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Host assemblage and environment shape β-diversity of freshwater parasites across diverse taxa at a continental scale

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Abstract

Aim: Positive relationships in compositional similarity between consumer and resource assemblages are widely known in free-living taxa, but less is known about parasites and their hosts. We investigated whether congruent patterns of assemblage similarity across diverse taxa of hosts and parasites exist at a continental scale and quantified the relative importance of host assemblages and environmental variables in shaping these relationships.

Location: European freshwaters.

Major taxa studied: The hosts were fishes, birds and mammals. The parasites were monogeneans, trematodes and copepods.

Methods: We extracted distribution data from the *Limnofauna Europaea* for three aquatic parasite taxa and for three vertebrate taxa functioning as their definitive hosts across 25 biogeographical regions in Europe. First, we investigated β-diversity congruence patterns between parasite and host assemblages, corrected for the distance between regions using partial Mantel tests. Second, we assessed the relative importance of host assemblages and environmental variables in shaping parasite β-diversity patterns using generalized dissimilarity models (GDMs).

Results: Spatial community dissimilarities of regional parasite assemblages were positively correlated with those of their respective host assemblages in all five parasite–host groups studied. The GDMs highlighted the equal importance of both host assemblages and environmental variables in shaping parasite assemblages. However, the direct effect of host assemblages was relatively small compared with the effect of environmental factors mediated by host assemblages. Climatic parameters (precipitation and temperature) contributed most to the variance explained by environmental variables.

Main conclusions: Our analyses indicate that spatially congruent patterns of assemblage similarity exist between parasites and their hosts at a continental scale. They also suggest that this congruence is driven not only by host assemblages but also by environmental (climatic) variables, either directly or indirectly via their effects on host assemblages. Thus, environmental variables are important for mapping, forecasting and management of parasites at a geographical scale.

KEYWORDS
β-diversity, aquatic parasites, aquatic vertebrates, biodiversity congruence patterns, dispersion, distribution, generalized dissimilarity modelling, macroparasites, Mantel test

1 | INTRODUCTION

Spatial congruence of species diversity across trophic levels (i.e., a positive correlation between resource and consumer diversity; Gaston, 1996) is a commonly observed diversity pattern. Positive correlations of α-diversity (species richness) between resources and consumers are well known for plant–herbivore, plant–pollinator and prey–predator systems (Biesmeijer et al., 2006; Castagneyrol & Jactel, 2012; Siemann, Tilman, Haarstad, & Ritchie, 1998). Such patterns are likely to be driven by bottom-up effects of the availability and distribution of resources: a more extensive range of resource types provided by plant and prey species can support a larger number of consumer species (herbivores, pollinators and predators) in a geographical region (Currie & Paquin, 1987; MacArthur & Levins, 1967). As a consequence, congruent spatial patterns in species richness can emerge (Su, Debinski, Jakubauskas, & Kindscher, 2004; Wolters, Bengtsson, & Zaitsev, 2006). Likewise, congruence is also observed when comparing the spatial patterns in compositional similarity of resource and consumer assemblages, which is indispensable in the context of evaluating ecological hypotheses, because species composition may reveal more about the mechanistic basis of community assembly than species richness (Lyashevska & Farnsworth, 2012; Su et al., 2004).

Congruent patterns of biodiversity have been studied mainly in free-living species, but they are also known from parasitic organisms (Clark et al., 2018; Maestri, Shenbrot, & Krasnov, 2017; Vinarski, Korallo, Krasnov, Shenbrot, & Poulin, 2007). Indeed, the parasite richness (α-diversity) of a region has been shown to covary with host richness across various parasitic taxa (see meta-analysis by Kamiya, O'Dwyer, Nakagawa, & Poulin, 2014 and references therein), both at small spatial scales within local ecosystems (Hechinger & Lafferty, 2005) and among larger biogeographical regions (Krasnov, Shenbrot, Khokhlova, & Degen, 2004; Thieltges, Hof, Dehling, et al., 2011). However, much less is known about the congruence of spatial patterns in compositional similarity (β-diversity) of host and parasite assemblages and about the general importance of the composition of host assemblages in shaping parasite assemblages. Parasite assemblages might be more reliant on resource diversity (Clark et al., 2018) than free-living species, because parasite species depend on their respective host species to be present in order to occur in an assemblage. Additionally, environmental variables and (host) phylogeny are assumed to play a role in shaping local assemblages of free-living (Barnagaud et al., 2014) and parasitic species (Clark et al., 2018; Maestri et al., 2017). For example, temperature can limit habitat suitability for parasites but not for their hosts (Galaktionov & Bustnes, 1999). Consequently, parasite assemblages can largely be shaped by host assemblages and the environment in three ways. First, the environment directly shapes the host assemblage, and the host assemblage shapes the parasite assemblage. In this scenario, the environmental variables do not shape parasite assemblages directly (indirect/host-mediated; Figure 1a). Second, the environmental variables and host assemblage might both shape parasite assemblages directly (direct; Figure 1b), but there are no observable indirect effects of the environment through the host assemblages. Third, the environment could affect parasite assemblages both directly and

