A Journal of Macroecology

Global Ecology and Biogeography

RESEARCH PAPER

Geographic isolation and climate govern the functional diversity of native fish communities in European drainage basins

Diana Schleuter[1]*, Martin Daufresne[1], Jacques Veslot[1], Norman W. H. Mason[2], Cédric Lanoiselée[1], Sébastien Brosse[3], Olivier Beauchard[4] and Christine Argillier[1]

[1]*Irstea, UR Hydrobiologie, 3275 Route de Cézanne, CS 40061, 13182 Aix en Provence, France,* [2]*Landcare Research, Private Bag 3127, Hamilton 3240, New Zealand,* [3]*Laboratoire Evolution et Diversité Biologique, UMR 5174, CNRS-Université Paul Sabatier, Toulouse, France,* [4]*University of Antwerpen, Campus Drie Eiken, DC 223, Universiteitsplein 1, 2610 Wilrijk, Belgium*

ABSTRACT

Aim In times of biodiversity crisis, it is extremely important to understand diversity gradients. In particular, the study of the diversity of ecological functions is a key issue for the management of ecosystem integrity. Here we identify areas of low functional diversity of the native fish fauna in European drainage basins and we determine the relative importance of three underlying mechanisms: environmental filtering, geographic isolation and climatic history.

Location The European continent.

Methods Based on 14 morphological traits that are closely related to fish function (habitat and dietary niches), three independent functional diversity indices [functional richness (FR), functional evenness (FE), functional divergence (FD)] were calculated for 128 European drainage basins with a total of 230 fish species. The indices were standardized for species richness using null models. The patterns of the standardized indices are described and three potentially underlying mechanisms are tested using variance partitioning and multi-linear regression models.

Results FR and FD were highest in eastern European drainage basins and in Great Britain and lowest in the Mediterranean. FE patterns were less pronounced. All observed patterns were mainly governed by geographic isolation and present environmental conditions. Within the environmental conditions, average annual temperature and precipitation were good predictors for functional diversity. The role of habitat diversity and size was negligible.

Main conclusions Geographic isolation coupled with harsh environmental conditions such as extreme temperatures and low precipitation, as in Mediterranean regions, can lead to low FR and FD. This can be explained by extinction that could not be compensated by re-colonization and high speciation. Due to their high functional redundancy, communities in these areas might better withstand further species extinctions on a small scale. Over the short term, however, their often extremely low FR suggests a less flexible functioning that can hinder their ability to withstand today's rapid environmental and anthropogenic threats.

Keywords
Dispersal limitation, environmental filtering, Europe, functional divergence, functional diversity, functional evenness, functional richness, glaciations, morphological traits, native fish fauna.

*Correspondence: Diana Schleuter, Limnological Institute, University of Konstanz, 78457 Konstanz, Germany. E-mail: DianaSchleuter@web.de

INTRODUCTION

In times of high and rapid loss of biodiversity, it is especially important to identify regions of low diversity and to understand the causes of the patterns observed (Dudgeon *et al.*, 2006), since 'cold' spots of diversity are generally assumed to be extremely vulnerable to environmental changes and anthropogenic impacts (Tilman, 1996; Worm *et al.*, 2006). Several studies have already recognized hot and cold spots of diversity. In these studies, the importance of different, partly collinear triggers such as environmental conditions (e.g. temperature and precipitation), the size of the system (geographic area) and history (e.g. extinction during glaciations and re-colonization) were emphasized (Currie *et al.*, 2004; Mittelbach *et al.*, 2007; Field *et al.*, 2009; Hugueny *et al.*, 2010).

Large-scale studies on biodiversity are almost exclusively based on taxonomic richness. However, to consider solely species identity does not help us to understand the underlying ecological processes and to disentangle the role played by the different triggers. A functional diversity approach better considers species ecology as well as their complementarity and redundancy and can thus be a helpful tool in biodiversity studies (Tilman *et al.*, 1997; Díaz & Cabido, 2001; Petchey & Gaston, 2006).

Three independent aspects of functional diversity can be calculated: functional richness (FR), functional evenness (FE) and functional divergence (FD) (Villéger *et al.*, 2008; Schleuter *et al.*, 2010). FR measures how much of a functional niche space is filled; FE and FD measure how this niche space is filled. While FE measures how evenly traits are distributed in trait space, FD is a measure of the traits' variance. Functional diversity can help us to better understand the mechanisms that underlie observed diversity patterns and to better discriminate between competing hypotheses explaining species richness gradients (Mason *et al.*, 2007, 2008). Applying functional diversity indices at a regional scale, Mason *et al.* (2007, 2008) were able to consider the underlying mechanisms. With increasing temperature they found a decrease in FR, whereas FE increased. Their results provide evidence for the species–energy hypothesis that postulates higher species richness with increasing temperature due to the facilitation of niche specialization with increasing resource availability (Srivastava & Lawton, 1998). However, despite these advantages, large-scale studies including functional diversity remain scarce.

At a continental scale, the study of Stevens *et al.* (2003) is to our knowledge the only study that has included functional diversity. For the American continent, based on functional groups of bats, they found a latitudinal gradient in functional diversity which could not be explained by species richness alone. In the present study, we applied for the first time the concept of functional diversity based on individual trait measurements on a continental scale, examining fish communities in European drainage basins. The patterns of functional diversity of the freshwater fish communities of 128 European drainage basins are described using three different diversity measurements: FR, FE and FD. Based on recent studies on European fish species richness patterns and community similarities (Griffiths, 2006; Reyjol *et al.*, 2006; Leprieur *et al.*, 2009), we tested three different hypotheses that might explain these patterns by applying regression analysis and variation partitioning (Table 1).

1. The environmental filtering hypothesis, which assumes that the present environmental conditions are responsible for the observed diversity patterns. Here we concentrate on two sub-hypotheses based on the influence of climatic conditions and habitat diversity and size. (a) The environmental harshness hypothesis, analogous to the physiological tolerance hypothesis or niche volume hypothesis defined by Currie *et al.* (2004) and Mason *et al.* (2008), respectively. This hypothesis predicts, for instance, that in harsh environments fewer species are able to cope with the present conditions. In areas with extreme climates (e.g. cold temperature or aridity), we would either expect only highly adapted individuals with a low combination of characters to survive or generalists that can cope with fluctuating environments (Clavero *et al.*, 2004) and therefore low FR and FD, while FE might be either low or high. Besides these climate-based hypotheses the habitat size hypothesis (b) postulates that community diversity increases with increasing habitat size (Oberdorff *et al.*, 1995; Field *et al.*, 2009). It is generally assumed that habitat diversity increases with area, and thus also niche availability. With niche availability, FR is in turn expected to increase, while patterns of FE and FD are less predictable.

2. The isolation hypothesis postulates that dispersal barriers such as high mountain chains explain diversity patterns (Field *et al.*, 2009; Leprieur *et al.*, 2009). In isolated areas such as the Iberian Peninsula and Italy, we would expect functional diversity to differ from Central Europe with comparatively low FR and high FE in the isolated areas. Indeed, due to speciation in the

Hypothesis	Variable	Min	Max	Median
Environment	Temperature (°C), annual mean	−3.3	18.0	9.0
	Precipitation (mm), annual sum	316	2604	738
	Area (km²)	11	1410 951	3151
	Average elevation (m)	12	1700	229
Dispersal limitation	Isolation through mountain chains	No	Yes	95/32†
Climatic history	Ice coverage during LGM (%)	0	100	33
	Distance to the Black Sea (km)*	540	4170	3140

Table 1 Hypotheses tested to explain the European patterns of functional diversity, variables used, minimum, maximum and median for each variable on the basis of the 128 drainage basins used in this study.

