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Research

Spatial mismatch in morphological, ecological and phylogenetic diversity, in historical and contemporary European freshwater fish faunas

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Biodiversity encompasses multiple facets, among which taxonomic, functional and phylogenetic aspects are the most often considered. Understanding how those diversity facets are distributed and what are their determinants has become a central concern in the current context of biodiversity crisis, but such multi-faceted measures over large geographical areas are still pending. Here, we measured the congruence between the biogeographical patterns of freshwater fish morphological, ecological and phylogenetic diversity across Europe and identified the natural and anthropogenic drivers shaping those patterns. Based on freshwater fish occurrence records in 290 European river catchments, we computed richness and evenness for morphological, ecological and phylogenetic diversity using standardized effect sizes for each diversity index. We then used linear models including climatic, geo-morphological, biotic and human-related factors to determine the key drivers shaping freshwater fish biodiversity patterns across Europe. We found a weak spatial congruence between facets of diversity. Patterns of diversity were mainly driven by elevation range, climatic seasonality and species richness while other factors played a minor role. Finally, we found that non-native species introductions significantly affected diversity patterns and influenced the effects of some environmental drivers. Morphological, ecological and phylogenetic diversity constitute complementary facets of fish diversity rather than surrogates, testifying that they deserve to be considered altogether to properly assess biodiversity. Although the same environmental and anthropogenic factors overall explained those diversity facets, their relative influence varied. In the current context of global change, non-native species introductions may also lead to important reshuffling of assemblages resulting in profound changes of diversity patterns.

Keywords: global change, null models, historical assemblages



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Introduction

Biodiversity is a multifaceted concept that encompasses taxonomic, functional and phylogenetic dimensions (Gaston and Spicer 2004). While the taxonomic diversity accounts for the number of species in an assemblage (i.e. species richness), functional diversity represents the variety of functional traits within the assemblage whereas the phylogenetic diversity measures its evolutionary breadth. Functional diversity encompasses a wide breadth of functional traits among which morphological and ecological traits are the most frequently considered (Ricklefs 2012, Schleuter et al. 2012, Ulrich et al. 2016). Nevertheless, the relationship between diversity measures based on morphological and on ecological traits remains unclear and seldom investigated. On the other hand, phylogenetic diversity is assumed to be a good surrogate for functional diversity (Vitousek et al. 1997) because it encapsulates the overall variability of functional traits (Gerhold et al. 2015). Nevertheless, such an approach is constrained by the hypothesis of phylogenetic conservatism of functional traits, and no longer applies when trait convergence along the phylogeny is observed (Losos 2008). Moreover, lability in traits has been increasingly found (Losos et al. 2003, Pearman et al. 2008), indicating that phylogeny could not always be used as proxy for functional traits (Gerhold et al. 2015, Lopez et al. 2016). Previous studies have reported diversity patterns over continental scales for taxonomic (Reyjol et al. 2007), functional and phylogenetic facets (Schleuter et al. 2012, Zupan et al. 2014) separately. While some authors have compared several dimensions of diversity at a local scale (Devictor et al. 2010, Strecker et al. 2011, Monnet et al. 2014, Thuiller et al. 2014), few focused on the comparison of these different facets simultaneously at a large continental scale (but see Arnan et al. 2015).

Indeed, even if previous studies considered simultaneously morphological, life-history and habitat use traits at a continental scale (Blanchet et al. 2013), to our knowledge, only Safi et al. (2011) and Arnan et al. (2015) took into account several diversity facets on a continental or global scale, but those approaches provided mixed conclusions. While Arnan et al. (2015) reported a strong spatial congruence between diversity facets for European ants, Safi et al. (2011) detected, once the effect of taxonomic richness was accounted for, a mismatch between functional and phylogenetic mammal diversity across the world. Species richness might blur differences between diversity facets since functional and phylogenetic diversity are mechanistically correlated to the number of species. Accounting for species richness is therefore a prerequisite to compare those diversity facets.

The responses of the different facets of diversity to environmental conditions investigated simultaneously remains poorly explored. The influence of environmental drivers has been investigated separately on taxonomic (Bernard-Verdier et al. 2013), functional (Schleuter et al. 2012) and phylogenetic (Liu et al. 2016) diversity. For instance, Schleuter et al. (2012) underlined the importance of current climate (temperature and precipitation) in shaping spatial patterns of

functional diversity in stream fish assemblages across Europe. In contrast, past climatic events (e.g. glaciations) shaped the taxonomic structure of fish assemblages, which was strongly influenced by refuge areas during the last glaciation events (Reyjol et al. 2007). Such refugia are currently characterized by functionally and/or phylogenetically rich assemblages (Schleuter et al. 2012). This could be due to the fact that historical climatic conditions are related to the percentage of endemic species (Oberdorff et al. 1999, Tedesco et al. 2012). Endemic species might influence more strongly diversity patterns than widespread species, likely because they are generally more functionally specialized (Griffiths et al. 2014). Current environmental harshness is also prone to affect functional and phylogenetic diversity by selecting functionally adapted species to harsh environments, that can (or not) belong to closely related clades. For instance, Tallents et al. (2005) showed that tree phylogenetic diversity declined with altitude, whereas Baessler et al. (2016) reported a decline of lichens functional diversity with altitude despite an altitudinal increase in taxonomic richness.

