host group with the lowest number of parasite species (reptiles), where post-hoc tests identified a particular genus (*Patagium*) and family (Auridistomidae, *Patagium* being the only genus in this family) as being significantly different from others. However, excluding this genus did not affect the results of the analyses and thus we decided to present the full data.

## Discussion

The geographic range size distributions of parasites in all definitive host groups showed the typical right-skewed pattern observed in free-living species: most parasite species occupy small to medium ranges, and only a few species occupy very large ones. The total area occupied by each parasite species is likely to be an overestimate as species do not necessarily occur everywhere within a region. This may particularly affect the range size measures of parasites occurring in large regions. However, the number of regions occupied is not biased in this respect as it simply notes presence/absence of a species no matter what the size of the region is, and thus the general trend of a right-skewed pattern seems to be robust. In the only other study on patterns in geographic range sizes of parasites on large spatial scales, fleas (Siphonaptera) ectoparasitic on small mammals showed a similar patterns (Krasnov et al. 2005). The fleas' geographic range sizes were negatively correlated with their degree of host specificity: flea species with a wide range of host species had larger ranges than highly specific species (Krasnov et al. 2005). Host specificity may also affect the pattern observed in European trematode species, but, unfortunately, we cannot test this formally as no information on host specificity is currently available. However, analyses of regional parasite faunas of vertebrates suggest that the majority of helminth species are relatively host specific (Gregory et al. 1991, Poulin 1992, 2007). Being restricted to

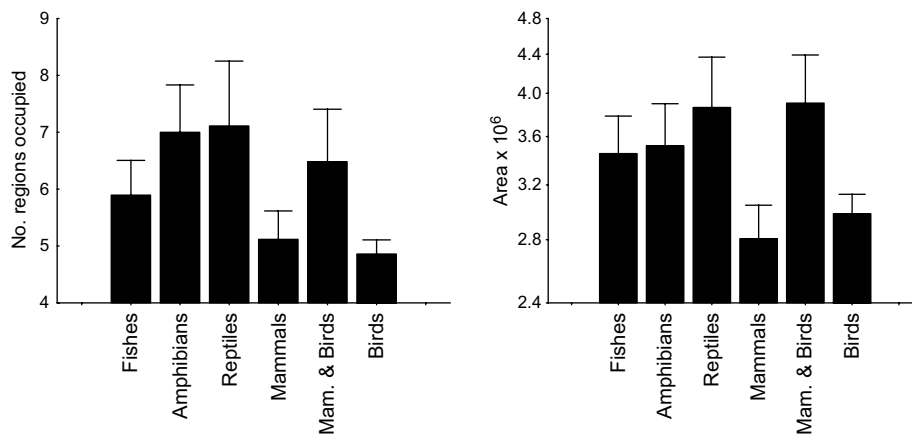


Figure 2. Mean (+SE) geographic range sizes (number of regions occupied and area occupied) of European freshwater trematodes utilising different types of definitive hosts. Note the truncated y-axes. For the number of trematode species per type of definitive host see Fig. 1.

