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Correlations between broad-scale taxonomic and genetic differentiations suggest a dominant imprint of historical processes on beta diversities

Running title: Broad-scale β -SGDCs in freshwater fishes

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23 **Abstract**

- 24 – **Aim:** Dispersal limitation, environmental selection and drift are known to influence both
25 taxonomic similarity between communities and genetic similarity between populations.
26 However, disentangling the relative roles of these processes on spatial patterns of
27 differentiation - whether regarding taxonomic differentiation between communities or
28 genetic differentiation between populations - is challenging. Investigating whether spatial
29 patterns of taxonomic differentiation and genetic differentiation are correlated (β -SGDCs)
30 is a promising approach to address this issue. Here, we investigated β -SGDCs over broad
31 spatial scales and 22 freshwater fish species to elucidate the processes shaping taxonomic
32 and genetic differentiations between drainage basins.
- 33 – **Location:** Global scope, data mainly from Europe and North America.
- 34 – **Taxon:** Actinopterygii and Petromyzontiformes (freshwater fishes).
- 35 – **Methods:** We used Mantel tests to investigate the raw correlation between taxonomic and
36 genetic differentiations. We carried out multiple regressions to characterise the effects of
37 geographic distance (proxy of dispersal limitation), environmental distance (proxy of
38 environmental selection) and pairwise harmonic mean area between basins (proxy of drift)
39 on taxonomic differentiation and genetic differentiation taken separately. We then
40 analysed the correlation between the residuals of these two regressions with Mantel tests.
41 Finally, we investigated whether the variation in β -SGDC between species was related to
42 species traits.
- 43 – **Results:** We detected an overall positive β -SGDC, both for the raw and the residual
44 correlations. This implies that, unmeasured effects, other than geographic distance,
45 environmental distance and harmonic mean area, influence the β -SGDC observed. Values
46 of β -SGDCs greatly varied between species, but this was not explained by any species
47 traits.

– **Main conclusions:** Independently of the effects of geographic distance, environmental distance and harmonic mean area, the β -SGDC we observed suggests that historical processes strongly shaped the patterns of taxonomic and genetic differentiations between basins. Consequently, taxonomic differentiation may be an appropriate proxy to explain the influence of historical processes on genetic differentiation.

Keywords

β -SGDC, dispersal limitation, distance decay, drift, environmental selection, freshwater fishes, historical processes, macrogenetics, Mantel tests, multiple regression of distance matrices

58 **Introduction**

59 Understanding the mechanisms that shape taxonomic differentiation between spatially
60 separated communities and those influencing genetic differentiation between spatially
61 separated populations are long-standing issues in ecology and evolution (Wright, 1943, 1951;
62 Whittaker, 1960, 1972; Preston, 1962; Mayr, 1963). More recently, these issues have been
63 united (Vellend, 2003; Vellend & Geber, 2005; Kahilainen, Puurtinen, & Kotiaho, 2014),
64 emphasising that drift, dispersal and selection influence both taxonomic differentiation
65 between communities and genetic differentiation between populations. Drift and selection
66 affect the species frequencies within communities and gene frequencies within populations,
67 which tend to increase differentiation. Conversely, dispersal of individuals between
68 populations and dispersal of species between communities will tend to decrease
69 differentiation.

70 Among the factors that can affect both taxonomic and genetic differentiation,
71 geographic distance is probably the most studied. The similarity in taxonomic composition
72 between communities tends to decrease with the geographic distance that separates them; a
73 pattern long-recognised in biogeography and formalised as the distance decay of similarity
74 (Nekola & White, 1999; Soininen, McDonald, & Hillebrand, 2007). Similarly, the genetic
75 similarity between populations tends to decrease with the geographic distance separating
76 them; a pattern long-recognised in population genetics and referred to as isolation-by-distance
77 (IBD; Wright, 1943; Rousset, 1997). Two main non-mutually exclusive explanations can
78 account for the distance decay of taxonomic and genetic similarity (see Soininen et al., 2007
79 and Orsini et al., 2013 for reviews). First, similarity decreases with geographic distance
80 because the dispersal of organisms (i.e. their movement from a place to another) is limited by
81 their intrinsic dispersal ability, which hence does not counteract anymore the differentiating
82 effect of drift. Secondly, similarity decays with geographic distance because of decreasing

similarity in spatially correlated environmental features; in such cases, the underlying explanation is environmental selection of different species (community differentiation) or genotypes (genetic differentiation) in distinct environments. However, differentiation between sites does not always increase with geographic distance. This is the case when the migrants are competitively excluded by already established communities (e.g. Almany, 2003) or populations (e.g. Fraser et al., 2018) at high densities, therefore counteracting the homogenising effect of dispersal whatever the intrinsic dispersal ability of the migrants. This may also happen when the environmental variation between sites displays no – or negative – spatial autocorrelation (e.g. Derry et al., 2009).

Although spatial patterns of taxonomic and genetic differentiations can be explained by environmental selection independently of limited dispersal and vice-versa, disentangling the relative strengths of these mechanisms is challenging, as communities and populations that are geographically distant are also likely to inhabit different environments. Using modern spatial statistical methods, some recent studies have nonetheless taken up the challenge. In their study of global patterns of species turnover in terrestrial vertebrates, Qian & Ricklefs (2012) have shown that both dispersal limitation and environmental selection have played important roles in determining the patterns they observed. Similarly, in their reinterpretation of 34 representative studies, Orsini *et al.* (2013) highlighted that patterns associated with dispersal limitation were as common as those associated with local genetic adaptation in structuring population genetic differentiation in the wild. However, the relative strength of dispersal limitation and environmental selection on differentiation patterns seems to vary according to the species and the spatial scale under consideration, both for taxonomic (Astorga et al., 2012; Moritz et al., 2013) and genetic (Orsini et al., 2013) differentiations. Comparative studies of multiple taxonomic groups suggest that the influence of dispersal limitation on taxonomic differentiation is stronger for species with low dispersal ability than

for more effective dispersers, and this result holds true both at the broad-scale (e.g. Qian & Ricklefs, 2012) and at the fine-scale (e.g. Astorga et al., 2012). Comparative studies of multiple species have also been identified as a promising avenue to reveal the factors influencing patterns of genetic differentiation (Wang et al., 2013). Yet, such studies are scarce and mainly carried out at relatively small spatial scales (e.g. Wang et al., 2013; Fourtune, Paz-Vinas, Loot, Prunier, & Blanchet, 2016) despite the increasing availability of broad-scale datasets in population genetics, suggesting that it is now time to embrace macrogenetics (Blanchet, Prunier, & De Kort, 2017).

Theories in population genetics and community ecology acknowledge that dispersal, selection and drift together shape the differentiation between populations and between communities (see e.g. Vellend & Orrock, 2009 for a review of processes in both disciplines). However, the contribution of drift to taxonomic or genetic differentiation has been the subject of few empirical investigations, in contrast with dispersal limitation and environmental selection (Gilbert & Levine, 2017; Prunier, Dubut, Chikhi, & Blanchet, 2017). Genetic drift is the evolutionary process of random fluctuations in allelic frequencies occurring naturally in all populations due to their finite size, although it is stronger in small ones (Allendorf, 1986). Similarly, ecological drift corresponds to the random fluctuations in species frequencies occurring naturally in all communities due to their finite size and this too is stronger in small ones. Drift is the result of random sampling during the processes of birth, death and reproduction and ultimately leads to the loss of genetic diversity within populations, and species diversity within communities. Therefore, drift increases the differentiation between populations and between communities depending on their respective sizes: the smaller they are, the more they will differentiate. Dispersal of organisms between populations and between communities counteracts the differentiating effect of drift while environmental selection can accelerate it. Attributing the observed spatial patterns of genetic or taxonomic differentiation

to dispersal limitation or to environmental selection without accounting for drift may thus be misleading.

Most of the explanatory variables used in analyses to infer the role of dispersal limitation and environmental selection on differentiation patterns are proxies representing present-day conditions. Thus, using current explanatory variables to investigate dispersal limitation and environmental selection on differentiation patterns is only relevant if the contemporary geography and environment of the study area has not changed substantially since these patterns were established (Wang et al., 2013). Otherwise, the historical processes that may have shaped the observed differentiation patterns, including those explaining colonisation histories, may be overlooked. In addition, if dispersal is not continuous (as generally assumed) but rather intermittent because of landscape dynamics which have induced the appearance and disappearance of dispersal barriers, then two geographically close localities sharing a similar environment could, nevertheless, be dissimilar in terms of community composition and allele frequencies provided they have been isolated for a sufficiently long time (given their sizes) for drift to be effective. Nonetheless, examining which part of differentiation patterns is not explained by current explanatory variables may help to elucidate the influence of historical processes on those patterns.

In such complex contexts, understanding the rules that govern differentiation patterns (both taxonomic and genetic) may be enhanced by comparing taxonomic dissimilarities between communities and genetic dissimilarities between populations of a focal species (Lamy, Laroche, David, Massol, & Jarne, 2017). The few empirical studies that have examined these correlations, called beta species-genetic diversity correlations (β -SGDCs) (Kahilainen et al., 2014), revealed a majority of positive correlations (reviewed by Lamy et al., 2017). This suggests that the processes affecting taxonomic dissimilarity affect genetic dissimilarity of the species under study in the same way (Baselga et al., 2013; Baselga,

Gómez-Rodríguez, & Vogler, 2015). However, because the relative strength of processes shaping patterns of taxonomic and genetic differentiation is expected to vary according to the species and the spatial scale under consideration, so is the strength of the putative resulting β -SGDCs. Among the rare studies of β -SGDCs over multiple species, some have highlighted that positive β -SGDCs were stronger for focal species with low dispersive abilities (e.g. Papadoulou et al., 2011) while others did not find strong differences between species (e.g. Fourtune et al., 2016), and all were carried out at relatively small spatial scales. These contrasting results call for more studies of β -SGDCs for multiple species to gain a better understanding of whether and how variations in species traits lead to distinct patterns of β -SGDCs. In addition, β -SGDCs for multiple species have not been examined yet at broad spatial scales.

Freshwater fishes are a relevant model to start investigating this question for at least three reasons. First, as β -SGDCs for multiple freshwater fish species have been conducted at small scales within a single drainage basin (Fourtune et al., 2016), computing β -SGDCs for multiple freshwater fish species at broader scales will permit the comparison of β -SGDC variations across scales for the same biological model. Secondly, for strictly freshwater fishes, at present, almost no exchange of individuals occurs between drainage basins (hereafter “basins”) because they are isolated from each other by land and/or sea (although dispersal may occasionally occur between adjacent basins). Therefore, if basins are isolated from each other independently of the geographic distance between them, we can expect dispersal limitation to play a minor role on the broad-scale between-basin patterns of taxonomic and genetic differentiations. On the contrary, if basins have been isolated from each other for a long time, we can expect drift to play a significant role on the broad-scale between-basin patterns of taxonomic and genetic differentiations, as dispersal no longer counteracts the effect of drift. This is particularly true if population sizes and community sizes are small: the

larger they are, the longer it will take to observe differentiation. Finally, while several recent studies have tried to disentangle the role of dispersal limitation, environmental selection and historical processes on patterns of taxonomic differentiation between basins (Leprieur et al., 2009, 2011; Dias et al., 2014), the processes shaping genetic differentiation at such broad scales have rarely been examined together. Studying β -SGDCs may therefore reveal whether the processes influencing between-basin taxonomic differentiation, affect between-basin genetic differentiation in the same way.

In this meta-analysis of 22 freshwater fish species, our main goal was to elucidate the processes underlying β -SGDCs at broad spatial scales. In particular, we wanted to test whether β -SGDCs can be explained by the parallel action of measurable processes (dispersal limitation, environmental selection and drift) on taxonomic and genetic differentiation, or are due to other, non-measurable processes. To that end, we first computed measures of genetic differentiation between basins for each fish species. Then, for each species, we investigated i) the raw correlation between taxonomic and genetic differentiations, ii) the effects of geographic distance (as a proxy of dispersal limitation), environmental distance (as a proxy of environmental selection) and pairwise harmonic mean area between basins (as a proxy of drift) on taxonomic differentiation and genetic differentiation taken separately and iii) the correlation between taxonomic and genetic differentiations independent of the effects of geographic distance, environmental distance and harmonic mean area (Fig. 1). Such independent correlation integrates the effects of unmeasured processes, including the historical processes of dispersal, environmental selection and drift related to the historical connectivity of basins. This allowed us to characterise the overall (i.e. mean over the species) raw β -SGDC, the overall effects associated with each predictor for each response variable, and the overall independent β -SGDC. Finally, we tested whether the variation in β -SGDCs between species could be attributed to variations in species traits.