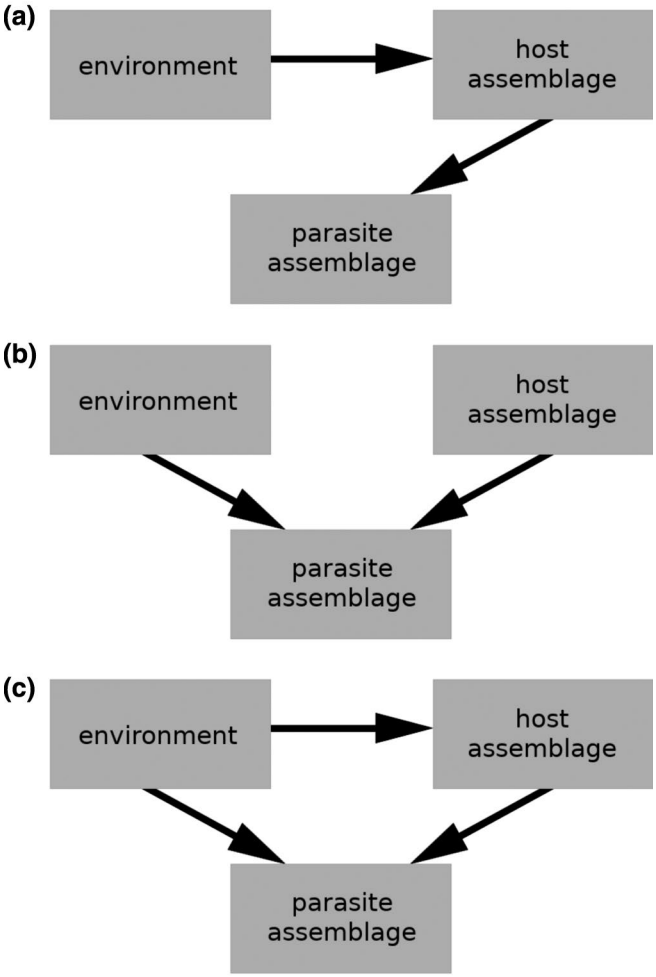

FIGURE 1 Conceptual relationships between environmental variables, host assemblages and parasite assemblages. Parasite assemblages can be affected by the environment in three ways. (a) The environment directly shapes host assemblages, and host assemblages shape the parasite assemblage, but the environmental variables do not. (b) Both environmental variables and host assemblages directly shape parasite assemblages, but there is no effect of the environment through host assemblages. (c) Finally, the environment can affect parasite assemblages both directly and indirectly through host assemblages. Note that the arrows only indicate effects on parasite assemblages; for example, in (b) it is still expected that environmental variables influence host assemblages, but this does not impact parasite assemblages

indirectly through host assemblages (mixed; Figure 1c). Which of these mechanisms are at play, and the relative strength of these interactions, is mostly unknown for parasite assemblages. It is, thus, fundamental to disentangle the relative contributions of environmental variables and host assemblages in shaping patterns of β-diversity in parasites.

Here, we analyse the congruence of host and parasite assemblage similarity in the European freshwater fauna, based on data presented by Illies (1978). This monograph documents the distribution of freshwater animal species among 25 biogeographical regions in Europe with a general focus on free-living organisms but also includes data on several parasitic taxa. Biogeographical regions are based on geographical and climatic properties of the areas (for details, see Hof, Brändle, & Brandl, 2008; Illies, 1978). This unique dataset has been used for various analyses of diversity patterns in free-living species (e.g., Dehling, Hof, Brändle, & Brandl, 2010; Griffiths, 2006; Hof et al., 2008) and in parasites (Thieltges, Hof, Borregaard, et al., 2011; Thieltges, Hof, Dehling, et al., 2011). One of the latter studies identified a positive relationship between vertebrate (definitive) host and trematode parasite richness (Thieltges, Hof, Dehling, et al., 2011). Our study expands on these analyses, which focused on patterns of α-diversity, by looking into the spatial congruence of compositional similarity of host and parasite assemblages (β-diversity). Additionally, we include environmental variables to compare the relative contribution of host assemblages and environmental factors. To maximize the generality of our inferences, we investigated three different parasite groups from three different host groups, resulting in five different host–parasite combinations: monogeneans, trematodes and copepods infecting fish, and trematodes infecting birds or mammals. Monogeneans are ectoparasites that infect the gills and fins of fish and have a direct life cycle (i.e., no intermediate hosts; Goater, Goater, & Esch, 2013). In contrast, endoparasitic trematodes usually have complex life cycles (i.e., including intermediate hosts; Goater et al., 2013). They typically use a vertebrate as their definitive host, in which sexual reproduction occurs, molluscs as first intermediate hosts and invertebrates or vertebrates (depending on the trematode species) as second intermediate hosts. Host specificity is generally very low in second intermediate hosts, and only a few widely distributed mollusc species serve as first intermediate hosts. Hence, the diversity of the definitive (and not the intermediate) hosts is considered to be the primary driver of regional trematode richness (Thieltges, Hof, Dehling, et al., 2011). Parasitic copepods are ectoparasites that infest the gills, fins and skin of fishes, and most have direct life cycles (Goater et al., 2013).

We estimated β-diversity using the Jaccard index and further partitioned β-diversity into species replacement/turnover and nestedness components (Baselga, 2012). This allowed us to investigate whether congruence patterns in compositional similarity exist between the regional host (fishes, birds and mammals) and parasite assemblages (monogeneans, trematodes and copepods) in the European freshwater fauna. Subsequently, we used generalized dissimilarity models (GDMs; Ferrier, Manion, Elith, & Richardson, 2007) to distinguish between environmental and pure host assemblage effects on parasite assemblages and to investigate which of the proposed models (indirect/host-mediated, direct or mixed; Figure 1) fitted our data best.