*For non-isolated basins (*n* = 95).
†Number of non-isolated to number of isolated basins.

Table 2 Description of the functional traits, describing aspects of habitat and diet niche axes (Gatz, 1979; Labropoulou & Markakis, 1998; Sibbing & Nagelkerke, 2001).

Niche axis	Morphological trait	Interpretation
Habitat and swimming ability	Pectoral fin length	Manoeuvring speed, habitat velocity
	Vertical position of pectoral fin	Turning capacity
	Body depth	Manoeuvrability, hydrodynamics in the habitat
	Caudal peduncle length	Swimming speed, endurance, acceleration
	Caudal peduncle length relative to body depth	Swimming speed
	Caudal peduncle depth relative to body depth	Swimming ability
	Caudal fin length	Swimming ability
	Eye position	Vertical position in the water column
Diet and food acquisition	Mouth position	Location of food acquisition
	Eye diameter	Adaptation to light conditions (turbidity, night activity) and size of prey items
	Length of longest barbel	Non-visual food detection (turbidity, night activity), also indicates benthic feeders
	Head length	Relative prey size
	Length of upper jaw	Relative prey size
	Maximum size	Actual prey size (in combination with head and upper jaw length)

If not stated, the different traits were standardized by the standard length of the fish (apart from traits giving a character's position and maximum size).

isolated areas, species are more similar than in areas where the same number of species is reached through colonization (Reyjol *et al.*, 2006; Mittelbach *et al.*, 2007).

3. The climatic history hypothesis, which assumes that past climatic events such ice ages had a negative impact on diversity through mass extinctions (Oberdorff *et al.*, 1997; Tedesco *et al.*, 2005). In drainage basins with full ice coverage during the Last Glacial Maximum (LGM), lower functional diversity (i.e. low FR, low FE and high FD) is therefore expected.

Finally, discussing these results on functional diversity together with results on species richness patterns and the distribution of endemic species (e.g. Reyjol *et al.*, 2006; Leprieur *et al.*, 2009) can help us to understand how environmental and historical mechanisms such as isolation and the LGM together influenced the present diversity gradients. Considering different approaches simultaneously can also help to identify regions that could be at the highest risk because of changing environmental conditions and anthropogenic impacts.

METHODS

Data set

Data from drainage basins located throughout geographic Europe (from the Iberian Peninsula in the west to the Ural Mountains in the east and from southern Anatolia to northern Scandinavia) were used (Fig. S1 and Table S1 in Supporting Information). Fish occurrence data were collected from several published books and articles (Table S2). To exclude anthropogenic impacts, only native species were considered, including extirpated species. Fishes entering freshwater only sporadically (e.g. Mugilidae, Syngnathidae) or fishes assumed not to have reached their present range via the continental route, such as *Alosa* spp., *Coregonus* spp., *Gasterosteus aculeatus*, *Salmo* spp.

(Banarescu, 1989, 1992; Kottelat & Freyhof, 2007) were excluded from the analysis. Only drainage basins with at least three fish species after removal were retained for analyses, leading to a total of 230 species and 128 drainage basins.

The functional diversity of the fish communities was calculated based on 14 uncorrelated or only slightly correlated ($r < 0.65$) morphological traits related to diet and habitat niche axes (Table 2, Fig. 1) (Gatz, 1979; Labropoulou & Markakis, 1998; Sibbing & Nagelkerke, 2001). Traits were measured on photographs and scientific drawings (lateral view of the fish), since at the geographic scale of this study the collection and laboratory treatment of all occurring fish species were not possible. We used either our own photographs, pictures collected mainly from http://www.fishbase.org, Kottelat & Freyhof (2007) and Berg (1965), or pictures provided by helpful colleagues. If available, measurements were taken from five pictures per species. All traits were standardized to account for differently sized photographs and species (e.g. standard length; see Table 1 and Fig. 1 for greater detail).

As predictor variables, four environmental variables were selected (Table 1), describing present climatic and spatial heterogeneity without showing strong collinearity (correlation coefficients r ranging from -0.3 to 0.3). The selected variables are known to influence species richness (Oberdorff *et al.*, 1995; Field *et al.*, 2009), and for some their influence on functional diversity of fish communities was already shown on a regional scale by Mason *et al.* (2008). In total we used three sets of explanatory variables:

1. Present-day climatic conditions (average temperature and precipitation values) and habitat (drainage basin area and average elevation) (Leprieur *et al.*, 2008; Hugueny *et al.*, 2010 and references therein). Average elevation was chosen as a proxy for habitat diversity, because for this data set it correlated better with climatic variability (spatial and inter-annual) than range of
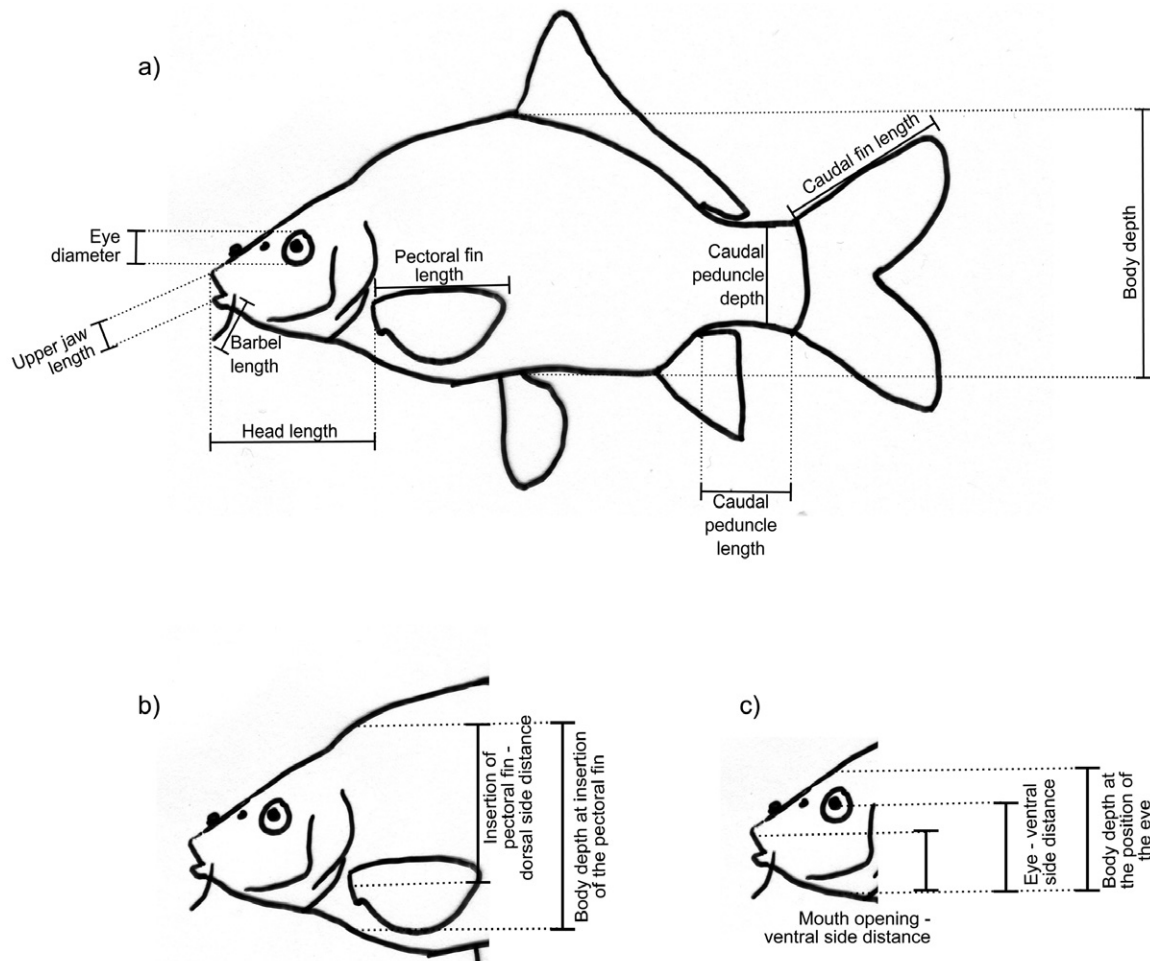
Figure 1 Functional character measurements. (a) All measurements are standardized by the standard length. Caudal peduncle length is also standardized by body depth; caudal peduncle depth was only standardized by body depth. (b) Pectoral fin position: pectoral fin dorsal side distance divided by body depth at the pectoral fin. (c) Eye position: eye–ventral side distance divided by body depth at the eye; mouth position: mouth–ventral side distance at the position of the eye divided by body depth at the position of the eye.