208

209 **Materials and methods**210 *Genetic differentiation and geographic distribution of genetic data*

211 As we wanted to investigate genetic differentiation at the broad scale, we restricted our
212 analyses of spatial genetic differentiation to species exhibiting a wide distribution. We
213 downloaded sequence records of the mitochondrial gene cytochrome c oxidase I (COI) from
214 BOLD (www.boldsystems.org) in May 2017 for the following widespread taxa: Cyprinidae,
215 Salmonidae, *Lampetra*, *Petromyzon*, *Cobitis*, *Misgurnus*, *Barbatula*, *Silurus*, *Esox*, *Lota lota*,
216 *Gymnocephalus* and *Sander*. We first cleaned and aligned sequences by taxon and then re-
217 aligned them together to keep the same fragment of 501 nucleotides for the analyses.
218 Sequence records without sufficient geographic information to assign them to a drainage
219 basin (hereafter “basin”) or without a species name were discarded from our dataset. We
220 defined a basin as the drainage area upstream from its mouth at the sea. According to this
221 definition, a basin is isolated from other basins by barriers (sea or land) which are impassable
222 for strictly freshwater fishes. The validity of species names was assessed using FishBase
223 (Froese & Pauly, 2017), resulting in a total of 6637 sequence records with a valid species
224 names belonging to 716 distinct species distributed in 218 basins. We checked the
225 environment (i.e. “freshwater”, “brackish”, “saltwater”) of each species using FishBase
226 (Froese & Pauly, 2017), the status (i.e. “native”, “exotic” or “unknown”) of each species in
227 each basin using the global database on freshwater fish species occurrence (Tedesco et al.,
228 2017). We conserved only native records of strictly freshwater species, i.e. 4894 records,
229 corresponding to a total of 509 species in 176 basins.

230 We calculated between-basin genetic differentiation (by pooling individuals in the
231 drainage basins) for the polymorphic species present in at least four basins with a minimum of

three individuals per basin. To calculate such genetic differentiation, we converted single nucleotide polymorphisms (SNPs) of the sequence data into a table of individual genotypes and then calculated pairwise genetic distances for each pair of basins using G''_{ST} (Meirmans & Hedrick, 2011), the corrected version of Hedrick's G'_{ST} (Hedrick, 2005). G''_{ST} is independent from within population diversity and does not underestimate genetic distance when the number of populations is small (Meirmans & Hedrick, 2011). As G''_{ST} likely removes the effect of drift, we also calculated the pairwise genetic distances for each pair of basins using F_{ST} (Nei, 1973) for comparison purpose.

All these different selection filters drastically reduced the number of species we included in analyses: we finally focused our analyses of between-basin genetic differentiation on a total of 22 species in 38 basins (for more details about these basins, see Appendix S1 in Supporting Information). For instance, from all the species of *Lampetra* and *Petromyzon* we searched in BOLD, we conserved only *L. planeri* for the analyses. The number of species with analysed genetic data per basin varies from one (for 20 basins) to seventeen (for one basin, the basin “Odra”; Fig. 2; Appendix S1). The number of basins per species varies from four (our minimum threshold) to eleven (for the species *Esox lucius*) covering on average 76 % (standard deviation (sd) = 18 %) of their native range, with species exhibiting on average 11.0 individuals per basin (sd = 11.0; Appendix S2). Most records are located in Europe and North-America (Fig. 2).

Taxonomic differentiation

We calculated pairwise taxonomic differentiation between each pair of basins based on the list of native species per basin extracted from the global database on freshwater fish species occurrence (Tedesco et al., 2017). We used Simpson dissimilarity (β_{sim}) - the turnover component of Sørensen dissimilarity (Sørensen, 1948) - which is independent from total

256 taxonomic richness (see Baselga 2012 for review).

257 *Geographic distance, environmental distance and pairwise harmonic mean area*

258 We computed between-basin geographic distance by calculating the distance between basin
259 centroids. The average distance between basins was 5 295 km (sd = 3 920 km). Measurements
260 of geographic distance were then centred and scaled before further analyses.

261 To characterise the environment of the basins, we used variables related to the
262 contemporary climate known to influence freshwater fish alpha diversity patterns at the global
263 scale (e.g. Dias et al. 2014; Oberdorff et al. 2011; Tedesco et al. 2012; Tisseuil et al. 2013) i.e.
264 mean annual temperature and precipitation (<http://www.worldclim.org/>), mean annual surface
265 runoff (<http://www.grdc.sr.unh.edu/>) and mean annual actual and potential evapotranspiration
266 (<http://csi.cgiar.org/Aridity/>). The mean values of all the variables were computed for each
267 basin. To compute pairwise environmental distances between each pair of basins, we
268 performed a principal component analysis (PCA) on these environmental variables
269 (previously centred and scaled) and calculated the Euclidean distance between basins based
270 on the first three PCA axes.

271 Finally, we calculated the pairwise harmonic mean area between each pair of basins.
272 Indeed, the harmonic mean population size between pairs allows the role of drift on genetic
273 differentiation (Serrouya et al., 2012) to be taken into account and can be computed using
274 environmental proxies for local carrying capacities (Prunier et al., 2017). In our case, we used
275 the surface area of the basin as a raw environmental proxy for local carrying capacity. The
276 basins studied had an average surface area of 257 589 km² (sd = 584 803 km²). Measurements
277 of harmonic mean area were centred and scaled before further analyses.

278 *Statistical analyses*

First, we investigated the raw correlation between taxonomic differentiation and genetic differentiation for each species individually using a Mantel correlation test with 999 permutations. To test the null hypothesis that there is no relationship between taxonomic differentiation and genetic differentiation using the information provided by all the species examined, we considered that this hypothesis has been tested independently n times, with n being the number of species included in the analyses. To combine the results from several independent tests bearing upon the same overall hypothesis, we used a modification of the Fisher's combined probability test. Under the null hypothesis that taxonomic and genetic differentiations are unrelated, observed p-values associated with the Mantel's test of each species are expected to be distributed according to a uniform distribution in $[0, 1]$. We therefore compared the observed mean p-value over the species to a null distribution of mean p-values obtained by sampling randomly 10 000 times one p-value by species in a uniform distribution in $[0, 1]$. We calculated the p-value associated with the combined test as the frequency at which null mean p-values were below the observed mean p-value. This procedure avoids some problems identified by the use of a chi-2 test (e.g. Whitlock, 2005) which was the method initially proposed by Fisher.

To investigate the putative roles of dispersal limitation, environmental selection and drift on taxonomic and genetic differentiations, for each species we built multiple regressions of geographic distance (D_{geo}), environmental distance (D_{env}) and harmonic mean area (D_{area}) on taxonomic differentiation (TD) and genetic differentiation (GD) taken separately (Fig. 1) as follows: $TD = \alpha_0 + \alpha_1 * D_{\text{geo}} + \alpha_2 * D_{\text{env}} + \alpha_3 * D_{\text{area}}$ and $GD = \beta_0 + \beta_1 * D_{\text{geo}} + \beta_2 * D_{\text{env}} + \beta_3 * D_{\text{area}}$. Our approach is very similar to multiple regressions on distance matrices (MRM; Lichstein 2007) except in the way we calculated p-values associated with partial regression coefficients. As in MRM, we permuted the rows and associated columns of the response distance matrix simultaneously. We repeated this operation 1999 times while holding the

explanatory distance matrices constant to generate null distributions for partial regression coefficients. Then, in MRM, the p-value associated with a partial regression coefficient is calculated with a two-sided permutation test using the pseudo-t of Legendre et al. (1994), i.e. it tests whether the t-statistic associated with each regression coefficient is lower or higher than expected under a null distribution of pseudo-t obtained by permutation. In our approach, we hypothesised that geographic distance and environmental distance have a positive effect on both taxonomic and genetic differentiations (dispersal limitation and environmental selection enhance differentiation and are positively related to geographic and environmental distances respectively) while harmonic mean area has a negative effect on taxonomic and genetic differentiations (drift enhances differentiation and is negatively related to the harmonic mean area). To increase the statistical power of the tests, we therefore carried out one-sided tests for calculating the p-values associated with each partial regression coefficient. We tested the overall (i.e. over the species) effects of geographic distance, environmental distance and harmonic mean area on taxonomic and genetic differentiations by performing a combined probability test as described for the raw correlation between taxonomic and genetic differentiations, but this time considering probabilities associated with partial regression coefficients.

To examine whether taxonomic and genetic differentiations were still correlated once the effects of geographic distance and environmental distance had been taken into account, we then performed a Mantel correlation test between the residuals of the multiple regression on taxonomic differentiation and the residuals of the multiple regression on genetic differentiation with 999 permutations for each species. We tested this overall (i.e. over the species) residual correlation using a combined probability test as described for the raw correlation between taxonomic and genetic differentiations.

Finally, we examined the heterogeneity between species regarding the residual correlation between taxonomic and genetic differentiations and tested whether some species traits could explain such heterogeneity. The species traits initially considered were body length, longevity in the wild, vulnerability, used in aquaculture, use as bait, use in the aquarium, habitat, migratory behaviour and dispersal ability – which was calculated using a formula giving dispersal distance as a function of body size and caudal fin aspect ratio (Radinger & Wolter, 2014). However, as migratory behaviour was ‘potamodromous’ for 16 out of the 22 species, ‘non-migratory’ for one species and the information was not available for the 5 species left, we excluded this non-informative trait from our analyses. Species traits were directly extracted from FishBase (Froese & Pauly, 2017). All the analyses and the corresponding figures were realised with R 3.5.1 (R Core Team 2018) using the packages ‘ade4’ (Dray & Dufour, 2007), ‘ape’ (Paradis, Claude, & Strimmer, 2004), ‘betapart’ (Baselga, Orme, Villeger, De Bortoli, & Leprieur, 2018), ‘Biostrings’ (Pagès, Aboyoun, Gentleman, & DebRoy, 2018), ‘broom’ (Robinson & Hayes, 2018), ‘ggplot2’ (Wickham, 2016), ‘ggthemes’ (Arnold, 2018), ‘hierfstat’ (Goudet & Jombart, 2015), ‘maptools’ (Bivand & Lewin-Koh, 2018), ‘mmod’ (Winter, 2012), ‘RColorBrewer’ (Neuwirth, 2014), ‘rgdal’ (Bivand, Keitt, & Rowlingson, 2018), ‘rgeos’ (Bivand & Rundel, 2018), ‘reshape2’ (Wickham, 2007), ‘seriation’ (Hahsler, Buchta, & Hornik, 2018) and ‘vegan’ (Oksanen et al., 2018).

Results

We detected an overall positive correlation between taxonomic and genetic differentiations, significantly different from 0. This result holds true both for the raw correlation between taxonomic and genetic differentiations ($r_{\text{mean} \pm \text{sd}} = 0.433 \pm 0.420$; Fig. 3a; Appendices S3, S4)

and for the residual correlation, i.e. the correlation between taxonomic and genetic differentiations independent of the effects of geographic distance, environmental distance and harmonic mean area ($r_{\text{mean} \pm \text{sd}} = 0.379 \pm 0.641$; Fig. 3b; Appendices S3, S4).

There was almost no overall effect of geographic distance on taxonomic differentiation ($\alpha_1_{\text{mean} \pm \text{sd}} = 0.032 \pm 1.051$) or on genetic differentiation ($\beta_1_{\text{mean} \pm \text{sd}} = -0.011 \pm 1.060$), and these overall effects did not differ significantly from 0 (Fig. 4; Appendices S5, S6, S7). In contrast, we detected an overall positive effect of environmental distance on both taxonomic differentiation ($\alpha_2_{\text{mean} \pm \text{sd}} = 0.405 \pm 0.956$) and genetic differentiation ($\beta_2_{\text{mean} \pm \text{sd}} = 0.229 \pm 0.865$), although it was only significantly different from 0 for taxonomic differentiation (Fig. 4; Appendices S5, S6, S7). There was an overall negative effect of harmonic mean area on both taxonomic differentiation ($\alpha_3_{\text{mean} \pm \text{sd}} = -0.178 \pm 0.617$) and genetic differentiation ($\beta_3_{\text{mean} \pm \text{sd}} = -0.092 \pm 0.713$), but it was only significantly different from 0 for taxonomic differentiation (Fig. 4; Appendices S5, S6, S7). Using F_{ST} as a measure of genetic differentiation did not change the trend we observed: there was an overall negative but not significant effect of harmonic area on F_{ST} (Appendices S6, S7).