In addition to natural environmental factors, anthropogenic activities may also drive diversity patterns, considering taxonomic (Vitousek et al. 1997), functional (D'agata et al. 2014) or phylogenetic (Thuiller et al. 2011) facets. For instance, D'agata et al. (2014) found a loss of functional diversity in coral reef fish assemblages when human population density increased. Similarly, Thuiller et al. (2011) projected a decrease in phylogenetic diversity in response to climate change. Human-mediated introductions of non-native species are also known to modify the functional structure of assemblages by the loss of functionally unique species (Matsuzaki et al. 2013, 2016).

Here, we focused on freshwater fish assemblages across Europe. Europe encompasses a wide variety of environmental conditions and anthropogenic pressures that are likely to affect fish assemblages. Moreover, European fish fauna studies benefit from detailed knowledge on species distribution, richness, functional features and phylogeny (Reyjol et al. 2007, Logez et al. 2013). We split functional diversity into ecological and morphological features as those two kinds of traits are usually considered independently in fish studies (Schleuter et al. 2012, Buisson et al. 2013). Our aim was first to describe the spatial patterns of morphological, ecological and phylogenetic diversity for European freshwater fish across Europe while controlling for species richness using standardized effect sizes. We then measured the spatial congruence between these three biodiversity facets. Finally, we identified which environmental variables were the main drivers of observed patterns and how human activities, through non-native species introductions but also human density and land-use, have modified those patterns.

Material and methods

Fish data

Freshwater fish occurrence records in 290 European river catchments ($24\,225 \pm 101\,960\text{ km}^2$) were compiled from

published data on species lists at the river-catchment scale (see Supplementary material Appendix 1 in for a full list of references). Only river catchments with at least 5 fish species were kept for analyses. Measuring functional diversity for catchments with less than 5 species was indeed not possible since only 4 functional dimensions were kept (see the Diversity indices section for more details). Thus, 39 catchments were not included ($1510 \pm 2000 \text{ km}^2$). Most of these basins were in Iceland (31 out of the 39 removed basins), which is characterized by specific biogeographical history as well as particular topographical and climatic conditions and hence contain almost only Salmonids and always less than five species. Our database included a total of 415 fish species from which 41 were non-natives, defined as species originating from outside Europe (i.e. exotic species) or native species to Europe introduced into river basins where they did not historically occur (i.e. translocated species). Non-native species translocations and introductions have occurred 1822 times (given that one species could be introduced in several different basins).

In order to describe morphological diversity of European fish assemblages, we used 14 morphological measures available for 300 species (Toussaint et al. 2016), which accounted for 95% of the total occurrences. These morphological measures were used to compute 14 unitless ratios linked to prey detection, prey capture, position in the water column and swimming abilities according to Villéger et al. (2010). Body length was also included in the analyses since it encapsulates most of fish functions (Blanchet et al. 2010). The measure of body length used was the maximal body length of the species recorded from Fishbase (Froese and Pauly 2017) and was checked for all species and errors were corrected using literature on the species. All the morphological traits have been detailed in Villéger et al. (2010).

To estimate ecological diversity, we used 14 qualitative ecological traits (Supplementary material Appendix 2) linked to feeding diet (i.e. feeding habitat and feeding diet), habitat use (i.e. rheophily, reproduction habitat, migration, salinity preference and position in the water column) and life-history strategies (i.e. fecundity, spawning time, egg diameter, life span, age of first female maturity, parental care, incubation period). Those traits were collected from the literature for all the species.

Finally, we used the time-calibrated phylogeny for fishes published by Rabosky et al. (2013) to describe phylogenetic diversity on 288 species accounting for 92% of the total occurrences.

We maximized the number of species for each facet by using all the species for which data were available for a given facet.