elevation or standard deviation of elevation. Data for elevation and climatic variables were obtained from http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/gtopo30_info and http://www.cru.uea.ac.uk (New *et al.*, 2002), respectively. Mean annual temperature and precipitation were calculated from the monthly means averaged over the basin grids (10′ longitude, latitude).

2. A two-factorial variable indicating whether or not a drainage basin was historically isolated. Basins were considered historically isolated when they lay in one of the areas which are geographically isolated from Central Europe by the main European mountain chains: the Iberian Peninsula (isolated by the Pyrenees), the Italian Peninsula (isolated by the Alps), the western Balkans (isolated by the Dinaric Alps) and southern Anatolia (isolated by the Taurus Mountains) (Banarescu, 1989, 1992; Ketmaier *et al.*, 2004; Leprieur *et al.*, 2009).

3. Variables on climatic history (Table 1), which are known to have influenced species extinctions and extirpations (ice cover during the LGM) and the re-colonization of the drainage basins

afterwards (distance to the Black Sea, from where Central Europe was re-colonized after the LGM) (Banarescu, 1989, 1992; Reyjol *et al.*, 2006; Field *et al.*, 2009). The extension of ice cover was taken from Dürr *et al.* (2005) and expressed in three levels (not covered at all, partly covered, fully covered). The distance to the Black Sea was calculated as the distance between the centre of the Black Sea and the centre of each drainage basin (Reyjol *et al.*, 2006).

Functional diversity

Three indices were calculated describing different independent aspects of functional diversity (Mason *et al.*, 2005; Villéger *et al.*, 2008; Schleuter *et al.*, 2010), namely FR, FE and FD. The morphological traits define a multidimensional space in which species are positioned, and each river basin consists of a volume filled with its respective species. FR is the volume of the functional trait space. Then, within this volume, FE characterizes the degree of trait aggregation (from a uniform to a patchy distri-

bution) and FD describes the degree of niche differentiation (maximal when all the species are positioned at the surface of the volume).

FR was calculated using FR_{Is} proposed by Schleuter *et al.* (2010). This index is based on intra-specific trait variability and considers gaps in the functional niche space and thus describes functional richness better than other indices. It is a one-dimensional index that calculates the union of the species trait ranges (i.e. intra-specific variability, here a species' range between minimum and maximum trait values) at one site, relative to the union of species trait ranges for all sites together. It is then averaged over all traits:

$$FR_{Is} = \frac{\int \max_{s \in S_c} [\mathbf{1}_{st}(x)] dx}{\int \max_{s \in \cup S_c} [\mathbf{1}_{st}(x)] dx},$$

where s is the species, S_c is the number of species present in a drainage basin, $\cup S_c$ the union of species of all drainage basins and $\mathbf{1}_{st}(x)$ is 1 if x is between the minimum and maximum value of trait t in species s, otherwise it is 0.

FE was calculated using the multidimensional index FE_m by Villéger *et al.* (2008) that calculates evenness based on the abundance-weighted Euclidean distances between all species pairs to calculate first the minimum spanning tree (MST) that links all the species in a multidimensional trait space and then compares the distribution of branch lengths to an optimal even distribution:

$$FE_m = \frac{\sum_{e \in E} \min \left[\frac{\mathrm{dist}(e)/(A_e/A)}{\sum_{e' \in E} \mathrm{dist}(e')/(A_{e'}/A)}, \frac{1}{|S_c|-1} \right] - \frac{1}{|S_c|-1}}{1 - \frac{1}{|S_c|-1}},$$

where S_c is the number of species in a community, E is the set of edges connecting species pairs in the MST, $\mathrm{dist}(e)$ is the distance between endpoint species of edge e, A is total abundance and A_e is the sum of the abundances of the endpoint species of edge e.

To calculate FD, Rao's quadratic entropy FD_Q (Rao, 1982) was used. This index is based on the Simpson index (Simpson, 1949), used to calculate species diversity, and weights the trait-based Euclidean distances between pairs of species ($\mathrm{dist}(s, s')$) by the product of their relative abundances (A_s/A for species s, whereby A_s is the abundance of species s and A the abundance of all species in the community):

$$FD_Q = \sum_{s \in S_c} \sum_{s' \in S_c} \frac{A_s A_{s'}}{A^2} \mathrm{dist}(s, s').$$

Since relative abundance was not available for this study, it was set to $1/S_c$ for each species.

Standardization of functional diversity indices

The mean FR_{Is} and the variances of the three indices strongly depend on local species richness (Schleuter *et al.*, 2010). To account for these dependences, the observed values of the functional diversity indices (I_{obs}) were standardized. To calculate the SES (standardized effect size) I_{obs} was centred and scaled using the mean (I_{rand}) and standard deviation (σ_{rand}) estimates based on the distribution of the corresponding indices computed for a set of random communities (Gotelli & McCabe, 2002):

$$SES = (I_{obs} - I_{rand})/\sigma_{rand}.$$

To keep row and column sums stable (Gotelli, 2000), while also considering the wide range of species richness, we did not follow the commonly used swap method to randomize communities, but applied a weighted re-sampling method that we specifically designed to control for the occurrence of each species in the whole data set. We started with one drainage basin, which was randomly drawn from the European basin pool. If the observed species richness in this basin was n, then n different species were randomly drawn from the European species pool with no replacement (the probability for each species to be drawn corresponds to the percentage of that species' occurrence). A second basin was then randomly drawn among the remaining basins; if its richness was m, then m species were randomly drawn from the European pool, but the probability of each species was now the number of occurrences of that species minus 1 divided by the total number of basins minus 1, if it was previously drawn, divided by the remaining number of basins, and so on, until the species were randomized for each drainage basin. The whole procedure was repeated 999 times leading to 999 simulated data sets used to compute the corresponding index values. This sample was then used to estimate I_{rand} and σ_{rand}.