The results of these multiple regressions as well as the residual correlations between taxonomic and genetic differentiations are summarised in Fig. 5. Overall, they suggest that the effect of geographic distance, environmental distance and harmonic mean area only explain a small part of the correlation between taxonomic and genetic differentiations.

Despite this strong overall independent correlation between taxonomic differentiation of freshwater fish communities and genetic differentiation of freshwater fish populations, the correlation between taxonomic and genetic differentiations varied greatly between species (Fig. 3b; Appendix S3). For some species, such as the common roach *Rutilus rutilus* (Fig. 6a, b), there was a sound correlation between taxonomic differentiation and genetic

differentiation, whether we considered the raw or residual correlation. In other species, such as the common chub *Squalius cephalus*, taxonomic differentiation and genetic differentiation were not correlated (Fig. 6c, d). In this species, genetic differentiation was better predicted by geographic distance and harmonic mean area (Appendix S5). However, none of the species traits examined explained this heterogeneity of responses between species (Appendix S8).

Discussion

Our analyses indicated that taxonomic and genetic differentiations are strongly correlated overall, and independently of the parallel effects of geographic distance, environmental distance and harmonic mean area on taxonomic and genetic differentiations. This suggests that the parallel influence of dispersal limitation, environmental selection and drift on taxonomic and genetic differentiations only partially explains the overall β -SGDC we observed. This independent, unexplained correlation between taxonomic and genetic differentiations thus probably results from processes that we did not explicitly consider in our study. The most probable explanation is that the independent β -SGDC we observed is due to the parallel action of historical processes, which occurred when the basins were still connected, on taxonomic and genetic differentiations. These historical processes include all the different processes that explain the colonisation history of basins (Orsini et al., 2013): i) the dispersal of individuals between previously connected basins in interaction with environmental and/or biotic selection on their dispersal route and ii) environmental and/or biotic selection in interaction with drift within their place of arrival and/or origin that may have led to extinction. This explanation is supported by previous studies on the influence of historical processes on broad-scale taxonomic differentiation between freshwater fish communities on the one hand and on broad-scale genetic differentiation between freshwater

400 fish populations on the other hand. Two recent studies on global freshwater fish biodiversity
401 have shown that present-day patterns of taxonomic dissimilarity across basins are well
402 explained by the historical connectivity of basins (Dias et al., 2014) and also historical
403 climatic oscillations that took place during the Quaternary and the Holocene (Leprieur et al.,
404 2011). For fish species, it is well known that historical dispersal influences genetic structure
405 across basins (Carvalho, 1993), especially for zones that were subject to intense post-glacial
406 recolonisation such as our study area. Multispecies comparisons at large spatial scales in
407 Europe (Seifertová, Bryja, Vyskočilová, Martínková, & Šimková, 2012) and in North
408 America (April, Hanner, Mayden, & Bernatchez, 2013) have shown that the climatic
409 fluctuations that caused glacial cycles during the Pleistocene had a generalised effect on the
410 patterns of fish genetic divergence. In addition, three other, non-exclusive hypotheses may
411 explain the independent β -SGDC we observed. First, the proxies we used to account for
412 dispersal limitation, environmental selection and drift may not fully represent these processes.
413 For instance, we may have overlooked some environmental variables that are important in
414 driving environmental selection. Alternatively, we may have poorly estimated the role of drift,
415 either because the area of the basin we used to account for drift may be too approximate to
416 accurately represent the carrying capacities of populations and communities or because we
417 did not consider that the influence of drift within a basin increases with its age of isolation.
418 Secondly, the sequence data we used to calculate genetic differentiation may not detect
419 dispersal limitation and/or environmental selection properly, either because they did not cover
420 the entire native ranges of species (see possible consequences of such sampling bias in e.g.
421 Meirmans, 2015), or because the mitochondrial gene COI is not directly under environmental
422 selection. Finally, the proposed frameworks to interpret SGDCs (Vellend & Geber, 2005;
423 Lamy et al., 2017) suggest that correlations between species diversity and genetic diversity
424 may also result from a causal action of species diversity on genetic diversity or vice-versa.

For instance, if the focal species (i.e. the species for which we studied genetic diversity) is a facilitator for the other component species of the community, we would expect their populations sizes to co-vary positively, resulting in a positive α -SGDC; the converse is expected if the focal species is a competitor. If the nature of the interaction between the focal species and the other species of the community is generally the same within each basin, such causal effect is not expected to influence the β -SGDC we observed. However, if the focal species is facilitator in one basin and competitor in another, we would expect the population sizes of the other component species of the community to increase in the first case and decrease in the second case. This would result in more ecological drift within the community where the focal species is competitor, and therefore more taxonomic differentiation between basins than would be expected without this causal effect. In the end, such causal effect would tend to reduce β -SGDC because it would increase taxonomic differentiation between basins without influencing genetic differentiation.

Moreover, our results contribute new insights into the study of β -SGDCs. With the study of 22 new β -SGDCs, we increased the number of β -SGDCs (43) previously reported in the literature by more than 50 % (see Lamy *et al.*, 2017 for the most recent review). We found an average raw correlation between taxonomic and genetic differentiations of 0.433, and an independent correlation (i.e. independent from the parallel effects of geographic distance, environmental distance and harmonic mean area on taxonomic and genetic differentiations) of 0.379. Both of these values are superior to the average value of 0.221 reported by Lamy *et al.* (2017). They are also around three times superior to the average value of 0.139 found by Fourtune *et al.* (2016) in their study of four freshwater fish species at a smaller scale, within one drainage basin. This suggests that the strong correlations we found are probably more related to the size and/or the isolation of the habitats we studied (i.e. large drainage basins isolated from each other) rather than our biological model. Previous syntheses have reported

that α -SGDCs (i.e. correlations between genetic diversity within populations and species diversity within communities) are stronger and more often positive in island-like habitats (Vellend & Geber, 2005; Vellend et al., 2014), in agreement with the predictions of theoretical models (Laroche et al., 2015). As drainage basins are typically island-like habitats (Sepkoski & Rex, 1974; Hugueny, 1989), our findings suggest that this explanation may hold true for β -SGDCs as well. The observed differences also suggest that for a system without present-day dispersal the β -SGDC is stronger than in systems with present-day dispersal. Actually, the opposite could have been expected (i.e. weaker β -SGDCs for systems without present-day dispersal than for systems with present-day dispersal) if the genetic similarity between two previously connected populations had been erased by genetic drift occurring after their isolation without changes in species composition (i.e. no species extinction). However, our results suggest that drift did not influence significantly the patterns of genetic differentiation we observed. As this result holds true both for G''_{ST} and F_{ST} , this is probably because we mainly focused on large drainage basins and consequently large population sizes.

Our results also indicate that the sign and magnitude of β -SGDCs varied greatly between the different species we examined. We provided two examples. On the one hand, we showed that the β -SGDC was strong for *Rutilus rutilus*, suggesting that historical processes largely shaped the patterns of genetic differentiation observed in this species. This is consistent with a previous study indicating that *R. rutilus* is composed of two historically isolated, independently evolving sets of populations (Larmuseau et al., 2009). On the other hand, our results indicate that genetic differentiation in *Squalius cephalus* was not correlated to taxonomic differentiation, but was well explained by geographic distance. This suggests that dispersal limitation has a more important effect than any other processes on broad-scale genetic differentiation in *S. cephalus*. This might seem surprising, since previous analyses of the mitochondrial gene cytochrome b in that species indicated four main lineages originating

from multiple glacial refugia (Durand, Persat, & Bouvet, 1999; Seifertová et al., 2012). However, the use of a combination of both mitochondrial and nuclear DNA, Seifertová et al. (2012) also suggested that genetic differentiation in *S. cephalus* resulted from a combination of different factors, i.e. post-glacial colonisation from different refugia or recent evolutionary processes such as drift or dispersal limitation. Our results based on the analysis of the mitochondrial gene COI strongly support the dispersal limitation hypothesis although, as we did not design the sampling, but analysed existing data, we might not have captured the whole picture. As *R. rutilus* and *S. cephalus* have similar dispersal abilities, this difference of β -SGDC between the two species does not seem to be related to their difference in dispersal abilities. Beyond these two species and this single trait, our analyses did not permit us to uncover any trait that could explain the variability of β -SGDC over the 22 species we examined. This is surprising because life-history traits of species are known to shape spatial patterns of genetic differentiation (e.g. Duminil et al., 2007; Kelly & Palumbi, 2010), and therefore β -SGDC. This unexpected finding may be due to different reasons. First, the variability of β -SGDC may be due to species traits that we did not consider. Secondly, the β -SGDC at the specific scale was sometimes examined for a small number of basins, which may result in wide variations in the estimated correlation coefficients. Therefore, single species outcomes should be interpreted with great caution.

To conclude, this study of broad-scale β -SGDC for multiple freshwater fish species suggests that historical processes greatly contributed to the shape of present-day patterns of taxonomic and genetic differentiations, independently of contemporary processes. This implies that taxonomic differentiation may be an appropriate proxy to explain the role of historical processes on patterns of genetic differentiation, which remains a challenging issue in landscape genetics (Dyer, Nason, & Garrick, 2010). We believe that further studies of broad-scale β -SGDCs comparing organisms whose dispersal is limited within habitat patches

500 with organisms that are able to disperse across habitat patches, will help to investigate the
501 extent to which our findings can be generalised.

Figures

Figure 1. Illustration of the different processes expected to act in parallel on between-basin taxonomic differentiation of freshwater fish communities (TD) and on between-basin genetic differentiation of freshwater fish populations (GD) at different periods and the proxies used in this study to infer those processes. The black frame encompasses the causal diagram depicting the relationships that we actually tested in this study, i.e. the effects of geographic distance (proxy of contemporary dispersal limitation), environmental distance (proxy of contemporary environmental selection) and pairwise harmonic mean area between basins (proxy of contemporary drift) on TD and GD. The double arrow between TD and GD represent the residual correlation, i.e. the correlation between TD and GD which is not explained by the parallel influence of contemporary dispersal limitation, contemporary environmental selection

515 and contemporary drift on TD and GD. The numbers on the arrows and the signs below them
516 correspond to our theoretical expectations regarding the different effects which are detailed in
517 the text below the black frame. The grey arrows represent the putative effects of historical
518 dispersal limitation, historical environmental selection and historical drift on TD and GD that
519 we did not directly test in our statistical approach. The grey polygons on the right side
520 represent the evolution of the basin configuration through time from one unique basin to two
521 distinct and disconnected basins, with almost no contemporary dispersal of individuals
522 between them (dispersal may occasionally occur between adjacent basins).

Figure 2. Spatial distribution of the number of species with analysed genetic data per basin studied in our analyses at the global scale. Top: the rectangle indicates the location of the enlarged area. Bottom: enlarged area including Europe and North America. In total, our study encompasses 22 species with analysed genetic data in 38 basins.

Figure 3. Violin plots showing the distribution and the probability density of (a) raw correlations coefficients and (b) residual correlation coefficients between taxonomic differentiation and genetic differentiation for the 22 fish species examined at global scale. Crossbars indicate mean $\pm$ standard deviation.

Figure 4. Violin plots showing the distribution and the probability density of the effect of geographic distance, environmental distance and harmonic mean area (as standardised regression coefficients) for the 22 fish species examined at global scale on (a) taxonomic differentiation and (b) genetic differentiation. Crossbars indicate mean $\pm$ standard deviation.

Figure 5. Causal diagram depicting the results of multiple regressions of geographic distance, environmental distance and harmonic mean area on TD and GD (taken separately). Arrows represent putative causal effects through the standardised regression coefficients (positive values: solid arrows; negative values: dotted arrows; arrow width is proportional to coefficient value). The R^2 represent the part of variance explained by the multiple regressions on TD (left) and GD (right). U_{TD} and U_{GD} represent unspecified factors influencing TD and GD respectively. The double arrow between SD and GD corresponds to the residual correlation. All numerical values represent means for the 22 fish species examined at global scale.