River catchment descriptors

Each river catchment was described in terms of climatic, geo-morphological and anthropogenic features. Five climatic variables were extracted from the WorldClim database

(Hijmans et al. 2005): mean annual air temperature (TEMP), total annual precipitation (PREC), seasonality of air temperature (TSEAS), seasonality of precipitation (PSEAS) and the percent of surface covered by ice during the last glacial maximum (LGM). Contemporary climatic conditions were averaged from 1960 to 1990. The area of river catchment (AREA) was extracted from CCM2 database (Vogt et al. 2007) and elevation range (ELE) from HYDRO1k database available from the U.S. Geological Survey (<https://lta.cr.usgs.gov/HYDRO1K>). Anthropogenic features were available for the year 2000 and were described using variables extracted from the Global Land Cover Network (GLCN) database (artificial areas, cultural areas, forest and shrub-herb areas) and the population density extracted from the HYDE 3.0 database (Klein Goldewijk et al. 2011). We then performed a principal component analysis (PCA) on these anthropogenic variables and kept the first axis (accounting for 38.4% of the total variability and strongly positively correlated to population density, artificial and cultural areas) to obtain a synthetic variable (HUM) describing the intensity of human activities. Finally, we quantified the proportion of non-native species (i.e. exotic and translocated species; NNS) for each European river catchment using Kottelat and Freyhof (2007). Proportions rather than occurrences were used to be comparable between river catchment.

Diversity indices

Historical diversity patterns

In order to quantify diversity while considering its facets (i.e. morphological, ecological and phylogenetic) and components (i.e. richness and evenness), we used different indices. Evenness has been proposed to complement richness in the taxonomic, functional and phylogenetic approaches (Villéger et al. 2008). For morphological and ecological richness measures, we used the diversity indices proposed by Villéger et al. (2008). Morphological and ecological richness (MORPHO-rich and ECOL-rich, respectively) were the volume occupied by co-occurring species in a morphological and ecological space, respectively (ranging from 0 to 1, 1 meaning that the maximal volume in the space is occupied). The morphological and ecological evenness (MORPHO-even and ECOL-even, respectively) measured how patchy the species were distributed within the morphological and ecological space, respectively (ranging from 0 to 1, 1 meaning an even distribution of species within the space). We computed those indices by calculating a Gower distance matrix between species based on morphological and ecological traits, separately. The distances between species were projected on 4 axes using a principal coordinates analysis (accounting for 86 and 94% of the total variance of morphological and ecological traits, respectively; Maire et al. 2015). Regarding phylogenetic diversity, we estimated phylogenetic richness (PHYLO-rich) and evenness (PHYLO-even) using Faith's PD (Faith 1992) and Villéger's FEve (Villéger et al. 2008).

Impact of non-native species on diversity patterns

In order to assess the impact of non-native species on the observed patterns, we computed each index by considering first all fish species co-occurring in the contemporary assemblages (i.e. entire assemblages) and historical assemblages (i.e. based on native species only). As there were very few recorded fish extirpations in the studied catchments (Villéger et al. 2011), we considered that native species constitute a good proxy of historical assemblages before non-native species introductions.

Null models and standardized effect sizes

Since ecological, morphological and phylogenetic diversity indices (richness and evenness) are known to be strongly influenced by species richness (Gotelli and Graves 1996), we used randomizations of species traits and phylogeny to control for this effect. We kept the same number of species per catchment and the same number of occurrence per species in the entire dataset while randomizing species identity. For analyses based on native assemblages, we considered only the combinations of traits as well as the species observed in the native species pool. We performed 999 randomizations and then obtained 999 null values of the six indices of diversity *per* assemblage. Then, we measured the standardized effect size (SES) as $(obs - \text{mean}(rand))/sd(rand)$, *obs* being the observed index and *rand*, the 999 null values of the index. A positive value of SES indicates a higher value of the index than expected by chance given the number of species while a negative SES indicates a lower value (Gotelli and Graves 1996). In the following parts of the paper, all the richness and evenness diversity measures (MORPHO-rich, ECOL-rich, PHYLO-rich and MORPHO-even, ECOL-even, PHYLO-even) are expressed as SES values.

In order to quantify the impact of non-native species on the observed patterns, we computed the difference between the SES based on contemporary assemblages and the SES based on historical assemblages. Positive values indicate that non-native species increase the SES value while negative values mean that non-natives decrease the SES value. In the following parts of the paper, the change of diversity measures from historical to contemporary periods (Δ MORPHO-rich, Δ ECOL-rich, etc.) are expressed as changes of SES from historical to contemporary periods.

Statistical analyses

We compared historical and contemporary SES using paired Student's t-test. Then, in order to better understand relationships between the different diversity facets, we quantified the phylogenetic signal (i.e. closely related species are more ecologically/morphologically similar than distant ones; Losos 2008) in ecological and morphological traits separately using Moran's I (Keck et al. 2016). To determine the spatial congruence for each component of diversity (i.e. richness and evenness), we measured the relation between all pairwise combinations of facets (i.e. ecological and

morphological, ecological and phylogenetic, phylogenetic and morphological).

To identify the potential drivers of the observed spatial patterns, we performed linear models with each index separately as the response variable, and river catchment descriptors as explanatory variables. All predictors were transformed to z-scores to standardize slope coefficients to compare the relative strength of the predictors. We found no evidence for multicollinearity between the explanatory variables (variance inflation factors all lower than 10; Zuur et al. 2007) and checked for spatial autocorrelation using Moran's I (Fan and Myint 2014). We chose the structure of spatial autocorrelation by fitting semi-variograms and took spatial autocorrelation into account in all the models performed on the historical and contemporary assemblages separately.