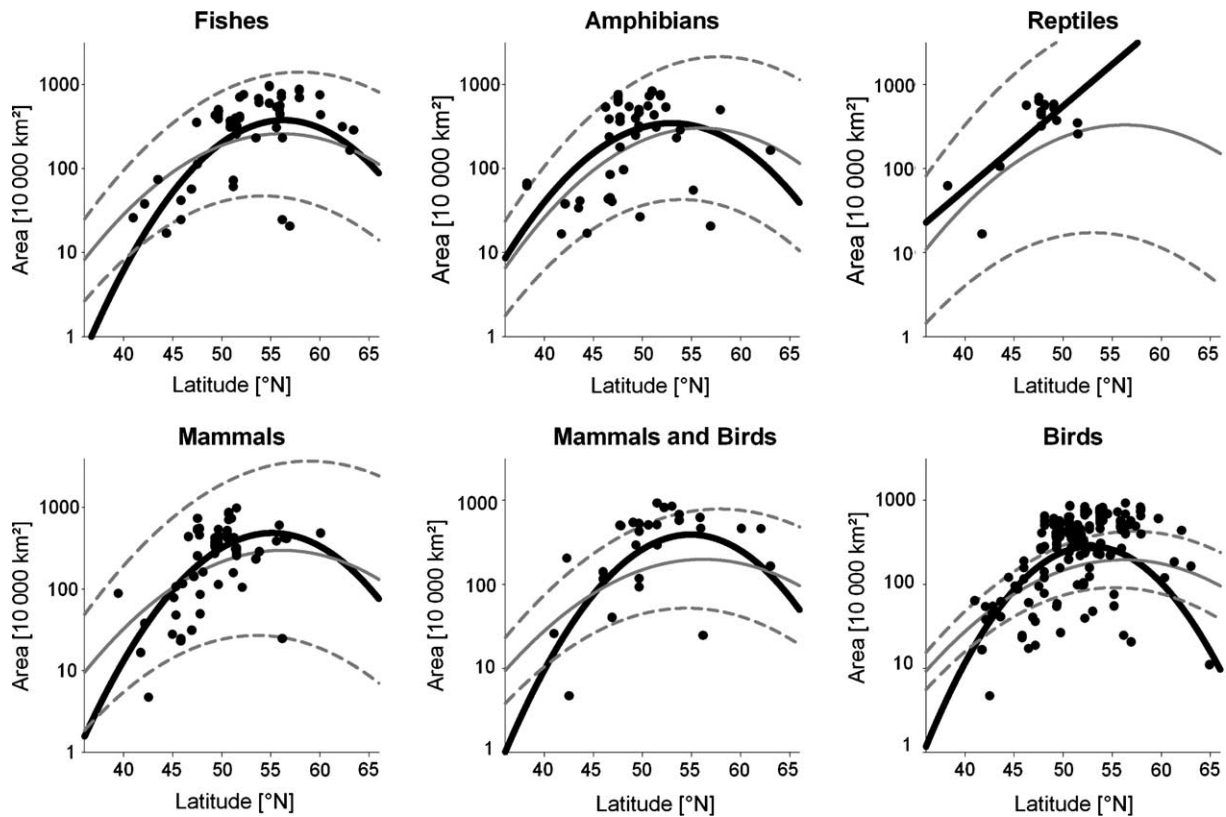


Figure 3. Relationships between the latitudinal centre ( $^{\circ}\text{N}$ ) and range size (area  $\times 10\,000\text{ km}^2$ ) for the six groups of definitive hosts showing values for each trematode species (black points). Black lines indicate the observed relationships fitted from these points (area vs linear and squared term of latitudinal centre; reptiles: area vs. linear term of latitudinal centre only). Grey lines indicate the relationships rendered by the null model simulations, based on slopes and intercepts from 1000 simulations (straight line) and the respective 95% confidence intervals (for values of observed and simulated slopes and intercepts, see Supplementary material Table S1).

a single or a few host species means that the spatial distribution of a parasite species should strongly depend on the spatial distribution of its particular host species. Because the majority of vertebrates have relatively small ranges (Gaston 2003), the geographic ranges of their parasites should also be relatively small, which could lead to the frequency distributions observed in our study.

Contrary to expectation, parasites utilising host groups that are presumed to have high dispersal capacities, e.g. birds, did not have, on average, larger range sizes than those utilising host groups with lower dispersal capacity. That we could not detect any statistical differences among host groups may be a consequence of the relatively coarse grain size of the data, not providing sufficient power to reject the null hypothesis. However, considering the well known importance of definitive host type for parasite dispersal, we would have expected strong differences among groups, well exceeding the resolution of our data. For example, local scale studies of parasite communities in fish hosts indicate the dispersal capacity of the definitive host to be crucially important for parasite dispersal (Esch et al. 1988). In addition, phylogeographic data suggest that parasites using birds should have much greater geographic ranges, especially when considering the large migrations of water birds in Europe. Typically, freshwater parasites using fish as definitive hosts show pronounced genetic differences among different populations on a scale of a few hundred