Figure 6. Observed (dots) and predicted (dashed line) raw values (a, c) and residual values from the multiple regressions (b, d) of genetic differentiation as a function of taxonomic differentiation for the two fish species (a, b) *Rutilus rutilus* and (c, d) *Squalius cephalus*.

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755 **Biosketch**

756 The authors are particularly interested in documenting and explaining spatial patterns of
757 biodiversity at large spatial scales. They try to disentangle the interplay between historical and
758 contemporary factors (including anthropogenic pressures) in shaping patterns of alpha and
759 beta diversities in aquatic populations and communities and value this knowledge to guide
760 conservation strategies of aquatic ecosystems.

761 **Supporting information**

762 Supporting information for this article may be found online.

763 **Data availability**

764 ~~The data and the script~~ Upon acceptance of this manuscript, all data and scripts used for the
765 analyses are available from the Dryad Digital Repository:
766 <https://doi.org/10.5061/dryad.8vb6160>. ~~will be uploaded in a Dryad repository.~~

Correlations between broad-scale taxonomic and genetic differentiations suggest a dominant imprint of historical processes on beta diversities

Running title: Broad-scale β -SGDCs in freshwater fishes

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23 **Abstract**

- 24 – **Aim:** Dispersal limitation, environmental selection and drift are known to influence both
25 taxonomic similarity between communities and genetic similarity between populations.
26 However, disentangling the relative roles of these processes on spatial patterns of
27 differentiation - whether regarding taxonomic differentiation between communities or
28 genetic differentiation between populations - is challenging. Investigating whether spatial
29 patterns of taxonomic differentiation and genetic differentiation are correlated (β -SGDCs)
30 is a promising approach to address this issue. Here, we investigated β -SGDCs over broad
31 spatial scales and 22 freshwater fish species to elucidate the processes shaping taxonomic
32 and genetic differentiations between drainage basins.
- 33 – **Location:** Global scope, data mainly from Europe and North America.
- 34 – **Taxon:** Actinopterygii and Petromyzontiformes (freshwater fishes).
- 35 – **Methods:** We used Mantel tests to investigate the raw correlation between taxonomic and
36 genetic differentiations. We carried out multiple regressions to characterise the effects of
37 geographic distance (proxy of dispersal limitation), environmental distance (proxy of
38 environmental selection) and pairwise harmonic mean area between basins (proxy of drift)
39 on taxonomic differentiation and genetic differentiation taken separately. We then
40 analysed the correlation between the residuals of these two regressions with Mantel tests.
41 Finally, we investigated whether the variation in β -SGDC between species was related to
42 species traits.
- 43 – **Results:** We detected an overall positive β -SGDC, both for the raw and the residual
44 correlations. This implies that, unmeasured effects, other than geographic distance,
45 environmental distance and harmonic mean area, influence the β -SGDC observed. Values
46 of β -SGDCs greatly varied between species, but this was not explained by any species
47 traits.

48 – **Main conclusions:** Independently of the effects of geographic distance, environmental
49 distance and harmonic mean area, the β -SGDC we observed suggests that historical
50 processes strongly shaped the patterns of taxonomic and genetic differentiations between
51 basins. Consequently, taxonomic differentiation may be an appropriate proxy to explain
52 the influence of historical processes on genetic differentiation.

53 **Keywords**

54 β -SGDC, dispersal limitation, distance decay, drift, environmental selection, freshwater
55 fishes, historical processes, macrogenetics, Mantel tests, multiple regression of distance
56 matrices

58 **Introduction**

59 Understanding the mechanisms that shape taxonomic differentiation between spatially
60 separated communities and those influencing genetic differentiation between spatially
61 separated populations are long-standing issues in ecology and evolution (Wright, 1943, 1951;
62 Whittaker, 1960, 1972; Preston, 1962; Mayr, 1963). More recently, these issues have been
63 united (Vellend, 2003; Vellend & Geber, 2005; Kahilainen, Puurtinen, & Kotiaho, 2014),
64 emphasising that drift, dispersal and selection influence both taxonomic differentiation
65 between communities and genetic differentiation between populations. Drift and selection
66 affect the species frequencies within communities and gene frequencies within populations,
67 which tend to increase differentiation. Conversely, dispersal of individuals between
68 populations and dispersal of species between communities will tend to decrease
69 differentiation.

70 Among the factors that can affect both taxonomic and genetic differentiation,
71 geographic distance is probably the most studied. The similarity in taxonomic composition
72 between communities tends to decrease with the geographic distance that separates them; a
73 pattern long-recognised in biogeography and formalised as the distance decay of similarity
74 (Nekola & White, 1999; Soininen, McDonald, & Hillebrand, 2007). Similarly, the genetic
75 similarity between populations tends to decrease with the geographic distance separating
76 them; a pattern long-recognised in population genetics and referred to as isolation-by-distance
77 (IBD; Wright, 1943; Rousset, 1997). Two main non-mutually exclusive explanations can
78 account for the distance decay of taxonomic and genetic similarity (see Soininen et al., 2007
79 and Orsini et al., 2013 for reviews). First, similarity decreases with geographic distance
80 because the dispersal of organisms (i.e. their movement from a place to another) is limited by
81 their intrinsic dispersal ability, which hence does not counteract anymore the differentiating
82 effect of drift. Secondly, similarity decays with geographic distance because of decreasing

similarity in spatially correlated environmental features; in such cases, the underlying explanation is environmental selection of different species (community differentiation) or genotypes (genetic differentiation) in distinct environments. However, differentiation between sites does not always increase with geographic distance. This is the case when the migrants are competitively excluded by already established communities (e.g. Almany, 2003) or populations (e.g. Fraser et al., 2018) at high densities, therefore counteracting the homogenising effect of dispersal whatever the intrinsic dispersal ability of the migrants. This may also happen when the environmental variation between sites displays no – or negative – spatial autocorrelation (e.g. Derry et al., 2009).

Although spatial patterns of taxonomic and genetic differentiations can be explained by environmental selection independently of limited dispersal and vice-versa, disentangling the relative strengths of these mechanisms is challenging, as communities and populations that are geographically distant are also likely to inhabit different environments. Using modern spatial statistical methods, some recent studies have nonetheless taken up the challenge. In their study of global patterns of species turnover in terrestrial vertebrates, Qian & Ricklefs (2012) have shown that both dispersal limitation and environmental selection have played important roles in determining the patterns they observed. Similarly, in their reinterpretation of 34 representative studies, Orsini *et al.* (2013) highlighted that patterns associated with dispersal limitation were as common as those associated with local genetic adaptation in structuring population genetic differentiation in the wild. However, the relative strength of dispersal limitation and environmental selection on differentiation patterns seems to vary according to the species and the spatial scale under consideration, both for taxonomic (Astorga et al., 2012; Moritz et al., 2013) and genetic (Orsini et al., 2013) differentiations. Comparative studies of multiple taxonomic groups suggest that the influence of dispersal limitation on taxonomic differentiation is stronger for species with low dispersal ability than

for more effective dispersers, and this result holds true both at the broad-scale (e.g. Qian & Ricklefs, 2012) and at the fine-scale (e.g. Astorga et al., 2012). Comparative studies of multiple species have also been identified as a promising avenue to reveal the factors influencing patterns of genetic differentiation (Wang et al., 2013). Yet, such studies are scarce and mainly carried out at relatively small spatial scales (e.g. Wang et al., 2013; Fourtune, Paz-Vinas, Loot, Prunier, & Blanchet, 2016) despite the increasing availability of broad-scale datasets in population genetics, suggesting that it is now time to embrace macrogenetics (Blanchet, Prunier, & De Kort, 2017).

Theories in population genetics and community ecology acknowledge that dispersal, selection and drift together shape the differentiation between populations and between communities (see e.g. Vellend & Orrock, 2009 for a review of processes in both disciplines). However, the contribution of drift to taxonomic or genetic differentiation has been the subject of few empirical investigations, in contrast with dispersal limitation and environmental selection (Gilbert & Levine, 2017; Prunier, Dubut, Chikhi, & Blanchet, 2017). Genetic drift is the evolutionary process of random fluctuations in allelic frequencies occurring naturally in all populations due to their finite size, although it is stronger in small ones (Allendorf, 1986). Similarly, ecological drift corresponds to the random fluctuations in species frequencies occurring naturally in all communities due to their finite size and this too is stronger in small ones. Drift is the result of random sampling during the processes of birth, death and reproduction and ultimately leads to the loss of genetic diversity within populations, and species diversity within communities. Therefore, drift increases the differentiation between populations and between communities depending on their respective sizes: the smaller they are, the more they will differentiate. Dispersal of organisms between populations and between communities counteracts the differentiating effect of drift while environmental selection can accelerate it. Attributing the observed spatial patterns of genetic or taxonomic differentiation

to dispersal limitation or to environmental selection without accounting for drift may thus be misleading.

Most of the explanatory variables used in analyses to infer the role of dispersal limitation and environmental selection on differentiation patterns are proxies representing present-day conditions. Thus, using current explanatory variables to investigate dispersal limitation and environmental selection on differentiation patterns is only relevant if the contemporary geography and environment of the study area has not changed substantially since these patterns were established (Wang et al., 2013). Otherwise, the historical processes that may have shaped the observed differentiation patterns, including those explaining colonisation histories, may be overlooked. In addition, if dispersal is not continuous (as generally assumed) but rather intermittent because of landscape dynamics which have induced the appearance and disappearance of dispersal barriers, then two geographically close localities sharing a similar environment could, nevertheless, be dissimilar in terms of community composition and allele frequencies provided they have been isolated for a sufficiently long time (given their sizes) for drift to be effective. Nonetheless, examining which part of differentiation patterns is not explained by current explanatory variables may help to elucidate the influence of historical processes on those patterns.

In such complex contexts, understanding the rules that govern differentiation patterns (both taxonomic and genetic) may be enhanced by comparing taxonomic dissimilarities between communities and genetic dissimilarities between populations of a focal species (Lamy, Laroche, David, Massol, & Jarne, 2017). The few empirical studies that have examined these correlations, called beta species-genetic diversity correlations (β -SGDCs) (Kahilainen et al., 2014), revealed a majority of positive correlations (reviewed by Lamy et al., 2017). This suggests that the processes affecting taxonomic dissimilarity affect genetic dissimilarity of the species under study in the same way (Baselga et al., 2013; Baselga,

Gómez-Rodríguez, & Vogler, 2015). However, because the relative strength of processes shaping patterns of taxonomic and genetic differentiation is expected to vary according to the species and the spatial scale under consideration, so is the strength of the putative resulting β -SGDCs. Among the rare studies of β -SGDCs over multiple species, some have highlighted that positive β -SGDCs were stronger for focal species with low dispersive abilities (e.g. Papadoulou et al., 2011) while others did not find strong differences between species (e.g. Fourtune et al., 2016), and all were carried out at relatively small spatial scales. These contrasting results call for more studies of β -SGDCs for multiple species to gain a better understanding of whether and how variations in species traits lead to distinct patterns of β -SGDCs. In addition, β -SGDCs for multiple species have not been examined yet at broad spatial scales.

Freshwater fishes are a relevant model to start investigating this question for at least three reasons. First, as β -SGDCs for multiple freshwater fish species have been conducted at small scales within a single drainage basin (Fourtune et al., 2016), computing β -SGDCs for multiple freshwater fish species at broader scales will permit the comparison of β -SGDC variations across scales for the same biological model. Secondly, for strictly freshwater fishes, at present, almost no exchange of individuals occurs between drainage basins (hereafter “basins”) because they are isolated from each other by land and/or sea (although dispersal may occasionally occur between adjacent basins). Therefore, if basins are isolated from each other independently of the geographic distance between them, we can expect dispersal limitation to play a minor role on the broad-scale between-basin patterns of taxonomic and genetic differentiations. On the contrary, if basins have been isolated from each other for a long time, we can expect drift to play a significant role on the broad-scale between-basin patterns of taxonomic and genetic differentiations, as dispersal no longer counteracts the effect of drift. This is particularly true if population sizes and community sizes are small: the

larger they are, the longer it will take to observe differentiation. Finally, while several recent studies have tried to disentangle the role of dispersal limitation, environmental selection and historical processes on patterns of taxonomic differentiation between basins (Leprieur et al., 2009, 2011; Dias et al., 2014), the processes shaping genetic differentiation at such broad scales have rarely been examined together. Studying β -SGDCs may therefore reveal whether the processes influencing between-basin taxonomic differentiation, affect between-basin genetic differentiation in the same way.