All analyses were performed with R software ver. 3.2.1 (R Core Team). Morphological and ecological indices as well as phylogenetic evenness were computed using the function 'multidimFD' available online at <<http://villeger.sebastien.free.fr/Rscripts.html>>. Phylogenetic richness was computed with 'picante' package. Linear models were performed with 'nlme' package and the autocorrelation structure was assessed with 'gstat' package.

Results

Patterns of European fish diversity

Historical diversity patterns

Richness – historical assemblages presented mean values of 0.83 (± 1.34 SD), 0.31 (± 1.23 SD) and 0.74 (± 0.89 SD) (Fig. 1a) for ecological, morphological and phylogenetic diversity, respectively. We nevertheless found a south-north gradient in ecological diversity which was low in southern basins and increased towards the northern part of Europe (Fig. 1a). In contrast, morphological and phylogenetic diversity were low in northwestern Europe and increased towards southeastern Europe (Fig. 1a), even if most of phylogenetic diversity values were positive, contrary to morphological diversity pattern for which northern catchments exhibited negative values and southern ones positive values.

Evenness – overall, historical MORPHO-even was low (mean MORPHO-even = -0.52 ± 1.05 SD), especially in the eastern part of Europe, with an increasing tendency from low to medium diversity from southeastern to northeastern Europe (Fig. 1b). In contrast, the historical values of ECOL-even and PHYLO-even were mainly high (0.25 ± 0.84 and 0.52 ± 0.95 , respectively) except for some river catchments in northern and southern Europe where low diversity was observed (Fig. 1b). Concerning PHYLO-even, the highest values were observed in two large river catchments (i.e. Danube and Volga; Fig. 1b).

Impact of non-native species on diversity patterns

Richness – non-native species led to decrease in MORPHO-rich (mean Δ MORPHO-rich = -0.38 ± 0.51 SD) and

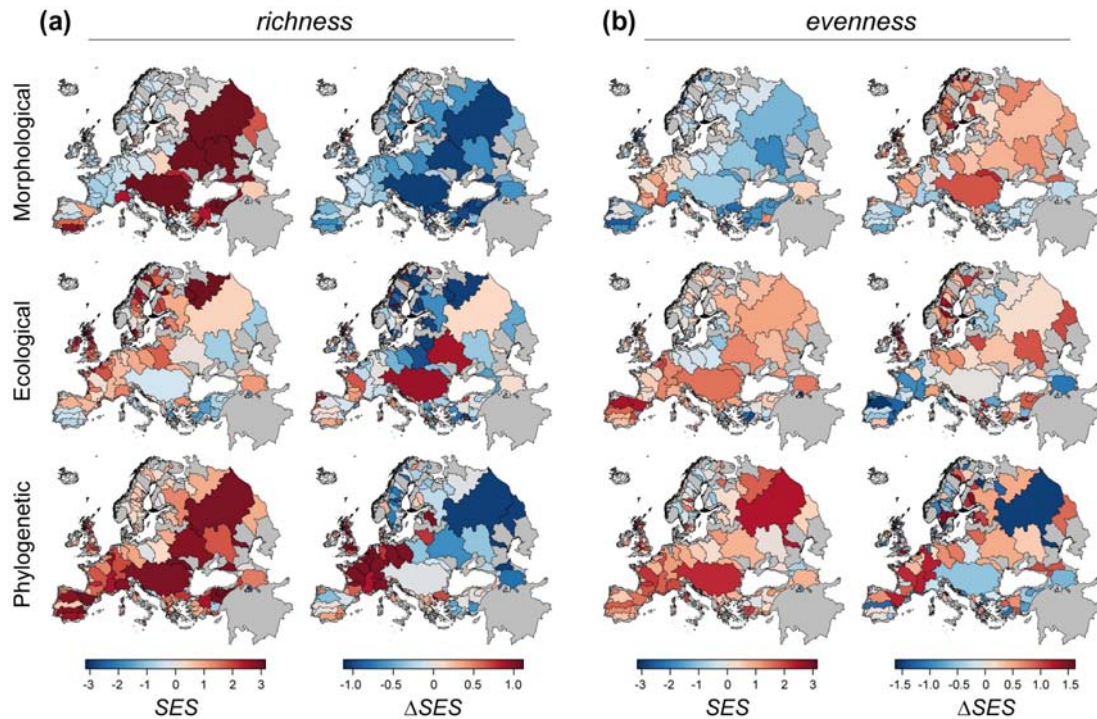


Figure 1. Spatial patterns of standardized effect sizes for (a) richness and (b) evenness in ecological, morphological and phylogenetic diversity based on historical assemblages (SES) and differences between SES based on historical and contemporary assemblages (Δ SES). Grey regions are European areas without fish information. Historical morphological and phylogenetic richness presents a northwest-southeast gradient while historical ecological richness presents a south-north gradient. Historical morphological evenness presents a southeast-northwest gradient while ecological and phylogenetic evenness present no clear gradient.