2 | METHODS

2.1 | Data sources

The *Limnofauna Europaea* monograph has been used as a data source for several previous macroecological or biogeographical studies, both on free-living and on parasitic groups (Dehling et al., 2010; Griffiths, 2006; Hof et al., 2008; Thieltges, Hof, Borregaard, et al., 2011; Thieltges, Hof, Dehling, et al., 2011). Occurrence data for both host and parasite species in each of 25 biogeographical regions (bioregions; based on geographical and climatic features) in Europe were extracted from this source (for a map and details on classifications, see Dehling et al., 2010; Hof et al., 2008; Illies, 1978). All host and parasite species listed in the book spend a considerable part of their life cycle in freshwater (for detailed inclusion criteria, see Illies, 1978). Given that the *Limnofauna Europaea* does not provide data on abundance or sampling effort, it was not possible to correct for biases in these factors. The composition of the European fauna is well known, and experts in their respective fields have compiled the data. It is, thus, assumed that the accuracy of the data is of a sufficient level for the results to be robust (see references above for further discussions on overall data quality). Unfortunately, modern parasite databases, such as the one from the Natural History Museum London, do not have the same spatial resolution as the *Limnofauna Europaea*, and therefore do not allow for similar analyses or investigation of the completeness of the survey of the *Limnofauna Europaea* data. We, therefore, acknowledge that the accuracy of the *Limnofauna Europaea* data remains to be assessed when more detailed databases become available in the future (including up-to-date distributional data with a high spatial resolution for parasite species).

To increase the robustness of our analyses, unique records (i.e., species that occur in only one bioregion, *c*. 25% of species) were excluded from the analyses, because these rare species often lead to an underestimation of assemblage similarity (Chao, Chazdon, Colwell, & Shen, 2005). We considered the removal of unique records from the analyses to be an appropriate precautionary measure to avoid a bias in the similarity metric. However, for completeness, analyses were repeated with unique records included, with summary statistics given in the Supporting Information (Table S1.1). Removal of unique records resulted in some bioregions without parasite species. These bioregions were removed from these analyses, resulting in a different number of host species and bioregions between analyses (see Table 1).

Three parasite taxa covered in detail by the *Limnofauna Europaea* (monogeneans, trematodes and copepods) were analysed separately. Furthermore, analyses were run separately for groups of trematodes based on the definitive host taxon (i.e., mammal, bird or fish; following an approach similar to that of Krasnov, Mouillot, Shenbrot, Khokhlova, & Poulin, 2010). Both freshwater monogeneans (excluding four species of polystomatids that parasitize amphibians exclusively) and the copepods parasitizing vertebrates typically parasitize only fish (Rohde, 1984).

TABLE 1 Results of the partial Mantel tests for the Jaccard index (β_{jac}) and its nestedness (β_{jne}) and turnover (β_{jtu}) components

Host group	Parasite group	Number of hosts	Number of parasites	Number of regions*	β_{jac}			β_{jne}			β_{jtu}			Mean occupied bioregions per parasite (± SD)
					r_{Mantel}	*p*-value	Multiple site	r_{Mantel}	*p*-value	Multiple site	r_{Mantel}	*p*-value	Multiple site	
Fish	Copepods	144	29	21	**0.53**	**.000**	0.927	0.20	.060	0.082	**0.27**	**.003**	0.845	7.69 ± 4.18
Fish	Trematodes	150	49	24	**0.41**	**.000**	0.939	**0.24**	**.010**	0.153	0.12	.094	0.787	7.69 ± 4.70
Birds	Trematodes	124	207	25	**0.29**	**.021**	0.949	**0.25**	**.001**	0.141	**0.25**	**.003**	0.807	6.72 ± 4.15
Mammals	Trematodes	12	67	25	**0.20**	**.032**	0.946	−0.04	.624	0.129	−0.22	.988	0.817	6.72 ± 4.80
Fish	Monogeneans	144	129	18	**0.45**	**.000**	0.948	−0.01	.515	0.114	0.16	.072	0.834	3.68 ± 1.86

Note: Also given are the numbers of hosts, parasites and regions per host–parasite group pairing, the multiple site dissimilarities and the mean number of bioregions where each parasite species occurs for each parasite group. Mantel correlations (r_{Mantel}) and *p*-values of significant partial Mantel tests are in bold.

*The number of regions differs between subsets based on the exclusion of singletons.

Environmental data, calculated as averages for each bioregion, for the GDMs were derived from GIS and climate databases, as described by Dehling et al. (2010). Briefly, the Global Lakes and Wetland Database and the Digital Chart of the World Server were used to compile data on water bodies. The GTOPO30 data were used to calculate the elevation range within each region. Temperature and precipitation data were obtained from Worldclim (for more details and references, see Dehling et al., 2010). Distances between pairs of bioregions were calculated as the distance between the geographical centroids of the regions based on data from Hof et al. (2008). The great circle distance ("as the crow flies") between the centroids of all possible pairs of regions was then calculated. The area of each bioregion was calculated from the same data. Given that host and parasite occurrence data were available only at a bioregion level (see Discussion for more details), environmental variables were averaged over the region to match this scale. Although some of the information is lost during this process, this was considered to be appropriate because bioregions are based on geographical and climatic features.