In this meta-analysis of 22 freshwater fish species, our main goal was to elucidate the processes underlying β -SGDCs at broad spatial scales. In particular, we wanted to test whether β -SGDCs can be explained by the parallel action of measurable processes (dispersal limitation, environmental selection and drift) on taxonomic and genetic differentiation, or are due to other, non-measurable processes. To that end, we first computed measures of genetic differentiation between basins for each fish species. Then, for each species, we investigated i) the raw correlation between taxonomic and genetic differentiations, ii) the effects of geographic distance (as a proxy of dispersal limitation), environmental distance (as a proxy of environmental selection) and pairwise harmonic mean area between basins (as a proxy of drift) on taxonomic differentiation and genetic differentiation taken separately and iii) the correlation between taxonomic and genetic differentiations independent of the effects of geographic distance, environmental distance and harmonic mean area (Fig. 1). Such independent correlation integrates the effects of unmeasured processes, including the historical processes of dispersal, environmental selection and drift related to the historical connectivity of basins. This allowed us to characterise the overall (i.e. mean over the species) raw β -SGDC, the overall effects associated with each predictor for each response variable, and the overall independent β -SGDC. Finally, we tested whether the variation in β -SGDCs between species could be attributed to variations in species traits.

208

209 **Materials and methods**210 *Genetic differentiation and geographic distribution of genetic data*

211 As we wanted to investigate genetic differentiation at the broad scale, we restricted our
212 analyses of spatial genetic differentiation to species exhibiting a wide distribution. We
213 downloaded sequence records of the mitochondrial gene cytochrome c oxidase I (COI) from
214 BOLD (www.boldsystems.org) in May 2017 for the following widespread taxa: Cyprinidae,
215 Salmonidae, *Lampetra*, *Petromyzon*, *Cobitis*, *Misgurnus*, *Barbatula*, *Silurus*, *Esox*, *Lota lota*,
216 *Gymnocephalus* and *Sander*. We first cleaned and aligned sequences by taxon and then re-
217 aligned them together to keep the same fragment of 501 nucleotides for the analyses.
218 Sequence records without sufficient geographic information to assign them to a drainage
219 basin (hereafter “basin”) or without a species name were discarded from our dataset. We
220 defined a basin as the drainage area upstream from its mouth at the sea. According to this
221 definition, a basin is isolated from other basins by barriers (sea or land) which are impassable
222 for strictly freshwater fishes. The validity of species names was assessed using FishBase
223 (Froese & Pauly, 2017), resulting in a total of 6637 sequence records with a valid species
224 names belonging to 716 distinct species distributed in 218 basins. We checked the
225 environment (i.e. “freshwater”, “brackish”, “saltwater”) of each species using FishBase
226 (Froese & Pauly, 2017), the status (i.e. “native”, “exotic” or “unknown”) of each species in
227 each basin using the global database on freshwater fish species occurrence (Tedesco et al.,
228 2017). We conserved only native records of strictly freshwater species, i.e. 4894 records,
229 corresponding to a total of 509 species in 176 basins.

230 We calculated between-basin genetic differentiation (by pooling individuals in the
231 drainage basins) for the polymorphic species present in at least four basins with a minimum of

three individuals per basin. To calculate such genetic differentiation, we converted single nucleotide polymorphisms (SNPs) of the sequence data into a table of individual genotypes and then calculated pairwise genetic distances for each pair of basins using G''_{ST} (Meirmans & Hedrick, 2011), the corrected version of Hedrick's G'_{ST} (Hedrick, 2005). G''_{ST} is independent from within population diversity and does not underestimate genetic distance when the number of populations is small (Meirmans & Hedrick, 2011). As G''_{ST} likely removes the effect of drift, we also calculated the pairwise genetic distances for each pair of basins using F_{ST} (Nei, 1973) for comparison purpose.

All these different selection filters drastically reduced the number of species we included in analyses: we finally focused our analyses of between-basin genetic differentiation on a total of 22 species in 38 basins (for more details about these basins, see Appendix S1 in Supporting Information). For instance, from all the species of *Lampetra* and *Petromyzon* we searched in BOLD, we conserved only *L. planeri* for the analyses. The number of species with analysed genetic data per basin varies from one (for 20 basins) to seventeen (for one basin, the basin “Odra”; Fig. 2; Appendix S1). The number of basins per species varies from four (our minimum threshold) to eleven (for the species *Esox lucius*) covering on average 76 % (standard deviation (sd) = 18 %) of their native range, with species exhibiting on average 11.0 individuals per basin (sd = 11.0; Appendix S2). Most records are located in Europe and North-America (Fig. 2).

Taxonomic differentiation

We calculated pairwise taxonomic differentiation between each pair of basins based on the list of native species per basin extracted from the global database on freshwater fish species occurrence (Tedesco et al., 2017). We used Simpson dissimilarity (β_{sim}) - the turnover component of Sørensen dissimilarity (Sørensen, 1948) - which is independent from total

256 taxonomic richness (see Baselga 2012 for review).

257 *Geographic distance, environmental distance and pairwise harmonic mean area*

258 We computed between-basin geographic distance by calculating the distance between basin
259 centroids. The average distance between basins was 5 295 km (sd = 3 920 km). Measurements
260 of geographic distance were then centred and scaled before further analyses.

261 To characterise the environment of the basins, we used variables related to the
262 contemporary climate known to influence freshwater fish alpha diversity patterns at the global
263 scale (e.g. Dias et al. 2014; Oberdorff et al. 2011; Tedesco et al. 2012; Tisseuil et al. 2013) i.e.
264 mean annual temperature and precipitation (<http://www.worldclim.org/>), mean annual surface
265 runoff (<http://www.grdc.sr.unh.edu/>) and mean annual actual and potential evapotranspiration
266 (<http://csi.cgiar.org/Aridity/>). The mean values of all the variables were computed for each
267 basin. To compute pairwise environmental distances between each pair of basins, we
268 performed a principal component analysis (PCA) on these environmental variables
269 (previously centred and scaled) and calculated the Euclidean distance between basins based
270 on the first three PCA axes.

271 Finally, we calculated the pairwise harmonic mean area between each pair of basins.
272 Indeed, the harmonic mean population size between pairs allows the role of drift on genetic
273 differentiation (Serrouya et al., 2012) to be taken into account and can be computed using
274 environmental proxies for local carrying capacities (Prunier et al., 2017). In our case, we used
275 the surface area of the basin as a raw environmental proxy for local carrying capacity. The
276 basins studied had an average surface area of 257 589 km² (sd = 584 803 km²). Measurements
277 of harmonic mean area were centred and scaled before further analyses.

278 *Statistical analyses*

First, we investigated the raw correlation between taxonomic differentiation and genetic differentiation for each species individually using a Mantel correlation test with 999 permutations. To test the null hypothesis that there is no relationship between taxonomic differentiation and genetic differentiation using the information provided by all the species examined, we considered that this hypothesis has been tested independently n times, with n being the number of species included in the analyses. To combine the results from several independent tests bearing upon the same overall hypothesis, we used a modification of the Fisher's combined probability test. Under the null hypothesis that taxonomic and genetic differentiations are unrelated, observed p-values associated with the Mantel's test of each species are expected to be distributed according to a uniform distribution in $[0, 1]$. We therefore compared the observed mean p-value over the species to a null distribution of mean p-values obtained by sampling randomly 10 000 times one p-value by species in a uniform distribution in $[0, 1]$. We calculated the p-value associated with the combined test as the frequency at which null mean p-values were below the observed mean p-value. This procedure avoids some problems identified by the use of a chi-2 test (e.g. Whitlock, 2005) which was the method initially proposed by Fisher.

To investigate the putative roles of dispersal limitation, environmental selection and drift on taxonomic and genetic differentiations, for each species we built multiple regressions of geographic distance (D_{geo}), environmental distance (D_{env}) and harmonic mean area (D_{area}) on taxonomic differentiation (TD) and genetic differentiation (GD) taken separately (Fig. 1) as follows: $TD = \alpha_0 + \alpha_1 * D_{\text{geo}} + \alpha_2 * D_{\text{env}} + \alpha_3 * D_{\text{area}}$ and $GD = \beta_0 + \beta_1 * D_{\text{geo}} + \beta_2 * D_{\text{env}} + \beta_3 * D_{\text{area}}$. Our approach is very similar to multiple regressions on distance matrices (MRM; Lichstein 2007) except in the way we calculated p-values associated with partial regression coefficients. As in MRM, we permuted the rows and associated columns of the response distance matrix simultaneously. We repeated this operation 1999 times while holding the

explanatory distance matrices constant to generate null distributions for partial regression coefficients. Then, in MRM, the p-value associated with a partial regression coefficient is calculated with a two-sided permutation test using the pseudo-t of Legendre et al. (1994), i.e. it tests whether the t-statistic associated with each regression coefficient is lower or higher than expected under a null distribution of pseudo-t obtained by permutation. In our approach, we hypothesised that geographic distance and environmental distance have a positive effect on both taxonomic and genetic differentiations (dispersal limitation and environmental selection enhance differentiation and are positively related to geographic and environmental distances respectively) while harmonic mean area has a negative effect on taxonomic and genetic differentiations (drift enhances differentiation and is negatively related to the harmonic mean area). To increase the statistical power of the tests, we therefore carried out one-sided tests for calculating the p-values associated with each partial regression coefficient. We tested the overall (i.e. over the species) effects of geographic distance, environmental distance and harmonic mean area on taxonomic and genetic differentiations by performing a combined probability test as described for the raw correlation between taxonomic and genetic differentiations, but this time considering probabilities associated with partial regression coefficients.

To examine whether taxonomic and genetic differentiations were still correlated once the effects of geographic distance and environmental distance had been taken into account, we then performed a Mantel correlation test between the residuals of the multiple regression on taxonomic differentiation and the residuals of the multiple regression on genetic differentiation with 999 permutations for each species. We tested this overall (i.e. over the species) residual correlation using a combined probability test as described for the raw correlation between taxonomic and genetic differentiations.

Finally, we examined the heterogeneity between species regarding the residual correlation between taxonomic and genetic differentiations and tested whether some species traits could explain such heterogeneity. The species traits initially considered were body length, longevity in the wild, vulnerability, used in aquaculture, use as bait, use in the aquarium, habitat, migratory behaviour and dispersal ability – which was calculated using a formula giving dispersal distance as a function of body size and caudal fin aspect ratio (Radinger & Wolter, 2014). However, as migratory behaviour was ‘potamodromous’ for 16 out of the 22 species, ‘non-migratory’ for one species and the information was not available for the 5 species left, we excluded this non-informative trait from our analyses. Species traits were directly extracted from FishBase (Froese & Pauly, 2017). All the analyses and the corresponding figures were realised with R 3.5.1 (R Core Team 2018) using the packages ‘ade4’ (Dray & Dufour, 2007), ‘ape’ (Paradis, Claude, & Strimmer, 2004), ‘betapart’ (Baselga, Orme, Villeger, De Bortoli, & Leprieur, 2018), ‘Biostrings’ (Pagès, Aboyoun, Gentleman, & DebRoy, 2018), ‘broom’ (Robinson & Hayes, 2018), ‘ggplot2’ (Wickham, 2016), ‘ggthemes’ (Arnold, 2018), ‘hierfstat’ (Goudet & Jombart, 2015), ‘maptools’ (Bivand & Lewin-Koh, 2018), ‘mmod’ (Winter, 2012), ‘RColorBrewer’ (Neuwirth, 2014), ‘rgdal’ (Bivand, Keitt, & Rowlingson, 2018), ‘rgeos’ (Bivand & Rundel, 2018), ‘reshape2’ (Wickham, 2007), ‘seriation’ (Hahsler, Buchta, & Hornik, 2018) and ‘vegan’ (Oksanen et al., 2018).