ECOL-rich (-0.11 ± 0.70) and for 85 and 56% of catchments, respectively. These decrease in diversity were mainly observed in catchments with high historical diversity (Fig. 1a). This was particularly true for large catchments such as Danube, Dniepr or Volga (Fig. 1a). Regarding PHYLO-rich, an opposite pattern was observed with an increase of diversity for 61% of the catchments (mean Δ PHYLO-rich = 0.10 ± 0.50 SD; Fig. 1a).

Evenness – overall, differences between historical and contemporary indices were significant for all indices except ECOL-even and PHYLO-even (all $p < 0.05$ except for ECOL-even: $p = 0.52$ and PHYLO-even: $p = 0.12$). Non-native species resulted in an increase, albeit weak on average, in evenness for all the three diversity facets (0.21 ± 0.53 , 0.03 ± 0.85 and 0.09 ± 0.93 for MORPHO-even, ECOL-even and PHYLO-even, respectively; Fig. 1b). MORPHO-even increased in 62% of the studied catchments, while ECOL-even and PHYLO-even increased in 53 and 51% of catchments, respectively, when non-native species were considered.

Congruence between facets

Morphological as well as ecological traits were both significantly phylogenetically conserved (Moran's $I = 0.29$ and 0.39 , respectively, $p < 0.001$).

For historical fish assemblages, we found significant and positive linear relationships between the SES values of MORPHO-rich and PHYLO-rich ($R^2 = 0.11$, $p < 0.001$, Fig. 2a), between the MORPHO-rich and ECOL-rich ($R^2 = 0.05$, $p < 0.001$, Fig. 2a) and between ECOL-even and PHYLO-even ($R^2 = 0.02$, $p = 0.02$, Fig. 2b). All the other pairwise indices were not significantly correlated.

For contemporary assemblages, a negative relationship was detected between the SES values computed on MORPHO-rich and ECOL-rich ($R^2 = 0.08$, $p < 0.001$; Fig. 2a) whereas positive relationships were observed between the SES values of MORPHO-rich and PHYLO-rich ($R^2 = 0.07$, $p < 0.001$; Fig. 2a) and the SES values of ECOL-even and PHYLO-even ($R^2 = 0.03$, $p < 0.001$; Fig. 2b).

Determinants of historical and contemporary assemblages

The effects of environmental drivers primarily varied according to the diversity facets and the considered index, with a major role of geomorphological and climatic variables. Overall, the models presented a better goodness-of-fit for richness indices (adjusted R^2 ranging from 0.56 to 0.63) than for evenness indices (adjusted R^2 ranging from 0.21 to 0.42; Table 1).