Data analysis

To test the relationship between the different environmental variables describing present climate and habitat and the values of the SES functional diversity index, multiple linear regression models were applied. For mean annual temperature and precipitation, we first checked whether the quadratic term should also be included in the model. Therefore, we regressed SES index values considering models including the linear term of the predictor variable only and those including the quadratic term as well. As the best-performing model for each variable, the model with the significantly lowest Akaike information criterion (AIC) was considered (Johnson & Omland, 2004). To be sure that the climatic variables were not biased for the large drainage basins, this analysis was also run without the largest 25% of drainage basins. However, removing the large drainage basins did not change the results of the linear regression models. For plots displaying the relationship between SES index values and drainage basin size see Fig. S2.

The relative importance of environmental conditions, dispersal limitation (geographic isolation by mountain chains) and climatic history (ice cover during the LGM) in explaining SES values was then tested using variation partitioning. This method divides the variation explained by the different sets of

explanatory variables into independent and joint effects. We applied the method according to Borcard *et al.* (1992) where partitioning is based on redundancy analysis (RDA), a popular ordination method in community ecology. The partition is based on adjusted R^2 as it provides unbiased estimates. Variance partitioning has recently been controversially discussed in the literature (e.g. Gilbert & Bennett, 2010). However, the discussion mostly concerns the analysis of community composition data, which are generally difficult to model, and the inclusion of spatial predictors such as principal components of neighbour matrices (PCNM) or Moran's eigenvector maps (MEM).

The residuals of the full model of the variance partitioning of each index were tested with a Mantel test (Mantel, 1967) for spatial autocorrelation using a higher-order neighbourhood matrix, where two basins were contiguous when their polygons shared at least one boundary point. Given that Scandinavia was re-colonized after the LGM through the Baltic Sea (Banarescu, 1989) and that the Baltic Sea was a freshwater lake (Ancylus Lake) until 8.0 kyr BP (Björck, 1995), basins draining into it were considered to be contiguous, as were the Thames and the Rhine, which were connected after the LGM (Banarescu, 1989). Direct neighbours were indicated with 1, otherwise geographic distance was indicated by the minimum number of boundaries which had to be crossed (Tedesco *et al.*, 2005). Drainage basins that were missing in the data base were also considered. Distance values higher than 5 were grouped in a sixth class, because spatial correlations of native species are normally only expected for short and medium distances (Tedesco *et al.*, 2005; Leprieur *et al.*, 2009).

The role of climatic history was additionally assessed through the relationship of re-colonization potential after LGM (distance to the Black Sea) and the SES values for the different indices using linear regressions. This analysis was done for the non-isolated drainage basins only because the isolated basins were not re-colonized after the LGM from the Black Sea (Banarescu, 1989; Durand *et al.*, 1999; Reyjol *et al.*, 2006).

All variables that did not meet the assumption of a normal distribution were log-transformed. Calculations were made using the open source program R (R development core team, 2008) and the implemented package vegan (Oksanen *et al.*, 2010).

RESULTS

General pattern of functional diversity

Functional diversity differed markedly between drainage basins. Standardized FR showed a strong north–south gradient and was lower than expected in southern Europe, with the lowest values found for drainage basins on the Iberian Peninsula and other Mediterranean areas, followed by the northern Scandinavian drainage basins, and the highest values being found in Central and eastern Europe and Great Britain (Fig. 2a). Standardized FE, in contrast, did not show a clear spatial gradient: FE was lower than expected in north-western Europe and in some drainage

basins in Central and eastern Europe, as well as in Greece and Turkey, while in other drainage basins in the same areas and on the Iberian Peninsula FE was higher than expected (Fig. 2b). The lowest index values were found for Greece, while the highest were found on the Iberian Peninsula. Similar to FR, FD also exhibited a north–south gradient with the highest FD values being in temperate Central Europe (Fig. 2c). Drainage basins in the western Balkans exhibited the lowest values, while the highest FD was found for the Danube and some drainage basins in Great Britain.

Environmental variables

For all functional diversity indices, the best-fit model for average annual temperature was the model that also included the quadratic term (lowest AIC) with the lowest SES index values in cold and warm areas for FR and FD, while for FE this relationship was inverted (Fig. 3). For precipitation, the relationship was linear for all indices. The multi-predictor models (Table 3) showed the explanatory importance of climatic variables: the average annual temperature was significant for all three functional diversity indices, and precipitation contributed to the explanation of variance for FR and FD. In contrast, variables representing habitat diversity and size were less important. Only average elevation contributed to the explanation of variance for FR and FD, while drainage basin size was not significant for any of the models.

The role of the environment, geographic isolation and climatic history

The combination of present environmental conditions, geographic isolation and climatic history best explained the variation of FR (75%), followed by FD (38%) and FE (17%) (Fig. 4). In all functional diversity indices, the observed gradients were best explained by isolation through insurmountable mountain chains followed by present environmental conditions (Fig. 4). For FR, the combined effect of isolation with environment and climatic history accounted for 64%, and 25% of the variation was explained solely by isolation. The present environmental conditions explained a total of 46%, while their independent effect accounted for only 6%. Climatic history in terms of ice cover during the LGM was the least important; although the combined effect accounted for 36%, its independent effect was only 1%. For FE (Fig. 4b) and FD (Fig. 4c), isolation explained a total of 9% and 27%, respectively, while each effect alone in both indices accounted for 9%, closely followed by present environmental conditions (combined effects 8% and 24%; independent effects 6% and 8%). As for FR, the role of climatic history was negligible. This was especially true for FE where climatic history did not contribute independently to the explanation of the observed variance.