Results

We detected an overall positive correlation between taxonomic and genetic differentiations, significantly different from 0. This result holds true both for the raw correlation between taxonomic and genetic differentiations ($r_{\text{mean} \pm \text{sd}} = 0.433 \pm 0.420$; Fig. 3a; Appendices S3, S4)

and for the residual correlation, i.e. the correlation between taxonomic and genetic differentiations independent of the effects of geographic distance, environmental distance and harmonic mean area ($r_{\text{mean} \pm \text{sd}} = 0.379 \pm 0.641$; Fig. 3b; Appendices S3, S4).

There was almost no overall effect of geographic distance on taxonomic differentiation ($\alpha_1_{\text{mean} \pm \text{sd}} = 0.032 \pm 1.051$) or on genetic differentiation ($\beta_1_{\text{mean} \pm \text{sd}} = -0.011 \pm 1.060$), and these overall effects did not differ significantly from 0 (Fig. 4; Appendices S5, S6, S7). In contrast, we detected an overall positive effect of environmental distance on both taxonomic differentiation ($\alpha_2_{\text{mean} \pm \text{sd}} = 0.405 \pm 0.956$) and genetic differentiation ($\beta_2_{\text{mean} \pm \text{sd}} = 0.229 \pm 0.865$), although it was only significantly different from 0 for taxonomic differentiation (Fig. 4; Appendices S5, S6, S7). There was an overall negative effect of harmonic mean area on both taxonomic differentiation ($\alpha_3_{\text{mean} \pm \text{sd}} = -0.178 \pm 0.617$) and genetic differentiation ($\beta_3_{\text{mean} \pm \text{sd}} = -0.092 \pm 0.713$), but it was only significantly different from 0 for taxonomic differentiation (Fig. 4; Appendices S5, S6, S7). Using F_{ST} as a measure of genetic differentiation did not change the trend we observed: there was an overall negative but not significant effect of harmonic area on F_{ST} (Appendices S6, S7).

The results of these multiple regressions as well as the residual correlations between taxonomic and genetic differentiations are summarised in Fig. 5. Overall, they suggest that the effect of geographic distance, environmental distance and harmonic mean area only explain a small part of the correlation between taxonomic and genetic differentiations.

Despite this strong overall independent correlation between taxonomic differentiation of freshwater fish communities and genetic differentiation of freshwater fish populations, the correlation between taxonomic and genetic differentiations varied greatly between species (Fig. 3b; Appendix S3). For some species, such as the common roach *Rutilus rutilus* (Fig. 6a, b), there was a sound correlation between taxonomic differentiation and genetic

differentiation, whether we considered the raw or residual correlation. In other species, such as the common chub *Squalius cephalus*, taxonomic differentiation and genetic differentiation were not correlated (Fig. 6c, d). In this species, genetic differentiation was better predicted by geographic distance and harmonic mean area (Appendix S5). However, none of the species traits examined explained this heterogeneity of responses between species (Appendix S8).

Discussion

Our analyses indicated that taxonomic and genetic differentiations are strongly correlated overall, and independently of the parallel effects of geographic distance, environmental distance and harmonic mean area on taxonomic and genetic differentiations. This suggests that the parallel influence of dispersal limitation, environmental selection and drift on taxonomic and genetic differentiations only partially explains the overall β -SGDC we observed. This independent, unexplained correlation between taxonomic and genetic differentiations thus probably results from processes that we did not explicitly consider in our study. The most probable explanation is that the independent β -SGDC we observed is due to the parallel action of historical processes, which occurred when the basins were still connected, on taxonomic and genetic differentiations. These historical processes include all the different processes that explain the colonisation history of basins (Orsini et al., 2013): i) the dispersal of individuals between previously connected basins in interaction with environmental and/or biotic selection on their dispersal route and ii) environmental and/or biotic selection in interaction with drift within their place of arrival and/or origin that may have led to extinction. This explanation is supported by previous studies on the influence of historical processes on broad-scale taxonomic differentiation between freshwater fish communities on the one hand and on broad-scale genetic differentiation between freshwater

400 fish populations on the other hand. Two recent studies on global freshwater fish biodiversity
401 have shown that present-day patterns of taxonomic dissimilarity across basins are well
402 explained by the historical connectivity of basins (Dias et al., 2014) and also historical
403 climatic oscillations that took place during the Quaternary and the Holocene (Leprieur et al.,
404 2011). For fish species, it is well known that historical dispersal influences genetic structure
405 across basins (Carvalho, 1993), especially for zones that were subject to intense post-glacial
406 recolonisation such as our study area. Multispecies comparisons at large spatial scales in
407 Europe (Seifertová, Bryja, Vyskočilová, Martínková, & Šimková, 2012) and in North
408 America (April, Hanner, Mayden, & Bernatchez, 2013) have shown that the climatic
409 fluctuations that caused glacial cycles during the Pleistocene had a generalised effect on the
410 patterns of fish genetic divergence. In addition, three other, non-exclusive hypotheses may
411 explain the independent β -SGDC we observed. First, the proxies we used to account for
412 dispersal limitation, environmental selection and drift may not fully represent these processes.
413 For instance, we may have overlooked some environmental variables that are important in
414 driving environmental selection. Alternatively, we may have poorly estimated the role of drift,
415 either because the area of the basin we used to account for drift may be too approximate to
416 accurately represent the carrying capacities of populations and communities or because we
417 did not consider that the influence of drift within a basin increases with its age of isolation.
418 Secondly, the sequence data we used to calculate genetic differentiation may not detect
419 dispersal limitation and/or environmental selection properly, either because they did not cover
420 the entire native ranges of species (see possible consequences of such sampling bias in e.g.
421 Meirmans, 2015), or because the mitochondrial gene COI is not directly under environmental
422 selection. Finally, the proposed frameworks to interpret SGDCs (Vellend & Geber, 2005;
423 Lamy et al., 2017) suggest that correlations between species diversity and genetic diversity
424 may also result from a causal action of species diversity on genetic diversity or vice-versa.

For instance, if the focal species (i.e. the species for which we studied genetic diversity) is a facilitator for the other component species of the community, we would expect their populations sizes to co-vary positively, resulting in a positive α -SGDC; the converse is expected if the focal species is a competitor. If the nature of the interaction between the focal species and the other species of the community is generally the same within each basin, such causal effect is not expected to influence the β -SGDC we observed. However, if the focal species is facilitator in one basin and competitor in another, we would expect the population sizes of the other component species of the community to increase in the first case and decrease in the second case. This would result in more ecological drift within the community where the focal species is competitor, and therefore more taxonomic differentiation between basins than would be expected without this causal effect. In the end, such causal effect would tend to reduce β -SGDC because it would increase taxonomic differentiation between basins without influencing genetic differentiation.

Moreover, our results contribute new insights into the study of β -SGDCs. With the study of 22 new β -SGDCs, we increased the number of β -SGDCs (43) previously reported in the literature by more than 50 % (see Lamy *et al.*, 2017 for the most recent review). We found an average raw correlation between taxonomic and genetic differentiations of 0.433, and an independent correlation (i.e. independent from the parallel effects of geographic distance, environmental distance and harmonic mean area on taxonomic and genetic differentiations) of 0.379. Both of these values are superior to the average value of 0.221 reported by Lamy *et al.* (2017). They are also around three times superior to the average value of 0.139 found by Fourtune *et al.* (2016) in their study of four freshwater fish species at a smaller scale, within one drainage basin. This suggests that the strong correlations we found are probably more related to the size and/or the isolation of the habitats we studied (i.e. large drainage basins isolated from each other) rather than our biological model. Previous syntheses have reported

that α -SGDCs (i.e. correlations between genetic diversity within populations and species diversity within communities) are stronger and more often positive in island-like habitats (Vellend & Geber, 2005; Vellend et al., 2014), in agreement with the predictions of theoretical models (Laroche et al., 2015). As drainage basins are typically island-like habitats (Sepkoski & Rex, 1974; Hugueny, 1989), our findings suggest that this explanation may hold true for β -SGDCs as well. The observed differences also suggest that for a system without present-day dispersal the β -SGDC is stronger than in systems with present-day dispersal. Actually, the opposite could have been expected (i.e. weaker β -SGDCs for systems without present-day dispersal than for systems with present-day dispersal) if the genetic similarity between two previously connected populations had been erased by genetic drift occurring after their isolation without changes in species composition (i.e. no species extinction). However, our results suggest that drift did not influence significantly the patterns of genetic differentiation we observed. As this result holds true both for G''_{ST} and F_{ST} , this is probably because we mainly focused on large drainage basins and consequently large population sizes.

Our results also indicate that the sign and magnitude of β -SGDCs varied greatly between the different species we examined. We provided two examples. On the one hand, we showed that the β -SGDC was strong for *Rutilus rutilus*, suggesting that historical processes largely shaped the patterns of genetic differentiation observed in this species. This is consistent with a previous study indicating that *R. rutilus* is composed of two historically isolated, independently evolving sets of populations (Larmuseau et al., 2009). On the other hand, our results indicate that genetic differentiation in *Squalius cephalus* was not correlated to taxonomic differentiation, but was well explained by geographic distance. This suggests that dispersal limitation has a more important effect than any other processes on broad-scale genetic differentiation in *S. cephalus*. This might seem surprising, since previous analyses of the mitochondrial gene cytochrome b in that species indicated four main lineages originating

from multiple glacial refugia (Durand, Persat, & Bouvet, 1999; Seifertová et al., 2012). However, the use of a combination of both mitochondrial and nuclear DNA, Seifertová et al. (2012) also suggested that genetic differentiation in *S. cephalus* resulted from a combination of different factors, i.e. post-glacial colonisation from different refugia or recent evolutionary processes such as drift or dispersal limitation. Our results based on the analysis of the mitochondrial gene COI strongly support the dispersal limitation hypothesis although, as we did not design the sampling, but analysed existing data, we might not have captured the whole picture. As *R. rutilus* and *S. cephalus* have similar dispersal abilities, this difference of β -SGDC between the two species does not seem to be related to their difference in dispersal abilities. Beyond these two species and this single trait, our analyses did not permit us to uncover any trait that could explain the variability of β -SGDC over the 22 species we examined. This is surprising because life-history traits of species are known to shape spatial patterns of genetic differentiation (e.g. Duminil et al., 2007; Kelly & Palumbi, 2010), and therefore β -SGDC. This unexpected finding may be due to different reasons. First, the variability of β -SGDC may be due to species traits that we did not consider. Secondly, the β -SGDC at the specific scale was sometimes examined for a small number of basins, which may result in wide variations in the estimated correlation coefficients. Therefore, single species outcomes should be interpreted with great caution.

To conclude, this study of broad-scale β -SGDC for multiple freshwater fish species suggests that historical processes greatly contributed to the shape of present-day patterns of taxonomic and genetic differentiations, independently of contemporary processes. This implies that taxonomic differentiation may be an appropriate proxy to explain the role of historical processes on patterns of genetic differentiation, which remains a challenging issue in landscape genetics (Dyer, Nason, & Garrick, 2010). We believe that further studies of broad-scale β -SGDCs comparing organisms whose dispersal is limited within habitat patches

500 with organisms that are able to disperse across habitat patches, will help to investigate the
501 extent to which our findings can be generalised.

Figures

504

Figure 1. Illustration of the different processes expected to act in parallel on between-basin taxonomic differentiation of freshwater fish communities (TD) and on between-basin genetic differentiation of freshwater fish populations (GD) at different periods and the proxies used in this study to infer those processes. The black frame encompasses the causal diagram depicting the relationships that we actually tested in this study, i.e. the effects of geographic distance (proxy of contemporary dispersal limitation), environmental distance (proxy of contemporary environmental selection) and pairwise harmonic mean area between basins (proxy of contemporary drift) on TD and GD. The double arrow between TD and GD represent the residual correlation, i.e. the correlation between TD and GD which is not explained by the parallel influence of contemporary dispersal limitation, contemporary environmental selection

515 and contemporary drift on TD and GD. The numbers on the arrows and the signs below them
516 correspond to our theoretical expectations regarding the different effects which are detailed in
517 the text below the black frame. The grey arrows represent the putative effects of historical
518 dispersal limitation, historical environmental selection and historical drift on TD and GD that
519 we did not directly test in our statistical approach. The grey polygons on the right side
520 represent the evolution of the basin configuration through time from one unique basin to two
521 distinct and disconnected basins, with almost no contemporary dispersal of individuals
522 between them (dispersal may occasionally occur between adjacent basins).