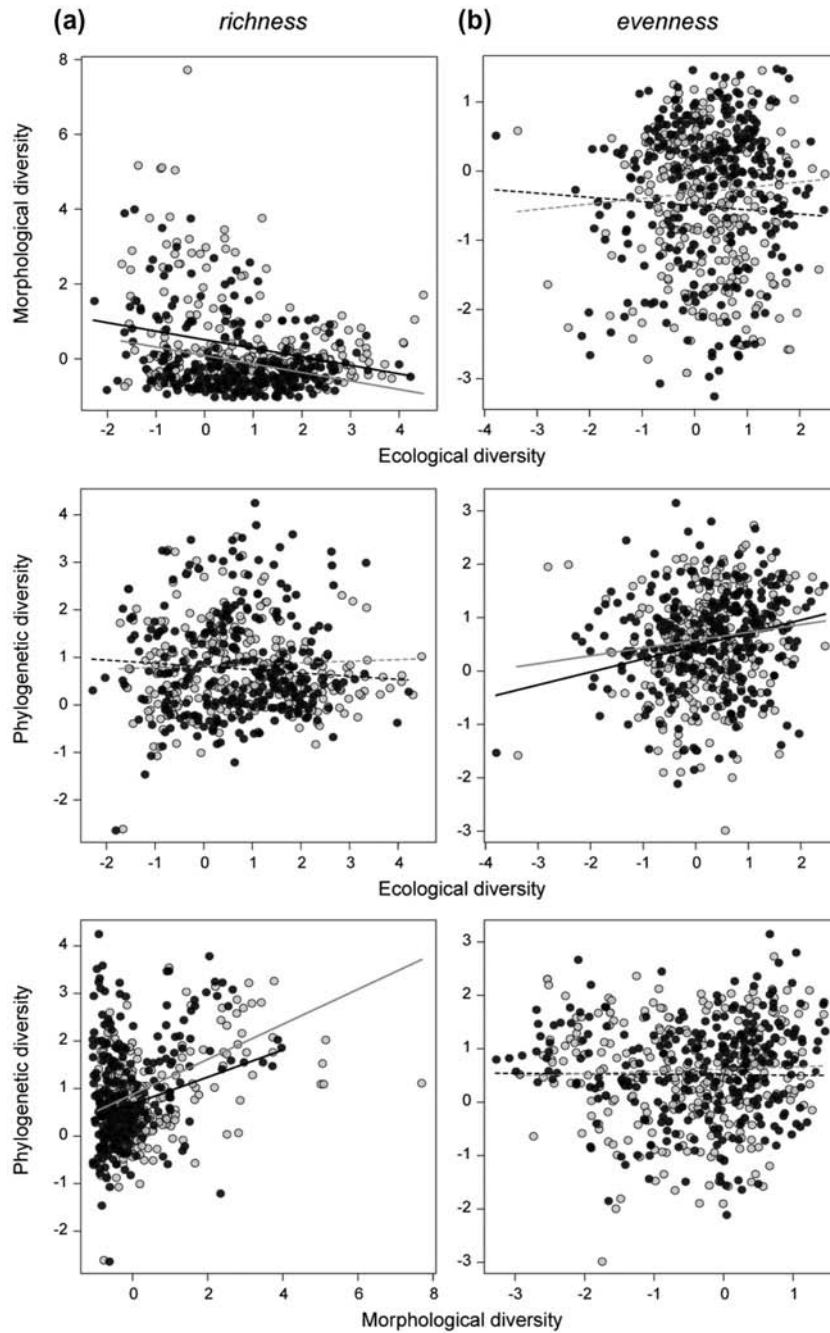


Figure 2. Relationships between the different facets of (a) richness and (b) evenness in morphological, ecological and phylogenetic diversity ($n=290$). Grey and black points correspond to standardized effect sizes (SES) based on historical and contemporary fish assemblages, respectively. Solid lines of best fit from linear models indicate significant ($p < 0.05$) relationships while dashed lines are non-significant relations.

For historical assemblages, MORPHO-rich was only positively impacted by species richness and the seasonality of rainfall and negatively by catchment area. ECOL-rich was negatively influenced by elevation range, average and seasonality of temperature but positively by the percentage of ice cover. PHYLO-rich increased with elevation range, species richness, seasonality of rainfall and catchment area but

decreased with temperature seasonality. MORPHO-even was negatively influenced by elevation range as well as seasonality and total annual precipitation. ECOL-even was not significantly impacted by any of the studied determinants. Finally, PHYLO-even increased with species richness and the percentage of ice cover but decreased with the seasonality of temperature.

Table 1. Results of linear models relating standardized effect sizes (SES) of diversity indices (MORPHO-rich, ECOL-rich and PHYLO-rich: morphological, ecological and phylogenetic richness, respectively; MORPHO-even, ECOL-even and PHYLO-even: morphological, ecological and phylogenetic evenness, respectively) computed on historical and contemporary fish assemblages to catchment descriptors (log-transformed when the distribution was not Gaussian). Given values are slope regression coefficients (in bold when significant at $p < 0.05$). AREA: area of river catchment, TEMP: mean annual temperature, TSEAS: seasonality of temperature, LGM: percent of surface covered by ice during the last glacial maximum, PREC: total annual precipitation, PSEAS: seasonality of precipitation, ELE: elevation range, HUM: human use, NNS: percentage of non-native species, SR: total fish species richness. HUM and NNS, considered as recent effects, have not been tested on historical assemblages.

Assemblage	Diversity indices (SES)	Adjusted R ²	log(AREA)	TEMP	TSEAS	LGM	PREC	PSEAS	log(ELE)	HUM	NNS	SR
Historical	MORPHO-rich	0.56	-0.30	0.03	0.10	0.02	-0.03	0.21	0.07	-	-	0.38
	ECOL-rich	0.63	-0.19	-0.47	-0.31	0.24	-0.02	-0.04	-0.42	-	-	0.18
	PHYLO-rich	0.59	0.13	0.16	-0.26	0.11	-0.05	0.20	0.23	-	-	0.49
	MORPHO-even	0.42	0.07	-0.01	-0.08	-0.09	-0.17	-0.31	-0.19	-	-	0.05
	ECOL-even	0.21	0.11	0.02	-0.15	0.07	-0.04	0.07	0.09	-	-	0.08
	PHYLO-even	0.38	0.24	0.17	-0.26	0.23	0.04	0.01	0.10	-	-	0.20
Contemporary	MORPHO-rich	0.54	-0.05	0.12	0.01	0.04	< 0.01	-0.09	0.09	-0.01	-0.17	0.11
	ECOL-rich	0.69	-0.21	-0.64	-0.47	0.03	0.05	-0.11	-0.32	-0.08	0.17	0.20
	PHYLO-rich	0.64	-0.09	0.16	-0.38	0.15	-0.11	0.13	0.20	-0.10	0.02	0.17
	MORPHO-even	0.54	-0.14	-0.37	-0.12	-0.03	-0.11	-0.23	-0.31	0.02	0.11	0.09
	ECOL-even	0.50	-0.22	-0.15	-0.11	0.30	-0.03	-0.03	0.09	-0.13	-0.01	0.80
	PHYLO-even	0.44	-0.04	0.01	-0.25	< 0.01	-0.02	0.05	0.01	-0.10	-0.07	0.46