2.2 | β-Diversity congruence patterns

To identify whether congruence patterns in compositional similarity exist between regional host and parasite assemblages, we investigated estimates of β-diversity. Given that β-diversity can be partitioned into turnover and nestedness components, β-diversity approaches also allow disentangling of the ecological processes that shape similarities in species assemblages (Baselga, 2010). The dissimilarity in assemblage composition between all pairs of bioregions was calculated using the Jaccard index (β_{jac}), which is the most commonly used index for analyses of parasite data (e.g., Poulin, Blanar, Thieltges, & Marcogliese, 2011; Thieltges et al., 2009). Additionally, we partitioned β_{jac} into the dissimilarity attributable to species replacement (β_{jtu}) and the dissimilarity attributable to nestedness (β_{jne}), following (Baselga, 2012). For each dissimilarity index (β_{jac}, β_{jtu} and β_{jne}), this resulted in two matrices for each analysis, one for the host group and one for the respective parasite group. These were then analysed using a third matrix with geographical distances between bioregions in a partial Mantel test with 100,000 permutations (Legendre & Fortin, 1989). Partial Mantel tests control for the influence of geographical distances between bioregions and were used because the similarity in species composition between two locations is known to decrease with increasing geographical distance between them (distance decay of similarity; Nekola & White, 1999; Soininen, McDonald, & Hillebrand, 2007). Multiple-site dissimilarities (Diserud & Ødegaard, 2007) were also calculated for the three Jaccard similarity indices (β_{JAC}, β_{JTU} and β_{JNE}; Baselga, 2012).

2.3 | Generalized dissimilarity models

Traditional β-diversity approaches generally allow for the investigation of congruence patterns only between two communities (e.g., hosts and parasites) and thus ignore environmental variables. During the last decades, methods have been developed that can also incorporate environmental information (GDMs; Ferrier, Drielsma, Manion, & Watson, 2002; Ferrier et al., 2007). These methods allow for the weighing of the relative importance of environmental factors and resource

assemblages in shaping consumer assemblages. Additionally, these allow for relationships between environmental variables and species assemblages to be nonlinear (Ferrier et al., 2007), which could be crucial for an accurate understanding of these relationships (Fitzpatrick et al., 2013). To investigate the relative importance of environmental variables and host assemblages in shaping parasite assemblages further, we implemented these GDMs. As with the partial Mantel tests, first the Jaccard dissimilarities for host and parasite matrices were calculated. Next, pairwise dissimilarities between each pair of sites for all predictor variables, including geographical distance, were calculated based on the mean values for each bioregion. These matrices were then used as explanatory matrices in the GDMs, following the instructions described by Manion et al. (2018). For each host–parasite group, a GDM with three I-splines was constructed. In short, for each environmental gradient, a flexible function is fitted that expresses the change in host or parasite (depending on the analysis) assemblage. The flexible function means that the nonlinear responses can be fitted, and the flexibility is constrained by the number of I-splines (i.e., the larger the number of I-splines, the more flexible the function). For further details, see Ferrier et al. (2007). Given that the nestedness and turnover analyses did not show clear patterns in the Mantel tests, GDMs were not calculated for these. Predictor variables used were as follows: (a) host dissimilarity; (b) geographical distance between the centroids of the bioregions; (c,d) river length and lake perimeter per unit area (total river length or lake perimeter divided by the size of the bioregion); (e) mean elevation; and (f,g) mean annual precipitation and temperature for each bioregion. Initially, predictor variables were input separately. However, to simplify the interpretation, all environmental predictors (b–g) were combined into one matrix to weigh their combined predictive power against host assemblages. Variables were inspected visually to ensure that no autocorrelation was present in the data. Only the latter of the two model types is shown here (models with separate environmental predictors are presented in the Supporting Information Figure S1.1 and S1.2). Using a leave-one-out method, the contribution of each explanatory variable was calculated, resulting in the proportion of variance explained by each of the predictor variables in addition to the variance explained equally well by multiple predictors (called "overlap" in explained variance). This "overlap" is likely to be attributable to indirect effects (Figure 1c). The difference in the explained variance was calculated, and I-splines were plotted (Borcard, Legendre, & Drapeau, 1992; Maestri et al., 2017).

In addition to these models focusing on parasite assemblages, we also ran GDMs with host assemblages as the response variables. This allowed us to separate the direct and indirect effects of environment and host assemblages on parasite assemblages (Figure 1), following similar approaches to those of Maestri et al. (2017). If the parasite-response GDMs indicated an effect of host assemblages but not of environmental variables, whereas the host-response GDMs showed an effect of environmental variables, this would support the mechanism of an indirect host-mediated relationship (Figure 1a). Effects of environment and host on parasite assemblages in the parasite-response GDMs but no effect of environment on host assemblages in the host-response GDMs would support a direct mechanism (Figure 1b). Finally, similar responses to environmental variables by host and parasite assemblages in the host- and parasite-response GDMs in addition to host effects in the parasite GDMs would indicate a mix of direct and indirect effects of environment and host assemblages (Figure 1c).

All analyses were run in R (v.3.4.4; R Core Team, 2018) with the "vegan" package (v.2.5-2; Oksanen et al., 2018) for Mantel tests. The GDMs were run using the package "gdm" (v.1.3.11; Manion et al., 2018). Dissimilarity indices were calculated in "betapart" (v.1.5.1; Baselga, Orme, Villeger, Bortoli, & Leprieur, 2018), and plots were produced using "ggplot2" (Wickham, 2016).

All scripts and data files are available online from data.4tu.nl as Berkhout et al. (2019).

3 | RESULTS

After exclusion of unique records (see Table 1), the analyses were run with 49 trematode parasite species associated with 150 fish host species, 207 trematodes associated with 124 species of birds, and 67 trematodes associated with 12 species of mammals that can serve as hosts. There were also 129 monogenean and 29 copepod species that co-occurred with 144 fish species.