We did not detect a spatial autocorrelation in the model residuals for FR ($P = 0.227$) or FE ($P = 0.183$), while the Mantel test was significant for the model residuals of FD ($P = 0.001$). The role of re-colonization potential after the
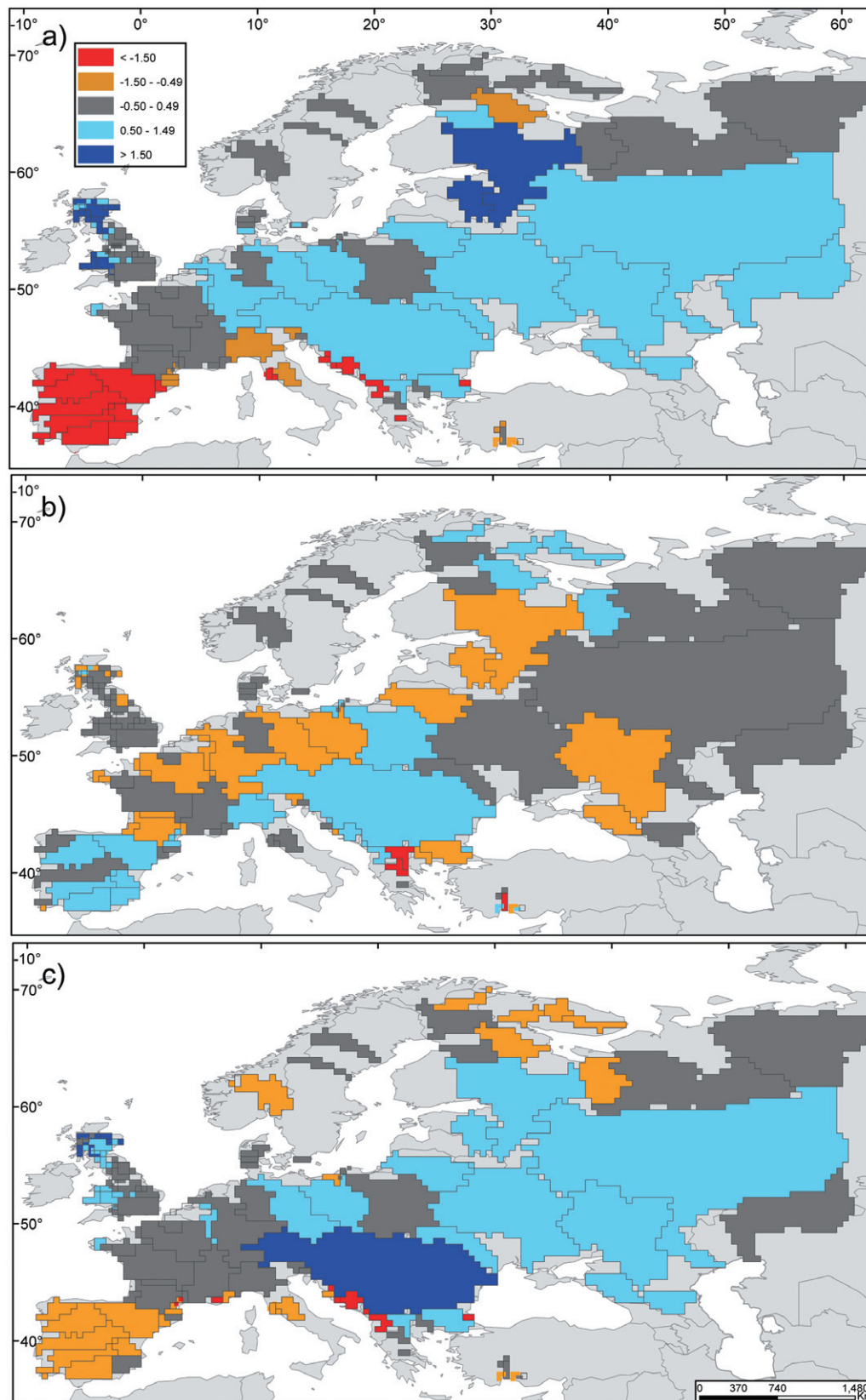
Figure 2 Functional diversity of drainage basins used in this study: (a) functional richness, (b) functional evenness, and (c) functional divergence. Different colours show different categories of the standardized effect size (SES) values (positive/negative values show that the observed index value is higher/lower than expected at random). For drainage basin names, index values and predictors, please see the Supporting Information (Fig. S1, Table S1).
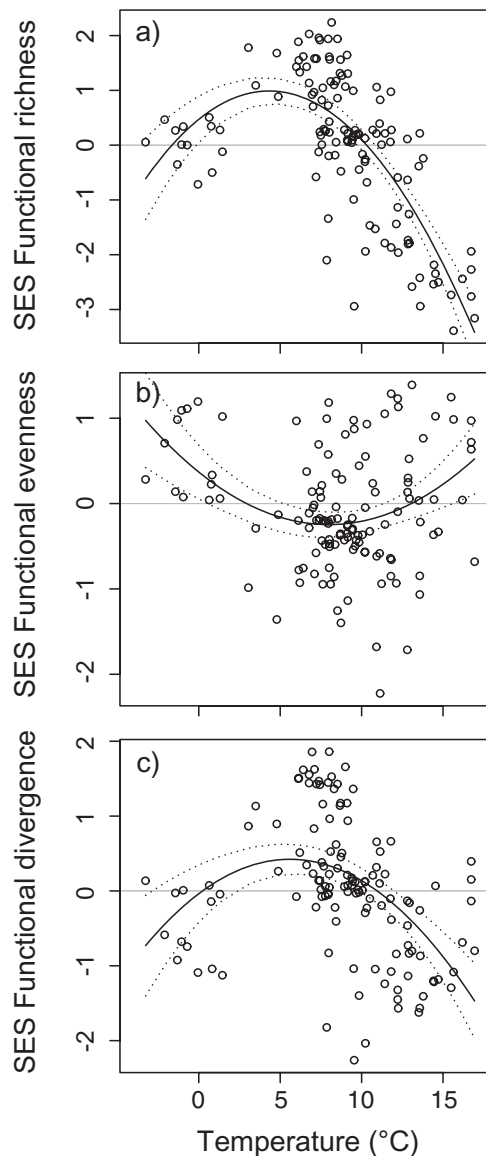
Figure 3 Relationship of the standardized effect size (SES) functional diversity index values with average annual temperature: (a) functional richness ($R^2 = 0.57$, $P < 0.001$), (b) functional evenness ($R^2 = 0.13$, $P < 0.001$) and (c) functional divergence ($R^2 = 0.23$, $p < 0.001$). The solid line represents the model's fit, dotted lines the 95% confidence intervals.

Table 3 Multiple-predictor models for the environmental variables for functional richness, evenness and divergence.

Predictor	Slope	SE	*t*-value	*P*-value
Functional richness				
Intercept	−4.12	1.81	−2.3	0.024*
Temperature	0.16	0.05	3.1	0.002**
Temperature^2	−0.022	0.003	−6.5	< 0.001***
Precipitation	1.93	0.59	3.3	0.001**
Area	0.14	0.10	1.4	0.171
Elevation	−0.60	0.19	−3.1	0.002**
Adjusted R^2	0.60			
Functional evenness				
Intercept	0.89	1.41	0.6	0.530
Temperature	−0.15	0.04	−3.6	< 0.001***
Temperature^2	0.009	0.003	3.2	0.001**
Precipitation	−0.27	0.46	−0.6	0.566
Area	−0.10	0.08	−1.2	0.215
Elevation	0.28	0.15	1.9	0.062
Adjusted R^2	0.12			
Functional divergence				
Intercept	−3.31	1.63	−2.0	0.045*
Temperature	0.11	0.05	2.3	0.025*
Temperature^2	−0.010	0.003	−3.3	0.001**
Precipitation	1.44	0.54	2.7	0.008**
Area	0.16	0.09	1.8	0.078
Elevation	−0.63	0.17	−3.7	< 0.001***
Adjusted R^2	0.29			

$P > 0.05$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.
Number of observations = 128. Area = drainage basin size. Elevation = average elevation. Temperature = average annual temperature. Precipitation = summed annual precipitation. SE = standard error.

terns for the fish communities in European drainage basins. Most particularly, FR, and to some extent FD, can be explained by these hypotheses.