Results were different for contemporary assemblages (Table 1). The goodness-of-fit of models was similar to what was previously found for richness indices (adjusted R² ranging from 0.54 to 0.69) but better for evenness indices (adjusted R² ranging from 0.44 to 0.54). Overall, compared to historical assemblages, some effects appeared and other ones were not detected anymore. The variability in drivers between historical and contemporary assemblages was especially remarkable for catchment area and percentage of ice cover. No effect of human use was detected on any of the diversity indices while non-native species were found to influence negatively MORPHO-rich and positively ECOL-rich. The effect of taxonomic species richness was higher than for historical assemblages, with a significant positive influence on most indices except for MORPHO-even.

Discussion

Spatial patterns of freshwater fish diversity in Europe varied depending on the facets (i.e. morphological, ecological or phylogenetic) and components (i.e. richness or evenness). Our results suggest that climatic conditions, especially the seasonality of temperature and precipitation, were the primary factors driving the observed patterns while the catchment geo-morphological characteristics played a secondary role. Moreover, we found that non-native species blurred the influence of both geo-morphological factors and species richness on diversity indices, therefore paralleling current knowledge on the role of non-native species on contemporary European fish biogeography (Leprieur et al. 2008), and extending it to functional and phylogenetic facets.

Spatial patterns of diversity

Two main spatial gradients of fish diversity were identified. First, a gradient was detected from south-east to north-west

for morphological and phylogenetic richness as well as morphological evenness. Second, a gradient from south to north was observed for ecological richness and in a lesser extent for ecological evenness highlighting harsher conditions for fish assemblages in the Mediterranean region than in northern Europe. The Ponto-Caspian region appears as a major region in spatial patterns of diversity likely due to the fact that it was a well-known refuge during the Pleistocene glaciation with a high diversity level (Reyjol et al. 2007). In the present study, we showed that this region is not only rich in terms of species number but also in terms of morphological and phylogenetic diversity. On the other hand, the northern, central and western parts of Europe (as defined by Reyjol et al. 2007) were often opposite to the Ponto-Caspian region in terms of diversity. Concerning evenness, patterns were clearer than those observed for richness and quasi-opposite to richness patterns for morphological and ecological diversity, suggesting that areas with strong morphological and ecological richness presented low evenness. Although species evenness received less attention than richness, some studies showed a decrease of evenness with latitude in fish (McClatchie et al. 1997) and invertebrates (Rex et al. 2000, Woodd-Walker et al. 2002, Tolimieri 2007), which was not in agreement with our findings for both phylogenetic and ecological diversity.

Congruence between facets

Here, we found weak congruence between spatial patterns in the different facets studied concerning both richness and evenness. Similarly, Devictor et al. (2010) reported that some regions differed in terms of functional and phylogenetic diversity for French bird communities. Nevertheless, for other geographical areas, the two facets were congruent (Safi et al. 2011, Arnan et al. 2015). We found stronger congruence between morphological and phylogenetic richness than between ecological and phylogenetic richness, likely due to a stronger

phylogenetic signal in morphological than in ecological traits. Surprisingly, we found a very weak relation between ecological and morphological diversity concerning both richness and evenness. While several studies used morphological traits as proxies for ecological traits (Ricklefs 2012, Schleuter et al. 2012, Ulrich et al. 2016), its ecological meaning remains vague, and a given morphological trait can have multiple meanings (Wainwright 2007). For instance, dorsal eyed fish can either be benthic species feeding on the bottom, or surface species feeding on terrestrial insects falling on the surface (Villéger et al. 2017). In addition, the morphological and ecological traits usually measured on fish represent distinct functions. Morphological traits that are often derived from fish external morphology provide information on feeding and dispersion (Gatz 1979, Webb 1984) while ecological traits classically used are rather linked to life history strategy. This could explain the absence of congruence detected between spatial patterns of fish morphological and ecological diversity, which encompassed mainly life history strategy diversity in the current study. In addition, since morphological and ecological facets describe distinct functions, while the phylogenetic facet accounts for a more general view of evolutionary-grounded functional diversity, these facets should not be considered as surrogates, but as complementary diversity metrics. They therefore need to be considered simultaneously, in order to get a more comprehensive view of biodiversity.