524

525 **Figure 2.** Spatial distribution of the number of species with analysed genetic data per basin
 526 studied in our analyses at the global scale. Top: the rectangle indicates the location of the
 527 enlarged area. Bottom: enlarged area including Europe and North America. In total, our study
 528 encompasses 22 species with analysed genetic data in 38 basins.

Figure 3. Violin plots showing the distribution and the probability density of (a) raw correlations coefficients and (b) residual correlation coefficients between taxonomic differentiation and genetic differentiation for the 22 fish species examined at global scale. Crossbars indicate mean $\pm$ standard deviation.

Figure 4. Violin plots showing the distribution and the probability density of the effect of geographic distance, environmental distance and harmonic mean area (as standardised regression coefficients) for the 22 fish species examined at global scale on (a) taxonomic differentiation and (b) genetic differentiation. Crossbars indicate mean $\pm$ standard deviation.

Figure 5. Causal diagram depicting the results of multiple regressions of geographic distance, environmental distance and harmonic mean area on TD and GD (taken separately). Arrows represent putative causal effects through the standardised regression coefficients (positive values: solid arrows; negative values: dotted arrows; arrow width is proportional to coefficient value). The R^2 represent the part of variance explained by the multiple regressions on TD (left) and GD (right). U_{TD} and U_{GD} represent unspecified factors influencing TD and GD respectively. The double arrow between SD and GD corresponds to the residual correlation. All numerical values represent means for the 22 fish species examined at global scale.

Figure 6. Observed (dots) and predicted (dashed line) raw values (a, c) and residual values from the multiple regressions (b, d) of genetic differentiation as a function of taxonomic differentiation for the two fish species (a, b) *Rutilus rutilus* and (c, d) *Squalius cephalus*.

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753 **Biosketch**

754 The authors are particularly interested in documenting and explaining spatial patterns of
755 biodiversity at large spatial scales. They try to disentangle the interplay between historical and
756 contemporary factors (including anthropogenic pressures) in shaping patterns of alpha and
757 beta diversities in aquatic populations and communities and value this knowledge to guide
758 conservation strategies of aquatic ecosystems.

759 **Supporting information**

760 Supporting information for this article may be found online.

761 **Data availability**

762 The data and the script used for the analyses are available from the Dryad Digital Repository:
763 <https://doi.org/10.5061/dryad.8vb6160>.

SUPPORTING INFORMATION

Correlations between broad-scale taxonomic and genetic differentiations suggest a dominant imprint of historical processes on beta diversities

Marine Robuchon, Boris Leroy, Céline Jézéquel and Bernard Hugueny

Appendix S1 Characteristics of the drainage basins analysed in our study

aet = mean annual actual evapotranspiration; pet = mean annual potential evapotranspiration; tmoy = mean annual temperature ; precsum = mean annual precipitation; runoff = mean annual surface runoff; Surface_area_km = surface area; N_species = number of species with genetic data. See main text for the source of data. Mean and standard deviation (SD) over the 38 basins are given at the end of the table.

Basins	aet	pet	tmoy	precsum	runoff	Surf_area_km	N_species
Acheloos	640	1066.1	123.27929	924.009	557.74899	5821.728156	1
Agly	630	906.3	125.49053	770.632	116.367	1125.200682	3
Arachthos	655	1034.7	113.31274	1004.44	742.65767	2473.939349	1
Aude	625	928.5	123.53473	781.976	130.21899	5283.136409	1
Axios	493	986.3	101.52936	601.732	154.31825	24583.23488	3
Charente	644	911.6	120.03306	867.967	233.5864	9561.56072	1
Churchill	398	582	-23.90383	475.655	118.85188	304248.866	1
Danube	574	850.7	87.342907	750.564	295.57456	802142.8624	16
Delaware	813	991.2	91.341375	1148.11	623.8048	28618.74225	1
Dordogne	682	935.2	111.27602	886.614	350.67982	24113.64285	1
Elbe	507	721.7	79.989063	623.004	178.65205	143864.5137	16
Evinos	629	1068.6	124.6515	898.565	462.55499	1105.990108	1
Evros	525	994.7	112.64752	622.026	233.69195	53005.94877	1
Garonne	653	932	111.66166	822.437	258.36741	55217.94818	2
Glomma	404	469.2	8.6601708	730.294	415.933	41930.43322	4
Grande.USA	333	1517.8	163.21044	395.802	11.279145	480465.5835	2
Guadalupe	714	1510	198.33098	844.73	31.73177	15777.64583	1
Hudson	756	924.8	71.827872	1118.13	526.25893	34795.07612	1
Loire	602	854.6	105.10719	750.497	196.85747	116661.6899	2
Louros	663	1121.3	145.51997	1040.27	713.57898	1080.177613	1
Mackenzie	329	521.7	-43.57659	392.294	160.29758	1680044.211	1
Meuse	588	732.3	91.633783	886.959	285.14163	32856.16342	1
Mississippi	618	1096.6	95.416708	759.456	222.75135	3017672.487	4
Nelson	418	726	12.974033	492.429	95.228112	1019864.883	1
Odra	489	737.8	81.363189	581.098	155.37879	118991.636	17
Pearl	1119	1437.3	178.64183	1495.1	483.74908	21790.63225	1

Po	635	788.2	92.085106	1020.21	519.70202	73831.63159	5
Rhine	588	738.1	82.161385	872.964	475.19941	163633.2382	16
Rhone	629	802.8	85.285926	1019.07	479.94488	96827.05122	10
Rihios	414	1063.9	139.98324	484.53	1.7229	2088.952236	2
Saint.Jean.USA	635	762.6	36.171725	1049.03	608.68723	54888.62971	1
Saint.Laurent	629	811.7	49.93017	884.414	343.00659	1056005.322	6
Sakarya	421	1033.3	106.13612	497.924	62.963135	70666.64849	2
Santee	985	1322.8	155.71445	1239.84	132.91453	39531.78697	1
Seine	559	811.4	101.43787	690.465	173.8974	75984.27645	3
Strymon	459	957.1	104.39717	545.061	93.719109	16826.18541	1
Susurluk.Cayi	578	1056.4	120.13898	727.301	111.40774	23768.99736	4
Tagus	459	1097.2	136.86304	565.262	214.13121	71216.07416	1
Mean	591.9	942.2	97.9	796.3	288.8	257588.6	3.6
SD	158.5	237.6	50.0	245.9	204.0	584802.5	4.8

Appendix S2 Descriptive statistics of the datasets used for analyses

N_basins_genet = number of basins with genetic data analysed; N_basins_native = number of basins where the species is recorded as native; Prop_basins_genet/native = proportion of basins with genetic data analysed over basins where the species is recorded as native; N_indiv_tot = total number of individuals; N_indiv_mean = mean number of individuals by basin; N_indiv_min = minimum number of individuals in a basin; N_indiv_max = maximum number of individuals in a basin. Mean and standard deviation (SD) over the 22 species are given at the end of the table.

Species	N_basins_genet	N_basins_native	Prop_basins_genet/native	N_indiv_tot	N_indiv_mean	N_indiv_min	N_indiv_max
<i>Abramis brama</i>	4	8	0.500	46	12	6	16
<i>Alburnoides bipunctatus</i>	5	5	1.000	31	6	4	13
<i>Alburnus alburnus</i>	5	8	0.625	43	9	3	18
<i>Barbatula barbatula</i>	4	4	1.000	55	14	5	22
<i>Campostoma anomalum</i>	4	6	0.667	30	8	5	15
<i>Chondrostoma nasus</i>	4	5	0.800	71	18	5	35
<i>Esox lucius</i>	11	16	0.688	97	9	3	15
<i>Gobio gobio</i>	7	8	0.875	71	10	3	22
<i>Lampetra planeri</i>	4	6	0.667	27	7	3	10
<i>Leuciscus aspius</i>	4	5	0.800	34	9	3	17
<i>Leuciscus leuciscus</i>	4	5	0.800	47	12	4	19
<i>Lota lota</i>	5	7	0.714	37	7	5	13
<i>Notropis atherinoides</i>	4	4	1.000	25	6	4	11
<i>Phoxinus phoxinus</i>	4	4	1.000	234	59	5	207
<i>Rhinichthys atratulus</i>	5	5	1.000	28	6	3	11
<i>Rhinichthys cataractae</i>	4	5	0.800	39	10	5	17
<i>Rutilus rutilus</i>	6	11	0.545	58	10	3	17
<i>Scardinius erythrophthalmus</i>	4	11	0.364	26	7	3	10
<i>Squalius cephalus</i>	11	16	0.688	87	8	3	21
<i>Telestes pleurobipunctatus</i>	4	6	0.667	20	5	3	9
<i>Thymallus thymallus</i>	6	7	0.857	41	7	4	11
<i>Tinca tinca</i>	5	7	0.714	32	6	3	13
Mean	5.2	7.2	0.762	53.6	11.0	3.9	24.6
SD	2.1	3.4	0.175	45.3	11.0	1.0	41.1

Appendix S3 Results of the Mantel tests between taxonomic differentiation and genetic differentiation (raw correlations) and between the residuals of taxonomic differentiation and genetic differentiation (residual correlations)

r is the Mantel r coefficient; mean and standard deviation (SD) over the 22 species are given at the end of the table

Species	Raw correlations		Residual correlations	
	r	pval	r	pval
<i>Abramis brama</i>	0.539	0.167	0.949	0.042
<i>Alburnoides bipunctatus</i>	0.963	0.100	0.885	0.008
<i>Alburnus alburnus</i>	-0.098	0.333	-0.781	0.975
<i>Barbatula barbatula</i>	0.327	0.458	0.716	0.083
<i>Campostoma anomalum</i>	0.333	0.250	-0.857	1.000
<i>Chondrostoma nasus</i>	0.841	0.042	0.784	0.042
<i>Esox lucius</i>	0.685	0.077	0.040	0.406
<i>Gobio gobio</i>	0.586	0.174	0.112	0.354
<i>Lampetra planeri</i>	-0.306	0.583	0.900	0.083
<i>Leuciscus aspius</i>	0.448	0.167	0.825	0.042
<i>Leuciscus leuciscus</i>	0.511	0.167	-0.989	1.000
<i>Lota lota</i>	0.918	0.050	0.793	0.008
<i>Notropis atherinoides</i>	0.725	0.208	0.221	0.375
<i>Phoxinus phoxinus</i>	-0.049	0.708	0.802	0.042
<i>Rhinichthys atratulus</i>	0.488	0.033	0.682	0.025
<i>Rhinichthys cataractae</i>	0.099	0.625	-0.588	1.000
<i>Rutilus rutilus</i>	0.918	0.006	0.724	0.008
<i>Scardinius erythrophthalmus</i>	0.970	0.250	0.978	0.042
<i>Squalius cephalus</i>	0.103	0.304	-0.004	0.507
<i>Telestes pleurobipunctatus</i>	-0.464	0.750	0.798	0.042
<i>Thymallus thymallus</i>	0.799	0.001	0.730	0.008
<i>Tinca tinca</i>	0.187	0.217	0.618	0.017
Mean	0.433	0.258	0.379	0.278
SD	0.420	0.229	0.641	0.376

Appendix S4. Tests of the overall correlation (over the 22 species) between taxonomic differentiation and genetic differentiation for (a) the raw correlations and (b) the residual correlations (i.e. the correlations between the residuals of the multiple regressions). The p-values associated to these tests were obtained by comparing the mean observed p-value over the species to a null distribution of p-values. Dashed vertical lines in test plots show the mean observed p-value over the species.

Appendix S5 Results of multiple regressions on taxonomic differentiation

All the coefficients are standardised partial regression coefficients; R2 is the total variance explained by the multiple regression; mean and standard deviation (SD) over the 22 species are given at the end of the table.