kilometres, whereas those using birds do not, suggesting that the latter have much greater dispersal potential (Criscione and Blouin 2004). However, even if range sizes among groups turned out to be significantly different with more finely resolved data, these differences would still be different from what was anticipated because parasites of the highly vagile birds showed much smaller range sizes than those of the more localised fish, amphibians and reptiles. This suggests that host dispersal is of less or different relevance on larger spatial scales than expected from small scale studies. Perhaps the structuring forces acting on local scales are superimposed by other forces on regional to continental scales.

Several non-exclusive mechanisms might be at work on these larger spatial scales. For instance, hosts with large range sizes may often also carry a high number of parasite species, as the number of parasite species exploiting a particular host species increases with that host's geographic range size (Dritschilo et al. 1975, Gregory 1990, Shenbrot et al. 2007). Hence, a few highly mobile and widely distributed host species (e.g. migratory fish) may distribute many parasite species over large spatial areas, although the host group in general has a relatively small dispersal capacity. The actual infection levels of parasite species in host populations (i.e. prevalence, or percentage of hosts infected) may also be of importance; mean helminth prevalences in fish hosts seem to be higher than in bird

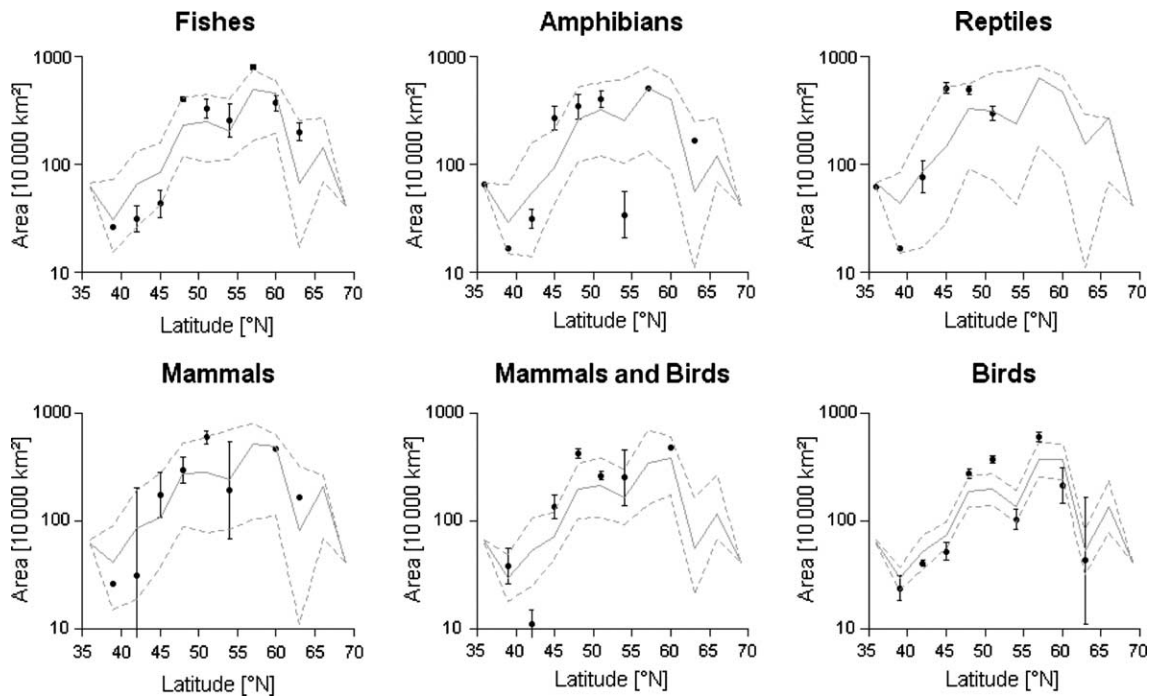


Figure 4. Relationships between the latitudinal centre (°N) and range size (area  $\times$  10 000 km<sup>2</sup>) for the six groups of definitive hosts using Rohde plots. Black points are the mean values of log<sub>10</sub>(area), calculated for the species whose latitudinal centres fall within latitudinal bands of 3° width. Error bars indicate the standard errors of the mean. Grey lines indicate the values rendered by the null model simulations (straight line) and their respective 95% confidence intervals (dashed lines). For the number of trematode species per type of definitive host see Fig. 1. For details on null model setup, see text.

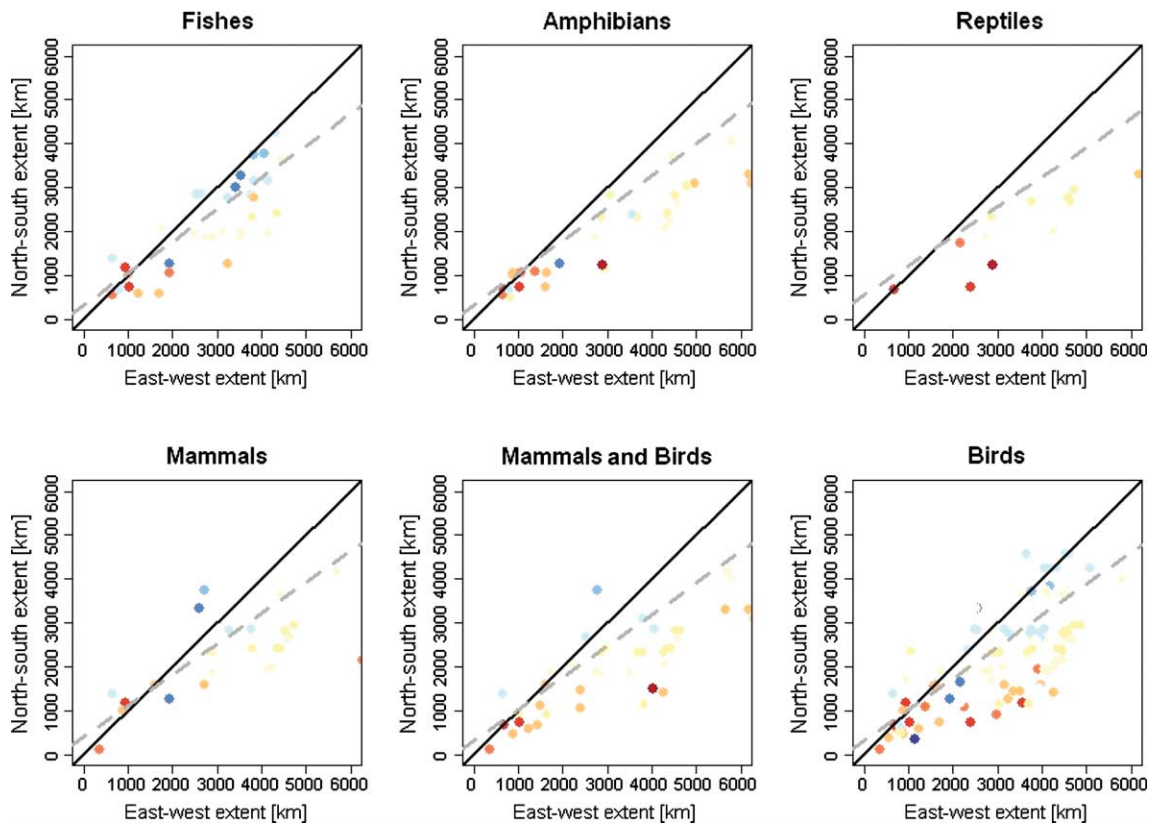


Figure 5. Relationships between the maximum north-south and east-west extent (km) of the geographic ranges of European freshwater trematodes utilising different types of definitive hosts. Black straight lines (slope = 1) indicate ranges of equal extent in north-south and east-west direction. Grey dashed lines indicate the regression line rendered from the null model simulations. Colours indicate the latitudinal centres of the species' ranges, ranging from southern (dark red) via central (light red and blue) to northern (dark blue) latitudes.