Drivers of freshwater fish diversity patterns in Europe

In the present study, we identified several key drivers of spatial patterns of diversity, among which temperature and precipitation seasonality were the most influencing factors. Although patterns differed according to the considered facets and indices of diversity, we found an overall consistency between the main factors shaping functional richness and evenness even if the effects of environmental conditions were weaker for the evenness component. While the impact of climate is generally assessed using mean temperature, we highlighted that this variable was not necessarily a good predictor of freshwater fish diversity compared to temperature and precipitation seasonality. There is a growing amount of evidence that temporal climatic variability might be a strong predictor of species diversity (Adler et al. 2006, Letten et al. 2013, Logez et al. 2013). High seasonality is expected to promote species diversity by temporally partitioning available niches allowing competition stabilization (White et al. 2010). In contrast to this expectation, our results showed that high temperature seasonality led to low phylogenetic and ecological traits diversity, suggesting that climatic variability may act as a strong environmental filter regarding phylogenetic and ecological trait diversity. If previous studies on fish highlighted the importance of climatic variability on functional richness, the effect of this driver was not so obvious on evenness, contrary to our observations (Pool et al. 2010).

Here, we found that elevation range was an important driver of richness of the three considered facets similarly to what was found in several taxa of vertebrates (Meynard et al.

2011, Sagouis et al. 2017). Elevation range seems to be a more integrative surrogate for the overall diversity of environmental conditions over the river catchment than the area of the catchment.

Concerning the effect of historical factors such as the percentage of ice cover which is known to strongly shape community structure (Ordonez and Svenning 2015), we detected a positive effect of the percentage of ice cover during the Last Glacial Maximum on ecological richness as well as on ecological and phylogenetic evenness. Historical climatic conditions have been shown to influence the proportion of endemic species (Oberdorff et al. 1999, Tedesco et al. 2012). Especially, a low percentage of endemic species has been observed in areas covered by ice during the Pleistocene (Oberdorff et al. 1999). These species are generally highly functionally specialized and could increase functional diversity in uncovered areas during the last glaciation event (Griffiths et al. 2014). However, these areas might then be colonized by migratory and marine derived families (Griffiths 2015) which ultimately increase functional diversity. Our results suggest that recolonizations by migratory and/or marine species could occur in the small northern catchments, previously under the ice. Moreover, although we used standardized effect sizes to account for the effect of species richness on diversity indices, we found that species richness had a positive influence on several facets and indices of diversity for both historical and contemporary fish assemblages. The catchments with the highest species richness were also the largest ones (e.g. Danube, Volga), presenting a higher local habitat diversity and consequently, a larger number of ecological niches available for species, evenly distributed in the functional space (Mason et al. 2008). On the contrary, this suggests that catchments with low species richness contain aggregates of functionally and phylogenetically close species, potentially due to strong environmental filtering. Finally, we found no or weak effect of human-related variables on freshwater fish diversity patterns in Europe. This result contrasts with previous studies in which intensity of human activities and urbanization were found as major drivers of diversity (Aronson et al. 2014). However, at the broad scale of catchments, it is likely that the effect of local stressors (e.g. pollution, urbanization, fragmentation) might not be detectable since intensity of human activities is not homogeneously distributed within catchment. This can result in the presence of areas less impacted that might prevent species extirpations at the catchment scale. The introduction of non-native species can modify relations between the facets of diversity and environmental factors. Although the spatial patterns of richness and evenness were both impacted by the introduction of non-native species, the changes were not in the same way for the two components. While the introduction of non-native species tended to decrease the values for richness, the effect was less marked for evenness, especially for morphological facet where an increase of SES values was clearly observed. This suggests that the introduction of non-native species increased the number of new morphological traits (species more evenly distributed within the morphological volume), but also the redundancy of current ecologi-

cal traits phylogenetically conserved (species more aggregated within the ecological traits volume).

While contemporary assemblages were mainly structured by climatic factors, historical assemblages were additionally shaped by geo-morphological features of river catchments. This difference in drivers was likely due to the fact that non-native species dispersal is often conducted by humans (directly or indirectly) and because those species are opportunistic and tolerant towards a large range of environmental features. It thus appears essential to study both contemporary and historical assemblages in order to deepen our understanding of biotic responses to environmental changes, especially in the on-going context of global change. Overall, the most striking effect of non-native species was to blur the influence of some environmental conditions on spatial patterns of fish diversity, except for the most important drivers such as temperature seasonality and elevation range for which the effect on diversity indices was similar for historical and contemporary assemblages. Leprieur et al. (2008) previously reported that non-native species introductions were not randomly distributed across space neither distributed according to environmental gradients but were facilitated by and thus related to human activities, independently of abiotic conditions they experienced.

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Supplementary material (Appendix ECOG-03611 at < www.ecography.org/appendix/ecog-03611 >). Appendix 1–2.