Among environment, geographic isolation and climatic history, the current environmental conditions (hypothesis 1) were the second most important component explaining the observed diversity gradient for FR (46% in total), FE (8%) and FD (24%). Considering environmental variables alone, those describing present climate, particularly temperature, fit best with the different functional diversity indices. Climate can act in different ways on functional diversity. We found evidence for the environmental harshness hypothesis, which predicts lower diversity in harsh environments (Currie *et al.*, 2004; Mason *et al.*, 2008); FR and FD were lowest in areas with extreme average annual temperature in southern and northern Europe. For fish communities in France, Mason *et al.* (2008) found increasing FR with increasing temperature, arguing that the increased temperature allowed for increased niche specialization, seemingly due to higher productivity and thus higher species richness. In the present study with a broader temperature range, FR also increased to a certain extent with temperature. The decrease in the Mediterranean regions might be attributed to some extent to the combination of high tempera-
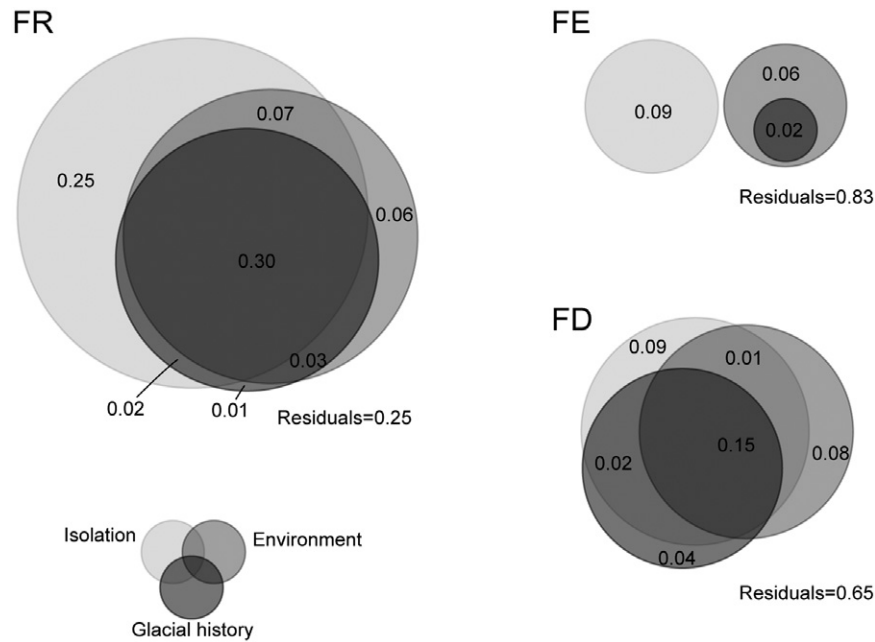
LGM for the non-isolated basins did not influence the observed functional diversity patterns. The relationship between distance to the Black Sea and the SES index values was only significant for FR ($P = 0.02$, slope = 0.019), but explained only 5% of the variation.

DISCUSSION

From the hypotheses postulated, the present environmental conditions, especially climate (hypothesis 1) and geographic isolation (hypothesis 2) best explain the functional diversity pat-

Figure 4 Fractions of adjusted percentage variation (R^2_{adj}) explained for functional richness (FR), functional evenness (FE) and functional divergence (FD) of freshwater fish communities of European drainage basins by environment (habitat diversity and climate), dispersal limitation/isolation (basins isolated from Central Europe by mountain chains) and climatic history (ice cover during the Last Glacial Maximum). Size of circles reflect the R^2_{adj} of the total effect, numbers indicate explained variation of different unique and combined effects. Please note that due to graphical limitations overlaps of circles are only approximations.

tures and low precipitation. Especially in small drainage basins, where the impact of droughts is more severe (Clavero *et al.*, 2004), annual precipitation can strongly affect FR. For the Iberian Peninsula, for instance, freshwater fish are largely habitat specialists, adapted to fluctuating water levels (Magalhães *et al.*, 2002; Clavero *et al.*, 2004), resulting in less space for functionally different species.

Among the environmental variables, we found no, or only weak, evidence for the habitat diversity/size hypothesis. Size of the drainage basin did not contribute significantly to explaining variance for any of the three indices. Average elevation within a drainage basin was significant for FR and FD, although with only a slight improvement in the model's goodness of fit. This is surprising, since habitat diversity, especially habitat size, has been identified as an important predictor for species richness in previous studies (Oberdorff *et al.*, 1995; Field *et al.*, 2009; Hugueny *et al.*, 2010), and we also expected FR to increase with habitat size and thus niche availability. One could argue that the drainage basin scale used in this study was too large, yet Mason *et al.* (2008) found no significant effect of area on functional diversity when working on lakes in France. It is possible that the habitat diversity of small and large basins differs less than is commonly assumed. The increase in species richness with increasing area could, in this case, be attributed to the increase in functionally similar species that can avoid competition when the basin size is sufficient, and less to the addition of functionally different species. This hypothesis is supported by the development of convergent species in isolated populations (Elmer *et al.*, 2010). It is also in accordance with the prediction that larger

areas have higher speciation rates (Mittelbach *et al.*, 2007; Hugueny *et al.*, 2010). In large basins, species might have wider ranges and populations can more easily become fragmented than in smaller basins. An increase in species richness then does not lead to a sharp increase in FR because closely related species are more similar. Another possible reason is that area is not as good a predictor for aquatic habitat diversity as is generally agreed. However, it should be noted that indices which are standardized for species richness are being considered here. As a consequence, these results do not oppose the species richness–area relationship.

In addition to hypothesis 1, we found strong evidence for hypothesis 2 postulating that geographic isolation strongly influences functional diversity. Geographic isolation was the component that explained most of the observed variation (FR 64%, FE 9%, FD 27% in total and FR 25%, FE 9%, FD 9% alone) and that could partially explain the very low FR values found in the Mediterranean areas (Iberian Peninsula, Italy, western Balkans). The strong effect of isolation on functional diversity might be caused by three mechanisms: extinction, dispersal limitation (inhibited re-colonization) and speciation. First, the Mediterranean drainage basins with extreme temperatures and droughts combined with a relatively small drainage basin size may have been more vulnerable to extinctions (Griffiths, 2006; Reyjol *et al.*, 2006). Due to the lack of glaciations in these climates, drainage basins have been isolated from each other for a longer time in the Mediterranean and the major faunal exchange between drainage basins is older in these areas than in Central Europe; thus these drainage basins have been subject to extinc-

tions for a longer period of time (Reyjol *et al.*, 2006). Second, re-colonization from the temperate zones was inhibited due to high mountain chains that acted as geographic barriers (Banarescu, 1989, 1992; Leprieur *et al.*, 2009), leading to a loss of functional characters. The relatively low FD values confirm the loss of extreme trait values. Finally, another effect of long-lasting isolation is the increase in allopatric speciation. However, in contrast to species richness that logically increases in the absence of extinction when the speciation rate is high, functional diversity might only increase slowly (FR) or even decrease (FE, FD). Apart from a few exceptions (parallelism in cichlids), closely related species are generally more similar than more distant ones (e.g. Richman & Price, 1992), resulting in relatively low FR for related species compared with unrelated ones at the same species richness level. FE might either decrease due to species clumping or increase, as observed in this study for the Mediterranean, if speciation leads to a more regular distribution than before. Depending on the position of the species cluster in trait space, FD might also either increase or decrease. The low FR values in the Mediterranean areas might therefore partly be a product of increased speciation rates. Actually, species richness is quite high in these regions (Reyjol *et al.*, 2006, 2008) and 10 out of the 29 *Barbus* species in Europe are native to the Iberian Peninsula (*c.* 25% of the species inventoried there), as with six of nine *Squalius* species. An indicator that the speciation rate is high in those areas is also the high number of endemic species (Griffiths, 2006; Reyjol *et al.*, 2006, 2008; Marr *et al.*, 2010). Reyjol *et al.* (2006) even suggested that in the Mediterranean drainage basins, allopatric as well as *in situ* speciation has occurred.

In general, different effects on functional richness are possible if extinction and speciation rates are considered in combination with geographic isolation. Without isolation, species richness and functional richness are expected to increase due to speciation and colonization until saturation is reached; then extinction, colonization and speciation balance each other. However, if this drainage basin becomes geographically isolated, colonization stops. Then the extinction rate and speciation rate might either balance each other or the extinction rate can be lower or higher than the speciation rate. When species loss is compensated by speciation, functional richness decreases slightly due to the greater similarity of the new sister species. Although extinction will not necessarily occur in the oldest species, due to the ongoing speciation process more similar species will accumulate over time. This might be especially true in the climates considered here and because of the low availability of empty niches that do not allow for the fast adaptive radiation that can be observed in the tropics when habitats are newly colonized. When the extinction rate exceeds the speciation rate, FR will decrease even more drastically.