3.1 | β-Diversity congruence patterns

The partial Mantel correlation (r) ranged from .20 to .53 (Table 1), indicating that dissimilarity in parasite assemblages increased with increasing dissimilarity in host assemblages after correcting for the geographical distance between assemblages (Figure 2). When partitioned into their turnover (β_{jtu}) and nestedness (β_{jne}) components, several relationships became non-significant (Table 1). In the significant relationships, the nestedness and turnover components of β-diversity correlations between host and parasite assemblages showed similar strength [$r(\beta_{jne})$ = .24–.25; $r(\beta_{jtu})$ = .25–.27; Table 1; Figure 2]. Similar patterns for all three dissimilarity indices were observed when using the full dataset (i.e., including unique records; Supporting Information Table S1.1). Multiple-site dissimilarities showed similarly high values for overall β-diversity in all parasite–host groups (β_{JAC}; .93–.95; Table 1). However, in all parasite–host groups, the spatial turnover component was responsible for most of the β-diversity (β_{JTU} = .79–.85), whereas the nestedness component made only a marginal contribution to β-diversity (β_{JNE} = .08–.15; Table 1).

In general, correlations of assemblage dissimilarity (β_{jac}) between hosts and parasites were stronger in parasite communities of fish (.41–.53 for trematodes, monogeneans and copepods) than in mammals and birds (.20 and .29, respectively; Table 1). Among parasite groups infecting fish, the correlation was strongest for copepod parasites (r = .53) and weaker for trematodes (r = .41) and monogeneans (r = .45; Table 1). Among the different host groups infected by trematodes, the weakest correlation between the dissimilarities in assemblages was found in mammal hosts (r = .20) and the highest in fish hosts (r = .41; Table 1).

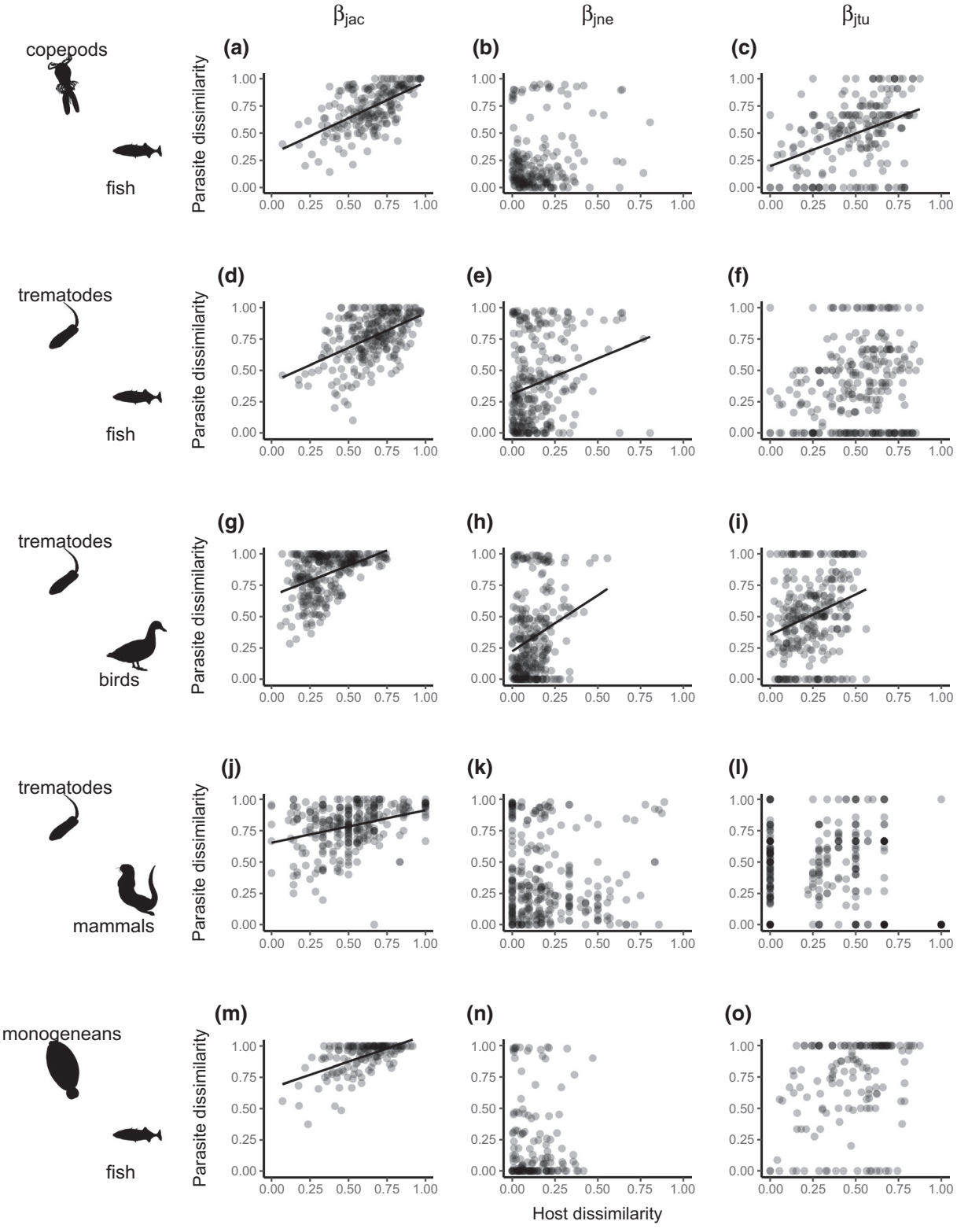

FIGURE 2 Dissimilarities (Jaccard index β_{jac}, β_{jne} and β_{jtu}) of parasite assemblage composition among bioregions (*y* axes) are plotted against dissimilarities of host assemblage composition (*x* axes). Each row (e.g., a,b,c) shows the plots for one host–parasite combination for β_{jac} (first subplot), β_{jne} (second subplot) and β_{jtu} (third subplot). The correlation fitted with the Mantel test is shown in black. The order of the rows of subplots is ranked by average host specificity from high (copepods in fish, 6.9) to low (monogeneans in fish, 1.6) as based on literature data (see main text for details). Overlapping points are indicated by proportional darker shading