hosts based on comprehensive compilations of published data (Poulin 1998a, b). The higher dispersal capacity of birds might thus be offset by their relatively low levels of infection, which decreases a parasite species' likelihood of being dispersed. Another mechanism blurring the expected pattern could be that birds have a higher proportion of highly host specific parasites compared to fish. These specialist parasites would be confined to the dispersal ranges of their single definitive hosts, most of which would have limited dispersal capacity themselves as suggested by the predominance of small ranges, and this may again offset any advantage associated with the high dispersal capacity of the host group in general. However, consistent comparative data from the different host groups are not available to test these ideas.

Regression analyses and Rohde plots showed that the relationship between latitudinal centre and range size was hump-shaped in all host groups (except for reptiles). The fact that most variation in the graphs follows the expectations from the null models suggests that geometric constraints imposed by the study area may be a parsimonious explanation for the observed pattern, i.e. the geographic shape and extent of the European continent and its biogeographical regions, with land masses in the south being interrupted by the Mediterranean Sea.

The pattern of range sizes stretching more in east-west than in north-south directions remained after controlling for geometric constraints of the study area with null models, and is similar to the one observed in European birds (Brown and Maurer 1989). If the orientation of ranges was only determined by the shape of Europe, we would expect the data to follow the null model expectations. However, the orientation is longer in the east-west direction than expected. This is probably an effect of the orientation of major climatic zones and major topographical features like mountain chains (e.g. the Alps) in Europe, which mostly run in an east-west direction (Brown and Maurer 1989). They act as a dispersal barrier for both free-living and parasite species. In our data the effect was most pronounced in trematodes with centres of distribution in southern to central Europe. This probably points to the particular importance of the southern mountain chains, i.e. the Alps and Pyrenees, as biogeographical barriers for hosts and parasites. In contrast, the pattern was more or less absent in trematode species with northern distributional centres. This may be interpreted as a legacy of the ice ages with highly dispersive northern species re-colonising large parts of northern Europe after a large-scale eradication of northern faunas (Hof et al. 2006, 2008, Dehling et al. in press).

Although our data base is the best available for trematodes for a large spatial scale, the resolution is rather coarse. Nonetheless, we think that our analyses are robust based on the following patterns: 1) the frequency distribution of range sizes was based on the number of regions occupied which is not biased in respect to overestimating range sizes (not all habitats of a region need to be occupied); 2) from previous small and regional scale studies, we would have expected strong differences in mean range sizes among different definitive host types by far exceeding the resolution of our data; 3) both latitudinal gradients in range sizes and 4) a more east-west than north-south orientation of ranges could be detected, indicating that data resolution was

sufficient to detect a pattern. Hence, we think our analyses are a valuable first step into the exploration of range size patterns of endoparasites. Should more detailed distributional data become available in the future, more elaborate and detailed analyses will be feasible, expanding on our basic findings.

In conclusion, the geographic range size patterns of European freshwater trematodes show a typical hollow curve distribution, with most species having small ranges. Dispersal capacity of host groups did not affect the range sizes of parasites, suggesting that the dispersal capacity of definitive hosts is of less importance than on small spatial scales. Range sizes of trematodes showed a hump-shaped distribution along a latitudinal gradient similar to null model expectations, suggesting that the observed pattern is caused by the extent and shape of the European continent. Finally, trematode ranges tended to stretch more in east-west than in north-south directions, and this orientation was stronger than expected from geometric constraints models, pointing to geographic features like the Alps as major barriers for the dispersal of parasites. Our analysis was confined to trematodes and it will be interesting to investigate other parasite groups (e.g. cestodes, nematodes, ectoparasites etc.) in future studies to see if the patterns hold true more generally.

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