Another less probable scenario in the European climate is that the speciation rate is higher than the extinction rate. In this case, species richness will increase, and depending on the extinction rate FR will decrease, increase or remain stable. The increase of species richness, however, and possibly FR, will always be lower than in non-isolated basins, where the re-colonization potential is higher. An example of this could be the relatively high FR and

FD in Great Britain that go along with relatively low FE. The species there re-colonized the drainage basins after the LGM and include quite a variety of different taxa and are therefore functionally more unique than species in the isolated drainage basins in the Mediterranean with the same number of species which are more similar due to higher speciation and extinction rates in these areas.

Although the effect of geographic isolation alone was 25% for FR, we could not completely disentangle the effect of temperature and isolation, as geographically isolated areas on the European continent are mostly in southern Europe. Similar studies on other continents could help to further clarify the effects of these variables.

Finally, we did not find clear evidence for the climatic history hypothesis 3. Neither the ice coverage during the LGM nor the distance to the Black Sea, from where drainage basins were re-colonized after the LGM, substantially influenced functional diversity. This is in contrast to what is known for species richness (Reyjol *et al.*, 2006). Our results therefore suggest that the species that dispersed further were functionally more unique, as the high FR in Great Britain already illustrates. With ongoing species dispersal, the probability of the arrival of functionally redundant species will increase. Additionally, drainage basins in Central Europe have been isolated from each other for a relatively short time and therefore have not been subject to extinction for a long time. Another reason for the low contribution of climatic history alone might be the collinearity between present temperature, geographic isolation (most isolated drainage basins are in southern Europe) and ice cover during the LGM, resulting in the relatively high proportion of combined effects in variance partitioning. However, the collinearity of distance to the Black Sea and present environmental variables (precipitation $R^2 = 0.28$) are accounted for by using the residuals from the multivariate model built with the variables describing present environmental conditions.

Lastly, we detected spatial autocorrelation in the residuals of the FD model; nevertheless, we believe that the results of the FD model are reliable. Hawkins *et al.* (2007) conclude from their study with a Monte Carlo experiment that autocorrelation is not as problematic as it is most often claimed to be. In their experiments, the regression results were not seriously affected by autocorrelation and R^2 values were even lower when autocorrelation was not removed. As there was no autocorrelation for the FR and FE model residuals, we suggest that in the present study an environmental predictor that explains the spatial distribution of this index was omitted. This could be, for example, temporal and spatial variability within a drainage basin that might not be sufficiently covered by drainage basin size and elevation.

Previous studies identified the European Mediterranean drainage basins as diversity hot spots based on their high species richness and their high number of endemic species (Reyjol *et al.*, 2006, 2008). The present study has shown that due to their low functional diversity these drainage basins are concurrently also extremely vulnerable to environmental fluctuations. However, these are the climates that will suffer most from ongoing climate change with increasing temperatures and droughts (Malcolm

et al., 2006). Given the strong anthropogenic activities that overwhelm the natural dispersal barriers and that Mediterranean areas are subject to very high invasion rates (Leprieur *et al.*, 2008; Marr *et al.*, 2010), further destabilization of these vulnerable ecosystems is likely.

CONCLUSION

In the present study, functional diversity is mainly governed by geographic isolation and climate. Within the limits of our work, the concept of habitat diversity and size do not seem to be applicable to functional diversity. Specifically, environmental harshness such as extreme temperatures and low precipitation as in the Mediterranean can lead to low FR. These areas also experience geographic isolation from Central Europe and a long-lasting isolation among drainage basins due to the lack of glaciations during the last ice age. These areas have therefore been subject to extinction for a longer time and these extinctions could not be compensated by re-colonization. Coupled with the comparatively high speciation in these areas, functional diversity, particularly FR, became extremely low. Due to the high number of endemic species, on a continental scale, Reyjol *et al.* (2006) identified peri-Mediterranean Europe as a biodiversity hotspot. Most particularly, the Iberian and Italian Peninsulas and the Balkans may be subject to further extinctions due to the highly seasonal Mediterranean climate and further warming and droughts due to climate change (Griffiths, 2006). The lower FR and FD in the Mediterranean basins suggest that species are more functionally redundant than those in basins from other areas. Hence, we could hypothesize that Mediterranean community functioning could better withstand further species extinctions than community functioning in temperate areas on a small scale. Indeed, in these latter areas, the higher FD assumes a higher niche differentiation and possibly a higher functional complementarity that is more susceptible to a loss of functions. However, over the short term, the lower FR of the Mediterranean areas could suggest a less flexible functioning that can withstand expected short-term climate change (hydrological stress) and actual pressures from non-native species introduction in these zones (Marr *et al.*, 2010).

ACKNOWLEDGEMENTS

REFERENCES

Banarescu, P. (1989) Zoogeography and history of the freshwater fish fauna of Europe. *The freshwater fishes of Europe Vol.1 / II: General introduction to fishes* (ed. by J. Holcik), pp. 88–107. Aula-Verlag GmbH, Wiesbaden.

Banarescu, P. (1992) *Zoogeography of fresh waters. Vol 2: Distribution and dispersal of freshwater animals in North America and Eurasia.* Aula-Verlag GmbH, Wiesbaden.

Berg, L.S. (1965) *Fishes of the USSR and adjacent countries, Vol. I– III*, 4th edn. Israel Program for Scientific Translation, Jerusalem.

Björck, S. (1995) A review of the history of the Baltic Sea, 13.0-8.0 ka BP. *Quaternary International*, **27**, 19–40.

Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045–1055.

Clavero, M., Blanco-Garrido, F. & Prenda, J. (2004) Fish fauna in Iberian Mediterranean river basins: biodiversity, introduced species and damming impacts. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **14**, 575–585.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'brien, E. & Turner, J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7**, 1121–1134.

Díaz, S. & Cabido, M. (2001) Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, **16**, 646–655.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, M.L.J. & Sullivan, C.A. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, **81**, 163–182.

Durand, J.D., Persat, H. & Bouvet, Y. (1999) Phylogeography and postglacial dispersion of the chub (*Leuciscus cephalus*) in Europe. *Molecular Ecology*, **8**, 989–997.

Dürr, H.H., Meybeck, M. & Dürr, S.H. (2005) Lithologic composition of the Earth's continental surfaces derived from a new digital map emphasizing riverine material transfer. *Global Biogeochemical Cycles*, **19**, GB4S10. doi:10.1029/2005GB002515.

Elmer, K.R., Kusche, H., Lehtonen, T.K. & Meyer, A. (2010) Local variation and parallel evolution: morphological and genetic diversity across a species complex of Neotropical crater lake cichlid fishes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 1763–1782.

Field, R., Hawkins, B., Cornell, A.H.V., Currie, D.J., Diniz-Filho, J.A.F., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G. (2009) Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, **36**, 132–147.

Gatz, A.J.J. (1979) Ecological morphology of freshwater stream fishes. *Tulane Studies in Zoology and Botany*, **21**, 91–124.

Gilbert, B. & Bennett, J.R. (2010) Partitioning variation in ecological communities: do the numbers add up? *Journal of Applied Ecology*, **47**, 1071–1082.

Gotelli, N.J. (2000) Null model analysis of species co-occurrence patterns. *Ecology*, **81**, 2606–2621.

Gotelli, N.J. & McCabe, D.J. (2002) Species co-occurrence: a meta-analysis of J. M. Diamond's assembly rules model. *Ecology*, **83**, 2091–2096.