3.2 | Generalized dissimilarity models

The variance in parasite assemblage dissimilarity explained by the full model (including both host assemblages and environmental variables) ranged from 37 to 67%, with most variance explained in the monogeneans and least in the trematodes in fish (Figure 3). In all groups, a more substantial part of the variance was explained by the environmental variables than by the host assemblages. The amount of variance explained by the environmental variables ranged from 11% (copepods) to 32% (monogeneans), whereas the variance explained by the host assemblage was between 0.92% (trematodes in mammals) and 5.1% (trematodes in fish; Figure 3). In the copepods on fish, and trematodes in fish and bird groups, the largest part of the explained variance could be explained by both the host species matrix and the environmental variables. The variance explained by either predictor is indicated by the "overlap" in variance explained by the different explanatory matrices (Figure 3). For the monogeneans in fish, the "overlap" was similar to the variance explained solely by the environment. For the trematodes in mammals, the environmental variables accounted for most of the explained variance (Figure 3).

Inspection of the sum of the I-splines for the predictors (Table 2; continuous lines in Supporting Information Figures S1.3–S1.7) showed that temperature was the highest ranking individual predictor overall, having the highest value for six out of 10 of the analyses. In others, temperature ranked second. For the parasite groups, in both the trematodes and parasitic copepods in fish the host assemblage ranked as the second most important predictor. In the others, host assemblage ranked third or fourth (Table 2). Note that the variance explained by fish host species was not the same for all parasite groups, because the parasite groups showed different patterns in their assemblages.

To test further how the variance explained by host assemblages related to the environmental variables (Figure 1), GDMs were also run with host assemblages as the response variable and the environmental data as predictors. In these, between 37 and 59% of the variance was explained (Supporting Information Figure S1.2). For

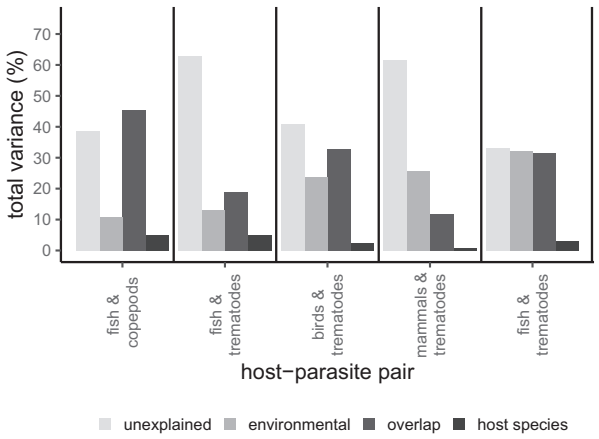

FIGURE 3 Percentage of variance explained by the different explanatory variables for each of the host–parasite pairs. Total variance explained is 61, 37, 59, 38 and 67% (in order of the figure from left to right)

TABLE 2 Sum of the coefficients of the I-splines for each predictor for each group analysed

	Parasitic copepods in fish	Fish associated with parasitic copepods	Trematodes in fish	Fish associated with trematodes	Trematodes in birds	Birds associated with trematodes	Trematodes in mammals	Mammals associated with trematodes	Monogeneans in fish	Fish associated with monogeneans
Geographical distance	0.107	0.370	0.000	0.344	0.034	0.179	0.246	0.354	0.421	0.377
Area	0.016	0.422	0.475	0.537	0.000	0.205	0.000	**0.623**	0.435	0.072
River length (m)	**1.585**	0.291	0.000	0.031	**2.736**	0.000	0.423	0.000	0.036	0.517
Lake perimeter (m)	0.456	0.197	0.049	0.172	0.000	0.010	0.000	0.071	0.322	0.114
Precipitation (mm)	0.480	0.805	0.206	0.670	0.503	0.175	0.737	0.416	2.226	**0.726**
Temperature (°C)	0.770	**0.955**	**1.333**	**0.969**	2.667	**0.606**	**2.420**	0.398	**3.162**	0.676
Elevation (m)	0.000	0.364	0.142	0.358	0.003	0.000	0.059	0.097	2.434	0.415
Host species	0.993	-	1.141	-	1.563	-	0.460	-	1.554	-

Note: Bold values indicate the dominant factor in each model (i.e., the largest value in each column). Note that analyses on host groups have one predictor fewer (i.e., host species).

the host assemblages, generally, the same environmental factors explained variance in these models as in the parasite models. Also, the I-splines mostly had the same shape (Supporting Information Figures S1.2–S11.8; dashed lines in I-spline figures). Together with the results from the parasite response GDMs, these results suggest direct and indirect effects of environment and host assemblages (i.e., the mixed mechanism proposed in Figure 1c). For both host and parasite assemblages, similar patterns were found when using the full dataset (Supporting Information Table S1.2); these will therefore not be discussed separately.