Species	Intercept	pval.Intercept	Geo	pval.Geo	Env	pval.Env	Area	pval.Area	R2	pval.R2
<i>Abramis brama</i>	0.659	0.701	0.521	0.398	0.475	0.298	-0.202	0.360	0.521	0.624
<i>Alburnoides bipunctatus</i>	2.261	0.207	0.338	0.207	-0.084	0.550	-0.763	0.207	0.784	0.020
<i>Alburnus alburnus</i>	2.194	0.199	0.416	0.079	-0.669	0.813	-0.670	0.164	0.388	0.367
<i>Barbatula barbatula</i>	0.659	0.628	0.521	0.326	0.475	0.138	-0.202	0.323	0.521	0.624
<i>Campostoma anomalum</i>	0.672	0.882	0.305	0.461	0.570	0.329	0.324	0.700	0.797	0.288
<i>Chondrostoma nasus</i>	0.659	0.705	0.521	0.406	0.475	0.301	-0.202	0.366	0.521	0.624
<i>Esox lucius</i>	0.317	0.092	0.558	0.090	0.073	0.267	0.410	0.989	0.702	0.000
<i>Gobio gobio</i>	1.402	0.445	0.150	0.331	0.015	0.438	-0.711	0.099	0.602	0.001
<i>Lampetra planeri</i>	1.962	0.844	0.470	0.387	0.195	0.503	-0.389	0.330	0.978	0.032
<i>Leuciscus aspius</i>	-0.253	0.908	-0.333	0.540	0.641	0.460	0.083	0.464	0.085	0.975
<i>Leuciscus leuciscus</i>	0.659	0.618	0.521	0.326	0.475	0.126	-0.202	0.331	0.521	0.624
<i>Lota lota</i>	0.421	0.794	0.770	0.233	0.568	0.142	0.036	0.628	0.853	0.007
<i>Notropis atherinoides</i>	0.605	0.710	0.101	0.461	0.426	0.379	-0.303	0.369	0.594	0.542
<i>Phoxinus phoxinus</i>	0.659	0.629	0.521	0.375	0.475	0.131	-0.202	0.332	0.521	0.624
<i>Rhinichthys atratulus</i>	0.344	0.859	0.061	0.510	-0.287	0.684	0.513	0.791	0.314	0.488
<i>Rhinichthys cataractae</i>	-9.883	0.373	-4.072	0.882	4.147	0.079	1.821	0.830	0.576	0.563
<i>Rutilus rutilus</i>	1.819	0.391	0.312	0.164	-0.132	0.559	-0.875	0.089	0.873	0.000
<i>Scardinius erythrophthalmus</i>	-0.590	0.748	-0.385	0.662	-0.219	0.670	-0.712	0.167	0.789	0.299
<i>Squalius cephalus</i>	0.034	0.956	-0.025	0.527	0.228	0.196	-0.044	0.423	0.052	0.434
<i>Telestes pleurobipunctatus</i>	-87.769	0.253	-1.617	0.829	1.548	0.171	0.086	0.423	0.867	0.192
<i>Thymallus thymallus</i>	1.903	0.715	0.215	0.368	-0.089	0.542	-0.654	0.120	0.353	0.172
<i>Tinca tinca</i>	7.394	0.550	0.839	0.397	-0.389	0.603	-1.071	0.196	0.802	0.016
Mean	-3.358	0.600	0.032	0.407	0.405	0.381	-0.178	0.395	0.592	0.342
SD	19.067	0.254	1.051	0.204	0.956	0.214	0.617	0.250	0.249	0.288

Appendix S6 Results of multiple regressions on genetic differentiation

All the coefficients are standardised partial regression coefficients; R2 is the total variance explained by the multiple regression; mean and standard deviation (SD) over the 22 species are given at the end of the table.

Table S6.1 Results when genetic differentiation is measured with G''_{ST}

Species	Intercept	pval.Intercept	Geo	pval.Geo	Env	pval.Env	Area	pval.Area	R2	pval.R2
<i>Abramis brama</i>	-7.853	0.142	-1.278	0.954	0.630	0.089	1.047	1.000	0.286	0.847
<i>Alburnoides bipunctatus</i>	1.667	0.375	0.156	0.349	0.045	0.496	-0.760	0.204	0.739	0.035
<i>Alburnus alburnus</i>	0.928	0.791	0.034	0.619	-0.084	0.442	-0.694	0.359	0.448	0.280
<i>Barbatula barbatula</i>	2.138	0.562	0.224	0.343	0.030	0.457	-0.854	0.174	0.466	0.682
<i>Campostoma anomalum</i>	3.536	0.001	1.136	0.000	-0.347	0.902	-0.042	0.310	0.931	0.101
<i>Chondrostoma nasus</i>	-0.458	0.952	-0.165	0.582	0.650	0.167	0.463	0.671	0.417	0.731
<i>Esox lucius</i>	1.025	0.097	1.021	0.097	-0.103	0.627	-0.138	0.335	0.927	0.000
<i>Gobio gobio</i>	5.610	0.120	0.768	0.132	-0.335	0.848	-0.511	0.144	0.737	0.000
<i>Lampetra planeri</i>	2.266	0.286	0.552	0.000	-0.742	1.000	0.397	1.000	0.335	0.806
<i>Leuciscus aspius</i>	-1.954	0.658	-0.992	0.711	0.147	0.437	-0.460	0.314	0.545	0.598
<i>Leuciscus leuciscus</i>	-2.365	1.000	-0.210	0.511	0.944	0.162	0.725	0.671	0.962	0.056
<i>Lota lota</i>	0.710	0.476	0.884	0.216	0.295	0.236	-0.094	0.507	0.757	0.028
<i>Notropis atherinoides</i>	-0.801	0.833	-0.255	0.594	0.500	0.244	-0.685	0.163	0.999	0.001
<i>Phoxinus phoxinus</i>	1.527	0.751	0.047	0.468	-0.304	0.754	-0.870	0.218	0.725	0.382
<i>Rhinichthys atratulus</i>	-1.992	0.417	-0.723	0.839	0.867	0.159	0.171	0.572	0.234	0.633
<i>Rhinichthys cataractae</i>	-1.374	0.198	-3.698	1.000	3.493	0.000	1.875	1.000	0.380	0.766
<i>Rutilus rutilus</i>	0.772	0.679	0.039	0.505	0.327	0.292	-0.682	0.130	0.872	0.000
<i>Scardinius erythrophthalmus</i>	-0.167	1.000	-0.275	0.523	-0.331	0.499	-0.799	0.242	0.929	0.105
<i>Squalius cephalus</i>	3.345	0.024	0.848	0.011	0.069	0.383	0.222	0.760	0.813	0.000
<i>Telestes pleurobipunctatus</i>	99.964	0.175	1.305	0.000	-0.826	1.000	0.275	0.825	0.657	0.467
<i>Thymallus thymallus</i>	2.520	0.570	0.255	0.330	0.175	0.378	-0.742	0.069	0.639	0.009
<i>Tinca tinca</i>	1.026	0.877	0.092	0.470	-0.054	0.496	0.131	0.591	0.036	0.972
Mean	5.003	0.499	-0.011	0.420	0.229	0.457	-0.092	0.466	0.629	0.341
SD	21.381	0.334	1.060	0.305	0.865	0.293	0.713	0.308	0.271	0.350

Table S6.2 Results when genetic differentiation is measured with F_{ST}

Species	Intercept	pval.Intercept	Geo	pval.Geo	Env	pval.Env	Area	pval.Area	R2	pval.R2
<i>Abramis brama</i>	0.808	0.810	0.170	0.481	-0.633	0.778	-0.813	0.277	0.698	0.416
<i>Alburnoides bipunctatus</i>	-1.278	0.198	-0.268	1.000	0.228	0.000	0.113	0.655	0.044	0.961
<i>Alburnus alburnus</i>	-3.214	0.108	-0.621	0.902	1.165	0.144	0.723	0.906	0.599	0.118
<i>Barbatula barbatula</i>	-4.092	0.543	-0.765	0.718	0.205	0.379	1.140	0.803	0.324	0.816
<i>Campostoma anomalum</i>	1.264	0.706	-0.093	0.530	-0.702	0.797	-0.207	0.627	0.675	0.446
<i>Chondrostoma nasus</i>	-0.127	0.870	-0.098	0.532	0.722	0.180	0.191	0.619	0.469	0.679
<i>Esox lucius</i>	0.230	0.357	-0.119	0.571	-0.155	0.726	0.051	0.538	0.038	0.578
<i>Gobio gobio</i>	1.649	0.540	0.183	0.298	-0.276	0.789	-0.120	0.338	0.047	0.839
<i>Lampetra planeri</i>	-4.038	0.379	-1.397	0.699	1.337	0.343	0.033	0.419	0.944	0.082
<i>Leuciscus aspius</i>	-1.608	0.309	-1.292	1.000	0.829	0.113	-0.268	0.340	0.380	0.766
<i>Leuciscus leuciscus</i>	-2.876	0.398	-0.536	0.763	0.103	0.326	-0.043	0.502	0.308	0.829
<i>Lota lota</i>	0.661	0.263	1.058	0.196	0.309	0.214	-0.275	0.262	0.971	0.000
<i>Notropis atherinoides</i>	-1.436	0.958	-0.390	0.505	0.609	0.495	-0.626	0.493	0.963	0.055
<i>Phoxinus phoxinus</i>	15.134	0.169	1.609	0.169	-0.234	0.792	-2.050	0.123	0.986	0.021
<i>Rhinichthys atratulus</i>	2.101	0.398	0.640	0.219	-0.560	0.778	-0.278	0.242	0.172	0.748
<i>Rhinichthys cataractae</i>	0.363	0.865	-0.235	0.553	0.169	0.443	0.630	0.756	0.282	0.850
<i>Rutilus rutilus</i>	-1.722	0.109	-0.469	0.991	1.028	0.033	0.102	0.603	0.582	0.019
<i>Scardinius erythrophthalmus</i>	6.458	0.254	0.950	0.000	-0.552	1.000	0.458	0.747	0.605	0.530
<i>Squalius cephalus</i>	0.188	0.808	-0.038	0.565	-0.065	0.511	0.019	0.453	0.010	0.913
<i>Telestes pleurobipunctatus</i>	100.388	0.339	1.331	0.159	-0.821	0.749	0.261	0.497	0.683	0.436
<i>Thymallus thymallus</i>	3.549	0.310	0.529	0.222	-0.608	0.855	-0.340	0.218	0.171	0.543
<i>Tinca tinca</i>	-0.616	0.847	-0.148	0.586	0.652	0.148	-0.214	0.375	0.512	0.202
Mean	5.081	0.479	0.000	0.530	0.125	0.481	-0.069	0.490	0.476	0.493
SD	21.673	0.277	0.774	0.295	0.648	0.310	0.623	0.209	0.324	0.333

Appendix S7. Tests of the overall effects (over the 22 species) of geographic distance, environmental distance and difference in area on (a) taxonomic differentiation, (b) genetic differentiation measured with G''_{ST} and (c) genetic differentiation measured with F_{ST} . The p-values associated to these tests were obtained by comparing the mean observed p-value over the species associated to each effect to a null distribution of p-values. Dashed vertical lines in test plots show the mean observed p-value over the species.

(c) Multiple regressions on genetic differentiation (F_{ST})

Geographic distance

Environmental distance

Harmonic mean area

Appendix S8. Variations of the residual correlation coefficient between taxonomic differentiation and genetic differentiation (r) according to different species traits: (a) length, (b) dispersal ability, (c) longevity in the wild, (d) vulnerability, (e) use in aquaculture, (f) use as baits, (g) use in aquarium and (h) habitat.

Disconnection time

Contemporary period
= basins disconnected

1

Taxonomic differentiation is expected to increase with geographical distance because of **dispersal limitation**

2

Genetic differentiation is expected to increase with geographical distance because of **dispersal limitation**

3

Taxonomic differentiation is expected to increase with environmental distance because of **environmental selection**

4

Genetic differentiation is expected to increase with environmental distance because of **environmental selection**

5

Taxonomic differentiation is expected to increase with **drift** which decreases with harmonic mean area

6

Genetic differentiation is expected to increase with **drift** which decreases with harmonic mean area

7

Residual correlation due to unmeasured processes including those depending on the historical connectivity of basins

(a) Raw correlations between taxonomic differentiation and genetic differentiation

(b) Residual correlations between taxonomic differentiation and genetic differentiation

(a) Multiple regressions on taxonomic differentiation

(b) Multiple regressions on genetic differentiation

**GEOGRAPHIC
DISTANCE**

**ENVIRONMENTAL
DISTANCE**

**HARMONIC MEAN
AREA**

Page 96 of 97

(c) Raw correlations

Squalius cephalus

(d) Residual correlations

Squalius cephalus