Griffiths, D. (2006) Pattern and process in the ecological biogeography of European freshwater fish. *Journal of Animal Ecology*, **75**, 734–751.

Hawkins, B.A., Diniz Filho, J.A.F., Mauricio Bini, L., De Marco, P. & Blackburn, T.M. (2007) Red herrings revisited: spatial autocorrelation and parameter estimation in geographical ecology. *Ecography*, **30**, 375–384.

Hugueny, B., Oberdorff, T. & Tedesco, P.A. (2010) Community ecology of river fishes: a large-scale perspective. *Community ecology of stream fishes: concepts, approaches, and techniques* (ed. by K.B. Gido and D.A. Jackson), pp. 29–62. American Fisheries Society Symposium 73. American Fisheries Society, Bethesda, Maryland.

Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology and Evolution*, **19**, 101–108.

Ketmaier, V., Bianco, P.G., Cobolli, M., Krivokapic, M., Caniglia, R. & De Matthaeis, E. (2004) Molecular phylogeny of two lineages of Leuciscinae cyprinids (*Telestes* and *Scardinius*) from the peri-Mediterranean area based on cytochrome *b* data. *Molecular Phylogenetics and Evolution*, **32**, 1061–1071.

Kottelat, M. & Freyhof, J. (2007) *Handbook of European freshwater fishes*. Kottelat, Cornol, Switzerland and Freyhof, Berlin, Germany.

Labropoulou, M. & Markakis, G. (1998) Morphological–dietary relationships within two assemblages of marine demersal fishes. *Environmental Biology of Fishes*, **51**, 309–319.

Leprieur, F., Beauchard, O., Blanchet, S., Oberdorff, T. & Brosse, S. (2008) Fish invasions in the world's river systems: when natural processes are blurred by human activities. *PLoS Biology*, **6**, 0404–0410.

Leprieur, F., Olden, J.D., Lek, S. & Brosse, S. (2009) Contrasting patterns and mechanisms of spatial turnover for native and exotic freshwater fishes in Europe. *Journal of Biogeography*, **36**, 1899–1912.

Magalhães, M., Beja, P., Canas, C. & Collares-Pereira, M. (2002) Functional heterogeneity of dry-season fish refugia across a Mediterranean catchment: the role of habitat and predation. *Freshwater Biology*, **47**, 1919–1934.

Malcolm, J.R., Liu, C.R., Neilson, R.P., Hansen, L. & Hannah, L. (2006) Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology*, **20**, 538–548.

Mantel, N. (1967) The detection of disease clustering and a generalized regression approach. *Cancer Research*, **27**, 209–220.

Marr, S.M., Marchetti, M.P., Olden, J.D., García-Berthou, E., Morgan, D.L., Arismendi, I., Day, J.A., Griffiths, C.L. & Skelton, P.H. (2010) Freshwater fish introductions in mediterranean-climate regions: are there commonalities in the conservation problem? *Diversity and Distributions*, **16**, 606–619.

Mason, N.W.H., Mouillot, D., Lee, W.G. & Wilson, J.B. (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, **111**, 112–118.

Mason, N.W.H., Lanoiselée, C., Mouillot, D., Irz, P. & Argillier, C. (2007) Functional characters combined with null models reveal inconsistency in mechanisms of species turnover in lacustrine fish communities. *Oecologia*, **153**, 441–452.

Mason, N.W.H., Irz, P., Lanoiselée, C., Mouillot, D. & Argillier, C. (2008) Evidence that niche specialization explains species–energy relationships in lake fish communities. *Journal of Animal Ecology*, **77**, 285–296.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V. *et al.* (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**, 315–331.

New, M., Lister, D., Hulme, M. & Makin, I. (2002) A high-resolution data set of surface climate over global land areas. *Climate Research*, **21**, 1–25.

Oberdorff, T., Guégan, J.-F. & Hugueny, B. (1995) Global scale patterns of fish species richness in rivers. *Ecography*, **18**, 345–352.

Oberdorff, T., Hugueny, B. & Guégan, J.-F. (1997) Is there an influence of historical events on contemporary fish species richness in rivers? Comparisons between western Europe and North America. *Journal of Biogeography*, **24**, 461–467.

Oksanen, J.F., Blanchet, G., Kindt, R., Legendre, P., O'hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2010) *Vegan: community ecology package*. Available at: http://CRAN.R-project.org/package=vegan (accessed 23 October 2010).

Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters*, **9**, 741–758.

R development core team (2008) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.

Rao, C.R. (1982) Diversity and dissimilarity coefficients: a unified approach. *Theoretical Population Biology*, **21**, 24–43.

Reyjol, Y., Hugueny, B., Pont, D., Bianco, P.G., Beier, U., Cailoa, N., Casals, F., Cowx, I.G., Economou, A., Ferreira, M.T., Haidvogl, G., Noble, R., de Sostoa, A., Vigneron, T. & Virbickas, T. (2006) Patterns in species richness and endemism of European freshwater fish. *Global Ecology and Biogeography*, **16**, 65–75.

Reyjol, Y., Hugueny, B., Bianco, P.G. & Pont, D. (2008) Congruence between riverine fish species richness and endemism at the biogeographical scale: the role of history. *Aquatic Conservation – Marine and Freshwater Ecosystems*, **18**, 1311–1314.

Richman, A.D. & Price, T. (1992) Evolution of ecological differences in the Old World leaf warblers. *Nature*, **355**, 817–821.

Schleuter, D., Daufresne, M., Massol, F. & Argillier, C. (2010) A user's guide to functional diversity indices. *Ecological Monographs*, **80**, 469–484.

Sibbing, F.A. & Nagelkerke, L.A.J. (2001) Resource partitioning by Lake Tana barbs predicted from fish morphometrics and prey characteristics. *Reviews in Fish Biology and Fisheries*, **10**, 393–437.

Simpson, E.H. (1949) Measurement of diversity. *Nature*, **163**, 688–688.

Srivastava, D.S. & Lawton, J.H. (1998) Why more productive sites have more species: an experimental test of theory using tree-hole communities. *The American Naturalist*, **152**, 510–529.

Stevens, R.D., Cox, S.B., Strauss, R.E. & Willig, M.R. (2003) Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal trends. *Ecology Letters*, **6**, 1099–1108.

Tedesco, P.A., Oberdorff, T., Lasso, C.A., Zapata, M. & Hugueny, B. (2005) Evidence of history in explaining diversity patterns in tropical riverine fish. *Journal of Biogeography*, **32**, 1899–1907.

Tilman, D. (1996) Biodiversity: population versus ecosystem stability. *Ecology*, **77**, 350–363.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997) The influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300–1302.

Villéger, S., Mason, N.W.H. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, **89**, 2290–2301.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J. & Watson, R. (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science*, **314**, 787–790.

SUPPORTING INFORMATION

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

Figure S1 All European drainage basins available for this study. Please see Table S1 for more detailed information.

Figure S2 Standardized functional diversity indices plotted against drainage basin size.

Table S1 Drainage basins available for this study.

Table S2 References for the fish occurrence data of European drainage basins.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCH

During this study **Diana Schleuter** was a post-doctoral research associate at Aix-en-Provence (France) Institut de Recherche en Sciences et Technologies pour l'Environnement (Irstea). During this period, she was funded by the National Research Agency of France (ANR) within the Freshwater Fish Diversity project (ANR-06-BDIV-010). Her research focused on functional diversity and fish community ecology. At present she is associated with the Limnological Institute in Konstanz (Germany) and is also working on behavioural ecology and social interactions in fish.

Editor: Janne Soininen