4 | DISCUSSION

Our analyses revealed that the similarity of regional assemblages of a diverse range of parasite taxa in the European freshwater fauna was correlated with the similarity of their host assemblages. Moreover, GDMs showed that parasite assemblages are equally shaped by the direct and indirect effects of environment and host assemblages (Figure 1c). However, the direct effect of host assemblages was relatively small compared with the effect of environmental factors mediated by host assemblages. Climatic parameters (precipitation and temperature) contributed most to the variance explained by environmental variables.

The results of the β-diversity analyses confirmed the expectation that it is the composition of host communities that drives diversity congruence in parasite assemblages on continental scales. This dependence of parasite assemblage composition on host assemblage composition may underlie the frequently observed positive correlation between parasite richness (α-diversity) and host richness in various parasitic organisms (see meta-analysis by Kamiya et al., 2014 and references therein). This correlation has also previously been found in trematodes across the 25 biogeographical regions of Europe (Thieltges, Hof, Dehling, et al., 2011). Whether species turnover or nestedness is the primary driver of the observed congruence in assemblage similarities between hosts and parasites appears to differ among the parasite–host pairs studied. Only copepods and trematodes in birds showed a significant correlation in host and parasite assemblage turnover (Table 1). This correlation indicates that replacement of hosts is linked to a predictable turnover in parasite assemblages. For nestedness, only trematodes in fish and birds showed a significant correlation (Table 1). Thus, for these taxa, subsets of host species are correlated with subsets of parasite species. Given that we found only a few significant relationships and contrasting patterns, it is unclear what the relative contributions of these processes are for shaping host–parasite congruence in general. Previous work has found that, among other factors, host phylogeny (Clark et al., 2018), ecological fitting (Hoberg & Brooks, 2008) and invasive species (Clark et al., 2018) can explain parasite species turnover. For example, the large number of trematode parasites in birds could hint at ecological fitting and subsequent speciation, potentially through the adaptation to intermediate hosts in the complex life cycle. This pattern, therefore, deserves further study, because the relative contributions of nestedness and turnover components could be important during host range shifts with warming climates, given that they might affect the shift of parasite assemblage composition under climate change (Guerin, Biffin, & Lowe, 2013).

Comparing the three host groups, the β-diversity analyses showed that the compositions of the fish assemblages were generally better at predicting the compositions of the respective parasite assemblages than were mammal and bird assemblages. Parasites in mammals and birds, which can travel over land, have an advantage in dispersal compared with parasites of freshwater fishes, which are dependent on the interconnectivity between water bodies. As a result, fish and fish-parasite assemblages are more structured genetically (Blasco-Costa & Poulin, 2013; Criscione & Blouin, 2004) and are thus expected to be more heterogeneous in space than those of mammals and birds (although this was not reflected in the multiple-site β-diversity values in our study, which were similar for all five parasite–host groups; Table 1; Supporting Information Table S1.3). The predictive power for bird parasites might be decreased further because of seasonal bird migrations, taking parasites with them (Viana, Santamaría, & Figuerola, 2016) and resulting in the mixing of parasite populations and species among regions (Gutiérrez, Rakhimberdiev, Piersma, & Thieltges, 2017; Koprivnikar & Leung, 2015). For mammal parasites, the low number of aquatic mammals and their broad spatial distribution may additionally limit the explanatory power of mammal host community composition in explaining mammal parasite community structure. Besides varying dispersal capabilities among host groups, host specificity could play a role in shaping the observed parasite–host congruence patterns. All parasites show some level of host specificity (Poulin & Mouillot, 2004) and thus depend on the presence of certain hosts, and it would be expected that more host-specific parasites have a stronger link to host congruence. However, in the absence of reliable data on host specificity for the parasite species in our database, this remains to be investigated.

In the analyses including environmental factors, in addition to host assemblages, as explanatory variables, a large part of the variance could be explained by the host assemblages or the environmental variables, or both (the "overlap" in variance explained; Figure 3). The similarity in environmental factors shaping host and parasite assemblages and the overlap in explained variance by environmental factors and host assemblages support the mixed hypothesis proposed in Figure 1c. This means that environmental factors shape host assemblages, which in turn shape parasite assemblages, in addition to a substantial direct contribution of environmental variables to parasite assemblages (Figure 1c). A similar pattern is seen in gamasid mites parasitic on small mammals in the northern Palaearctic. Here, the mite community in individual host species is shaped primarily by environmental variables, but parasite assemblages on host communities (i.e., many species) are predominantly shaped by host species assemblages (Vinarski et al., 2007). Parasite assemblages are, thus, shaped by the environment both directly and through the host species. In our study and in previous work, most of the variability in parasite assemblages explained by host assemblages can also be explained by environmental variables (i.e., there is considerable overlap). There is thus a relatively small contribution of host species assemblages to

shaping parasite assemblages, indicating that in general, it is not the distribution of host species that shapes parasite distributions, but it is the restrictions on both host and parasite distributions determined by environmental variables. Both here and in previous work (Maestri et al., 2017; Vinarski et al., 2007), a large portion of variance is equally well explained by host assemblages and environmental variables, with a small proportion of variance explained by host species assemblages alone.

Mean annual temperature was the most important environmental variable for most host–parasite groups in explaining variance. It was used as a proxy for temperature regime and, thus, appears to be an essential factor in shaping host and parasite assemblages in Europe. This implies that with increasing differences in mean annual temperatures between bioregions, the dissimilarity between regions increases, corroborating that in some cases it is not the host availability but the temperature regime that restricts the range of parasitic species (Galaktionov & Bustnes, 1999), directly or indirectly (Figure 1c). A similar role of temperature is seen in the northern part of the continent for the distribution of plants (Fitzpatrick et al., 2013), which are also unable to control their body temperature. Additionally, in Mongolia, air temperature and host turnover were also the two most important predictors for flea turnover (Maestri et al., 2017). Animals generally perform best at the temperatures at which they evolved and perform worse at diverging temperatures. Free-living, infective stages of endoparasites are particularly susceptible to changes in environmental factors, such as temperature (Morley, 2011, 2012). Thus, differences in thermal regimes can have substantial adverse effects on their fitness and therefore restrict their distribution. Extremes in summer or winter temperatures are likely to limit the distributions of the species studied, and future climate change may thus affect the distribution of these species (Lindgren, Tälleklint, & Polfeldt, 2000). In the analyses for parasites with fish hosts, precipitation also appeared to be a meaningful environmental predictor (Supporting Information Figures S1.3–S1.7), probably because levels of precipitation can determine stream size and permanence, and thus habitat availability for different fish species.

Another important factor, river length, measures the amount of flowing freshwater in a bioregion. For parasitic copepods and trematodes in birds, differences in the available river habitat shape the parasite assemblage. This difference reflects the different requirements of different species regarding water bodies for successful completion of their life cycle (Kanarek & Zalesny, 2014), either through host requirements or through direct restrictions on parasites. However, the lack of variance explained by the water body variables themselves (not more than 3.2%) could be attributable to the measures used here, river length and lake perimeter per unit area. These might not be the most appropriate predictors, and a more sophisticated measure that captures the interconnectivity between water bodies might be better suited (Clark et al., 2018). Unfortunately, such a variable was not available for the present data.

Generally, we did not find an effect of area (i.e., size of the bioregion) on parasite or host assemblages. This finding corresponds to earlier work on freshwater species in the same area (Dehling et al., 2010). However, for the mammal hosts, area was the most important predictor in our study. This might be attributable to the low number of mammal species in the study (n = 12), and larger areas might thus contain higher diversity (Pâslaru, 2014). In contrast, for the trematodes in mammals, temperature and precipitation are relevant predictors, but the size of the bioregion is not (Table 2). The overall large portion of unexplained variance in the trematode parasites might be attributable to their complex life cycle (Goater et al., 2013). As a result of their dependence upon intermediate hosts, variability in the absence and presence of intermediate hosts shaped by environmental variables, but not considered here, could play an additional role in shaping these assemblages.

For the host assemblages, the same environmental variables were important in explaining the variance in the data as in their corresponding parasite group (indicated by the similar shapes of the curves in Supporting Information Figures S1.1–S1.8). The similarity in environmental factors shaping host and parasite assemblages and the overlap in explained variance by environmental factors and host assemblages support the hypothesis that environmental factors shape host assemblages, which in turn shape parasite assemblages, in addition to a substantial direct contribution of the environment to parasite assemblages (Figure 1c). If the GDMs had shown that mainly host assemblage shapes parasite assemblages, this would have supported the "host-mediated" hypothesis (Figure 1a), especially given that host assemblages are shaped by the environment (Supporting Information Figures S1.3–S11.7). On the contrary, if no effect of environment on host assemblages was found, but there was still an effect of both environmental and host assemblages on parasites, this would support the "direct impact" hypothesis (Figure 1b). Given that we found both direct and indirect effects of the environment on parasite assemblages, in addition to environment-independent effects of host assemblage, most support is found for the "mixed impact" hypothesis (Figure 1c).

In summary, the similarity of regional assemblages of a diverse range of parasite taxa in the European freshwater fauna was relatively well predicted by their respective host assemblage composition, even when accounting for spatial distance among regions. We were unable to draw decisive conclusions on the importance of nestedness and turnover of β-diversity congruence patterns. However, we showed that environmental variables, especially temperature and precipitation, are key factors in shaping parasite assemblages, in part through their effects on host assemblages. The present analyses of a unique continental-scale dataset contribute significantly to our limited, but growing, understanding of the patterns and mechanisms that shape the diversity of parasite assemblages on large spatial scales. Further analyses should aim to unravel the relative contributions of nestedness and turnover to the observed β-diversity congruence patterns in more detail. This will help to establish the relative contribution of local host assemblage composition to parasite assemblage composition during the range expansion of host species in response to environmental change. Furthermore, our understanding of the effect of host specificity on congruence patterns could benefit from studies using data on the host specificity of individual parasite species. Our GDM models could potentially be improved by including other relevant environmental variables (while being cautious about autocorrelation between variables) and selecting the most relevant ones (Fitzpatrick et al., 2013) or reducing the

number using principal components analysis techniques (Maestri et al., 2017). However, care must also be taken to avoid overfitting. It is crucial to bear in mind that for different host–parasite groups, different environmental variables are likely to play key roles (Astorga et al., 2012). Also, our data divide Europe into 25 broad biogeographical regions; by decreasing the grain size of the analysis more, local data could be included, which could lead to increased explanatory power.

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AUTHOR CONTRIBUTIONS

D.W.T., R.B., R.P. and B.W.B. designed the study. C.H., M.K.B., D.M.D. and B.W.B. compiled the database, and D.M.D. provided the environmental data. B.W.B. conducted the analyses with input from R.B., M.B. and D.W.T., and B.W.B. led the writing with significant input from all co-authors.

DATA AVAILABILITY

The data and scripts will be uploaded to data.4tu.nl under Berkhout et al. (2019).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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